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Salicylic acid alleviates chilling injury in anthurium (*Anthurium andraeanum* L.) flowers

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ABSTRACT

We tested if salicylic acid (SA) can alleviate chilling injury in anthurium flowers (*Anthurium andraeanum*). Cut flowers of five cultivars, individually placed in water, were held at 4 °C and 12 °C. Symptoms of chilling injury (CI) were found in the flowers stored at 4 °C. These symptoms included desiccation of the spadix (the compound floral stalk) and a colour change of the spathe (the large floral bract) to pink and then to brown. The time to the CI symptoms depended on the cultivar. CI symptoms were accompanied by an increase in electrolyte leakage, by loss of fresh weight, and by an increase in catalase (CAT) and superoxide dismutase (SOD) activity. SA at 2.0 mM in water was applied as a 15 min dip. It delayed the CI symptoms, as well as the loss of fresh weight, the increase in electrolyte leakage, and the increase CAT and SOD activity. The data suggest that CI in this system is related to an increase in the concentrations of active oxygen species.

1. Introduction

Anthurium (*Anthurium andraeanum* L.) is a tropical flower that shows injury when stored at low temperatures. The recommended optimum temperature for storage is 12.5–20 °C (Reid, 2004). Anthurium flowers are very small, arranged on a stalk-like structure called the spadix. Pollinators are mainly attracted by a large colourful bract, called the spathe. The end of vase life of flowers that have not been stored is usually determined by a colour change in the spathe or spadix (Paull and Goo, 1982; Paull and Chantrachit, 2001; Elibox and Umaharan, 2010). When the flowers have been stored at a low temperature prior to vase life, colour changes in the spathe or spadix are often found very early during vase life. These parts often turn brown. This is different from the colour changes at the end of vase life in flowers that have not been stored at low temperature, where loss of glossiness is observed but no browning (Shirakawa et al., 1964; Paull, 1987).Salicylic acid (SA) is important in regulating normal plant growth and development (Hayat et al., 2010), but also in the response to plant pathogens (Vlot et al., 2009). Treatment with SA increased resistance to chilling injury in plants such as wheat (Tasgin et al., 2006) and maize (Janda et al., 1999) and in tomato (Ding et al., 2002), peach (Wang et al., 2006; Cao et al., 2010) and pomegranate (Sayyari et al., 2009) fruit. Treatment with SA prevented the increase in the concentration of H_2O_2, and in the increase in the activity of catalase, superoxide dismutase, and ascorbate peroxidase (Wang et al., 2006).

SA treatment also prevented chilling-induced increase in lipid peroxidation in membranes, which is the process whereby unsaturated fatty acids in lipids become degraded to lipid hydroperoxides (Senaratna et al., 2000). Lipid hydroperoxides then become degraded to compounds such as malondialdehyde (which are often detected by a method based on their reaction with thiobarbituric acid [TBA]). Lipid peroxidation can be due to reactive oxygen compounds, but might also relate to increased activity of enzymes such as lipoxygenase (LOX).

The increase in active oxygen compounds might be an early response during the processes leading to chilling injury, followed by membrane lipid peroxidation (Cao et al., 2010). The reactive oxygen compounds might act directly on membranes, but they also might be a signal transduction mechanism that induces membrane damage (Mittler, 2002; Miller et al., 2008). Moreover, the relationship between membrane lipid peroxidation and reactive oxygen compounds can be more complex, as LOX is also thought to be partly responsible for the formation of reactive oxygen species (Gardner, 1995).

The aim of this study was to test if *Anthurium* flowers would also respond favorably to SA. Treatment with SA might allow longer

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transport at low temperature. We included determination of the concentration of thiobarbituric acid (TBA)-reactive compounds, total antioxidant capacity, and the activity of enzymes such as lipoxygenase, catalase, and superoxide dismutase.

2. Materials and methods

2.1. Plant material, vase life

Cut flowers of *Anthurium andraeanum* L. were obtained from commercial growers in Thailand. Flowers were harvested when 40–50% of the true flowers on the spadix had fully opened. The cultivars studied were Tropical (red spathe), Casino (orange spathe), Cheers (pink spathe), Angel (white spathe), and Pistache (green spathe). Flowers were cut in the morning, placed in water at the growers' property and transported at 12 °C in water to the laboratory in less than 5 h. In the laboratory, the flower stems were recut to 30 cm length. Flowers were individually placed in 50 mL graduated cylinders containing distilled water and the cylinders were covered with a cellophane wrap to prevent evaporation. The cylinders with flowers were placed at 4 or 12 °C (85–90% RH). Light levels were about 15 $\mu mol\ m^{-2}\ s^{-1}$, partially from natural light and partially from Philips TL D 36W/54 cool white fluorescent tubes (12 h/day). They remained at the two temperatures for 50 days.

Flowers were evaluated individually and vase life was measured as the time until the flower were discarded because of spadix desiccation, loss of spathe gloss, spathe blackening and spathe wilting (Paull and Goo, 1982). The fresh weight (FW) of individual flowers was determined every four days throughout the experimental period. Relative FW was calculated as a percentage of initial FW.

2.2. Spathe browning

CI was evaluated every 4 days by determining the brown area on the spathes of 10 individual flowers using a scale from 1 to 5; 1 = no chilling injury; 2 = mild injury (1–20% of spathe affected); 3 = moderate injury (21–50% of spathe affected); 4 = severe injury (51–80% of spathe affected); 5 = very severe injury (81–100% of spathe affected). CI was calculated as $\sum$ (number on CI scale × number of flowers at that number on the CI scale)/total number of flower in each group.

2.3. Electrolyte leakage

Ten discs (2 mm thickness and 15 mm diameter) were excised from the spathe by a cork borer, rinsed with 50 mL of distilled water between excisions. They were incubated in 30 mL of 0.4 M mannitol solution and shaken at 100 cycles per min, at ambient temperature. Electrolyte leakage of the solution was determined following shaking for 3 h, using a conductivity meter (Consort model C831, Belgium). Maximum electrolyte leakage was determined after autoclaving the material at 121 °C for 1 h to release electrolytes. The percentage of electrolyte leakage was calculated using the equation:

$$\text{Electrolyte leakage (\%)} = \frac{\text{Initial electrolyte leakage}}{\text{Final electrolyte leakage}} \times 100.$$

2.4. TBA-reactive compounds

Five grams of spathe FW were homogenized with 25 mL of 5% (w/v) trichloroacetic acid (TCA). The mixture was centrifuged for 10 min at 4000 × *g*. Thiobarbituric acid (TBA) reactivity was determined by adding 2.5 mL of 0.5% TBA in 15% TCA to 1.5 mL of the supernatant. The reaction solution was held for 20 min in a bath containing boiling water, then cooled quickly and finally centrifuged at 12,000 × *g* for 10 min to clarify the solution. Absorbance was measured at 532 nm and corrected for non-specific turbidity by subtracting the absorbance at 600 nm, calculated with an extinction coefficient of 1.55 $nmol\ L^{-1}\ m^{-1}$. Data were expressed as $nmol\ g^{-1}$ FW.

2.5. Lipoxygenase (LOX) activity

LOX was extracted and assayed by the method described by Lara et al. (2003). Five grams of spathe were homogenized in 1 mL of extraction solution containing 0.1 M phosphate, pH 7.5, 2 mM DTT, 1 mM EDTA, 0.1% (v/v) Triton X-100 and 1% (w/v) PVPP. The homogenate was centrifuged at 12,000 × *g* for 20 min at 4 °C, and the supernatant held at 0 °C. LOX activity was assayed by mixing 100 μL of the supernatant with 2.5 mL 0.1 M phosphate, pH 8, 400 μL substrate solution (8.6 mM linoleic acid, 0.25% (v/v) Tween-20, 10 mM NaOH, in 0.1 M phosphate, pH 8). Activity was measured by following the increase in absorbance at 234 nm. One unit of enzyme activity was defined as the increase in absorbance per min and per mL enzyme solution.

2.6. Total antioxidant capacity and activities of catalase and superoxide dismutase

Ferric reducing/antioxidant power assay (FRAP assay) was used to estimate the antioxidant capacity, according to the original method of Benzie and Strain (1996) with some modifications. The FRAP reagent was freshly prepared from 300 mM acetate buffer (pH 3.6), 10 mM tripyridyltriazine (TPTZ) made up in 40 mM HCl and 20 mM $FeCl_3$. All three solutions were mixed in the ratio of 10:1:1(v/v/v). An aliquot of 0.1 mL of the tested sample solution was mixed with 3.0 mL of FRAP reagent. The absorption of the reaction mixture was measured at 593 nm after 2 min incubation at 37 °C. A calibration curve was prepared, using an aqueous solution of ferrous sulphate $FeSO_4{\cdot}7H_2O$ and the results, obtained from three replicate extractions, were expressed as mmol $FeSO_4{\cdot}7H_2O$ per 100 g of FW (noted as: mmol Fe^{2+} per 100 g FW).

CAT activities were assayed at 25 ± 2 °C, following the method described by Ali et al. (2005). CAT activity was determined by monitoring the decomposition of H_2O_2 at 420 nm. The reaction mixture contained 50 mM sodium phosphate buffer (pH 7.0), 30 mM H_2O_2, and 100 μL of enzyme extract.

SOD activity was measured using a modification of the method of Ukeda et al. (1997). The reaction mixture contained 50 mM sodium phosphate buffer (pH 8.0), 3 mM xanthine, 3 mM EDTA, 0.75 mM XTT (2,3-bis(2-methoxy-4-nitro-5-sulfophenyl)-2*H*-tetrazolium-5-carboxanilide), and 0.14 units of xanthine oxidase. Activity was determined by monitoring the reduction rate of XTT at 470 nm, using mixtures with and without the enzyme extract. The unit of SOD was defined as the amount of enzyme that produced half-maximal inhibition.

2.7. Treatment with salicylic acid (SA)

Prior to placing the flowers at low temperature a SA treatment was carried out in experiments with anthurium cv. Cheers (the most CI-sensitive cultivar in the present tests). Individual flower stems were dipped for 15 min in 2.0 mM SA at about 20 °C. Flowers that were removed from the SA solution were allowed to air-dry at room temperature. The flowers were then individually placed in water and stored at 4 °C (85% RH) for 20 days. Samples were collected for the measurements of spathe blackening, electrolyte leakage, lipid peroxidation MDA content, lipoxygenase

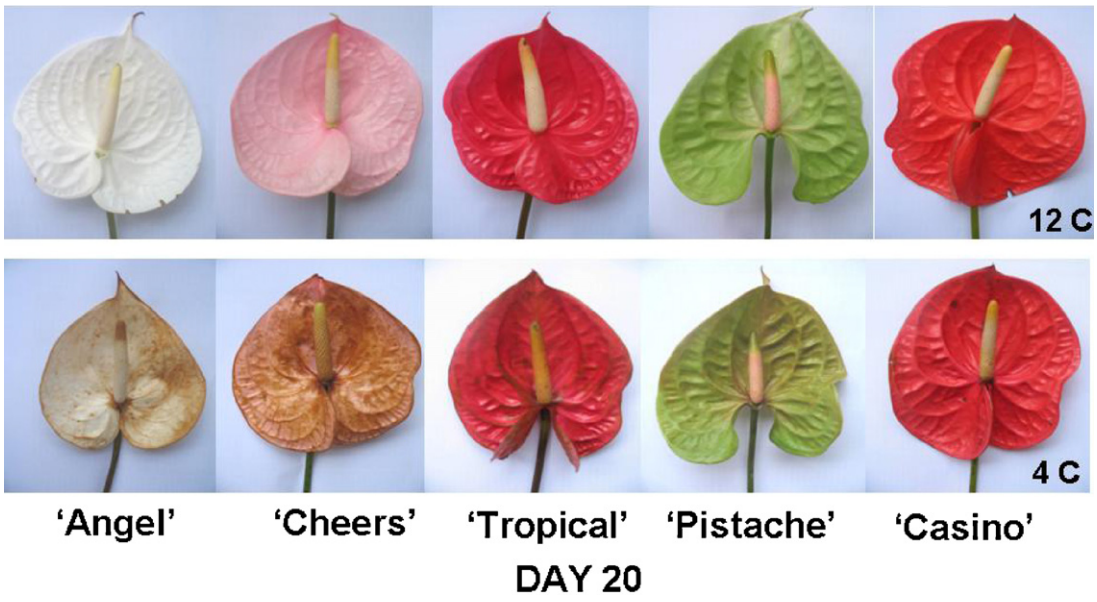

Fig. 1. Visible CI symptoms in the spathe of cut *Anthurium* flowers. Flowers of five cultivars were stored, with the stem ends in water, at 4 or 12 °C for 20 days. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

(LOX) activities, total antioxidant capacity, antioxidant enzymes activities (CAT and SOD), as described above.

2.8. Statistical analysis

We used ten replicate flowers in the storage treatments. Determinations of biochemical parameters used five replications per treatment. Each treatment was replicated five times, each replication consisting of the whole spathe from 10 to 15 randomly sampled flowers which were pooled together. In every replication the data were determined three times, whereby the values were averaged. Statistical differences were calculated using a Tukey–Kramer's multiple range test for comparison of more than two sets or Student's *t*-test when comparing two data sets, both at $p \leq 0.05$. All experiments were repeated once or twice at later dates.

3. Results

3.1. Chilling injury symptoms, cultivar-dependence

Cut flowers of all of the 5 cultivars tested showed virtually no chilling injury (CI) symptoms when stored in water at 12 °C, but did show CI symptoms during storage in water at 4 °C. The CI symptoms were mainly a change of spathe colour (Fig. 1). The colour change depended on the initial colour. The white spathe of cv. Angel and the light pink spathe of cv. Cheers turned brown (Fig. 1). The darker pink spathe of cv. Tropical lost glossiness and colour and turned to a brown-like colour at the main vascular bundles. The green spathe of cv. Pistache lost glossiness and developed brown areas. The red spathe of cv. Casino lost both glossiness and colour, but did not show browning even by day 20 (Fig. 1). Red and pink spathes tended to become bluish. The spadix became desiccated, starting from the top.

Fig. 2A shows that very light CI symptoms developed by the end of storage at 12 °C, and only in cv. Cheers. During storage at 4 °C, CI symptoms were first found in cv. Cheers, and were also most pronounced in this cultivar (Fig. 2B). Less CI was observed in the cvs. Angel, Pistache, and Tropical (Fig. 2B). Least sensitive was cv. Casino (Fig. 2B).

The average time to the CI symptoms (spathe discolouration) was also shortest (15 d) in cv. Cheers, and longest (28 d) in cv. Casino (Table 1). It was intermediate in the three other cultivars studied (Table 1).

3.2. Fresh weight (FW)

During the first eight days of storage at 12 °C, the FW of the flowers, in all five cultivars tested, showed no change. By day 20, however, FW was 91–98% of the initial value, with cv. Cheers showing the lowest FW (Fig. 3A). The decrease in FW started earlier during storage at 4 °C (Fig. 3B). By the end of the storage period at 4 °C, FW varied between 81 and 90% of initial values (Fig. 3B). Cv. Cheers lost most FW, and cv. Casino the least. The other three cultivars lost intermediate amounts of FW (Fig. 3B).

3.3. Electrolyte leakage (EL)

Electrolyte leakage of the spathe in all the *Anthurium* cultivars stored at 12 °C did not increase during the 20 d of storage (Fig. 4A). EL of the spathe increased in flowers stored at 4 °C. The largest increase was found in cv. Cheers and the lowest in cv. Casino (Fig. 4B).

Table 1
Time to spathe discoloration in five cultivars of anthurium flowers (*Anthurium andraeanum*) stored with the stems in water at 4 °C or 12 °C.

Cultivars	Time to discoloration (d)[a]	
	4 °C	12 °C
Angel (White)	20 c	43 a
Cheers (Pink)	15 d	41 b
Tropical (Red)	19 c	40 b
Pistache (Green)	25 b	40 b
Casino (Orange)	28 a	44 a

[a] Mean values followed by different letters in the same column are significantly different at $p \leq 0.01$, using Tukey–Kramer's multiple range test.

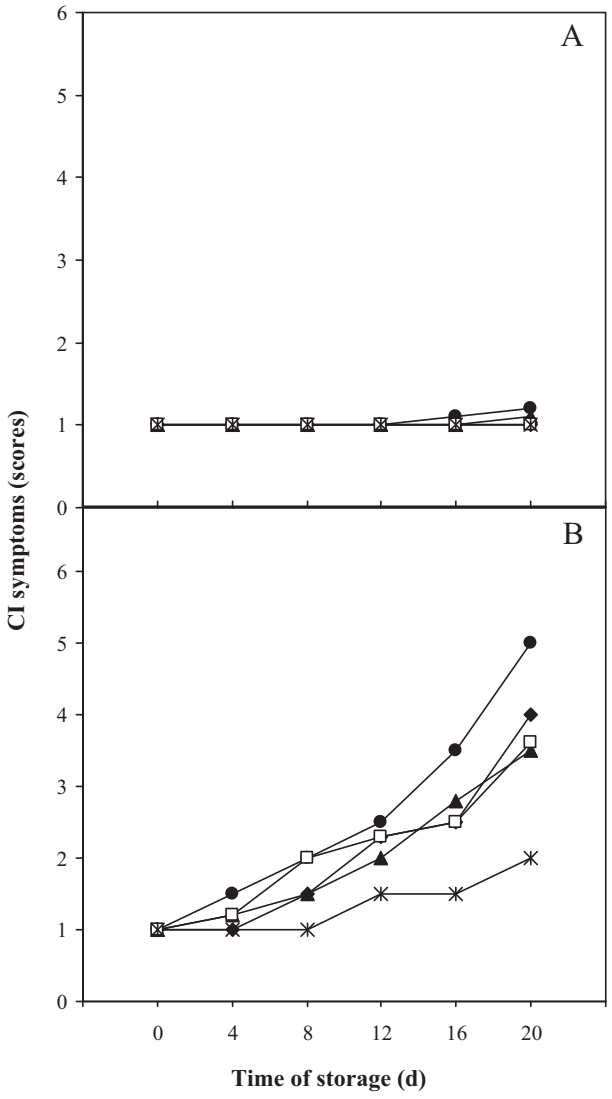

Fig. 2. Chilling injury (CI) scores in the spathe of cut *Anthurium* flowers. Flowers were stored, with the stem ends in water, at 12 °C (A) or 4 °C (B). The cultivars were Cheers (●), Angel (♦), Pistache (□), Tropical (▲), and Casino (∗).

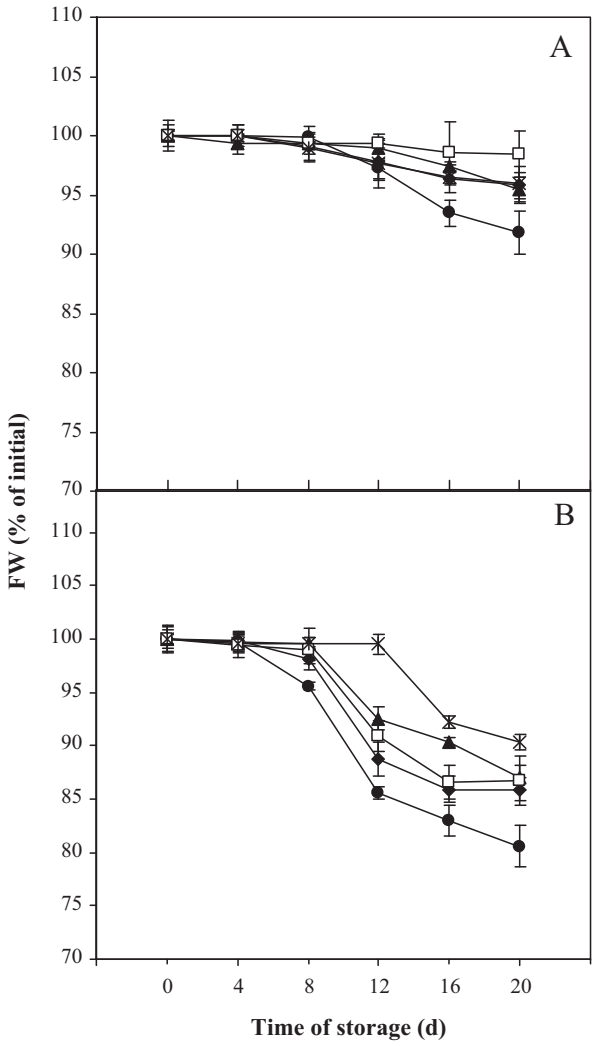

Fig. 3. Fresh weight of cut *Anthurium* flowers. Flowers were stored, with the stem ends in water, at 12 °C (A) or 4 °C (B). The cultivars tested were Cheers (●), Angel (♦), Pistache (□), Tropical (▲), and Casino (∗). Data are means ± S.E. of five replications (each consisting of 10 flowers).

3.4. Effect of salicylic acid

Cv. Cheers flowers were selected to test a pulse treatment with 1.0, 1.5 and 2.0 mM salicylic acid (SA) for 15 min at room temperature. The flowers were then stored at 4 °C. Dipping flowers in 1.0 and 1.5 mM SA had no protective effect against CI (data not shown). Dipping in 2.0 mM SA alleviated CI symptoms (mainly spathe browning) in cv. Cheers (Fig. 5A).

The FW of cv. Cheers flowers treated with 2.0 mM SA prior to storage at 4 °C, decreased less than that of the control flowers (Fig. 5B). The EL of the spathe of cv. Cheers treated with 2.0 mM SA remained lower than that in untreated control flowers (Fig. 5C).

TBA binds with degradation products of lipid peroxidation, such as malondialdehyde. However, this reaction is not specific, thus the TBA reaction is only an approximation of lipid peroxidation (Knight et al., 1988). During storage at 4 °C, the concentration of TBA-reactive compounds in the spathe of control cv. Cheers increased (Fig. 6A). Compared to the controls, a lower concentration of TBA-reactive compounds was found in the spathe of flowers treated with 2.0 mM SA than (Fig. 6A).

During storage at 4 °C, the LOX activity in the spathe of control cv. Cheers flowers had sharply increased by day 4 and then slightly decreased toward the end of the 20 d of storage. The LOX activity in the spathe of cv. Cheers flowers treated with 2.0 mM SA did not appreciably increase (Fig. 6B).

The total antioxidant capacity in the spathe of cv. Cheers flowers that were stored at 4 °C slightly decreased during vase life (Fig. 7A). No differences were found between the control flowers and the flowers that had been treated with SA prior to cold storage (Fig. 7A).

CAT activity of the spathe in control cv. Cheers flowers increased during the first 8 days of storage at 4 °C, then decreased (Fig. 7B). The CAT activity of the spathe of flowers that had been treated with SA increased more than in the controls (Fig. 7B).

The SOD activity in the spathe of cv. Cheers increased from day 0 to 4 of vase life, then gradually decreased (Fig. 7C). The spathe SOD activity of cut flowers treated with 2.0 mM SA was higher than in the control flowers, but had become the same by day 16 and day 20 of the experiment (Fig. 7C).

4. Discussion

Cut *Anthurium* flowers that were held in water at 4 °C showed severe CI symptoms. This confirms earlier work with *Anthurium* flowers that were stored at low temperature, (Shirakawa et al., 1964; Paull, 1987; Pritchard et al., 1991). Both when comparing

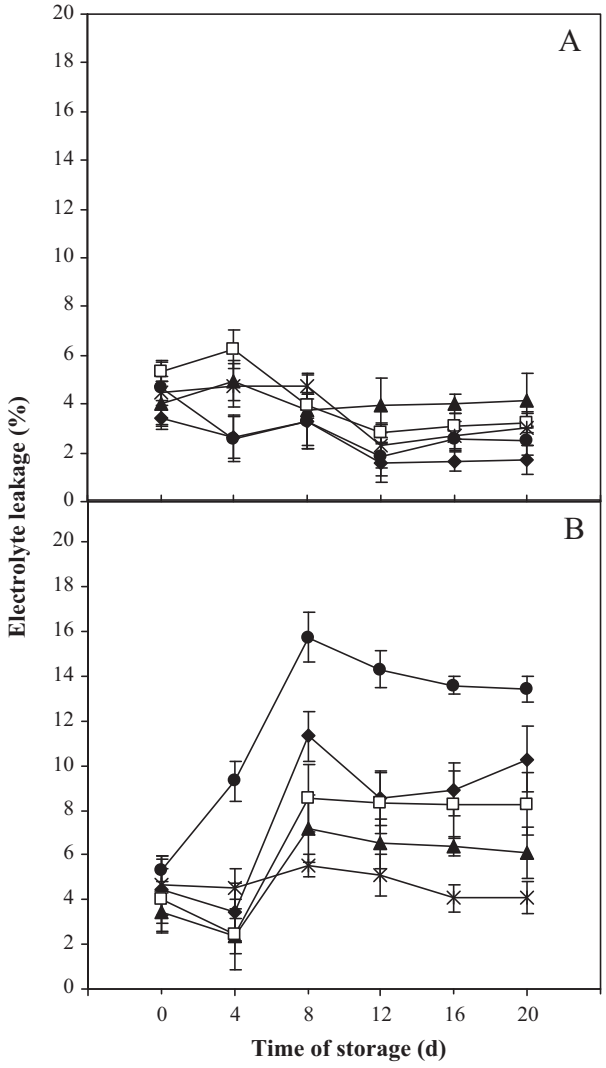

Fig. 4. Electrolyte leakage from the spathe of cut *Anthurium* flowers. Flowers were stored, with the stem ends in water, at 12 °C (A) or 4 °C (B). The cultivars were Cheers (●), Angel (♦), Pistache (□), Tropical (▲), and Casino (∗). Data are means ± S.E. of five replications (each consisting of the whole spathe from 10 flowers).

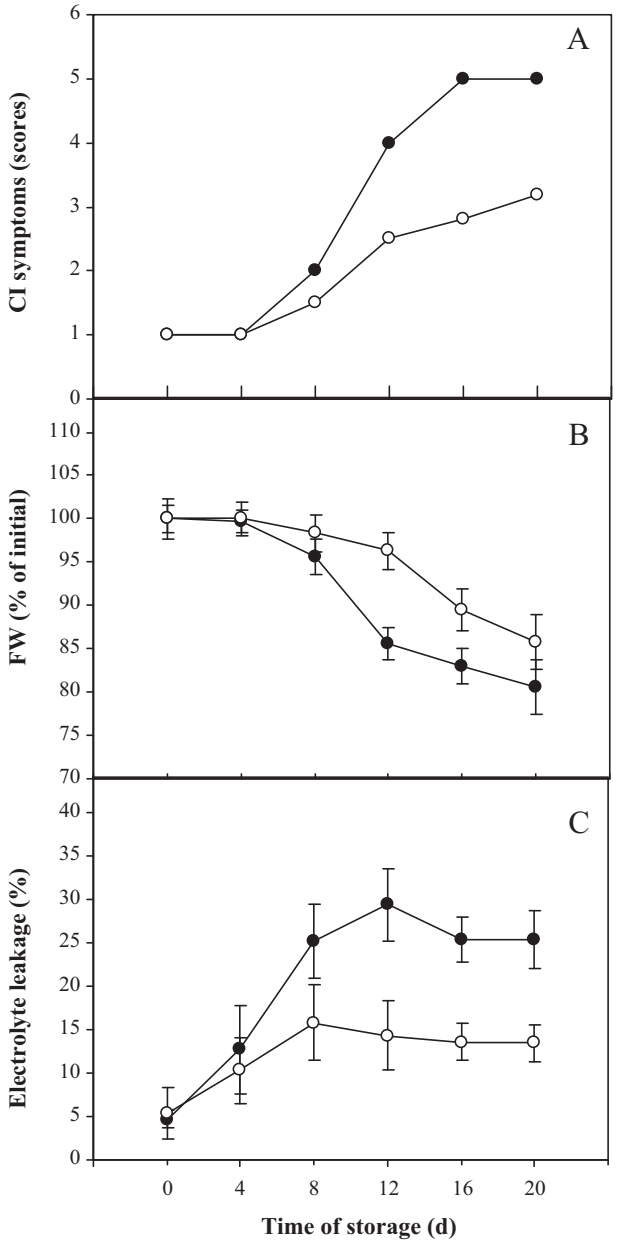

Fig. 5. Effects of treatment with salicylic acid in cut *Anthurium* cv. Cheers flowers. SA was applied as a 15 min dip of the stem ends in 2.0 mM aqueous solution, prior to cold storage. Data are the chilling injury (CI) score of the spathe (A), the FW of the flowers (B) and electrolyte leakage from the spathe (C), during storage at 4 °C, in flowers that had not been (●) or had been (○) treated with SA. Data are means ± S.E. of five replications (each consisting of the whole spathe from 10 flowers).

cultivars (Fig. 2) and when comparing controls and SA-treated flowers (Fig. 5A), we found that the visible CI symptoms showed a close correlation with loss of FW (Fig. 3). It is not clear what was cause or effect, if there is a causal relationship. The simplest explanation seems that the visible injury induced by low temperature storage represents dead cells, and that these dead cells easily lose water. Increased electrolyte leakage has often been used as an indicator of membrane damage during storage at low temperature. This leakage was generally correlated with the extent of visible CI (Saltveit, 2000). Our data also show a clear correlation between electrolyte leakage and the visible CI symptoms. An explanation for the release of electrolytes from the spathe is that the release is mainly due to cells that have died. Electrolytes can leave a cell only when the plasma membrane has lost semipermeability. This probably does not occur unless the cell is dead.

As noted in the Introduction, a treatment with SA protects against the development of visible CI symptoms in several whole plant and fruit species. SA often acts as a small signaling molecule in plants. It plays an important role in triggering the defense mechanisms against pathogens. It also acts as a molecule that counteracts CI (Raskin, 1992). We have now found a protective effect of SA against the damage induced by low temperature in cut anthurium flowers. In our experiments SA considerably reduced the rise in electrolyte leakage, reduced the increase in the concentration of TBA-reactive compounds, and also the increase in LOX activity. SA treatment also resulted in high activity of both catalase and SOD. These data suggest that the effect of SA occurs at a rather early step in the physiological changes leading to the damage induced by cold storage.

The concentration of TBA-reactive compounds and the activity of LOX often increase in response to storage at low temperature. These parameters are often used as indicators of membrane injury (Berger et al., 2001). Some examples of an increase in TBA-reactive compounds during low temperature storage, from our laboratory, are banana fruit (Promyou et al., 2008) and basil leaves (Wongsheree et al., 2009). The alleviating effect of SA on the rise in

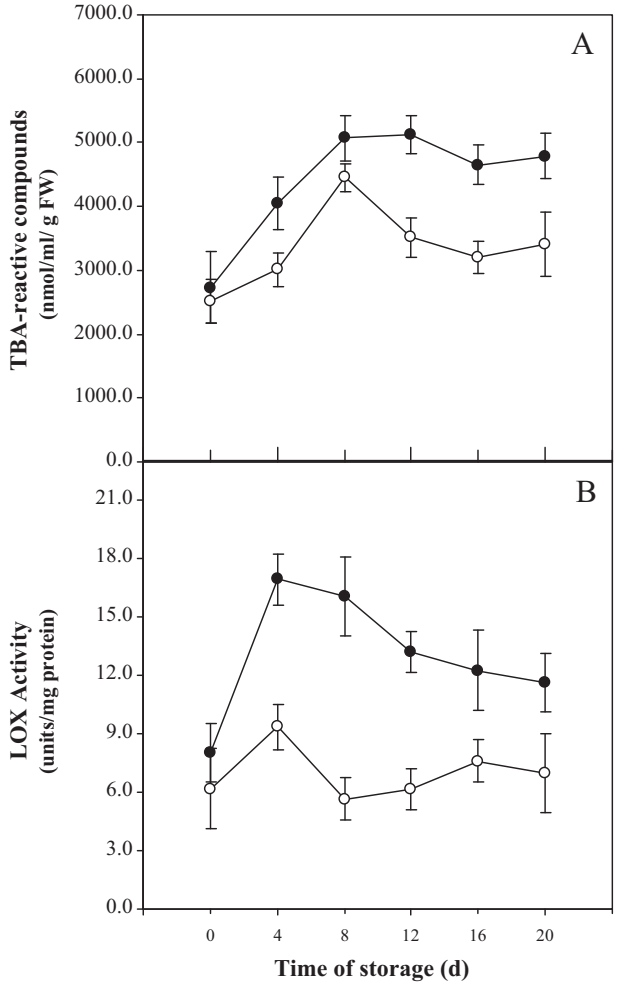

Fig. 6. Lipid degradation after treatment with salicylic acid in cut *Anthurium* cv. Cheers flowers. SA was applied as a 15 min dip of the stem ends in 2.0 mM aqueous solution, prior to cold storage. Data are the concentration of TBA-reactive compounds (A) and lipoxygenase (LOX) activities (B) of the spathe, during storage at 4 °C, in flowers that had not been (●) or had been (○) treated with SA. Data are means ± S.E. of five replications (each consisting of the whole spathe from 10 flowers).

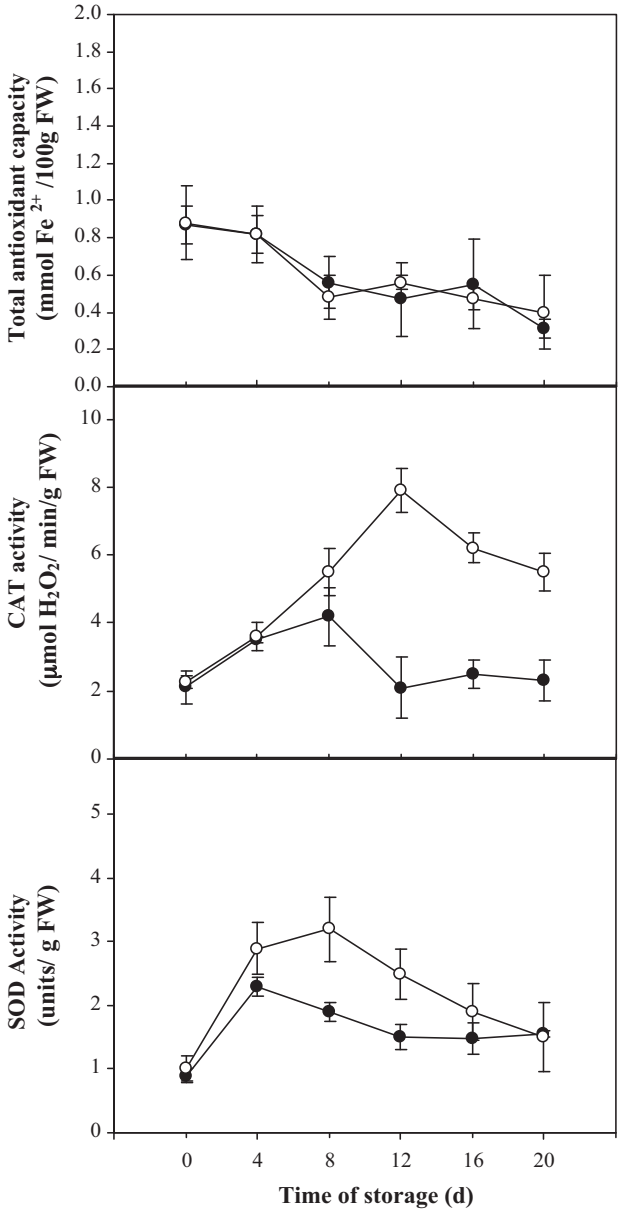

Fig. 7. Anti-oxidant systems after treatment with salicylic acid in cut *Anthurium* cv. Cheers flowers. SA was applied as a 15 min dip of the stem ends in 2.0 mM aqueous solution, prior to cold storage. Data are the total antioxidant capacity of the spathe (A) and the activities of catalase (B) and superoxide dismutase (C), during storage at 4 °C, in flowers that had not been (●) or had been (○) treated with SA. Data are means ± S.E. of five replications (each consisting of the whole spathe from 10 flowers).

the concentration of TBA-reactive compounds and the increase in LOX activity of *Anthurium* spathes clearly suggest a role of membrane damage in CI. Similarly, SA treatment resulted in a lower LOX activity in cold-stored peach fruit (Cao et al., 2010).

An increase in oxidative compounds such as free radicals based on oxygen, as well as H_2O_2, often accompanies visible CI symptoms. CI is also often correlated with an increase in total antioxidant capacity and in the activity of antioxidant enzymes such as catalase and SOD (Srivalli et al., 2003). These data suggest that cold storage induces an increase in the concentration of oxidative compounds, and that cells react by activating systems that render these innocuous. The failure of this protective system might be one of the possible causes of the cell death induced by cold.

We found no effect of SA on total antioxidant capacity. This is unlike the results with pomegranate fruit during storage at low temperature where SA treatment maintained total antioxidant capacity (Sayyari et al., 2011). Cold-stored *Anthurium* flowers treated with SA maintained higher activities of CAT and SOD, compared to control flowers. This is in agreement with data of Knorzer et al. (1999) who found increased catalase activity upon SA treatment of suspension-grown soybean cells. The data suggest that SA is able to mobilize the defense against oxidative compounds, at least partially converting these to H_2O_2 and then to water.

It is concluded that SA treatment induced chilling tolerance in *Anthurium* flowers. SA apparently resulted in better detoxification of reactive oxygen compounds and in better maintenance of membrane integrity, during low temperature storage. A 15 min dip in SA is a simple treatment that can be applied in practice.

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