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Postharvest Polyamine Application Alleviates Chilling Injury and Affects Apricot Storage Ability

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ABSTRACT: Fruit of two apricot cultivars 'Bagheri' and 'Asgarabadi' were treated with putrescine (Put) or spermidine (Spd) at 1 mM and then were stored at 1 °C for 21 days. Fruit were sampled weekly and stored 2 days at 20 °C for shelf-life study. The treatments reduced ethylene production and maintained the firmness and color of the fruit. Peroxidase (POX), catalase (CAT), superoxide dismutase (SOD), and polyphenol oxidase (PPO) activities and total phenol (TP) concentrations were measured during storage. Both cultivars showed chilling injury (CI) incidence, and the severity in control fruit was higher than either Put or Spd treatments. CI incidence in Spd-treated fruit was lower than that of Put-treated fruit. Polyamine (PA) treatment generally increased antioxidant enzyme activity of fruit during storage. PA treatments may help maintain the quality of apricot fruit during storage by inhibiting ripening and decreasing CI incidence.

KEYWORDS: *Postharvest, fruit quality, physiological disorder, antioxidant enzyme*

INTRODUCTION

Postharvest life of apricot fruit is short and affected by various factors, such as incidence from low temperatures during storage.[1,2] Generally, a reduction in the temperature can substantially reduce the rate of many metabolic processes, which lead to fruit senescence, deterioration, and loss of crop quality. Stone fruits are very sensitive to low temperatures, and peaches and nectarines exhibit chilling injury (CI) after a long cold storage period.[3] The main symptoms in the CI of peaches and nectarines are internal browning (IB) and flesh mealiness.[4] Plums and apricots can also be affected, although the symptoms are slightly different, with a gel-like region forming near the stone.[5] Because development of these chilling disorders reduces consumer acceptance, the onset of CI symptoms determines the postharvest storage potential of the fruit.

Different treatments that have potential to alleviate CI and prolong the fruit storage period have been evaluated. Intermittent warming heat shock was applied to control CI in apricot.[6] Plant growth regulators, such as jasmonic acid,[7] salicylic acid,[8] and polyamines (PAs),[9,10] may reduce the impact of different stress conditions on horticultural crops. In the present research, we used PAs, which are low-molecular-weight biogenic amines, ubiquitous in all organisms. The three major PAs that are normally found in the chloroplast of higher plants are putrescine (Put), spermidine (Spd), and spermine (Spm).[11] In plants, they have been implicated in a wide range of growth and developmental processes, such as cell division, dormancy breaking of tubers and germination of seeds, stimulation, support, and development of flower buds, embryogenesis, fruit set and growth, fruit ripening and senescence, plant morphogenesis, and response to environmental stresses.[12]

Treatment with exogenous PAs can maintain fruit firmness and delay ripening in lemons[13] and apples,[14,15] inhibit ethylene production, stabilize membrane systems, therefore minimizing changes in permeability and loss of fluid and, thus, reduce CI,[16] and provide protective action against lipid peroxidation.[17] Accumulation of Put is a general response to stress.[18]

Plant injury induced by chilling usually involves an imbalance between the production and consumption of active oxygen species.[19] Protection of cells from oxidative injury under stress is thought to be a major mechanism of resistance to plant stresses, and this resistance is likely to depend upon the competence of the antioxidant system. Superoxide dismutase (SOD) dismutates superoxide radicals to hydrogen peroxide and O_2 in a reaction that is spontaneous and extremely rapid, thus protecting the cells from damage by superoxide radical reaction products. The product, which is a potentially toxic compound, is then reduced to water by a number of enzymes, such as catalase (CAT) and peroxidase (POX).[20]

The effect of postharvest Put treatments on extending shelf life and reducing mechanical damage in apricot was evaluated,[21] but there are no reports of the effects of PAs on CI in apricot and associated enzyme activities, such as those involved in browning [polyphenol oxidase (PPO)] and antioxidant defense (CAT). The objective of the current study was to investigate if postharvest Put and Spd application to apricot before storage at 1 °C would prolong the fruit storage period. In addition, effects of treatments on flesh browning, changes in total phenol (TP) concentrations, and activities of antioxidant enzymes in the fruit were evaluated.

MATERIALS AND METHODS

Plant Material and Treatment. Two commercial apricot (*Prunus armeniaca* L.) cultivars, 'Bagheri' and 'Asgarabadi', were harvested according to the commercial harvest and fruit color change. Apricot fruit after harvest were immediately transported by a ventilated car to the Department of Horticultural Science Laboratory at Tarbiat

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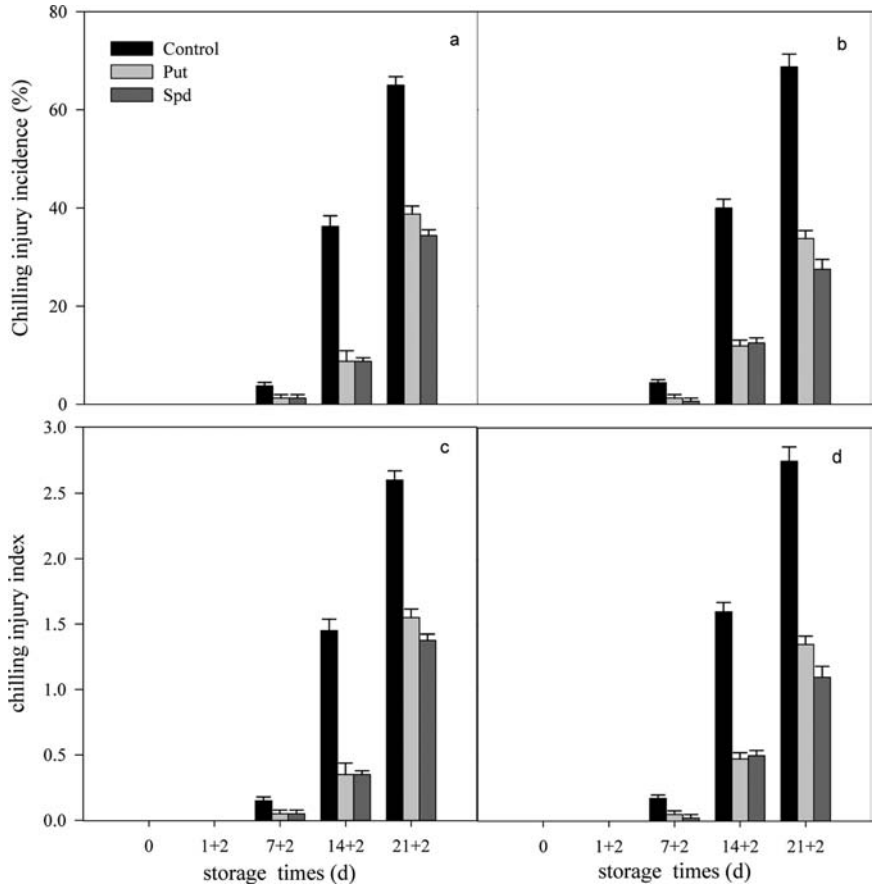

Figure 1. CI incidence (a, 'Bagheri'; b, 'Asgarabadi') and CI index (c, 'Bagheri'; d, 'Asgarabadi') of apricot after treatment with 1 mM Put or Spd at harvest and storage at 1 °C. Mean ± standard error (n = 4).

Modares University (TMU) in Tehran, Iran. Fruit were selected for uniformity in size, shape, and color and without any mechanical damage, blemishes, disease, and pest damage. A total of 30 fruit were sampled for immediate analysis to monitor fruit characteristics at harvest before application of treatments (day 0). Also, sufficient harvested apricot fruit were randomly distributed into 12 groups of 140 fruit each for treatment application in four replicates. Fruit were dipped at 20 °C for 4 min in 1 mM Put, 1 mM Spd, or distilled water as the control. The selected concentration was based on published effects of these compounds on plums and pomegranates.[22,23] All solutions contained Tween-20 (2 g L^{-1}). Fruit were then placed on desiccant Kraft paper and allowed to dry before storage. All of the control and treated fruit were stored in storage at 1 °C, and after 1, 7, 14, and 21 days, samples were transferred and stored at 20 °C for another 2 days prior to measurements and analysis, to simulate the marketing process.

Fruit Quality Measurements. Fruit flesh color was determined on the opposite pared check of each fruit (15 fruit per replicate) using a self-contained color measurement spectrophotometer (Hunter Lab, Color Flex, Reston, VA). Values a^* and b^* were recorded and converted to hue angle using the formula $h^\circ = \tan^{-1}(b^*/a^*)$. Subsequently, flesh firmness was measured using a hand-held Effegi penetrometer fitted with an 8 mm tip. Values were expressed as Newton. A wedge-shaped slice of flesh taken from each fruit was pooled and juiced. Soluble solids content (SSC) was measured using a temperature-compensated refractometer (Atago, NSG Precision Cells, Inc., Hicksville, Japan). Titratable acidity (TA) was measured by titrating 10 mL of juice with 0.1 N NaOH to an end point of pH 8.2 and expressed as a percentage of malic acid.

Ethylene Production. Fruit were removed from storage and allowed to reach 20 °C. Four replicates of three fruit per treatment were placed in a 1 L glass jar hermetically sealed for 1 h. A total of 1 mL of headspace gas was withdrawn with a gas syringe, and ethylene was quantified using gas chromatography (GC, Agilent 6890N, Santa Clara, CA) equipped with a flame ionization detector (FID) and a 50 m stainless-steel column (Agilent Technology, Inc. model 19095P-S25 HP-Plot AL/S). The carrier gas (helium) flow rate was 30 mL min^{-1}. The column temperature was 70 °C, and injector and detector temperatures were 180 °C. Ethylene production rates were expressed as nL g^{-1} h^{-1}.

CI Evaluation in the Fruit. Symptoms of CI, including gel breakdown, flesh woolliness, and flesh browning,[24] were visually assessed, and the incidence was recorded. A severity index was determined as follows: [(percentage of fruit with no disorder × 0) + (percentage of fruit with slight disorder × 1) + (percentage of fruit with medium disorder × 2) + (percentage of fruit with severe disorder × 4)]/4. Slight disorder meant that less than 25% of the fruit flesh was affected. Medium disorder meant that between 25 and 50% of the flesh was affected. Severe disorder meant that more than 50% of the fruit flesh showed symptoms.

TP Content and Enzyme Activities. After CI evaluation, two wedged-shaped slices of flesh tissue from two opposite sides of each fruit were removed, immediately frozen in liquid nitrogen, and stored at −80 °C until used for extraction and analysis of the TP content and enzyme activity.

TP concentrations are measured by homogenizing 1 g of frozen tissue from each replicate with 5 mL of ice cold 1% HCl−methanol solution and then centrifuged at 4 °C for 10 min at 12000g. The supernatant was collected and used for phenol determination. The TP content in the extracts was determined according to the Folin−Ciocalteu procedure,[25] using gallic acid for the standard curve. Results are expressed as milligrams of gallic acid equivalent (GAE) per 100 g of fresh weight (FW).

The activity of CAT, POX, and SOD was measured using 1 g of sample homogenized in 6 mL of freshly prepared 25 mM phosphate buffer (pH 6.8). The homogenate was centrifuged at 18000*g* for 15 min, and the supernatant was used as a source of crude enzyme. All steps to obtain enzyme preparations were carried out at 4 °C.

CAT activity was determined according to Cakmak and Horst.[26] Aliquots of the supernatant were added to 25 mM phosphate buffer (pH 6.5) and hydrogen peroxide at a final concentration of 10 mM. The enzyme activity was measured at 240 nm and expressed as units of enzyme per milligram of protein.

POX activity was determined by the rate of guaiacol oxidation in the presence of hydrogen peroxide at 470 nm for 1 min, as described previously.[27] The reaction mixture contained 25 mM phosphate buffer (pH 6.8), 28 mM guaiacol, and enzyme extract in a 3 mL assay volume, and the reaction was initiated by adding hydrogen peroxide at a final concentration of 5 mM. The enzyme activity was expressed as units of enzyme per milligram of protein.

SOD activity was determined by measuring the ability of SOD to inhibit the photochemical reduction of nitroblue tetrazolium (NBT) at 560 nm after exposure to a light for 30 min.[28] The assay mixture contained 25 mM phosphate buffer (pH 6.8), 12 mM L-methionine, 75 μM NBT, 1 μM riboflavin, 50 mM Na−carbonate (pH 10.2), and enzyme extract in a total volume of 3 mL. The blank mixture had the same composition but was kept in the dark. A total of 1 unit of SOD activity is defined as the amount of enzyme that inhibits the NBT photoreduction by 50% under the assay conditions.

PPO enzyme was extracted by blending 1 g of frozen sample in freshly prepared 100 mM phosphate buffer (pH 6.8) containing Triton X-100 and polyvinylpyrrolidone (PVP), followed by centrifugation at 15000*g* for 20 min, as described previously.[29] Aliquots of the supernatant were added to solution containing catechol at a final concentration of 0.05 M. The increase in absorbance was monitored at 410 nm for 2 min at 25 °C, and the activity of enzyme was expressed as units per milligram of protein of the homogenate.

The protein concentration in each sample was determined by the method described in the literature using bovine serum albumin (BSA) as a standard.[30]

Statistical Analysis. The results were subjected to analysis of variance (ANOVA). The sources of variance were PA treatments and storage time, and data were expressed as the mean ± standard error (SE) (n = 4). Mean comparisons were performed using the least significant difference (LSD) test to examine if differences were significant at $p < 0.05$. All analyses were performed with MSTATC software.

RESULTS

CI. CI was first detected after 7 days of storage for both 'Bagheri' and 'Asgarabadi'; thereafter, CI incidence and severity increased with a longer storage life (Figure 1). However, CI was strongly suppressed in fruit treated with either Put or Spd.

Ethylene Production. At harvest, ethylene production was low, but it increased rapidly in control fruit until 14 days, reaching a maximum of 27.8 and 36.2 nL g^{-1} h^{-1} in 'Bagheri' and 'Asgarabadi', respectively. Production then decreased until the end of storage (panels a and b of Figure 2). Put and Spd treatments of both cultivars suppressed ethylene production, and the difference between treated and control was significant ($p < 0.05$) until the end of storage. However, ethylene production in PA-treated fruit slightly increased over time (panels a and b of Figure 2).

Fruit Quality. Fruit firmness decreased regardless of treatment, but Put- and Spd-treated fruit softened more slowly. The effect of Spd on softening was greater than that for Put (panels c and d of Figure 2). Untreated fruit loss 85% of their firmness, while treated fruit with Put and Spd retained 40 and 50% of firmness, respectively, after 21 days of storage. Fruit firmness loss after 14 days of storage for control, Put, and Spd

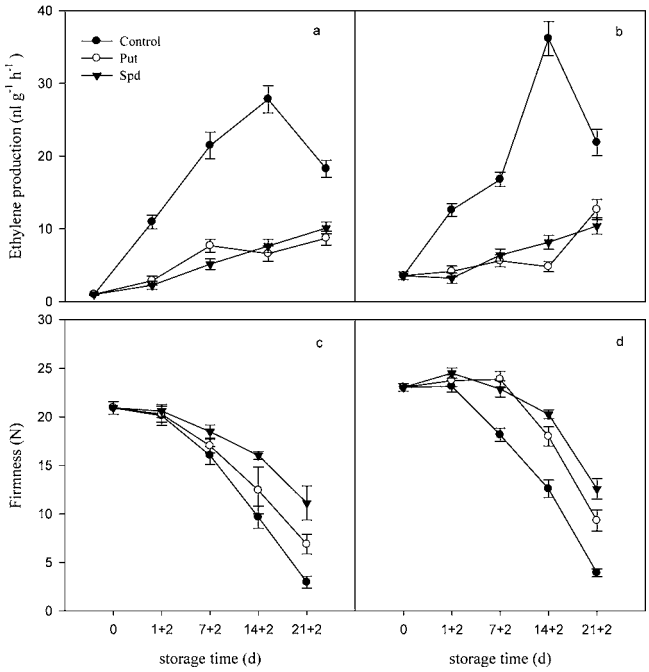

Figure 2. Ethylene production (a, 'Bagheri'; b, 'Asgarabadi') and fruit firmness (c, 'Bagheri'; d, 'Asgarabadi') of apricot after treatment with 1 mM Put or Spd at harvest and storage at 1 °C. Mean ± standard error (n = 4).

treatments in 'Bagheri' fruit was 54, 40, and 23% and in 'Asgarabadi' fruit was 45, 22, and 12%, respectively.

Neither Put nor Spd affected SSC and TA. However, Put and Spd delayed the decrease of $h°$ during storage. There was no difference in fruit color after treatment with either Spd or Put (panels a and b of Figure 3).

TP Content and PPO Activity. TP was relatively stable during storage of fruit at low temperatures, although in 'Asgarabadi', the TP of control fruit was higher at days 1 and 14 than at other times. The TP content of 'Bagheri' fruit was affected by treatment, with the average TP contents in control and Put- and Spd-treated fruit being 132, 130, and 127 mg of GAE/100 g of FW, respectively. PPO activity decreased rapidly during the 14 days of storage of 'Asgarabadi', especially in Spd- and Put-treated fruit, but that of control fruit was generally higher than that in treated fruit and was almost stable after 7 days (panels a and b of Figure 4). After day 1, PPO activity had no significant changes during storage time in 'Bagheri' but the effects of PA treatment were significant ($p < 0.05$) and enzyme activity in control was higher than PA treatment during storage at 1 °C (panels a and b of Figure 4).

Antioxidant Enzyme Activity. CAT activity in control fruit decreased during the first week of storage and then remained relatively stable, while that in Put- and Spd-treated fruit was higher during storage (panels c and d of Figure 4). CAT activity was higher in Spd- than Put-treated fruit during storage.

POX increased during storage of 'Asgarabadi' but not for 'Bagheri', but activity was higher in Spd-treated fruit than the control and Put-treated fruit in both cultivars (panels e and f of Figure 4).

SOD activity increased during 7 days of storage at low temperatures and then decreased. Changes in 'Asgarabadi' were significant ($p < 0.05$) during storage (panels g and h of Figure 4). Although enzyme activity of Put and Spd at day 1 and Spd

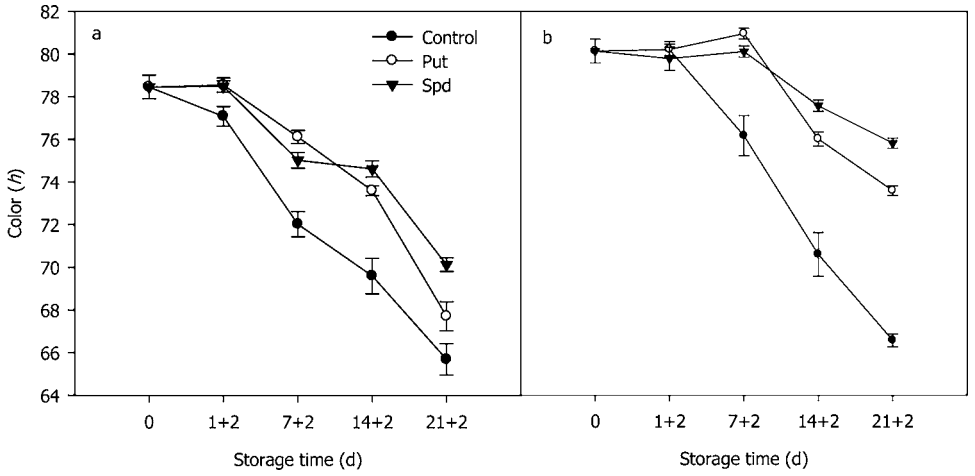

Figure 3. Color (a, 'Bagheri'; b, 'Asgarabadi') of apricot after treatment with 1 mM Put or Spd at harvest and storage at 1 °C. Mean ± standard error (n = 4).

at day 14 was higher than the control, treatment had no significant effect on enzyme activity during storage.

DISCUSSION

Stone fruit are susceptible to CI when stored at low temperatures.[3] Both cultivars in the current study developed CI after 7 days at 1 °C, and the incidence increased thereafter. However, PAs markedly reduced CI incidence in both cultivars to about 50% of control levels after 21 days of storage. CI incidence in Spd treatment was lower than in Put treatments, so that CI incidence of Put treatment on day 21 was 5 and 6% higher than Spd treatment in 'Bagheri' and 'Asgarabadi', respectively. PAs have been reported to act protective of cold stress in tomato[31] and prevented CI in cucumber[10] and zucchini.[32] Moreover, the protective role of PAs has also been reported in other types of stress, such as mechanical damage.[33] Recent work reported that the effect of exogenous PA application could induce the acclimation of pomegranate to low temperatures and, in turn, protect the fruit from CI by increasing the levels of endogenous Put and Spd, because the normal levels would not be high enough to induce this adaptation to cold storage.[23]

It has been reported that treatment with 1-methylcyclopropene (1-MCP) decreased ethylene production in apricots during the storage and shelf-life period, and this effect was reflected in lower firmness loss in treated fruit than in control.[1,34,35] Apricot softening was also delayed by PA application in the current study (panels c and d of Figure 2). The slower softening is probably associated with effects of PAs on ethylene production, with Spd and to a lesser extent Put suppressing ethylene production of fruit during storage (panels a and b of Figure 2). These results are similar to those who found that apricots treated with Put led to firmer fruit, delayed color change, and inhibited ethylene production.[21,36] These effects could be the result of the capacity of PA to bind pectic substances at the cell wall level[37] and the inhibition of enzyme activity that degrades pectic acids.[9] PAs may compete directly with the synthesis of ethylene because they share a common precursor *S*-adenosylmethionine (SAM).[38]

Antioxidative systems play an important role in protecting plants from damage caused by reactive oxygen species (ROS) at low temperatures.[39] Plant injury induced by chilling usually involves an imbalance between the production and elimination of ROS,[19] and tolerance to chilling stress is often associated with the enhanced capacity of the antioxidant defense system under low-temperature conditions.[7,8] The appearance of CI disorders in the fruit flesh of stone fruit also occurs at low temperatures, which may be related to tissue deterioration, resulting from membrane lipid oxidation.[3] It is well-known that SOD, CAT, and POX are important active free-radical scavenging enzymes, and the decreased activities of these enzymes may lead to high levels of ROS.[39] Sustained accumulation of ROS could cause lipid peroxidation, aggravate oxidative damage, and accelerate senescence.[40] The SOD enzyme is the first line of cell defense against free radicals, and its greater activity in fruits has been related to a higher resistance to stress and a longer commercial life.[41] High SOD activity has been associated with stress tolerance in plants because it neutralizes the reactivity of the superoxide radical, which is overproduced under stress.[42] SOD activity showed different patterns in two cultivars. In 'Bagheri', SOD activity increased and then was stable, while Spd effectively increased SOD activity during storage. Although enzyme activity in 'Asgarabadi' increased in the first 7 days and then decreased but SOD activity in PA treatments, especially Spd was always higher than the control. These results was in agreement with recent work that found that SOD activity in control peach fruit decreased, while the treatment with heat alone or the combination of heat and salicylic acid induced an increase in SOD activity and reduced CI.[8] Also others reported that 1-MCP treatment improved SOD activity and delayed senescence in apricot fruit.[1]

CAT protects cells against ROS because it catalyzes the decomposition of hydrogen peroxide to form oxygen and water.[43] Spd retains CAT activity in a stable level, while in control and Put treatment, enzyme activity decreased and was always lower than Spd treatment (panels c and d of Figure 4). Although CAT activity in Put-treated fruit decreased during storage, activity in 'Bagheri' was higher than that of the control fruit. Thus, the increase of CAT activity in PA treatments indicates that the hydrogen peroxide may be removed, and therefore, the formation of the hydroxyl radical and chilling-induced damage was mitigated. These results support the finding where γ-amino butyric acid treatment reduced CI in peach and enhanced CAT activity.[44] Also others indicated that a high level of CAT activity was accompanied by alleviated CI

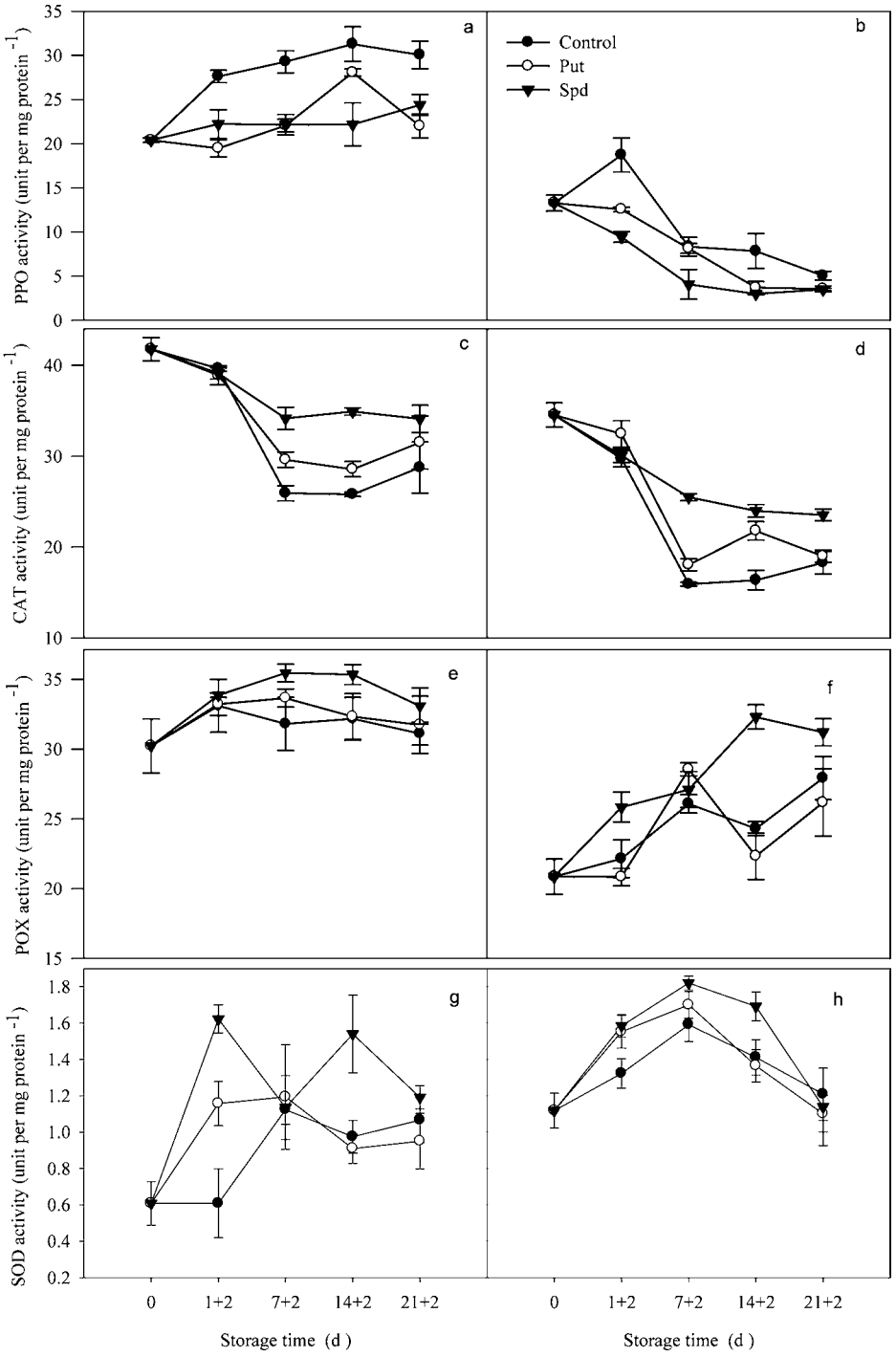

Figure 4. Activities of PPO (a, 'Bagheri'; b, 'Asgarabadi'), CAT (c, 'Bagheri'; d, 'Asgarabadi'), POX (e, 'Bagheri'; f, 'Asgarabadi'), and SOD (g, 'Bagheri'; h, 'Asgarabadi') in apricot after treatment with 1 mM Put or Spd at harvest and storage at 1 °C. Mean ± standard error (n = 4).

in mume fruit.[43] POX activity in PA treatment, especially in Spd-treated fruit, was higher than the control, and in 'Asgarabadi', POX activity in Spd-treated fruit was about 2-fold of the harvest on day 14. Although the increase of POX in Spd-treated fruit of 'Bagheri' was less than that of 'Asgarabadi', it was still higher. PAs enhanced POX production in both cultivars, and POX activity was higher than the control, especially after 14 and 21 days of storage.

During the cold storage of 'Bagheri', TP concentrations in control fruit were higher than in PA-treated fruit. An increase of TPs has been reported in peaches that are developing CI.[45,46] PPO is considered to be the key enzyme in tissue browning of cold-damaged fruit and vegetables.[47−49] However, there are no studies on changes of PPO activity in apricot fruit stored at low temperatures. Therefore, the physiological function of PPO in the development of CI symptoms of apricot remains unclear. Some evaluation reported that a marked increase in PPO activity during the period of 21 and 28 days at 0 °C may result from CI.[50] PPO activity changes in the two cultivars were different. PPO in control fruit of 'Bagheri' increased during storage time, while a marked decrease was observed for 'Asgarabadi'. In peach, PPO activity decreased by day 4 and

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then increased to a maximum over 8−12 days of storage.[51] Although changes in the patterns of enzymes in two cultivars was different, low PPO activity appears to be related to a lower CI incidence. The CI is related to tissue deterioration, which leads to changes in membrane permeability and the interaction between phenols and PPO, which are generally found in separate compartments in the cell. PAs affected the TP content and PPO activity and, on the other side, mitigated the chance of the reaction between the enzyme and substrate through maintaining fruit firmness and integrity.

In conclusion, our research indicates that Put and Spd could maintain fruit quality and increase CI resistance of apricot by suppression of ethylene production and improving protective enzyme activity.

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