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Genotypic variability and response to water stress of pre- and post-anthesis phases in triticale

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Abstract

A better understanding of responsiveness of time to anthesis to water stress in triticale and wheat might help to explain their differences in performance under stress and to identify which attributes or components of time to anthesis are most affected. Three experiments were carried out during the 2004 and 2005 growing seasons to (i) evaluate genotypic variability in phenology responsiveness to drought in triticale and to (ii) explore the variation in the duration of pre-anthesis phases occurring before and after the onset of stem elongation as well as their responsiveness to water stress. Important variation was found among triticale cultivars on time to anthesis, allowing classification of cultivars into long, intermediate and short cycle. Differences in the duration of the stem elongation phase (i.e. from terminal spikelet initiation (TS) to anthesis (ANT)) were as high as 200 °Cd for cultivars with similar time to flowering. Although water stress reduced the time to anthesis (in average by ca. 125 °Cd), cultivars showed a differential responsiveness to drought in phases occurring before or after TS. Some cultivars that were highly sensitive to drought in the emergence (Eme)–TS phase were insensitive in the phase TS–ANT and vice-versa. Water shortage tended to reduce the grain filling period and was most evident when a Mediterranean environment treatment was simulated.

Keywords: Water stress; Crop development; Triticale; Wheat

1. Introduction

Triticale seems to be an interesting alternative to other cereals, particularly bread wheat, in environments where growing conditions are unfavorable or in low-input systems (Karpenstein-Machan et al., 1994; Erekul and Köhn, 2006). As an appropriate timing of anthesis is a critical determinant of crop adaptability (Worland, 1996; Slafer and Whitechurch, 2001), it might be speculated that responsiveness of triticale and wheat to environmental stresses could be associated, at least in part, with their likely differences in phenological responses to stress. Although it is well known that the major environmental factors determining the rate of crop development are temperature and photoperiod (see Slafer and Rawson, 1994; and references quoted therein), it has been reported that factors such as water and nutrient stresses could modify the rate of development and consequently, time to anthesis (e.g. Longnecker et al., 1993; Grieve et al., 1994; Otegui et al., 1995; Jalal Kamali and Boyd, 2000; Arisnabarreta and Miralles, 2004; Salvagiotti and Miralles, 2007). A better understanding of responsiveness of time to anthesis in triticale might help explaining adaptability to stressful environments.

As time to anthesis is actually composed of different sub-phases, whose rates of development differ in sensitivity to environmental factors (e.g. Slafer and Rawson, 1994), understanding which attributes or components of time to anthesis are most affected in response to water and nutritional stress may be relevant. This is particularly relevant when considering that partitioning of developmental time between different sub-phases (e.g. before and after the onset of stem elongation) has been shown to be potentially useful to improve yield in wheat and barley (Slafer et al., 1996; Miralles et al., 2000; Gonzalez et al., 2003), due to the physiological relevance for yield of duration of this phase (Slafer, 2003). There are evidences of considerable genetic variability for partitioning of the development time to anthesis and between pre- and post-onset of stem elongation phases both, in wheat (Whitechurch et al., 2007) and barley (Kernich et al., 1997).

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Our understanding of these particularities in triticale is extremely poor. Some evidences in triticale have shown genotypic variability in the duration of time to anthesis due to factors such as temperature and photoperiod (Brouwer, 1977; Ewert, 1996; Ewert et al., 1996; Naylor and Su, 1998; Giunta et al., 2001; Santiveri et al., 2004), but no evidences of sensitivity of time to anthesis to water or nitrogen stress are available. There are no evidences either on genetic variation in partitioning of the total cycle to anthesis into different durations of pre- and post-onset of stem elongation.

The objectives of the present work were (i) to evaluate genotypic variability in phenology responsiveness to drought in triticale and (ii) to determine the variation in the duration of pre-anthesis phases occurring before and after the onset of stem elongation as well as their responsiveness to water stress. In two of the three experiments, wheat was also included to evaluate the potential difference in phenological response to water restrictions.

2. Materials and methods

The study comprised three experiments. The first one focused on variability among several triticale cultivars while the others two compared a pair of triticales selected from experiment 1 with a wheat cultivar well adapted to the growing conditions.

2.1. Experiment 1

In 2004 a field experiment was conducted in the rain-shelter facility of the Institute for Agricultural Plant Physiology and Ecology (IFEVA) of the University of Buenos Aires (34°35′S, 58°29′W). The soil was an 180 cm deep layer of typic argiudoll plow layer resting on native loess (C) (Chimenti et al., 2002).

Treatments consisted of the factorial combination of 11 commercial triticale cultivars and 2 water regimes. The cultivars included (nine bred in Argentina, provided by the National Institute of Agricultural Technology and two Mexican cultivars, provided by The Autonomous University of the State of Mexico (Table 1). Water regimes included an irrigated (700 mm throughout the growing season) and a droughted condition (350 mm), in both cases without nutrient limitations. A watering power station controlled the water supply in each of the treatments, through a drip irrigation system with dripping lines in between the crop rows. The treatments were arranged in a completely randomized design over sites with two replicates. The water regimes corresponded to the sites.

Table 1
Name of the cultivars, species (T, triticale; W, wheat) and origin of the cultivars used in the study

Entry	Cultivar	Species	Origin	Experiment
1	Remedios	T	Argentina	1
2	Tehuelche	T	Argentina	1
3	Presto	T	Argentina	1
4	Yagan	T	Argentina	1–3
5	Genú	T	Argentina	1
6	Quiñe	T	Argentina	1
7	Ñinca	T	Argentina	1
8	Tizne	T	Argentina	1–3
9	Boaglio	T	Argentina	1
10	Cerrillo	T	Mexico	1
11	Maravilla	T	Mexico	1
12	Escudo	W	Argentina	2, 3

The experiment was hand-sown at 350 seeds m^{-2} on 21 July 2004 in plots of four rows, 0.175 m apart and 1.4 m long. Weeds were removed by hand, to avoid any negative effect of hormonal herbicides that may have differentially affected the cultivars, fungicides and insecticides were sprayed to prevent or control fungal diseases and insect damages.

Haun stage (Haun, 1973) was determined from seedling emergence (Eme) until the flag leaf was completely emerged (ligule visible), on three plants per plot three times per week, randomly chosen, Haun stage was determined (Haun, 1973). Phyllochron (°Cd $leaf^{-1}$) was calculated as the reciprocal of the slope of the relationship between the cumulative number of emerged leaves and thermal time from seedling emergence. To determine the timing of terminal spikelet stage (TS) three plants were randomly sampled twice weekly and dissected under binocular microscope. The date of anthesis (ANT) was recorded for each plot when 50% of the spikes of the main shoots had either visible exerted anthers or when anthers that had dehisced were observed through the palea. At anthesis, 20 plants in each plot were labelled and then a single spike was sampled twice a week and the dry weight of the four grains of the central spikelets was recorded from 7 days after anthesis until that the end of the experiment, after physiological maturity. Time of physiological maturity was estimated as when grain growth ceased, estimated by fitting a bilinear regression between grains dries weight and thermal time from anthesis (for details see Miralles and Slafer, 1995).

Air temperature data were recorded hourly using a meteorological station (Davis, weather monitor II) in the experimental area. Thermal time for all phases was calculated using 0 °C as base temperature.

2.2. Experiment 2

The experiment was carried out during the 2005 growing season in the IFEVA's facilities described above. Treatments consisted of three genotypes (two triticales and one wheat), two water regimes and two levels of N availability. The triticale cultivars (Yagan and Tizne) were selected from experiment 1 due to they had similar durations to anthesis phase but differential responsiveness to drought of their pre-anthesis phases. Thus, while the Eme–TS phase showed a high and low response to drought in Yagan and Tizne, respectively; the TS–ANT phase was unaffected in Yagan and very sensitive in Tizne when plants were exposed to water stress. In addition to these triticales one wheat cultivar (Escudo) was also included in this experiment. This wheat possess, under non-limiting conditions, a similar cycle to anthesis to that of the two triticale cultivars chosen. The regimes of water supply were similar to those used in experiment 1 (irrigated = 530 mm and droughted = 250 mm) and treatments applied using the system described therein.

The nitrogen availability treatments consisted of an unfertilized control (N_0) which had 115 kg N ha^{-1} in the soil at sowing and a fertilised with urea (N_1) to increase the availability by 102 kg N ha^{-1} (N_1 = 217 kg N ha^{-1}). The urea application was split into two identical quantities (51 kg N ha^{-1}) broadcasted at the beginning of tillering and at the onset of stem elongation. Treatments were arranged in a randomized complete block design combined over sites (water regimes). The two nitrogen treatments were randomized within water regimes and within each nitrogen × water condition, cultivars were sown in three randomized blocks.

The experiment was hand-sown at 350 seeds m^{-2} on 27 June 2005 in plots of 8 rows, 0.175 m apart and 1.6 m long. The lengths of each development phase were determined as in experiment 1. Weed competition, fungal diseases and insect damages were avoided or controlled as in experiment 1. In this experiment, canopy temperature was recorded for 81, 90, 95 and 105 days after seedling emergence (DAE), in both water regimes using an infrared thermometer (BK PRECISION model 635, California, USA).

2.3. Experiment 3

The same two triticales (Yagan and Tizne) and the wheat (Escudo) used in experiment 2 were grown in a third experiment run in parallel in which they were grown under two regimes of water supply simulating contrasting conditions: irrigated to anthesis and then droughted (Mediterranean environment treatment) and droughted to anthesis and then irrigated (Monsoon environment treatment). The Mediterranean environment treatment received 380 mm of irrigation until anthesis (similar to the "irrigated" treatment of experiment 2 for pre-anthesis) but no further irrigation was provided, while the Monsoon environment treatment was poorly irrigated, with only 180 mm, before anthesis and with another 150 mm during grain filling (similar to water added during grain filling in the irrigated treatment of experiment 2). The treatments were arranged in a randomized complete block design combined over sites. Within each of the two regimens of water supply considered as sites, three replicates of each cultivar were randomized. The experiment was carried out without nutrient limitations and weeds, diseases and pest were controlled as described in experiment 1.

3. Results

In experiment 1, the mean squares of the main effects and the interaction for the duration of period from seedling emergence to terminal spikelet (Eme–TS) were significant ($P < 0.01$). On the other hand, the duration from terminal spikelet initiation to anthesis (TS–ANT) was not affected significantly by the water regime. Also a large and significant variation ($P < 0.01$) was observed in final leaf number (FLN), phyllochron, duration of the period Eme–ANT and from anthesis to physiological maturity (ANT–PM) ($P < 0.05$). The interaction water regime × cultivar in this experiment was only significant for the Eme–TS period (Table 2). In experiment 2, both Eme–TS and TS–ANT periods were affected by moisture treatment ($P < 0.01$) and cultivars only affected the duration Eme–TS. In experiment 2, the moisture treatment affected significantly ($P < 0.01$) the phyllochron and the duration of period Eme–ANT. The cultivars were significantly affected in all variables, except in the duration of period ANT–PM. The mean squares for all variables due to the nitrogen availability (either directly or in interaction with water regime, cultivars or both) were always smaller and never significant (Table 2). Therefore, in this paper the results of the moisture and cultivars treatments are shown averaging both nitrogen availabilities.

3.1. Variability in time to anthesis

Cultivars differed markedly in time to anthesis (Fig. 1). The two Mexican cultivars had much faster rate of development than the Argentine cultivars, which in turn, ranged in thermal time to anthesis from less than 1500 to more than 1700 °Cd. The

Table 2
Mean squares and its statistical significance for final leaf number (FLN), phyllochron and the periods from seedling emergence to terminal spikelet (Eme–TS), emergence to flowering (Eme–ANT) and flowering to physiological maturity (ANT–PM) for 11 triticale cultivars (season 2004) grown in two regimes to water supplied and two triticale and one wheat cultivars (season 2005) grown in two water regimes and two levels of nitrogen availability (115 and 217 kg N ha^{-1})

Season	Source of variation	FLN	Phyllochron (°Cd leaf^{-1})	Eme–TS (°Cd)	Eme–ANT (°Cd)	ANT–PM (°Cd)
2004	Water regime (W)	0.12 ns	29.8 ns	141,931.8**	173,629.4**	100.6 ns
	Cultivar (G)	11.03**	504.3**	110,262.4**	116,321.9**	19,827.2*
	W × G	0.40 ns	94.2 ns	9,850.0**	1,740.3 ns	5,293.5 ns
	C.V. (%)	5.2	8.1	3.4	2.2	10.5
2005	Water regime (W)	0.44 ns	204.8**	24,903.4**	95,511.9**	33,831.4 ns
	Nitrogen (N)	0.44 ns	9.22 ns	1,563.5 ns	4,932.7 ns	1,497.9 ns
	Entry (G)	17.6**	302.8**	38,677.8**	19,154.7**	78,778.9 ns
	W × N	0.00 ns	8.08 ns	3,591.0 ns	378.9 ns	1,290.0 ns
	W × G	0.36 ns	7.04 ns	6,905.2*	1,032.6 ns	16,331.2 ns
	N × G	0.19 ns	4.4 ns	1,240.8 ns	1,669.9 ns	5,321.7 ns
	W × N × G	0.08 ns	17.6 ns	1,927.1 ns	454.9 ns	3,378.7 ns
	C.V. (%)	4.3	4.4	4.8	2.7	14.7

**, * and ns stand for differences that were significant at $P < 0.01$, $P < 0.05$ or not significant, respectively.

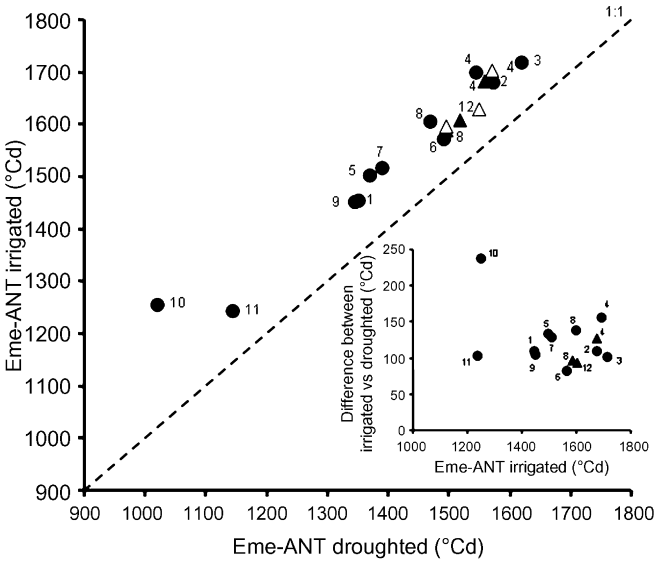

Fig. 1. Relationship between thermal time from emergence (Eme) to anthesis (ANT) in irrigated and droughted conditions in 11 triticale cultivars and one wheat. Inset is the relationship between the difference in thermal time to anthesis in irrigated vs. droughted conditions and thermal time to anthesis in irrigated. Data corresponding to experiment 1 (circles), experiment 2 (close triangles) and experiment 3 (open triangles). Numbers labeling each symbol refer to cultivars as numbered in Table 1. Dashed line correspond to the 1:1 ratio, $y = x$.

duration of the period Eme–ANT was longer in irrigated than in droughted conditions (averaged across cultivars the difference was around 125 °Cd in experiment 1 and 95 °Cd in experiment 2). The cultivars could be grouped, regarding their time to anthesis into long, intermediate and short cycle, being the differences largely due to their differences in final leaf number ($r = 0.74$ and $P < 0.001$). The triticales that were also grown in experiments 2 and 3 had a performance consistent with that exhibited in experiment 1 (Fig. 1). The wheat cultivar used in experiments 2 and 3 had almost the same duration to anthesis to Tizne under both water regimes, and therefore were shorter than Yagan (Fig. 1). Overall, the magnitude of the response to water stress was largely independent of the actual duration of the cycle to anthesis under well-watered conditions (Fig. 1, inset).

Table 3
Final leaf number and phyllochron in 11 triticale cultivars (experiment 1, season 2004) and two triticale and one wheat cultivars (experiment 2, season 2005) grown in two regimens of water supplied

Season	Cultivar	Final leaf number		Phyllochron (°Cd leaf^{-1})	
		Irrigated	Droughted	Irrigated	Droughted
2004	Remedios	11.8 abcd	11.6 cde	110.5 a	99.4 b
	Tehuelche	14.6 a	14.5 a	118.1 a	114.9 ab
	Presto	14.1 abc	13.6 ab	129.1 a	145.4 a
	Yagan	14.5 ab	14.5 a	113.2 a	121.4 ab
	Genú	11.5 bcd	11.1 cde	118.7 a	111.5 b
	Quiñe	11.3 cd	11.8 bc	125.9 a	114.8 ab
	Ñinca	11.2 cd	12.8 abc	129.5 a	115.9 ab
	Tizne	10.9 d	11.6 cd	120.8 a	123.0 ab
	Boaglio	11.9 abcd	11.3 cde	115.4 a	108.0 b
	Cerrillo	9.8 d	9.8 ed	92.8 a	102.5 b
	Maravilla	9.7 d	9.7 e	101.1 a	100.7 b
	Mean	11.9	12.0	115.9	114.3
2005	Escudo	11.3 b	11.6 a	119.7 a	115.6 a
	Tizne	12.0 b	11.7 a	122.8 a	112.9 ab
	Yagan	14.0 a	13.3 a	109.9 a	106.8 b
	Mean	12.4	12.2	117.4 a	111.7 b

Means followed by different letters are significantly ($P < 0.05$) different.

3.2. Components and sub-phases of the period emergence to anthesis

Regarding responsiveness to drought of phases occurring before or after TS, cultivars showed clear differences (Fig. 2a and b), and due to these differences among cultivars there was no clear relationship between responsiveness of the total cycle to anthesis and that of either Eme–TS or TS–ANT. The comparison of the cultivars Ñinca and Tehuelche illustrates this variation. While in Ñinca (labelled with #7), the Eme–TS phase was very responsive to drought (Fig. 2a), the TS–ANT was virtually insensitive (Fig. 2b) and the opposite trend occurred in Tehuelche (#2, cf. Fig. 2a and b).

In both experiments, final leaf number (FLN) was generally unresponsive and phyllochron was slightly sensitive to water regime (Table 3).

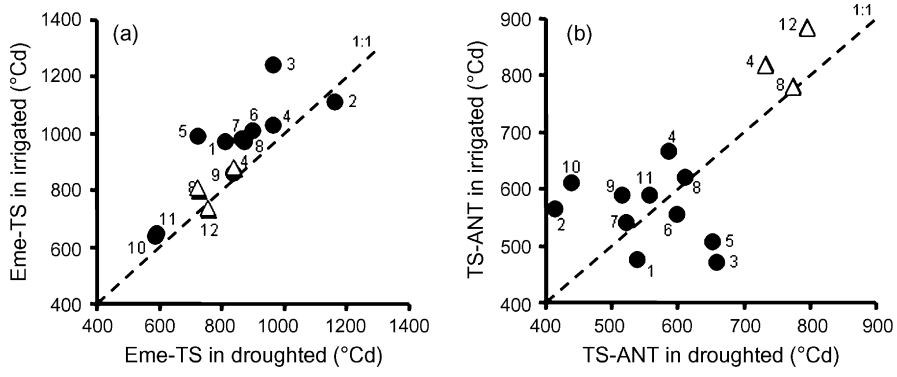

Fig. 2. Relationship between duration (thermal time) from (a) seedling emergence to terminal spikelet (Eme–TS) and (b) from terminal spikelet to anthesis (TS–ANT) under irrigated and droughted conditions. For symbols and numbers see Fig. 1 and Table 1. Dashed lines correspond to the 1:1 ratio.

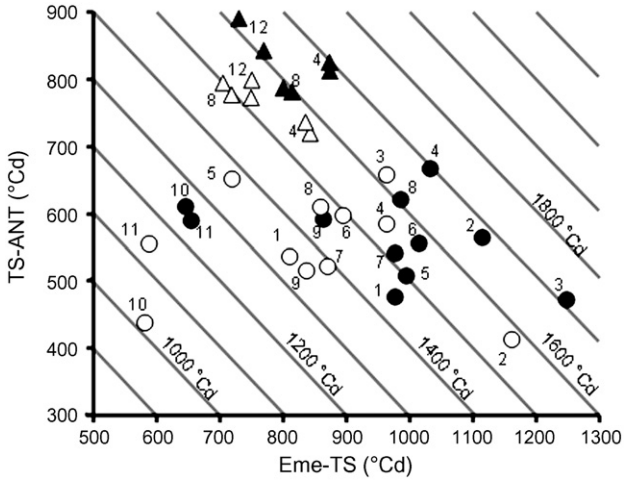

Fig. 3. Duration of phase from terminal spikelet to anthesis (TS–ANT) vs. the duration of phase from emergence (Eme) to TS for 11 triticale cultivars grown under irrigated (close symbols) and droughted (open symbols) conditions. Lines represent iso-thermal times from emergence to anthesis. Cultivars on the same line have similar cycle to anthesis duration, though they may differ strongly in the partitioning of the time between pre- and post-terminal spikelet phases. For symbols and numbers see Fig. 1 and Table 1.

3.3. Partitioning of time to anthesis (Eme–TS and TS–ANT)

There was no relationship between the duration of the stem elongation phase (TS–ANT) and the emergence to terminal spikelet (Eme–TS). It was possible to identify cultivars in which, for a similar pre-anthesis duration, the length of period from terminal spikelet to anthesis differed significantly. Some examples have been selected to illustrate this variability (Fig. 3). Cultivars numbered 2–4 were the longest cultivars and they had virtually the same Eme–ANT duration (1699, 1680 and 1719 °Cd, respectively under well watered conditions), while the duration of stem elongation was 29 and 16% longer in Yagan and Tehuelche than in Presto, respectively (668, 566 and 473 °Cd, respectively; Fig. 3). In the intermediate cultivars Boaglio and Remedios time to anthesis was the same (1453 and 1452 °Cd, respectively) but the duration from terminal spikelet to anthesis was 20% longer in the former than in the latter cultivar (592 and 478 °Cd, respectively). Cerrillo and Maravilla (Mexican cultivars) were the shortest and they did not differ in their duration to anthesis neither in the duration of the previous stages (Fig. 3).

3.4. Effect of water stress on the partitioning of time to anthesis

Depending on the cultivar, water restriction shortened the duration of phases in relation to the plants grown under irrigated conditions. Taking into account the pairs of cultivars selected for the same duration from Eme–ANT under irrigated condition, water restriction slightly reduced the timing to anthesis in all pairs and depending on the particular pair selected, altered the relative duration of the pre-anthesis phases. For instance, while the differences in stem elongation phase between Remedios and Boaglio was ca. 20% under irrigation, when they were grown under drought, the difference in that phase was negligible (Fig. 3). Timing to anthesis was not different between both cultivars, although it was shortened at ca. 100 °Cd with respect to the irrigated treatment. Presto and Tehuelche showed virtually the same duration from emergence to anthesis under irrigated (1700 °Cd) as well as under droughted conditions (1600 °Cd). However, the longer duration of the terminal spikelet to anthesis phase observed in Tehuelche under irrigated treatment was reverted when grown in droughted conditions, where that phase was shorter than in Presto (Fig. 3).

In experiment 2 and 3, Tizne and Escudo (wheat) had almost the same duration to anthesis in irrigated treatment but when were grown under drought Escudo (symbol labeled with #12) changed in ranking, reducing 10% the duration of TS–ANT whereas in Tizne (#8) a reduction of a similar magnitude was observed in Eme–TS instead (Fig. 3).

3.5. Duration of period from anthesis to physiological maturity (ANT–PM)

Duration of ANT–PM did not change significantly in most cultivars, but in Presto, Tizne and Tehuelche in experiment 1 and Tizne and Yagan in experiment 2, in which post-anthesis duration was reduced because of water restrictions. On the other hand, the opposite was observed in Genú and Remedios, in which duration was lengthened. Cultivar Presto had a shorter duration of this phase than the rest of the cultivars (Fig. 4).

When compared against the treatment irrigated in the whole cycle (experiment 2), the Mediterranean environment treatment (terminal drought) reduced by ca. 16% the ANT–PM phase (22, 7 and 17% for Escudo, Tizne and Yagan, respectively). On the other hand, when compared against the droughted treatment (experiment 2), the Monsoon environment treatment tended to increase slightly the post-anthesis period, although the effect was non-significant in statistical terms ($P > 0.50$) (Table 4).

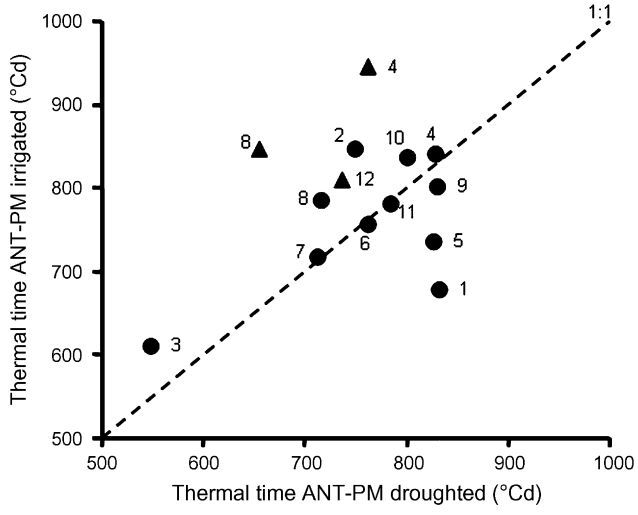

Fig. 4. Relationship between thermal time from anthesis (ANT) to physiological maturity (PM) for plants grown under irrigated vs. droughted conditions in triticale and wheat cultivars. For symbols and numbers see Fig. 1 and Table 1. Dashed line indicates the 1:1 ratio.

Table 4
Thermal time (°Cd) from anthesis to physiological maturity for two triticale cultivars (Tizne and Yagan) and a wheat (Escudo) growing in four contrast water regimes

Treatment	Cultivars			Mean
	Escudo	Tizne	Yagan	
Irrigated	808.2 a	846.5 a	944.8 a	866.5 a
Mediterranean	624.3 b	787.9 b	778.8 b	730.3 b
Droughted	737.1 a	656.4 a	763.9 a	719.2 a
Monsoon	755.8 a	679.5 a	755.9 a	730.4 a

Irrigated and droughted treatments representing the controls correspond to experiment 2; means followed by the same letter comparing cultivars between pairs of environments (irrigated vs. Mediterranean and droughted vs. Monsoon environments treatments) not differ significant at 5% for a Tukey test.

4. Discussion

A nitrogen effect on triticale development phases was not significant and then it was not considered in the results description. Although development responsiveness to nitrogen has been reported in wheat (Dale and Wilson, 1978; Longnecker et al., 1993; Salvagiotti and Miralles, 2007) and barley (Arisnabarreta and Miralles, 2004) normally very large differences in N availability are required to produce significant but relative small changes in the rate of development. This is likely why in many others studies no effects were reported (Frank and Bauer, 1982; Bauer et al., 1984; Prystupa et al., 2003). In addition, the lowest N level used in this study was relatively high and probably this is the reason for the lack of significant effects of both N treatment.

A great genotypic variation in time to anthesis could be successfully used for adaptability improvement to specific environments (Brouwer, 1977; Giunta et al., 2001). The results of this study emphasize great variation between cultivars on time to anthesis, allowing to classify the cultivars into classes of long, intermediate and short cycle. Similar classification was used by Giunta et al. (2001) when evaluated wheat and triticale cultivars in the Mediterranean environment treatment. The differences observed between the cultivars in time to anthesis were mainly due to a differential number of leaves and phyllochron in agreement with Giunta et al. (2001) who found that variation in anthesis date was mostly explained by the total number of leaves. The large variability in the duration pre-anthesis phases may be also important, as the duration of stem elongation could be a physiological determinant for the number of grains per spike and per unit land area (Slafer et al., 2001; Miralles et al., 2000; Gonzalez et al., 2003). In this study, differences in the duration of the TS–ANT phase were as high as 200 °Cd for cultivars with similar time to flowering. The identification of the variability in the duration of the stem elongation phase is the first step to select parental lines with a longer stem elongation phase to be used in crossings to obtain genotypes with the same flowering time (which is critical in terms of adaptability), but different relative duration of the pre-flowering phases (Miralles and Slafer, 2007).

Water stress under field conditions reduced time to anthesis (measured in calendar days as well as in thermal time) of the triticale cultivars, in line with other previous evidences that have shown that a restriction of water availability hastens development stages not only in triticale (Krenzer et al., 1991; Ivandic et al., 2000; McMaster and Wilhelm, 2003) also in other species as barley (Day et al., 1978). The reductions in time to anthesis could be ascribed to increases in canopy temperature produced by water restriction: drought increased canopy temperature, on average of the four measurements made, by ca. 1.3 °C with respect to the irrigated treatment. Unfortunately, canopy temperature was not registered throughout the whole crop cycle and thereby, thermal time could not be re-calculated using the canopy temperature instead of air temperature.

The triticale cultivars showed a differential responsiveness to drought in those phases before or after TS. Some cultivars were highly sensitive to drought in the Eme–TS phase when they were in the TS–ANT phase were not and vice-versa. In general terms, and specially in the 2005 growing season, the shortening of the pre-flowering phase, due to water stress, was associated with reductions in phyllochron more than with changes in FLN as was previously observed by Arisnabarreta and Miralles (2004) and Salvagiotti and Miralles (2007). This behavior was expected, as FLN is a clear developmental event (hardly affected by changes in nutrients and/or water availability) while phyllochron include growing events (e.g. leaf expansion). However, the effects of water stress on the phyllochron were extremely low (between 2 and 5%) and cannot fully explain the shortening observed in the time to anthesis by water restriction. In fact, drought also affected the length of the peduncle elongation phase, i.e. between flag leaf appearance and anthesis.

Water shortage tended to reduce the grain filling period, mainly during the 2005 growing season, in agreement with other evidences (Royo et al., 2000; Santiveri et al., 2002; Garcia del Moral et al., 2005). This was particularly evident when a Mediterranean environment was simulated. Interestingly, the reduction of the grain filling period by water stress was not reverted when a Monsoonal environment treatment was simulated. In other words, grain weight potential probably was set immediately after anthesis (Brocklehurst, 1977; Reddy and Daynard, 1983; Jenner et al., 1991; Jones et al., 1996) or even immediately before anthesis (Calderini et al., 1999, 2001), determining that potential grain size cannot be modified when water restrictions were released few days after anthesis at the onset of grain filling.

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