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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

Table 2
Comparison of yield and its determinants between the CIMCOG panel and the subset of ten genotypes. Data are the adjusted means from a combined analysis of the wheat genotypes grown during the 2010–2011 and 2012 at CENEB, near Ciudad Obregon, Mexico.

Trait	Average		CIMCOG		Subset	
	CIMCOG	Subset	Range	$LSD_{0.05}$	Range	$LSD_{0.05}$
Yield (Mg ha^{-1})	6.42	6.40	4.99–7.63	0.7	6.13–6.61	0.7
Biomass (Mg ha^{-1})	14.12	13.97	11.73–15.76	1.5	13.23–14.72	1.5
Harvest index	0.46	0.46	0.41–0.52	0.02	0.43–0.49	0.03
Number of grains (m^2)	15,072	16,554	11,626–21,769	1848	13,752–21,950	2639
Number of grains (spike^{-1})	50	50	41–63	8.3	45–56	9.1
Grain weight (mg grain^{-1})	43	39	30–52	3.1	30–45	4.4
Days to anthesis	87	87	78–95	2.5	80–95	1.2

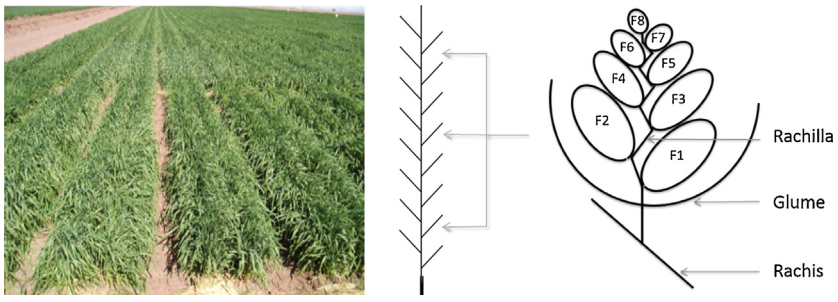

Fig. 1. The 60 CIMCOG lines were grown under raised beds (left panel); and schematic diagram illustrating spikelet positions within the spike as well as the position of florets within the spikelet that were used in this study to characterize floret development in CIMCOG (right panel).

gynoecium development from floret primordia present (W3.5), to styles curved outwards and stigmatic branches spread wide with pollen grains on well-developed stigmatic hairs (W10), which are considered fertile florets (for details see Fig. 1 in Ferrante et al., 2013a).

The analysed spikelets were those on the apical (fourth spikelet from the top of the spike), central (middle spikelet of the spike), and basal (fourth spikelet from the bottom of the spike) positions of the spike (Fig. 1, right panel). Naming of florets within the spikelets followed the same system described by González et al. (2003a); that is, from F1 to the last developed floret depending on their position with respect to the rachis (F1 was the floret most proximal to the rachis and the most distal floret primordia was F6–F8, depending on the specific spikelet and genotype analysed; Fig. 1, right panel).

To analyse the dynamics of development we plotted the developmental score of the particular florets against thermal time (°C d), which was calculated daily assuming, as it is standard, that the mean temperature was the average of the maximum and minimum values and the base temperature was 0 °C for all genotypes and stages of development. Then, for each sampling date we calculated the number of floret primordia which were alive and developing normally; the timing when floret primordia were considered not developing normally any longer was that when the maximum stage of development of a particular floret primordium was reached. Then the number of floret primordia was plotted against thermal time around anthesis for each particular genotype and experiment. For this analysis we considered a primordia to be a floret when it reached at least the stage 3.5 in the scale of Waddington et al. (1983).

The data were subjected to analysis of variance (ANOVA), and the relationships between variables were determined by regression analysis (SAS statistics program, 2002). The adjusted means across the 2 years were obtained by using PROC MIXED procedure of the SAS statistical package (SAS statistics program, 2002). All the effects, years, replications within years, blocks within years and replications, and genotype by year interaction (G × E) were considered as random effects and only the genotypes were considered as fixed effects.

3. Results

There were significant differences in number of fertile florets per spikelet in each of the two experiments, and in addition these differences were reasonably consistent between years, with the unique exception of line 2 (Fig. 2). Line 8 was within the lines exhibiting the highest levels of spike fertility in both experiments, and line 9 was within those exhibiting the lowest values (Fig. 2).

There was significant variation in both components of the number of fertile florets: the maximum number of floret primordia initiated and the proportion of primordia surviving to become fertile florets at anthesis. However, the number of fertile florets was much more strongly related to the survival of floret primordia than to the maximum number florets initiated (Fig. 3).

To further understand the processes involved in the genotypic differences within the CIMCOG panel we studied the dynamics of generation and survival of floret primordia in apical, central and basal spikelets. The general dynamics was similar in all cases (genotypes × spikelet positions): during stem elongation the number of floret primordia firstly increased rapidly, reaching a

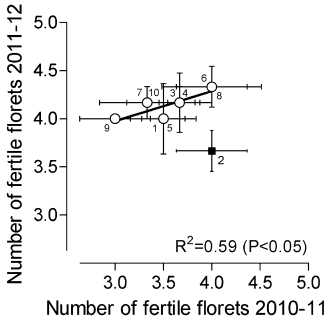

Fig. 2. Fertile florets per spikelet in both experiments for the subset of the CIMCOG panel. Bars on each data-point show the standard error of the mean. Genotypes were labelled as in Table 1. Genotype 2 was the exception, not behaving consistently between the 2 years, and genotypes 8 and 9 were those having respectively the highest and the lowest number of fertile florets per spikelet of the lines analysed consistently between years. Data points of some genotypes are overlapped.

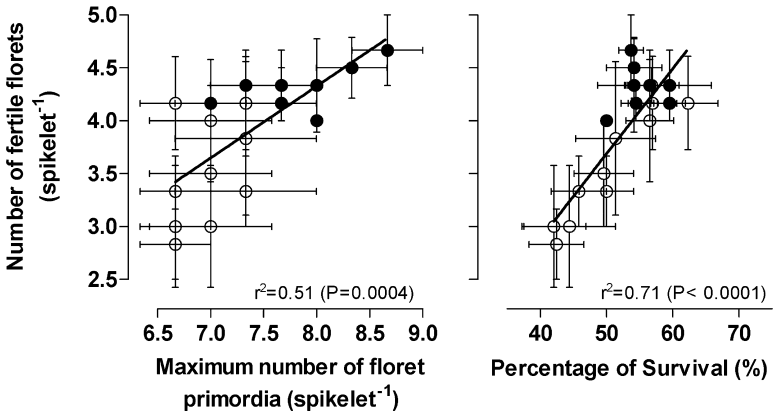

Fig. 3. Number of fertile florets per spikelet related to either the maximum number of floret primordia initiated (left panel) or the percentage of these primordia which developed normally surviving to produce fertile florets at anthesis (right panel). Open circles represent season 2010–11 and closed circles season 2011–12.

peak representing the maximum number of floret primordia and finally decreased sharply until a certain number of fertile florets is established as the balance of the generation and degeneration process (Table A.1). Cultivars varied in the dynamics of generation/degeneration of floret primordia determining the number of fertile florets per spikelet at different spikelet positions (Fig. A.1). To illustrate these genotypic differences we compared this dynamics of floret generation/degeneration for the apical, central and basal spikelets of the two genotypes exhibiting the extreme cases of floret fertility (Fig. 2): lines 8 and 9 representing high and low spike fertilities, respectively. Both genotypes had a similar maximum number of floret primordia initiated in the apical and central spikelets, whilst genotype 9 had a slightly lower maximum number of florets initiated in the basal spikelets than genotype 8 (Fig. 4). On the other hand, in all spikelets the decrease in number of floret primordia (floret mortality) was more noticeable in genotype 9 than in 8 (Fig. 4). Interestingly it seemed that in all spikelet positions genotype 9 reached the maximum number of floret primordia closer to anthesis than genotype 8, implying that the time for floret survival was consistently shorter in the genotype with lowest final number of fertile florets at anthesis (Fig. 4).

When analysing the development of the individual florets it was clear that florets 1 and 2 developed normally and always reached the stage of fertile florets: in all spikelets and all genotypes (Fig. A.2). Thus, none of the differences between genotypes in spike fertility were related to the fate of the two most proximal florets. Similarly, none of the genotypic differences in spike fertility were related to the fate of florets 6, 7 and 8; as none of these florets developed normally to reach the stage of fertile florets ever (Fig. A.3). Therefore, genotypic differences in the developmental patterns of intermediate florets (3, 4 and 5) were critical for establishing the genotypic variation in spike fertility. Focusing on these particular florets it became clear that:

(i) floret 3 developed normally, achieving the stage of fertile florets, in the two genotypes and in all the spikelets: even when the difference in spike fertility was not due to the fate of floret 3, a difference in developmental rates was noticeable: it seemed that floret 3 in genotype 9 developed with some delay compared to that in genotype 8 (Fig. 5, left panels).
(ii) floret 4 in the central spikelets did also develop normally achieving the stage of fertile florets in both genotypes, though again it seemed that this floret started its development in genotype 9 with some delay respect to the timing of development initiation in genotype 8 (Fig. 5, central panel).
(iii) floret 4 in the basal and apical spikelets developed normally to become fertile only in genotype 8 (in the apical spikelets only in some of the plants analysed) but was never fertile in apical and basal spikelets of genotype 9 (Fig. 5, top and bottom of the central panels).
(iv) floret 5 was never fertile in the apical spikelets of any of the two genotypes (Fig. 5, top-right panel), while in the central and basal spikelets it was fertile in some of the plants of genotype 8 and in none of the plants of genotype 9 (Fig. 5, central- and bottom-right panels).

Even in the case of the floret × spikelet positions in which primordia did not continue developing normally to achieve the stage of fertile florets, there was a clear trend, though with few

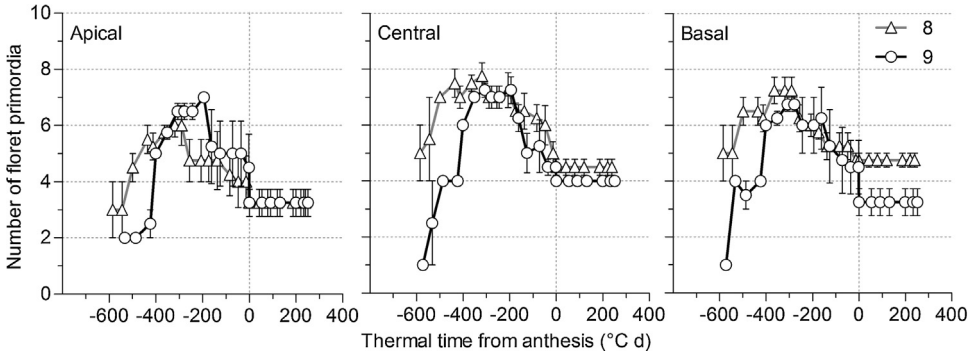

Fig. 4. Dynamics of the number of living floret primordia (those developing normally at the time of measurement) from the onset of stem elongation onwards, plotted against thermal time from anthesis in genotypes 8 and 9, which consistently had high and low spike fertility, respectively, within the subset analysed from the CIMCOG panel in the apical (left panel), central (middle panel) and basal spikelets (right panel).

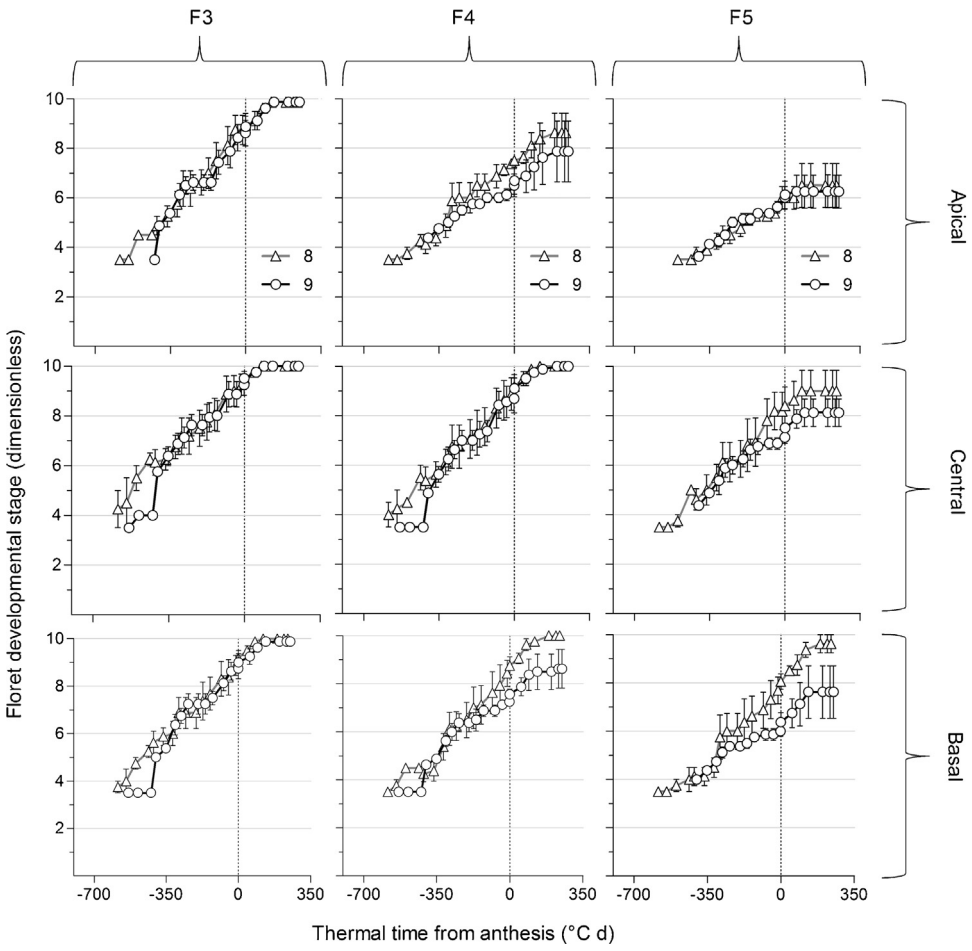

Fig. 5. Developmental progress of floret primordia 3, 4 and 5 (from left to right panels) in apical, central and basal spikelets (from top to bottom panels) from the onset of stem elongation onwards, plotted against thermal time from anthesis in genotypes 8 and 9 of the subset analysed from the CIMCOG panel. The florets are fertile when achieving the stage 10 in the scale developed by Waddington et al. (1983).

exceptions, for the floret primordia of genotype 8 to have developed more than the equivalent florets of genotype 9 (Figs. 5 and A.3).

4. Discussion

Future wheat breeding needs to be extremely efficient as the land allocated to wheat (and most other major food crops) is unlikely to increase significantly, and the use of inputs cannot increase at similar rates as they have in the last half-century (Chand, 2009; Reynolds et al., 2012; Hall and Richards, 2013). Although farm yields may be much lower than yield potential, they seem to be related (Slafer and Araus, 2007; Fischer and Edmeades, 2010) and therefore there is agreement that genetic gains in yield potential will need to be accelerated (Reynolds et al., 2009). To identify opportunities for major improvements in crop photosynthesis is essential (Reynolds et al., 2000; Parry et al., 2011), but will not translate in yield gains without further gains in sink strength, the major determinant of which is grain number. In fact, genotypic differences in yield are most frequently associated with those in grains per m^2 (Slafer et al., 2014) and genetic gains in yield have been mostly explained by improvements in this component (Calderini et al., 1999 and references quoted therein). Further improving grain number would require the identification of variation in its physiological determinants within high-yielding, well adapted populations for breeding. As wheat is a cleistogamous plant, a major determinant of grain number is the number of fertile florets produced. Unfortunately, studies on the dynamics of floret primordia generation/degeneration, which ultimately determines spike fertility, are rather rare, likely because the intrinsic difficulties of determining these dynamics.

Most of the relatively few studies on floret development dynamics were focused on the effects of environmental factors affecting grain number. In these cases, it was consistently revealed that floret survival was more critical than the initiation of primordia for most environmental factors affecting the number of fertile florets at anthesis. Examples of this include cases in which spike growth during pre-anthesis was altered by shading (Fischer and Stockman, 1980), nitrogen availability (Sibony and Pinthus, 1988; Ferrante et al., 2010), photoperiod condition (González et al., 2003b) and combinations of some of these environmental treatments (Langer and Hanif, 1973; Whingwiri and Stern, 1982; González et al., 2003b, 2005). Regarding genotypic variation, which is key for genetically improving a trait, there have been reports only based on the introgression of semi-dwarfing genes. Miralles et al. (1998) reported that Rht1 and Rht2 alleles increased the likelihood of relatively distal floret primordia to successfully progress to the production of fertile florets and attributed this to an improved assimilate allocation of resources to the growing spike before anthesis (Siddique et al., 1989; Slafer and Andrade, 1993). As opportunities to further increase partitioning to the juvenile spike in respect of most modern cultivars are restricted, variation in floret development and spike fertility within elite germplasm must be identified. In the present study we reported variation in the dynamics of floret primordia in a panel assembled for its potential relevance for breeding to further raise yield potential. The genotypic variation in maximum number of florets initiated was marginal whereas variation

in floret primordia survival was found to be the main determinant of the genotypic variation in the number of fertile florets at anthesis. The fact that final number of fertile florets was related to floret primordia survival and rather independent of the maximum number of florets initiated is in agreement with results reported with a comparison of four modern durum wheats by Ferrante et al. (2010, 2013a). Thus, it seems that the differences between elite genotypes in spike fertility are based on similar processes responsible for differences in spike fertility when plants are grown under contrasting environmental conditions.

The model hypothetically applicable is that wheat (and all other cereals) may produce an excessive number of floret primordia without penalties as it is energetically inexpensive. However, when progressing to later developmental stages, growth of these primordia requires increasing amounts of resources, so the plant adjusts the number of primordia that become fertile florets (Sadras and Slafer, 2012). This adjustment would be quantitatively related with the availability of resources for the growing juvenile spike before anthesis. This is further reinforced by evidence that the triggers for floret primordia death are not purely developmental processes (Ferrante et al., 2013b) but likely resource-driven (González et al., 2011). Bancal (2009) suggested that floret death starts when the first floret of the central position reaches a Waddington scale of 7–8; which in the panel of elite lines analysed is not true for all the cultivars (e.g., the onset of floret death in genotype 7 is when the proximal floret at the central position scores 9.3 in the Waddington scale (Table A.1)).

Much of the differences between the set of genotypes analysed from the CIMCOG panel, in terms of spike fertility, were associated with differences in floret survival that can be traced back to the processes of floret development. Comparing the two extreme genotypes of this study (in terms of fertile florets produced per spikelet), it seemed clear that the cultivar maximizing floret survival has a consistently longer period of floret development. Thus, it seemed possible to speculate that advancing development progress of labile florets increases the likelihood of a floret primordia becoming fertile floret. For instance growing a particular genotype under relatively shorter photoperiods during the period of floret development (and spike growth) before anthesis normally brings about significant increases in floret primordia survival (González et al., 2003b; Serrago et al., 2008). It seems consistent with this that genotypes having slightly longer periods of floret development may increase the number of fertile florets through reducing the proportion of primordia dying, in line with the earlier hypothesis that lengthening the stem elongation phase would bring about increases in the number of grains per m^2 (Slafer et al., 2001).

5. Conclusion

We concluded that within elite wheat germplasm, which could be used directly in breeding programmes, there is variation in developmental dynamics of the florets which are ultimately responsible for differences in spike fertility. Genotypes with more fertile spikes exhibited an improved survival of floret primordia related to a longer period of floret mortality: the longer the period the more time (and resources) will be available for allowing labile primordia to continue developing normally therefore reducing floret mortality. Selecting lines exhibiting this property as prospective parents may help in further raising yield potential in wheat.

Acknowledgements

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Appendix A. Appendix

See Fig. A.1.
See Fig. A.2.
See Fig. A.3.
See Table A.1.

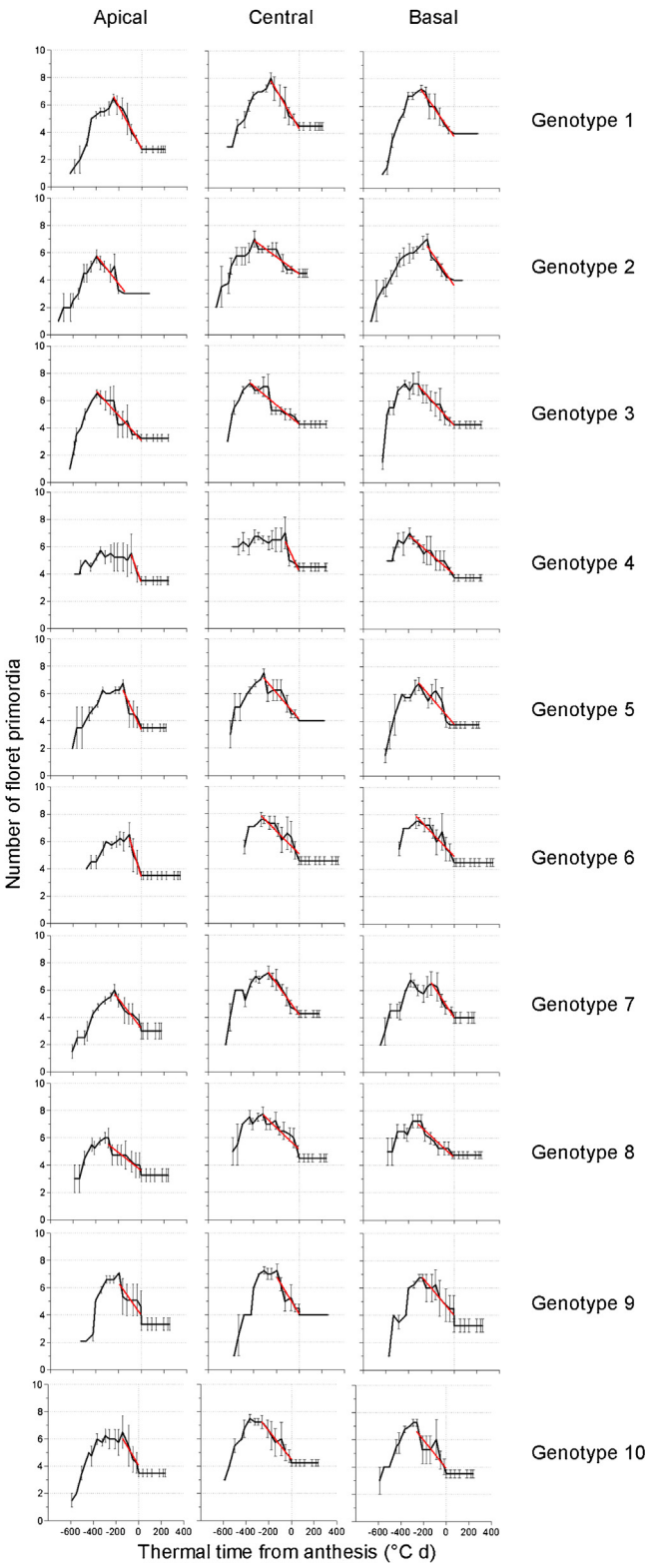

Fig. A.1. Dynamics of the number of living floret primordia from the onset of stem elongation onwards, plotted against thermal time from anthesis, in the apical (left panel), central (middle panel) and basal spikelets (right panel).

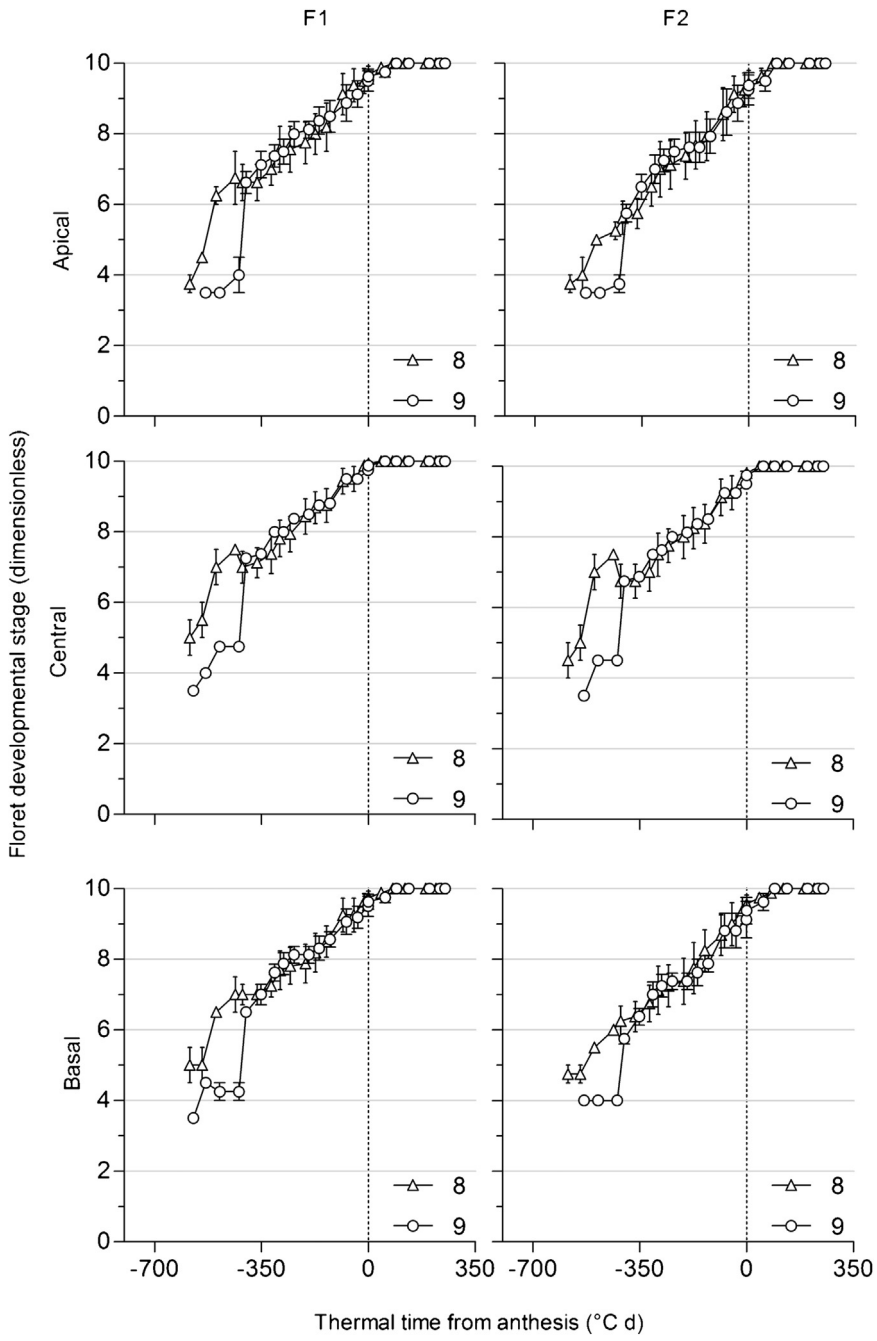

Fig. A.2. Developmental progress of floret primordia 1 and 2 in apical, central and basal spikelets (from top to bottom panels) from the onset of stem elongation onwards, plotted against thermal time from anthesis.

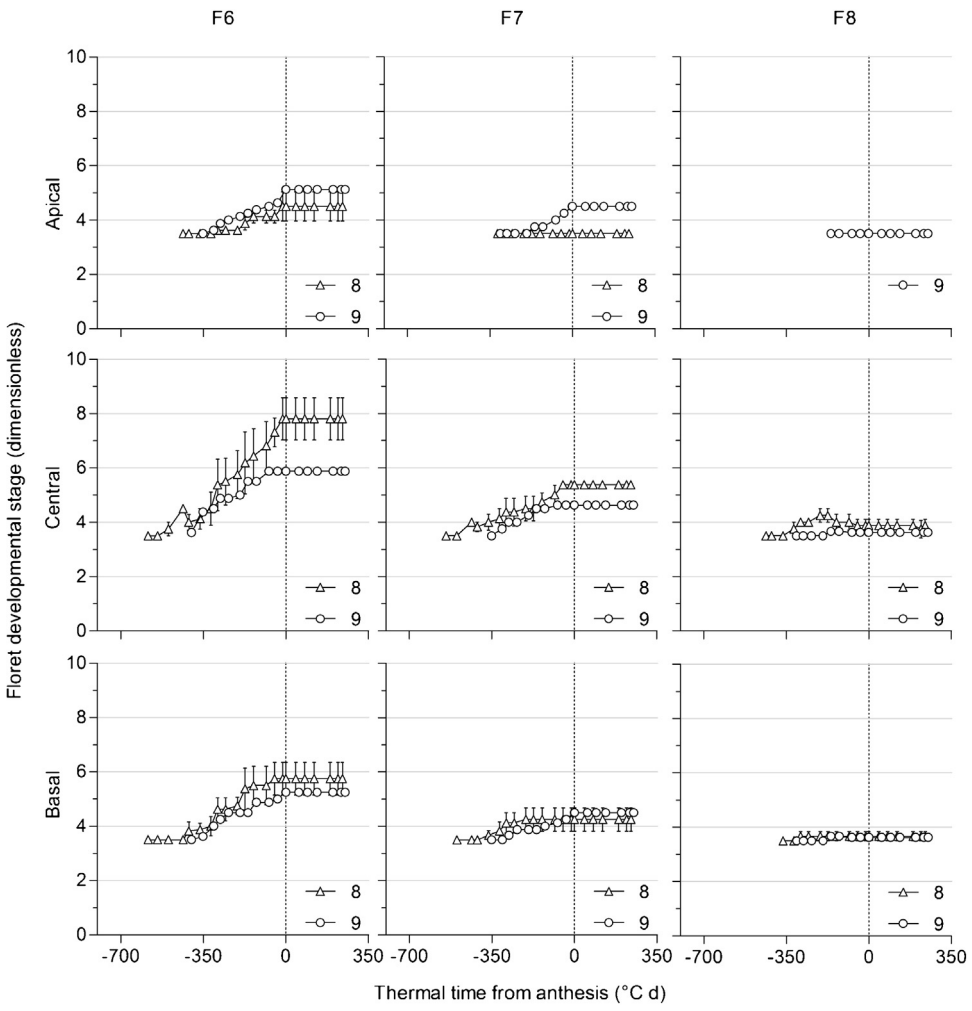

Fig. A.3. Developmental progress of floret primordia 6, 7 and 8 (from left to right panels) in apical, central and basal spikelets (from top to bottom panels) from the onset of stem elongation onwards, plotted against thermal time from anthesis.

Table A.1
Floret mortality rate as a linear model from the maximum number of floret primordia vs. the number of fertile florets for the mean of season 2010–11 and 2011–12.

Position	Entry	Maximum number of floret primordia				Number of fertile florets			Floret mortality rate		
		Floret primordia	TT (before anthesis)	Waddington Scale of F1	SE	Fertile florets	SE	TT (before anthesis)	Primordia °C d^{-1} (×100)	r^2	P
Apical	1	6.5	250	7.6	±0.31	2.75	±0.25	0	−1.536 ± 0.1060	0.977	<0.0001***
	2	5.75	394	5.9	±0.55	3	±0	145.5	−1.055 ± 0.2146	0.829	0.0044**
	3	6.5	391.5	7.2	±0.25	3.25	±0.25	0	−0.911 ± 0.0995	0.903	<0.0001***
	4	5.5	88	9.3	±0.42	3.5	±0.289	0	−2.318 ± 0.3824	0.974	0.1041ns
	5	6.75	159.5	8.3	±0.37	3.5	±0.289	0	−1.802 ± 0.4563	0.839	0.029*
	6	6.5	104.5	8.8	±0.42	3.5	±0.289	0	−2.708 ± 0.4124	0.956	0.0224*
	7	6	236.5	7.5	±0.35	3	±0.577	0	−1.070 ± 0.1264	0.935	0.0004***
	8	6	290	7.6	±0.51	3.25	±0.479	0	−0.652 ± 0.1182	0.813	0.0009***
	9	7	194.5	8.1	±0.23	3.25	±0.479	0	−1.182 ± 0.3567	0.687	0.0211*
	10	6.5	141.5	8.8	±0.37	3.5	±0.25	0	−1.398 ± 0.3334	0.854	0.0247*
Central	1	8	250	8.2	±0.27	4.5	±0.289	0	−1.403 ± 0.0998	0.975	<0.0001***
	2	7	394	7	±0.35	4.5	±0.289	0	−0.614 ± 0.0832	0.872	<0.0001***
	3	7.25	432	7.5	±0.35	4.25	±0.25	0	−0.695 ± 0.0914	0.853	<0.0001***
	4	7	123.5	9.3	±0.27	4.5	±0.289	0	−1.785 ± 0.7602	0.734	0.1433ns
	5	7.5	312	7.7	±0.43	4	±0	0	−0.965 ± 0.1405	0.871	0.0002***
	6	7.5	334	8.3	±0.37	4.5	±0.289	0	−0.802 ± 0.1218	0.844	0.0002***
	7	7.25	269.5	8	±0.32	4.5	±0.25	0	−1.148 ± 0.0730	0.976	<0.0001***
	8	7.75	318.5	7.3	±0.55	4.5	±0.289	0	−0.800 ± 0.1220	0.843	0.0002***
	9	7.25	194.5	8.5	±0.17	4	±0	0	−1.355 ± 0.2463	0.858	0.0027**
	10	7.25	260	8.3	±0.23	4.25	±0.25	0	−1.054 ± 0.1124	0.936	<0.0001***
Basal	1	7.25	288	7.6	±0.31	4	±0	0	−1.182 ± 0.0847	0.970	<0.0001***
	2	7	235.5	7.5	±0.20	4	±0	0	−1.208 ± 0.1999	0.901	0.0038**
	3	7.25	315	8.1	±0.24	4.25	±0.25	0	−0.918 ± 0.0672	0.964	0.0001***
	4	7	391.5	7	±0.61	3.75	±0.25	0	−0.718 ± 0.0587	0.943	<0.0001***
	5	6.75	312	7.2	±0.43	3.75	±0.25	0	−0.969 ± 0.1770	0.811	0.0009***
	6	7.5	334	7.7	±0.25	4.5	±0.289	0	−0.849 ± 0.1226	0.857	0.0001***
	7	6.5	200.5	8.1	±0.27	4	±0.408	0	−1.269 ± 0.1534	0.945	0.0012**
	8	7.25	318.5	7.25	±0.32	4.75	±0.25	0	−0.762 ± 0.0830	0.913	<0.0001***
	9	6.75	278	7.8	±0.31	3.25	±0.479	0	−0.988 ± 0.1540	0.855	0.0004***
	10	7.25	260	8.1	±0.23	3.5	±0.289	0	−1.036 ± 0.2817	0.693	0.0103*

SE = standard error of the mean.
* <0.05.
** <0.01.
*** <0.001.

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