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Ecophysiological determinants of biomass and grain yield of wheat under P deficiency

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ABSTRACT

Grain yield of crops can be expressed as a function of the intercepted radiation, the radiation use efficiency and the partitioning of above-ground biomass to grain yield (harvest index). When a wheat crop is grown under P deficiency the grain yield is reduced but it is not clear how these three components are affected. Our aim was (i) to identify which of these components were affected in spring bread wheat under P deficiency at field conditions and (ii) to relate the grain yield responses to processes of grain yield formation during the spike growth period. Three field experiments were conducted in the potentially high wheat yielding environment of southern Chile. All experiments had two levels of P availability: with (155 kg P ha^{-1}) or without P fertilization (average soil P-Olsen concentration of 10 ppm, a medium level of P availability). High wheat grain yields were obtained varying between 815 and 1222 g m^{-2} with P applications. Experiments showed a grain yield reduction caused by P deficiencies of 35, 16 and 18% in experiments 1, 2 and 3, respectively. This was related ($R^2 = 0.99$, $P < 0.01$) to a reduction in the total above-ground biomass at harvest and not to the harvest index. Reductions in above-ground biomass were due to a reduction in radiation intercepted under P deficiency without effecting radiation use efficiency. Grain number per square meter was the main yield component ($R^2 = 0.99$, $P < 0.01$) that explained the grain yield reduction caused by the P deficiency which was due to low spike biomass at anthesis ($R^2 = 0.96$, $P < 0.05$). The reduction in spike biomass at anthesis was related ($R^2 = 0.86$, $P < 0.01$) to reductions in crop growth rate during the spike growth period as a consequence of a lower radiation intercepted during this period. This study showed that under high wheat yield conditions the main effect of a P deficiency on grain yield reduction was a negative impact on the total above-ground biomass due to the negative impact on intercepted radiation, particularly during the spike growth period, affecting negatively spike biomass at anthesis and consequently grain number and yield.

1. Introduction

According to Monteith (1977) crop biomass accumulation is related to the amount of photosynthetically active radiation intercepted by the crop. Several studies have shown the strong linear relationship between biomass accumulation and the cumulative solar radiation intercepted by different crops. The slope of this relationship represents the radiation use efficiency, defined as crop biomass produced per unit of total solar radiation or photosynthetically active radiation (PAR) intercepted by the canopy (Sinclair and Muchow, 1999). In this context, grain yield (g m^{-2}) of crops (Eq (1)), can be expressed in its simplest form as a product of the cumulative solar radiation intercepted (RI, MJ m^{-2}) during the crop cycle, radiation use efficiency (RUE, g MJ^{-1}), and the partitioning of biomass to yield, or harvest index (HI, g g^{-1}):

$$\text{Grain yield} = \text{RI} \times \text{RUE} \times \text{HI} \tag{1}$$

The RI depends on the fraction of radiation intercepted by the canopy (FRI) each day during the crop cycle and the total incident solar radiation. The FRI depends on the leaf area index (LAI) and the light extinction coefficient (k) (Massignam et al., 2009). Several studies have shown that RI is negatively affected by N deficiency (Hall et al., 1995; Salvagiotti and Miralles, 2008; Massignam et al., 2009), sulfur deficiency (Salvagiotti and Miralles, 2008) and aluminum toxicity (Sierra et al., 2003; Valle et al., 2009a) during crop cycle due to reductions in LAI associated with those restrictions. Today there is much less information, particularly in wheat, about the effects of P deficiency on RI and its impact on above-ground biomass and grain yield. In the same way that was described for other nutrients, P deficiency in maize and sunflower decreased

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RI due to smaller LAI development (maize: Pellerin et al., 2000; Colomb et al., 2000; Plenet et al., 2000a; Fletcher et al., 2008a; sunflower: Rodríguez et al., 1998a). In wheat, grown at field conditions for 61 days after emergence, Rodríguez et al. (2000) found that P deficiency reduced above-ground biomass, LAI and the FRI by 61, 69 and 46%, respectively respect to the control without restrictions. More recently, Lázaro et al. (2009), in an environment of medium wheat grain yield (ranges of 490–520 g m^{-2}), showed that during spike growth period of wheat P deficiency resulted in a reduction RI.

In addition to RI, the evaluation of RUE sensitivity to soil stresses is essential for a complete understanding of the above-ground biomass and grain yield constraints. Theoretical analyses have consistently indicated a dependence of RUE on leaf photosynthetic activity and considerable information about the negative response of RUE under N deficiency has been published (Hall et al., 1995; Sinclair and Muchow, 1999; Muurinen and Peltonen-Saino, 2006; Massignam et al., 2009). On the contrary, RUE is little affected by aluminum toxicity (Sierra et al., 2003; Valle et al., 2009a). Much less information is available about RUE response to P deficiency. However, several studies in pot experiments have shown that the leaf photosynthesis rate has been negatively affected by P deficiency in sunflower (Plesnicar et al., 1994; Rodríguez et al., 1998a), wheat (Rodríguez et al., 1998b), tobacco (Pieters et al., 2001) and in other species including C$_3$ and C$_4$ metabolisms (Halsted and Lynch, 1996). In maize, under controlled conditions, RUE was slightly affected by P deficiency (Mollier and Pellerin, 1999). On the other hand, under field conditions, contrasting results have been found since RUE was not affected in maize under P deficiency (Plenet et al., 2000b; Fletcher et al., 2008b), while in wheat, Rodríguez et al. (2000) found that during the period of 61 days after emergence RUE was reduced on averaged 35% under P deficiency. Recently Lázaro et al. (2009), reported in one of two experiments reported, a significant reduction (36%) in RUE during the spike growth period (ca. 27 d) under P deficiency. However, neither of them evaluated the whole wheat growth cycle and, moreover, in the study of Lázaro et al. (2009) RUE was not correctly calculated by regression between biomass and cumulative RI (Sinclair and Muchow, 1999). Therefore, more studies are needed in wheat to assess the sensitivity of this biomass factor under P deficiency at field conditions throughout the entire crop cycle.

The other source of variation for grain yield determination, HI, seems to be conservative under soil stress conditions such as N (Dreccer et al., 2000; Salvagiotti and Miralles, 2008) or sulfur deficiencies (Salvagiotti and Miralles, 2008), aluminum toxicity (Valle et al., 2009b) and mechanical impedances (Sadras et al., 2005). Similar stability on HI has been found under different P availabilities (Manske et al., 2000; Plenet et al., 2000b), suggesting that a P deficiency decreases grain yield mainly through its negative impact on ecophysiological mechanisms of above-ground biomass determination (e.g., RI and/or RUE).

Using the assimilate-based approach proposed by Fischer (1985), the grain number per square meter is considered the direct driving force for yield, and considerable evidence shows a close relationship between yield and grain number (wheat: Slafer et al., 2005; Fischer, 2008; Peltonen-Sainio et al., 2007; barley: Arisnabarreta and Miralles, 2008a; triticale: Estrada-Campuzano et al., 2008). In this approach, grain numbers are positively correlated to the photothermal quotient (MJ m^{-2} d^{-1} °C^{-1}) recorded during the critical period of grain number determination where spikes are growing actively (Fischer, 1985; Savin and Slafer, 1991; Abbate et al., 1995). Spike biomass at or around anthesis is the earliest predictive physiological trait measured with which grain number has been shown to be closely related over a range of studies evaluating source-sink manipulation in wheat (Savin and Slafer, 1991; Lázaro et al., 2009), triticale (Estrada-Campuzano et al., 2008) and barley (Arisnabarreta and Miralles, 2008b). The photothermal quotient could be negatively affected by P deficiency because RI decreased under this nutritional condition (Rodríguez et al., 2000). Until now only Lázaro et al. (2009) has reported that P deficiency reduces RI during the spike growing period, affecting the photothermal quotient and decreasing spikes biomass around anthesis and consequently grain number and yield. However, it is important to highlight that this study was carried out in an environment of intermediate yield potential (<5.2 Mg ha^{-1}). Therefore, in order to improve our knowledge about the effect of P on grain number and yield determination more studies are needed to evaluate these variables in high yielding environments like southern Chile where wheat grain yield can over-yield 10 Mg ha^{-1} (Valle et al., 2009b; Sandaña et al., 2009).

The objective of the present study was to evaluate under field conditions, how the physiological mechanisms of biomass and grain yield determination of wheat responded to a P deficiency in the high yielding environments of southern Chile.

2. Materials and methods

2.1. Site, experimental design and management

Three field experiments were conducted during the 2007–2008 (Experiment 1), 2008–2009 (Experiment 2) and 2009–2010 (Experiment 3) growing seasons. The soil was a Duric Hapludand located at the experimental station of the Universidad Austral de Chile, Valdivia (39°47′S, 73°14′W, 19 m a.s.l.), Chile. The same spring bread wheat cultivar (Pandora) was used in all experiments. In all experiments, treatments consisted of two levels of P: with or without P fertilization. In each experiment, treatments were arranged in a randomized complete block design with three replicates. The initial soil available P concentration in experiments 1, 2 and 3 were 8.1, 10.8 and 11.4 ppm P-Olsen, respectively, these values are considered as a medium soil P level.

In experiment 1, each plot consisted of seven rows width, 3 m long and 0.15 m apart, while in experiment 2 plots consisted of nine rows width, 2.5 m long and 0.15 m apart. In experiment 3 plots consisted of thirty rows width, 1.5 m long and 0.15 m apart. Sowing dates were August 30th, September 5th and September 3th for experiment 1, 2 and 3, respectively. In experiment 1, wheat seeds were sown at a rate of 300 seeds m^{-2}, while in experiment 2 and 3 the seed rate was 350 seeds m^{-2}. In all experiments, in order to have a good seed distribution along rows, strip paper containing seeds were used. In experiment 1, plots were fertilized with 83 kg K ha^{-1}, 150 kg N ha^{-1} and 100 kg S ha^{-1} at sowing and with 150 kg N ha^{-1} at the beginning of tillering. In experiment 2 and 3, plots were fertilized at sowing with 125 kg K ha^{-1}, 100 kg N ha^{-1} and 100 kg S ha^{-1} at sowing and with 150 kg N ha^{-1} at the beginning of tillering. In all experiments, plots with P fertilization were fertilized with 155 kg P ha^{-1} at sowing. At sowing all fertilizers were incorporated homogeneously in each row below the strip paper, while at tillering N was allocated between rows.

All experiments to avoid water shortages until harvest, plots were surface-irrigated weekly in order to replace the cumulative daily difference between daily rainfall and daily evaporation. The experiments were maintained free of biotic stresses. Thus, weeds were periodically removed by hand, while diseases and insects were prevented with the use of fungicides and insecticides at the rates recommended by their manufacturers.

2.2. Plant measurements

In all experiments, phenological observations were done weekly. The anthesis date of wheat was recorded using the dec-