PLANT SCIENCE TODAY
Vol 12(sp4): 1-6
https://doi.org/10.14719/pst.11490

eISSN 2348-1900

RESEARCH ARTICLE

Influence of different organic acids on enzymatic activity and postharvest quality in strawberry

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Received: 27 August 2025; Accepted: 05 October 2025; Available online: Version 1.0: 31 October 2025

Cite this article: Jashanpreet K, Chetak B, Navprem S, Sudha B, Gurpreet KD. Influence of different organic acids on enzymatic activity and postharvest quality in strawberry. Plant Science Today. 2025; 12(sp4): 1-6. https://doi.org/10.14719/pst.11490

Abstract

Strawberries are highly perishable fruits that suffer rapid quality loss during postharvest storage due to water loss, softening and microbial decay. Preserving their freshness, texture and nutritional value is essential to reduce postharvest losses and extend shelf life. This study evaluated the effectiveness of organic acids, such as ascorbic acid (AA), salicylic acid (SA) and oxalic acid (OA), at concentrations of 1, 2 and 3 mM in extending postharvest life. The study focused on preserving the quality of 'Winter Dawn' strawberries during 15 days of cold storage (5 ± 1 °C; 90-95 % relative humidity (RH)). The findings revealed that applying SA at a 3 mM concentration significantly reduced physiological weight loss and decay. This treatment also minimized fruit softening by inhibiting cell wall-degrading enzymes, such as polygalacturonase and pectin methyl-esterase. Furthermore, SA at 3 mM enhanced the activity of reactive oxygen species (ROS) scavenging enzymes, including peroxidase and superoxide dismutase (SOD). Moreover, it preserved fruit quality by maintaining higher levels of titratable acidity, total phenolics and antioxidant activity. Additionally, strawberries treated with 3 mM SA retained stable sensory attributes, including color, taste, glossiness and overall acceptability, throughout storage. Therefore, SA at 3 mM is a promising, natural postharvest treatment for maintaining the quality and extending the shelf life of strawberries during cold storage.

Keywords: enzymes; organic acids; pectin-esterase; post-harvest storage; salicylic acid

Introduction

Strawberry (*Fragaria × ananassa* Duch.) is one of the most widely cultivated fruit crops globally, with major production in China, USA and Europe. In India, the area under strawberry cultivation is around 2000 ha and is commercially cultivated in Himachal Pradesh, Maharashtra, Uttarakhand, Punjab, Haryana, Western Uttar Pradesh and Madhya Pradesh (1). It is enjoyed worldwide for its distinctive color, shape, aroma, delightful flavor and appealing texture. Strawberries are rich in nutrients such as vitamins, minerals, anthocyanins, flavonoids and phenolic acids, which provide health benefits in humans by combating cancer, oxidative stress, inflammation and neurodegenerative diseases (2). Although non-climacteric, strawberries are highly perishable owing to physical damage, water loss, tissue softening and fungal spoilage (3). The primary approach to extending the shelf life of strawberries is low-temperature storage. However, relying solely on cold storage is insufficient due to the highly perishable nature of strawberries when exposed to ambient temperatures. Therefore, alongside low-temperature storage, other postharvest methods have been documented to prolong the storage life of strawberry fruits, including techniques such as hot water treatment (4). Strawberries are highly perishable due to their delicate texture, elevated respiration rate and vulnerability to fungal decay (5). Postharvest, strawberry fruit quality declines quickly due to moisture loss and softening. To maintain fruit quality, strawberries should be stored at (5±1 °C; 90-95 % RH) immediately after harvest (6). Salicylic acid (SA), recognized as a signalling hormone, enhances resistance to oxidative stress, suppresses ethylene production and delays fruit senescence during storage (7). SA and its derivatives, such as acetyl SA, can delay fruit ripening, preserve quality and manage postharvest diseases (8). External application of SA triggers systemic acquired resistance at the site of pathogen infection and promotes the production of pathogenesis-related proteins in plants (9). Pre- and postharvest application of SA on the 'Camarosa' strawberry cultivar delayed fruit ripening, enhanced vitamin C levels and slowed metabolic activities and carbohydrate depletion (10). Applying SA during storage delayed kiwi fruit ripening by reducing ethylene production (11). Research indicates that SA inhibited fungal decay in peaches and grapes (12, 13). During storage, SA application bolstered the defence system by boosting antioxidant enzyme activities, enhancing resistance to fungal attacks (14). SA also delays banana fruit ripening and softening by slowing the action of cell wall-degrading enzymes (15). Synthetic fungicides containing harmful chemicals are commonly used to manage postharvest fruit decay in many regions, posing risks to human health (16). Strawberry, despite optimal success on production front, it faces myriad postharvest and marketing problems due to its short shelf life. In view of the above

facts, experiment would be carried out to determine the effect of organic acids with the aim to increase their shelf life and to maintain the quality characteristics of strawberry at refrigerated condition.

Materials and Methods

Fruit material

In February 2025, mature 'Winter Dawn' strawberry fruits, free from bruises and blemishes, were picked early in the morning at the experimental farm of Punjab Agricultural University, Ludhiana, India. The fruits were carefully harvested using fruit clippers, retaining short peduncles and calyxes. They were promptly transported to the post-harvest laboratory, where they were sorted by size, shape and any visible damage. The fruits were then disinfected with a 1.0 % sodium hypochlorite solution, rinsed with water and air-dried. Subsequently, they were divided into 10 treatments (T1-T10) with 6 replications. The treatment includes, T1- AA (1 mM), T2- AA (2 mM), T3- AA (3 mM), T4- SA (1 mM), T5- SA (2 mM), T6- SA (3 mM), T7- OA (1 mM), T8- OA (2 mM), T9- OA (3 mM), T10- control. After packaging of strawberry fruits in punnets, they were stored for 15 days under refrigerated conditions (5±1 °C; 90-95 % relative humidity (RH)).

Chemicals

Sodium acetate buffer (Trihydrate granular, reagent grade), sodium chloride (Sisco Research Laboratories (SRL) Pvt. Ltd.), polygalacturonic acid (Merck Sigma Pvt. Ltd.), guaiacol (Ultra Pure Chem Lab Industries), pectin (SRL Pvt. Ltd) etc., are used in this study.

Preparation of treatment solutions

To prepare the treatment solutions, AA was dissolved in distilled water at concentrations of 1 mM (176 mg/L), 2 mM (352 mg/L) and 3 mM (528 mg/L), mixed thoroughly using a magnetic stirrer. SA was prepared by dissolving the required amount in lukewarm (35 °C to 40 °C) distilled water at concentrations of 1 mM (138 mg/L), 2 mM (276 mg/L) and 3 mM (414 mg/L). Similarly, OA solutions were prepared at concentrations of 1 mM (126 mg/L), 2 mM (252 mg/L) and 3 mM (378 mg/L) using distilled water, with all solutions thoroughly mixed on a magnetic stirrer.

Polygalacturonase (U/mg protein)

To isolate the enzyme, fruit pulp tissue was combined with sodium citrate buffer. The mixture was filtered using Whatman filter paper and then centrifuged at 15000 × g for 30 min at 4 °C. The resulting supernatant was used to assess polygalacturonase (PG) activity. The PG activity was determined according to the method described elsewhere (17). The assay involved mixing 0.4 mL of sodium acetate buffer (trihydrate granular), 0.1 mL of NaCl (sodium chloride), 0.4 mL of polygalacturonic acid and 0.1 mL of the enzyme supernatant extract. The mixture was incubated at 37 °C for 30 min, followed by the addition of 3,5-dinitrosalicylic acid (DNS). The mixture was then heated in a boiling water bath for 5 min. PG activity was quantified at 540 nm by using spectrophotometer (Spectra Max plus 384 spectrophotometer).

Pectinesterase (U/mg protein)

The pectin methyl esterase (PME) activity assay was performed as described elsewhere (18). A 3 mL glass cuvette was used to prepare the reaction mixture, consisting of 0.2 mL of 0.15 M NaCl, 0.1 mL of 0.01 % bromothymol blue solution, 0.2 mL of water, 0.1 mL of homogenate and 1 mL of 0.01 % pectin solution (adjusted to pH 7.5 with 0.1 N NaOH (sodium hydroxide). After adding the enzyme preparation, the cuvette was gently shaken. Absorbance was measured at 620 nm immediately and again after 3 min. The change in absorbance between 0 and 3 min served as the indicator of PME activity, which was quantified using the standard curve.

Peroxidase (U/mg protein)

For peroxidase (POD) enzyme extraction from fruit tissue, 2 mL of potassium phosphate buffer (pH 7.5) (lab grade 99.5 %) was utilized, followed by centrifugation at 10000 × g for 30 min at 4 °C. To assess enzyme activity, a mixture was prepared in a cuvette containing 0.2 mL of enzyme extract, 3.0 mL of 0.05 M guaiacol and 0.1 mL of 0.8 M H_2O_2 (hydrogen peroxide) for reaction initiation. The change in absorbance at 470 nm was measured to determine POD activity, expressed as U/ mg protein (19).

Superoxidase dismutase (U/mg protein)

The activity of the superoxide dismutase (SOD) enzyme was determined following the method described previously (20). After enzyme extraction in potassium phosphate buffer (pH 7.5), the supernatant was used as the enzyme extract for SOD activity evaluation. The reaction mixture in the spectrophotometric cuvette consisted of 1.5 mL tris-HCl buffer (pH 8.2), 0.5 mL of 6 mM ethylenediaminetetraacetic acid, 1.0 mL of 6 mM pyrogallol and 0.1 mL of enzyme extract supernatant. One unit of SOD activity is defined as the enzyme quantity needed to reduce pyrogallol by 50 %. Absorbance changes were continuously monitored at 420 nm for 3 min and expressed as U/ min g fresh weight (FW).

Statistical analysis

Results were statistically analyzed by using R Studio software. A completely randomized design (CRD) with factorial arrangement of 2 factors was employed. To test the overall significance of the data, ANOVA (analysis of variance) techniques were employed. To compare the differences among treatment means (CD ≤ 0.05) least significant differences (LSD) test was used.

Results

Polygalacturonase (U/mg protein)

Table 1 shows the impact of organic acids on PG (U/mg protein) activity in the strawberry during low-temperature storage. The data show a significant increase in PG activity with longer storage time, rising from 3.79 to 4.70 over 15 days. Among the treatments, SA at 3 mM (T6) resulted in the lowest mean PG activity (4.00), followed closely by SA at 2 mM (T5) with a mean of 4.05. The highest PG activity was observed in the untreated control (T10) at 5.14, followed by OA at 1 mM (T7) at 4.31. Overall, higher concentrations of SA, particularly 3 mM, were most effective in reducing PG activity, followed by AA and OA treatments. These findings highlight the potential of SA at 3 mM as an effective postharvest treatment to minimize PG activity and preserve fruit quality during storage.

Pectinesterase (U/mg protein)

Table 2 shows the impact of organic acids on pectinesterase (U/ mg protein) in strawberries stored at low temperatures. The results show a significant increase in PME activity, rising from 0.037 to 0.0466 over 15 days of storage. Among the treatments, SA at 3 mM (T6) recorded the lowest mean PME activity at 0.0403, closely followed by SA at 2 mM (T5) at 0.0412. The highest pectinesterase levels were observed in the untreated control

Table 1. Effect of organic acids on polygalacturonase (U/mg protein) of strawberry fruits during storage

	Storage days						
Treatment	**0**	**3**	**6**	**9**	**12**	**15**	**Mean**
T1	3.79	3.93	4.06	4.32	4.57	4.77	4.24^{bc}
T2	3.79	3.87	3.98	4.16	4.37	4.57	4.12^{de}
T3	3.79	3.84	3.97	4.12	4.19	4.39	4.05^{ef}
T4	3.79	3.86	3.99	4.17	4.32	4.52	4.10^{e}
T5	3.79	3.85	3.98	4.15	4.19	4.39	4.05^{ef}
T6	3.79	3.83	3.97	4.05	4.09	4.29	4.00^{f}
T7	3.79	3.94	4.18	4.45	4.66	4.86	4.31^{b}
T8	3.79	3.89	4.04	4.31	4.48	4.68	4.19^{cd}
T9	3.79	3.85	3.99	4.14	4.23	4.43	4.07^{ef}
T10	3.79	4.54	5.07	5.39	5.95	6.15	5.14^{a}
Mean	3.79^{f}	3.94^{e}	4.12^{d}	4.32^{c}	4.50^{b}	4.70^{a}	
LSD at 0.05		D = 0.060		T = 0.078		D×T = 0.191	

D = Days

T = Treatments

U/mg protein = Enzyme units per milligram of protein

Means values within column that have different superscript letters are significantly different from one another under the LSD test at 0.05 probability level.

Table 2. Effect of organic acids on pectinesterase (U/mg protein) of strawberry fruits during storage

	Storage days						
Treatment	**0**	**3**	**6**	**9**	**12**	**15**	**Mean**
T1	0.037	0.043	0.044	0.045	0.046	0.048	0.0435^{bc}
T2	0.037	0.042	0.042	0.043	0.043	0.045	0.0420^{de}
T3	0.037	0.041	0.042	0.042	0.043	0.045	0.0416^{ef}
T4	0.037	0.042	0.042	0.043	0.044	0.046	0.0421^{de}
T5	0.037	0.041	0.041	0.042	0.043	0.045	0.0412^{f}
T6	0.037	0.040	0.040	0.041	0.041	0.043	0.0403^{g}
T7	0.037	0.043	0.044	0.045	0.046	0.048	0.0430^{b}
T8	0.037	0.042	0.043	0.044	0.045	0.047	0.0428^{cd}
T9	0.037	0.042	0.042	0.042	0.044	0.046	0.0421^{de}
T10	0.037	0.044	0.046	0.048	0.051	0.053	0.0462^{a}
Mean	0.037^{f}	0.0418^{e}	0.0426^{d}	0.0434^{c}	0.0446^{b}	0.0466^{a}	
LSD at 0.05		D = 0.0005		T = 0.0007		D×T = 0.0017	

D = Days

T = Treatments

U/mg protein = Enzyme units per milligram of protein

Means values within column that have different superscript letters are significantly different from one another under the LSD test at 0.05 probability level.

(T10) with a mean of 0.0462, followed by OA at 1 mM (T7) at 0.043. Overall, higher concentrations of SA, particularly 3 mM, were most effective in suppressing PME activity, followed by AA and OA treatments. These findings highlight the potential of SA at 3 mM as an effective postharvest treatment to reduce PME activity and preserve fruit quality during storage (Fig. 1).

Peroxidase (U/mg protein)

Table 3 displays the effects of organic acids on POD activity (U/mg protein) in strawberries during low-temperature storage. The data reveal a significant rise in POD activity, increasing from 2.28 to 2.35 over a 15-day storage period. Among the treatments, SA at 3 mM (T6) showed the highest mean POD activity with a mean of 2.83, followed closely by SA at 2 mM (T5) at 2.73. The lowest POD activity was observed in the untreated control (T10) with a mean of 2.20, followed by OA at 1 mM (T7) at 2.46. Overall, higher concentrations of SA, particularly 3 mM, were most effective in enhancing POD activity, followed by AA and OA treatments. These results suggest that SA at 3 mM could be a valuable postharvest treatment for increasing POD activity and maintaining fruit quality during storage.

Superoxidase dismutase (U/mg protein)

Table 4 presents data on the impact of organic acids on SOD activity (U/mg protein) in the strawberry during low-temperature storage. The results show a significant rise in SOD activity with extended storage time, increasing from 2.71 to 2.83 over 15 days. Among treatments, SA at 3 mM (T6) recorded the highest mean SOD activity at 3.18, followed by SA at 2 mM (T5) at 3.08. The lowest SOD activity was observed in the untreated control (T10) with a mean of 2.73, followed by OA at 1 mM (T7) at 2.94. Overall, higher concentrations of SA, especially 3 mM, proved most effective in enhancing SOD activity, followed by AA and OA treatments. These findings highlight the potential of SA at 3 mM as a postharvest treatment to boost SOD activity and preserve fruit quality during storage.

Table 3. Effect of organic acids on peroxidase (U/mg protein) of strawberry fruits during storage

	Storage days						
Treatment	**0**	**3**	**6**	**9**	**12**	**15**	**Mean**
T1	2.28	2.54	2.81	2.61	2.49	2.29	2.50^{fg}
T2	2.28	2.58	2.95	2.66	2.59	2.39	2.57^{de}
T3	2.28	2.63	3.02	2.72	2.68	2.48	2.63^{c}
T4	2.28	2.58	2.92	2.76	2.62	2.42	2.59^{cd}
T5	2.28	2.64	3.09	2.94	2.83	2.63	2.73^{b}
T6	2.28	2.69	3.29	3.06	2.94	2.74	2.83^{a}
T7	2.28	2.53	2.71	2.62	2.43	2.23	2.46^{g}
T8	2.28	2.55	2.83	2.68	2.54	2.34	2.53^{ef}
T9	2.28	2.61	2.94	2.73	2.62	2.42	2.59^{cd}
T10	2.28	2.48	2.65	2.32	1.85	1.65	2.20^{h}
Mean	2.28^{e}	2.58^{c}	2.92^{a}	2.71^{b}	2.55^{c}	2.35^{d}	
LSD at 0.05		D= 0.032		T = 0.041		D×T = 0.101	

D = Days

T = Treatments

U/mg protein = Enzyme units per milligram of protein

Means values within column that have different superscript letters are significantly different from one another under the LSD test at 0.05 probability level.

Fig. 1. Images showing comparison of control and treated fruits with SA after 15 days under refrigerated condition.

Table 4. Effect of organic acids on superoxidase dismutase (U/mg protein) of strawberry fruits during storage

	Storage days						
Treatment	**0**	**3**	**6**	**9**	**12**	**15**	**Mean**
T1	2.71	3.14	3.17	3.13	3.01	2.81	2.99^{de}
T2	2.71	3.19	3.22	3.15	3.09	2.89	3.04^{bcd}
T3	2.71	3.21	3.25	3.19	3.11	2.91	3.06^{bc}
T4	2.71	3.18	3.24	3.18	3.12	2.92	3.05^{bc}
T5	2.71	3.21	3.26	3.22	3.14	2.94	3.08^{b}
T6	2.71	3.28	3.37	3.35	3.31	3.11	3.18^{a}
T7	2.71	3.08	3.14	3.11	2.92	2.72	2.94^{e}
T8	2.71	3.15	3.18	3.12	3.06	2.86	3.01^{cd}
T9	2.71	3.19	3.22	3.17	3.09	2.89	3.04^{bcd}
T10	2.71	3.04	3.11	2.65	2.54	2.34	2.73^{f}
Mean	2.71^{e}	3.16^{b}	3.21^{a}	3.12^{b}	3.03^{c}	2.83^{d}	
LSD at 0.05		D = 0.0401		T = 0.0518		D×T = 0.127	

D = Days

T = Treatments

U/mg protein = Enzyme units per milligram of protein

Means values within column that have different superscript letters are significantly different from one another under the LSD test at 0.05 probability level.

Discussion

Strawberry softening primarily results from pectin solubilization, degradation of cell wall polysaccharides and loss of neutral sugars such as galactose and arabinose during ripening and postharvest storage. Cell wall-degrading enzymes, particularly PG, play a significant role in degrading cell wall polysaccharides, leading to reduced fruit firmness and cell wall cohesion. Postharvest treatments that reduce these enzymes' activity can slow the softening process, extending shelf life (21). Edible coatings form a protective barrier on the fruit surface, limiting oxygen availability, which reduces the activity of cell wall-degrading enzymes and improves fruit membrane integrity (22). Table 1 indicates that strawberries treated with 3 mM SA (T6) had the lowest activity compared to the untreated control group. During storage, PG levels in fruits rose significantly, with control samples showing the highest PG activity. In contrast, fruits treated with SA displayed lower PG activity than controls. Among treated samples, those exposed to 100 µL/L SA exhibited the lowest PG activity. PG is the primary enzyme involved in pectin degradation and fruit softening during the ripening process (23). Comparable results were also noted that PG activity in fruit peels was lower on day 9 than on day 3 of shelf life across all treatments. After 3 days, PG activity was lower in the GA combined with SA treatment compared to other treatments, except for the low-dose SA treatment. By day 6, PG activity was reduced in both the low-dose SA and GA plus SA treatments compared to the control (24) whereas the effects of SA were found to differ when 'Hari chhal' bananas were treated with 0.5 mM or 1 mM solution. SA may reduce fruit softening and suppress the activities of invertase, cellulase, PG, xylanase, catalase (CAT) and POD. Pectin-degrading enzymes are strongly associated with alterations in pectins, which significantly contribute to the softening of fruit and vegetable tissues (25). In higher plants, PME degrades pectins, which are essential components of the fruit's middle lamella and primary cell wall, generating demethylated pectins that are more vulnerable to hydrolysis by PG. PG promotes the cleavage of α-(1→4)- galacturonan bonds in demethylated pectins, resulting in shorter chains and leading to the depolymerization and dissolution of pectins (26, 27).

According to Table 2, the lowest PME activity was observed in strawberries treated with 3 mM SA (T6) compared to the control group. PME activity in all samples increased gradually during storage, but the rise was significantly lower in SA-treated fruits. By day 15, PME activity in SA-treated strawberries was markedly reduced compared to the control ($p < 0.05$). These findings suggest that SA treatment effectively inhibited PME activity, thereby delaying cell wall degradation and maintaining fruit firmness during storage (28). CTS-g-SA treatment reduced PME activity in fruit during the mid to late storage phases, showing significantly lower activity ($p < 0.05$) in treated fruit compared to controls from days 45 to 75. The expression of the PME gene in fruit peel consistently decreased throughout the storage period (29). This decrease could be attributed to CTS-g-SA's capacity to maintain a sustained release of SA, which suppresses the activity of cell wall hydrolases (30). POD promotes lignin synthesis and counteracts ROS, enhancing pathogen defense and mitigating oxidative stress. According to Table 3, the highest POD activity was recorded in fruits treated with 3 mM SA (T6) compared to the control group. POD activity in fruit peels was higher on day 9 than on day 3 of shelf life (SL), except for the low-dose gibberellic acid (GA) treatment. After 3 days of SL, no notable differences in POD activity were observed across treatments. By day 6, both GA treatment levels showed elevated POD activity compared to the control. By day 9, both SA treatment levels demonstrated increased POD activity relative to the control. Treatments with GA and SA enhanced the activity of the antioxidant enzyme POD in both fruit peel and pulp, particularly after 6 and 9 days of shelf life (31). POD and polyphenol oxidase (PPO) are recognized as protective enzymes that defend against stress and pathogen attacks (32).

Strawberry fruits treated with 3 mM SA displayed the highest POD activity (0.39 U/mg protein) after 15 days compared to other treatments. Fruits treated with different concentrations of calcium chloride ($CaCl_2$) and SA sustained POD activity during storage, whereas the control group exhibited the lowest activity (0.15 U/mg protein). These findings suggest that a moderate SA concentration (5 mM) was most effective in maintaining peak POD activity in strawberry fruits during storage (33).

SA, an important phenylpropanoid compound, enhances fruit resilience against stress by promoting ascorbate peroxidase activity, which aids in preventing oxidative cellular damage (34). SOD, a key protective enzyme, shields plant cells from damage during stress conditions. Under stress, the enzymatic actions of CAT, SOD and POD preserve cell integrity by directly neutralizing ROS, such as superoxide radicals and H_2O_2, transforming them into less harmful compounds (35).

According to Table 4, the highest SOD activity was observed in fruits treated with 3 mM SA, (T6) compared to the control group. Fruits treated with 3 mM SA showed the highest SOD activity after 15 days of storage. The control group experienced the most significant decrease in SOD activity throughout the storage period. These results indicate that treatment with 3 mM SA was the most effective in preserving maximum SOD activity during storage (36). SA-treated peaches exhibited enhanced CAT and SOD activity by lowering superoxide radical levels during storage (37).

Conclusion

This study demonstrates that postharvest treatment of strawberries with 3 mM SA effectively delays quality deterioration during cold storage by reducing the activity of cell wall-degrading enzymes (PEG and PME) and enhancing antioxidant defence systems (POD and SOD). These effects collectively contribute to slower fruit softening, improved membrane stability and prolonged storage life without compromising sensory quality. Therefore, SA at 3 mM can be considered a promising, safe and eco-friendly alternative to chemical fungicides for maintaining the postharvest quality and extending the shelf life of strawberries during cold storage. Further research should investigate the combined application of SA with other natural treatments or packaging technologies to enhance postharvest benefits, as well as evaluate its effectiveness across different cultivars to ensure broader applicability to maximize postharvest benefits.

Acknowledgements

The facilities provided by Punjab Agricultural University for conducting the work are gratefully acknowledged.

Authors' contributions

JK conducted experiments and collected the data. CB drafted the manuscript. NS checked for plagiarism and finalized it according to the journal guidelines. SB helped in the data analysis. GKD provided technical support. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors do not have any conflict of interest to declare.

Ethical issues: None

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