Field Crops Research 203 (2017) 94–105

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Strategies for yield determination of bread wheat and two-row barley growing under different environments: A comparative study

Santiago Alvarez Prado[a,c,*], José M. Gallardo[a], Betina C. Kruk[a], Daniel J. Miralles[a,b]

[a] Cátedra de Cerealicultura, Departamento de Producción Vegetal, Universidad de Buenos Aires, Av San Martín 4453 (C 1417 DSE), Ciudad de Buenos Aires, Argentina
[b] IFEVA and CONICET, Av San Martín 4453 (C 1417 DSE), Ciudad de Buenos Aires, Argentina
[c] Present address: INRA, Unité Mixte de Recherche 759 Laboratoire d'Ecophysiologie des Plantes sous Stress Environnementaux (LEPSE), F-34060 Montpellier, France

ARTICLE INFO

Article history:
Received 4 August 2016
Received in revised form
18 December 2016
Accepted 19 December 2016

Keywords:
Numerical components
Biomass accumulation
Yield strategies
Environments
Night temperature

ABSTRACT

Grain yield variations in bread wheat and two-row barley are better explained by changes in grain number (GN) than mean grain weight. However, the strategies for building GN are different in both species because in two-row barley the variations in GN are more frequently related to the number of spikes m^{-2}, due to its higher tillering capacity than wheat, whereas in bread wheat both grain number $spike^{-1}$ and the number of spikes m^{-2} contribute to the establishment of GN. The higher tillering capacity and leaf area index at the beginning of the crop cycle in two-row barley allows a higher radiation accumulation than in bread wheat. We hypothesize that the higher early vigor of two-row barley, associated with its greater leaf area exposure relative to wheat, represents an initial advantage that is capitalized at the end of the cycle as higher biomass accumulation driven by a larger GN and consequently higher grain yield. The main objective of this work was to compare different physiological traits of bread wheat and two-row barley growing together under different temperature and radiation conditions. We evaluated two genotypes of each species, with similar phenology, growing under four different environments without water or nutritional deficiencies. Numerical yield components, biomass, radiation interception and harvest index were measured. Despite no differences being observed between genotypes of bread wheat and two-row barley in terms of total grain yield and total grain number when exposed to different environments, each species had a different strategy for establishing the final yield. Although two-row barley showed initial advantages in radiation interception, bread wheat genotypes accumulated more intercepted photosynthetic active radiation (iPAR) and used it in a more efficient way than two-row barley, thus allowing a higher biomass accumulation. Both species showed a reduction in grain weight due to increases in mean night and high temperatures. Grain weight reductions were higher in bread wheat than in two-row barley, and were directly associated with shortening of the duration of grain filling without consequences for the grain-filling rate. This suggested a direct effect of temperature on grain development rather than a growth limitation due to a lack of source.

1. Introduction

Different methods have been developed for analyzing yield determination in grain crops (Tardieu, 2013). One of the most common approaches is numerical component analysis, which expresses yield by a multiplicative series of yield components. In this approach, yield is the product of grain number (GN) per unit area and mean grain weight. Generally, grain yield variations in wheat and barley are better explained by changes in GN than changes in mean grain weight (Calderini et al., 1999a; Arisnabarreta and Miralles, 2008; Slafer et al., 2014 and reference herein). In barley, variations in GN in response to the environment are more frequently related to the number of spikes m^{-2} than to the number of grains $spike^{-1}$, especially in two-row barley, which is usually more stable due to a lower plasticity relative to wheat (Abeledo et al., 2003; García del Moral et al., 2003; Arisnabarreta and Miralles, 2008; Peltonen-Sainio et al., 2009). In general, two-rowed barley cultivars clearly possess a greater ability to establish fertile tillers than six-rowed barley cultivars (Kirby and Riggs, 1978; Le Gouis et al., 1999; Peltonen-Sainio et al., 2009), which have greater spike

* Corresponding author at: INRA, Unité Mixte de Recherche 759 Laboratoire d'Ecophysiologie des Plantes sous Stress Environnementaux (LEPSE), F–34060 Montpellier, France.
E-mail addresses: santiago.alvarez-prado@supagro.inra.fr, saprado@unr.edu.ar (S. Alvarez Prado).

http://dx.doi.org/10.1016/j.fcr.2016.12.013
0378-4290/

plasticity when establishing grains per spike and therefore different strategies are required to establish yield in both barely spike types (Arisnabarreta and Miralles, 2006). On the other hand, GN in bread wheat is strongly related to the combination of both grain number spike^{-1} and the number of spikes m^{-2} (Peltonen-Sainio et al., 2009; Alzueta et al., 2012) with a reduced tillering capacity compared to two-row barley (Peltonen-Sainio et al., 2009).

Comparisons of bread wheat and two-row barley growing under contrasting environments (*e.g.* different types of stresses and/or crop management practices) indicated differences in GN m^{-2} between the two species (Prystupa et al., 2004; Alzueta et al., 2012; Marti and Slafer, 2014; Arisnabarreta and Miralles, 2015). For instance, longer days, which are typical at high latitudes or in late sowings, are known to depress tillering, due to a shortening of the vegetative period under inductive photoperiods (Kirby et al., 1985; Peltonen-Sainio et al., 2009). Despite this negative effect, two-row barley outperforms bread wheat under these conditions with its relatively high tillering capacity and survival, which determines a greater number of fertile spikes and consequently more GN m^{-2} than bread wheat (Peltonen-Sainio et al., 2009). Different sowing dates modify the cycle length and therefore the amount of solar radiation that is captured by the crops. For instance, late sowings with shorter cycles (associated with higher temperatures and longer photoperiod) reduce the spike growth period, diminishing the cumulative radiation during that phase, affecting the number spikes m^{-2} and yield negatively (Alzueta et al., 2012; Alzueta et al., 2014).

Within the numerical component method, grain weight usually has less impact than GN m^{-2} for yield determination (Peltonen-Sainio et al., 2007). However, the stability of two-row barley grain weight has great significance for the malting industry, as penalties apply if grains have a smaller size than industrial requirements. Grain weight reductions in bread wheat and two-row barley are commonly observed under water stresses and high temperatures during pre-anthesis (Wardlaw and Wrigley, 1994; Calderini et al., 1999b; Ugarte et al., 2007) as well as during the grain-filling period (Albrizio et al., 2010). Grain weight reductions due to increases in temperature are commonly explained by shortening of the duration of grain filling (Savin and Nicolas, 1996; Savin et al., 1997). Hence, although two-row barley outperforms bread wheat under inductive photoperiods, non-suitable grain-filling conditions negatively affect grain weight, reducing grain quality below the standards required by the industry (Savin and Nicolas, 1996).

Other methods commonly used to analyze yield determination in grain crops consider functional relationships regulated by the environment. Grain yield is considered as a function of incident light, the fraction of light intercepted by the crop, the efficiency of the conversion of light into biomass, i.e. radiation-use efficiency (RUE) (Monteith, 1977), and the fraction of accumulated biomass across the crop cycle that is transferred to harvested grains, i.e. harvest index (Donald and Hamblin, 1976). During the 20th century, harvest index was one of the main determinants of yield improvement in bread wheat (Calderini et al., 1995; Hay, 1995). In two-row barley this trend has been less clear and has varied among different countries (Hay, 1995; Abeledo et al., 2003).

Radiation interception by the crop can be further described in terms of the total amount of incident radiation and the fraction of it that is intercepted by the canopy. Delays in sowing dates normally reduce the length of the crop cycle due the exposure to higher temperatures and more inductive photoperiods than in early sowings, limiting the cumulative intercepted radiation by the crops and thereby reducing yield (Kirby et al., 1985). During the early stages of the crop cycle, two-row barley accumulates higher amounts of intercepted photosynthetic active radiation (iPAR) than bread wheat (López-Castañeda et al., 1995; Sieling et al., 2016) due to its stronger early vigor, which is reflected in a larger leaf area that is associated with a greater interception of radiation early in the season. Regarding RUE, values ranging from 1.46 to 2.93 g MJ^{-1} and 1.79 to 2.33 g MJ^{-1} have been reported for bread wheat and two-row barley, respectively (Gregory et al., 1992; Muurinen and Peltonen-Sainio, 2006). Similarities in RUE suggest that differences in grain yield between species should be associated with the amount of intercepted radiation.

We hypothesize that in comparison to wheat the higher early vigor of two-row barley (associated with higher leaf area index and tiller capacity than wheat) represents an initial advantage that at the end of the crop cycle manifests as higher biomass accumulation driven by a larger grain number and consequently higher grain yield when both species are grown in the same environmental conditions. Regarding the numerical yield components, higher tillering capacity in barley determines more fertile spikes m^{-2} and thereby higher GN m^{-2} compared to wheat. This advantage will persist under late sowings where higher temperature and radiation shorten the phenological stages depressing tillering capacity, negatively affecting fertile florets spike^{-1} and consequently reducing grain yield in both species. The main objective of this work was to compare physiological strategies for yield determination of wheat and barley growing together under different temperature and radiation conditions (given by different sowing dates and growing seasons).

2. Materials and methods

2.1. General description

Field experiments were carried out during two consecutive growing seasons (2007 and 2008) in the experimental fields of the Department of Plant Production, Faculty of Agronomy, University of Buenos Aires, Argentina (34°35′S, 58°29′W). The soil was a silty clay loam, classified as Vertic Argiudoll. Within each growing season, treatments were a combination of two genotypes of bread wheat (Chaja and Cronox) and two genotypes of two-row barley (Ayelen and Scarlett) sown simultaneously at two contrasting sowing dates (early and late sowings), arranged in a split-plot design with three replicates. Sowing dates were assigned to main plots, and genotypes to sub-plots. Both species were hand-sown on 21 May and 23 July in 2007 and 6 June and 13 August in 2008 at a density of 330 seeds m^{-2}. As both wheat and barley crops experienced different climatic conditions throughout the crop cycle we considered each combination of sowing date by growing season as an environment. Each plot corresponding to the genotypes (sub-plots) consisted of 7 rows 15 cm apart and 2 m long.

In the present work, we focus on the genotypes of wheat (Klein Chaja and Cronox) and two-row barley (Quilmes Ayelen and Scarlett) most commonly used by farmers in Argentina in the period when the experiments were conducted and with similar cycle lengths. The latter characteristic allows comparison of sowing dates without a strong influence due to changes in phenology. From this point forward, the wheat and barley cultivars will be referred to as "wheat" and "barley" throughout the text.

All the experiments were irrigated throughout the growing season to avoid water stress, and fertilized with mono-ammonium phosphate at sowing (100 kg ha^{-1}) and with urea (150 kg ha^{-1}) split at two different times: i) Z2.0 (Zadoks et al., 1974): beginning of tillering (75 kg ha^{-1}) and ii) Z3.0: first node detectable in main stems (75 kg ha^{-1}). Pests and diseases were prevented or controlled by spraying recommended fungicides and insecticides, and weeds were periodically removed by hand. To prevent lodging, structures with nets were installed from tillering to maturity in the plots.

2.2. Sampling, measurements and estimations

2.2.1. Numerical components model

At anthesis, defined as 50% of the spikes from each plot showing anthers, five spikes from both main stems and tillers of each plot were sampled and the number of fertile florets was determined as indicated in the scale of Waddington et al. (1983).

To determine the maximum water content in grains, three spikes per experimental unit were sampled two or three times a week from flowering to after commercial maturity, immediately enclosed in a hermetic plastic bag, and transported to the laboratory. Proximal grains from central spikelets in wheat and grains from central spikelets in barley were separated from the spikes in a humidified box to prevent moisture loses during sampling. Fresh weight was determined immediately and dry weight was measured after drying the grains in a forced-air oven at 70 °C for at least 72 h.

Water content was calculated as the difference between grain fresh weight (F_W) and grain dry weight (D_W). A tri-linear model was fitted for the relationship between water content and thermal time:

$$W_C = a + bx, \quad if\, x \leq c; \tag{1}$$

$$W_C = a + bc, \quad if\, x > c < e; \tag{2}$$

$$W_C = a + bc + d(x\text{-}e)x, \quad if\, x \geq e \tag{3}$$

where x is thermal time, W_C is water content, a the Y-intercept, b the water accumulation rate (mg [°Cd]$^{-1}$), c the beginning of the hydric plateau (°Cd), d the water loss rate (mg [°Cd]$^{-1}$) and e the end of the hydric plateau (°Cd). The value of water content during the hydric plateau was considered as the maximum water content (For details see Alvarez Prado et al., 2013).

During the grain-filling period the rate and duration of grain filling were determined over 4 grains located at central positions of the spike for both species by fitting a bi-linear model to the grain dry weight against the number of days after flowering:

$$GW = a + b\text{DAF}, \quad \text{for DAF} <= c \tag{4}$$

$$GW = a + bc, \quad \text{for DAF} > c \tag{5}$$

where GW is grain weight, DAF is days after flowering, a the Y-intercept (mg), b the grain-filling rate (mg day^{-1}) and c the total grain-filling duration (days). The bi-linear model was fitted to the grain dry weight data using the iterative optimization technique in GraphPad Prism version 5 (Raduschev, 2007).

At physiological maturity, identified as the moment when grains reach their maximum dry weight (Alvarez Prado et al., 2013), the central row of each plot was harvested to determine grain yield and its main components: grain number and grain weight. Grain yield was determined individually for main stems and tillers and was obtained from the product between grain number and grain weight. Mean grain weight was obtained from the sum of main stem and tillers weighted by their contribution to total grain yield. Main stems and tillers were separated and counted to obtain the spikes m^{-2} for each fraction of the plant (i.e. main stems and tillers). Grains spike^{-1} was estimated as the ratio between the grain number and spike number per unit area. The number of spikelets per spike was obtained from five randomly chosen spikes from both main stem and tillers. Grain set was estimated as the ratio between grains spike^{-1} and fertile florets spike^{-1}.

2.2.2. Biomass accumulation and allocation model

The biomass growth and allocation model was used to dissect the physiological mechanisms behind yield determination across environments. Thus, grain yield was considered as the product of aboveground biomass (AGB) at physiological maturity and harvest index. As mentioned for the yield component model, at physiological maturity the central row of each plot was harvested and aboveground biomass was determined after drying samples for at least 72 h at 60 °C. Harvest index (HI) was determined as the ratio between grain yield and aboveground biomass.

Radiation interception was measured during the whole cycle with a one meter linear ceptometer (Cava Rad®, Cavadevises Co., Buenos Aires, Argentina). Measurements were made during sunny days between 12:00 and 13:00 h in the central row of each plot by determining the incident solar radiation immediately above the canopy and transmitted radiation at the base of the crop (on soil surface) by placing the sensor in three positions along the central row (left, center and right positions) and considering an average for the three measurements for each plot (repetition). A polynomial adjustment was made to the fraction of intercepted radiation (measured on a number of several days) during the crop cycle. Daily intercepted photosynthetic active radiation (iPAR) was calculated as the product of the daily fraction of intercepted radiation and the daily incident solar radiation obtained from meteorological station, multiplied by 0.48 (Szeicz, 1974). Radiation use efficiency was calculated as the ratio between aboveground biomass at physiological maturity and accumulated iPAR during the crop cycle.

2.2.3. Meteorological data

Meteorological data (air temperature, photosynthetically active radiation and relative humidity) were recorded every hour throughout the crop cycle by an automatic meteorological station (Davis Vantage Pro2, USA) placed 20 m from the experimental fields. The vapor pressure deficit (VPD, kPa) was estimated as the difference between the actual vapor pressure (e_a, kPa) and the saturated vapor pressure (e_s, kPa) for the day i following the Clausius-Clayperon equation:

$$e_{s(i)} = \exp\left(19.0177 - \left(5327 * \left((Tm_{(i)} + 273)^{-1}\right)\right)\right) \tag{6}$$

where $Tm_{(i)}$ is the mean temperature of the day (i) (°C).

$$e_{a(i)} = e_{s(i)} * HR_{(i)} * 100^{-1} \tag{7}$$

where $HR_{(i)}$ is the mean daily relative humidity (%).

During the grain-filling period, temperatures equal to or higher than 30 °C were considered as "moderately high temperatures" and were recorded as the number of hours above 30 °C for each genotype by repetition combination to calculate a "heat stress index".

2.3. Statistical analysis

As was described above, treatments were arranged in a split-plot design, with environments assigned to main-plots and genotypes to sub-plots. Under the variant of split-plot design, linear mixed models were used to test trait variability. The linear model fitted to each of the traits comprises a blocking structure including the effect of the block within each environment, and a treatment structure. In order to compare species, a "Species" factor was added to the analysis. In a global analysis, species and genotypes nested within species were considered as fixed effects. Environment, block within environment and all possible interactions were considered as random effects. Residual variation was dissected into different random sources of variation for testing fixed effect (Gomez and Gomez, 1984). Then, a second analysis by environment was performed where genotypes were considered as a fixed effect and blocks as random effects. Mixed models were performed using the R package, *AsremL*, and differences between means within environments were assessed through Duncan's test using the R package, *agricolae* (R Core Team, 2014).

To assess trait associations by considering variations in both "x" and "y" variables we used model II linear regressions (Ludbrook,

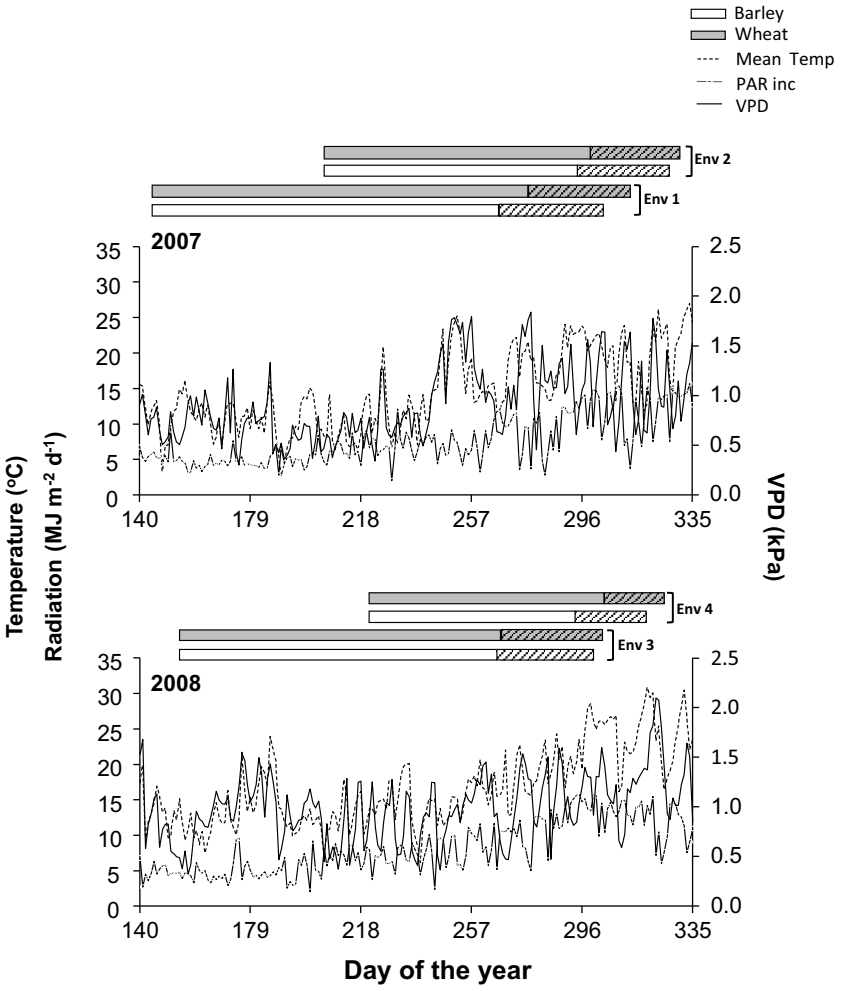

Fig. 1. Meteorological conditions during the crop cycle in all sowing dates. Values are daily mean temperature, daily photosynthetic incident solar radiation, and air vapor pressure deficit (VPD). Bars on each graph represent the average cycle length of bread wheat (gray bars) and two-row barley (white bars). Each bar is divided into sowing-anthesis (plain bar) and anthesis-physiological maturity (striped bar).

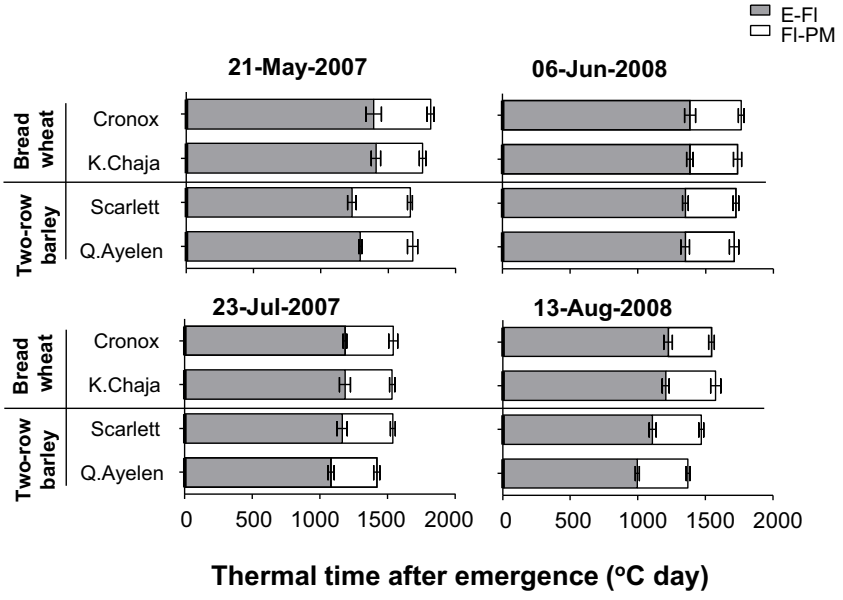

Fig. 2. Duration of developmental phases in bread wheat and two-row barley sown in four different environments. Filled and empty bars represent the duration of the phases from emergence to flowering (E-Fl) and flowering to physiological maturity (Fl-PM), respectively. Horizontal bars at the end of each phase indicate the standard error.

2012). Correlation analysis was used for testing trait correlation in both species. Slope tests were performed in order to compare species for different trait correlations using GraphPad Prism (Raduschev, 2007).

3. Results

3.1. Weather conditions

Mean temperature, total incident solar radiation and vapor pressure deficit (VPD) during the periods from sowing to flowering and flowering to physiological maturity are shown in Fig. 1. Average air temperature from sowing to physiological maturity varied across sowing dates from 14 to 19 °C, with it being higher in later sowings (Environment 2 and 4; Fig. 1). These differences between earlier (Environment 1 and 3) and later sowings were consistent during the phenological phases of sowing-flowering (12–17 °C) and flowering-physiological maturity (19–24 °C).

As expected, global radiation followed a similar pattern to temperature, with it being higher in later sowings than earlier sowings (Fig. 1). Global radiation for the whole crop cycle ranged from 7.0 to 10.4 MJ m^{-2} d^{-1}. Average radiation was 32% lower in environment 1 compared to environment 4. Regarding the evaporative demand, air vapor pressure deficit (VPD) increased from 0.89 to 1.04 kPa as the sowing was delayed (Fig. 1). Differences between environments were slightly higher for pre-anthesis stages (16%) than during the grain-filling period (13%).

3.2. Phenology

On average, the duration of the bread wheat cycle up to physiological maturity (1658 ± 105 °Cd; 144 days) was slightly longer than the two-row barley cycle (1572 ± 124 °Cd; 139 days; $p < 0.05$). Differences in the crop cycle duration between species were related to differences in the duration of the pre-anthesis phase (Alvarez Prado et al., 2013), which on average was five days longer in bread wheat than in two-row barley ($p < 0.05$; Fig. 2). The period from Emergence to Flowering also varied according to the environment, being longer in earlier sowings than later sowings ($p < 0.05$; Fig. 2). Differences in grain-filling duration were more important between environments (243 °Cd) than between species (86 °Cd) ($p > 0.05$; Fig. 2).

3.3. Grain yield: numerical components model

Total grain yield varied from c.a. 360–700 g m^{-2}, showing no significant differences between bread wheat and two-row barley ($p > 0.05$; Table 1). Yield variability across environments ranged from 10 to 45% ($p < 0.01$) and no genotype x environment interaction was observed (Table 1). Final grain yield was dissected into main stems and tiller performance in order to evaluate different plant fraction contributions. The general tendency in two-row barley yield was for a more than 50% tiller contribution, while bread wheat genotypes differed in their plant fraction contribution with the tiller contribution being between 28 and 50% (Table 1). The yields of both main stems and tillers differed between species ($p < 0.05$; Table 1). Bread wheat showed a higher main stem yield than two-row barley ($p < 0.05$) in all cases, with the exception of environment 4 where both species had similar levels (Table 1). On the other hand, two-row barley's tiller yield was higher than in bread wheat ($p < 0.05$), with the differences being higher under early sowings (environments 1 and 3; Table 1).

Over all sources of variation, the yield of both bread wheat and two-row barley was positively associated with GN m^{-2} (Fig. 3A). No association was found between GN m^{-2} and mean grain weight ($p > 0.05$; Fig. 3B), and as a consequence no relationship was found between yield and mean grain weight (Fig. 3C). No differences between species were observed for total GN (Table 1), which was explained by a significant variability in tillers and main stems ($p < 0.05$) that compensated total GN (Table 1). The environmental effect on both yield and GN was practically the same (Table 1).

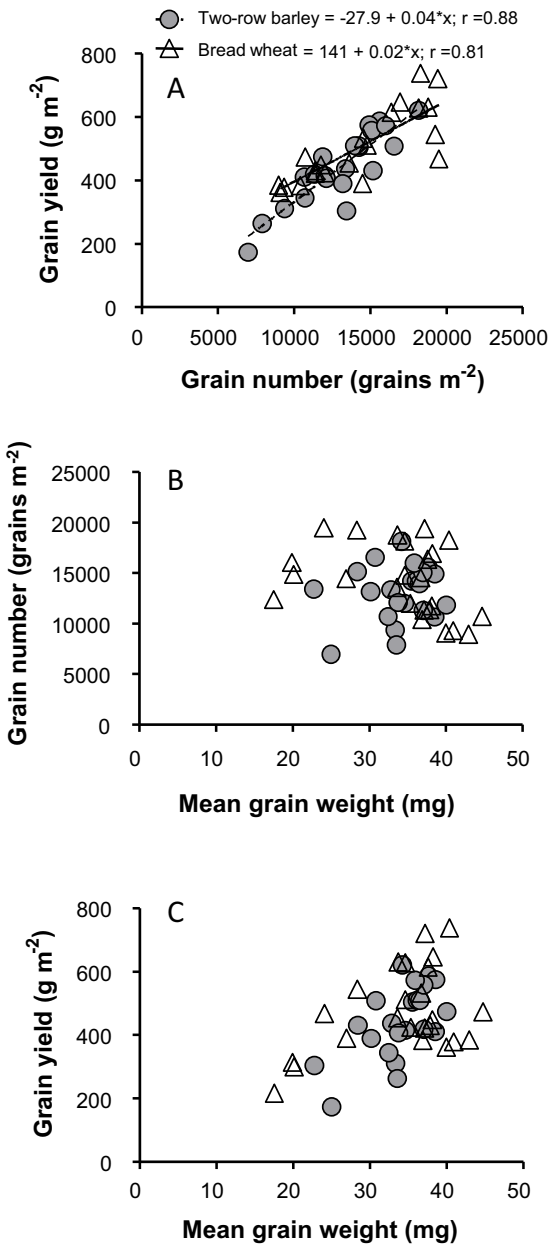

Fig. 3. Relationship between grain yield (A) and grain number m^{-2}, mean grain weight and grain number m^{-2} (B) and grain yield and mean grain weight (C) in bread wheat (open triangles) and two-row barley (closed circles).

As mentioned above, under the late sowing date of 2008 a strong reduction in the mean grain weight was evident with average values of 23 and 28 mg $grain^{-1}$ for bread wheat and two-row barley, respectively, and consequently the final grain yield was reduced (Fig. 3C). Mean grain weight reductions were mainly explained by temperature increases due to delays in the sowing date. In this sense, grain weight was negatively associated with the number of hours above 30 °C (Fig. 4A; $p < 0.0001$; $r = -0.83$ and -0.81 for two-row barley and bread wheat, respectively), and also with increases in minimum ($p < 0.0001$; $r = -0.76$ and -0.86 for two-row barley and bread wheat, respectively), daily mean ($p < 0.0001$;

Table 1
Grain yield, grain number and 1000 grain weight from main stems, tillers and total of wheat (K. Chaja and Cronox) and barley (Q. Ayelen and Scarlett) under four different environments. Relative contribution of main stems and tiller are listed between brackets. Species mean values, mean squares of each factor from the split-plot analysis and its significance are listed at the end of the table. Letters comparing genotypes within each environment reflect mean comparison through Duncan test.

Env	Specie	Genotype	Grain yield (gr m^{-2})			Grain number ($grains\ m^{-2}$)			1000 grain weight (gr)		
			MS	Tillers	Total	MS	Tillers	Total	MS	Tillers	Total
1	Barley	Q.Ayelen	175.4 (39%)^{b}	269.2 (61%)^{a}	444.6^{ab}	4545 (38%)^{b}	7530 (62%)^{a}	12076^{ab}	38.5^{a}	36.1^{a}	37.0^{a}
		Scarlett	218.7 (39%)^{ab}	338.3 (61%)^{a}	557.0^{a}	5921 (40%)^{ab}	8898 (60%)^{a}	14818^{a}	36.9^{a}	38.0^{a}	37.6^{a}
	Wheat	K.Chaja	268.4 (65%)^{a}	144.2 (35%)^{b}	412.6^{b}	7165 (64%)^{a}	4099 (36%)^{b}	11263^{b}	37.4^{a}	35.2^{a}	36.7^{a}
		Cronox	251.2 (47%)^{a}	281.0 (53%)^{a}	532.2^{a}	6819 (48%)^{a}	7400 (52%)^{a}	14219^{ab}	37.0^{a}	38.0^{a}	37.5^{a}
2	Barley	Q.Ayelen	212.1 (51%)^{c}	199.8 (49%)^{a}	411.9^{a}	5700 (48%)^{b}	6165 (52%)^{a}	11865^{ab}	37.0^{ab}	32.3^{a}	34.7^{b}
		Scarlett	203.9 (55%)^{c}	165.2 (45%)^{ab}	369.1^{a}	5782 (52%)^{b}	5337 (48%)^{a}	11119^{ab}	35.3^{b}	30.8^{a}	33.4^{b}
	Wheat	K.Chaja	373.1 (88%)^{a}	52.0 (12%)^{b}	425.1^{a}	8971 (86%)^{a}	1499 (14%)^{b}	10470^{b}	41.8^{a}	33.7^{a}	40.9^{a}
		Cronox	280.1 (53%)^{b}	252.3 (47%)^{a}	532.4^{a}	7906 (50%)^{a}	7816 (50%)^{a}	15721^{a}	35.4^{b}	32.2^{a}	34.0^{b}
3	Barley	Q.Ayelen	238.6 (44%)^{c}	308.8 (56%)^{ab}	547.4^{a}	6316 (42%)^{c}	8680 (58%)^{ab}	14996^{a}	40.2^{a}	33.2^{a}	37.5^{a}
		Scarlett	275.2 (49%)^{bc}	290.1 (51%)^{a}	565.4^{a}	7297 (47%)^{bc}	8231 (53%)^{a}	15529^{a}	36.0^{a}	34.5^{a}	35.2^{a}
	Wheat	K.Chaja	479.5 (81%)^{a}	110.5 (19%)^{b}	590.0^{a}	11834 (80%)^{a}	2892 (20%)^{b}	14726^{a}	40.9^{a}	37.6^{a}	40.5^{a}
		Cronox	339.6 (60%)^{ab}	231.0 (40%)^{a}	570.6^{a}	9052 (58%)^{ab}	6490 (42%)^{a}	15541^{a}	37.6^{a}	36.6^{a}	37.8^{a}
4	Barley	Q.Ayelen	165.1 (46%)^{a}	194.4 (54%)^{a}	359.5^{a}	5710 (44%)^{b}	7383 (56%)^{a}	13094^{a}	29.6^{a}	26.1^{a}	27.9^{a}
		Scarlett	167.7 (47%)^{a}	189.4 (53%)^{a}	357.1^{a}	5320 (44%)^{b}	6909 (56%)^{a}	12229^{a}	31.2^{a}	26.0^{a}	28.6^{a}
	Wheat	K.Chaja	235.3 (55%)^{a}	193.7 (45%)^{a}	429.0^{a}	8608 (56%)^{a}	6847 (44%)^{a}	15455^{a}	23.5^{a}	21.9^{a}	22.8^{a}
		Cronox	178.3 (41%)^{a}	251.5 (59%)^{a}	429.8^{a}	6578 (39%)^{ab}	9644 (58%)^{a}	16734^{a}	24.4^{a}	21.8^{a}	25.1^{a}
		Barley mean	202.2 (46%)	239.0 (54%)	441.2	5712.6 (44%)	7305.1 (56%)	13071.7	35.6	32.1	34.0
		Wheat mean	300.7 (61%)	189.5 (39%)	490.2	8366.7 (59%)	5836.0 (41%)	14266.7	34.8	32.1	34.3
		Sp	*81260****	*40904***	*6926*	*70397177****	*21465558**	*14116620*	*8.5*	*0.003*	*0.1*
		Gen(Sp)	*16571****	*51929****	*11763*	*7867299***	*51212652****	*20351163*	*22.2*	*1.2*	*17.8*
		Env	*57853****	*18612**	*81885****	*16978642****	*14894623**	*18558555*	*275.6****	*289.2****	*289.1****
		*Env*Sp*	*9859***	*8814*	*11763*	*1798481*	*13291098**	*10164746*	*46.7***	*30.5**	*47.6****

ns: not significant, $p > 0.05$.
* Significant for $p < 0.05$.
** Significant for $p < 0.01$.
*** Significant for $p < 0.001$.

r = −0.76 and −0.81 for two-row barley and bread wheat, respectively) and mean night temperatures (Fig. 4B; $p < 0.0001$; r = −0.81 and −0.89 for two-row barley and bread wheat, respectively) during the grain-filling period. The rate of reduction in mean grain weight per degree of increase in night temperature (determined by the slope of the regression) was higher in bread wheat than in two-row barley ($p < 0.05$ for the slope test; Fig. 4B) without genotypic differences within each species ($p > 0.05$). Reductions in mean grain weight due to increases in both the number of hours above 30 °C and mean night temperature were mostly associated with shortening of the duration of grain filling, which had a similar rate of reduction in both bread wheat and two-row barley (Fig. 4C and D, respectively), while no effect was observed on the grain-filling rate (Fig. 4E and F, respectively). High temperatures (number of hours above 30 °C) also impacted on the maximum water content of both species (Fig. 5). Despite the high temperature effect being evident under the latest sowing date in both species, wheat genotypes experienced hotter environments than two-row barley (Fig. 5).

3.3.1. Grain number sub-component model

No significant differences ($p > 0.05$) were observed in total GN m^{-2} between bread wheat and two-row barley across environments. When the contributions of main stems and tillers to final GN m^{-2} were compared, significant differences ($p < 0.05$) were observed in the main stem contribution with 8367 ± 1798 and 5713 ± 819 grains m^{-2} for bread wheat and two-row barley, respectively; representing contributions to the total GN of 58 and 44% (Table 2). Also, significant differences between species were observed for GN m^{-2} from tillers ($p < 0.05$; 5836 ± 3055 and 7305 ± 1347 grains m^{-2} for bread wheat and two-row barley, respectively) across the experienced environments, with a relative contribution to total GN m^{-2} of 42 and 56% in bread wheat and two-row barley, respectively (Table 2).

When dissecting GN m^{-2} into its numerical components, differences between species ($p < 0.05$) were observed for all evaluated traits except for grain set, which was on average 0.60 ± 0.03 and 0.65 ± 0.11 for two-row barley and bread wheat, respectively (Table 2). Variations in GN m^{-2} were positively correlated with changes in the number of spikes m^{-2}, the number of spikelets per spike and the number of grains $spike^{-1}$ in two-row barley and with the number of spikes m^{-2} and the number of spikelets per spike in bread wheat (Table 3). Two-row barley produced 34% more spikes m^{-2} ($p < 0.01$) than bread wheat and those differences were related to the number of tiller spikes m^{-2}, which was 60% higher in two-row barley than in bread wheat (Table 3). Regarding grains $spike^{-1}$, differences between species were observed in all plant fractions ($p < 0.05$) with bread wheat showing c.a. 50 and 40% higher number of grains $spike^{-1}$ than two-row barley for main stems and tillers, respectively (Table 2). The lack of correlation between GN m^{-2} and grains $spike^{-1}$ in bread wheat was explained by the negative correlation observed between grains $spike^{-1}$ and spikes m^{-2} (Table 3).

As expected, the variation in grains $spike^{-1}$ was positively related to variations in the number of fertile florets $spike^{-1}$ ($p < 0.01$, Table 3) and to the grain set ($p < 0.05$, Table 3) in bread wheat, but in two-row barley changes in grains $spike^{-1}$ were associated with the number of spikelets $spike^{-1}$ and the grain set (Table 3). In both species, the number of spikelets $spike^{-1}$ was strongly and positively correlated with the number of fertile florets $spike^{-1}$. Bread wheat showed 30% more fertile florets per spike than two-row barley, which was mostly associated with similar differences (33% more fertile florets per spikes) in main stems ($p < 0.05$, Table 2), while no differences in this trait were observed in tillers (Table 2).

Table 2
Sub-components of grain number m^{-2} in wheat and barley growing under different environments (i.e. sowing dates and growing season combinations). Mean values, mean squares of each factor from the split-plot analysis and its significance for main factors and their interactions were listed. Letters comparing genotypes within each environment reflect mean comparison through Duncan test.

Env	Specie	Genotype	Fertile florets $spike^{-1}$			Fertile spikelet $spike^{-1}$			Number of grains $spike^{-1}$			Grain Set			Number of spikes m^{-2}		
			MS	Tiller	Total	MS	Tiller	Total	MS	Tiller	Total	MS	Tiller	Total	MS	Tiller	Total
1	Barley	Q.Ayelen	26.2^{b}	20.8^{b}	22.5^{b}	19.8^{a}	15.4^{a}	16.9^{a}	13.1^{c}	11.1^{ab}	11.8^{b}	0.50^{b}	0.54^{a}	0.52^{b}	330^{a}	688^{a}	1018^{a}
		Scarlett	26.3^{b}	21.4^{ab}	22.9^{b}	21.8^{a}	17.2^{a}	18.6^{a}	17.3^{b}	12.1^{ab}	13.7^{b}	0.66^{ab}	0.57^{a}	0.61^{ab}	330^{a}	754^{a}	1084^{a}
	Wheat	K.Chaja	36.2^{a}	24.0^{a}	29.8^{a}	13.8^{b}	10.5^{b}	12.1^{b}	26.8^{a}	14.2^{a}	20.3^{a}	0.74^{a}	0.59^{a}	0.67^{a}	267^{b}	289^{b}	556^{b}
		Cronox	27.5^{b}	19.5^{b}	22.1^{b}	13.3^{b}	10.6^{b}	11.4^{b}	20.4^{b}	10.8^{b}	13.9^{b}	0.75^{a}	0.56^{a}	0.65^{a}	324^{a}	688^{a}	1012^{a}
2	Barley	Q.Ayelen	25.4^{c}	22.3^{ab}	23.5^{c}	22.2^{a}	16.9^{a}	18.9^{a}	17.8^{b}	12.2^{bc}	14.3^{c}	0.70^{a}	0.55^{c}	0.49^{b}	314^{ab}	508^{a}	822^{a}
		Scarlett	23.2^{c}	17.9^{b}	20.0^{d}	21.5^{a}	14.8^{ab}	17.6^{a}	16.9^{b}	10.6^{c}	13.1^{c}	0.73^{a}	0.60^{bc}	0.68^{ab}	330^{a}	501^{a}	831^{a}
	Wheat	K.Chaja	37.2^{a}	26.1^{a}	35.1^{a}	13.2^{b}	9.8^{c}	12.5^{b}	25.9^{a}	21.7^{a}	25.2^{a}	0.70^{a}	0.83^{a}	0.56^{a}	330^{a}	83^{b}	413^{b}
		Cronox	31.0^{b}	24.1^{a}	26.9^{b}	12.9^{b}	11.4^{bc}	12.0^{b}	25.4^{a}	16.7^{b}	20.3^{b}	0.82^{a}	0.69^{b}	0.80^{a}	311^{b}	462^{a}	773^{a}
3	Barley	Q.Ayelen	31.9^{b}	28.8^{a}	29.8^{b}	25.5^{b}	22.4^{a}	23.3^{a}	19.6^{b}	11.0^{a}	13.7^{b}	0.61^{a}	0.37^{a}	0.63^{a}	300^{b}	755^{a}	1055^{a}
		Scarlett	31.9^{b}	32.7^{a}	32.4^{b}	31.1^{a}	27.7^{a}	28.9^{a}	25.3^{ab}	18.3^{a}	20.9^{ab}	0.79^{a}	0.56^{a}	0.66^{a}	289^{b}	789^{ab}	1078^{ab}
	Wheat	K.Chaja	55.8^{a}	39.1^{a}	51.2^{a}	17.7^{c}	13.9^{b}	16.5^{b}	36.1^{a}	18.6^{a}	30.4^{a}	0.69^{a}	0.42^{a}	0.76^{a}	322^{a}	158^{c}	480^{c}
		Cronox	43.9^{ab}	22.6^{a}	32.9^{b}	16.9^{c}	14.2^{b}	15.6^{b}	32.2^{a}	19.5^{a}	25.9^{a}	0.74^{a}	0.86^{a}	0.76^{a}	280^{b}	320^{a}	600^{bc}
4	Barley	Q.Ayelen	28.1^{c}	25.0^{c}	25.9^{c}	26.0^{a}	24.7^{a}	25.2^{a}	22.9^{b}	12.1^{b}	15.2^{bc}	0.81^{a}	0.49^{a}	0.65^{a}	249^{a}	622^{a}	871^{a}
		Scarlett	26.7^{c}	24.3^{c}	25.1^{c}	26.5^{a}	23.9^{a}	24.9^{a}	18.7^{b}	10.3^{b}	13.1^{c}	0.70^{ab}	0.42^{a}	0.56^{a}	284^{a}	627^{a}	911^{a}
	Wheat	K.Chaja	53.3^{a}	45.5^{a}	48.7^{a}	16.7^{b}	16.2^{b}	16.4^{b}	34.5^{a}	18.1^{a}	24.7^{a}	0.65^{ab}	0.40^{a}	0.53^{a}	249^{a}	373^{a}	622^{a}
		Cronox	43.5^{b}	38.4^{b}	40.0^{b}	15.4^{b}	13.9^{c}	14.4^{c}	23.3^{b}	15.8^{ab}	18.1^{b}	0.54^{b}	0.41^{a}	0.48^{a}	284^{a}	644^{a}	929^{a}
		Barley mean	27.5	24.1	25.3	24.3	20.4	21.8	19.0	12.2	14.5	0.69	0.51	0.60	305	644	949
		Wheat mean	41.0	29.9	35.8	15.0	12.6	13.9	28.1	16.9	22.3	0.70	0.60	0.65	296	377	673
		Sp	*2214****	*401***	*1341****	*1047.2****	*731.6****	*890.6****	*996.1****	*347.4****		*0.003*	*0.088*	*0.029*	*177.1*	*620823****	*641971****
		Gen(Sp)	*511****	*341**	*692****	*23**	*6.6*	*90.9***	*190.8***	*19.6*		*0.026*	*0.045*	*0.030*	*2640*	*551358****	*579616****
		Env	*1307****	*1254****	*1334****	*279****	*477.9****	*189.4****	*546.4****	*31.4*		*0.039*	*0.333**	*0.136**	*21565****	*441012****	*403631****
		*Sp*Env*	*456****	*577***	*370****	*23.5*	*68.7**	*4.7*	*25.7*	*31.9*		*0.160**	*0.118*	*0.096*	*4805*	*69239*	*62173*

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

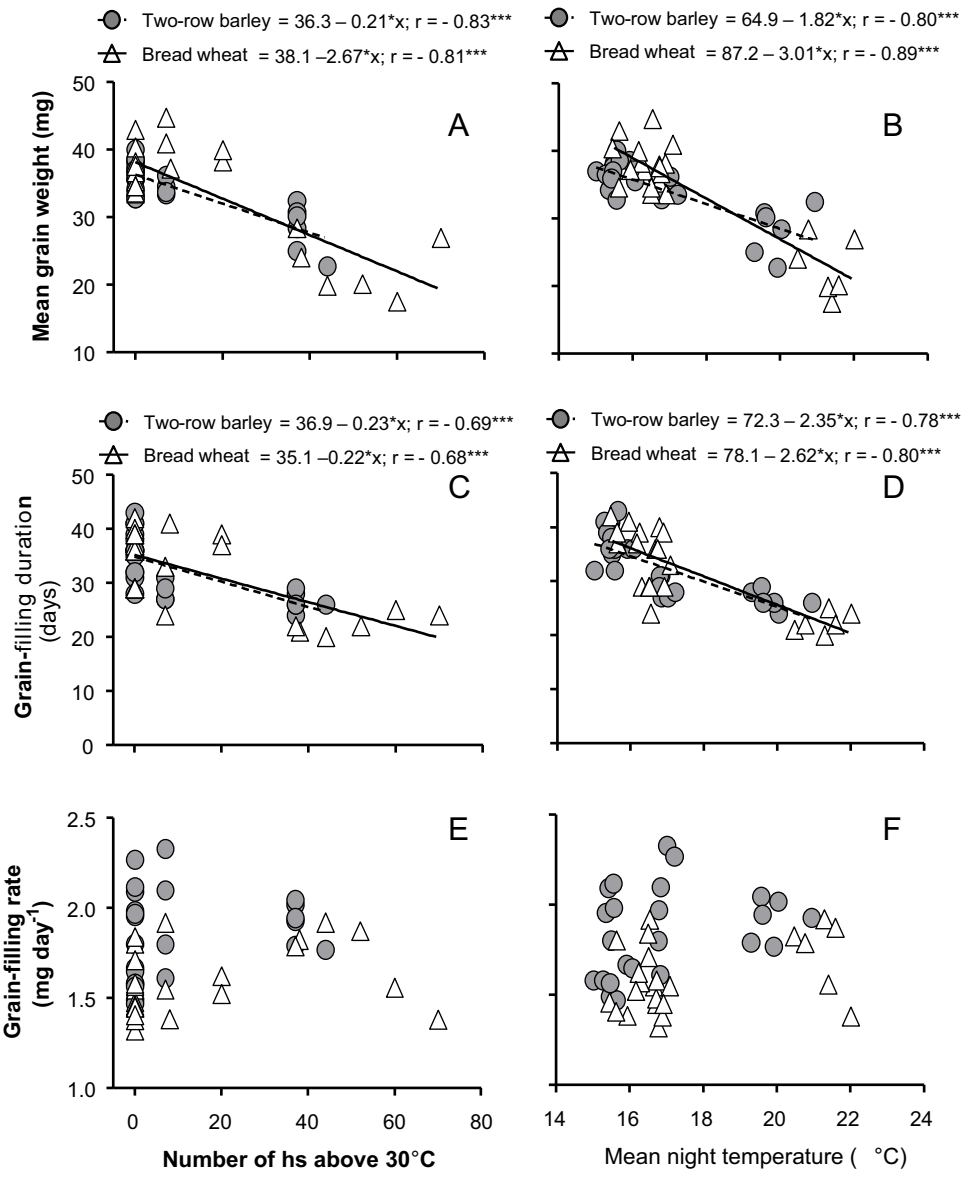

Fig. 4. A, B) Mean grain weight, C, D) grain-filling duration and E, F) grain-filling rate versus the number of hours above 30 °C (A, C and E) and mean night temperature (B, D and F) during the grain-filling period for bread wheat (open triangles) and two-row barley (closed circles). Bold and dotted lines represent the regression adjusted for bread wheat and two-row barley, respectively.

Table 3
Correlation coefficients of grain number m^{-2} (Grain m^{-2}) and its sub-components (spikelet $spike^{-1}$, spikes m^{-2}, grains $spike^{-1}$, fertile florets $spike^{-1}$ and grain set) in wheat (below the diagonal) and barley (above the diagonal).

		BARLEY					
		Grain m^{-2}	Spikelet $spike^{-1}$	Spikes m^{-2}	Grains $spike^{-1}$	Fertile florets $spike^{-1}$	Grain set
WHEAT	Grains m^{-2}		0.44* ns	0.87***	0.58**	0.47*	0.25 ns
	Spikelet $spike^{-1}$	0.52**		0.21 ns	0.45*	0.85***	0.13 ns
	Spikes m^{-2}	0.50*	−0.11 ns		−0.08 ns	0.35 ns	−0.10 ns
	Grains $spike^{-1}$	0.33 ns	−0.16 ns	−0.62**		0.32 ns	0.68***
	Fertile florets $spike^{-1}$	0.12 ns	0.72***	−0.42*	0.56**		−0.05 ns
	Grain set	0.30 ns	−0.16 ns	−0.15 ns	0.44*	−0.46*	

ns, non significant correlation.
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

3.4. Grain yield: biomass accumulation and allocation model

A significant variation in AGB was obtained across studied environments ($p < 0.05$; Table 4), and it was always higher in bread wheat than in two-row barley ($p < 0.05$; Table 4) without interactions with the environment (Table 4). The AGB ranged from 908 to 1607 g m^{-2} and from 1074 to 1670 g m^{-2} in two-row barley and

Table 4
Aboveground biomass at physiological maturity, cumulative intercepted photosynthetic active radiation (iPAR) and radiation use efficiency (RUE), estimated from emergence to physiological maturity, and harvest index of wheat and barley growing under different environments (i.e. sowing dates and growing seasons). Mean values, mean squares of each factor from the split-plot analysis and its significance for the main factors and their interactions were listed. Letters comparing genotypes within each environment reflect mean comparison thorough Duncan test.

Environment	Specie	Genotype	Biomass ($g\,m^{-2}$)	IPAR ($MJ\,m^{-2}$)	RUE ($g\,MJ^{-2}$)	Harvest index
1	Barley	Q. Ayelen	1299.7^{b}	640.6^{a}	2.03^{ab}	0.34^{b}
		Scarlett	1291.0^{b}	635.3^{a}	2.03^{ab}	0.43^{a}
	Wheat	K. Chaja	1286.7^{b}	654.9^{a}	2.03^{b}	0.31^{b}
		Cronox	1618.5^{a}	696.3^{a}	2.32^{a}	0.33^{b}
2	Barley	Q. Ayelen	1013.2^{a}	536.4^{a}	1.88^{a}	0.40^{a}
		Scarlett	908.0^{a}	495.2^{a}	1.84^{a}	0.40^{a}
	Wheat	K. Chaja	1074.1^{a}	514.5^{a}	2.09^{a}	0.40^{a}
		Cronox	1037.5^{a}	467.1^{a}	2.30^{a}	0.42^{a}
3	Barley	Q. Ayelen	1302.7^{a}	629.3^{b}	2.07^{a}	0.35^{a}
		Scarlett	1607.4^{a}	647.6^{a}	2.48^{a}	0.37^{a}
	Wheat	K. Chaja	1670.0^{a}	646.5^{a}	2.59^{a}	0.35^{a}
		Cronox	1640.5^{a}	644.2^{a}	2.21^{a}	0.40^{a}
4	Barley	Q. Ayelen	968.7^{a}	563.9^{a}	1.72^{a}	0.37^{a}
		Scarlett	1098.9^{a}	555.6^{a}	1.95^{a}	0.36^{a}
	Wheat	K. Chaja	1296.4^{a}	593.0^{a}	2.2^{a}	0.27^{a}
		Cronox	1332.3^{a}	591.3^{a}	2.26^{a}	0.29^{a}
		Barley mean	1184	583	2.0	0.37
		Wheat mean	1377	613	2.2	0.35
		Sp	*241967**	*3375*	*0.628**	*0.006*
		Gen(Sp)	*2088*	*324*	*0.072*	*0.007*
		Env	*585695****	*47984****	*0.209*	*0.056***
		*Env*Sp*	*43307*	*1502*	*0.048*	*0.019**

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

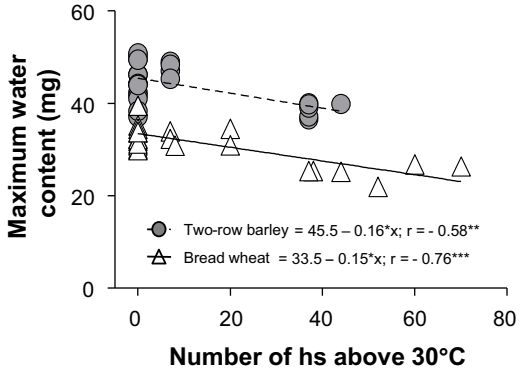

Fig. 5. Relationship between grain maximum water content and the number of hours above 30 °C during the grain-filling period for bread wheat (open triangles) and two-row barley (closed circles).

bread wheat, respectively (Table 4). Both species showed similar partitioning patterns when all studied environments were considered (Table 4). In fact, yield and GN variations were mainly explained by changes in AGB (Fig. 6A, B) at maturity rather than by variations in harvest index ($p > 0.05$), which was more stable than biomass in both species (Table 4).

Aboveground biomass was dissected into its physiological components: intercepted photosynthetic active radiation (iPAR) and radiation use efficiency (RUE). Accumulated radiation during the whole cycle (i.e. from emergence to PM) varied across environments ($p < 0.05$; Table 4), ranging from 420 to 696 $MJ\,m^{-2}$ in bread wheat and from 495 to 648 $MJ\,m^{-2}$ in two-row barley (Table 4). On average, bread wheat showed a higher RUE than two-row barley ($p < 0.05$; Table 4) varying across environments from 1.57 to 2.48 $g\,MJ^{-1}$ and from 1.75 to 2.62 $g\,MJ^{-1}$, respectively (Table 4). Increases in AGB were positively associated with the accumulated iPAR (Fig. 6C) and RUE (Fig. 6D) in both species.

Comparing the dynamic of iPAR during the crop cycle in both species, a higher radiation interception was observed for two-row barley than in bread wheat from the beginning of the cycle up to the point where nearly 50% of the intercepted radiation was reached, but thereafter both crops followed common interception patterns (Fig. 7). When considering the entire crop cycle, the total iPAR accumulated by bread wheat was slightly higher than in two-row barley, regardless of the environment tested (Table 4). Unlike the observations for iPAR, RUE values remained stable across environments (Table 4).

4. Discussion

The present study compared bread wheat and two-row barley growing simultaneously under different environments. Across the studied environments, no consistent yield advantage was observed for either of the species (at least for genotypes included in the present study). Similar studies have been carried out under Mediterranean conditions and have reported contrasting results, and in some cases barley outperformed wheat (Josephides, 1993), while no differences were observed in others (Simpson and Siddique, 1994; Cossani et al., 2009). Despite similarities in final grain yield, different physiological strategies were identified in both species. For the studied genotypes, grain yield variability was associated with variations in GN m^{-2} and changes in both traits were closely associated with differences in growth of AGB (García et al., 2013; de San Celedonio et al., 2014). When dissecting the contributions of main stems and tillers to final yield or GN, there were clear differences between species. Bread wheat genotypes showed higher GN and consequently higher yield than two-row barley genotypes in the main stems, while the opposite occurred in the tillers where two-row barley genotypes outperforming those of bread wheat.

Previous evidence has revealed that the number of spikes m^{-2} is the main component that explains GN m^{-2} variation in two-

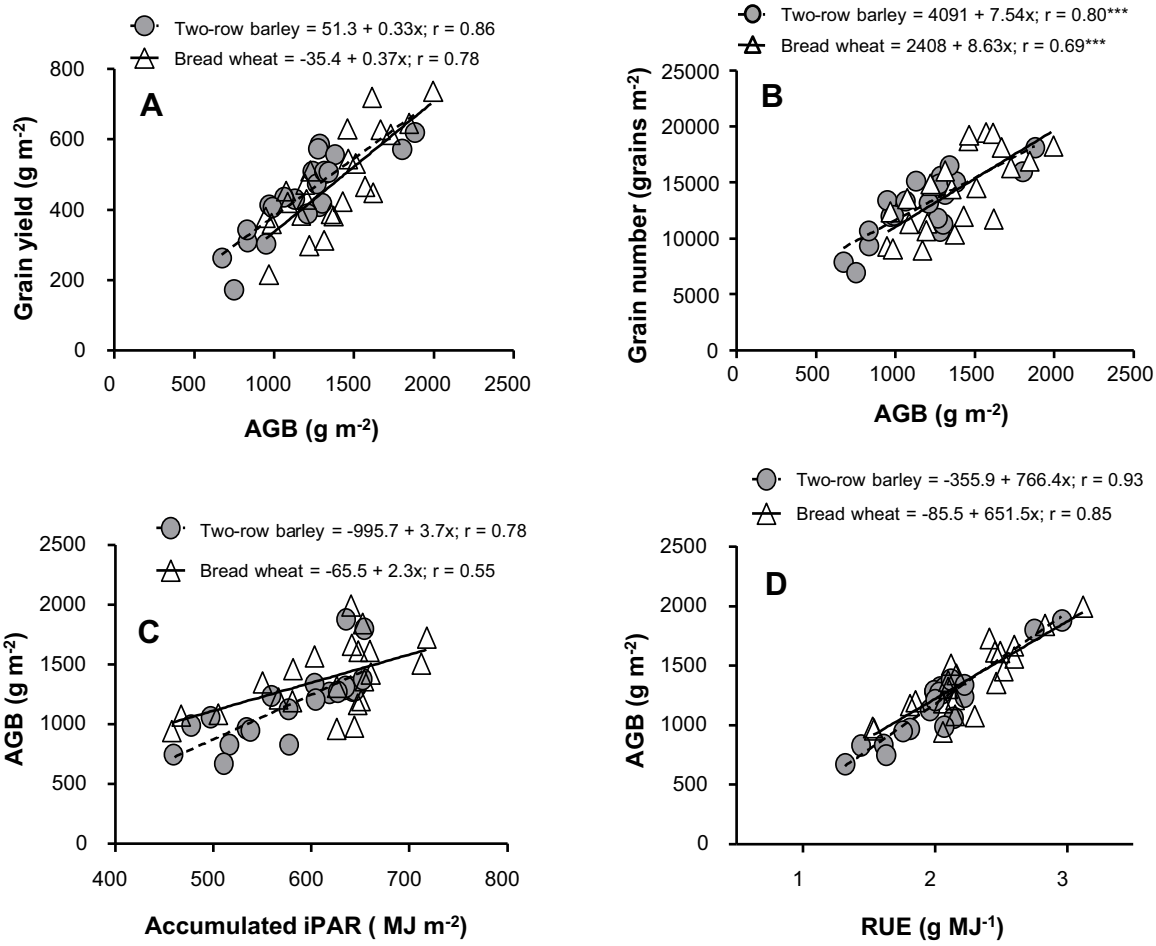

Fig. 6. Relationship between A) grain yield and aboveground biomass (AGB), B) grain number per unit area and AGB, C) AGB with accumulated intercepted PAR (iPAR), and D) AGB with radiation use efficiency (RUE) for bread wheat (triangles) and two-row barley (circles).

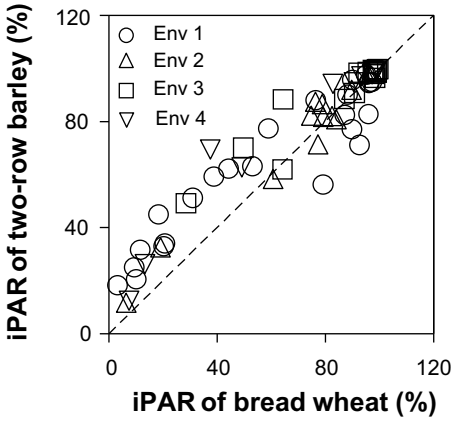

Fig. 7. Relationship between the proportion of wheat and barley iPAR calculated during the whole cycle for bread wheat and two-row barley across four environments. The dotted line represents the 1:1 relationship.

row barley (Abeledo et al., 2003; García del Moral et al., 2003; Arisnabarreta and Miralles, 2006, 2008; Peltonen-Sainio et al., 2009). Our results showed that variations in GN m^{-2} were significantly associated with changes in both grains $spike^{-1}$ and spikes m^{-2} in two-row barley genotypes, although the association was stronger with spikes m^{-2}, as also reported by Arisnabarreta and Miralles (2006) and de San Celedonio et al. (2014). A stronger association with spikes m^{-2} in barley is explained by a high tillering capacity, which is associated with grain number determination (Arisnabarreta and Miralles, 2006; Bingham et al., 2007; Alzueta et al., 2012; Slafer et al., 2014). This higher tillering capacity of two-row barley over wheat is supported by a faster tiller appearance rate (Alzueta et al., 2012), which determines higher intercepted radiation than wheat and explained a higher iPAR accumulation at early stages of the cycle (López-Castañeda et al., 1995). However, the larger number of spikes m^{-2} observed in barley was not enough to promote a higher GN m^{-2} compared to wheat due to the lower spike plasticity.

On the other hand, for bread wheat the strategies for GN determination are usually focused on both spikes m^{-2} and grains $spike^{-1}$ determinations, the former (spikes m^{-2}) being more capable of accommodating larger changes in GN than the latter (Slafer et al., 2014). Wheat genotypes evaluated in the present study differed from some reports in the literature (Abbate et al., 1997; de San Celedonio et al., 2014) because variations in GN m^{-2} were significantly associated with changes in the number of spikes m^{-2} alone (Table 3). This lack of association between GN m^{-2} and grains $spike^{-1}$ for the evaluated wheat genotypes could be explained by a trade-off between spikes m^{-2} and grains $spike^{-1}$ (Table 3). The overlap of stem and spike growth dynamics (Slafer and Savin, 2006) implies a feedback control between spikes m^{-2} and grains $spike^{-1}$ determined by resource availability. This negative association between components was previously reported by Slafer et al. (2014) and was defined as a fine-tuning mechanism where the spikes m^{-2} are mainly responsible for coarse regulations driven

by environmental factors while grains spike^{-1} are mainly driven by genotypic differences.

When the physiological components of biomass were dissected, i.e. iPAR accumulated and RUE, results showed that the higher intercepted radiation of barley compared to wheat, at early stages of the cycle, was not maintained during the whole cycle. In fact, bread wheat genotypes included in the present study accumulated more iPAR during the whole cycle and used it in a more efficient way than two-row barley genotypes. The higher sink strength of wheat, given by a higher GN m^{-2} than in barley (10% higher), probably resulted in a more efficient use of the radiation (10% higher in wheat than in barley), and together with a higher iPAR accumulated (5%) promoted a higher biomass accumulation (16%) at physiological maturity with respect to two-row barley. Reynolds et al. (2005) demonstrated in wheat that an increased RUE was directly associated with larger sink strength, resulting in an increased proportion of biomass partitioned to the spike at anthesis.

Regarding grain weight variations, both species followed a common pattern because grain weight was reduced due to exposure to high temperatures (measured as a stress index during the number of hours above 30 °C that crops were exposed during grain filling) and increases in mean night temperature during grain filling. Both negative effects were associated with delays in the sowing date. The reductions in grain weight were driven by shortening of the duration of the grain-filling period, which was not compensated by increases in the grain-filling rate. Moreover, the grain-filling rate did not change with increases in night temperature and/or the number of hours above 30 °C. Although it is not possible to separate temperature effects (high temperature and mean night temperature) because both temperatures rose due to delays in the sowing date, the current results are in line with those reported in the literature following crops exposure to high temperature (Sofield et al., 1977; Wardlaw and Moncur, 1995; Savin et al., 1997) and to warmer nights (Prasad et al., 2008; Garcia et al., 2016). Although high temperatures during grain filling did not affect the grain-filling rate, a slightly negative impact on the maximum water content was observed. As maximum water content is a proxy of potential grain weight and therefore the grain-filling rate, it is possible that high temperatures (probably during the lag phase) were associated with delays in flowering time as a consequence of supra optimal sowing dates, and impacted on grain weight through reductions in potential grain weight (Tashiro and Wardlaw, 1990). However, the limitation imposed by reductions in maximum water content was almost negligible compared to reductions in the grain-filling duration.

In addition, the mean night temperature effects observed in this work are in line with the results of García et al. (2016) who showed a direct effect of mean night temperature increases on grain development and not on grain growth. The results observed by these authors (García et al., 2016) were not associated with source availability (measured as senescence and stem water soluble carbohydrates), suggesting that the negative effects of warm nights on grain weight were directly related to processes within the grain itself. The results of Garcia et al. (2016) are also in line with our previous work (see Alvarez Prado et al., 2013) where increases in source availability (through Source: sink treatments) did not impact on grain weight determination. Differences between species could be explained by differences in phenology as two-row barley reached flowering time earlier than bread wheat, thus avoiding high temperatures (except for the latest sowing date) and therefore reducing the influence of temperature on ovary development (Alvarez Prado et al., 2013).

The present study compared two genotypes of both bread wheat and two-row barley growing together in different environments. Both species showed different strategies linked with grain number determination. While two-row barley genotypes focused on tillering capacity and survival during early stages, those of bread wheat intercepted more light and used it in a more efficient way across the whole cycle. Thus, results from this work do not support the hypothesis that a higher radiation capture by barley compared to wheat during the early stages of crop cycle represents an initial advantage in barley that is capitalized at the end of the cycle as higher biomass accumulation and consequently higher grain yield.

Acknowledgements

The authors thank Diego Cattoni and Florencia Cappiello for valuable comments on a previous version of the manuscript. This study was funded by UBACyT (University of Buenos Aires) and PICT (National Agency of Science and Technology) grants.

References

Abbate, P.E., Andrade, F.H., Culot, J.P., Brindaban, P.S., 1997. Grain yield in wheat: effects of radiation during spike growth period. Field Crops Res. 54, 245–257.
Abeledo, G.L., Calderini, D.F., Slafer, G.A., 2003. Genetic improvement of barley yield potential and its physiological determinants in Argentina (1944-1998). Euphytica 130, 325–334.
Albrizio, R., Todorovic, M., Matic, T., Stellacci, A.M., 2010. Comparing the interactive effects of water and nitrogen on durum wheat and barley grown in a Mediterranean environment. Field Crops Res. 115, 179–190.
Alvarez Prado, S., Gallardo, J.M., Serrago, R.A., Kruk, B.C., Miralles, D.J., 2013. Comparative behavior of wheat and barley associated with field release and grain weight determination. Field Crops Res. 144, 28–33.
Alzueta, I., Abeledo, G.L., Mignone, C.M., Miralles, D.J., 2012. Differences between wheat and barley in leaf and tillering coordination under contrasting nitrogen and sulfur conditions. Eur. J. Agron. 41, 92–102.
Alzueta, I., Arisnabarreta, S., Abeledo, L.G., Miralles, D.J., 2014. A simple model to predict phenology in malting barley based on cultivar thermo-photoperiodic response. Comput. Electron. Agric. 107, 8–19.
Arisnabarreta, S., Miralles, D.J., 2006. Yield responsiveness in two- and six-rowed barley grown in contrasting nitrogen environments. J. Agron. Crop Sci. 192, 178–185.
Arisnabarreta, S., Miralles, D.J., 2008. Critical period for grain number establishment of near isogenic lines of two- and six-rowed barley. Field Crops Res. 107, 196–202.
Arisnabarreta, S., Miralles, D.J., 2015. Grain number determination under contrasting radiation and nitrogen conditions in 2-row and 6-row barleys. Crop Pasture Sci. 66, 456–465.
Bingham, I.J., Blake, J., Foulkes, M.J., Spink, J., 2007. Is barley yield in the UK sink limited? I. Post-anthesis radiation interception, radiation-use efficiency and source-sink balance. Field Crops Res. 101, 198–211.
Calderini, D.F., Dreccer, M.F., Slafer, G.A., 1995. Genetic improvement in wheat yield and associated traits: a re-examination of previous results and the latest trends. Plant Breed. 114, 108–112.
Calderini, D.F., Reynolds, M.P., Slafer, G.A., 1999a. Genetic gains in wheat yield and associated physiological changes during the twentieth century. Wheat: Ecology and physiology of yield determination. The Haworth Press, Inc., New York, pp. 351–377.
Calderini, D.F., Abeledo, L.G., Savin, R., Slafer, G.A., 1999b. Final grain weight in wheat as affected by short periods of high temperature during pre- and post-anthesis under field conditions. Aust. J. Plant Physiol. 26, 453–458.
Cossani, C.M., Slafer, G.A., Savin, R., 2009. Yield and biomass in wheat and barley under a range of conditions in a Mediterranean site. Field Crops Res. 112, 205–213.
de San Celedonio, R.P., Abeledo, G.L., Miralles, D.J., 2014. Identifying the critical period for waterlogging on yield and its components in wheat and barley. Plant Soil 378, 265–277.
Donald, C.M., Hamblin, J., 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Adv. Agron. 28, 361–405.
García del Moral, L.F., García del Moral, M.B., Molina-Cano, J.L., Slafer, G.A., 2003. Yield stability and development in two- and six-rowed winter barleys under Mediterranean conditions. Field Crops Res. 81, 109–119.
García, G.A., Hasan, A.K., Puhl, L.E., Reynolds, M.P., Calderini, D.F., Miralles, D.J., 2013. Grain yield potential strategies in an elite wheat double-haploid population grown in contrasting environments. Crop Sci. 53, 2577–2587.
García, G.A., Serrago, R.A., Dreccer, M.F., Miralles, D.J., 2016. Post-anthesis warm nights reduce grain weight in field-grown wheat and barley. Field Crops Res. 195, 50–59.
Gomez, K.A., Gomez, A.A., 1984. Statistical Procedures for Agricultural Research. Wiley.
Gregory, P.J., Tennant, D., Belford, R.K., 1992. Root and shoot growth, and water and light use efficiency of barley and wheat crops grown on a shallow duplex soil in a Mediterranean-type environment. Aust. J. Agric. Res. 43, 555–573.

Hay, R.K.M., 1995. Harvest index – a review of its use in plant-breeding and crop physiology. Ann. Appl. Biol. 126, 197–216.
Josephides, C.M., 1993. Analysis of adaption of barley, triticale, durum and bread wheat under Mediterranean-type environment. Aust. J. Plant Physiol. 43, 555–573.
Kirby, E.J.M., Riggs, T.J., 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., Appleyard, M., Fellowes, G., 1985. Variation in development of wheat and barley in response to sowing date and variety. J. Agric. Sci. 104, 383–396.
López-Castañeda, C., Richards, R.A., Farquhar, G.D., 1995. Variation in early vigor between wheat and barley. Crop Sci. 35, 472–479.
Le Gouis, J., Delebarre, O., Beghin, D., Heumez, E., Pluchard, P., 1999. Nitrogen uptake and utilisation efficiency of two-row and six-row winter barley cultivars grown at two N levels. Eur. J. Agron. 10, 73–79.
Ludbrook, J., 2012. A primer for biomedical scientists on how to execute model II linear regression analysis. Clin. Exp. Pharmacol. Physiol. 39, 329–335.
Marti, J., Slafer, G.A., 2014. Bread and durum wheat yields under a wide range of environmental conditions. Field Crops Res. 156, 258–271, Research 119, 48–58.
Monteith, J.L., 1977. Climate and efficiency of crop production in Britain. Philos. Trans. R. Soc. Lond. Ser. B: Biol. Sci. 281, 277–294.
Muurinen, S., Peltonen-Sainio, P., 2006. Radiation-use efficiency of modern and old spring cereal cultivars and its response to nitrogen in northern growing conditions. Field Crops Res. 96, 363–373.
Peltonen-Sainio, P., Kangas, A., Salo, Y., Jauhiainen, L., 2007. Grain number dominates grain weight in temperate cereal yield determination: evidence based on 30 years of multi-location trials. Field Crops Res. 100, 179–188.
Peltonen-Sainio, P., Jauhiainen, L., Rajala, A., Muurinen, S., 2009. Tiller traits of spring cereals under tiller-depressing long day conditions. Field Crops Res. 113, 82–89.
Prasad, P.V.V., Pisipati, S.R., Ristic, Z., Bukovnik, U., Fritz, A.K., 2008. Impact of nightime temperature on physiology and growth of spring wheat. Crop Sci. 48, 2372–2380.
Prystupa, P., Savin, R., Slafer, G.A., 2004. Grain number and its relationship with dry matter: n and P in the spikes at heading in response to N × P fertilization in barley. Field Crops Res. 90, 245–254.
R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Raduschev, D., 2007. Graph Pad Prism Version 5.0. Graph Pad Software, Inc., San Diego, CA.
Reynolds, M.P., Pellegrineschi, A., Skovmand, B., 2005. Sink-limitation to yield and biomass: a summary of some investigations in spring wheat. Ann. Appl. Biol. 146, 39–49.
Savin, R., Nicolas, M.E., 1996. Effects of short periods of drought and high temperature on grain growth and starch accumulation of two malting barley cultivars. Aust. J. Plant Physiol. 23, 201–210.
Savin, R., Stone, P.J., Nicolas, M.E., Wardlaw, F., 1997. Grain growth and malting quality of barley. 1: Effects of heat stress and moderately high temperature. Aust. J. Plant Physiol. 48, 615–624.
Sieling, K., Böttcher, U., Kage, H., 2016. Dry matter partitioning and canopy traits in wheat and barley under varying N supply. Eur. J. Agron. 74, 1–8.
Simpson, P.G., Siddique, K.H.M., 1994. Soil type influences relative yield of barley and wheat in a Mediterranean-type environment. J. Agron. Crop Sci. 172, 147–160.
Slafer, G.A., Savin, R., 2006. Physiology of crop yield. In: Goodman, R. (Ed.), Encyclopedia of Plant and Crop Science. Taylor & Francis, New York, NY.
Slafer, G.A., Savin, R., Sadras, V.O., 2014. Coarse and fine regulation of wheat yield components in response to genotype and environment. Field Crops Res. 157, 71–83.
Sofield, I., Evans, L.T., Cook, M.G., Wardlaw, I.F., 1977. Factors influencing the rate and duration of grain filling in wheat. Aust. J. Plant Physiol. 4, 795–797.
Szeicz, G., 1974. Solar radiation for plant growth. J. Appl. Ecol. 11, 617–636.
Tardieu, F., 2013. Plant response to environmental conditions: assessing potential production, water demand, and negative effects of water deficit. Front. Physiol. 4, 1–11.
Tashiro, T., Wardlaw, I.F., 1990. The effects of high temperature at different stages of ripening on grain set, grain weight and grain dimensions in the semi-dwarf wheat 'banks'. Ann. Bot. 65, 51–61.
Ugarte, C., Calderini, D.F., Slafer, G.A., 2007. Grain weight and grain number responsiveness to pre-anthesis temperature in wheat: barley and triticale. Field Crops Res. 100, 240–248.
Waddington, S.R., Cartwright, P.M., Wall, P.C., 1983. A quantitative scale of spike initial and pistil development in barley and wheat. Ann. Bot. 51, 119–130.
Wardlaw, I.F., Moncur, L., 1995. The response of wheat to high temperature following anthesis: i. The rate and duration of kernel filling. Aust. J. Plant Physiol. 22, 391–397.
Wardlaw, I.F., Wrigley, C.W., 1994. Heat tolerance in temperate cereals – an overview. Aust. J. Plant Physiol. 21, 695–703.
Zadoks, J.C., Chang, T.T., Konzak, C.F., 1974. A decimal code for the growth stages of cereals. Weed Res. 14, 415–421.