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Relationship between yield, growth and spike weight in wheat under phosphorus deficiency and shading

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SUMMARY

The effect of phosphorus deficiency on yield formation in spring wheat (*Triticum aestivum* cv. Prointa Oasis) was investigated, focusing on crop growth and dry matter partitioning during the spike growth period (SGP), which is critical for grain number determination. Two experiments combining shading and P deficiency were performed at Balcarce, Argentina (37°45′S). The main treatments were two levels of soil P-availability: low P, a naturally low P fertility soil (7·0 and 5·5 mg Bray extractable P/kg soil, in the first and second experiments respectively) and high P, a P dose that does not limit growth. The sub-treatments were two levels of radiation (shaded and control). Phosphorus deficiency affected yield mainly through the number of grains/unit surface (m^2). Differences in grain number/m^2 were related to differences in dry weight of spikes/m^2, measured 7 days after anthesis, excluding grain weight. The duration of the SGP did not change much as result of P deficiency: 27 days with high P and only 3 days more with low P. Therefore, changes in spike dry weight were mainly due to differences in spike growth rate. In turn, the spike growth rate of all treatments was linearly related to crop growth rate, with little effect of dry matter partitioning to spikes. Finally, differences in crop growth rate between P treatments were mainly determined by the amount of intercepted radiation. It was concluded that P deficiency resulted in a reduction in intercepted radiation during the SGP, thus causing a reduction in grain number and crop yield.

INTRODUCTION

Phosphorus is one of the least available macronutrients in soil (Vance *et al.* 2003) and frequently limits wheat yield in many areas of the world, e.g. Argentina (Berardo 1994; Rodriguez *et al.* 2000), Australia (Elliott *et al.* 1997; Norrish 2003), Mexico (Egle *et al.* 1999; Manske *et al.* 2000, 2001, 2002), Brazil (Rosa & Camargo 1991) and sub-Saharan Africa (Daroub *et al.* 2003). For this reason, wheat crops are habitually supplied with inorganic P fertilizers. Projections for the year 2020 predict a 50% increase in the demand for phosphorus fertilizers because of the increasing demand for food by the growing world population (Manske *et al.* 2000). Today, phosphorus is an expensive input used by farmers to achieve a desired crop yield; however, the non-renewable nature of inorganic P fertilizers means that cheap sources of P will be exhausted within the next 60–90 years (Hammond *et al.* 2004). In addition, an excess of P added to crops may pollute local watercourses and contribute to the process of eutrophication (Withers *et al.* 2001). Within the general context of environmental and economic concerns, accurate management of phosphorus becomes a key factor for achieving a successful wheat crop.

There is evidence that the main effect of P availability on wheat yield is observed in the number of grains/unit ground area (Elliott *et al.* 1997; Manske *et al.* 2000). It has been reported that P deficiency reduces the leaf expansion rate, decreases the number of tillers and increases the thermal time between successive leaf expansions, thus controlling the amount of intercepted solar radiation (Rodriguez *et al.* 1999,

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2000). However, most of these studies have been carried out either on young plants grown in controlled environments, using short time scales (Plenét *et al.* 2000*a*), or in small containers with other crops, such as barley (Prystupa *et al.* 2004). Other studies of P deficiency at the grain yield level, carried out in fields, have been based on the numerical yield components analysis (Egle *et al.* 1999; Manske *et al.* 2000, 2001, 2002) and not on an assimilate-based approach. In the latter approach, grain number/m² is interpreted in terms of dry weight of spikes/m² before grain filling and number of grains/unit of spike weight (Fischer 1984, 1993; Abbate *et al.* 1995; Demotes-Mainard & Jeuffroy 2001). The dry weight of spikes reflects the quantity of photoassimilates allocated by the crop for the production of flowers (future grains) until anthesis. The photoassimilate supply may determine the survival of initiated flowers and, subsequently, the number of grains/m² (Fischer 1984; Abbate *et al.* 1995).

Abbate *et al.* (1995, 1997) have analysed wheat crops without water or nutrient limitations at Balcarce (latitude, 38°S), and confirmed Fischer's (1985) results that: (i) intercepted radiation is the main factor determining crop and spike growth until anthesis, (ii) grain number/m² is positively related to spike dry weight (SDW) and (iii) grain number/m² is positively related to accumulated intercepted solar radiation during the spike growth period (SGP). However, when the model was used in situations with variable N availability, the conclusions differed between authors. Fischer (1993) and Demotes-Mainard & Jeuffroy (2001) concluded that the number of grains is limited by the supply of carbon assimilates, whereas Abbate *et al.* (1995) compared the effects of N and shading and concluded that low N during the SGP reduces the number of grains not only by lowering dry weight of the spike but also by producing other effects which could not be explained in terms of crop carbon economy. More recently, Sinclair & Jamieson (2006) have highlighted the importance of resource accumulation, particularly that of N, for both grain number and yield determination, an approach that Fischer (2008) criticized.

In contrast to nitrogen, there are no reports on the effects of P deficiencies on the relationships between grain number, crop growth, SDW and the quantity of intercepted radiation. The aim of the present paper was to compare the effect of P deficiency with that resulting from reductions in incident radiation, in order to clarify the effect of P on wheat grain number determination. This analysis provides a better understanding of the effects of P deficiency and will thus guide crop management and allow estimation of wheat yield when P supply is limiting. Some of the high P treatment results reported in the present paper have been presented previously by Abbate *et al.* (1997).

MATERIALS AND METHODS

Management and experimental design

Two experiments were carried out at the Unidad Integrada Balcarce, Argentina (37°45′S, 58°18′W, altitude 130 m asl) during the 1994/95 (Expt 1) and 1995/96 (Expt 2) growing seasons. The soil was a loamy, illitic, thermic, typic Argiudoll (Soil Survey Staff 2003) with approximately 6·0 g organic matter/kg soil in the top 250 mm and adequate K fertility (>2·8 mmol/100 g). A commercial spring bread wheat cultivar (Prointa Oasis) was tested. The experiments combined two P levels (low and high as main treatments) and two radiation levels (shade and control as sub-treatments) in a split-plot design with three (Expt 1) and four (Expt 2) complete randomized blocks. The available P in the top 200 mm of the low P level treatment was 7 mg P/kg (Bray I) in Expt 1 and 5·5 mg P/kg in Expt 2. These soil P levels were deficient according to the local calibration (Berardo, 1994). The high P treatments were fertilized with 80 and 84 kg P/ha in experiments Expt 1 and Expt 2, respectively, in order to assure non-limiting P availability. The fertilizer was broadcast and incorporated before sowing. Two levels of radiation were applied during the SGP. The levels were natural radiation incidence (0·00 shading) and shade (0·56 of the natural radiation incidence). Shade was achieved by means of black nets placed 100–200 mm above the canopy. Mean temperature under the nets over a 24 h cycle was 1·5 °C lower, while mean maximum temperature was 5·2 °C lower and mean minimum temperature was 0·9 °C higher, than in unshaded plots (Abbate *et al.* 1997). The subplots were 7·5 m long, 7 or 10 rows wide and with rows 0·15 m apart in Expt 1 and 0·20 m apart in Expt 2. All treatments received 253 kg N/ha applied in three equal applications to ensure adequate N supply. These amounts of fertilizer were enough to ensure adequate nutrient supply. Expt 1 was rain fed, whereas Expt 2 was irrigated until maturity to ensure sufficient water availability. The experiments were free of pests and diseases. Seeds were treated with a benomyl–thiram mixture before seeding and weeds were controlled with a commercial mixture of *metsulfuron metil* (5 g a.i./ha) and *dicamba* (60 g a.i./ha) (Misil II). The number of established plants, duration of the period, levels of shading recorded at noon and relevant dates of experiments are presented in Table 1.

Plant sampling and measurements

Emergence date was considered as the date when half of the plants had their first leaf emerged to approximately 10 mm. Date of terminal spikelet (when the first floral primordium was observed in the terminal spikelet) was determined by dissection of four randomly selected main stem shoot apices per plot every

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Table 1. *Dates and number of days from emergence of wheat* (*cv. Prointa Oasis*) *to key growth stages for experiments Expt 1 and Expt 2, at Balcarce* (*high P data from Abbate* et al. *1997*)

Experiment:	Expt 1				Expt 2			
P level:	Low		High		Low		High	
Shading proportion	0·00	0·56	0·00	0·56	0·00	0·56	0·00	0·56
Preceding crop	Sunflower				Pasture			
Sowing date	8 Aug 1994				18 Aug 1995			
Emergence date	23 Aug 1994				30 Aug 1995			
Plants established/m²	270				349			
Days from emergence to:								
Terminal spikelet	49	49	49	49	49	49	47	47
Anthesis	89	88	86	87	88	88	84	85
Beginning of shading	–	65	–	65	–	70	–	70
End of shading	–	97	–	97	–	91	–	91
Beginning of SGP*	65	65	66	67	70	70	64	64
End of SGP	95	95	93	94	96	96	91	92

* SGP, spike growth period.

2–4 days. Date of anthesis was defined as the moment when half of the spikes exposed at least one anther. The dates were determined by linear interpolation from measurements made on 40 randomly selected spikes per plot, every 2–3 days. To measure crop dry weight (CDW), plants were cut at ground level, dried at 56 °C for 10 days to constant weight and weighed. Sample size was four to five innermost rows wide and 0·4–0·6 m long before anthesis, 0·6–0·7 m long after anthesis and 0·7–0·8 m long after maturity. A distance of at least 0·35 m was left as borders between successive quadrants. A subsample of shoots was dissected into leaf lamina stems (including leaf sheaths) and spikes, even when they were small (length >5 mm). After anthesis, the number of spikes per unit of area was calculated. In a subsample of spikes, the immature grains were removed to determine dry weight of non-grain spikes. The green area index (GAI) was determined by measuring the area (one side) of all green organs (i.e. leaves, stems and spikes when present) in a subsample of shoots, with an area meter LI-3000 (LI-COR, Lincoln, Nebraska, USA). After physiological maturity, plots were hand-harvested and all spikes of the sample were threshed. The grains were winnowed and afterwards dried and weighed to determine yield. A grain subsample was taken and manually cleaned to determine dry weight/grain by counting, drying and weighing two groups of 500 grains each. The number of grains/unit area (GN) was estimated by dividing yield by the individual grain dry weight.

The SGP was considered as in Abbate *et al.* (1997), i.e. the interval during which the spikes achieved from 0·05 to 1·00 of the non-grain weight they had accumulated by day 7 after anthesis. Linear interpolation of spike and CDW through time was used to estimate CDW at the beginning of spike growth. All treatments were sampled on the same date; the difference between sampling time and the end of spike growth was −1 to 3 days. During the SGP, mean growth rates (g/m²/d) of crop (CGR) and spikes (SGR) were calculated, and mean dry weight partitioning to spikes was calculated as SGR/CGR and expressed as a proportion. Weather records (Table 2) were obtained from a meteorological station located approximately

Table 2. *Mean temperature, incident PAR and rainfall from emergence to beginning of the SGP* (*period 1*), *during the SGP* (*period 2*) *and from anthesis to 35 d after* (*period 3*), *for high P and unshaded treatments of 1994 and 1995 experiments* (*from Abbate* et al. *1997*) *and historical values at Balcarce*

Experiments	Period 1	Period 2	Period 3
	Temperature (°C)		
Expt 1 – 1994	11·8	17·3	19·4
Expt 2 – 1995	12·4	16·2	18·3
Historical*	11·2	15·4	18·0
	Incident PAR (MJ/m²/d)		
Expt 1 – 1994	6·7	12·9	11·6
Expt 2 – 1995	7·6	10·5	13·1
Historical*	7·2	10·2	11·0
	Precipitation (mm)		
Expt 1 – 1994	175	31	202
Expt 2 – 1995	111	160	89
Historical*	123	76	88

* Mean of 1970–2005 period.

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Table 3. *The effects of P deficiency and crop shading on dry grain yield, grain number and dry weight per grain at maturity; grain number per unit of spike weight (excluding grain weight) at the end of the SGP; partitioning to spikes and SGR, during the SGP, in Expt 1 and Expt 2 for cv. Prointa Oasis at Balcarce (high P data from Abbate* et al. *1997)*

Treatment		Grain yield (g/m^2)	Grain number ($10^3/m^2$)	Weight per grain (mg)	Spike weight (g/m^2)	Grain/g of spike (num./g)	Duration of SGP (days)	Partitioning to spike	SGR ($g/m^2/d$)
Shading (%)	P level								
Expt 1									
0	High	490	17	29·0	228	74	27	0·34	7·7
0	Low	345	13	25·8	181	74	30	0·31	5·5
56	High	346	11	31·4	140	79	28	0·44	4·6
56	Low	245	9	27·0	101	90	30	0·29	3·0
S.E.D. (6 D.F.)*		20·9	6	0·59	7·2	2·7	0·6	0·022	0·28
S.E.D. (6 D.F.)†		20·3	5·6	0·67	5·7	2·9	ns	0·020	0·22
Expt 2									
0	High	520	14·6	35·4	170	86	27	0·28	6·0
0	Low	202	7	31	80	84	26	0·38	2·9
56	High	368	11	35	107	97	28	0·35	3·8
56	Low	148	5	32	50	98	26	0·62	1·8
S.E.D. (6 D.F.)*		29·9	7·1	1·0	5·9	13·1	0·3	0·034	0·21
S.E.D. (6 D.F.)†		28·7	7·3	1·6	5·8	9·8	ns	0·056	0·21

ns: not significant ($P > 0·05$).
* Standard errors of mean differences to compare P treatments at the same levels of shading.
† Standard errors of mean differences to compare shading at the same or different levels of P deficiency.

1 km away from the experimental site. Daily proportion of incident photosynthetically active radiation (PAR = 0·5 of total radiation) that was intercepted by the crop (intercepted PAR (IPAR)) was calculated as $(1 - PAR_i/PAR_o)$, where PAR_i was the incident PAR just above the lowest layer of dead leaves and PAR_o was the incident PAR above the crop canopy. The values of PAR_i and PAR_o were measured with a line quantum sensor (LI-COR 191SB, LI-COR, Lincoln, Nebraska, USA) connected to a radiometer (LI-COR 188 B). The measurements were taken at midday, placing the sensor perpendicularly to the rows. Approximately one recording per metre of plot was taken. IPAR was measured every 10–15 days; IPAR between measurements was obtained by linear interpolation over time. IPAR ($MJ/m^2/d$) for each day was calculated as the product of the corresponding daily IPAR fraction and daily incident PAR. Radiation-use efficiency (RUE, g/MJ) was calculated as the ratio between CGR and the mean IPAR during the SGP. Also, the Fischer's (1985) photothermal quotient ($MJ/m^2/d/°C$), defined as the ratio of mean IPAR to mean air temperature minus 4·5 °C (developmental base temperature) during the period from 20 days before to 10 days after anthesis (Abbate *et al.* 1995) was calculated for each plot.

In Expt 2, pairs of main shoots or first tiller spikes with the same number of spikelets and same day of anthesis were selected and tagged 3–5 days after anthesis. Five pairs were selected in each plot. Spikelets in one member of each pair were removed with scissors, leaving only the four central ones, two on each side of the rachis. At maturity, the grains of the trimmed spikes and the corresponding grains of untrimmed spikes were harvested. Grains were counted, dried and weighed. Weight per grain of trimmed spikes was considered as an estimator of potential weight/grain and the difference between the weights/grain of trimmed and untrimmed spikes was used as an estimator of the degree of source limitation (Fischer & HilleRisLambers 1978).

Statistical analyses

Differences between treatment means in each experiment were examined if the analysis of variance revealed significant differences. Regression analysis was used with treatment means. The level of significance used was $P < 0·05$ in all statistical tests.

RESULTS

Yield and components

Phosphorus deficiency reduced yield by 30% in Expt 1 and by 61% in Expt 2 (Table 3). In Expt 2, yield in low P was 41% lower than that in Expt 1, and the

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Table 4. *Weight per grain* (*weight per grain of central spikelets of untrimmed spikes*), *potential weight per grain* (*weight of grain of trimmed spikes*) *and degree of sink limitation* (*actual*/*potential*), *with and without P fertilization, in experiment Expt 2 for cv. Prointa Oasis, at Balcarce*

P level	Weight per grain (mg)	Potential weight (mg)	Sink limitation
High	39	37	0·94
Low	33	31	0·98
S.E.D. (3 D.F.)*	3·4	1·6	ns

ns: not significant (test F, $P > 0{\cdot}05$).
* Standard error of mean differences to compare P level.

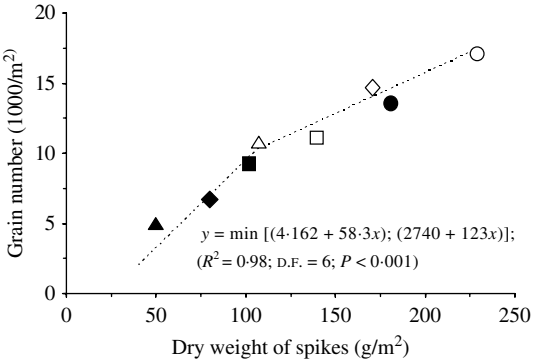


Fig. 1. Number of grains (measured 7 days after anthesis) as a function of dry weight of spikes by the end of their growth period in experiments Expt 1 and Expt 2, with cv. Prointa Oasis at Balcarce (high P data from Abbate *et al.* 1997). The two-line regression was obtained by Abbate *et al.* (1997) without deficiency. Symbols in Expt 1: ○ without shading, high P level; ● without shading, low P level; □ with shading, high P level; ■ with shading, low P level and in Expt 2: ◇ without shading, high P level; ◆ without shading, low P level; △ with shading, high P level; ▲ with shading, low P level. The S.E.D. are shown in Table 3.

available soil P was 21 % lower in Expt 2 than in Expt 1. On the other hand, yield with high P was only 5 % greater in Expt 2 as compared to that in Expt 1. Shading, which reduced incident radiation during the SGP to 0·56 of full (unshaded) incident radiation, reduced yield by 30 % in both experiments. The effect of P deficiency and shading on yield can be analysed in terms of their effect on weight/grain and GN.

Weight per grain was affected by P deficiency, but the reduction on weight in low P as compared with high P was only 12 % (mean of both experiments, Table 3). This reduction is far smaller than that observed for grain yield. In Expt 2, weight/grain of whole and trimmed spikes was compared and found to be similar (Table 4). Both grain number and yield were reduced by P deficiency and shading, without a significant P × shading interaction. The decrease in GN in low P as compared with that in high P was 19 % in Expt 1 and 56 % in Expt 2 (mean of with and without shading, Table 3).

Grain yield was highly and positively correlated with GN ($R^2 = 0{\cdot}99$, $P \leqslant 0{\cdot}001$) but not with weight per grain ($R^2 = 0{\cdot}38$, $P = 0{\cdot}08$). To remove secondary environmental effects on Expt 1 and Expt 2, the correlations were carried out using standardized deviations calculated as: (treatment value − experiment mean)/experiment mean. The above results clearly indicate that the effects of P deficiency and shading on yield were mainly due to a proportional reduction in GN and not in the weight/grain.

Grain number and dry weight of spikes

The effects of P deficiency and shading on GN were analysed in terms of (i) the dry weight of spikes/m² (SDW) before grain filling and (ii) the number of grains/unit of spike weight. The number of grains/unit of spike weight was not affected by P deficiency or shading in Expt 2, but an increase in the number of grains/unit of spike weight in the shading treatment was observed in Expt 1 (Table 3). The GN and SDW of all treatments were compared with the two regression lines obtained by Abbate *et al.* (1997) to obtain more information about the relationship between both variables (Fig. 1). No particular deviation was observed in the relationship between GN and SDW for P deficiency with respect to the regression lines obtained without P deficiency with the same cultivar as that described in Abbate *et al.* (1997). Therefore, the reduction in GN as a result of P deficiency and shading is explained by a reduction in SDW.

SDW was reduced notably by both P deficiency and shading (Table 3). Low P reduced SDW by 24 % in Expt 1 and by 53 % in Expt 2 (Table 3) as compared with high P (mean of with and without shading). Shading reduced SDW by 42 % in Expt 1 and by 37 % in Expt 2 (mean of with and without P deficiency) and P × shading interaction effects were not statistically significant.

SDW before grain filling is a product of the SGR and the duration of the SGP. The mean duration of SGP was 28 days, with differences of less than 3 days between treatments and experiments (Table 1). No differences were found in the duration of the SGP between shaded and non-shaded treatments; however, P deficiency slightly increased the SGP (Table 3) in Expt 1.

The SGR is a product of CGR and the proportion of crop growth that is partitioned to the spike. Dry matter partitioning towards the spikes was different in each experiment (mean value: 0·41 for Expt 1 and

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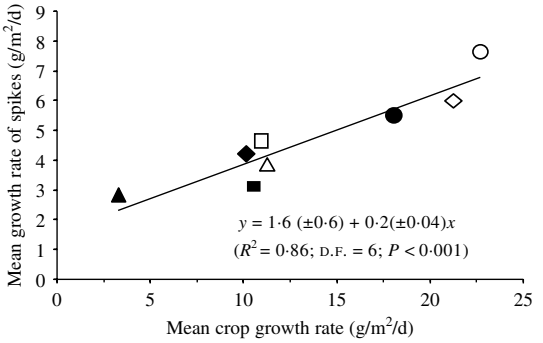


Fig. 2. SGR mean and mean CGR during the SGP, in experiments Expt 1 and Expt 2 with cv. Pronta Oasis at Balcarce (high P data from Abbate *et al.* 1997). Symbols in Expt 1: ○ without shading, high P level; ● without shading, low P level; □ with shading, high P level; ■ with shading, low P level and in Expt 2: ◇ without shading, high P level; ◆ without shading, low P level; △ with shading, high P level; ▲ with shading, low P level. The S.E.D. are shown in Tables 3 and 5.

0·34 for Expt 2, Table 3). In Expt 1, P deficiency diminished dry weight partitioning to shoots but did not affect the partitioning to spikes (Table 3). In Expt 2, partitioning was increased by both P deficiency and shading. A clear linear relationship between SGR and CGR (Fig. 2) was found throughout all treatments ($R^2 = 0{\cdot}86$; D.F. = 6; $P \leqslant 0{\cdot}01$). The slope of this relation was $0{\cdot}23 \pm 0{\cdot}038$ and the intercept was greater than zero ($1{\cdot}6 \pm 0{\cdot}56$ g/m²/d; Fig. 2). Furthermore, partitioning to spikes was not related to SDW at the end of the SGP.

Crop growth during the SGP

Crop growth was reduced by P deficiency from very early stages of crop development (Table 5). As compared with high P, low P decreased CDW and GAI at the beginning of the SGP by 62% in Expt 1 and by 50% in Expt 2 (Table 5). At the end of the SGP, 7 days after anthesis, CDW in low P was 35 and 60% lower than in high P treatments in Expt 1 and Expt 2, respectively (mean of with and without shading). Reductions in GAI due to P deficiency were 54% in Expt 1 and 73% in Expt 2 (Table 5).

Shading during the SGP decreased CDW by 30% in both experiments (Table 5) but no effects on GAI were detected (Table 4). No P × shading interaction was found for CDW or GAI. IPAR was affected by P deficiency and shading. P deficiency reduced IPAR more in Expt 2 than in Expt 1 (Table 5). The CGR was linearly related to IPAR ($R^2 = 0{\cdot}92$; $P = 0{\cdot}004$). The slope of this relationship ($2{\cdot}2 \pm 0{\cdot}09$ g/MJ) represented the mean RUE since the constant term did not differ from zero.

With high P, the RUE of the non-irrigated experiment Expt 1 was 2·0 g/MJ (Table 5) whereas that corresponding to the irrigated experiment Expt 2 reached 2·5 g/MJ. Shading did not affect RUE. Phosphorus deficiency reduced RUE by 36% in Expt 2, but no effect was found in Expt 1 (Table 5). However, the effect of P deficiency on CGR during the SGP was higher than on RUE (mean fall for both experiments in CGR was 67%, Table 4).

Despite the changes in grains/spike weight and RUE (Table 5 and Fig. 2) among treatments and experiments, there was a unique and highly significant correlation between GN and the photothermal quotient (Q) ($GN = 2810(\pm 1220) + 15820(\pm 2190)Q$; $R^2 = 0{\cdot}90$; $P \leqslant 0{\cdot}05$; Fig. 3). The temperature during the SGP changed less than 7% between experiments (Table 2) and even less between shading treatments. Therefore, the relationship between GN and Q was mostly controlled by intercepted radiation. Consequently, GN was linearly correlated with the mean IPAR during the SGP ($R^2 = 0{\cdot}85$; $P \leqslant 0{\cdot}01$; Fig. 4).

DISCUSSION

Yield

Grain yield was reduced by P deficiency and shading. However, while the reduction in yield produced by shading was similar in both experiments, the reduction produced by P deficiency was higher at Expt 2 (Table 3). These differences in the effects of P stress between experiments may be attributed to differences in soil P availability. In Expt 2, available soil P was 21% lower than in Expt 1 and yield in low P was 41% lower in Expt 2 than in Expt 1; however, yield with high P was very similar in both years.

Although weight/grain was slightly lower (10–14%) with P deficiency, the effects of P-stress and shading on yield were mainly associated with a reduction in GN (Table 3). Rodriguez (personal communication) and Egle *et al.* (1999) also found that weight/grain is relatively unaffected by P deficiency and that the differences in grain yield under P stress are determined only by its effects on the yield components defined early in the growing season. Moreover, the equivalence of the weight/grain of whole and trimmed spikes (Table 4) indicates that the degree of source limitation was not affected when P deficiency reduced sink number. Plenét *et al.* (2000*b*) reached a similar conclusion for maize. Nevertheless, potential grain weight with P deficiency was lower than that of non P-stressed plants (Table 4).

SDW

SDW just before grain filling is the result of the product between the duration of the SGP and the SGR. Although differences were found in the present work in the duration of the SGP (Table 3), these results are not conclusive. Phosphorus deficiency

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Table 5. *The effects of P deficiency and shading on: CDW and GAI at the beginning and at the end of the SGP; CGR; IPAR; RUE during the SGP in experiments Expt 1 and Expt 2 for cv. Prointa Oasis at Balcarce (high P data partially taken from Abbate* et al. *1997)*

Treatment		CDW* (g/m^2)	GAI* (m^2/m^2)	CDW† (g/m^2)	GAI† (m^2/m^2)	CGR ($g/m^2/d$)	IPAR ($MJ/m^2/d$)	RUE (g/MJ)
Light	P level							
Expt 1								
1·00	High	541	4·6	1210	3·3	23	11·5	2·0
1·00	Low	204	2·2	798	1·3	18	9·0	2·0
0·56	High	–	–	859	3·4	11	5·3	2·1
0·56	Low	–	–	500	1·7	9	4·2	2·2
S.E.D. (6 D.F.)‡		25·1	0·22	51·9	0·23	ns	0·11	ns
S.E.D. (6 D.F.)§		–	–	42·2	ns	1·4	0·20	ns
Expt 2								
1·00	High	265	2·5	843	3·2	21	8·4	2·5
1·00	Low	122	1·3	334	0·9	8	4·4	1·8
0·56	High	291	2·8	592	3·2	11	4·5	2·5
0·56	Low	156	1·8	241	0·8	3	2·2	1·6
S.E.D. (6 D.F.)‡		17·0	0·19	40·2	1·43	1·4	0·34	0·30
S.E.D. (6 D.F.)§		ns	0·17	36·8	1·49	1·5	0·27	0·33

ns: not significant ($P > 0·05$).
* Beginning of SGP.
† End of SPG.
‡ Standard errors of mean differences to compare P treatments at the same levels of shading.
§ Standard errors of mean differences to compare shading at the same or different levels of P deficiency.

increased the SGP slightly (Table 3) in Expt 1; while, on the contrary, in Expt 2 the duration was only 1 day shorter in low P treatments. Rodriguez (1998) found a greater effect of P deficiency on wheat development, reporting a 14-day delay in anthesis with severe P stress. However, the difference in the duration of the double ridge to anthesis period was only 4 days. With P levels similar to those used in the present experiments, Rodriguez *et al.* (2000) found that different P treatments reached terminal spikelet at the same moment, in spite of a delay in early developmental states. A delay in the anthesis date (12 days) has also been found in severely P deficient soils in Australia (Elliott *et al.* 1997).

Working with N deficiency, neither Abbate *et al.* (1995) nor Demotes-Mainard *et al.* (1999) observed important changes on the duration of the SGP. Those authors concluded that the duration of the SGP was slightly altered by the N treatments, and that the changes in SDW near anthesis may be mainly attributed to differences in the SGR. This conclusion is also valid for P deficiency.

The SGR was analysed through the CGR and the proportion of biomass partitioned to the spikes. The slope of the relationship between the SGR and the CGR was positive and the intercept was greater than zero (Fig. 2). A positive intercept has also been found in other field experiments by Wall (1979), Fischer (1985) and Abbate *et al.* (1995, 1997). This positive intercept indicates an increase in partitioning towards reproductive organs in poor growth conditions. An increase in the partitioning to reproductive organs has been found when treatments of shading or N deficiency were used (Fischer 1993; Abbate *et al.* 1995; Demotes-Mainard & Jeuffroy 2001). Shading and P deficiency clearly increased the partitioning toward the spikes in Expt 2 but not in Expt 1 (Table 3). The mean partitioning to spikes of both experiments in high P treatments was 0·31, which is within the range (0·30–0·33) found for the same cultivar by Abbate *et al.* (1998) when studying modern Argentinean cultivars. Additionally, Fischer (1993) found that N-stress before the SGP appears to lead to greater partitioning to the spike during the preanthesis period than when the N stress was later. In Expt 2, the CGR before the SGP was lower than in Expt 1 (Table 5). This could explain the greater partitioning to spike in Expt 2 as compared with Expt 1. The same reasoning could be applied to the increased partitioning to spike observed in low P in Expt 2. In barley, Prystupa *et al.* (2004) found no or only slight effects of P deficiency on partitioning to the spike measured as the ratio of spike and crop dry matter at flowering. However, these results could not be fully comparable with those from the present work, because this proportion can be affected by differences in crop growth previous to the SGP and also because they were obtained in plants grown in containers. The

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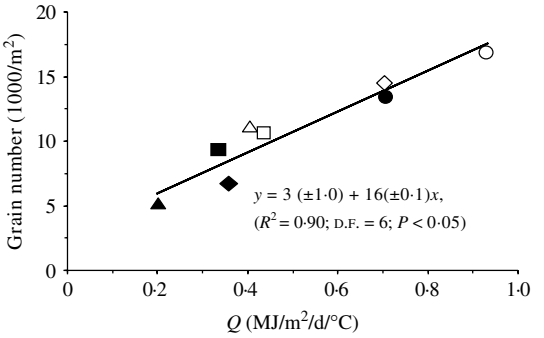


Fig. 3. Number of grains per unit of surface as a function of the photothermal quotient (Q) in experiments Expt 1 and Expt 2, with cv. Prointa Oasis at Balcarce (high P data from Abbate *et al.* 1997). Symbols in Expt 1: ○ without shading, high P level; ● without shading, low P level; □ with shading, high P level; ■ with shading, low P level and in Expt 2: ◇ without shading, high P level; ◆ without shading, low P level; △ with shading, high P level; ▲ with shading, low P level. The S.E.D. of grain number are shown in Table 3.

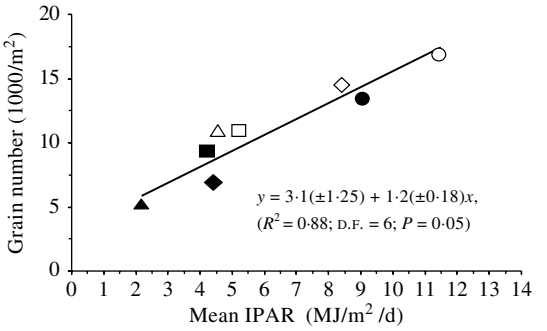


Fig. 4. Number of grains per unit of surface as a function of IPAR during the SGP in experiments Expt 1 and Expt 2, with cv. Prointa Oasis at Balcarce (high P data from Abbate *et al.* 1997). Symbols in Expt 1: ○ without shading, high P level; ● without shading, low P level; □ with shading, high P level; ■ with shading, low P level and in Expt 2: ◇ without shading, high P level; ◆ without shading, low P level; △ with shading, high P level; ▲ with shading, low P level. The S.E.D. are shown in Tables 3 and 5.

SDW at the end of the SGP was not correlated to partitioning but to the CGR; therefore, the main effect of P deficiency on SDW is the result of its effect on the CGR instead of on partitioning to the spike.

Crop growth during the SGP

The lower dry weight of spikes/m² induced by P deficiency and low radiation was mainly due to a reduction in the CGR during the SGP. This is because differences in the duration of that period and dry matter partitioning to spikes were not relevant. However, the CGR was linearly related to the mean IPAR during the SGP ($R^2 = 0{\cdot}92$, $P \leqslant 0{\cdot}01$), but not to RUE ($R^2 = 0{\cdot}18$, $P = 0{\cdot}30$).

The RUE during the SGP, without P deficiency, of Expt 2 (2·5 g/MJ) was close to that reported by Abbate *et al.* (1997) for the same cultivar and phenologic period (2·7 g/MJ), and also to the values found for other cultivars by other authors (Gallagher & Biscoe 1978; Whitfield & Smith 1989; Fischer 1993; Robertson & Giunta 1994; Abbate *et al.* 1998; Shearman *et al.* 2005) for wheat growth until anthesis in non-limiting nutritional and water availability. However, RUE of Expt 1 was 26 % lower. Loomis & Amthor (1996) calculated that the theoretical upper limit of dry matter production by wheat crops is in the range of 3–4 g/MJ based PAR. Warm temperature, low concentration of CO_2 relative to O_2 and the limit of light saturation inhibit the attainment of greater RUE (Loomis & Amthor 1996), but none of these appear to be the cause of the lower RUE in Expt 1. Fischer (1993) suggested that frosts could explain low RUE values, but no frost episodes occurred in either of the experiments presented here. In the unwatered Expt 1, rainfall during the SGP was 80 % lower than that in Expt 2 (Table 1); consequently, its low RUE is likely to be due to water stress in this period. Gallagher & Biscoe (1978), Whitfield & Smith (1989) and Robertson & Giunta (1994), among others, have reported reduced RUE in water-stressed crops.

Sinclair & Shiraiwa (1993) hypothesized that increased diffuse radiation coupled with decreased irradiance in soybean crops results in increased RUE. This could have happened in the shading treatments; however, shading did not change the RUE in either of the two experiments (Table 4). This consistency in RUE coincides with that measured in other works with shading (Fischer 1985; Abbate *et al.* 1997; Rodriguez *et al.* 2000).

In the present study, P deficiency reduced RUE by 15 % (Table 5). Rodriguez *et al.* (2000), with the same cultivar but during the period preceding the SGP, also observed that RUE was significantly affected by P deficiency. However, in the present study, the effect of P deficiency on the GAI (mean reduction 64 %) and the CGR (mean reduction 44 %) during the SGP was higher (Table 5) than the effect on RUE. In maize crops grown in field conditions, Plenét *et al.* (2000*a*, *b*) also showed that P deficiency primarily affects leaf area and subsequently the amount of absorbed PAR, but only affects the RUE slightly.

Grain number and SDW

Phosphorus deficiency decreased the GN and SDW (Table 3). When water and nutrients are non-limiting, changes in the GN can be interpreted by the 'assimilate approach', i.e. through the carbohydrate supply to reproductive organs (Fischer 1984, 1985; Abbate

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et al. 1995, 1997; Demotes-Mainard & Jeuffroy 2004). This supply can be quantified by means of SDW 7 days after anthesis excluding grain weight (Abbate *et al*. 1997). The GN and SDW of all treatments of the present study were compared with the two-line relationship obtained by Abbate *et al*. (1997) (Fig. 1). As this last relationship was obtained by natural or imposed changes in incident radiation, it can be considered that it shows the effect of crop photosynthesis and assimilate supply to the spikes and grains. No particular deviation was observed between the GN and SDW of treatments with P deficiency with respect to Abbate's regression obtained with the same cultivar and without P deficiency. Moreover, the association between the GN of all treatments of the present study with Q was highly significant ($R^2 = 0{\cdot}90$; $P = 0{\cdot}03$). In contrast with the present study, when clustered with and without N deficiency treatments, no unique linear regression was obtained (Abbate *et al*. 1995). In addition, the relationship between SDW of all treatments (with and without P deficiency or shading) and Q was strong ($R^2 = 0{\cdot}93$; $P \leqslant 0{\cdot}01$, D.F. = 6). The regression coefficient of $231 \pm 25{\cdot}8$ g of spikes/m^2 per unit of photothermal quotient was greater than that obtained by Abbate *et al*. (1995) ($114 \pm 12{\cdot}4$) with an older cultivar and the treatments with the highest levels of N.

The present results support the idea that the effects of P deficiency on the GN could be fully explained by variations in the availability of assimilates to sustain flower growth. This is in contrast to the additional depressor effect of N-deficiency on the GN observed by Abbate *et al*. (1995). Possible differences between the responses of the GN to changes in SDW could be due to greater growth reduction in the early growth stages; while Abbate *et al*. (1995) showed greater growth reduction during the SGP. In the present study, the reduction in growth caused by P deficiency was 56% at the beginning of the SGP (mean of all shading treatments of both experiments) and 38% during the SGP. However, Abbate *et al*. (1995) showed that the reduction in growth caused by N deficiency was 7% at the beginning and 25% during the SGP (mean of extreme N treatments). These differences in evolution between P and N stress are typical of the Argentine Pampas, and several sets of data (Spiertz & Ellen 1978; Ellen & Spiertz 1980; Spiertz 1980; Fischer 1993; Abbate *et al*. 1995; Rodriguez & Goudriaan 1995; Plenét *et al*. 2000*b*) suggest that this is the case in other wheat regions of the world. However, if N deficiency is severe early in the crop growth cycle and remains stable during the SGP, no particular N-effect is expected on GN (Fischer 1993; Abbate 1999; Demotes-Mainard & Jeuffroy 2004).

Abbate *et al*. (1995) and Sinclair & Jamieson (2006) have hypothesized that spike N concentration in addition to SDW (i.e. spike N-accumulation) are critical factors in determining both the GN and yield in wheat. The strong relationship between GN and SDW (Fig. 1), even with P deficiencies, suggests that spike N would be a critical estimator of grain number only in the presence of N deficiencies.

The conclusions from this work are that phosphorus deficiency did not have a significant effect on the relationship between the GN and SDW. This suggests that the decrease in yield induced by P deficiency is due mainly to the fact that the crops produce lower quantities of photoassimilates during the SGP and have a reduced GN, which is, in turn, due mainly to a reduction in the IPAR during the SGP. The GN of the treatments with and without P deficiency was linearly correlated with the mean IPAR during the SGP. This relationship was close to that obtained by Abbate *et al*. (1997) in crops without P deficiency. This occurred because: (i) temperature during the SGP changed less than 5% between years and treatments, (ii) the duration of the SGP and partitioning to spike were slightly affected by P deficiency and (iii) intercepted radiation was the main factor that determined both crop and spike growth.

As the P deficiency controls the GN through light interception, the estimation of growth and yield of wheat under P deficiency requires measurement of IPAR accumulated during the SGP. This would improve calculation of yield in regions subjected to P deficiency using remote data of interception radiation.

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