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Exogenous dopamine ameliorates chilling injury of banana fruits during cold storage

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This study investigated postharvest dopamine treatment efficiency in ameliorating chilling injury of banana fruits during storage at 7 ºC for 21 days. Our results showed that dopamine treatment at 150 µM promoted phenols and flavonoids biosynthesis acquired by higher phenylalanine ammonia-lyase (*PAL*) expression and activity concurrent with lower polyphenol oxidase (*PPO*) expression and activity leading to higher DPPH, FRAP, and ABTS radicals scavenging activity. In addition, dopamine treatment at 150 µM promoted endogenous proline biosynthesis by activating pyrroline-5-carboxylate synthetase (*P5CS*) and ornithine δ-aminotransferase (*OAT*) expression and activity concurrent with suppressing proline dehydrogenase (*ProDH*) expression and activity. Furthermore, higher endogenous γ-aminobutyric acid (GABA) biosynthesis in banana fruits by 150 µM dopamine treatment was accompanied by higher glutamate decarboxylase (*GAD*) and GABA transaminase (*GABA-T*) expression and activity. Therefore, our results suggest that dopamine treatment at 150 µM might be employed for banana fruits chilling injury amelioration by enhancing phenylpropanoid pathway activity and boosting endogenous proline and GABA biosynthesis.

Keywords GABA accumulation, ROS scavenging activity, Postharvest cold storage, Proline accumulation, Phenylpropanoid pathway

Thanks to higher health-promoting reactive oxygen species (ROS) scavenging molecules, banana fruits have gained worldwide attention. By employing low temperatures during transportation, handling, and storage, banana fruits suffer from chilling damage, which significantly challenges economic value, commercial quality, and consumer acceptance[1–3]. Hence, employing postharvest technologies to ameliorate chilling damage in banana fruits has received growing attention.

During cold storage (7 °C), the impairment of the mitochondrial electron transport system in banana fruits accelerates ROS overaccumulation and suppresses adenosine triphosphate (ATP) production. In addition, boosting NADPH oxidase (respiratory burst oxidase homologs; *RBOHs*) expression and activity in banana fruits might be crucial for higher O_2^- generation and H_2O_2 accumulation during cold storage. By boosting cytosolic calcium (Ca^{2+}) accumulation acquired by Ca^{2+}-ATPase activity impairment under cold storage, boosting phospholipase D (*PLD*), phospholipase C (*PLC*), diacylglycerol kinase (*DGK*) and lipoxygenase (*LOX*) expression and activity accompanied by suppressing fatty acid desaturases (*FADs*) expression and activity accelerates membrane fluidity and integrity deterioration in banana fruits. In banana fruits during cold storage, lower membrane unsaturated/saturated fatty acids (unSFA/SFA) accumulation was associated with membrane fluidity and integrity deterioration demonstrated by lower electrolyte leakage and malondialdehyde (MDA) accumulation. In banana fruits during cold storage, phenylpropanoid pathway activity is promoted, as shown by higher phenylalanine ammonia-lyase (*PAL*) expression and activity, which supports higher phenols biosynthesis. By membrane fluidity and integrity deterioration during cold storage, higher polyphenol oxidase (*PPO*) expression and activity accelerates phenols oxidation while boosting pericarp browning in banana fruits[4–13].

In recent years, postharvest technologies such as melatonin, brassinosteroid (BR), nitric oxide (NO), hydrogen sulfide (H_2S), hot water dipping (HWD), γ-aminobutyric acid (GABA), glycine betaine (GB), dopamine, methyl jasmonate (MeJA), azacytidine (5-azaC), adenosine triphosphate (ATP) and phytosulfokine α (PSKα) have been employed by researchers for ameliorating chilling damage while maintaining quality in banana fruit during cold storage (7 °C) by boosting ROS scavenging system activity accompanied by suppressing ROS generating system activity, suppressing membrane deteriorating enzymes activity accompanied by boosting membrane unsaturation, boosting phenylpropanoid pathway activity accountable for higher phenols and flavonoids

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biosynthesis and higher DPPH, FRAP and ABTS radicals scavenging activity, boosting molecular chaperones heat shock proteins (*HSPs*) expression, boosting cold-responsive ICE1-CBFs signaling pathway, suppressing programmed cell death (PCD) by preserving RNA and proteins homeostasis, boosting intracellular ATP and NADPH availability, boosting endogenous H_2S, proline, GABA, dopamine, GB, NO, polyamines and jasmonic acid (JA) biosynthesis, and suppressing ethylene biosynthesis[2,3,14–37].

By exogenous treatment or endogenous accumulation acquired by activating tyrosine decarboxylase (*TyrDC*) expression, dopamine is an illustrative signaling catecholamine molecule displaying ROS scavenging strength conferring biotic and abiotic stress tolerance in horticultural crops[38]. By apple trees spraying and watering with dopamine, apple fruits displayed higher endogenous dopamine accumulation acquired by activating *TyrDC* expression, which promotes flavonoids and anthocyanins biosynthesis associated with boosting fructose and sucrose biosynthesis, which are crucial for improving apple fruits quality[32]. Ali et al.[2] reported that ameliorating chilling damage in banana fruits by dopamine treatment during cold storage (7 °C) might be attributed to boosting endogenous dopamine biosynthesis acquired by higher *TyrDC* expression concurrent with boosting endogenous glycine betaine biosynthesis, higher chlorophyll accumulation, and suppressing H_2O_2 accumulation acquired by catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX) and glutathione reductase (GR) activity, all are crucial for preserving membrane integrity revealing by lower electrolyte leakage and MDA accumulation. Recently, Aghdam et al.[39] reported that dopamine treatment ameliorated chilling damage in kiwifruits by boosting target of rapamycin (*TOR*) expression accompanying by suppressing sucrose non-fermenting 1-related kinase 1 (*SnRK1*) expression, which enhances intracellular ATP and NADPH availability, higher endogenous salicylic acid biosynthesis, lower *PLD* and *LOX* expression and higher phenols, flavonoids, and ascorbic acid biosynthesis concurrent with lower H_2O_2 accumulation, all are promising for preserving membrane integrity revealing by lower electrolyte leakage and MDA accumulation.

The present study focused on discovering how the dopamine treatment ameliorates chilling damage in banana fruits during storage at 7 °C for 21 days. This was accompanied by assaying (1) *PAL* and *PPO* expression and activity regulating phenols and flavonoids biosynthesis and DPPH, FRAP, and ABTS radicals scavenging activity, (2) endogenous proline biosynthesis by *P5CS*, *OAT*, and *ProDH* expression and activity, and (3) endogenous GABA biosynthesis by *GAD* and *GABA-T* expression and activity.

Materials and methods

Dopamine and banana fruits treatment

Banana fruits (*Musa acuminate*, AAA group, cv. Cavendish) at the mature green stage were obtained from a wholesale market without any exposure to ethylene de-greening treatment. Then, they were separated into fingers and selected for uniformity of size and color and against mechanical injury and disease. For dopamine treatment at 0 and 150 µM for 10 min at 20 °C according to Ali et al.[2], 120 fingers were randomly divided into 2 lots, comprising three replicates of 20 fingers. The fingers were immersed in 0 (ddH_2O as control), and 150 µM dopamine for 10 min at 20 °C. After that, fingers were air-dried at room temperature and packaged in unsealed 0.04 mm-thick polyethylene film bags for storage at 7 ± 1 °C for 21 days. During 7, 14, and 21 days of storage at 7 ± 1 °C, peels of fingers were separated, mixed, powdered in liquid nitrogen, and stored at − 80 °C for biochemical and genes expression analyses.

Fruits phenols and flavonoids accumulation

Folin–Ciocalteu procedure was used for phenols accumulation (g GAE kg^{-1} FW) assaying, as stated by Perini et al.[40]. The aluminium chloride ($AlCl_3$) colorimetric method was used for flavonoids accumulation (g QE kg^{-1} FW) assaying, as stated by Duarte-Sierra et al.[41].

Fruits ABTS, DPPH, and FRAP radicals scavenging activity

ABTS, DPPH, and FRAP radicals scavenging activity were assayed accordant with Xu and Chen[42]. ABTS, DPPH, and FRAP radicals scavenging activity were expressed as the mmol of Trolox equivalents (TE) per mass of fresh weight, mmol TE kg^{-1} FW.

Fruits PAL and PPO enzymes activity

PAL and PPO enzymes activity were assayed in accordance with Li et al.[43] and Yang et al.[44]. PAL and PPO enzymes activity were expressed in mkatals produced per mass of protein, mkat kg^{-1}.

Fruits proline biosynthesis and P5CS, OAT, and ProDH enzymes activity

The acid ninhydrin method was used for proline accumulation (mg kg^{-1} FW) assaying, as stated by Zhang et al.[45]. P5CS, PDH, and OAT enzymes activity were assayed, as stated by Shan et al.[46]. P5CS, PDH, and OAT enzymes activity were expressed in mkatals produced per mass of protein, mkat kg^{-1}.

Fruits GABA biosynthesis and GAD and GABA-T enzymes activity

GABA accumulation (mg kg^{-1} FW) was assayed enzymatically using the GABase procedure, as stated by Deewatthanawong et al.[47]. GAD activity was assayed based on GABA production, as stated by Bartyzel et al.[48], while GABA-T activity was assayed based on alanine production, as stated by Ansari et al.[49]. GAD and GABA-T enzymes activity were expressed in mkatals produced per mass of protein, mkat kg^{-1}.

Fruits genes expression by qRT-PCR analysis

Total RNA extraction and cDNA synthesis were accompanied, as stated by Liu et al.[50]. *PAL*, *PPO*, *P5CS*, *ProDH*, *OAT*, *GAD*, and *GABA-T* expression (Table 1) were analyzed as stated by Ali et al.[2] and calculated by formula $2^{-\Delta\Delta Ct}$ as stated by Livak and Schmittgen[51].

Gene name	Functional annotations	Accession numbers	Primer sequences (5′-3′)
PAL	Phenylpropanoid pathway	NC_088357	F: ATCTCGTCCCGCTGTCTTAC R: TCCCCTCCAGTATGTGCTCCA
PPO	Phenylpropanoid pathway	NC_088347	F: TCTACGACGAGAATGCTGACT R: CCTTCAAGGCTTTGGGAGT
P5CS	Proline biosynthesis	NC_088345	F: TGGATGCTGCTTGGAGAAGA R: CAAAATCTTCTTGCGGGCCT
OAT	Proline biosynthesis	NC_088347	F: CGGTGATGTTTTGGGGCTAG R: ATACAAATCACGCCCGCATC
ProDH	Proline biosynthesis	NC_088337	F: TTCTTGCTGGAGAGGGTCAG R: TTCCTTTCCGATTCCCAGCT
GAD	GABA biosynthesis	NC_088352	F: CCAGACCTGACATGGGACTT R: TGATCGGTGCCAAGGTAGTT
GABA-T	GABA biosynthesis	NC_088342	F: GTAGGGGAAGGGTAGCGATC R: TCAGATTGAAGAGGTGCCGT
Actin	Housekeeping gene	NC_088338	F: TGGTATGGAAGCCGCTGGTA R: CTGCTGGAATGTGCTGAGG

Table 1. Primers used in the qRT-PCR analysis of expression.

Results and discussion

Fruits phenylpropanoid pathway activity

As presented in Fig. 1, banana fruits treated with 150 µM dopamine displayed higher PAL expression and activity (Fig. 1A, B; $P > 0.05$) accompanied by lower PPO expression and activity (Fig. 1C, D; $P > 0.05$) during storage at 7 °C for 21 days. By higher PAL/PPO expression and activity, banana fruits treated with 150 µM dopamine displayed higher phenols (Fig. 2A; $P > 0.05$) and flavonoids (Fig. 2B; $P > 0.05$) biosynthesis accompanied by higher DPPH, FRAP, and ABTS radicals scavenging activity (Fig. 2C-E; $P > 0.05$) during storage at 7 °C for 21 days.

Through dopamine treatment, employing GPCR/cAMP/PKA signaling pathway[52] ameliorating chilling damage in banana fruits by boosting endogenous dopamine biosynthesis acquired by higher *TyrDC* expression concurrent with boosting endogenous glycine betaine biosynthesis, suppressing chlorophyll degradation and suppressing H_2O_2 accumulation, which is important for preserving membrane integrity revealing by lower electrolyte leakage and MDA accumulation[2]. Exogenous dopamine treatment ameliorated chilling damage in banana fruits, which is associated with lower pericarp browning and might be attributed to preserving membrane integrity. By membrane integrity maintenance, higher phenols and flavonoids biosynthesis acquired by higher *PAL/PPO* expression and activity alleviating banana fruits chilling damage. By heat treatment accompanied by employing 2-aminoindan-2-phosphonic acid (AIP) as a PAL inhibitor, Chen et al.[4] reported that higher *PAL1/2* expression concurrent with higher PAL protein accumulation and activity is crucial for ameliorating chilling damage in banana fruits[4]. Higher *PAL* expression and activity, concurrent with lower *PPO* expression and activity, might be crucial for ameliorating chilling damage in banana fruits by boosting phenols and flavonoids biosynthesis and improving ROS scavenging activity[4,9]. Wang et al.[53] reported that melatonin treatment ameliorated chilling damage in banana fruits by suppressing *PPO1*/2/3 expression accompanied by PPO activity acquired by higher miR528 expression, which contributes to preserving membrane integrity demonstrated by lower electrolyte leakage and MDA accumulation. Song et al.[54] reported that ABA treatment ameliorated chilling damage in banana fruits by boosting endogenous ABA biosynthesis and activating ABI5 transcription factor expression in the ABA signaling pathway, enhancing phenols and flavonoid biosynthesis. By ABA treatment, the ABI5 transcription factor activating phenols and flavonoids biosynthesis (*PAL*, *C4H*, *4CL*, *CHS*, and *FLS*) expressions by directly binding to ABRE/G-box binding site in the promoter of flavonoid biosynthesis genes[54]. Chen et al.[55] reported that DNA methylation inhibitor 5-azacytidine (5-azaC) treatment ameliorated chilling damage in banana fruits by boosting phenols biosynthesis and improving DPPH and FRAP radicals scavenging activity acquired by lower *PPO1/2* expression and PPO activity. Pongprasert et al.[56] reported that conferring chilling damage in banana fruits treated with UV-C might be attributed to higher phenols biosynthesis acquired by higher PAL activity concurrent with lower PPO activity. Wang et al.[28] reported that ameliorating chilling damage in banana fruits by NO treatment might be attributed to higher phenols biosynthesis and FRAP radicals scavenging activity acquired by higher PAL activity. Wang et al.[29] reported that ameliorating chilling damage in banana fruits by GABA treatment might be attributed to boosting phenols biosynthesis acquired by higher PAL activity, leading to improving FRAP and DPPH radicals scavenging activity. Luo et al.[20] reported that H_2S treatment ameliorated chilling damage in banana fruits by boosting PAL activity and suppressing PPO activity accountable for higher phenols biosynthesis and higher DPPH and FRAP radicals scavenging activity. Wang et al.[30] reported that ameliorating chilling damage in banana fruits by NO treatment was associated with higher phenols biosynthesis and DPPH radicals scavenging activity acquired by higher PAL activity concurrent with lower PPO activity. Lo'ay and El-Khateeb[57] reported that ascorbic acid treatment ameliorated chilling damage in banana fruits by boosting phenols and flavonoid biosynthesis acquired by lower PPO activity. Ali et al. 14 reported that H_2S treatment ameliorated chilling damage in banana fruits by boosting phenols biosynthesis acquired by higher PAL and lower PPO activity. Tian et al.[58] reported that astragalus polysaccharides treatment ameliorated chilling damage in banana fruits by boosting phenols biosynthesis and DPPH radicals scavenging activity acquired by higher *PAL* and *CHS* expression and activity concurrent with lower *PPO* expression and

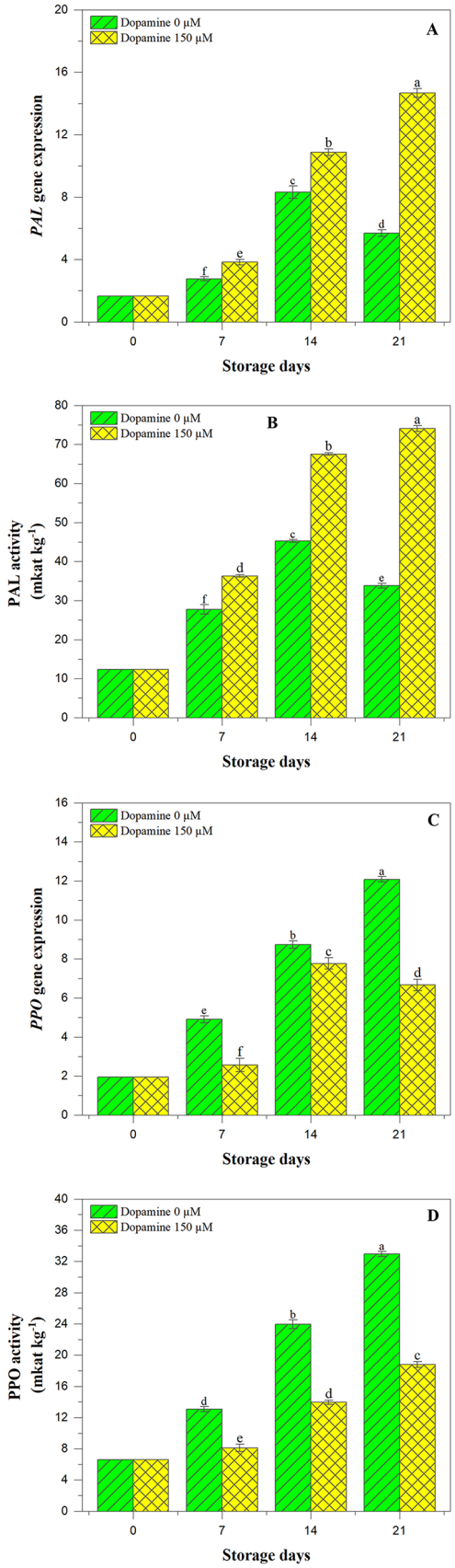

Fig. 1. *PAL* and *PPO* expression and activity in banana fruits treated with dopamine at 150 µM during storage at 7 °C for 21 days.

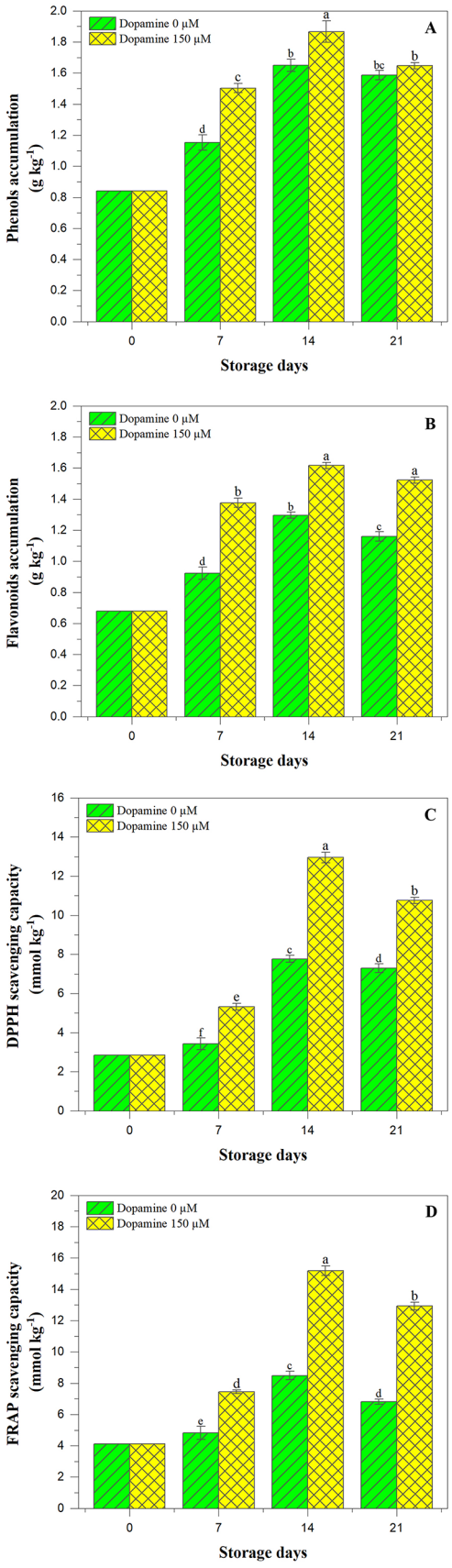

Fig. 2. Phenols and flavonoids biosynthesis concurrent with ABTS, FRAP, and DPPH radicals scavenging activity in banana fruits treated with dopamine at 150 µM during storage at 7 °C for 21 days.

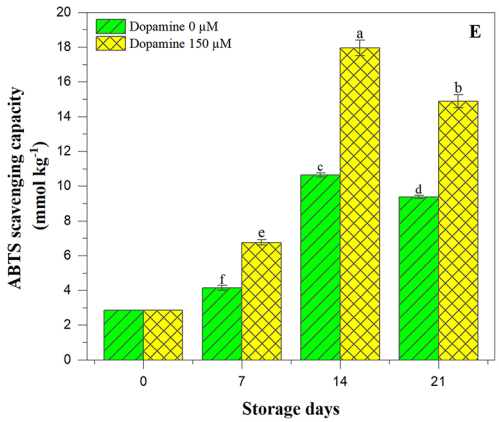

Figure 2. (continued)

activity. Charoenphun et al.[59] reported that ameliorating chilling damage in banana fruits by melatonin treatment might be attributed to boosting phenols such as gallic acid, chlorogenic acid, quinic acid, protocatechuic acid, and catechin accumulation acquired by higher PAL activity concurrent with lower PPO activity. Therefore, improving ABTS, FRAP, and DPPH radicals scavenging activity acquired by higher phenols and flavonoids biosynthesis by activating *PAL* concurrent with suppressing *PPO* expression and activity might be crucial for ameliorating chilling damage in banana fruits by 150 μM dopamine treatment during cold storage.

Fruits proline metabolism

As presented in Fig. 3, banana fruits treated with 150 μM dopamine displayed higher *P5CS* and *OAT* expression and activity (Fig. 3A-D; $P > 0.05$) accompanied by lower *ProDH* expression and activity (Fig. E, F; $P > 0.05$) during storage at 7 °C for 21 days. By higher *P5CS/ProDH* and *OAT/ProDH* expression and activity, banana fruits treated with 150 μM dopamine displayed higher proline biosynthesis (Fig. 3G; $P > 0.05$) during storage at 7 °C for 21 days.

During cold storage, P5CS activity is accountable for pyroline 5-carboxylate biosynthesis from glutamate by utilizing ATP and NADPH, and P5CR activity is responsible for proline biosynthesis from pyroline 5-carboxylate by using NADPH. In addition to proline biosynthesis from glutamate supplied from GS/GOGAT cycle activity, ornithine provided from arginine by arginase activity is accountable for proline biosynthesis by OAT and P5CR activity. During cold storage, P5CS and OAT activity is responsible for endogenous proline biosynthesis, while ProDH activity is responsible for endogenous proline degradation[60,61]. During cold storage, proline is not only advantageous for osmoregulation as an osmoprotectant but also exhibits ROS scavenging activity advantageous for preserving membrane integrity, in addition to serving as a chaperoning molecule for keeping ROS scavenging proteins stability[60,61]. Wang et al.[28] reported that ameliorating chilling damage in banana fruits by NO treatment might be attributed to higher endogenous proline biosynthesis acquired by higher P5CS activity concurrent with lower ProDH activity. Wang et al.[29] reported that ameliorating chilling damage in banana fruits by GABA treatment might be attributed to boosting endogenous proline biosynthesis acquired by higher P5CS activity concurrent with lower ProDH activity. Luo et al.[20] reported that H_2S treatment ameliorated chilling damage in banana fruits by boosting endogenous proline biosynthesis acquired by higher P5CS and lower ProDH activity. Wang et al.[31] reported that ameliorating chilling damage in banana fruits by NO treatment might be attributed to boosting endogenous proline biosynthesis acquired by higher OAT activity. Ali et al.[14] reported that H_2S treatment ameliorated chilling damage in banana fruits by boosting endogenous proline biosynthesis acquired by higher P5CS and OAT activity and lower ProDH activity. Wang et al.[3] reported that ameliorating chilling damage in banana fruits by PSKα treatment might be attributed to boosting endogenous proline biosynthesis acquired by higher P5CS and OAT activity concurrent with lower ProDH activity. As shown in kiwifruits, higher endogenous proline biosynthesis in banana fruits by dopamine treatment might be attributed to boosting *TOR* expression concurrent with suppressing *SnRK1* expression[39,60,62]. Therefore, boosting endogenous proline biosynthesis acquired by activating *P5CS* and *OAT* and suppressing *ProDH* expression and activity might be crucial for ameliorating chilling damage in banana fruits by 150 μM dopamine treatment during cold storage.

Fruits GABA metabolism

As presented in Fig. 4, banana fruits treated with 150 μM dopamine displayed higher *GAD* and *GABA-T* expression and activity (Fig. 4A-D; $P > 0.05$) during storage at 7 °C for 21 days. By lower *GAD/GABA-T* expression and activity, banana fruits treated with 150 μM dopamine displayed higher GABA biosynthesis (Fig. 4E; $P > 0.05$) during storage at 7 °C for 21 days.

During cold storage, cytosolic Ca^{2+}/CaM accumulation and cytosolic acidification promote GAD activity and cytosolic GABA biosynthesis. During GABA biosynthesis by GAD activity, H^+ consumption might be crucial for preventing cytosolic acidification. In addition, GABA serves as an osmoprotectant molecule and exhibits ROS-scavenging activity[63,64]. During cold storage, intracellular ROS overaccumulation confining tricarboxylic acid cycle activity by succinyl-CoA synthetase and α-ketoglutarate dehydrogenase enzymes

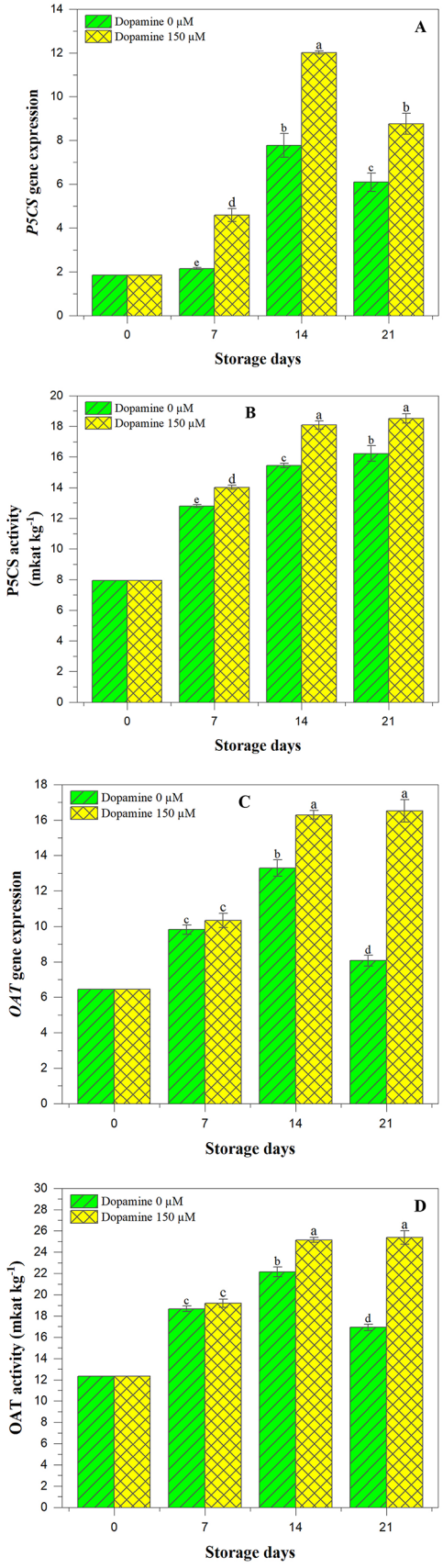

Fig. 3. *P5CS*, *OAT*, and *ProDH* expression and activity concurrent with endogenous proline biosynthesis in banana fruits treated with dopamine at 150 μM during storage at 7 °C for 21 days.

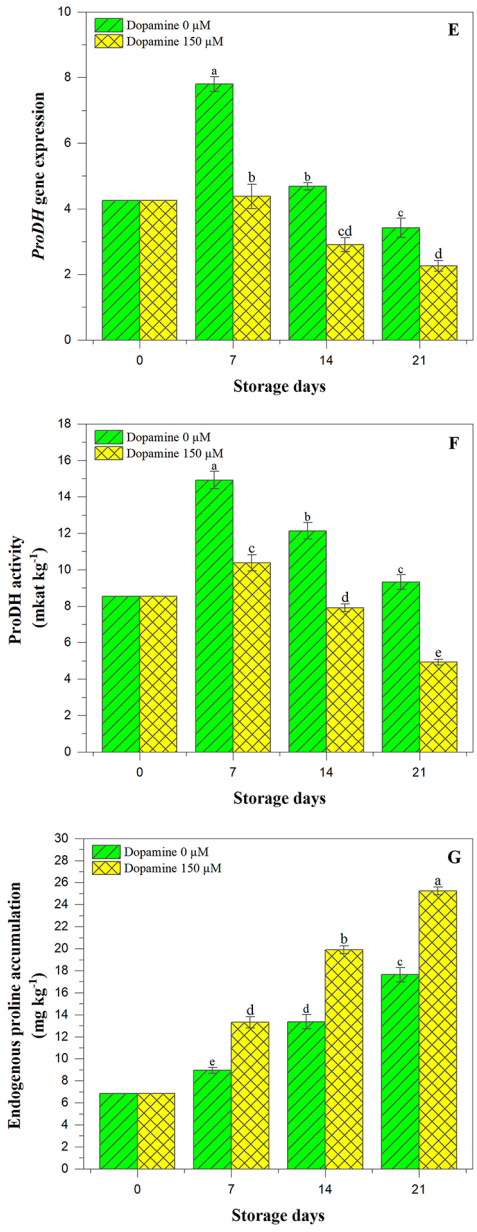

Figure 3. (continued)

inactivation, which is accountable for insufficient NADH supplying confining ATP generation, intracellular ROS overaccumulation and insufficient carbon skeletons supplying restraining protective metabolic pathways activity[63,64]. Supplying sufficient GABA through GAD activity is crucial for activating GABA shunt activity to supply succinate and NADH in mitochondria through GABA-T and SSADH activity. GABA shunt activity allows TCA cycle activity to continue by providing succinate from SSADH activity, leading to intracellular NADH and ATP availability and avoiding ROS overaccumulation.

Furthermore, higher GABA shunt activity is promising for boosting carbon skeleton phosphoenolpyruvate availability, which accompanied by erythrose 4-phosphate supplying from oxidative pentose phosphate pathway, is accountable for activating shikimate pathway, responsible for boosting phenylalanine availability for activating phenylpropanoid pathway, in addition tryptophan supplying for boosting melatonin biosynthesis[63–66]. Wang et al.[31] reported that ameliorating chilling damage in banana fruits by NO treatment might be attributed to boosting endogenous GABA biosynthesis acquired by higher GAD activity concurrent with lower GABA-T activity. Ali et al.[14] reported that H_2S treatment ameliorated chilling damage in banana fruits by boosting endogenous GABA biosynthesis acquired by higher GAD and GABA-T activity. Wang et al.[3] reported that ameliorating chilling damage in banana fruits by PSKα treatment might be attributed to boosting endogenous GABA biosynthesis acquired by higher GAD activity concurrent with lower GABA-T activity. Therefore, boosting endogenous GABA biosynthesis by enhancing GAD expression and activity might be crucial for ameliorating chilling damage in banana fruits by 150

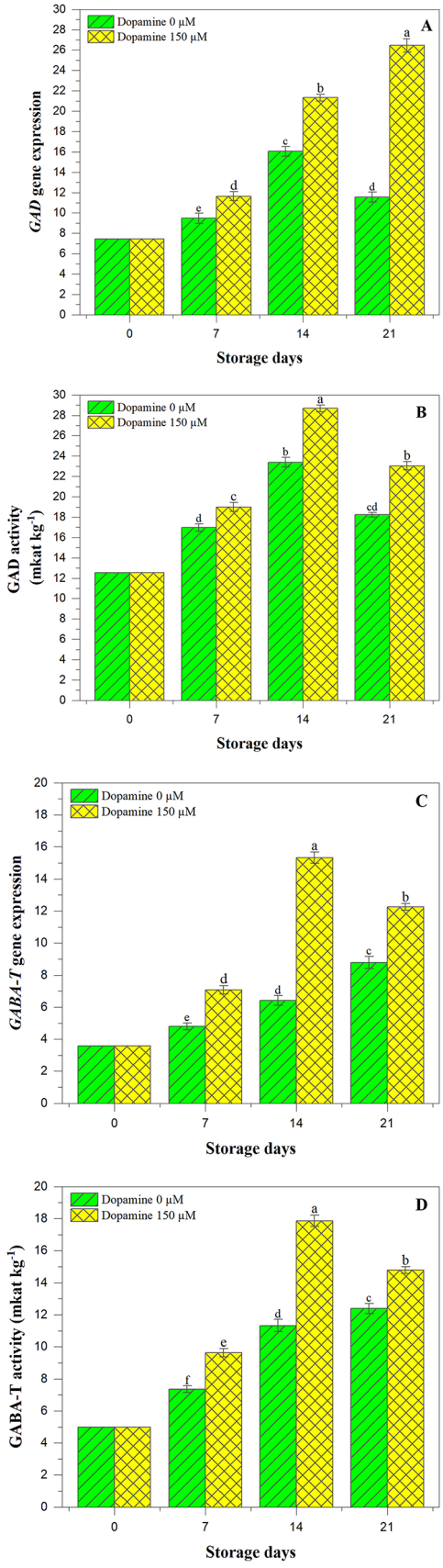

Fig. 4. *GAD* and *GABA-T* expression and activity concurrent with endogenous GABA biosynthesis in banana fruits treated with dopamine at 150 μM during storage at 7 °C for 21 days.

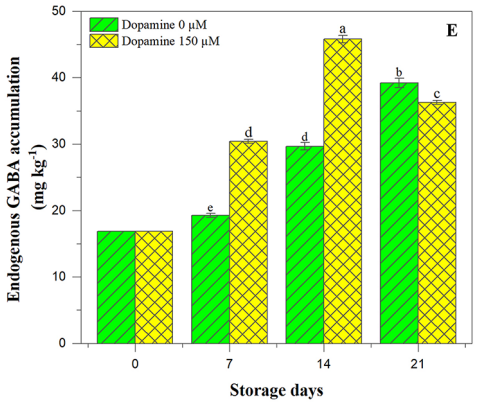

Figure 4. (continued)

µM dopamine treatment. In addition, GABA shunt pathway activation, cytosolic GAD activity concurrent with mitochondrial GABA-T and SSADH activity are accountable for supporting succinate for TCA cycle activity and NADH for electron transport system activity[65,66]. By exogenous dopamine treatment, endogenous dopamine signaling promotes signaling H_2O_2 dependent *PAL* expression and activity, which not only improves ROS scavenging activity by boosting phenols, flavonoids, and anthocyanins biosynthesis but also accelerates glutamate supplying by providing NH_4^+ for glutamine synthetase /glutamate synthase (GS/GOGAT) cycle activity. By sufficient glutamate supply, enhancing *GAD* expression and activity promotes GABA shunt activity, conferring biotic and abiotic stress tolerance by boosting intracellular ATP and carbon skeletons availability and suppressing intracellular ROS overaccumulation[67]. Sharafi et al.[66] reported that ameliorating chilling damage in tomato fruits by melatonin treatment might be attributed to boosting GABA shunt activity represented by higher GAD, GABA-T, and SSADH activity concurrent with boosting phenylpropanoid pathway activity represented by higher *PAL* expression and activity leading to higher phenols biosynthesis and higher DPPH radical scavenging activity. Wang et al.[68] reported that suppressing *THM27* transcription factor expression during cold stress might be crucial for ameliorating chilling damage in tomato plants by activating *GAD2* expression and boosting endogenous GABA biosynthesis, which promotes anthocyanins biosynthesis and ROS scavenging activity. Therefore, GABA shunt activity revealed by higher *GABA-T* expression and activity could ameliorate chilling damage in banana fruits by 150 µM dopamine treatment by avoiding intracellular ROS overaccumulation and supporting intracellular ATP and carbon skeleton availability. By boosting GABA shunt activity, supporting intracellular ATP and carbon skeletons availability was associated with higher fatty acids biosynthesis, elongation, and unsaturation concurrent with higher phenylpropanoid pathway activity[65,66].

Conclusions

Our results shed light on dopamine treatment potential in ameliorating chilling damage in banana fruits through improving ABTS, FRAP, and DPPH radicals scavenging activity acquired by higher phenols and flavonoids biosynthesis through activating *PAL* concurrent with suppressing *PPO* expression and activity. In addition to promoting ROS scavenging molecules accumulation by enhancing phenylpropanoid pathway activity, in ameliorating chilling damage in banana fruits treated with dopamine could be ascribed to boosting endogenous proline biosynthesis, as osmoprotectant, protein chaperone, and ROS scavenger molecule, acquired by activating *P5CS* and *OAT* concurrent with suppressing *ProDH* expression and activity. Furthermore, activating *GAD* and *GABA-T* expression and activity by dopamine treatment could be responsible for enhancing endogenous GABA biosynthesis, which is beneficial for avoiding intracellular ROS overaccumulation and supporting intracellular ATP and carbon skeleton availability, in addition to osmoprotectant function (Fig. 5). Therefore, dopamine could be exogenously applied to alleviate chilling injury in banana fruits by enhancing phenylpropanoid, GABA shunt and proline biosynthesis pathways activity. However, further studies at biochemical and molecular levels are needed for a illustration of dopamine effects on sensory and nutritional quality of banana fruits during postharvest storage.

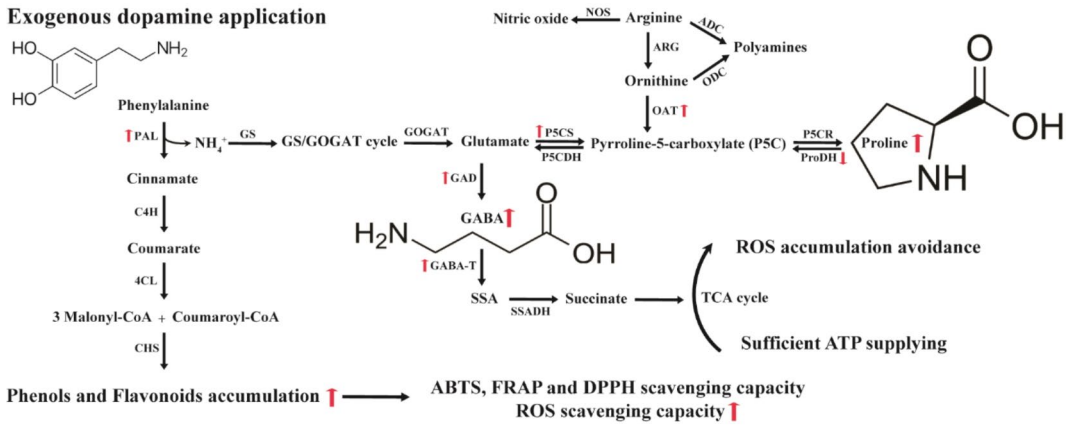

Fig. 5. A schematic diagram exhibiting phenylpropanoid, proline and GABA metabolism pathways in banana fruits treated with dopamine at 150 μM during storage at 7 °C for 21 days.

Data availability

Data availabilityThe data that support the findings of this study are available from the corresponding author upon reasonable request. There are no restrictions on data availability.

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Declarations

Competing interests

The authors declare no competing interests. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article.

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