INTERNATIONAL JOURNAL OF AGRICULTURE & BIOLOGY
ISSN Print: 1560–8530; ISSN Online: 1814–9596
15–102/2016/18–1–46–51
DOI: 10.17957/IJAB/15.0060
http://www.fspublishers.org

Full Length Article

Dry Matter and N Contributions to the Formation of Sink Size in Early- and Late-maturing Rice under Various N Rates in Central China

Fengxian Yao[1], Jianliang Huang[2], Lixiao Nie[2], Kehui Cui[2], Shaobing Peng[2] and Fei Wang[2*]
[1]*College of Life and Environment Sciences, Gannan Normal University, Ganzhou, 341000, China*
[2]*National Key Laboratory of Crop Genetic Improvement, MOA Key Laboratory of Crop Ecophysiology and Farming Systemin the Middle Reaches of the Yangtze River, College of Plant Science and Technology, Huazhong Agricultural University, Wuhan, Hubei 430070, China*
[*]For correspondence: fwang@mail.hzau.edu.cn

Abstract

Sink size with spikelets number (m^{-2}) is one of the critical factors determining grain yield in cereals including rice. Nitrogen and dry matter are regarded as the two main factors controlling the formation of sink size and the objectives of present study were to examine the potential mechanisms underlying the difference in sink size between the late maturing YLY6 and HY3 an early maturing and drought resistant variety. The difference in the contribution of N and dry matter to the formation of sink size between the two varieties was also investigated. Growth duration of YLY6 was 20 days longer than of HY3. YLY6 produced significantly larger sink size than HY3 due to more secondary branches and spikelets, which resulted in higher grain yield for YLY6. Application of N fertilizer increased spikelets number for both YLY6 and HY3. Sink size of HY3 significantly correlated with N accumulation from mid-tillering (MT) to panicle initiation stage (PI) (R^2=0.68) and N concentration in stem at PI (R^2=0.74). However, for the late-maturing variety-YLY6, formation of sink size was more associated with biomass accumulation from PI-FL (flowering, R^2=0.82). Both N and biomass accumulation significantly contributed to the difference in sink size between HY3 and YLY6, with R^2 of 0.45 and 0.84, respectively. Taken together, this study indicated that contribution of N and dry matter to the formation of sink size was different in rice varieties with different growth duration. © 2016 Friends Science Publishers

Keywords: Rice; Spikelets; Sink size; Growth duration; Nitrogen; Dry matter

Introduction

Stagnation in rice yield potential and production has been observed frequently in last decade (Ray *et al*., 2012; Zhang *et al*., 2014). Three main components are used in the estimation of grain yield in cereal crops including rice, namely spikelet number (m^{-2}), percentage of filled spikelets and 1000-grain weight. Maximum grain yield is determined by the number of spikelets (sink size), since grain weight is relatively genetically stable (Yoshida, 1981). Therefore, a large sink size is regarded as one of the essential traits in the new plant type (NPT) breeding at IRRI and China's super hybrid rice (Peng *et al*., 2008).

Sink size includes panicles (m^{-2}) and spikelets per panicle. Since there is often a trade-off between these two traits, Yoshida *et al*. (2006) suggested that analysis of spikelet number per m^{-2} would be more effective than separate analysis of each of them. There were significant genotypic variation in the sink size among different varieties (Peng *et al*., 2000) and it is also influenced by various environmental factors, like temperature (Munakata, 1976), CO_2 concentration (Yoshida, 1973; Kim *et al*., 2010) and N fertilizer (Hasegawa *et al*., 1994; Kamiji *et al*., 2011). Horie *et al.* (1997) found a significant difference in sink size of Kishihikari when the variety was planted in three different locations. Despite of the close relationship between sink size and grain yield, very few studies highlight about the eco-physiological mechanisms underlying the formation of sink size in rice.

Studies indicates that formation of sink size is associated with N accumulation and dry matter production in the reproductive growth stage, however, there is still controversy about the specific period which determines the spikelet number (Hasegawa *et al*., 1994; Yoshida *et al*., 2006). Previous studies have reported that N accumulation before the spikelet differentiation is important for the final spikelet number (Wada, 1969), however, N accumulation at panicle initiation stage was found to correlate with spikelet number (Shiga and Sekiya, 1976; Kamiji and Horie, 1989). Similar results have been reported by Hasegawa *et al*. (1994), but it was suggested that variation in spikelet number from 157 field experiments could be more accounted for by

To cite this paper: Yao, F., J. Huang, L. Nie, K. Cui, S. Peng and F. Wang, 2016. Dry matter and N contributions to the formation of sink size in early- and late-maturing rice under various N rates in central china. *Int. J. Agric. Biol.*, 18: 46–51

considering both of plant N concentration and aboveground biomass at the panicle formation stage. Yoshida *et al*. (2006) summarized the following factors essential for increasing sink size: (1) larger N accumulation in the vegetative stage and early reproductive stage (up to two weeks before flowering), (2) higher crop growth rate (CGR) in the last two weeks before heading, and (3) genotypes with high spikelet production efficiency per unit N. Kamiji *et al*. (2011) examined the effect of time of top-dressing N fertilizer on sink size in four years with two varieties and found N top-dressing at panicle initiation stage was most efficient in increasing spikelet number. Furthermore, two CO_2 enrichment studies indicated that both N and dry matter are necessary for increasing spikelet number (Kim *et al*., 2010) and plant growth in the first week after panicle initiation was the most essential for determining the spikelet number (Yoshida, 1981).

In our previous study, late-maturing super-hybrid rice (YLY6) produced significantly higher grain yield than HY3 (early-maturing water-saving and drought-resistance rice) under both flooding and alternate wetting and drying condition and sink size was the main reason for the difference between the two varieties (Yao *et al*., 2012). In present study, the objectives were to: (1) compare grain yield of YLY6 and HY3 under rainfed condition; (2) examine the reasons causing the difference in sink size between YLY6 and HY3; and (3) discuss the effect of growth duration on the contribution of N accumulation and dry matter production to the formation of sink size, which will facilitate the improvement in grain yield for water-saving and drought-resistance rice.

Materials and Methods

Two varieties were used in this study, namely Yangliangyou 6 (YLY6) and Hanyou 3 (HY3). YLY6 is a widely disseminated two-line hybrid variety, which has strong disease-resistance, high yield potential and grain quality (Zhao *et al*., 2006). HY3 is popular water-saving and drought-resistance rice, which has good agronomic performance under rainfed condition (Yu *et al*., 2005; Luo, 2010). Growth duration of YLY6 and HY3 are around 135 and 115 days in both 2009 and 2010, respectively.

In 2009 and 2010, field experiments were conducted at Zhangbang Village, Dajin town, Wuxue County, Hubei Province, China (29°51′N, 115°33′E). Soil from the upper 15 cm contained 31.1 g kg^{-1} organic matter, 137 mg kg^{-1} alkali hydrolyzable N, 19.5 mg kg^{-1} Olsen-P and 66.2 mg kg^{-1} exchangeable K and a pH of 5.53. The total precipitation during the rice growth duration was 533 mm in 2009 and 684 mm in 2010. A split-plot design was adopted in the experiments with four replications. N treatments and varieties were in main- and subplots, respectively. Plot size was 30 m^2 in both 2009 and 2010. Plots were separated by bunds covered with plastic film (20 cm in the soil) to reduce seepage between plots. One to 3 cm water was kept in the field during the first two weeks after transplanting and then no irrigation was applied in rest of growth period. Totally, the amount of irrigation water was 116 mm in 2009 and 60 mm in 2010 for both varieties. The total amount of rainfall received was 489 mm for HY3 and 533 for YLY6 in 2009, 579 mm for HY3 and 684 mm for YLY 6 in 2010 during the rice growing season. The soil water potential was kept within -15 kpa in 2009 and -35 kpa in 2010.

Two 27-day and 26-day old seedlings were transplanted per hill at a spacing of 13.3 cm × 30 cm in 2009 and 2010, respectively. There were four N treatments (0, 108, 148 and 189 kg ha^{-1}) in 2009 and three N treatments (0, 108 and 175 kg ha^{-1}) in 2010. Fertilizer N in the form of urea was applied with 39% as basal, 28% at tillering (TL) and 33% at panicle initiation stage (PI). Phosphorus (60 kg P ha^{-1}) and zinc (5 kg Zn ha^{-1}) were applied once as basal fertilizer. Potassium fertilizer at 90 kg K ha^{-1} was applied a rate of 1:1 at MT and PI. The experiments were intensively managed to minimize the damage caused by diseases, insects and weeds.

Twelve plants (0.48 m^2) from each plot were sampled at MT, PI and FL in 2009 and 2010. The plants were separated into green leaf blades, culm plus leaf sheath and panicle when present. Dry weight of each tissue was determined after oven-drying at 70℃ to constant weight. N concentration in the tissues was determined by micro-Kjeldahl digestion, distillation and titration (Bremner and Mulvaney, 1982). Details for grain yield and yield components are given in Yao *et al*. (2012).

The main culms were continuously marked with ink from seedling emergence and panicles on the main culms of six plants with medium size were collected from each plot after the full heading stage. Survived spikelets per panicle (SSPP), differentiated secondary rachis branches (SB) were determined. The frequency of abortion was the ratio of the number of aborted rachis branches over differentiated ones. Rachis branches with spikelets remaining were regarded as surviving; otherwise, the aborted branches were counted (Kato *et al*., 2006).

Statistical Analysis

Analysis of variance was performed using Statistix 8.0 and significance comparison was based on the least significant difference (LSD) test at the 0.05 probability level. Figures were made using SigmaPlot 12.5.

Results

Grain Yield and Yield Components

Grain yield and harvest index (HI) of YLY6 was significantly higher than of HY3 across all the N treatments in both 2009 and 2010 (Table 1 and 2). However, grain weigh and grain filling percentage were lower in YLY6 and produced significantly more spikelets (m^{-2}) than HY3 in both years (Table 1 and 2). Difference in the spikelets between the two varieties was mainly due to difference in spikelets per panicle (Table 1). Application of N fertilizer significantly increased grain yield for both varieties across the two years, due to a higher biomass production and more spikelets (Table 1). No statistically significant difference was observed in number of spikelets per panicle among different N treatments (Table 1).

Branch and Spikelet Numbers and Spikelet Production Efficiency

There was no significant difference in the number of primary branches between the two varieties across the three N treatments (Fig. 1). YLY6 produced significantly more secondary branches (SB) and spikelets in the secondary branches (SSB) than HY3 and N fertilizer application increased the number of SB and SSB (Fig. 1). The effect of N on decrease in SB was completely opposite for YLY6 and HY3. Nitrogen fertilizer increased number of degenerated SB for YLY6, but decreased it for HY3, which resulted in number of degenerated SB in YLY6 lower than of HY3 under N0, but higher at N rates of 108 and 175 kg ha^{-1} (Fig. 1). The infertile spikelets were similar for the two varieties, and among the three N treatments (Fig. 1). YLY6 had significant higher SPE_b than HY3, while no difference in SPE_N between the two varieties (Table 3). Application of N fertilizer did not affect SPEb, but reduced SPE_N for both the two varieties (Table 3). SPE_N under N treatment of 175 kg ha^{-1} was significantly lower than N0 treatment (Table 3).

Table 1: Analysis of variance for grain yield, biomass, harvest index (HI), spikelets m^{-2}, spikelets per panicle, panicles m^{-2}, grain filling percentage and grain weight at Wuxue county, Hubei province, China in 2009 and 2010

ANOVA	Grain yield	Biomass	HI	Spikelets m^{-2}	Spikelets per panicle	Panicles m^{-2}	Grain filling percentage	Grain weight
2009								
N	**	**	*	**	ns	***	*	ns
V	***	**	**	***	***	**	ns	***
N*V	*	ns	ns	ns	ns	ns	ns	ns
2010								
N	***	**	ns	**	ns	**	*	**
V	***	***	***	***	***	ns	**	***
N*V	ns	ns	ns	*	*	ns	ns	***

Levels of significance indicated: ns=not significant, *significant at p<0.05, **significant at p<0.01, ***significant at p<0.001.

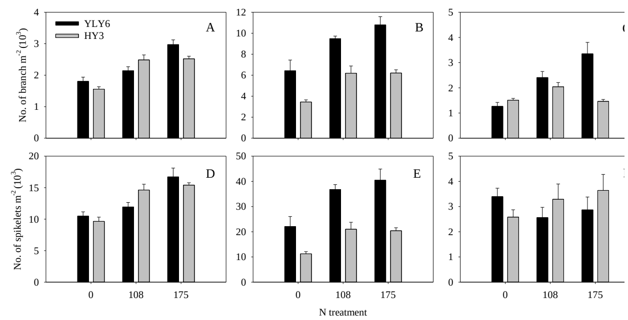

Fig. 1: Number of primary (A), secondary (B) and degenerated (C) branches and spikelets in primary (D) and secondary (E) branches, and empty spikelets (E) under different N treatments at Wuxue county, Hubei province, China in 2010

Table 2: Yield components of YLY6 and HY3 under different N treatments (kg N ha^{-1}) at Wuxue county, Hubei province, China in 2009 and 2010

Treatment	Grain yield (t ha^{-1})	Biomass (t ha^{-1})	HI (%)	Spikelets (m^{-2})	Spikelets per panicle	Panicles (m^{-2})	Grain filling percentage (%)	Grain weight (mg)
2009								
YLY6								
0	7.41 b	12.4 b	53.1 a	27150 b	136 a	198.0 b	87.2 a	27.5 a
108	8.74 a	15.7 a	48.7 b	36813 a	143 a	257 a	77.4 b	26.7 a
148	9.03 a	16.1 a	48.5 b	35332 a	137 a	256 a	81.7 b	27.0 a
189	8.83 a	15.9 a	46.0 b	33678 a	134 a	251 a	81.4 b	26.5 a
Mean	8.05 A	15.0 A	49.1 A	33243 A	138 A	240 A	81.9 A	26.9 B
HY3								

Correlation Between Spikelets (m^{-2}) and Dry Matter Production, N accumulation, N concentration

Linear correlation was found between spikelets (m^{-2}) (sink size) with biomass and N accumulation in the period from MT-PI and from PI-FL. No significant correlation was found for YLY6 between N accumulation and sink size (Fig. 2A and B), but sink size significantly correlated with N accumulation from MT-PI for HY3 (R^2=0.69) (Fig. 2C and D). When data for both YLY6 and HY3 was used, N accumulation between PI-FL correlated significantly with sink size (Fig. 2 E, F). Nonetheless, no significant correlations were observed between sink size and N concentration in the stem at PI and FL stage, except for HY3 at PI stage (R^2=0.74, Fig. 3).

When data for YLY6 under three N treatments were used, there was significant correlation between sink size and biomass accumulation both from MT-PI and PI-FL, but the latter correlation was more significant (R^2=0.82) (Fig. 4A, B). For HY3, sink size didn't significantly correlate with biomass accumulation from MT-PI and PI-FL (Fig. 4C, D). When both YLY6 and HY3 were analyzed, correlation between sink size and biomass accumulation from PI-FL was strong (R^2=0.85, Fig. 4E, F).

Discussion

Genetic link between growth duration and sink size (spikelets number m^{-2}) has been found in the past few years. *Ghd7*, a gene regulating heading date, also control panicle size (Xue

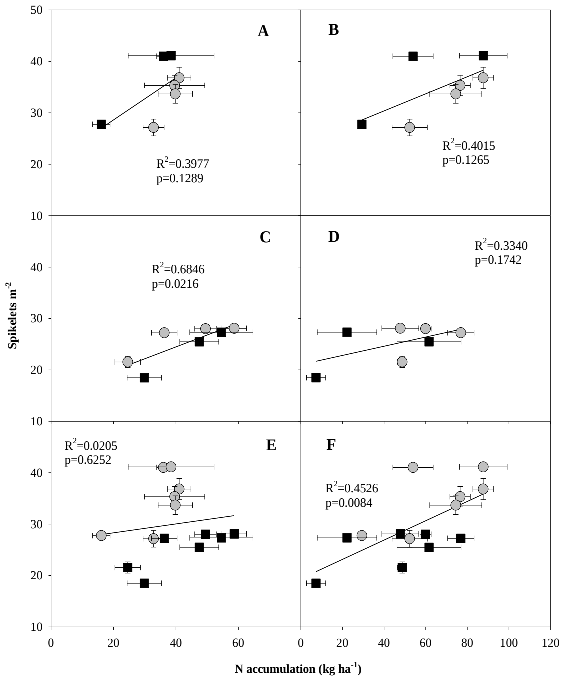

Fig. 2: Correlation between N accumulation and spikelets number (m^{-2}) in 2009 and 2010. N accumulation was from MT-PI in A, C, E, and PI-FL in B, D and F. Data in A and B were for YLY6, C and D for HY3, while E and F for both YLY6 and HY3. The grey cycles and the dark boxes represent date in 2009 and 2010, respectively in A, B, C and D, while they represent YLY6 and HY3, respectively in E and F.

et al., 2008; Liu *et al*., 2013). Endo-Higashi and Izawa (2011) found that two genes controlling flowering time (*Heading date 1* and *early heading date 1*) together showed significant influence on panicle size through reducing primary branches. However, underlying physiological mechanisms for such link is not clear yet. In this study, two varieties with significant difference in growth duration (YLY6 and HY3) were used to examine whether the critical factors influence the formation of sink size are influenced by growth duration and to identify the possible reasons for a large sink size in the late-maturing variety YLY6. The results showed that YLY6 produced significantly bigger sink size than HY3 and N fertilizer application could increase sink size too (Table 2). The bigger sink size of YLY6 lead to a significantly higher grain yield than HY3 (Table 2).

Nitrogen and carbohydrates were taken as the two major factors affecting sink size from the previous studies (Hasegawa *et al*., 1994; Kamiji *et al*., 2011; Tamura *et al*., 2011). Nitrogen application as basal fertilizer or at midtillering increased sink size mainly through more panicles (Table 2), while N application at panicle initiation stage could increase spikelets per panicle (Kamiji *et al*., 2011). Nitrogen top-dressing at panicle initiation stage i.e. 30 days before heading could promote the differentiation of spikeletes and at late spikelet formation stage i.e. 20 days before heading reduce degeneration of spikelets (Kamiji *et al*., 2011). Sink size was linearly correlated with plant N content 14 days before heading (Kamiji *et al*., 2011). From

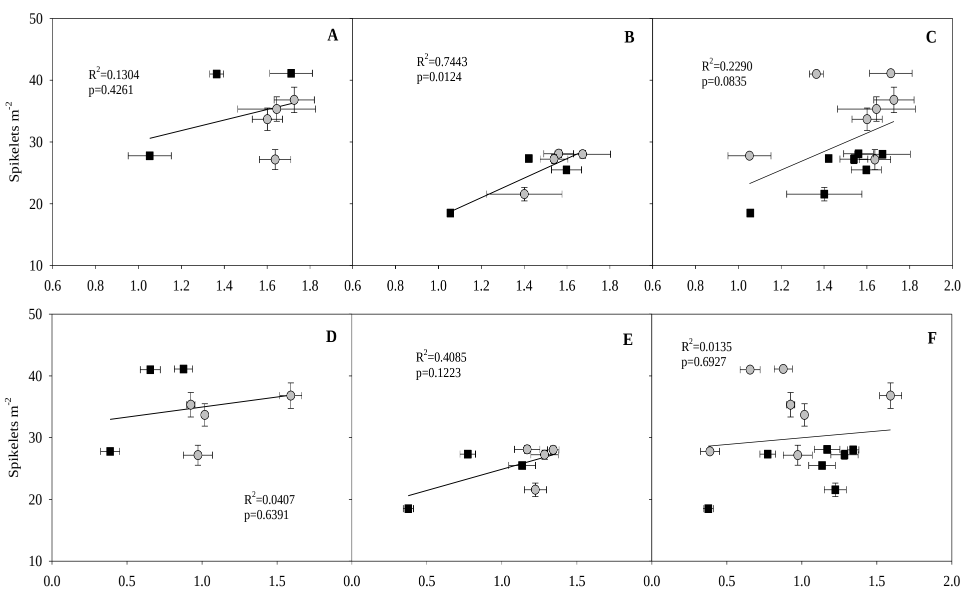

Fig. 3: Correlation between spikelets number (m^{-2}) and N concentration in the stem at PI (A, B, C) and FL (D, E, F). A and D are for YLY6, B and E for HY3, while C and F stand for the data from both YLY6 and HY3. The grey cycles represent data in 2009, and the dark boxes are from 2010

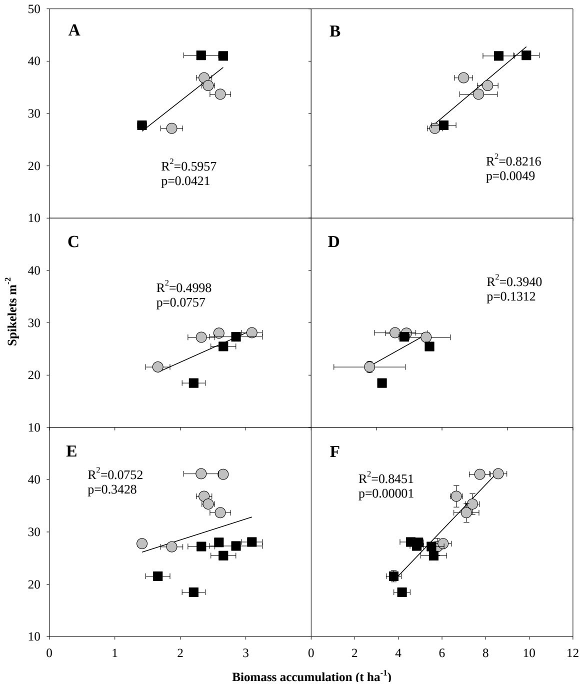

Fig. 4: Correlation between biomass accumulation and spikelets number (m^{-2}) in 2009 and 2010. Biomass accumulation was from MT-PI in A, C, E, and PI-FL in B, D and F. Data in A and B were for YLY6 at different N treatments, C and D for HY3, while E and F for both YLY6 and HY3. The grey cycles and the dark boxes represent date in 2009 and 2010, respectively in A, B, C and D, while they represent YLY6 and HY3, respectively in E and F

the FACE study under three N treatments by Kim *et al.* (2010), N is indispensable for the formation of sink size. This was also demonstrated from the evidence that a NADH-glutamate synthase2 gene functions in remobilization of leaf N through phloem to panicle, significantly reduced sink size (Tamura *et al.*, 2011).

In present study, N application exhibited different effects on the formation of sink size between the two varieties with different growth duration. Nitrogen could increase the number of primary and secondary branches and spikelets for YLY6, while degenerated branches also increased as N application increased (Fig. 1). For HY3, there was no difference in the number of differentiated branches among the three N treatments; however, N application decreased branch degeneration (Fig. 1). Increment in sink size under high N treatment in HY3 was more dependent on N accumulation before PI (Fig. 2). Moreover, N from PI-FL contributed to the difference in sink size between the two varieties (Fig. 3).

The effect of non-structural carbohydrates on the formation of sink size is still controversy. Kobayashi *et al.* (2001) and Ding and Maruyama (2004) concluded that spikelet differentiation was not influenced by non-structural

Table 3: Spikelets production efficiency of biomass (SPE_b) and N (SPE_N) in YLY6 and HY3 under various N treatments at Wuxue county, Hubei province, China in 2010

Var	N	SPE_b (no. g^{-1})	SPE_N (no. g^{-1})
YLY6	0	32.5 a	3870 a
	108	34.3 a	2902 ab
	175	30.7 a	2086 b
	Mean	32.5 A	2953 A
HY3	0	24.6 a	2956 a
	108	29.7 a	2272 ab
	175	28.6 a	1695 b
	Mean	27.6 B	2308 A

Within a column for each variety, means followed by the same letter are not significantly different according to LSD (0.05). Lower-case and upper-case letters indicate comparisons within each variety and between two varieties, respectively
YLY6-Yangliangyou6, HY3-Hanyou3

carbohydrates contents in the stem or panicle. However, CO_2 enrichment experiments demonstrated that sink size was increased under high CO_2 concentration (Yoshida, 1973; Kim *et al.*, 2010). Number of spikelets on an individual tiller significantly correlated with the stem dry weight (Shiratsuchi *et al.*, 2007). On the other hand, aboveground biomass or crop growth rate during the panicle formation period was used in the model to explain the varietal and environmental effects on sink size (Hasegawa *et al.*, 1994; Yoshida *et al.*, 2006). In this study, there was significant difference in SPE_b between the two varieties, but not among the three N treatments (Table 3). Compared with the early-maturing variety-HY3, the formation of sink size in YLY6 was more dependent on dry matter production, especially from PI to FL (Fig. 4). Moreover, the difference in dry matter accumulation from PI-FL significantly contributed to the difference in sink size between the two varieties (R^2=0.85) (Fig. 4). Similarly, the much longer reproductive stage could result in significantly more kernel number (m^{-2}) in wheat, which was due to the increase in dry matter production (Fischer, 1985; Kobayashi *et al.*, 2001).

Popular early maturing WDR variety-HY3 and late maturing hybrid variety-YLY6 was used to examine the effect of growth duration on the critical factors influencing sink size. It was found that for HY3, N accumulation before panicle initiation and N concentration in the stem at PI were important for increasing sink size. On the contrary, YLY6 was more dependent on biomass accumulation both from MT-PI and PI-FL, especially the latter period. Both N (R^2=0.45) and biomass (R^2=0.85) accumulation from PI-FL contributed to the difference in sink size between the two varieties. Further studies with more varieties should be conducted to verify this finding and clarify the physiological mechanism.

Acknowledgment

This study was supported by MOA Special Fund for Agroscientific Research in the Public Interest of China (No. 201203096).

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(Received 28 January 2015; Accepted 28 May 2015)