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Progress in genetic improvement of grain yield and related physiological traits of Chinese wheat in Henan Province

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ABSTRACT

Wheat is one of the staple food crops worldwide and breeding for high yield wheat is critical to meet the need of increasing world population. To determine the factors that limit wheat yield potential in Henan province, China, 30 wheat cultivars that have been widely grown in Henan province since 1940s were evaluated for grain yield and related physiological traits. The results show that grain yield has been significantly increased since 1940s, with an annual genetic gain of 1.09%, and the increased yield after 1900s was attributed to the introduction of 1BL/1RS translocation. The significant yield increase mainly resulted from a significant increase in grain number per spike (GNPS), thousand kernel weight (TKW) and harvest index (HI), and a significant decrease in plant height due to utilization of semi-dwarfing genes. The genetic improvement of assimilate accumulation and translocation was mainly reflected by the improvement in post-anthesis assimilate accumulation (PoAAA) and post-anthesis transportion rate (PoATR) of pre-anthesis assimilates (PrAA), with genetic gains of 0.63% and 1.89%, respectively. The improvement of the PoAAA was closely related to an increase in net photosynthetic rates (P_n) of flag leaves at anthesis and 20 days after anthesis, and leaf area index (LAI) at 20 days after anthesis; whereas the improvement of the PoATR of the PrAA was closely associated with the improvement of accumulation and redistribution of the assimilates accumulated in stems and sheaths. As yield increased, the source-sink ratio significantly decreased, reflecting that the source has been gradually becoming a limiting factor to grain yield increase. Therefore, diverse strategies should be adopted to improve biomass (source) in future wheat breeding to meet the need of continuous increasing in wheat yield.

1. Introduction

Food security has become an urgent problem that needs to be solved due to continuous increasing in world population, justifying improvement of crop yield as the main target of crop production (Edgerton, 2009; Long et al., 2015). Information on the contribution of physiological traits to wheat yield potential (*Triticum aestivum* L.) and understanding of the limiting factors for wheat yield improvement are important to continuous improvement of wheat yield in wheat breeding programs. Many studies on improvement of wheat yield have been conducted in China (Zhou et al., 2007a,b) and other countries (Brancourthulmel et al., 2003; Morgounov et al., 2010; Green et al., 2012; Manès et al., 2012; Beche et al., 2014; Pozo et al., 2014). Average annual genetic gains in wheat yield varied with studies, ranging from 5.8 kg ha^{-1} yr^{-1} from 1860 to 1982 in Australia (Perry and D'Antuono, 1989) to 123 kg ha^{-1} yr^{-1} from 1950 to 1996 in France (Brisson et al., 2010). In China, the range of the genetic gains was from 22.8 kg ha^{-1} yr^{-1} from 1940s to 2010s in Shaanxi province (Sun et al., 2014) to 103.5 kg ha^{-1} yr^{-1} from 1975 to 2007 in Xinjiang province (Zhang et al., 2011). Harvest index (HI) that positively correlated with grain yield in most studies increased significantly through wheat breeding, which resulted not only from reduced plant height through deployment of semi-dwarf *Rht* genes during the Green Revolution in middle of the 20th century, but also from increased grain number and weight (Reynolds et al., 2009; Xiao et al., 2012). A comparison of genetic progresses made in wheat HI indicate a systematic increase over time with the

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Abbreviations: SNPUA, spike number per unit area; GNPS, grain number per spike; TKW, thousand kernel weight; GNPUA, grain number per unit area; AB, aboveground biomass; PrAAA, pre-anthesis assimilate accumulation; PoAAA, post-anthesis assimilate accumulation; PoATR of PrAA, post-anthesis transport rate of pre-anthesis assimilate; HI, harvest index; Pn, net photosynthesis rate; LAI, leaf area index.

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HI values reaching about 0.50 in spring wheat (Sayre et al., 1997; Reynolds et al., 1999) and 0.55 in winter wheat (Shearman et al., 2005), which is close to a hypothetical limit of 0.60 in wheat (Austin et al., 1980). Thus further improvement of HI will be falter in the future breeding.

Wheat biomass yield significantly affects grain yield. The contribution of aboveground biomass (AB) to wheat yield has been widely investigated, but the conclusions are still dispuTable Some studies shown that AB contributed significantly to increased grain yield (Sadras and Lawson, 2011; Bustos et al., 2013), while others indicated the AB contribution was not significant (Giunta et al., 2007; Sun et al., 2014). Biomass formation stage can be split into pre-anthesis assimilates and post-anthesis assimilates, and both play important roles in formation of grain yield. Bidinger et al. (1977) studied assimilate accumulation in wheat and barley (*Hordeum vulgare* L.) using an isotope tracing technique, and reported that the contribution of pre-anthesis assimilates to grain yield was approximately 80 g m^{-2}. Subsequently, Foulkes et al. (2002) and Shearman et al. (2005) reported that the values could be as high as 400 g m^{-2}. Fischer and Stockman (1986) indicated that amount of pre-anthesis assimilates was closely correlated to number of florets per spike, and grain number per spike could be improved by availability of assimilates in developing spikes. In a normal condition, post-anthesis assimilate is mainly used for grain filling in wheat (Xu et al., 1999; Liu et al., 2013). Dreccer et al. (2009) reported that grain weight was high in the lines with high water soluble carbohydrates in early grain filling stages, indicating that more available assimilates contribute to a higher grain weight potential in the stage when the number of endosperm cells and starch granules are established. The amount of post-anthesis assimilates is, therefore, also very important to grain yield.

Study of the source-sink relationship by manipulating the source-sink ratios at the grain filling stage is another approach to understand mechanisms of yield formation. Borrás et al. (2004) determined the magnitude of grain weight changes in response to manipulation of assimilate availability during grain filling, and found that wheat yield was mainly sink-limited in all growing conditions, which agrees with Reynolds et al. (2005) and Zhang et al. (2010). A case of source-sink co-limitation has also been reported in wheat (Álvaro et al., 2008), however, this research was conducted under water-limited conditions that could cause a reduction of biomass at 40%. Modern wheat cultivars may respond more to the changes in source-sink ratios than the old ones (Álvaro et al., 2008), indicating that the increased yield through breeding in the past has led to a growing limitation of the source.

Henan province is a major wheat production province located in the east-central China. In 2011, 5.32 million ha of wheat were planted, which accounted for 21.9% of the total wheat planted in China (Wu et al., 2014). Wheat-maize system is the major production system in Henan, except in Xinyang region where a wheat-rice system is predominant. Before the 1970s, wheat grown in Henan province was mostly landraces or some cultivars introduced from other provinces or countries. Since the 1970s, locally bred cultivars have gradually become dominant in Henan and many of them have also been expended to other neighboring provinces (He et al., 2001). With increased grain yield and changed market demands, the objectives of wheat breeding in Henan province has gradually changed from yield only to balancing the yield potential with end-use quality, disease resistance and eurytopicity. Several studies were conducted to assay the genetic gain of wheat yield in Henan province, but the results were controversial. Zheng et al. (2011) studied 18 cultivars released from 1981 to 2008 and concluded that the improvement of grain yield were awing to the increased grain weight and harvest index (HI), and that the net photosynthesis rate (P_n) after anthesis was closely correlated with grain yield; whereas Zhou et al. (2014) investigated 10 wheat cultivars released from 1995 to 2014, however, concluded that HI, grain number per unit area (GNPUA) and AB were the major contributors to the increased yield. Therefore it is necessary to investigate the impact of the changes in agronomic and physiological traits on yield increase to identify a new strategy for further yield improvement. The objectives of this study were to (i) evaluate the genetic progresses in wheat grain yield and related traits through modern breeding in Henan province from 1940s to 2010s, (ii) investigate the genetic changes of assimilate accumulation and translocation traits in relation to the increased yield and determine the factors that are responsible for such changes, (iii) understand the impact of breeding activities on the source-sink relationship and explore the new strategies to further improve the grain yield potential.

2. Materials and methods

2.1. Plant materials

Thirty wheat cultivars, including three landraces and 27 bred wheat cultivars, were selected for this study (Table 1). They have been widely grown in Henan province from 1940s to 2010s with a maximum annual planting area over 0.1 million ha each, except for the landraces.

2.2. Experimental design

The experiments were conducted from 2012 to 2015 (three growing seasons) in the Henan Research and Development Center for Modern Agriculture (Yuanyang, Henan, China; 35°00′N, 113°40′E, 77 m a.s.l.). Table 2 listed weather data from 2012 to 2015. The soil type of the experimental field was highly organic and slightly alkaline sandy clay. Urea (ca. 13 kg ha^{-1} of N), ammonium phosphate (ca. 170 kg ha^{-1} of P, 67 kg ha^{-1} of N) and potassium chloride (ca. 75 kg ha^{-1} of K) were applied prior to planting, and then an additional 120 kg ha^{-1} of N was top-dressed at stem elongation stage (GS31) (Zadoks et al., 1974). The trial was arranged in a completely randomized block design with six replications, of which three replications were used to assay grain yield (yield plots) and the rest three replications were used for sample collection to evaluate other traits (sampling plots). Each plot consisted of six rows at 4.25 m in length and 0.23 m in width, giving a total plot area of 6.67 m^2. Seed was planted on October 6 each year at a seeding rate of 180 kernels m^{-2} using a plot planter. According to the local cultivation practice, furrow irrigation (60 mm each) was applied at the tillering (before winter) (GS25), stem elongation (GS31) and anthesis (GS60) stages. Fungicides and pesticides were applied at stem elongation (GS33) and grain filling (GS73) stages to prevent attack by diseases and pests. Bamboo sticks (2–3 m long) were used to prevent tall plants from lodging so that the maximum yield potential could be reached.

2.3. Plant sampling and trait evaluation

2.3.1. Evaluation of yield and agronomic traits

At the physiological maturity (GS92), each yield plot was hand-harvested, threshed, dried, and weighed separately to determine grain yield at 13% moisture content.

Spike number per unit area (SNPUA) was recorded at the milk stage (GS87) in each sampling plot, and 20 spikes were collected from each sampling plot to evaluate grain number per spike (GNPS) and thousand kernel weight (TKW) at the physiological maturity (GS92). Grain number per unit area (GNPUA) was calculated by SNPUA x GNPS. Plant height was measured at 5 days after anthesis (GS71) from soil surface to the top of the main spike (excluding awns) in each representative plant, and three representative plants