TÜBİTAK

Research Article

Turk J Agric For
35 (2011) 319-331

doi:10.3906/tar-0911-407

Stem reserve accumulation and mobilization in wheat (*Triticum aestivum* L.) as affected by sowing date and N – P – K levels under Mediterranean conditions

Amir AYNEHBAND*, Maryam VALIPOOR, Esfandiar FATEH

[1]Department of Agronomy & Plant Breeding, Faculty of Agriculture, University of Shahid Chamran, Ahvaz - IRAN

Received: 25.11.2009

Abstract: Some parts of the dry matter accumulated in the wheat stem during the vegetative period are translocated to grain during the grain-filling period. This study assesses the changes in dry matter accumulation in wheat, and the translocation of different internodes of the main stem as affected by some cultural practices. Field experiments, including 3 sowing dates (early, conventional, and late), and 4 N – P – K levels, F_1 - (0 – 0 – 0), F_2 - (110 – 90 – 80), F_3 - (70 – 50 – 40) and F_4 - (150 – 130 – 120), were conducted at the Agricultural Faculty of Shahid Chamran University during 2008 and 2009. The main stem internodes length, weight, dry matter accumulation, and mobilization were measured. Our results showed that the behaviors of the 4 N– P – K levels were similar as they ranged in the same order for pre-anthesis and post-anthesis dry matter accumulation; also, differences in fertilizer application induced similar changes in dry matter accumulation and remobilization. Dry matter translocation was an average of 2% higher for all fertilized treatments, when compared to the control, which has shown the low influence of fertilization on this efficiency in our study. The effect of sowing dates in pre-anthesis dry matter contribution to reproductive organs was much more than the influence associated with the N – P – K levels. However, we recorded differences in dry matter, mobilization efficiency, and mobilization dry matter among sowing dates. The early sowing dates show the best value for mobilized dry matter and dry matter in all stem internodes. Nevertheless, mobilization efficiency had lowest value at this time. The highest mobilization efficiency in all stem internodes was associated with lowest N – P – K level application; also, mobilized dry matter decreased with increasing fertilizer application with all sowing dates and stem internodes, except with early sowing dates for peduncle internodes. With a delay in sowing date, and/or increase in N – P – K levels, the amount of dry matter remobilization decreased, mainly due to a decrease in stem weight. However, the sowing dates had greater influence on dry matter accumulation and remobilization than the fertilizer application.

Key words: Dry matter, mobilization efficiency, N – P – K levels, sowing date, wheat

Introduction

In all grain crops, the supply of assimilates to the developing grain originates both from current assimilation transferred directly to kernels, and from the remobilization of assimilates stored temporarily in vegetative plant parts (Gebbing et al. 1999). The reserves deposited in vegetative plant parts before anthesis may buffer grain yield when conditions become adverse to photosynthesis and mineral uptake during grain filling (Tahir and Nakata 2005).

* E-mail: aynehband@scu.ac.ir

The relative importance of current assimilation and remobilization changes among genotypes, and is strongly related to environmental conditions (Arduini et al. 2006).

In recent years, there has been an improved understanding of yield responses to alterations in assimilates availability during different phonological phases, as affected by sowing dates (Takahashi and Nakaseko 1993). It was shown that crops experience periods during the growth cycle when yield is mainly limited by the source strength, the sink capacity, or both (Borras et al. 2004). There are many factors that can affect the source-sink relation during the different growth phases, including genotype, sowing date, rainfall, and fertilization (Dordas 2009).

The contribution of pre-anthesis assimilates to seed may be crucial for maintaining seed yield when adverse climatic conditions reduce photosynthesis, water, and mineral uptake (Arduini et al. 2006). It is known that winter wheat transfers a large percentage (7%-57%) of its pre-anthesis storage of assimilates to the seed. However, under unfavorable conditions stored C and N contributed 64% and 81% of total grain C and N, respectively (Plaut et al. 2004). In fact, the reserves in stems or other vegetative tissues can be used for seed filling under any stress that depresses the photosynthesis reserves, which varies in different species, genotypes, and environmental conditions; also, a large movement of assimilates can occur under low soil fertility conditions (Masoni et al. 2007). The remobilization of assimilates originates from plant senescence, an active and ordered process that involves the translocation of stored reserves from stems and sheets to grain (Ercoli et al. 2008). In bread wheat, heavy use of N fertilizer delay senescence, which results in additional nonstructural carbohydrates left in the straw leading to reduced grain yield (Yang and Zhang 2006).

In Mediterranean environments, the hot and dry conditions, occurring during grain filling, reduce the photosynthesis rate after anthesis, limiting the contribution of current assimilates to the grain (Alvaro et al. 2008). Under these circumstances, dry matter accumulation before anthesis in vegetative parts of the plant, and its remobilization to the grain during grain filling becomes particularly important (Palta et al. 1994). It was reported that late sowing dates (i.e. unfavorable environmental conditions) reduced both shoot biomass and grain yield, in addition to their N content when compared to the optimum sowing dates. However, since reductions in these characters were proportional, the mean harvest index and nitrogen harvest index with late and optimum sowing were similar (Chatha et al. 1999). In another study, it was reported that early sowing showed no advantage over optimum sowing, except that more N was removed from the soil in the former than in the latter. However, more N was lost from the crop with early rather than in optimum sowing, counterbalancing, to some extent, the advantage of early sowing. (Ehdaie and Waines 2001)

These results indicated that the estimation of the amount of stem reserves accumulated and mobilized were dependent on environmental conditions (i.e. sowing date) genotype, and cultural practices. For instance, a rise in temperature that occurs constantly during the grain filling stage of wheat under Mediterranean conditions also has a negative effect on dry matter production (Alvaro et al. 2008). Moreover, different stresses, such as high temperature (and water deficit) limited the production of new photosynthetic products. Therefore, the contribution of stored carbohydrates may become the predominant source of transported materials (Blum et al. 1994).

There is little information regarding the effect of sowing dates on the accumulation and translocation of assimilates in the wheat stem. The objectives of this research were to study the status of stem dry matter accumulation during the vegetative period, and the contribution of pre-anthesis assimilates to the reproductive organs of wheat grown with 2 cultural practices, including sowing dates and N – P – K levels.

Materials and methods

This field study was conducted at an experimental farm of the Faculty of Shahid Chamran University of Ahvaz, Iran (31°20′ N latitude and 48°41′ E longitudes) at an elevation of 20 m above mean sea level during the 2008-2009 growing seasons. The soil type was sandy loam with pH 7.5, and a 0.54% average organic matter concentration. The 0-30 cm soil layers contained 0.043% nitrogen, 12 mg kg^{-1} phosphorus, and a 190 mg kg^{-1} exchangeable potassium. The experimental design was a split plot based on RCB with 3 replications. The main plot had sowing dates (SD) in 3 levels, including early SD (27 Oct), conventional SD (6 Nov), and late SD (6 Dec). The sub-plot had different N – P – K levels including F_1 - control (0 – 0 – 0), F_2 - optimum (110 – 90 – 80), F_3 - 40% lower than optimum (70 – 50 – 40), and F_4 - 40% higher than optimum (150 – 130 – 120). Each plot consisted of 7 rows, 3 m in length; also, inter row spacing was 20 cm and interplant spacing was 3 cm.

In each plot, 30 main tillers from the 2 middle rows next to the guard rows were tagged as spikes that emerged from the flag leaf sheaths. Three main tillers were harvested randomly at anthesis and at 10-day intervals after anthesis until maturity. After each harvest, leaf blades and sheaths were removed and main tillers were immediately dried in a drier at 70 °C for 48 h. Then each main tiller was divided by spike and stem; each stem was divided into 3 segments, namely peduncle (first internode below the spike), penultimate (the internode below the peduncle), and the lower internodes the stem segments. The length and weight of each segment was measured, and its specific weight was calculated as the ratio of its weight to its length. The magnitude of mobilized dry matter in each internode segment was estimated as the difference between post-anthesis maximum and minimum weight. Mobilization efficiency of dry matter in each internode segment was estimated by the proportion (%) of mobilized dry matter relative to post-anthesis maximum weight of that segment. The mean of the 3 samples in each harvest was used in the statistical analysis.

The data was processed by an analysis of the variance (ANOVA) and analyzed with the SAS program. The means were compared using the LSD test.

Results

Stem segments length and weight

Different sowing dates significantly changed internode length, and thus reduced the length of the main stem (Table 1). A greater reduction in length was found for low internodes than for penultimates. There was little variation for internode and stem length among the fertilizer levels. Late SD had the shortest peduncle (29.5 cm), then penultimate (18.5 cm), and lower internodes (27.3 cm). In contrast, early SD had the longest peduncle (34.9 cm), then penultimate (19.9 cm), and lower internodes (36.9 cm). However, no significant different was found for penultimate internode between early SD and conventional SD. The proportion of the main stem length, partitioned into the length of different segments, varied among sowing dates. It ranged from 38% (early SD) to 39% (late SD) from peduncle, from 22% (early SD) to 25% (late SD) for penultimate internode, and from 35% (late SD) to 40% (early SD) for the lower internodes (Table 1).

Sowing date significantly influenced on internode weight, which consequently reduced the weight of main stem (Table 2). The largest reduction was observed from lower internodes followed by peduncle and the penultimate. A significant variation was found among the sowing dates, from peduncle, penultimate, and the lower internode weight. Peduncle weight ranged from 167 mg for $S_3 \times F_4$ interaction to 303 mg for $S_1 \times F_3$ interaction (Table 2). Penultimate internode weight varied from 140 mg for $S_3 \times F_3$ to 243 mg for $S_1 \times F_3$. The lower internodes, which consisted of 2 to 4 internodes, had a much greater weight compared with each of the top internodes. Weight of the lower internodes ranged from 237 mg for $S_2 \times F_1$ to 550 mg for $S_1 \times F_2$. Among the sowing dates, early SD also had higher basal internode weights (Table 2).

Since internode weight is a function of internode length, internode weight was divided by length to determine internode specific weight or linear density (Table 3). Sowing dates, on average, reduced specific weight. The lower internode and the penultimate showed the highest reduction followed by the peduncle. Significant variation for internode specific weight was observed among the sowing dates, but not for fertilizer levels. Peduncle specific weight were maximum in both $S_2 \times F_2$ (8.3 mg cm^{-1}), and $S_1 \times F_4$ (8.2 mg cm^{-1}) treatments. In contrast, $S_3 \times F_4$ (5.6 mg cm^{-1}), and $S_2 \times F_1$ (5.7 mg cm^{-1}), showed the minimum specific weight from peduncle (Table 3). Penultimate internode specific weight was the highest for $S_1 \times F_3$ (12 mg cm^{-1}). In contrast, $S_3 \times F_4$ (7.7 mg cm^{-1}) had the lowest penultimate specific weight. Specific

Table 1. Length of main stem internodes for sowing date, N – P – K, and interaction of sowing date and N – P – K.

Treatment	Length of main stem			
	Peduncle (cm)	Penultimate internodes (cm)	Lower internodes† (cm)	Stem‡ (cm)
Sowing date				
S_1 - Early	34.9 a§	19.9 a	36.9 a	91.9 a
S_2 - Conventional	31.9 b	20.0 a	28.2 b	80.1 b
S_3 - Late	29.5 c	18.5 b	27.3 b	75.3 c
N – P - K (kg/ha)				
F_1- (0 – 0 – 0)	30.6 b	18.8 a	28.6 a	78.1 b
F_2- (110 – 90 – 80)	32.7 a	19.6 a	31.5 a	83.8 a
F_3- (70 – 50 – 40)	32.8 a	19.7 a	31.5 a	84.0 a
F_4- (150 –130 – 120)	31.3 ab	19.9 a	31.6 a	83.8 a
Interaction (S × F)				
$S_1 \times F_1$	34.2 ab	19.2 ab	35.9 ab	89.5 abc
$S_1 \times F_2$	35.3 a	20.3 a	37.7 a	93.3 a
$S_1 \times F_3$	36.0 a	20.3 a	37.2 a	93.6 a
$S_1 \times F_4$	34.2 ab	19.9 ab	36.9 a	91.0 ab
$S_2 \times F_1$	29.4 ef	19.0 ab	26.2 c	74.7 de
$S_2 \times F_2$	33.3 abc	20.2 ab	28.1 c	81.6 cd
$S_2 \times F_3$	31.8 bcde	20.2 a	29.4 bc	81.5 cd
$S_2 \times F_4$	33.2 abcd	20.5 bc	28.9 bc	82.6 bcd
$S_3 \times F_1$	28.2 f	18.2 b	23.6 c	70.0 e
$S_3 \times F_2$	29.8 def	18.6 ab	28.7 c	77.1 de
$S_3 \times F_3$	30.4 cdef	18.2 b	27.9 c	76.5 de
$S_3 \times F_4$	29.6 ef	19.1 ab	29.1 bc	77.8 de

† Internodes below penultimate.
‡ Length of all internodes.
§ In each section, means followed by the same letter within columns are not significantly different (P < 0.05) according to LSD test.

weight for the lower internodes ranged from 8.9 mg cm^{-1} for $S_2 \times F_1$ to 14.7 mg cm^{-1} for $S_1 \times F_3$ (Table 3).

Internodes dry matter trends

Different trends for post-anthesis changes in peduncle weight were observed among the sowing dates (Figure 1). The early SD was different from the other sowing dates examined with regarded to peduncle weight, but its trend was similar to those of conventional SD and late SD. These sowing dates showed the greatest increase in peduncle weight during the first 10 days after anthesis and reached their maximum weight 20 days post-anthesis. No

Table 2. Weight of main stem internodes for sowing date, N – P – K, and interaction of sowing date and N – P – K.

Treatment	Weight of main stem			
	Peduncle (mg)	Penultimate internodes (mg)	Lower internodes† (mg)	Stem‡ (mg)
Sowing date				
S_1 - Early	287 a§	231 a	538 a	1057 a
S_2 - Conventional	207 b	198 b	266 b	641 b
S_3 - Late	180 c	152 b	277 b	609 b
N – P - K (kg/ha)				
F_1- (0 – 0 – 0)	210 a	174 a	342 a	727 a
F_2- (110 – 90 – 80)	230 a	187 a	361 a	804 a
F_3- (70 – 50 –40)	232 a	189 a	383 a	778 a
F_4- (150 – 130 – 120)	227 a	184 a	356 a	767 a
Interaction (S × F)				
$S_1 \times F_1$	267 abc	203 ab	517 a	987 a
$S_1 \times F_2$	297 a	240 a	550 a	1087 a
$S_1 \times F_3$	303 a	243 a	547 a	1093 a
$S_1 \times F_4$	283 ab	237 a	540 a	1060 a
$S_2 \times F_1$	170 e	147 c	237 b	553 b
$S_2 \times F_2$	220 cde	180 bc	300 b	700 b
$S_2 \times F_3$	207 de	177 bc	260 b	643 b
$S_2 \times F_4$	230 bcd	170 bc	267 b	667 b
$S_3 \times F_1$	193 de	173 bc	273 b	640 b
$S_3 \times F_2$	180 de	147 c	300 b	627 b
$S_3 \times F_3$	180 de	140 c	277 b	597 b
$S_3 \times F_4$	167 e	147 c	260 b	573 b

† Internodes below penultimate
‡ Weight of all internodes.
§ In each section, means followed by the same letter within columns are not significantly different (P < 0.05) according to LSD test.

significant change in peduncle weight was observed with late SD between 10 and 20 days post-anthesis (Figure 1). Trends in the subsequent decrease in peduncle weight were also different among the sowing dates. The fastest reduction in peduncle weight over 20 to 30 days post-anthesis belonged to early SD. Peduncle weight was not reduced in conventional SD over 30 to 50 days post-anthesis. No decrease in peduncle weight over 40 to 50 days post-anthesis was observed for all sowing dates. However, late SD showed some increase in peduncle weight during 30 to 40 days post-anthesis.

Table 3. Specific weight of main stem internodes for sowing date, N – P - K, and interaction of sowing date and N – P – K.

Treatment	Specific weight of main stem			
	Peduncle (mg cm^{-1})	Penultimate internodes (mg cm^{-1})	Lower internodes† (mg cm^{-1})	Stem‡ (mg cm^{-1})
Sowing date				
S_1 - Early	8.2 a§	11.5 a	14.6 a	11.5 a
S_2 - Conventional	6.4 b	8.4 b	9.5 b	8.0 b
S_3 - Late	6.1 b	8.2 b	10.2 b	8.1 b
N – P – K (kg/ha)				
F_1 - (0 – 0 – 0)	6.8 a	9.2 a	11.7 a	9.1a
F_2 - (110 – 90 – 80)	6.9 a	9.5 a	11.2 a	9.1 a
F_3 - (70 – 50 – 40)	7.0 a	9.5 a	12.0 a	9.4 a
F_4 - (150 – 130 – 120)	6.9 a	9.2 a	10.9 a	9.0 a
Interaction (S × F)				
$S_1 \times F_1$	7.8 ab	10.6 ab	14.5 a	11.0 a
$S_1 \times F_2$	8.4 a	11.8 a	14.6 a	11.6 a
$S_1 \times F_3$	8.3 a	12.0 a	14.7 a	11.7 a
$S_1 \times F_4$	8.2 a	11.8 a	14.5 a	11.6 a
$S_2 \times F_1$	5.7 c	7.6 c	8.9 c	7.3 b
$S_2 \times F_2$	6.6 bc	8.9 bc	11.0 bc	8.6 b
$S_2 \times F_3$	6.5 abc	8.7 bc	9.0 bc	7.9 b
$S_2 \times F_4$	6.9 bc	8.3 c	9.3 bc	8.1 b
$S_3 \times F_1$	6.9 bc	9.5 bc	11.6 b	9.1 b
$S_3 \times F_2$	6.0 c	7.8 c	10.4 bc	8.1 b
$S_3 \times F_3$	5.9 c	7.8 c	9.9 bc	7.8 b
$S_3 \times F_4$	5.6 c	7.7 c	9.0 bc	7.4 bd

† Internodes below penultimate.
‡ Specific weight of all internodes.
§ In each section, means followed by the same letter within columns are not significantly different ($P < 0.05$) according to LSD test.

The early SD and conventional SD had similar trends for post-anthesis changes in peduncle specific weight (Figure 2). Trends with late SD were different. The peduncle in all of the sowing dates reached maximum specific weight at 20 days post-anthesis (Figure 2). The extent and rate of increase in the peduncle specific weight (accumulation of dry matter per unit length of peduncle) during the first 20 days after anthesis with late SD, 2.2 mg cm^{-1} and 0.11 mg cm^{-1} day^{-1}, respectively, were highest among the sowing dates. The extent and rate of the subsequent decrease (mobilization of dry matter) over the next

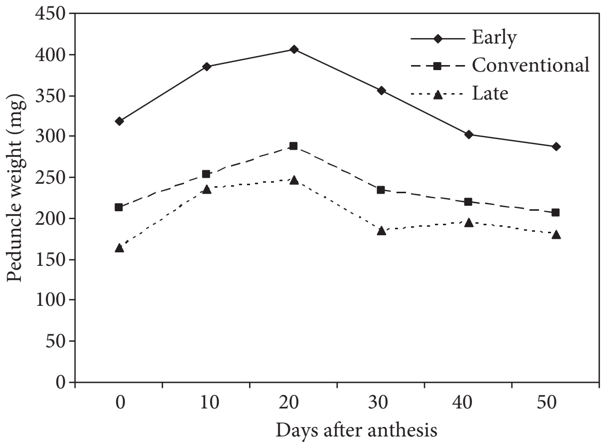

Figure 1. Changes in main stem peduncle dry weight during grain filling from 3 sowing dates. Each point is a mean of 9 observations.

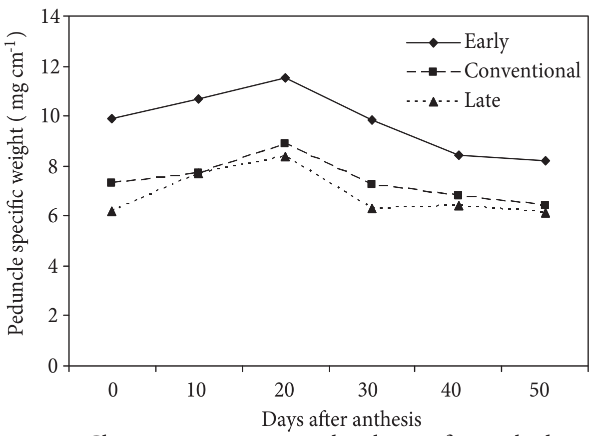

Figure 2. Changes in main stem peduncle specific weight during grain filling from 3 sowing dates. Each point is a mean of 9 observations.

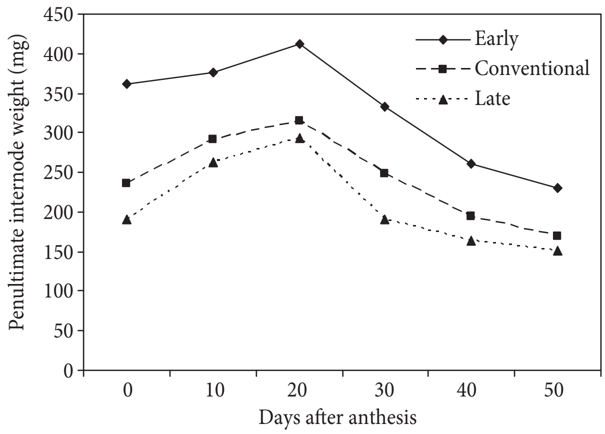

Figure 3. Changes in main stem penultimate dry weight during grain filling from 3 sowing dates. Each point is a mean of 9 observations.

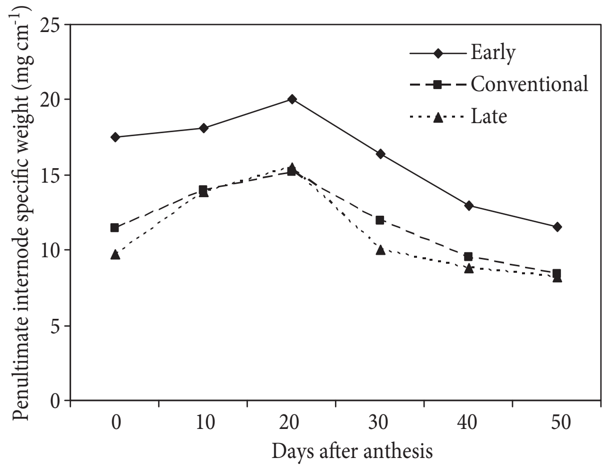

Figure 4. Changes in main stem penultimate specific weight during grain filling from 3 sowing dates. Each point is a mean of 9 observations.

30 days with early SD, 3.3 mg cm^{-1} and 0.11 mg cm^{-1} day^{-1}, respectively, were also the highest.

Trends in post-anthesis changes in penultimate internode weight are shown in Figure 3. Maximum penultimate weight for all sowing dates was reached 20 days post-anthesis. Post-anthesis penultimate internode weight with early SD was the highest, and significantly greater than other sowing dates (Figure 3). Sowing dates showed little difference in trends for post-anthesis penultimate internode specific weight (Figure 4). Late SD showed the highest extent and rate of increase in penultimate specific weight, 5.4 mg cm^{-1} and 0.27 mg cm^{-1} day^{-1}, respectively, during 20 days post-anthesis. The extent and rate of subsequent decrease over the next 30 days with early SD, 8.5 mg cm^{-1} and 0.28 mg cm^{-1} day^{-1}, respectively, were the highest. Conventional SD and late SD were the lowest and showed, more or less, similar trends for these traits.

The lower internodes, taken together as a stem segment, from all sowing dates reached their maximum weight at anthesis (Figure 5). The lower internodes with early SD had the highest weights, whereas those from conventional SD and late SD had

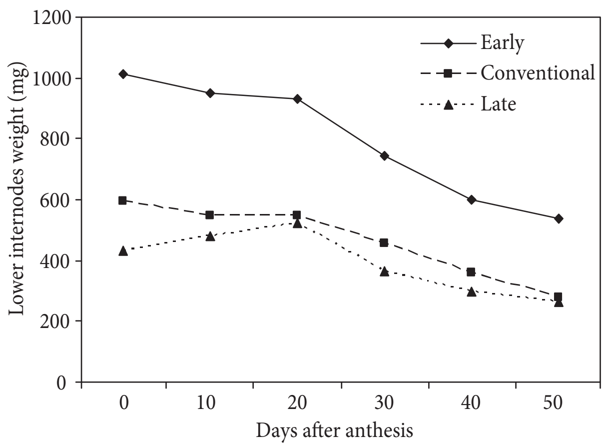

Figure 5. Changes in main stem lower internodes dry weight during grain filling from 3 sowing dates. Each point is a mean of 9 observations.

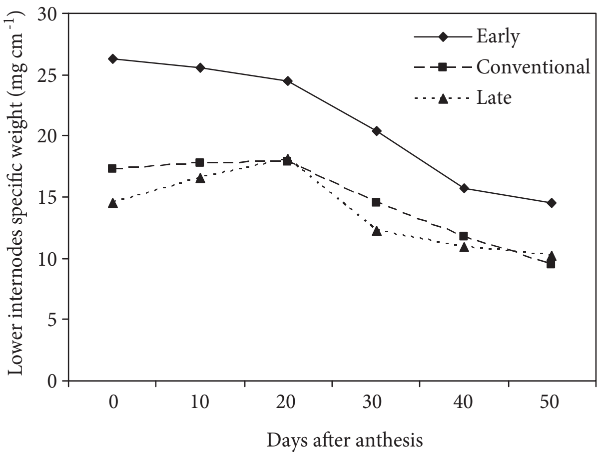

Figure 6. Changes in main stem lower internodes specific weight during grain filling from 3 sowing dates. Each point is a mean of 9 observations.

the lowest weights. All sowing dates showed, more or less, similar trends for post-anthesis lower internodes weight. The lower internodes, taken together as a stem segment, with early SD reached their maximum specific weight at anthesis, and from conventional SD and late SD in 20 days post-anthesis (Figure 6). Again, late SD showed the highest extent and rate of increase in the lower internodes specific weight, 3.6 mg cm^{-1} and 0.18 mg cm^{-1} day^{-1}, respectively, during 20 day post-anthesis. The extent and rate of the subsequent decrease over the next 30 days with early SD, 9.9 mg cm^{-1} and 0.33 mg cm^{-1} day^{-1}, respectively, were also the sharpest followed by conventional SD and late SD.

It was mentioned earlier that early SD responded differently to sowing dates when compared with others, in regard to peduncle penultimate and lower internode weight. While peduncle weight of all sowing dates was reduced under different N – P – K levels, the amount of reduction was lowest in the control plot (267 mg vs. 193 mg), and was highest in optimum fertilizer (303 mg vs. 180 mg). The amount of reduction in penultimate internode weight caused by fertilizer levels was lowest in the control plot (203 mg vs. 147 mg), whereas the highest reduction was observed as 40% lower than the optimum fertilizer rate (243 mg vs. 140 mg). Therefore, peduncle and penultimate internode weights from sowing dates were depressed more in the lower fertilizer application treatment.

Dry matter mobilization and efficiency

Sowing dates reduced post-anthesis maximum and minimum weights from peduncle on average, by 39% and 48%, respectively (Table 4). However, the amount of reduction varied for different fertilizer levels. The estimate of mobilized dry matter, calculated as the difference between post-anthesis maximum and minimum weight in peduncle, varied more in conventional SD than in other dates among fertilizer levels. Mobilization efficiency, estimated as the ratio of mobilized dry matter to maximum weight, showed similar trends (Table 4). Mobilized dry matter from the peduncle, on average, was greater with early SD than in conventional SD and late SD by 28%. However, fertilizer levels responded differently to sowing date in respect to the amount of dry matter mobilized from the peduncle (Table 4). Mobilization efficiency in peduncle, on average, was greatest in conventional SD (37%) treatment. Lower fertilizer levels (the control and 40% lower than optimum fertilizer levels) had greater dry matter mobilization efficiency from all sowing dates (Table 4).

The sowing date reduced the penultimate internode post-anthesis maximum and minimum weights by 28% and 34%, respectively (Table 5). All fertilizer levels reduced mobilized dry matter at the penultimate internode at different sowing date treatments. The amount of mobilized dry matter at the penultimate internode, on average, was greater with early SD than with others by 20%. However,

Table 5. Postanthesis maximum and minimum means for penultimate weight, estimate of penultimate mobilized dry matter (MDM), and mobilization efficiency (ME) in wheat sowing date and different (N – P – K).

(N – P – K) kg ha-1	Early sowing date				Conventional sowing date				Late sowing date			
	Max.	Min.	MDM†	ME‡	Max.	Min.	MDM†	ME‡	Max.	Min.	MDM†	ME‡
	mg			%	mg			%	mg			%
F_1 - (0 : 0 : 0)	393	203	190	48	323	147	177	55	290	173	117	40
F_2 - (110 : 90 : 80)	413	243	170	41	320	177	143	45	330	140	190	58
F_3 - (70 : 50 : 40)	437	240	197	45	303	180	123	41	277	147	130	47
F_4 - (150 : 130 : 120)	403	237	167	41	313	170	143	46	287	147	140	49
Mean	411	231	181	44	315	168	146	47	296	152	144	48

† Maximum weight – minimum weight.
‡ (Mobilized dry matter / maximum weight) × 100.

mobilization efficiency of dry matter from the penultimate internode, on average, was greater with late SD (48%) than with early SD (44%) (Table 5). Similar to peduncle, lower fertilizer levels (control and 40% lower than optimum fertilizer levels) had the highest mobilization efficiency under all sowing dates for penultimate (Table 5).

Post-anthesis maximum and minimum weights for the lower internodes also were reduced at different sowing dates by 48% and 51%, respectively (Table 6). However, the amount of reduction varied among fertilizer levels. Sowing dates, on average, reduced the amount of mobilized dry matter by 47%, but increased mobilization efficiency by 26% in conventional SD. Fertilizer levels respond differently to sowing dates with regards to the amount of dry matter mobilized and the efficiency of mobilization from the lower internodes (Table 6). For example, mobilization efficiency in conventional SD increased by 31% with lower fertilizer (40% lower than optimum fertilizer level) when compared with control conditions, whereas no change in mobilization efficiency was observed with early SD across the lower fertilizer levels.

Table 6. Postanthesis maximum and minimum means for lower internodes weight, estimate of lower internodes mobilized dry matter (MDM), and mobilization efficiency (ME) in wheat sowing date and different fertilizer rate (N – P – K).

(N – P – K) kg ha-1	Early sowing date				Conventional sowing date				Late sowing date			
	Max.	Min.	MDM†	ME‡	Max.	Min.	MDM†	ME‡	Max.	Min.	MDM†	ME‡
	mg			%	mg			%	mg			%
F_1 - (0 : 0 : 0)	1010	517	493	49	570	236	333	58	493	273	220	45
F_2 - (110 : 90 : 80)	1087	547	540	50	740	260	480	65	587	277	310	53
F_3 - (70 : 50 : 40)	1017	550	467	46	657	300	357	54	503	300	203	40
F_4 - (150 : 130 : 120)	943	540	403	43	620	267	353	57	537	260	277	33
Mean	1014	538	476	47	647	266	381	58	530	277	252	43

† Maximum weight – minimum weight
‡ (Mobilized dry matter / maximum weight) × 100.

Discussion

The diverse group of sowing dates examined demonstrated considerable variation for internode attributes at anthesis and during the grain-filling period in all N – P – K levels. The lower and penultimate internodes, on average, reached their maximum length in $S_1 \times F_2$ treatment. However, the peduncle reached maximum length in $S_1 \times F_3$. The peduncle was, on average, longer than the penultimate for all the sowing dates and fertilizer levels.

Sowing dates, on average, significantly reduced main stem length by 18%. The reduction in stem length was reflected more on lower internode length (26%) than on peduncle length (16%), and the penultimate internode length (7%). The partitioning of the main stem length into peduncle, penultimate, and the lower internodes length was different among the sowing dates. Partitioning of stem length into different internodes between N – P – K levels was longest in penultimate internode. The peduncle internode in the $S_1 \times F_3$ treatment made up 37%, the penultimate internode in the $S_1 \times F_2$ treatment was 22% and the lower internodes in the $S_1 \times F_2$ treatment was 40% of the main stem length; in which all of them were at the highest percentages observed among sowing dates × fertilizer levels interaction.

Sowing dates, on average, reduced main stem weight by 42%. This reduction was reflected more on lower internodes (51%) and peduncle (37%) than on the weight of the penultimate (34%). These differences among internode weights in response to sowing dates were due to the time of the wheat seedlings emergence, and the time each segment attained its maximum weight. Among the internode traits, the greatest variation was observed in internode weight; in contrast, with fertilizer levels, none of the sowing dates had a similar weight for peduncle, penultimate, and the lower internodes. A large variability in the contribution of assimilates stored prior to anthesis to grain yield has been reported in wheat. Most of this variability can be attributed to differences in sowing date (Ehdaie and Waines 2001), soil type effects (Masoni et al. 2007), genotypes (Alvaro et al. 2008), and crop management (Arduini et al. 2006). Environmental conditions during the pre- and post-anthesis periods are likely to have different effects on dry matter and N accumulation (Plaut et al. 2004).

The peduncle and penultimate internodes in the $S_1 \times F_3$ treatment made up 28% and 22%, respectively and the lower internodes in the $S_1 \times F_2$ treatment was 51% of the main stem weight; in which all of them were at the highest percentages observed among sowing dates × fertilizer levels interaction. It seems that the sowing dates differences in maximum stem weight were not related to the fertilizer levels. For example, in each sowing date the stem weights for the all N – P – K levels were not significantly different. Chatha et al. (1999) reported that the relative growth rates of shoots planted on different dates were different from one another throughout the crop growing season of wheat. The early planted crop grew faster because of a higher relative growth rate than that of wheat planted later. In the middle of the vegetative period, absolute growth rates of wheat shoots were higher in plots planted on earlier sowing dates than the absolute growth rates shoots in plots sown later. In addition, the allometric relationships of the root and shoot growth revealed that the date of sowing had significant effect on root-shoot ratio. The early sown wheat plants had higher root-shoot ratios than that those planted later (Takahashi and Nakaseko 1993).

Significant sowing date differences were found for internode specific weight. As internodes lengths remained constant after reaching their maximum length, increase in specific weight represented deposition of dry matter and the subsequent decrease represented mobilization and translocation of dry matter. The specific weight of stem segments from top to bottom internodes was greatest at lower internodes, and with early SD. The sowing date decreased stem specific weight by 30%. This reduction was mainly due to reduction in stem weight (42%) rather than stem length (18%). These observations indicate that early SD rather than conventional SD had the highest stem weight. Therefore, it seems that focus on specific weight is a better criterion than shorter stem length when selecting sowing date. Dry matter accumulation and the partitioning into different plant parts were different between the fertilization treatments and the control. Total aboveground biomass increased after anthesis in all fertilization treatments. Basically, dry matter production was directly related to N and P supply, and when N and P supply was low there was also low production of dry matter (Dordas 2009) and the distribution of assimilates to the reproductive organs (Gebbing et al. 1999).

Late SD reduced maximum weight in the peduncle by 39%, in the penultimate internode by 28%, and in the lower internodes by 48%. These differences in percentage reduction, in response to sowing date, were due to a delay in plant establishment, and shorten stem elongation duration. The mean mobilized dry matter, calculated as the difference between post-anthesis maximum and minimum weight, was greater with early SD than in other sowing dates for peduncle, and a similar trend was found for penultimate and for the lower internodes. However, for each segment, different trends for mobilized dry matter were found among the fertilizer levels in different sowing dates. Wheat in optimum fertilizer showed greater dry matter mobilized from penultimate with late SD than with early SD conditions. It was reported that the optimum period for sowing date for a wheat crop in each region depended upon location, timing and the distribution of rainfall (Jackson et al. 2000). Therefore, delay in sowing beyond the optimum period reduces wheat yields (Blum et al. 1994). The percent reduction in yield due to late sowing depends on the type of wheat cultivars. Sowing wheat crops early has been recommended as a means of reducing nitrate leaching. Therefore, an increase in shoot N content at anthesis was mainly due to an increase in dry matter accumulation rather than to N concentration (Ehdaie and Waines 2001).

Conventional SD had greater dry matter mobilization efficiency by 37% in peduncle, and by 58% at the lower internodes. The stem segments responded differently to sowing dates because of their differences in vegetative stage and the duration of elongation periods. Post-anthesis maximum weight with early SD when compared with that from conventional SD was reduced by 39% in peduncle, by 28% in penultimate internode, and by 48% in the lower internodes, whereas post-anthesis minimum weight was reduced by 48%, 34%, and 48%, respectively. As a result, the penultimate internode at conventional SD and late SD had similar mobilization efficiency (47% and 48%, respectively), but were greater than that with early SD (44%). However, significant sowing date variation for mobilization efficiency of dry matter was observed under all N – P – K treatments. It was suggested that one of the ways to achieve future durum wheat yield increases under Mediterranean conditions is to keep improving dry matter translocation in grains, which may result from an enlargement of the source size (biomass) at anthesis or from increase in dry matter translocation efficiencies (Alvaro et al. 2008). Even though, variability for the rate and duration of biomass production still has to be demonstrated (Arduini et al. 2006).

The maximum stem reserve accumulation and percentage of mobilization in wheat depends on stem length and stem specific weight. Our study showed sowing date variations for these traits in different internodes of the main stem. However, dry matter accumulation and mobilization varied little along the stem and at different fertilization levels. More than 63% of the stem dry matter was, on average, stored in the peduncle and penultimate with conventional SD, followed by 55% with late SD, and 69% with early SD. Dry matter translocation efficiency was not significantly different between the different treatments. Masoni et al. (2007) reported that the contribution of pre-anthesis assimilates to seed fill was not different at the different fertilization treatments when compared with the control. Nevertheless, dry matter partitioning was strongly associated with assimilate availability at flowering.

The stem weight from early SD was the highest among sowing dates examined, and it had more mobilized stem dry matter than the other sowing dates (it was obtain by the calculation of mobilization dry matter of peduncle, penultimate and lower internodes). This was due to prolonging the vegetative duration and a longer peduncle and lower internodes during this sowing date, which increased the accumulation of a large amount of stem reserves, especially before anthesis. A delay in SD demonstrated a greater rate and/or extent of dry matter accumulation, but early SD had subsequently higher mobilization per unit stem length. Therefore, early SD with greater rates of dry matter mobilization were exposed less to effects of heat terminal stress than others. Van Herwaarden et al. (1998) demonstrated that in bread wheat the water deficit during grain filling reduced assimilation, and consequently grain yield and high-N crops suffered greater reduction when compared with unfertilized ones. The lower grain yield of crops with high-nitrogen levels and low water availability appears to be due to either an incomplete remobilization of reserves, or a reduction in the amount of reserves available for remobilization (Yang and Zhang 2006). However, increasing the storage capacity of high pre-anthesis growth will not be effective in increasing grain yield, if growth shortly before and after anthesis is limited by periods of drought or by N supply (Plaut et al. 2004). Also, the decrease due to water stress was higher in high-N application (1.6 t ha^{-1}) than in low (0.7 t ha^{-1}) or no N application (Ercoli et al. 2008).

The peduncle, penultimate, and lower internode weights from all sowing dates were less affected by different fertilizer applications. Dry matter mobilized from peduncle and penultimate with early SD and conventional SD decreased in response to fertilizer application when compared with the control. Ercoli et al. (2008) reported that the amount of remobilized dry matter during grain filling was increased by water stress only in N fertilized plants. However, the magnitude of the N effect was greatest at full irrigation, so that when water stress occurred accumulation and remobilization of dry mater and N was greatly reduced, especially in high-N plants. Thus, the nitrogen status of the plant was found to modify plant tolerance to water stress, as the high-N plants were more sensitive to drought than the unfertilized ones (Dordas 2009). With the optimal planting date, the highest grain yield was obtained with the varieties that showed the highest post-heading accumulation of both dry matter and nitrogen and the best N remobilization efficiency, but, in some of them, the dry matter translocation was lowest (Takahashi and Nakaseko 1993; Chatha et al. 1999; Ehdaie and Waines 2001).

Conclusion

On the basis of the results of this study, cultural practices aiming to maximum wheat stem reserve accumulation and mobilization in heat terminal stressful environments should consider balanced the partitioning of stem length and weight with greater stem specific weight, because specific weight had a positive relationship with stem mobilized dry matter treatments. Also, the results presented here show that mean main stem dry matter at anthesis with early sowing (1831 mg) was greater than that with conventional (1250 mg) and late (1075 mg) sowings. However, differences in mean stem MDM and ME between early and conventional sowing dates were significant. It was from late sowing dates that the main stem weight displayed a minimum rate and variation for sowing date × N – P – K interactions. With early sowing, plants had a longer vegetative period when compared to optimum and late sowings; therefore, they produced greater internode lengths while weight and specific weight remained the same or was reduced slightly at different N – P – K levels. In fact, the current photosynthetic source is depressed by any unfavorable condition, and grain filling becomes more dependent on a mobilized resource. Therefore, in our study the environmental conditions caused by different sowing dates had the most influence on both storage and mobilization of stem reserves.

References

Alvaro F, Isidro J, Villegas D, Garcia del Moral LF, Royo C (2008) Breeding effect on grain filling, biomass partitioning, and remobilization in Mediterranean durum wheat. Agron J 100: 361-370.

Arduini I, Masoni A, Ercoli L, Mariotti M (2006) Grain yield, and dry matter and nitrogen accumulation and remobilization in durum wheat as affected by variety and seeding rate. Eur J Agron 25: 309-318.

Blum A, Sinmena B, Mayer J, Golan G, Shpiler L (1994) Stem reserve mobilization supports wheat grain filling under heat stress. Aust J Plant Physiol 21: 771-781.

Borras L, Slafer GA, Otegui ME (2004) Seed dry weight response to source-sink manipulations in wheat, maize and soybean: a quantitative reappraisal. Field Crops Res 86: 131-146.

Chatha E, Ghaffar A, Randhawa MA (1999) Dry matter partitioning into root and shoot of wheat genotypes sown at different depths and dates under rainfed conditions. Int J Agri Biol 1: 250-253.

Dordas C (2009) Dry matter, nitrogen and phosphorus accumulation, partitioning and remobilization as affected by N and P fertilization and source–sink relations. Eur J Agron 30: 129-139.

Ehdaie B, Waines JG (2001) Sowing date and nitrogen rate effects on dry matter and nitrogen partitioning in bread and durum wheat. Field Crops Res 73: 47-61.

Ercoli L, Lulli L, Mariotti M, Mosani A, Arduini I (2008) Post-anthesis dry matter and nitrogen dynamics in durum wheat as affected by nitrogen supply and soil water availability. Eur J Agron 28: 138-147.

Gebbing T, Schnyder H, Kuhbauch W (1999) The utilization of pre-anthesis reserves in grain filling of wheat. Assessment by steady-state $^{13}CO_2$ / $^{12}CO_2$ labelling. Plant Cell Environ 22: 851-858.

Jackson LF, Dubcovsky J, Gallagher LW, Wenning RL, Heaton J, Vogt H, Gibbs LK, Kirby D, Canevari M, Carlson H, Kearney T, Marsh B, Munier D, Muttere C, Orloff S, Schmierer J, Vargas R, Williams J, Wright S (2000) 2000 regional barley, common and durum wheat, triticale, and oat performance tests in California. Agronomy Progress Report No. 272. University of California, Davis, CA. 1999.

Masoni A, Ercoli L, Mariotti M, Arduini I (2007) Post-anthesis accumulation and remobilization of dry matter, nitrogen and phosphorus in durum wheat as affected by soil type. Eur J Agron 26: 179-186.

Palta JA, Kobata T, Fillery IR, Turner NC (1994) Remobilization of carbon and nitrogen in wheat as influenced by postanthesis water deficits. Crop Sci 34: 118-124.

Plaut Z, Butow BJ, Blumenthal CS, Wrigley CW (2004) Transport of dry matter into developing wheat kernels and its contribution to grain yield under post-anthesis water deficit and elevated temperature. Field Crops Res 86: 185-198.

Tahir ISA, Nakata N (2005) Remobilization of nitrogen and carbohydrate from stems of bread wheat in response to heat stress during grain filling. J Agron Crop Sci 191: 106-115.

Takahashi T, Nakaseko K (1993) The influence of sowing time on dry matter partitioning in spring wheat. Jpn J Crop Sci 62: 88-94.

Van Herwaarden AF, Farquhar GD, Angus J F, Richards RA, Howe GN, Van Herwaarden AF (1998) 'Haying-off', the negative grain yield response of dry land wheat to nitrogen fertilizer. I. Biomass, grain yield, and water use. Aust J Agr Res 49: 1067-1081.

Yang J, Zhang J (2006) Grain filling of cereals under soil drying. New Phytol 169: 223-236.