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Dynamics of floret development determining differences in spike fertility in an elite population of wheat

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ABSTRACT

Further increases in wheat yield potential could be achieved through a better understanding of the dynamics of floret primordia generation/degeneration, a process which has received little attention. We quantified genotypic variation among elite genotypes of the CIMCOG panel assembled by CIMMYT for its usefulness for wheat breeding. Ten genotypes, representing the range of variation for yield and its components of the whole panel, were grown under high-yielding conditions in NW Mexico for two growing seasons. The stage of development of floret primordia was determined 2–3 times weekly during stem elongation for apical, central and basal spikelets within the spike. The dynamics of floret initiation/death, and the resulting number of fertile florets, were determined for each spikelet position. We found that the variation in number of fertile florets within this elite germplasm was much more related to the survival of floret primordia than to the maximum number of florets initiated. As the two floret primordia most proximal to the rachis were almost always fertile and most distal florets (florets 6–8) were never fertile, the differences in number of fertile florets were clearly attributed to the differential developmental patterns of intermediate florets (floret primordia 3, 4 and 5, counted from the rachis, depending on the spikelet position). We found significant differences among elite germplasm in dynamics of floret development. Differences in floret survival seemed positively related to those in the length of the period of floret development: the longer the duration of floret development the higher the likelihood of that floret becoming fertile. It is proposed that this type of study may be instrumental for identifying prospective parents for further raising yield potential wheat breeding programmes.

1. Introduction

Due to the increasing global population together with a growing demand for meat and dairy products (implying a growing amount of grains should be used to produce animal food at a low rate of conversion), a substantial increase of grain production in the next decades is critical. This is particularly challenging as the basic manageable resources for crop growth and yield (water, nutrients) will not increase (Connor and Mínguez, 2012) and the land available for crop production is likely to decline (Albajes et al., 2013 and references quoted therein). These challenges together with the need of making future production of crops more sustainable amount to a 'perfect storm' (Godfray et al., 2010; Fischer et al., 2014). Among the major crops, wheat is one of the most critical for warranting human nourishment: it is the most widely crop grown globally and is the primary source of protein for the world population, representing c. 20% of the daily intake for developing countries (Braun et al., 2010). In order to maintain balance between demand and supply alternative ways and means to further raise wheat yield must be found (Chand, 2009). A major way to navigate this 'perfect storm', facing the restrictions mentioned above, is through re-gaining high rates of genetic gains in yield. However, this may not be easily achieved as there is mounting evidence that genetic gains in yield have recently been much lower than what it would be required (Reynolds et al., 2012; Fischer et al., 2014). The likelihood of accelerating breeding progress would increase with knowledge of genetic variation available for traits putatively determining yield (Slafer, 2003; Reynolds and Borlaug, 2006; Reynolds et al., 2009).

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Yield in wheat is generally more related to grain number than to the average weight of the grains (Fischer, 2008, 2011) as the number of grains is far more plastic than the size of the grains (Sadras and Slafer, 2012). Consequently, genetic gains in wheat yield have been more related to improvements in the number than in the size of the grains (e.g. Canevara et al., 1994; Calderini et al., 1995; Sayre et al., 1997; Shearman et al., 2005; Acreche et al., 2008). As even in modern cultivars grain growth seems not strongly limited by the source (Borrás et al., 2004; Pedro et al., 2011), it seems likely that further increases in yield potential may require additional improvements in grain number (Reynolds et al., 2001, 2005; Acreche and Slafer, 2009; González et al., 2014). The identification of potential traits to increase grain number is of great interest to ensure that increased photosynthetic potential is fully utilized by matching it with adequate sink demand (Reynolds et al., 2012; Slafer et al., 2014). To achieve this aim, it would be useful to understand the degree of variation of physiological drivers of grain number within elite lines. Grain number is largely determined during the stem elongation (SE) phase (Fischer, 1985; Slafer and Rawson, 1994). Therefore improvements of traits determined during SE would be required to further increase grain number (Slafer et al., 2005).

Beyond increasing crop growth rate and further improving biomass partitioning before anthesis, it may also be relevant to optimize the developmental attributes to maximize spike fertility (Foulkes et al., 2011; Reynolds et al., 2012). This involves two different aspects of development: [i] the pattern of partitioning of time to anthesis into different phases (Slafer et al., 2001), as lengthening the duration of the SE phase may increase yield (Slafer, 2003; Miralles and Slafer, 2007); and [ii] the dynamics of floret development (Kirby, 1988), as grain number is the consequence of the developmental process of floret generation/degeneration resulting in a certain number of fertile florets (González et al., 2011).

Looking for variation in dynamics of floret development within modern elite cultivars, could contribute to the elucidation of the mechanisms which are most likely to provide opportunities to identify sources for a potential increase in grain number. Floret development in wheat has been long studied (Stockman et al., 1983; Sibony and Pinthus, 1988; Miralles et al., 1998; Wang et al., 2001; González et al., 2003a; Bancal, 2008; Shitsukawa et al., 2009; Dreccer et al., 2014), especially its response to nitrogen applications (Holmes, 1973; Langer and Hanif, 1973; Ferrante et al., 2010). It seems that due to the difficulties involved with the developmental analysis of spike morphogenesis there is an absence of research describing variation for this trait among elite wheat cultivars.

The objective of the present study was to determine the degree of variation within elite germplasm of wheat in patterns of floret development responsible for differences in number of fertile florets, and to further understand the differences in generation of fertile florets among genotypes differing in yield components.

2. Materials and methods

2.1. General conditions

Two field experiments were conducted in the Mexican Phenotyping Platform (MEXPLAT) established at the research station "Centro Experimental Norman E. Borlaug" (CENEB), near Ciudad Obregón, Sonora, Mexico (27°33′ N, 109°09′ W, 38 masl), with conditions that represent the high-yielding environments of wheat worldwide (Braun et al., 2010). The soil is a Chromic Haplotorrert (Vertisol Calcaric Chromic), low in organic matter (<1%), and slightly alkaline (pH = 7.7).

2.2. Treatments and experimental design

Experiments were sown on 06 December 2010 and 09 December 2011, within the optimal sowing period for the winter–spring cycle of cereals in the region. Sowing density was 101.5 and 108.8 kg ha^{-1} respectively, and 200 units of N fertilizer (urea) were applied. Weeds were removed by hand throughout the growing season and diseases and insects prevented by applying recommended fungicides and insecticides at the doses suggested by their manufacturers.

Table 1
Subset selected from the CIMCOG panel. For each entry, the name of the cultivar or cross is indicated, as well as the main trait for which the genotype was selected to be part of the CIMCOG.

Entry	Name	Trait
1	BACANORA T88	High grains/m^2
2	BCN/RIALTO	Late development
3	BRBT1*2/KIRITATI	Large grains
4	CROC_1/AE.SQUARROSA (205)//BORL95/3/PRL/SARA//TSI/VEE#5/4/FRET2	High floret number
5	ATTILA/PASTOR	High floret number; late development
6	PFAU/SERI.1B//AMAD/3/WAXWING	Early development
7	SERI M 82	Wide adaptation
8	SIETE CERROS T66	Benchmark
9	TRAP#1/BOW/3/VEE/PJN//2*TUI/4/BAV92/ RAYON/5/KAUZ//ALTAR 84/AOS/3/MILAN/KAUZ/4/HUITES	Wide adaptation
10	WHEAR/SOKOLL	Wide adaptation

The treatments consisted of the ten wheat genotypes (Table 1), all elite material belonging to the CIMMYT Mexico Core Germplam Panel (CIMCOG) with good agronomic adaptation. The full set of 60 genotypes of the CIMCOG panel are potentially useful in practical breeding programmes aiming to further raising yield potential and for that reason is the main germplasm studied so far by the Wheat Yield Consortium (Reynolds et al., 2011). For this particular study, the number of genotypes had to be restricted to ten because of the detailed measurements required, particularly regarding floret development (see below). However, it is worth noting that the selected genotypes do represent fairly well the whole CIMCOG panel in terms of yield and its major determinants both considering average values as well as range of variation (Table 2).

The experiment was designed in randomized complete blocks with two replicates, where plots were assigned to genotypes. In season 2010–2011 plots were 5 m long and 3.2 m wide, consisting of four raised beds 0.80 m wide, with two rows per bed (0.24 m apart), and in season 2011–2012 plots were 8.5 m long and 1.84 m wide, consisting of two raised beds 0.80 m wide, with two rows per bed (0.24 m apart) (Fig. 1, left panel).

2.3. Measurements and analyses

Plots were inspected periodically and one plant per plot regularly sampled and dissected under binocular microscope (Carl Zeiss, Germany) to detect the timing of initiation of the terminal spikelet in each case. From then on until a week after anthesis, one plant per plot was randomly sampled twice or thrice weekly. The samples were taken to the lab and the apex of the main shoot dissected under binocular microscope. On the dissected juvenile spikes the total number of floret primordia was counted in each of the analysed spikelets. In addition the stage of development of each of the florets within particular spikelets was determined. Together these measurements represent the variability expected in the spikes, in developmental terms (see below). To determine the stage of development of the floret primordia, we followed the scale of Waddington et al. (1983). This scale is based on