Effect of Water Stress during the Spike Growth Period on Wheat Yield in Contrasting Weather

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***Abstract*—** *The effect of water deficit on spring wheat yield (Triticum aestivum L.) was analyzed focusing on crop growth and dry weight partitioning during the spike growth period (SGP). Two levels of water availability (rainfed and irrigated) were tested in two locations (Córdoba and Balcarce, Argentina). The degree of source limitation for grain filling was greater under rainfed conditions (12%) than under irrigation (5%); however, water stress affected yield by 40% (mean of all experiments), mainly through grain number m*$^{-2}$ *(GN) rather than by differences in weight per grain. The decrease in GN due to water stress was associated with spikes dry weight (SDW = total spikes weight – grain weight) measured 7 days after anthesis, but some additional experiment effect was detected on GN. Analysis of different weather variables showed the vapor pressure deficit (VPDX) as the one that best explained GN deviations. A model for GN estimation with or without water stress, was developed including the effect of water stress on SDW reduction* (ΔSDW)*, where H represents no water stress:*

$$\text{GN} = 4878 + 51 \cdot \text{SDW}_\text{H} - \max\left(-10 + 91 \cdot \text{VPDX}, 51\right) \cdot \Delta\text{SDW} \quad (R^2=0.93).$$

The SDW was analyzed as the product between spike growth rate (SGR) and the spike growth period (SGP) duration. SGP duration was not affected by water level, but anthesis date was up to 9 days earlier under water stress in Córdoba. SGR was more associated with crop growth rate (CGR) than with assimilates partition to spikes, and this effect increased when CGR was reduced. CGR was associated with the amount of intercepted photosynthetic active radiation during the SGP but not with the radiation use efficiency. Thus, GN was affected for both water stress reducing the availability of assimilates for spike growth and VPDX of each environment.

I. INTRODUCTION

Increases in world population will lead to sustained increases in food demand for incoming years (FAO, 2009). Possibilities of supplying food to increasing population will come mainly from an increase in yield per unit area (Andrade, 2011). However, food security is at serious risk in the long term (Fischer et al., 2014). Indeed, climate change has been associated with the occurrence of extreme meteorological episodes, including an increase in the frequency of droughts, which may have strong impact on agricultural production (FAO, 2009).

In Argentina, wheat production is mostly concentrated in greats plains with reduced rainfall from east to west regions, where water availability is the main limiting factor.

The crop-physiological approach proposed by Fischer (1984) considers that in wheat, grain number per unit area (GN) is the component most highly associated with yield, and this variable can be analyzed as the product between: (i) the duration of the rapid spike growth period previous grain filling (SGP), (ii) crop growth rate during this phase (CGR), (iii) dry weight partitioning to spikes (PE), and (iv) number of grains g^{-1} of spike produced, which is an indicator of spike fertility (SF). This approach has been previously used to examine the effects of solar radiation (Fischer, 1985; Abbate et al., 1997), cultivar (Slafer et al., 1991; Abbate et al., 1998), nitrogen (Thorne and Wood, 1987; Fischer et al., 1993; Abbate et al., 1995), phosphorus (Lázaro et al., 2010) and water (Robertson and Giunta, 1994) on wheat. A change in any of these ecophysiological components may cause variations in GN. The first three components define the spike dry weight per unit area at the start of grain filling (SDW) which reflects the amount of assimilates used by the crop for the formation and growth of reproductive organs, i.e. the survival of differentiated flowers, and therefore the GN. Several studies have shown that GN and SDW are positively related in the absence of water and nutritional deficiencies, *i.e.* across changes in intercepted radiation and temperature (Fischer, 1985; Thorne and Wood, 1987; Abbate et al., 1995; Abbate et al., 1997; Lázaro and Abbate, 2012). At the same time, SDW was directly associated with variations in crop growth during SGP (Fischer, 1984; Fischer, 1985; Abbate et al., 1995; Abbate et al., 1997; Lázaro et al., 2010; Fischer, 2011). In the absence of water and nutritional limitations, crop growth and GN are lineal function of the amount of intercepted radiation during the SGP (Fischer, 1985; Abbate et al., 1997; Lázaro and Abbate, 2012).

Water stress reduces crop growth by decreasing the amount of intercepted radiation (Gallagher and Biscoe, 1978; Robertson and Giunta, 1994) through a reduction in leaf expansion, less exposure of leaf surface (e.g. leaf curling) or leaf death. In addition, water stress can also reduce crop growth due to a decrease in photosynthesis (Subrahmanyam et al., 2006) and in radiation use efficiency (RUE; Gallagher and Biscoe, 1978; Robertson and Giunta, 1994). Therefore, water stress during SGP could reduce GN mainly due to a lower crop growth. However, it has been indicated that although water stress operates mainly through a reduction in the assimilates supply to the spikes during SGP (Fischer, 1984; Fischer, 2011), an additional reduction in GN per spike (Fischer, 2011) has been observed due to male sterility (Fischer, 1973). The existence of GN reduction due to N deficiencies during SGP has been previously shown by Abbate et al. (1995). Similar effect was not found by early P deficiencies (Lázaro et al., 2010). However, additional effects (*i.e.* supplementary GN decreases as a function of SDW reduction) of water stress over yield and GN in wheat has not yet been clearly analyzed or quantified under field conditions.

The aim of this work was to compare wheat the yield obtained under natural water stress scenarios with that achieved under non-limiting water conditions in two contrasting environments of Argentina and obtain GN estimations under both conditions.

II. MATERIALS AND METHODS

Three experiments were conducted to examine the effects of water stress: one in Córdoba (31°30´ S, 64°00´ W; altitude 360 m) during 1998, involving two sowing dates (denominated CA98-1 and CA98-2), and two in Balcarce (37°45´ S, 58°18´ W; altitude 130 m) during 1995 (BP95) and 1998 (BA98). Soil in Córdoba was a Typic Haplustoll with silt loam texture (Soil Survey Staff, 2003), 23 g kg^{-1} of organic matter in the surface layer (0-20 cm), whereas soil in Balcarce was a Typic Argiudoll with loam texture (Soil Survey Staff, 2003), with 55 g kg^{-1} of organic matter in the surface layer (0-20 cm). The bread wheat, spring, awned Argentinean PROINTA Oasis cultivar was used in all experiments.

2.1 Experiments

Detailed information of the experiments is shown in Table 1. Sowing density ranged from 250 to 350 seeds m^{-2}, where lower values were used in June sowings and the highest ones in August sowings. Plots were 7-15 m long and 21-25 rows wide (0.20 m between rows). Drip irrigation was used, keeping soil water content above 50% of plant available soil water in 2 m deep in Córdoba or up to the presence of petrocalcic layer (*ca.* 1 m) in Balcarce.

TABLE 1
RELEVANT CHARACTERISTICS AND DATES OF IMPORTANT EVENTS OF THE MAIN EXPERIMENTS CONDUCTED IN BALCARCE AND CÓRDOBA, AND OF THE EXPERIMENTS USED FOR VALIDATION

Location	Expt. Code	Water level	*Expt. design	Sowing date	Anthesis date	Beginning #SGP date	End SGP date
Balcarce	**BP95**	Irrigated	RB (4)	18-Aug-95	22-Nov	02-Nov	28-Nov
		Rainfed			22-Nov	02-Nov	28-Nov
	BA98	Irrigated	RB (4)	14-Jul-98	11-Nov	18-Oct	18-Nov
		Rainfed			11-Nov	17-Oct	18-Nov
Córdoba	**CA98-1**	Irrigated	SP (4)	16-Jun-98	15-Oct	18-Sep	19-Oct
		Rainfed			07-Oct	12-Sep	12-Oct
	CA98-2	Irrigated		23-Jul-98	30-Oct	12-Oct	04-Nov
		Rainfed			22-Oct	06-Oct	29-Oct
Data for validation							
Paraná†	**PN94**	Rainfed	RB (3)	26-Jun-94	27-Sep	07-Sep	04-Oct
	PA99	Rainfed	RB (3)	05-Jul-99	04-Oct	14-Sep	11-Oct

* RB, randomized complete blocks; SP, split-plot in complete blocks (sowing date as main treatment), number of replications in parentheses.
# SGP: Spike growth period, see Materials and Methods
†data from Caviglia et al. (2001).

Treatments with low water availability were performed under natural rainfed conditions; thus, water supply varied between sowing dates, years and locations. All experiments were conducted free of nutrient limitations, pests and diseases. Plastic nets with a 20 x 20 cm mesh were placed horizontally at 0.3-0.5 cm height to prevent lodging. Plots were fertilized with 11.1 to 20.0 g N m^{-2} divided in two applications, and 1.2 to 2.8 g P m^{-2}, according to local recommendations, applied broadcast and incorporated before sowing.

2.2 Measured and calculated variables

In all experiments, anthesis dates (when 50% of spikes showed at least one anther) were determined by linear interpolation from measurements taken on 40 spikes per plot every 2 to 4 d. Crop growth and its components (leaves, stems including leaf sheaths, spikes greater than 0.5 cm and grains, including immature ones) were measured from aboveground biomass samples of 0.5 m^{-2} before anthesis, and of 0.8-1.0 m^{-2} after anthesis. Crop dry weight (CDW) was determined in all plots at four stages: (i) just before the beginning of SGP, (ii) 10 days after the previous measurement, (iii) 7 days after anthesis (end of SGP, Abbate et al., 1997) and (iv) after phisiological maturity. All samples were dried at 56°C until constant weight, and weighed.

According to Abbate et al. (1997), SGP duration was considered to be the time in days when SDW increased from 5 to 100% of the their total weight attained 7 d after anthesis, deducting grain weight. Beginning of SGP date was obtained by linear interpolation between sampling dates as a function of SDW (Abbate et al., 1997). Crop dry weight at the beginning of SGP was estimated by linear interpolation between the first two samplings as a function of date (Abbate et al., 1997). Differences between the third sampling date and the end of SGP was 0 to 2 d, and no corrections were made. CGR and spike growth rate (SGR) during SGP were calculated as the ratio of their dry weights increment during SGP and SGP duration. PE during the SGP was calculated as the ratio between SGR and CGR. Specific leaf area (SLA, cm^{-2} g^{-1}) was obtained by measuring the projected green area of a subsample on all the green organs (leaves, stems and spikes, when present) with a leaf area integrator LI-3000 (LI-COR, Lincoln, Nebraska, USA). A green area index (GAI) was calculated as the product between crop dry weight (g m^{-2}) and SLA.

At maturity, grain samples were collected to determine grain yield. A grain subsample was taken and manually cleaned to determine dry weight per grain (WG) by counting and weighing at least 500 grains. The GN was calculated as the ratio of yield and WG. SF was calculated by the ratio of GN and SDW (without grains) (Abbate et al., 1997). In BP95 and BA98, potential weight per grain (PWG) was measured in trimmed spikelets according to Fischer and HilleRisLambers (1978) and Abbate et al. (1997). Between 3 and 5 days after anthesis, five pairs of spikes with the same number of spikelets and anthesis date in each plot were selected. The spikelets of a member of each pair were removed with scissors, leaving only four central ones, two on each side of the rachis. At maturity, grains of the trimmed and untrimmed spikes were harvested and grains were dried and weight. Sink limitation degree (DSL), was calculated as the ratio between WG of untrimmed and trimmed spikes (Abbate et al., 2001b); and the source degree limitation, as the complement to 100% of DSL. The PWG was estimated as the ratio between WG and DSL (Abbate et al., 2001b).

Photosynthetically active radiation fraction (PAR=0.5 total radiation) intercepted by the crop (R_i) was calculated as ($1-PAR_i/PAR_0$), where PAR_i was the PAR incident on the bottom layer of dry leaves and PAR_0 was the PAR incident on the top of canopy. The PAR_i and PAR_0 were measured with a linear quantum sensor (LI-COR 191SB, LI-COR) of a length equal to four inter-rows and connected to a radiometer (LI-COR 188 B). Measurements were taken at noon, every 15 days, placing the sensor perpendicularly to the rows, with approximately one record per meter of plot. The R_i between days of measurement was calculated by linear interpolation. Daily amount of intercepted PAR (IPARi, in MJ m^{-2} d^{-1}) was calculated as the product of R_i and incident PAR. Radiation use efficiency (RUE, g MJ^{-1}) was calculated as the ratio between CGR and mean $IPAR_i$ (IPAR) during the SGP.

Volumetric soil water content was measured every 7 days up to crop maturity. Measurements were taken at 20 cm depth intervals with a field calibrated neutron probe. Depth of measurement was 2 m in irrigated plots and 3 m in rainfed ones in Córdoba; in Balcarce, measurements were taken only to the depth of the petrocalcic layer. Soil water content at the deepest measured layer changed ≤10% through the experimental period; therefore, water loss by deep drainage was assumed to be negligible. The volumetric content of each layer was accumulated across depths to calculate the water stored within the soil profile. Cumulative water use (WU, mm) was determined by accumulating the water balance between successive soil moisture measurements by the following equation:

$$WU = EP + I + \Delta S \quad [1]$$

Where EP (mm) is water supplied to soil by effective precipitation, *I* (mm) is irrigation and ΔS (mm) is the change in the stored water within the soil profile. The EP was calculated from daily precipitation (PP, mm), using an equation proposed by Dardanelli et al. (1992) for daily values higher than 15 mm and for soils with surface characteristics similar to those in these experiments:

$$\mathrm{EP} = 2.43\,\mathrm{PP}^{0.667} \qquad [2]$$

Irrigation application efficiency was assumed to be 100%.

Weather records were obtained from meteorological stations located within 0.5 and 2.0 km from each experimental site.

2.3 Statistical analysis

A mixed linear model was used to analyze the variance of data. The model included two main effects (experiment and water level) and their interaction as classification criteria, and allowed for heteroscedastic residual variances among experiments. Differences between treatment means in each experiment were examined when the analysis of variance revealed significant differences. The level of significance used was $P<0.05$ in all statistical tests.

Linear regression models were fitted to evaluate the relationship between yield components through water levels or locations, then comparisons of regression coefficients were performed (Steel & Torrie 1980). When regression coefficients were not significantly different, a pooled regression was fitted.

2.4 Data analysis

GN and SDW for all treatments were compared with the bi-linear relationship obtained by Abbate et al. (1997) and Lázaro and Abbate (2012), who used the same cultivar as in this study, without water limitation. To evaluate the effect of the weather stress on the relationship between GN and SDW were tested the following 14 weather variables, measured during the SGP:

1. TMAX: mean daily maximum air temperature (°C) obtained in a weather cabinet.
2. TMIN: mean daily minimum air temperature (°C) obtained in a weather cabinet.
3. TAVG: mean daily average air temperature (°C) obtained as the average between TMAX and TMIN.
4. TAD: mean daily evaporation (mm d^{-1}) of tank type A, without the correction suggested by FAO 24.
5. TAA: cumulative evaporation, obtained as the sum of TAD (mm).
6. VPD: mean daily vapor pressure deficit (kPa), calculated for θ=0.5 (Abbate et al., 2004):

   $$\mathrm{VPD} = e_s - e_a \qquad \text{Eq. [1]}$$

   $$e_s = e_{s(d)}\,\theta + e_{s(n)}(1-\theta) \qquad \text{Eq. [2]}$$

   $$e_{s(d)} = 0.611 \cdot \exp\left(\frac{17.27 \cdot \mathrm{TMAX}}{\mathrm{TMAX} + 237.3}\right) \qquad \text{Eq. [3]}$$

   $$e_{s(n)} = 0.611 \cdot \exp\left(\frac{17.27 \cdot \mathrm{TMIN}}{\mathrm{TMIN} + 237.3}\right) \qquad \text{Eq. [4]}$$

   $$e_a = \left(e_{s(d)}\,\mathrm{RHMIN}/100 + e_{s(n)}\,\mathrm{RHMAX}/100\right)/2 \qquad \text{Eq. [5]}$$

   where RHMAX and RHMIN were the daily maximum and minimum humidity, respectively and the subindex *d* and *n* denoted day and night value.

7. VPDX: mean daily vapor pressure deficit (kPa) weighting day saturated vapor pressure by θ=0.72 (Eq. [2]) (Abbate et al., 2004).
8. ETPF56D: mean daily potential evapotranspiration (mm d^{-1}) according to Penman-Monteith method (Allen et al., 1998) calculated using the AGROCLIMA software (Abbate, 2004).
9. ETPF56A: cumulative potential evapotranspiration, obtained as the sum ETPF56D (mm).

10. RHMAX: mean daily maximum relative humidity (%) obtained in a weather shelter.
11. RHMIN: mean daily minimum relative humidity (%) obtained in a weather shelter.
12. RHAVG: mean daily relative humidity (%) obtained in a weather shelter.
13. IPAR: mean daily incident photosynthetically active radiation (MJ m^{-2} d^{-1}).
14. PTQ: photothermal quotient (MJ m^{-2} d^{-1} $°C^{-1}$), calculated as the ratio between mean daily PAR_o and mean daily TAVG minus 4.5 °C (Fischer, 1985).

The Table 2 resumes the values of these variables for each experiment.

TABLE 2
THE WEATHER VARIABLES FOR EACH FIELD EXPERIMENTS, DURING THE SPIKE GROWTH PERIOD IN THE HIGH WATER AVAILABILITY (IRRIGATED) TREATMENTS OF EXPERIMENTS PERFORMED IN BALCARCE (BP95 AND BA98) AND CÓRDOBA (CA98-1 AND CA98-2) USING THE CULTIVAR PROINTA OASIS. THE LAST COLUMN INDICATES THE PERCENTAGE RANGE OF VARIATION (%).

Weather variable	BA98	BP95	CA98	CA98	%
TMAX (°C)	22.1	22.3	23.6	27.3	22
TMIN (°C)	8.7	10.8	10.1	14.4	51
TAVG (°C)	15.4	16.5	16.9	20.8	31
TAD (mm d^{-1})	4.2	4.2	6.1	7.4	59
TAA (mm)	131.1	109.5	189.5	170.9	53
VPD (kPa)	0.60	0.58	1.16	1.33	83
VPDX (kPa)	0.94	0.89	1.55	1.81	71
ETF56D (mm d^{-1})	3.2	3.9	2.8	3.1	36
ETF56A (mm)	98.0	102.0	85.6	71.1	35
RHMAX (%)	84.5	98.0	77.4	84.5	24
RHMIN (%)	62.5	60.7	34.1	40.4	57
RHAVG (%)	73.5	79.3	55.8	62.4	35
IPAR (MJ m^{-2} d^{-1})	10.7	10.4	9.7	9.0	17
PTQ (MJ m^{-2} d^{-1} $°C^{-1}$)	0.98	0.87	0.78	0.55	54

The models fitted with each weather variable were tested according to the following assumption: when water availability is not limiting, it is expected that GN will respond linearly to SDW according to the following relationship (where subscript H denotes high water availability):

$$\mathrm{GN_H} = a_\mathrm{H} + b_\mathrm{H} \cdot \mathrm{SDW_H} \quad \text{Eq. [6]}$$

On the other hand, the decrease in GN ($\Delta\mathrm{GN}$) and SDW ($\Delta\mathrm{SDW}$) under water stress can be expressed as:

$$\Delta\mathrm{GN} = \mathrm{GN_H} - \mathrm{GN} \quad \text{Eq. [7]}$$

$$\Delta\mathrm{SDW} = \mathrm{SDW_H} - \mathrm{SDW} \quad \text{Eq. [8]}$$

and the corresponding exchange rate (slope *b*) can be defined as:

$$b = \frac{\Delta\mathrm{GN}}{\Delta\mathrm{SDW}} \quad \text{Eq. [9]}$$

a priori can be established that:

$$b \geq b_\mathrm{H} > 0 \quad \text{Eq. [10]}$$

Then, if *b* increases linearly in response to a weather variable (V), can be defined the relationship:

$$b = \max\left(c + d \cdot V, b_H\right) \quad \text{Eq. [11]}$$

From Eq. [9] can be written:

$$\Delta \text{GN} = b \cdot \Delta \text{SDW} \qquad \text{Eq. [12]}$$

Turning Eq. [11] into Eq. [12]:

$$\Delta \text{GN} = \max\left(c + d \cdot V, b_H\right) \cdot \Delta \text{SDW} \qquad \text{Eq. [13]}$$

From Eq. [7], GN can clean up and replacing Eq. [6] and Eq. [13]:

$$\text{GN} = a_{\text{H}} + b_{\text{H}} \cdot \text{SDW}_{\text{H}} - \max\left(c + d \cdot V, b_H\right) \cdot \Delta \text{SDW} \qquad \text{Eq. [14]}$$

The Eq. [14] allows us to estimate GN with or without water stress. Under high water availability, the term $\max\left(c + d \cdot V, b_H\right) \cdot \Delta \text{SDW}$ takes a value of zero, so Eq. [14] is transformed into Eq. [6]. Moreover, *a priori* is not expected that water stress increase the GN, and:

$$V > 0 \qquad \text{Eq. [15]}$$

since the studied variables cannot take negative values except for temperature, but negative temperature near GN determination period is a severe adversity. These conditions are met in Eq. [11] when:

$$\text{if } d > 0 \Rightarrow c < b_H \qquad \text{Eq. [16]}$$

$$\text{if } d < 0 \Rightarrow c > b_H \qquad \text{Eq. [17]}$$

These constraints define reasonable values limits for parameters c and d.

The values of c and d were fitted using an iterative procedure, fixing a_{H} = 4878 grains m^{-2} and b_{H} = 51 grains g^{-1}, values previously obtained by Lázaro and Abbate (2012) for the cultivar PROINTA Oasis from 22 data sets without water deficiencies from several locations across the world.

For model validation, values of GN and SDW obtained in two previous experiments were used (PN94 and PA99; Caviglia et al. 2001) at the Paraná site (31°30´ S, 60°19´ W, 110 m), whose main characteristics are reported in Table 1. The GN and SDW for these experiments were obtained as described for previous experiments.

III. RESULTS

3.1 Weather variation among experiments

The highest range of variation was observed for VPD and VPDX (83 and 71% respectively, Table 2); the lowest values of these variables were for the experiments of Balcarce and higher than those of Córdoba. The range of variation of TAD, RHMIN, PTQ, TAA and TMIN was between 59 and 51%. TAD and TAA for Córdoba were higher than that for Balcarce. RHMIN and PTQ were higher in Balcarce than in Cordoba. TMIN differences were not related with the location. The range of variation of other weather variables was lower (36 to 17%) and their values were similar between locations.

3.2 Water use

WU for each treatment at the beginning and end of SGP is shown in Table 3. WU was significantly affected by both the experiment and the treatment (water level), although the interaction between these factors was significant. WU during SGP for rainfed treatments was always lower than in irrigated ones. Average WU during SGP for rainfed treatment across all experiments was 46%. The highest value of water decrease at the beginning of SGP was reported in BP95 (69%). The lowest value was reported in experiment BA98, whereas CA98-1 and CA98-2 showed intermediate values (28 and 51%, respectively; Fig. 1).

TABLE 3
EFFECTS OF WATER AVAILABILITY ON: WATER USE (WU), CROP DRY WEIGHT (CDW) AND GREEN AREA INDEX (GAI) AT THE START AND END OF THE SPIKE GROWTH PERIOD (SGP); CROP GROWTH RATE (CGR), INTERCEPTED PHOTOSYNTHETICALLY ACTIVE RADIATION (IPAR) AND RADIATION-USE EFFICIENCY (RUE) DURING SGP, IN EXPERIMENTS PERFORMED IN BALCARCE (BP95 AND BA98) AND CÓRDOBA (CA98-1 AND CA98-2) USING THE CULTIVAR PROINTA OASIS.

		WU		CDW		GAI				
Experiment	Treatment	start*	end†	start*	end†	start*	end†	CGR	IPAR	RUE
	(water level)	mm	mm	g m^{-2}	g m^{-2}	m^2 m^{-2}	m^2 m^{-2}	g m^{-2} d^{-1}	MJ m^{-2} d^{-1}	g MJ^{-1}
BP95	**Irrigated**	115	216	265	843	2.5	3.2	21	8.4	2.5
	Rainfed	36	87	117	393	1.1	1.4	10	5.0	2.0
BA98	**Irrigated**	117	244	508	1283	7.5	5.3	25	10.1	2.5
	Rainfed	116	196	432	1131	5.3	3.4	22	9.6	2.3
CA98-1	**Irrigated**	226	390	725	1273	6.2	3.8	18	8.5	2.1
	Rainfed	163	245	381	771	2.3	2.1	13	6.0	2.2
CA98-2	**Irrigated**	288	437	787	1224	7.7	3.3	19	8.4	2.2
	Rainfed	142	221	315	626	2.1	1.2	14	5.6	2.5
Experiment Means										
BP95	---	75	152	191	618	1.8	2.3	16	6.7	2.3
BA98	---	116	220	470	1207	6.4	4.4	24	9.9	2.4
CA98-1	---	194	318	553	1022	4.2	2.9	15	7.2	2.1
CA98-2	---	215	329	551	925	4.9	2.2	16	7.0	2.3
Water Level Means										
---	**Irrigated**	186	322	571	1156	5.9	3.9	21	8.9	2.3
---	**Rainfed**	114	187	311	730	2.7	2.0	15	6.5	2.3
S.E.D.$_1$ (12 D.F.)		4.4	3.7	23.3	35.4	0.26	0.20	0.9	0.16	ns
S.E.D.$_2$ (12 D.F.)		3.1	2.6	16.5	25.1	0.18	0.14	0.6	0.12	ns
S.E.D.$_3$ (12 D.F.)		6.3	5.2	33.0	50.1	0.36	ns	1.3	0.23	ns

*Start of the SGP; †End of the SGP

ns: non-significant difference between means (P>0.05).

S.E.D.$_1$: Standard error of mean differences to test significance between Experiment Means.

S.E.D.$_2$: Standard error of mean differences to test significance between Water Level means.

S.E.D.$_3$: Standard error of mean differences to test significance of Experiment× Water Level interaction.

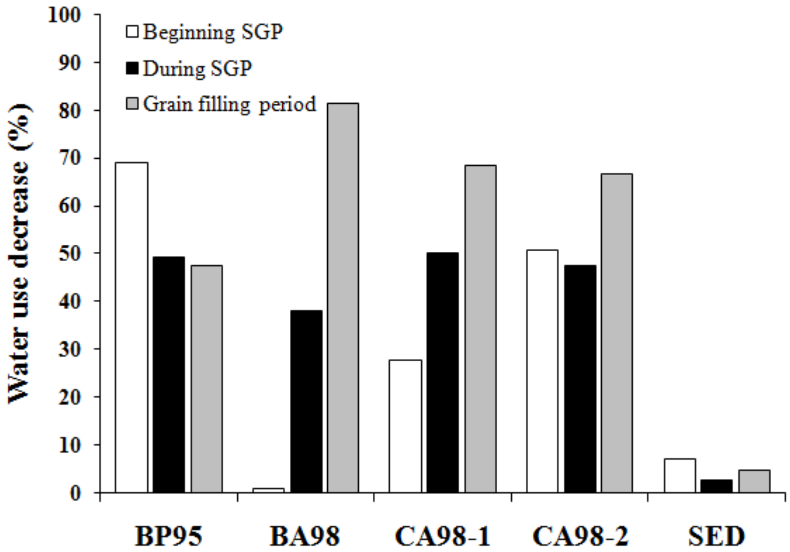

FIG. 1. DECREASES IN WATER USE AT THE BEGINNING OF SPIKE GROWTH PERIOD (SGP), DURING OF SGP AND GRAIN FILLING PERIODS, FOR EXPERIMENTS PERFORMED IN BALCARCE (BP95 AND BA98) AND CÓRDOBA (CA98-1 AND CA98-2) USING THE CULTIVAR PROINTA OASIS. S.E.D.: STANDARD ERROR OF MEAN DIFFERENCES TO TEST SIGNIFICANCE BETWEEN EXPERIMENTS IN THE SAME GROWTH PERIOD.

3.3 Crop dry weight

A suitable indicator of water stress level is the variation in CDW between irrigated and rainfed treatments (Table 3). CDW was higher for irrigated treatments than rainfed ones from the beginning to the end of SPG (Fig. **2**). The level of stress in Balcarce was similar at the start and during SPG and in Córdoba, the stress at the beginning of SPG was more important than during the period. CDW for rainfed treatment in Córdoba at the beginning of SGP decreased 54% in comparison with the irrigated ones (average of CA98-1 and CA98-2). In BP95, the decrease in CDW at the beginning of SGP was similar than the reported in Córdoba, whereas for BA98 it was 15% below (Fig. **2**). A similar effect was observed for the GAI between experiments (Table 3). Reductions in CDW at the beginning and end of SGP were significantly associated with reductions in WU efficiency (R^2=0.75; D.F.=6; P<0.006).

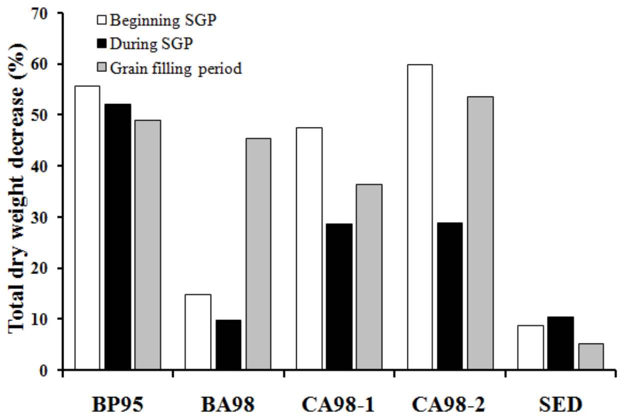

FIG. 2. DECREASES IN TOTAL DRY WEIGHT AT THE BEGINNING OF SPIKE GROWTH PERIOD (SGP), AND DURING OF SGP AND GRAIN FILLING PERIODS FOR EXPERIMENTS CONDUCTED IN BALCARCE (BP95 AND BA98) AND CÓRDOBA (CA98-1 AND CA98-2), USING THE CULTIVAR PROINTA OASIS. S.E.D.: STANDARD ERROR OF MEAN DIFFERENCES TO TEST SIGNIFICANCE BETWEEN EXPERIMENTS IN THE SAME GROWTH PERIOD.

CGR and IPAR during SGP were always lower for rainfed than irrigated treatments (Table 3). However, RUE was not consistently affected by water levels (Table 3). CGR was significantly associated with IPAR during SGP (R^2=0.92; D.F.=6; P<0.0001; Fig. 3) but not with RUE (R^2=0.34; P=0.12).

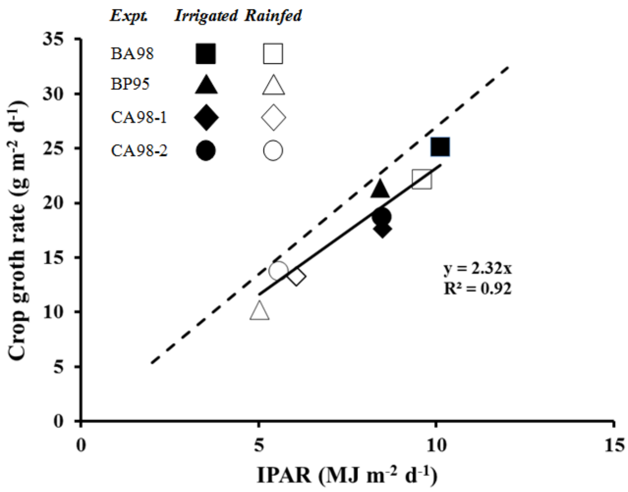

FIG. 3. MEAN CROP GROWTH RATE AS A FUNCTION OF MEAN INTERCEPTED PHOTOSYNTHETIC ACTIVE RADIATION DURING THE SPIKE GROWTH PERIOD, FOR EXPERIMENTS PERFORMED IN BALCARCE (BP95 AND BA98) AND CÓRDOBA (CA98-1 AND CA98-2) USING THE CULTIVAR PROINTA OASIS. THE INTERCEPT OF THE RELATIONSHIP IS NOT SIGNIFICANTLY DIFFERENT FROM 0. FILLED SYMBOLS CORRESPOND TO THE IRRIGATED TREATMENTS AND OPEN SYMBOLS, TO RAINFED TREATMENTS. THE S.E.D. FOR CGR AND IPAR ARE SHOWN IN TABLE 3. THE DOTTED LINE WAS OBTAINED FROM ABBATE ET AL. (1997).

3.4 Yield and their components

Yield was significantly affected by water level (Table 4). The highest and lowest yields under irrigation were obtained in BA98 and CA98-2, respectively. Grain yield decreased by 40% due to the effect of water stress (mean of all experiments). However, the magnitude of the differences changed across environments (Table 4).

TABLE 4
EFFECT OF WATER AVAILABILITY ON: GRAIN YIELD (GY), GRAIN NUMBER (GN) AND DRY WEIGHT PER GRAIN (WG) AT MATURITY; SPIKE WEIGHT (NOT INCLUDING GRAIN WEIGHT) AT THE END OF THEIR GROWTH PERIOD (SDW), SPIKE FERTILITY, DURATION OF SPIKE GROWTH PERIOD (DSGP); PARTITIONING TO SPIKE (PS) AND SPIKE GROWTH RATE (SGR) DURING THE SPIKE GROWTH PERIOD, IN EXPERIMENTS PERFORMED IN BALCARCE (BP95 AND BA98) AND CÓRDOBA (CA98-1 AND CA98-2) USING THE CULTIVAR PROINTA OASIS

Experiment	Treatment	GY	GN	WG	SDW	SF	DSGP	PS	SGR
	(Water level)	g m^{-2}	10^3 m^{-2}	mg	g m^{-2}	grains g^{-1}	days	%	g m^{-2} d^{-1}
BP95	**Irrigated**	520	14.6	35	170	86	27	28	6.3
	Rainfed	256	7.9	32	88	94	27	31	3.2
BA98	**Irrigated**	542	14.4	37	212	68	31	26	6.5
	Rainfed	417	12.4	34	175	78	32	24	5.3
CA98-1	**Irrigated**	494	14.3	35	197	74	31	35	6.1
	Rainfed	294	9.3	32	150	62	30	37	4.9
CA98-2	**Irrigated**	382	12.0	32	162	75	23	36	6.7
	Rainfed	204	7.6	27	131	58	23	41	5.5
Experiment Means									
BP95	---	388	11.3	34	128	90	27	29	4.7
BA98	---	479	13.4	36	193	70	31	25	5.9
CA98-1	---	394	11.8	33	173	68	30	36	5.5
CA98-2	---	293	9.8	29	147	66	23	38	6.1
Water Level Means									
---	**Irrigated**	485	13.9	35	185	76	28	31	6.4
---	**Rainfed**	293	9.3	31	136	71	28	33	4.7
S.E.D.$_1$ (12 D.F.)		17.9	0.51	0.6	5.0	5.4	0.5	1.8	0.24
S.E.D.$_2$ (12 D.F.)		12.7	0.36	0.5	3.6	ns	ns	ns	0.17
S.E.D.$_3$ (12 D.F.)		ns	0.72	ns	7.1	ns	ns	ns	ns

ns: non-significant difference between means (P>0.05).
S.E.D.$_1$: Standard error of mean differences to test significance between Experiment Means.
S.E.D.$_2$: Standard error of mean differences to test significance between Water Level means.
S.E.D.$_3$: Standard error of mean differences to test significance of Experiment×Water Level interaction.

The WG decreased 11% on average across treatments, with a range of variation between 9 and 16% (Table 4). The experiment × water level interaction for WG was not significant (Table 4). Variations in WG were almost four times lower than those found for yield. On the other hand, the effect of water stress on GN ranged from 14% to 46% between treatments (Table 4). The experiment × water availability interaction for GN was significant, but it represented only 7% of the total variability and was no crossed (Table 4); thus, although in all experiments the rainfed treatment produced a smaller number of grains than the irrigated treatment (Table 4). Within each experiment, the relationships between yield and WG or GN did not differ significantly (P>0.05) from those found using combined data from all experiments. Yield was more strongly associated with GN (R^2=0.95; P<0.0001) than with WG (R^2=0.64; P<0.0001). The relationship between WG and GN was positive and significant (R^2=0.46; P<0.0001).

No significant differences in PWG between experiments or between water levels were found, and the experiment × water availability interaction was not significant (Table 5). However, DSL was significantly affected by the water availability

(Table 5). Thus, the degree source limitation (100-DSL) was greater under rainfed conditions (mean 12%) than under irrigation (mean 5%) (Table 5).

TABLE 5
EFFECT OF WATER AVAILABILITY ON GRAIN WEIGHT (WG), POTENTIAL WEIGHT PER GRAIN (PWG) AND DEGREE OF SINK LIMITATION (DSL), IN EXPERIMENTS PERFORMED IN BALCARCE (BA98 AND BP95), USING THE CULTIVAR PROINTA OASIS.

Experiment	Water level	WG (mg)	PWG (mg)	DSL (%)
BP95	**Irrigated**	35	38	94
	Rainfed	32	37	89
BA98	**Irrigated**	37	39	96
	Rainfed	34	39	87
Experiment Means				
BP95	---	34	37	91
BA98	---	36	39	92
Water level Means				
---	**Irrigated**	36	39	95
---	**Rainfed**	33	38	88
S.E.D.$_1$ (6 D.F.)		0.5	ns	ns
S.E.D.$_2$ (6 D.F.)		0.5	ns	1.8
S.E.D.$_3$ (6 D.F.)		ns	ns	ns
ns: non-significant difference between means (P>0.05).				
S.E.D.$_1$: Standard error of mean differences to test significance between Experiment Means.				
S.E.D.$_2$: Standard error of mean differences to test significance between Water Level means.				
S.E.D.$_3$: Standard error of mean differences to test significance of Experiment×Water Level interaction.				

3.5 Spike dry weight relationship

The effect of water stress on GN was analyzed through the product between SDW and SF. The SF was not affected by water stress, but it showed differences between experiments (Table 4). The SDW showed a significant experiment × water level interaction (Table 4); however, the magnitude of the variability explained by this interaction was always smaller than that explained by the effect of experiment or water level individually (Table 4). Reduced water availability resulted in a decrease in SDW between 17 and 48% across experiments, with the highest values in BP95 (Table 4).

SDW was analyzed as the product between SGP duration and SGR. Duration of SGP was not affected by water availability. The main source of variation affecting the duration of the SPG was the location. SPG duration was 23 d in CA98-2 and 31 d in BA98 (Table 4). Rate of development (*i.e.* the inverse of the duration) during SGP of each experiment was positively associated with mean temperature (range: 15-21°C; R^2=0.89; *D.F.*=3; *P*=0.02). The ordinate to the origin of this relationship was not statistically different from 0 (*i.e.* T_b=0 °C) and the thermal time obtained was 474 °Cd; however, using the traditional value of T_b = 4.5 °C (Fischer, 1985), the fitted regression line was also significant (R^2=0.78; *D.F.*=4; *P*=0.02). According to this last model, the thermal time during SGP was 354 °C. Although duration of SGP was not affected by water level, anthesis date was about 9 days earlier by water stress effect in CA98-1 and CA98-2; however, in BA98 and BP95, anthesis date did not differed for treatments under rainfed and irrigated conditions. (Table 1).

SGR was significantly affected by water level. The effect of experiment × water level interaction was not significant over the SGR (Table 4). Rainfed condition reduced SGR by 25% (mean of all experiments), with a range of variation from 47% for BP95 to 20% for the rest of experiments (Table 4). SGR was analyzed as the product between CGR and PE. Location effect in the relationship between SGR and CGR was found. Models considering individually each location effect were significant (p <0.05; Fig. 4). Both relationships had an intercept significantly greater than 0, indicating an increase in the partition of assimilates when the CGR was reduced. The partitioning to spikes under rainfed conditions (mean of all experiments) was slightly higher than under irrigation, although this difference was not statistically significant. The highest values of assimilates partition to spikes were found in Córdoba (Table 4).

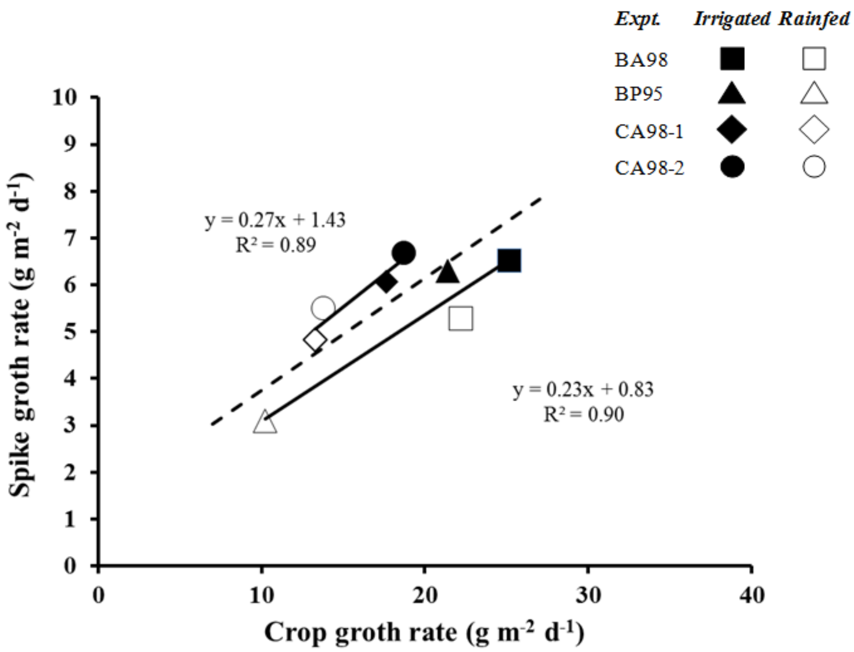

FIG. 4. MEAN SPIKE GROWTH RATE AS A FUNCTION OF MEAN CROP GROWTH RATE, FOR EXPERIMENTS PERFORMED IN BALCARCE (BP95 AND BA98) AND CÓRDOBA (CA98-1 AND CA98-2) USING THE CULTIVAR PROINTA OASIS. FILLED SYMBOLS CORRESPOND TO IRRIGATED TREATMENTS AND OPEN SYMBOLS, TO RAINFED TREATMENTS. THE S.E.D. FOR SGR IS SHOWN IN TABLE 4 AND FOR CGR IN TABLE 3. THE DOTTED LINE WAS OBTAINED FROM ABBATE ET AL. (1997).

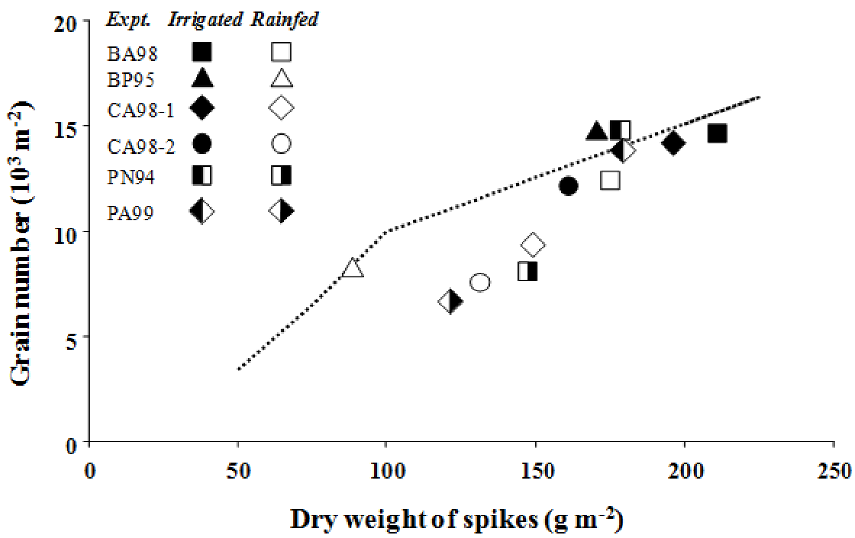

FIG. 5. RELATIONSHIP BETWEEN GRAIN NUMBER AND SPIKE DRY WEIGHT FOR EXPERIMENTS PERFORMED IN BALCARCE (BP95 AND BA98) AND CÓRDOBA (CA98-1 AND CA98-2) USING THE CULTIVAR PROINTA OASIS. DATA FROM PN94 AND PA99 WERE TAKEN FROM CAVIGLIA ET AL. (2001). THE DOTTED LINE OR REFERENCE WAS OBTAINED FROM ABBATE ET AL. (1997) AND LÁZARO AND ABBATE (2012) THE S.E.D. FOR NG AND SDW ARE SHOWN IN TABLE 4.

3.6 Grain number and climatic variables relationship

The relationship between GN and SDW for irrigated treatments did not differ from the bi-linear reference model of Abbate et al. (1997) and Lázaro and Abbate (2012) (Fig. 5). However, the GN obtained in some of the rainfed treatments was below that the expected under such relationship. The effect of water stress on GN was not observed in Balcarce, even with SDW decreases in rainfed treatments equal or greater than those in Córdoba (Fig. 5). This decrease was related to a weather variable according to Eq. [14]. Table 6 shows the contribution of several weather variables to the goodness of fit of Eq. [14]. The model obtained when VPDX was included in Eq. [14]

$$GN = 4878 + 51 \cdot SDW_H - \max(-10 + 91 \cdot VPDX,\ 51) \cdot \Delta SDW \qquad \text{Eq. [18]}$$

reduced to 8% the estimation error of GN, while estimation error for the bi-linear model of reference was 21%. Although other climatic variables also improved GN estimation, VPDX reported the greatest statistical significance (*P*=0.004), highest determination coefficient (R^2=0.93) and meets the conditions of Eq. [16] and Eq. [17] (*i.e.* $d > 0$ and $c < 0$). When the model using VPDX was validated with complementary data of Paraná (Fig. 5), it was able to predict accurately the GN with an estimation error of 11%, while the error for the bi-linear model of reference was 29%.

TABLE 6

STANDARD ERROR OF ESTIMATION (SEE) OF GRAIN NUMBER (GN) BY MEANS OF DIFFERENT WEATHER VARIABLES, WITH EQ. [14], FULFILLING THE CONDITIONS OF EQ. [16] AND EQ. [17], COEFFICIENT OF DETERMINATION (R^2) AND PROBABILITY OF FITTED MODEL (P-VALUE); VARIABLES ORDERED BY SEE.

Weather variable (independent variable)	SEE		R^2	P-value
	grain m^{-2}	%†		
VPDX (kPa)	917	7.9	0.93	0.0001
TAD (mm d^{-1})	928	8.0	0.92	0.0001
VPD (kPa)	945	8.2	0.92	0.0002
ETF56A (mm)	1050	9.1	0.90	0.0003
TAA (mm)	1093	9.4	0.90	0.0004
RHAVG (%)	1139	9.8	0.89	0.0005
RHMIN (%)	1155	10.0	0.88	0.0005
RHMAX (%)	1200	10.4	0.87	0.0007
TMAX (°C)	1220	10.5	0.87	0.0007
ETF56D (mm d^{-1})	1340	11.6	0.84	0.0013
IPAR (MJ m^{-2} d^{-1})	1357	11.7	0.84	0.0014
PTQ (MJ m^{-2} d^{-1} $°C^{-1}$)	1358	11.7	0.84	0.0014
TAVG (°C)	1461	12.6	0.81	0.0022
TMIN (°C)	1646	14.2	0.76	0.0046
Abbate et al. (1997) and Lázaro & Abbate (2012) model ‡	2406	20.8	0.49	0.0522
† SEE as percentage of mean GN.				
‡ Dotted line of Fig. 5; the statistical corresponds to error of estimation of data of this study.				

IV. DISCUSSION

4.1 Water stress

By comparing crop growth and GAI at the beginning of SGP between treatments (Fig. 2, Table 3), it is clear that initial water deficiency in BP95 was as high as in Córdoba experiments. This growth reduction did not occur in BA98, where WU until the start of SGP was similar to the condition under irrigation, showing a low level of stress in terms of CDW up to that moment. On the other hand, in experiments CA98-1 and CA98-2, water deficiency was evident before the beginning of SGP. These differences in water supply were frequently reported in the Argentine sub-humid and semi-arid wheat region (Magrín, 1990; Savin et al., 1995; Brisson et al., 2001; Abbate et al., 2001a). For the sub-humid southeast wheat region (i.e. Balcarce) the crop is usually exposed to water stress from the beginning of SGP. In the semi-arid northwest wheat region (i.e. Córdoba), crop growth is more related with the water stored in the soil profile at planting, with the possibility of extreme drought before SGP. According to Lázaro (1996), in Balcarce accumulated rainfall between March and August is usually (95% of years) restores the soil available water (1 m depth) and this amount of water is enough for the crop to reach full radiation interception before the start of SGP. However, this was not the case for the year 1995 in Balcarce or in semi-arid areas such as Cordoba, where it is difficult to achieve a high soil profile recharge of water before planting.

4.2 Crop dry weight

The CDW was reduced by water stress at the beginning and end of SGP (Fig. 2), with variable magnitude among experiments (Table 3). However, despite these differences, CGR was linearly associated with IPAR during SGP and not with RUE. Then, growth during SGP was more conditioned by the low amount of radiation captured by the crop during that period, due to a low GAI under water stress, than by a decrease in its photosynthetic activity per unit of leaf area (Table 3). This is consistent with previous reports indicating that reductions in crop growth may be better explained by decreases in light capture rather than by decreases in photosynthetic activity (Hsiao, 1973) or RUE (Gallagher and Biscoe, 1978; Whitfield and Smith, 1989; Robertson and Giunta, 1994; O'Connell et al., 2004). The average value of RUE found in this study was 2.3 g MJ^{-1} (Table 3), this value was lower than the found by Abbate et al. (1997) for the same cultivar in Balcarce. Kemanian et al. (2004) found that RUE decreased with increasing VPDX. According to the equation proposed by those authors, it could be estimated a mean RUE of 2.7 and 2.4 g MJ^{-1} PAR intercepted, for data of Abbate et al. (1997) and for the present work, respectively. These estimated values are similar to those observed in both studies; therefore, most of the differences in RUE between these studies can be explained by differences in VPDX.

4.3 Yield and their components

Water stress produced a significant reduction in yield in all experiments. Although water stress reduced WG, the greatest effect was observed in GN, being this component the most associated with yield. These results are consistent with those of García del Moral et al. (2003) and the calculated from data of Robertson and Giunta (1994), who reported that decreases in GN was obtained as a result of reduction in water supply close to anthesis.

The WG was less affected by water stress than GN, despite the high decrease in WU and CDW during the grain-filling period (Fig. 1; Fig. 2).This behavior can be attributed to two causes. First, while water stress significantly reduced, in mean, crop growth during grain filling, from 375 g m^{-2} with irrigation to 206 g m^{-2} without irrigation (equivalent to 45%, Fig. 2), when this growth was expressed per grain, the difference resulted of less magnitude (average 13%). Second, a proportion of assimilates accumulated during pre-anthesis had to be remobilize to the grain during the filling period. The calculated mean remolization was 9% of the crop weight at the end of SGP, value close to that reported by Bidinger et al. (1977) and Blum (1983). Third, the PWG was not affected by water level, although there was a significant source limitation under rainfed conditions (Table 5). This limitation was not important enough to significantly reduce WG. In addition, there were no negative effects on WG in the presence of a greater GN. The relationship between WG and GN was positive (R^2=0.73; P<0.007). Borrás et al. (2004) indicated that the magnitude of the limitation by source of assimilates in wheat during the filling period is of little importance in comparison to the sinks capacity. This fact would be of more importance as more early the stress occurs.

4.4 Spike dry weight

SDW was analyzed as the product of the duration of SGP and SGR. Duration of SGP was not affected by water availability (Table 4), and the differences found between experiments were due to changes in temperature. The thermal time during SGP found using a T_b of 4.5 °C was statistically similar to that reported for Lázaro and Abbate (2012) in the same cultivar (354 vs. 305 °Cd, respectively) and within the range found in different wheat cultivars reported by Whitechurch et al. (2007). However, in Córdoba experiments, crop cycle until anthesis was shorter due to low water availability (Table 1). Idso et al. 1980 and Jensen et al. (1990) data showed small differences in canopy temperature between irrigation and rainfed treatments under low VPD, but these were differences up to 4°C with VPD comparable to those of Córdoba. Therefore, the high VPD in the Córdoba experiments may have led to a higher canopy temperature and a shorter crop cycle. In Balcarce the lower VPD did not produce differences in canopy temperature between irrigation and rainfed treatments. There are records of a reduction in crop cycle under moderate water stress conditions (Angus and Moncur, 1977; Magrín, 1990; van den Boogaard et al., 1996) as that observed in the experiments in Córdoba. However, no reports were found regarding the dependence of SGP duration of water stress (Table 4), the result of the present work indicates that SGP duration is not directly influenced by water supply. Other authors found no influences of N stress (Abbate et al., 1995; Demotes-Mainard et al., 1999) or P stress (Lázaro et al., 2010) on SGP duration in wheat. Then, differences in SDW due to water stress can be explained mainly by changes in SGR.

The SGR was analyzed through the CGR and the proportion of CDW partitioned to spikes. A positive relationship was found between SGR and CGR, and a larger PE towards reproductive organs in the presence of lower growth values. Boogaard et al. (1996) reported a higher harvest index in wheat under water stress, suggesting a higher PE towards reproductive organs with water stress. However, Robertson and Giunta (1994) reported equal or less partition to spikes at anthesis with water stress. Other authors working with shading (Abbate et al., 1997), N deficiencies (Abbate et al., 1995) or P deficiencies (Lázaro et al., 2010) also observed increases in PE to spikes in the presence of lower values of CGR during SGP.

In the present work, although partitioning to spikes was not significantly affected by water stress, an increase in partitioning to spikes at environments where CGR was lower was found, indicated by a positive intercept in Fig. 4. In BA98, CGR decreased by 12% by water stress, whereas in BP95, CA98-1 and CA98-2, CGR decreased by 52, 24 and 26%, respectively (Table 3). However, no association between SDW and PE to spikes was found. Thus, changes observed in SDW under water stress, cannot be attributed to this component. These results are consistent with those found previously in response to environmental changes (Fischer, 1985; Abbate et al., 1995; Abbate et al., 1997; Lázaro et al., 2010), indicating that SGR was more related to CGR than PE to spikes.

4.5 Grain number and spikes dry weight relationship

GN variations could be well explained by changes in assimilates supply (i.e. SDW) when water was not limiting, but SDW is not enough as the only estimator of GN under water stress conditions. Thus, the bi-line relationship proposed by Abbate et al. (1997) and Lázaro and Abbate (2012) under irrigated conditions (Fig. **5**) overestimated the GN obtained in the rainfed treatments in Córdoba experiments. Additional data from the experiment conducted in Paraná also separated from that relationship (Fig. **5**).

Larger decreases in GN than the reference values of the bi-linear relationship in Fig. **5**, suggests the presence of an additional mechanism that regulates GN determination under water stress. Fischer (2011) also showed that, under water stress conditions, there are additional depressors of the grain number per spike, due to effects on the spikes fertility. Data of the present work did not reveal significant differences in SF due to water stress; however, the expected response without water stress (according to Abbate et al., 1997, Lázaro and Abbate, 2012, and the line of Fig. **5**) is the increase in SF when SDW is reduced. Nevertheless, in Córdoba water stress always tended to reduce SF, and this decrease was greater in CA98-2. In Balcarce, water stress affected GN through a reduction in SDW, while in Córdoba, water stress also reduced directly GN. These effects could be related to different weather variables between experiments. VPDX was the weather variable that best explained GN under water stress condition in comparison with the relationship found by Abbate et al. (1997) and Lázaro and Abbate (2012) under irrigation. The prediction model obtained (Eq. [18]) involves a reduction in GN by water stress due to a lower spike growth. There is also an additional negative effect which is controlled by the VPDX. Others weather variables had a good model fit and the VPDX could summarized most of them and can be calculated easily. Historical VPDX mean for Balcarce close to anthesis average date (10-Nov) is 0.85 kPa, while in Córdoba is 1.40 kPa for an anthesis date at 10-Oct. For an average SDW_H in Balcarce and Cordoba of 185 g m^{-2} and 136 g m^{-2} for irrigated and rainfed conditions (Table 4), using Eq. [18] estimations indicates that GN reduction in Cordoba would be close to 40% while in Balcarce should be only 23%. It is expected that under similar reductions in WU or crop growth during SGP, Córdoba will present a greater decrease in GN due a more restrictive environmental conditions for wheat than Balcarce.

No studies have linked GN reduction by water stress with climatic factors as in this work. Fischer (1973) found GN reduction induced by male sterility, suggesting the existence of an additional negative effect in the presence of water stress and therefore the decrease in GN would not only controlled by crop photosynthesis. Changes in the histology, hormone and gene expression have been also associated to these mechanisms (Koonjul et al., 2005). Additional effects reducing GN, similar to those reported in this work for water stress conditions, have been previously found (Abbate et al., 1995) under N limiting situations.

In conclusion, under water stress conditions, grain yield decreased more closely associated with a decrease in GN than in WG. The relationship between GN and SDW was affected by water deficit. This suggests that decreases in GN under water stress is not only influenced by assimilates availability for spike growth; there are also weather variables causing additional effects. The inclusion of VPDX in a model for GN predictions increases the accuracy of estimations. This could be helpful to understand and estimate wheat yields in regions where water stress is a limiting production factor.

This work is part of a thesis submitted by M. Cantarero in partial fulfillment of the requirements for the Doctoral degree, Universidad Nacional de Córdoba.

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