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Correlation of Reduced Softening and Increased Polyamine Levels during Low-oxygen Storage of 'McIntosh' Apples

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Additional index words. *Malus domestica*, postharvest physiology, putrescine, spermidine, spermine

Abstract. **The rate of postharvest softening of 'McIntosh' apples (*Malus domestica* Borkh.) was reduced by storage in a 1% O_2 atmosphere at 1 or 3.5C. Apples stored in controlled atmosphere (CA) also maintained higher levels of the polyamines putrescine (PUT), spermidine (SPD), and spermine (SPN) in both skin and flesh tissues than those stored in air. The levels of putrescine and spermidine increased by 2- to 6-fold in CA-stored apples, while spermine decreased, but remained 2- to 5-fold higher than in air-stored fruit at both temperatures. Polyamines were also found to inhibit the in vitro activity of the cell wall-degrading enzyme polygalacturonase (PG). SPD and SPN were more effective than PUT, with SPN possessing the greatest inhibitory activity. These results are consistent with a hypothesis that increased polyamine levels are involved in the beneficial effects of CA storage and that polyamine activity could include the inhibition of cell wall degradation.**

CA storage is effective in delaying onset of ripening and senescence in a variety of fruits and vegetables. The mechanism of CA action appears to involve several factors, including: 1) suppression of respiratory activity, 2) inhibition of ethylene production, 3) changes in the levels of growth regulators, and 4) inhibition of the increase in the activity of softening-related enzymes, such as polygalacturonase (PG; EC 3.2.1.15) (Kader, 1986; Wang, 1989; Weichman, 1986).

Polyamines appear to be potent inhibitors of senescence-related processes in plant tissues (Galston and Kaur-Sawhney, 1987). These compounds have been shown to inhibit the degredative enzymes RNase (EC 3.1.27.5), protease (EC 3.4.24.4) (Galston and Kaur-Sawhney, 1987), and peroxidase (EC 1.11.1.7) (Srivastava and Rajbabu, 1983), and to inhibit the senescence of detached leaves (Altman, 1982). The anti-senescent activity of polyamines may also be related to their ability to stabilize and protect membranes (Ballas et al., 1983; Roberts et al., 1986) and their anti-oxidant properties (Drolet et al., 1986). Also, the resistance of zucchini squash to chilling injury has been correlated with elevated polyamine levels (Kramer and Wang, 1989). Given this relationship between polyamines and senescence, the possible involvement of these compounds in the mechanism of CA action has been of interest (Wang, 1988; Wang, 1989; Wang and Ji, 1988). The delay of senescence in Chinese cabbage and the reduction of chilling injury in zucchini squash by CA storage has been shown to be correlated with increased levels of polyamines (Wang, 1988; Wang and Ji, 1988).

The treatment of apples with Ca^{++} has been shown to inhibit softening (Betts and Bramlage, 1977; Conway and Sams, 1987; Drake and Spayd, 1983). The mechanism of Ca^{++} activity may involve inhibition of the activity of softening-related enzymes such as PG (Conway et al., 1987; Drake and Spayd, 1983). Since polyamines are also cationic, it seemed possible that they could likewise inhibit PG. The purpose of this study was thus to investigate the effect of CA storage on polyamine levels in 'McIntosh' apples and to investigate a possible mechanism (PG inhibition) of polyamine anti-senescent activity.

Materials and Methods

Fruit from mature standard-size 'McIntosh' apple trees in the orchard of Cornell Univ., Ithaca, N.Y. were harvested on 9

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Sept. 1987—the optimum harvest date for storage as predicted by the method of Blanpied (1973). The fruit were transferred to Beltsville, Md. the next day. They were then randomly divided into two lots of 400 each and stored at either 1 or 3.5C. Within each temperature group, the fruit were further divided into two lots of 200 each and stored in either air or 1% O_2.

Stainless steel chambers (200 liters) with glass doors were used as storage containers and 200 fruit (placed in ten 20-fruit trays) were stored in each chamber for each treatment. To establish a 1% O_2 atmosphere, the sealed chambers were flushed initially with N_2 at a high rate, followed by 1% O_2 (argon-free) from a premixed gas cylinder. The flow rate was maintained at 100 ml·min^{-1} throughout the storage, with 90% to 95% RH. For air storage, the chambers were flushed with air from a compressed air cylinder at the same flow rate. The 1% O_2 atmosphere was verified and monitored by an Orsat gas analyzer and a gas chromatograph (Shimadzu) equipped with a thermal conductivity detector. About 300 g of Purafil and 500 g of lime were placed in each chamber to absorb ethylene and CO_2, respectively.

Fruit firmness was measured on a pared surface (three per fruit) with a Magness–Taylor penetrometer equipped with an 11-mm plunger. Samples were taken at harvest and at 2-week intervals during storage. Fifteen fruit were used at harvest and six were removed biweekly at random from each group for measurement of firmness and polyamine analysis. Samples (2.0 g) of skin and flesh tissue (as a wedge) were removed and stored at −80°C. The 1% O_2 atmosphere was re-established as described above immediately after each sampling.

Extracts for polyamine analysis were prepared by homogenizing 2.0 g of tissue in 15 ml of 5% perchloric acid using a Polytron (Brinkman). Before homogenization, 1,8-octanediamine (150 nmol·g^{-1} fresh weight) (Sigma) was added as an internal standard. The homogenate was then centrifuged at 47,800× *g* for 20 min. The supernatant was removed for use in polyamine analysis.

Polyamines were analyzed using high-pressure liquid chromatography (HPLC) with methods similar to those described by Kramer and Wang (1989). Dansylation was performed by mixing 400 µl of 10 mg dansyl chloride (Sigma)/ml (in acetone) and 150 µl of saturated sodium bicarbonate with 200 µl of extract. After incubation overnight at room temperature, 250 µl of 50 mg proline/ml was added and the incubation was continued another 1 hr. After centrifugation for 10 min in a microcentrifuge, the pH of the supernatant was checked and adjusted close to neutral (6 to 8) as necessary. Samples of 100 µl of the supernatant were used for HPLC analysis. HPLC was performed on a system consisting of two pumps (Waters 6000A). Samples were injected using a Waters U6K injector onto a reverse-phase C-18 column (Supelco 25 cm LC-18 with a Supelguard LC-18 5-µm guard column). Samples were eluted from the column at a flow rate of 1.5 ml·min^{-1} with a programmed solvent gradient of 0, 100, 0; 15, 0, 100; 19, 0, 100; where the first number is the time (minutes), the second number is the percent of buffer A (60 methanol : 40 water), and the third number is the buffer B (100% methanol). Elution was completed in 18 min. Eluates were detected by a spectrofluorometer (Perkin-Elmer 650-10S) using an excitation wavelength of 365 nm and an emission wavelength of 510 nm. The pumps were controlled and data were collected and analyzed using a NEC APCIV PowerMate 2 computer system equipped with a Maxima 820 Chromatography Workstation (Dynamic Solutions). Polyamines were quantitated by the comparison of peak areas with those of standards. Each data point is the average of three independent samples.

The effect of polyamines on PG activity was assayed by measuring the increase in reducing sugars with 2-cyanoacetamide (Gross, 1982). PG was extracted from 'Golden Delicious' apples inoculated with *Penicillium expansum* Link ex Thom as described by Conway et al. (1988). Reaction mixtures contained 100 µl of 0.4% citrus polygalacturonic acid (Sigma, washed with 80% ethanol before use) in 100 mM of sodium acetate (pH 5.5), 50 µl polyamine (Sigma) solution, and 50 µl of the enzyme preparation. To determine activity in the absence of inhibitor, 50 µl of water was used instead of the polyamine solution. For quantifying released reducing groups with 2-cyanoacetamide, reactions were terminated after 20 min of incubation at 30C by adding 1 ml of cold borate buffer (pH 9.0). Then, 200 µl of 1% 2-cyanoacetamide (Aldrich) was added and each sample was mixed and immersed in a boiling water bath for 10 min. After equilibration to 25C, the absorbance at 276 nm was determined. Each data point presented is the average of six independent assays.

The figures were prepared using SigmaPlot software (Jandel Scientific). The traces presented are computer-generated regression lines.

Results

Effect of CA on softening. The average firmness value at harvest was 73 N. Low-O_2 atmosphere significantly inhibited the softening of apples at both 1 and 3.5C (Fig. 1), with the overall rate of softening being greater at the higher temperature. These results are similar to those previously reported (Dewey and Bourne, 1982; Lau et al., 1987).

Effect of CA on polyamines. The effects of CA storage on the polyamine levels in the skin are shown in Figs. 2 (1C) and 3 (3.5C). At both temperatures, storage in air resulted in a slight increase (<2-fold) in PUT, a slight decrease (30% to 50%) in

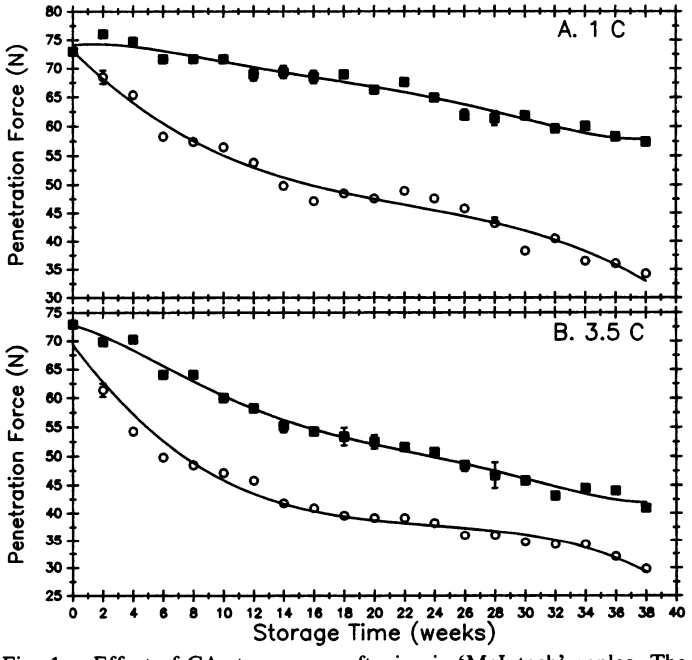

Fig. 1. Effect of CA storage on softening in 'McIntosh' apples. The fruit were held in 1% O_2 (■) or air (○) at 1C (**A**) or 3.5C (**B**). Vertical bars represent ± SE.

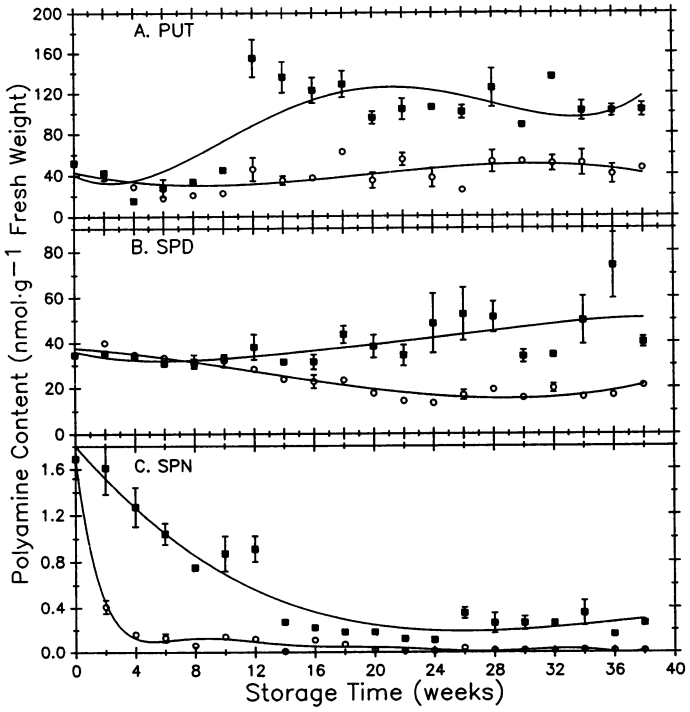

Fig. 2. Effect of CA storage on the polyamine content of skin tissue from apples held at 1C in 1% O_2 (■) or air (○). Vertical bars represent ± SE.

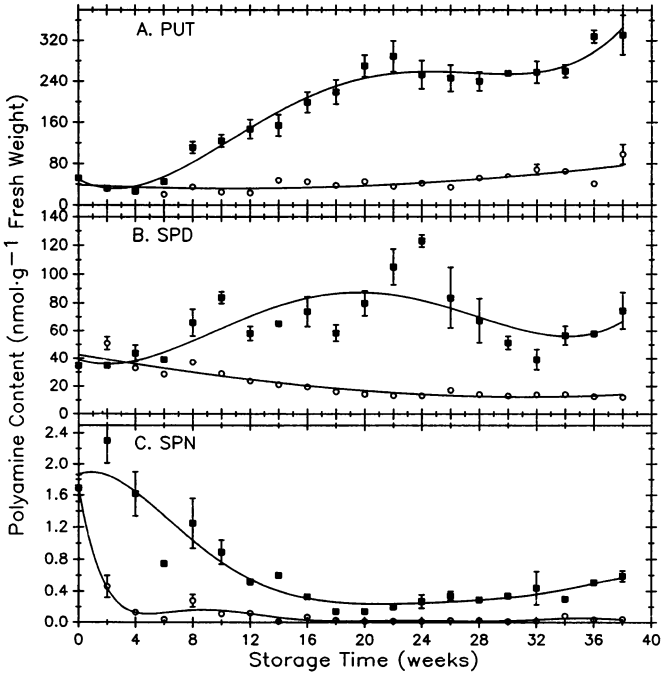

Fig. 3. Effect of CA storage on the polyamine content of skin tissue from apples held at 3.5C in 1% O_2 (■) or air (○). Vertical bars represent ± SE.

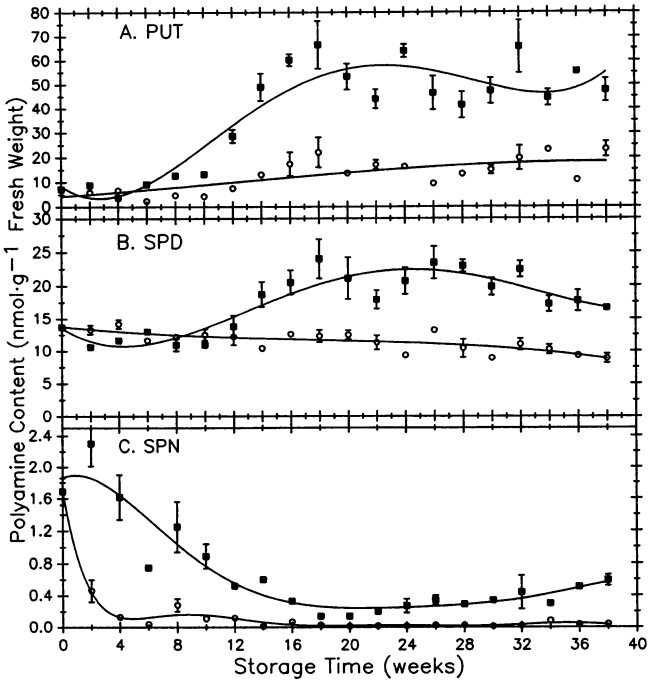

Fig. 4. Effect of CA storage on the polyamine content of flesh tissue from apples held at 1C in 1% O_2 (■) or air (○). Vertical bars represent ± SE.

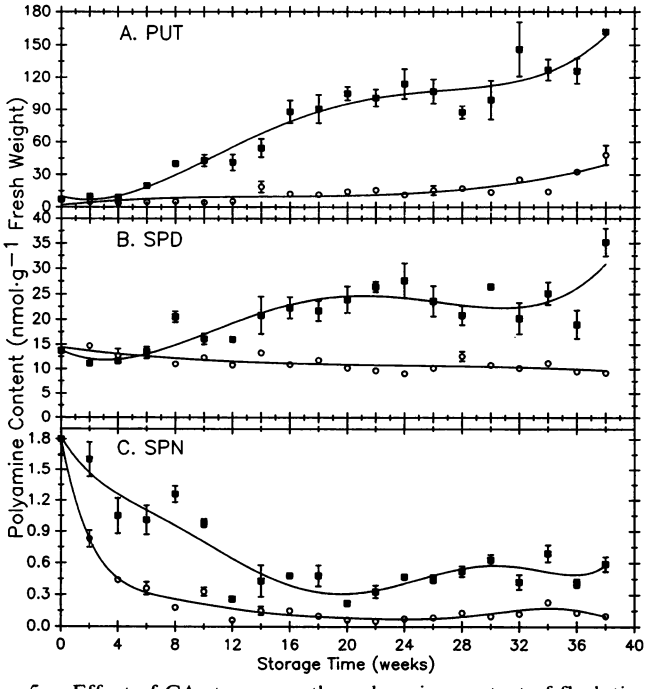

Fig. 5. Effect of CA storage on the polyamine content of flesh tissue from apples held at 3.5C in 1% O_2 (■) or air (○). Vertical bars represent ± SE.

SPD, and a major decrease (≈90% by week 4) in SPN over time. The polyamine levels in CA-stored apples were higher than those in the air-stored fruit. PUT (3- to 5-fold) and SPD increased over time (2- to 3-fold) while SPN decreased, but all remained higher (4- to 10-fold) than in the air-stored apples. Some differences due to storage temperature were observed. PUT and SPD levels were elevated by the CA to a greater extent at 3.5C and SPD was induced earlier at 3.5C than at 1C. Similar results were observed in the flesh (Figs. 4 and 5). Storage of

the fruit in air induced slight increases (1.5- to 3-fold) in PUT, SPD decreased slightly (30%), and SPN decreased rapidly. CA storage resulted in increases in PUT (5- to 10-fold) and SPD (2-fold); SPN levels decreased, but all remained higher (3- to 5-fold) than those of the air-stored fruit. These differences in PUT levels were apparent in both skin and flesh tissues after 6 to 8 weeks of storage; in SPD, after 8 to 12 weeks; and in SPN, after only 2 weeks. The polyamine levels were higher in apples kept at 3.5 than those stored at 1C, and generally lower in the flesh tissue than in the skin tissue. These results demonstrate that the inhibition of senescence in apples by CA storage at both 1 and 3.5C is coincident with elevated polyamine levels.

Inhibition of PG activity by polyamines. As Ca^{++} has been shown to retard apple softening and inhibit the softening-related enzyme PG (Conway et al., 1987; Drake and Spayd, 1983), we investigated the effects of polyamines on PG activity in vitro. The polyamines PUT, SPD, and SPN inhibited the activity of purified PG, with SPN having been most potent (Fig. 6).

Discussion

We have shown that CA storage of apples results in increased polyamine levels (as compared to air-stored fruit) concomitant with a decrease in the rate of fruit softening. These results are consistent with the hypothesis that polyamines are involved in the mechanism by which CA retards senescence in stored fruits and vegetables. CA storage of Chinese cabbage and zucchini squash was found to result in the elevation of polyamine levels (Wang, 1988; Wang and Ji, 1988). Polyamines have been shown to possess anti-senescent properties (Galston and Kaur-Sawhney, 1987), including the inhibition of degradative enzymes (Galston and Kaur-Sawhney, 1987; Srivastava and Rajbabu, 1983), the stabilization of membranes (Ballas et al., 1983; Roberts et al., 1986), and action as an anti-oxidant (Drolet et al., 1986).

The treatment of apples with Ca^{++} has been shown to inhibit softening (Betts and Bramlage, 1977; Conway and Sams, 1987; Drake and Spayd, 1983) and reduce fungal decay (Conway et al., 1987; Conway et al., 1988). This activity appears to involve the ability of Ca^{++} to associate with the cell wall and form cation cross-bridges with pectic acid and other polysaccharides that would limit the access of softening enzymes to the cell wall (Conway et al., 1987; Drake and Spayd, 1983). Since polyamines are also polycations, the mechanism by which softening is retarded by CA could involve protection of cell walls. We have tested this hypothesis by determining the effect of polyamines on PG, a major softening enzyme in fruit (Bennett and DellaPenna, 1987). Polyamines were, in fact, found to inhibit the activity of PG in vitro. The relative inhibitory activity of the polyamines tested corresponded with the number of charges per molecule; i.e., tetravalent SPN was a much more potent inhibitor than trivalent SPD, which was more effective than divalent PUT. Similar to Ca^{++}, polyamines, therefore, appear to inhibit PG by a mechanism that involves ionic association with the cell wall. The suggestion of polyamines acting at the cell wall is consistent with reports of SPD binding to the wall (Pistocchi et al., 1987) and with the localization of polyamine catabolic enzymes at the cell wall (Kaur-Sawhney et al., 1981). Our results suggest another possible anti-senescent polyamine activity (inhibition of cell wall degradation) and that this activity may play a role in the inhibition of softening by storage.

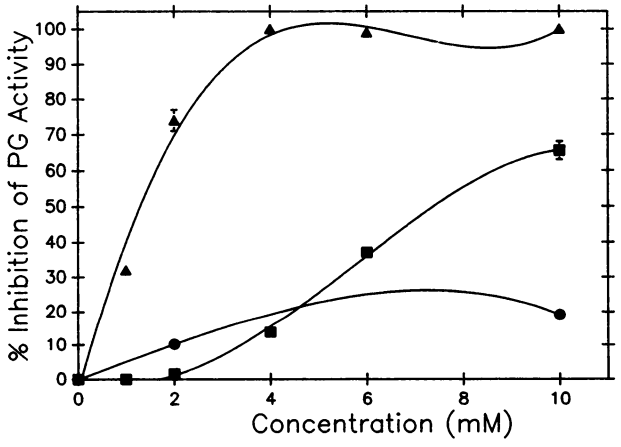

Fig. 6. Effect of SPN (▲), SPD (■), and PUT (●) on the in vitro activity of purified polygalacturonase. Vertical bars represent ± SE.

Several questions remain to be answered concerning the role of polyamines in CA storage. It is unclear to what extent the effects of CA are related to polyamine accumulation and to what extent these effects are related to other processes. The regulatory mechanism by which CA increases polyamine levels is also unknown. CA could inhibit polyamine catabolism that is catalyzed by the oxygen-requiring enzyme polyamine oxidase (Kaur-Sawhney et al., 1981) or affect polyamine biosynthetic enzymes. The further delineation of the regulation and effects of polyamines during CA storage could suggest techniques for increasing the storage life of apples by augmenting polyamine levels. Such augmentation could include either postharvest application or genetic manipulation to increase endogenous polyamine levels.

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Decay Control and Quality Maintenance after Moist Air Heat Treatment of Individually Plastic-wrapped Nectarines

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Abstract. **Moist air heat treatment at 52C for 15 min prevented decay in individually plastic-wrapped or naked nectarine [*Prunus persica* (L.) Batsch var. nectarina (Ait.) Maxim.] fruit puncture-inoculated with *Monilinia fructicola* (Wint.) Honey. Heat treatment for 5 or 10 min slowed decay development, but did not prevent it. In treatments where decay occurred, the wrap increased decay. Heat treatment tests at 52C for 15, 30, 45 min slowed softening and ethylene production of fruit. Wrapping alone reduced ethylene production 75% and respiration 12%, but did not significantly influence softening. The wrap reduced or eliminated undesirable skin browning associated with heat treatments.**

Postharvest heat treatment has been used for control of fruit decay (Jones and Burton, 1973; Jones et al., 1973; Smith, 1971; Tindale et al., 1958). A 2.5-min dip in 52C water effectively controls decays in peaches caused by *M. fructicola* and *Rhizopus stolonifer* (Smith, 1962). Moist air at 54C for 15 min (Smith et al., 1964) also may be used to control decay in stone fruit. Hot-water treatment of nectarines may slow ripening of nectarines (C.M. Harris, personal communication) and, in other fruit, heat has been found to alter some of the ripening processes (Chan et al., 1981; Chan, 1986a, 1986b; Field, 1985; Yu et al., 1980). In addition, heat may cause surface browning and increased susceptibility of fruit to decay (Phillips and Austin, 1982; Phillips and Harris, 1979; Smith, 1962).

Heat treatment may not offer control of pathogens that may contaminate the fruit after the treatment, although hot water containing fungicides has been used to provide residual protection to decay (Harvey, 1978; Jones and Burton, 1973; Jones et al., 1973; Wells, 1971; Wells, 1972; Wells and Harvey, 1970).

Plastic wrap reduces water loss (Ben-Yehoshua, 1985; Hulbert and Bhowmik, 1987; Smith et al., 1964), alters respiration rate (Ben-Yehoshua, 1985), and may reduce microbial contamination of heat-treated fruit. Wrapping fruit individually is a relatively new technique (Ben-Yehoshua, 1985; Bhowmik and Sebris, 1988). The advantages of wrapping fruit individually over wrapping several fruit together are: a) the elimination of secondary infection, b) decrease in condensation of water droplets found in bags, c) avoidance of severe modification of in-

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