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# Agronomic and Physicochemical Properties Facilitating the Synchronization of Grain Yield and the Overall Palatability of *Japonica* Rice in East China

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**Abstract:** Understanding the agronomic and physicochemical characteristics related to grain yield and grain quality is an ongoing hotspot. In 2018 and 2019, high-yielding rice with good palatability (HYGP), high-yielding rice with poor palatability (HYPP), and low-yielding rice with good palatability (LYGP) were grown in paddy fields to explore the main traits underlying the better grain yield and overall palatability of HYGP. HYGP and HYPP demonstrated a 18.1–20.7% higher grain yield ($p < 0.05$) than LYGP; HYGP and LYGP gave an overall palatability from 75.2 to 77.0, higher ($p < 0.05$) than HYPP. The higher grain yield of HYGP compared to that of LYGP resulted from a larger sink size because of the spikelets per panicle and the higher total shoot biomass weight ($p < 0.05$). HYGP exhibited more ($p < 0.05$) panicles per $m^2$ but lower spikelets per panicle and 1000-grain weight than HYPP and maintained a similar grain yield to HYPP. Compared with HYPP and LYGP, HYGP exhibited more ($p < 0.05$) biomass accumulation from heading to maturity, supported by the higher leaf area index, post-heading leaf photosynthetic rate, and SPAD values. HYGP had higher ($p < 0.05$) adenosine diphosphate glucose pyrophosphorylase and starch branching enzyme activities at the middle and late grain-filling stages than HYPP and LYGP. HYGP and LYGP had a lower ($p < 0.05$) chalky area, chalky degree, amylose content, setback, grain protein content, and prolamin content than HYPP, while it had a higher ($p < 0.05$) gel consistency, breakdown, and ratio of glutelin content to prolamin content. Our results suggested that optimized yield components, more biomass accumulation through improved leaf photosynthetic capacities, a lower amylose content with coordinated enzyme activities involved in starch synthesis, and a lower grain protein content with a better composition were the main traits facilitating the better grain yield and overall palatability of rice in east China.

**Keywords:** rice; grain yield; overall palatability; agronomic and physicochemical characteristics



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## 1. Introduction

Rice (*Oryza sativa* L.), one of the most important staple cereals worldwide, supplies rich carbohydrates and protein with balanced amino acids for humans worldwide [1]. It has been the top priority to chase for high rice yields in order to meet the daunting challenges brought by the ever-growing population all over the world [2,3]. In recent years, more consumers are prioritizing good-quality rice with the rapid improvement in living standards [4,5]. Such a shift in consumer demand drives the pace of breeding rice cultivars with superior grain yield and the quality in breeding programs and cultivation practices nowadays [6,7].

Rice grain quality, including the qualities of milling, appearance, cooking, eating, and nutritional value, is receiving more and more attention from researchers [8]. Generally, cooking and eating quality is widely considered the most crucial indicator for evaluating grain quality, considering that rice is consumed as one of the food rations [9,10]. Starch and protein, occupying 80–90% and 4–18%, respectively, of grain dry weight, are two key factors influencing rice grain quality [11]. Compared with other major rice-producing countries, China's rice is always characterized by superior grain yield but inferior grain quality, especially cooking and eating quality [12–14]. The poor grain quality of China's rice is mainly attributed to higher amylose content and grain protein content, which leads to hard and rough-cooked rice and lowers cooking and eating quality [13,15,16]. The over-application of nitrogen (N) fertilizers also led to unsatisfactory rice grain quality in China [17,18]. China's rice occupies about 19% of the world's rice fields and 36% of the total N fertilizers consumption worldwide [19]. Excessive N application led to lower N use efficiency and deteriorated rice grain quality [17,20–22].

It is an ongoing hot topic to achieve synergistic improvements in rice grain yield and grain quality, especially cooking and eating quality [3,6]. The existing literature reported some key agronomic and physicochemical characteristics underlying the superior cooking and eating quality of rice [23–26]. For instance, rice cultivars with good cooking and eating quality were reported to exhibit lower amylose content and setback and higher peak viscosity and setback [24,25]. Peng et al. [26] concluded that the activities of adenosine diphosphate glucose pyrophosphorylase (AGP) and the starch branching enzyme (SBE) correlated positively with the cooking and eating quality in rice. *Japonica* rice is a dominant cultivar type in the northeast and east of China [27,28]. For a long time, rice production in east China was always characterized by a higher grain yield but poor cooking and eating quality compared to rice in northeast China. The provincial average grain yield of *japonica* rice average about 8.8 t ha$^{-1}$ in recent years in Jiangsu, east China, which ranked first among the main rice-production provinces in China [29]. It is widely recognized that *japonica* rice in northeast China produces better cooking and eating quality than the corresponding in east China, mainly due to specific good-quality rice, fertile soil, and the large difference between day and night temperatures during rice-growing periods [30]. In recent years, success was achieved in developing high-yielding *japonica* rice with excellent overall palatability in east China, such as Nanjing 9108 and Wuyunjing 30 [7]. Due to such superior characteristics, this high-yielding rice with good palatability (HYGP) is grown widely in production [21,31]. In addition, several N-efficient strategies such as reduced N rate with dense planting and site-specific N management were proposed for rice production [19,28]. These improved N application methods were reported to not only maintain grain yield and N use efficiency but also to benefit rice grain quality [5,32]. Still, little attention is paid to investigate the main traits underlying the better grain yield and overall palatability of HYGP under improved N-efficient management.

The present study was conducted to determine the main traits underlying the superior grain yield and overall palatability of HYGP. The agronomic and physicochemical characteristics included grain yield components, shoot biomass weight and accumulation, harvest index, leaf area index (LAI), plant N concentration and accumulation, the activities of enzymes involved in the grain starch synthesis, and grain quality characteristics. We hope our results will bring new insights for rice breeders to improve the grain yield and quality of *japonica* rice.

## 2. Materials and Methods

### *2.1. Plant Materials, Experimental Site, and Field Management*

Before this study, 54 *japonica* rice cultivars with widespread planting in east China were selected and planted in paddy fields in 2016 and 2017, which varied greatly in terms of grain yield (ranging from 8.1 t ha$^{-1}$ to 10.2 t ha$^{-1}$) and cooking and eating quality (overall palatability ranging from 55.3 to 79.4) across two years. Among these 54 *japonica* rice cultivars, nine representative rice cultivars were screened and classified into three types—HYGP, high-yielding rice with poor palatability (HYPP), and low-yielding rice with good palatability (LYGP)—based on distinct differences in grain yield and cooking and eating quality. The HYGP were Nanjing 9108, Wuyunjing 30, and Naning 3908; the HYPP were Huaidao 5, Huajing 4, and Changnongjing 8; the LYGP were Suxiangjing 3, Songzaoxiang 1, and Yangjing 103. For instance, the cumulative planting area of Nanjing 9108 exceeded more than 1.8 Mha since it was released in 2013 (www.ricedata.cn, accessed on 21 April 2022). The specific information about the year of release, cross information, and growth period of the rice cultivars is listed in Table 1.

**Table 1.** The specific information about the year of release, cross information, and growth period of rice cultivars.

| Cultivar Type | Cultivar | Year of Release | Cross Information | Duration from Heading to Maturity (d) | Total Growth Period (d) |
|---|---|---|---|---|---|
| HYGP | Nanjing 9108 | 2013 | Wuxiangjing 14 × Guandong 194 | 57 | 146–147 |
| | Wuyunjing 30 | 2014 | Kuifeng/Wuxiangjing 19 × Tai 0206 | 58 | 147–148 |
| | Nanjing 3908 | 2018 | Nanjing 5055 | 57–58 | 146 |
| HYPP | Huaidao 5 | 2000 | 7208 × Wuyujing 3 | 50–51 | 140 |
| | Huajing 4 | 2005 | Zhendao 88 × Fengwei 6 | 50 | 140–141 |
| | Changnongjing 8 | 2014 | H 07–37 × Wuyunjing 23 | 50–51 | 141–142 |
| LYGP | Suxiangjing 3 | 2010 | Wujing 13 × Beiming | 47–48 | 137 |
| | Songzaoxiang 1 | 2014 | Zaoxiangruanfan 2 × Zaoxiangchanglijing | 48 | 138–139 |
| | Yangjing 103 | 2017 | Jindao 1007 × Yangjing 4227 | 48–49 | 137–138 |

HYGP, high-yielding rice with good palatability; HYPP, high-yielding rice with poor palatability; LYGP, low-yielding rice with good palatability.

In both 2018 and 2019, field experiments were conducted at the farm (119.25° E, 32.30° N) of Yangzhou University, Jiangsu, east China. The meteorological data during the rice-growing period were recorded through an automated weather station (Figure 1). The soil of the experimental field was sandy loam in texture, and 0–20 cm soil contained organic carbon 19.4 g $kg^{-1}$, total N 1.6 g $kg^{-1}$, Olsen phosphorus (P) 33.4 mg $kg^{-1}$, and available potassium (K) 83.2 mg $kg^{-1}$.

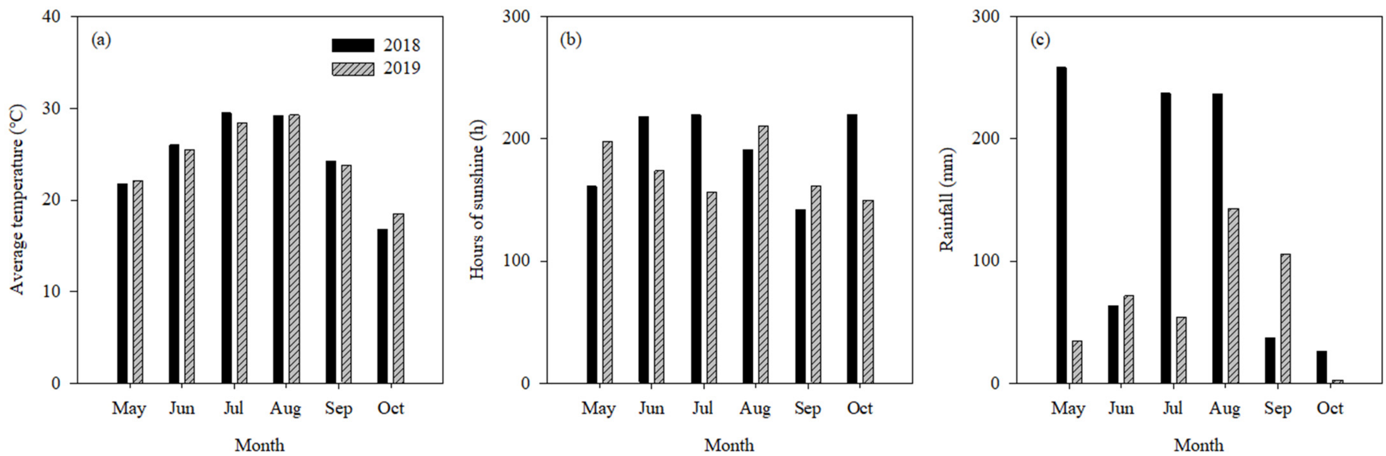


**Figure 1.** Average temperature (**a**), hours of sunshine (**b**), and rainfall (**c**) per month during rice growing periods in 2018 and 2019.

A randomized block design with three replications was adopted in these field experiments, and each plot covered 24 $m^2$ (6 m $\times$ 4 m) at two study years. Seeds of rice were sown on the 20th of May, and 20-day seedlings were transplanted with four seedlings per hill at a density of 27.8 hills per $m^2$ on the 9th of June. At one day before transplanting, the experimental plots received a total of 90 kg N $ha^{-1}$, 180 kg $P_2O_5$ $ha^{-1}$, and 150 kg $K_2O$ $ha^{-1}$. The N application at 1 week after transplanting, panicle initiation, and the penultimate-leaf appearance followed the site-specific N management based on the measurements of leaf N status through the soil-plant analysis development meter (SPAD) [19]. When SPAD $\leq$ 40, 40 < SPAD < 42, and SPAD $\geq$ 42, the N application rates were 90, 60, and 30 kg $ha^{-1}$ at 1 week after transplanting and 75, 60, and 45 kg $ha^{-1}$ at the penultimate leaf appearance. When SPAD $\leq$ 38, 38 < SPAD < 40, and SPAD $\geq$ 40, the N application rates at panicle initiation were 90, 60, and 30 kg $ha^{-1}$, respectively [28]. For all rice cultivars, the N rates at 1 week after transplanting, panicle initiation, and the penultimate-leaf appearance were 60, 45, and 60 kg $ha^{-1}$ at two years, respectively, following the methods above. In this study, the total N rate was 255 kg $ha^{-1}$ at two years, lower than the normal rate (averaged 300 kg $ha^{-1}$) of rice production in east China [17,28]. Irrigation methods and the management of pests, disease, and weeds followed local recommendations.

### *2.2. Sampling and Measurement*

#### 2.2.1. LAI, Shoot Biomass, N Concentration, Leaf Photosynthetic Rate, SPAD Values, Enzymatic Activity

Five hills of plants were collected to measure the LAI, shoot biomass, and N concentration at jointing, heading, and maturity. The LAI was determined by a LI-3100C Leaf Area Meter (Lincoln, NE, USA). The sampled plants were divided into leaves, stems, and panicles (at heading and maturity) and placed well in Kraft paper bags to determine the shoot biomass weight after being oven-dried at 75 °C for 80 h. After that, the dried samplings were ground through a 0.5-mm sieve in a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) for the N concentration, referring to the micro-Kjeldahl method [33].

The leaf photosynthetic rate and SPAD values of the rice cultivars were measured at the early grain-filling stage (EGS), middle grain-filling stage (MGS), and late grain-filling stage (LGS). Here, EGS, MGS, and LGS of HYGP were set at 16–17, 33–34, and 50–51 days after heading (DAH); EGS, MGS, and LGS of HYPP and LYGP were set at 13–14, 27–28, and 41–42 DAH. The sampling periods of three cultivar types were set mainly considering their different durations from heading to maturity (Table 1). The flag leaf photosynthetic rate was determined around 9:30 h to 11:00 h by three LICOR-6400 photosynthetic instruments (Lincoln, NE, USA) under sunny conditions. The SPAD values of the top three leaves were measured by a SPAD meter (SPAD-502 plus) around 15:00 h to 16:30 h in the field.

In each plot, plants with the same heading and flowering date were tagged as single stems, and 200 single stems were selected in total. The tagged panicles were sampled at EGS, MGS, and LGS, and the grains located in the middle position of the tagged panicles were collected for measuring key enzymes involved in grain starch synthesis, including adenosine diphosphate glucose pyrophosphorylase (AGP), granule bound starch synthetase (GBSS), soluble starch synthase (SSS), and starch branching enzyme (SBE). Such enzymes were measured using commercial assay kits (BC0430, BC3295, BC1855, BC1865, Solarbio Science & Technology, Beijing, China).

#### 2.2.2. Grain Yield and Grain Quality

In each plot, 200 representative hills of plants were harvested at maturity for determining the grain yield at 14% moisture. In each plot, 100 representative hills of plants were collected for measuring the panicles per $m^2$, and 10 representative hills of plants were sampled for determining the spikelets per panicle, the filled-grain percentage, and the 1000-grain weight. The harvested rice grains were air-dried and stored at room temperature for three months to determine rice grain quality, following the standard method (GB/T17891-2017, Ministry of Agriculture and Rural Affairs, China).

To determine the milling and appearance qualities, 150 g rice grains were dehulled into milled rice through a dehusker (SY88-TH, Sangyong, Korea), and the brown rice was polished into milled rice through a Pearlest mill (Kett, Tokyo, Japan). After that, 30 g of milled rice was collected and scanned (SC-E, Wanshen, Hangzhou, China) to measure the chalky rice percentage, chalky area, and chalky degree.

Representative milled rice grains were oven-dried at 60 °C until constant weight and ground with a stainless steel grinder for determining the cooking and eating quality and nutritional quality. The amylose content was determined following the iodine colorimetric method [34]. The gel consistency of the rice paste (4.4% $w/v$) was determined by measuring the length of the cold gel in the culture tube after placing it horizontally for 1 h. The overall palatability was evaluated by a rice taste analyzer (STA1A, Satake, Japan). The pasting properties of rice flour were determined using a rapid visco-analyzer (RVA-3D, Newport Scientific, Sydney, Australia). The peak viscosity, hot viscosity, and cool viscosity in centipoise (cP) units and the derivative parameters breakdown and setback were recorded with the software of Thermal Cline for Windows.

The protein content was determined by the Infratec 1241 automatic analyzer (Foss, Copenhagen, Denmark). Grain protein compositions were extracted following the method of Tran et al. [35]. Distilled water, 0.06 mol $L^{-1}$ NaCl solution, 80% ethanol solution, and 0.04 mol $L^{-1}$ NaOH solution were successively applied to extract different protein compositions. Then, the content of each protein composition was measured through the Coomassie brilliant blue method [36].

### *2.3. Statistical Analysis*

The data were processed using analysis of variance (ANOVA) with the least significant difference. The ANOVA showed that there were no differences ($p > 0.05$) in the grain yield and the related agronomic and physiochemical traits among three cultivars in the same cultivar type, and the data in the same cultivar type were presented as the means of three cultivars. The means were tested by the least significant difference at $p = 0.05$ ($LSD_{0.05}$). Additionally, Pearson's correlation analysis was used to analyze the correlations between the determined agronomic and physiochemical traits and the grain yield and overall palatability of the rice.

## 3. Results

### *3.1. Grain Yield, Overall Palatability, and Yield Components*

There was no significant difference in grain yield between the HYGP and HYPP, which were 18.1–20.7% higher ($p < 0.05$) than that of LYGP. The overall palatability of HYGP ranged from 76.0 to 77.9 (averaged 77.0) across two years, similarly to LYGP. HYGP and LYGP both exhibited higher ($p < 0.05$) overall palatability than HYPP. There existed differences ($p < 0.01$) in the yield components among cultivar types. HYGP and LYGP showed similar panicles per $m^2$ and were both higher ($p < 0.05$) than that of HYPP. The spikelets per panicle of HYPP were the highest, followed by those of HYGP and LYGP, respectively. HYGP and HYPP had higher ($p < 0.05$) spikelets per $m^2$ but a lower ($p < 0.05$) filled-grain percentage than LYGP. Generally, HYGP and LYGP exhibited lower 1000-grain weights than HYPP (Table 2).

**Table 2.** Grain yield, overall palatability, and yield components of rice cultivar types.

| Year | Cultivar Type | Grain Yield (t $ha^{-1}$) | Overall Palatability | Panicles per $m^2$ | Spikelets per Panicle | Spikelets per $m^2$ | Filled-Grain Percentage (%) | 1000-Grain Weight (g) |
|---|---|---|---|---|---|---|---|---|
| 2018 | HYGP | 9.9 a | 76.0 a | 328 a | 134 b | 43.7 a | 90.8 b | 25.8 b |
| | HYPP | 9.8 a | 61.1 b | 286 b | 150 a | 42.9 a | 91.6 b | 27.3 a |
| | LYGP | 8.2 b | 74.7 a | 331 a | 112 c | 36.9 b | 92.9 a | 25.1 c |

**Table 2.** *Cont.*

| Year | Cultivar Type | Grain Yield (t ha$^{-1}$) | Overall Palatability | Panicles per m$^2$ | Spikelets per Panicle | Spikelets per m$^2$ | Filled-Grain Percentage (%) | 1000-Grain Weight (g) |
|---|---|---|---|---|---|---|---|---|
| 2019 | HYGP | 9.8 a | 77.9 a | 333 a | 133 b | 44.2 a | 91.8 b | 25.4 b |
| | HYPP | 9.9 a | 56.9 b | 285 b | 149 a | 42.2 ab | 91.2 b | 27.6 a |
| | LYGP | 8.3 b | 75.6 a | 334 a | 111 c | 36.8 b | 92.9 a | 25.3 b |
| Analysis of variance (ANOVA) | | | | | | | | |
| Year | | ns | ns | ns | ns | ns | ns | ns |
| Cultivar type | | ** | ** | ** | ** | ** | ** | ** |
| Year × Cultivar type | | ns | ns | ns | ns | ns | ** | * |

HYGP, high-yielding rice with good palatability; HYPP, high-yielding rice with poor palatability; LYGP, low-yielding rice with good palatability. Values in the same year and the same column followed by different lowercase letters are significantly different at the $p < 0.05$ level. In the ANOVA: ns, not significant at the $p < 0.05$ level; *, significant at the $p < 0.05$ level; **, significant at the $p < 0.01$ level.

### 3.2. Shoot Biomass, Harvest Index, N Accumulation, and LAI

There existed differences ($p < 0.01$) in the shoot biomass weight at the main stages, as well as in the shoot biomass accumulation and harvest index, among the cultivar types. HYGP and HYPP showed similar shoot biomass weights at jointing and heading and similar biomass accumulation from jointing to heading, which were higher ($p < 0.05$) than those of LYGP. HYGP had the highest shoot biomass weight at maturity and biomass accumulation from heading to maturity, followed by HYPP and LYGP, respectively ($p < 0.05$). The harvest indexes of HYGP and LYGP were similar and lower ($p < 0.05$) than that of HYPP (Table 3).

**Table 3.** Shoot biomass weight and accumulation and harvest index of rice cultivar types.

| Year | Cultivar Type | Shoot Biomass Weight (t ha$^{-1}$) | | | Shoot Biomass Accumulation (t ha$^{-1}$) | | Harvest Index |
|---|---|---|---|---|---|---|---|
| | | Jointing | Heading | Maturity | Jointing-Heading | Heading-Maturity | |
| 2018 | HYGP | 4.2 ab | 10.8 a | 17.7 a | 6.6 a | 6.9 a | 0.48 b |
| | HYPP | 4.5 a | 10.6 a | 16.6 b | 6.1 b | 6.0 b | 0.51 a |
| | LYGP | 3.7 b | 9.1 b | 14.7 c | 5.4 c | 5.6 c | 0.48 b |
| 2019 | HYGP | 4.3 ab | 10.7 a | 17.5 a | 6.4 a | 6.8 a | 0.48 b |
| | HYPP | 4.6 a | 10.7 a | 16.8 b | 6.1 a | 6.1 b | 0.51 a |
| | LYGP | 3.7 b | 9.2 b | 14.7 c | 5.5 b | 5.5 c | 0.49 b |
| Analysis of variance (ANOVA) | | | | | | | |
| Year | | ns | ns | ns | ns | ns | ns |
| Cultivar type | | ** | ** | ** | ** | ** | ** |
| Year × Cultivar type | | ns | ns | ns | * | ns | ns |

HYGP, high-yielding rice with good palatability; HYPP, high-yielding rice with poor palatability; LYGP, low-yielding rice with good palatability. Values in the same year and the same column followed by different lowercase letters are significantly different at the $p < 0.05$ level. In the ANOVA: ns, not significant at the $p < 0.05$ level; *, significant at the $p < 0.05$ level; **, significant at the $p < 0.01$ level.

The differences in the N accumulation at jointing, heading, and maturity were significant ($p < 0.05$ or $p < 0.01$) among cultivar types. Compared with LYGP, HYGP and HYPP had a higher ($p < 0.05$) N accumulation at jointing, heading, and maturity. For example, the N accumulation at maturity (kg ha$^{-1}$) of HYGP averaged 205 across two years and was 18.8% higher than that of LYGP. The N concentration at maturity in leaves and panicles differed significantly ($p < 0.01$) among cultivar types. Compared with HYPP, HYGP and LYGP showed higher leaf N concentrations at maturity and lower ($p < 0.05$) panicle N concentrations at maturity (Table 4).

**Table 4.** N accumulation at the main growth stages and plant N concentration at the maturity of rice cultivar types.

| Year | Cultivar Type | N Accumulation (kg ha$^{-1}$) | | | N Concentration at Maturity (%) | | |
|---|---|---|---|---|---|---|---|
| | | Jointing | Heading | Maturity | Stem | Leaf | Panicle |
| 2018 | HYGP | 92 a | 175 a | 205 a | 0.87 a | 1.2 a | 1.1 a |
| | HYPP | 98 a | 179 a | 199 a | 0.85 a | 0.9 c | 1.3 b |
| | LYGP | 82 b | 147 b | 173 b | 0.89 a | 1.1 b | 1.1 a |
| 2019 | HYGP | 96 a | 173 a | 205 a | 0.87 a | 1.2 a | 1.1 a |
| | HYPP | 100 a | 173 a | 197 b | 0.84 a | 0.9 b | 1.3 b |
| | LYGP | 80 b | 151 b | 172 c | 0.91 a | 1.1 ab | 1.1 a |
| Analysis of variance (ANOVA) | | | | | | | |
| Year | | ns | ns | ns | ns | ns | ns |
| Cultivar type | | * | ** | ** | ns | ** | ** |
| Year × Cultivar type | | ns | * | ns | ns | ns | ns |

N, nitrogen; HYGP, high-yielding rice with good palatability; HYPP, high-yielding rice with poor palatability; LYGP, low-yielding rice with good palatability. Values in the same year and the same column followed by different lowercase letters are significantly different at the $p < 0.05$ level. In the ANOVA: ns, not significant at the $p < 0.05$ level; *, significant at the $p < 0.05$ level; **, significant at the $p < 0.01$ level.

Generally, HYGP and HYPP both had a higher ($p < 0.05$) LAI at jointing and heading than LYGP. For instance, the LAI at the heading of HYGP was 7.8% higher than that of LYGP in 2019. The LAIs at the maturity of HYPP and LYGP were both lower ($p < 0.05$) than that of HYGP (Figure 2).

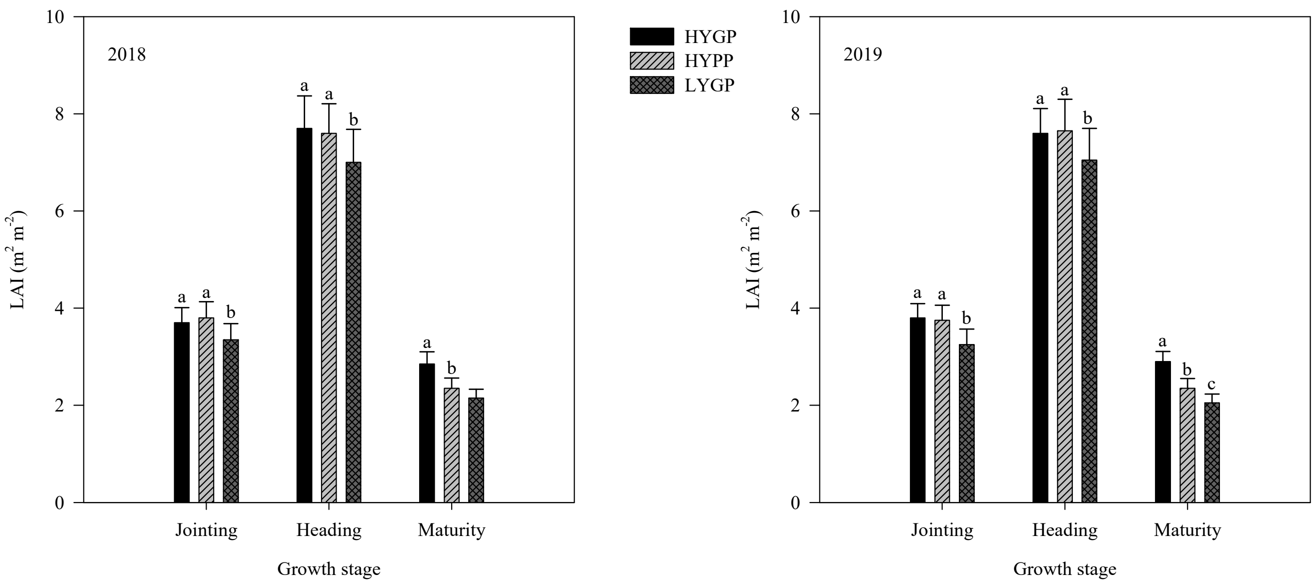


**Figure 2.** LAI at the jointing, heading, and maturity of rice cultivar types. LAI, leaf area index; HYGP, high-yielding rice with good palatability; HYPP, high-yielding rice with poor palatability; LYGP, low-yielding rice with good palatability. Different lowercase letters in the same growth stage above the histogram indicate statistical significance at the $p < 0.05$ level.

### *3.3. Leaf Photosynthetic Rate, SPAD Values, and Enzymatic Activities*

No consistent trends were detected in the flag leaf photosynthetic rate and SPAD values across the top three leaves at EGS among the three cultivar types in both years. HYGP exhibited a higher ($p < 0.05$) flag leaf photosynthetic rate at MGS and LGS than HYPP and LYGP. For instance, the flag leaf photosynthetic rate at the MGS of HYGP was 14.7% and 17.0% higher than those of HYPP and LYGP, respectively. Similarly, HYGP had higher ($p < 0.05$) SPAD values across the top three leaves at MGS and LGS compared with HYPP and LYGP (Figure 3).

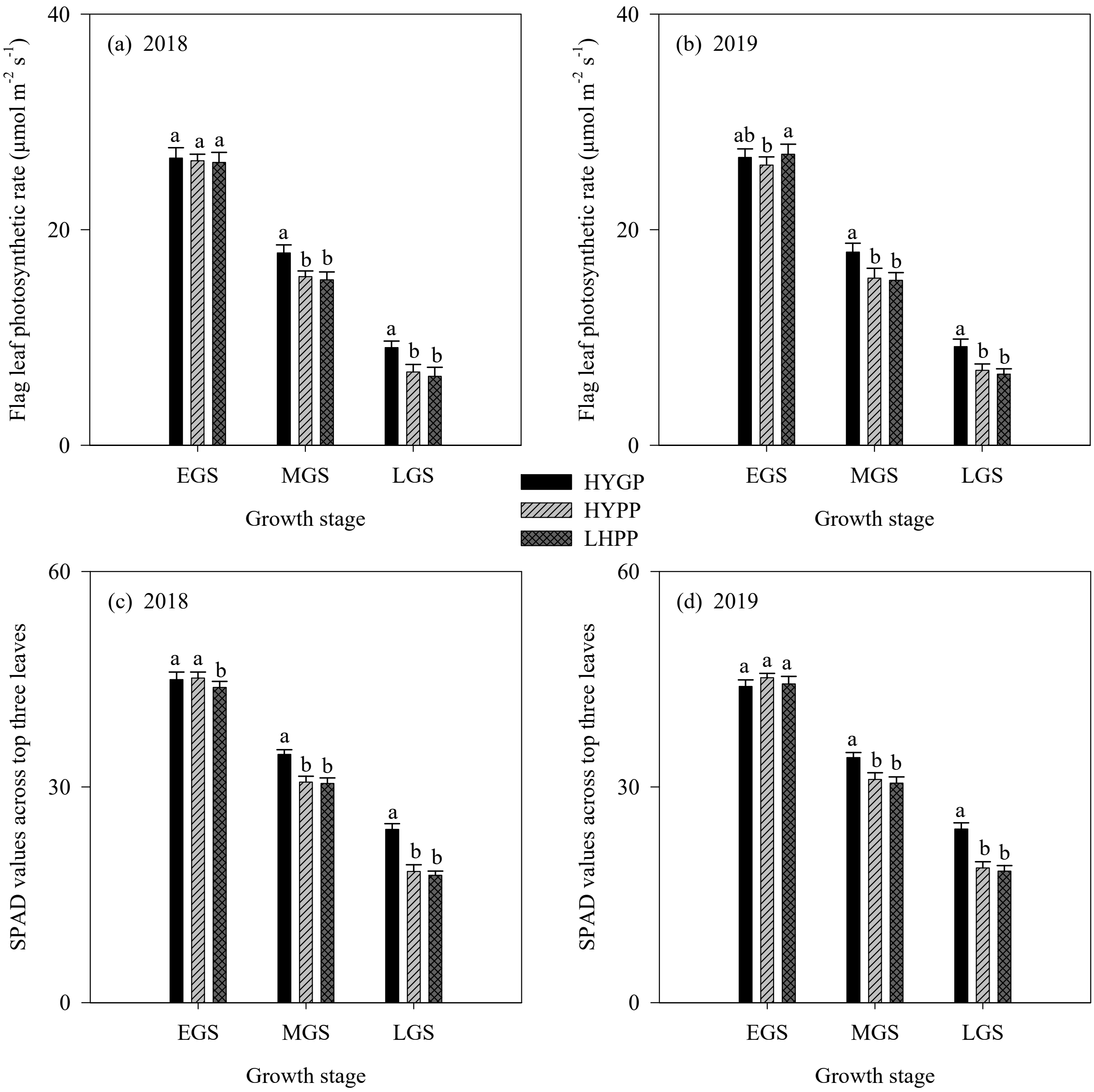


**Figure 3.** Flag leaf photosynthetic rate (**a**,**b**) and SPAD values across the top three leaves (**c**,**d**) after the heading of rice cultivar types. HYGP, high-yielding rice with good palatability; HYPP, high-yielding rice with poor palatability; LYGP, low-yielding rice with good palatability; EGS, early grain-filling stage; MGS, middle grain-filling stage; LGS, late grain-filling stage. Different lowercase letters in the same growth stage above the histogram indicate statistical significance at the $p < 0.05$ level.

HYGP had higher ($p < 0.05$) AGP and SBE activities at EGS than HYPP and LYGP. HYGP showed higher ($p < 0.05$) AGP activity at MGS and LGS than HYPP and LYGP. Compared with HYPP and LYGP, HYGP exhibited higher ($p < 0.05$) SBE activity at MGS and LGS (Figure 4). Generally, the trends in the SSS and GBSS activities among the three cultivar types were not consistent at the two study years (Figure 5).

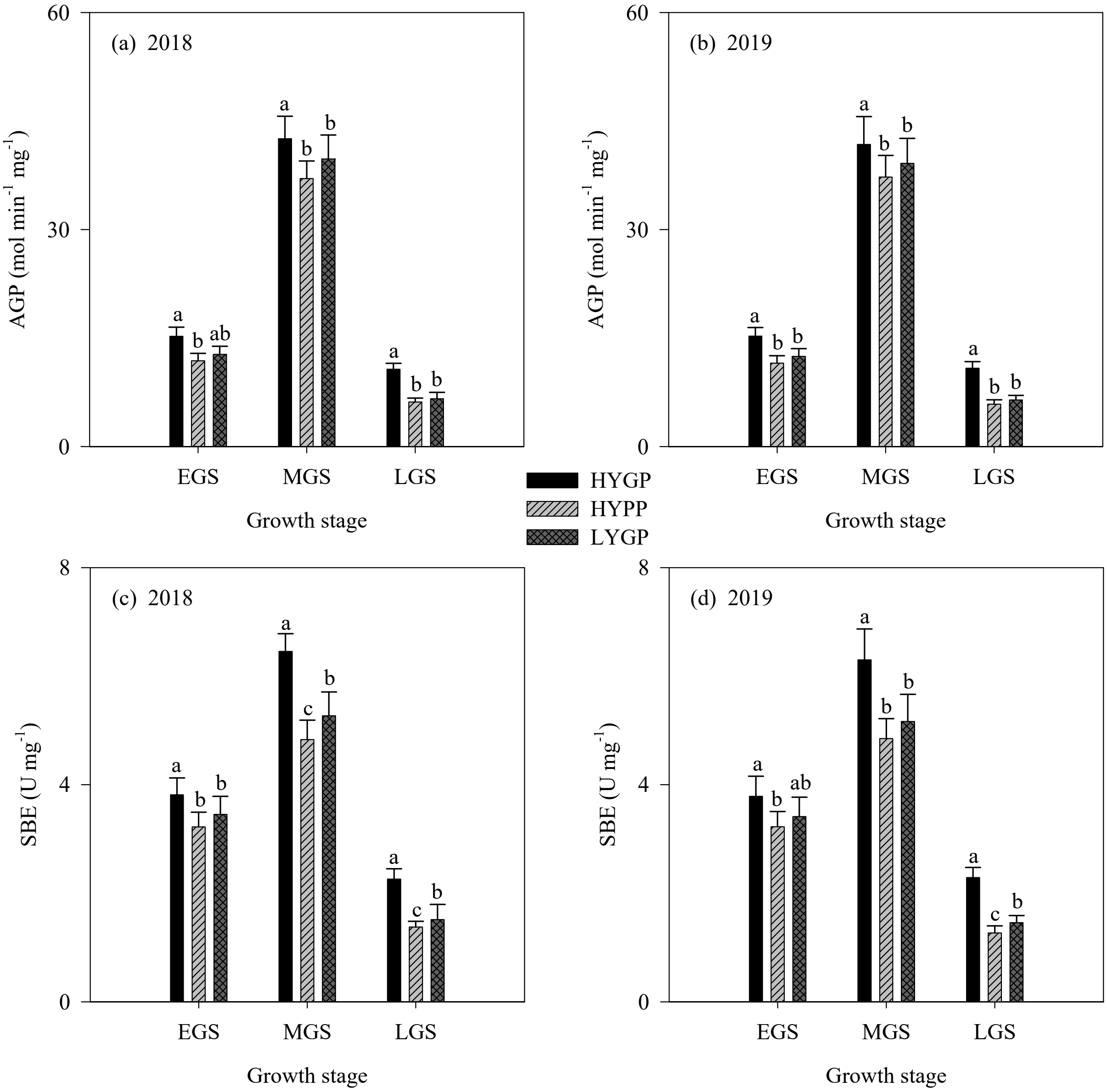


**Figure 4.** AGP (**a**,**b**) and SBE (**c**,**d**) activities in the grains after the heading of rice cultivar types. AGP, adenosine diphosphate glucose pyrophosphorylase; SBE, starch branching enzyme; HYGP, high-yielding rice with good palatability; HYPP, high-yielding rice with poor palatability; LYGP, low-yielding rice with good palatability; EGS, early grain-filling stage; MGS, middle grain-filling stage; LGS, late grain-filling stage. Different lowercase letters in the same growth stage above the histogram indicate statistical significance at the $p < 0.05$ level.

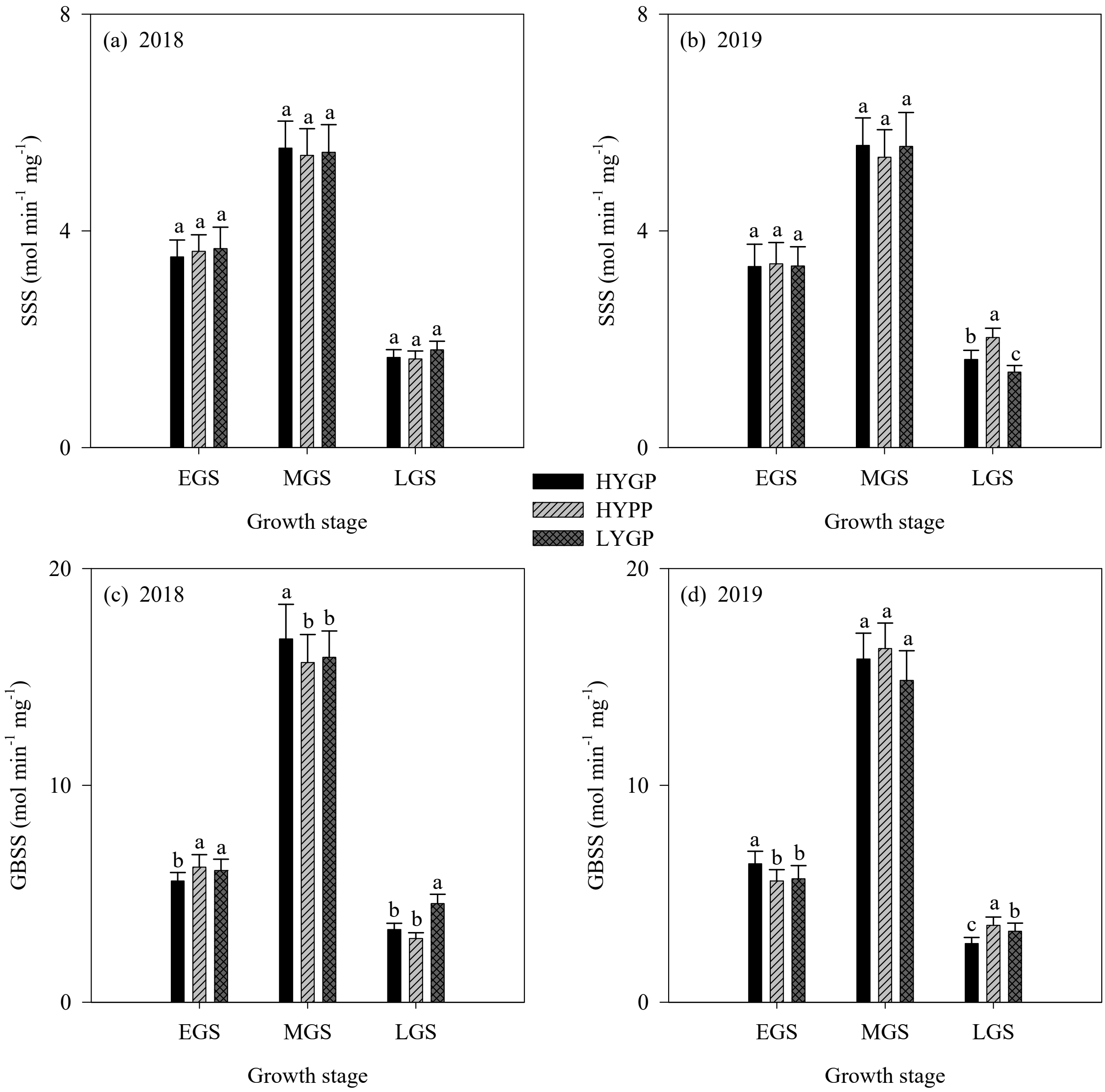


**Figure 5.** SSS (**a**,**b**) and GBSS (**c**,**d**) activities in grains after the heading of rice cultivar types. SSS, soluble starch synthase; GBSS, granule bound starch synthetase; HYGP, high-yielding rice with good palatability; HYPP, high-yielding rice with poor palatability; LYGP, low-yielding rice with good palatability; EGS, early grain-filling stage; MGS, middle grain-filling stage; LGS, late grain-filling stage. Different lowercase letters in the same growth stage above the histogram indicate statistical significance at the $p < 0.05$ level.

### *3.4. Milling, Appearance, Nutritional Qualities, and RVA*

There existed differences ($p < 0.01$) in the appearance quality among the three cultivar types, but not for milling quality. HYGP showed a similar chalky rice percentage to HYPP, while it was higher ($p < 0.05$) than that of LYGP. HYGP and LYGP had lower ($p < 0.05$) chalky areas than HYPP. The chalky degree of HYPP was the highest, followed by HYGP and LYGP, respectively. The chalky rice percentage and chalky degree also differed ($p < 0.01$ or $p < 0.05$) between the two study years; the chalky rice percentage and chalky degree of rice were higher in 2018 than in 2019 (Table 5).

**Table 5.** Milling and appearance qualities of rice cultivar types.

| Year | Cultivar Type | Milling Quality | | | Appearance Quality | | |
|---|---|---|---|---|---|---|---|
| | | Brown Rice Percentage (%) | Milled Rice Percentage (%) | Head Rice Percentage (%) | Chalky Rice Percentage (%) | Chalky Area (%) | Chalky Degree (%) |
| 2018 | HYGP | 83.9 a | 71.7 a | 70.6 a | 32.8 a | 21.2 b | 6.9 b |
| | HYPP | 83.0 a | 70.0 b | 69.4 b | 31.1 ab | 25.1 a | 7.8 a |
| | LYGP | 83.5 a | 71.4 a | 69.1 b | 28.6 b | 20.9 b | 6.0 c |
| 2019 | HYGP | 83.5 a | 71.6 a | 70.8 a | 29.6 a | 21.0 b | 6.2 b |
| | HYPP | 82.7 b | 70.7 a | 70.2 a | 29.7 a | 26.0 a | 7.7 a |
| | LYGP | 83.4 a | 71.8 a | 70.7 a | 27.4 b | 20.9 b | 5.7 c |
| Analysis of variance (ANOVA) | | | | | | | |
| Year | | ns | ns | * | ** | ns | * |
| Cultivar type | | ns | ns | ns | ** | ** | ** |
| Year × Cultivar type | | ns | ns | * | ns | ns | ns |

HYGP, high-yielding rice with good palatability; HYPP, high-yielding rice with poor palatability; LYGP, low-yielding rice with good palatability. Values in the same year and the same column followed by different lowercase letters are significantly different at the $p < 0.05$ level. In the ANOVA: ns, not significant at the $p < 0.05$ level; *, significant at the $p < 0.05$ level; **, significant at the $p < 0.01$ level.

The amylose content, gel consistency, and RVA spectrum characteristics were affected ($p < 0.01$) by the cultivar type, while the cool viscosity was also affected ($p < 0.01$) by the year. HYGP and LYGP had lower ($p < 0.05$) amylose contents and higher ($p < 0.05$) gel consistency contents than HYPP. For example, the gel consistency (mm) of HYGP was 76.1 and 24.8% higher than that of HYPP. The cultivar types differed significantly ($p < 0.01$) in terms of RVA spectrum characteristics. HYGP and LYGP had higher peak viscosities and hot viscosities than HYPP. There was not a consistent trend in the cool viscosity among the three cultivar types. HYGP and LYGP exhibited a higher ($p < 0.05$) breakdown and a lower ($p < 0.05$) setback than HYPP (Table 6).

**Table 6.** Amylose content, gel consistency, and RVA spectrum characteristics of rice cultivar types.

| Year | Cultivar Type | Amylose Content (%) | Gel Consistency (mm) | Peak Viscosity (cP) | Hot Viscosity (cP) | Cool Viscosity (cP) | Breakdown (cP) | Setback (cP) |
|---|---|---|---|---|---|---|---|---|
| 2018 | HYGP | 13.2 b | 75.7 a | 2936 a | 2039 a | 2514 b | 897 a | −422 b |
| | HYPP | 15.0 a | 60.5 b | 2287 b | 1855 b | 2320 a | 432 b | 33 a |
| | LYGP | 12.8 b | 73.7 a | 2817 a | 1951 ab | 2450 c | 866 a | −367 b |
| 2019 | HYGP | 12.9 b | 76.4 a | 2970 a | 2001 a | 2487 b | 969 a | −483 b |
| | HYPP | 15.2 a | 61.5 b | 2391 b | 1904 b | 2425 b | 487 b | 34 a |
| | LYGP | 13.3 b | 73.8 a | 2897 a | 2081 a | 2548 a | 816 a | −349 b |
| Analysis of variance (ANOVA) | | | | | | | | |
| Year | | ns | ns | ns | ns | ** | ns | ns |
| Cultivar type | | ** | ** | ** | ** | ** | ** | ** |
| Year × Cultivar type | | ns | ns | ns | * | * | ns | ns |

HYGP, high-yielding rice with good palatability; HYPP, high-yielding rice with poor palatability; LYGP, low-yielding rice with good palatability; cP, centipoise. Values in the same year and the same column followed by different lowercase letters are significantly different at the $p < 0.05$ level. In the ANOVA: ns, not significant at the $p < 0.05$ level; *, significant at the $p < 0.05$ level; **, significant at the $p < 0.01$ level.

HYGP and LYGP showed similar protein contents, both lower ($p < 0.05$) than that of HYPP. Differences ($p < 0.01$ or $p < 0.05$) in the albumin and glutelin contents existed among the years, cultivar types, and their interactions, while the prolamin contents differed ($p < 0.01$) among the cultivar types. There were no consistent trends in the albumin, globulin, and glutelin contents among the three cultivar types. HYGP and LYGP showed lower ($p < 0.05$) prolamin contents than HYPP. The ratios of the glutelin content to the prolamin content for HYGP and LYGP were similar and higher than that of HYPP (Table 7).

**Table 7.** Protein content and its composition of rice cultivar types.

| Year | Cultivar Type | Protein Content (%) | Albumin Content (%) | Globulin Content (%) | Prolamin Content (%) | Glutelin Content (%) | Ratio of Glutelin Content to Prolamin Content |
|---|---|---|---|---|---|---|---|
| 2018 | HYGP | 8.1 b | 0.68 a | 0.91 a | 0.93 b | 7.5 a | 8.0 a |
| | HYPP | 9.8 a | 0.71 a | 0.93 a | 0.99 a | 7.4 a | 7.4 b |
| | LYGP | 8.2 b | 0.70 a | 0.92 a | 0.95 b | 7.5 a | 7.8 a |
| 2019 | HYGP | 8.3 b | 0.67 b | 0.91 a | 0.91 b | 7.2 a | 8.0 a |
| | HYPP | 9.7 a | 0.65 b | 0.96 a | 0.97 a | 7.2 a | 7.5 b |
| | LYGP | 8.3 b | 0.71 a | 0.93 a | 0.90 b | 7.1 a | 7.9 a |
| Analysis of variance (ANOVA) | | | | | | | |
| Year | | ns | ** | ns | ns | ** | ns |
| Cultivar type | | ** | * | ns | ** | ** | ** |
| Year × Cultivar type | | * | * | ns | ns | * | ns |

HYGP, high-yielding rice with good palatability; HYPP, high-yielding rice with poor palatability; LYGP, low-yielding rice with good palatability. Values in the same year and the same column followed by different lowercase letters are significantly different at the $p < 0.05$ level. In the ANOVA: ns, not significant at the $p < 0.05$ level; *, significant at the $p < 0.05$ level; **, significant at the $p < 0.01$ level.

### *3.5. Correlation Analysis*

The determined agronomic and physiochemical traits greatly affected the rice grain yield and overall palatability. The panicles per $m^2$, shoot biomass accumulation from heading to maturity, leaf N concentration at maturity, and AGP and SBE activities at MGS and LGS were all positively ($p < 0.01$ or $p < 0.05$) correlated with the grain yield and overall palatability. The spikelets per panicle, 1000-grain weight, and amylose content were positively ($p < 0.01$) correlated with the grain yield and negatively ($p < 0.01$) correlated with the overall palatability. The breakdown and the ratio of glutelin content to prolamin content were positively ($p < 0.01$) correlated with the overall palatability, while the harvest index, panicle N concentration at maturity, chalky degree, setback, protein content, and prolamin content were negatively ($p < 0.01$) correlated with the overall palatability (Table 8).

**Table 8.** Pearson's correlation coefficients between the determined agronomic and physiochemical traits and the grain yield and overall palatability of the rice.

| Determined Parameters | Grain Yield | Overall Palatability |
|---|---|---|
| Panicles per $m^2$ | 0.63 ** | 0.79 ** |
| Spikelets per panicle | 0.89 ** | −0.75 ** |
| 1000-grain weight | 0.67 ** | −0.92 ** |
| Shoot biomass weight at maturity | 0.85 ** | −0.31 |
| Shoot biomass accumulation from heading to maturity | 0.77 ** | 0.62 ** |
| Harvest index | 0.42 | −0.79 ** |
| Leaf N concentration at maturity | 0.49 * | 0.86 ** |
| Panicle N concentration at maturity | 0.25 | −0.67 ** |
| LAI at maturity | 0.73 ** | 0.72 ** |
| AGP activity at MGS | 0.56 * | 0.48 * |
| AGP activity at LGS | 0.62 ** | 0.54 * |
| SBE activity at MGS | 0.55 * | 0.64 ** |
| SBE activity at LGS | 0.57 * | 0.51 * |
| Chalky area | 0.41 | −0.69 ** |
| Chalky degree | 0.37 | −0.86 ** |
| Amylose content | 0.60 ** | −0.77 ** |
| Gel consistency | −0.27 | 0.79 ** |
| Breakdown | −0.32 | 0.87 ** |
| Setback | 0.36 | −0.85 ** |

**Table 8.** *Cont.*

| Determined Parameters | Grain Yield | Overall Palatability |
|---|---|---|
| Protein content | 0.45 | −0.89 ** |
| Prolamin content | 0.19 | −0.70 ** |
| Ratio of glutelin content to prolamin content | −0.28 | 0.86 ** |

N, nitrogen; LAI, leaf area index; AGP, adenosine diphosphate glucose pyrophosphorylase; MGS, middle grain-filling stage; LGS, late grain-filling stage; SBE, starch branching enzyme; *, significant at the $p < 0.05$ level; **, significant at the $p < 0.01$ level.

## 4. Discussion

For rice, cooking and eating quality was previously evaluated by manual tasting modality, which was easily susceptible to the subjective factors of tasters [37,38]. In this study, the cooking and eating quality of rice was scored by the STA1A taste analyzer, a more objective evaluation of rice cooking and eating quality. The negative correlation between the rice grain yield and the cooking and eating quality was widely reported in the existing literature [39–42]. For example, Chen et al. [39] observed that rice with a higher yield performance often produced the poor palatability of cooked grains in late-season cropping systems in central China. Over recent years, special attention has been paid to grain quality, particularly cooking and eating quality in breeding programs in China, in addition to grain yield; such a breeding target was achieved mainly by lowering the amylose content of grains [7]. Overall, this breeding strategy was proven effective, and rice cultivars with superior grain yield and overall palatability were available in production, such as HYGP in this study. In addition, some studies with similar experimental conditions to our study reported that the overall palatability of HYGP was averaged at approximately 65 [43,44]; such a value was lower than that (>75) in this study (Table 2). The differences might be mainly attributed to the N management; site-specific N management was adopted in this study (255 kg N $ha^{-1}$), while the conventional N application method with a higher rate (300 kg N $ha^{-1}$) was adopted in the studies of Hu et al. [43] and Zhu et al. [44]. These results might indicate a better response of rice cooking and eating quality to N-efficient management [17,32].

Zhang et al. [45] reported that high-yielding rice with improved grain quality always exhibited more panicles per $m^2$ and spikelets per panicle, while it exhibited a smaller grain weight in the Taihu region, east China; the spikelets per panicle were negatively correlated with cooking and eating quality and positively correlated with the grain yield of rice in northeast China [42]. This information suggests that the contribution of yield components to the grain yield and grain quality varied with the experimental conditions and rice cultivars [42,45,46]. In this study, more spikelets per panicle facilitated the higher grain yield of HYGP in comparison with LYGP; HYGP exhibited higher panicles per $m^2$ and lower spikelets per panicle and 1000-grain weight compared with HYPP (Table 2). These results indicate that an optimized yield component is the basis of the superior grain yield and grain quality of rice (Table 8). It is noteworthy that the 1000-grain weights of HYGP and LYGP were both smaller than that of HYPP (Table 2). As previously mentioned, it is effective to develop high-yielding rice with good grain quality through the down-regulation of amylose content by the antisense Waxy gene nowadays in China [7]. Hori et al. [38] and Ni et al. [47] found that such a breeding method would decrease the 1000-grain weight of high-quality rice in breeding practices.

Compared with HYPP and LYGP, HYGP exhibited a higher ($p < 0.05$) shoot biomass weight at maturity and more biomass accumulation from heading to maturity (Table 3), indicating that assimilate production after heading is critical to maintaining grain yield and overall palatability in rice (Table 8). The improved post-heading biomass production of HYGP is supported by the higher LAI after heading and the flag leaf photosynthetic rate and SPAD values across the top three leaves at MGS and LGS in comparison with HYPP and LYGP (Figures 2 and 3). e HYGP exhibited a longer duration from heading to maturity (Table 1), which could promote a sustainable and steady grain-filling process;

such a process is beneficial for filling the grains, especially inferior grains, and improving grain quality [34,48]. It is observed that HYGP and LYGP both had lower ($p < 0.05$) harvest indexes than HYPP, which might be closely associated with the final grain N concentration (Tables 3 and 4). For crops, higher seed (or grain) N concentration caused more translocation of assimilates and N, faster plant senescence, and an increase in the harvest index [49–51]. Here, HYPP had a higher ($p < 0.05$) panicle N concentration at maturity, which would over-stimulate assimilates translocation from the leaf, increase the harvest index, and result in more pronounced reductions in the LAI, leaf photosynthetic rate, SPAD values, and biomass accumulation after heading (Table 3, Figures 2 and 3).

Starch, the main component of rice grains, determines rice grain yield and grain quality properties. For rice, the synthesis of starch is catalyzed by key enzymes, e.g., AGP, GBSS, SSS, and SBE [52]. The relationship between the key enzymes involved in starch synthesis and cooking and eating quality is still not well established. For example, Gong et al. [53] concluded that lower GBSS activity and higher activities of SSS and SBE benefit rice cooking and eating quality, while higher GBSS activity decreases amylose content and improves cooking and eating quality [54]. Herein, HYGP had higher ($p < 0.05$) activities of AGP and SBE at MGS and LGS compared with HYPP and LYGP; there were no clear trends in SSS and GBSS among the three cultivar types (Figures 3 and 4). Our results suggested that higher AGP and SBE activities at the middle and late grain-filling stages were important traits underlying the superior grain yield and overall palatability of HYGP (Table 8).

In China, *japonica* rice was previously reported to exhibit inferior appearance quality relative to *indica* hybrid rice due to the high chalky degree [21,55]. In recent years, great efforts have been made to reduce the chalkiness during the breeding process towards the superior cooking and eating quality of *japonica* rice [7]. In this study, HYGP and LYGP demonstrated a lower ($p < 0.05$) chalky area and chalky degree than HYPP (Table 5); higher grain chalkiness might partially explain the poor palatability of HYPP, as indicated by negative ($p < 0.01$) correlations between the chalky area and chalky degree and the overall palatability (Table 8). These results suggested an improved appearance quality of *japonica* rice with good palatability in east China, consistent with the observations of Gu et al. [17] and Hu et al. [43]. Nonetheless, the chalky degree of HYGP and LYGP is still higher than that in northeast China, a well-known rice production region characterized by superior grain quality [29,30]. Such a comparison suggests that the appearance quality of *japonica* rice in east China may still be improved further. The chalky rice percentage and chalky degree were affected not only by the cultivar type but also by the year; the chalky rice percentage and chalky degree of rice in 2018 were higher than those in 2019 (Table 5). Such a difference might be associated with the climatic factors between the two study years. In our study, the heading dates of the tested cultivars occurred in mid-late August, and the early grain-filling period of rice received more rainfall and fewer hours of sunshine (Figure 1). It was reported that the appearance quality of rice was susceptible to light deficiency stress after heading, especially during the early grain-filling period [56,57].

The level of amylose is a primary factor determining the palatability, digestibility, and end-use of starch during cooking and food processing [38,58]. Our results demonstrated that HYGP and LYGP both exhibited lower ($p < 0.05$) amylose contents than HYPP, which could give soft and sticky cooked grains with good palatability (Tables 6 and 8). Such an improved cooking and eating quality was preferred by people in east China due to their appreciation for soft *japonica* rice [7,21]. RVA spectrum characteristics were identified indicators for assessing rice cooking and eating quality. Generally, the breakdown correlated positively with the gel consistency and stickiness of cooked rice and correlated negatively with its hardness [9,59]. Allahgholipour et al. [25] and Ma et al. [29] concluded that rice cultivars with good grain quality had a higher peak viscosity and breakdown and a lower setback. Our results also demonstrated that, compared with HYPP, HYGP and LYGP had higher ($p < 0.05$) peak viscosities, hot viscosities, and breakdowns and lower setbacks (Table 6); breakdown was positively correlated while setback was negatively correlated

($p < 0.01$) with the overall palatability of rice grains (Table 8). Our results indicated that *japonica* rice with good palatability was characterized by a lower amylose content, a higher breakdown, and a lower setback.

Compared with HYGP and LYGP, HYPP exhibited a higher ($p < 0.05$) grain protein content, which might result from the higher final grain N concentration and another factor for poor palatability (Table 4, Table 7, and Table 8). We observed that the prolamin content and the ratio of glutelin content to prolamin content differed ($p < 0.01$) among the three cultivar types, while the albumin, globulin, and glutelin contents did not. Here, HYGP and LYGP exhibited lower ($p < 0.05$) prolamin contents and higher ($p < 0.05$) glutelin content to prolamin content ratios than HYPP (Table 8), indicating that rice cultivars with lower prolamin contents and higher glutelin content to prolamin content ratios might produce a softer texture and better palatability of cooked grains [9,60].

## 5. Conclusions

HYGP produced a grain yield of 9.9 t $ha^{-1}$ and an overall palatability of over 75; therefore, it could be considered as high yielding rice with superior cooking and eating quality. The yield superiority of HYGP over LYHP was supported by a large sink size through the spikelets per panicle and the greater biomass accumulation after heading through improved leaf photosynthetic capacities. The higher AGP and SBE activities after heading, the lower amylose content and grain protein content, the higher breakdown with a lower setback, and the lower prolamin content with a higher ratio of glutelin content to prolamin content contributed to the better overall palatability of HYGP compared to HYPP. These improved agronomic and physicochemical characteristics underlie the better grain yield and overall palatability of HYGP.

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