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Research Article

Regulation of curcuminoids, photosynthetic abilities, total soluble sugar, and rhizome yield traits in two cultivars of turmeric (*Curcuma longa*) using exogenous foliar paclobutrazol

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Abstract

Paclobutrazol (PBZ) is a member of plant growth retardants, commonly applied for growth regulation, yield improvement, and biotic and abiotic stress alleviation. However, the effects of PBZ on turmeric (*Curcuma longa* L.; Zingiberaceae), a rhizomatous herb, have not been well established. The objective of this investigation was to gain a better understanding of the effect of PBZ on two different varieties of turmeric plants, 'Surat Thani' ('URT'; high curcuminoids >5% w/w) and 'Pichit' ('PJT'; low curcuminoids <3% w/w). Pseudostem height of cv. 'PJT' treated by 340 μM PBZ was significantly decreased by 14.82% over control, whereas it was unchanged in cv. 'URT'. Interestingly, leaf greenness (SPAD value), maximum quantum yield of PSII (F_v/F_m) and photon yield of PSII (Φ_{PSII}) in cv. 'PJT' treated by 340 μM PBZ were significantly elevated by 1.47, 1.28 and 1.23 folds, over control respectively. Net photosynthetic rate (P_n) in cv. 'PJT' declined by 38.58% (340 μM PBZ) over control, as a result of low levels of total soluble sugars (TSS; 127.8 mg g^{-1} DW) in turmeric rhizome. A positive relation between photosynthetic abilities and aerial fresh weight was demonstrated. In addition, a negative relationship between TSS and total curcuminoids was evidently found (R^2 = 0.4524). Curcuminoids yield in turmeric rhizomes significantly dropped, depending on the degree of exogenous foliar PBZ applications. In summary, cv. PJT was found to be very sensitive to PBZ application, whereas rhizome yield and growth traits and high amount of curcuminoids were retained in cv. 'URT'. Plant growth retention in turmeric cv. 'URT' using 170 mM PBZ foliar spray without negative effects on rhizome biomass and total curcuminoids content was demonstrated.

Keywords: *Curcuma longa*; curcuminoids; growth parameters; paclobutrazol; physiological responses; total soluble sugar

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Introduction

Turmeric (*Curcuma longa* L.; Zingeberaceae) is a rhizomatous herb, which has been widely cultivated as a spice in tropical regions, especially in India (Akram *et al.*, 2010). Turmeric plant contains curcuminoids and has been used as food ingredient, edible dye and traditional medicine (Sharma *et al.*, 2005; Anandaraj and Sudharshan, 2011). There are three major kinds of curcuminoids, namely curcumin (CUR), demethoxycurcumin (DEM) and bis-demethoxycurcumin (BIS) (Akram *et al.*, 2010; Li *et al.*, 2011). Of these, CUR is the dominant and biologically important active constituent (Prasad *et al.*, 2014; Kocaadam and Şanlier, 2017) with high potent antioxidant, anti-inflammatory and cancer preventive properties (Frank *et al.*, 2003; Akram *et al.*, 2010; Gupta *et al.*, 2012, 2013). An increasing demand of turmeric varieties for the food, pharmaceutical, and cosmetic industries has been reported due to its medicinal properties. A novel cultivation system to yield high curcuminoids and high biomass of rhizomes in turmeric plant still needed to be discovered (Deepa *et al.*, 2017; Sandeep *et al.*, 2017). In India, high yielding turmeric cultivars (HYTCs), namely 'Palam Pitamber' (32.94 t ha^{-1}) and 'Palam Lalima' (32.35 t ha^{-1}) are cultivated as elite varieties, with high rhizome productivity, profitability, and curcuminoids yield (Choudhary and Rahi, 2018). However, in Thailand has only two cultivars, namely 'Trang 1' and 'Trang 2', have been approved by the department of Agriculture, but they have low rhizome productivity and curcuminoids content. Recently, turmeric cv. 'URT' with high curcuminoids (>5% w/w) has been reported (Chintakovid *et al.*, 2021 a, b). In addition, low curcuminoids genotype, cv. PJT have been selected from the turmeric plant characterization to play as negative check.

Paclobutrazol [PBZ; (2RS, 3RS)-1-(4-chlorophenyl)-4,4-dimethyl-2-(1H-1,2,4-triazol-1-yl)pentan-3-ol] is a plant growth retardant, which affects the growth rate in higher plants, especially potted ornamental species (Whipker and Hammer, 1997; Krung *et al.*, 2007; Carver *et al.*, 2014). It also regulates carbohydrate metabolism to control off-season flowering and fruit set in several fruit species (Yeshitela *et al.*, 2004; Arzani *et al.*, 2009; Brar, 2010; Martínez-Fuentes *et al.*, 2013; Upreti *et al.*, 2014) and lignin synthesis and produce a strong stalk against lodging in rice (Sinniah *et al.*, 2012), maize (Kamran *et al.*, 2018a) and wheat (Kamran *et al.*, 2018b). Physiological adapted strategies, yield attributes and qualities in PBZ treated plants in various microclimate environments have been validated in many plant species (Meena *et al.*, 2014; Tekalign and Hammes, 2005a, b; Kamran *et al.*, 2018c). Moreover, it has been widely applied to alleviate abiotic stresses including drought, salinity and extreme temperature (Soumya *et al.*, 2017; Chandra and Roychoudhury, 2020). In *C. alismatifolia*, PBZ application has been reported to enhance off-season production (Boontiang *et al.*, 2019) and drought tolerant abilities (Jungklang *et al.*, 2017). *C. gracillima* and *C. thorelii* and *C. alismatifolia* were found to be most sensitive (Sarmiento and Kuehny, 2003). However, the basic information of foliar application and optimum doses of PBZ in *C. longa* is still lacking. In addition, pseudostem (up to 1 m) and plant canopy (8-12 leaves with up to 1 m long) of turmeric require a long distance between row and plant spacing in agricultural practices (Ravindran 2007). We hypothesized that PBZ-treatment can retard the pseudostem height and plant canopy in turmeric without having negative effects on rhizome yield traits and total curcuminoids in rhizomes. Compact canopy control using PBZ is an alternative way to make a high density of turmeric plant production in SMART greenhouse. The rationale of this study indicating that we used PBZ to investigate whether it can regulate the curcuminoid content and, thus, morpho-physiological traits. The objective of present study was to investigate the regulation of morphological growth characters, physiological changes, rhizome yield traits, and total curcuminoids in *C. longa* using PBZ foliar spray under controlled greenhouse conditions.

Materials and Methods

Plant materials and PBZ treatments

Master stock of turmeric rhizomes, cvs. 'Surat Thani' ('URT'; high curcuminoids) and 'Pichit' ('PJT'; low curcuminoids) were procured from Department of Agriculture, Ministry of Agriculture and Cooperative, Thailand. The rhizomes were incubated into peat moss until two true leaves were emerged and then individual plantlet was transferred into plastic bags (15 × 30 cm) containing 10 kg garden soil (EC=2.687 dS m^{-1}; pH=5.5; organic matter=10.36%; total N=0.17%; total P=0.07%; total K=1.19%) under greenhouse conditions (32±2 °C Day/28±2 °C night air temperature and 85±5% relative humidity) for 5 months. Slow releasing fertilization (Osmocoat; 13:13:13; N:P:K) was applied twice to each plant, i) 10 g bag^{-1} before planting into soil substrate, and ii) 10 g bag^{-1} at four months after transplanting (Akamine *et al.*, 2007). Uniform plant materials were selected for exogenous application of different concentrations of PBZ, i.e., 0 (control), 170 and 340 µM (100 mL $plant^{-1}$ together with 0.25 mL 9.6% w/v linear alkalbenzene sulfonate, 6.4% w/v sodium laurylether sulfate and 0.125% w/v alkyl polygucoside) from four and five months-old seedlings, which were harvested after eight months. Two times of exogenous PBZ foliar-spray at 4 and 5 months after planting were practically applied and then cultivated until harvesting period at 8 months. At harvesting period, overall growth performance, leaf greenness (SPAD), chlorophyll fluorescence, net photosynthetic rate, and soluble sugars were measured in the leaf tissues as well as total curcuminoids and total soluble sugars in rhizomes were assayed.

Growth performances

Pseudostem height, leaf length, leaf width, pseudostem fresh weight, pseudostem dry weight, leaf area, root length, number of roots, root fresh weight and root dry weight were measured as growth parameters. Leaf area was measured by Leaf Area Meter (Model CL-203, CID® Inc, WA, USA). In addition, rhizome yield traits like rhizome width, fresh and dry weight of rhizomes were measured.

Physiological measurements

Leaf greenness (SPAD value) in the second fully expanded leaf from the shoot tip of each treatment was measured using Chlorophyll Meter (SPAD-520 Plus, Konica Minolta, Osaka, Japan) according to Hossain *et al.* (2000).

Chlorophyll fluorescence emission was measured from the adaxial surface of second fully expanded leaf from the shoot tip using a fluorescence monitoring system (model FMS 2; Hansatech Instruments Ltd., Norfolk, UK) in the pulse amplitude modulation mode (Loggini *et al.*, 1999). A leaf kept in dark for 30 min was initially exposed to the modulated measuring beam of far-red light (LED source) with typical peak at wavelength 735 nm. Initial fluorescence (F_0) and maximum (F_m) fluorescence yields were measured under weakly modulated red light (<0.5 µmol m^{-2} s^{-1}) with 1.6 s pulses and then exposed to saturating light (>1,500 µmol m^{-2} s^{-1} PPFD) and calculated using FMS software for Windows®. The variable fluorescence yield (F_v) was calculated using the equation: $F_v=F_m-F_0$. The ratio of variable to maximum fluorescence (F_v/F_m) was calculated as the maximum quantum yield of PSII photochemistry. The photon yield of PSII (Φ_{PSII}) in the light was calculated as: $\Phi_{PSII} = (F_m'-F)/F_m'$ after 45 s of illumination, when steady state was achieved (Maxwell and Johnson, 2000).

Net photosynthetic rate (P_n; µmol m^{-2} s^{-1}), stomatal conductance (g_s; mmol CO_2 m^{-2} s^{-1}), transpiration rate (E; mol m^{-2} s^{-1}) and a ratio of P_n/E (water use efficiency, WUE) in second fully expanded leaf were measured using a portable photosynthesis system fitted with an infrared gas analyzer (LI 6400, LI-COR, Lincoln, NE, USA), according to the method of Cha-um *et al.* (2007). The E and g_s were measured continuously by monitoring the H_2O content of air entering and exiting the IRGA head space chamber. The flow rate of air in sample line and micro-chamber temperature was set at 500 µmol m^{-2} s^{-1} and 27±1 °C block temperature, respectively. The light intensity was adjusted to 1,000 μmol m^{-2} s^{-1} PPFD using 6400-02B red-blue LED light source.

Biochemical assays

For the estimation of curcumin content, the dry-harvested rhizomes were cleaned thoroughly with tap water, cut into small pieces and allowed to dry in hot air oven at 50 °C for 96h. The pieces are then powdered by using Moulinex™ Blender (Groupe SEB, France). Fifty milligrams of dried powder were transferred into vial and then 5 mL of methanol were added for extraction. The mixture was vortexed vigorously, sonicated for 30 min and then the supernatant was filtered through Whatman® No.1. The extracted solution was dried and stored in the deep freezer (-20 °C) prior to curcuminoids assay. For curcuminoids analysis, dried extracted samples were suspended in 1 mL methanol and then filtrated through 0.45 μm pore size (MilliporeTM nylon filter). Ten microliters of sample were injected into injection loop and analyzed by HPLC (Waters Associates, Milford, MA, USA) equipped with Water 2998 photodiode array detector at 425 nm. BIS, DEM and CUR were separated using C_{18} (VertisepTM UPS) column incubating under 25 °C. The mobile phase consisted of acetonitrile (100% HPLC grade) and acetic acid (0.25%, v/v). The elution was carried out with a gradient set with a flow rate of 0.8 mL min^{-1}. The solvent gradient was: 50% acetonitrile up to 8 min, 50 to 40% acetonitrile from 8 to 10 min, 40% acetonitrile constant from 10 to 15 min, and 40 to 50% acetonitrile from 15 to 16 min (Pothitirat and Grisanapan, 2007).

Soluble sugars (sucrose, glucose, and fructose) in the leaf tissues (second fully expanded leaf from the shoot tip) and primary rhizome were assayed following the method of Karkacier *et al.* (2003). In brief, fifty-milligrams of freeze-dried sample were ground in a mortar with liquid nitrogen. One mL of nanopure water was added and centrifuged at 12,000 ×g for 15 min. The supernatant was collected and filtered through a 0.45 μm membrane filter (VertiPure™, Vertical®, Vertical Chromatography Co., Ltd., Thailand). Ten microliters of the filtrate were injected into a Waters HPLC equipped with a MetaCarb 87C column and a guard column (Agilent Technologies, Santa Clara, CA, USA). Deionized water was used as the mobile phase at a flow rate of 0.5 mL min^{-1}. The online detection was performed using a Waters 410 differential refractometer detector and the data was analysed by Empower® software. Sucrose, glucose, and fructose (Fluka, USA) were used as the standards.

Statistical analysis

The experiment was designed as 3 × 2 factorials in a Completely Randomized Design (CRD) with 6 replications (n = 6) in each treatment. Analysis of variance (ANOVA) in each parameter was analysed using SPSS software. The mean values were compared using Tukey's HSD and analysed by SPSS software version 11.5. Pearson's correlation between SPAD and F_v/F_m, F_v/F_m and Φ_{PSII}, P_n and pseudostem dry weight, TSS in rhizomes and total curcuminoids was calculated.

Results

Growth performances

Overall morphological characteristics were studied in both aerial and underground parts of two turmeric genotypes sprayed with different PBZ treatments (Figure 1). Pseudostem height of cv. 'PJT' (54.3 cm) without PBZ treatment was higher than cv. 'URT' (37.0 cm) by 1.47 folds. Pseudostem height in 'PJT' was sensitive to 340 μM PBZ treatment, and significantly retarded by 14.73% over control, whereas it was unchanged in 'URT' (Figure 2a). Retardation of psudostem height in recent study depended on the turmeric genotypes and the degree of PBZ treatments. In aerial part, pseudostem fresh weight (STFW), pseudostem dry weight (STDW), leaf length (LL) and leaf width (LW) in 'PJT' without PBZ treatment were higher than in 'URT' by 1.67, 1.81, 1.26 and 1.39 folds, respectively (Table 1). Under 340 μM PBZ treatment, STFW (121.1 g) and STDW (11.4

g) in 'URT' turmeric plants were lower than in 'PJT' by 45.10% and 47.71%, respectively. Under without PBZ condition, LL and LW in 'PJT' were greater than in 'URT'. Additionally, leaf area (LA) in both genotypes were unchanged (Table 1). Moreover, LL, LW and leaf area (LA) in both genotypes were unchanged (Table 1). In underground part, root fresh weight (RTFW), root dry weight (RTDW), root length (RTL), number of roots (NRT) and rhizome width (RhW) in 'PJT' was greater than in 'URT' by 1.63, 1.82, 1.37, 1.68 and 1.2 folds, respectively (Table 2). Under 340 μM PBZ treatment, RTFW, RTDW, RTL and NRT in 'URT' were significantly decreased by 38.68%, 47.34%, 32.73% and 54.43% over 'PJT', respectively (Table 2). In addition, RTFW, RhW and rhizome fresh weight (RhFW) in 'PJT' plants treated with 340 μM PBZ were significantly declined by 34.16%, 26.55% and 55.96% over control (0 μM PBZ), respectively. Reduction in RhW and RhFW parameters was dependent on exogenous PBZ foliar concentrations (Table 2).

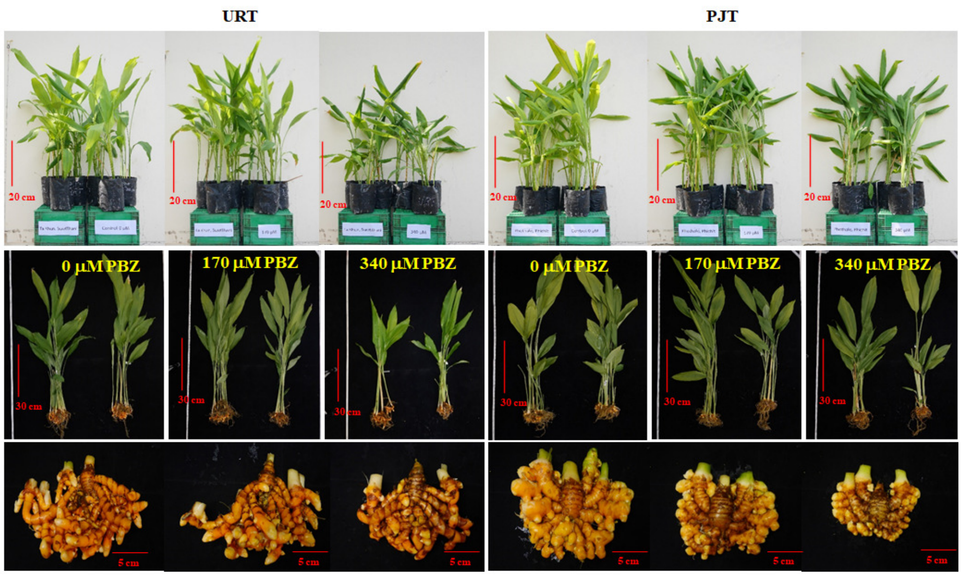

Figure 1. Morphological characteristics of two turmeric varieties, URT and PJT, upon exogenous foliar application by 0 (control), 170 and 340 μM PBZ at vegetative stage prior to harvest at maturity (8 months-old) under the greenhouse conditions

Table 1. Pseudostem fresh weight (STFW), pseudostem dry weight (STDW), leaf length (LL), leaf width (LW) and leaf area (LA) of two turmeric cultivars, URT and PJT, upon exogenous foliar application by 0 (control) 170 and 340 μM PBZ at vegetative stage prior to harvest at maturity (8 months-old) in the greenhouse conditions. Data presented as mean ± SE (n = 6)

Variety	PBZ (μM)	STFW (g)	STDW (g)	LL (cm)	LW (cm)	LA (cm^2)
URT	0	171.6±18.1bc	14.8±1.6bc	40.3±1.7b	8.7±1.0b	2300±253ab
	170	164.8±25.9bc	15.5±2.4bc	45.2±1.9ab	9.6±0.5ab	2200±409ab
	340	121.1±13.4c	11.4±1.2c	44.1±2.8ab	10.7±0.5ab	1507±198b
PJT	0	287.1±23.3a	26.8±2.5a	50.8±2.6a	12.1±0.6a	2773±273ab
	170	295.7±22.5a	27.4±2.2a	47.1±2.2ab	11.4±0.6ab	3486±422a
	340	220.6±14.9ab	21.8±1.7ab	46.7±2.8ab	13.0±0.4a	2831±315ab
Significant level						
Var		**	**	*	**	**
PBZ		**	*	ns	*	ns
Var × PBZ		ns	ns	ns	ns	ns

ns, * and ** represent non-significant, significant ($p \le 0.05$) and highly significant ($p \le 0.01$), respectively. Different letters in each column represent significant difference at $p \le 0.05$ according to Tukey's HSD test.

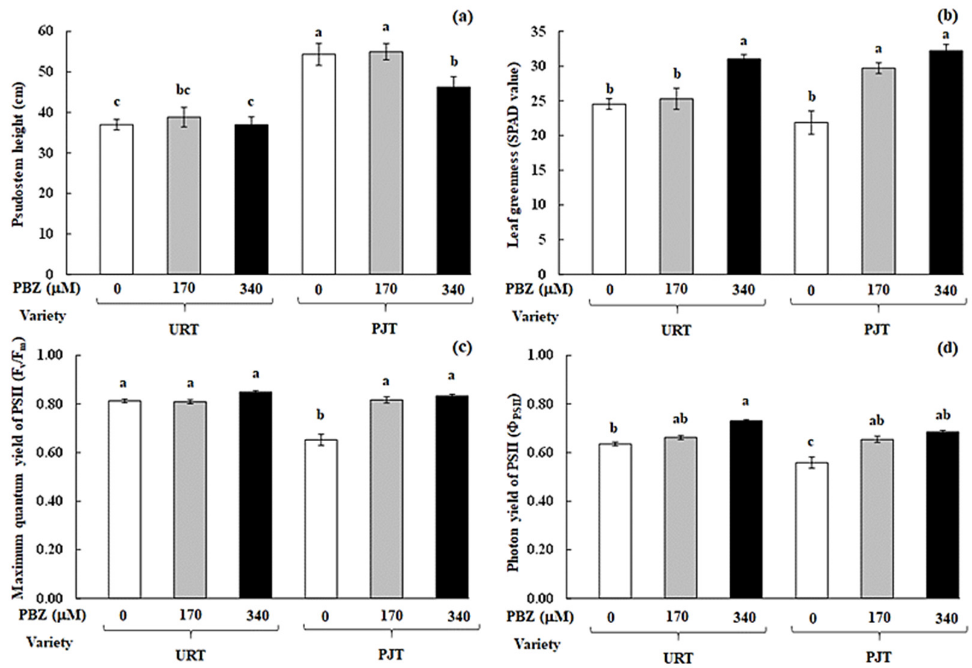

Figure 2. Pseudostem height (a), leaf greenness (SPAD; b), maximum quantum yield of PSII (F_v/F_m; c) and photon yield of PSII (Φ_{PSII}; d) of two turmeric varieties, URT and PJT, upon exogenous foliar application by 0 (control), 170 and 340 µM PBZ at vegetative stage prior to harvest at maturity (8 months-old) under the greenhouse conditions

Data presented as mean ± SE ($n = 6$). Different letters along each bar represent significant difference according to Tukey's HSD test at $p \leq 0.05$.

Table 2. Root fresh weight (RTFW), root dry weight (RTDW), root length (RTL), number of roots (NRT), rhizome width (RhW) and rhizome fresh weight (RhFW) of two turmeric cultivars, URT and PJT, upon exogenous foliar application by 0 (control), 170 and 340 µM PBZ at vegetative stage prior to harvest at maturity (8 months-old) in the greenhouse conditions

Variety	PBZ (µM)	RTFW (g)	RTDW (g)	RTL (cm)	NRT	RhW (cm)	RhFW (g)
URT	0	39.5±2.6bc	2.74±0.21cd	37.2±0.6b	50±4b	14.7±0.6b	208.8±14.6ab
	170	34.7±4.4bc	2.97±0.51cd	42.2±2.6ab	44±6b	14.3±1.0b	181.9±18.4b
	340	26.0±3.4c	1.98±0.17d	37.2±3.1b	36±6b	14.2±0.9b	159.1±12.4bc
PJT	0	64.4±4.6a	4.98±0.33ab	51.0±3.9a	84±13a	17.7±0.7a	287.0±11.2a
	170	62.5±3.5a	5.67±0.51a	42.8±5.1ab	100±7a	14.8±0.5b	179.0±19.4b
	340	42.4±2.4b	3.76±0.21bc	55.3±8.6a	79±5a	13.0±0.4b	126.4±9.7c
Significant level							
Var		**	**	**	**	ns	**
PBZ		**	**	ns	ns	**	**
Var × PBZ		ns	ns	ns	ns	*	ns

Data presented as mean ± SE ($n = 6$).

ns, * and ** represent non-significant, significant ($p \leq 0.05$) and highly significant ($p \leq 0.01$), respectively. Different letters in each column represent significant difference at $p \leq 0.05$ according to Tukey's HSD test.

Physiological changes

Leaf greenness (SPAD value) in 340 µM PBZ treated turmeric plants cvs. 'URT' and 'PJT' was significantly increased by 1.26 and 1.48 folds over control, respectively (Figure 2b). In 'PJT', leaf greenness in 170 µM PBZ treated plants was 29.70 SPAD unit, which was 1.36 folds greater over control (Figure 2b).

Interestingly, the maximum quantum yield of PSII (F_v/F_m) and photon yield of PSII (Φ_{PSII}) in 'PJT' sprayed with 340 µM PBZ were promoted by 1.28 and 1.23 folds over control, respectively (Figure 2c-d). In 'URT', only Φ_{PSII} was up-regulated by 340 µM PBZ (1.15 folds over control) (Figure 2c-d). Positive relationships between leaf greenness and F_v/F_m (Figure 3a; $R^2 = 0.5912$) and F_v/F_m and Φ_{PSII} (Figure 3b; $R^2 = 0.8361$) were demonstrated. Photosynthetic abilities of the light reaction in 'PJT' treated with PBZ was significantly improved. In contrast, net photosynthetic rate (P_n), in 'PJT' sprayed with 340 µM PBZ was significantly declined by 38.58% over control, while it was unaffected in 'URT' (Figure 3c). A positive relationship between P_n and STDW was found (Figure 3d; $R^2 = 0.4559$). Transpiration rate (E) and stomatal conductance (g_s) in 'PJT' without PBZ treatment were greater than those in 'URT' by 1.99 and 1.87 folds, respectively (Figure 4a-b). In PBZ treated plantlets of 'PJT', E was significantly dropped by 61.63% (170 µM PBZ) and 74.90% (340 µM PBZ) over control (Figure 4a). Similarly, g_s was decreased by 61.63% (170 µM PBZ) and 75.35% (340 µM PBZ) over control (Figure 4b). A positive relation between g_s and E was observed (Figure 4c; $R^2 = 0.9955$). Water use efficiency (P_n/E) in 'PJT' treated with 170 and 340 µM PBZ was significantly improved by 2.13 and 2.45 folds over control (without PBZ), respectively, whereas it was unchanged in 'URT' (Figure 4d).

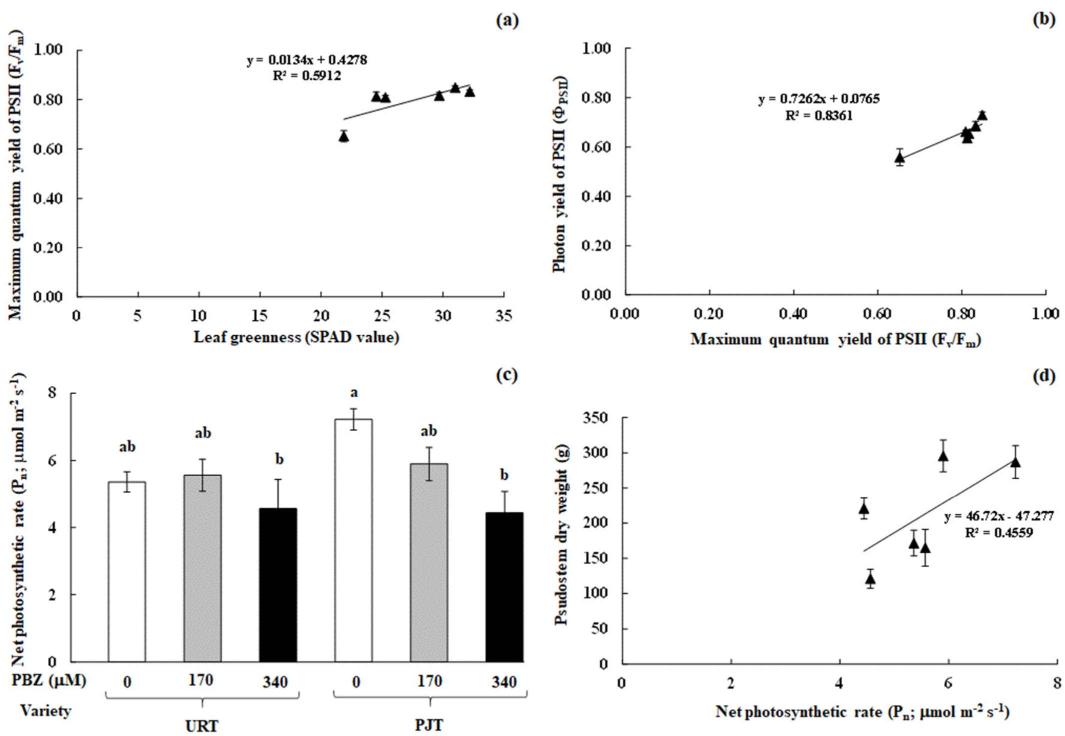

Figure 3. Relationships between SPAD and F_v/F_m (a), F_v/F_m and Φ_{PSII} (b), net photosynthetic rate (P_n, c) and relationship between P_n and pseudostem dry weight (d) of two turmeric varieties, URT and PJT, upon exogenous foliar application by 0 (control), 170 and 340 µM PBZ at vegetative stage prior to harvest at maturity (8 months-old) under the greenhouse conditions

Data presented as mean ± SE (n = 6). Different letters along each bar represent significant difference according to Tukey's HSD test at $p \leq 0.05$.

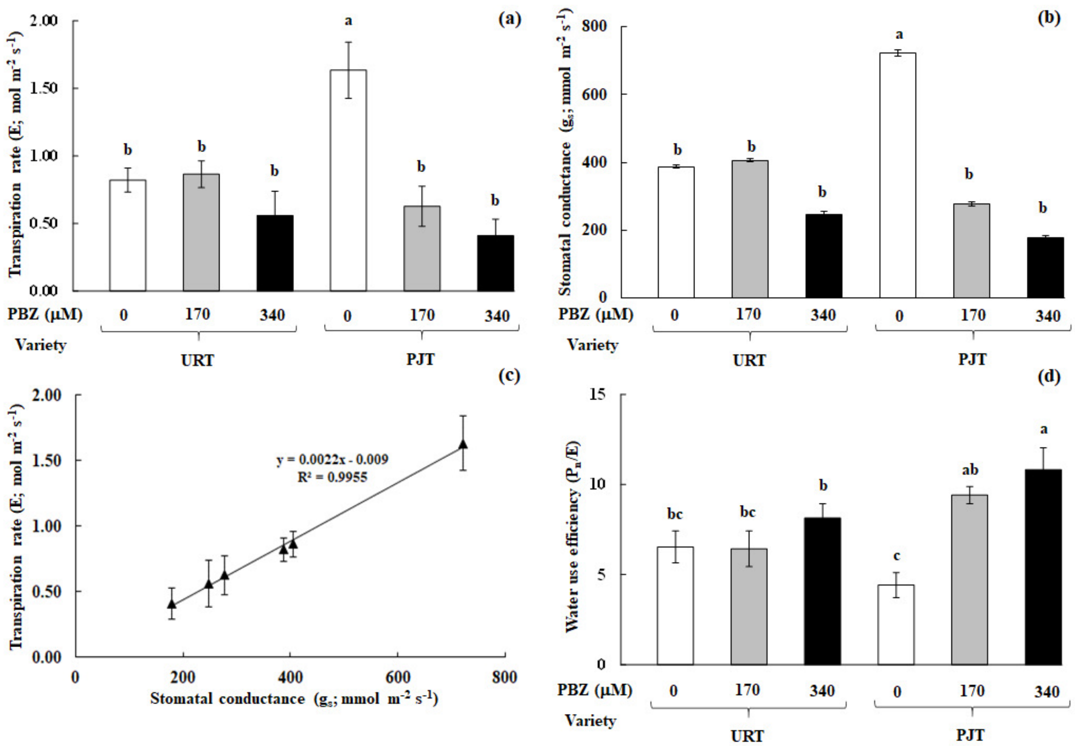

Figure 4. Transpiration rate, E (a), stomatal conductance, g_s (b), relationship between E and g_s (c) and water use efficiency, P_n/E (d) of two turmeric varieties, URT and PJT, upon exogenous foliar application by 0 (control), 170 and 340 μM PBZ at vegetative stage prior to harvest at maturity (8 months-old) under the greenhouse conditions. Data presented as mean ± SE (n = 6). Different letters along each bar represent significant difference according to Tukey's HSD test at $p \leq 0.05$.

Biochemical changes

Sucrose in the leaf tissues of 'URT' treated with 340 μM PBZ was significantly decreased by 34.76% over control in contrast to glucose, which was increased by 1.25 folds over control (Table 3). In 'PJT', glucose and fructose in plantlets treated with 340 μM PBZ were increased by 1.29 and 1.41 folds over control and the maximum value of sucrose was found to be 42.7 mg g^{-1} DW (1.18 folds over control) in 170 μM PBZ treated plants (Table 3). In rhizome, sucrose>fructose>glucose was evidently observed, especially in cv. 'URT'. Sucrose in 'PJT' rhizome (140.9 mg g^{-1} DW) was greater compared with 'URT' (55.7 mg g^{-1} DW), whereas fructose level in 'PJT' rhizome was lower by 45.90% over 'URT' (Table 3). In 'PJT' rhizome of 340 μM PBZ treated plants, sucrose and glucose significantly declined by 46.84% and 50.80% over control, respectively (Table 3). Upon 340 μM PBZ exogenous spray, total soluble sugars (TSS) in 'PJT' were increased by 1.18 folds over 'URT' (Figure 5a). A positive relation between TSS and total curcuminoids was demonstrated in rhizome (Figure 5b; R^2 = 0.4524).

Table 3. Sucrose (Suc; mg g^{-1} DW), glucose (Gluc; mg g^{-1} DW) and fructose (Fruc; mg g^{-1} DW) in the leaf and rhizome tissues of two turmeric (*Curcuma longa*) varieties, URT and PJT, upon exogenous foliar application by 0 (control), 170 and 340 µM PBZ at vegetative stage prior to harvest at maturity (8 months-old) in the greenhouse conditions

Variety	PBZ	Leaf			Rhizome		
	(µM)	Suc	Gluc	Fruc	Suc	Gluc	Fruc
URT	0	32.8±5.3b	17.8±0.8b	28.5±1.1ab	55.7±6.8c	23.3±1.5ab	39.6±3.1a
	170	32.3±5.8b	18.6±1.3b	25.7±1.4ab	56.3±4.0c	22.1±3.7ab	36.4±4.2a
	340	21.4±4.4c	22.3±1.9a	29.9±1.7a	73.3±6.4bc	26.9±4.0a	27.6±5.7ab
PJT	0	36.1±6.3b	18.2±3.4b	21.0±3.3b	140.9±10.0a	18.7±4.8b	19.8±6.1bc
	170	42.7±5.5a	17.7±1.0b	23.9±1.0ab	100.7±9.0b	16.1±0.7b	30.1±6.4ab
	340	33.9±2.8b	23.4±1.1a	29.7±1.9a	74.9±16.7bc	9.2±1.4c	13.7±2.2c
Significant level							
Var		*	ns	*	**	**	**
PBZ		ns	*	*	*	**	*
Var × PBZ		ns	ns	ns	**	*	ns

Data presented as mean ± SE (n = 6).
ns, * and ** represent non-significant, significant ($p \le 0.05$) and highly significant ($p \le 0.01$), respectively. Different letters in each column represent significant difference at $p \le 0.05$ according to Tukey's HSD test.

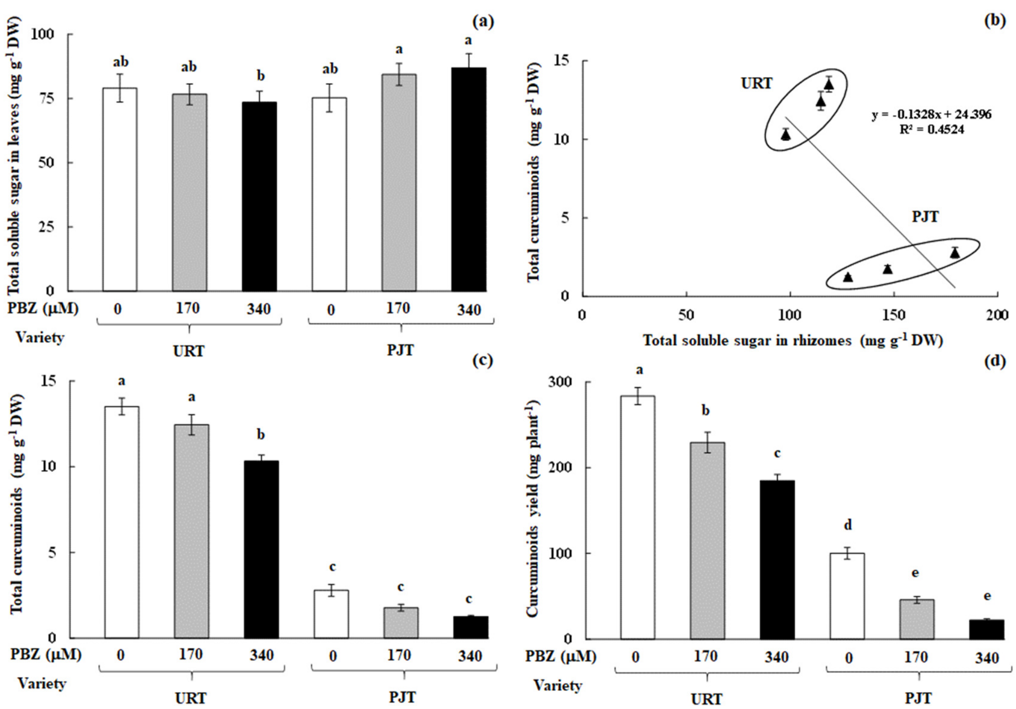

Figure 5. Total soluble sugar (TSS) in the leaf tissues (a), relationship between TSS in rhizome tissues and total curcuminoids (b), total curcuminoids (c) and curcuminoids yield (d) of two turmeric varieties, URT and PJT, upon exogenous foliar application by 0 (control), 170 and 340 µM PBZ at vegetative stage prior to harvest at maturity (8 months-old) in the greenhouse conditions
Data presented as mean ± SE (n = 6). Different letters along each bar represent significant difference according to Tukey's HSD test at $p \le 0.05$.

Total curcuminoid content (mg g^{-1} DW) and curcuminoids yield (mg $plant^{-1}$) in 'URT' were greater by 4.84 and 2.83 folds over 'PJT', confirming 'URT' as elite variety (Figure 5c-d). In 'URT', total curcuminoid content in 340 µM PBZ treated plants was significantly dropped by 23.61% over control, whereas it was unchanged in 'PJT' (Figure 5c). Interestingly, curcuminoids yield per plant in 'PJT' rhizome was sensitive to PBZ treatments, resulting in a significant decrease by 54.22% under 170 µM PBZ treatment and 77.63% under 340 µM PBZ treatment (Figure 5d). Similarly, curcuminoids yield per plant in 'URT' treated with 170 µM and 340 µM PBZ was also declined by 19.10% and 34.75% over control, respectively (Figure 5d). In plantlets without PBZ treatment, RhDW per plant of 'PJT' was significantly greater than 'URT' by 1.71 folds (Figure 6a). RhDW per plant in 'PJT' was retarded in relation to PBZ concentrations, leading to a decrease of 28.13% (170 µM PBZ) and 50.70% (340 µM PBZ) over control (Figure 6a). BIS, DEM and CUR in 'URT' rhizome was sensitive to PBZ, especially at the concentration of 340 µM, where a decrease of 34.5%, 25.85% and 18.17% was observed over control, respectively (Figure 6b-d). In 'PJT' rhizome, only DEM in 340 µM PBZ treated plants was significantly decreased by 58.25% over control (Figure 6c), whereas BIS and CUR were unchanged (Figure 6b and 6d).

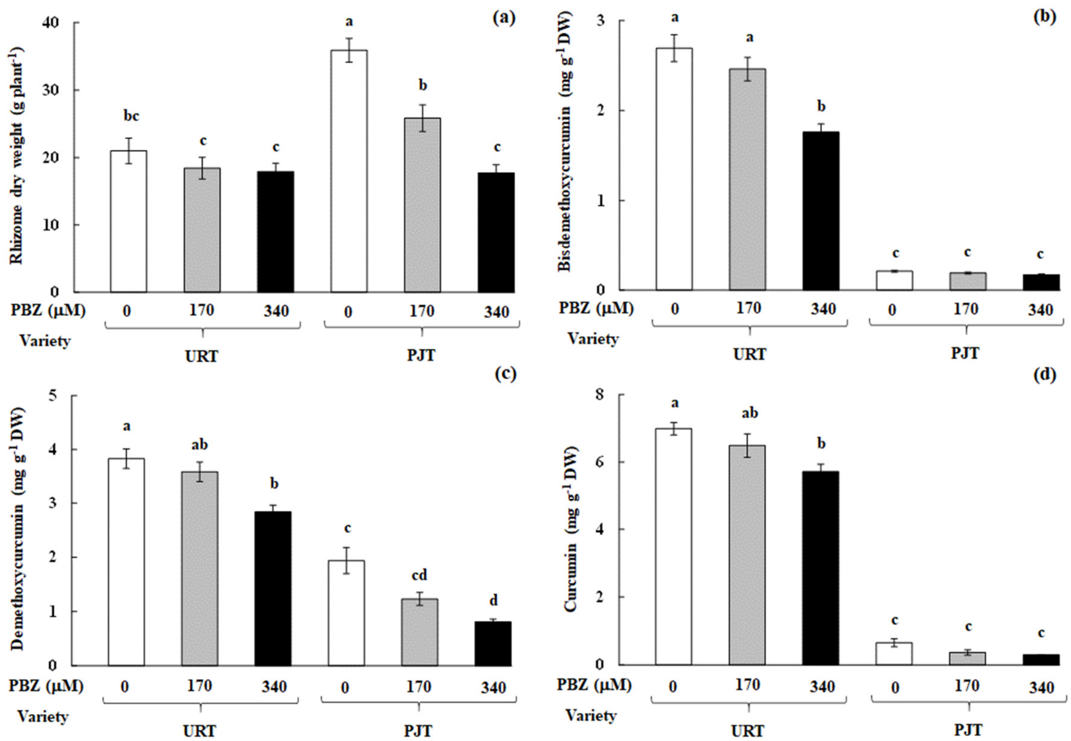

Figure 6. Rhizome dry weight (a), bisdemethoxycurcumin (b), demethoxycurcumin (c) and curcumin (d) in the rhizomes of two turmeric varieties, URT and PJT, upon exogenous foliar application by 0 (control), 170 and 340 µM PBZ at vegetative stage prior to harvest at maturity (8 months-old) in the greenhouse conditions.

Data presented as mean ± SE (n = 6). Different letters along each bar represent significant difference according to Tukey's HSD test at $p \leq 0.05$.

Discussion

Pseudostem height of turmeric cv. 'PJT' was significantly retarded by 340 µM PBZ exogenous foliar application, whereas it was unchanged in cv. 'URT'. It is possible that PBZ response in turmeric plants depends on the application method (soil drenching or foliar spray), degree of PBZ doses, and genotypic factor. In Patumma (*Curcuma alismatifolia*) cv. 'Chiang Mai Pink'), pseudostem height of 1,500 mg L^{-1} PBZ-treated plants were retarded by 50% of control and slow growth rate was observed when compared with control plants (Jungklang *et al.*, 2017). Pseudostem height in Patumma cv. 'Kimono Pink' (Boontiang *et al.*, 2019), ginger (*Zingiber officinale*; Rusmin *et al.*, 2015) and torch ginger (*Etlingera elatior*; Muangkaewngam and Te-chato, 2018) was also retarded in response to the degree of PBZ application and period of cultivation. Interestingly, plant height of *Zantedeschia elliottiana* treated with 2-4 mg PBZ $rhizome^{-1}$ was unchanged in both greenhouse and field trial conditions, whereas it was highly declined in *Z. rehmannii* (Corr and Widmer, 1991). In general, pseudostem height of cv. 'PJT' was extremely susceptible to PBZ treatment than cv. 'URT'. Previously, shoot height of *C. alismatifolia* 'Chiang Mai Pink' (88 cm) was found to be sensitive to PBZ and retarded by 3.08 and 4.94 folds compared with *C. gracillima* 'Violet' (28.6 cm) and *C. thorelii* (17.8 cm), respectively (Sarmiento and Kuehny, 2003). Inhibitory effects of PBZ in higher plants are closely related to GA inhibitors and result in dwarfed plants (Zhu *et al.*, 2016; Seesangboon *et al.*, 2018). Overall growth performances, i.e., STFW, STDW, LL and LW in turmeric plants of cv. 'PJT' were greater than those in cv. 'URT', whereas these parameters were maintained in PBZ-treated plants. Genotype has a significant effect on the plant's response to PBZ as reported in Curcuma (Sarmiento and Kuehny, 2003) and Zantedeschia (Corr and Widmer, 1991). Plant height, leaf area and dry matter in two rose cultivars, 'Yellow Terrazza' and 'Shiny Terrazza' tend to decline with increase in a PBZ concentration (Carvalho-Zanão *et al.*, 2018). In pepper (*Capsicum chinense* cvs. 'Bode Amarela' and 'Biquin Vermelha'), plant height and total leaf number were unchanged after 10 μM PBZ foliar spray, whereas only plant height was retarded after soil drenched PBZ application (França *et al.*, 2017). In the root zone, overall root and rhizome traits in cv. 'PJT' were better than 'URT'. The RTFW, RhW, RhFW and RhDW in 'PJT' were significantly dropped, especially in 340 μM PBZ treated plants. Similarly, RTDW and number of tubers in two potato genotypes (*Solanum tuberosum* cvs. 'Granola' and 'Agria') treated with 90 mg L^{-1} PBZ were significantly decreased when compared with control (Esmaielpour *et al.*, 2011) and number of tubers, tuber fresh mass, tuber dry mass and total yield of potato was significantly declined in relation to the rate of PBZ treatments (Tekalign and Hammes, 2004; de Araújo *et al.*, 2020). In cassava (*Manihot esculenta* cv. 'Rocha'), fibrous roots fresh mass, tuberous root fresh mass, number of tuberous roots and tuberous root length were sharply dropped in plants treated with 45-90 mg PBZ $plant^{-1}$ over the control (Medina *et al.*, 2012).

It was observed that the leaf greenness or SPAD unit of turmeric plant cvs. 'PJT' and 'URT' treated with PBZ foliar spray was significantly increased over control, especially after 340 μM PBZ treatment. In *C. alismatifolia* and *Zingiber officinale*, total chlorophyll content in the leaf tissues of PBZ treated plants was increased, depending on the degree of PBZ concentrations (Rusmin *et al.* 2015; Boontiang et al. 2019). A positive relationship between SPAD and maximum quantum yield of PSII (F_v/F_m) in herbaceous peony (*Paeonia lactiflora*) with PBZ treatment was demonstrated (r = 0.739; Xia *et al.*, 2018). Similarly, Φ_{PSII} in peanut (*Arachis hypogaea*) was found to be improved with PBZ treatment (Senoo and Isoda, 2003). Increased chlorophyll content in the leaves of PBZ-treated plants of *Viola* × *wittrockiana* (Gliožeris *et al.*, 2007) and *Syzygium myrtifolium* (Roseli *et al.*, 2012) was evidently observed. Stomatal functions including P_n, g_s, and E in PBZ-treated plants were significantly decreased, especially in cv. 'PJT', while WUE was increased. Negative effects of PBZ treatment in terms of P_n, g_s and E reduction have been well established in *S. myrtifolium* (Roseli *et al.*, 2012), *Caryopteris incana* (Harmath *et al.*, 2014), *Litchi chinensis* (Pandey *et al.*, 2018), *S. tuberosum* (Tekalign and Hammes, 2005a), Camelina sativa (Kumar *et al.*, 2012) and Arbutus unedo (Navarro *et al.*, 2007). In contrast, WUE was up-regulated by PBZ treatment (Pal *et al.*, 2016; Xia *et al.*, 2018). Therefore, genotypic variation strongly regulates P_n, g_s and E in PBZ-treated plants (Rodrigues *et al.*, 2016).

Glucose in the leaf tissues of 340 μM PBZ treated plants of cvs. 'URT' and 'PJT' was significantly increased over control. However, fructose was increased only in the leaves of cv. 'PJT'. TSS in pseudostems of 5 mg L^{-1} PBZ treated wheat cvs. 'Puntal' and 'Estrella' were enriched over control, depending on the genetic background of the crop (Assuero *et al.*, 2012). In maize (*Zea mays* cv. 'Zhengdan958'), TSS in the leaf tissues of PBZ treated plants was promoted at early stage after silking (15 d DAS) and then, declined (Kamran *et al.*, 2020). Sucrose level in the leaf tissues of turmeric plants was lower than in rhizome, especially in cv. 'PJT', whereas both glucose and fructose were improved with PBZ treatment. It is possible that greater sucrose accumulation rate in the rhizome is due to the fact that rhizome act as sink organ (storage), and the leaf tissues represent source organ (biosynthesis) (Zheng *et al.*, 2012; Dewi and Darussalam, 2018; Smith *et al.*, 2018). In Ethiopian mustard (*Brassica carinata* cv. 'PC5'), TSS in the leaf tissues of PBZ-treated plants were accumulated in relation to the degree of PBZ foliar spray (Setia *et al.* 1995). In rhizome of cv. 'PJT', sucrose and glucose in 340 μM PBZ treated plants were significantly decreased when compared with control, whereas those were unchanged in cv. 'URT'. Similarly, soluble and non-soluble carbohydrate levels in PBZ treated grapevines (*Vitis vinifera* cv. 'Seyval blanc') were declined in relation to an increasing rate of PBZ concentrations (Hunter and Proctor, 1994). In contrast, total carbohydrate content in *C. alismatifolia* cv. 'Kimono Pink' treated with PBZ was increased over control in the rhizome, whereas it was unchanged in the leaf tissues (Boontiang *et al.*, 2019). In tuber of potato (cv. 'Markies'), TSS, reducing sugars and non-reducing sugars in PBZ-treated plants (10 and 100 mg L^{-1} PBZ) were largely enriched over control (de Araújo *et al.*, 2020).

Interestingly, curcuminoids including BIS, DEM and CUR in non-elite 'PJT' and elite 'URT' genotypes were found to be negatively affected by PBZ treatment, especially in cv. 'URT'. In *Ophiopogon japonicus*, ophiopogonin B, D and D′ concentrations, in the PBZ sprayed plants were sharply dropped when compared with control plants (Sun *et al.*, 2020). Likewise, inulin content in the tuber of *Helianthus tuberosus* treated with 100 mg L^{-1} PBZ was decreased by 7.57% over control (Phasri *et al.*, 2019). In fruit of *Lichi chinensis*, vitamin C and anthocyanin contents in PBZ-treated plants were lower than in control (Pandey *et al.*, 2018). In agreement, oil yield of Ethiopian mustard treated with 20 mg L^{-1} PBZ was significantly declined by 4.6% over control (Setia *et al.*, 1995). In contrast, ἀ-tocopherol in tuber of *Dioscorea rotundata* treated with 15 mg L^{-1} PBZ was unchanged when compared with control (Jaleel *et al.*, 2007). In general, anthocyanin content in flower bracts (Boontiang *et al.*, 2019) and vitamin C in leaf tissues (Jungklang *et al.* 2017) of *C. alismatifolia* treated by PBZ was increased over control.

Conclusions

Pseudostem height, root fresh weight, rhizome width, rhizome fresh weight and rhizome dry weight in cv. 'PJT' treated with 340 μM PBZ were significantly retarded as along with stomatal functions, i.e., P_n, g_s, E and WUE and sucrose and glucose content. Similarly, curcuminoids yield (mg $plant^{-1}$) and DEM in cvs. 'URT' and 'PJT' treated with 340 μM PBZ were significantly decreased. Therefore, selecting a candidate cultivar (elite variety) with high curcuminoid levels and compact plant canopy (high density cultivated practices) using PBZ in the greenhouse needs further validation together with microclimatic controlled conditions.

Authors' Contributions

DC, RT, TS, TS; Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration. SC-U; Supervision; Validation; Visualization; Writing - original draft; Writing - review and editing. All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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