THE CROP JOURNAL 2 (2014) 235–243

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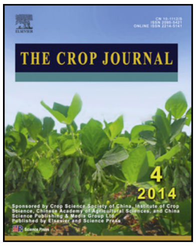

Optimal yield-related attributes of irrigated rice for high yield potential based on path analysis and stability analysis

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ARTICLE INFO

Article history:
Received 19 August 2013
Received in revised form
27 January 2014
Accepted 23 April 2014
Available online 14 May 2014

Keywords:
Irrigated rice
Grain yield
Yield-related attributes
Sequential path analysis
Stability analysis

ABSTRACT

Improvement of yield in rice (*Oryza sativa* L.) is vital for ensuring food security in China. Both rice breeders and growers need an improved understanding of the relationship between yield and yield-related traits. New *indica* cultivars (53 in 2007 and 48 in 2008) were grown in Taoyuan, Yunnan province, to identify important components contributing to yield. Additionally, two standard *indica* rice cultivars with similar yield potentials, II You 107 (a large-panicle type) and Xieyou 107 (a heavy-panicle type), were planted in Taoyuan, Yunnan province and Nanjing, Jiangsu province, from 2006 to 2008 to evaluate the stability of yield and yield-related attributes. Growth duration (GD), leaf area index (LAI), panicles per m^2 (PN), and spikelets per m^2 (SM) were significantly and positively correlated with grain yield (GY) over all years. Sequential path analysis identified PN and panicle weight (PW) as important first-order traits that influenced grain yield. All direct effects were significant, as indicated by bootstrap analysis. Yield potential varied greatly across locations but not across years. Plant height (PH), days from heading to maturity (HM), and grain weight (GW) were stable traits that showed little variation across sites or years, whereas GD (mainly the pre-heading period, PHP) and PN varied significantly across locations. To achieve a yield of 15 t ha^{-1}, a cultivar should have a PH of 110–125 cm, a long GD with HM of approximately 40 days, a PN of 300–400 m^{-2}, and a GW of 29–31 mg.

Abbreviations: PHP, pre-heading period; HM, days from heading to maturity; GD, growth duration; PH, plant height; LAI, leaf area index; MT, maximum tiller number per square meter; PR, panicle rate; PN, panicle number per square meter; SP, spikelet number per panicle; SFP, spikelet filling percentage; GW, grain weight; PW, panicle weight; SM, spikelet number per square meter; GY, grain yield; PI, panicle initiation.

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Peer review under responsibility of Crop Science Society of China and Institute of Crop Science, CAAS.

Production and hosting by Elsevier

http://dx.doi.org/10.1016/j.cj.2014.03.006
2214-5141

1. Introduction

Rice (*Oryza sativa* L.) is a staple grain for more than half of the world's population, and over 90% of world rice production occurs in Asia [1]. An increase in rice production is urgent, because the populations of major rice-producing countries are expected to consume 70% more rice by the year 2025 [2]. However, it is difficult to expand the area devoted to rice production because most arable land suitable for this purpose has already been developed with urban infrastructure. Further increase in rice production must be achieved largely by increasing yield per unit area. Improving rice yield has accordingly become one of the major objectives of breeders and growers in many countries over the past several decades. Grain yield is the result of a complex causal mechanism of plant ontogeny. From the beginning of a plant's life, environmental factors affect plant and crop traits, which, in turn, determine the final GY. Complex causal systems have been developed to study the traits that influence the final GY during plant development [3–6]. Many investigators have studied the correlations and causal associations of rice GY and yield-related traits, such as PH, PW, SP, GD, HM, and GW [4,7–11]. Although simple correlation analysis may not sufficiently explain the causal system, path analysis, developed by Wright [12], enables study of the complex relationships among traits of interest. Kozak et al. [13] performed a path analysis of a complex causal mechanism among 15 traits in lowland rice that determined GY and milling quality. For GY per plant, they found the highest positive correlation with the number of branches per panicle, followed by PN, PH, and flag leaf area. Sarawgi et al. [14] used path analysis to interpret the correlations of traits with GY and harvest index in tested rice accessions. All of these studies focused on GY per plant. Although GY per unit area is the product of GY per plant and plant density, GY per plant is influenced by plant density, meaning traits that correlate causally with GY per plant are different from those of GY per unit area.

Moreover, several traits closely correlated with GY show large variation across years and sites [15–17], possibly producing unstable GY results. Traits with unstable results cannot be recommended to breeders as an effective index for improving the yield potential. Stability analysis of yield-related traits is accordingly important for construction of a breeding index.

The highest rice yield records in China were >13 t ha^{-1} [18–20] and 18.5 t ha^{-1} [21] obtained in Taoyuan village, Yongsheng county, Yunnan province. Taoyuan is a well-known location for evaluating high-yield potential of rice, owing to its favorable ecological conditions such as light and temperature resources. In this study, several new hybrid cultivars or genotypes were collected from different provinces of China and grown in Taoyuan during the 2007 and 2008 growing seasons. Additionally, two representative *indica* hybrids with similar yield potentials, II You 107 of a large-panicle type and Xieyou 107 of a heavy-panicle type, were selected and grown in Taoyuan village and Qinglongshan village, Nanjing, Jiangsu province, from 2006 to 2008. The main objectives of this study were (i) to evaluate the GY potential of new *indica* hybrid cultivars in China; (ii) to explore the complex correlations between rice GY and yield-related traits in a large pool of high-yield genotypes or cultivars; and (iii) to evaluate the stability of yield-related traits over time and across locations for the new *indica* hybrid cultivars.

2. Materials and methods

2.1. Experimental design

Two experiments were performed. The first was performed over the 2007–2008 growing seasons in Taoyuan village, Yongsheng county, Yunnan province (26°13′ N, 100°34′ E, 1170 m a.s.l.), to investigate the relationships between several traits influencing yield. Newly released *indica* rice cultivars (53 cultivars in 2007 and 48 cultivars in 2008) were grown on a farm during the rice growing seasons, which occurs from mid-March to mid-September. The second experiment was performed in both Taoyuan and Nanjing, Jiangsu province (32°2′ N, 118°42′ E, 80 m a.s.l.) from 2005 to 2008, to investigate variation in yield-related traits. Two typical Chinese *indica* F_1 hybrid cultivars, a large-panicle cultivar, II You 107, and a heavy-panicle cultivar, Xieyou 107, were planted during the rice growing seasons. The soil at Taoyuan was an OrthicAcrisol (FAO taxonomy) with pH 8.0, an organic carbon content of 12.4 g kg^{-1}, and a total nitrogen content of 2.0 g kg^{-1}. The soil at the Nanjing site was an OrthicAcrisol with pH 7.3, an organic carbon content of 6.7 g kg^{-1}, and a total nitrogen content of 1.1 g kg^{-1}. Both experiments were arranged in a completely randomized block design with three replicates. The area of a plot was 4 m × 5 m = 20 m^2.

2.2. Crop management

Seedlings 30-day-old raised in a wet nursery were transplanted in early April at the Taoyuan site, and seedlings 35-day-old raised in a dry nursery were transplanted in mid-June at the Nanjing site, with hill spacing of 0.3 m × 0.13 m and one seedling per hill at both sites. Nitrogen (125 kg ha^{-1} N as urea), phosphorus (150 kg ha^{-1} P_2O_5 as single superphosphate), potassium (150 kg ha^{-1} K_2O as K_2SO_4), and zinc fertilizer (15 kg ha^{-1} Zn as magnesium–zinc fertilizer) were incorporated in the Taoyuan site, and 105 kg ha^{-1} N as urea, 75 kg ha^{-1} P_2O_5 as single superphosphate, 75 kg ha^{-1} K_2O as KCl, and 15 kg ha^{-1} Zn as magnesium–zinc fertilizer were incorporated in plots in the Nanjing site one day before transplanting. In the Taoyuan site, additional N was applied 7 days after transplanting (125 kg ha^{-1}), 12 days after transplanting (62.5 kg ha^{-1}), panicle initial (PI) (187.5 kg ha^{-1}), and the stage of the 2nd leaf from the top extension (125 kg ha^{-1}). An additional 150 kg ha^{-1} K_2O was also supplied at the PI stage. In the Nanjing site, N at the rates of 70, 105, and 70 kg ha^{-1} was applied 7 days after transplanting, at the PI stage and the 2nd leaf from the top extension stage, respectively, and 75 kg ha^{-1} K_2O were applied at the PI stage.

Except for the chemical fertilizer applications described above, similar crop management and experimental methods were adopted for both sites and years. Water, weeds, insects, and diseases were controlled as required to avoid yield loss.

2.3. Parameter measurements

Data were collected in the same way for each experiment in each year. Tiller numbers in the 30 hills from each plot were counted every five days to determine tiller density. Five hills were sampled from each plot during the heading and maturity stages in each experiment. Stem (main stems plus tillers) and panicle numbers were recorded. Plant samples were separated into green leaf blades (leaf), culms plus sheaths (including dead tissues) and panicles. The area of all green leaves was measured with an LI-3000 (LI-COR, Lincoln, NE, USA) and expressed as LAI at heading stage. In each plot, plant heights of 20 main stems were measured from the ground to the panicle tip. For the samples taken at maturity, panicles were hand-threshed and filled spikelets were separated by submersion in tap water. To determine individual GW, the filled spikelets were oven-dried at 70 °C to constant weight. SP, SFP, and SM were calculated and GY was determined from a 5 m^2 area in each plot with the moisture content adjusted to 13.5%. The traits observed included PHP, HM, GD, PH, LAI, MT, PR, PN, SP, SFP, SM, PW, GW, and GY.

A Micro Station Data Logger (H21-002, Hobo, USA) was used to record daily PAR, temperature, and relative humidity (RH) with a PAR sensor (S-LIA-M003 and Temp/RH sensor (S-THA-M006)) at Taoyuan and Nanjing, respectively. The data for each year are listed in Table 1 for both sites.

2.4. Data analysis

The datasets from Experiment 1 for each year were tested for skewness and kurtosis using SPSS 20.0 (IBM SPSS statistics 20). An appropriate transformation was applied to traits that showed non-normal distributions. Pearson linear correlation coefficients were calculated for all pairwise combinations of GY and the 13 traits listed above. Correlation coefficients were partitioned into direct and indirect effects using conventional path coefficient analysis [22]. Then, a sequential stepwise multiple regression was performed to organize the predictor variables into first- and second-order paths on the basis of their respective contributions to the total variation in GY and on minimal colinearity. The sequential path model consisted of both predictor and response variables. The level of multi-colinearity in each component path was calculated from two common measures, the “tolerance” value and the “variance inflation factor” (VIF), as suggested by Hair et al. [23]. Small tolerance values (much lower than 0.1) or high VIF values (>10) indicate high colinearity [23,24]. Partial coefficients of determination (analogous to linear regression coefficients) were calculated from the path coefficients for all predictor variables. To estimate the standard error path coefficients, bootstrap analysis [25] was performed with SPSS. For Experiment 2, a one-way ANOVA (analysis of variance) was used to test the difference between GY and the yield-related traits across both years and locations. The environmental variance (S^2), indicating the stability of both yield and yield-related traits [26,27], was determined. The environmental variance (S^2) is defined as the variance of genotype yields recorded across test or selection environments (i.e., individual trials):

$$S_i^2 = \sum(R_{ij} - m_{ij})/(e-1) \quad (1)$$

where, R_{ij} = the observed genotype yield response in the environment j, m_{ij} = the genotype mean yield across environments, and e = the number of environments. The greatest stability occurs when $S^2 = 0$.

In addition, the coefficient of variation (CV) was calculated as a stability measure. A CV value close to 0 indicates the greatest stability.

3. Results

3.1. Distribution of GY potential and yield-related traits

For Experiment 1, GY of the 53 tested cultivars ranged from 7.1 to 18.1 t ha^{-1} in 2007. The GY for these cultivars was normally distributed, with an average value of 13.7 t ha^{-1} and a standard deviation of 2.24 (Fig. 1-A). Of the 53 cultivars, 13 had a GY above 15.0 t ha^{-1}. In 2008, the GY of 48 tested cultivars was also normally distributed, with an average value of 15.1 ± 1.57 t ha^{-1} (Fig. 1-B). The GY in 2008 increased approximately 10% over the values observed in 2007. In 2008, the minimum GY was 10.7 t ha^{-1} for cultivar 08 TJ-Fan 4, whereas the maximum GY was 18.50 t ha^{-1} for cultivar II You 107. Of the 48 cultivars tested, 17 had a GY above 15.0 t ha^{-1}.

The average GD, PH, SFP, and SM values in 2007 and 2008 were almost identical. The MT and PN values decreased in 2008, whereas the SP, GW, and PW increased. The average GY increased from 13.7 t ha^{-1} in 2007 to 15.1 t ha^{-1} in 2008 (Table 2).

Table 1 – Daily average, minimum and maximum temperatures, average relative humidity, and average solar radiation in Taoyuan and Nanjing from 2005 to 2008.

Year	Average temperature (°C)	Maximum temperature (°C)	Minimum temperature (°C)	Relative humidity (%)	PAR (μmol m^{-2} s^{-1})
Taoyuan, Yunnan province					
2005	25.0	30.3	17.1	64.6	275.4
2006	23.9	29.7	19.3	54.9	459.8
2007	23.8	29.3	18.7	57.3	421.2
2008	23.0	28.9	17.7	63.9	409.0
Nanjing, Jiangsu province					
2005	24.7	29.0	21.3	78.0	–
2006	25.0	29.3	21.4	79.0	256.1
2007	24.3	28.6	21.1	81.0	324.9
2008	24.1	27.1	21.5	79.0	277.5

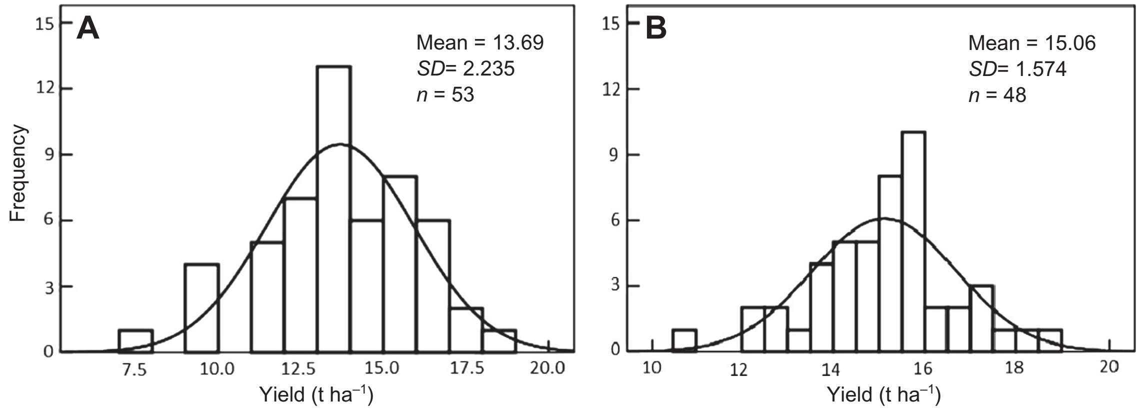

Fig. 1 – Frequency distribution of grain yield for the cultivars planted in Taoyuan in 2007 (A) and 2008 (B). *SD*: standard deviation.

3.2. Correlation of GY with other yield-related traits

Correlation matrices for the GY and the yield-related traits for both years of Experiment 1 are presented in Table 3. In general, the correlation coefficients among the variables were low. Growth duration, LAI, PN, and SM were all significantly and positively correlated with GY for both years ($P < 0.01$), but the correlation coefficient (r) above 0.5 was for SM only. Growth duration was strongly correlated with PHP, with r of 0.82 in 2007 and 0.83 in 2008, but was weakly correlated with HM. Pre-heading period was significantly and positively correlated with PH and PW in both years and positively correlated with GY in 2008. Plant height was significantly and positively correlated with GW and significantly and negatively correlated with SFP, with absolute r values above 0.50 in 2007. Maximum tiller number per square meter was negatively correlated with PR and positively correlated with PN for both years. Panicle number per square meter was significantly and positively correlated with LAI and SM for both years and with GY only in 2007, but negatively correlated with PW for both years. Moreover, a highly positive correlation was

Table 2 – Descriptive statistics for grain yield and yield-related traits of tested cultivars in 2007 and 2008.

Trait	Minimum	Maximum	Mean	SD	Skewness	Kurtosis
2007						
PHP (d)	107	150	135.6	7.9	−0.9	2.9
HM (d)	25	44	35.3	4.6	−0.3	−0.3
GD (d)	140	185	170.9	7.6	−1.4	5.1
PH (cm)	83	129	116.4	9.3	−1.5	3.8
LAI	5.2	10.4	7.4	1.5	0.5	−0.9
MT	398.9	931.8	637.9	132.7	0.5	−0.5
PR (%)	30.3	68.4	48.4	8.3	0.0	0.2
PN	240.7	407.2	308.3	43.6	0.3	−0.6
SP	120.7	252.9	179.6	27.4	0.2	0.2
SFP (%)	67.4	96.4	86.1	7.7	−0.6	−0.5
GW (mg)	18.8	35.6	29.2	3.5	−1.0	1.4
PW (g)	2.4	5.8	4.5	0.8	−0.5	0.0
SM	36.4	72.9	55	9.2	−0.2	−0.6
GY (t ha^{-1})	7.1	18.1	13.7	2.2	−0.5	0.6
2008						
PHP (d)	105	144	131	7.0	−1.7	4.2
HM (d)	31	47	40.3	4.0	−0.7	0.1
GD (d)	146	180	171.2	7.3	−1.0	2.0
PH (cm)	94.4	137.2	117.5	8.7	−1.4	2.5
LAI	2.5	9.5	6.2	1.4	0.5	1.0
MT	214.5	714.0	459.3	94.4	0.4	1.4
PR (%)	42.0	95.1	60.1	11.1	1.5	2.9
PN	204.0	428.8	274.6	43.6	1.8	3.7
SP	155.7	287.0	204.7	26.6	0.5	1.1
SFP (%)	64.5	95.9	86.8	5.4	−1.3	5.1
GW (mg)	21.1	36.7	31.5	2.9	−1.0	2.2
PW (g)	3.1	6.6	5.6	0.7	−1.3	2.8
SM	37.4	72.6	55.7	7.5	0.2	−0.1
GY (t ha^{-1})	10.7	18.5	15.1	1.6	−0.2	0.5

Table 3 – Correlation coefficients among yield-related traits.

	PHP	HM	GD	PH	LAI	MT	PR	PN	SP	SFP	SM	GW	PW	GY
PHP		−0.32*	0.83**	0.47**	0.20	0.05	−0.28	−0.19	0.22	−0.19	0.03	0.33*	0.33*	0.25
HM	−0.23		0.27	−0.18	0.33*	0.14	0.22	0.46**	0.08	0.13	0.44**	−0.33*	−0.09	0.23
GD	0.82**	0.36*		0.44**	0.51**	0.12	−0.17	0.07	0.27	−0.06	0.27	0.14	0.28	0.39**
PH	0.44**	0.10	0.46**		0.35*	−0.33	0.06	−0.29	0.37*	−0.53**	0.12	0.57**	0.39*	0.22
LAI	0.19	0.24	0.37*	0.39**		0.41*	−0.00	0.79**	−0.21	0.04	0.53**	0.08	−0.12	0.48**
MT	0.45**	0.04	0.49**	−0.11	0.51**		−0.78**	0.50**	−0.32	0.35*	0.09	−0.35*	−0.29	0.02
PR	−0.71**	0.09	−0.63**	−0.14	−0.12	−0.78**		0.12	0.07	−0.20	0.16	0.05	−0.05	0.04
PN	−0.06	0.19	0.10	−0.21	0.84**	0.62**	−0.06		−0.32*	0.03	0.57**	−0.38**	−0.50**	0.31*
SP	0.27	0.11	0.32*	0.17	−0.39**	−0.03	−0.24	−0.49**		−0.35**	0.59**	−0.11	0.59**	0.35*
SFP	−0.06	−0.17	−0.17	−0.31*	0.01	0.06	0.03	0.12	−0.50**		−0.27*	0.12	0.28*	0.29*
SM	0.22	0.28	0.41**	−0.04	0.52**	0.53**	−0.29	0.57**	0.43**	−0.31*		−0.41**	0.09	0.58**
GW	0.29	−0.20	0.12	0.41**	−0.19	−0.23	−0.09	−0.40**	−0.25	0.10	−0.65**		0.59**	0.34*
PW	0.47**	−0.17	0.32*	0.31*	−0.53**	−0.16	−0.31*	−0.72**	0.55**	0.11	−0.22	0.52**		0.65**
GY	0.58**	0.06	0.59**	0.21	0.52**	0.52**	−0.48**	0.44**	0.02	0.28	0.51**	0.15	0.28	

Correlation coefficients in 2007 and 2008 are shown in the upper and lower panels, respectively.

* Significant at $P < 0.05$.

** Significant at $P < 0.01$ (2-tailed test).

found between LAI and SM for both years. Panicle weight was positively related to SP and GW for both years.

3.3. Sequential path coefficient analysis of GY with respect to the other yield-related traits

Conventional path coefficient analysis determines the contribution of various factors by partitioning the correlation coefficients into components of direct and indirect effects (Fig. 2).

Analysis of multi-colinearity indicated inconsistent patterns of relationships among the variables. For example, in 2007, PN and PW showed both positive and high direct effects on GY, whereas in 2008 the direct effect of PN on GY was negative. In addition to inconsistent patterns for direct effects, high multi-colinearity was observed for some traits (Table 4), particularly for those showing high direct effects, such as PW (VIF = 164.03 for 2007 and 90.95 for 2008).

The mean direct effects estimated from a set of 200 bootstrap samples were in close agreement with the observed direct effects of various traits (Table 5). All the direct effects were significant based on *t*-test. Panicle number per square meter and PW, as first-order variables, accounted for nearly 94% of the variation in GY in both 2007 and 2008 (Table 5), and both variables displayed high and positive direct effects on GY. The direct path coefficient of PN was higher in 2007 but lower in 2008 than PW (Fig. 2). The correlation between PN and PW was significant and negative. These results indicate that both PN and PW influence GY and PN and PW influence each other. The path analysis of second-order variables over the first-order variable showed that 90.9% in 2007 and 82.3% in 2008 of the total variation for PN were explained by MT and PR (Table 5). The path coefficients of MT were higher than those of PR in both 2007 and 2008, showing that PN was determined mainly by MT. Panicle weight was dependent on SP, SFP, and GW, and the coefficients of determination were 0.982 and 0.985 in 2007 and 2008, respectively. The path coefficients for all three traits were significant for both years ($P < 0.0.1$) in the order SP > GW > SFP. These results demonstrate that rice cultivars with large panicles and grain could improve PW.

3.4. Static stability of yield-related traits across both years and sites

To elucidate the difference in yield-related traits over years and sites, two rice cultivars with high-yield potentials, II You

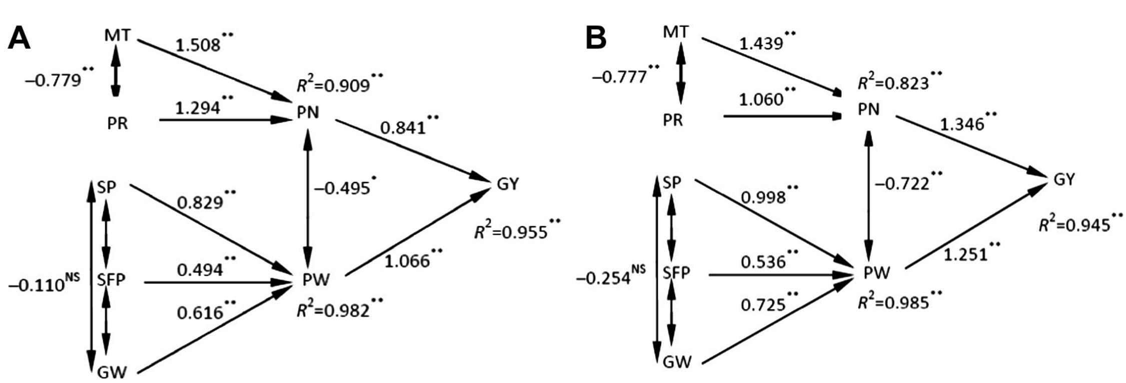

Fig. 2 – Sequential path model illustrating interrelationships among the various traits contributing to grain yield. A: 2007 dataset; B: 2008 dataset. The coefficient of determination (R^2) for each component of the path analysis is shown below its respective response variable. *: significant at $0.01 \le P < 0.05$. **: significant at $P < 0.01$. NS: not significant at $P \ge 0.05$.

Table 4 – Tolerance and variance inflation factor (VIF) values for predictor variables for both conventional path analysis and sequential path analysis.

Year	Predictor variable	Response variable	Tolerance		VIF	
			M1	M2	M1	M2
2007	PN	GY	0.013	1.325	79.64	0.755
	PW		0.006	1.325	164.03	0.755
	MT	PN	0.087	2.542	11.45	0.393
	PR		0.131	2.542	7.64	0.393
	SP	PW	0.007	1.150	138.21	0.870
	SFP		0.041	1.153	24.45	0.868
	GW		0.015	1.020	64.87	0.980
2008	PN	GY	0.006	2.089	156.44	0.479
	PW		0.011	2.089	90.95	0.479
	MT	PN	0.041	2.525	24.56	0.396
	PR		0.054	2.525	18.68	0.396
	SP	PW	0.011	1.406	93.32	0.711
	SFP		0.034	1.327	29.61	0.753
	GW		0.017	1.071	58.96	0.934

M1: conventional path analysis; and M2: sequential path analysis.

107 and Xieyou 107, were planted in Taoyuan and Nanjing from 2006 to 2008 (Experiment 2). The GY was virtually identical for both cultivars, but yield-related traits, including GW, SP, and PN, were significantly different ($P < 0.01$). For II You 107, a standard large-panicle cultivar, SP was greater than 200, more than 1.3-fold that of Xieyou 107. Conversely, for Xieyou 107, a standard heavy-panicle variety, PN and grain size were larger than those of II You 107.

For both cultivars, GY varied greatly across sites. At Taoyuan, the GY of II You 107 was 17.7 t ha^{-1}, and the GY of Xieyou 107 was 17.0 t ha^{-1}. At Nanjing, the GY for II You 107 was 1.92-fold lower and the GY for Xieyou 107 was 1.83-fold lower than the values recorded at Taoyuan. The CV of the GY across sites ranged from 41% to 47% (Table 6).

For the four yield components, PN, SP, SFP, and GW, only SP was not significant between sites. Maximum tiller number per square meter in Nanjing was 313 m^{-2} for II You 107 and 335 m^{-2} for Xieyou 107, compared with 731 m^{-2} for II You 107 and 738 m^{-2} for Xieyou 107 in Taoyuan ($P < 0.05$). Panicle rate was significantly higher at Nanjing than at Taoyuan. The difference of source capacity (LAI at heading stage) and sink capacity between Taoyuan and Nanjing was also significant. The SM at Taoyuan was 1.68-fold higher for II You 107 and 1.63-fold higher for Xieyou 107 than at Nanjing. Leaf area indexes at heading stage for II You 107 and Xieyou 107 were 1.36 and 1.30-fold higher at Taoyuan than at Nanjing. The CV for SM was larger than that for LAI at heading stage and was identical for the two cultivars. The GD at Taoyuan was 42 d longer for II You 107 and 38 days longer for Xieyou 107 than at Nanjing. The difference in GD between the two sites was caused mainly by PHP, with averages of 43 days for II You 107 and 39 days for Xieyou 107. No significant difference was found in HM across sites or years. There was a small difference in PH between Taoyuan and Nanjing for both cultivars, and PH was stable at approximately 110 cm. Overall, the significant differences between Taoyuan and Nanjing, in descending order, were PHP > GD > PN > MT > SM > LAI > PW > GW > SFP. PH, HM, and SP were relatively stable across locations, and the differences were not significant. The stability of yield-related traits was identical for both cultivars.

Compared with the large differences between locations, the differences in the yield-related traits, with the exception of PR, SFP, and GW, between years for both cultivars were not significant. The CV of 13 yield-related traits was nearly identical for both cultivars. Overall, GD, PH, GW, SFP, and PN were relatively stable across years, with CVs of smaller than 10%.

Environment variance (S^2) of the two cultivars, II You 107 and Xieyou 107, showed similar stability for GY (Table 6). However, the stability of PW, GW, and SM of the large-panicle variety, II You 107, was higher than that of the heavy-panicle cultivar, Xieyou 107. Among the yield-related traits, independent of large-panicle or heavy-panicle type, HM, PH, SFP, and GW were the most stable with a CV lower than 10%, followed by PW, GD, PHP, LAI, and SP with a moderate CV of 10%–20%. In comparison, MT, PR, and GY were the most unstable traits with the CV above 30%.

Table 5 – Estimation of the standard error values of path coefficients using bootstrap analysis.

Year	Predictor variables	Response variables	R^2-adj	Direct effect	Bootstrap		
					SE	Mean	Bias
2007	PN	GY	0.95	0.841	0.003	0.043	0.000
	PW			1.066	0.114	2.967	−0.013
	MT	PN	0.90	1.508	0.026	0.445	0.001
	PR			1.294	0.491	6.101	0.014
	SP	PW	0.98	0.829	0.001	0.024	0.000
	SFP			0.494	0.003	0.052	0.000
	GW			0.616	0.005	0.142	0.001
2008	PN	GY	0.94	1.346	0.002	0.049	0.000
	PW			1.251	0.185	2.908	−0.030
	MT	PN	0.82	1.439	0.059	0.520	−0.001
	PR			1.060	0.565	3.255	0.059
	SP	PW	0.98	0.998	0.001	0.025	0.000
	SFP			0.536	0.004	0.067	0.000
	GW			0.725	0.008	0.168	0.002

R^2-adj, adjusted determination coefficient.

Table 6 – Analysis of variance for grain yield and yield-related traits for II You 107 and Xieyou 107.

Year	Site	PHP (d)	HM (d)	GD (d)	PH (cm)	LAI	MT (m^{-2})	PR (%)	PN (m^{-2})	SP	SFP (%)	SM ($\times 10^3$)	GW (g)	PW (g)	GY (t ha^{-1})
II You 107															
2006	Nanjing	97	41	138	109.2	7.3	298.1	75.1	223.6	185.6	79.3	41.5	26.5	3.9	8.7
	Taoyuan	139	41	180	113.0	9.5	839.5	48.2	403.6	195.8	84.5	79.0	27.8	4.6	18.5
2007	Nanjing	97	41	138	111.1	5.9	410.9	48.8	199.5	247.9	71.7	49.1	26.6	4.7	9.4
	Taoyuan	139	41	180	109.8	10.4	642.8	55.5	350.2	199.2	89.6	69.8	28.3	5.0	17.8
2008	Nanjing	97	41	138	115.3	7.9	230.7	93.2	214.6	177.9	85.9	38.2	28.4	4.4	9.3
	Taoyuan	140	38	178	109.4	9.4	684.7	47.1	321.9	228.9	90.0	73.7	28.2	5.8	18.7
Xieyou 107															
2006	Nanjing	95	40	135	109.2	8.2	285.2	88.8	253.0	137.1	82.2	34.7	29.3	3.3	8.3
	Taoyuan	135	40	175	108.3	10.2	845.9	51.6	431.8	161.6	85.3	69.7	30.8	4.2	18.4
2007	Nanjing	95	40	135	108.8	6.3	456.7	51.8	232.0	186.9	74.5	43.2	28.7	4.0	9.2
	Taoyuan	135	40	175	110.7	9.0	708.5	55.9	394.9	158.3	88.1	62.6	30.2	4.2	16.7
2008	Nanjing	95	40	135	113.7	8.6	263.9	100.2	263.2	137.9	89.5	36.3	31.6	3.9	10.3
	Taoyuan	135	39	174	110.2	9.9	668.4	53.2	353.5	149.0	90.3	52.7	32.8	4.4	15.6
F-value															
Year		0.1	2.4	1.1	1.2	1.5	2.1	4.338**	1.1	1.7	5.7**	1.4	4.9*	1.4	0.7
Site		3157.8**	2.3	3134.5**	1.2	48.5**	178.3**	27.3**	214.3**	0.1	23.2**	128.2**	5.0**	11.9**	408.7**
Cultivar		0.4	0.7	0.5	0.4	0.7	1.7	1.1	1.0	23.0**	2.4	1.7	26.8**	9.8**	0.1

* Significant at $P < 0.05$.
** Significant at $P < 0.01$.

4. Discussion

4.1. *Grain yield potential*

Grain yield potential is defined as the yield of a cultivar when grown in an environment to which it is adapted, with unlimited nutrients and water and with pests, disease, weeds, lodging, and other stresses effectively controlled [28]. Taoyuan village, an eco-site for high-yield rice because of its favorable light and temperature conditions, has produced yields of rice from 13 to 18 t ha^{-1} [18–20], with many new hybrid cultivars being planted there to test their yield potential. In this study, the cultivars chosen for testing came from breeding units throughout China with unrelated parents. The average GY of the 53 cultivars grown in 2007 was 13.7 t ha^{-1} and the average GY of the 48 cultivars grown in 2008 was 15.1 t ha^{-1}. These values were close to the highest rice yield recorded [18–21]. In 2007, Xieyou 107, II You 2186, and II You 318 were the top three cultivars, with GY above 16.5 t ha^{-1}. In 2008, the two highest-yielding cultivars were Xieyou 107 and II You 107, with GY of 18.5 and 18.4 t ha^{-1}, respectively.

4.2. *Growth period*

Final yield is a function of the length of growing season [29]. If the potential size of a crop is predetermined, the length of PHP is also important. In this study, PHP was significantly and positively correlated with PH and PW for both years and was positively correlated with GY in 2008, suggesting that a longer PHP can benefit the growth of vigorous rice plants and improve GY. Because GY is determined during grain filling between heading and maturity stages, crop physiologists have indicated the importance of increased biomass production after heading in rice for high GY [30,31]. Yang et al. [32] reported that HM was a crucial determinant of genotypic variation of GY in field-grown tropical irrigated rice. Days from heading to maturity was not significantly correlated with GY, given that the values of HM in the 101 tested cultivars were all around 40 days. Although no comparison of dry matter accumulation after heading was calculated, the results clearly revealed that the improvement of GY was mainly the result of an increase in the crop growth rate after heading. Similar findings were reported by Takai et al. [33] and Li et al. [31]. Pre-heading period varied significantly across sites but not across years, whereas HM did not vary significantly across sites or years [21].

4.3. *Plant height*

Plant height is an important morphological index and criterion for rice breeders. In this study, PH varied minimally across sites and years. The first significant advance in rice yield potential was a result of dwarf breeding. The new plant type proposed by the International Rice Research Institute (IRRI) is a PH of 90–100 cm. Yuan [34] proposed a PH of at least 100 cm from the soil surface to the unbent plant tip at maturity. Peng et al. [35] reviewed the PH of popular Chinese rice cultivars, which included Xieyou 9308 (PH of 120–135 cm) and Liangyoupeijiu (115–125 cm). Although PH was positively correlated with GW, increases in PH could enhance the risk of lodging. Therefore, the suitable PH for high-yielding rice is hypothesized to be 110–125 cm.

4.4. *Source and sink*

LAI is one of the major determinants of crop photosynthesis [36]. LAI was significantly correlated with SM and GY, verifying that LAI could be a basic index for rice yield [37]. Sink size as SM is the primary determinant of rice GY [18,37–39] and has often been considered in breeding programs to be the limiting factor in the process of increasing GY. In this study, sink size was the yield-related trait most significantly positively correlated with GY. In this study, SM of the cultivars with yields over 15.0 t ha^{-1} was more than 50,000.

4.5. *Yield component traits*

Grain yield in rice depends upon PN, SP, SFP, and GW. Direct path coefficients of PN and PW to GY were similar, indicating that the effects on GY were equal for these two factors. Panicle number per square meter was significantly influenced by location, but PW was not.

Panicle number per square meter was significantly and positively correlated with LAI, SM, and GY, suggesting that PN is the basis for increasing source and sink and the guarantee of higher yields. Gravois and Helms [40] reported that optimum rice yield could not be attained without optimum panicle density at uniform maturity. Panicle number per square meter was significantly and negatively correlated with individual PW for both years, showing that high yields could be attributed to factors other than PN. These results are supported by the statistic analysis, showing that the average PN of the 48 cultivars tested in 2008 was lower than those in 2007, whereas the average GY was higher in 2008 than in 2007.

Panicle weight is the product of SP, SFP, and GW. The direct path coefficient to PW declined from SP to GW to SFP, in contrast to the results of Yuan et al. [19]. Given that only two cultivars were used by Yuan et al. [19], their results may have been limited. Spikelet number per panicle, ranging from 121 to 287 with an average of 191, differed significantly across cultivars but not across locations or years. Spikelet filling percentage was influenced mainly by the environment, but was relatively stable under high yield cultivation, reaching 80% at Nanjing and 87% at Taoyuan. Grain weight is a stable varietal factor, because grain size is rigidly controlled by the size of the hills in which the rice is planted [41]. Consequently, average GW is nearly constant and minimally influenced by the environment. Similar results were observed in this study; the GWs of II You 107 and Xieyou 107 were 27.6 ± 0.8 g and 30.6 ± 1.3 g across locations and years. However, the GW of the 101 cultivars tested ranged from 18.8 g to 35.6 g, with an average of 30.3 g. The cultivars with lower GW values also showed low GY. These results indicate that larger grain size has been an objective of high-yield hybrid rice breeding. Grain weight ranged from 29.0 to 31.0 mg for cultivars with a GY of more than 17 t ha^{-1} in this study.

Although the average PN decreased from 308 m^{-2} in 2007 to 274 m^{-2} in 2008, SP increased from 180 to 205 over the same period, resulting in similar sink size for the two years. However, the average GW increased from 29.2 mg in 2007 to 31.5 mg in 2008, resulting in a higher GY in 2008 than in 2007. Clearly, the newly developed hybrid rice cultivars have changed from heavy-panicle to large-panicle types.

5. Conclusion

The yield potential varied greatly over locations, but not across growing seasons. Sequential path analysis identified both PN and PW as important first order traits influencing grain yield. All direct effects were significant, as indicated by bootstrap analysis. PH, HM, and GW were stable variety traits that were not affected by the location or year. To achieve a yield of 15 t ha^{-1}, a cultivar should have a PH of 110–125 cm, a long GD with an HM of approximately 40 days, and a GW of 29–31 mg. A decreased PN and increased GW indicate that rice breeding has shifted from selecting heavy-panicle cultivars to large-panicle cultivars. Yield potential in rice can be improved by increasing PHP, strengthening the source capacity, and enlarging the sink size.

Acknowledgments

This study was jointly supported by the National Key Technology R&D Program of China (2011BAD16B14, 2012BAD20B05, 2012BAD04B08, and 2013BAD20B05). We thank the staff of the Agricultural Station of Taoyuan town in Yongsheng county, Yunnan province, for the generous support.

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