Improvements in Plant Morphology Facilitating Progressive Yield Increases of *japonica* Inbred Rice since the 1980s in East China

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Abstract: Grain yield was greatly increased during the genetic improvement of *japonica* inbred rice since the 1980s in Jiangsu, east China; thus, an improved plant morphology should be expected, considering that plant morphology is a decisive factor determining grain yield. Twelve representative *japonica* inbred rice released from 1983 to 2013 were grown in the same fields in 2019 and 2020. Grain yield increased (*p* < 0.01) at 63.3 kg ha⁻¹ year⁻¹ across 2 years among rice cultivars released in different periods. The genetic improvement in grain yield was associated with increased spikelets per panicle. Single panicle weight, number of primary and secondary branches, and number of grains on primary and secondary branches were all increased with a year of release. Generally, the width of top three leaves positively correlated (while angle of top three leaves and light extinction coefficient negatively) correlated (*p* < 0.01) with year of release. Leaf area per tiller and leaf area index at heading and maturity, specific leaf weight, leaf photosynthetic rate, and SPAD values after heading were all increased linearly with year of release. Plant height exhibited a positive (*p* < 0.01) trend with year of release, as well as stem weight per tiller and K and Si concentrations of stem. Spikelets per panicle, width of top three leaves, plant height, and leaf area index, and specific leaf weight after heading positively correlated (while angle of top three leaves and light extinction coefficient negatively) correlated (*p* < 0.01) with grain yield and single panicle weight. Our results suggested that modern *japonica* inbred rice exhibited expanded sink size by spikelets per panicle, higher leaf area through leaf width, optimized leaf photosynthetic capacity, lower leaf angle and light extinction coefficient, and enhanced stem strength. These improved plant morphologies facilitated yield increases of *japonica* inbred rice since the 1980s in east China.

Keywords: genetic improvement; plant morphology; *japonica* inbred rice; grain yield

1. Introduction

Rice production in China has increased fourfold over the past seven decades (National Bureau of Statistics, China, 2019). From the 1950s to the 1980s, the increased rice yields were attributed to the promotion of semi-dwarf and dwarf cultivars and the expansion of rice-growing areas [1,2]. From the 1980s to the present, the yield increases were achieved mainly via utilization of heterosis that greatly enhanced rice yield potential, improved cultivation managements (such as rice precise and quantitative cultivation technique), and climate change [3–5]. For example, Yu et al. [5] estimated the increased rice yields in China after 1980 were achieved via genetic improvement (38.9%), crop management (9.3%), and climate change (4.4%).
Genetic improvement is a determinant factor for increased yields across many rice-growing countries, such as India, Japan, the Philippines, and Thailand [6–10]. In China, genetic progress in rice grain yield was reported in the northeast [11,12], southwest [13], south [14], and central China [15,16]. Such studies suggested that genetic progress greatly increased rice grain yield, which was associated with prolonged growth period [6,14], expanded sink size through spikelets per panicle [12,15], and increased biomass accumulation, harvest index, or both [9,10,15].

Plant morphology is a decisive factor influencing grain yield formation of rice, which encompasses plant height, leaf shape and arrangement, and panicle branching pattern. The effects of genetic improvement on plant morphology were studied in maize [17,18], wheat [19,20], and soybean [21]. For example, Ma et al. [18] concluded that the genetic improvement in maize grain yield was attributable to the reduced plant height and more upright leaf posture. For rice, Wu et al. [12] reported that plant height decreased during the genetic improvement of *japonica* inbred rice in northeast China, while Li et al. [14] reported that plant height increased during the genetic improvement of *indica* and *japonica* inbred rice in south China. Such research on rice indicated that the changes of plant morphology to cultivar improvement varied with the specific cultivar types and experimental regions.

In China, *indica* hybrid rice and *japonica* inbred rice are two main cultivar types in production [22]. The past four decades have seen a dramatic shift in the cultivation area between *indica* hybrid rice and *japonica* inbred rice in Jiangsu, east China; the rate of *japonica* inbred rice planting area has increased from 10% in the 1980s to 90% today [23]. Such a pronounced shift increased the provincial average rice yield from 7.3 t ha$^{-1}$ in the 1980s to 8.6 t ha$^{-1}$ nowadays [23,24]. To date, little information is available on changes in grain yield and related plant morphology during the genetic improvement of *japonica* inbred rice since the 1980s in Jiangsu, east China.

In this study, twelve representative *japonica* inbred rice released from 1983 to 2013 in east China were collected and grown in the same paddy fields. The main purposes of the current study were (1) to evaluate changes in grain yield and plant morphological traits of *japonica* inbred rice released since the 1980s in Jiangsu, and (2) to elucidate possible causes for changes in grain yield from the viewpoint of plant morphology during the genetic improvement of *japonica* inbred rice.

2. Materials and Methods

2.1. Experimental Site and Meteorological Information

Field experiments were conducted at the experimental farm (119.25° E, 32.30° N) of Yangzhou University, Jiangsu, China in 2019 and 2020. The experimental field soil belonged to sandy loam type with the following properties measured at 2 years: 15.8 g kg$^{-1}$ organic carbon, 1.4 g kg$^{-1}$ total nitrogen (N), 29.7 mg kg$^{-1}$ Olsen phosphorus (P), and 70.3 mg kg$^{-1}$ available potassium (K). Generally, the rice experienced higher temperature and sunshine hours, and lower rainfall during the growing period in 2019 than the corresponding growth period in 2020.

2.2. Rice Cultivar, Experimental Design, and Field Management

Twelve *japonica* inbred rice released from 1983 to 2013 were grown in this field experiment. These rice cultivars were selected because they were all released by local breeding institutes, and well-adapted to the agro-ecological conditions of the study area. The rice cultivars were very popular and widely adopted by local farmers during historical periods. For example, Wuyujing 3 was famous for its high and stable grain yield and was widely planted with a cumulative area of 6.1 Mha as of 2020. Nanjing 5055 and Nanjing 9108 were grown in a large area for their excellent grain quality in recent years [25]. Besides, these rice cultivars were generally considered representative during the breeding process of *japonica* inbred rice since the 1980s, and were always chosen as the control (CK) in the crop variety regional trials conducted in Jiangsu, east China [23]. The rice cultivars were kindly
provided by breeding institutes. The information on year of release, cross information, cumulative planting area, and breeding institute was seen in Table 1.

Table 1. The information on year of release, cross information, cumulative planting area, and breeding institute of rice cultivars.

| Cultivar     | Year of Release | Cross Information                                      | Cumulative Planting Area (Mha) | Breeding Institute                                      |
|--------------|-----------------|--------------------------------------------------------|-------------------------------|---------------------------------------------------------|
| Yanjing 2    | 1983            | Nanjing 11                                             | 1.0                           | Institute of Agricultural Sciences, Yancheng, Jiangsu    |
| Sidao 8      | 1986            | Aijing 22/Sidao 5 × Chengbao 1                          | 0.4                           | Farm of Cotton Raw Seed, Siyang, Jiangsu                |
| Wuyujing 2   | 1989            | Zhongdan 1/79-51 × Zhongdan 1/Yangjing 1                 | 1.6                           | Farm of Rice–Wheat Breeding, Wujin, Jiangsu             |
| Wuyujing 3   | 1992            | Zhongdan 1/79-51 × Zhongdan 1/Yangjing 1                 | 6.1                           | Farm of Rice–Wheat Breeding, Wujin, Jiangsu             |
| Wuyujing 5   | 1997            | Wuyujing 3 × Bing 627                                   | 1.0                           | Xuhuai Institute of Agricultural Sciences, Jiangsu      |
| Huaidao 5    | 2000            | 7208 × Wuyujing 3                                       | 2.2                           | Farm of Rice–Wheat Breeding, Wujin, Jiangsu             |
| Wuxiangjing 14 | 2003        | Jing 58 × 248-5/254-13/ Wuxiangjing 9                   | 1.3                           | Xuhuai Institute of Agricultural Sciences, Jiangsu      |
| Wujing 15    | 2004            | Zaozong 9/Chunjiang 03 Jing × Wuyujing 7                 | 0.9                           | Farm of Rice–Wheat Breeding, Wujin, Jiangsu             |
| Wuyunjing 21 | 2007            | Yun 9707 × Yun 9726                                     | 0.7                           | Institute of Agricultural Sciences, Wujin, Jiangsu      |
| Wuyunjing 24 | 2010            | Nongken 57/Kuihuahuang × 9746                           | 0.8                           | Institute of Agricultural Sciences, Wujin, Jiangsu      |
| Nanjing 5055 | 2011            | Wujing 13 × Guandong 194                                | 1.0                           | Jiangsu Academy of Agricultural Sciences                |
| Nanjing 9108 | 2013            | Wuxiangjing 14 × Guandong 194                           | 1.8                           | Jiangsu Academy of Agricultural Sciences                |

The information on year of release, cross information, cumulative planting area, and breeding institute of rice cultivars is available from the website http://www.ricedata.cn (accessed on: 12 April 2021).

This field experiment was laid in a randomized block design with three replicates. Each plot area was 24 m² (6 m × 4 m) at 2 years. Pregenerated rice seeds were sown in seedbeds on May 20 and transplanted with four seedlings per hill into open fields for 2 years. The hill spacing was 30 cm row and 12 cm plant. The total N rate was 270 kg ha⁻¹ with a ratio of 3:3:2:2 at 1 d before transplanting, 7 d after transplanting, at panicle initiation, and at penultimate–leaf appearance stages, respectively. The total P and K rates were both 180 kg ha⁻¹ and were applied once as base dressing at 1 d before transplanting. The irrigation regime adopted in field experiment followed the alternate wetting and drying method, which applied multiple flooding and drainage during the rice–growing cycle [26]. The weed and pest management were identical during the rice–growing period in all experimental plots. In the two–year field experiment, no lodging phenomenon was observed in each plot.

2.3. Sampling and Measurement

The plants of five hills were sampled at heading and maturity to measure biomass weight and leaf area index. The sampled plants were divided into panicles, leaves, and stems. Leaf area index was determined through a leaf area meter (LI-3100C, Li-Cor, Lincoln, NE, USA), then the weights of the panicles, leaves, and stems were measured after oven–drying at 75 °C for 80 h. After weighing, stems were collected to grind through a 0.5 mm sieve using a Wiley mill (Thomas-Wiley Corp., Swedesboro, NJ, USA) to measure the K and silicon (Si) concentrations. The K concentration was determined through flame atomic absorption spectrophotometry; Si concentration was determined referring to the method of Tamai and Ma. [27].

Leaf morphologies, including leaf length, width, and angle of top three leaves, were measured at 30 days after heading (DAH) in the field. The photosynthesis active radiation (PAR) was measured using a line quantum sensor (LI-250, Li-Cor, Lincoln, NE, USA) at
30 DAH. Such a measurement was conducted between 9:30–11:30 a.m. in the field on a sunny day. The line quantum sensor was positioned 50 cm above the canopy to measure the incident PAR \( (I_0) \), then the sensor was positioned 5 cm above the field water level to measure the incident PAR at the bottom \( (I) \). The light extinction coefficient \( (k) \) was calculated by the following formula based on Beer–Lambert’s law:

\[
k = \frac{\log_n \left( \frac{I_0}{I} \right)}{LAI}
\]

where \( \log_n \) is the natural log of the number. \( I_0 \) is the incident PAR above the canopy and \( I \) is the incident PAR at the bottom.

The plants of four hills were collected at full heading stage to measure specific leaf weight, and photosynthetic rate and SPAD values of flag leaves. Specific leaf weight was calculated as the ratio of leaf dry mass to leaf area. Leaf area was determined by a leaf area meter (LI-3100C, Li-Cor, Lincoln, NE, USA), and leaf dry mass was weighted after oven-drying at 75 °C for 80 h. The leaf photosynthetic rate was determined between 9:30 and 11:30 by three portable photosynthetic instruments (LI-6400, Li-Cor, Lincoln, NE, USA).

At maturity, the plants of 50 hills were collected to determine plant height, single panicle weight, number of primary and secondary branches, and number of grains on primary and secondary branches. In each plot, rice plants from 200 hills were harvested manually for grain yield measurement with a moisture content of 14%; rice plants from 100 hills were sampled to determine grain yield components, including panicles per m\(^2\), spikelets per panicle, filled-grain percentage, and grain weight.

2.4. Data Analysis

Data analyses were conducted with SAS version 9.4 (SAS Institute Inc., Cary, NC, USA). Means were compared by analysis of variance (ANOVA), followed by the least significant difference (LSD) test. In the ANOVA, the source of variation included year, cultivar, and the interaction year \( \times \) cultivar. The results of ANOVA showed that there were no significant differences in grain yield and plant morphological traits between the two study years, therefore data averaged across 2 years were used for the following analysis (Table 2). The correlation coefficients were calculated using the Pearson method.

Table 2. Analysis of variance (ANOVA) of grain yield and the related morphological traits among year, cultivar, and the interaction.

| Source          | df | Grain Yield | Spikelets per Panicle | Single Panicle Weight | Light Extinction Coefficient | Leaf Area Index | Leaf Photonic Rate | SPAD Values | Specific Leaf Weight | Plant Height |
|-----------------|----|-------------|-----------------------|-----------------------|-----------------------------|----------------|-------------------|-------------|----------------------|--------------|
| Year            | 1  | ns          | ns                    | ns                    | ns                          | ns             | ns                | ns          | ns                   | ns           |
| Cultivar        | 11 | **          | **                    | **                    | **                          | **             | **                | **          | **                   | **           |
| Year \( \times \) Cultivar | 11 | **          | ns                    | ns                    | ns                          | ns             | ns                | ns          | ns                   | ns           |
| Total           | 71 | ns          | ns                    | ns                    | ns                          | ns             | ns                | ns          | ns                   | ns           |

ns, not significant at the 0.05 probability level according to the LSD test; *, significant at the 0.05 probability level according to the LSD test; **, significant at the 0.01 probability level according to the LSD test.

3. Results

3.1. Grain Yield and Panicle Traits

Grain yield differed significantly \( (p < 0.01) \) in rice cultivars released from 1983 to 2013. Grain yield increased \( (p < 0.01) \) linearly with year of release, and the annual increment was 63.3 kg ha\(^{-1}\) across 2 years. Panicles per m\(^2\) and filled-grain percentage exhibited negative \( (p < 0.01) \) trends, while spikelets per panicle and spikelets per m\(^2\) exhibited positive \( (p < 0.01) \) trends with year of release (Table 2 and Figure 1).
Results was 63.3 kg ha⁻¹ across 2 years. There existed a positive correlation between single panicle weight and number of grains on primary branches (0.83) (Figure 3). The number of primary and secondary branches increased (P < 0.01) trends with year of release (Table 2 and Figure 1). Grain yield differed significantly (P < 0.01) linearly with year of release, and the annual increment of primary branches was more than that of secondary branches. Similarly, the number of grains on primary and secondary branches varied significantly (P < 0.01) trends with year of release; the annual increase in number of secondary branches was more than that of primary branches. Spikelets per panicle and spikelets per m² exhibited positive (P < 0.01) trends with year of release (Table 2 and Figure 1).

Single panicle weight varied significantly (P < 0.01) in rice cultivars from 2.3 g to 3.6 g across 2 years. There existed a positive correlation between single panicle weight and year of release among rice cultivars released from 1983 to 2013, with an annual increase of 0.04 g (Table 2 and Figure 2).

Figure 1. Relationships between year of release and panicles per m² (a), spikelets per panicle (b), spikelets per m² (c), filled-grain percentage (d), grain weight (e), and grain yield (f) of rice cultivars. Data were fitted by linear regression (y = ax + b). In the linear regression, x was reassigned as years after 1983; for example, x was valued as 1 in 1983 and so on. **, significant at the 0.01 probability level according to the LSD test; ns, not significant at the 0.05 probability level according to the LSD test. Vertical bars represent ± standard error of the mean (n = 6).

Figure 2. Relationship between year of release and single panicle weight of rice cultivars. Data were fitted by linear regression (y = ax + b). In the linear regression, x was reassigned as years after 1983; for example, x was valued as 1 in 1983 and so on. **, significant at the 0.01 probability level according to the LSD test. Vertical bars represent ± standard error of the mean (n = 6).
The number of primary and secondary branches increased ($p < 0.01$) with year of release, and the annual increase in the number of secondary branches was more than that of primary branches. Similarly, the number of grains on primary and secondary branches both exhibited positive ($p < 0.01$) trends to year of release; the annual increase in number of grains on secondary branches averaged 1.30 across 2 years and was higher than that of grains on primary branches (0.83) (Figure 3).

![Graphs showing trends in number of branches and grains over years](image)

**Figure 3.** Relationships between year of release and number of primary and secondary branches (a,b) and number of grains on primary and secondary branches (c,d) of rice cultivars. Data were fitted by linear regression ($y = ax + b$). In the linear regression, $x$ was reassigned as years after 1983; for example, $x$ was valued as 1 in 1983 and so on. **, significant at the 0.01 probability level according to the LSD test. Vertical bars represent ± standard error of the mean ($n = 6$).

### 3.2. Leaf Length, Width, and Angle, and Light Extinction Coefficient

The width of the 1st top leaf was increased ($p < 0.01$) linearly with year of release, and such trend was detected for the 2nd and 3rd top leaves. Generally, the length of the 3rd top leaf did not change significantly during rice cultivar improvement; the lengths of the 1st and 2nd top leaves increased ($p < 0.01$) linearly with year of release (Figure 4).
Figure 4. Relationships between year of release and length and width of 1st top leaves (a,d), 2nd top leaves (b,e), and 3rd top leaves (c,f) at 30 DAH of rice cultivars. DAH, days after heading. Data were fitted by linear regression \(y = ax + b\). In the linear regression, \(x\) was reassigned as years after 1983; for example, \(x\) was valued as 1 in 1983 and so on. **, significant at the 0.01 probability level according to the LSD test; ns, not significant at the 0.05 probability level according to the LSD test. Vertical bars represent ± standard error of the mean (\(n = 6\)).

The angle of the top three leaves showed negative (\(p < 0.01\)) trends to year of release. Generally, the angle of the 3rd top leaf decreased by 0.33° year\(^{-1}\), and was higher than that of the 1st (0.29° year\(^{-1}\)) and 2nd (0.19° year\(^{-1}\)) top leaves. Light extinction coefficient varied significantly (\(p < 0.01\)) from 0.57 to 0.42 in rice cultivars released from 1983 to 2013 across 2 years. Light extinction coefficient showed a negative (\(p < 0.01\)) trend against year of release, with an annual reduction of 0.005 (Table 2 and Figure 5).
Figure 5. Relationships between year of release and angle of top three leaves (a-c) and light extinction coefficient (d) at 30 DAH of rice cultivars. DAH, days after heading. Data were fitted by linear regression \( y = ax + b \). In the linear regression, \( x \) was reassigned as years after 1983; for example, \( x \) was valued as 1 in 1983 and so on. **, significant at the 0.01 probability level according to the LSD test. Vertical bars represent ± standard error of the mean (\( n = 6 \)).

3.3. Leaf Area, Specific Leaf Weight, Leaf Photosynthetic Rate, and SPAD Value

Leaf area per tiller at heading and maturity were increased linearly with year of release, with an annual increase of 3.3 cm\(^2\) and 1.6 cm\(^2\) across 2 years, respectively. Leaf area index increased obviously before 2000 but fluctuated after 2000. Overall, leaf area index at heading increased (\( p < 0.01 \)) linearly with year of release; such a trend was detected at maturity (Figure 6).

Specific leaf weight differed significantly (\( p < 0.01 \)) in rice cultivars released from 1983 to 2013. Specific leaf weight exhibited a positive (\( p < 0.01 \)) trend to year of release, increased by 0.43 g m\(^{-2}\) year\(^{-1}\) across 2 years. Leaf photosynthetic rate and SPAD values varied significantly (\( p < 0.01 \)) among rice cultivars. Leaf photosynthetic rate and SPAD values both increased (\( p < 0.01 \)) linearly with year of release (Table 2 and Figure 7).
Figure 6. Relationships between year of release and leaf area per tiller (a, b), and leaf area index (c, d) at heading and maturity of rice cultivars. Data were fitted by linear regression ($y = ax + b$). In the linear regression, $x$ was reassigned as years after 1983; for example, $x$ was valued as 1 in 1983 and so on. **, significant at the 0.01 probability level according to the LSD test. Vertical bars represent ± standard error of the mean ($n = 6$).

Figure 7. Relationships between year of release and specific leaf weight (a), leaf photosynthetic rate (b), and SPAD values (c) at full heading stage of rice cultivars. Data were fitted by linear regression ($y = ax + b$). In the linear regression, $x$ was reassigned as years after 1983; for example, $x$ was valued as 1 in 1983 and so on. **, significant at the 0.01 probability level according to the LSD test. Vertical bars represent ± standard error of the mean ($n = 6$).
3.4. Plant Height, Stem Weight, K and Si Concentrations

The difference in plant height was significant \((p < 0.01)\) in rice cultivars, which ranged from 90.3 cm to 117.0 cm across 2 years. Plant height correlated positively \((p < 0.01)\) with year of release, and the annual increase in plant height was 0.82 cm (Table 2 and Figure 8).

![Figure 8. Relationship between year of release and plant height of rice cultivars. Data were fitted by linear regression \((y = ax + b)\). In the linear regression, \(x\) was reassigned as years after 1983; for example, \(x\) was valued as 1 in 1983 and so on. **, significant at the 0.01 probability level according to the LSD test. Vertical bars represent ± standard error of the mean \((n = 6)\). Generally, stem weight per tiller at heading increased stably before 2000 and fluctuated after that. Stem weight per tiller at heading correlated positively \((p < 0.01)\) with year of release and increased by 0.02 g year \(^{-1}\) across 2 years. Similarly, stem weight per tiller at maturity increased \((p < 0.01)\) linearly with year of release, and the annual rate was 0.03 g. The K concentration of stem increased \((p < 0.01)\) linearly with year of release, with an annual increase of 0.01%. The Si concentration of stem also correlated positively \((p < 0.01)\) with year of release (Figure 9).

![Figure 9. Cont.](image-url)
The K concentration of stem increased ($p < 0.01$) linearly with year of release, with an annual increase of 0.01%. The Si concentration of stem also correlated positively ($r = 0.86$, $p < 0.01$) with grain yield and single panicle weight. Correlation analysis also showed that specific leaf weight correlated positively ($p < 0.01$) with leaf photosynthetic rate and with SPAD values (Table 3).

### 3.5. Correlation Analysis

Most of the plants’ morphological traits, such as spikelets per panicle, width of top three leaves, leaf area index at heading and maturity, specific leaf weight, and plant height, correlated positively ($r < 0.01$ or $r < 0.05$) with grain yield and single panicle weight. Conversely, the angle of the top three leaves and light extinction coefficient correlated negatively ($p < 0.01$) with grain yield and single panicle weight. Correlation analysis also showed that specific leaf weight correlated positively ($p < 0.01$) with leaf photosynthetic rate and with SPAD values (Table 3).

### Table 3. Correlation matrix between grain yield and plant morphological traits of rice cultivars.

|        | GY | SPP | SPW | LEC | LAIH | LAIM | SLW | LPR | SPAD Values | PH | STH |
|--------|----|-----|-----|-----|------|------|-----|-----|-------------|----|-----|
| **GY** |    |     |     |     |      |      |     |     |             |    |      |
| **SPP**|    | 0.92** | 0.97** | 0.88** |      |      |     |     |             |    |      |
| **SPW**|    | 0.92** | 0.97** | 0.88** |      |      |     |     |             |    |      |
| 1st Leaf Width | -0.83 | -0.86 | -0.88 | -0.66 |      |      |     |     |             |    |      |
| 2nd Leaf Width | 0.90** | 0.94** | 0.86** | 0.81 |      |      |     |     |             |    |      |
| 3rd Leaf Width | -0.79 | -0.84 | -0.88 | -0.62 | 0.66* |      |     |     |             |    |      |
| 1st Leaf Angle | -0.71 | -0.69 | -0.66 | 0.77** | -0.65 | 0.64* |      |     |             |    |      |
| 2nd Leaf Angle | -0.78 | -0.66 | -0.69 | 0.88** | -0.78 | 0.83** | -0.65 |      |             |    |      |
| 3rd Leaf Angle | -0.71 | -0.69 | -0.66 | 0.77** | -0.65 | 0.64* |      |     |             |    |      |

GY, grain yield; SPP, spikelets per panicle; SPW, single panicle weight; LEC, light extinction coefficient; LAIH, leaf area index at heading; LAIM, leaf area index at maturity; SLW, specific leaf weight; LPR, leaf photosynthetic rate; PH, plant height; STH, stem weight per tiller at heading; STM, stem weight per tiller at maturity. Data used for calculations are from Figures 1–9. *, significant at the 0.05 probability level according to the LSD test; **, significant at the 0.01 probability level according to the LSD test.
4. Discussion

The contribution of genetic improvement to increased yields was studied across rice-growing countries. Genetic improvement increased at 26.3 (low N condition) and 42.0 (high N condition) kg ha\(^{-1}\) year\(^{-1}\) of rice released from 1944 to 1992 in the United States [28], 15.7 to 45.0 kg ha\(^{-1}\) year\(^{-1}\) of upland rice released from 1992 to 2009 in Brazil [29], and 75 to 81 kg ha\(^{-1}\) year\(^{-1}\) of rice released from 1966 to 1995 in the Philippines [9]. In China, the annual yield increase reached 137.9 kg ha\(^{-1}\) from 1958 to 2005 in the northeast [12], and 60 to 70 kg ha\(^{-1}\) from 1936 to 2005 in central China [15]. In this study, the genetic improvement achieved a 63.3 kg ha\(^{-1}\) year\(^{-1}\) yield gain across 2 years of japonica inbred rice since the 1980s in east China (Figure 1); this value was close to the estimated value of 58 kg ha\(^{-1}\) year\(^{-1}\) based on changes in grain yield in China after 1980 [5]. These results suggested that great success was achieved in breeding high-yielding japonica inbred rice since the 1980s [24].

Previous studies reported that yield improvement was achieved by expanding sink size through panicles per m\(^2\) and spikelets per panicle in northeast China [12], panicles per m\(^2\) in Japan [6], and spikelets per panicle in central China [15]. Our results showed that progressive yield increase was attributed to the enlarged sink size by spikelets per panicle (Figure 1, Table 3), consistent with Zhu et al. [15]. In this study, single panicle weight increased \((p < 0.01)\) linearly with year of release (Figure 2), indicating more attention has been given to improving individual-plant yield in the breeding progress of japonica inbred rice in east China. Such a breeding strategy could balance the contradiction between the quantity and quality of crop population, as more quantity was always associated with poor quality during the process of crop population formation [30]. Similar observations were reported in the genetic improvement of maize [31,32] and wheat [33,34]. Our results showed that modern rice produced more primary and secondary branches than old ones, as well as grains on primary and secondary branches (Figure 3), which laid the foundation of large panicles in modern rice. Besides, annual increases in number of secondary branches and grains on secondary branches were consistently higher than those of primary branches and grains on primary branches (Figure 3). This result indicated it was efficient to increase spikelets per panicle from promoting panicle branching, especially for secondary branches, consistent with Gong et al. [35] and Huang et al. [36].

Leaf area increased \((p < 0.01)\) with year of release during the genetic improvement of japonica inbred rice since the 1980s (Figure 6). Notably, the width of the top three leaves increased \((p < 0.01)\) linearly with year of release, while such a trend was not present for length (Figure 4), indicating that an increase in leaf area was mainly resulted from higher leaf width rather than leaf length during cultivar evolution. It was reported that excessive growth of leaf length would easily result in leaf curling [37,38], despite a feasible way to increase leaf area. Hence, such an improvement in leaf width not only increased leaf area but also helped make leaves more upright, confirmed by lower leaf angle with year of release (Figures 5 and 6). Leaf angle and light extinction coefficient correlated negatively \((p < 0.01)\) with year of release (Figure 5), suggesting that modern rice exhibited compact plant architecture. Similar results were also reported during the genetic improvement of rice in the central and northeast China [12,16]. This result indicated that the canopy architecture of modern japonica inbred rice was greatly optimized during genetic breeding, which allowed the modern rice to have a large leaf area with improved light interception and distribution into the crop canopy.

In the present study, leaf photosynthetic rate and SPAD values both correlated positively \((p < 0.01)\) with year of release (Figure 7), suggesting stay–green characteristics in modern japonica inbred rice bred in east China. Meanwhile, specific leaf weight increased \((p < 0.01)\) linearly with year of release (Figure 7), indicating thicker leaves in modern rice than the old ones. Previous studies reported that compared with a thin leaf with low specific leaf weight, a thick leaf with high specific leaf weight absorbed more radiation resources and exhibited higher leaf photosynthesis [39–41]. Our results also showed that specific leaf weight correlated positively both with leaf photosynthetic rate and SPAD
values (Table 3), suggesting that a higher specific leaf weight might be an important parameter for reflecting improved leaf photosynthetic capacity and biomass production in high-yielding rice breeding [16,42].

Most existing literature reported a reduced trend of plant height during the genetic improvement across maize- and wheat–production countries [18,43–45]. However, such a trend was not consistent during rice cultivar evolution. It was reported that plant height was increased [46,47], or reduced [12,28,29] during rice genetic improvement. In this study, plant height was increased ($p < 0.01$) among rice released from 1983 to 2013 in east China (Figure 8). The increased plant height promoted leaf extension, benefited light interception and leaf photosynthesis, and enhanced grain yield [46]. Besides, we observed that plant height stabilized at nearly 115 cm in recently bred rice cultivars (released after 2010) (Figure 8), which met the recommended plant height (110–120 cm) in the future breeding program of japonica inbred rice in China [48,49].

The larger sink size and heavier single panicle weight acquired a stronger stem to realize a higher yield potential in modern rice of our study (Figures 1 and 2). In this study, stem weight per tiller at heading and maturity both correlated positively ($p < 0.01$) with year of release (Figure 9), indicating available assimilates production for stem enrichment after heading, which was beneficial for stem lodging resistance. Our results herein demonstrated that K and Si concentrations of stem both correlated with year of release (Figure 9). Generally, K and Si elements could help enhance lignified portions and increased the strength of epidermal cells [50,51]. Therefore, higher stem weight per tiller and K and Si concentrations contributed to the improvement of lodging resistance in modern japonica inbred rice in east China.

The coordination of the sink–source relationship is a critical factor for grain yield. It is well documented that rice grain yield is generally sink–limited [52,53]. Our above results exhibited that sink (such as spikelets per m$^2$, and single panicle weight) and source (such as leaf area, specific leaf weight, and leaf photosynthetic rate) both increased along with genetic cultivar improvement. Such results indicated that genetic progress has reduced sink limitation and maintained sink–source balance. Noteworthy, there existed a negative correlation between filled–grain percentage and year of release (Figure 1), indicating it is still a great challenge to improve synergistically sink size and sink–filling efficiency in modern japonica inbred rice. This information also suggested that source increased relatively slowly to meet the enlarged sink during the genetic improvement of japonica inbred rice since the 1980s. Therefore, source-related capacities should receive more attention for rice future high-yielding breeding and cultivation practices.

5. Conclusions

The genetic improvement achieved a 63.3 kg ha$^{-1}$ year$^{-1}$ yield increase across 2 years of japonica inbred rice since the 1980s in east China. The morphological changes in japonica inbred rice have enlarged sink size through spikelets per panicle, increased leaf area by leaf width, optimized leaf orientation and light distribution within the canopy, improved plant height and leaf photosynthetic capacity, and enhanced stem strength. These improved plant morphologies contributed to yield improvement of japonica inbred rice since the 1980s. The declined filled-grain percentage in modern rice cultivars might be attributable to more attention for sink, while relatively less for source during the genetic improvement. Future breeding should focus more on source improvement on the basis of expanding sink to develop high–yielding cultivars.

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