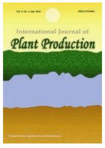

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Physiological processes associated with high yield traits in modern rice varieties

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Abstract

Understanding the physiological processes associated with high yield traits in modern crop varieties is essential to further increase grain yield and improve nutrient management strategies. Field trials were conducted to study the effects of fertilization and variety on the grain yield of rice (*Oryza sativa* L.) with two fertilizer levels and 18 modern varieties. The objectives were to evaluate yield components, time courses of dry matter production and time courses of N, P_2O_5 and K_2O accumulation among different yield categories and to determine physiological processes associated with yield-trait relationships. Variation among varieties had a considerable impact on rice grain yield, regardless of fertilization. Close correlations were observed between grain yield and effective panicles, dry matter production and N, P_2O_5 and K_2O accumulation. Differences in dry matter production and P_2O_5 accumulation among different yield categories began at anthesis; differences in N and K_2O accumulation emerged earlier. It can be concluded that consistent increases in dry matter production (especially post-anthesis) and N, P_2O_5 and K_2O accumulation are crucial for further improvements in rice yield-trait relationships.

Keywords: Dry matter production; Nutrients uptake; Variety; Fertilization; Rice.

Introduction

Continuously growing population and consumption growth mean that the global demand for food will increase for at least another 40 years (Godfray et al., 2010). Achieving and sustaining optimal yield is a continuous challenge in agricultural systems which are already one of the major forces causing global environmental degradation (Foley et al., 2005). Much of the world experiences yield gaps where productivity may be limited by management (Foley et al., 2011). Understanding the physiological processes associated with yield-trait relationships in modern crop varieties is essential to further increase grain yield and improve management strategies (Shearman et al., 2005).
Rice (*Oryza sativa* L.) is a primary cereal crop in China. The annual yield of approximate 200 million tons and sowing area of around 30 million ha since 1995 rank the first and the second in the world, respectively (Yang et al., 2006). Therefore, it is very important to realize that rice production contributes to global food security (Yao et al., 2007). Previous studies have shown that the largest contribution to increased yield potential of modern crop varieties has come from increases in harvest index (HI),

following the introduction of semidwarf traits into rice in the 1960s (Evans, 1997; Donmez et al., 2001). However, information is lacking on which traits determine yield and when the HI can be increased to get close to the biological maximum in most modern rice varieties (Richards, 2000).

Ye et al. (2012) hypothesize that, with relatively little possibility of HI increase, greater yield potential must come from increases in net primary productivity. In practice, Yang et al. (2006) observed that there was a highly significant linear correlation between grain yield and dry matter production post-anthesis. However, few studies (Sinclair and Jamieson, 2008; Xiao et al., 2012) have focused on the relationships between yield components and time courses of dry matter production or nutrient accumulation.

In this study, field trials were conducted to evaluate the relationships between rice grain yield and yield components, time course of dry matter production and time course of N, P_2O_5 and K_2O accumulation. Two fertilizer levels and 18 modern rice varieties were used. The objectives were (1) to determine whether a consistent increase in dry matter production and nutrient uptake could further increase rice grain yield, (2) to identify which physiological processes can contribute to further gains in rice grain yield and (3) how yield components and time courses of dry matter production and nutrient accumulation differ among yield levels. Progress in answering these questions is essential to better understand yield-limiting factors and to inform future breeding strategies and crop management procedures.

Materials and Methods

Description of Study Site

On farm experiments were carried out on the Agricultural Research Station of Datonghu Administration District, Jingzhou, Hubei Province, China (30° 3′ N, 113° 45′ E). The climate of Datonghu is sub-tropical, humid and monsoonal; winters are cold and summers hot. The annual precipitation is 1000-1300 mm, with about 60% of rainfall occurring in the rice-growing season (Jun. - Oct.). The experimental soil is classified as a fluvo-aquic soil. The texture is clay. Soil organic matter, total N, Olsen-P, NH_4OAc-K and pH in the top 20 cm soil profile was 32.3 g kg^{-1}, 2.24 g kg^{-1}, 22.5 mg kg^{-1}, 218.8 mg kg^{-1} and 6.34, respectively.

Experimental Design

The experiment evaluated a single factor design with two treatments, including no fertilizer (CK) and fertilization (NPK). Nitrogen fertilizer in the forms of urea was applied uniformly to the soil at rates equivalent to 165 kg N ha^{-1}. Fifty percent of the N fertilizer was applied as a basal dose and the other 35% and 15% N was applied as top dressing at the tillering stage and the panicle stage, respectively. All plots received 45 kg P_2O_5 ha^{-1} as superphosphate and 75 kg K_2O ha^{-1} as potassium chloride pre-transplanting. No organic manure was applied.

The 18 rice varieties selected are currently the most widely grown in Jingzhou, Hubei Province, China. The variety names, years of introduction, locations of introduction and selected physiological traits are listed in Table 1. We used a randomized complete block design with three replicates of each treatment combination. Each plot was measured 20 m^2. Field experiments were conducted in a typical riceoilseed rape (*Brassica napus* L.) rotation system. Rice was transplanted with the density of 19.5×10^4 ha^{-1} into all the plots on June 6 and was harvested on October 3.

Table 1. The name, year and location of release and the date for anthesis and maturity for selected 18 rice varieties.

No.	Variety	Abbreviation	Year of release	Location	Anthesis date	Maturity date
1	Huanghuazhan	HHZ	2007	Hubei	8-16	9-30
2	Yangliangyou6	YLY6	2005	Hubei	8-18	10-1
3	Luoyou8	LY8	2006	Hubei	8-19	10-2
4	Fengliangyou4	FLY4	2009	Anhui	8-18	10-1
5	Neixiang2128	NX2128	2008	Sichuan	8-18	10-1
6	Zhenzhunuo	ZZN	2010	Henan	8-19	10-2
7	Yangliangyou542	YLY542	2009	Anhui	8-15	9-30
8	Guofeng1	GF1	2005	Hubei	8-16	9-30
9	Fengliangyouxiang1	FLYX1	2007	Anhui	8-17	10-1
10	Jinyou527	JY527	2004	Sichuan	8-19	10-3
11	Liangyou6326	LY6326	2007	Anhui	8-18	10-1
12	Liangyou036	LY036	2008	Hubei	8-19	10-3
13	Xinliangyou6	XLY6	2007	Jiangsu	8-17	10-1
14	Wandao131	WD131	2004	Anhui	8-16	9-30
15	Tianliangyou616	TLY616	2008	Hubei	8-17	10-1
16	Liangyou234	LY234	2010	Hubei	8-17	10-1
17	Liangyoupeijiu	LYPJ	2001	Hubei	8-19	10-2
18	Yangliangyou609	YLY609	2001	Hubei	8-16	9-30

Sampling and Laboratory Procedures

Soil samples from the 0-20 cm soil layer collected pre-planting were air-dried, sieved and then used to measure organic matter, total N, Olsen-P (0.5 mol L^{-1} $NaHCO_3$), 1.0 mol L^{-1} NH_4OAc-extractable K (1.0 Mammonium acetate at pH 7) and pH (1:2.5, soil: water) (Sparks et al., 1996). Plant samples were collected to determine dry matter and N, P, K content on five occasions: transplanting stage (June 6), tillering stage (June 17), panicle stage (July 24), anthesis stage (August 22) and harvest (October. 3).

At maturity, an area of 3 m × 2 m was harvested manually; straw (all above-ground biomass except grain at maturity) and grain yield were determined after oven drying at 60 °C, N, P and K content was measured. Grain yield value was adjusted to 14% moisture. Sub-samples of the grain and straw were taken to determine N, P and K content using the Kjeldahl procedure, Mo-Sb colorimetry and Flame photometry methods, respectively (Thomas et al., 1967; Bao, 2000).

Numbers of effective panicles were counted manually from a randomized 12 plants. The number of grains per panicle was counted manually to estimate a mean value from 20 panicles. For thousand kernel weight, 1000 grains were randomly counted and weighed.

Statistical Analysis

Data were analyzed using SAS software (SAS Institute, 1998), a mixed ANOVA model with rice variety (degrees of freedom [df]=17) and fertilization treatments (df=2) was used to assess the overall variability of grain yield.

To assess the yield level among different fertilization treatments, the 18 rice varieties were divided into four categories according to their grain yield in the CK treatment and NPK treatment: low yield at CK (Low efficiency, LE), high yield at CK (High efficiency, HE), low increased yield at NPK compared to CK (Low response, LR) and high increased yield at NPK compared to CK (High response, HR).

For all varieties, grain yield of the CK treatment below the varietal mean was categorized as low efficiency; grain yield above the varietal mean yield was categorized as high efficiency. Increased grain yield of the NPK treatment compared to CK below the varietal mean was categorized as low response; grain yield above the varietal mean yield was categorized as high response.

Results

Grain Yield

Variation among varieties had a considerable impact on rice grain yield, regardless of fertilization (Figure 1). Yield in the CK treatment ranged from 4215 (HHZ) to 6831 kg ha^{-1} (YLY542). Yield in NPK treatment ranged from 4695 (HHZ) to 8337 kg ha^{-1} (XLY6). Although the yield varied across the different varieties, NPK had significant influences on it. Yield increase in response to NPK varied from 4.9% (JY527) to 66.8% (YLY609).

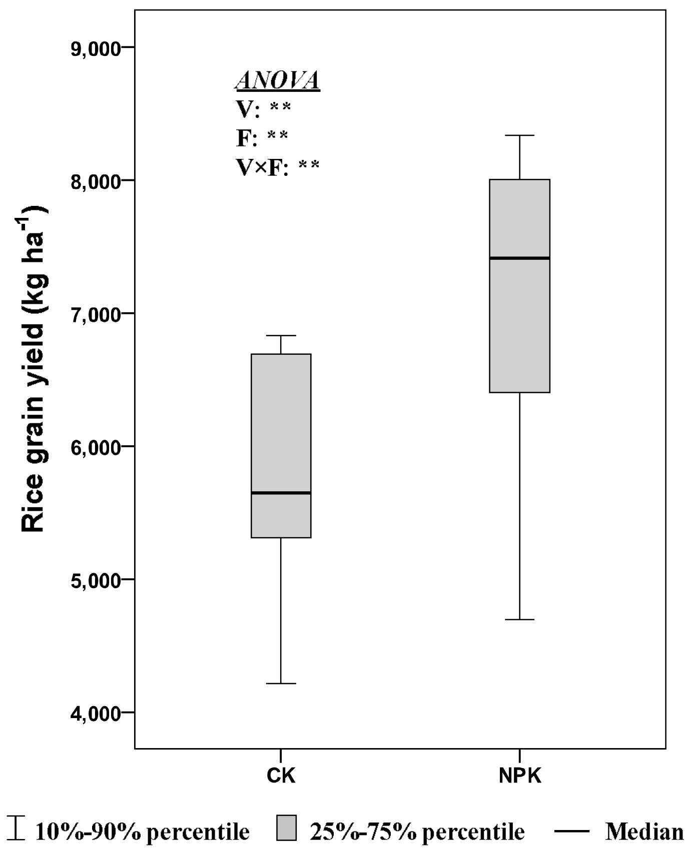

Figure 1. Rice grain yield as affected by varieties and fertilization. ** Statistically significant at P<0.01.

Relationships between grain yield and (1) yield components, (2) dry matter production and (3) nutrient accumulation are presented in Table 2. Among yield components, effective panicle was strongly correlated with rice yield-trait relationships, whereas grain per panicle, grain weight and seed setting rate were not. A close correlation (r=0.51–0.55) was noted between grain yield and biomass. Similarly, a close correlation was observed between grain yield and N accumulation (r=0.62–0.83), P_2O_5 accumulation (r=0.75–0.78) and K_2O accumulation (r=0.80–0.82).

Table 2. Average yield components, biomass, nutrient uptake and the correlative coefficient (r) between grain yield and these parameters with different fertilization.

Item	CK		NPK	
	Mean	r	Mean	r
Effective panicle ($\times 10^4$ ha^{-1})	9.6±1.7	0.51*	12.6±2.2	0.55*
Grain per panicle	230.7±35.1	0.41	239.5±42.2	0.35
Grain weight (g 1000^{-1})	28.2±7.6	0.24	29.9±2.9	0.37
Seed setting rate (%)	78.6±21.8	0.04	80.5±9.6	0.05
Biomass (kg ha^{-1})	12376±1517	0.97**	14709±1870	0.98**
N accumulation (kg ha^{-1})	112.3±15.6	0.83**	168.5±19.8	0.62**
P_2O_5 accumulation (kg ha^{-1})	54.7±6.5	0.75**	67.6±7.3	0.78**
K_2O accumulation (kg ha^{-1})	185.6±35.7	0.80**	246.3±30.7	0.82**

* Statistically significant at P<0.05.
** Statistically significant at P<0.01.

Dry Matter Production, Nutrient Accumulation and Partitioning at Different Yield Levels and among Genotypes

To further compare the partitioning of dry matter production and nutrient accumulation among different rice varieties, pooled grain yield data in CK treatment and increase of grain yield in NPK compared to CK (NPK-CK) were grouped into four yield categories: low yield at both CK and NPK-CK (Low Efficiency, Low Response), low yield at CK and high yield at NPK-CK (Low Efficiency, High Response), high yield at CK and low yield at NPK-CK (High Efficiency, Low Response) and high yield at both CK and NPK-CK (High Efficiency, High Response). Varieties with LE, LR were HHZ (No. 1), ZZN (No. 6), JY527 (No. 10) and LY234 (No. 16) and varieties with HE, HR were YLY6 (No. 2) and XLY6 (No. 13) (Figure 2).

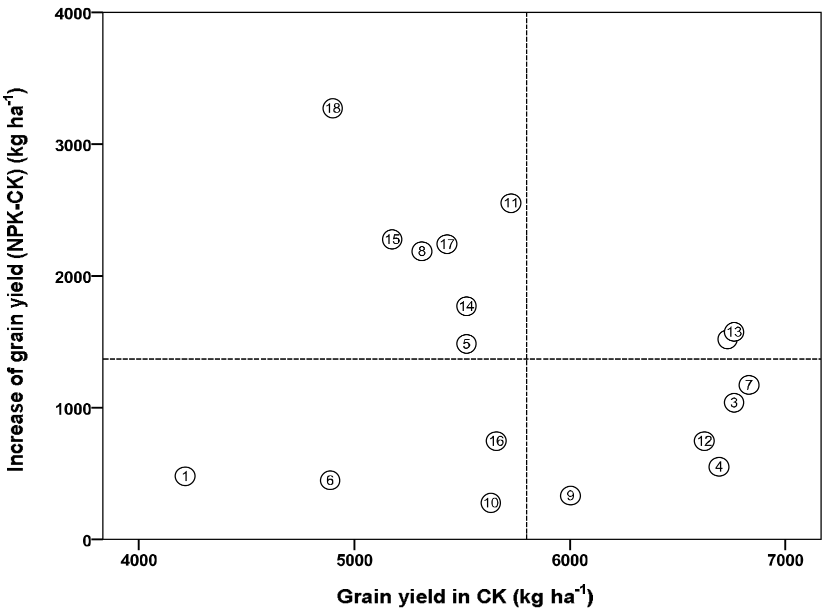

Figure 2. Relationship rice grain yield between CK and NPK. The line in figure means average value of rice grain yield in CK treatment and increase of grain yield in NPK compared to CK.

Rice grain yield for the two HE, HR varieties averaged 6747 and 8294 kg ha^{-1} in the CK and NPK treatments, respectively (Figure 3). For comparison, mean rice yield for the four LE, LR varieties averaged 5098 and 5586 kg ha^{-1} in the CK and NPK treatments, respectively. The increased yield between these two categories was mainly attributed to effective panicle number per unit area. The effective panicle number for HE, HR increased by 71.4% (from 7.6×10^4 ha^{-1} to 13.0×10^4 ha^{-1}) and 56.6% (from 10.2×10^4 ha^{-1} to 16.0×10^4 ha^{-1}) in the CK and NPK treatment, over those for LE, LR ($P<0.05$).

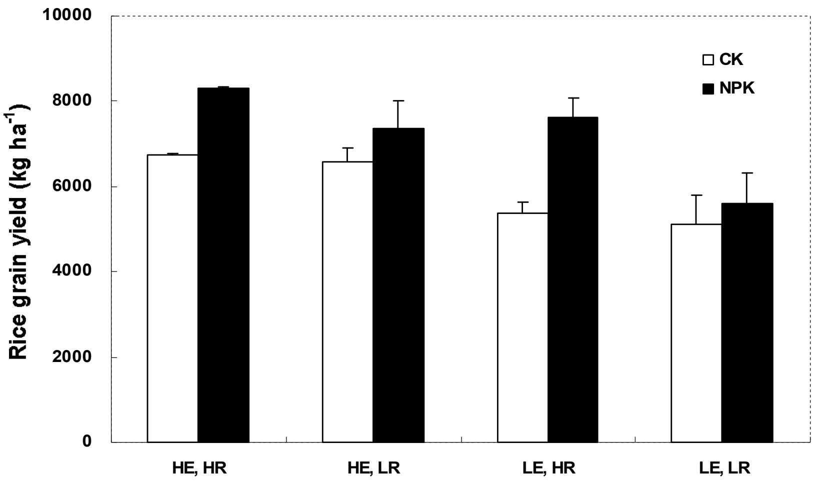

Figure 3. Average rice grain yield for in CK and NPK treatments with different rice genotypes: HE, HR (n=2, varieties No. 2 and 13); HE, LR (n=5, varieties No. 3, 4, 7, 9 and 12); LE, HR (n=7, varieties No. 5, 8, 11, 14, 15, 17 and 18) and LE, LR (n=4, varieties No. 1, 6, 10 and 16). HE, HN means grain yield was more than mean yield for both CK and increase of grain yield in NPK compared to CK; HE, LR means grain yield in CK was more than mean yield and increase of grain yield in NPK compared to CK was less than mean yield; LE, HR means grain yield in CK was less than mean yield and increase of grain yield in NPK compared to CK was more than mean yield; LE, LN means grain yield was less than mean yield for both CK and increase of grain yield in NPK compared to CK.

Time courses of rice dry matter production and N, P_2O_5, K_2O accumulation for rice strains categorized as LE, LR and HE, HR are shown in Figure 4.

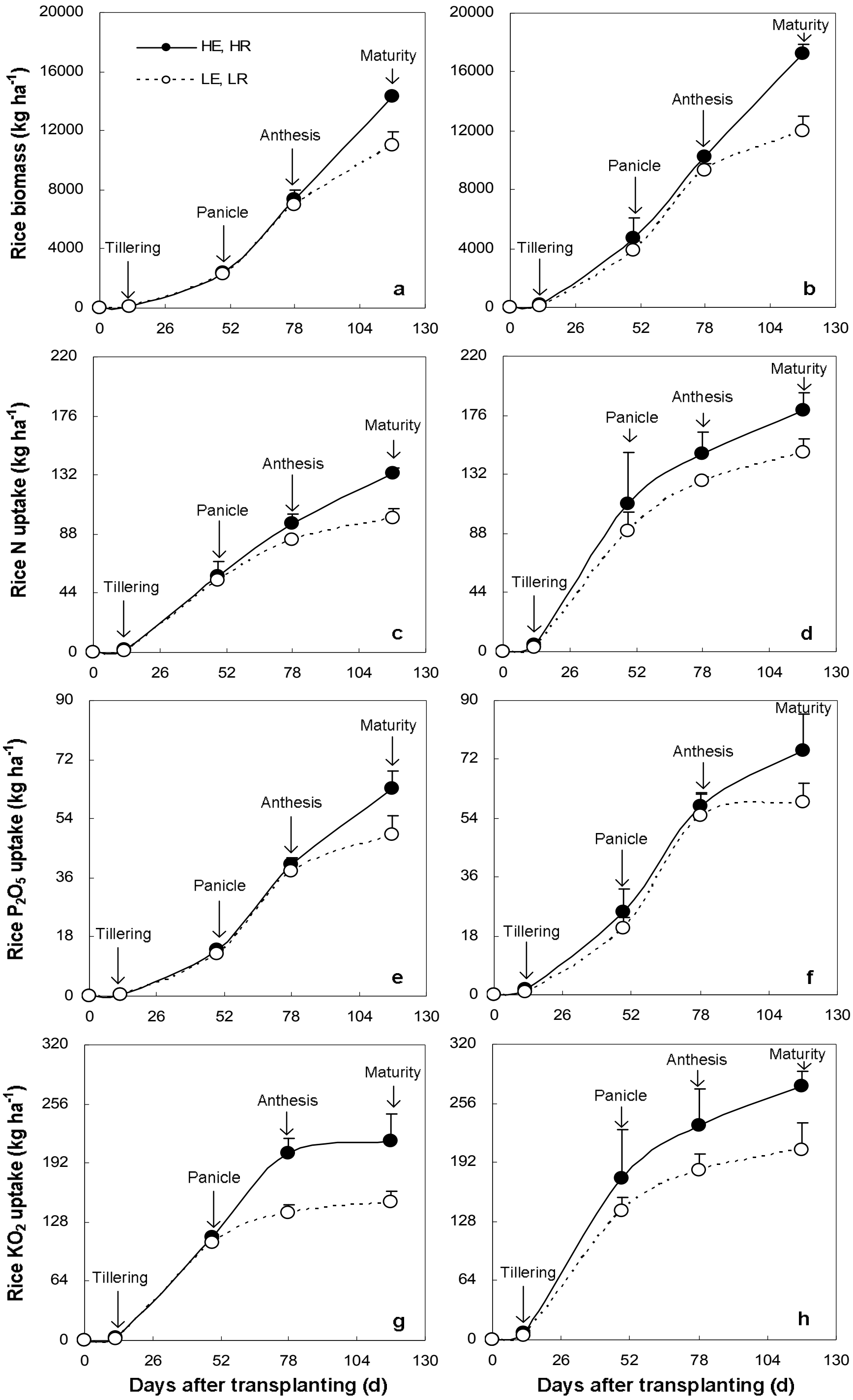

Figure 4. Rice dry matter production (a and b), N uptake (c and d), P_2O_5 uptake (e and f), K_2O uptake (g and h) curves for in CK (a, c, e and g) and NPK treatments (b, d, f and h) with different rice genotypes: LE, LR (n=4, varieties HHZ, ZN, JY527 and LY234) and HE, HR (n=2, varieties YLY6 and XLY6). LE, LN means grain yield was less than mean yield for both CK and increase of grain yield in NPK compared to CK; and HE, HN means grain yield was more than mean yield for both CK and increase of grain yield in NPK compared to CK.

Before the anthesis stage, no significant difference in dry matter production was found between these two yield categories. However, dry matter production from anthesis to maturity for HE, HR increased by 95.3% (from 7313 to 14285 kg ha^{-1}) and 67.5% (from 10269 to 17195 kg ha^{-1}) in the CK and NPK treatments, respectively, over those for LE, LR ($P<0.05$) (Figure 4 a and b). No significant differences in harvest index (HI) were observed between these two categories. These results further support the notion that grain yield was mainly determined by dry matter production in the post-anthesis and not by HI.

At the panicle stage, no significant difference in N accumulation was found among these two yield categories. At the anthesis stage, significant differences in N accumulation were found between the two yield categories ($P<0.05$); N accumulation increased for HE, HR by 14.3% (from 83.9 to 95.9 kg ha^{-1}) and 15.9% (from 127.4 to 147.6 kg ha^{-1}) for the CK and NPK treatments, respectively, over those for LE, LR (Figure 4 c and d). Similarly, at the panicle stage, no significant difference in K_2O accumulation was found among these two yield categories. At the anthesis stage, significant differences in K_2O accumulation were found between the two yield categories ($P<0.05$); K_2O accumulation increased for HE, HR by 45.7% (from 138.7 to 202.0 kg ha^{-1}) and 26.8% (from 183.2 to 232.3 kg ha^{-1}) for the CK and NPK treatments, respectively, over those for LE, LR (Figure 4 g and h).

P_2O_5 accumulation was similar to the dry matter production. P_2O_5 accumulation from anthesis to maturity for HE, HR increased by 108.1% (from 11.1 to 23.0 kg ha^{-1}) and 314.0% (from 4.1 to 17.1 kg ha^{-1}) in the CK and NPK treatments, respectively, over those for LE, LR ($P<0.05$) (Figure 4 e and f). This difference was attributable to increasing straw nutrient concentration (N, P and K) at higher grain yields. For example, straw N concentration at the anthesis stage in HE, HR increased by 15.1% and 13.6% for the CK and NPK treatments, respectively, over those for LE, LR. At maturity, straw and grain N concentration were also similar for these two yield categories. Consequently, the difference in N accumulation at anthesis and maturity were mainly attributed to variation in dry matter accumulation.

Discussion

Intensive high-yield agriculture is dependent on addition of fertilizers, especially industrially produced nitrogen fertilizers (Matson et al., 1997). Without the use of synthetic fertilizers, world food production could not have increased at the rate it did and more natural ecosystems would have been converted to agriculture for feeding 6 billion people (Tilman et al., 2002). Our results showed that NPK treatment had significant influences on the grain yields of rice although they varied across the different varieties. Yield increase rate in response to NPK varied from 4.9% (JY527) to 66.8% (YLY609). But, Cassman and Dobermann (2001) pointed out that the average yields in those rice producing regions of Japan, Korea and China where farmers were early adopters of green-revolution technologies were about 80% of the climate-adjusted genetic yield potential ceiling. The large yield gap for rice in many parts of south and southeast Asia indicates that these regions could have significant yield increases with use of appropriate technologies (Tilman et al., 2002).

HI, the ratio of grain weight to total plant weight, is an important trait associated with the dramatic increases in crop yields. Most progress in improving HI occurred following the introduction of semidwarf traits into rice in the 1960s (Sinclair, 1998). However, the scope for continued HI increases in modern rice varieties was limited by the need to maintain sufficient leaf area and stem biomass for interception of solar radiation, physical support and storage of assimilates and N used in grain filling (Cassman, 1999). Ye et al. (2012) also did not observe significant correlations between HI and grain yield among modern wheat varieties. With relatively little possibility for increases in grain yield by improving HI, greater yield potential must come from increases in net primary productivity (Cassman, 1999). Our results showed that it was important to increase net dry matter production over the entire growing season to achieve a high grain yield (r=0.97-0.98). It was consistent with the opinion of Donmez et al. (2001). In our research, dry matter accumulation amount before the anthesis stage was similar for different yield categories (HE, HR and LE, LR), while yield increase was mainly attributable to dry matter increase from anthesis to maturity. Yang et al. (2006) demonstrated that postanthesis dry matter production of high-yield rice differs between different yield categories.

Unlike the similar dry matter production before the anthesis stage, significant differences in N and K_2O accumulation were observed between HE, HR and LE, LR varieties after NPK fertilizer applications ($P<0.05$). This indicated that carbon assimilate availability at the panicle stage was not the critical factor in determining yield differences between HE, HR and LE, LR varieties, while straw N and K_2O concentration and amount of N and K_2O may have an important role in yield development. An increase in the amount of N at this stage allows leaf area to be sustained for a longer period to increase solar radiation interception and carbon accumulation (Sinclair and Horie, 1989). As a result, dry matter and N, P_2O_5, K_2O accumulation at anthesis for HE, HR, across two fertilizer levels, increased by 7.9% and 15.1%, 5.4%, 36.3% respectively, compared to those for LE, LR varieties. The connections among N status, canopy size and grain set at anthesis were also apparent in tillering population quality. Higher N concentration was reflected in more surviving tillering with panicles (Sinclair and Jamieson, 2006). Consequently, the effective panicles per unit area for HE, HR was higher than that for LE, LR varieties.

Moreover, more post-anthesis N, P_2O_5 and K_2O accumulation was observed for HE, HR varieties than for LE, LR varieties. The increase in post-anthesis nutrients accumulation for different yield categories was attributed to higher accumulation of dry matter biomass, not N, P and K concentrations of straw and grain. As a result, large amounts of N, P_2O_5 and K_2O in the crop pre- and post-anthesis delayed the loss of leaf photosynthetic activity and had potential for increasing yields. Yang et al. (2006) pointed out that an ideal crop canopy group should have a large total storage capacity, high dry matter production and elevated N accumulation post-anthesis. Extension of the duration of green leaf area to increase photosynthetic production post-anthesis can promote transfer of photosynthetic production and thus increased grain yield. So, we think that consistent increases in dry matter production (especially post-anthesis) and N, P_2O_5 and K_2O accumulation are crucial for further improvements in rice yield-trait relationships.

Conclusion

The close relationship between yield and dry matter or N, P_2O_5 and K_2O accumulation indicated that consistently improved dry matter production and nutrients accumulation over the entire rice growing season will be crucial to further improve grain yield. The increase in dry matter production and P_2O_5 accumulation among different yield categories began at anthesis, while increased N and K_2O accumulation emerged at the panicle stage. In practice, establishing ideal crop canopy groups and high dry matter and N, P_2O_5 and K_2O accumulation post-anthesis should enhance biological yield per unit area, promote optimum agronomic performance in individual plants and populations and consequently, increase the potential for yield increase.

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