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Historical Trends Analysis of Main Agronomic Traits in South China Inbred *Indica* Rice Varieties since Dwarf Breeding

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Abstract: Studying the evolutionary patterns of rice agronomic traits in South China and analyzing the characteristics of rice improvement can provide insights into the developmental trajectory of rice breeding in South China and can guide further enhancement of variety yield. In this study, widely promoted varieties and core parents developed through dwarf breeding in the southern region, as well as landraces, were collected and planted in three different ecological regions. A total of 18 agronomic traits were investigated related to heading date, plant type, panicle type, grain type, and yield, and multiple comparisons, a correlation analysis, and a path analysis were conducted. The results indicate that dwarf breeding has significantly increased the yield of inbred *indica* rice varieties in South China. However, a reduction in plant height has also resulted in a reduction in flag leaf, shorter panicles, and decreased biomass, which have led to metabolic source and storage capacity deficiencies and limited yield potential. To address these limitations, breeders have employed strategies such as increasing flag leaf width, spikelet density, number of primary branches, and grain number per panicle. These measures have led to a gradual increase in yield. Additionally, starting from the 1980s, high-quality rice breeding has been pursued in South China, resulting in slender grain shape and reduced thousand grain weight. Given that total grain number per panicle has already increased significantly and the thousand grain weight cannot be reduced further, enhancing the effective tiller number, which decreases year by year, becomes an important approach to increasing the yield of inbred *indica* rice varieties in South China.

Keywords: South China; inbred *indica* rice; heading date; yield; plant type; trait evolution

1. Introduction

Rice serves as a staple food for more than 60% of China's population, making it an essential dietary component. Remarkably, rice accounts for nearly 40% of the nation's total calorie intake [1]. The rice region of South China is located at the southernmost part of China and is one of the main rice-producing regions in the country. Fluctuations in rice production within this region have a significant impact on China's overall rice output. Due to its tropical and subtropical monsoon climate, this region in South China is frequently affected by typhoons. Since the 1950s, the Rice Research Institute, Guangdong Academy of Agricultural Sciences has pioneered the development of dwarf rice breeding by utilizing dwarfing genes, and thus has initiated the first "Green Revolution" [2,3]. With the promotion of dwarf varieties and extensive use of fertilizers, China's rice yield per unit area has nearly doubled from 1961 to 2006. However, in recent years, rice production has remained stagnant or even shown a negative growth trend [4].

There is a significant correlation between many agronomic traits and rice yield, and improving yield-related agronomic traits is an important approach for enhancing productivity [5,6]. Different ecological regions display variations in critical agronomic traits that constrain rice yield potential, and the emphasis on genetic enhancement of these agronomic traits also diverges accordingly. To establish a breeding theory for ideal plant type, rice breeders have proposed numerous models based on the ecological characteristics of different regions. These models have included the compact plant type with large panicles from the International Rice Research Institute (IRRI); the short and erect plant type of temperate *japonica* rice in northern China; the high canopy and short panicle type in the middle and lower reaches of the Yangtze river; the post-functional ideal plant type in eastern China; the heavy panicle type between subspecies in southwestern China; and the "semi-dwarf, early-maturing, deep-rooted, and super-high-yielding (special) superior breeding" plant type in the double-cropping rice region of South China [7–12].

Since dwarf breeding in the 1950s, there have been four notable variety iterations in inbred *indica* rice varieties in the South China, each having a significant impact on rice production in the region. The continuous upgrading and improvement of traits such as plant architecture and panicle type have been one of the important factors driving variety iterations [13]. Conducting systematic research on the evolution of key agronomic traits in rice varieties developed during different periods can provide insights into the breeding trajectory in South China and can serve as a theoretical basis for further advancements in rice breeding. Some studies have reported on the evolution of agronomic traits during the process of variety replacement in rice, both domestically and internationally [14–18]. However, there is a lack of research that has specifically focused on the evolution of important breeding traits in rice within a particular ecological region. Cheng et al. reported on the evolution of agronomic traits during the replacement of *indica* rice varieties in the southern region of China from the 1950s to the early 1980s [19]. Liu et al. conducted a study on the evolution of yield and plant type characteristics using 65 widely promoted inbred *indica* rice varieties developed in the southern region of China from dwarf breeding until 2005 [20]. However, the existing research has limited quantities of experimental materials, lacks representativeness, and is also lacking in studies related to heading date under different environments and grain sizes. Additionally, there is still a lack of research on the evolution of characteristics between tall stalk landraces and the dwarf varieties of different generations.

Therefore, in this experiment, we collected extensively adopted varieties and core parents spanning over 60 years of dwarf breeding history in the rice region of South China rice. We also used 36 landraces as a control. A total of 231 samples of inbred *indica* rice from South China were used as experimental materials. By analyzing the significant differences in the mean values of 18 agronomic traits, including heading date, plant type, panicle type, grain type, and yield components, among varieties from different time periods, along with the execution of correlation and path analyses for the traits among different generations of varieties, we clarified the components and changes that influence yield. Based on this, we explored the main factors affecting rice yield in South China, providing a theoretical foundation for the development direction of rice breeding for plant type in this area. The research results are very significant with respect to guiding further improvements in rice yield.

2. Materials and Methods

2.1. Rice Materials

For this experiment, a total of 195 inbred *indica* varieties (Figure 1A) that have been extensively promoted in production were selected from rice cultivation areas in South China, spanning from the 1960s to the present. The cultivars included widely cultivated varieties as well as important parental lines. Additionally, 40 cultivars derived directly from South China rice and bred in other rice-growing regions such as Hunan, Hubei, Jiangxi, and Anhui were also included. Based on the year of cultivar development, the materials were divided into six breeding stages: 1960s (28 cultivars), 1970s (27 cultivars), 1980s (40 cultivars), 1990s (41 cultivars), and modern varieties developed after the year 2000 (59 cultivars). Additionally, 36 landraces were selected as controls (Figure 1B). In total, there were 231 accessions used for the study.

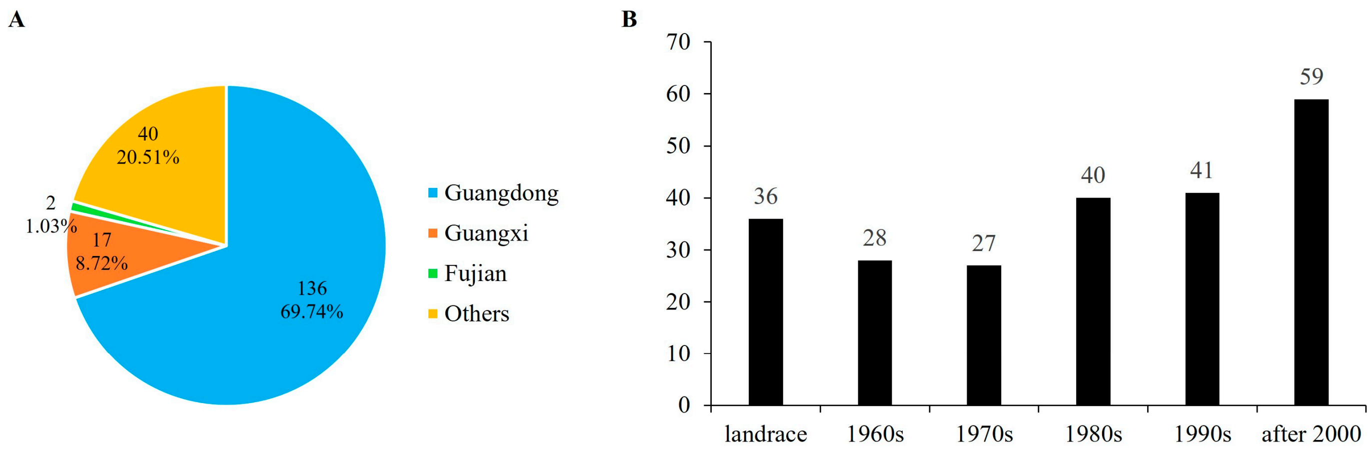

Figure 1. Sources and distribution of varieties in different ages in South China: (**A**) Sources of varieties; (**B**) quantity distribution of varieties in different ages.

2.2. Field Experiments

The field trials were conducted across three distinct locations: the Agricultural Science Research Institute in Pingxiang, Jiangxi Province (27.6° N, 113.8° E); the Institute of Agricultural Genomics at Shenzhen, the Chinese Academy of Agricultural Sciences, Guangdong Province (22.6° N, 114.1° E); and the Nanbin Experimental Station of the Crop Science Research Institute, Chinese Academy of Agricultural Sciences, in Sanya, Hainan Province (18.3° N, 109.3° E). A completely randomized block design was adopted, with three replicates. Each variety was planted in three rows, and each row consisted of eight plants with a spacing of 20 cm × 25 cm.

The three locations represented three different ecological regions based on different growing seasons. Pingxiang is in a subtropical humid monsoon climate zone, Shenzhen has a subtropical monsoon climate, while Sanya has a tropical oceanic monsoon climate. The sowing date at the Pingxiang experimental site was 31 May 2017, representing mid-season rice; the sowing date at the Shenzhen experimental site was 12 July 2017, representing late-season rice; and the sowing date at the Sanya experimental site was 3 December 2017, representing winter cropping. The temperature and precipitation conditions during vegetation of the rice panel can clearly distinguish the three ecological regions (Table S1). Field management practices followed local conventional practices.

2.3. Phenotypic Investigation

Before conducting the phenotypic assessment, weak and diseased plants were removed. To avoid marginal effects, four individual plants were selected with the same growth in the middle of each row. The following traits were investigated: heading days (HD, 50% of individuals within the plot exhibiting heading); plant height (PH); flag leaf length (FLL); flag leaf width (FLW); flag leaf area (FLA, calculated as flag leaf length × flag leaf width × 0.7); and effective tiller number per plant (ETN). After maturity, the above-ground portion of each plant was harvested, dried, and measured for individual biomass and grain yield per plant (GY). The harvest index (H-index) was calculated as (grain yield per plant/biomass per plant) × 100%. Other traits examined included panicle length (PL); number of primary branches per panicle (NPB); total grain number per panicle (GNP); filled grain number per panicle (FGNP); grain density (GD, calculated as total spikelet number per panicle/panicle length); thousand grain weight (TGW); grain length (GL); grain width (GW); and length-to-width ratio (LWR). The GNP, TGW, GL, GW, and LWR were determined using a Wanshen SC-G automatic seed analyzer and a thousand grain weight analyzer.

2.4. Statistical Analysis

The data for agronomic traits were collected from 12 plants per variety. Multiple replicates of the mean values for each trait were subjected to a statistical analysis. The data in the main text are presented as phenotypic averages for all varieties at this stage, and the standard deviations (SDs) are calculated and listed in the supplementary tables. Duncan's multiple range tests were employed to determine significant differences. A correlation analysis was performed to explore the relationships among various agronomic traits. The results were deemed statistically significant when $p < 0.05$ (*) and extremely significant when $p < 0.01$ (**). A path analysis was conducted to examine the direct and indirect effects of other traits on the grain yield per plant. The data were organized using Microsoft Office Excel 2016 (Redmond, WA, USA), and the software SPSS 19.0 (Chicago, IL, USA) was used for data statistical analysis.

3. Results

3.1. Performance of Agronomic Traits of Inbred Indica Rice under Different Environments in South China

3.1.1. Heading Date

From the frequency distribution of heading days (HD) in the three environments (Figure 2), it can be observed that the frequency distribution of heading days for landraces and varieties in the 1960s and 1970s was the most complex, showing the widest range. When the rice panel was cultivated in Pingxiang as mid-season rice, the distribution of HD was the most dispersed, while the varieties developed in the 1980s and later exhibited a more concentrated distribution of HD. The frequency distribution range for varieties developed after 2000 was the smallest, with a difference of only 10–19 days across the three ecological regions (Table S2). When cultivated in Pingxiang, there were no significant differences for the HD of varieties from different decades. When the rice panel was cultivated in Shenzhen as late-season rice, the average HD ranged from 63.5 to 66.6 days, which was the shortest among the three environments. When the rice panel was planted in Sanya during winter, there was an increasing trend in HD among decades, with the longest average HD ranging from 89.6 to 100.7 days. The different patterns of HD dynamics in Pingxiang, Shenzhen, and Sanya may be explained by the different light and temperature conditions in these locations, considering the planting season and latitude of the trial sites.

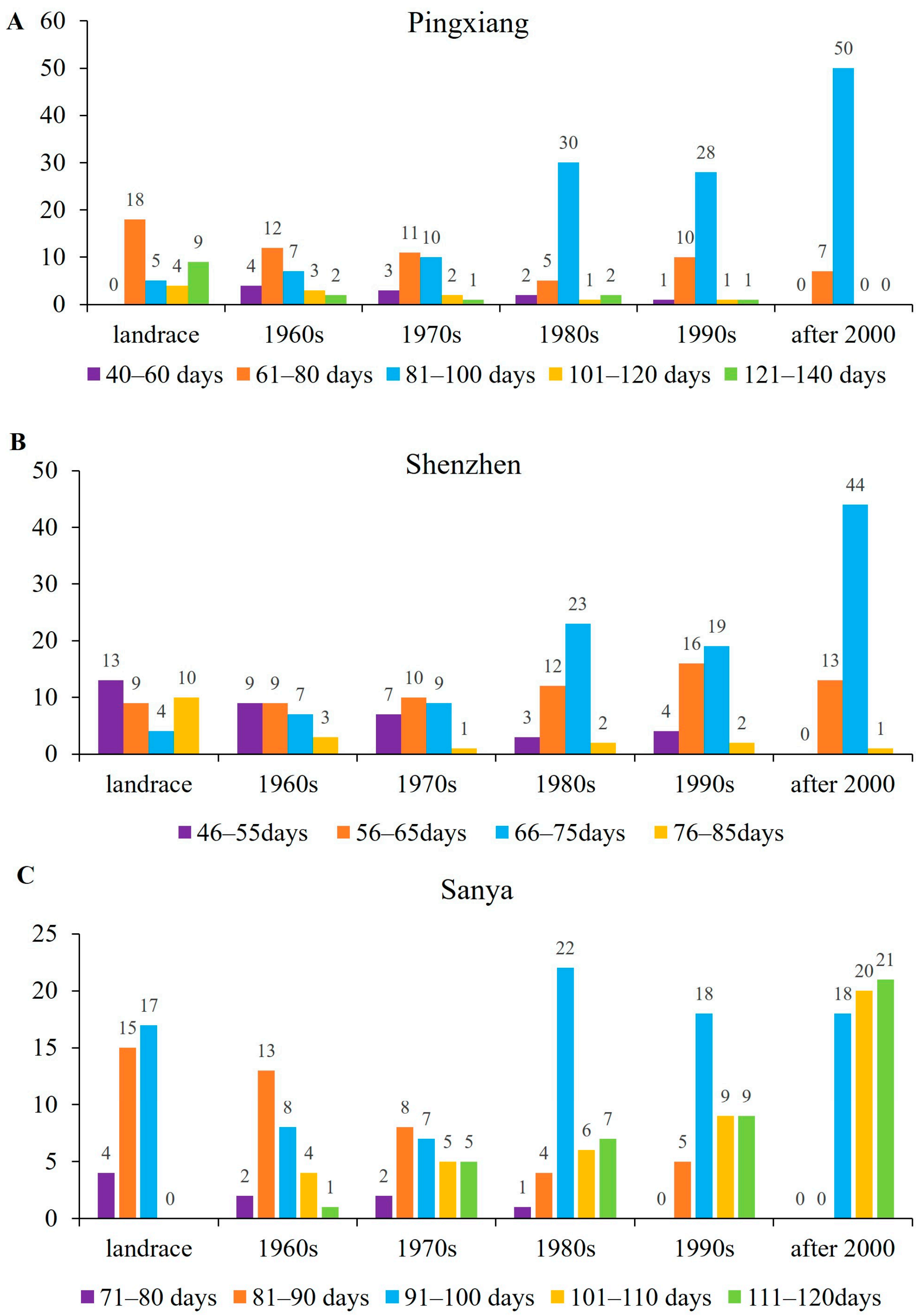

Figure 2. Frequency distribution of heading days of rice at different ages, across three different environments. (**A**–**C**) display the frequency distribution in Pingxiang, Shenzhen and Sanya, respectively.

3.1.2. Plant Type-Related Traits

By comparing the changes in plant architecture among different varieties across multiple decades and three distinct environments, it can be observed that after dwarf breeding, the plant height (PH) of the 1960s varieties decreased by approximately 30% compared to that of the landraces, followed by a slight recovery (Figure 3, Table S2). In addition, along with a decrease in plant height, the flag leaf length (FLL) of the 1960s varieties also showed a significant decrease of 15–20% and then remained relatively stable. However, after a significant increase in flag leaf width (FLW) during the 1960s, there was no significant increasing trend in the subsequent breeding stages, except for a gradual increase observed in Shenzhen. Regarding the flag leaf area (FLA), there were no significant differences among different stages in Pingxiang and in Sanya, while in Shenzhen, varieties developed after the 1990s showed a significant increase in FLA compared to earlier varieties (Figure 3, Table S2).

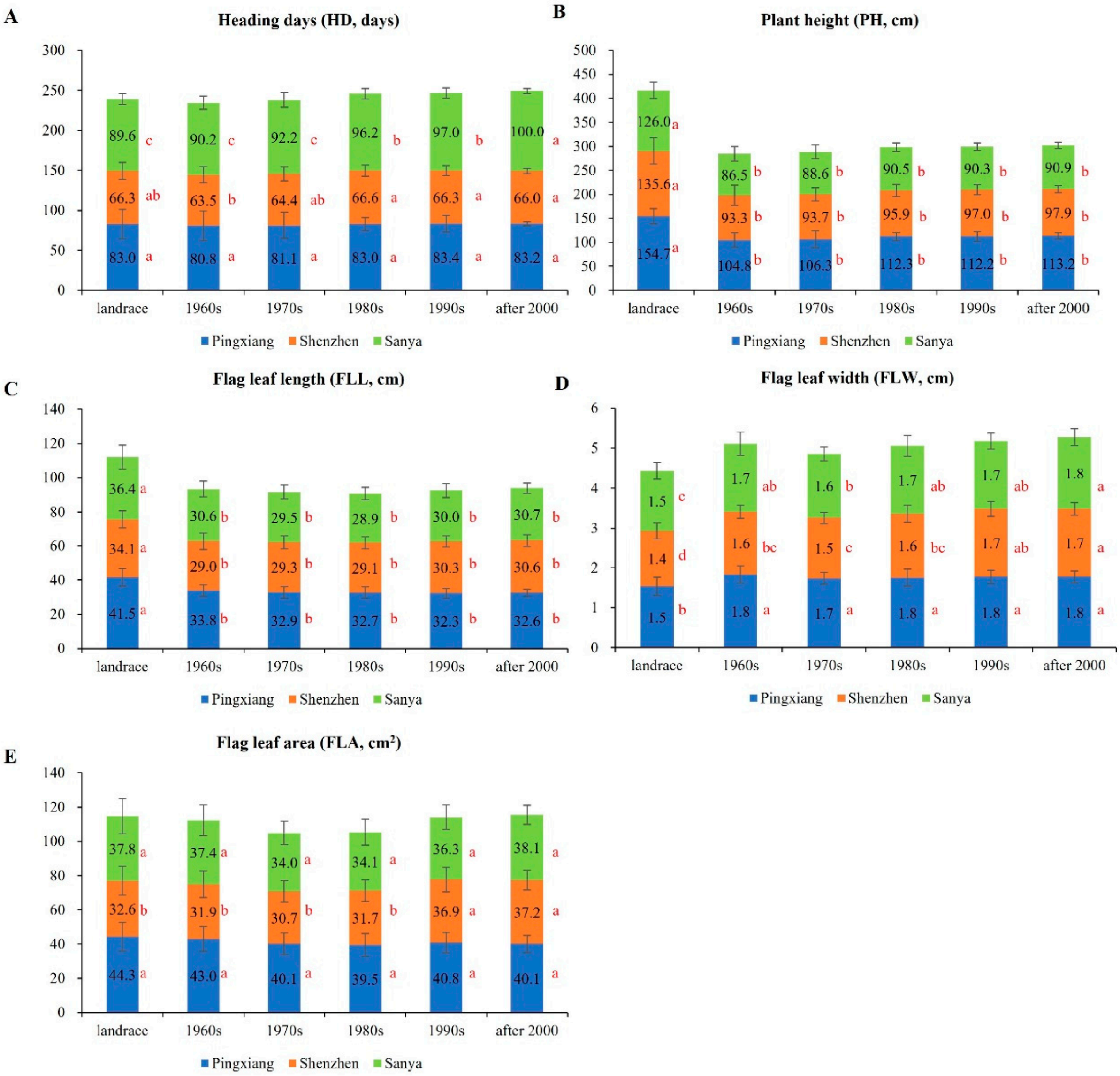

Figure 3. Heading days and plant architecture traits of rice at different breeding stages under different environments. Different letters next to the bar chart denote significant differences among decades by Duncan's multiple range test within each location. (**A**) heading days; (**B**) plant height; (**C**) flag leaf length; (**D**) flag leaf width; (**E**) flag leaf area.

3.1.3. Panicle Type-Related Traits

During the dwarf breeding stage, although the panicle length (PL) shortened with a decrease in plant height, other traits of the panicle were significantly improved. The grain density (GD) increased significantly every 20 years across all three environments, from 4.9–5.3 in landraces to 5.6–6.4 in the 1960s–1970s, then to 7.3–8.3 in the 1980s–1990s, and further increased to 8.3–9.8 in the past 20 years (Figure 4, Table S3). Breeders slightly lagged behind in improving the number of primary branches per panicle (NPB). By the 1980s, the average NPB increased by 1.3, and after 2000, it further increased by approximately 1 on average. The improvement in total grain number per panicle (GNP) by breeders was also remarkable. In Pingxiang, except for the insignificant changes in GNP during the 1960s–1970s and 1980s–1990s, there were significant increases in GNP during other breeding stages (Figure 4, Table S3). GNP increased from 122 in landrace to 190 in varieties of the recent 20 years. In Shenzhen and in Sanya, the GNP increased gradually in each stage, especially in the 1980s and after 2000, with increases of 16–32% and 12–17%, respectively, compared to the previous stage, reaching a maximum of 315 spikelets per panicle in certain varieties. The variation pattern of filled grain number per panicle (FGNP) was similar to that of the GNP, especially in the breeding stages of the 1980s and after 2000. The FGNP increased significantly in all three environments. However, the increments were limited in other breeding stages (Figure 4, Table S3). The average seed setting rate of varieties at different breeding stages ranged from 84.6% to 86.6%, and there were no significant differences among different breeding stages.

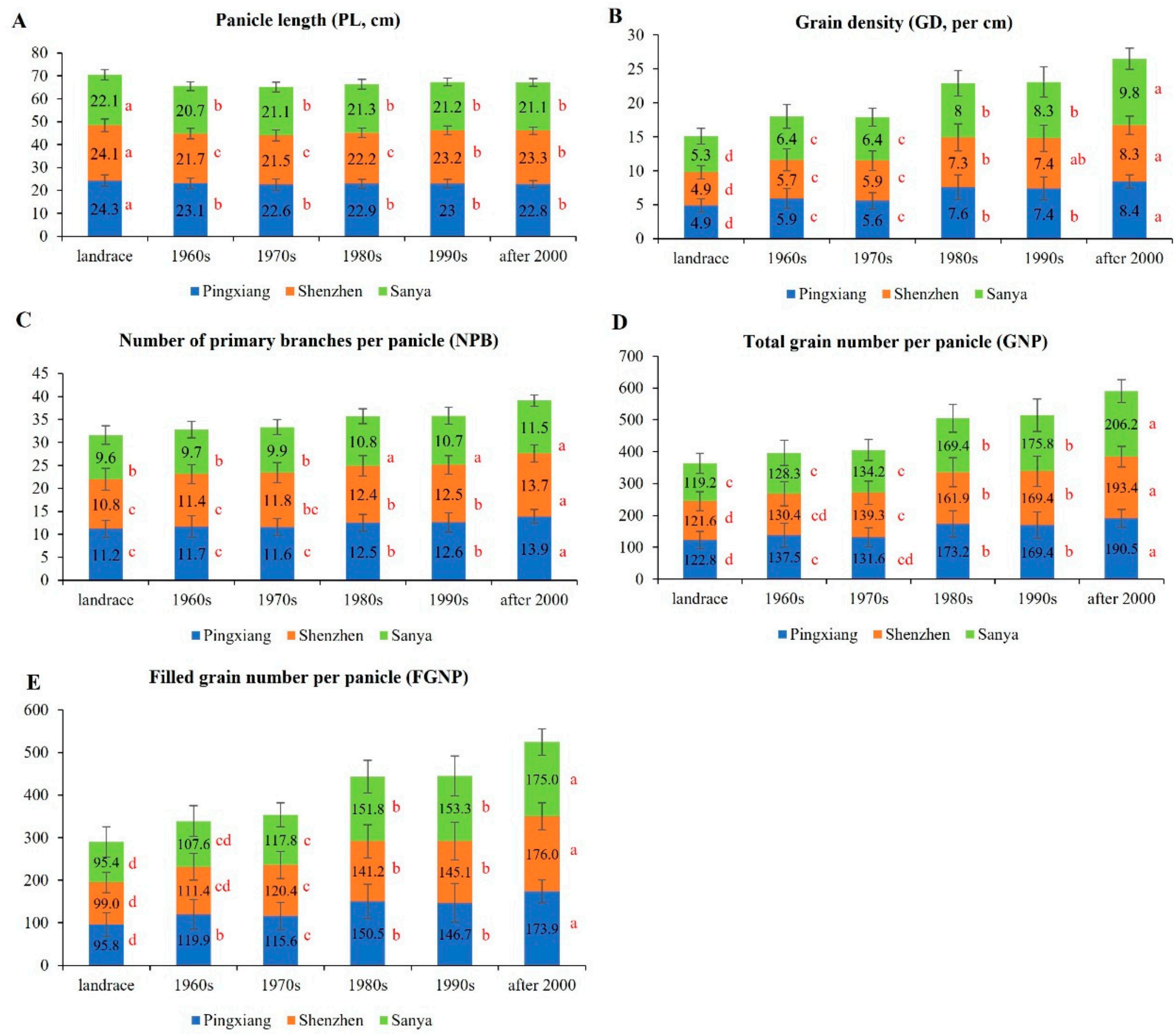

Figure 4. Panicle type-related traits of rice at different breeding stages under different environments. Different letters next to the bar chart denote significant differences among decades by Duncan's multiple range test within each location. (**A**) panicle length; (**B**) grain density; (**C**) number of primary branches per panicle; (**D**) total grain number per panicle; (**E**) filled grain number per panicle.

3.1.4. Grain Type-Related Traits

The grain type of rice varieties in the 1960s and 1970s did not show significant changes compared to landraces, indicating that breeders did not focus on improving grain shape during this period (Figure 5, Table S4). It was not until the 1980s that significant changes in grain length (GL) and width (GW) were observed, transitioning from oval-shaped to slender-shaped grains, accompanied by smaller grain size and decreased thousand grain weight (TGW). Compared to the 1980s, rice grains became longer and narrower in the 1990s. By the 2000s, the TGW decreased further, resulting in a higher grain length-to-width ratio (LWR), with some varieties reaching a maximum value of 4.1 (Figure 5, Table S4). This gave rise to the characteristic slender-shaped grain in South China.

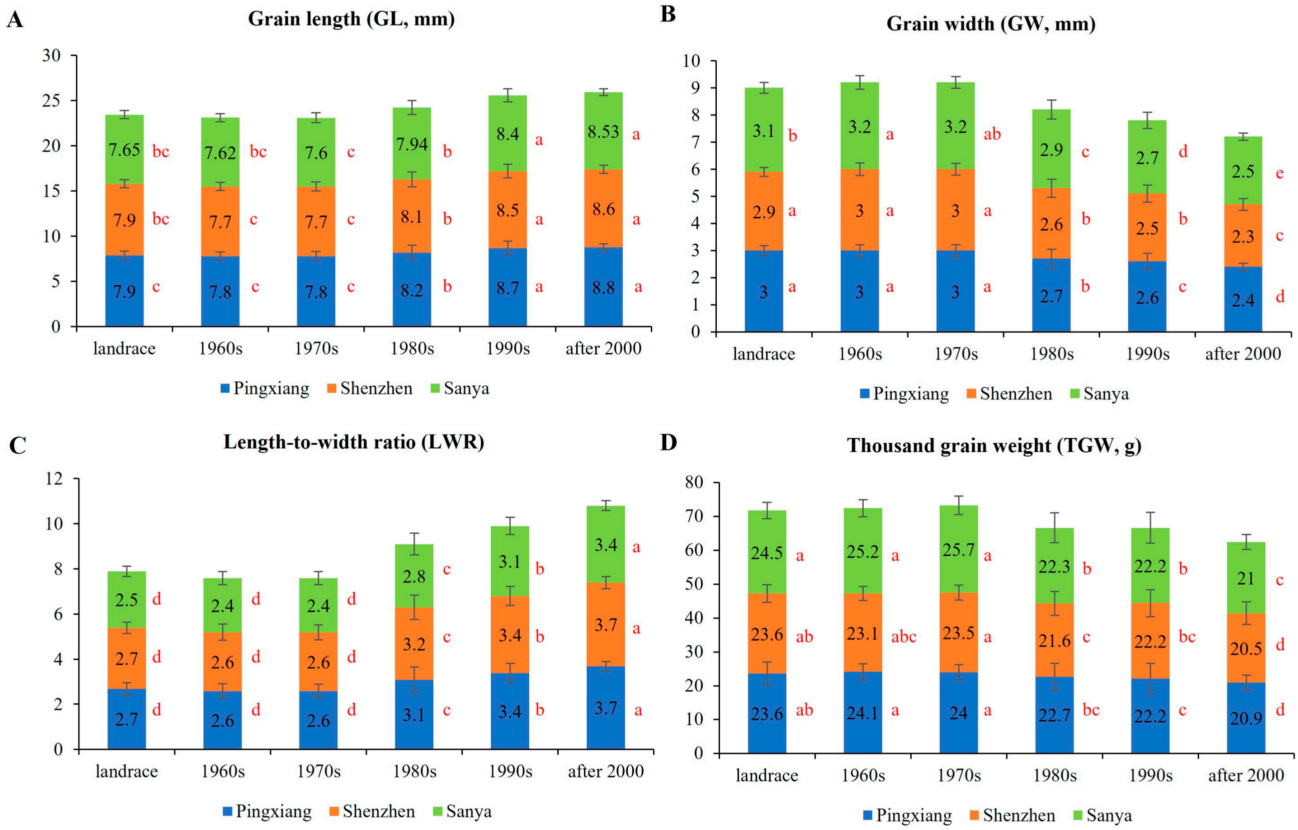

Figure 5. Grain type characteristics of rice at different breeding stages under different environments. Different letters next to the bar chart denote significant differences among decades by Duncan's multiple range test within each location. (**A**) grain length; (**B**) grain width; (**C**) grain length-to-width ratio; (**D**) Thousand grain weight.

3.1.5. Yield-Related Traits

The effective tiller number per plant (ETN) is an important factor contributing to yield. The ETN did not increase but rather decreased in distinct environments and across different generations of varieties (Figure 6, Table S5). In Shenzhen and in Sanya, modern varieties exhibited a significant decrease in the ETN compared to landraces and varieties in the 1960s. In Pingxiang, the ETN in different breeding stages showed an initial increase followed by a decrease, reaching 13.0 panicles per plant in the 1970s, and then decreasing to 10.5 panicles per plant in the 2000s. After dwarf breeding, the biomass per plant showed a trend of an initial decrease followed by an increase across all three environments. For example, in Shenzhen, the biomass per plant in varieties of the 1970s decreased to 46.5 g, and then began to increase, reaching 52.1 g in the 2000s. In Sanya, the biomass per plant decreased to 42.9 g in the 1960s, and then increased to 54.4 g in the 2000s. The harvest index (H-index) reflects the efficiency of converting crop biomass into yield. In the 1960s, the H-index significantly increased in all three environments. In Shenzhen, there was another significant increase in the H-index for the varieties in the 1970s. Although there were varying degrees of increases in the H-index in Pingxiang and in Sanya, they were not significant. Dwarf breeding led to a significant increase in grain yield per plant (GY) until the 1970s, and then it stabilized or increased slowly (Figure 6, Table S5).

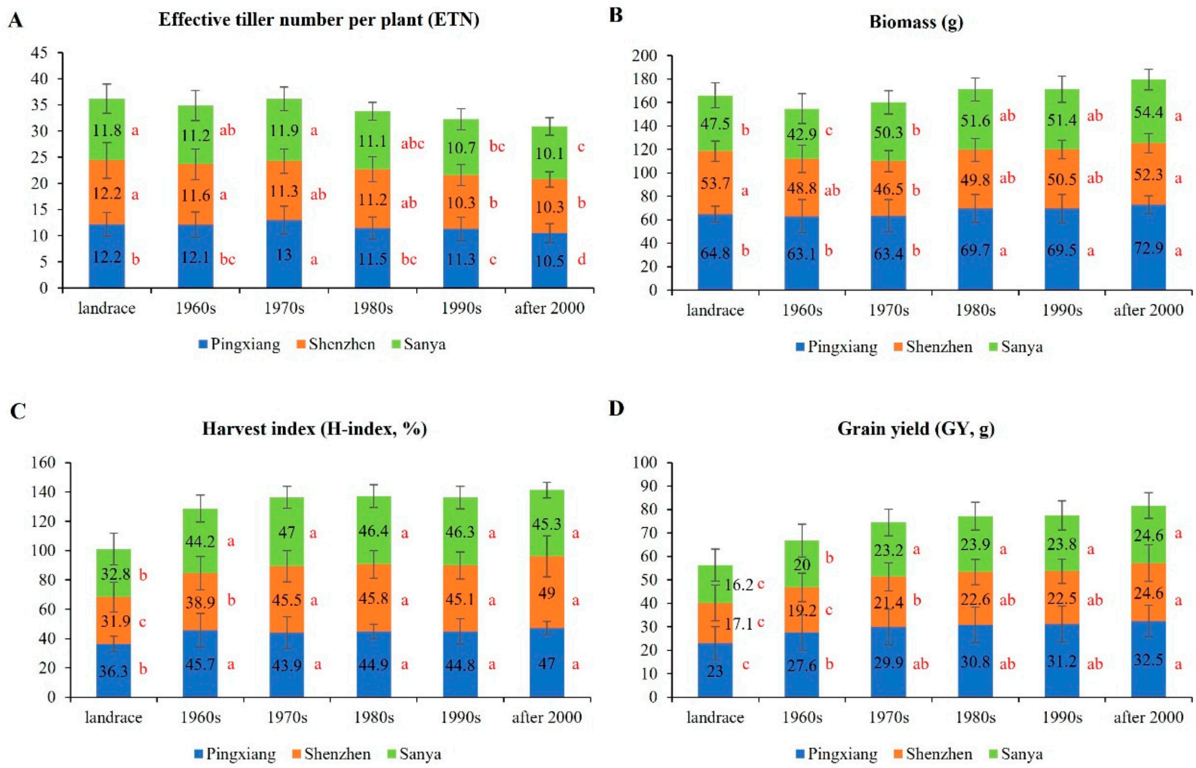

Figure 6. Yield characteristics of rice at different breeding stages under different environments. Different letters next to the bar chart denote significant differences among decades by Duncan's multiple range test within each location. (**A**) effective tiller number per plant; (**B**) biomass per plant; (**C**) harvest index; (**D**) grain yield per plant.

A two-factor ANOVA was performed on the 18 agronomic traits of 231 rice accessions across three locations (see Table S6). Notably, all traits displayed significant differences within the rice panel, indicating a substantial level of genetic diversity. In addition, significant differences were also detected among the three locations, except for the traits of FGNP, ETN, and H-index (Table S7). Broad sense heritability (H^2) for each trait was estimated and separately by decade; grain type-related traits (including GL, GW, LWR, and TGW), PH, FLW, and GD showed high H^2, ranging from 82.0% to 98.9%, while FLL, FLA, and GY showed relatively low H^2 (Table S7).

3.2. Correlations among Important Agronomic Traits and Grain Yield per Plant

The correlation analysis results among agronomic traits, such as plant type, panicle type, grain type, yield components, and grain yield per plant (GY), are shown in Figure 7. GY showed highly significant positive correlations with flag leaf width, flag leaf area, grain density, number of primary branches per panicle, total grain number per panicle, filled grain number per panicle, grain length, length-to-width ratio, biomass per plant, and harvest index, across all three environments (Figure 7, Tables S8 and S9). Additionally, in Shenzhen, panicle length and the number of effective tillers per plant also showed a highly significant positive correlation with GY (Table S9). In Sanya, heading days and panicle length were also significantly positively correlated with GY. Compared to plant type and grain type, the panicle-related traits exhibited a stronger correlation with GY (Table S10). In all three environments, the trait that showed the highest correlation with GY was the number of filled grains per plant, followed by grain density and primary branches. In Shenzhen, the number of effective tillers per plant was positively correlated with GY, while in Pingxiang and in Sanya, no significant correlation was observed between the number of effective tillers and GY.

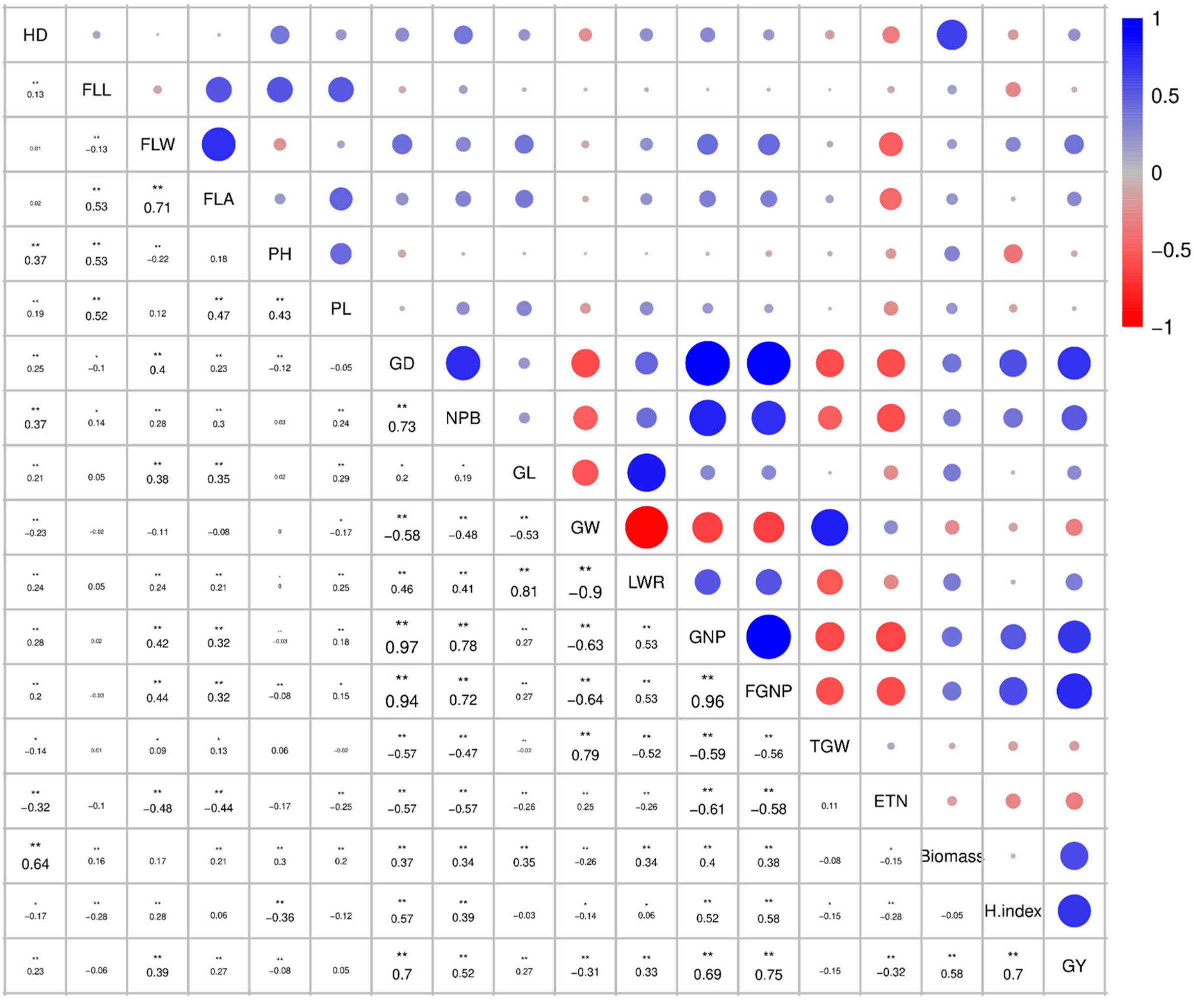

Figure 7. Correlation coefficients among 18 main agronomic traits. The data were derived from the average phenotype of each trait across three different locations. FLL, flag leaf length; FLA, flag leaf area; PL, panicle length; FLW, flag leaf width; HD, heading date; NPB, number of primary branches per panicle; GNP, total grain number per panicle; GY, grain yield per plant; FGNP, filled grain number per panicle; GL, grain length; GD, grain density; H-index, harvest index; LWR, length-to-width ratio; ETN, effective tiller number per plant; GW, grain width; TGW, thousand grain weight; PH, plant height. * and ** denote significant difference at $p < 5\%$ and $p < 1\%$ levels, respectively.

In the three environments, the flag leaf length was positively or significantly positively correlated with flag leaf area and biomass per plant, but it showed a significant negative correlation with the harvest index (Tables S8 and S9). This indicates that the longer flag leaf indeed improves photosynthetic efficiency and biomass to some extent, but it also brings negative effects, as it does not lead to an increase in the harvest index. The flag leaf width was positively or significantly positively correlated with flag leaf area, biomass per plant, and harvest index. This suggests it is feasible that increasing flag leaf width enlarges leaf area, enhances photosynthetic efficiency, accumulates dry matter, improves the harvest index, and ultimately increases yield. Plant height was highly positively correlated with panicle length and biomass per plant and significantly or highly significantly negatively correlated with grain density, filled grain number per panicle, and harvest index. On the one hand, this indicates that, while dwarf breeding reduces plant height, it also leads to a decrease in panicle length and single plant biomass. However, on the other hand, due to the excellent improvement in grain density and filled grain number per panicle, it increases the harvest index, achieving an increase in yield, which is consistent with the results by the Duncan analysis.

In the three environments, grain length and grain width were positively or highly positively correlated with thousand grain weight (TGW), while the length-to-width ratio was negatively or highly negatively correlated with TGW. Interestingly, across all three environments, there was no correlation detected between TGW, which is one of the three yield components. This may be due to the fact that, since the 1980s, rice breeding in South China has been focused on improving grain quality, and breeders have tended to select slender grains with a large length-to-width ratio, which has led to a reduction in TGW. Therefore, in this experiment, the correlation between TGW and GY was not significant.

3.3. Path Analysis of Agronomic Traits and Grain Yield per Plant

The regression coefficients between 17 agronomic traits and GY were calculated, and the significance testing for multiple linear regression was conducted by F-test. The results indicate that these traits have significant linear relationships with GY and can be subjected to a path analysis. The coefficient of determination (R^2) values in Pingxiang, in Shenzhen, and in Sanya were 0.977, 0.951, and 0.982, respectively, indicating that these agronomic traits can explain at least 95% of the variation in GY under all three environments. The path analysis results are shown in Table S11; biomass per plant and harvest index make the largest direct contributions to GY (0.685 and 0.691 in Pingxiang, 0.449 and 0.801 in Shenzhen, 0.707 and 0.604 in Sanya), while grain density, number of primary branches per panicle, total grain number per panicle, and filled grain number per panicle have significant indirect effects (0.699, 0.398, 0.373, and 0.585, respectively, in Pingxiang; 0.46, 0.403, 0.627, and 0.48, respectively, in Shenzhen; 0.848, 0.461, 0.344, and 0.622, respectively, in Sanya). These results indicate that these traits have limited direct contributions to GY and indirectly affect yield through other pathways. It is worth noting that among all the traits with positive indirect path coefficients, the sum of coefficients for panicle-related traits is much larger than the sum of coefficients for plant type and grain type traits. This suggests that panicle-related traits make the greatest contribution to GY, which is consistent with the results of the correlation analysis, indicating a higher correlation between panicle-related traits and GY compared to plant type and grain type traits.

4. Discussion

Improving rice yield potential beyond the current high levels is an important topic in rice research both domestically and internationally [21]. Expanding sink capacity is the foundation for improving yield, and the main approaches are to increase the number of effective panicles or the number of grains per panicle. However, there is a significant negative correlation between effective panicle number and grains per panicle. Therefore, balance and coordination between these two factors is necessary to achieve the goal of expanding sink capacity [22].

Many scholars, through studies on rice in different ecological regions, generally believe that increasing grain number per panicle to cultivate large-panicle varieties and expanding individual sink capacity to increase the overall population sink capacity are the main ways to improve the yield potential of varieties [13,15,16,20]. This study shows that the grain number per panicle of rice varieties developed in different years in the South China region have shown a linear increase over the past 50 years, and the yield level has also exhibited a year-on-year increase from the 1950s to the mid-late 1980s. This is consistent with the breeding approach in the rice region of South China, which has primarily focused on selecting large-panicle varieties and increasing grain weight per panicle to improve yield levels.

Since the early 1990s, the grain number per panicle of rice varieties in South China has further increased, but grain weight and the number of effective tillers have significantly decreased. As a result, the sink capacity of the varieties has not been substantially improved, and the yield level has stagnated without achieving new breakthroughs [20]. Some studies have suggested that increasing the harvest index can enhance the sink capacity and further optimize the source–sink relationship, leading to increased yields [23]. However, other scholars have put forward the opposite view; they have claimed that the main approach to increasing rice yield through dwarf breeding was by significantly improving the harvest index. However, in the past decades, the rice yield level has not made further breakthroughs, primarily because the yield-increasing effect by improving the harvest index has reached its limit. To further enhance the yield potential of rice, new approaches must be explored [21,24]. Liu et al. deemed that, over the past 50 years since dwarf breeding, genetic improvement of rice varieties in South China has focused on cultivating large-panicle varieties. Currently, the grain number per panicle of rice varieties in South China has reached a relatively high level, and merely increasing the grain number per panicle has limited potential for improving yield. Therefore, he proposed that, based on the premise of increasing biological yield, it was necessary to appropriately raise the grain weight level on the basis of existing large-panicle varieties. This would create a new balance between the factors of grain number and grain weight at a higher level, which would be an important approach to further increase rice yield in South China [25].

This study showed that both the effective tiller number (ETN) and the thousand grain weight (TGW) of rice varieties in South China have shown a downward trend in recent decades. The decrease in ETN is due to the need to maintain the balance of plant type, and therefore ensures the centralized supply of nutrients and breed large panicle [26,27]. The decrease in TGW is influenced by market demand and climatic conditions. By the 1980s, the average yield per unit area of inbred *indica* rice in South China had increased by approximate 30% (Table S5). Breeders have consciously shifted their focus from high and super-high yields to developing new varieties with high quality and yield. Considering the characteristics of high temperature and high humidity in South China, breeders have chosen the long and slender grain type to change grain shape from oval type to slender type while maintaining the original yield level. The elongated grain type has a faster filling rate, making the grains easier to become plump, and thus achieving better quality [28–30]. We believe that under the background of the current rice quality breeding in South China, it is not suitable to increase yield by increasing the TGW. Considering that the GNP has been greatly improved, the potential for further improvement is limited. Therefore, there is significant potential to increase the effective tiller number per plant. An increase in effective tiller number (ETN) must be accompanied by adjustments in plant type, such as top-three leaves and plant height, to ensure an adequate supply of metabolic sources without causing ineffective tillering or small tillering.

The timing of heading in rice plants, i.e., early or late, can affect the accumulation of photosynthetic products in rice, and then affect the grain filling process in the rice filling stage, and ultimately affect the yield and quality of rice. The heading stage of rice also determines the adaptability and yield of rice varieties in different regions, making it one of the main target traits for artificial selection [31–33]. In this study, various varieties across different breeding stages displayed variations in heading time under diverse ecological conditions, and a trend towards a concentrated distribution began to emerge from the 1980s. This may be attributed to breeders developing early and late season double-cropping rice varieties that can be used for both early and late cropping. Prior to the 1970s, rice varieties in the double-cropping areas of South China were categorized as early or late rice. If early rice varieties were used for late season planting, their growth duration would be significantly shortened, resulting in early heading and a significant decrease in yield. Late rice varieties used for early planting would typically delay head or failure to head, resulting in reduced yield or even no harvest. Such materials were highly light and temperature sensitive, with high requirements for light conditions and poor adaptability to the environment, leading to their scattered distributions in different environments. In 1978, with the development of the first dual-purpose rice variety in South China, i.e., Guichao 2, a large number of early and late season double-cropping rice varieties with low light sensitivity and moderate temperature sensitivity were subsequently bred. This reduced their susceptibility to environmental and seasonal influences, ensured a moderate growth duration, and improved the adaptability of the varieties.

In this study, it was observed that as the plant height decreased, the length of the flag leaf also decreased, while its width increased. This observation aligns with the objective fact that, while addressing problems of fertilizer tolerance and lodging resistance and given the climatic attributes of vigorous winds and substantial rainfall in South China, breeders tend to appropriately shorten the flag leaf length and minimize the susceptibility of leaves to wind-induced damage. This approach also subsequently reduces the risk of bacterial leaf blight infection. Increasing the flag leaf width can compensate for the decrease in leaf area caused by short leaves, thereby preventing a decline in photosynthetic efficiency and ensuring an adequate supply of metabolic source. Studies have shown that reducing plant height also brings negative consequences such as decreased biomass, which hinders the accumulation and conversion of dry matter, resulting in a decline in yield potential. Therefore, breeders have, once again, improved plant height since the 1980s, making slight increases, and an adequate increase in plant height could enhance biomass and yield [34,35]. Panicle length is an important factor affecting rice yield, and it is highly positively correlated with plant height. Due to the influence of dwarf breeding, panicle length has significantly decreased. In order to prevent a decrease in yield per plant, breeders have sequentially improved other panicle traits such as grain density, grain number per panicle, filled grain number, and number of primary branches, while maintaining the panicle length relatively unchanged.

The process of morphological changes in rice varieties of South China is essentially the selection process of breeders for desirable traits. Breeders' improvements in traits are not limited to a single trait but consider the overall performance, involving the coordinated improvement of multiple traits to achieve complementary advantages and dynamic balance [36–38]. For further study, we intend to disclose the landscape of genetic variations and to summarize the trend of rice breeding in South China rice collection, providing informative insights regarding agronomical traits, pedigrees, introgressions, and QTLs by integrating phenotypic, genomic, and historical clues.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy13082159/s1, Table S1. Temperature and precipitation conditions during vegetation of rice panel in Pingxiang, Shenzhen and Sanya from June 2017 to April 2018. Table S2. Heading date and plant architecture traits of rice at different stages under different environments. Table S3. Panicle type related traits of rice at different stages under different environments. Table S4. Grain type characteristics of rice at different stages under different environments. Table S5. Yield characteristics of rice at different breeding stages under different environments. Table S6. Phenotype of 18 main agronomic traits of 231 rice accession in Pingxiang, Shenzhen and Sanya. Table S7. Two-way ANOVA and broad sense heritability for 18 traits investigated. Table S8. Correlation coefficients of main agronomic traits in Pingxiang. Table S9. Correlation coefficients of main agronomic traits in Shenzhen. Table S10. Correlation coefficients of main agronomic characters in Sanya. Table S11. Path coefficient of important agronomic traits and grain yield per plant.

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