

Physiological traits associated with recent advances in yield of Chinese wheat

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Physiological traits associated with recent advances in yield of Chinese wheat

(Rasgos fisiológicos asociados con los recientes avances en el rendimiento del trigo chino)

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CHAPTER 1

General introduction

This introduction aims to provide a broad view on the recent advances in grain yield of Chinese winter bread wheats and the relevant physiological and agronomical traits involved. In addition, current phenotypic approaches to select biotic stress resistance have also been included. Therefore, the purpose of the introduction is to define the background that connects the different chapters of this thesis.

This introduction has been divided into the following sections:

- Wheat production in China
- Breeding for grain yield
- Traits contributing to yield improvements
- High-throughput phenotyping for grain yield loss by stress
- Objectives
- References

1. Wheat production in China

China is the largest bread wheat (*Triticum aestivum* L.) producer in the world, totaling 120.6 million Mg (FAO, 2012), with the second largest planting area (about 24.1 million ha) after India (29.9 million ha). China, with a population that already accounts for one fifth of the world's total, is facing a fast economic development that demands increased amounts of food and feed and thus greater agricultural productivity. At the same time environmental concerns from intensive agriculture are increasing, associated with the low use efficiency of inputs such as fertilizer and water, and this is occurring alongside stagnation and even shrinkage of the area available for planting. Moreover, this situation will become more acute during the next few decades (Cui et al. 2008). Increasing wheat production through a higher grain yield per unit area has become the most important breeding target for wheat in China.

In China, there are two main wheat planting regions characterized by diverse

environments and cropping systems (Zhou et al. 2007). In the winter wheat planting regions of the North China Plain Winter Wheat Zone (NCPWWZ), the true winter type wheat is cultivated around Hebei, Beijing and Tianjin provinces. Facultative or intermediate wheat is grown in the Yellow River and Huai Valleys Winter Wheat Zone (YRHVWWZ), which includes the regions around Henan, Shandong and Anhui provinces. The production of YRHVWWZ accounts for more than 70% of the total wheat production in China (Xiao et al. 2012) with wheat-maize double cropping being the main rotation system in this region (Zhou et al. 2007). The national average grain yield has increased from less than 2 Mg ha⁻¹ in 1980s to approximately 5 Mg ha⁻¹ in 2013 (Figure 1). This has been the consequence of a breeding program, with the introduction of more productive varieties, together with an increase of fertilizer and irrigation inputs (Cui et al. 2008; Xiao et al. 2012). However, the total arable area is shrinking (Figure 2), particularly that of the spring wheat region, because the demand of land for industry and urbanization has increased. In addition, the average grain yield has increased more slowly in recent years than before (Figure 3). Meanwhile, the wheat-maize double crop rotation encourages farmers to apply more inputs to maize, rather than in wheat, in their search for higher economic benefits (Liu et al. 2003). Moreover, the ongoing change in the climate makes agricultural productivity less predictable, which highlights the urgency to develop more input-efficient genotypes. Additionally, yellow rust (*Puccinia striiformis* f. sp. *tritici*) is still the major disease constraint for wheat production in YRHVWWZ (Huang et al. 2007; Zheng et al. 2011). He et al. (2011) reported that the annual average yellow rust-infected area accounted for 4.2 million ha during 2004-2009, and increasing the multiple disease tolerance of wheat has become one of the main breeding objectives in recent breeding strategies.

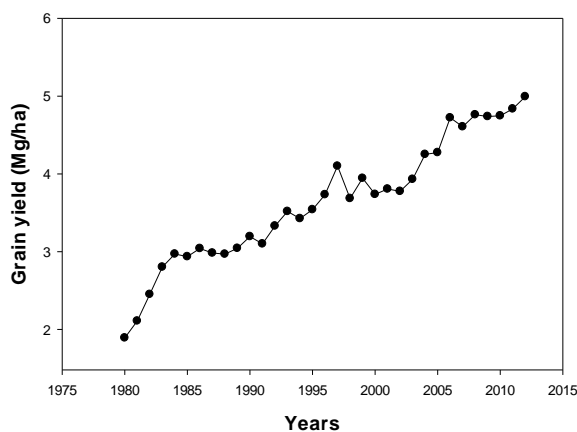


Fig. 1 Winter wheat grain yield from 1980 to 2012 in China. (FAO, 2014)

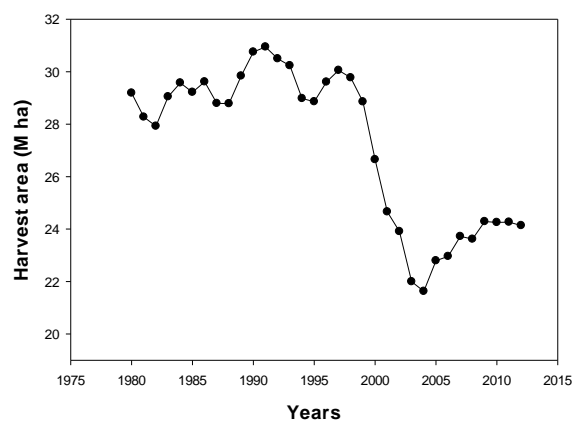


Fig. 2 Winter wheat total production from 1980 to 2012 in China. (FAO, 2014)

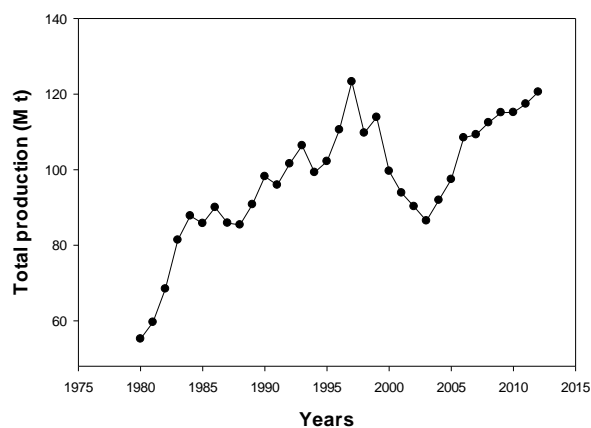


Fig. 3 Winter wheat harvest area from 1980 to 2012 in China. (FAO, 2014)

2. Breeding for grain yield

Genetic improvements have made substantial contributions to increase wheat yields all around the world (Tester and Langridge 2010; Zheng et al. 2011). In China the release of new cultivars, together with a significant progress in breeding methodologies, have started to bear fruit in terms of increased yield (Li et al. 2006a; Zhu et al. 2010b). During the last 20 years, Chinese wheat breeding has made remarkable progress by releasing two sets of cultivars, with the primary set characterized by improved yield potential and the secondary set having improved

grain quality, with both sets having dwarf genes and multi-resistance to various diseases. They are represented by many widely distributed genotypes in different wheat zones, such as Shi 4185, Jimai 22, Zhengmai 9023, Yumai 34, Zhoumai 18, Aikang 58, and Xinong 979 (He et al. 2011). Three elite parents were used extensively in the breeding strategies: Zhou 8425B, Lumai 14 and the 6VS/6AL translocation line. More than 20 cultivars have been bred from the well-known donor material, Zhou 8425B, as a source for high yield potential together with genes for yellow rust (YrZH84) and leaf rust (LrZH84) resistance (Li et al. 2006b; Zhao et al. 2008; Yin et al. 2009).

The annual genetic gains in China have been analysed by comparing cultivars released from 1960-2006 in the NCPWWZ and YRHVWWZ (Zhou et al. 2007; Zheng et al. 2011; Xiao et al. 2012). Average annual genetic gains (the improvement in grain yield as a result of the introduction of new germplasm) ranged from 32.07 to 72.11 kg ha⁻¹ per year, with the most significant increase taking place in the early 1980s, largely because of the utilization of dwarfing genes and the 1BL/1RS translocation (Zhou et al. 2007; Zheng et al. 2011; Xiao et al. 2012). This outcome agrees with previous studies reporting that the primary agronomical trait contributing to the yield improvement worldwide was harvest index (HI), which increased after the “Green Revolution” as a result of reduced plant height due to the successful utilization of dwarfing genes and translocation of the 1B/1R chromosome from rye (*Secale cereale* L.) (Reynolds et al. 1999; Zhou et al. 2007). As a consequence more kernels can be produced from a given total above-ground biomass. In the case of China, increases in grain yields during recent decades were largely associated with a larger number of kernels per unit area (Xiao et al. 2012) as a result of increases in the number of kernels per spike. The increasing kernels per unit area was also achieved through an increase in the number of spikes per unit area, resulting from improving the tiller capacity and supplying larger fertilization (Zheng et al. 2011). By contrast, the total above-ground biomass has not contributed to the increases in grain yield in either the YHVWWZ (Zheng et al. 2011), although there have been a few reports

claiming the opposite in other region (Xu et al. 2000; Xiao et al. 2012). However, while all these genetic gain studies have been carried out under irrigated conditions, the contribution of the different yield components to grain yield improvement under the less optimal field conditions of China needs to be determined.

Although a significant grain yield potential (approximately 12 Mg ha⁻¹ in the case of YHVWWZ) has been recorded at agricultural research stations (Zhou et al. 2007), maintaining such a yield potential in farmers' fields, which is a daunting challenge due to a variety unfavourable factors, is unfeasible (Reynolds et al. 2011). In China the grain yield of modern Chinese genotypes can easily be affected by poor agronomical adaptations (e.g. due to the widely divergent latitudes and climate, or simply due to climate change) and the consequence is a low yield performance. The reason is that nearly all recently released cultivars have been bred for higher yield under favourable agronomical conditions, but the adaptation to less favourable or stressful planting environments has been neglected (Zheng et al. 2011). In that context it is important to evaluate the performance of the modern Chinese wheat cultivars, bred for high-input agronomical conditions, under the environmental conditions expected in the coming decades. Regarding this, Mediterranean conditions may represent a useful scenario to test the adaptation capacity of modern Chinese wheat.

3. Traits contribute to yield improvements

In November of 2009, a Wheat Yield Consortium (WYC) was established by the International Maize and Wheat Improvement Center (CIMMYT), constituted by world-renowned crop experts, who aim to bring together a broad range of agricultural research to rise the yield potential of wheat and assist farmers in improving (Reynolds et al. 2009; Foulkes et al. 2011; Parry et al. 2011; Reynolds et al. 2011). WYC reviewed that improving yield potential could be optimized via key physiological traits including improved photosynthetic capacity, optimizing partitioning to grain yield and increasing lodging tolerance (Reynolds et al. 2009; Foulkes et al. 2011;

Parry et al. 2011; Reynolds et al. 2011). By contrast, even in recent years Chinese breeders have relied on their experienced ‘eye’ to select for what are considered to be appropriate plant ideotypes and in later generations yield testing is used. Actually, such skills could be complemented by selecting for traits considered key by the world research community, therefore increasing the efficiency of breeding in China. This includes the use of proper approaches to identify traits that increase crop production of genotypes in multiple environments (e.g. drought, salinity). Secondary traits used to phenotype for higher yield should be highly heritable, and not result in penalties when conditions are favourable, nor should they be associated with negative pleiotropic effects on other important agronomic or marketable attributes (Richards 2006). Moreover, the traits must be relatively easy and affordable to measure.

Nitrogen is considered the most important element for crop growth. Excessive use of nitrogen (N) fertilizer is very common in the Chinese wheat-maize cropping systems, particularly in regions with high population densities. In the NCPWWZ for example, rates of N application are usually beyond 300 kg N ha⁻¹ for winter wheat and 250 kg N ha⁻¹ for maize (Liu et al. 2003; Cui et al. 2008). Such high N rates greatly exceed the N requirements of both crop species in these environments and will inevitably lead to large losses of N and eventually pollution. In fact, nitrogen use efficiency (NUE) in wheat is only around 15%, therefore lower than the world average (around 33%) for wheat (Ma et al. 2008). Thus, optimizing the traits related to N use is one strategy to breed high yield wheat, and not only in China. Selecting for high NUE genotypes represents a major goal in breeding programs in many cropping regions (Kichey et al. 2007). In this context, it is paramount to find a useful proxy method for evaluating NUE and detecting the general status of N metabolism during different plant growth stages. The approach based on analysing the stable nitrogen isotope composition ($\delta^{15}\text{N}$) in its natural abundance in dry matter has proved to be potentially useful in screening the genotypic performance of N metabolism (Yousfi et al. 2012) under irrigation (Masclaux-Daubresse et al. 2008), drought (Robinson et al. 2000) or salinity (Yousfi et al. 2013), even though a complete knowledge of the

underlying biochemical mechanisms is still lacking (Tcherkez 2010). On the other hand, the use of ^{15}N labelling is a good alternative that generally allows the estimation of N uptake, accumulation and remobilization from source organs to the sink organs with a less biased and more precise manner than analysing ^{15}N in its natural abundance (Kichey et al. 2007; Masclaux-Daubresse et al. 2008). However, the use of ^{15}N tracing to estimate N metabolism in wheat has not been deployed before in high yielding genotypes from China.

In genetic-gain experiments, the photosynthesis rate per unit area at saturated photosynthetic photon flux density (Pn) and stomatal conductance (gs) is reported to have positively contributed to raising yield potential during the last 60 years in China (Jiang et al. 2003; Zheng et al. 2011). However, these results are challenged by many reports in other wheat growing regions of the world where photosynthetic rates have not changed with genetic gain of grain yield, or have even been negatively correlated (Reynolds et al. 2000; Richards 2000). Pn can be increased by increasing the activity of Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (Araus et al. 1993; Parry et al. 2011), or in terms of increasing the total organ photosynthesis capacity (e. g. flag, ears) (Tambussi et al. 2007; Maydup et al. 2010). However, the photosynthesis of the ear, and its potential implication in breeding for grain yield, has been much less researched (Maydup et al. 2010). Beside the above considerations, Parry et al. (2011) reviewed how improvements in photosynthesis could be achieved without necessarily increasing Pn per unit area or per total organ, but by raising the ability of the canopy to intercept and capture light, increasing the duration of light capture and improving the photosynthetic efficiency of the canopy.

Unlike the instantaneous photosynthesis measurements of the ear or the flag leaf, the carbon isotope composition ($\delta^{13}\text{C}$) when analysed in plant dry matter provides information on the long-term transpiration efficiency of plants. The $\delta^{13}\text{C}$ of the total organic matter (TOM) has been proposed as a selection criterion for high water use efficiency (WUE) for wheat breeding in many regions such as the Mediterranean,

North America, Australia and China (Farquhar and Richards 1984; Sun et al. 1996; Araus et al. 2003; Xu et al. 2007). In the case of China, Xu et al. (2007) reported that TOM $\delta^{13}\text{C}$ is a useful tool to evaluate grain yield in irrigated, rain-fed and saline conditions. Therefore, the TOM $\delta^{13}\text{C}$ in kernels and leaves could be used to estimate yield performance in breeding (Zhu et al. 2010a). However, $\delta^{13}\text{C}$ may be affected not only by growing conditions, which mainly affect stomatal opening, but also by intrinsic changes in photosynthetic metabolism (Tcherkez and Hodges 2008; Araus et al. 2013). In that sense, stable oxygen isotope composition ($\delta^{18}\text{O}$) provides an approach to help separate the independent effects of intrinsic Pn and gs on $\delta^{13}\text{C}$ because $\delta^{18}\text{O}$ is unaffected by photosynthesis (Barbour and Farquhar 2000; Araus et al. 2013). TOM $\delta^{18}\text{O}$ integrates the evaporative conditions throughout the crop cycle (Barbour and Farquhar 2000); therefore, $\delta^{18}\text{O}$ has been proposed as a proxy method for measuring transpiration and water use in different crop species (Barbour and Farquhar 2000; Cabrera-Bosquet et al. 2011). However, the applications of TOM $\delta^{18}\text{O}$ in breeding and related to other eco-physiological studies have only been implemented in wheat in recent years.

4. High-throughput phenotyping for grain yield loss by stress

Avoidance of stress by plants is a way to increase actual grain yield in farmers' fields. In this content, breeding for increasing resistance to stress without a penalty in yield potential is an alternative approach. To meet these needs it is necessary to phenotype large numbers of lines rapidly and accurately, and identify the best progeny under abiotic and biotic stresses, preferably using high-throughput, fast and inexpensive methods of phenotyping (Cabrera-Bosquet et al. 2012). Proximal (remote) sensing and imaging are among the most promising high-throughput approaches (Araus and Cairns 2014). Proximal sensing with different categories of sensors is a non-destructive and non-invasive method based mostly on information provided by reflection (or transmission) of visible/near-infrared radiation (e.g. using spectroradiometers or multispectral cameras for recording) and by far-infrared

radiation (e.g. capture by infrared thermometers or thermal cameras) emitted by the crop (Berger et al. 2010; Vadivambal and Jayas 2011). An economical alternative to some of the spectroradiometrical approaches is the use of conventional red/green/blue (RGB) images that use a low-cost sensor (e.g. a conventional camera) and that may be processed using open software. This approach enables estimation of a vegetation index as affected, for example, by rain-fed conditions or biotic stresses (Mirik et al. 2006; Casades ús et al. 2007; Lenthe et al. 2007; Moller et al. 2007). In this way, high-throughput phenotyping platforms could be particularly useful for obtaining detailed measurements of plant characteristics that collectively provide reliable estimates of phenotypic traits relevant to breeding (Cabrera-Bosquet et al. 2012). Therefore, the aim is to find effective and affordable approaches to evaluate the abiotic and biotic stresses, such as the yellow rust that is threatening Chinese wheats and hindering production at the farmers' field level.

