Field Crops Research 203 (2017) 114–127

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Yield determination, interplay between major components and yield stability in a traditional and a contemporary wheat across a wide range of environments

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ARTICLE INFO

Article history:
Received 15 June 2016
Received in revised form
27 December 2016
Accepted 28 December 2016

Keywords:
Nitrogen
Irrigation
Photoperiod
Sink
Triticum *aestivum*

ABSTRACT

Physiological bases of Mediterranean wheat yield improvements have been less explored than in other regions, particularly so during the period following the Green Revolution. Due to the common terminal stress of Mediterranean regions, it could be hypothesized that contemporary cultivars would exhibit improved average grain weight and yield stability compared with a traditional cultivar. Despite the lack of clear evidence in the literature, farmers in Mediterranean regions may prefer growing traditional cultivars over modern ones under the poorest environments and allocate the best lands to more contemporary cultivars. For instance, in our region this has been the case with Anza (a traditional, but semi-dwarf, cultivar) and Soissons (more modern and with a putatively higher potential yield than Anza). We analysed in detail for these two cultivars yield determination and its responsiveness to a very wide range of growing conditions (across six experiments, yield ranging from less than 1 to more than 8 Mg ha^{-1}). Both cultivars responded to the improved yielding conditions noticeably but Soissons did so more strongly, revealing a clearly higher yield potential. The higher yield stability of the traditional cultivar did not imply consistently better performance under the lowest yielding conditions. The main component explaining the yield advantage of the contemporary cultivar was the number of grains per m^2 though the traditional cultivar exhibited a sort of partial compensation due to possessing a consistently higher average grain weight. Across all conditions, the overall fruiting efficiency of the contemporary cultivar (111.4 ± 7.5 grains g_{spike}^{-1}) was significantly higher than that of the traditional one (88.3 ± 3.9 grains g_{spike}^{-1}), which was the basis of a higher spike fertility in the contemporary than in the traditional cultivar, observed in most of the spikelets consistently across environmental conditions with a clear trend to increase the number of spikelets exhibiting a significant difference in fertility between the two cultivars and the overall difference in spike fertility between them. Analysing in detail the weight of each individual grain in the last two experiments, we showed that the improved spike fertility due to a higher fruiting efficiency did not bring about reductions in grain weight potential and the dominant cause of the partial compensation was the increase in the proportion of grains in distal positions (constitutively smaller than proximal grains) in the contemporary cultivar.

1. Introduction

Improvement of wheat yield during the last century has been achieved mainly by increasing harvest index through raising the number of grains both per spikelet and per spike (e.g. Acreche et al., 2008; Austin et al., 1989; Calderini et al., 1999; Shearman et al., 2005; Siddique et al., 1989a) with no major changes in above ground biomass (e.g. Calderini et al., 1995), although focusing in the last few decades of breeding at CIMMYT Lopes et al. (2012) and Aisawi et al. (2015) found biomass has increased more than harvest index. As grain number is the main component determining yield (Prystupa et al., 2004; Slafer et al., 2005; Peltonen-Sainio et al., 2007; Zhang et al., 2007; Slafer et al., 2014) yield gains have been usually strongly associated with gains in the number of grains per unit land area (e.g. Frederick and Bauer, 1999; Slafer et al., 2005).

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http://dx.doi.org/10.1016/j.fcr.2016.12.028
0378-4290/

This has been extensively reported for a relatively wide range of environments (Calderini et al., 1999 and references quoted therein). However, less has been explored under Mediterranean conditions (and with less consistent effects; e.g. Sener et al., 2009), where cereal yields are commonly restricted by frequent and unpredictable water and heat stresses during the last part of the growing season, mainly coinciding with grain filling (Acevedo et al., 1999; López et al., 1996; López-Bellido et al., 2000; Rana and Katerji, 2000; Olesen and Binbi, 2002; Savin et al., 2015). This is particularly important as drought and high temperatures during grain filling can reduce grain weight (Loss and Siddique, 1994) and, due to the spatial and temporal variability in their occurrence, can reduce yield stability. Although there were studies conducted in Australia and in the Mediterranean Basin, conclusions cannot be taken into account straightforwardly as most of these studies considered long periods of breeding and reported a strong reduction in time to anthesis mainly because very old cultivars had an inappropriately long phenology, particularly in Australia (e.g. Siddique et al., 1989a) but also in the Mediterranean basin (Motzo et al., 2004; De Vita et al., 2007; Isidro et al., 2011). When comparing cultivars released during the second half of the 20th century, whilst in European countries where wheat has been grown for centuries, breeding did not change time to anthesis consistently, as the old cultivars were already well adapted. As time to flowering may have a strongly confounding effect in general (Pinto et al., 2010; Lopes et al., 2015) and more particularly in Mediterranean conditions of frequent terminal stress, conclusions from studies involving drastic changes in phenology cannot reveal the actual changes made by breeding in the Mediterranean region during the last decades.

Therefore, it could be hypothesized that contemporary cultivars performing better than traditional ones (considering as such those released soon after the green-revolution, already semi-dwarf) under Mediterranean scenarios might exhibit different physiological attributes determining their improved performance and that a contemporary wheat cultivar would exhibit improved average grain weight and yield stability compared with a traditional cultivar. In other words, that the background environmental condition may alter which are the traits more relevantly explaining genetic gains in yield. This hypothesis would match with agronomic improvement in Mediterranean regions which stimulated strategies to defer water use ensuring grain filling (Slafer et al., 2014). On the other hand, if physiological bases for yield gains are similar to those reported in non-Mediterranean regions, it could be interpreted as that the evolutionary constraints imposed on wheat yield physiology (on wheat reproductive output) are so strong that the consequences of breeding are virtually identical disregarding the environmental constraints in which the release of cultivars were made. This last alternative would be true if yield were mechanistically related to grain number per m^2, which might be the case not only in bread (Slafer et al., 2006; Reynolds et al., 2009) and durum wheat (Ferrante et al., 2012; Giunta et al., 2007) but also in most grain crops (Sadras and Slafer, 2012). If so, understanding the mechanisms controlling grain number determination between contrasting cultivars may be relevant to further raising yield (Fischer 2011; and referenced quoted therein).

Most papers concluding that breeding has increased yield through increasing grain number involved cultivars released before and after the Green Revolution produced by introgressing semi-dwarfism. When “old” cultivars considered were recessive for Rht alleles (tall phenotype) the driving force for increasing grain number was the relatively large transfer of assimilates to growth of the juvenile spikes during pre-anthesis period produced by the introgression of dominant Rht alleles in “modern” cultivars (Brooking and Kirby, 1981; Miralles and Slafer, 1995; Flintham et al., 1997; Miralles et al., 1998). The improved partitioning to the juvenile spikes growing during pre-anthesis led to an increase in spike dry weight at anthesis (Siddique et al., 1989b; Slafer et al., 1994; Slafer and Andrade, 1993), which in turn was pivotal for increasing grain number associated with plant height reduction (Fischer, 2007). However, if when comparing the physiological bases of yield differences between a traditional and a contemporary cultivar both are semi-dwarf, any differences in grain number must have been achieved through a different process to that commonly described when comparing tall and semi-dwarf cultivars, and such bases have been not explored in depth yet, even though they may be more relevant for future breeding than the bases comparing tall vs semi-dwarf cultivars. For instance, genetic gains achieved during the last decades in NW Mexico was associated with an increased grain weight (Lopes et al., 2012; Aisawi et al., 2015), but this is a high-yielding environment and results in Mediterranean region might differ. As modern cultivars already possess plant heights within the range optimising yield, alternatives to increase grain number must be envisaged (Reynolds et al., 2012; and referenced quoted therein). Recently, other possible pathway to raise grain number could be to increase the efficiency with which a certain growth of the juvenile spike before anthesis may be used to set a certain number of grains, or fruiting efficiency (i.e. the number of grains set per unit of spike dry weight at anthesis, see Slafer et al., 2015).

Modern cereal cultivars with improved potential yield have shown more responsiveness to improved growing conditions but less yield stability (Slafer and Kernich, 1996; Abeledo et al., 2003). This has given room to the concept that genotypes with low potential yield would outyield cultivars of high yield potential under stress conditions, as there would be a crossover interaction revealed by a change in yield rank of the genotypes so that those performing well under stress environments would possess low potential yield and *vice-versa* (e.g. Ceccarelli, 1996). However, despite of its higher stability old cultivars do not frequently outyield modern ones under low-yielding environments (Calderini and Slafer, 1999). Similarly in the Spanish Mediterranean region modern cultivars yielded more than their predecessors when tested under higher yielding environments though under relatively poorer environmental conditions yield did not noticeably differ (Acreche et al., 2008), indicating that in general modern cultivars used in Spain are also less stable due to its improved responsiveness to better environments rather than due to their lower yields under poor conditions. Results from Pswarayi et al. (2008) confirmed that high-yielding modern cultivars consistently outyield landraces in high-yielding environments, but the expected reverse advantage was not consistent in low-yielding conditions (see Fig. 1 in Pswarayi et al., 2008) Part of the controversy might be due to what are defined as “low-yielding” environments (in which a cross-over interaction might be expected) between the different studies. To deal with this issue properly, in the present study we explored a huge range of yielding conditions, including extremely low-yielding environments. Based on the belief that cultivars of limited potential yield would perform consistently better under stress conditions, farmers in Mediterranean regions, such as that of the Ebro Valley area (a semi-arid region in Catalonia, north-eastern Spain), tend to prefer growing traditional cultivars over modern ones under the poorest environments and allocate the best lands to more contemporary cultivars. Thus, at the time when the experiments were designed and carried out, the farmers with more aversion to the risk frequently chose Anza (a traditional, but semi-dwarf, cultivar) and those with less risk-aversion generally preferred Soissons (more modern and with a putatively higher potential yield than Anza) but nitrogen (N) fertilisation management was similar for any of the cultivars sown (Jaume Gregory, Department of Agriculture of Catalonia at the Agramunt Office, personal communication).

There is scarce information from field experiments in Mediterranean regions, such as the Ebro valley, regarding yield responsiveness to changes in yielding conditions when compar-