Contribution of main culm and tillers to grain yield of durum wheat: Influence of sowing date and plant traits

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Abstract

The question of whether tillers are a burden or a resource in durum wheat is of concern in the variable Mediterranean climates. The contribution of tillers to grain yield was investigated in commercial cultivars differing in time to anthesis, tillering and spike size, in response to three sowing dates:mid-autumn (recommended), winter, and early spring. The thermal time of phenological phases was calculated, and yield-components and floret production were analysed separately in main culm and tillers. Tiller spikes showed higher spikelet abortion coupled to lower spikelet fertility and mean kernel weight, so that grain yield was 40-60% lower than in main culm spikes. Despite this, tillers contributed 35 to 50% to plant yield. The sowing date affected tiller number rather than one tiller yield. In winter sowings (December), lower main culm yield was fully compensated by increased tiller yield, whereas shifts of sowing date to early spring (February) reduced tillering, which caused a yield loss ranging from 12 to 20%. Cultivars differed in one tiller yield rather than in tiller number, and higher grain yield of tillers was primarily due to increased grain recovery. A more equal partitioning of resources within main culm and tillers corresponded to better yield stability across sowing dates. Starting from this, we suggest that early anthesis, a long stem elongation phase, a high primordium initiation-rate and small spikes, could be positive traits for durum wheat yield stability in changing environ-

ments, since they allow plants directing more time and resources to floret production and grain filling both in main culm and tiller spikes. From a methodological point of view, our results show that the number of fertile florets per spike is highly correlated with the average floret number of five given spikelets.

Introduction

Wheat plants are formed by one main culm and a number of tillers varying from null to several tenths, depending on cultivar and environmental conditions. Grain yield of wheat crops is a quantitative trait determined by the product of three principal components: spike number per plant, or unit surface, mean kernel weight and kernel number per spike. Moreover, the last is a complex component resulting from the product of the number of spikelets per spike and the number of kernels per spikelet, and both these sub-components depend on their initiation and abortion rates, which occur at different stages during the crop cycle. Distinct components may compete or compensate and yield gain can be obtained by selecting for one or the other (Rharrabti *et al.*, 2010; Ferrante *et al.*, 2012; Slafer *et al.*, 2014). The most outstanding success of past wheat breeding was to increase grain number per unit surface, which was primary obtained by increasing kernel number per spike, whereas the number of fertile tillers per plant was even reduced in order to uniform the achievement of maturity and reduce within plant competition (De Vita *et al.*, 2007; Uzik and Zofajova, 2007; Fischer, 2016). In Italy and Spain, however, the genetic improvement of durum wheat in the last century increased both the number of grains per spike and the number of fertile tillers, despite the two yield components directly compete for assimilates (Brdar *et al.*, 2008; Subira *et al.*, 2015). This is because in Mediterranean semiarid environments, characterized by variable and unpredictable climatic conditions, high tillering may compensate for the poor crop establishment caused by late drought or early frost (Acevedo *et al.*, 2002; Elhani *et al.*, 2007). In addition, Dreccer *et al.* (2013) reported that tillers assist in competing against weeds, and, according to Spink *et al.* (2000), the production of more fertile tillers per plant can be a strategy to reduce seed costs.

Tiller number is the yield component with the highest plasticity (Slafer *et al.*, 2014). Nevertheless, the genetic control of tiller production and the potential of tillers in wheat yield optimization have not been fully elucidated (Xie *et al.*, 2016). According to Dreccer *et al.* (2013), low tillering wheat lines accumulate more water-soluble carbohydrates in stems, which leads to a higher grain number per spike and heavier kernels, though to only minimal yield increase. Artificial detillered plants and *tin* mutants have obtained a higher grain yield, which was associated with longer spikes and higher spikelet fertility (Kebrom *et al.*, 2012; Hendriks

et al., 2016). On the opposite, Xie *et al.* (2016) found that more fertile tillers per plant did not affect the yield of individual shoots and increased yield, and it was also reported that detillered plants yielded more in greenhouse conditions, but not in the field (Guo and Schnurbusch, 2015). In general, free-tillering was found detrimental in unfavourable environmental conditions (Mitchell *et al.*, 2013; Hendriks *et al.*, 2016), but was considered essential to take advantage of favourable conditions (Sadras and Rebetzke, 2013; Slafer *et al.*, 2014). However, Elhani *et al.* (2007) reported that tillers contributed to grain yield more than the main culm in rainfed durum wheat. Therefore, to find an association between distinct morpho-phenological traits of wheat genotypes and the tiller contribution to yield in response to environmental conditions could be of help in selecting for those traits that are more adapt to changing environments.

Durum wheat (*Triticum turgidum* L. var. *durum*) is a staple cereal crop in the Mediterranean basin, where it is cultivated under rainfed conditions from autumn to early summer. Shifts from the recommended sowing dates are often necessary because soils are either too dry or too waterlogged, and these events are predicted to become more frequent in the near future (Bassu *et al.*, 2009; Trnka *et al.*, 2014). Wheat yield components are differently sensitive to delays in sowing date, and a Cultivar x Environment interaction exists (Subira *et al.*, 2015). In general, late planting reduces grain yield (Inagaki *et al.*, 2007; Arduini *et al.*, 2009; Kumar *et al.*, 2016), primarily because it shortens the period from emergence to anthesis, thus reducing the time for tiller and spike development (Whitechurch *et al.*, 2007; Fischer, 2016). However, both lower (Akhtar *et al.*, 2012) and higher (Arduini *et al.*, 2009) numbers of spikes per unit surface were found in delayed sowings: the former due to reduced emergence in winter and to a shorter vegetative phase (Mahdi *et al.*, 1999; Dreccer *et al.*, 2013), the latter due to enhanced tiller growth rate at higher temperatures and longer day lengths (Kebrom *et al.*, 2012). Yield losses in delayed sowings are generally associated with a lower kernel number per spike (Bassu *et al.*, 2010; Kumar *et al.*, 2016), but there is no agreement on whether the most affected determinant is the number of spikelets or the spikelet fertility (Li *et al.*, 2001; Fischer, 2008; Arduini *et al.*, 2009; González-Navarro *et al.*, 2015).

Elhani *et al.* (2007) reported that environmental conditions influenced the determination of yield components differently in the two spike types, but, to the best of our knowledge, the effect of sowing date on spike yield components has never been analysed separately in the main culm and tiller spikes. In addition, the response of distinct spikelets to delays in sowing has not been previously investigated, though it is known that floret production and grain recovery differ among spikelets according to their position within the spike (Álvaro *et al.*, 2008; Bancal, 2009).

The aim of our research was thus to i) determine the contribution of main culm and tiller spikes to grain yield of durum wheat; ii) analyse the influence of sowing date on the determination of yield components and sub-components in the two spike types; and iii) highlight if spikelet position within the spike may influence spikelet fertility in response to sowing date. Hypothesizing that phenological and morphological traits influence the contribution of tillers to plant yield, investigations were carried out on four durum wheat cultivars differing in time to anthesis, tillering capacity and spike traits (Ercoli *et al.*, 2014), which were sown at three dates between mid-autumn and early spring.

Materials and methods

Site and experimental design

A two-year experiment was carried out from 2011 to 2013 at the Research Station of the Department of Agriculture, Food and Environment (University of Pisa, Italy), which is located approximately 4 km away from the sea (43°40′N, 10°19′E) and is 1 m above sea level. The climate of the area is hot-summer Mediterranean (Csa): the mean annual maximum and minimum daily air temperatures are 20.2°C and 9.5°C, respectively, and the mean rainfall is 971 mm per year. For the period of the research, the minimum and maximum daily temperatures and daily rainfall were obtained from a weather station located at the experimental site.

In both years, experimental treatments consisted of three sowing dates and four cultivars of durum wheat (*Triticum turgidum* L. ssp. *durum*). Sowing dates were: November (mid-autumn, recommended sowing for central Italy), December (winter sowing) and February (early spring sowing). The tested cultivars were Claudio (Cl), Normanno (Nm), Saragolla (Sg) and Svevo (Sv), all semidwarf modern genotypes selected in Italy for good-quality pasta production (Ercoli *et al.*, 2011). The cultivars Normanno and Svevo are promoted as good tillering types, whereas for Saragolla and Claudio no information on tillering is given. Other cultivar features are reported in Table 1.

Each year, treatments were arranged in a split-plot factorial design, with four replicates. Sowing dates were the main plots and cultivars the subplots.

Experimental equipment and crop management

Plants were grown outdoors in 29-L pots. The pots were made from polyvinyl chloride (PVC) tubes (60 cm long by 25 cm diameter) fitted with a PVC base serving as a bottom. A 30-mm-diameter hole was drilled in the bottom of each pot and a 5-cm layer of drainage gravel was added before soil. Pots were filled with 30 kg of soil, the main characteristics of which were similar over the two years and were approximately 54.9% sand (2-0.05 mm), 33.5% silt (0.05-0.002 mm), 11.6% clay (<0.002 mm), 7.7 pH, 0.7 g kg⁻¹ total N (Kjeldahl method), 4.4 mg kg⁻¹ available phosphorus (Olsen method) and 69.3 mg kg⁻¹ available potassium (BaCl₂-TEA method). Pots were placed side-by-side into growth boxes built with a reticular net in order to allow plants to form a relatively normal and uniformly distributed aerial canopy structure. Edge effects were avoided by supplement pots placed around those used for harvests. All pots were embedded in expanded clay and growth boxes

Table 1. Genetic background and year of release of wheat cultivars used in the research.

Cultivar	Genetic origin	Year of release
Claudio	Cimmyt35/Durango//IS193B/Grazia	1998
Normanno	Simeto/F22//L35	2002
Saragolla	Iride/LineaPSB 0114	2004
Svevo	Linea Cimmyt/Zenit	1996

surrounded by polystyrene panels to reduce daily fluctuations in soil temperature.

Sowing dates were 9 and 19 November, 28 and 20 December, and 9 and 19 February, in the growing seasons 2011-2012 and 2012-2013, respectively. Pots were sown with 20 seeds, placed in two rows spaced 12.5 cm. After emergence, the seedlings were thinned to ten plants per pot, corresponding to approximately 200 plants m^{-2}. This density is low compared to that of 300-400 plant m^{-2} conventionally applied in central Italy, but it was chosen to reduce inter-plant competition for tiller development. Due to pot arrangement, canopy density was slightly lower, approximately 160 plants m^{-2}. As a whole, 96 pots per year were harvested: 48 were harvested at anthesis for the determination of floret number, and 48 at maturity for the determination of grain yield and its components.

Phosphorus and potassium were applied pre-planting as triple mineral phosphate and potassium sulphate, at rates of 100 kg ha^{-1} of P$_2$O$_5$ and K$_2$O. Following the management techniques typically used (Ercoli *et al.*, 2013), nitrogen was applied at a rate of 150 kg ha^{-1} and was split into three applications: at sowing as ammonium sulphate, at pseudo-stem erection and at first node detectable as urea, in the following proportions: 30-60-60 kg N ha^{-1}. Weed control was performed by hand hoeing and pots were watered near to field capacity throughout the growing season. As the pots were well drained, both limiting and excess water conditions were avoided and therefore the effects of the very different rainfall in the two years were minimized.

Plant measurements

Over the entire growth cycle, phenological stages were recorded following the Zadoks' scale (Zadoks *et al.*, 1974), as were the time of reaching emergence, anthesis and maturity, as reported in Table 2. In each pot, stages were considered achieved when they were observed on more than 50% of the plants. To distinguish main culm from tillers, at the stage 3-leaves unfolded (stage 13) the 3rd leaf blade of all plants was marked with a spot of black nail polish, and at the stage the 5th leaf tip was visible (stage 14) a red wool-thread was tied around the sheath of the 4th leaf. As low order leaves are hard to detect at maturity, at later stages the 5th and the 7th leaf blades were also marked with different coloured nail polish.

At anthesis, five main culm (MC) and five tiller (T) spikes per pot were randomly chosen and immediately analysed, or stored in a refrigerator for maximum 48 h. The number of spikelets per spike was counted and classified as *complete* (with well-developed glumes and awns) and *aborted* (with very small glumes and awns missing or very short). The number of fertile florets was counted under a stereomicroscope (Leica Z16 APO) with a magnification up to 92x on five sample spikelets (two basal, two central, and the terminal spikelet), as shown in Figure 1. Florets were considered *fertile* when they had green anthers and a *bifidum* stigma (Álvaro *et al.*, 2008).

At maturity, plants were harvested and separated into main culm, fertile tillers (bearing a spike) and sterile tillers. On each plant we determined the number of fertile and sterile tillers, the number of leaves formed on the main culm, and the number of complete and aborted spikelets of MC and T spikes. In addition, on five MC and five T spikes per pot, we counted the number of kernels on five spikelets where the position was the same as chosen for floret counts (Figure 1). Main culm and tiller spikes of each pot were separately threshed with a laboratory thresher and the grain yield and kernel numbers were determined for each spike type.

Calculations

The duration of phenological stages was expressed in thermal time, calculated as the sum of heat units measured in growing degree-days (GDD), as GDD = ((Tmax + Tmin)/2) – Tb. In the formula, Tmax and Tmin are the daily maximum and minimum air temperatures, and Tb is the base temperature below which no significant crop development occurs. If Tmin < Tb then Tmin = Tb was also incorporated into the equation. An upper threshold temperature (Tut), above which crop development is negatively affected, was also incorporated, *i.e.*, if Tmax > Tut then Tmax = Tut (McMaster and Wilhelm, 1997). The utilized cardinal intervals were 0-25°C up to the stage the first node was detectable and 7-30°C for the following phases (Porter and Gawith, 1999; Eshaghi *et al.*, 2011).

The number of total primordia initiated on main culms was obtained as the sum of final leaves and total spikelets. Spikelet abortion rate was calculated as the percentage ratio of aborted and total (complete+aborted) spikelets. Mean kernel weight was calculated separately for MC and T spikes by dividing MC (or T) grain yield per pot by the number of MC (or T) kernels per pot. The number of florets, or kernels, in basal and central spikelets was averaged for the two spikelets analysed for each position. Grain recovery was calculated for each position, as the percentage of the number of kernels per spikelet on the number of florets per spikelet.

Floret counts are laborious and time-consuming and must be carried out over a short time span, so it is more convenient to estimate the total number of florets within a spike from that of a few sample spikelets. Thus, in the first year of the research, we counted
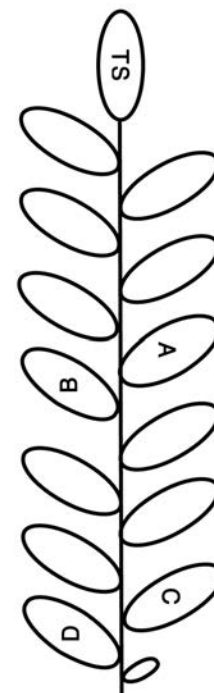

Figure 1. Position of spikelets utilised for floret counts: basal (C, D); central (A, B); terminal spikelet (TS).

all fertile florets of one MC and one T spike per pot (96 in total) and plotted the obtained values against the average floret numbers of two basal, two central and the terminal spikelet of the same spikes, multiplied by the number of complete spikelets. We found that counted and estimated values were closely related when the average of two basal, two central and the terminal spikelet were used (Figure 2). In addition, we also found a significant relationship between the counted kernels per spike and the average kernel number of two basal, two central and the terminal spikelet multiplied by the number of complete spikelets (Figure 2). These findings allowed usto estimate the number of fertile florets per spike by multiplying the average number of florets of the five chosen spikelets per the number of complete spikelets per spike, and then calculating grain recovery on a spike basis.

Statistical analysis

Results were subjected to analysis of variance (Tables 3 and 4). The experimental design was a split-split-plot with four replicates: years were located as main plots, sowing dates as subplots and cultivars as sub-subplots. To assess if the number of florets and kernels per spikelet and grain recovery were affected by spikelet posi-

tion within the spike, we arranged these data in a split-split-split-plot experimental design. Years were located as main plots, sowing dates as subplots, cultivars as sub-subplots, and spikelet positions as sub-sub-subplots. Percentage data were arcsin transformed before analysis. Significantly different means were separated at a 0.05 probability level by Tukey's test (Steel *et al.*, 1997).

Results

Climate

The mean temperature of the entire wheat growing season (November-July) was quite similar in 2011-12 and 2012-13, at 11.6 and 12°C, respectively. However, in the first season the average minimum temperature was lower (4.9 *vs* 6.9°C) and the maximum temperature higher (18.3 *vs* 17.1°C) than in the second (Figure 3). Rainfall differed more than twofold (499 *vs* 1155 mm) in the two growing seasons. Differences were greatest in winter, with a cumulative rainfall of 70 mm in 2011-2012, and 596 mm in

Table 2. Time (days after sowing) to emergence, anthesis and maturity, as affected by sowing date and cultivar, in the growing seasons 2011-2012 and 2012-2013.

Stage	Cultivar	09-Nov 2011	19-Nov 2012	28-Dec 2011	20-Dec 2012	09-Feb 2012	19-Feb2013
Emergence		13	14	32	36	20	19
Anthesis	Claudio	172	165	134	138	97	90
	Normanno	180	170	134	139	97	90
	Saragolla	169	162	131	134	93	86
	Svevo	169	162	131	134	95	87
Maturity		224	218	186	190	146	140

Table 3. Results of ANOVA for the experimental design split-split-plot Year × Sowing date × Cultivar.

Treatments	Grain yield (g plant⁻¹)	Leaves (n)	Total primordia (n)	Grain yield (g spike⁻¹)	Main culm Kernels (n spike⁻¹)	MKW (g)	Complete spikelets (n spike⁻¹)	Initiated spikelets (n spike⁻¹)	Spikelet abortion (%)	Fertile florets (n spike⁻¹)
Year (Y)	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Sowing date (S)	*	*	*	*	*	*	*	*	*	n.s.
Y × S	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Cultivar (C)	*	*	*	*	n.s.	*	*	*	*	*
Y × C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S × C	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Y × S × C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

	Tiller (n plant⁻¹)	Spikes (n plant⁻¹)	Cumulative grain yield (g plant⁻¹)	CTY (%)	Grain yield (g spike⁻¹)	Kernels (n spike⁻¹)	MKW (g)	Complete spikelets (n spike⁻¹)	Initiated spikelets (n spike⁻¹)	Spikelet abortion (n spike⁻¹)	Fertile florets (n spike⁻¹)
Year (Y)	n.s.	n.s.	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Sowing date (S)	*	*	*	*	n.s.	n.s.	*	*	*	*	*
Y × S	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Cultivar (C)	*	n.s.	*	*	*	*	*	*	*	*	*
Y × C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S × C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Y × S × C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

2012-2013 (Figure 3). Around anthesis and during grain-filling, conversely, rainfall was 83 mm higher in the dryer growing season.

Phenology

In the warmer growing season of 2012-2013, growth cycles were 4-6 days shorter than in 2011-2012, whereas anthesis occurred approximately one week earlier in November and February sowings, but four days later in December, probably because of slower emergence (Table 2). Time to anthesis was reduced with the delay of sowing, by approximately 40 days in December and by 77 days in February, so that the length of the entire growth cycle decreased from approximately 221 days in November to 188 in December and

Table 4. Results of ANOVA for the experimental design split-split-split-plot Year × Sowing date × Cultivar × Spikelet position.

Treatments	Main culm Fertile florets (n spikelet⁻¹)	Kernels (n spikelet⁻¹)	Grain recovery per spikelet (%)	Tillers Fertile florets (n spikelet⁻¹)	Kernels (n spikelet⁻¹)	Grain recovery per spikelet (%)
Year (Y)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Sowing date (S)	*	n.s.	*	n.s.	n.s.	n.s.
Y × S	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Cultivar (C)	*	*	*	n.s.	*	*
Y × C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S × C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Y × S × C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Spikelet position (P)	*	*	*	*	*	*
Y × P	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S × P	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
C × P	*	n.s.	n.s.	*	n.s.	n.s.
Y × S × P	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Y × C × P	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S × C × P	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Y × S × C × P	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
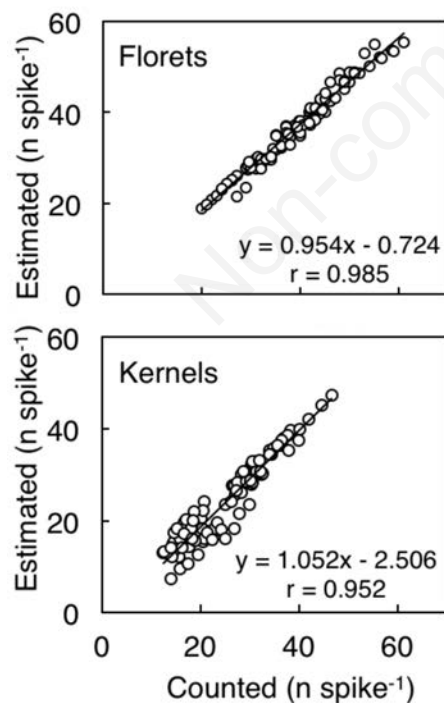
Figure 2. Relationships between the numbers of florets, or kernels, per spike counted and estimated as the mean value of five spikelets per spike (two basal, two central and the terminal spikelet) multiplied by the number of complete spikeletsper spike (n=96).
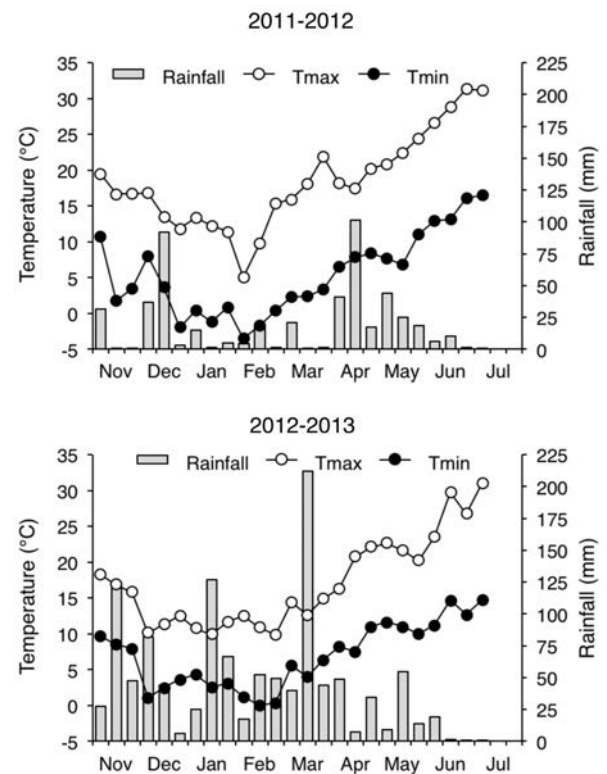
Figure 3. Decadic maximum and minimum temperatures and rainfall over the durum wheat growing seasons 2011-12 and 2012-13.

143 in February. In both years and all sowings, Saragolla and Svevo reached anthesis earlier than Claudio and Normanno, whereas maturity was achieved by all cultivars on the same date.

The thermal time of plant phases was differently affected by the delay of sowing. In November and February sowings plants needed approximately 130°Cd to complete emergence, whereas they required 215°Cd in December (data not shown). The length of the vegetative phase (emergence-1st node detectable) decreased up to 48% from November to February, with the highest reduction between November and December (Figure 4A). The duration of stem elongation (1st node detectable-anthesis) was less affected by sowing date and patterns differed slightly among cultivars (Figure 4B). Finally, the grain-filling phase (anthesis-maturity) increased between November and December and then did not change further (Figure 4C). Cultivars did not differ in the time to emergence and differences in the length of following phases were more appreciable in November than in later sowings. The thermal time of the vegetative phase decreased in the order Normanno>Claudio> Saragolla>Svevo, with an overall 13% decrease; the stem elongation phase was 18% longer in Normanno and Svevo compared to Claudio and Saragolla, and the grain filling phase was 14% shorter in Normanno (Figure 4). As a result the thermal time to anthesis equalled in the cultivars Saragolla and Svevo and was from 5 to 12% longer in the cultivars Claudio and Normanno, respectively.

Grain yield of plants

Analysis of variance highlighted a significant year mean effect for the grain yield per plant, the cumulative grain yield of tillers, and the contribution of tillers to yield (Table 3). The interactions with year were never significant, and those between sowing date and cultivar were only found to be significant for grain yield per plant. Accordingly, all data were presented as means of the two growing seasons and, except for grain yield per plant, they were presented as sowing date and cultivar mean effects.

Averaged over years, in all cultivars grain yield per plant did not change significantly between November and December sowings and decreased in February, but the decrease was by 12% in Svevo and by approximately 20% in the other cultivars (Figure 5). The cultivar Claudio yielded 8% less than the others in November. Averaged over seeding dates and cultivars, grain yield was 16%

lower in the growing season 2012-2013 (2.6 *vs* 3.1 g plant^{-1}), which was a consequence of the lower contribution of tillers to plant yield (Table 5). Tiller number, fertility and yield slightly and not significantly increased with the delay of sowing from November to December, whereas a further delay to February sig-
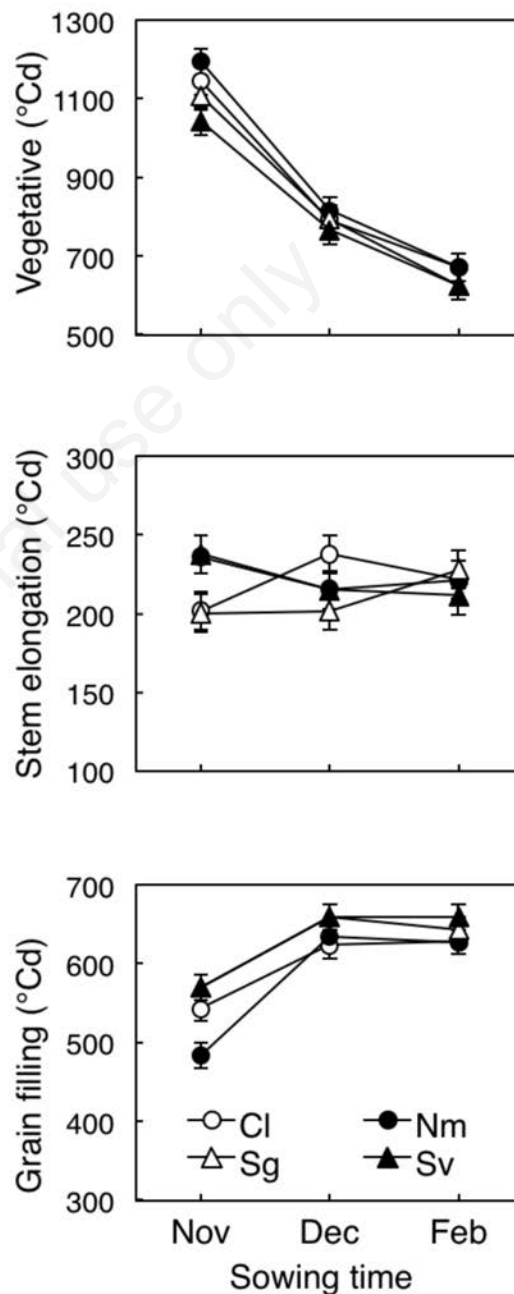
Figure 4. Thermal times of the vegetative (emergence-1st node detectable, A), stem elongation (1st node detectable-anthesis, B) and grain filling (anthesis-maturity, C) periods, as affected by sowing date and cultivar. Cl, Claudio; Nm, Normanno, Sg, Saragolla; Sv, Svevo. Data are means of two years and four replicates (n=8). Vertical bars represent honest significant difference at P<0.05.

Table 5. Number of tillers and tiller spikes per plant, tiller yield, and contribution of tillers to grain yield per plant (CTY), as affected by the growing season, sowing date, and cultivar mean effects.

Treatment	Tillers (n plant^{-1})	T spikes (n plant^{-1})	T yield (g plant^{-1})	CTY (%)
Growing season				
2011-2012	4.2[a]	1.8[a]	1.4[a]	46.1[a]
2012-2013	4.1[a]	1.4[a]	1.0[b]	39.0[b]
Sowing date				
November	4.3[a]	1.8[a]	1.3[a]	44.4[a]
December	4.7[a]	2.0[a]	1.5[a]	49.9[a]
February	3.6[b]	1.3[b]	0.9[b]	35.5[b]
Cultivar				
Claudio	4.4[ab]	1.9[a]	1.2[b]	41.7[b]
Normanno	3.8[b]	1.7[a]	1.2[b]	41.4[b]
Saragolla	4.9[a]	1.5[a]	1.2[b]	40.7[b]
Svevo	3.6[b]	1.7[a]	1.5[a]	49.2[a]

Within each block, values followed by different letters are significantly different (P<0.05).

nificantly decreased these parameters. Accordingly, the contribution of tillers to plant yield ranked in the order December≥November>February (Table 5). Despite differences in tiller production, cultivars did not significantly differ in the number of tiller spikes. Conversely, the cumulative grain yield of tillers per plant was 25% higher in Svevo, which increased the contribution of tillers to plant yield by approximately eight percentage points.

Grain yield and yield components of main culm and tiller spikes

Sowing date only slightly affected the grain yield of MC spikes and did not affect that of T spikes (Table 6). Yield components responded differently to sowing date, with similar trends in MC and T spikes. The mean kernel weight was lowest in November, whereas the number of kernels per spike was highest. The number of complete spikelets per spike progressively decreased with the delay of sowing, whereas the number of kernels per spikelet was unaffected.

Grain yield per spike significantly differed among cultivars, with different rankings for MC and T (Table 6). The former yielded more in Normanno and Saragolla, whereas the latter in Svevo and Saragolla. Accordingly, the grain yield of MC spikes was always markedly higher than that of T spikes, but the increase was by 67%, 111%, 139% and 159%, in Svevo, Saragolla, Normanno and Claudio, respectively. The mean kernel weight was significantly lower in the cultivar Normanno in both spike types, while the highest values were recorded in Claudio. The number of kernels per spike did not differ among cultivars in MC and was approximately five kernels lower in Claudio in T. In both spike types, the number of complete spikelets ranked in the order Saragolla>Normanno>Claudio>Svevo, with significant higher values in Saragolla compared to Claudio and Svevo. Finally, the number of kernels per spikelet was lower in Saragolla in MC spikes and higher in Svevo in T spikes.

Despite the above differences among cultivars and independently of sowing date, in MC and T spikes, grain yield per spike was positively and significantly correlated with the number of kernels per spike, which in turn was correlated with the number of kernels per spikelet (Figure 6). Otherwise, no relationships were found for grain yield per spike, or kernels per spike, with other yield components and sub-components (data not shown).
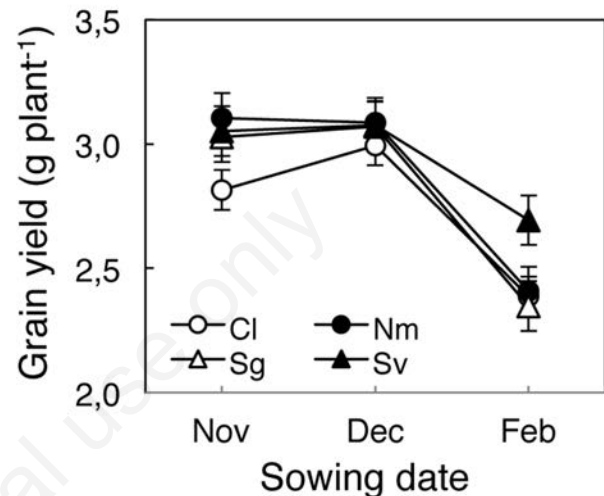

Figure 5. Grain yield per plant, as affected by sowing date and cultivar. Cl, Claudio; Nm, Normanno, Sg, Saragolla; Sv, Svevo. Data are means of two years and four replicates (n=8). Vertical bars represent honest significant difference at P<0.05.

Table 6. Grain yield and yield components of main culm and tiller spikes, as affected by the sowing date and cultivar mean effects.

Treatment	Grain yield (g spike⁻¹)	Mean kernel weight (mg)	Kernels (n spike⁻¹)	Complete spikelets (n spike⁻¹)	Kernels (n spikelet⁻¹)
			Main culm spike		
Sowing date					
November	1.7[a]	46.1[b]	36.4[a]	16.5[a]	2.2[a]
December	1.5[b]	51.1[a]	30.0[b]	14.7[b]	2.1[a]
February	1.6[ab]	51.3[a]	30.6[b]	13.5[c]	2.3[a]
Cultivar					
Claudio	1.6[ab]	53.7[a]	29.6[a]	13.6[b]	2.2[a]
Normanno	1.7[a]	45.7[b]	36.0[a]	15.8[ab]	2.3[a]
Saragolla	1.7[a]	50.4[a]	33.2[a]	17.2[a]	1.9[b]
Svevo	1.5[b]	48.2[ab]	30.5[a]	13.1[b]	2.3[a]
Tiller spike					
Sowing date					
November	0.76[a]	43.6[b]	17.6[a]	13.1[a]	1.4[a]
December	0.76[a]	46.3[a]	16.4[a]	11.6[ab]	1.4[a]
February	0.70[a]	46.2[a]	14.9[a]	10.3[b]	1.4[a]
Cultivar					
Claudio	0.61[b]	47.4[a]	12.8[b]	11.0[bc]	1.2[b]
Normanno	0.69[b]	41.4[b]	16.5[a]	12.4[ab]	1.4[b]
Saragolla	0.79[a]	45.4[a]	17.4[a]	13.0[a]	1.3[b]
Svevo	0.87[a]	47.2[a]	18.5[a]	10.2[c]	1.8[a]

Within each block, values followed by different letters are significantly different (P<0.05).

Primordia initiation and abortion

The number of complete spikelets in a spike is a function of the number of spikelet primordia initiated by the culm apex and their abortion rate. Our results highlighted that the number of initiated spikelets was less than two units lower in T compared to MC, whereas the abortion rate was markedly higher in the former, at 13 *vs* 4% (Table 7). The delay in sowing reduced both the initiation and the abortion of spikelets, so that the decrease in complete spikelets was lower than that in total spikelets, particularly in tillers (Tables 6 and 7). Averaged over sowing dates, the number of initiated spikelets was significantly higher in the cultivars Normanno and Saragolla, and the latter cultivar also showed the lowest abortion rate (Table 7).

The number of leaves formed on the main culm decreased progressively from November to February, averaged over cultivars (Table 8). Thus, the total leaf and spikelet primordial initiated on the main culm apex decreased by approximately five units, from 28.3 to 23 with the delay of sowing. Averaged over sowings, the number of MC leaves was significantly higher in Claudio and lower in Saragolla, while intermediate values were recorded in Normanno and Svevo. Accordingly, the total number of initiated MC primordia was significantly lower in Svevo compared with the other cultivars.

Floret formation and grain recovery

Analysis of variance highlighted that sowing date, cultivar and spikelet position affected floret number and grain recovery per spikelet, but no year effect was detected (Table 4). The only significant interaction was found between cultivar and spikelet position for the floret number.

The number of fertile florets per spikelet increased progressively with the delay of sowing, but the increment was significant only in MC between November and February (Table 7). In MC spikes, the number of fertile florets per spikelet did not differ significantly among cultivars in the basal spikelets, whereas it was

approximately 0.5 florets lower in Claudio in the other positions (Figure 7). In T spikes, differences were found only in the terminal spikelet, with Svevo and Normanno showing approximately 2.1 florets and Claudio and Saragolla 1.6. The number of fertile florets per spikelet was always higher in MC than in T spikes and depended on spikelet position, decreasing significantly in the order central>basal≥terminal in both spike types. On average, the number of
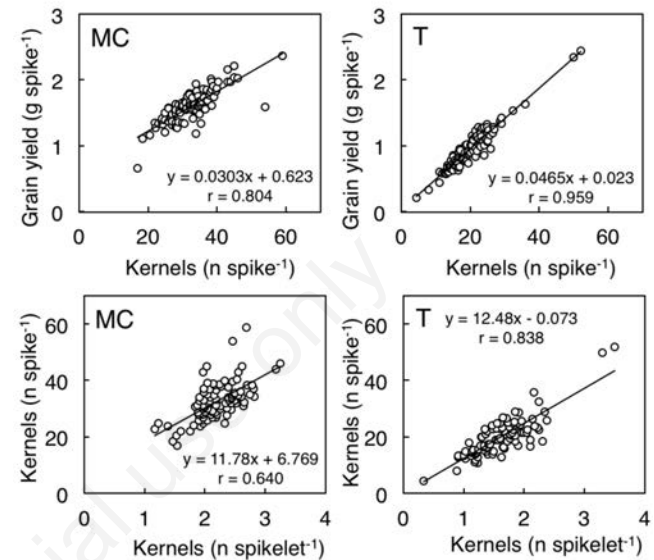

Figure 6. Relationship between grain yield per spike and kernels per spike, and between kernels per spike and kernels per spikelet, in main culms (MC) and tillers (T) (n=96).

Table 7. Determinants of the numbers of spikelets and kernels in main culm and tiller spikes, as affected by the sowing date and cultivar mean effects.

Treatment	Initiated spikelets (n spike^{-1})	Spikelet abortion (%)	Fertile florets (n spikelet^{-1})	Grain recovery per spikelet (%)	Fertile florets (n spike^{-1})
			Main culm spike		
Sowing date					
November	17.4[a]	5.3[a]	2.5[b]	88.0[a]	42.0[a]
December	15.1[b]	2.5[b]	2.7[ab]	77.8[b]	41.8[a]
February	13.9[c]	2.7[b]	3.0[a]	76.7[b]	38.7[a]
Cultivar					
Claudio	14.2[b]	4.4[a]	2.5[b]	88.0[a]	34.2[b]
Normanno	16.5[a]	4.8[a]	2.9[a]	79.3[b]	44.7[a]
Saragolla	17.3[a]	0.3[b]	2.9[a]	65.5[c]	49.2[a]
Svevo	13.9[b]	5.6[a]	2.8[a]	82.1[a]	35.4[b]
			Tiller spike		
Sowing date					
November	15.8[a]	16.9[a]	2.1[a]	66.7[a]	27.3[a]
December	12.8[b]	9.5[b]	2.2[a]	63.6[a]	28.3[a]
February	11.9[b]	13.4[ab]	2.3[a]	60.9[a]	23.8[b]
Cultivar					
Claudio	12.7[b]	13.2[b]	2.1[a]	57.1[b]	22.6[b]
Normanno	15.0[a]	17.3[a]	2.3[a]	60.9[b]	28.2[a]
Saragolla	14.2[a]	7.9[c]	2.2[a]	59.1[b]	28.1[a]
Svevo	12.1[b]	15.7[ab]	2.3[a]	78.3[a]	27.0[a]

Within each block, values followed by different letters are significantly different (P<0.05).

florets per MC spikelet was 2.5 in Claudio compared to approximately 2.9 in the other cultivars, whereas in T spikelets it was not affected by sowing date and cultivar and was approximately 2.2.

Grain recovery per spikelet, *i.e.*, the proportion of fertile florets that actually produced kernels within each spikelet, was markedly higher in MC than in T spikes, at 80 *vs* 63% on average (Table 7). In MC, grain recovery was significantly higher in the November sowing, whereas in T it was not affected by the sowing date. Grain recovery differed among varieties: in MC it ranked in the order Claudio>Svevo>Normanno>Saragolla, whereas in T it was significantly higher in Svevo. Finally, grain recovery was significantly affected by spikelet position. In MC spikes it was 87% in the central spikelets and approximately 76% in the other positions, while in T spikes it was approximately 71% in the basal and central spikelets but only 47% in the terminal one (Figure 8).

Table 8. Number of leaves and total primordia formed on the main culm apex, as affected by the sowing date and cultivar mean effects.

Treatment	Leaves (n culm^{-1})	Total primordia (n apex^{-1})
Sowing date		
November	10.9[a]	28.3[a]
December	9.8[b]	24.9[b]
February	9.1[c]	23.0[b]
Cultivar		
Claudio	10.8[a]	25.0[ab]
Normanno	9.8[b]	26.3[a]
Saragolla	9.3[c]	26.6[a]
Svevo	9.9[b]	23.8[b]

Within each block, values followed by different letters are significantly different (P<0.05).
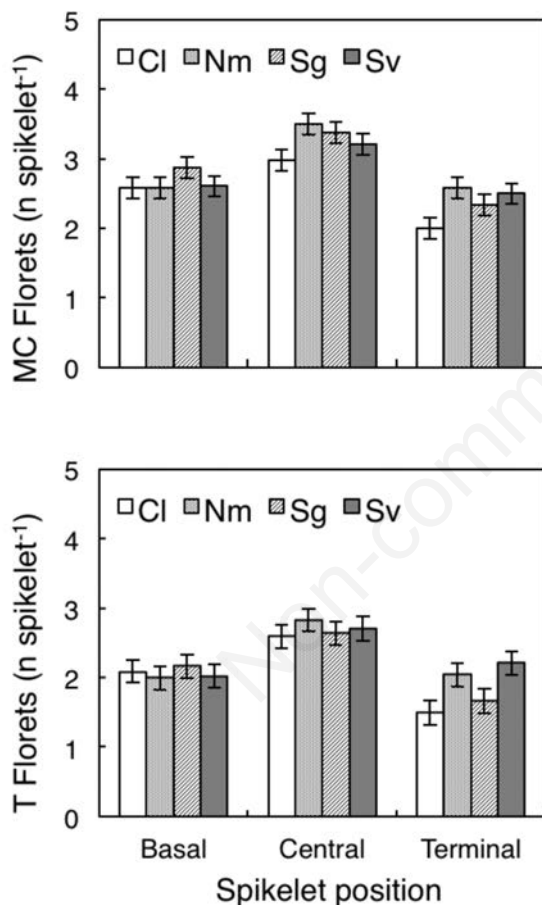

Figure 7. Number of florets per spikelet of main culm (MC) and tiller (T) spikes, as affected by cultivar and spikelet position within the spike. Cl, Claudio; Nm, Normanno, Sg, Saragolla; Sv, Svevo. Data are means of two years, three sowing dates and four replicates (n=24). Vertical bars represent honest significant difference at P<0.05.
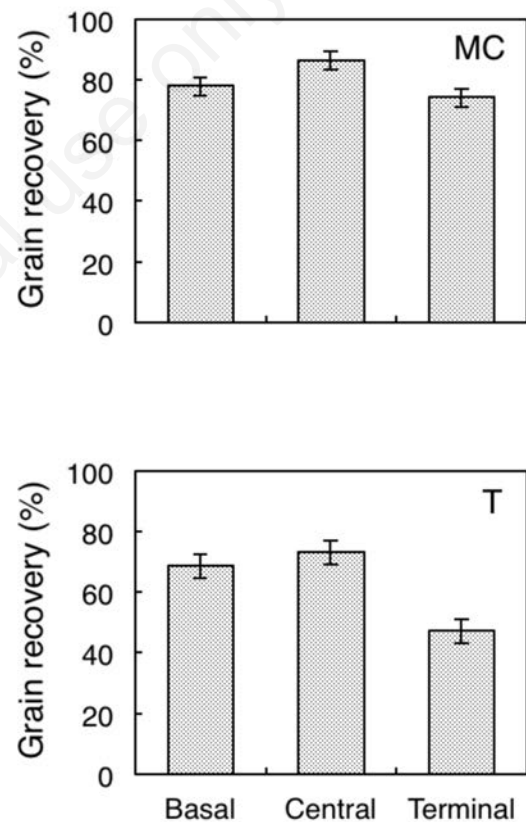

Figure 8. Grain recovery in spikelets of main culm (MC) and tiller (T) spikes, as affected by spikelet position within the spike. Data are means of two years, three sowing dates, four cultivars and four replicates (n=96). Vertical bars represent honest significant difference at P<0.05.

The number of fertile florets per spike, estimated from the product of the average floret number of five sample spikelets and the number of complete spikelets per spike, was lower in February than in earlier sowings, but differences were significant only in T (Table 7). In MC spikes, the number of florets was approximately 30% higher in Saragolla and Normanno compared to Claudio and Svevo, whereas in T spikes it was approximately 20% lower in Claudio than in the other cultivars. Grain recovery calculated on spike basis showed patterns similar to those calculated for spikelets (data not reported).

Discussion

The durum wheat cultivars utilized in this research produced between 2.3 and 3.1 g of grain per plant. Between-years differences in grain yield were low compared to the marked differences in rainfall, probably because plants were grown in well-drained pots, which avoided waterlogging in 2012-2013, and also received artificial irrigation, which avoided drought stress up to anthesis in 2011-2012, and during grain filling in both years.

Variations in grain yield per plant were not significant between mid-autumn and winter sowings (November and December), while the delay to early spring (February) markedly decreased grain yield, primarily because of the lower tiller production, whereas the yield of single spikes did not, or only slightly, decreased. Yield decrease was less pronounced in Svevo, which was associated with the higher yield of tiller spikes compared to the other cultivars. The number of fertile tillers did not vary significantly among cultivars and, on average, the promoted good-tillering cv. Normanno and Svevo showed only 5% higher yield compared to Claudio and Saragolla. These findings confirm that the plasticity in the number and yield of tiller spikes is crucial to responding positively to high yielding conditions (Sadras and Rebetzke, 2013; Slafer et al., 2014; Subira et al., 2015), and to compensate for the lower yield of main culm spikes (Elhani et al., 2007). They also highlight that the four tested cultivars perform similarly at stand densities ideal for good-tillering genotypes when grown in optimal water conditions (Valério et al., 2009).

Although tillers contributed substantially to grain yield, the average yield of one tiller spike was approximately half that of one main culm spike, which resulted from the sum of slightly lower spikelet initiation and higher spikelet abortion, on one hand, and a lower number of florets per spikelet, grain recovery and mean kernel weight, on the other.

Effect of sowing date on spike yield components

The delay of sowing markedly shortened the vegetative phase, which reduced the initiation of both leaf and spikelet primordia. Spikelet abortion also decreased, possibly because of lower intra-spike competition, so that the reduction in the number of complete spikelets was less pronounced. According to Serrago et al. (2008), later sowings expose plants to a longer photoperiod during the phase of rapid stem elongation, thus reducing its duration and the number of fertile florets per spike. In contrast, we found that the thermal time of the period was only slightly affected and the number of florets per spikelet tended to increase, with a higher degree in main culm than in tiller spikes. Li et al. (2001) also reported that spikelet number was more sensitive to delays in sowing than floret production, which can be interpreted as an adjustment to the lower number of spikelets (Sinclair and Jamieson, 2006). We found, however, that excess florets were not fertilized, as shown by the

lower grain recovery in later sowings, and, therefore, the number of kernels per spikelet was generally unaffected, and the number of kernels per spike decreased. It is worth noting that though floret production and grain recovery differed according to spikelet position, all spikelets responded similarly to sowing date, suggesting that they equally suffered from assimilates shortening in later sowings.

Mean kernel weight is the last-determined yield component, and thus it may compensate for the lower number of kernels produced in later sowings, provided that environmental conditions are favourable to ovary growth around anthesis and to grain filling later on (Moragues et al., 2006; Ferrise et al., 2010; Slafer et al., 2014). In many wheat growing areas, however, this does not occur because heat stress and terminal drought reduce grain growth duration and kernel weight (Brdar et al., 2008; Modarresi et al., 2010; Mitchell et al., 2013). In our research, grain-filling duration was not greatly affected and the thermal time was even longer in later sowings. The kernels were accordingly heavier in December and in February compared to November, but increments were not enough to compensate for the lower kernel number. Though our results could be influenced by the fact that the pots were irrigated, Khaledian et al. (2013) estimated that in the northern Mediterranean area, terminal growth is generally also maintained in rainfed field conditions.

In summary, delays from the conventional sowing date slightly decreased the yield of MC spikes, reducing primarily spikelet number, which was not compensated by higher production of florets per spikelet and only in part by increased kernel weight. As grain yield per plant did not differ significantly between November and December sowings, our results highlight that in the winter sowing, tillers fully compensated for the smaller MC spike by slightly increasing the number of fertile spikes per plant and by maintaining their size and grain set. Tillers thus play a key role in maintaining yield stability across autumn-winter sowings.

Effect of genotype on spike yield components

The four durum-wheat cultivars differed in the strategies of yield determination (Fischer, 2008), primarily in spike size, spikelet fertility, mean kernel weight, and in the contribution of tillers to yield, and also differed in the duration of phenological phases. Nevertheless, for all yield components, the response to sowing date showed similar patterns among cultivars, but differences in amplitude, so that a Cultivar × Sowing date interaction existed only for grain yield per plant.

Genotypic variation in response to the environment is often associated with differences in phenology (Miralles and Slafer, 2007; Modarresi et al., 2010; Borrás-Gelonch et al., 2012) and in our research it could depend on the wide variation in daylength sensitivity of durum wheat genotypes released in Italy (Motzo and Giunta, 2007; Subira et al., 2015). We found that cultivars differed in the relative length of vegetative, stem elongation and grain-filling phases, but, similar to the findings of Whitechurch et al. (2007), these differences tended to disappear in the winter and early spring sowings. Accordingly, differences in yield stability in late sowings cannot be ascribed to differences in the duration of phenological phases.

Tillering capacity is another trait associated with the responsiveness of genotypes to the environment (Dreccer et al., 2013; Sadras and Rebetzke, 2013; Hendriks et al., 2016). In our research, the cultivar Svevo exhibited the highest contribution of tillers to plant yield and the smallest yield loss in the February sowing, which relied on the elevated grain yield of single tiller spikes rather than on their number. Consistently, Slafer et al. (2014) reported

that, while environment mainly drives variations in spike number, genotype drives those in kernels per spike. The good tiller yield was associated with higher grain recovery and mean kernel weight compared to those of other cultivars. Analysing the performances of Svevo against phenological and yield-component traits, we hypothesize that the higher yield stability depended on its more pronounced spring habit and very low sensitivity to daylength (Motzo and Giunta, 2007), which supported a faster initiation of both leaf and spikelet primordia and a higher growth rate of tillers (Arduini *et al.*, 2010; Dreccer *et al.*, 2013). This allowed Svevo to shorten the vegetative phase maintaining high leaf number and tiller yield (Borrás-Gelonch *et al.*, 2012), and lengthen the stem elongation phase without delaying anthesis (Miralles and Slafer, 2007). Indeed, we found that both leaf number and tiller yield were higher in Svevo compared to the other early flowering cultivar Saragolla. In addition, because of the earlier start of stem elongation, Svevo formed overall less primordia (leaves + initiated spikelets) on the main culm compared to Saragolla, which probably reduced within and between spike competitions. These are both crucial for adequate floret development and fertilization (Bancal, 2009; González-Navarro *et al.*, 2015). Our hypothesis is supported by the higher grain recovery and tiller contribution to yield in Svevo than in Saragolla, despite coincident anthesis, and according to Li *et al.* (2001), this can be consistent with the spring habit.

Conversely, the worse yield performance of the cultivar Claudio was primarily because of low spikelet fertility, which was due to lower floret production in both spike types, particularly in the central and upper spikelets, and to the lower grain recovery in tillers. We associated these traits with the longer vegetative phase, evidenced by the higher main-culm leaf number compared to other cultivars, and the short stem elongation phase, which reduces the time for floret differentiation and makes this cultivar similar to older genotypes (Motzo and Giunta, 2007; Álvaro *et al.*, 2008). Ferrante *et al.* (2012) associated the lower yield of Claudio with lower grain set and fruiting efficiency. In our research, however, reduced spikelet fertility was in part compensated during grain filling, so that this cultivar showed the highest mean kernel weight.

The length of the entire growth cycle was equal in the four cultivars, so that earlier anthesis corresponded to longer grain filling. Accordingly, the latest flowering Normanno had the lowest mean kernel weight both in main culm and tillers, suggesting that late anthesis is detrimental to grain filling in Mediterranean photothermal conditions, independently of sowing time and despite an optimal water supply.

In line with the variability in spike size within Italian durum wheat germoplasm (De Vita *et al.*, 2007; Álvaro *et al.*, 2008), the four cultivars differed in spike size, Normanno and Saragolla showing larger spikes than Claudio and Svevo. In our research, larger main culm spikes produced more florets per spike, but suffered from intra-spike competition, as suggested by lower grain recovery and mean kernel weight. The higher yield of tiller spikes observed in Svevo compared to Normanno and Saragolla suggests that large main culm spikes are also more competitive for resources against tillers. In summary, we suggest that the higher yield stability of Svevo relies on the lowest difference in grain yield between main culm and tiller spikes, the former being the lowest yielding and the latter the highest.

Independent of sowing date and cultivar, the grain yield of both main culm and tiller spikes was closely related to the number of kernels per spike, but not to the mean kernel weight, which confirms compensation and less plasticity for the latter yield component (Slafer *et al.*, 2014). In addition, we found that the number of kernels per spike was significantly and positively related to the number of kernels per spikelet, but not to the number of spikelets per spike, suggesting that lower spikelet numbers accommodate higher floret production and recovery.

Conclusions

We suggest that the question of whether tillers are a burden or a resource in durum wheat should be reconsidered. In fact, our results highlight that, at low plant density, tillers contributed at least 40% to plant yield and a better yield stability in later sowings was associated with a higher contribution of tillers to yield. We found that variations in tiller yield in response to sowing date depended primary on tiller number, whereas differences among cultivars relied on the yield of single tiller spikes. A Cultivar × Sowing date interaction was revealed for grain yield per plant, but not for the yield of main culm and tiller spikes and their components.

The analysis of spike types and their components showed that large main culm spikes are more competitive against tiller spikes, but also suffer from intra-spike competition and are more sensitive to delays in the sowing date. Therefore, we hypothesize that higher yield stability can be achieved with a more equal partitioning of resources within main culm and tillers, which can be obtained by reducing the number of main culm primordia and increasing their initiation rate. This allows for the stem elongation and grain filling phases to be longer without delaying anthesis, but it also reduces the sink strength of the main culm spike. Accordingly, more time and resources can be allocated to floret production and to grain filling both in main culm and tillers.

From a methodological point of view, our results show that the number of florets per spike can be effectively estimated by counting florets on only five spikelets from given positions: two basal, two central and the terminal spikelet.

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