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FLOODING STRESS

Waterlogging Affects Leaf and Tillering Dynamics in Wheat and Barley

R. P. de San Celedonio[1,2,3], L. G. Abeledo[1,3], J. M. Brihet[1] & D. J. Miralles[1,2,3]

1 Cátedra de Cerealicultura, Departamento de Producción Vegetal, Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires, Argentina
2 IFEVA, Facultad de Agronomía, Universidad de Buenos Aires – CONICET, Buenos Aires, Argentina
3 CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina

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Correspondence
R. P. de San Celedonio
Cátedra de Cerealicultura
Departamento de Producción Vegetal
Facultad de Agronomía, Universidad de Buenos Aires
Av. San Martín 4453, (C1417DSE) Buenos Aires, Argentina; and IFEVA, Facultad de Agronomía
Universidad de Buenos Aires – CONICET
Av. San Martín 4453
(C1417DSE) Buenos Aires, Argentina
Tel.: +54 11 45248053
Fax: +54 11 45248039
Email: romina@agro.uba.ar

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Abstract

The aim of this study was to analyse (i) the crop attributes that determine flowering time (i.e. final leaf number, FLN; and phyllochron, Phy), (ii) the dynamics of tiller appearance and (iii) the synchrony between leaf and tiller appearance in wheat and barley plants exposed to waterlogging. Two experiments were carried out in pots, in which wheat and barley cultivars were exposed to five waterlogging treatments, during different periods throughout the crop cycle, from emergence to maturity. The appearance of leaves and tillers on the main stem was measured twice a week in labelled plants. Waterlogging from emergence to flag leaf appearance significantly delayed time to flowering. The delay was greater when waterlogging occurred at the beginning of tillering, lengthening the period from emergence to flowering 24 % (13–15 days) in barley and 10–15 % (6–10 days) in wheat, as compared to control. Phy was the main attribute explaining the delay in flowering, as FLN was not altered. Waterlogging during the early stages of development reduced tiller appearance rate (TAR) in both species, but this effect was partially counterbalanced by a lengthening of the tillering phase, so the effect on final tiller number at maturity was limited. In conclusion, the exposure of wheat and barley to waterlogging during early stages of development delayed time to flowering and reduce TAR in both species. Waterlogging during more advanced crop stages produced slight effects on tillering dynamics, which would indicate that waterlogging affected structure generation more than mortality.

Introduction

Waterlogging is an important constraint that affects crops worldwide. The main origin of this stress is when water from precipitation or irrigation accumulates in the soil profile for a period of time, as a consequence of heavy rainfall, soil compaction, flat topography or bad drainage systems (Van Ginkel et al. 1997). Many agricultural soils of the world destined to wheat and barley cultivation are frequently exposed to waterlogging (Sayre et al. 1994, Samad et al. 2001, Reussi Calvo and Echeverria 2006; Shaw et al. 2013, de San Celedonio et al. 2014a), affecting crop yield, and causing economic losses. Moreover, it is expected in the near future that there will be more risk of waterlogging due to an increase of occurrence of more intense precipitations and extreme events of high rainfall around the world, as a result of climate change (Wollenweber et al. 2003, Trenberth et al. 2007, IPCC 2014).

The negative effects of waterlogging on the attributes related to growth (i.e. biomass accumulation and its partition) in wheat and barley have been widely described in the literature (Cannell et al. 1980, Musgrave 1994, Setter and Waters 2003, de San Celedonio et al. 2014b, Marti et al. 2015). However, its effects on crop development have been analysed to a lesser extent. The final number of leaves that appeared on the main stem, as well as the leaf appearance rate, determine the duration of the phase from emergence to flowering (Em–Fl). Changes in the rate of leaf appearance or phyllochron (i.e. thermal time required between the appearance of two successive leaves; Cao and Moss 1989) influence the dynamics of tiller appearance (Hay and Kirby 1991), which in turn affects yield, through the

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determination of spike number per plant (García del Moral and García del Moral 1995, Elhani et al. 2007, de San Celedonio et al. 2014b).

Tillering is a process that takes place throughout the entire crop cycle. In wheat and barley, under potential conditions (i.e. a crop growing without abiotic restrictions or biotic adversities), the first tiller emerges when the first 2–3 leaves have appeared on the main stem and afterwards tillers continue appearing regularly until the maximum number of tillers is reached. After that, some of the tillers die (this process being quantified via the rate of tiller mortality), until the final tiller number (FTN) is reached (Kirby and Riggs 1978, Hay and Kirby 1991, Ishag et al. 1998, Alzueta et al. 2012). Waterlogging significantly reduces biomass accumulation in wheat, this associated with negative effects on initiation and growth of tillers (Malik et al. 2001, Collaku and Harrison 2002), and, as a consequence, decreases in the number of spikes per plant occur, thus affecting yield (de San Celedonio et al. 2014b). In wheat and barley several authors have reported a counterbalance between the rate of tiller appearance and the rate of tiller mortality, as the more tillers initiated the fewer tillers survive (García del Moral and García del Moral 1995, Berry et al. 2003, Salvagiotti and Miralles 2007).

Most of works that evaluate the effect of waterlogging on tillering focused the studies into a particular moment of the crop cycle, in general at the end of the treatment, or after some time of recovery. For example, exposing wheat plants to 14 days of waterlogging during tillering reduced the number of initiated tillers from 62 % to 70 % (Malik et al. 2001, 2002); and even 3 days of waterlogging reduced the number of tillers 40 %, after 25 days of recovery (Malik et al. 2002). In barley, 2 weeks of waterlogging during tillering resulted in reductions in the number of tillers established per plant from 20 % to 40 % at the end of treatment, depending on the genotype, while after 2 week of recovery the reductions were from 28 % to 53 % (Pang et al. 2004). However, waterlogging effects on number of tillers initiated, do not reflect necessarily the penalizations on the number of tillers at the end of the crop cycle. Under field conditions, Collaku and Harrison (2002) evaluated the number of tillers at maturity, after applying waterlogging during tillering, and found reductions respect to the control from 8 % to 66 %, depending on the genotype. Robertson et al. (2009) found a 50 % reduction in the number of tillers initiated when wheat plants suffered waterlogging during tillering, but at maturity there was no difference in the number of fertile tillers between waterlogged and drained treatments, due to the production of higher order tillers in waterlogged plants. The previous evidence shows the importance of evaluating the effect of waterlogging on tiller dynamics, considering the whole cycle, from the emergence of the first tiller until the final number of tillers is reached. The analysis carried out in the present study will allow to understand which of the phases of tillering dynamic is affected by waterlogging, especially when it is applied at different moments of the crop cycle.

It is well-known that temperature, day length and vernalization are the main environmental factors that govern the rate of development in wheat and barley, and determine the duration of the different phenological phases (Hay and Kirby 1991, Slafer and Rawson 1994, Kernich et al. 1995). However, several papers have demonstrated that abiotic stress, such as nutrient deficiency, can also modify the duration of the phenological phases in wheat and barley, although the responses are controversial (Rodríguez et al. 1998, Prystupa et al. 2003, Arisnabarreta and Miralles 2004, Guarda et al. 2004, Salvagiotti and Miralles 2007). In a recently published review, Hall et al. (2014) concluded that the currently available evidence concerning the response of time to flowering to the level of nitrogen in both species is not unanimous.

Although several works have been published about the effect of abiotic stress on crop development, extremely few have studied the effect of waterlogging. Robertson et al. (2009) reported that waterlogging during tillering increased the production of higher order tillers, despite a reduction in the number of tillers initiated, contributing to delayed ear emergence in wheat. Similar results were found by Amri et al. (2014), who reported a delay of ca. 10 days in flowering time when six cultivars of wheat were exposed to waterlogging during tillering. For barley the evidences are scarce; in a recent study, de San Celedonio et al. (2014b) showed that flowering time was delayed ca. 15 days compared to control plants, when wheat and barley crops were waterlogged early during the crop cycle (i.e. previous to the beginning of stem elongation). However, what remains unknown is which of the attributes regulating time to flowering, either the number of final leaves appeared on the main stem and/or the rate of leaf appearance, were affected by waterlogging.

The process of leaf appearance regulates the dynamics of tiller emergence (Kirby et al. 1985). The total number of tillers appeared per plant in relation to the number of leaves appeared on the main stem is called synchrony (Abeledo et al. 2004, Salvagiotti and Miralles 2007, Alzueta et al. 2012). The synchrony between leaf and tiller appearance is in general affected by the environment, because the tillering process is strongly influenced by resource availability. Different works have shown that the number of tillers appeared per emerged leaf increased under high nutritional levels (Abeledo et al. 2004, Salvagiotti and Miralles 2007, Alzueta et al. 2012) and the effect was higher in barley than in wheat (Abeledo et al. 2004, Salvagiotti and Miralles 2007, Alzueta et al. 2012).

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However, the synchrony between leaf appearance and tiller emergence has not been evaluated under waterlogging conditions.

The aim of this study was to analyse (i) the crop attributes that determine flowering time [i.e. final leaf number (FLN) and phyllochron], (ii) the dynamics of tiller appearance, and (iii) the synchrony between leaf and tiller appearance in wheat and barley plants exposed to waterlogging treatments applied during different moments of the crop cycle. The study will allow a better understanding of the effects of waterlogging on attributes regulating crop development comparatively in both species. We hypothesized that, (i) if a delay in flowering time occurred as a consequence of waterlogging, it would be explained by an effect on leaf appearance rate (phyllochron) more than by an effect on FLN, as the phyllochron involves growth and development attributes; (ii) waterlogging events would affect the tillering phase taking place during the stress [i.e. waterlogging during early stages of development would reduce tillering appearance rate, while waterlogging during late stages of development would affect tiller survival (TS)]; (iii) finally, the effect of waterlogging would be higher on tillering than on leaf appearance rate and, as a consequence, it would affect the coordination of appearance of leaves and tillers (synchrony).

Materials and Methods

Growing conditions

Two experiments (Exp 1 and Exp 2) were conducted at the School of Agronomy of the University of Buenos Aires (34° 35′ S, 58° 29′ W) during the 2010/11 growing season.

In order to explore contrasting environmental conditions between experiments, Exp 1 was sown in an early sowing date (2nd July) and conducted in a greenhouse, while Exp 2 was sown in a later sowing date (6th September) under natural field conditions. Both experiments were carried out in 12 l plastic pots (24 cm depth), filled with 5 cm gravel starting at the bottom and then completed with clay loam soil (Typic Arguidoll, USDA) in Exp 1 and a mix 3 : 1 of sand and clay loam soil (Typic Argiudoll, USDA) in Exp 2. A mixture with sand was chosen for Exp 2 to facilitate the drainage in the control pots and waterlogging pots when necessary in case of heavy rainfall. The seeds were uniformly placed 2 cm deep at a rate of 6 seeds per pot. At sowing, 2.5 g of fertilizer 15 % N : 15 % P_2O_5 : 15 % K_2O (Triple 15; Yara Argentina S.A., Buenos Aires, Argentina) was applied per pot. The level reached of soil nutrients was 42 ppm of N and 19 ppm of P in Exp 1, and 34 ppm of N and 19 ppm of P in Exp 2, enough to reach an optimal crop yield under the explored conditions. Both experiments were conducted without biotic stresses by applications of insecticides and fungicides. Weeds were periodically removed by hand.

Treatments

Treatments were arranged following a completely randomized design with four replications in Exp 1, and three replications in Exp 2. In each experiment, treatments consisted of the combination of one wheat and one barley cultivar and six waterlogging conditions, including a control without waterlogging. The wheat cultivars used in Exp 1 and Exp 2 were Klein Chajá and Baguette 13, respectively. The barley cultivar was Scarlett in both experiments. Under non-waterlogging conditions, these cultivars have similar phenology (measured as days to flowering) and high yield potential, according to the Argentinean National Evaluation Trials (Conti et al. 2013, INTA 2013, INASE 2014).

Six waterlogging treatments were imposed during five different periods throughout the crop cycle: (i) from leaf 1 to leaf 4 appeared on the main stem (L1–4), (ii) from leaf 4 to leaf 7 (L4–7), (iii) from leaf 7 to leaf 10 (L7–10), (iv) from leaf 10 to flowering (L10–Fl), (v) from flowering to maturity (Fl–M) and (vi) control without waterlogging throughout the entire crop cycle (Ctl). To match the phenological stages at the beginning and end of each waterlogging treatment, duration of each waterlogging treatment was 20 days in Exp 1 and 15 days in Exp 2.

In order to impose waterlogging treatments, pots were placed into containers (1 m × 1 m × 0.5 m) with 1 cm layer of free water above the surface of the pots during the whole period of each waterlogging treatment. Out of the waterlogging treatment, pots were maintained at 80 % field capacity through irrigation. Once each waterlogging treatment was finished, the pots were taken out of the containers and remained without irrigation during ca. 10 days, allowing free drainage, and after that they were re-watered normally. Control pots, from sowing to maturity, were always maintained at 80 % field capacity. Volumetric humidity content was continuously monitored on the top and bottom of the pots (AT Theta Kit HH2 Moisture content; Delta Devices, Cambridge, England).

Measurements

Crop phenology was determined following the decimal code of Zadoks et al. (1974). Phenological stages measured were emergence (Z10), first visible node (Z31; exclusively measured in Exp 1) and flowering time (Z65). As in barley the true flowering (when pollen of anthers is released over the stigma of the ovary) occurs in general when the spike is in the sheath of flag leaf (Fernández Gómez and Wilson 2012), flowering time in the barley cultivar was determined by opening the spikelets and visualizing pollen release. At

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emergence, one plant per pot (representative of the pot) was labelled to follow the dynamics of leaf and tiller appearance throughout the crop cycle. Leaf number appearance in main stems was measured twice a week from seedling emergence to complete flag leaf appearance using the scale proposed by Haun (1973). Twice weekly the tiller number per plant was measured from the appearance of the first tiller to maturity. The tiller per plant dynamics was done on the same plants in which leaf number was characterized.

Data analysis

The duration of the phenological stages was expressed using thermal time units, calculated as the cumulative difference between mean daily temperature and a base temperature of 0°C (Cao and Moss 1989). Daily air temperature was recorded every hour throughout the crop cycle in both experiments by an automatic meteorological station (Davis Vantage Pro2, Hayward, California, USA) placed in the same site where each experiment was carried out. Daily values of maximum, minimum and average air temperature and photoperiod during crop cycle in both experiments are presented in Fig. 1.

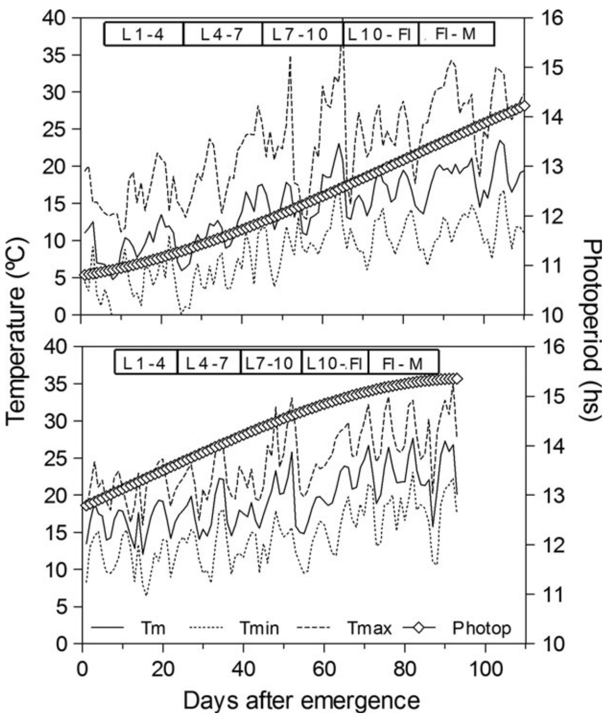

Fig. 1 Daily values of mean (T_m), maximum (T_{max}) and minimum (T_{min}) air temperature and photoperiod during crop cycle in Exp 1 (upper panel) and Exp 2 (bottom panel). Bars indicate timing of waterlogging treatments, where L stands for the number of leaves appeared on the main stem, Fl flowering and M maturity.

Phyllochron was calculated as the inverse of the slope of the linear relationship between the cumulative number of emerged leaves on the main stem and the thermal time from seedling emergence (Fig. 2a), according to the following equation:

$$Y = a + bx, \qquad (1)$$

where Y represents the number of leaves on the main stem (leaf pl^{-1}), x the cumulated thermal time from seedling emergence (°Cd), a the intercept (leaf pl^{-1}), and b the rate of leaf appearance (leaf pl^{-1} °Cd^{-1}). Phyllochron (°Cd leaf^{-1}; Phy) was estimated as the inverse of b parameter.

The dynamics of tillering during the crop cycle was analysed using a tetra-linear model (Fig. 2b), according to the following equation:

$$Y = a + bx(x \le c) + bc(x > c) + e(x - d)(x \ge d) + e(f - x)(x \ge f), \qquad (2)$$

where Y represents the tiller number per plant (tiller pl^{-1}), x the cumulated thermal time from seedling emergence (°Cd), a the intercept (tiller pl^{-1}), b the tiller appearance rate (tillers pl^{-1} °Cd^{-1}; TAR), c the thermal time at which the maximum tiller number was reached (°Cd; TT MTN), d the thermal time at the beginning of tiller mortality (°Cd; TT BTM), e the tiller mortality rate (tillers dead pl^{-1} °Cd^{-1}; TMR) and f the thermal time at which the final tiller number was defined (°Cd; TT FTN). This model also allowed to determine the thermal time at the beginning of tillering (°Cd; TT BT), the maximum tiller number per plant (tillers pl^{-1}; MTN) and the final tiller number per plant (tillers pl^{-1}; FTN). Tiller survival (%; TS) was calculated as the ratio between the MTN and the number of fertile tillers (i.e. with a spike) at maturity (as an average of the pot). The number of spikes per plant was measured at maturity.

The synchrony between leaf and tiller appearance was estimated adjusting a bi-linear regression model between the number of total tillers appeared per plant and the number of leaves appeared on the main stem (Fig. 2c), according to the following equation:

$$Y = a + bx(x \le c) + bc(x > c), \qquad (3)$$

where Y represents the tiller number per plant (tiller pl^{-1}), x the leaf number on the main stem, a the intercept (tiller pl^{-1}), b the synchrony (tillers leaf^{-1}; Sync) and c the number of leaves at which the maximum tiller number per

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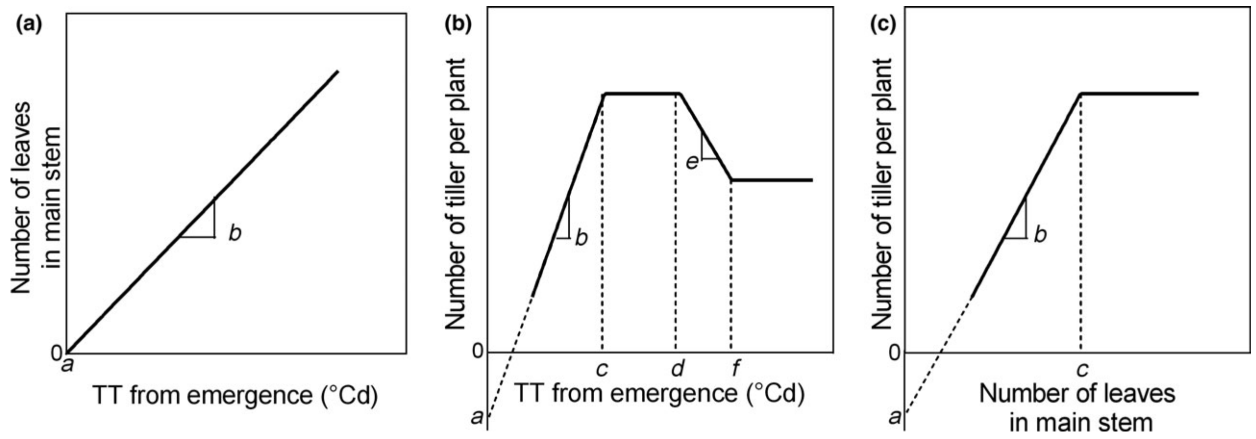

Fig. 2 Diagrams showing the models used to determine the parameters of: (a) phyllochron (°Cd leaf^{-1}), according to Eqn 1 (*a*, intercept; *b*, rate of leaf appearance), estimated as the inverse of *b* parameter; (b) tillering dynamics in wheat and barley according to Eqn 2 (*a,* intercept; *b* tiller appearance rate; *c* thermal time at which the maximum tiller number (MTN) was reached; *d* thermal time at the beginning of tiller mortality; *e* tiller mortality rate; *f* thermal time at which the final tiller number was defined) and (c) the synchrony between the number of tillers appeared per plant and the number of leaves appeared on the main stem according to Eqn 3 (*a*, intercept; *b*, synchrony; *c*, number of leaves at which MTN was reached).

plant was reached (leaf pl^{-1}; LMTN). This model also allowed to determine the number of leaves at which tillering began (leaf pl^{-1}; LBT).

Parameters of Eqns 1–3 were iteratively estimated using an optimization model (Motulsky and Christopoulos 2003).

Statistical analysis

Statistical differences between treatments were tested through analyses of variance (ANOVA) using InfoStat Professional v.1.1 (Di Rienzo et al. 2011). The mean treatment values were compared using Tukey test with significance level of 0.05.

Results

Phenology and leaf appearance

There was a significant interaction on the duration of the Em–Fl phase between waterlogging treatments and the species ($P < 0.001$). Waterlogging significantly ($P < 0.001$) delayed flowering time of wheat and barley when it was applied in L1–4, L4–7 and L7–10 in Exp 1 while in Exp 2 the delay in flowering was only detected in barley for waterlogging treatments applied in L1–4 and L4–7 (Table 1). Although waterlogging from L1 to L10 delayed flowering time, the treatment that produced the highest effect in both species and experiments was L4–7, barley being more affected than wheat. In barley, the delay of the Em–Fl phase, when waterlogging was applied in L4–7, was ca. 260 °Cd compared to the control in both experiments ($P < 0.05$), while in wheat the delay was 152 °Cd and only observed in Exp 1 ($P < 0.05$). Those delays in flowering time represented around 13–15 days for barley and 6–10 days for wheat, compared to the control. Waterlogging treatments most affected the first visible node to flowering (FVN–Fl) sub-phase which was 41 % longer in barley and 33 % in wheat, compared to the control, and in all cases associated with the L4–7 treatment (Exp 1). When waterlogging was applied later in the ontogeny (L10–Fl and Fl–PM), the duration of the Em–Fl phase or time to maturity were not affected ($P > 0.05$; Table 1).

The analysis of the traits associated with the duration of time to flowering (i.e. number of leaves and phyllochron) showed that barley initiated one leaf more than wheat in Exp 1 ($P < 0.001$), but waterlogging treatments did not modify FLN in any species or experiment ($P > 0.10$) (Table 1). However, phyllochron was significantly affected by waterlogging, in L4–7 phyllochron was 13 % higher than the control in both species, in Exp 2 ($P < 0.001$). In Exp 1, there was also an increase in phyllochron of 9 % in wheat and 5 % in barley, but the difference was not significant in statistical terms ($P > 0.05$; Table 1). Thus, phyllochron was the trait that better explained the delay in flowering due to waterlogging during pre-flowering ($r^2 = 0.47$; $P < 0.01$), as the FLN was not associated to time of flowering ($r^2 = 0.09$; $P > 0.1$).

Tillering dynamics

Tillering dynamics followed a pattern of four phases: (i) tiller appearance, (ii) maintaining of the maximum number of tillers per plant, (iii) tiller mortality, and (iv) the phase from the definition of the final number of tillers per plant (fertile plus non-fertile tillers) to maturity (Fig. 3).

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Table 1 Duration of the phase measured in thermal time (°Cd) from emergence to first visible node (Em–FVN), from first visible node to flowering (FVN–Fl) and from emergence to flowering (Em–Fl), phyllochron (Phy; °Cd $leaf^{-1}$) and final leaf number on the main stem (FLN; leaf pl^{-1}) in wheat and barley cultivars (Cv) exposed to waterlogging during different moments of the crop cycle in Exp 1 (early sowing date under greenhouse conditions) and Exp 2 (late sowing date under natural conditions). Waterlogging treatments (WL) indicate the moment of the crop cycle in which waterlogging was applied: L stands for the number of leaves appeared on the main stem, Fl flowering, M maturity and Ctl control without waterlogging. Linear regression used to calculate phyllochron showed a coefficient $r^2 > 0.95$ in all replicates ($P < 0.001$)

		Exp 1					Exp 2		
Cv.	WL	Em–FVN	FVN–Fl	Em–Fl	Phy	FLN	Em–Fl	Phy	FLN
Wheat	Ctl	667	371	1038	89.7	10.0	1168	90.3	10.0
	L1–4	697	430	1127	96.3	9.5	1168	92.6	10.0
	L4–7	697	493	1190	97.3	10.3	1287	101.8	10.3
	L7–10	637	468	1105	91.0	9.8	1241	94.1	10.5
	L10–Fl	713	325	1038	83.8	10.0	1113	90.9	10.0
	Fl–M	637	412	1050	89.3	9.8	1195	85.4	10.7
Barley	Ctl	667	417	1084	92.1	11.8	1031	90.8	10.3
	L1–4	697	478	1176	97.7	11.3	1195	91.3	11.0
	L4–7	757	589	1346	96.8	12.0	1287	102.0	10.3
	L7–10	697	493	1190	99.6	11.8	1148	95.6	10.7
	L10–Fl	757	327	1084	96.6	11.5	1031	87.3	10.3
	Fl–M	727	357	1084	95.8	11.5	1031	92.9	9.7
h.s.d. WL		79.1	85.7	30.8	7.4	ns	84.6	7.2	ns
h.s.d. Cv		30.8	ns	12.0	2.9	0.3	32.6	ns	ns
h.s.d. WL × Cv		ns	ns	50.5	12.2	ns	139.5	ns	ns

h.s.d., honest significant difference for Tukey's test at P = 0.05; ns, not significantly different (P > 0.05).

The parameters of tillering dynamics estimated using Eqn 3 are described in Table 2 ($r^2 > 0.90$ in all cases). With the exception of treatment L1–4 in barley (Exp 1), where the phase of tiller mortality was not evident, tillering dynamics was well represented in all cases by this four phase model. In the case of barley treatment L1–4 in Exp 1, the appearance of later tillers (from immediately previous to flowering to advanced grain filling) made it impossible to capture the moment in which tillers began to die. These later tillers were included in Fig. 3 (bicolour squares), but were no considered for the description of tiller mortality in barley (Table 2). For that reason, parameters of tiller mortality (TT BTM; TMR; TT FTN and FTN) in treatment L1–4 in both species were not included in the statistical analysis of variance (ANOVA) (Table 2).

Waterlogging significantly affected TT BT in both experiments (P < 0.01). L1–4 was the treatment that most delayed the beginning of tillering, especially in barley (76 °Cd and 99 °Cd later than the control in Exp 1 and Exp 2, respectively) (Table 2). In the rest of the treatments there was no clear pattern of waterlogging on TT BT, as in some cases waterlogging accelerated the beginning of tillering compared to the control, while in others it produced a slight delay in TT BT. TAR was also reduced ca. 20 % in average by waterlogging treatments (P < 0.01). In both species, the treatments producing the greatest reductions in TAR were L1–4 (−47 % compared to the control) in Exp 1, and L4–7 (−57 % compared to the control) in Exp. 2. The moment MTN was reached (TT MTN) did not differ between wheat and barley under control conditions (P > 0.05). However, in barley, waterlogging treatments applied early in the crop cycle (L1–4 and L4–7) significantly delayed the TT MTN (Table 2). Although the general trend was the earlier the waterlogging treatment the longer the delay in TT MTN, the impact varied depending on cultivar and experiment. In three of the four cases, the longest delays in TT MTN were in the L1–4 treatment (Table 2). Thus, the negative effect of waterlogging on TAR was partially counterbalanced by a lengthening of the tillering phase. For example, in the case of barley, the reductions in the MTN in treatments L1–4 (Exp 1) and L4–7 (Exp 2) were 15 % and 30 %, respectively, which were lower in proportion than the reduction in TAR (Table 2).

Tiller mortality was analysed excluding treatment L1–4 of wheat and barley in Exp 1 because, as previously explained, this treatment did not fit a tetra-linear model in barley, due to the appearance of later tillers during grain filling. The beginning of tiller mortality (TT BTM) was 10 % later in barley than in wheat, independently of the treatment (P < 0.05). Waterlogging treatments did not significantly modify TT BTM in Exp 1 (P > 0.05), but in Exp 2 TT BTM was earlier in general in waterlogging treatments than in the control. In Exp 1, the TMR was accelerated by

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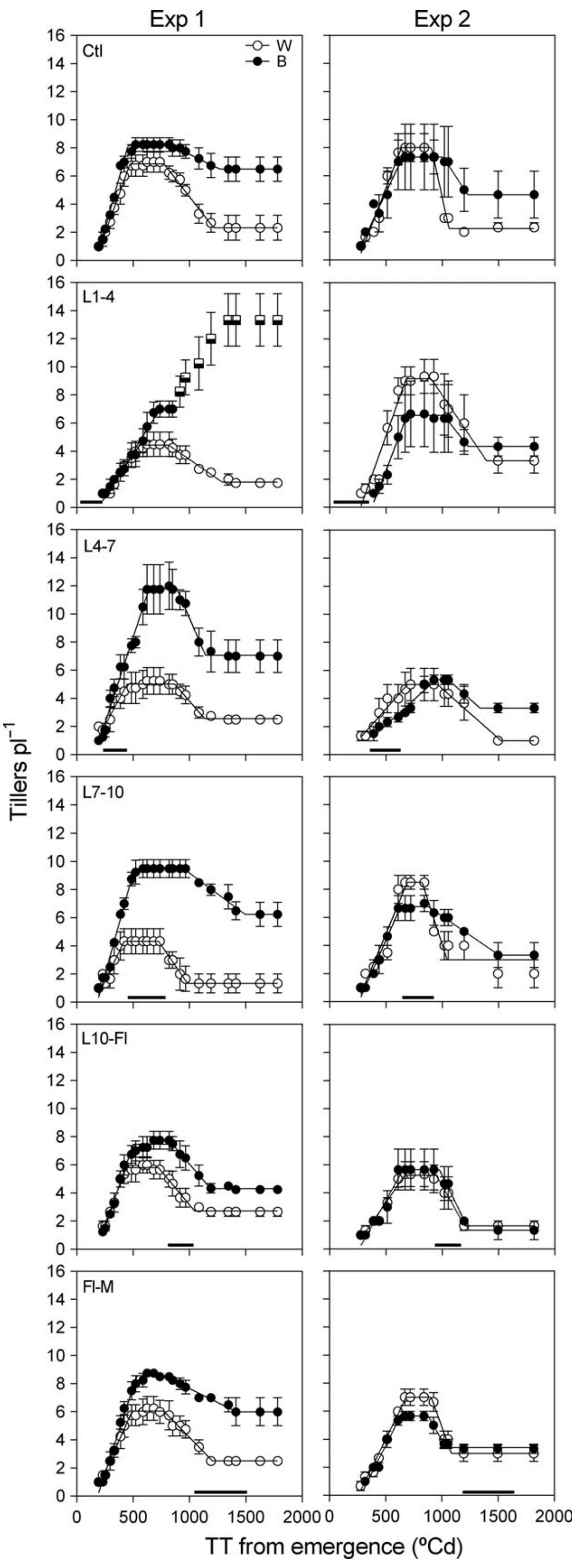

Fig. 3 Dynamics of tiller appearance and mortality throughout the crop cycle from seedling emergence for wheat (W) and barley (B) cultivars exposed to waterlogging in different moments during the crop cycle (L stands for the number of leaves appeared on the main stem, Fl flowering, M maturity and Ctl control without waterlogging), in two experiments (Exp 1, left panels; Exp 2, right panels). Bicolour symbols in L1–4 Exp 1 represent new tillers emerged during grain filling, that were not considered in the adjustment. Full horizontal bars indicate the timing of waterlogging treatments. The lines were fitted following Eqn 2; results of the adjustments are shown on Table 2. Standard errors are represented by vertical lines.

waterlogging in barley ($P < 0.05$). However, in Exp 2 no significant differences ($P > 0.05$) were found in TMR when the Ctl was compared with the waterlogging treatments, even when waterlogging was applied during this process (L10–Fl; Fl–PM; Table 2). Finally, tiller mortality rate (TMR) did not differ between wheat and barley in any experiment or treatment.

The moment in which the final tiller number was reached (TT FTN) and the FTN were not significantly affected by waterlogging treatments. There was a significant cultivar effect on FTN, which was in average higher in barley than in wheat in both experiments ($P < 0.05$), but in Exp 1 the cultivar effect depended on the waterlogging treatment (interaction Cv × WL; $P < 0.05$). Tiller survival was also higher in barley than in wheat in both experiments ($P < 0.05$) and was different between waterlogging treatments L4–7 (38 % average for both species) and L7–10 (17 % average for both species) in Exp 2 ($P < 0.05$), although differences were not significant when compared to the control (Fig. 4). The number of spikes per plant at maturity was also higher in barley than in wheat in both experiments ($P < 0.001$). Spikes were affected by waterlogging only in Exp 2 ($P < 0.05$), L7–10 treatment mostly reducing the number of spikes per plant (Fig. 4).

Synchrony between leaf and tiller dynamics

The coordination between the appearance of leaves and tillers (synchrony) was higher in barley than in wheat in Exp 1 (as barley produced 0.3 more tillers per appeared leaf than wheat; $P < 0.01$). However, in Exp 2 synchrony was similar in wheat and barley (Table 3). Waterlogging applied during the early stages affected synchrony ($P < 0.01$), by reducing the number of tillers appeared per emerged leaf in both species. However, treatments producing the more negative effects varied with experiments. In Exp 1, L1–4 treatment produced the lowest synchrony in both species ($P < 0.01$), whereas in Exp 2 L4–7 treatment significantly reduced synchrony ($P < 0.01$). In Exp 2, waterlogging applied in L4–7 significantly anticipated the beginning of tillering compared to leaf appearance, as the first tiller emerged when plants had one leaf less than the

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Table 2 Thermal time from seedling emergence to beginning of tillering (TT BT; °Cd), tiller appearance rate (TAR; tillers pl^{-1} $°Cd^{-1}$), thermal time from seedling emergence to maximum tiller number (TT MTN; °Cd), maximum tiller number per plant (MTN; tillers pl^{-1} $°Cd^{-1}$), thermal time from seedling emergence to beginning of tiller mortality (BTM; °Cd), tiller mortality rate (TMR; tillers pl^{-1} $°Cd^{-1}$), thermal time from seedling emergence to the moment in which the final tiller number was reached (TT FTN; °Cd) and final tiller number per plant (FTN; tillers pl^{-1}) in wheat and barley cultivars (Cv) exposed to waterlogging in different moments during the crop cycle in Exp 1 (early sowing date under greenhouse conditions) and Exp 2 (late sowing date under natural conditions). Waterlogging treatments (WL) indicate the moment of the crop cycle during which waterlogging was applied: L stands for the number of leaves appeared on the main stem, Fl flowering, M maturity and Ctl control without waterlogging.

Exp.	Cv.	WL	TT BT	TAR	TT MTN	MTN	BTM	TMR	TT FTN	FTN
Exp 1	Wheat	Ctl	153	0.021	492	7.0	797	0.013	1172	2.3
		L1–4	155	0.012	609	4.8	8781	0.010[1]	1174[1]	1.8[1]
		L4–7	111	0.015	490	5.3	860	0.014	1137	2.5
		L7–10	202	0.021	379	3.8	769	0.019	953	1.0
		L10–Fl	151	0.019	477	6.0	792	0.018	982	2.7
		Fl–M	155	0.019	493	6.3	810	0.014	1092	2.5
	Barley	Ctl	172	0.029	459	8.3	873	0.007	1212	6.5
		L1–4	248	0.015	714	7.0	–	–	–	–
		L4–7	176	0.024	643	12.0	895	0.024	1111	7.0
		L7–10	185	0.029	508	9.5	1073	0.017	1449	6.3
		L10–Fl	188	0.025	496	7.8	884	0.017	1150	4.3
		Fl–M	190	0.025	534	8.8	784	0.009	1202	6.3
h.s.d. WL			50	0.008	93	2.4	ns	0.009	ns	ns
h.s.d. Cv			19	0.003	36	0.9	77	ns	89	0.8
h.s.d. WL × Cv			82	ns	153	4.0	ns	ns	335	1.7
Exp 2	Wheat	Ctl	256	0.021	632	8.0	984	0.026	1220	2.3
		L1–4	274	0.022	707	9.3	942	0.019	1355	3.7
		L4–7	176	0.011	647	5.0	968	0.012	1409	1.7
		L7–10	250	0.019	691	8.5	839	0.023	1263	2.0
		L10–Fl	212	0.012	659	5.3	924	0.016	1179	1.7
		Fl–M	258	0.017	677	7.3	911	0.030	1085	1.7
	Barley	Ctl	306	0.022	624	7.7	1009	0.015	1230	4.7
		L1–4	405	0.024	674	6.7	948	0.024	1074	4.3
		L4–7	242	0.008	914	5.3	1148	0.010	1396	3.3
		L7–10	235	0.017	660	7.0	970	0.015	1261	3.3
		L10–Fl	341	0.020	638	6.0	992	0.018	1278	2.0
		Fl–M	281	0.016	631	5.7	896	0.018	1029	3.0
h.s.d. WL			82	0.009	99	ns	155	ns	ns	ns
h.s.d. Cv			32	ns	ns	ns	60	ns	ns	1.0
h.s.d. WL × Cv			ns	ns	163	ns	ns	ns	ns	ns

h.s.d., honest significant difference for Tukey's test at P = 0.05; ns, not significantly different (P > 0.05).
[1]Data was not included in the ANOVA due to the absence of the corresponding values for barley.

control in both species ($P < 0.01$) (Table 3). In that treatment, not only was the beginning of tillering anticipated in comparison to leaf appearance, but the end of tillering was also delayed, since plants had approximately two leaves more than the control at the beginning of tillering mortality, in both experiments (Table 3). Similarly, in Exp 1, waterlogging treatment L4–7 also delayed the end of tillering compared to leaf appearance in barley, as the last tiller appeared when plants had 1.8 leaves more than the control ($P < 0.05$).

Discussion

Waterlogging applied early during the crop ontogeny (from emergence to appearance of leaf 10) significantly affected phenological development in wheat and barley by delaying the time to flowering, although its effect differed according to the timing of exposition to waterlogging (Table 1). The effect on phenology was more pronounced when waterlogging occurred at the beginning of tillering (L4–7), lengthening the Em–Fl period 24 % in barley and 10–15 % in wheat. Thus, waterlogging delayed flowering time 13–15 days in barley and 6–10 days in wheat, compared to the control. In wheat, Robertson et al. (2009) showed that waterlogging during the early stages of wheat delayed time to anthesis; however, in a flooding tolerant species such as rice, there was no difference in time to flowering under continuous flooding compared to non-flooding conditions (Stuerz et al. 2014). Contrasting these results with those observed under other abiotic stresses, such as nutrient defi-

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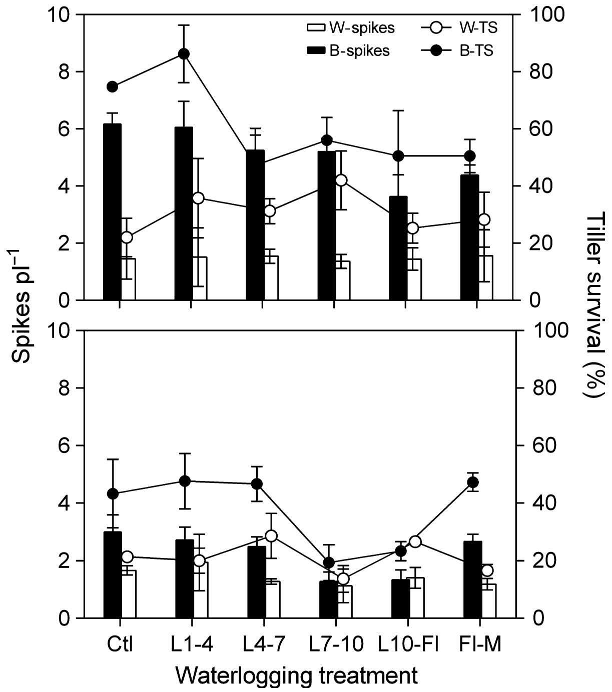

Fig. 4 Number of spikes per plant at maturity (spikes pl^{-1}; bars) and tiller survival (%; lines), quantified as the ratio between the maximum tiller number and the number of fertile tillers (i.e. with a spike) at maturity in wheat (empty bars) and barley (full bars) cultivars (Cv) exposed to waterlogging during different moments of the crop cycle in Exp 1 (upper panel) and Exp 2 (bottom panel). Waterlogging treatments (WL) indicate the moment of the crop cycle in which waterlogging was applied: L stands for the number of leaves appeared on the main stem, Fl flowering, M maturity and Ctl control without waterlogging.

Table 3 Synchrony between tiller and leaf appearance (Sync; tillers leaf^{-1}), number of leaves appeared on the main stem at the beginning of tillering (LBT; leaf pl-1) and number of leaves appeared on the main stem when tillering ended (LMTN; leaf pl-1) in wheat and barley cultivars exposed to waterlogging during different moments of the crop cycle in Exp 1 (early sowing date under greenhouse conditions) and Exp 2 (late sowing date under natural conditions). Waterlogging treatments (WL) indicate the moment of the crop cycle in which waterlogging was applied: L stands for the number of leaves appeared on the main stem, Fl flowering, M maturity and Ctl control without waterlogging.

		Exp 1			Exp 2		
Cv.	WL	Sync	LBT	LMTN	Sync	LBT	LMTN
Wheat	Ctl	1.7	3.2	6.3	1.8	4.0	7.5
	L1–4	1.0	3.0	7.1	1.9	4.0	8.0
	L4–7	1.6	3.2	5.4	1.0	3.0	7.3
	L7–10	1.6	3.7	5.0	1.7	3.9	8.0
	L10–Fl	1.5	3.3	6.3	1.0	3.3	7.4
	Fl–M	1.6	3.4	6.3	1.3	4.0	8.2
Barley	Ctl	1.9	3.6	7.0	2.2	4.6	6.8
	L1–4	1.5	4.5	8.3	2.0	5.3	7.9
	L4–7	1.9	5.5	8.8	0.8	3.8	9.6
	L7–10	2.0	3.8	7.5	1.6	4.1	7.4
	L10–Fl	1.7	3.4	7.2	1.7	4.9	7.2
	Fl–M	1.9	3.8	7.5	1.6	4.3	6.9
h.s.d. WL		0.5	ns	1.0	0.8	0.8	1.2
h.s.d. Cv		0.2	0.3	0.4	ns	0.3	ns
h.s.d. WL × Cv		ns	1.1	1.5	ns	ns	ns

h.s.d., honest significant difference for Tukey's test at P = 0.05; ns, not significantly different (P > 0.05).

ciencies, the effect of waterlogging on development was of higher magnitude. Under P deficiency, a delay of 10 % in time to flowering was reported in barley (Prystupa et al. 2003) and 14 % in wheat (Rodríguez et al. 1998), while no phenological differences were found by Alzueta et al. (2012) in wheat or barley, due to different N and S nutrition levels. Other studies, however, showed a delay in flowering time in barley due to N deficiencies (Arisnabarreta and Miralles 2004). In general terms, and as highlighted in Hall et al. (2014), changes in time to flowering in wheat and barley triggered by N responses, are in general of lower magnitude (<5 %).

Delays in time to flowering can occur as a result of a greater number of leaves on the main stem or a higher phyllochron. Number of leaves on main stem is usually a very conservative trait under stressful conditions, but exist evidences where the FLN was reduced by abiotic stresses, as Al toxicity in wheat (Valle and Calderini 2010). In the present study, waterlogging did not modify the FLN in any case, and this response was consistent with those recorded under other abiotic stresses, like nutrient deficiencies (Salvagiotti and Miralles 2007, Alzueta et al. 2012). Phyllochron appeared to be more susceptible to be modified, as under waterlogging conditions it tended to be higher than in the control (Table 1), similarly to what was shown for wheat under water shortage (Cabeza et al. 1993) or in wheat as well as barley under N (for wheat: Longnecker et al. 1993, Salvagiotti and Miralles 2007, for barley: Arisnabarreta and Miralles 2004) or P deficiencies (for wheat: Rodríguez et al. 1998, for barley: Prystupa et al. 2003). Moreover, in the case of rice, the emergence of leaves under complete submergence was delayed more in a cultivar without the submergence tolerant Sub1 gene, than in one having this gene (Gautam et al. 2014). In Exp 2, phyllochron was 13 % higher when waterlogging was applied at the beginning of tillering (L4–7) than in the control, and it could partly explain the delay in flowering observed in the same treatment. In Exp 1, the effect of waterlogging on phyllochron was lower and did not differ statistically from the control, despite the fact that the Em–Fl period was longer under waterlogged conditions. Waterlogging is expected to affect phyllochron more than FLN, as the latter is an attribute of development (affected by photoperiod and vernalization), while the former, although considered a developmental trait, can be influenced by

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abiotic stresses (e.g. nutrients and water restrictions), as it involves growth and development attributes (Dreccer et al. 2013).

Phyllochron was the main attribute analysed in our work that explained the delay in flowering, when wheat and barley were exposed to early waterlogging events. However, as the effect of waterlogging on phyllochron is not consistent enough to explain the delays observed in flowering, and the FLN did not change with waterlogging treatments, we hypothesize that other attributes could also be involved in explaining the delay in flowering time. On the one hand, it is possible to speculate that waterlogging also affected the phase of peduncle elongation, determining a longer period from the appearance of the last leaf (flag leaf) to flowering time. On the other, as the flowering time was recorded when 50 % of the stems of the pot reached anthesis, the appearance of higher order tillers in the waterlogging treatment applied during tillering phase (L4–7), with a delayed rate of development compared to main stems, could be responsible for this delay in flowering time. In this way, Robertson et al. (2009) reported that waterlogging during tillering increased the production of higher order tillers and contributed to delayed ear emergence in wheat.

The beginning of tillering was earlier in wheat than in barley in both experiments, independently of the waterlogging treatments, but when plants were exposed to waterlogging very early during the cycle (i.e. L1–4) the appearance of the first tiller tended to be delayed, especially in barley (Table 2). Moreover, waterlogging during early stages of development (L1–4 and L4–7) significantly reduced TAR in both experiments. This is consistent with the literature, that shows that waterlogging during tillering of wheat severely decrease the number of tillers produced at the end of the waterlogging treatment compared to plants grown under continuously drained soil (Malik et al. 2001, 2002). In barley, our results showed compensation between the reduction of TAR and the duration of the tillering period (TT MTN), by lengthening the phase of tillering appearance 40–55 % (depending on the treatment and the experiment). Similarly, wheat also showed a lengthening of the tillering phase, when waterlogging was applied during tillering, but of a lower magnitude than that observed in barley (24 % and 12 %, for Exp 1 and Exp 2, respectively). Thus, the negative effect of waterlogging on TAR, when plants were exposed during tillering, was partially counterbalanced by a lengthening of the phase, diminishing the effects of waterlogging on MTN.

The BTM occurred subsequently to the beginning of stem elongation in all situations, in agreement with what was stated in the literature (Davidson and Chevalier 1990, Hay and Kirby 1991) and was independent of the waterlogging condition in both species (Table 2). Although previous evidence showed that different abiotic stresses as water deficits (Davidson and Chevalier 1990, Elhani et al. 2007) or nutritional deficiencies (Alzueta et al. 2012) increased tiller mortality, in our study waterlogging did not significantly modify nor TMR or MTN.

Considering that waterlogging at early stages of development produces significant reductions in the TAR, the negative effect of this abiotic stress was more important for initiation than for mortality of tillers. It is consistent with the results of Alzueta et al. (2012) that proposed that the final number of tillers (FTN) is pre-established from an early stage of the crop cycle, and is determined by the TAR. In our work, FTN did not differ between the control and the waterlogging treatments, despite the fact that TAR was significantly reduced (Table 2). However, it is important to highlight that in our study FTN does not mean fertile tillers at maturity, but jointed tillers. The number of fertile tillers (spikes pl^{-1}; Fig. 2) was affected in a greater extent than FTN by waterlogging treatment. Moreover, there was a compensation of the lower TAR through a longer tillering period, as was described above.

The reduction in the TAR that occurred under early waterlogging also affected the coordination between the emergence of tillers and the appearance of leaves. A significant reduction in the synchrony occurred when wheat and barley plants were exposed to waterlogging during L1–4 and L4–7 (Table 3), similarly to plants of winter cereals exposed to nutritional deficiencies (Prystupa et al. 2003, Abeledo et al. 2004, Salvagiotti and Miralles 2007). Moreover, treatment L4–7 delayed tillering compared to leaf appearance in barley, as the last tillers appeared when plants had two or three leaves more in the main stem, under waterlogging conditions than in the control. However, this delay of tillering could not compensate for the reduction of TAR, as the synchrony in this treatment was significantly lower than that of the control.

In conclusion, exposure of wheat and barley cultivars to waterlogging during early stages of development (i.e. from leaf 1 to leaf 7 appeared in the main stem) significantly delayed flowering time, barley being the most affected. This delay was explained in part by reductions in the leaf appearance rate (higher phyllochron), but other mechanisms (e.g. elongation rate of the peduncle or production of higher order tillers) could be involved in the phenology delay. Even though waterlogging affected the leaf appearance rate, the TAR was reduced to a greater extent, affecting the coordination between tillering and emergence of leaves. The exposure of wheat and barley to waterlogging during more advanced stages of development produced lower effects, indicating that waterlogging affected structure generation more than mortality.

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References

Abeledo, L. G., D. F. Calderini, and G. A. Slafer, 2004: Leaf appearance, tillering and their coordination in old and modern barleys from Argentina. Field Crops Res. 86, 23–32.

Alzueta, I., L. G. Abeledo, C. M. Mignone, and D. J. Miralles, 2012: Differences between wheat and barley in leaf and tillering coordination under contrasting nitrogen and sulfur conditions. Eur. J. Agron. 41, 92–102.

Amri, M., M. H. El Ouni, and M. B. Salem, 2014: Waterlogging affect the development, yield and components, chlorophyll content and chlorophyll fluorescence of six bread wheat genotypes (*Triticum aestivum* L.). Bulg. J. Agric. Sci. 20, 647–657.

Arisnabarreta, S., and D. J. Miralles, 2004: The influence of fertiliser nitrogen application on development and number of reproductive primordia in field-grown two- and six-rowed barleys. Aust. J. Agric. Res. 55, 357–366.

Berry, P. M., J. H. Spink, M. J. Foulkes, and A. Wade, 2003: Quantifying the contributions and losses of dry matter from non-surviving shoots in four cultivars of winter wheat. Field Crops Res. 80, 111–121.

Cabeza, C., A. Kin, and J. F. Ledent, 1993: Effect of water shortage on main shoot development and tillering of common and spelt wheat. J. Agron. Crop Sci. 170, 243–250.

Cannell, R. Q., R. K. Belford, K. Gales, C. W. Dennis, and R. D. Prew, 1980: Effects of waterlogging at different stages of development on the growth and yield of winter wheat. J. Sci. Food Agric. 31, 117–132.

Cao, W., and D. N. Moss, 1989: Temperature effect on leaf emergence and phyllochron in wheat and barley. Crop Sci. 29, 1018–1021.

Collaku, A., and S. A. Harrison, 2002: Losses in wheat due to waterlogging. Crop Sci. 42, 444–450.

Conti, V. A., F. Moreyra, G. A. Gonzalez, A. R. Vallati, and F. J. Gimenez, 2013: Red Nacional de Cebada Cervecera. E.E.A. INTA Bordenave. http://inta.gob.ar/documentos/red-nacional-de-cebada-cervecera-campana-2012 [last accessed 15 September 2014].

Davidson, D. J., and P. M. Chevalier, 1990: Preanthesis tiller mortality in spring wheat. Crop Sci. 30, 832–836.

Di Rienzo, J. A., F. Casanoves, M. G. Balzarini, L. Gonzalez, M. Tablada, and C. W. Robledo, 2011: InfoStat Profesional. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Córdoba, Argentina.

Dreccer, M. F., S. C. Chapman, A. R. Rattey, J. Neal, Y. Song, J. J. T. Christopher, and M. Reynolds, 2013: Developmental and growth controls of tillering and water-soluble carbohydrate accumulation in contrasting wheat (*Triticum aestivum* L.) genotypes: can we dissect them? J. Exp. Bot. 64, 143–160.

Elhani, S., V. Martos, Y. Rharrabti, C. Royo, and L. F. García del Moral, 2007: Contribution of main stem and tillers to durum wheat (*Triticum turgidum* L. var. durum) grain yield and its components grown in Mediterranean environments. Field Crops Res. 103, 25–35.

Fernández Gómez, J., and Z. A. Wilson, 2012: Non-destructive staging of barley reproductive development for molecular analysis based upon external morphology. J. Exp. Bot. 63, 4085–4094.

García del Moral, M. B., and L. F. García del Moral, 1995: Tiller production and survival in relation to grain yield in winter and spring barley. Field Crops Res. 44, 85–93.

Gautam, P., A. K. Nayak, B. Lal, P. Bhattacharyya, R. Tripathi, M. Shahid, S. Mohanty, R. Raja, and B. B. Panda, 2014: Submergence tolerance in relation to application time of nitrogen and phosphorus in rice (*Oryza sativa* L.). Environ. Exp. Bot. 99, 159–166.

Guarda, G., S. Padovan, and G. Delogu, 2004: Grain yield, nitrogen-use efficiency and baking quality of old and modern Italian bread-wheat cultivars grown at different nitrogen levels. Eur. J. Agron. 21, 181–192.

Hall, A. J., R. Savin, and G. A. Slafer, 2014: Is time to flowering in wheat and barley influenced by nitrogen?: A critical appraisal of recent published reports. Eur. J. Agron. 54, 40–46.

Haun, J. R., 1973: Visual quantification of wheat development. Agron. J. 65, 116–119.

Hay, R. K. M., and E. J. M. Kirby, 1991: Convergence and synchrony – a review of the coordination of development in wheat. Aust. J. Agric. Res. 42, 661–700.

INASE, 2014: Red de ensayos comparativos de variedades de trigo. http://www.inase.gov.ar/index.php?option=com_content&view=article&id=102&Itemid=91 [last accessed 15 September 2014].

INTA, 2013: Red de evaluación de cultivares de trigo pan. http://inta.gob.ar/documentos/red-de-evaluacion-de-cultivares-de-trigo-pan [last accessed 15 September 2014].

IPCC, 2014: Summary for policymakers. In: C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, and L. L. White, eds. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, pp. 1–32. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Ishag, H. M., B. A. Mohamed, and K. H. M. Ishag, 1998: Leaf development of spring wheat cultivars in an irrigated heat-stressed environment. Field Crops Res. 58, 167–175.

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Kernich, G. C., G. A. Slafer, and G. M. Halloran, 1995: Barley development as affected by rate of change of photoperiod. J. Agric. Sci. 124, 379–388.

Kirby, E. J. M., and T. J. Riggs, 1978: Developmental consequences of two-row and six-row ear type in spring barley: 2. Shoot apex, leaf and tiller development. J. Agric. Sci. 91, 207–216.

Kirby, E. J. M., M. Appleyard, and G. Fellowes, 1985: Leaf emergence and tillering in barley and wheat. Agronomie 5, 193–200.

Longnecker, N., E. J. M. Kirby, and A. Robson, 1993: Leaf Emergence, Tiller Growth, and Apical Development of Nitrogen-Deficient Spring Wheat. Crop Science Society of America, Madison, WI, USA, ETATS-UNIS.

Malik, A. I., T. D. Colmer, H. Lambers, and M. Schortemeyer, 2001: Changes in physiological and morphological traits of roots and shoots of wheat in response to different depths of waterlogging. Aust. J. Plant Physiol. 28, 1121–1131.

Malik, A. I., T. D. Colmer, H. Lambers, T. L. Setter, and M. Schortemeyer, 2002: Short-term waterlogging has long-term effects on the growth and physiology of wheat. New Phytol. 153, 225–236.

Marti, J., R. Savin, and G. A. Slafer, 2015: Wheat yield as affected by length of exposure to waterlogging during stem elongation. J. Agron. Crop Sci., in press DOI: 10.1111/jac.12118.

Motulsky, H., and A. Christopoulos, 2003: Fitting Models to Biological Data Using Linear and Non Linear Regression. A Practical Guide to Curve Fitting. GraphPad Software Inc., San Diego, CA, USA.

Musgrave, M. E., 1994: Waterlogging effects on yield and photosynthesis in eight winter wheat cultivars. Crop Sci. 34, 1314–1318.

Pang, J., M. Zhou, N. Mendham, and S. Shabala, 2004: Growth and physiological responses of six barley genotypes to waterlogging and subsequent recovery. Aust. J. Agric. Res. 55, 895–906.

Prystupa, P., G. A. Slafer, and R. Savin, 2003: Leaf appearance, tillering and their coordination in response to NxP fertilization in barley. Plant Soil 255, 587–594.

Reussi Calvo, N. I., and H. E. Echeverria, 2006: Estrategias de fertilización nitrogenada en trigo: balance hídrico para el sur bonaerense. Ci Suelo 24, 115–122.

Robertson, D., H. Zhang, J. A. Palta, T. Colmer, and N. C. Turner, 2009: Waterlogging affects the growth, development of tillers, and yield of wheat through a severe, but transient, N deficiency. Crop Pasture Sci. 60, 578–586.

Rodríguez, D., M. C. Pomar, and J. Goudriaan, 1998: Leaf primordia initiation, leaf emergence and tillering in wheat (*Triticum aestivum* L.) grown under low-phosphorus conditions. Plant Soil 202, 149–157.

Salvagiotti, F., and D. J. Miralles, 2007: Wheat development as affected by nitrogen and sulfur nutrition. Aust. J. Agric. Res. 58, 39–45.

Samad, A., C. A. Meisner, M. Saifuzzaman, and M. Van Ginkel, 2001: Waterlogging tolerance. In: M. P. Reynolds, J. I. Ortiz-Monasterio, and A. McNab, eds. Application of Physiology in Wheat Breeding, pp. 135–144. CIMMYT, Mexico City, Mexico.

de San Celedonio, R. P., J. R. Micheloud, G. L. Abeledo, D. J. Miralles, and G. A. Slafer, 2014a: Riesgo de anegamiento en trigo (*Tritucum aestivum* L.) para distintas localidades de la región triguera argentina. Ciencia Suelo 32, 233–246.

de San Celedonio, R. P., L. G. Abeledo, and D. J. Miralles, 2014b: Identifying the critical period for waterlogging on yield and its components in wheat and barley. Plant Soil 378, 265–277.

Sayre, K., M. Van Ginkel, S. Rajaram, and I. Ortiz-Monasterio, 1994: Tolerance to waterlogging losses in spring bread wheat: effect of time of onset on expression. Annu Wheat Newsl 40, 165–171.

Setter, T. L., and I. Waters, 2003: Review of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats. Plant Soil 253, 1–34.

Shaw, R. E., W. S. Meyer, A. McNeill, and S. D. Tyerman, 2013: Waterlogging in Australian agricultural landscapes: a review of plant responses and crop models. Crop Pasture Sci. 64, 549–562.

Slafer, G. A., and H. M. Rawson, 1994: Sensitivity of wheat phasic development to major environmental factors: a re-examination of some assumptions made by physiologists and modellers. Aust. J. Plant Physiol. 21, 393–426.

Stuerz, S., A. Sow, B. Muller, B. Manneh, and F. Asch, 2014: Leaf area development in response to meristem temperature and irrigation system in lowland rice. Field Crops Res. 163, 74–80.

Trenberth, K. E., P. D. Jones, P. Ambenje, R. Bojariu, D. Easterling, A. Klein Tank, D. Parker, F. Rahimzadeh, J. A. Renwick, M. Rusticucci, B. Soden, and P. Zhai, 2007: Observations: surface and atmospheric climate change. In: S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, eds. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Valle, S. R., and D. F. Calderini, 2010: Phyllochron and tillering of wheat in response to soil aluminum toxicity and phosphorus deficiency. Crop Pasture Sci. 61, 863–872.

Van Ginkel, M., K. Sayre, and G. Boru, 1997: La tolerancia al anegamiento en el trigo: problemas relacionados con el fitomejoramiento. In: M. Mohan Kohli, and D. L. Martino, eds. Explorando Altos Rendimientos en Trigo, pp. 193–208. CIMMYT, INIA, Colonia, Uruguay.

Wollenweber, B., J. R. Porter, and J. Schellberg, 2003: Lack of interaction between extreme high-temperature events at vegetative and reproductive growth stages in wheat. J. Agron. Crop Sci. 189, 142–150.

Zadoks, J. C., T. T. Chang, and C. F. Konzak, 1974: A decimal code for the growth stages of cereals. Weed Res. (Oxf.) 14, 415–421.

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