Field Crops Research 196 (2016) 251–260

Contents lists available at ScienceDirect

Field Crops Research

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

Genetic improvement of nitrogen uptake and utilization of winter wheat in the Yangtze River Basin of China

Zhongwei Tian, Yu Li, Zhihui Liang, Hua Guo, Jian Cai, Dong Jiang, Weixing Cao, Tingbo Dai*

National Technology Innovation Center for Regional Wheat Production, Key Laboratory of Crop Physiology Ecology and Production Management of Ministry of Agriculture, Jiangsu Collaborative Innovation Center for Modern Crop Production, Nanjing Agricultural University, No. 1 Weigang, Nanjing, Jiangsu 210095, PR China

ARTICLE INFO

Article history:
Received 24 September 2015
Received in revised form 7 July 2016
Accepted 9 July 2016
Available online 18 July 2016

Keywords:
Winter wheat
Genetic improvement
Nitrogen utilization efficiency
Nitrogen uptake
Nitrogen translocation

ABSTRACT

Verifying the ongoing genetic improvement of nitrogen use efficiency (NUE) and determining the physiological basis of the improvement will aid breeders and agronomists in developing new wheat (*Triticum aestivum* L.) cultivars, with the aim of high yields and low N fertilizer requirements. A two-year field experiment was conducted with 32 wheat cultivars, which were bred or widely planted in the Yangtze River Basin from 1950 to 2005 under two N application rates (0 and 225 kg N ha^{-1}) in Nanjing, China, to examine the improvement of N uptake and utilization, as well as its physiological basis. Grain yield, harvest index (HI), N recovery efficiency (NRE), and N agronomic efficiency (NAE) increased with cultivar development from the 1950s to the 2000s. N accumulation at maturity of modern cultivars was higher than for the older cultivars, which mainly resulted in increased N accumulation amount and N accumulation rate during the jointing to anthesis (J–A) growth period. With cultivar development, the activities of nitrate reductase (NR) and glutamine synthetase (GS) in leaves increased at the booting and anthesis stages, while remained stable during the grain filling stage, indicating that N assimilation increased prior to anthesis, resulting in an increase in pre-anthesis N concentration and uptake in plants. Leaf N concentration (LNC) increased at anthesis, and the increase was larger than that observed in other organs. At maturity, LNC and grain N concentration (GNC) decreased, while the amount of N in stems, chaff, and the total plants increased, indicating that increased N in leaves at anthesis enhances N remobilization to grain. The N distribution amount to leaves at anthesis increased with cultivar development, but decreased at maturity. Post-anthesis N translocation amount and N translocation efficiency of vegetative organs increased, and the N translocation efficiencies of leaves were higher than those of other organs. NRE and NAE were positively correlated with grain yield, kernel number, kernel weight, HI, N uptake during the J–A growth period, and post-anthesis N translocation. Grain yield and HI were positively correlated with pre-anthesis N uptake, and N translocation of each organ, while there was no relationship with biomass or post-anthesis N uptake. Therefore, increased pre-anthesis N assimilation ability and post-anthesis N translocation were strongly associated with grain yield, and N uptake and utilization efficiency.

1. Introduction

The increased crop yields in the past five decades have been associated with a 20-fold increase in nitrogen (N) fertilizer application globally, and a further 3-fold increase is expected by 2050 (Kant et al., 2011). However, crop yields have been increasing at a much lower rate than the increase in N fertilizer applied (Vitousek et al., 2009). Wheat, as an important food crop in the human diet, accounts for a large fraction of N fertilizer used in crop production (Zhu and Chen, 2002). The application of N fertilizer increases wheat yield; however, its excessive use has become a major prob-

Abbreviations: N, nitrogen; NUE, N use efficiency; NRE, N recovery efficiency; NAE, N agronomic efficiency; HI, harvest index; TKW, 1000-kernel weight; LNC, leaf N concentration; GNC, grain N concentration; PNC, plant N concentration; E–J, the growth periods of emergence to jointing; J–A, the growth periods of jointing to anthesis; A–M, the growth periods of anthesis to maturity; NR, nitrate reductase; GS, glutamine synthetase.

* Corresponding author.
E-mail address: tingbod@njau.edu.cn (T. Dai).

http://dx.doi.org/10.1016/j.fcr.2016.07.007

Table 1
Wheat cultivars released in different eras that were tested in this study.

Type	Year of release	Cultivars
1950s	1950–1959	Zaoyangmai, Huoshaotou, Nanda 2419, Bimamai, Wangshuibai
1960s	1960–1969	Xiaoyan 4,Youbaomai, Abbondanza, Funo, Jiangdongmen
1970s	1970–1979	Zhengyi 1, Yangmai 1, Bodijiang
1980s	1980–1989	Lumai1, Xiaoyan 107, Shannong 7859
1990s	1990–1999	Lumai 15, Lumai 22, Yumai 34, Yumai 50, Ningmai 9, Yangmai 158, Xuzhou 25
2000s	2000–2005	Zhengmai 9023, Yannong 19, Xiaoyan 54, Ningmai 13, Yangmai 11, Yangmai 13, Yangmai 14, Yangmai 15, Yangmai 16

lem in China. N fertilizer use in China increased by 50% during 1990–2008, but crop yields increased by only 10% (Duan et al., 2014). This overuse has resulted in low N use efficiency (NUE) of crops. In China, NUE for wheat is as low as 26–31%, and a large amount of applied N (180 kg ha^{-1} $year^{-1}$) is lost to the environment (Miao et al., 2011) and remains a serious threat to human health (Jing et al., 2007). The Yangtze River Basin constitutes 16.4% of the national wheat production area and accounts for 25% of total national production. N fertilizer has been extensively and widely used since the 1980s in the Yangtze River Basin, and application rates have increased from 87 kg ha^{-1} in 1980–234 kg ha^{-1} in 2004.

Improved wheat NUE will be of economic benefit to farmers and will help reduce environmental contamination associated with excessive inputs of N fertilizers. Increased NUE is unlikely, unless a systems approach is implemented that incorporates NH_4-N fertilizer and low N rates at sowing, thereby improving the fertilizer quality and N management strategies. N management strategies of application at a late growth period could improve grain yield and NUE. However, there may be many limitations depending on soil type and ecological environment (Haby et al., 1993). Genetic differences in N uptake and utilization have also been reported in different crops including wheat, rice, maize, sorghum, and barley (Ortiz-Monasterio et al., 1997; Muchow, 1998; Anbessa et al., 2009; Namai et al., 2009; Kant et al., 2011), and among cultivars of the same species, including wheat (Cornelius et al., 1991; Przulj and Momcilovic, 2001; Anbessa et al., 2009). Thus, breeding new cultivars with higher yield and NUE has become a new and effective approach to improve NUE. Crop breeders and agronomists are attempting to develop wheat cultivars (Guarda et al., 2004; Laperche et al., 2006; Hirel et al., 2007; Li et al., 2008; Foulkes et al., 2009) and wheat N management strategies (Raun et al., 2002; Shanahan et al., 2008) for higher NUE, while maintaining an acceptable yield.

Genetic improvement in N uptake and utilization of wheat has been reported in many countries, including Argentina (Calderini et al., 1995), Mexico (Ortiz-Monasterio et al., 1997), Finland (Muurinen et al., 2006), France (Brancourt-Hulmel et al., 2003), the UK (Foulkes et al., 1998), and America (Dhugga and Waines, 1989). These studies indicated that modern cultivars normally have higher yields than older cultivars, but wheat breeding has not resulted in consistent improvements in N uptake efficiency. However, improved NUE is associated with a higher harvest index. In contrast, many studies have shown that increases in NUE can be explained approximately equally by N uptake efficiency and N utilization efficiency (Ortiz-Monasterio et al., 1997; Foulkes et al., 1998; Muurinen et al., 2006). In China, breeding efforts in the past few decades have increased wheat yields, but the genetic improvement in NUE of Chinese wheat cultivars remains unclear. Information on the factors determining NUE of Chinese wheat cultivars is required, which will be helpful for breeding wheat with improved N uptake and utilization.

High yields and NUE are considered by-products of favorable N accumulation, distribution, and translocation (Schenk, 1996; Hocking and Stapper, 2001). In wheat, 70–95% of grain N originates from the remobilization of N stored in roots and shoots before anthesis (Barraclough et al., 2010). A less important fraction of grain N comes from post-anthesis N uptake (Hirel et al., 2007). High grain N accumulation results from higher NUE and N translocation efficiency (Schenk, 1996), and wheat grain yield and N accumulation are directly influenced by N absorption, assimilation, and translocation, which affects N uptake and utilization efficiency. However, it remains unclear whether N uptake post-anthesis or remobilized N from pre-anthesis limits grain yield and NUE (Martre et al., 2003). Specifically, genetic improvement in N assimilation and spatiotemporal N accumulation, distribution, and translocation, and their relationships to NUE in China remains unclear.

In this study, field experiments were conducted in two successive years using cultivars developed between 1950 and 2005. The development of grain yield characteristics and main agronomic traits of these cultivars, and their responses to N fertilizer rates were reported in an earlier publication from the same experiments (Tian et al., 2011). The objectives of the current study were to: (1) explore the development of N uptake and NUE characteristics and (2) identify the key factors that constrain NUE in these cultivars. The results are intended to provide information for wheat breeding and cultivation management targeting high yield and NUE.

2. Materials and methods

2.1. Field experiments

The experiments were conducted from 2007 to 2009 in Nanjing, China (32°02′N, 118°37.5′E), using 32 wheat cultivars that were released and grown in the Yangtze River Basin from 1950 to 2005 (Table 1). Wheat production in the Yangtze River Basin is characterized by a wheat-rice rotation system south of the Huai River in Jiangsu and Anhui Provinces, in the north of Hubei Province, and the south of Henan Province. The soil of this region is mainly paddy soil, the climate is humid and warm, and annual rainfall is 800–1400 mm. Weather conditions at the experimental sites during the wheat growing season are presented in Fig. 1. The soil properties of fields were tested at a depth of 0–25 cm before sowing, with an organic matter content of 19.50 g kg^{-1}, a total N of 0.87 g kg^{-1}, available N of 14.50 mg kg^{-1}, available phosphate of 17.50 mg kg^{-1}, and available potassium of 93.76 mg kg^{-1} in 2007–2008, and an organic matter content of 21.62 g kg^{-1}, a total N of 1.20 g kg^{-1}, available N 15.39 mg kg^{-1}, available phosphate of 18.40 mg kg^{-1}, and available potassium of 105.52 mg kg^{-1} in 2008–2009. The plot size was 2.0 m × 2.5 m. The basic seeding was 1.8×10^6 seeds ha^{-1} with a spacing of 0.25 m between rows (10 rows). The sowing date was 5 November in both 2007 and 2008. Two N rates were applied: 0 (N0) and 225 kg N ha^{-1} (N225). The N fertilizers were applied at sowing with a jointing ratio of 1:1, together with 150 kg P_2O_5 ha^{-1} and 150 kg K_2O ha^{-1}. The experiment was a completely randomized block design with three replications. Weeds were controlled by hand. Fungicides and pesticides were applied at jointing, booting, and 10 days after anthesis to prevent diseases and pests. Because of abundant rainfall during both study years, no irrigation was applied throughout the growing seasons.