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Characterization of high-yield performance as affected by genotype and environment in rice*

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Abstract: We characterized yield-relevant characters and their variations over genotypes and environments (locations and years) by examining two rice varieties (9746 and Jinfeng) with high yield potential. 9746 and Jinfeng were planted in two locations of Shanghai, China, during 2005 and 2006. The results show that there was a large variation in grain yield between locations and years. The realization of high yield potential for the two types of rice was closely related to the improved sink size, such as more panicles per square meter or grains per panicle. Stem and leaf biomasses were mainly accumulated from tillering stage to heading stage, and showed slow decline during grain filling. Meanwhile, some photosynthetic characters including net photosynthesis rate (P_n), leaf area index (LAI), specific leaf area (SLA), fluorescence parameter (maximum quantum yield of PSII, F_v/F_m), chlorophyll content (expressed as SPAD value), as well as nutrient (N, P, K) uptake were also measured to determine their variations over genotypes and environments and their relationships with grain yield. Although there were significant differences between years or locations for most measurements, SLA at tillering and heading stages, F_v/F_m and LAI at heading stage, stem biomass at heading and maturity stages, and leaf nitrogen concentration at tillering and heading stages remained little changed, indicating their possible applications as selectable characters in breeding programs. It was also found that stem nitrogen accumulation at tillering stage is one of the most important and stable traits for high yield formation.

Key words: Environment, Photosynthesis, Nutrition, Rice, Yield
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INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most important food crops in the world. Yield potential of modern rice cultivars in irrigated tropical areas has been greatly increased since the first semi-dwarf tropical indica cultivar, IR8, was released three decades ago (Khush *et al*., 2001), which, to a great extent, alleviated the pressure of food shortage caused by increasing population. However, food security is still a serious issue facing the world, and there is a need for more food production to keep pace with increasing world population. The demand for increasing rice production is particularly urgent, because the population of traditional rice-producing countries will require 70% more rice by year 2025 (IRRI, 1995; Swaminathan, 2007). Hence, the world rice production must increase by approximately 1% annually to meet the growing demand (Rosegrant *et al*., 1995). Recently, so-called super-rice cultivars or hybrids have been released in China, which have shown a markedly high yield potential when planted in the special areas (Amano *et al.*, 1996; Cheng and Min, 2001). However, these super-rice cultivars or hybrids are commonly characterized by unstable yields across environments (locations and years) (Horie *et al*., 1997; Ying *et al*., 1998). Therefore, it is imperative to clarify the responses of their growth and yield formation to environments. Understanding of the physiological processes associated with these responses may provide effective information for improving breeding

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and agronomy practices.

There have been some reports on determination of the physiological traits closely linked with yield formation. Horie *et al*.(1997) suggested the importance of increasing sink size and radiation use efficiencies during grain filling. Ying *et al*.(1998) reported that further improvement in rice yield potential depended more on the ability of increasing biomass production than on that of increasing harvest index (HI). As a matter of fact, in the breeding programs focused on improving plant type at IRRI (International Rice Research Institute, Philippines), large panicle and high biomass production are considered as the main selection criteria (Khush *et al*., 2001).

It is well known that final yield (phenotype) of a given cultivar is dependent on both genetic factors (genotype) and growth conditions (environment). Much effort has been done in breeding to improve genetic potential of rice cultivars or hybrids by optimizing plant type and light utilization. However, little research has been done in understanding the effect of environmental factors on the performance of physiological traits in super-rice cultivars or hybrids. The objectives of the current experiments were to determine the relationship between yield formation and environments, and to clarify the physiological traits closely linked with high yield under field conditions.

MATERIALS AND METHODS

Experimental sites and soil properties

Field experiments were conducted at experimental stations of Qingpu and Jinshan, Shanghai (30°53′ N, 120°08′ E, and altitude 6 m) in 2005 and 2006. The two locations, around 35 km apart, have the same climate. Basic soil fertility in these two locations is shown in Table 1. On the whole, year 2005 had more total precipitation and lower mean temperature than year 2006. A japonica hybrid Jinfeng and a japonica cultivar 9746 were used.

Table 1 Basic soil fertility in the two experiment locations

Location	Organic C (g/kg)	Available P (mg/kg)	Available K (mg/kg)	Available N (g/kg)	pH
Jinshan	1.14	12.39	68.27	3.55	7.35
Qingpu	0.65	21.23	54.42	1.45	5.97

Rice seeds were immersed in water for 2 d before sowing, and were sown on May 25 and transplanted on June 20 as single season rice (monocropping), and hill space was 25 cm×20 cm with one plant per hill. A completely random block design with 3 replications was used and plot area was 50 m^2. N fertilizer was supplied in the form of urea at a rate of 270~300 kg N/ha, with 30% of total N being applied before seeding, 30%, 20% and 20% top-dressed at tillering, booting and heading stages, respectively. K fertilizer was applied in the form of potash chloride at a rate of 370~450 kg/ha, with 70% being applied before transplanting and 30% top-dressed at booting stage. During growth, weeds, insects and diseases were chemically controlled as required.

Measurements of photosynthesis, fluorescence and SPAD value

The plant sampling and measurements were carried out at mid-tillering (35 d after transplant), booting (56 d after transplant) and heading (82 d after transplant) stages. Net photosynthetic rate (P_n), stomatal conductance and transpiration rate were measured with a LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE, USA) on the upper-most fully expanded leaves. Meanwhile, chlorophyll fluorescence was measured using a portable pulse-modulated fluorometer (mini-PAM, H. Walz, Germany) and chlorophyll content, expressed as SPAD value, was determined using an SPAD meter (SPAD-502, 1989 Minolta Co. Ltd., Japan). P_n and chlorophyll fluorescence were determined on 6 and 10 leaves respectively for each replication, while SPAD measurement was done on 15 leaves.

Biomass and nutrient analysis

Fifteen plants were harvested at each sampling stage and used for biomass and nutrient analyses. The plants were separated into different parts, dried in an oven at 70 °C and weighted. N concentration in plant tissue was determined with Kjeldahl method. K concentration was determined by atomic absorption spectrophotometer and P concentration by ammonium-vanadomolybdate method. Nutrient accumulation was calculated by product of nutrient concentration and tissue biomass (dry weight). At maturity stage, all plants of each plot were harvested for yield determination (expressed as grain yield with water content of 14%).

Statistical analysis

All data were subjected to ANOVA using statistical software SAS 8.0 for Windows, and comparisons between the treatments with $P<0.05$ were considered significantly different.

RESULTS

Yield and its components

Table 2 shows grain yield and its components for all the treatments. Grain yield varied between cultivars and environments (locations and years), ranging from 8.61~10.68 t/ha for 9746 and 7.61~10.58 t/ha for Jinfeng. There was a significant difference in grain yield between years or locations, with the yield in 2006 being higher than that in 2005, and the one of Qingpu being higher than that of Jinshan. In addition, the higher yield of 9746 was associated with more panicles per square meter and greater grain weight. In contrast, higher yield of Jinshan is attributed to more grains per panicle. Obviously, the yield components showed the great changes between years. Thus, panicles per square meter, the percentage of filled grains and grain weight were greater in 2006 than in 2005, but spikelet per panicle was just opposite. The difference in yield components between the two locations was relatively small.

Biomass accumulation

Stem biomass reached the maximum at heading stage and then declined during grain filling (Table 3). The two rice cultivars showed obvious difference in the change of stem biomass: 9746 had little increase after booting stage, whereas Jinfeng had a marked increase from booting stage to heading stage. The change of leaf biomass was basically similar for the two cultivars, with the maximum value occurring at heading stage and slight reduction during grain filling. Although grain biomass was mainly accumulated during grain filling for the two cultivars, there was a distinct difference between the cultivars in the relative proportion of biomass accumulated during grain filling, with the one of 9746 being much less than that of Jinfeng.

Table 2 Yield and its components for the two cultivars under different conditions

		Panicles (m^{-2})	Grains per panicle	Percentage of filled grains (%)	Grain weight (mg)	Yield (t/ha)
Variety	9746	243.29a	184.32b	91a	29.02a	9.97a
	Jinfeng	223.48b	205.45a	92a	24.30b	9.01b
Location	Jinshan	234.11a	190.82b	91a	26.71a	9.36b
	Qingpu	232.66a	199.50a	93b	26.61a	9.62a
Year	2005	221.49b	199.60a	91b	26.07b	9.10b
	2006	245.28a	190.18b	93a	27.24a	9.88a
Interaction	Var.×loc.	NS	NS	NS	NS	NS
	Var.×year	NS	S	NS	NS	NS

Means followed by different letters in the same column are significantly different at the $P<0.05$ level according to Turkey test. Var.: Variety; Loc.: Location; NS: Nonsignificant; S: Significant

Table 3 Biomass accumulation (g/m^2) of different plant tissues in different growth stages

		MT		BS		HS			MS		
		Stem	Leaf	Stem	Leaf	Stem	Leaf	Panicle	Stem	Leaf	Panicle
Variety	9746	109.99a	107.13a	350.32a	248.41a	397.66b	263.77a	450.61a	356.68b	227.46b	742.31a
	Jinfeng	103.29a	103.38a	324.07b	248.23a	498.95a	254.24a	344.63b	439.42a	253.93a	839.41a
Location	Jinshan	102.50a	98.67a	356.07a	257.58a	456.60a	260.74a	428.24a	392.26a	243.43a	847.91a
	Qingpu	109.79a	110.70a	319.08b	240.28a	447.87a	256.74a	364.01b	408.58a	240.09a	739.22b
Year	2005	72.11b	82.96b	251.07b	211.30b	428.44a	229.47b	391.57a	389.60b	223.64b	758.37b
	2006	140.62a	127.23a	421.13a	285.32a	476.61a	287.75a	394.83a	413.40a	259.96a	831.44a
Interaction	Var.×loc.	NS	NS	S	S	NS	NS	S	NS	NS	NS
	Var.×year	S	S	NS	S	NS	S	NS	NS	NS	NS

Means followed by different letters in the same column are significantly different at the $P<0.05$ level according to Turkey test. MT: Mid-tillering stage; BS: Booting stage; HS: Heading stage; MS: Maturity stage; Var.: Variety; Loc.: Location; NS: Nonsignificant; S: Significant

The environmental effect on the tissue biomass accumulation varied with years and locations. For stem biomass, little difference was found after heading stage regardless of years or locations, but a significant difference was found at mid-tillering stage between years, with the stem biomass in 2006 being greater than that in 2005, and at booting stage between years and locations, with the one in 2006 being greater than that in 2005, and the one of Qingpu being greater than that of Jinshan. For leaves, the biomass in 2006 was constantly higher than that in 2005 and no significant difference was found between locations through the whole growth stages, except for the leaf biomass of Qingpu being greater than that of Jinshan at mid-tillering stage. For panicles, the biomass of Jinshan was higher than that of Qingpu at both heading and maturity stages.

Photosynthetic rate, fluorescence parameter and SPAD value

Photosynthetic rate (P_n) of leaf at mid-tillering stage was significantly higher than that at heading stage, while for fluorescence parameter (maximum quantum yield of PSII, F_v/F_m), the opposite was observed (Table 4). However, there was no significant difference in SPAD value between the two measurements. Photosynthetic rate (P_n) differed significantly between the two cultivars at heading stage, with P_n of 9746 being higher than that of Jinfeng, and there was a significant difference between years, with P_n in 2005 being higher than that in 2006. For F_v/F_m, significant differences were not detected between cultivars, locations and years at heading stage, but were observed at mid-tillering stage. The F_v/F_m ratios of 9746, Jinshan and year 2005 were significantly higher than those of Jinfeng, Qingpu and year 2006, respectively. For SPAD value, no significant difference was found between cultivars or locations, whereas the difference was significant between years, with SPAD in 2005 being higher than that in 2006, irrespective of growth stage.

Specific leaf area (SLA) and leaf area index (LAI)

SLA showed obvious changes with the growth stages, and the higher changes were observed in mid-tillering stage compared with the heading stage. However, no significant difference was found between cultivars, locations or years, indicating that it is a relatively stable character. For LAI, the two cultivars showed no significant difference at mid-tillering stage, but at heading stage, 9746 displayed significantly higher LAI than Jinfeng. The difference in LAI between locations or years was found at early stage, and became smaller at heading stage.

Nutrient concentration and accumulation

The nutrient concentrations in different plant parts of the two rice genotypes under the two locations are shown in Table 5. N concentration in leaves and stems of the two genotypes showed dramatic decreases from mid-tillering stage to booting stage, remained less changed from booting stage to heading stage, and then declined rapidly during grain filling. N concentration in panicles remained relatively constant or had a slight decrease during grain filling. The difference in tissue N concentration between genotypes, locations and years varied with growth stages. At mid-tillering and heading stages, there was no

Table 4 Leaf photosynthetic rate (P_n), fluoresence parameter (F_v/F_m), SPAD value, specific leaf area (SLA) and leaf area index (LAI) at mid-tillering and heading stages

		P_n (μmol CO_2/(m^2·s))		F_v/F_m		*SPAD*		*SLA* (dm^2/g)		*LAI*	
		MT	HS	MT	HS	MT	HS	MT	HS	MT	HS
Variety	9746	24.63a	18.65a	0.77a	0.80a	43.93a	43.73a	2.34a	1.99a	2.85a	6.51a
	Jinfeng	22.87a	17.11b	0.69b	0.79a	44.33a	44.29a	2.25a	2.17a	2.56a	5.45b
Location	Jinshan	24.54a	19.12a	0.76a	0.79a	43.20b	44.17a	2.19a	2.09a	2.43b	6.04a
	Qingpu	22.96a	16.64b	0.70b	0.80a	45.05a	43.85a	2.39a	2.07a	2.98a	5.91a
Year	2005	25.57a	19.21a	0.75a	0.79a	44.85a	47.52a	2.29a	2.18a	2.15b	5.74a
	2006	21.93b	16.56b	0.71b	0.79a	43.40b	40.50b	2.28a	1.98a	3.25a	6.22a
Interaction	Var.×loc.	NS	NS	S	NS	NS	S	NS	NS	NS	NS
	Var.×year	S	NS	S	S	S	NS	NS	S	S	S

Means followed by different letters in the same column are significantly different at the $P<0.05$ level according to Turkey test. MT: Mid-tillering stage; HS: Heading stage; Var.: Variety; Loc.: Location; NS: Nonsignificant; S: Significant

Table 5 Nutrient concentrations of the different plant parts for 9746 and Jinfeng under different conditions

		N, P, K concentrations (%)									
		MT		BS		HS			MS		
		Stem	Leaf	Stem	Leaf	Stem	Leaf	Panicle	Stem	Leaf	Panicle
Variety	9746	2.02a, 0.45a, 1.96b	3.89a, 0.36a, 1.32a	1.25a, 0.52a, 1.60b	2.72a, 0.37a, 1.37a	1.11a, 0.48a, 2.44a	2.30a, 0.38a, 1.28a	1.42a, 0.32a, 0.49b	0.72a, 0.19a, 1.84a	1.12a, 0.13a, 0.71b	0.89b, 0.30a, 0.24a
	Jinfeng	1.79b, 0.41a, 2.29a	3.69a, 0.36a, 1.46a	1.18a, 0.53a, 2.02a	2.53b, 0.34a, 1.43a	0.89b, 0.43a, 2.09b	2.44a, 0.35a, 1.44a	1.34b, 0.27b, 0.55a	0.60b, 0.14b, 1.62b	0.87b, 0.14a, 0.88a	0.98a, 0.29a, 0.24a
Location	Jinshan	1.91a, 0.43a, 2.20a	3.86a, 0.36a, 1.41a	1.22a, 0.47b, 1.82a	2.60a, 0.32b, 1.49a	0.96a, 0.44a, 2.33a	2.29a, 0.34a, 1.42a	1.42a, 0.29b, 0.50b	0.63a, 0.18a, 1.67a	0.91b, 0.13b, 0.75a	0.80b, 0.30a, 0.23b
	Qingpu	1.90a, 0.43a, 2.05a	3.71a, 0.35a, 1.37a	1.21a, 0.59a, 1.79a	2.66a, 0.39a, 1.31b	1.04a, 0.48a, 2.19a	2.46a, 0.38a, 1.30a	1.33b, 0.31a, 0.55a	0.69a, 0.16b, 1.80a	1.07a, 0.15a, 0.84a	1.07a, 0.29a, 0.25a
Year	2005	2.05a, 0.47a, 2.21a	3.89a, 0.43a, 1.34a	1.35a, 0.49b, 2.06a	3.08a, 0.39a, 1.62a	1.01a, 0.38b, 2.41a	2.46a, 0.25b, 1.65a	1.29b, 0.24b, 0.62a	0.65a, 0.17a, 1.78a	1.00a, 0.13a, 0.87a	0.95a, 0.32a, 0.32a
	2006	1.76b, 0.39b, 2.04a	3.63a, 0.29b, 1.45a	1.07b, 0.58a, 1.56b	2.17b, 0.32b, 1.19b	1.00a, 0.53a, 2.11b	2.28a, 0.46a, 1.07b	1.49a, 0.36a, 0.42b	0.67a, 0.16a, 1.68a	0.98a, 0.14a, 0.72b	0.92a, 0.29b, 0.16b
Interaction	Var.×loc.	S, S, S	S, NS, NS	NS, S, NS	S, S, NS	NS, S, NS	S, NS, S	NS, NS, NS	S, NS, S	S, NS, S	S, NS, NS
	Var.×year	NS, S, S	NS, NS, S	NS, S, S	NS, NS, S	NS, S, S	S, NS, S	NS, NS, NS	S, NS, NS	S, S, NS	NS, NS, S

Means of the same nutrient followed by different letters in the same column are significantly different at the $P<0.05$ level according to Turkey test. MT: Mid-tillering stage; BS: Booting stage; HS: Heading stage; MS: Maturity stage; Var.: Variety; Loc.: Location; NS: Nonsignificant; S: Significant

significant difference in leaf N concentration between genotypes, locations and years. However, the difference was significant between genotypes and years at both booting and mid-tillering stages. The 9746 had constantly higher N concentration than Jinfeng, but for panicle N concentration, the opposite was observed.

For P concentration, there was no significant difference between the two genotypes in leaves through the whole growth duration and in stems before maturity stage. At maturity stage, 9746 had higher P concentration than Jinfeng. The difference between locations was dependent on growth stages. At mid-tillering and heading stages, no significant difference was detected in both leaves and stems, while at booting and maturity stages, the difference was significant. Relatively, the difference between years was more obvious. Thus at heading stage, the significant difference was found in both leaves and stem.

For K, there is no significant difference in leaf K concentration between the two genotypes until maturity, while difference in stem K concentration between the two genotypes was significant in all growth stages, with Jinfeng having higher values at mid-tillering and booting stages and smaller values at heading and maturity stages. The significant difference between the locations was only found for leaf at booting stage and for panicle at heading stage. On the whole, K concentration was found dramatically higher in 2005 than that in 2006.

Table 6 shows the nutrient accumulation in different plant parts of the two genotypes under different conditions. For N, the difference in stem between the genotypes was only found at mid-tillering stage, whereas in the leaves the difference was significant at booting and maturity stages. It may be suggest that more N in leaf and stem was remobilized and transferred into panicle for Jinfeng than for 9746 from booting stage to maturity stage.

Table 6 Nutrient accumulation of the different plant parts for 9746 and Jinfeng under different conditions

		N, P, K accumulations (g/m^2)									
		MT		BS		HS			MS		
		Stem	Leaf	Stem	Leaf	Stem	Leaf	Panicle	Stem	Leaf	Panicle
Variety	9746	2.19a,	4.14a,	4.27a,	6.66a,	4.45a,	6.08a,	6.49a,	2.58a,	2.54a,	6.58b,
		0.48a,	0.38a,	1.86a,	0.90a,	1.95b,	0.98a,	1.48a,	0.70a,	0.31b,	2.25a,
		2.15a	1.43a	5.58a	3.41a	9.75b	3.42a	2.21a	6.56b	1.63b	1.78b
	Jinfeng	1.80b,	3.81a,	3.75a,	6.11b,	4.54a,	6.07a,	4.65b,	2.69a,	2.25b,	8.02a,
		0.43b,	0.35a,	1.80a,	0.84b,	2.21a,	0.95a,	0.98b,	0.64b,	0.35a,	2.44a,
		2.26a	1.50a	6.02a	3.40a	10.47a	3.43a	1.90b	7.18a	2.21a	1.98a
Location	Jinshan	1.92b,	3.79a,	4.29a,	6.53a,	4.38a,	6.02a,	6.17a,	2.47b,	2.24b,	6.97b,
		0.43b,	0.34a,	1.81a,	0.81b,	2.05a,	0.93a,	1.30a,	0.73a,	0.31b,	2.57a,
		2.21a	1.39a	6.05a	3.78a	10.50a	3.63a	2.12a	6.51b	1.86a	1.97a
	Qingpu	2.03a,	4.11a,	3.74a,	6.22a,	4.59a,	6.12a,	4.93b,	2.79a,	2.51a,	7.68a,
		0.48a,	0.38a,	1.85a,	0.91a,	2.13a,	1.00a,	1.14b,	0.61b,	0.35a,	2.16b,
		2.21a	1.53a	5.61a	3.03b	9.81a	3.25a	1.98b	7.23a	2.01a	1.81b
Year	2005	1.49b,	3.23b,	3.42b,	6.53a,	4.27a,	5.57a,	5.13b,	2.53a,	2.21b,	7.13b,
		0.35b,	0.36a,	1.21b,	0.83b,	1.64b,	0.59b,	0.98b,	0.67a,	0.30b,	2.47a,
		1.54b	1.09b	5.11b	3.43a	10.43a	3.73a	2.41a	6.91a	1.96a	2.46a
	2006	2.46a,	4.69a,	4.57a,	6.19b,	4.72a,	6.57a,	5.86a,	2.75a,	2.55a,	7.59a,
		0.56a,	0.36a,	2.45a,	0.91a,	2.55a,	1.34a,	1.44a,	0.67a,	0.37a,	2.23a,
		2.88a	1.84a	6.52a	3.39a	9.84a	3.11b	1.68b	6.89a	1.92a	1.31b
Interaction	Var.×loc.	S,	NS,	S,	S,	NS,	S,	S,	S,	S,	S,
		S,	S,	S,	S,	S,	NS,	S,	NS,	S,	NS,
		S	NS	S	S	NS	S	S	S	S	NS
	Var.×year	S,	S,	S,	NS,	S,	S,	NS,	S,	NS,	NS,
		S,	S,	S,	S,	NS,	S,	NS,	NS,	NS,	NS,
		S	S	S	NS	S	S	NS	S	NS	S

Means of the same nutrient followed by different letters in the same column are significantly different at the $P<0.05$ level according to Turkey test. MT: Mid-tillering stage; BS: Booting stage; HS: Heading stage; MS: Maturity stage; Var.: Variety; Loc.: Location; NS: Nonsignificant; S: Significant

For P accumulation, there was a significant difference between the two genotypes, with 9746 having greater P accumulation at early stage, but Jinfeng having greater P accumulation in panicles at maturity stage. The difference between the locations varied with growth stages. At mid-tillering and booting stages, Qingpu had more leaf and stem P accumulations, whereas at heading and maturity stages, Jinshan had more. The significant difference was found between years, with more leaf and stem P accumulation in 2006 than in 2005.

For K accumulation, the difference in leaves between the two genotypes was only found at maturity stage, while in the stems the difference was also significant at heading stage. Although 9746 had more K accumulation in the panicles than Jinfeng at heading stage, the opposite was true at maturity stage. There was no difference between locations in leaf and stem K accumulations through the whole stage, except for the stems in maturity stage and the leaves in booting stage. The difference between years was quite dominant and varied with growth stages. At early stage, the plants in 2006 had more K accumulation than those in 2005, whereas at later stage the case was just opposite.

DISCUSSION

There have been a great number of studies on the relationships between yield components and yield in rice. Li *et al*.(2005) reported that there were positive correlations between yield and harvest index (HI), grain weight per plant, and grains per panicle. Rice yield is mainly dependent on producing ability of dry matter before heading (Katsura *et al*., 2007). It is commonly observed in rice as well as other cereals that fertile floret percentage and floret number per unit area are negatively correlated (Fischer *et al*., 1977; Matsushima, 1957). Matsushima (1957) proposed that sink size was mainly responsible for yield difference. Moreover, grain number, which is the

major part of sink size, is positively correlated with yield (Matsushima, 1957; Yoshida *et al.*, 2006). In the current study, it was found that the higher yield of 9746 was associated with more panicles per square meter and greater grain weight, but the higher yield of Jinfeng was mainly attributed to more grains per panicle (Table 2). It was reported that hybrid rice accumulated more biomass before heading than conventional cultivars. Sarker *et al*.(2001) showed that the degree of heterosis in dry matter accumulation was relatively lower at the later growth stage than at the early growth stage. Khan *et al*.(1998) found that dry matter accumulation during ripening stage would be slightly lower in hybrid rice than in their mid-parental varieties. In this study, two rice genotypes showed a similar change in leaf biomass, but an obvious difference in stem biomass; 9746 had little increase after booting stage, while Jinfeng showed a marked increase from booting stage to heading stage. The results suggest that biomass accumulated before heading has a great contribution to final yield performance. Obviously, the biomass accumulated in the stems (and leaf sheath) will be transported into developing grains during filling stage.

Murayama *et al*.(1987) considered that hybrid rice had a higher photosynthetic rate due to heterosis. However, photosynthetic rate of the same genotypes showed the marked difference during growth stage (Sarker *et al*., 2001; Tang *et al*., 2002). It is well known that there was an optimum LAI for CGR (crop growth rate) (Bunce, 1989). In this study, the photosynthetic rate and LAI of 9746 at heading stage were found significantly higher than those of Jinfeng (Table 4). However, little difference in biomass between the two genotypes was found, indicating that photosynthetic rate, at least at heading stage, might not be a main factor responsible for high grain yield in "super rice".

It is well documented that tillering capacity is one of the most important characters determining yield potential, as it is closely related with the number of panicle per unit area (Zou *et al*., 1991). On the other hand, the stem acts as an important storage organ and affects yield formation by accumulating biomass (Katsura *et al*., 2007). It has been shown that N concentration in rice plants is an important factor affecting tiller initiation and higher N concentration enhances tillering and stem development (Weerakoon *et al*., 1999; Zhong *et al*., 2003). Thus more N accumulation at mid-tillering stage means greater tillering capacity and better stem development. It can be assumed that N accumulation at mid-tillering stage is one of the most important and stable traits for determination of high yield formation.

Cooper and Somrith (1997) reported that the interaction between genotype and environment (G×E) played a relatively large role in the yield of rice grown in the rain fed lowlands. It was also reported that the physiological traits, such as photosynthesis rate (Hu *et al*., 2007), nitrogen uptake (Shan *et al*., 2005), floret number per unit area (Yoshida *et al*., 2006), which are closely related to the yield, showed wide variation over genotypes and environments. Furthermore, the G×E interaction may be partitioned into the interactions of genotype-by-location (G×L), genotype-by-year (G×Y) and genotype-by-location-by-year (G×L×Y). In this study, almost all the traits examined showed the significant differences between years or locations. On the other hand, some traits, including SLA at mid-tillering and heading stages, F_v/F_m and LAI at heading stage, stem biomass at heading and maturity stages, and leaf N concentration at mid-tillering and heading stages, kept little change over years and locations, indicating that these characters may be used in evaluation of yield potential or breeding program.

References

Amano, T., Shi, C., Qin, D., Tsuda, M., Matsumoto, Y., 1996. High-yielding performance of paddy rice achieved in Yunnan Province, China: I. High yielding ability of Japonica F1 hybrid rice, Yu-Za 29. *Japanese Journal of Crop Science*, **65**(1):16-21.

Bunce, J.A., 1989. Growth rate, photosynthesis and respiration in relation to leaf area index. *Annals of Botany*, **63**(4): 459-463.

Cheng, S.H., Min, S.K., 2001. Super-rice breeding in China. *Chinese Rice Research Newsletter*, **9**(2):13-15.

Cooper, M., Somrith, B., 1997. Implications of Genotype-by-Environment Interactions for Yield Adaptation of Rain Fed Lowland Rice: Influence of Flowering Date on Yield Variation. Proc. Workshop, Plant Breeding Strategies for Rain fed Lowland Rice in Drought Prone Environments. ACIAR, Canberra, Australia, p.104-114.

Fischer, R.A., Aguilar, I., Laing, D.R., 1977. Post-anthesis sink size in a high-yielding dwarf wheat: yield response to grain number. *Australian Journal of Agricultural Research*, **28**(2):165-175. [doi:10.1071/AR9770165]

Horie, T., Ohnishi, M., Angus, J.F., Lewin, L.G., Tsukaguchi,

T., Matano, T., 1997. Physiological characteristics of high-yielding rice inferred from cross-location experiments. *Field Crops Research*, **52**(1-2):55-67. [doi:10.1016/S0378-4290(96)03458-2]

Hu, M.L., Zhang, Y.X., Kong, L.N., Yang, Q.H., Wang, C.M., Zhai, H.Q., Wan, J.M., 2007. Quantitative trait locus for photosynthesis and its related physiological traits in rice (*Oryza sativa* L.). *Acta Agronomica Sinica*, **33**(2):183-188 (in Chinese).

IRRI (International Rice Research Institute), 1995. Rice Facts. IRRI, Los Banos, Philippines.

Katsura, K., Maeda, S., Horie, T., Shiraiwa, T., 2007. Analysis of yield attributes and crop physiological traits of Liangyoupeijiu, a hybrid rice recently bred in China. *Field Crops Research*, **103**(3):170-177. [doi:10.1016/j.fcr.2007.06.001]

Khan, M.N.A., Murayama, S., Ishimine, Y., 1998. Physiomorphological studies of F1 hybrids in rice (*Oryza sativa* L.). Photosynthetic ability and yield. *Plant Production Science*, **1**(4):233-239.

Khush, G.S., Coffman, W.R., Beachell, H.M., 2001. The History of Rice Breeding: IRRI's Contribution. *In*: Rockwood, W.G. (Ed.), Rice Research and Production in the 21st Century: Symposium Honoring Robert F. Chandler, Jr. Metro Manila, Philippines, p.117-135.

Li, C.S., Ye, S.H., Chen, Y.Z., Ruan, G.H., Huang, F.D., Zhang, X.M., 2005. The study on yield component factors of high yielding Japonica rice varieties. *Acta Agriculture Zhejiangensis*, **17**(4):177-181 (in Chinese).

Matsushima, S., 1957. Analysis of developmental factors determining yield and yield prediction in lowland rice. *Bulletin of the National Institute of Agricultural Science Japan*, **5**:203-206 (in Japanese).

Murayama, S., Miyazatv, K., Nost, A., 1987. Studies on matter production of F1 hybrid in rice. I. Heterosis in the single leaf photosynthetic rate. *Japanese Journal of Crop Science*, **56**(2):198-203.

Rosegrant, M.W., Agcaoili-Sombilla, M., Perez, N.D., 1995. Global Food Projections to 2020: Implications for Investment. Food, Agriculture, and Environment Discussion. Paper No. 5, IFPRI, Washington, DC.

Sarker, M.A.Z., Murayama, S., Ishimine, Y., Tsuzuki, E., 2001. Heterosis in photosynthetic characters and dry matter production in F1 hybrids of rice. *Nippon Sakumotsu Gakkai Koenkai Yoshi, Shiryoshu*, **211**:48-49.

Shan, Y.H., Wang, Y.L., Pan, X.B., 2005. Mapping of QTLs for nitrogen use efficiency and related traits in rice (*Oryza sativa* L.). *Agricultural Sciences in China*, **4**(10):721-727.

Swaminathan, M.S., 2007. Can science and technology feed the world in 2025? *Field Crops Research*, **104**(1-3):3-9. [doi:10.1016/j.fcr.2007.02.004]

Tang, J.J., Chen, X., Katsuyoshi, S., 2002. Varietal differences in photosynthetic characters and chlorophyll fluorescence induction kinetics parameters among intergeneric progeny derived from *Oryza*×*Sorghum*, its parents, and hybrid rice. *Journal of Zhejiang University SCIENCE B*, **3**(1):113-117.

Weerakoon, M.W., Olszkyb, D.M., Mossc, D.N., 1999. Effects of nitrogen nutrition on responses of rice seedlings to carbon dioxide. *Agriculture, Ecosystems and Environment*, **72**(1):1-8. [doi:10.1016/S0167-8809(98)00166-2]

Ying, J.F., Peng, S.B., He, Q.R., Yang, H., Yang, C.D., Visperas, R.M., Cassman, K.G., 1998. Comparison of high yield rice in tropical and subtropical environments I. Determinants of grain and dry matter yields. *Field Crops Research*, **57**(1):71-84. [doi:10.1016/S0378-4290(98)00077-X]

Yoshida, H., Horie, T., Shiraiwa, T., 2006. A model explaining genotypic and environmental variation of rice spikelet number per unit area measured by cross-locational experiments in Asia. *Field Crops Research*, **97**(2-3):337-343. [doi:10.1016/j.fcr.2005.11.004]

Zhong, X.H., Peng, S.B., Sanico, A.L., Liu, H.X., 2003. Quantifying the interactive effect of leaf nitrogen and leaf area on tillering of rice. *Journal of Plant Nutrition*, **26**(6):1203-1222. [doi:10.1081/PLN-120020365]

Zou, Y., Tang, Q., Hu, C., Liu, S., Xiao, D., 1991. Dynamic simulation for rice growth and yield. II. The comparison and application of rice tillering statistical models. *Crop Research*, **5**(4):18-22.