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Leaf Photosynthesis During Grain Filling Under Mediterranean Environments: Are Barley or Traditional Wheat More Efficient Than Modern Wheats?

L. G. Abeledo[1], R. Savin[2] & G. A. Slafer[2,3]

1 Departamento de Producción Vegetal, Facultad de Agronomía, Universidad de Buenos Aires, and CONICET, Buenos Aires, Argentina
2 Department of Crop and Forest Sciences and AGROTECNIO (Center for Research in Agrotechnology), University of Lleida, Lleida, Spain
3 ICREA (Catalonian Institution for Research and Advanced Studies), Lleida, Spain

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Correspondence
L.G. Abeledo
Departamento de Producción Vegetal
Facultad de Agronomía, Universidad de Buenos Aires
Av. San Martín 4453
(C1417DSE) Buenos Aires
Argentina
Tel. / Fax: +54 11 4524 8039 / 8053
Email: abeledo@agro.uba.ar

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Abstract

Barley is one of the most popular crops in dryland agricultural systems of Mediterranean areas, where it is assumed that barley, or traditional wheat cultivars, performs better than modern wheat under low-yielding conditions. It was tested whether variations in net leaf photosynthetic rate (P_N) during grain filling provide any basis for the potential better performance of barley and traditional wheat compared to modern wheats in Mediterranean areas. Two groups of field experiments were conducted in Agramunt (NE Spain) during 2005/06 (06) and 2006/07 (07) growing seasons combining low and high nitrogen (N) availabilities under rain-fed and irrigated conditions. Cultivars used in the first group of experiments were a traditional (Anza) and a modern (Soissons) wheat, whilst in a second group of experiments, a wheat (Soissons) and a barley (Sunrise) modern cultivars were used. Both wheat cultivars showed a similar P_N during grain filling but higher than that of the modern barley cultivar. Differences between species in P_N were maximized under high-yielding conditions. There were no differences between cultivars in instantaneous water-use efficiency. The barley cultivar showed a higher specific leaf area, but lower N content *per* unit of leaf area, than wheat. Photosynthetic nitrogen-use efficiency was similar between the traditional and the modern cultivar but lower than barley. Decreases in P_N after anthesis were not exactly observable in SPAD measurements. In conclusion, we found no consistent differences between cultivars in terms of post-anthesis photosynthetic activity to support the assumption of better performance under Mediterranean farm conditions of traditional wheat or barley against modern wheat.

Introduction

Wheat and barley are the most important cereal crops in Mediterranean areas, in which high temperatures and water scarcity impose a restriction to yield generation during grain filling (Araus et al. 2007, Francia et al. 2011, Jacobsen et al. 2012). Modern wheat cultivars have been normally selected for improved productivity under high-yielding conditions, whereas barley or traditional wheat cultivars have been usually defined as crops with better performance under poor environments than modern high-yielding wheats (Ceccarelli et al. 2007, Ryan et al. 2008). In fact, barley is the dominant cereal crop in the dryland systems of the Mediterranean basin (as well as in many other low-yielding systems) as farmers assume that barley performs better than wheat under these conditions (see Gibbon 1981, Cossani et al. 2007, Ryan et al. 2008) and, when growing wheat, farmers in these systems tend to favour the use of traditional rather than high-yielding modern cultivars (assuming that high-yielding cultivars are more sensitive to stresses than their traditional counterparts; Byerlee 1996). Conflicting with these assumptions, the performance of a cultivar of high potential yield under stressful growing conditions is frequently equal or better than that of cultivars of lower yielding capacity (Richards 2000, Araus et al. 2002, Abeledo et al. 2003, Slafer and Araus

2007, Sadras and Lawson 2011). For instance, Calderini and Slafer (1999) showed for different countries that modern wheat cultivars outyielded their older counterparts not only in high-yielding conditions but also along a wide range of environments. We were interested in determining whether photosynthetic rates during grain filling (frequently the most stressed phase in Mediterranean dryland systems) provide any basis for the assumed improved performance of barley and traditional wheat compared to high-yielding wheats in the Mediterranean region of Catalonia.

Regarding breeding effects on leaf photosynthesis, there are no generalized conclusions. In some cases, it was increased (soybean, Morrison et al. 1999), whilst in others it remained virtually constant (maize, Tollenaar and Wu 1999) or even decreased (wheat, Koç et al. 2003). In the case of wheat and barley, increasing grain yield through improved partitioning (i.e. harvest index) has been far more important than through increasing photosynthesis. Consequently, despite that breeding increased yield, photosynthesis *per* unit leaf area did not seem to have been consistently improved so far (Richards 2000). Sadras et al. (2012) found, working with a set of old and modern Australian wheat cultivars, that radiation-use efficiency improved with year of cultivar release (due to changes in the leaf nitrogen concentration along the canopy profile) but without significant changes in flag leaf photosynthesis (measured at anthesis). Additional evidences at the crop level of organization showed that modern cultivars have higher radiation-use efficiency than old wheat cultivars (Calderini et al. 1995, Shearman et al. 2005), even in Mediterranean conditions with terminal stresses (Acreche et al. 2008a). This is in line with improvements in the post-anthesis radiation-use efficiency in modern cultivars (Acreche and Slafer 2009). Modern cultivars, in wheat (Shearman et al. 2005, Acreche et al. 2008b, Sadras and Lawson 2011) as well as in barley (Schittenhelm et al. 1996, Abeledo et al. 2003), sets up more grain number than old ones and, as a result, there was an increase on the demand for photoassimilates during grain filling (e.g. Reynolds et al. 2005). Accordingly, wheats with larger number of grains showed an increase in net photosynthetic rates during grain filling due to a feedback response associated with the increasing sink strength (Sharma-Natu and Ghildiyal 1994, Reynolds et al. 2005, Acreche and Slafer 2009). Although wheat and barley yields seem mostly limited by the sink size rather than by the source strength (Slafer and Savin 1994, Borrás et al. 2004, Cartelle et al. 2006, Bingham et al. 2007), modern cultivars could experience a certain degree of source–sink co-limitation (Shearman et al. 2005, Acreche et al. 2008b). Thus, it might be possible that modern cultivars had increased leaf photosynthetic rates during grain filling.

In this paper, we analysed comparatively variations in leaf photosynthetic rate during grain filling between a traditional and a modern wheat cultivar and between a modern barley and wheat cultivar. Experiments were always grown on a real farm located in a Spanish Mediterranean region. Within each experiment, genotypes were subjected to a wide range of water and nitrogen (N) conditions. Although results from this sort of field studies are more variable than those in which single factor effects are studied under controlled conditions, the approach provides a situation very close to reality of actual farmers.

Materials and Methods

General conditions and treatments

Two independent studies were conducted under field conditions in Agramunt (41° 47′ 17″N, 1° 5′ 59″E, altitude 337 m; Spain), a typical Mediterranean location, on soils classified as Xerofluvent typic (SSS 1999). Each study (one comparing a modern and a traditional wheat, and the other comparing modern wheat and barley, hereafter WW and WB experiments, respectively) was carried out in two consecutive growing seasons (2005/06 and 2006/07, from now on designated by their harvest year 06 and 07, respectively). These studies were not conducted in an experimental station but in a field at a real farm, that was rented to install the experiments, sown with the farmer machinery and in which weeds, insects and diseases were controlled with the practices used by the farmers. In each experiment, the treatments comprised a factorial combination of two genotypes, two N levels (unfertilized and fertilized) and two water regimes (rain-fed and irrigated). Cultivars used in experiments WW06 and WW07 were a traditional (Anza) and a modern (Soissons) bread wheat (*Triticum aestivum* L.), while in experiments WB06 and WB07, they were Soissons and a modern two-rowed barley (*Hordeum distichum* L. cv. Sunrise). Although we are aware that there is genotypic variability within each species, we had to choose only one cultivar for each genotypic treatment to manage different N × water availabilities and take several measurements during the growth cycle, particularly photosynthetic measurements in the field within few hours (see below). These cultivars represent the actual choices made by farmers in the Catalonian Mediterranean region in NE Spain (Cossani et al. 2007, Acreche et al. 2008b), and they were used as standard controls to test the performance of other cultivars for at least 10 years, including the period of the present experiments, by GENVCE (Group for the Evaluation of the New Cereals Varieties in Spain).

Previous to sowing, soil moisture and nitrate content were measured for the 0–100 cm depth. Initial N content (N0) was 80 (WW06), 115 (WB06), 215 (WW07) and 150 kg N ha^{-1} (WB07). N fertilization treatments consisted of 0 and 150 kg N ha^{-1} applied as urea. The high fertilizer application represents a common fertilization level in the region. Fertilizer applications were split in two identical quantities at seedling emergence and beginning of tillering (DC21, Zadoks et al. 1974). Thus, nitrogen availabilities for the fertilized treatments (N1) were 230 (WW06), 265 (WB06), 365 (WW07) and 300 kg N ha^{-1} (WB07). Soil moisture content at sowing (0–100 cm) was, in both studies, 90 and 191 mm in 2005 and 2006, respectively. The rain-fed treatments (Rf) received 92 (06) and 333 mm (07) of water as rainfall during the crop cycle. The irrigated treatments (Ir) consisted of a weekly irrigation of ~10 mm each from beginning of stem elongation (DC31) to maturity (DC94) in both studies and both years. Throughout the crop cycle, ~121 mm and 220 mm were irrigated in WW06 and WW07 and 85 and 327 mm in WB06 and WB07, respectively, of which 25–30 % were irrigated from anthesis to maturity. A drip irrigation system was used for the distribution of water. The irrigation system was a set of hoses, parallel to the crop rows, derived from a central pipe connected to a bomb.

The experiments were arranged in a split block–split plot design with three replicates. Main plots were assigned to the combination of cultivars and irrigation treatments, and sub-plots to fertilization treatments. Each of the experimental units (sub-plots) was 3 m wide and 5 m long. The experiments of both studies were sown in the same dates, on 30 November 2005 and 06 November 2006. Planting density was, for both studies, 180 plants m^{-2} in the first season and 245 plants m^{-2} in the second season.

Measurements

Single leaf photosynthetic rate and related traits were determined weekly in each experimental unit from anthesis (DC65) to the end of grain filling using a portable photosynthesis system (Model LCi, ADC BioScientific, Great Amwell, UK). Measurements were performed in the leaf contributing most photoassimilates to the growing grains: the flag leaf in wheat (Cruz-Aguado et al. 1999, Yin et al. 2009) and the penultimate leaf in barley (Jenkyn and Anilkumar 1990). The flag leaf in wheat and the penultimate leaf in barley are the largest leaves in each case, and they are commonplace to measure post-anthesis photosynthesis in each species (see, for example, Pearman et al. 1979, Austin et al. 1982, Shearman et al. 2005, Zheng et al. 2011, for measurements in flag leaf in wheat, and Planchon et al. 1989, Sicher and Bunce 1997, Rybiñski and Garczyñski 2004, for measurements in the penultimate leaf in barley). Measurements were taken between middle morning and noon on cloudless days by holding the photosynthetic chamber perpendicularly to the direction of the sunrays (incident radiation always above 1000 μmol photons m^{-2} s^{-1}). The traits measured were net CO_2 assimilation (net photosynthetic rate, P_N) and leaf transpiration rate (E). To compare across time, transpiration rate was adjusted to the air vapour pressure deficit of each day (E_{VPD}) (Turner and Sinclair 1983). Instantaneous water-use efficiency (WUE_i; Tambussi et al. 2007) for each treatment was calculated as the slope of the linear regression between P_N and E_{VPD} during the grain-filling period.

Leaf chlorophyll concentration was estimated *in situ* using a portable chlorophyll metre (SPAD-520; Minolta, Tokyo, Japan) from anthesis to maturity. Measurements were made in each leaf used to determine gas exchange plus in three-additional leaves (four leaves per sub-plot in total) taking three readings *per* leaf, and their average was recorded. At anthesis, immediately after the gas exchange measurements were taken, the four leaves were harvested and green area *per* leaf was recorded using a leaf area metre (AT Dias II, Delta-T Devices, Cambridge, UK); and individual leaf dry weight (after oven-drying for 72 h at 65 °C) was measured with an electronic precision balance (HR-200-AC; A&D Instruments Ltd., Tokyo, Japan). Specific leaf area (SLA) was estimated as the ratio of leaf area to dry weight. Leaves were then milled using a pestle and a mortar, and leaf N concentration was measured through the Dumas method (AACC 2000). Leaf N content was calculated by multiplying leaf dry matter and N concentration. Specific leaf nitrogen (SLN) was calculated as the ratio of leaf nitrogen content to leaf area. Photosynthetic nitrogen-use efficiency (*PNUE*) was assessed as the ratio of P_N to nitrogen content per unit leaf area.

Dynamics of leaf photosynthesis and SPAD measurements were related to time using thermal time units with a base temperature of 8.2 °C for wheat (Slafer and Savin 1991) and 7.1 °C for barley (Wallwork et al. 1998). For integrating the effects of treatments on P_N throughout grain filling, we calculated the integral of the area underneath the curve joining the data points for the relationship between P_N and thermal time, and by analogy with the term 'leaf area duration' (Welbank et al. 1966), this integral was termed post-anthesis P_N duration. P_N was regressed against accumulated thermal time using a linear equation as follows:

$$y = a + bx$$

where y is the net photosynthetic rate (P_N, μmol CO_2 m^{-2} s^{-1}), a the intercept, b the rate of decrease of P_N throughout the grain-filling period (μmol CO_2 m^{-2} s^{-1} $°Cd^{-1}$) and x the thermal time from anthesis (°Cd). Parameters were iteratively estimated using an optimization model (Jandel Scientific 1991).

Environmental conditions

The main environmental difference between years was related to the amount and timing of rainfall. Total precipitation

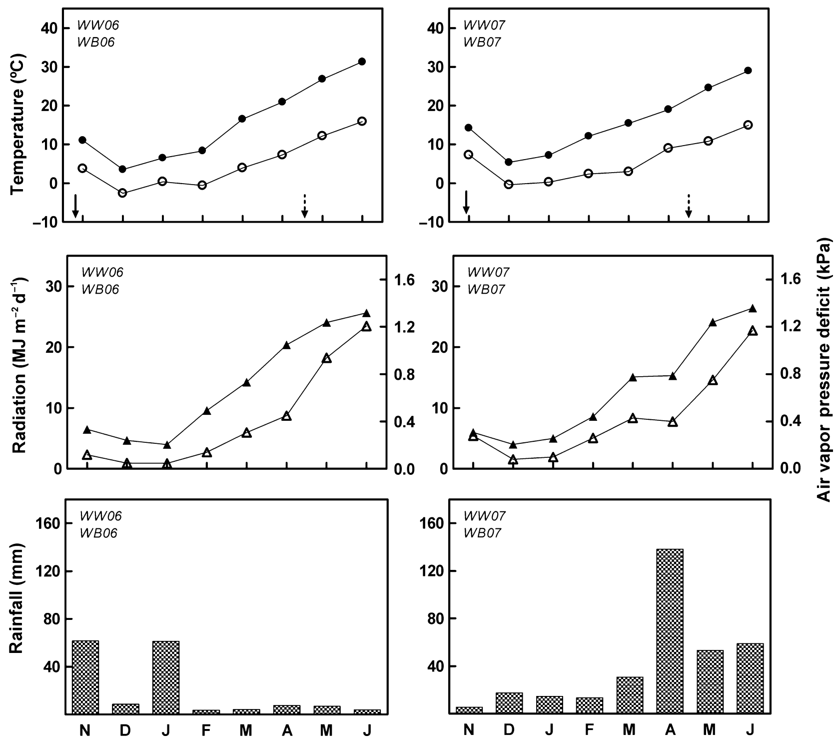

Fig. 1 Maximum (closed circles) and minimum (open circles) temperatures (up panels), global solar radiation (closed triangles) and air vapour pressure deficit (open triangles, right Y axis) (middle panels), and rainfall (dashed columns) (down panels) during experiments carried out under field conditions comparing a traditional and modern wheat cultivar (WW experiments) and comparing a modern wheat and barley cultivar (WB experiments) during the 2005/06 (06) and 2006/07 (07) growing seasons in Agramunt, NE Spain. The arrows indicate sowing (solid arrow) and average anthesis date (open arrow).

throughout the 2005/06 growing season was 92 mm, but only 5 mm precipitated from anthesis to maturity. Precipitation in 2006/07, a wet season, was 333 mm, of which 74 mm fall from anthesis to maturity (Fig. 1). Temperature, solar radiation and air vapour pressure deficit regimes were quite similar between both growing seasons (Fig. 1). The period between anthesis and maturity had a mean temperature of 20.9 °C in 2005/06 and 20.5 °C in 2006/07, while the mean solar radiation was 25.8 and 25.3 MJ m^{-2} d^{-1}, respectively. The daily air vapour pressure deficit increased during the grain-filling period from 0.85 (near anthesis) to 1.17 KPa (at the end of the period) (Fig. 1).

Statistical analyses

Data were subjected to analysis of variance (Statistix 2000) and differences among treatments established at a level of significance of $P < 0.05$. The degree of association between variables was estimated by linear regression models.

Results

Photosynthetic traits throughout grain filling

P_N in 2006, a dry season (Fig. 1), was significantly lower than P_N in 2007 when the plots remained rain-fed in both WW and WB experiments (Figs 2 and 3), and irrigation increased P_N far more in the dry than in the wet year (Figs 2 and 3). But, in any condition, no consistent differences were found in P_N (neither at anthesis nor in overall P_N during grain filling) between the traditional and the modern wheat cultivars (Fig. 2, WW experiments). Integrating post-anthesis P_N, measuring the area underneath the values, revealed no significant statistically differences between the traditional and the modern wheat cultivars (Table 1), although the tendency of the traditional wheat to show a higher integral photosynthesis due to an extended grain-filling period (mean of ~4 days). In experiment WB, Soissons showed a greater mean P_N at anthesis than Sunrise (Fig. 3, WB experiments). Although the rate of P_N reduction during grain filling was higher in the wheat (mean of −0.633 μmol CO_2 m^{-2} s^{-1} 10 °Cd^{-1}) than in the barley cultivar (mean of −0.563 μmol CO_2 m^{-2} s^{-1} 10 °Cd^{-1}), the differences between wheat and barley in P_N at anthesis overrode those in rate of P_N decrease during grain filling and, consequently, mean post-anthesis P_N duration in Soissons was either equal to, or higher than, Sunrise independently of the water or N level (Table 2). As the rate of decrease in P_N during grain filling was positively associated with P_N at anthesis ($R^2 = 0.75$, $P < 0.001$), differences between cultivars tended to be higher at the early phase of the post-anthesis period than at the end phase.

During grain filling, P_N was positively related to E_{VPD} in both experiments and both growing seasons (Fig. 4). WUE_i (the slope of the relationship between P_N and E_{VPD}) showed no consistent differences between the traditional and the modern wheat or between the modern barley and wheat (Fig. 4).

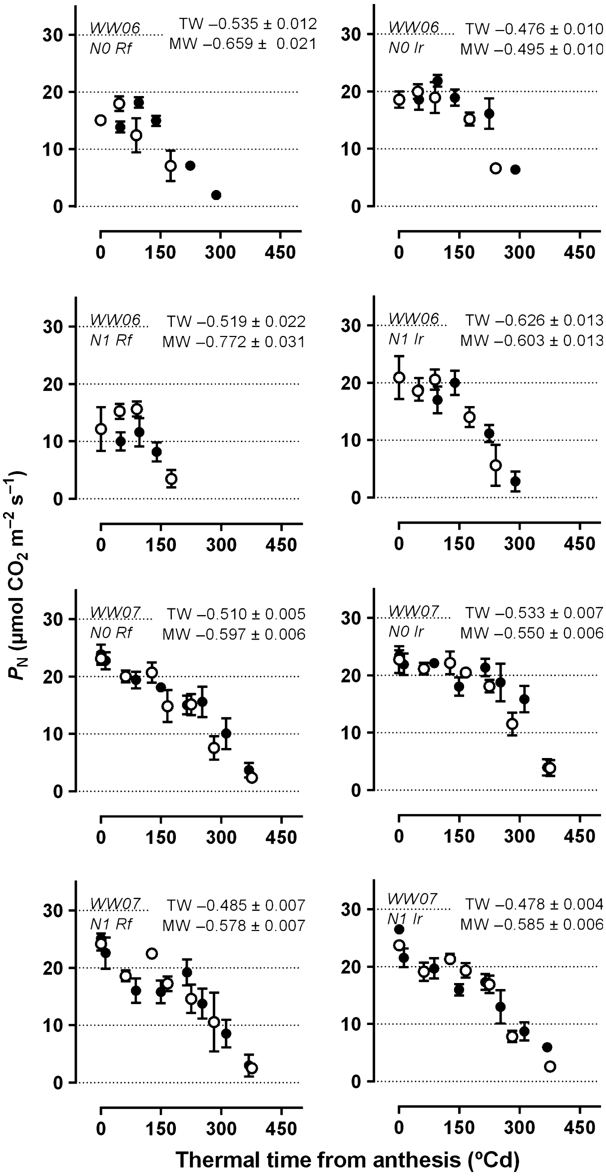

Fig. 2 Relationship between net leaf photosynthetic rate (P_N) and thermal time from anthesis for a traditional (Anza, TW, closed circles) and modern (Soissons, MW, open circles) wheat cultivar (WW experiments), grown under two nitrogen levels (unfertilized N0 and fertilized N1) and two water regimes (rain-fed Rf and irrigated Ir) in Agramunt, NE Spain, in 2005/06 (06) and 2006/07 (07) growing seasons. Each data point is the average of the experimental replicates, and vertical bars indicate 1 S.D. (when not seen it is because the length of the bar was smaller than the symbol). It is shown the overall rate of decrease in P_N during grain filling (µmol CO_2 m^{-2} s^{-1} 10 °Cd^{-1}) (±1 S.D.).

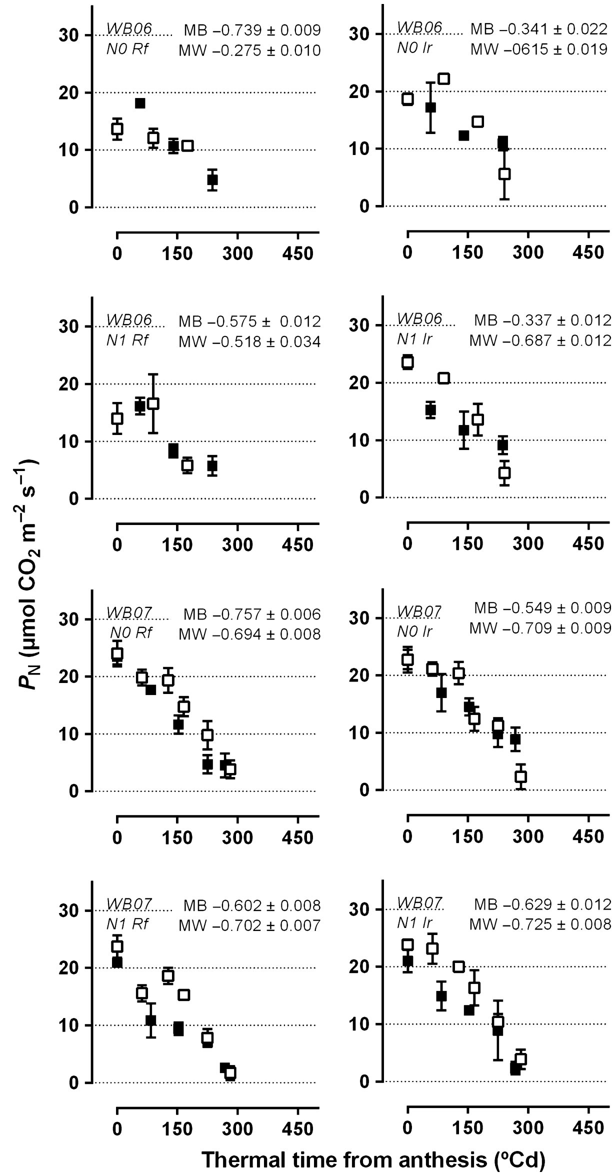

Fig. 3 Relationship between net leaf photosynthetic rate (P_N) and thermal time from anthesis for a modern barley (Sunrise, MB, closed squares) and wheat (Soissons, MW, open squares) cultivar (WB experiments), grown under two nitrogen levels (unfertilized N0 and fertilized N1) and two water regimes (rain-fed Rf and irrigated Ir) in Agramunt, NE Spain, in 2005/06 (06) and 2006/07 (07) growing seasons. Each data point is the average of the experimental replicates, and vertical bars indicate 1 S.D. (when not seen it is because the length of the bar was smaller than the symbol). It is shown the overall rate of decrease in P_N during grain filling (µmol CO_2 m^{-2} s^{-1} 10 °Cd^{-1}) (±1 S.D.).

Leaf traits and its relationship with photosynthetic rate

In WW, there were relatively small variations in SLA between the traditional and the modern wheat cultivar (Table 1), and there was no clear association between P_N and SLA ($P > 0.10$). In WB, the SLA was higher ($P < 0.005$) in Sunrise than in Soissons (mean SLA of 193 and 230 mm^2 g^{-1} for Sunrise, and of 126 and 171 mm^2 g^{-1} for Soissons in the 06 and 07 growing seasons, respectively). Differences between wheat and barley in P_N were negatively related to SLA, and this relationship was

Table 1 Post-anthesis P_N duration, specific leaf area (SLA), specific leaf nitrogen (SLN), and photosynthetic nitrogen use efficiency (PNUE) (±one standard deviation) for a traditional (Anza) and modern (Soissons) wheat cultivar (WW experiments), grown under two nitrogen levels (unfertilized N0 and fertilized N1) and two water regimes (rain-fed Rf and irrigated Ir) in Agramunt, NE Spain, in 2005/06 (06) and 2006/07 (07) growing seasons

			Post-anthesis P_N duration (μmol CO_2 m^{-2} s^{-1} °Cd)		SLA (cm^{-2} g^{-1})		SLN (mg N cm^{-2})		PNUE (μmol CO_2 g^{-1} N s^{-1})	
Exp	N	Water	Anza	Soissons	Anza	Soissons	Anza	Soissons	Anza	Soissons
WW06	N0	Rf	3714 ± 227	3212 ± 190	116.9 ± 18.7	126.3 ± 14.1	0.33 ± 0.05	0.32 ± 0.02	4.23 ± 0.87	4.67 ± 1.59
		Ir	6428 ± 450	4717 ± 611	135.0 ± 11.1	148.8 ± 13.7	0.31 ± 0.08	0.26 ± 0.05	6.37 ± 1.94	7.29 ± 0.54
	N1	Rf	3533 ± 148	2326 ± 157	126.7 ± 10.9	130.4 ± 32.6	0.34 ± 0.02	0.28 ± 0.03	2.93 ± 0.71	3.67 ± 2.43
		Ir	4821 ± 643	4578 ± 919	142.3 ± 4.4	156.0 ± 22.9	0.32 ± 0.02	0.27 ± 0.07	5.91 ± 0.67	8.57 ± 5.00
WW07	N0	Rf	6130 ± 855	5285 ± 218	143.8 ± 17.3	117.7 ± 35.0	0.24 ± 0.04	0.38 ± 0.06	9.65 ± 2.26	6.92 ± 3.47
		Ir	8086 ± 133	6388 ± 571	98.0 ± 13.4	123.8 ± 19.4	0.36 ± 0.08	0.34 ± 0.07	6.96 ± 2.20	7.14 ± 2.73
	N1	Rf	6091 ± 172	5833 ± 737	145.3 ± 25.4	75.9 ± 11.5	0.26 ± 0.05	0.60 ± 0.09	8.80 ± 2.76	3.73 ± 0.55
		Ir	6329 ± 949	5752 ± 62	104.6 ± 14.7	85.5 ± 17.0	0.37 ± 0.08	0.49 ± 0.04	6.18 ± 1.94	4.33 ± 0.72
LSD	Year		948*		23.9 ns		0.07 *		1.25 *	
	Cv		1063 ns		7.2*		0.07 *		1.62 ns	
	N		803*		14.8 ns		0.06 *		1.75 ns	
	Water		1173 ns		27.8 ns		0.09 ns		1.94 ns	
	Year × Cv		1341 ns		10.2 *		0.08 *		2.30 *	
	Year × N		1136 ns		21.0 ns		0.08 *		2.47 ns	
	Year × Water		1660 ns		39.3 ns		0.11 ns		2.74 *	
	Cv × N		570 *		17.5 *		0.06 *		2.05 ns	
	Cv × Water		966 ns		15.2 *		0.06 *		2.42 ns	
	N × Water		1136 ns		21.0 ns		0.09 ns		2.47 ns	

LSD values for main treatments and first degree interactions (ns $P > 0.05$, $*P \leq 0.05$).

particularly evident under wetter conditions, where differences in P_N between species were maximized. Differences in SLA between wheat and barley determined that wheat showed a higher N content *per* unit of leaf area (SLN) than barley (general mean of 0.28 mg N cm^{-2} and 0.18 mg N cm^{-2}, respectively) (Table 2), which implied that the conditions with high P_N values were those with the greater SLN. SLN followed a linear and negative relationship with SLA ($R^2 = 0.83$, $P < 0.001$ for the whole dataset). For the global set of experiments, leaf N concentration explained just a 35 % of variations in P_N ($P < 0.05$). There were no consistent differences between the traditional and the modern wheat cultivar in *PNUE* (Table 1), but barley tended to show a higher *PNUE* than wheat (general mean of 10.7 μmol CO_2 g^{-1} N s^{-1} for barley and 8.1 μmol CO_2 g^{-1} N s^{-1} for wheat; Table 2). Variations in *PNUE* were independent of *WUEi* ($P > 0.10$).

Chlorophyll metre readings measured at anthesis were similar between the traditional and the modern wheat cultivars (Fig. 5) as well as between wheat and barley (Fig. 6). Chlorophyll metre readings maintained constant until 100–200 °Cd after anthesis and from then on decreased at a rate that was similar between cultivars in both experiments. Variations in P_N during post-anthesis between cultivars (particularly observed in WB) were not reflected in concomitant differences in SPAD measurements. Thus, decreases in P_N after anthesis were partially related to SPAD measurements ($R^2 = 0.64$, $P < 0.001$), being the major departure from linear fitness concentrated in the days immediately after anthesis (the stage in which photosynthesis began to decrease but SPAD measurements still remained constant).

Discussion

The present work was carried out with the aim of analysing differences in photosynthetic traits during grain filling between wheat and barley (experiments WB) and between a traditional and a modern wheat cultivars (experiments WW) in a Mediterranean environment, to ascertain whether the preference of growers to use barley or traditional wheat instead of modern and high-yielding wheats is supported in their photosynthetic performances. It was not part of this study the analysis of yield and yield generation, but agronomic data, collected by others in these experiments, showed that under the lowest yielding conditions explored, the modern wheat effectively yielded less than the traditional wheat (2.9 and 3.6 Mg ha^{-1}) and both wheats yielded less than barley (4.4 Mg ha^{-1}; Cossani et al. 2009). However, even when in the present study the assumption

Table 2 Post-anthesis P_N duration, specific leaf area (SLA), specific leaf nitrogen (SLN), and photosynthetic nitrogen use efficiency (PNUE) (±one standard deviation) for a modern barley (Sunrise) and wheat (Soissons) cultivar (WB experiments) grown under two nitrogen levels (unfertilized N0 and fertilized N1) and two water regimes (rain-fed Rf and irrigated Ir) in Agramunt, NE Spain, in 2005/06 (06) and 2006/07 (07) growing seasons

			Post-anthesis P_N duration (μmol CO_2 m^{-2} s^{-1} °Cd)		SLA (cm^{-2} g^{-1})		SLN (mg N cm^{-2})		PNUE (μmol CO_2 g^{-1} N s^{-1})	
Exp	N	Water	Sunrise	Soissons	Sunrise	Soissons	Sunrise	Soissons	Sunrise	Soissons
WB06	N0	Rf	2991 ± 62	2311 ± 62	184.0 ± 9.1	126.2 ± 11.4	0.17 ± 0.01	0.31 ± 0.03	6.69 ± 1.67	5.23 ± 1.65
		Ir	3280 ± 441	3800 ± 333	199.3 ± 3.2	126.4 ± 3.8	0.16 ± 0.01	0.32 ± 0.03	7.00 ± 1.70	6.30 ± 0.80
	N1	Rf	3043 ± 19	2682 ± 151	190.3 ± 13.2	126.4 ± 26.2	0.22 ± 0.04	0.32 ± 0.08	4.72 ± 0.89	4.99 ± 0.17
		Ir	3011 ± 65	4015 ± 192	198.2 ± 12.9	124.2 ± 12.2	0.19 ± 0.03	0.34 ± 0.09	4.66 ± 0.00	6.42 ± 2.83
WB07	N0	Rf	3530 ± 142	4164 ± 462	258.8 ± 92.8	157.9 ± 34.4	0.12 ± 0.05	0.24 ± 0.06	21.37 ± 6.04	10.29 ± 1.22
		Ir	4032 ± 315	4385 ± 144	190.2 ± 80.8	189.3 ± 33.7	0.27 ± 0.08	0.20 ± 0.05	12.50 ± 10.5	12.00 ± 2.71
	N1	Rf	2839 ± 223	4385 ± 144	239.5 ± 88.2	170.4 ± 44.8	0.16 ± 0.07	0.26 ± 0.08	15.02 ± 5.96	9.32 ± 1.44
		Ir	3460 ± 192	4601 ± 109	233.0 ± 15.9	167.0 ± 23.7	0.18 ± 0.03	0.24 ± 0.04	11.67 ± 2.44	10.08 ± 1.07
LSD	Year		312 *		53.2 *		0.08 ns		3.05 *	
	Cv		561 *		41.0 *		0.05 *		2.47 *	
	N		294 *		11.0 ns		0.04 ns		1.62 ns	
	Water		206 *		36.4 ns		0.03 ns		3.08 ns	
	Year × Cv		793 ns		58.0 ns		0.07 *		3.49 ns	
	Year × N		416 ns		15.6 ns		0.06 ns		2.29 ns	
	Year × Water		291 *		51.4 ns		0.03 *		4.35 ns	
	Cv × N		395 ns		35.2 ns		0.04 ns		2.42 ns	
	Cv × Water		490 ns		96.6 ns		0.09 ns		6.34 ns	
	N × Water		416 *		15.6 ns		0.06 ns		2.29 ns	

LSD values for main treatments and first degree interactions (ns $P > 0.05$, *$P \leq 0.05$).

that traditional wheat and barley would yield more than the modern wheat under low-yielding conditions was in line with observed, this cannot be considered a proof of concept for that assumptions as when in the same region the analysis is wider (considering more experiments and treatments), there was no support for a consistently better performance of barley than wheat (Cossani et al. 2009), or of traditional and modern cultivars (Acreche et al. 2008b). In our experiments, we found no consistent differences in terms of post-anthesis photosynthetic activity to support the assumption of better performance under farm conditions of traditional wheat or barley against modern wheat. In fact, and despite the range of environments explored, traditional wheat or barley did not show a superior overall P_N than modern wheat (quite the opposite in general for the WB experiments). This is in line with the report from Dias et al. (2010), comparing photosynthetic rates in bread and durum wheat cultivars under heat stress conditions, where the leaf photosynthesis was similar between both species under heat stress and superior in bread wheat under optimal conditions.

The lack of consistent relation between differences in grain yield and flag leaf photosynthesis reinforces the concept that measurements carried out at individual plant level do not always correlate with the performance of the crop. Photosynthetic capacity at the crop level is determined by total leaf area and photosynthesis capacity of each individual leaf. Thus, inconsistencies in photosynthesis between the plant and the crop level can be related to (i) flag leaf is not the only green leaf during post-anthesis (specially at the beginning of the grain-filling period when the relative importance of flag leaf area is lower comparing with the area of the rest of the leaves in the whole crop), and it can be a counterbalance between leaf area at the crop level and photosynthesis per unit of leaf area, (ii) changes in canopy architecture alter the gradient of incident and absorbed irradiance through the canopy (de Pury and Farquhar 1997, Chenu et al. 2005) and, as a consequence, the canopy photosynthesis, (iii) changes in vertical leaf nitrogen distribution in canopy modified photosynthesis of the whole canopy (Werger and Hirose 1991, Dreccer et al. 2000) and (iv) the alternative importance of ear photosynthesis as source of photoassimilates (Blum 1985, Abbad et al. 2004), which is greater in barley than in wheat (Johnson et al. 1974).

Although there was in our work a contraposition between P_N at anthesis and its rate of decrease from then on, the rate of decrease did not compensate differences in P_N at anthesis (i.e. even though P_N decreased faster in wheat, it was always equal to or higher than P_N in barley during the whole grain-filling period). The relatively low value of P_N of the barley cultivar was related to its differen-

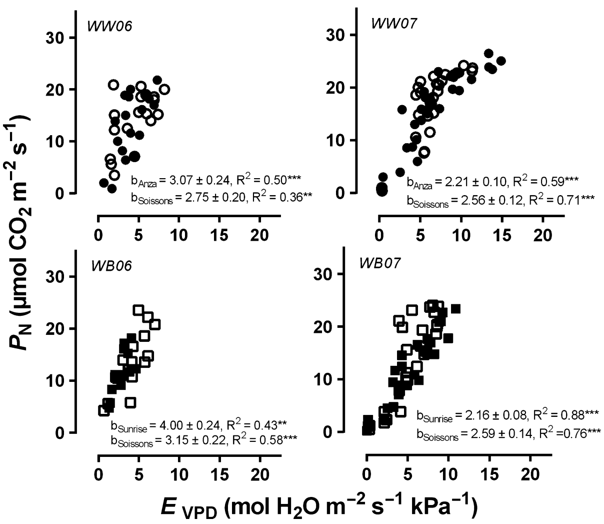

Fig. 4 Relationship between net leaf photosynthetic rate (P_N) and transpiration rate adjusted to VPD (E_{VPD}) during grain filling for a traditional (Anza, closed circles) and modern (Soissons, open circles) wheat cultivar (WW experiments), and a modern barley (Sunrise, closed squares) and wheat (Soissons, open squares) cultivar (WB experiments), grown under different nitrogen and water availabilities in Agramunt, NE Spain, in 2005/06 (06) and 2006/07 (07) growing seasons. It is shown the slope b of the linear regression (±1 S.E.), which represents the instantaneous water-use efficiency (µmol CO_2 mol H_2O^{-1} kPa).

tial characteristics with respect to wheat in (i) stomatal behaviour (i.e. rate of transpiration) and (ii) leaf levels of organization (i.e. SLA, SLN).

At the leaf level, water-use efficiency can be estimated as the ratio of P_N to the water transpired E (Tambussi et al. 2007, Cabrera-Bosquet et al. 2009). In our work, WUE_i showed no consistent differences between wheats or between wheat and barley. This is in line with the evidences provided by Cossani et al. (2012), who found no consistent advantages in water-use efficiency at the crop level of organization (kg_{grain} ha^{-1} mm^{-1}) between barley and wheat under a wide range of Mediterranean conditions.

SPAD measurements remained constant for about 150–200 °Cd after anthesis, and from then on it decreased at a rate that was similar between the traditional and the modern wheat and between wheat and barley. Thus, variations in P_N between cultivars throughout the grain-filling period were not exactly observable in SPAD measurements. As photosynthesis decreased earlier than SPAD, SPAD measurements were a better predictor of P_N when advancing the grain-filling period. The maintenance of SPAD measurements from anthesis to mid-grain-filling was consistent with the maintenance of chlorophyll content of the flag leaf observed in previous works (Ommen et al. 1999, Prasad et al. 2011). Part of the failure of SPAD in copying P_N differences at the initial phase of the post-anthesis rate could

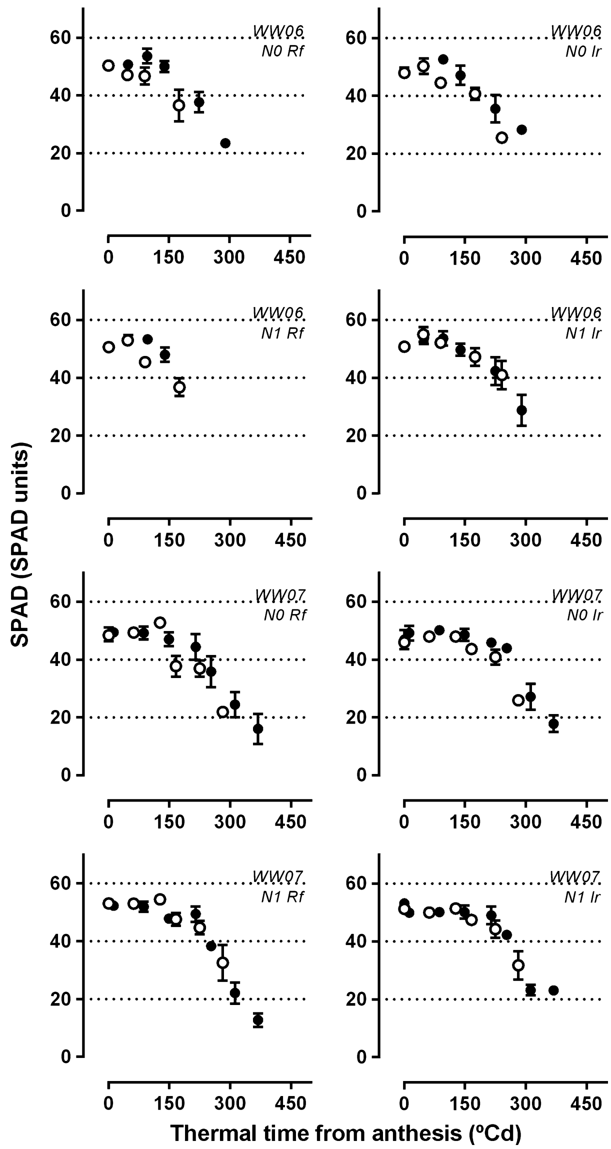

Fig. 5 Relationship between SPAD readings and thermal time from anthesis for a traditional (Anza, closed circles) and modern (Soissons, open circles) wheat cultivar (WW experiments), grown under two nitrogen levels (unfertilized N0 and fertilized N1) and two water regimes (rain-fed Rf and irrigated Ir) in Agramunt, NE Spain, in 2005/06 (06) and 2006/07 (07) growing seasons. Each data point is the average of the experimental replicates, and vertical bars indicate 1 S.D. (when not seen it is because the length of the bar was smaller than the symbol).

be related to the fact that there were no significant differences between cultivars in leaf N concentration, which is one of the determinants of SPAD measurements (Giunta et al. 2002, Lopez-Bellido et al. 2004).

In conclusion, the traditional and modern wheat showed a similar trend of leaf photosynthetic rate during grain filling, but these rates were higher than in barley. The modern wheat, in comparison with the barley culti-

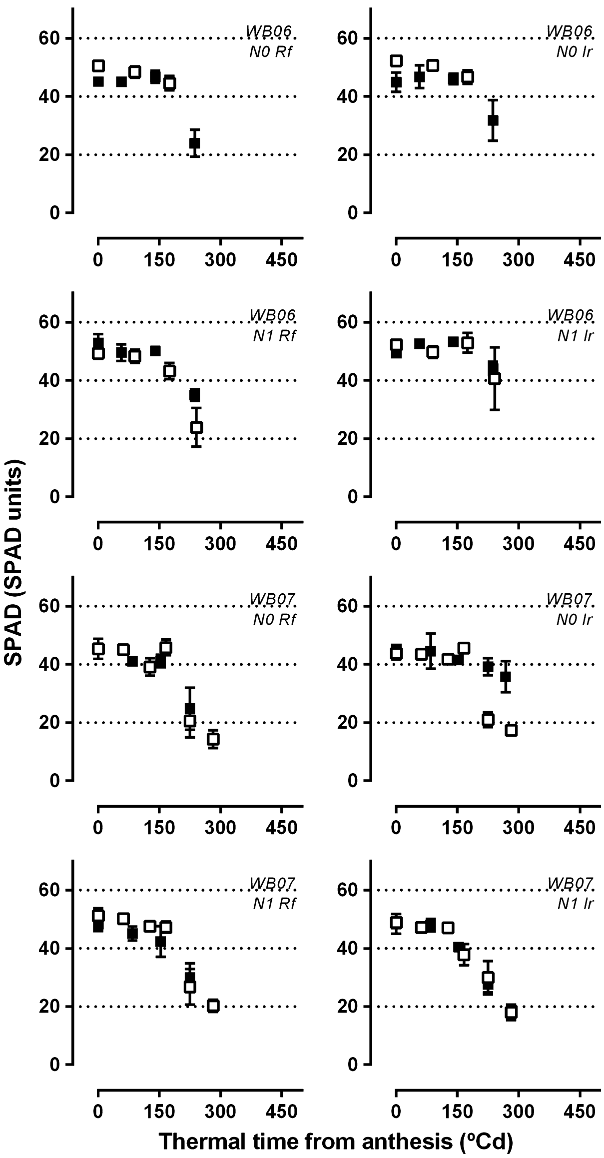

Fig. 6 Relationship between SPAD readings and thermal time from anthesis for a modern barley (Sunrise, closed squares) and wheat (Soissons, open squares) cultivar (WB experiments), grown under two nitrogen levels (unfertilized N0 and fertilized N1) and two water regimes (rain-fed Rf and irrigated Ir) in Agramunt, NE Spain, in 2005/06 (06) and 2006/07 (07) growing seasons. Each data point is the average of the experimental replicates, and vertical bars indicate 1 S.D. (when not seen it is because the length of the bar was smaller than the symbol).

var, showed higher P_N and higher degree of response with improving the environmental conditions associated with a greater transpiration rate (which did not result in differences between cultivars in water-use efficiency at the leaf level). Measurements of P_N under field conditions allow recognizing restrictions to biomass production at the crop level. No consistent evidences were found for an improved photosynthetic performance of barley or traditional wheat over modern high-yielding wheat.

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