



Differences between wheat and barley in leaf and tillering coordination under contrasting nitrogen and sulfur conditions

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ABSTRACT

It is traditionally assumed that barley has a higher tillering capacity than wheat whatever the environmental condition; however, this supposition has not been formally tested under experimental conditions nor analyzed its relationship with leaf appearance. In the present work, leaf appearance and tillering dynamics were studied in wheat and barley genotypes grown under contrasting nitrogen and sulfur levels at sowing. There was no difference in phenology (seedling emergence, first visible node and flowering) between wheat and barley or due to different nutrients. Phyllochron in barley tended to be higher than (or at least equal to) that observed in wheat, without effect of the N or S levels on this trait. Differences in final leaf number were negligible. Tillering dynamics was analyzed considering the tillering appearance rate (TAR), the maximum number of tillers appeared (MTN), the tillering mortality rate (TMR), and the final number of tillers per plant (FTN). TAR was significantly greater in barley than in wheat genotypes in all experiments. In both species, TAR was enhanced as N supply was increased while S promoted TAR only under high N conditions. The MTN was positively and significantly associated with TAR. Although cessation of tillering was similar between both species, the maximum number of tillers was superior in barley than in wheat, due to the differences between species in tiller appearance rate. A high MTN was related to a high tiller mortality rate. In spite of that counterbalance, FTN was closely related to MTN; as a consequence, FTN was pre-defined during the early phase of the tillering process. Barley showed higher values of tiller initiated per leaf appeared (synchrony) than wheat, while N and S deficiencies decreased that synchrony.

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1. Introduction

It is empirically assumed that barley has a higher tiller production than wheat; however, there are few works reported in the literature in which the tillering process has been studied comparatively between both species under different environmental conditions. Several studies have analyzed the effect of N on the phenology and dynamics of leaves and tillers in wheat (Rodríguez

et al., 1998; Berry et al., 2003; Evers et al., 2006; Salvagiotti and Miralles, 2007) as well as in barley (Baethgen et al., 1995; García del Moral and García del Moral, 1995; Prystupa et al., 2003; Abeledo et al., 2004; Borrás et al., 2009), but there is little evidence analyzing those attributes in both crops growing simultaneously under contrasting nutritional conditions.

Wheat and barley have important intraspecific variability in its tillering capacity. In barley, one of the causes of the differences in tillering dynamic between cultivars are associated with the ear type as six-rowed genotypes establishes less tillers per plant than two-rowed genotypes with similar cycle to flowering (Kirby and Riggs, 1978; García del Moral and García del Moral, 1995; Arisnabarreta and Miralles, 2004). In both species, there is a synchrony between leaf and tillers appearance (Kirby et al., 1985). Differences in tillering dynamics could be related to variability between wheat and barley genotypes in phenology and leaf appearance. Both in wheat and barley, flowering date depends on the final number of leaves in the main stem and the leaf appearance rate. It was widely reported that temperature, photoperiod and vernalization are the main factors that regulate the rate of development in both crops

Abbreviations: B, barley genotypes; BTM, beginning of tiller mortality ($^{\circ}\text{Cd}$); EM, seedling emergence; FL, flowering time; FTN, final tiller number (tillers pl^{-1}); FTNO, final tiller number occurrence ($^{\circ}\text{Cd}$); FVN, first visible node; IPAR, photosynthetically active radiation interception; MTN, maximum tiller number per plant (tillers pl^{-1}); NO, low soil nitrogen availability at sowing; N1, high soil nitrogen availability at sowing; LAR, leaf appearance rate (leaf $^{\circ}\text{Cd}^{-1}$); S0, low soil sulfur availability at sowing; S1, high soil sulfur availability at sowing; TAR, tillering appearance rate (tillers $\text{pl}^{-1} \text{ } ^{\circ}\text{Cd}^{-1}$); TMR, tillering mortality rate (tillers dead $\text{pl}^{-1} \text{ } ^{\circ}\text{Cd}^{-1}$); W, wheat genotypes.

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(Davidson et al., 1985; Hay and Kirby, 1991; Slafer and Rawson, 1994), while water and nutritional conditions are secondary factors that can modify the duration of the ontogenic phases from emergence to flowering (Arisnabarreta and Miralles, 2004; Salvagiotti and Miralles, 2007). However, the effects of nutrients availability on developmental processes are not conclusive. For example, for wheat, Fischer et al. (1993) reported a delay in flowering date with extreme nitrogen deficiencies, while in other studies, the effect of N deficiencies on the duration of ontogenic phases was not noticeable (Cartelle et al., 2006). Divergences between studies on the effect of N conditions on development could be related to differences in the timing, the intensity and/or the duration of the stress: the higher the intensity and the duration of the N stress, the stronger its impact on crop development (Fischer et al., 1993). A delay in flowering date under low soil N levels has also been reported in barley (Arisnabarreta and Miralles, 2004) as the result of a higher phyllochron, with a nil (Prystupa et al., 2003; Arisnabarreta and Miralles, 2004) or minor effect of the N deficiency (Longnecker et al., 1993) on the final leaf number. The effect of N on these processes is conditioned by the availability of other nutrients such as sulfur. Burke et al. (1986) showed that deficiencies in S reduced the size and the number of cells in wheat, and Salvagiotti and Miralles (2007) proposed that limitations in S could modify the occurrence of flowering by affecting the size of the leaf and modifying leaf appearance rate. We are not aware of the existence of works in which the effect of the N and S interaction have been analyzed in barley for leaf appearance.

The tillering process can be divided in four phases: (i) an initial phase characterized by tillering appearance, (ii) a second phase in which the maximum number of tillers per plant is reached, (iii) a phase in which a proportion of the tillers dies until, (iv) the final tiller number is defined. Generally, the first tiller appears when the 3rd or 4th leaf emerges on the main stem. Once the first tiller has emerged, the next tillers appear following a synchrony of a tiller per phyllochron according to the Fibonacci series (Skinner and Nelson, 1992; Bos and Neuteboom, 1998; Salvagiotti and Miralles, 2007). However, as tillering dynamics is strongly dependent on genotype and environment, changes in one or both variables could modify not only the dynamic of tiller but also the synchrony between leaf and tiller appearance. Increases in N availability promote tiller appearance rate determining, as a consequence, a higher maximum number of tillers per plant (Prystupa et al., 2003). Similarly, the addition of S increased tiller appearance rate, especially under non limiting N conditions evidencing NxS interaction (Salvagiotti and Miralles, 2007). In spite of the advantages of the nutrients on tiller production, Berry et al. (2003) reported that the higher the tillers initiated the lower the tillers survival, causing a counterbalance between the rates of tiller initiation and tiller mortality. Some evidences showed that the appearance of new tillers began to decrease strongly at a particular leaf area index in sorghum (Lafarge and Hammer, 2002), while Evers et al. (2006) reported in wheat that the end of tiller appearance occurred when the fraction of radiation intercepted by the canopy exceeds a specific threshold (0.40–0.45) and red:far-red ratio drops below 0.35–0.40.

It is assumed that the end of tiller appearance is related to the stage of first visible node in coincidence with the beginning of stem elongation (García del Moral and García del Moral, 1995; Miralles and Richards, 2000), while the beginning of tiller mortality starts during stem elongation (Davidson and Chevalier, 1989; Sparkes et al., 2006; Borràs-Gelonch et al., 2012). Thus, it is important not only to analyze how these tillers are generated, but also to evaluate how the tiller mortality rate influences the final number of tillers and its relationship with phenology. Most of the works focused in the study of tillering dynamics have studied the process of tillering generation, but few works have advanced to the study of tiller mortality, specially comparing both wheat and barley genotypes.

The general aim of the present study was to analyze the dynamics of leaf appearance and its coordination with tillering appearance in wheat and barley crops grown under contrasting combinations of N and S soil conditions.

2. Materials and methods

2.1. General conditions, treatments and experimental design

In order to achieve the objective, we carried out two types of experiments from 2004 to 2009 at the experimental field of the Department of Plant Production, University of Buenos Aires (34°35'S, 58°29'W). The first group of experiments was carried out under field conditions on a silty clay loam soil (Vertic Argiudoll) during the 2004 (Exp 1), 2006 (Exp 2.I), 2007 (Exp 2.II) and 2008 (Exp 2.III) growing seasons. These experiments combined different wheat and barley genotypes and two levels of soil N at sowing (natural N soil plus N fertilizer) named as “low” (N0) or “high” (N1) N availabilities (see for details Table 1). The genotypes used in each experiment were chosen considering their similarities in time to flowering (FL) and due to they represent genotypes widely used by farmers in Argentina. In the case of barley we included only two-rowed types because represent almost 100% of the cultivars used for the malting industry in Argentina. The experiments were sown on typical dates for Argentina at a density of ca. 300 plants m⁻². Within each experimental year, plots were arranged in a split-plot design with three replications where the main plots were assigned to the N levels and the genotypes were randomized into the main plots. Each experimental unit (plots) was 3 m wide × 8 m long.

The second group of experiments was designed to analyze the NxS interaction. These experiments were carried out during the 2005 (Exp 3), 2008 (Exp 4) and 2009 (Exp 5) growing seasons. Treatments consisted of the combination of genotypes of wheat and barley, two initial levels of nitrogen (N0 and N1) and two levels of sulfur (S0 and S1) (see for details Table 1). In 2005, the experiment was carried out under field conditions on the same soil previously detailed and plots (24) were arranged in a complete randomized design. In 2008 and 2009, the experiments were sown in containers of 1000-L capacity (1 m wide × 1 m high × 1 m long) filled with a mixture of 66% sand and 33% soil. The 24 containers were arranged in a complete randomized design with three replications. These experiments were carried out in containers in order to diversify the nutritional conditions explored.

In each experiment (Exp 1–5), the initial amount of mineral N (measured as NO₃⁻) and S (measured as SO₄⁼) was evaluated for the top 60 cm of the soil, previous to sowing, and plots were fertilized with urea (46:0:0) and ammonium sulfate (21:0:0 24% S) to achieve the N or S objective levels (Table 1). The experiments were conducted under non limiting water conditions and without presence of weed, pests or diseases.

2.2. Measurements and analysis

External phenology was characterized by taking into account the occurrence of seedling emergence (Z1.0, EM) and first visible node (Z3.1) stages using the Zadoks et al. (1974) scale. First visible node was exclusively measured in Exp 2, 4 and 5. Flowering time was determined in both species when pollen liberation occurred inside the spike (Waddington et al., 1983). At EM, two plants per experimental unit were labeled in the inner rows of each plot to follow the dynamics of leaf and tiller appearance throughout the crop cycle. Leaf number on the main stem was measured every 3–4 days from EM to FL, using the scale proposed by Haun (1973). The

Table 1
Summary of the different experiments carried out in the present study indicating name of the experiment, experimental year, sowing date (SOW), field condition, plant density (pl m^{-2}), codes of the nitrogen treatments (NT) in relation to the soil nitrogen level at sowing (natural nitrogen in the soil plus fertilizer, NL; kg N ha^{-1}), codes of the sulfur treatments (ST) in relation to the sulfur fertilizer rate (SF; kg S ha^{-1}) and wheat (W) and barley (B) genotypes used.

Experiment	Year	SOW	Condition	Density	NT	NL	ST	SF	Genotypes
Exp 1	2004	July 7th	Containers	300	N0	40			Klein Chajá (Kcha, W) Buck Manantial (Man, W)
					N1	200			Quilmes Alfa (QAlf, B) Quilmes Ayelén (QAye, B)
Exp 2.I	2006	August 12th	Field plots	320	N0	60			Buck 75 Aniversario (B75, W) Baguette 13 Premium (Bg13, W)
					N1	150			Klein Chajá (Kcha, W) Scarlett (Sca, B)
Exp 2.II	2007	July 12th	Field plots	305	N0	90			Buck 75 Aniversario (B75, W) Baguette 13 Premium (Bg13, W)
					N1	190			Klein Chajá (Kcha, W) Scarlett (Sca, B)
Exp 2.III	2008	July 15th	Field plots	305	N0	70			Buck 75 Aniversario (B75, W) Baguette 13 Premium (Bg13, W)
					N1	170			Klein Chajá (Kcha, W) Scarlett (Sca, B)
Exp 3	2005	July 20th	Field plots	300	N0	40	S0	0	Quilmes Ayelén (QAye, B)
					N1	200	S1	30	Klein Chajá (Kcha, W)
Exp 4	2008	July 30th	Containers	350	N0	60	S0	0	Buck 75 Aniversario (B75, W)
					N1	150	S1	30	Klein Chajá (Kcha, W)
Exp 5	2009	July 16th	Containers	350	N0	90	S0	0	Buck 75 Aniversario (B75, W)
					N1	190	S1	60	Baguette 13 Premium (Bg13, W)

appearance of leaf number was regressed against the accumulated thermal time from emergence using a linear model:

$$y = a + bx \quad (1)$$

where y is the number of leaves per main stem (leaf pl^{-1}), a the intercept (leaf pl^{-1}), b the leaf appearance rate ($\text{leaf } ^\circ\text{Cd}^{-1}$; LAR), and x the accumulated thermal time from seedling emergence. Parameters a and b were estimated using an optimization procedure (Radushev et al., 2007a). The phyllochron ($^\circ\text{Cd leaf}^{-1}$) was estimated as the inverse of the b slope.

Total tiller number per plant (without discriminating between primary, secondary or tertiary tillers) was measured once or twice a week from seedling emergence to physiological maturity. In all the experiments, the tillering dynamics during the crop cycle was analyzed using a tetralinear model as described in Fig. 1 (Radushev

et al., 2007b):

$$y = a + bx(x \leq c) + bc(x > c) + e(x - d)(x \geq d) + e(f - x)(x \geq f) \quad (2)$$

where y represents the tiller number per plant (tillers pl^{-1}), a the intercept (tillers pl^{-1}), b the tiller appearance rate ($\text{tillers pl}^{-1} \text{ } ^\circ\text{Cd}^{-1}$; TAR), c the thermal time at which the maximum tiller number was achieved ($^\circ\text{Cd}$), d the thermal time at the beginning of tiller mortality ($^\circ\text{Cd}$), e the rate of tiller mortality ($\text{tillers dead pl}^{-1} \text{ } ^\circ\text{Cd}^{-1}$; TMR), f the thermal time at which the final number of tillers was defined (final tiller number occurrence, FTNO, $^\circ\text{Cd}$) and x the accumulated thermal time from seedling emergence ($^\circ\text{Cd}$) (Fig. 1).

Photosynthetically active radiation interception (IPAR) was measured from seedling emergence to flowering with a linear cep-tometer (LI-191 S, LI-COR Inc. Lincoln NE, USA) between 12:00 and 14:00 h on clear days. Four measurements were taken in each replicate. The first measurement was made above the canopy to determine incident PAR (I0). The other three measurements were taken at the soil surface or following the senescence profile placing the sensor in three positions along the rows (left, center and right) to determine transmitted PAR (It) as indicated by Charles-Edwards and Lawn (1984). The fraction of PAR intercepted (IPAR) was calculated as $[I0 - It]/I0$.

Thermal time units were calculated from mean air temperature with a base temperature of 0°C (Rozen and Skaletsky, 2000). Daily air temperature was calculated by averaging maximum and minimum air temperature, measured hourly. Data were obtained with a standard meteorological station (Weather Monitor II, Davis Instruments, USA) located at the experimental field.

The synchrony between leaf and tiller appearance was estimated adjusting a linear regression model between the total number of tillers per plant and the Haun index, considering the phase that took place between the appearances of the first tiller until the point in which the maximum number of tillers was achieved. The slope of the model was defined as synchrony (tillers leaf^{-1}) (Salvagiotti and Miralles, 2007).

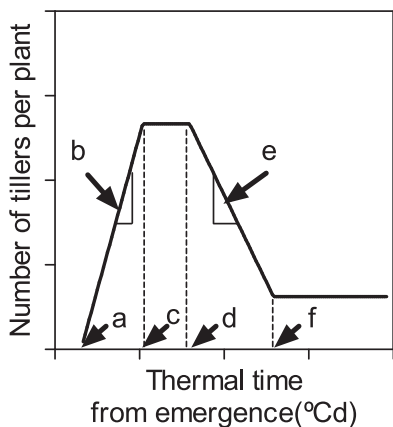


Fig. 1. Scheme showing the tetralinear model used to determine parameters of tillering dynamics (a , intercept; b , rate of tillering appearance; c , thermal time when tiller appearance ceased; d , thermal time at the beginning of tiller mortality; e , rate of tiller mortality; f , thermal time in which the final number of tillers was defined).

Statistical differences between treatments were tested through standard analyses of variance with first level interactions, for each experiment. In Exp 2, the year was considered as a main source of variation together with the nitrogen and genotype effects. When the analysis of variance revealed significant differences, the mean treatment values were compared using the Tukey's test with a significance level of $p < 0.05$. The software used for statistical analysis was *INFOSTAT Professional v.1.1* (2009).

3. Results

3.1. Phenology

The duration of the sowing to seedling emergence phase was similar ($p > 0.10$) between treatments in all the experiments, with a general mean duration of 151°Cd . The emergence to flowering phase showed a mean duration of 1200°Cd . With the exception of the wheat genotype Buck Manantial (Man), which showed a time to flowering *ca.* 230°Cd longer than the other wheat and barley genotypes (Exp 1; Table 2), there was no difference in flowering time between wheat and barley. N treatments, with the exception of Exp 2 and 5, did not produce significant differences in the duration of the emergence to flowering phase. In those cases where the N effect was significant, N addition delayed the duration of the phase but with differences between N0 and N1 lower than 60°Cd (on average less than 20°Cd), which is agronomically irrelevant when it is measured in days. There was no effect of S treatments on the time to flowering or interaction between genotypes or N and S in any experiment ($p > 0.10$; Table 3).

The effect of the treatments on the duration of the sub-phases from emergence to first visible node and first visible node to flowering was similar to that observed for the whole all period to flowering: the duration of the pre-flowering phases showed significant differences among genotypes and was slightly modified by effect of N, although the differences, even though significant in statistical terms, were negligible in the agronomical context (Tables 2 and 3).

3.2. Leaf appearance

The cumulative leaf number was linearly related to thermal time from emergence, with a coefficient $r^2 \geq 0.95$ in all the regressions ($p < 0.001$). For the set of experiments, phyllochron varied from *ca.* 85 to $120^\circ\text{Cd leaf}^{-1}$, mainly associated with genotypic variations (Table 2). Phyllochron in barley tended to be higher (*ca.* 8%) than (or at least equal to) that observed in wheat (Tables 2 and 3). For example, in Exp 1 the phyllochron of the barley genotypes QAlf and QAye was 108 and $120^\circ\text{Cd leaf}^{-1}$, respectively; while the wheat genotype Man and Kcha showed values of 100 and $104^\circ\text{Cd leaf}^{-1}$, respectively (Table 2). In most of the experiments, there was no effect either by N or by S on phyllochron or interaction between treatments ($p > 0.10$; Tables 2 and 3). The only exception was Exp 3, where the mean phyllochron of the high N availability was $5^\circ\text{Cd leaf}^{-1}$ lower than that of the low N availability treatment (Table 2).

Final leaf number varied between 10 and 12 leaves per plant for the whole set of experiments. The mean final leaf number on the main stem was 11, 10, 12, 11, 11, 10 and 10 in Exp 1, 2.I, 2.II, 2.III, 3, 4, and 5, respectively (Tables 2 and 3). Differences among genotypes in final leaf number were significant only in Exp 1 and 2 but, when existing, this difference was only of ≤ 0.5 leaf pl^{-1} (Table 2). Changes in the availability of N or S did not affect the final number of leaves per plant ($p > 0.10$) in any experiment (Tables 2 and 3).

No association was found between the duration of the emergence to flowering phase and the phyllochron or the final leaves number ($p > 0.10$), probably due to the range explored for thermal

time duration of the emergence to flowering period was narrow. The number of leaves at FVN stage was similar ($p > 0.10$) between treatments in all the experiments, with a general mean of 4.3 leaves appeared at that stage, representing *ca.* 40% of the final number of leaves. Therefore, the crop expanded *ca.* 6.4 leaves between FVN and FL (60% of the final leaf number).

3.3. Tillering dynamics

Tillering dynamics was analyzed considering the rate of tillering appearance (TAR), the maximum number of tillers appeared (MTN), the rate of tillering mortality (TMR), and the final number of tillers per plant (FTN). The timing of tillering initiation was independent of the genotype or of the N or S availabilities ($p > 0.05$). The first tiller appeared between the second and the fourth leaf emerged in the main stem in all treatments. Once the first tiller appeared, TAR of the barley genotypes was on average 20% higher than that of the wheat genotypes in all the experiments (general mean of 1.87×10^{-2} tillers $\text{pl}^{-1}^\circ\text{Cd}^{-1}$ vs. 1.53×10^{-2} tillers $\text{pl}^{-1}^\circ\text{Cd}^{-1}$, respectively). Improvements in the N condition increased the TAR *ca.* 23% (general mean of 1.83×10^{-2} tillers $\text{pl}^{-1}^\circ\text{Cd}^{-1}$ vs. 1.41×10^{-2} tillers $\text{pl}^{-1}^\circ\text{Cd}^{-1}$ for the N1 and N0 treatments, respectively). For example, in Exp 2, the barley genotype showed a TAR of 1.8×10^{-2} tillers $\text{pl}^{-1}^\circ\text{Cd}^{-1}$ for the N0 treatment, while TAR for the wheat genotypes B75, Bg13, and Kcha was 1.2×10^{-2} , 1.0×10^{-2} , and 1.3×10^{-2} tillers $\text{pl}^{-1}^\circ\text{Cd}^{-1}$, respectively; and, on average, TAR for the N1 treatment was 1.6×10^{-2} tillers $\text{pl}^{-1}^\circ\text{Cd}^{-1}$ vs. 1.1×10^{-2} tillers $\text{pl}^{-1}^\circ\text{Cd}^{-1}$ under the N0 condition ($p < 0.05$) (Fig. 2; Table 4). No GxN interaction was observed for this attribute (Table 4). In the experiments designed to evaluate the response of the genotypes to N and S (Exp 3–5), TAR showed interaction between both nutrients. Increases in TAR in response to the S addition were only observed when the N availability was high, with a TAR of 2.5×10^{-2} tillers $\text{pl}^{-1}^\circ\text{Cd}^{-1}$ for N1S1 and, on average, of 1.8×10^{-2} tillers $\text{pl}^{-1}^\circ\text{Cd}^{-1}$ for the other availabilities of N and S. That trend was similar in all genotypes (Fig. 3a). The average duration of the phase between the first tiller appearance until the point in which MTN was reached was *ca.* 506°Cd and did not show significant differences among treatments ($p > 0.10$; Table 4).

When MTN was reached the fraction of PAR intercepted in barley genotypes was on average 27% higher than that of the wheat genotypes in all the experiments (general mean of 0.56 vs. 0.44 of FPAR, respectively). However, it was wide the range of FPAR explored (between 0.20 and 0.80) in both crops at the point in which MTN was reached. That range of FPAR was mainly explained by the different N availabilities, being 70% higher under N1 than under N0 conditions (0.36 vs. 0.61 of FPAR, respectively) (Fig. 4). S addition promoted higher FPAR in both species under low N soil conditions (0.50 for barley vs. 0.23 for wheat) as well as under high N levels (0.77 vs. 0.60, respectively).

MTN in barley was 18% higher than that observed in wheat genotypes (general mean of 7.4 vs. 6.1 tillers per plant, respectively). Increases in N promoted a higher MTN, which was 24% greater in N1 condition than in N0 treatment (7.3 vs. 5.5 tillers per plant, respectively). The response of MTN to increases in the N availability was higher in barley than in wheat (Fig. 2; Table 4). For example, in Exp 2 the three wheat genotypes B75, Bg13 and Kcha established on average a MTN of 4.5 and 5.4 tillers per plant, while the barley genotype Sca established 5.2 and 9.5 tillers per plant, when grown under "low" or "high" N availabilities, respectively (Fig. 2; Table 4). Similar to what happened with TAR, MTN responded to S only when N availability was high, being MTN of 9.7 tillers per plant for the N1S1 treatment, and of 7.0 tillers per plant on average for the other combinations of N and S (Fig. 3b).

Once MTN was achieved, the emergence of tillers stopped and then tiller mortality began. The duration of the plateau for MTN

Table 2
Duration in thermal time ($^{\circ}\text{Cd}$) of the emergence (EM) to first visible node (FVN), FVN to flowering (FL), and EM–FL phases, phyllochron ($^{\circ}\text{Cd leaf}^{-1}$), and final main stem leaf number (FLN) in wheat (W) and barley (B) genotypes (G) grown under different soil N availabilities at sowing (N). Mean values for the main source of variation for Exp 1 and 2. Within each column and experiment, values followed by the same letter are not significantly different according to Tukey's test ($p < 0.05$).

Exp	Source of variation	Treatment	EM–FVN	FVN–FL	EM–FL	Phyllochron	FLN	
Exp 1	G	QAIf (B)	–	–	1251 bc	107.9 ab	11.4 ab	
		QAye (B)	–	–	1294 b	119.7 a	11.0 b	
		Kcha (W)	–	–	1207 c	103.9 b	10.7 b	
		Man (W)	–	–	1477 a	99.7 b	12.1 a	
		N0	–	–	1337 a	111.0 a	11.3 a	
	N	N1	–	–	1278 a	104.6 a	11.3 a	
		G			**	*	*	
	Exp 2	G				ns	ns	ns
			N				*	*
		G × N					ns	ns
Year						*	*	
Year		G	2006 (Exp 2.I)	620 a	551 a	1170 a	100.0 a	10.4 b
			2007 (Exp 2.II)	597 b	541 b	1138 b	102.3 a	12.0 a
			2008 (Exp 2.III)	619 a	461 c	1080 c	91.8 a	11.0 a
			B75 (W)	609 a	512 b	1121 c	98.1 a	11.2 ab
			Bg13 (W)	611 a	529 a	1140 b	101.9 a	10.8 b
		N	Kcha (W)	608 a	500 b	1108 d	95.8 a	10.9 ab
	Sca (B)		620 a	529 a	1149 a	96.4 a	11.6 a	
	N0		616 a	511 b	1127 b	99.8 a	11.0 a	
	N1		607 a	525 a	1132 a	96.3 a	11.2 a	
	Year			**	**	**	ns	*
Year × G	G		ns	*	**	ns	*	
	N		ns	**	*	ns	ns	
	Year × G		ns	ns	**	ns	*	
	Year × N		ns	ns	*	ns	ns	
	N × G		ns	ns	**	ns	ns	
	Year × N × G		ns	ns	*	ns	ns	

ANOVA: ns $p > 0.05$; * $p < 0.05$; ** $p < 0.01$.

Table 3
Duration in thermal time ($^{\circ}\text{Cd}$) of the emergence (EM) to first visible node (FVN), FVN to flowering (FL), and EM–FL phases, phyllochron ($^{\circ}\text{Cd leaf}^{-1}$), and final main stem leaf number (FLN) in wheat (W) and barley (B) genotypes (G) grown under different soil N and S availabilities at sowing. Mean values for the main source of variation for Exp 3–5. Within each column and experiment, values followed by the same letter are not significantly different according to Tukey's test ($p < 0.05$).

Exp	Source of variation	Treatment	EM–FVN	FVN–FL	EM–FL	Phyllochron	FLN	
Exp 3	G	Kcha (W)	–	–	1198 a	88.5 b	11.3 a	
		QAye (B)	–	–	1214 a	99.6 a	10.9 a	
	N	N0	–	–	1198 a	96.9 a	11.3 a	
		N1	–	–	1214 a	91.2 b	10.9 a	
	S	S0	–	–	1198 a	96.2 a	11.0 a	
		S1	–	–	1214 a	91.9 a	11.3 a	
	G × N	G				ns	**	ns
		N				ns	*	ns
		S				ns	ns	ns
		G × N				ns	*	ns
G × S					ns	ns	ns	
N × S					ns	ns	ns	
Exp 4	G	B75 (W)	543 a	476 b	1020 b	87.5 a	10.2 a	
		Kcha (W)	526 b	526 a	1052 a	85.1 a	10.2 a	
		N0	535 a	500 a	1035 a	86.0 a	10.2 a	
		N1	534 a	502 a	1036 a	86.6 a	10.2 a	
		S0	532 a	505 a	1037 a	86.4 a	10.2 a	
	S	S1	537 a	497 a	1034 a	86.2 a	10.2 a	
		G		*	*	*	ns	ns
		N		ns	ns	ns	ns	ns
		S		ns	ns	ns	ns	ns
		G × N		ns	ns	ns	ns	ns
Exp 5	G	B75 (W)	740 b	480 b	1221 b	112.4 a	10.1 a	
		Bg13 (W)	796 a	498 a	1294 a	110.7 a	10.2 a	
		N0	763 b	487 a	1250 b	111.8 a	10.0 a	
		N1	773 a	491 a	1265 a	111.3 a	10.3 a	
		S0	765 a	490 a	1255 a	109.0 a	10.4 a	
	S	S1	771 a	489 a	1260 a	114.1 a	9.8 a	
		G		*	*	*	ns	ns
		N		*	ns	*	ns	ns
		S		ns	ns	ns	ns	ns
		G × N		ns	ns	ns	ns	ns
G × S	G × S		ns	ns	ns	ns	ns	
	N × S		ns	ns	ns	ns	ns	
	G × S		ns	ns	ns	ns	ns	
	N × S		ns	ns	*	ns	ns	

ANOVA: ns $p > 0.05$; * $p < 0.05$; ** $p < 0.001$.

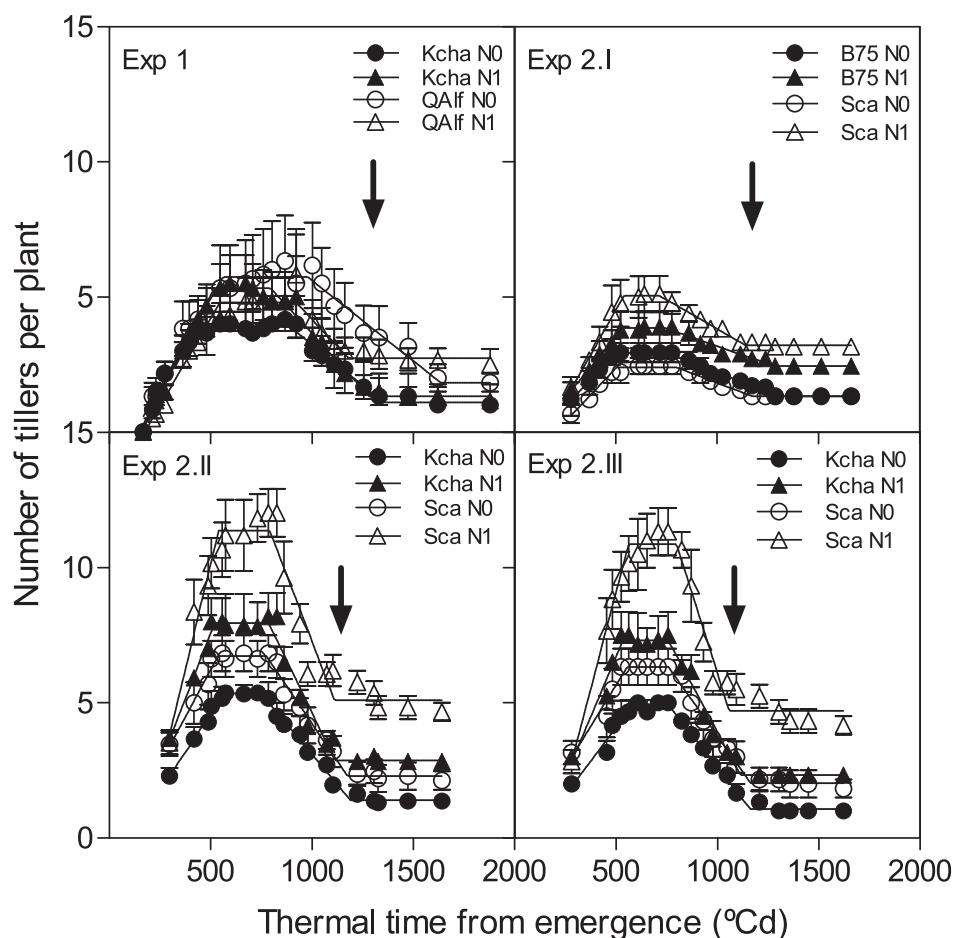


Fig. 2. Relationship between number of tillers per plant and thermal time from seedling emergence for wheat (Kcha, B75) and barley (QAIf, Sca) genotypes grown under low (N0) or high (N1) soil N availabilities at sowing. Data for Exp 1 (a), Exp 2.I (b), Exp 2.II (c) and Exp 2.III (d). The solid lines represent the adjustment of the analysis of regression using Eq. (2). The parameters of the adjustments are detailed in Table 4. Arrows indicate the flowering time.

Table 4

Tiller appearance rate (TAR; 10^{-2} tillers $pl^{-1} \text{ } ^\circ\text{Cd}^{-1}$), tiller appearance duration (TAD; $^\circ\text{Cd}$), maximum tiller number per plant (MTN; tillers pl^{-1}), beginning of tiller mortality (BTM; $^\circ\text{Cd}$), tiller mortality rate (TMR; 10^{-2} tillers dead $pl^{-1} \text{ } ^\circ\text{Cd}^{-1}$), tiller mortality duration (TMD; $^\circ\text{Cd}$), final tiller number per plant (FTN; tillers pl^{-1}) and final tiller number occurrence (FTNO; $^\circ\text{Cd}$), in wheat (W) and barley (B) genotypes (G) grown under different soil N availabilities at sowing (N). Mean values for the main source of variation for Exp 1 and 2. Within each column and experiment, values followed by the same letter are not significantly different according to Tukey's test ($p < 0.05$).

Exp	Source of variation	Treatment	TAR	TAD	MTN	BTM	TMR	TMD	FTN	FTNO
Exp 1	G	QAIf (B)	1.3 a	552 a	6.4 a	944 a	0.9 a	510 a	2.3 a	1454 a
		QAIf (W)	1.2 a	591 a	4.9 a	931 a	0.6 a	459 a	2.0 a	1390 a
		Kcha (W)	1.8 a	448 a	5.2 a	850 a	0.9 a	451 a	0.9 a	1301 a
		Man (W)	1.1 a	561 a	4.7 a	908 a	0.7 a	495 a	1.1 a	1402 a
	N	N0	1.3 a	518 a	5.0 a	964 a	0.6 a	527 a	1.3 a	1490 a
		N1	1.4 a	557 a	5.6 a	851 a	0.9 a	430 a	1.9 a	1281 a
	G		ns ns	ns ns	ns ns	* ns				
	N		ns ns	ns ns	ns ns	* ns				
	G × N		ns ns	ns ns	ns ns	ns ns				
	Exp 2	Year	2006 (Exp 2.I)	0.8 b	550 a	3.2 b	792 a	0.4 a	388 a	1.8 b
2007 (Exp 2.II)			1.7 a	543 a	7.0 a	791 a	1.6 b	318 a	2.2 a	1108 b
2008 (Exp 2.III)			1.5 a	562 a	6.4 a	785 a	1.6 b	314 a	1.8 b	1099 b
G		B75 (W)	1.2 b	557 a	5.1 bc	803 a	1.2 ab	327 a	1.7 b	1130 a
		Bg13 (W)	1.0 b	542 a	4.5 c	780 a	0.9 a	320 a	1.4 b	1100 a
		Kcha (W)	1.3 b	552 a	5.4 b	787 a	1.1 ab	364 a	1.7 b	1151 a
		Sca (B)	1.8 a	556 a	7.3 a	786 a	1.5 b	349 a	2.9 a	1136 a
N		N0	1.1 b	556 a	4.7 b	783 a	0.9 a	377 a	1.3 b	1160 a
		N1	1.6 a	548 a	6.4 a	795 a	1.4 b	303 b	2.5 a	1098 b
Year			* ns	ns	** ns	* ns		ns	*	*
G			*	ns	** ns	* ns		ns	** ns	ns
N			*	ns	* ns	* ns		*	** ns	*
Year × G			*	ns	* ns	* ns		*	ns	ns
Year × N			ns	ns	ns	ns		ns	ns	ns
G × N		ns	ns	** ns	ns		ns	** ns	ns	
Year × G × N		ns	ns	ns	ns		ns	ns	ns	

ANOVA: ns $p > 0.05$; * $p < 0.05$; ** $p < 0.01$.

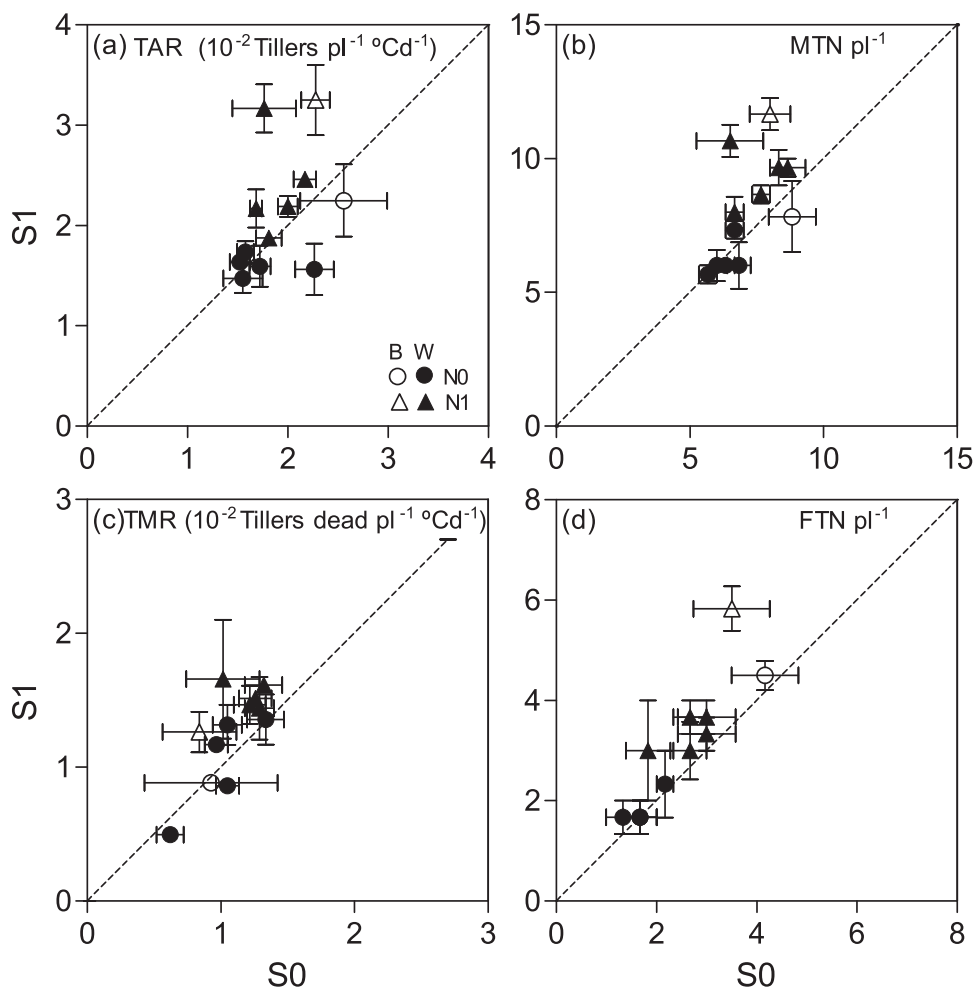


Fig. 3. (a) Tiller appearance rate (TAR), (b) maximum tillers number per plant (MTN), (c) tiller mortality rate (TMR) and (d) final tiller number per plant (FTN) in wheat (W) and barley (B) genotypes grown under low (N0) or high (N1) soil N availabilities at sowing. Each variable is contrasted for S1 and S0, with and without sulfur addition treatments, respectively. Data for Exp 3, Exp 4 and Exp 5. The dotted lines represent the 1:1 ratio.

was on average *ca.* 245 °Cd (general mean for all experiments), and the beginning of tiller mortality started *ca.* 775 °Cd from emergence. The timing of both events was independent of the treatments applied ($p > 0.05$). There was no association between beginning

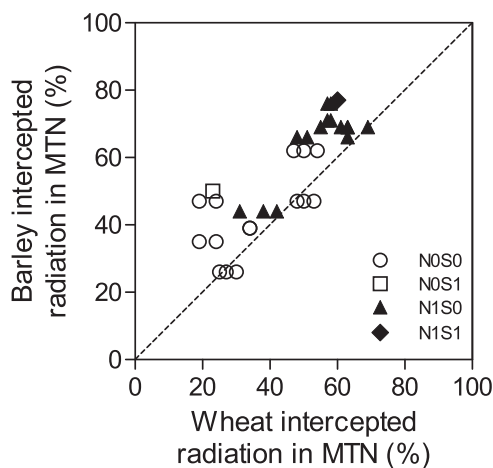


Fig. 4. Relationship between fraction of intercepted photosynthetically active radiation when the maximum tiller number (MTN) was reached for barley and wheat genotypes grown under low and high soil N (N0, N1) and S (S0, S1) availabilities at sowing. Data for Exp 1–3. The dotted lines represent the 1:1 ratio.

of tiller mortality and first visible node ($p > 0.10$). Tiller mortality was initiated after beginning of stem elongation (*ca.* 1170 °Cd from emergence; parameter *f* in Eq. (2)) (Fig. 5). The duration of the phase between the beginning and the end of tiller mortality was *ca.* 400 °Cd (as general mean), without significant differences for any treatment in any experiment ($p > 0.10$) (Fig. 5).

Barley genotypes showed a higher TMR than wheat genotypes, with average values of 1.12×10^{-2} tillers dead $\text{pl}^{-1} \text{°Cd}^{-1}$ vs. 1.03×10^{-2} tillers dead $\text{pl}^{-1} \text{°Cd}^{-1}$, respectively (Fig. 2; Table 4). Increases in N availability enhanced TMR (Table 4). For instance, in Exp 2 the N1 condition showed an average value of TMR *ca.* 35% greater than that of the N0 condition (*ca.* 1.4×10^{-2} tillers dead $\text{pl}^{-1} \text{°Cd}^{-1}$ vs. 0.9×10^{-2} tillers dead $\text{pl}^{-1} \text{°Cd}^{-1}$) ($p < 0.05$) (Fig. 2; Table 4). Similar to that observed for TAR and MTN, S increased TMR only when N availability was high. TMR showed values of 1.6×10^{-2} tillers dead $\text{pl}^{-1} \text{°Cd}^{-1}$ for the N1S1 treatment and of 1.0×10^{-2} tiller dead $\text{pl}^{-1} \text{°Cd}^{-1}$ as mean of the other treatments (Fig. 3c).

Finally, FTN was significantly higher in barley than in wheat genotypes (3.1 vs. 1.9 tillers per plant, respectively; Table 4). FTN was reached around 1235 °Cd from emergence (Table 4). As in the other attributes of tiller production, FTN increased with both N and S addition, showing values of 3.8 tillers per plant for the N1S1 treatment and 2.4 tillers per plant for the other N and S treatments (Fig. 3d).

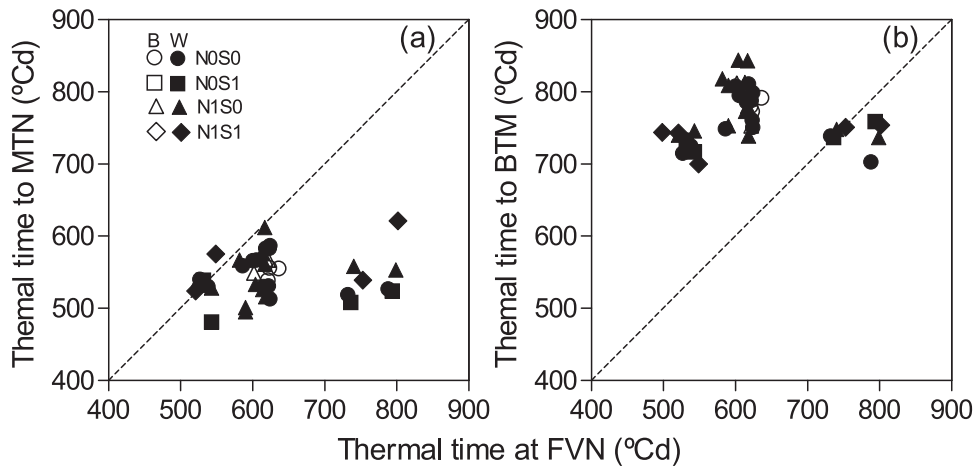


Fig. 5. Relationship between (a) the thermal time when reached the maximum tiller number per plant (MTN), and between (b) the thermal time at beginning of tiller mortality (BTM) and thermal time at occurrence of first visible node (FVN) in wheat (W) and barley (B) genotypes grown under low and high soil N (N0, N1) and S (S0, S1) availabilities at sowing. Data for Exp 2, 4 and 5. The dotted line represents the 1:1 ratio.

The maximum number of tillers was positively and significantly associated with the tiller appearance rate (Fig. 6a), but also determined a higher tiller mortality rate (Fig. 6b). Thus, the higher the tiller appearance rate, the higher the tiller mortality (Fig. 6c).

However, as increases in TAR were higher than increases in TMR (the slope of that relationship was less than 1; Fig. 6c), FTN was closely related to MTN (Fig. 6d). FTN was not significantly related to tiller mortality ($p > 0.10$).

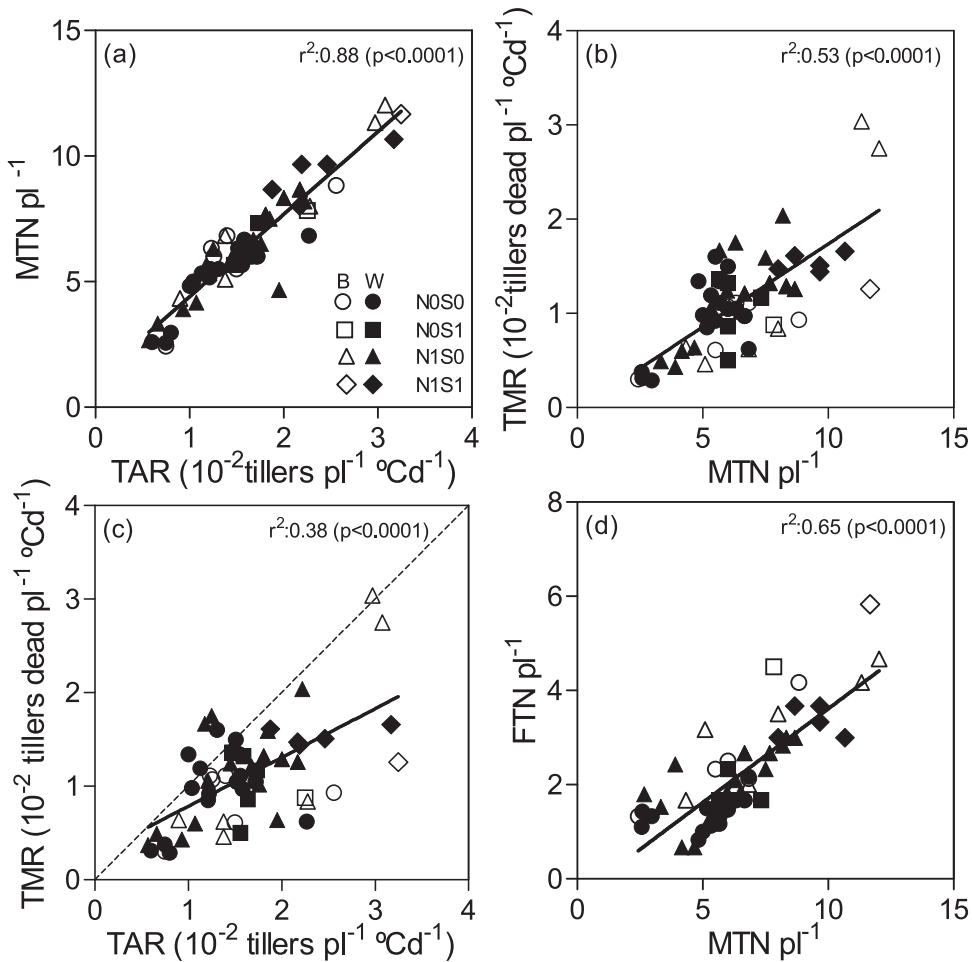


Fig. 6. Relationship between (a) maximum tiller number per plant (MTN) and tiller appearance rate; (b) tiller mortality rate (TMR) and maximum tiller number per plant (MTN); (c) tiller mortality rate (TMR) and tiller appearance rate (TAR), and (d) final tiller number per plant (FTN) and maximum tiller number per plant in wheat (W) and barley (B) genotypes grown under low and high soil N (N0, N1) and S (S0, S1) availabilities at sowing. Data for Exp 1–5. The solid lines represent the linear regression. In (c), the dotted line represents the 1:1 ratio.

3.4. Synchrony between leaves and tillers

The synchrony between the appearance of tillers and leaves showed significant differences among genotypes. On average, barley initiated more tillers per leaf (1.41) than wheat (1.23). The barley genotype Sca showed the highest value of tillers per leaf appeared (*ca.* 1.25 tillers leaf⁻¹), while the lowest value was recorded in the wheat genotype Bg13 (0.77 tillers leaf⁻¹; Fig. 7). The synchrony was *ca.* 25% greater for the crops grown under high N conditions than for those grown under low N availabilities (general mean of 1.45 and 1.10 tillers per leaf, respectively). For example, in Exp 1, the synchrony for N1 was *ca.* 20% higher ($p < 0.05$) than for the low N availability (*ca.* 1.12 and 0.89 tillers per leaf, respectively), without interaction between genotype and nitrogen (Fig. 7).

The synchrony in the experiments designed to evaluate the combined effects of N and S (Exp 3, 4 and 5) showed significant interaction N×S ($p < 0.05$). In Exp 3, for example, the highest value of synchrony was observed when both the initial N and S availabilities were high, with values of 2.2 and 2.6 tillers per leaf for Kcha and QAy, while the average values for the other treatments were 1.3 and 1.8 tillers per leaf, respectively, without interaction between the genotype and the combination of nutrients (Fig. 7). Following the same pattern observed in Exp 3, the synchrony in Exp 4 and 5 showed the highest values for the N1S1 treatment, with a mean value of 2.0 tillers per leaf, while in the other treatments the average value was 1.4 tillers per leaf.

4. Discussion

The present study highlights the differential response of leaf and tiller appearance between wheat and barley genotypes under contrasting soil N and S conditions. The phyllochron was modified only by the genotype, showing barley higher phyllochron than wheat in line to that reported by Miralles and Richards (2000). Modifications in N and S levels did not generate changes in phyllochron or in final leaves number. Thus, as phyllochron and final leaves number were not affected by N and S levels, duration of the emergence to flowering phase was not modified by changes in the nutritional conditions (the statistically significant differences observed were irrelevant in agronomic terms), similar to that observed by other authors (Cantero-Martinez et al., 1995; Cartelle et al., 2006; Salvagiotti and Miralles, 2007). However, other studies reported a delay in flowering date as the result of increases in the phyllochron under restrictions in N (Fischer et al., 1993; Arisnabarreta and Miralles, 2004) or S (Longnecker and Robson, 1994; Salvagiotti and Miralles, 2007). These divergences among studies on the effect of N or S on development could be related to differences in the magnitude and timing of the nutritional stress, as it is expected that the higher the severity and the duration of N stress, the higher its influence on crop development (Fischer et al., 1993). In our study the N or S deficiency were relatively moderated explaining the lack of nutrient effects on development.

Tillering dynamics was significantly affected by the genotype as well as by changes in N and S availabilities. Barley showed a 30% higher tiller appearance rate than wheat, as found by Lopez-Castaneda et al. (1995) and Miralles and Richards (2000). Differences between wheat and barley in tillering dynamics were evident from the initiation of the tillering process, presenting barley greater tillering capacity than wheat independently of the nutritional condition.

Cessation of tillering could be related (i) to the beginning of stem elongation and/or (ii) to changes in light conditions inside the canopy (reduction in the low red:far red ratio). The response of tillering to both factors could determine that even when the first mechanism (stem elongation) was triggered, tillering could

continue with high red:far red ratio. In this way, Evers et al. (2006) reported in wheat that tillering cessation occurred when the fraction of PAR intercepted by the canopy exceeds a specific threshold (0.40–0.45) and red:far-red ratio drops below 0.35–0.40. Although in the present work light quality inside the canopy was not measured, the fact that barley promotes a higher rate of tillering respect to wheat under higher conditions of PAR intercepted (barley showed greater FPAR at MTN than wheat crops, Fig. 4), suggests that barley buds (where tillers are initiated) could have different sensitivity to light quality (red:far-red) conditions than wheat ones. Thus, even when the light conditions into the canopy of barley have reached FPAR interception levels higher than 40%, as proposed for wheat by Evers et al. (2006), tillering in barley continue determining a higher MNT than wheat. This particular topic related to the different sensitivity between species to the light conditions inside the canopy have not been studied until now and should be explored in future researches to understand the tillering differences between species.

Nitrogen fertilization increased tiller appearance rate (*ca.* 23%) in both crops, in line with what was observed in other studies for both wheat (Rodríguez et al., 1998; Salvagiotti and Miralles, 2007) and barley (Prystupa et al., 2003; Arisnabarreta and Miralles, 2004). Barley has been traditionally considered a crop with low response to nitrogen addition (*i.e.* yield response per unit of N applied) in comparison to wheat (Christensen and Killorn, 1981; Delogu et al., 1998). However, that assumption was not properly tested in the literature; in fact, Cossani et al. (2009) did not found differences between wheat and barley in the response to N supply. In our work, the tillering response of wheat and barley to nitrogen addition was similar. Although N and S promoted increases in the tiller appearance rate and thereby in the maximum tiller number, the S effect was in general only evident when the N levels were high (demonstrating interaction between both nutrients). Probably, S promoted N absorption by the plant (Salvagiotti et al., 2009) increasing the status of N into the plants and promoting tillering appearance rate. Genotype and nutrients mostly modified crop growth attributes (such as the rate of tillering) rather than changes in development (such as duration of tillering phase).

In spite of the fact that the tiller appearance rate was the main driving force to determine the maximum tiller number, this positive relation was counterbalanced by the fact that the higher the number of tillers, the higher the tiller mortality rate. Nevertheless, as the relationship between TAR and TMR was less than proportional, FTN depended on the tiller appearance rate, promoted by species (barley vs. wheat) and/or by nutrients (*e.g.* “low” N vs. “high” N), and determined that the final number of tillers was pre-established from an early stage of the crop cycle. The association between MTN and TMR was also observed in other works (Sharma, 1995; Borrás et al., 2009). Non-surviving tillers could be beneficial if the amount of carbon fixed is re-distributed to other parts of the plants after their death (Palta et al., 2007). In this line, Ao et al. (2010) showed that the reduction of unproductive tillers did not contribute to increase grain yield in irrigated rice crops. However, Berry et al. (2003) showed that the carbon retained in non-surviving tillers was not re-distributed, determining a negative balance in the use of resources. Similarly, Thorne and Wood (1987) observed that, when water was limited, the production of non-surviving tillers was detrimental to crop yield because the carbon of dying tillers was not completely re-distributed to fertile shoots. Therefore, a high TAR and high MTN could be problematic in environments with limited water conditions (and/or in environments where crops start with high water content in the soil but precipitations become drastically reduced during the rest of the cycle). That situation is an opposite environmental condition to that explored in our study, where water availability was not limited.

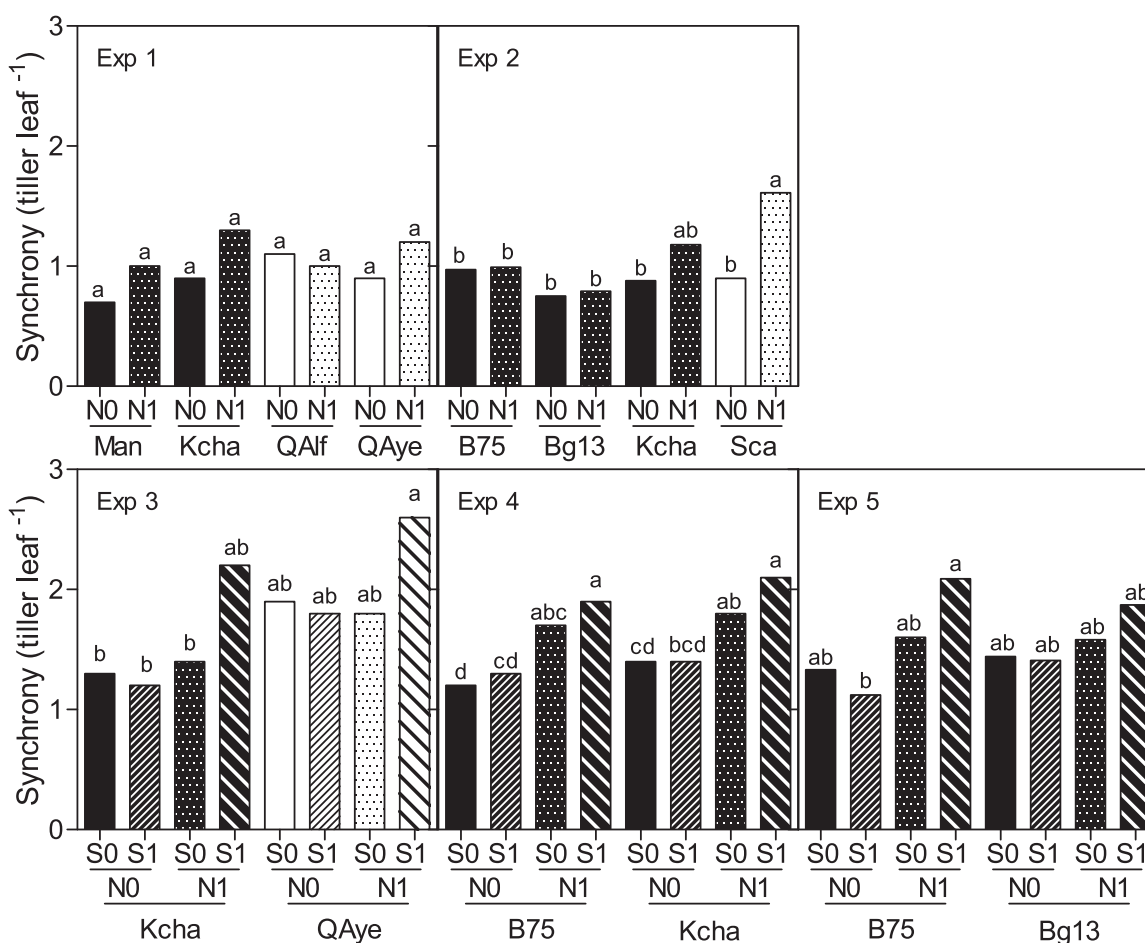


Fig. 7. Synchrony between tiller and leaf appearance in the main stem in wheat (Man, Kcha, B75, Bg13) and barley (QAlf, QAYe, Sca) genotypes grown under low and high soil N (NO, N1) and S (S0, S1) availabilities at sowing. Data for Exp 1–5. In Exp 2, data are the mean of three years. Within each panel, values with the same letter are not significantly different according to Tukey's test ($p < 0.05$).

In Gramineae, tillering appearance is related to the leaf appearance rate of the main stem through a pattern of tiller production based on the Fibonacci series (Neuteboom and Latinga, 1989; Boone et al., 1990; Miralles and Richards, 2000). As a result of the differences among genotypes and among nutrient levels on leaf and tillering appearance, the synchrony between tiller and leaf appearance showed differences due to the effect of the species (barley showed a higher synchrony than wheat) as well as due to the effect of the nutrients (deficiencies in N and S decreased the synchrony). One interesting point is that although barley showed a higher phyllochron (*i.e.* a lower leaf appearance rate) than wheat, its capacity for establishing tillers per leaf was higher than wheat. The increases in the synchrony between tiller appearances per emerged leaf in barley respect to wheat could be related to the barley capacity of generating tillers of superior orders (*i.e.* secondary or tertiary tillers). As secondary and tertiary tillers are more labile than primary tillers, this strategy to promote this order of tillers in barley could explain the higher TMR observed in this specie than in wheat. Future researches should be focus on analyzing the dynamics of tillering segregating between different orders of tillers and quantifying the number of leaves and the time of stem elongation in each of these tillers.

In conclusion, the final tiller number in wheat and barley was pre-defined during the early phase of the tillering process, and the high tillering capacity of barley was based on its high tillering rate despite its lower leaf appearance rate (respect to wheat). The differences between species in leaf appearance and tillering dynamics and their response to variations in the N or S condition represent

important tools to be incorporated in breeding programs (Borrás et al., 2009) and in modelization (Lafarge and Hammer, 2002) as determinants of the fraction of radiation intercepted by the crop (Abeledo et al., 2004; Kemanian et al., 2004) and yield generation (García del Moral et al., 1999; Arisnabarreta and Miralles, 2006). The differences between species in leaf and tillering appearance and their coordination, and the understanding of the mechanisms involved in those differences, constitute one of the main bases for understanding the adaptation of both crops to different environments and their response to nutrient fertilizers.

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