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Article

Grain Yield, Quality and 2-Acetyl-1-Pyrroline of Fragrant Rice in Response to Different Planting Seasons in South China

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Abstract: Climate conditions is an important factor affected the fragrant rice growth and development. In order to study the effects of different planting seasons on fragrant rice performance in South China, present study was conducted with three planting seasons (early season (April to July), middle season (June to September) and late season (August to November)) and three fragrant rice cultivars, '*Basmati-385*', '*Meixiangzhan-2*' and '*Xiangyaxiangzhan*'. The results showed that the highest grain yield and grain 2-acetyl-1-pyrroline (2-AP, key component of fragrant rice aroma) content were both recorded in late season treatment while the fragrant rice in middle season treatment produced the lowest grain yield, grain filling percentage, 1000-grain weight and gain 2-AP content. The highest contents of precursors (proline, pyrroline-5-carboxylic acid and 1-pyrroline) which related to 2-AP biosynthesis were recorded in late season treatment compared with early season treatment and middle season treatment. The highest activities of enzymes (proline dehydrogenase, pyrroline-5-carboxylic acid synthetase and ornithine transaminase) which involved in 2-AP biosynthesis were also observed in late season treatment. Moreover, the fragrant rice cultivars in late season possessed the lowest chalk rice rate, chalkiness as well as the highest brown rice rate, head rice and protein content. Thus, the optimal season for fragrant rice production in South China is the late season.

Keywords: 2-acetyl-1-pyrroline; climate; fragrant rice; grain qulity; yield formation

1 Introduction

Fragrant rice varieties are a series of special rice varieties which possess good grain quality and particular aroma with 2-acetyl-1-pyrroline (2-AP) as key compound [1]. In recent years, fragrant rice has attracted more and more attention and favor in international markets compared with other varieties of rice [2].

The yield formation and 2-AP biosynthesis of fragrant rice were affected by many environment factors and agronomic measures. For example, previous study revealed that shading during the grain filling stage would greatly increase grain 2-AP content and severely reduce grain yield of fragrant rice [3]. The study of Ren et al. [4] showed that the application of extra nitrogen fertilizer could increase the grain proline content and grain 2-AP concentration. Li et al. [5] also demonstrated that manganese fertilizer would induce the regulation of 2-AP biosynthesis in fragrant rice.

The climate factors especially the air temperature have significant influences on growth and development of rice varieties including fragrant rice. For example, Liu et al. [6] demonstrated the high air temperature during the flowering stage severely decreased the seed-setting rate and spikelets per panicle and caused the yield loss of super hybrid rice. The study of Kong et al. [7] revealed the high temperature stress would cause yield loss and grain quality decline of fragrant rice while the short-term water management could alleviate those negative effects. He et al. [8] indicated that the different temperatures during the grain filling stage had significant impacts on chlorophyll contents and the antioxidant system of fragrant rice.

Normally, the period of sowing or transplanting would directly determine the temperature and other climatic conditions during the growth period of fragrant rice in the field production. However, the effects of different planting seasons on yield formation, grain quality and 2-AP of fragrant rice were rarely reported. Therefore, present study was conducted with three different planting seasons and three fragrant rice cultivars in order to investigate how fragrant rice performances in response to different climate conditions.

2 Materials and Methods

2.1 Experimental Designs

The seeds of three fragrant rice cultivars, *Meixiangzhan-2* (*Lemont* × *Fengaozhan*, bred by Rice research institute of Guangdong academy of agricultural sciences), *Basmati-385* (local fragrant rice cultivar in India, improved and introduced by Rice research Institute of Guangdong Academy of Agricultural Sciences) and *Xiangyaxiangzhan* (*Xiangsimiao126* × *Xiangyaruanzhan*, bred by Taishan institute of agricultural science), which were widely used in fragrant rice production in South China, were used in present study. A pot experiment was conducted in Experimental Research Farm, College of Agriculture, South China Agricultural University, Guangzhou, China (23°09’N, 113°22’E and 11 m from mean sea level) in 2016. The germinated seeds of fragrant rice were sown in PVC trays (58 cm (leghth) × 25 cm (width) × 2 cm (height)) for raising nursery and then twenty-day-old seedlings were transplanted into pots filled with paddy soil (five hills per pot and four seedlings per hill). Each pot was filled with 10 kg of paddy soil which was sandy loam consisting 20.11 g/kg organic matter, 2.34 g/kg total nitrogen, 1.06 g/kg total phosphorus, 17.66 mg/kg total potassium and 6.23 pH. The first planting season was called ‘early season’ (ES, sowing on March 12, transplanting on April 1 and harvesting on July 10); The second season was called ‘middle season’ (MS, sowing on May 12, transplanting on June 1 and harvesting on September 10); The third season was called ‘late season’ (LS, sowing on July 12, transplanting on August 1 and harvesting on November 7). The climate conditions of three planting seasons were shown in Tab. 1.

Each pot was applied with 11 g ‘Special biological organic fertilizer (Dao Feng Xiang)’ manufactured by Guangzhou Huayuan Agricultural Ltd., China comprised of N+ P2O5+K2O ≥6%, active living bacteria ≥20 milliong^{-1}, and organic matter ≥12% with 60% at basal and 40% at tillering stage. The water layer was maintained at 3–4 cm at whole period. The fresh panicles were harvested at maturity and stored at −80°C for bio-chemical analysis.

2.2 Bio-Chemical Analysis

The determination of 2-AP, proline, pyrroline-5-carboxylic acid (P5C) and 1-pyrroline were according to the methods described by Luo [9]. The 2-AP concentration was determined by the synchronization distillation and extraction (SDE) method combined with a GCMS-QP 2010 Plus (Shimadzu Corporation, Japan) and expressed as μg kg^{-1} FW. The grain proline content was determined using sulfosalicylic acid,

Table 1: Climatic conditions during the experiment (from transplanting to harvest)

Planting season	Accumulated temperature (°C)	Sunshine duration (hour)	Percentage of sunshine (%)	Daily average temperature (°C)	Daily average temperature during the grain filling stage (°C)
Early season (ES)	2663.65	376.89	93.37	26.64	29.91
Middle season (MS)	2923.24	575.78	143.6	28.94	29.10
Late season (LS)	2633.62	498.06	135.27	26.87	24.69

ninhydrin and toluene and expressed as μg g^{-1}. The P5C concentration was estimated while the mixture contained enzyme extraction supernatant, trichloroacetic acid and 2-aminobenzaldehyde. After the reaction, the absorbance was read at 440 nm.

The activities of proline dehydrogenase (PDH), pyrroline-5-carboxylic acid synthetase (P5CS) and ornithine transaminase (OAT) were measured according the methods described by Du [10]. The PDH activity was assayed after the reaction absorbance was read at 440 nm, and the activity was calculated using a molar extinction coefficient. The P5CS activity was determined while the reaction mixture included Tris-HCL buffer, $MgCl_2$, sodium glutamate, ATP, hydroxamate-HCL and enzyme extract and expressed as μmol g^{-1} h^{-1} FW. The absorbance of the supernatant fraction which used for OAT activity determination was read at 440 nm while the OAT activity was expressed as μmol g^{-1} h^{-1} FW.

2.3 Determination of Yield and Related Trails

At maturity, five pots were randomly harvested from each season and threshed by machine. Then, the harvested grains were sun-dried and weighted to determinate the grain yield, average effective panicles number per hill, grain number per panicle, seed-setting rate and 1000-grain weight.

2.4 Determination of Grain Quality

After drying, the rice grains were taken to determinate the grain quality. The brown rice rate was estimated using a rice huller (Jiangsu, China). The milled rice and head rice recovery rates were calculated by using a Jingmi testing rice grader (Zhejiang, China). Grains with chalkiness and chalkiness degree were estimated by using an SDE-A light box (Guangzhou, China) while an Infratec-1241 grain analyzer (FOSS-TECATOR) was used to determine the grain amylose and protein contents.

2.5 Statistical Analyses

Data were analyzed using statistical software ‘Statistix 8.1’ (Analytical Software, Tallahassee, FL, USA) while differences amongst means were separated by using least significant difference (LSD) test at 5% probability level. Graphical representation was performed via Sigma Plot 14.0 (Systat Software Inc., California, USA).

3 Result

3.1 Grain Yield and Yield Related Traits

There were some differences among different planting seasons in grain yield and related traits of fragrant rice cultivars (Tab. 2). For *Basmati-385*, the highest grain yield, effective panicle number, grain number per

Table 2: Effect of planting seasons on yield and yield related traits in fragrant rice

Cultivar	Treatment	Effective panicle number (pot^{-1})	Grains number per panicle	Grain filling percentage (%)	1000-grain weight (g)	Grain yield ($g \cdot pot^{-1}$)
Basmati-385	ES	27.00 ± 1.22b	99.25 ± 3.00b	77.61 ± 3.02b	26.80 ± 0.06b	53.43 ± 2.14b
	MS	25.78 ± 2.21b	99.82 ± 1.35b	71.64 ± 3.23c	24.67 ± 0.22c	44.99 ± 3.11c
	LS	33.00 ± 1.22a	108.05 ± 2.11a	86.40 ± 2.14a	27.35 ± 0.07a	63.20 ± 3.81a
Meixiangzhan-2	ES	27.40 ± 1.12a	98.10 ± 2.76b	82.64 ± 1.03a	19.38 ± 0.12ab	55.43 ± 2.39a
	MS	27.60 ± 0.51a	102.00 ± 4.18ab	80.80 ± 1.46a	18.60 ± 0.51b	42.34 ± 2.40b
	LS	28.87 ± 2.66a	110.66 ± 1.63a	83.77 ± 1.63a	19.93 ± 0.17a	64.01 ± 3.31a
Xiangyaxiangzhan	ES	26.88 ± 0.88b	75.48 ± 3.12b	85.01 ± 1.23b	19.48 ± 0.06a	55.56 ± 1.00b
	MS	28.00 ± 1.22ab	73.89 ± 1.83b	79.51 ± 3.35c	17.52 ± 0.12b	50.82 ± 3.17b
	LS	29.40 ± 0.48a	92.55 ± 2.98a	94.22 ± 1.33a	20.17 ± 0.47a	61.24 ± 2.04a

Values ± SE sharing a common letter within a column don't differ significantly at ($P \leq 0.05$) according to least significant difference (LSD) test. ES: Early season; MS: Middle season; LS: Late season. The same as below.

panicle, grain filling percentage and 1000-grain weight were all recorded in LS treatment while the MS treatment had the lowest grain yield, 1000-grain weight and grain filling percentage. There was no remarkable difference between ES treatment and MS treatment in effective panicle number and grains number per panicle; For *Meixiangzhan-2*, there was no significant difference among three planting seasons in effective panicle number and grain filling percentage. The grain yield in LS treatment and ES treatment were significantly higher than MS treatment; For *Xiangyaxiangzhan*, the highest yield and grain number per panicle were both recorded in LS treatment and there was no significant difference between ES treatment and MS treatment in grain yield and grain number per panicle.

3.2 Grain Quality

Different planting seasons affected grain quality attributes of fragrant rice cultivars differently (Tab. 3). The highest brown rice rate and head rice rate were both recorded in LS treatment for three fragrant rice cultivars while LS treatment had the lowest or equally lowest chalk rice rate, chalkiness and amylose content. Furthermore, LS treatment significantly increased the grain protein content compared with ES treatment and MS treatment. There was no remarkable difference among different planting season in Akali value.

3.3 2-AP Concentration

As shown in Fig. 1, different planting seasons significantly influenced the grain 2-AP concentration of fragrant rice cultivars. For *Basmati-385* and *Xiangyaxiangzhan*, the highest 2-AP contents were both recorded in LS treatment while there was no significant difference between ES treatment and MS treatment; For *Meixiangzhan-2*, the trend of grain 2-AP content was recorded as: LS > MS > ES.

3.4 Proline, P5C and 1-Pyrroline Content

As shown in Fig. 2, the grain proline, P5C and 1-pyrroline contents were significantly affected by planting seasons. For proline, the grain proline content in ES treatment were significantly higher than both MS treatment and LS treatment for three fragrant rice cultivars. There was no significant difference between MS treatment and LS treatment for *Meixiangzhan-2* and *Xiangyaxiangzhan*; For P5C, the lowest grain P5C contents were recorded in MS treatment for all fragrant rice cultivars and there was no remarkable difference between ES treatment and LS treatment for *Basmati-385* and

Table 3: Effect of different planting seasons on grain quality in fragrant rice

Cultivar	Treatment	Brown rice rate (%)	Milled rice rate (%)	Head rice rate (%)	Chalky rice rate (%)	Chalkiness (%)	Length-width ratio	Protein (%)	Amylose content (%)	Akali
Basmati-385	ES	79.92 ± 0.26b	67.25 ± 0.22b	47.68 ± 1.38b	18.75 ± 1.57a	3.05 ± 0.35a	3.02 ± 0.01b	7.47 ± 0.03b	18.70 ± 0.10a	6.07 ± 0.07a
	MS	78.04 ± 0.43c	68.98 ± 0.12ab	47.69 ± 0.48b	10.27 ± 0.61b	2.02 ± 0.09b	3.08 ± 0.01a	7.23 ± 0.03c	18.43 ± 0.12a	6.10 ± 0.06a
	LS	81.26 ± 0.28a	70.68 ± 0.88a	66.57 ± 0.83a	8.68 ± 0.33b	1.67 ± 0.06b	2.99 ± 0.01c	8.27 ± 0.03a	17.70 ± 0.10b	6.27 ± 0.03a
Meixiangzhan-2	ES	79.91 ± 0.40b	69.29 ± 0.14a	45.65 ± 0.85b	16.88 ± 1.79a	3.26 ± 0.29a	3.01 ± 0.01a	9.37 ± 0.03a	18.10 ± 0.31a	6.30 ± 0.10a
	MS	79.16 ± 0.57c	69.74 ± 0.27a	48.78 ± 1.04b	10.57 ± 0.95b	2.28 ± 0.08b	2.93 ± 0.04a	9.30 ± 0.06a	17.83 ± 0.12a	6.33 ± 0.03a
	LS	80.66 ± 0.43a	70.94 ± 1.65a	62.88 ± 1.46a	7.15 ± 0.97b	1.47 ± 0.13c	2.99 ± 0.02a	9.23 ± 0.03a	17.63 ± 0.22a	6.40 ± 0.06a
Xiangyaxiangzhan	ES	78.47 ± 0.12b	65.43 ± 0.47b	47.47 ± 2.75ab	12.06 ± 0.94a	2.73 ± 0.13a	3.58 ± 0.04c	7.47 ± 0.09b	24.93 ± 0.50a	6.77 ± 0.07a
	MS	76.18 ± 0.89c	66.42 ± 0.18ab	40.64 ± 3.70b	6.26 ± 0.34b	2.28 ± 0.09a	3.73 ± 0.01b	7.07 ± 0.03c	18.67 ± 0.12b	6.77 ± 0.03a
	LS	80.61 ± 0.15a	67.55 ± 0.11a	53.64 ± 0.38a	4.27 ± 0.54b	0.86 ± 0.11b	3.95 ± 0.01a	9.37 ± 0.03a	17.93 ± 0.03b	6.80 ± 0.06a

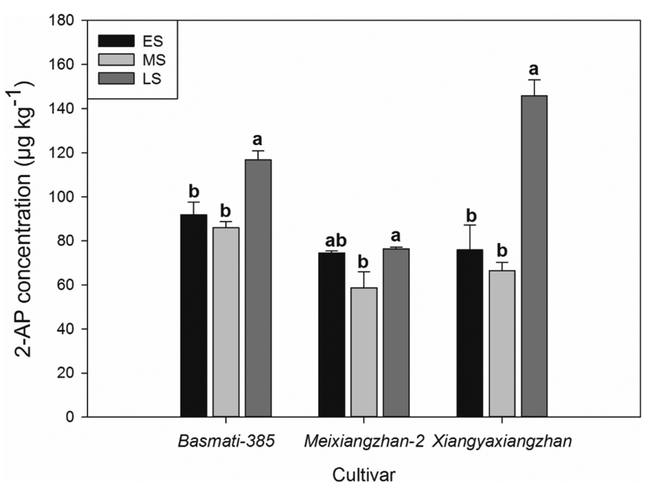

Figure 1: Effect of different planting seasons on grain 2-AP content in fragrant rice. Capped bars represent S.E. of three replicates. Means sharing a common letter don't differ significantly at ($P \leq 0.05$) according to least significant difference (LSD) test. The same as below

Meixiangzhan-2; For 1-pyrroline, the trend of grain 1-pyrroline content in three fragrant rice cultivars were all recorded as: LS > MS > ES.

3.5 Activities of PDH, P5CS and OAT

As shown in Fig. 3, different planting seasons significantly influenced the activities of enzymes involved in 2-AP biosynthesis. The highest activities were recorded in LS treatment and the lowest activities were

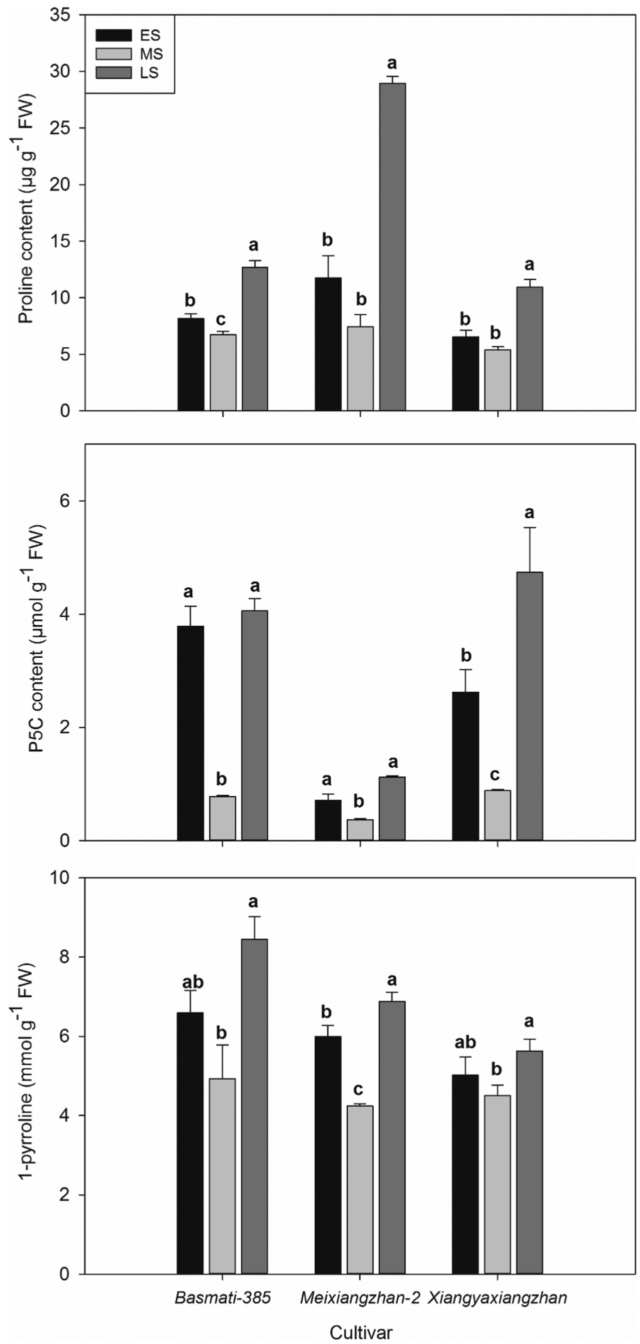

Figure 2: Effect of different planting seasons on grain proline, P5C and 1-pyrroline content in fragrant rice

recorded in MS treatment for *Basmati-385*, *Meixiangzhan-2* and *Xiangyaxiangzhan*. On the other hand, Fig. 3 showed that there was no remarkable difference among three planting seasons in P5CS activities and OAT activities for all fragrant rice cultivars.

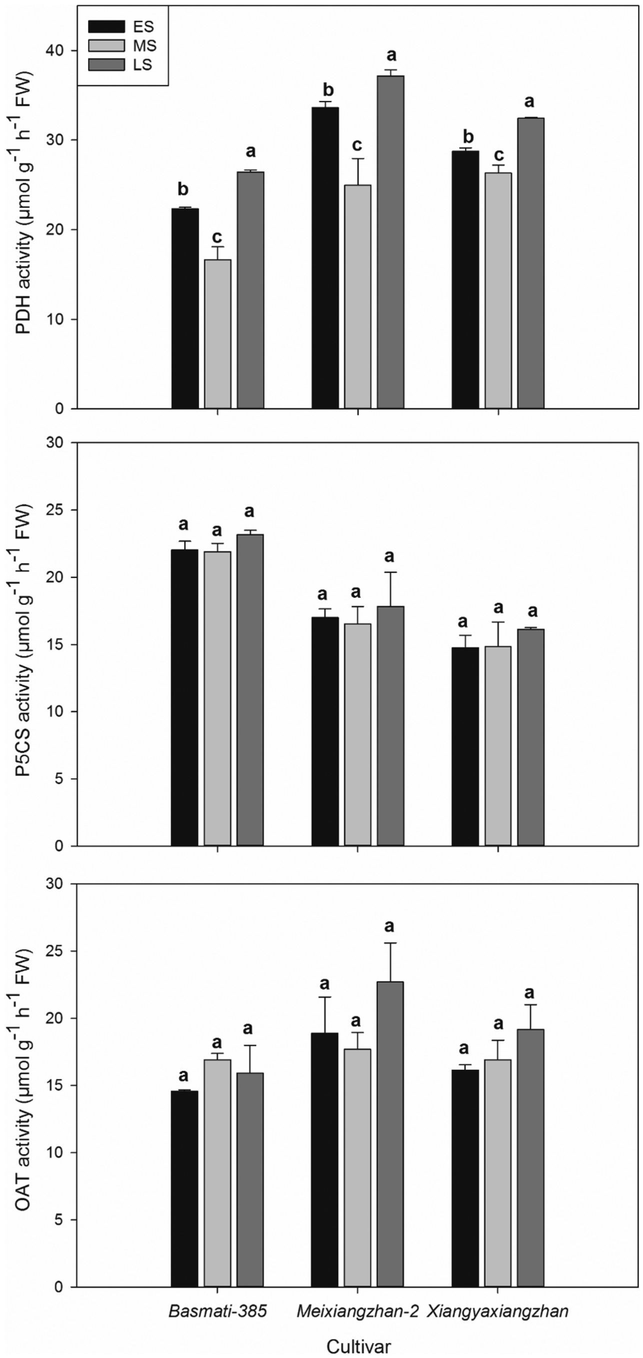

Figure 3: Effect of different planting seasons on activities of PDH, P5CS and OAT in fragrant rice

4 Discussion

Present study depicted the effects of different planting seasons on yield formation, grain quality and 2-AP biosynthesis in three different fragrant rice cultivars. Different planting seasons significantly affected the grain yield in '*Basmati-385*', '*Meixiangzhan-2*' and '*Xiangyaxiangzhan*'. The trend of grain yield was recorded as: LS > MS > ES and this difference was caused by the changes of grain filling percentage, effective panicle number and 1000-grain weight. Compared with early season and late season, the middle season had a much higher accumulated temperature as well as daily average temperature and it might be the directed reason for the lowest grain yield, grain filling percentage and 1000-grain weight were recorded in middle season for three fragrant rice cultivars. In 1991, Tashiro et al. [11] demonstrated that the suitable temperature range for rice growth and development was 21–26°C and the temperature exceed 27°C may cause reduction in seed-setting rate and 1000-grain weight. In present study, the daily average temperature in middle season was 28.94°C which definitely exceed this standard. Our results also agreed with the study of Sanchez et al. [12] who indicated that 28°C is the optimal temperature at tillering stage of rice and 24°C is optimal temperature at grain filling period, which are highest and lowest optimal temperatures, respectively compared with other growth stages of rice. On the other hand, the grain yield of fragrant rice cultivars in late season was significantly higher than early season except *Meixiangzhan-2* didn't reach the significant level. The difference could be explained by the different sunshine duration and percentage of sunshine. Previous study had shown that the light intensity had significant impacts on yield formation of rice by influencing the photosynthesis [13,14]. The results of present study were also consistent with the study of Mo et al. [3] which indicated that less sunshine would cause the yield loss of fragrant rice.

Grain quality is an important factor which affected the price of fragrant rice in international supermarket. In our study, the milled quality, appearance quality, nutrient quality and taste quality of three fragrant rice cultivars all significant affected by different planting seasons. Compared with early season and late season, the fragrant rice cultivars in late season possessed higher brown rice rate and head rice rate as well as crude protein content. Meanwhile, the lower chalk rice rate and chalkiness were also recorded in late season than early season and late season. The improvements in grain quality in late season treatment might be related to the lower daily average temperature which was 24.69°C. The research of Morita [15] showed that high air temperature during the grain filling phase would affected the grain quality severely. The study of Jin et al. [16] also showed that increased chalk rice rate and chalkiness were related to starch biosynthesis in endosperm under high temperature condition.

As the key flavor compound, the content of 2-AP was significantly influenced by different planting seasons. Our study observed that the fragrant rice cultivars in late season possessed higher grain 2-AP concentration than early season and middle season. Similar trend was recorded in content of 1-pyrroline which is the limited intermediate in 2-AP biosynthesis in fragrant rice [17]. The difference in grain 2-AP concentration might be attributed to the differences in both grain proline content and PDH activity. The investigation of Yoshihashi et al. [18] revealed that the proline is an important precursor in 2-AP biosynthesis which also is the nitrogen source for 2-AP in fragrant rice cultivars. The results of present study were also consistent with the research of Prodhan et al. [19] who discovered that the fragrant rice cultivars under 25°C had highest grain 2-AP concentration and the excellent phenotypic aroma score.

5 Conclusion

The grain yield, grain quality and grain 2-AP content of fragrant rice cultivars response to different planting seasons differently. The fragrant rice cultivars in middle season possessed the lowest grain yield, grain 2-AP concentration and grain quality and thus, the fragrant rice cultivars were not suitable to plant in the middle season in South China. On the other hand, the highest yield, grain quality and grain 2-AP content were recorded in late season treatment. Therefore, our results indicated that the optimal season for fragrant rice production is the late season.

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Conflicts of Interest: The authors declare that they have no conflicts of interest to report regarding the present study.

References

1. Wakte, K., Zanan, R., Hinge, V., Khandagale, K., Nadaf, A. et al. (2017). Thirty-three years of 2-acetyl-1-pyrroline, a principal basmati aroma compound in scented rice (Oryza sativa L.): a status review. *Journal of the Science of Food and Agriculture, 97(2),* 384–395. DOI 10.1002/jsfa.7875.
2. Bao, G., Ashraf, U., Wang, C., He, L., Wei, X. et al. (2018). Molecular basis for increased 2-acetyl-1-pyrroline contents under alternate wetting and drying (AWD) conditions in fragrant rice. *Plant Physiology and Biochemistry, 133,* 149–157. DOI 10.1016/j.plaphy.2018.10.032.
3. Mo, Z., Li, W., Pan, S., Fitzgerald, T. L., Xiao, F. et al. (2015). Shading during the grain filling period increases 2-acetyl-1-pyrroline content in fragrant rice. *Rice, 12,* 1–16.
4. Ren, Y., Ashraf, U., He, L. X., Mo, Z. W., Wang, F. et al. (2017). Irrigation and nitrogen management practices affect grain yield and 2-acetyl-1-pyrroline content in aromatic rice. *Applied Ecology and Environmental Research, 15(4),* 1447–1460. DOI 10.15666/aeer/1504_14471460.
5. Li, M., Ashraf, U., Tian, H., Mo, Z., Pan, S. et al. (2016). Manganese-induced regulations in growth, yield formation, quality characters, rice aroma and enzyme involved in 2-acetyl-1-pyrroline biosynthesis in fragrant rice. *Plant Physiology and Biochemistry, 103,* 167–175. DOI 10.1016/j.plaphy.2016.03.009.
6. Liu, K., Deng, J., Lu, J., Wang, X., Lu, B. et al. (2019). High nitrogen levels alleviate yield loss of super hybrid rice caused by high temperatures during the flowering stage. *Frontiers in Plant Science, 10,* 357. DOI 10.3389/fpls.2019.00357.
7. Kong, L., Ashraf, U., Cheng, S., Rao, G., Mo, Z. et al. (2017). Short-term water management at early filling stage improves early-season rice performance under high temperature stress in South China. *European Journal of Agronomy, 90,* 117–126. DOI 10.1016/j.eja.2017.07.006.
8. He, L. X., Chen, Y. L., Zhang, T. T., Zheng, A. X., Cheng, Y. et al. (2019). Effects of different temperature conditions on yield and physiological properties of rice (Oryza Sativa L.). *Applied Ecology and Environmental Research, 17(1),* 199–211. DOI 10.15666/aeer/1701_199211.
9. Luo, H., Du, B., He, L., He, J., Hu, L. et al. (2019). Exogenous application of zinc (Zn) at the heading stage regulates 2-acetyl-1-pyrroline (2-AP) biosynthesis in different fragrant rice genotypes. *Scientific Reports, 9(1),* 19513. DOI 10.1038/s41598-019-56159-7.
10. Du, P., Luo, H., He, J., Mao, T., Du, B. et al. (2019). Different tillage induces regulation in 2-acetyl-1-pyrroline biosynthesis in direct-seeded fragrant rice. *BMC Plant Biology, 19(1),* 308. DOI 10.1186/s12870-019-1913-9.
11. Tashiro, T., Wardlaw, I. F. (1990). The response to high temperature shock and humidity changes prior to and during the early stages of grain development in wheat. *Functional Plant Biology, 17(5),* 551–561. DOI 10.1071/PP9900551.
12. Sanchez, B., Rasmussen, A., Porter, J. R. (2014). Temperatures and the growth and development of maize and rice: a review. *Global Change Biology, 20(2),* 408–417. DOI 10.1111/gcb.12389.
13. Pan, S., Liu, H., Mo, Z., Patterson, B., Duan, M. et al. (2016). Effects of nitrogen and shading on root morphologies, nutrient accumulation, and photosynthetic parameters in different rice genotypes. *Scientific Reports, 6(1),* 32148. DOI 10.1038/srep32148.
14. Liu, K., Yang, R., Lu, J., Wang, X., Lu, B. et al. (2019). Radiation use efficiency and source-sink changes of super hybrid rice under shade stress during grain-filling stage. *Agronomy Journal, 111(4),* 1788–1798. DOI 10.2134/agronj2018.10.0662.
15. Morita, S. (2000). Effects of high air temperature on ripening in rice plants. Analysis of ripening performance in growth chamber experiments. *Japanese Journal of Crop Science, 69(3),* 391–399. DOI 10.1626/jcs.69.391.
16. Jin, Z., Yang, J., Qian, C., Liu, H., Jin, X. et al. (2005). Effects of temperature during grain filling period on activities of key enzymes for starch synthesis and rice grain quality. *Zhongguo Shuidao Kexue, 19,* 377–380.

17. Poonlaphdecha, J., Gantet, P., Maraval, I., Sauvage, F., Menut, C. et al. (2016). Biosynthesis of 2-acetyl-1-pyrroline in rice calli cultures: demonstration of 1-pyrroline as a limiting substrate. *Food Chemistry, 197,* 965–971. DOI 10.1016/j.foodchem.2015.11.060.
18. Yoshihashi, T., Huong, N. T. T., Inatomi, H. (2002). Precursors of 2-Acetyl-1-pyrroline, a potent flavor compound of an aromatic rice variety. *Journal of Agricultural and Food Chemistry, 50(7),* 2001–2004. DOI 10.1021/jf011268s.
19. Prodhan, Z. H., Faruq, G., Taha, R. M., Rashid, K. A. (2017). Agronomic, transcriptomic and metabolomic expression analysis of aroma gene (badh2) under different temperature regimes in rice. *International Journal of Agriculture and Biology, 19(03),* 569–576. DOI 10.17957/IJAB/15.0340.