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Original Article

Enhanced Impacts of Spermine Compared to Putrescine and Spermidine on Fruit Performance and Quality of Strawberry cv. Camarosa under Pre- and post-harvest Analyses

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ABSTRACT

Polyamines play a key role in regulating fruit quality, but the comparative effects of the major polyamines—putrescine (Put), spermine (Spm), and spermidine (Spd)—on strawberry fruit quality are still unclear. The current study sought to determine the effects of various polyamines to maximize the quality of the strawberry cv. Camarosa. The Pre-harvest experiment using varying amounts of Put, Spm, and Spd (0, 25, 50, 75, and 100 mg/L) was included in this investigation. In the post-harvest experiment, the ideal concentration determined in the initial trial was employed to submerge the fruits. Following that, these fruits were kept for 12 days, with samples being collected for examination on days 3, 6, 9, and 12. The application of polyamines, especially Spm, at 75 mg/L enhanced Chl a+b (35%), RWC (10%), fruit yield (40%), anthocyanin (36%), ascorbic acid (AsA, 33%), and DPPH scavenging activity (25%), while reducing the TSS/TA ratio at harvest by 24% compared with the untreated control. In the second experiment, the quality of the fruits decreased when they were stored. In fruits without polyamines, firmness (62%), anthocyanin (35%), and DPPH scavenging activity (29%) decreased by day 12 compared to the first day of storage. However, fruit weight loss (15.3%), fruit decay (24.7%), malondialdehyde (MDA, 75%), and TSS/TA (56%) all increased during storage. Polyamine treatments—particularly Spm—significantly reduced fruit decay, weight loss, MDA, and helped maintain antioxidant capacity, likely through enhanced membrane stability and modulation of ethylene-related senescence processes. Therefore, the application of Spm at 75 mg/L is recommended to enhance fruit yield and preserve strawberry fruit quality during storage.

Keywords: Antioxidant capacity, Anthocyanin, Fruit decay, Polyamines, Titratable acidity

INTRODUCTION

Polyamines, including spermine (Spm), spermidine (Spd), and putrescine (Put), are organic compounds that play crucial roles in plant growth, development, and postharvest storage of fruits. They are essential for modulating plant responses to environmental stress, regulating gene expression, and influencing cellular functions [1]. Polyamines are involved in cell division and elongation, promoting the synthesis of DNA, RNA, and proteins. They also stabilize the structure of DNA and RNA, facilitating efficient transcription and translation processes [2]. Exogenous application of polyamines can enhance plant growth by promoting root and shoot development. They interact synergistically with phytohormones like auxins, gibberellins, and cytokinins, regulating plant growth [2, 3].

Polyamines play a crucial role in fruit storage by delaying senescence, a process that leads to aging and decay. They inhibit the biosynthesis of ethylene, a plant hormone that accelerates ripening and deteriorates fruit quality. Polyamines help regulate ethylene levels, extending the shelf life of fruits and preventing over-ripening. Polyamines compete with ethylene for the common precursor, S-adenosylmethionine (SAM), thereby reducing the availability of SAM for ethylene biosynthesis. This results in a decrease in ethylene production, which helps delay the ripening process. Additionally, exogenous polyamines inhibit key enzymes involved in ethylene biosynthesis, further suppressing ethylene levels and extending shelf life [4, 5]. They also contribute to postharvest preservation by reducing oxidative stress and maintaining cell membrane integrity [3, 4]. Oxidative stress, caused by reactive oxygen species (ROS), damages cellular components, leading to deterioration of texture and appearance. Polyamines, with their strong antioxidative properties, help scavenge ROS and mitigate damage, preserving cell membrane integrity and preserving fruit firmness, color, and overall quality [6]. By stabilizing cellular structures and protecting against oxidative damage, polyamines extend the marketable life of fruits, reduce postharvest losses, and ensure fruits retain their nutritional and sensory qualities [2]. Polyamines bind to phospholipids and membrane components, strengthening and preventing lipid peroxidation, which can damage the cell membrane. This helps maintain fluidity and stability, controlling water, ions, and other molecules. It also helps maintain cellular turgor, structural integrity, and fruit quality during postharvest storage. Exogenous polyamines mitigate oxidative stress, preserving membrane selective permeability, extending shelf life, and preserving fruit quality [7, 8].

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Pre-harvest application of polyamines has been shown to influence plant growth and fruit quality in several crops, including jujube [9], black plum [10], and sesame [11], while post-harvest studies have reported beneficial effects on fruit quality and antioxidant capacity in papaya [12] and guava [13]. Strawberry (*Fragaria* × *ananassa*), despite its high nutritional value and commercial importance, is highly perishable and prone to rapid post-harvest deterioration. Although conventional storage methods such as temperature and humidity control can delay quality loss, they are often insufficient, highlighting the need for alternative and sustainable approaches to improve strawberry shelf life [14,15]. In strawberries, however, research on polyamines remains limited and fragmented, with most studies focusing on post-harvest treatments or individual polyamines rather than comprehensive comparative evaluations. For example, Jalali *et al*. [15] demonstrated that post-harvest application of Spm and Spd at relatively high concentrations (approximately 150–250 mg/L) delayed senescence by reducing weight loss and decay, maintaining firmness, and enhancing antioxidant activity during storage. Similarly, Orman *et al*. [16] reported that post-harvest treatment of strawberry fruits with spermidine at concentrations equivalent to approximately 150–300 mg/L significantly preserved biochemical and quality traits during cold storage, with 2.0 mM identified as the most effective dose. However, the effects of polyamine concentrations below 100 mg/L remain unclear, and most previous studies have investigated only one or two polyamines, primarily under post-harvest conditions.

Therefore, comparative information regarding the relative effectiveness and optimal concentrations of the three major polyamines—Put, Spm, and Spd—particularly under pre-harvest conditions, is still lacking. It is hypothesized that Spm may exert stronger physiological and protective effects than Put or Spd due to its higher positive charge density and greater capacity to stabilize cellular membranes and interact with macromolecules involved in stress regulation and senescence. To address this gap, the present study aimed to identify optimal concentrations of Put, Spm, and Spd for improving plant physiological traits, fruit yield, and antioxidant potential, and to subsequently evaluate their effects on post-harvest fruit quality and storage performance in strawberry cv. Camarosa under both pre- and post-harvest conditions.

MATERIALS AND METHODS

Experimental Treatments and Growth Circumstances

This study comprised two experiments evaluating the effects of polyamines under pre- and post-harvest conditions. In the pre-harvest experiment, strawberry plants (Camarosa cultivar) were treated with three polyamines—Put, Spm, and Spd—each applied at four concentrations (25, 50, 75, and 100 mg/L), in addition to an untreated control, resulting in a total of 13 treatments (1 control + 3 polyamine types × 4 concentrations). Each pot contained one plant. The experiment was conducted in a greenhouse under average temperatures of 16 °C at night and 27 °C during the day, with a relative humidity of 65–70%. The seeds were grown in grow boxes with a 2:1 ratio of cocopeat to perlite, and the plants were nourished with Hogland nutritional solution. The experiment was designed in a completely randomized design (CRD) with three replicates for each treatment in 2023. A total of 13 treatments of these polyamines at different concentrations were used, which were sprayed on the leaves three times at 15-day intervals. The first spraying was conducted at the 4-leaf stage. For the first experiment, the following parameters were used: Chlorophyll (Chl) content, relative water content (RWC), fruit yield, total soluble solids (TSS), titratable acidity (TA), anthocyanin, ascorbic acid (AsA), and DPPH scavenging activity.

In the second experiment, the optimal concentration identified from the first experiment was used to immerse the fruits. The treated fruits were then stored at 4 °C for 12 days, with samples collected on days 1, 3, 6, 9, and 12 for analysis. The experiment was arranged in a factorial design based on a completely randomized design (CRD), with polyamine type at four levels (control, Put, Spd, and Spm) and storage time at five levels (days 1, 3, 6, 9, and 12), resulting in a total of 20 treatments (4 polyamine treatments × 5 storage times), each with three replicates.

Chlorophyll Measurement

Arnon's method [17] was used to quantify the amounts of Chl in leaves with three replicates. Fresh leaves weighing 0.1 g were ground using liquid nitrogen. After adding 10 mL of acetone (80%), a centrifuge was run for 10 min at 6000 rpm. All procedure steps were conducted under dim light to minimize Chl degradation. Sample absorbance was measured at wavelengths of 645 and 663 nm using a Shimadzu UV-160 spectrophotometer. The following formulas made use of the findings:

Chl a (mg/g) = $12.7\times A_{663}-2.69\times A_{645}$

Chl b (mg/g) = $22.9\times A_{645}-4.68\times A_{663}$

Where:

A663 and A645 are the absorbance values at 663 nm and 645 nm, respectively.

Determination of Relative Water Content (RWC)

To calculate RWC, the developed leaves were utilized. Saturation weight (SW) was obtained by immersing the leaves in distilled water for a full day following the measurement of fresh weight (FW). To determine their dry weight (DW), the leaf samples were then dried for 24 h at 70 °C. In the end, the following equation was used to determine RWC [18].

$$\mathrm{RWC} = \frac{(\mathrm{FW}-\mathrm{DW})}{(\mathrm{SW}-\mathrm{DW})}\times 100$$

Yield, Weight loss, Decay, and Firmness of Fruits

Fruit yield was calculated by measuring the weight of all fruits per plant [19].

The weight loss of a fruit over time is measured by weighing the fruit at its start, storing it under specific conditions, and weighing it regularly. The percentage weight loss can be calculated using the formula:

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Initial weight - Final weight - 100. This method helps in understanding the process of fruit decay and its impact on moisture and mass.
Weight loss percentage= [(Initial Weight−Final Weight)/Initial weight] ×100
Fruit decay was assessed visually by estimating the proportion of the fruit surface area affected by decay symptoms. Decay was expressed as a percentage of the decayed surface area relative to the total fruit surface area.
A penetrometer (FT011 Fruit hardness Tester; Wagner Instruments, Italy) was used to measure the firmness of fruits. Fruit firmness was measured by inserting the penetrometer into two opposite sides of the fruit and recording the hardness values in kg cm^{-2}. This method helps identify the degree of decay or ripening based on changes in firmness over time [19].

Preparation of Fruit Extraction

Samples of fruit tissue were frozen using liquid nitrogen. After that, 5 g of fruit tissue was homogenized in 10 mL of 50 mmol L^{-1} phosphate buffer at pH 7.8. The homogenate was centrifuged for 20 min at 4 °C at 15000 rpm to decide on further analysis. It was decided to collect the fruit extract [19].

Anthocyanins Measurement

Total anthocyanin content was determined using the pH differential method as described previously [20]. Two buffer systems were used: 25 mM potassium chloride (KCl) buffer at pH 1.0 and 0.4 M sodium acetate buffer at pH 4.5. Fruit juice samples were first diluted with KCl buffer (pH 1.0) until the absorbance at 520 nm was within the linear range of the spectrophotometer, and the same dilution factor was then applied using sodium acetate buffer (pH 4.5). Absorbance was measured at 520 nm against distilled water as a blank.
The absorbance difference (A) was calculated as:
A=A520 (pH 1.0) − A520(pH 4.5)
Total anthocyanin content was calculated as cyanidin-3-glucoside (C3G) equivalents using the following equation:
Total anthocyanin (mg/L) = A×MW×DF×1000 / ε×l
where *A* is the absorbance difference, *MW* is the molecular weight of cyanidin-3-glucoside (449.2 g mol^{-1}), *DF* is the dilution factor, *ε* is the molar extinction coefficient (26,900 L/mol/cm), and *l* is the path length of the cuvette (1 cm). Anthocyanin content was finally expressed as mg C3G per 100 g fresh weight (mg C3G 100 g/FW).

Ascorbic Acid Measurement

Ascorbic acid (vitamin C) was measured by titrating 2,6-dichlorophenolindophenol. After 10 g of fruit flesh was digested with 3% metaphosphoric acid, the mixture's volume was expanded to 100 mL with the help of 3% metaphosphoric acid, and it was then filtered. To get a pale pink tint, 10 milliliters of filtered solution were titrated using dichlorophenol-indophenol. The quantity of ascorbic acid in mg 100/g of extract was determined using the pigment volume used in the titration [19].

Total Soluble Solids (TSS)

Fruit juice droplets were placed in a refractometer to quantify TSS. Brix was measured, and the refractometer's calibration was done using distilled water prior to the measurement [21].

Titration Acidity (TA) Determination

TA was determined by titration following a standard method [21]. Briefly, 5 mL of fruit extract was diluted with 20 mL of distilled water in an Erlenmeyer flask. The solution was titrated with 0.1 N NaOH at 20 °C while continuously monitoring pH using a calibrated pH meter. The titration endpoint was identified by a sharp change in pH, corresponding to neutralization of organic acids. TA was calculated based on the volume of NaOH consumed during titration and expressed as grams of citric acid per 100 mL of fruit extract (%). A citric acid conversion factor of 0.064 was used, assuming citric acid as the predominant organic acid in strawberry fruit, which is consistent with previous reports on strawberry organic acid composition [21]. Standardization of the titration procedure and operator training were applied to ensure consistency and accuracy in endpoint determination.

$$\text{TA\%} = \frac{\text{Titre (mL)} \times \text{NaOH Normality (0.1)} \times \text{Citric acid weight (0.064)}}{\text{Volume of sample for titrate (5 mL)}}$$

Data Analysis

Following data collection, the SAS (version 9.3, SAS Institute, Cary, NC, USA) tool was used to analyze the data for factorial design. Duncan's multiple range test was used to compare the data means at a 5% probability level ($P \leq 0.05$). EXSTAT performed PCA, and CIMMiner created a heat map, which may be found at https://discover.nci.nih.gov/cimminer/home.do.

RESULTS

Pre-harvest Test

This pre-harvest test of polyamines on strawberry plants included measurements of Chl, RWC, fruit yield and quality, and antioxidant capacity.

Chlorophyll and Relative Water Content

Polyamines significantly improve Chl content and RWC in plants, with Spm showing the most significant effects. Put, at concentrations of 25, 50, 75, and 100 mg/L, increased total Chl content by 13%, 22%, 24%, and 16% compared to the untreated control. Spm, at the same concentrations, further amplified Chl content, resulting in increases of 19%, 30%, 36%, and 20%, indicating its superior efficacy in promoting

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Chl accumulation (Table 1). Furthermore, polyamines, particularly Spm, significantly improved RWC of plants, a crucial indicator of their water status and overall health. The control plants had a water content of 81.6%, but when Spm was applied foliarly at 75 mg/L, the RWC increased to 90%, indicating the potential of polyamines in enhancing plant water balance (Table 1).

Fruit Yield and Maturity Index

Polyamines significantly increased fruit yield, with concentrations of 75 mg/L showing the most significant effects. Put, Spm, and Spd significantly increased fruit yield by 36%, 40%, and 37%, respectively, compared to the control. Polyamines also affected the TSS: TA ratio, a maturity index used to assess fruit taste and texture quality. The most pronounced reductions were observed at 75 mg/L, with Put, Spm, and Spd lowering the TSS: TA ratio by 14%, 24%, and 18%, respectively. This suggests that while polyamines enhance fruit yield, they may also affect the balance between sweetness and acidity, potentially affecting the overall taste and texture of the fruit (Table 1).

Table 1 Chlorophyll (Chl), relative water content (RWC), fruit yield, and total soluble solid (TSS)/ titratable acidity (TA) strawberry fruits under polyamines.

Polyamine (mg/L)	Chl a+b (mg/g)	RWC (%)	Fruit yield (g/plant)	TSS/TA
Control	0.9 ± 0.06 e	81.7 ± 1.5 j	380 ± 17.6 f	12.3 ± 0.38 a
Put 25	1.01 ± 0.05 d	83 ± 1.6 i	450 ± 17.6 e	11.4 ± 0.09 bc
Put 50	1.09 ± 0.07 bcd	86.7 ± 1.5 def	473.3 ± 23.8 d	10.9 ± 0.24 bcd
Put 75	1.1 ± 0.07 bcd	87 ± 1.2 de	516.7 ± 18 b	10.6 ± 0.07 d-g
Put 100	1.03 ± 0.05 cd	85.7±1.5 fg	453.3 ± 22.3 e	11.5 ± 0.49 b
Spm 25	1.06 ± 0.02 bcd	84.7 ± 1.8 gh	463.3 ± 18 de	10.6 ± 0.14 def
Spm 50	1.16 ± 0.06 ab	89.3 ± 1.8 ab	496.7 ± 18.9 c	9.9 ± 0.21 g
Spm 75	1.21 ± 0.07 a	90 ± 2.1 a	533.3 ± 23.8 a	9.3 ± 0.09 h
Spm 100	1.1 ± 0.06 bcd	88.7 ± 1.5 bc	470.7 ± 26.1 d	10.4 ± 0.01 d-g
Spd 25	1.07 ± 0.05 bcd	85 ± 1.6 gh	466.7 ± 14.8 de	10.8 ± 0.08 cde
Spd 50	1.12 ± 0.08 abc	86.3 ± 1.2 ef	476.7 ± 12.2 d	10.1 ± 0 efg
Spd 75	1.16 ± 0.05 ab	87.7 ± 1.5 cd	520 ± 21.2 ab	10 ± 0.16 fg
Spd 100	1.09 ± 0.05 bcd	84.3 ± 1.7 h	480 ± 17.6 d	10.6 ± 0.12 def

Small letters show the mean comparison and bars are standard errors (SE).

Anthocyanin, Ascorbic Acid, and DPPH Scavenging Activity

The antioxidant capacity of strawberries increased significantly under polyamine treatments (Table 2). The greatest anthocyanin was achieved under 75 mg/L Spm with a 36% increase relative to the control, boosted by polyamines. Moreover, this concentration of Put and Spd resulted in increases of 17% and 15%, respectively, in comparison to the control. AsA followed a similar pattern, reaching its maximum at 75 mg/L Spm, 33% higher than the control. Following a 75 mg/L spraying of Put and Spd, fruits exhibited increases in AsA of 10% and 23%, respectively.At Put concentrations of 25, 50, 75, and 100 mg/L, DPPH scavenging activity increased by 8%, 14%, 15%, and 8%, respectively. Similarly, foliar application of Spm resulted in increases of 12%, 22%, 25%, and 16% at the corresponding concentrations (Table 2).

Table 2 Anthocyanin, ascorbic acid (AsA), and DPPH scavenging activity strawberry fruits under polyamines.

Polyamine (mg/L)	Anthocyanin (mg /00 g)	AsA (mg /100 g)	DPPH scavenging activity (%)
Control	45 ± 6.5 d	58 ± 2.1 h	54.7 ± 5.3 f
Put 25	52.7 ± 3.9 bc	60.3 ± 2.4 h	59 ± 2.4 e
Put 50	50.7 ± 1.9 bc	64 ± 3.1 g	62.7 ± 2.1cd
Put 75	54 ± 2.1 bc	66.3 ± 2.7 fg	63 ± 2.4 cd
Put 100	49.7 ± 1.8 c	65.7 ± 1.9 fg	59 ± 2.1 e
Spm 25	53.3 ± 3.2 bc	69.7 ± 3.3 de	61.3 ± 1.8 de
Spm 50	55.3 ± 1.5 b	74.3 ± 2.8 b	66.7 ± 2.7 ab
Spm 75	61.3 ± 3.2 a	77.3 ± 2.4 a	68.3 ± 3.2 a
Spm 100	55 ± 1.8 b	72.7 ± 3.4 bc	63.7 ± 2.7 bcd
Spd 25	51.7 ± 1.5 bc	66 ± 2.1 fg	61.7 ± 1.9 de
Spd 50	52.7 ± 1.9 bc	71.3 ± 1.8 cd	64 ± 2.9 bcd
Spd 75	55.7 ± 2.9 b	71 ± 1.8 cd	65.7 ± 2.1 abc
Spd 100	51.3 ± 2.2 bc	68 ± 2.9 ef	63.7 ± 2.4 bcd

Small letters show the mean comparison and bars are standard errors (SE).

Post-harvest Test

The optimal polyamine concentration (75 mg/L) was chosen for fruit storage over a 12-day period in the post-harvest test.

Weight Loss, Decay, and Firmness

Throughout the storage period, fruit weight loss increased in all treatments; however, polyamine application significantly mitigated this reduction. In untreated fruits, the highest weight loss (15.3%) was observed on day 12 of storage. By contrast, on day 12, fruits treated with Put, Spm, and Spd exhibited 28%, 46%, and 41% lower weight loss, respectively, relative to the control, indicating a proportional reduction compared with untreated fruits (Fig. 1 a).

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Furthermore, fruit decay accelerates during storage, although polyamines slow the process. The greatest degradation, 24.7%, was seen on day 12 without poluyamines. By using Put, Spm, and Spd on day 12, the decay was reduced by 34%, 46%, and 42%, respectively, in comparison to the control (Fig. 1 b). Fruit firmness significantly decreased over the storage period, with noticeable declines observed as the days progressed. Specifically, on days 3, 6, 9, and 12, firmness in fruits without polyamine treatment decreased by 13%, 32%, 41%, and 62%, respectively. This trend highlights the natural softening process that occurs during storage, leading to a substantial loss of firmness over time in untreated fruits. Polyamines significantly improved fruit firmness in fruits treated with Put, Spm, and Spd. These treatments increased firmness by 47%, 65%, and 58%, respectively (Fig. 1 c).

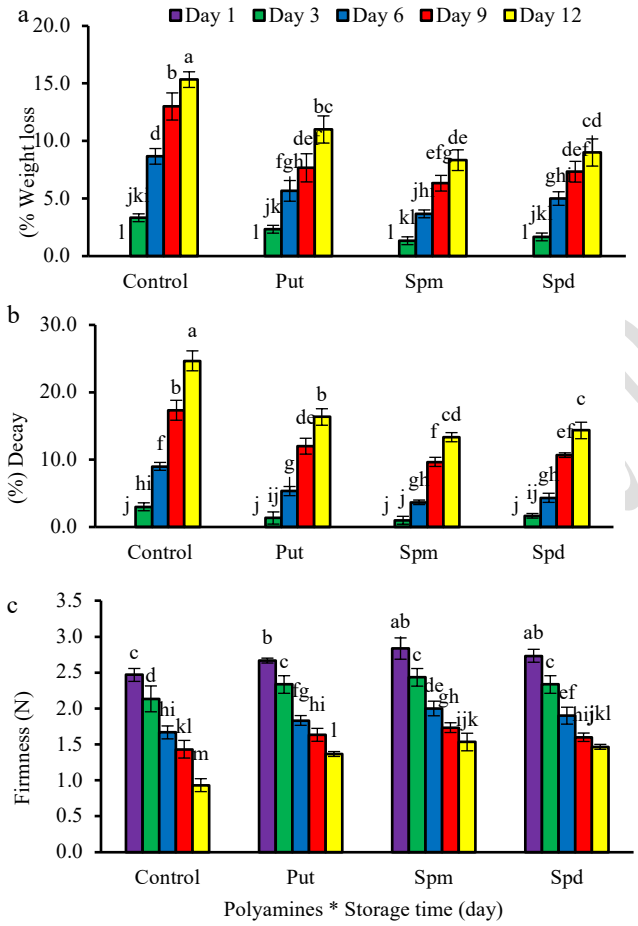

Fig. 1 Weight loss (a), decay (b), and firmness (c) of strawberry fruits under polyamines during storage. Small letters above the columns show the differences in mean comparison and bars are standard errors (SE).

Total Soluble Solids and Titratable Acidity

Polyamines reduced TSS, but storage time increased it. On day 12, a 13% rise in TSS was recorded without the use of plyamines. TSS dropped when polyamines were applied. On day 12, the application of Put, Spm, and Spd reduced TSS in fruit storage by 9%, 12%, and 10%, respectively (Fig. 2 a). In contrast, TA had a reverse reaction, declining during storage but increasing as it reduced by 28% at the end of storage in comparison to the first day of the storage. Furthermore, Spm demonstrated a 10% rise in TA on day 12 in response to non-polyamine treatment (Fig. 2 b). The ratio of TSS: TA increased noticeably during storage. In the absence of polyamine therapy, increases of 14%, 30%, 52%, and 57% were seen on days 3, 6, 9, and 12 as compared to the control. TSS/TA in fruit storage decreased by 13%, 19%, and 14% for Put, Spm, and Spd, correspondingly, on day 12 (Fig. 2 c).

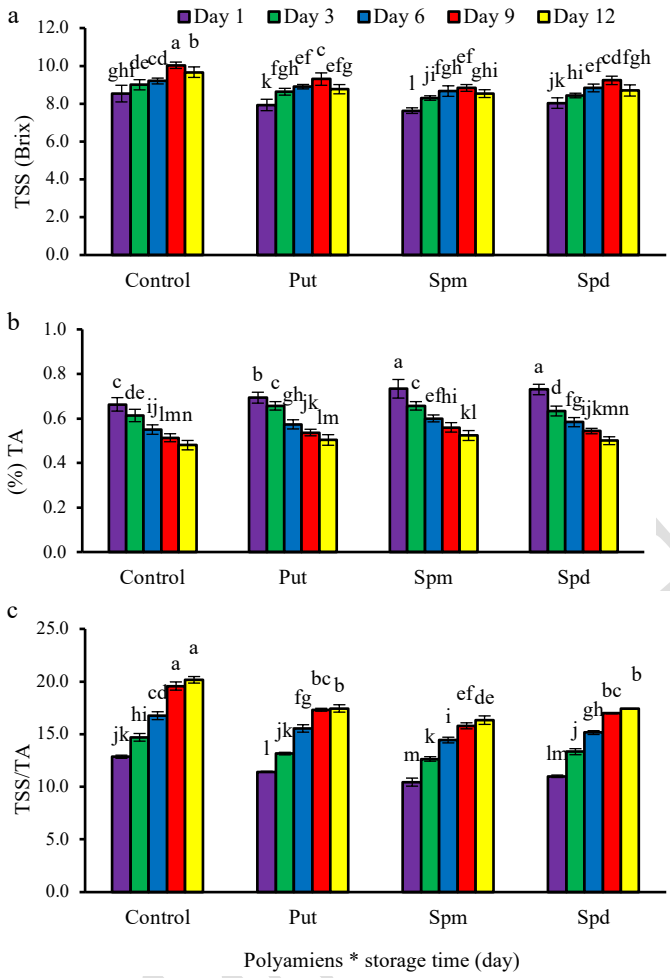

Fig. 2 Total soluble solids (TSS, a), titratable acidity (TA, b) and TSS/TA (c) of strawberry fruits under polyamines during storage. Small letters above the columns show the differences in mean comparison and bars are standard errors (SE).

Anthocyanin and Ascorbic Acid

During storage, fruits without polyamine treatment showed a significant decline in anthocyanin content, indicating a reduction in antioxidant capacity. In contrast, polyamine-treated fruits exhibited higher anthocyanin levels, with Put, Spm, and Spd resulting in increases of 10%, 14%, and 10%, respectively, by day 12 of storage (Fig. 3 a). AsA content in untreated fruits increased significantly by 44% on day 3 compared with day 1; however, AsA levels subsequently declined and by day 12 were not significantly different from the initial storage values. In polyamine-treated fruits, AsA content was better maintained throughout storage and was significantly higher than in the control, with Put, Spm, and Spd increasing AsA levels by 13%, 17%, and 18%, respectively, on day 12 (Fig. 3 b).

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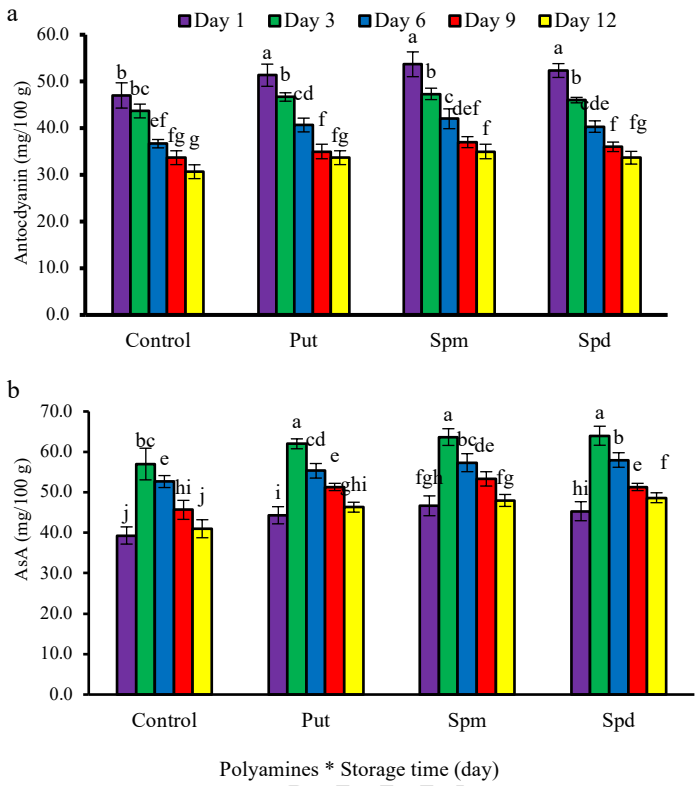

Fig. 3 Anthocyanin (a) and ascorbic acid (AsA, b) of strawberry fruits under polyamines during storage. Small letters above the columns show the differences in mean comparison and bars are standard errors (SE).

DPPH Scavenging as Activity and Malondialdehyde

The study found that the antioxidant capacity of fruits during storage decreased by 28% compared to day 1 without polyamine treatment. However, the addition of polyamines like Put, Spm, and Spd increased the DPPH scavenging activity by 12%, 17%, and 15% compared to the control group. This suggests that polyamines can protect the antioxidant capacity of fruits during storage, potentially mitigating the decline in antioxidant activity (Fig. 4 a). MDA levels in fruits increased during storage without polyamine treatment, indicating lipid peroxidation and oxidative stress. The highest MDA levels were observed on day 12 of storage without polyamine treatment, indicating high levels of oxidative damage (75%) relative to the control. However, the use of polyamines effectively reduced MDA levels, indicating their protective effect against lipid peroxidation and oxidative stress. On day 12, Put decreased MDA levels by 17%, Spm by 23%, and Spd by 19% compared to the control group, indicating polyamines' protective effect against lipid peroxidation and oxidative stress, thereby preserving fruit integrity and quality (Fig. 4 b).

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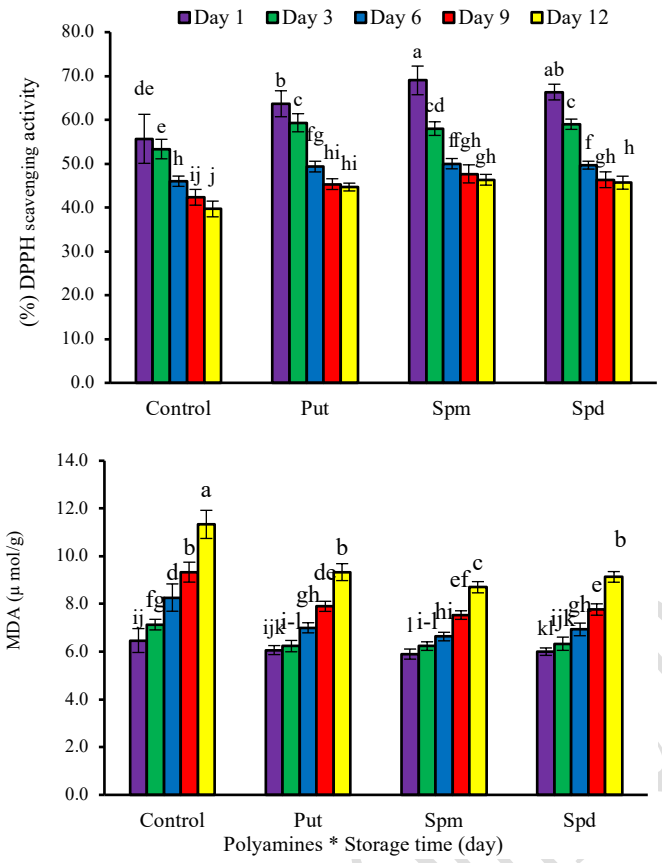
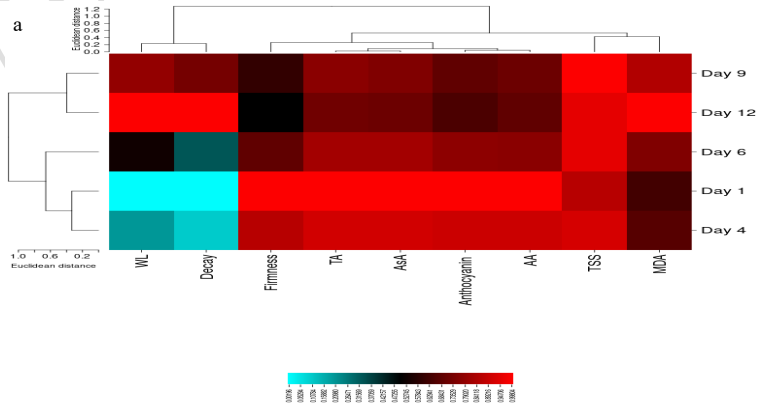


Fig. 4 DPPH scavenging activity (a) and malondialdehyde (MDA, b) of strawberry fruits under polyamines during storage. Small letters above the columns show the differences in mean comparison and bars are standard errors (SE).

Heat Map

The heat map analysis revealed clear clustering patterns among both storage duration and polyamine treatments. Fruits stored for 9 and 12 days clustered separately from earlier storage periods and were characterized by higher weight loss, decay, TSS, and MDA levels, as indicated by warmer color intensities, reflecting advanced senescence and quality deterioration. In contrast, earlier storage days showed higher firmness, TA, anthocyanin, AsA, and DPPH scavenging activity, which clustered together and were represented by cooler color gradients. Trait-based clustering indicated a close association between weight loss and decay, while antioxidant-related traits grouped with firmness and TA, suggesting coordinated physiological responses during storage (Fig. 5a). Similarly, polyamine-treated fruits, particularly those treated with Spm, formed distinct clusters from the control and exhibited lower weight loss, decay, and MDA accumulation, along with better maintenance of firmness and antioxidant capacity, highlighting the protective role of polyamines during cold storage (Fig. 5 b).



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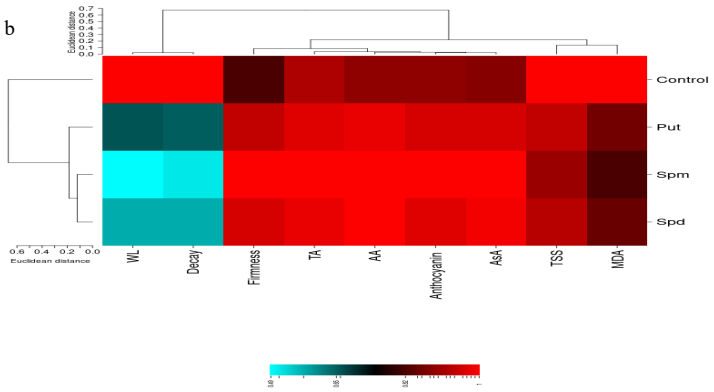

Fig. 5 Heat map analysis of strawberry fruits during storage (a) under polyamines (b). WL: weight loss, TA: titratable acidity, TSS: total soluble solids, AA: antioxidant activity, AsA: ascorbic acid. MDA: malondialdehyde.

Principal Component Analysis

PCA further clarified relationships among quality traits, storage time, and polyamine treatments (Fig. 6 a, b). For storage duration, the first component (F1) explained 94.7% of the total variance, while the second component (F2) accounted for 4.6%, indicating that most variability in fruit quality was driven by storage-related changes. The high contribution of F1 reflects the strong, coordinated response of multiple traits to storage progression rather than data scaling issues. Storage days were primarily separated along F1, with day 6 positioned near the origin, suggesting a transitional stage. Senescence-related traits (weight loss, decay, TSS, and MDA) showed strong positive loadings on F1, whereas firmness, TA, anthocyanin, AsA, and DPPH scavenging activity exhibited negative loadings, indicating inverse relationships. Similarly, in the PCA of polyamine treatments, F1 explained 98.9% of the variance and clearly separated the control from polyamine-treated fruits, highlighting the dominant influence of polyamines—particularly Spm—on maintaining fruit quality and antioxidant capacity.

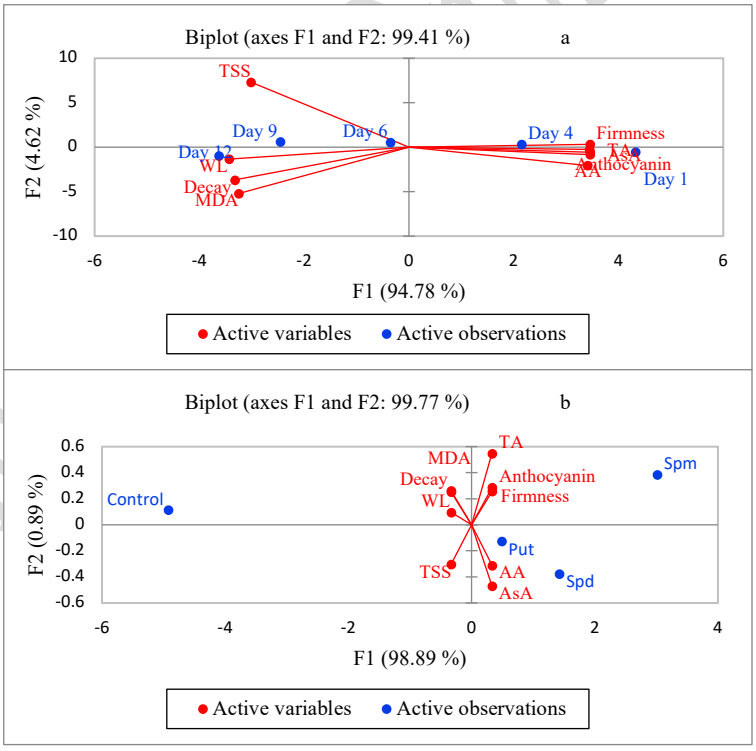

Fig. 6 Principal component analysis (PCA) of strawberry fruits during storage (a) under polyamines (b). WL: weight loss, TA: titratable acidity, TSS: total soluble solids, AA: antioxidant activity, AsA: ascorbic acid. MDA: malondialdehyde.

DISCUSSION

Pre-harvest

The application of polyamines, particularly Spm at a concentration of 75 mg/L, significantly enhanced leaf Chl content in strawberry plants. This is due to several biochemical mechanisms. Firstly, polyamines stabilize Chl-protein complexes, which helps maintain higher Chl levels

in the leaves. Secondly, it stimulates enzymes involved in Chl biosynthesis, such as δ-aminolevulinic acid (ALA) synthase, leading to increased Chl production [3]. Secondly, polyamines protect against oxidative stress by scavenging ROS, preserving chloroplast integrity and functionality. Spm can regulate antioxidant enzyme activity, allowing plants to maintain higher levels of Chl under stress conditions. Thirdly, polyamine, specially Spm enhances nitrogen assimilation, leading to increased nitrogen uptake and assimilation. It also activates nitrogen metabolism enzymes, enhancing nitrogen incorporation into Chl molecules [22]. Lastly, these polyamines regulate gene expression, influencing the expression of genes related to chloroplast development and Chl synthesis. Lastly, they inhibit Chl degradation, preventing its breakdown and increasing its accumulation in the leaves. Thus, foliar application of polyamines, particularly Spm, significantly contributes to the overall health and photosynthetic efficiency of strawberry plants [23]. In accordance with the findings of the current investigation, Zhao *et al*. [22] demonstrated the beneficial effects of polyamines on increasing Chl in wheat plants.

Foliar-applied polyamines significantly improved RWC in strawberry leaves. This is due to its role in maintaining cellular turgor pressure, enhancing water retention, and regulating ion channels in plant cell membranes. Polyamines, particularly Spm, also stabilize cell membranes by interacting with membrane phospholipids and proteins, reducing membrane permeability and minimizing water loss [13, 24]. It also protects cell membranes from lipid peroxidation, ensuring fluidity and function. Polyamines regulate aquaporin activity, enhancing their efficiency in water uptake and transport within plant tissues. Under stress conditions, Spm can counteract the downregulation of aquaporin expression by upregulating genes or maintaining their activity [25]. Polyamines also reduce transpiration rates by influencing stomatal behavior and interacting with plant hormones like abscisic acid (ABA). This helps maintain higher RWC in the leaves and contributes to better water status and overall plant resilience, especially under stress conditions [13, 25]. The current study was supported by Tan *et al*. [26], who demonstrated the effective impact of Spm on enhancing RWC.

Polyamines significantly improved fruit yield in strawberry plants. These mechanisms include promoting cell division and expansion, enhancing nutrient uptake, improving stress tolerance, and regulating plant hormonal balance. Stimulation of cell division is crucial during early fruit development, where rapid cell division determines the final size and number of [27]. Cell expansion is also promoted by modulating enzymes involved in cell wall loosening, leading to larger fruit sizes. Improved nitrogen uptake and assimilation are also enhanced by polyamines, particularly Spm, which plays a crucial role in nutrient uptake and assimilation. This leads to the growth and development of larger and more numerous fruits [28]. Polyamines can also upregulate the expression of nutrient transporter genes, enhancing the uptake of key nutrients such as potassium, phosphorus, and calcium. Polyamines enhance stress tolerance by acting as antioxidants, protecting plant cells from ROS damage, and maintaining water [10]. They interact with plant hormones like auxins, gibberellins, cytokinins, and ABA, ensuring optimal fruit development and yield. Polyamines also enhance photosynthetic efficiency, maintaining Chl content and optimizing energy utilization, making them an effective tool for improving fruit production [27,28].

Fruit antioxidant capacity was better impacted by polyamines, specifically Spm. Polyamines are polycationic compounds that play crucial roles in plant growth and stress responses. Recent studies have shown that polyamines can significantly enhance the antioxidant capacity of fruits by increasing levels of key antioxidant compounds such as anthocyanins and AsA, as well as improving DPPH radical scavenging activity [12]. Polyamines enhance anthocyanin production through several mechanisms, including activation of the phenylpropanoid pathway, gene expression modification, and interaction with stress response pathways. The increase in anthocyanin content in response to polyamine treatment may also be linked to their role in mitigating oxidative damage, as anthocyanins are effective scavengers of ROS [29]. Polyamines, particularly Spm, influence AsA biosynthesis through several mechanisms, including regulation of ascorbate biosynthetic enzymes, polyamine oxidation and H_2O_2 production, stabilization of cellular membranes, and improvement of DPPH scavenging activity [9]. The DPPH assay measures the ability of antioxidants to neutralize free radicals, and polyamines themselves can directly scavenge free radicals, including DPPH. Understanding these biochemical mechanisms opens up potential applications in agricultural practices to improve fruit quality and extend shelf life, ultimately benefiting human health through increased dietary antioxidant intake [30]. Overall, understanding these biochemical mechanisms opens up potential applications in agricultural practices to enhance fruit quality and extend shelf life, ultimately benefiting human health through increased dietary intake of antioxidants. Mishra *et al*. [12] showed that exogenous polyamine antioxidant compounds are present in black plum fruit.

Post-harvest

During the storage period of fruits, weight loss and decay can significantly reduce their quality and market value. These issues are primarily driven by physiological processes such as respiration, water loss, and microbial decay [6]. Polyamines have been shown to mitigate these adverse effects, thereby extending the shelf life of fruits. They play a crucial role in weight loss reduction by stabilizing cell membranes, regulating stomatal aperture, reducing respiration rates, and enhancing the fruit's natural defense mechanisms against pathogens [9]. Polyamines stabilize cell membranes by binding to phospholipids and interacting with membrane proteins, reducing permeability and minimizing water loss through transpiration. They also regulate stomatal aperture by modulating ion channels in guard cells, reducing transpiration rates and minimizing weight loss. Polyamines also reduce fruit rot, primarily caused by microbial infections, particularly by fungi and bacteria [31]. They exhibit direct antimicrobial properties by disrupting microbial cell membranes, interfering with microbial metabolism, and inhibiting the synthesis of nucleic acids and proteins. They can induce defense-related enzymes in fruits, such as chitinases, glucanases, and peroxidases, which degrade the cell walls of invading pathogens, preventing infection and decay [32]. Polyamines enhance lignin biosynthesis by upregulating phenylpropanoid pathway genes, acting as a barrier against microbial invasion, and regulate reactive oxygen species levels by modulating antioxidant enzymes [31]. In a related study, Jalali *et al*. [14] demonstrated the beneficial effects of applying 1.5 mM Spm and Spd, which were the most effective treatments in reducing fruit deterioration and weight loss. Out of the three primary polyamines, Spm was shown to be more effective in this investigation.

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Fruit firmness is a crucial quality attribute that affects consumer preference and market value. During storage, fruits often undergo a natural softening process due to cell wall degradation, which is primarily driven by enzymatic activities that break down the structural components of the cell wall and middle lamella, including pectins, hemicelluloses, and cellulose [33,34]. Polyamines, specially Spm have been shown to counteract this softening process and maintain fruit firmness. Polyamines inhibit the activity of cell wall-degrading enzymes, such as polygalacturonase (PG), pectin methylesterase (PME), cellulase, and β-galactosidase, by binding to enzyme molecules or substrates, preventing them from accessing their substrates [35]. They can also modulate gene expression, reducing the synthesis of these enzymes during storage, further contributing to the preservation of cell wall structure and fruit firmness. Polyamines stabilize cell wall structure by enhancing cross-linking of pectic substances, reducing solubilization of pectins, and maintaining intercellular adhesion [33]. They also influence calcium binding to pectin, reinforcing the cell wall structure and reducing its degradation during storage. Polyamines have antioxidant properties, scavenging reactive oxygen species, reducing oxidative damage, and maintaining fruit firmness. They also regulate hormonal pathways, particularly ethylene, which promotes ripening and softening processes. In summary, polyamines play a crucial role in preserving fruit firmness during storage [32].

During fruit storage, biochemical changes impact the taste, texture, and overall quality of the fruit. TSS and TA are key indicators of fruit quality. TSS is the concentration of sugars and other soluble substances, while TA measures the organic acid content in fruits. Typically, during storage, fruits exhibit an increase in TSS due to the conversion of starches to sugars and a decrease in TA as organic acids are metabolized. This ultimately affects the TSS/TA ratio, which determines fruit flavor and perceived sweetness [36]. TSS increases during storage due to the conversion of starches into simpler sugars, water loss, and the concentration of soluble solids, including sugars. Polyamines can inhibit sugar accumulation by modulating enzymes involved in carbohydrate metabolism, reducing the accumulation of sugars and reducing respiration rate [37]. They also help maintain lower TSS levels by decelerating metabolic processes. TA decreases during storage due to the metabolism of organic acids, such as citric acid and malic acid, which are often metabolized through the tricarboxylic acid (TCA) cycle to produce energy. Ethylene, a ripening hormone, accelerates the breakdown of organic acids, contributing to the decline in TA during storage. Polyamines can inhibit the metabolism of organic acids by interfering with enzymes involved in the TCA cycle, retaining higher acid levels and increasing TA during storage. The TSS/TA ratio is a key determinant of fruit flavor, reflecting the balance between sweetness and acidity. During storage, this ratio generally increases due to rising TSS and declining titratable acidity (TA), resulting in a sweeter taste profile [35]. In the present study, the reduction in TSS/TA observed following polyamine application is primarily associated with delayed fruit maturation and senescence, which is beneficial for extending storage life and maintaining post-harvest quality. Although a lower TSS/TA ratio may temporarily reduce perceived sweetness, it can contribute to improved firmness and controlled ripening, with potential implications for consumer acceptance depending on the marketing stage. Polyamines regulate the TSS/TA ratio by limiting sugar accumulation and preserving organic acids, and among them, Spm was more effective than Spd and Put, likely due to its higher positive charge density and greater influence on sugar metabolism and organic acid preservation [11, 14].

During fruit storage, antioxidant capacity declined due to the degradation of key antioxidant compounds like anthocyanins and a reduction in free radical scavenging activity. This decline is associated with the natural aging process, enzymatic degradation, and oxidative stress. Polyamines have been shown to counteract this decline by enhancing antioxidant capacity during storage.

Anthocyanin degradation is primarily driven by oxidative reactions, where ROS are generated during cellular respiration and stress conditions [12]. Enzymes such as polyphenol oxidases (PPO) and peroxidases (POD) can catalyze the oxidation of anthocyanins, further contributing to their decline during storage. These enzymes are often activated by physiological stresses associated with storage, such as changes in temperature, light exposure, and ethylene production [38]. Reduction in DPPH scavenging activity is also a result of decreased levels of antioxidants, which are directly correlated with the levels of antioxidants like anthocyanins, AsA, and other phenolic compounds. As the storage period progresses, the levels of these antioxidants typically decrease due to oxidative degradation and metabolic consumption, leading to reduced DPPH scavenging activity [39]. Polyamines, particularly Spm and Spd, can help counteract the decline in antioxidant capacity during storage by inhibiting oxidative degradation, upregulating anthocyanin biosynthesis, inhibiting enzymes like PPO and POD, and enhancing DPPH scavenging activity [40]. They also interact with other antioxidant systems, such as the ascorbate-glutathione cycle, stabilizing and regenerating other antioxidants. Polyamines can also induce the expression and activity of endogenous antioxidant enzymes, such as superoxide dismutase, catalase, and ascorbate peroxidase, which play critical roles in detoxifying ROS and maintaining higher levels of antioxidant compounds. This enzymatic defense mechanism supports the overall antioxidant capacity of the fruit during storage [14, 39]. Comparably, Mishra *et al*. [12] showed that treating black plum fruit with exogenous polyamines increases the antioxidant components in the fruit, preserving its postharvest quality.

AsA is a crucial antioxidant in fruits, protecting cells from oxidative stress and contributing to the nutritional quality of the fruit. During storage, AsA levels often show an initial increase followed by a gradual decrease due to various biochemical processes, including biosynthesis, oxidation, and degradation [41, 42]. The initial increase in AsA during storage is due to stress response activation, such as biosynthesis induction, respiration rate adjustment, and oxidation and degradation. Ascorbate oxidase activity, an enzyme that converts AsA to dehydroascorbic acid (DHA), becomes more active as storage progresses, leading to a net decrease in AsA levels [43]. Increased respiration rates and ethylene-induced ripening also contribute to a decline in AsA levels. Polyamines have been shown to enhance and stabilize AsA levels during storage. They can upregulate enzymes involved in the AsA biosynthesis pathway, promote continuous production of AsA, protect against oxidative degradation, inhibit ascorbate oxidase activity, and stabilize cellular structures. These actions help maintain higher levels of AsA throughout the storage period, preserving the antioxidant capacity and nutritional quality of the fruit [9].

MDA is a marker of oxidative stress and lipid peroxidation in plant tissues, including fruits. During storage, MDA levels often increase due to oxidative damage to cell membranes, leading to deterioration of fruit quality. The increase in MDA during storage is due to ROS accumulation,

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increased cellular metabolism, and depletion of antioxidants [44]. Polyamines can reduce MDA levels during storage by ROS, stabilizing cell membranes, enhancing antioxidant defense systems, and inhibiting ethylene biosynthesis. These properties help reduce the likelihood of ROS initiating lipid peroxidation and lowering MDA production. Polyamines also interact with phospholipids in cell membranes, reducing susceptibility to oxidative damage. Additionally, they can inhibit ethylene biosynthesis, thereby maintaining lower MDA levels during storage [12, 45]. Spm was more effective than Spd and Put in reducing MDA levels due to its higher polycationic nature and stronger interactions with negatively charged cell membrane components and reactive oxygen species. Its four amine groups provide greater ROS scavenging capacity, preventing oxidative damage and MDA formation. Spm's longer aliphatic chain stabilizes cell membranes and upregulates antioxidant enzymes, making it the most potent polyamine in lowering MDA levels. Zhang *et al*. [11] demonstrated the decrease in MDA when polyamine was applied to jujube fruit, which is similarly in parallel with no outcomes. Furthermore, Mishra *et al*. [12] demonstrated the same tendency with polyamines.

CONCLUSION

The study reveals that the application of polyamines, specifically spermine, putrescine, and spermidine, on strawberry yield and quality has shown significant differences in their effectiveness. Spermine treatment significantly increased fruit weight and justified soluble solids content, which are crucial indicators of fruit quality and consumer appeal. Post-harvest analyses showed that spermine-treated strawberries showed improved firmness, reduced decay rates, and lipid peroxidation, extending the fruit's shelf life. The sustained antioxidant activity also enhanced resistance to oxidative stress, contributing to the overall longevity and quality of the strawberries during storage. Putrescine and spermidine also provided some positive effects, but their impacts were less pronounced compared to spermine. These findings suggest that spermine's superior efficacy in enhancing strawberry agricultural productivity and post-harvest marketability could lead to optimized cultivation strategies, particularly in commercial strawberry production. By integrating spermine, particularly at 75 mg/L, into pre-harvest and post-harvest management practices, growers could achieve better economic returns, reduce spoilage losses, and meet consumer demands for high-quality strawberries with extended shelf life. This study positions spermine as a promising tool for advancing strawberry cultivation and other horticultural crops.

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Consent for Publication

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Declaration of Competing Interest

The authors declare that they have no known competing interests.

Data Availability

The data will be available on request.

Mehran Abdi: Conceptualization, Writing – original draft; Vahid Abdossi: Supervision, Methodology, Writing – review & editing, Project administration; Alireza Ladan-Moghadam: Writing – review & editing; Kambiz Larijani: Validation; Ali Mohammadi Torkashvand: Data curation, Visualization.

REFERENCES

1. Gao F., Mei X., Li Y., Guo J., Shen Y. Update on the roles of polyamines in fleshy fruit ripening, senescence, and quality. Frontiers in Plant Science. 2021;12:610313. https://doi.org/10.3389/fpls.2021.610313
2. Stolarska E., Paluch-Lubawa E., Grabsztunowicz M., Tanwar U.K., Arasimowicz-Jelonek M., Phanstiel O., Mattoo A.K. Sobieszczuk-Nowicka E. Polyamines as universal bioregulators across kingdoms and their role in cellular longevity and death. Critical Reviews in Plant Sciences. 2023;42:364-84. https://doi.org/10.1080/07352689.2023.2247886
3. Liu S., Zhang J., Sun X., Xu N. Characterization of spermidine synthase (SPDS) gene and RNA− Seq based identification of spermidine (SPD) and spermine (SPM) involvement in improving high temperature stress tolerance in *gracilariopsis lemaneiformis* (Rhodophyta). Frontiers in Marine Science. 2022;9:939888. https://doi.org/10.3389/fpls.2022.944358
4. Asija S., Seth T., Umar S., Gupta R. Polyamines and their crosstalk with phytohormones in the regulation of plant defense responses. Journal of Plant Growth Regulation. 2023;42:5224-46. https://doi.org/10.1007/s00344-022-10837-5
5. Khan E.A., Souri Z., García-Gaytán V. Polyamine metabolism and ethylene signaling in plants. Ethylene in Plant Biology. 2022;420-36. https://doi.org/10.1002/9781119744719.ch20
6. Ogurlu F., Kucuker E., Aglar F., Ozcengiz C.K., Uyak C. New approaches in pear preservation: Putrescine and modified atmosphere packaging applications to maintain fruit quality during cold storage. Food Science & Nutrition. 2024;12:6627-36. https://doi.org/10.1002/fsn3.4290
7. Choudhary S., Wani K.I., Naeem M., Khan M.M., Aftab T. Cellular responses, osmotic adjustments, and role of osmolytes in providing salt stress resilience in higher plants: polyamines and nitric oxide crosstalk. Journal of Plant Growth Regulation. 2023;42:539-53. https://doi.org/10.1007/s00344-022-10584-7
8. Farooq S., Lone M.L., Altaf F., Parveen S., Waseem W., Tahir I. Polyamines delay the senescence of *Antirrhinum majus* L. flowers by coordinating various physiological and biochemical mechanisms. Biology Bulletin. 2024;51:1691-701. https://doi.org/10.1134/S1062359024609455

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9. Zhang J., Wu Z., Ban Z., Li L., Chen C., Kowaleguet M.G.G.M., Wang L. Exogenous polyamines alleviate chilling injury of jujube fruit (*Zizyphus jujuba* Mill). Journal of Food Processing and Preservation. 2020;44:e14746. https://doi.org/10.1111/jfpp.14746
10. Mishra S., Barman K., Singh A.K., Kole B. Exogenous polyamine treatment preserves postharvest quality, antioxidant compounds and reduces lipid peroxidation in black plum fruit. South African Journal of Botany. 2022;146:662-8. https://doi.org/10.1016/j.sajb.2021.12.002
11. Desoky E.S.M., Alharbi K., Rady M.M., Elnahal A.S., Selem E., Arnaout S.M., Mansour E. Physiological, biochemical, anatomical, and agronomic responses of sesame to exogenously applied polyamines under different irrigation regimes. Agronomy. 2023;13:875. https://doi.org/10.3390/agronomy13030875
12. Hanif A., Ahmad S., Jaskani M.J., Ahmad R. Papaya treatment with putrescine maintained the overall quality and promoted the antioxidative enzyme activities of the stored fruit. Scientia Horticulturae. 2020;268:109367. https://doi.org/10.1016/j.scienta.2020.109367
13. Thapa S., Barman K., Singh A.K. Exogenous putrescine treatment maintains postharvest quality and delays senescence of guava fruit. Erwerbs-Obstbau. 2023;65:951-957. https://doi.org/10.1007/s10341-022-00721-7
14. Qaderi R., Mezzetti B., Capocasa F., Mazzoni L. Stability of Strawberry Fruit (Fragaria x ananassa Duch.) Nutritional Quality at Different Storage Conditions. Applied Sciences. 2022;13:313. https://doi.org/10.3390/app13010313
15. Jalali P., Zakerin A.R., Aboutalebi-Jahromi A.H., Sadeghi H. Improving postharvest life, quality and bioactive compounds of strawberry fruits using spermine and spermidine. Brazilian Journal of Biology. 2023;83:e273886. https://doi.org/10.1590/1519-6984.273886
16.Orman E., Yavic A., Gundogdu M., Aglar E., Celik K., Kan T. Polyamines in cold storage: impact of postharvest spermidine on strawberry quality. Journal of Food Measurement and Characterization. 2024;18: 9618-9630. 10.1007/s11694-024-02908-w
17. Arnon D.I. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. Plant Physiology. 1949;24(1):1. https://doi.org/10.1104/pp.24.1.1
18. Khosropour E., Weisany W., Tahir N.A.R., Hakimi L. Vermicompost and biochar can alleviate cadmium stress through minimizing its uptake and optimizing biochemical properties in *Berberis integerrima* bunge. Environmental Science and Pollution Research. 2022;29:17476-86. https://doi.org/10.1007/s11356-021-17073-6
19. Yaghubi K., Vafaee Y., Ghaderi N., Javadi T. Potassium silicate improves salinity resistant and affects fruit quality in two strawberry cultivars grown under salt stress. Communications in Soil Science and Plant Analysis. 2019;50:1439-51.
20. Giusti M.M., Wrolstad R.E. Wrolstad, Acylated anthocyanins from edible sources and their applications in food systems. Biochemical Engineering Journal. 2003;14(3):217-25. https://doi.org/10.1016/S1369-703X(02)00221-8
21. Urraca R., Sanz-Garcia A., Tardaguila J., Diago M.P. Estimation of total soluble solids in grape berries using a hand-held NIR spectrometer under field conditions. Journal of the Science of Food and Agriculture. 2016;96:3007-16.
22. Zhao P., Chen X., Xue X., Wang Y., Wang Y., Li H., Li, Y. Improvement of polyamine synthesis maintains photosynthetic function in wheat during drought stress and rewatering at the grain filling stage. Plant Growth Regulation. 2024;102:497-513. https://doi.org/10.1007/s10725-023-01075-0
23. Islam M.A., Pang J.H., Meng F.W., Li Y.W., Ning X.U., Chao Y.A.N.G., Jun L.I.U. Putrescine, spermidine, and spermine play distinct roles in rice salt tolerance. Journal of Integrative Agriculture. 2020;19:643-55. https://doi.org/10.1016/S2095-3119(19)62705-X
24. Li Z., Cheng B., Wu X., Zhang Y., Feng G., Peng, Y. Spermine-mediated metabolic homeostasis improves growth and stress tolerance in creeping bentgrass (*Agrostis stolonifera*) under water or high-temperature stress. Frontiers in Plant Science. 2022;13:944358. https://doi.org/10.3389/fpls.2022.944358
25. D'Incà R., Mattioli R., Tomasella M., Tavazza R., Macone A., Incocciati A., Tavladoraki P. A *Solanum lycopersicum* polyamine oxidase contributes to the control of plant growth, xylem differentiation, and drought stress tolerance. The Plant Journal. 2024;119:960-81. https://doi.org/10.1111/tpj.16809
26. Tan M., Hassan M.J., Peng Y., Feng G., Huang L., Liu, L., Li, Z., Li Z. Polyamines metabolism interacts with γ-aminobutyric acid, proline and nitrogen metabolisms to affect drought tolerance of creeping bentgrass. International Journal of Molecular Sciences. 2022;23:2779. https://doi.org/10.3390/ijms23052779
27. Yang H., Fang Y., Liang Z., Qin T., Liu J.H., Liu, T. Polyamines: pleiotropic molecules regulating plant development and enhancing crop yield and quality. Plant Biotechnology Journal. 2024;22:3194-201. https://doi.org/10.1111/pbi.14440
28. Huang Y., Wu S., Xu Q., Chen X., Qi, X. Spermidine enhances parthenocarpic fruit formation in cucumber by promoting efficient distribution of soluble sugars and photosynthates. Scientia Horticulturae. 2024;330:113103. https://doi.org/10.1016/j.scienta.2024.113103
29. Sayyad-Amin P., Davarynejad G., Abedi B. Effects of preharvest application of chemical compounds on pear (*Pyrus communis* cv.'Shekari') fruit traits. Erwerbs-obstbau. 2022;64:657-62.. https://doi.org/10.1007/s10341-022-00756-w
30. Raychaudhuri S.S., Pramanick P., Talukder P., Basak A. Polyamines, metallothioneins, and phytochelatins—Natural defense of plants to mitigate heavy metals. Studies in Natural Products Chemistry. 2021;69:227-61. https://doi.org/10.1016/B978-0-12-819487-4.00006-9
31. Yaviç A. Detailed study on cold storage of mulberry fruits: Effect of postharvest putrescine treatments on quality characteristics and biochemical properties of mulberry fruits. Journal of Food Composition and Analysis. 2024;126:105916. https://doi.org/10.1016/j.jfca.2023.105916
32. Liu Y., Hou Y., Yi B., Zhao Y., Bao Y., Wu Z., Jin P. Exogenous phytosulfokine α alleviates chilling injury of loquat fruit via regulating sugar, proline, polyamine and γ-aminobutyric acid metabolisms. Food Chemistry. 2024;436:137729. https://doi.org/10.1016/j.foodchem.2023.137729
33. Kibar H., Taş A., Gündoğdu M. Evaluation of biochemical changes and quality in peach fruit: Effect of putrescine treatments and storage. Journal of Food Composition and Analysis. 2021;102:104048. https://doi.org/10.1016/j.jfca.2021.104048
34. Javed H.U., Kularathnage N.D., Du J., Liu R., Yang Z., Zhong S., Zeng L.Y. A novel synthesized Vanillin-Based Deep Eutectic Agent (V-DEA) mitigates postharvest fungal decay and improve shelf life and quality of cherry tomatoes. Food Chemistry. 2024;453:139612.
35. Taş A., Berk S.K., Kibar H., Gündoğdu M. An in-depth study on post-harvest storage conditions depending on putrescine treatments of kiwifruit. Journal of Food Composition and Analysis. 2022;111:104605. https://doi.org/10.1016/j.jfca.2022.104605
36. Zhao Y., Zhu X., Hou Y., Pan Y., Shi L., Li X. Effects of harvest maturity stage on postharvest quality of winter jujube (*Zizyphus jujuba* Mill. cv. Dongzao) fruit during cold storage. Scientia Horticulturae. 2021;277:109778. https://doi.org/10.1016/j.scienta.2020.109778
37. Xiao Q., Ye S., Wang H., Xing S., Zhu W., Zhang H., Lv X. Soluble sugar, organic acid and phenolic composition and flavor evaluation of plum fruits. Food Chemistry: X. 2024;24:101790. https://doi.org/10.1016/j.fochx.2024.101790
38. Habibi F., García-Pastor M.E., Puente-Moreno J., Garrido-Auñón F., Serrano M., Valero D. Anthocyanin in blood oranges: A review on postharvest approaches for its enhancement and preservation. Critical Reviews in Food Science and Nutrition. 2023;63(33):12089-101. https://doi.org/10.1080/10408398.2022.2098250
39. Mahmoudi R., Razavi F., Rabiei V., Palou L., Gohari G. Postharvest chitosan-arginine nanoparticles application ameliorates chilling injury in plum fruit during cold storage by enhancing ROS scavenging system activity. BMC Plant Biology. 2022;22:555. https://doi.org/10.1186/s12870-022-03952-8
40. Javed H.U., Liu Y.S., Hao J.G., Hayat F., Hasan M. Aromatic Perspectives: An In-Depth review on Extracting, influencing Factors, and the origins of raisin aromas. Food Chemistry: X. 2024;22:101285. https://doi.org/10.1016/j.fochx.2024.101285

41. Sinha A., Gill P.P., Jawandha, S.K., Kaur P., Grewal S.K. Chitosan-enriched salicylic acid coatings preserves antioxidant properties and alleviates internal browning of pear fruit under cold storage and supermarket conditions. Postharvest Biology and Technology. 2021;182:111721. https://doi.org/10.1016/j.postharvbio.2021.111721
42. Khaliq G., Ali S., Gapper N., Nicola S. Recent advances and approaches in the application of elicitors to enhance resistance mechanisms in fresh produce. Frontiers in Sustainable Food Systems. 2023;6:1061079. https://doi.org/10.3389/fsufs.2022.1061079
43. Arabia A., Munné-Bosch S., Muñoz P. Ascorbic acid as a master redox regulator of fruit ripening. Postharvest Biology and Technology. 2024;207:112614. https://doi.org/10.1016/j.postharvbio.2023.112614
44. Khedr E.H., Khedr N. Optimization of postharvest progesterone treatment to alleviate chilling injury in mango fruit, maintaining intracellular energy, cell wall stability, and antioxidant activity. Postharvest Biology and Technology. 2023;206:112572. https://doi.org/10.1016/j.postharvbio.2023.112572
45. Khaliq G., Ali S., Ejaz S., Abdi G., Faqir Y., Ma J., Ali A. γ-Aminobutyric acid is involved in overlapping pathways against chilling injury by modulating glutamate decarboxylase and defense responses in papaya fruit. Frontiers in Plant Science. 2023;14:1233477. https://doi.org/10.3389/fpls.2023.1233477

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