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RESEARCH ARTICLE

Paclobutrazol Application Improves Grain 2AP Content of Thai Jasmine Rice KDML105 under Low-Salinity Conditions

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Abstract

KDML105 rice (*Oryza sativa* L.) cultivar, also known as the jasmine rice, is the most valuable fragrant rice of Thailand. The aroma is attributed to a highly 2-acetyl-1-pyrroline (2AP) compound, which is abundantly produced when rice plants are cultivated in the infertile saline soil in northeastern Thailand. The area suitable for production of KDML105 has been limited, and the farmers suffer low grain yield as a trade-off for the premium quality. In this study, we investigated whether foliar application of paclobutrazol (PBZ), which is a plant growth retardant, could mimic the effect of salt stress in promoting the 2AP content of the Thai fragrant rice. PBZ was sprayed on KDML105 rice leaves during the vegetative or reproductive growth stages. PBZ application up to 150 ppm during the vegetative stage was found to have mild effects on growth performances and yield components compared to the reproductive stage. The 100 ppm PBZ foliar spray during the vegetative stage was also found to increase the levels of 2AP and proline, which might be directed toward the 2AP production, in KDML105 rice grains to nearly the levels found in rice cultivated under 0.4% NaCl. The effects of PBZ were found on other tested aromatic verities: PT1 and RD43, and a non-aromatic variety: RD31. However, the amylose content of RD31 was significantly reduced in response to the PBZ application. These results showed that PBZ application is a promising strategy for improving grain quality of fragrant rice, although the effects may vary among rice genetic backgrounds.

Key words : Jasmine rice, paclobutrazol, 2AP, yield, aroma, salinity stress

Introduction

Thailand is one of the major rice exporters, contributing over 11 million tons in 2017 (FAO 2017). The rice production in Thailand, totaling more than 20 million tons annually, covers an area of 9 million ha – however, nearly half of which is under threat of drought periods and approximately one-third is affected by inland salinity. These poor growth conditions lead to the unceasing problem of low grain yield at 2 - 3 ton/ha for the Thai rice production (Papademetriou et al. 2000). Adding to this problem, these infertile areas are also the sites where fragrant rice is usually cultivated. Fragrant rice is preferred by the domestic consumers and is an important export commodity of Thailand. Approximately one half of the rice produced and one-fourth of the exported Thai rice is fragrant rice (FAO 2017). Even though commanding a higher price, 1.5 - 2 times the value of non-fragrant white rice, the fragrant rice varieties are often associated with low grain yield (Giraud 2013). Therefore, strategies to improve the productivity of the fragrant rice in the saline, arid soil and/or to boost the aromatic quality of the fragrant rice varieties cultivated in the fertile lands are urgently needed.

The Thai fragrant rice varieties are classified into two major groups: the highly fragrant "Thai Hom Mali" or "Thai Jasmine" rice and the less fragrant "Khao Hom" The "Thai Hom Mali," which is considered the most premium due to its soft-textured and aromatic cooking quality, consists mainly of the Khao Dawk Mali 105 (KDML105) variety and its mutagenized modern varieties such as RD15 and RD6 (Vanavichit et al. 2018). The "Khao Hom" rice, including Pathum Thani 1 (PT1) and RD43, has comparable cooking

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quality, e.g. low amylose content, but has significantly lower levels of aromatic compounds (Suwannaporn et al. 2007). KDML105 is the most well-known Thai fragrant rice variety. KDML105 was selected from its origin at Chonburi province, Thailand (Bureau of Rice Research and Development 2010). To achieve the highest quality, KDML105 is typically grown in selected areas in the north and northeastern Thailand where soil salinity is 2-8 dS m^{-1} EC (Vanavichit et al. 2018). KDML105 cultivated in the saline soil of the northeast contained a high content of 2-acetyl-1-pyrroline (2AP), e.g. 525 ppb 2AP compared to 87 ppb 2AP in the rice cultivated in the low-salinity soil of Thailand's central region (Yoshihashi et al. 2004). The increase in 2AP content is partly attributed to the accumulation of compatible solutes such as proline, which cannot be converted to γ-amino butyric acid in the fragrant rice varieties due to the non-functional *BADH2* allele and is instead redirected toward the synthesis of 2AP (Vanavichit and Yoshihashi 2010; Wakte et al. 2017). In contrast, the "Khao Hom" cultivars such as PT1 and RD43 are typically cultivated in the irrigated, low-salnity regions, resulting in a higher grain yield but a substantially lower amount of 2AP (Vanavichit et al. 2018).

Triazole-type plant growth retardants (PGR) such as paclobutrazol (PBZ) act as anti-gibberellins. PBZ is known to block the conversion of kaurene to kaurenoic acid in the gibberellin biosynthesis pathway through inhibition of kaurene oxidase (Dalziel and Lawrence 1984). PBZ application usually results in plant height and root length reduction by decreasing cell wall expansion along with increasing cell wall stiffness (Behringer et al. 1990; Potter and Fry 1993; Yang et al. 1996). Effects of PBZ on the reduction of vegetative growth had been reported in apricot tree (Arzani and Roosta 2004) and potato (Tekalign and Hammes 2005). In chrysanthemum, PBZ caused a decrease in stem diameter and pith cell length, leading to increased secondary xylem development, but adversely altered root cortical cell length leading to inhibited secondary vascular development (Burrows et al. 1992). As the vegetative growth is retarded by PBZ, nutrients become accumulated inside the plants. Thus, PBZ application can be beneficial to the plant productivity. For example, PBZ treatment at the vegetative stage increased potato tuber yield (Mabvongwe et al. 2016). Rice plants treated with PBZ had been shown to have increased chlorophyll content, tiller number, and yield (Pan et. al. 2013; Yim et al. 1997). Several studies also found that PBZ increased various kinds of compatible solutes and osmoprotectants, including proline, leading to higher water-deficit tolerance (Tesfahun 2018). Nonetheless, successful usage of PGR depends on various factors including chemical type, concentration, plant species, and plant growth stage (Mabvongwe et al. 2016).

Benefits of PBZ application to improve rice productivity, stress tolerance, and grain quality have not been intensively investigated and some of the previous studies showed variable results among rice genetic backgrounds. Since one of the clear effects of PBZ treatment is the accumulation of proline, which is linked with the production of 2AP in fragrant rice, we therefore tested whether foliar PBZ application at a suitable dosage and growth stage, which would not severely affect plant growth and grain yield performance, could enhance 2AP content of the KDML105 rice variety cultivated under low-salinity conditions. We also tested the effects on other "Khao Hom" fragrant varieties and a non-fragrant Thai rice variety. Our study demonstrated the potential use of PBZ to enhance the grain 2AP content of KDML105, thus allowing for cultivation of this high-value Thai Jasmine rice in low-salinity condition which would have less adverse effects on the plant growth and grain yield.

Materials and Methods

Plant materials

Seeds of rice *Oryza sativa* L. ssp. indica cv. KDML 105 were obtained from a propagating field in Mukdahan province, Thailand. Seeds of Pathum Thani 1 (PT1), Rice Department 43 (RD43), and Rice Department 31 (RD31) were obtained from the Rice Department, Ministry of Agriculture and Cooperatives, Thailand.

Growth conditions and treatments

Dry seeds were soaked in tap water for two days. Germinated seeds were densely sown into soil in a 4-inch pot. Average-size seedlings were individually transplanted into plastic planting bags (5 x10 inches) and placed in a plot flooded with about 1 inch of tap water for low-salinity condition. Plots were situated in a greenhouse until harvest. KDML105 rice plants were cultivated at NSTDA, Pathum Thani province, Thailand (N 13.76352, E 100.52868), while the other cultivars were planted at the Faculty of Science, Mahidol University, Bangkok, Thailand (N 14.04515, E 100.36090). Salt stress was simulated by 0.4% NaCl supplementation in water at 45 days after sowing (DAS).

Commercial PBZ solution (Sotus International, Thailand) at 50, 100, or 150 ppm were sprayed once directly onto whole leaf blade until runoff. Water was similarly applied as control (0 ppm). For KDML105 rice plants, results from PBZ application at two different growth stages were compared: vegetative stage (60 DAS) and reproductive stage (80 DAS). For PT1, RD43, and RD31 rice plants, 100 ppm PBZ was sprayed during vegetative stage (66 DAS). Three plants were used for each treatment group.

Measurement of growth performance, yield, and grain quality

At the mature grain stage of each studied cultivar, shoot height, root length, and leaf area were measured. Yield components in terms of panicle length, 100-grain weight, percentage of filled grains, and grain yield per plant were examined. Grain quality was determined using 2AP levels and amylose content. Levels of 2AP were measured by headspace gas chromatography following a method by

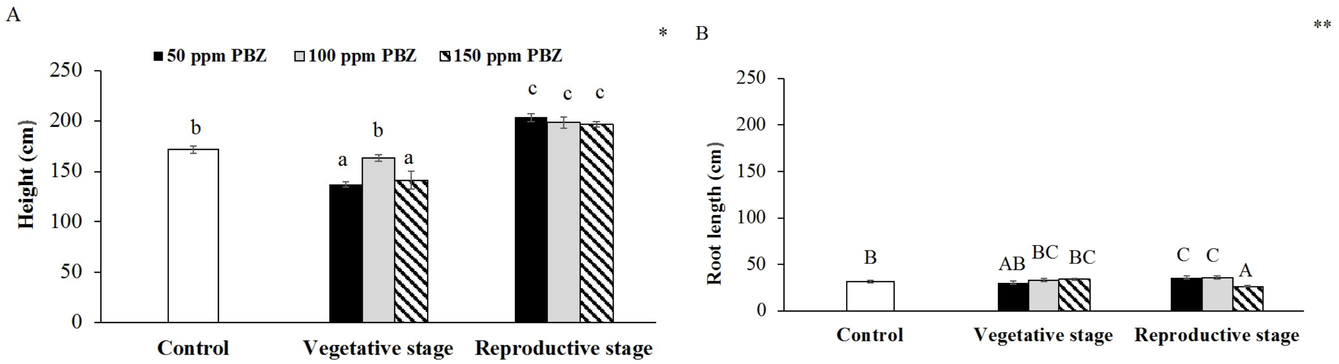

Fig. 1. Shoot height (A) and root length (B) at mature grain stage of KDML105 under control (untreated) or in response to 50, 100, or 150 mg L^{-1} paclobutrazol PBZ)) application at vegetative and reproductive stages. * and ** indicates significant difference at $P \leq 0.01$ and $P \leq 0.05$, respectively, (one-way ANOVA). Values that share a letter are not significant different (*post-hoc* DMRT, $P \leq 0.05$).

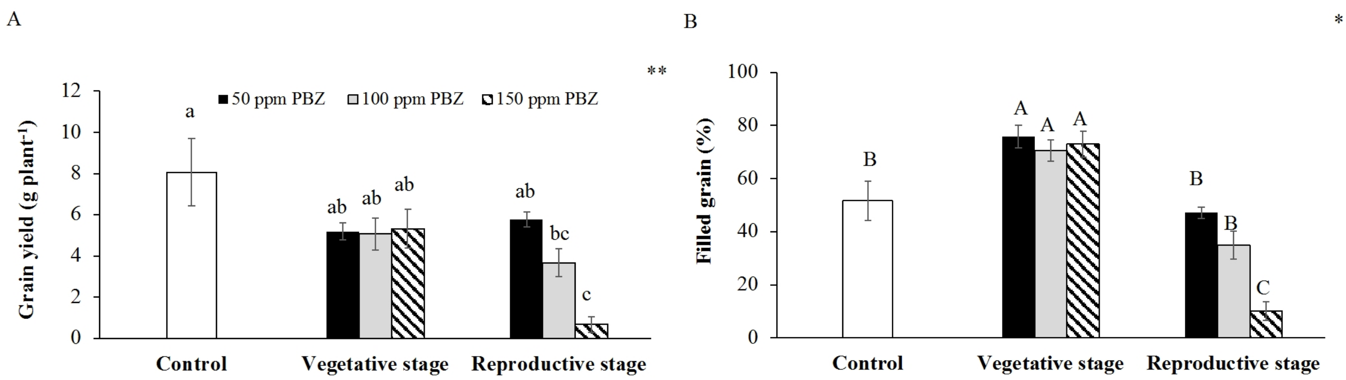

Fig. 2. Grain yield (A) and percent of filled grains (B) at mature grain stage of KDML105 under control (untreated) or in response to 50, 100, or 150 mg L^{-1} paclobutrazol (PBZ) application at vegetative and reproductive stages. * and ** indicates significant difference at $P \leq 0.01$ and $P \leq 0.05$, respectively (one-way ANOVA). Values that share a letter are not significant different (*post-hoc* DMRT, $P \leq 0.05$).

Sriseadka et al. (2006). Amylose content was measured using the AMYLOSE/AMYLOPECTIN assay kit (Megazyme International, Ireland) according to the manufacturer's protocol. Proline content of 'KDML105' grains was measured according to Bates et al. (1973).

Statistical analysis

The study was conducted using factorial experiments with completely randomized design. Mean values were compared using one-way ANOVA followed by Duncan's new multiple range test (DMRT). The paired-sample T-test was used to assess the differences between cultivars. The mean values of 3 replications were shown at significant level of $P \leq 0.05$ or ≤ 0.01 using SPSS software (SPSS Inc. USA).

Results

PBZ application affected growth and yield performances in KDML105 rice plants

PBZ at 50, 100, and 150 ppm was sprayed onto KDML105 rice plants at vegetative or reproductive stages. Growth responses of KDML105 showed significant shoot height reduction of about 17-20% compared to the control plant after 50 or 150 ppm PBZ was sprayed at the vegetative stage, although the application of PBZ at all three concentrations during the reproductive stage led to a slight but noticeable shoot height increase (Fig. 1A). The PBZ application had little or no effect on root length, except the 150 ppm PBZ treatment at the reproductive stage, which slightly decreased the root length (Fig. 1B). PBZ did not significantly alter other shoot performances, including the total leaf area (data not shown).

The application of 50, 100, or 150 ppm PBZ during the vegetative stage also resulted in a decrease, although not statistically significant in our study, in grain yield of KDML105 (Fig. 2A). Further yield reduction and a decrease in percent filled grains were observed in a dose-dependent manner when PBZ was sprayed during the reproductive stage (Fig. 2B). In contrast, the percentage of filled grains was improved upon the PBZ application at the vegetative stage.

PBZ application led to a higher level of 2AP in KDML105 rice grains under low-salinity conditions

Based in the results described above for KDML105, the PBZ application at the vegetative stage was shown to be less detrimental to the plant growth and grain yield compared to the application at reproductive stage. Thus, to test the effects on 2AP production, PBZ was sprayed only at the vegetative stage in two concentrations at 50 and 100 ppm. Fig. 3A shows the effect of PBZ on the grain 2AP content, which is a main aromatic compound of the KDML105 jasmine rice. Under the control low-salinity growth condition (tap water, no NaCl added) and no PBZ application, the KDML105 grains were shown to produce about 1.0 µg/g of 2AP which is considered to be a low level of the aroma. In comparison, under the salt-stress condition (0.4% NaCl), the KDML105 grains accumulated approximately 1.6 µg/g 2AP. The application of 100 ppm PBZ to the KDML105 rice plants grown under the low-salinity condition enhanced the 2AP level as their grains produced approximately 1.4 µg/g 2AP, which is nearly the level found under the salt-stress condition. Since proline is linked to the 2AP biosynthesis in fragrant rice, we also tested whether the effect of PBZ on 2AP production was attributable to an increase in the proline content. The results showed a 4.9-fold increase in proline concentration in response to the 100 ppm PBZ application (Fig. 3B).

PBZ application marginally affected growth, yield, and grain quality in PT1, RD43, and RD31 cultivars

Because the PBZ foliar spray at vegetative stage was beneficial for the aromatic quality of KDML105, it was hypothesized that PBZ might also improve productivity and/or aroma of other rice cultivars. To test this hypothesis, two fragrant cultivars namely PT1 and RD43, and a non-fragrant cultivar RD31 were sprayed with 100 ppm PBZ at the vegetative stage. The PBZ spray caused significant height reduction of both fragrant cultivars: PT1 and RD4, but not RD31 (Fig. 4). The root length was unaffected in PT1 and RD43, and increased slightly in the RD31. Similarly to KDML105, the grain yields of all three rice varieties decreased in response to the PBZ application, whereas the percentage of filled grains was largely unchanged (Fig. 5). However, it should be noted that the reductions in grain yield and percent filled grains were minimal in comparison to the effects of salt stress. The influence of PBZ and salt stress (0.4% NaCl) on panicle length and 100-grain weight is shown in Table 1. Although PBZ significantly reduced panicle length, the

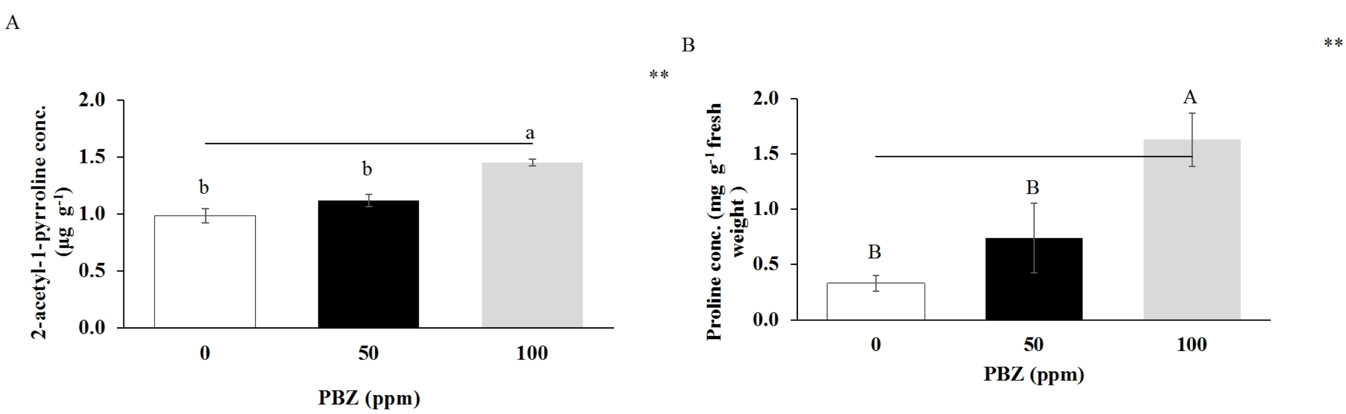

Fig. 3. Concentration of grain 2-acetyl-1-pyrroline (A) and flag-leaf proline (B) of KDML105 at milky stage in response to 0, 50, or 100 mg L^{-1} paclobutrazol (PBZ) application at vegetative stage. Line indicates 2-acetyl-1-pyrroline or proline concentration at milky stage of KDML105 plant grown under salt stress condition, without paclobutrazol application. * and ** indicates significant difference at $P \leq 0.01$ and $P \leq 0.05$, respectively (one-way ANOVA). Values that share a letter are not significant different (*post-hoc* DMRT, $P \leq 0.05$).

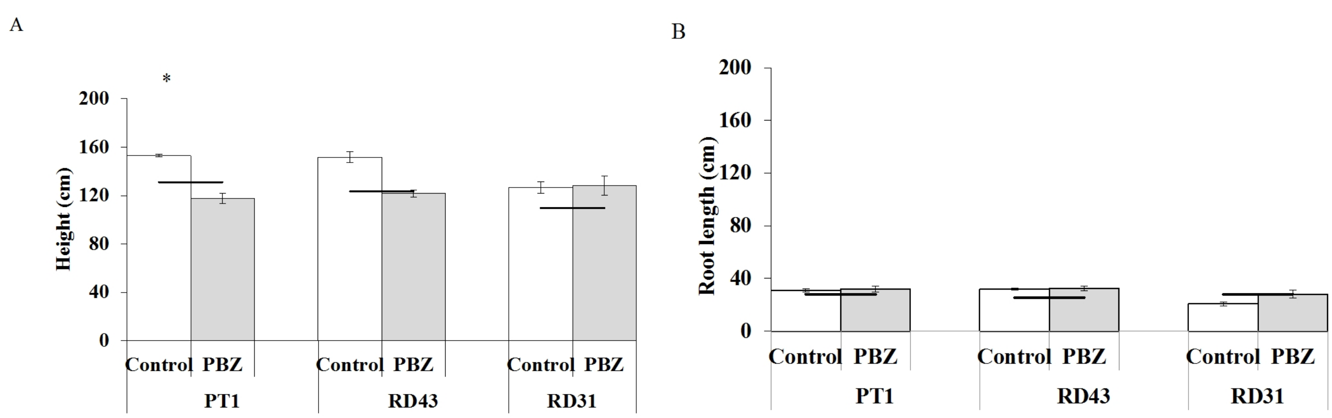

Fig. 4. Height (A) and root length (B) at mature grain stage of PT1, RD43 and RD31 in response to 0 or 100 mg L^{-1} paclobutrazol application at vegetative stage. Line indicates performance of rice plants grown under salt stress condition, without paclobutrazol application. ** indicates significant difference at $P \leq 0.01$(paired-sample T-test).

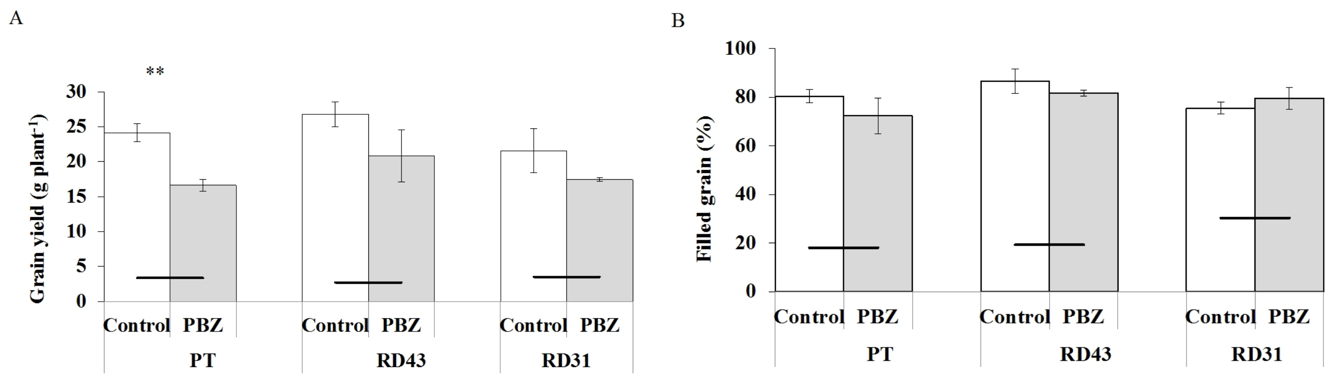

Fig. 5. Grain yield (A) and percent of filled grains (B) of PT1, RD43 and RD31 in response to 0 or 100 mg L^{-1} paclobutrazol application at vegetative stage. Line indicates performance of rice plants grown under salt stress condition, without paclobutrazol application. ** indicates significant difference at $P \leq 0.01$ (paired-sample T-test).

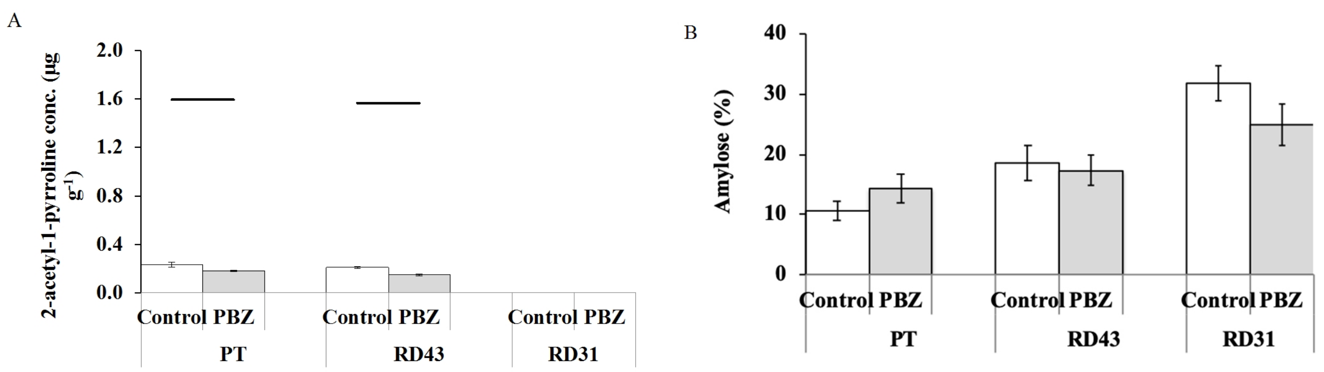

Fig. 6. 2-Acetyl-1-pyrroline concentration (A) and amylose content (B) in grain of PT1, RD43 and RD31 in response to 0 or 100 mg L^{-1} paclobutrazol application at vegetative stage. Line indicates 2-acetyl-1-pyrroline level in grain of KDML105 grown under salt stress condition. * indicates significant difference at $P \leq 0.05$ using (paired-sample, T-test).

Table 1. Yield components at mature grain stage of PT1, RD43, RD31 grown under various conditions: control, salt stress (0.4% NaCl), and 100 mg L^{-1} paclobutrazol application at vegetative stage (no salt stress).

Cultivars	Conditions	Panicle length (cm)†	100-grain weight (g)†
PT1	Stress	24.21 b*	1.94
	Control	27.91 a	2.28
	Paclobutrazol	21.77 c	2.53
RD43	Stress	15.34 e	2.30
	Control	23.59 b	2.54
	Paclobutrazol	21.46 c	2.58
RD31	Stress	18.48 d	2.04
	Control	22.83 bc	2.25
	Paclobutrazol	19.35 d	2.46
Significant level			
Cultivars		**	**
Conditions		**	**
Cultivars x Conditions		**	ns

†Values that share a letter are not significantly different at $P \leq 0.01$ (*post-hoc* DMRT). ** indicates significant difference at $P \leq 0.01$ (two-way ANOVA); ns, not significant.

100-grain weight was not significantly affected.

Next, we examined whether PBZ could improve the aroma content of PT1, RD43, and RD31 rice grains. As expected, the untreated 2AP contents of PT1 and RD43 grains were approximately 0.2 µg/g, which was about eight-time lower than that found in KDML105 grown under salt-stress condition. The non-fragrant RD31 did not produce the 2AP compound. In contrast to KDML105, the PT1, RD43, and RD31 grains did not increase in the 2AP levels in response to the PBZ application.

The amylose content is another important factor of the rice grain quality, with low amylose preferable among many consumers of aromatic rice. The amylose content in the control RD31 grains was above 30%, which placed it under the category of high-amylose rice (IRRI 2006). After PBZ treatment, the amylose level was improved to a level categorized as an intermediate-amylose rice (20-25%). The amylose contents of PT1 and RD43 grains were largely unaffected.

Discussion

The shoot growth and grain yield reduction observed for the KDML105 rice plants sprayed with PBZ at the vegetative stage was consistent with the fact that PBZ is a plant growth retardant. The reduction of plant height may be viewed as advantageous since there has already been a trend to develop modern cultivars with shorter plant height (Sasaki et al. 2002). The height reduction observed in this experiment was indeed a confirmation that the PBZ concentration and method of application were effective in interfering with the endogenous gibberellin. The spray time-dependent effect was interesting, although not unexpected, since the plant during different growth stages is likely to be differentially affected by PGR. Nonetheless, these results suggest that PBZ should be applied at a suitable concentration and growth stage to achieve desirable effects.

Previous research found that rice grain yield and grain weight were comparable in control plants and plants with 25 ppm PBZ (Goufo et al. 2011) or 50 ppm PBZ (Pan et al. 2013) applied at heading stage. However, higher PBZ levels caused reduction in grain yield. In this study, PBZ application at the early growth or vegetative stage gave marginal, statistically insignificant grain yield reduction and higher percentage of filled grain. This might be attributed to the accumulation of assimilates due to the reduction of shoot growth conferred by the PBZ application, leading to the increased percent filled grain.

The use of PBZ application to increase the 2AP content in rice has previously been reported with no success. For example, Goufo et al. (2011) found that fragrant rice 'Guixiangzhan' and 'Peizaruanxiang' had 30-37% lower 2AP content after 25 ppm PBZ treatment at heading stage compared to the control plants. In this study, we showed more than 40% increase in the 2AP obtained from the rice plants grown under low-salinity condition following the 100 ppm PBZ application at vegetative stage. Therefore, this finding might permit cultivation of the KDML105 rice in irrigated, fertile areas to obtain a high grain yield simultaneously with a high level of 2AP production. The discrepancy in our results and that of Goufo et al. (2011) could be attributed to several factors including the differences in PBZ concentrations and growth stage at which PBZ was applied. However, as discussed below, it is quite likely due to the differences in physiology and metabolism imparted by the rice genetic backgrounds. The mechanism of the 2AP induction by PBZ has not been fully elucidated. Previous studies showed that some PGRs including PBZ could increase the levels of proline and polyamines, such as spermidine and spermine (Grossmann et al. 1993; Rabert et al. 2014). Both proline and polyamines may be metabolized toward the 2AP biosynthesis (Yoshihashi et al. 2002). This effect was confirmed by the rise in proline level in response to the PBZ treatment in our study and suggested that the elevated level of 2AP in PBZ-treated KDML rice grains was attributed at least in part to the increased accumulation of proline.

We examined the effect of PBZ on the 2AP production in additional rice cultivars, including PT1 and RD43. PT1 and RD43 were chose because these "Khao Hom" fragrant rice cultivars have good cooking quality and a higher grain yield than KDML105, but a much lower amount of fragrance – thus, despite their potential in the rice market, they are not as preferred by the consumers and not as widely cultivated, about 0.24 million ha in total. However, our results did not show an increase in 2AP content in PT1 and RD43 as well as the non-fragrant rice RD31. Therefore, the effect of PBZ application on the 2AP content may be specific to KDML105, or may be variable among rice varieties. In fact, factorial analysis of panicle length and 100-grain weight revealed that there was significant interaction between the treatment and the genetic background. Although the PBZ did not cause significant reduction of yield in KDML105, even at the 150 ppm concentration, it did lower the yield in PT1 and RD43. A previous report showed that the yield of 'Peizataifeng' and 'Huayou 86' increased after 50 ppm PBZ treatment (Pan et al. 2013). Likewise, the filled grain percentage of KDML105 was increased by PBZ, but unchanged in other cultivars. Based on this result and the others, application of PBZ must be tailored to each cultivar to achieve the desired outcome and further studies are needed.

In this study, we also examined the effect of PBZ on amylose content because a large sector of consumers, especially those who prefer fragrant rice, prefer the low-amylose, soft-textured cooked rice. RD31, 31% amylose, is categorized as high amylose, whereas RD43, 18%, is considered as low amylose but still much higher than KDML105 and PT1. Although amylose content is largely determined by genetic background, several environmental factors such as air temperature and soil nutrients had been demonstrated to affect the amylose content (Patindol et al. 2015). Amylose content could also be improved by some PGRs. For example, PBZ had been previously shown to increase the amylose content of the super hybrid rice 'Peizataifeng' (Pan et al. 2013). Our results also demonstrated the effect of PBZ to substantially lower the amylose content of RD31 and to a smaller extent of RD43. Nonetheless, the effect of PBZ on amylose content may depend on the genetic background, as the PBZ application slightly increases the amylose content of PT1. Thus, PBZ may have an additional benefit on the amelioration of amylose content and should be further investigated.

Conclusions

PBZ had a possibility to enhance productivity, aroma, and amylose content of rice grains when applied at a suitable rate and growth stage. For the KDML105 cultivar, PBZ application was shown to increase the 2AP grain content to a level that is comparable to the amount produced under salt-stress condition. Moreover, PBZ also improved percent filled grains without significant yield loss. The potential use of PBZ therefore provides an opportunity for obtaining high-quality KDML105 grains at a greater yield when cultivated in areas with low-salinity. For RD31, the amylose content could be improved with PBZ application. These beneficial effects of PBZ should be further validated in field trials. The variable responses to PBZ application among cultivars warrants further studies to determine suitable dosage, timing, and other factors concerning the methods of PBZ application, and further studies to understand the basis of genetic interactions.

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