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Variability of duration of pre-anthesis phases as a strategy for increasing wheat grain yield

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ABSTRACT

In wheat, stem elongation phase (SEP) duration is critical for grain number (GN) per unit of area determination, as it is the phase in which the spikes grow. Lengthening SEP, for instance by photoperiodic sensitivity, without altering the cycle to anthesis (AT) has been proposed as an alternative way to increase spike dry weight, and in turn GN. As most works supporting this idea have modified only SEP by artificial manipulation (e.g. photoperiod extensions), it is relevant to evaluate this hypothesis in populations segregating for this attribute in natural conditions. The aim of this work was to analyse the variability in SEP duration relative to AT in two F4 populations; in order to select contrasting phenotypes to evaluate the impact of this attribute on grain yield components and to analyse the selection response of this attribute. These segregating populations (Las Rosas INTA × Triguero 230 (A) and Klein Estrella × ProINTA B. Alazán (B)) were derived from parental lines with similar flowering time but different relative duration of their pre-anthesis phases. Two field experiments with previous vernalization treatment in cool chamber were carried out. In 2006, F4 populations were characterized and from one of them (population B, which presented higher variability) four groups were selected, which presented contrasting phenotypes in the attribute under study. Progenies of these groups (F5), together with remnant F4 full-sib of each one, were studied during 2007. Grain yield per plant was higher, due to GN increases, when duration of the SEP was lengthened. However, selection response to longer SEP with similar cycle to AT could not be found, possibly as the result of a high environmental influence on this attribute. The phenotypic variability evidenced in this attribute was not clearly associated with major adaptation genes evaluated (i.e. Ppd and/or Vrn), suggesting that other minor genes could be associated.

1. Introduction

Improving wheat (*Triticum aestivum* L.) grain yield potential is required to match expected population growth. From the beginning of the twentieth century, wheat grain yield was consistently increased, mainly after the introgression of dwarfing genes (*Rht*) into the background of adapted varieties (Siddique et al., 1989; Calderini et al., 1999). However, during the last decades, strategies of conventional breeding have been insufficient to keep improvement rate similar to the past (Calderini and Slafer, 1998; Miralles and Slafer, 2007), suggesting efficiency losses in breeding programs (Fischer, 2007). Therefore, since this cereal is an essential component of the global food security (Reynolds et al., 2011), increasing wheat production is necessary to follow the pace of population growth in the near future (Evans, 1998; Borlaug, 2007). In this scenario, progress in grain yield is still the factor of greatest impact on productivity growth, and the genetic gain in grain yield potential is still the main component of this progress (Fischer, 2007).

Genetic improvement in grain yield potential could be accelerated if ecophysiological attributes are used as selection criteria, especially in a crop such as wheat, which has already been subjected to an intense selection pressure (Shorter et al., 1991; Reynolds et al., 2001, 2011). For this purpose, it is necessary not only to identify

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Abbreviations: TR, transplant; FN, first node detectable; SEP, stem elongation phase; SGP, spike growth period; AT, anthesis; GN, grain number; GW, grain weight; SD, standard deviation; ES, early flowering time and short SEP; EL, early flowering time and long SEP; LS, late flowering time and short SEP; LL, late flowering time and long SEP.

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ecophysiological attributes functionally linked to grain yield potential, but also to improve the understanding of the genetic basis controlling those traits for easy handling (Slafer, 2003). In this sense, interdisciplinary approaches that combine studies at different approximation levels (i.e. molecular, crop ecophysiology and genetic improvement) are required to raise this genetic gain in wheat grain yield potential, which will probably be harder to achieve than in the past (Slafer, 2003; Edmeades et al., 2004; Sinclair et al., 2004).

Considering a wide range of environmental conditions, grain number (GN) per unit of area is the main component that explains the variations in grain yield (Magrin et al., 1993; Calderini et al., 1999; Fischer, 2008). This component, although it is generated during the whole period, from sowing to immediately after anthesis (AT), is determined a few weeks before flowering (Fischer, 1983, 1985). The stem elongation phase (SEP) (i.e. from terminal spikelet initiation to AT), during which the spike growth period (SGP) is included, is critical to GN setting, as assimilates allocated in spikes at the end of this period are crucial for floret establishment (Kirby, 1988; Slafer et al., 1994; Miralles and Slafer, 1999). In fact, a strong relationship was found between the spike dry weight at flowering and the number of fertile florets (the majority set a grain) under a wide range of conditions (e.g. Siddique et al., 1989; Miralles et al., 2000; González et al., 2005c; Serrago et al., 2008). As future increases in biomass partitioning to spike through genetic reduction of height seem to be unlikely, it is necessary to find alternatives to raise spike growth maintaining high levels of partition as a way to improve GN (Miralles and Slafer, 2007).

Development manipulation during the pre-anthesis phases has been proposed as a way to reduce source competition between stems and spikes during SGP. Along this line, lengthening the duration of SEP (or more specifically SGP) without altering the flowering time has been hypothesized as an alternative way to increase spike dry weight, and GN in turn (Slafer et al., 1996; Miralles et al., 2000; Slafer, 2003). Following that hypothesis, previous evidence demonstrated: (i) the existence of variability in SEP duration in commercial wheat cultivars with similar flowering time (Whitechurch et al., 2007a,b); (ii) the sensitivity to actual photoperiod during SEP is physiologically independent of the response in previous development phases, using artificial manipulation of photoperiod both under controlled conditions (Miralles and Richards, 2000) and in field studies (Whitechurch and Slafer, 2002); and (iii) the number of fertile florets raised as spike dry weight was increased, due to a longer SEP (Miralles et al., 2000; González et al., 2005c; Serrago et al., 2008), suggesting that increased spike fertility was mediated by a greater accumulation of carbohydrates (Ghiglione et al., 2008).

The evidence described above supports the idea that any genetic factor (e.g. photoperiod sensitivity) lengthening SEP, independently of the total flowering time, will improve spike dry weight at AT and increase its fertility (Slafer et al., 2001). However, most of the experiments to test the hypothesis were carried out using different commercial cultivars. Besides, changes in SEP duration were made by artificial manipulation of environmental factors, such as photoperiod, focusing on particular phases. Those approaches were important to establish the physiological bases of the spike growth and floret survival response to SEP duration. Nevertheless, they cannot be extrapolated to real crops, as the environment manipulation described above cannot be artificially made in a commercial crop. Therefore, it is necessary to demonstrate the advantage of a longer SEP duration on grain yield in natural field conditions, employing genetic populations specifically designed for this purpose. This approach constitutes a starting point for new research assisted by molecular tools, which can be focused on a precise determination of these genetic bases.

The objective of this work was, firstly, to analyse the variability in SEP duration relative to AT in two F4 populations obtained from contrasting cultivars for this attribute. Secondly, to select divergent phenotypes to evaluate the impact of SEP duration relative to AT on the main grain yield components and to analyse the selection response of this attribute.

2. Materials and methods

2.1. Experimental conditions and plant material

Two field experiments were carried out in the experimental field of the Department of Plant Production of the University of Buenos Aires (34° 35′S, 58° 29′W, 25 m.a.s.l.) during 2006 and 2007 growing seasons. Trials were irrigated and adequate nutrients applied (i.e. fertilization was adequate to obtain more than 35 ppm of phosphorus and 200 kg of nitrogen per hectare). Plant pathogens and pests were prevented by chemical treatments, and weeds were removed by hand to avoid any negative effect of hormonal herbicides on crop development. Seedlings were vernalized before transplant (TR) to avoid any difference in vernalization requirement among materials. Thus, seeds were germinated in pots filled with an inert substrate (i.e. vermiculite) and, after 24 h, they were transferred to a cold chamber (4–6 °C, 8 h daylength) for 15 days. Vernalized seedlings were transplanted to the field on 19 July 2006 and 13 July 2007. Both dates were taken as the beginning of each experiment (indicated through the text as TR). Seeds of each material, previous to vernalization treatment, were equally distributed in strips of biodegradable paper which were finally transplanted ensuring a uniform seedling depth and distance distribution in the field.

In the first experiment (2006), two F4 populations, called A and B in this work, were evaluated. They derived from parental lines with similar flowering time but different SEP duration. Population A was obtained from cultivars Las Rosas INTA and Triguero 230, and population B was obtained from Klein Estrella and ProINTA Bonaerense Alazán. These cultivars were selected screening more than 60 Argentinean commercial cultivars (Whitechurch et al., 2007a). Population A consisted of a smaller number of F4 individuals than population B (73 and 173, respectively). Both F4 were derived from F2 by single seed descendant methodology (SSD) (Goulden, 1939; Brim, 1966). Both F4 populations (A and B) and parental lines were randomly distributed in the field (i.e. they were randomly distributed in the strips of biodegradable paper) and each individual was tagged in order to be identified.

In the second experiment (2007), four groups of F5 progenies, obtained from contrasting F4 (2006) phenotypes in SEP duration relative to AT were evaluated. Divergent selection was carried out to obtain contrasting groups for that attribute from data obtained only from population B. Firstly, two sets of ca. 20 individuals, classified as early or late flowering time, were selected considering those whose cycle to AT differed more than 1.5 standard deviation (SD) from the mean of the whole population. Within each set with similar flowering time, two groups of 6 individuals according to their SEP were selected. The selection of extreme phenotypes within each set (early and late) was carried out based on differences of at least one SD from its mean SEP, obtaining materials with long and short SEP within early and late flowering time. Therefore, the resulting groups combined the following phenology: (i) early flowering time with short (ES) and long (EL) SEP, and (ii) late flowering time with short (LS) and long (LL) SEP. Besides, this second experiment included remnant seeds of F4 full-sib of each individual selected in 2006 for the progeny test, which were disposed in contiguous rows to the corresponding F5 progeny. The experimental arrangement was a complete randomized design with 6 replicates