

Effects of Exogenous Propylene on Softening, Glycosidase, and Pectinmethylesterase Activity during Postharvest Ripening of Apricots

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Apricots (*Prunus armeniaca* L. cv. *Boccuccia spinosa*) picked at the commercial ripening stage [soluble solids content (SSC) 12.6%] were left to reach full ripening in continuously humidified air at 20 °C. Changes in the rate of ethylene production, firmness, soluble solids concentration, and titratable acidity were measured. The α -D- and β -D-glucosidases, α -L-arabinofuranosidase, α -D- and β -D-galactosidases, β -D-xylosidase, and α -D-mannosidase activities were assayed. To evaluate the influence of ethylene on glycosidase activity, propylene (500 μ L L⁻¹) was applied to apricots for 24 and 48 h. In apricots ripened in air, ethylene production increased on the first day and exhibited a typical climacteric pattern. Good edible quality was reached in 5 days when SSC was at least 14% and acidity was between 1.1 and 1.2% (% malic acid). During postharvest ripening, α -L-arabinofuranosidase activity increased from 1.9 to 11.6 nkat until day 7. α -D-Galactosidase, α -D-mannosidase, and β -D-galactosidase activity increased continuously but at a lower rate. β -D-Xylosidase activity also increased, but the level of activity was lower than the other glycosidases assayed. Pectinmethylesterase (PME) decreased during the postharvest ripening, and propylene enhanced this pattern, by stimulating ethylene production. Even the activities of α -L-arabinofuranosidase, β -D-xylosidase, α -D-mannosidase, and β -D-galactosidase were greatly stimulated by the propylene treatment, which consequently induced rapid softening of the fruits.

KEYWORDS: Softening, ethylene, sugars, acidity, color

INTRODUCTION

Rapid softening and the associated susceptibility to physical damage and disease is the major commercial problem for apricot distribution.

Apricots are harvested early, compromising the development of full aroma and eliciting consumer dissatisfaction (1). Fruit softening is brought about by the action of cell wall degrading enzymes that break down the rigid structure of the fruit, resulting in the observed textural changes (2). Research has focused on pectin degradation, resulting from the action of the ripening-related enzyme polygalacturonase, as the key element of the softening process, but molecular genetic studies have shown that this enzyme is not the main determinant of fruit softening (3). Synergistic enzyme action involving pectinmethylesterase, expansins, Egases (endo-1,4- β -D-glucanases), XETs (xyloglucan endotransglycosylases), and exo-glycosylhydrolases (glycosidases) is probably crucial for coordinated cell wall disassembly during fruit ripening (4). The demethylesterification catalyzed by pectinmethylesterase (PME) influences the interactions between cell wall components (5) and modulates cell wall hydrolases activity (6), making pectins more degradable by

pectinolytic enzymes. Glycosidases progressively hydrolyze mono- or disaccharides from the nonreducing ends of oligo- or polysaccharides. Even though the removal of the glycosyl residues has probably less dramatic effects on cell wall disassembly than endo-acting enzymes, glycosidases have been proposed to promote wall loosening by indirect mechanisms (4).

In melons, glycosidase activity changes during ripening (7), and its activity is enhanced by exogenous ethylene in ACC (1-amino-1-cyclopropane carboxylic acid) oxidase (ACO) antisense melon (8). β -D-Galactosidase, which releases galactosyl residues from cell walls, has been studied and proposed to play an important role in softening of papaya and mango (9, 10), tomato (11, 12), avocado (13), kiwifruit (14), melon (15), and grape (16). Because different mono- and disaccharides are strictly bound to the backbone of the cell wall, other glycosidases also may contribute to fruit softening.

At ripening, apricots exhibit a peak in respiration and ethylene production, in parallel with the increase of sugars and loss of acidity and firmness (17). However, there have been no studies on cell wall-degrading enzymes of apricots that might contribute to ripening-associated softening, while Nanos et al. (18) has reported the influence of ethylene on rapid softening of apricots.

Here we report a study examining the enzymes involved in

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cell wall degradation with a focus on changes in glycosidases activity during postharvest apricot ripening in relation to softening and other quality changes. To clarify the role of ethylene in the changes in enzymatic activity associated with the occurrence of softening, harvested fruit were also treated with propylene, an ethylene analogue known to promote ripening and stimulate the respiratory climacteric (19).

MATERIALS AND METHODS

Materials and Treatments. Apricot fruits (*Prunus armeniaca* L. cv. Boccuccia spinosa) were harvested at an average penetrometer reading of 32.6 ± 0.6 N and a soluble solids content of $12.6 \pm 0.2\%$. After samples were sorted for uniform size, appearance, and absence of defects, the fruits (160 fruits divided in 2 jars) were placed into 14 L glass jars in a humidified continuous air flow system (CO_2 was less than 0.4%) and left to ripen at 20 ± 1 °C (postharvest ripening experiment).

Quality and physiological measurements were carried out at harvest and for a period of 11 days. At each sampling time, after quality analyses, fruits were frozen in liquid nitrogen and stored at -82 °C for enzymatic analyses.

For propylene treatments, another lot of 160 apricots coming from the same orchard of the postharvest ripening experiment, was sorted as previously described. The apricots were divided in two sublots and placed into 14 L glass jars, flushed for 24 or 48 h with humidified air containing propylene ($500 \mu\text{L L}^{-1}$), and then transferred to a continuous humidified air flow for 3 days.

Ethylene Measurement. For C_2H_4 measurements, three lots of 10 fruits each were removed from the 14 L jar and placed into 1 L glass jars and sealed for 1 h at 18 °C.

C_2H_4 was monitored by injecting 1 mL of a headspace gas samples into a Carlo Erba Fractovap 4200 gas chromatograph (GC) (Carlo Erba Spa, Milano, Italy) equipped with a 1-m alumina column (80/100 mesh) with a flame ionization detector (Carlo Erba Spa), oven temperature 100 °C. Results were expressed as μL of $\text{C}_2\text{H}_4 \text{ kg}^{-1} \text{ h}^{-1}$. CO_2 levels remained below 0.2% after 1 h.

Quality Measurements. External color measurement was performed by using a HunterLab colorimeter D25 (HunterLab D25-PC2-Hunter, Reston, VA) taking the reading on both sides of equatorial part of the fruit.

Firmness was measured with a penetrometer (Fruit Pressure Tester 327; EFFEGI, Gaiarine, Ravenna, Italy), after removing the peel, by carefully pushing the 8-mm diameter probe into the equatorial part of the fruit to avoid hitting the seed.

Whole flesh firmness was monitored using a deformation test under nondestructive force (20, 21). Fruits were placed widthwise over the plate of an Instron Universal Testing machine (model 4301; Instron, Canton, MA) and compressed with a flat compression anvil (55 mm in diameter) at a rate of 25 mm min^{-1} (chart speed = 10 mm min^{-1}). The deformation of whole fruit to a load of 3 N (full scale range = 100 N) was recorded. Data were expressed in terms of millimeter deformation under a force of 3 N.

Titrateable acidity (TA) was measured by titration of 2 g of puree diluted with 100 mL of water to pH 8.1 with 0.1 N NaOH, using three drops of phenolphthalein as a colorimetric indicator (22). Results were expressed as a percentage of malic acid.

SSC (%) was detected with a model RL-2 table refractometer (Abbè, Officine Galileo, Florence, Italy) calibrated at 20 °C. Flesh of apricots was sliced, homogenized with an UltraTurrax, and centrifuged to extract the juice.

Enzymes Extraction and Assay. Mesocarp tissue (2 g) was homogenized in 4 mL of 50 mM sodium acetate extraction buffer (pH 6) containing 1.4 M NaCl, 0.2% (w/v) cysteine, and 1% (w/v) poly(ethylene glycol) (PEG) (7). Homogenate was stirred for 2 h and then centrifuged at 17 000 rpm for 30 min. Supernatant was desalted using a NAPTH 10 Sephadex G-25 column which had been preequilibrated with the same buffer 50 mM sodium acetate (pH 6). All of the above steps were carried out at 4 °C.

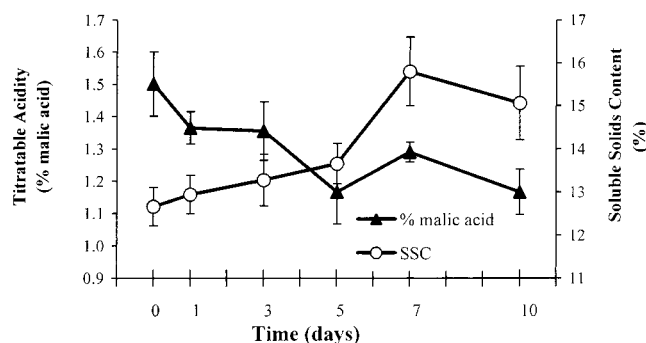


Figure 1. Changes in titratable acidity and total soluble solids content of apricots during postharvest ripening in air. Data are the means of 10 samples. Vertical bars indicate SD.

Assay mixture for glycosidase activities consisted of 50 μL of enzyme extract in 950 μL of corresponding *p*-nitrophenyl derivatives of specific substrate (7). Optimal pH, K_m , and V_m for each glycosidase were found to measure activities under ideal conditions. Final concentrations in 50 mM sodium acetate buffer were 10.8 mM for α -L-arabinofuranoside (pH 4), 15 mM for α -D-mannopyranoside (pH 4.6), 9.5 mM for α -D-glucopyranoside (pH 5.4), 16 mM for β -D-glucopyranoside (pH 5.4), 1.5 mM for α -D-galactopyranoside (pH 5), 10 mM for β -D-galactopyranoside (pH 4.4), and 10 mM for β -D-xylopyranoside (pH 4.4). Results were presented as maximal activity after calculating velocities using the Michaelis–Menten equation.

Reaction mixture was incubated at 37 °C in a water bath for 60 min. Enzyme controls were incubated under the same conditions but with the enzyme solutions previously boiled for 10 min. To terminate the reaction, 5 mL of 0.1 M Na_2CO_3 was added and the formed *p*-nitrophenol was determined from the absorbance at 405 nm with a Lambda 3B UV/VIS spectrophotometer (Perkin-Elmer).

All glycosidases activities increased linear for more than 1 h, with respect to substrate. Resulting values were expressed as nanomoles of *p*-nitrophenol formed per second (nkat) per gram of fresh weight.

PME has been extracted by homogenization of 2 g of tissue with 4 mL of 1 M K_2HPO_4 (pH 7.5) for 1 h at 4 °C (23). A total of 0.4 mL of apricot extract was incubated with 0.6 mL of 0.75% (w/v) pectic solution (68% esterified) (Sigma, Co.) in 1 mM phosphate buffer (pH 7.5) for 15 min at 37 °C. Transformation of alcohol in nitrite has been obtained by adding 2.5 mL of 7% (v/v) H_3PO_4 and 2.5 mL of 5% (w/v) KNO_2 and keeping the sealed vials in ice. After 15 min, 0.5 mL of headspace atmosphere was removed and analyzed by GC (Fractovap 4200, Carlo Erba Instruments) adapted with 3-m long metal column of Chromosorb W 80/100 mesh and Ucon (LB 1715) nonpolar phase. Methanol (Carlo Erba Co.) was used as a standard.

Protein Determination. Protein concentration was measured by the Bradford method using a protein-dye reagent (Bio-Rad) and BSA as a standard.

RESULTS

Ethylene Production and Quality Analysis in Air and Propylene-Treated Fruits during Postharvest Ripening.

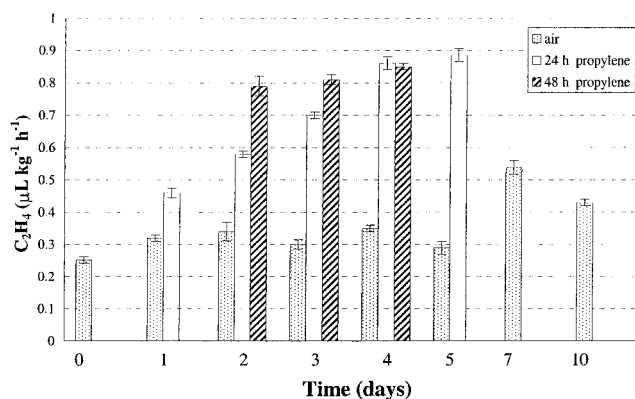
Apricots reached good edible quality after the fifth day following harvest when a large increase of SSC was observed (Figure 1). Increase of sugars was approximately 1% in the first 5 days, then increasing an additional 1% in 2 days, and then remaining stable until the fruits were overripe. Acidity decreased until day 5, then remained stable for the rest of the period (Figure 1). Propylene treatments did not affect SSC and acidity (data not shown). External color was not a good indicator of ripening in this variety, showing no change of color during the period following harvest (data not shown). The ratio malic acid/SSC showed a decrease during the postharvest ripening, with a significant drop between days 3 and 5 (Table 1).

Ethylene production of apricots was very low starting from $0.25 \mu\text{L kg}^{-1} \text{ h}^{-1}$, reaching a peak of $0.54 \mu\text{L kg}^{-1} \text{ h}^{-1}$ on day

Table 1. Penetrometer Values and Malic Acid/SSC Ratios during Postharvest Ripening of Apricots in Air at 20 °C^a

days of storage	penetrometer (N)	malic acid/SSC
0	32.6 ± 5.3	0.118 ± 0.023
1	24.8 ± 7.5	0.109 ± 0.013
3	12.7 ± 3.3	0.102 ± 0.018
5	10.1 ± 2.1	0.082 ± 0.009
7	4.9 ± 3.0	0.079 ± 0.004
10	2.2 ± 0.9	0.069 ± 0.006

^aData are the means of 10 individual fruit samples ± SD.

**Figure 2.** Changes in ethylene production of apricot fruit during postharvest ripening. Data are the means of three replicates each one of 10 fruit. Vertical bars indicate SD.

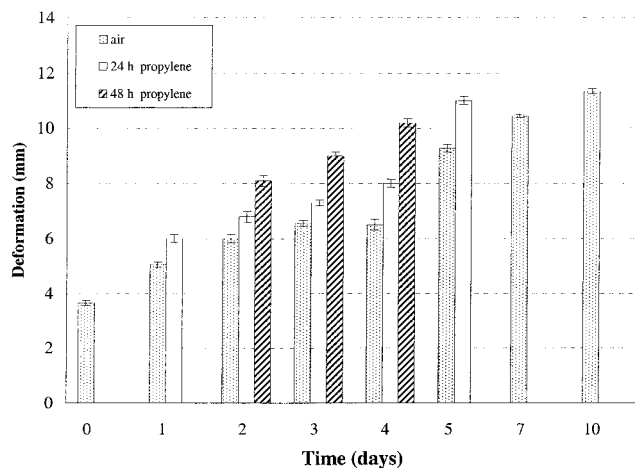
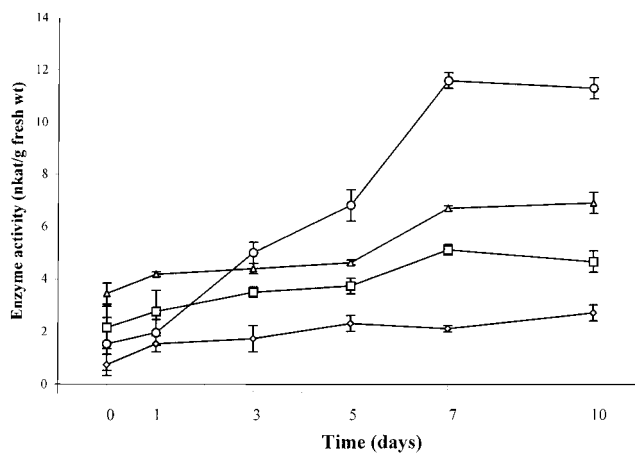
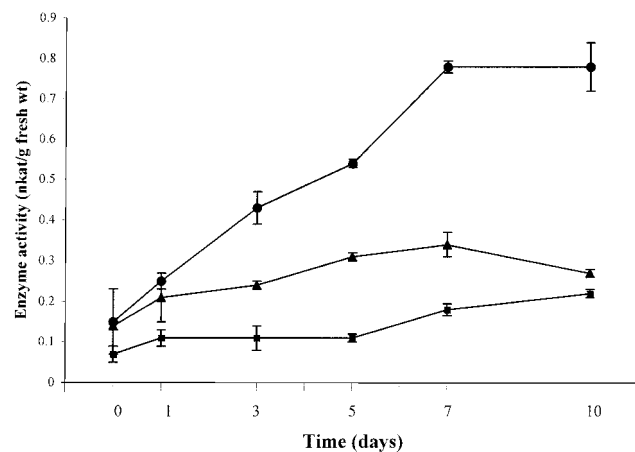
7, and then declining (**Figure 2**). Ethylene biosynthesis was greatly enhanced by propylene treatment. After 24 h of propylene treatment, ethylene production was slightly higher than in air-treated fruits, but in the following 3 days in air, ethylene production was much higher. Forty-eight hours of propylene treatment induced even greater ethylene production, but after 3 days in air the level of production was not changed.

Fruit firmness decreased during the experimental period, especially from day 5 until day 10 (**Table 1**). Minimum tissue resistance for eating quality was defined as 10 N.

Fruit deformation using the Instron measurement increased progressively with time, and on day 5, the fruit became very soft (**Figure 3**). Propylene treatment accelerated fruit softening. With 48 h of propylene treatment, fruit softening increased continuously after the treatment, reaching the same value as air-treated fruits, but approximately 5 days earlier.

Glycosidases Activity in Control and Propylene-Treated Fruits during Postharvest Ripening. α -L-Arabinofuranosidase, α -D-galactosidase, α -D-mannosidase, and β -D-galactosidase were the enzymes with the highest activities, showing 10-fold higher activity than other glycosidases. α -L-Arabinofuranosidase activity rose from from 1.9 (day 0) to 11.6 nkat (day 7), and then remained stable (**Figure 4**). α -D-Galactosidase activity was initially higher than α -L-arabinofuranosidase but increased to a lesser extent during ripening so that at the end of the analysis exhibited nearly 50% less activity. α -D-Mannosidase and β -D-galactosidase activities were also lower. Even though the total activity was lower, β -D-xylosidase increased from 0.15 (day 0) to almost 0.8 nkat on day 7 (**Figure 5**). For all enzymes, optimal pH was between 4 (α -L-arabinofuranosidase) and 5.4 (α -D- and β -D-glucosidases). Enzymes activity was computed even on the basis of protein content by obtaining the same patterns.

Effect of propylene treatments was only on activities of β -D-xylosidase, β -D-galactosidase, α -D-mannosidase, and α -L-ara-

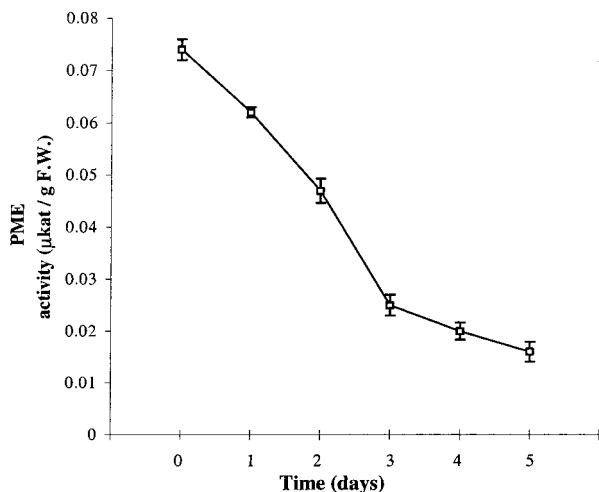
**Figure 3.** Deformation of apricots during postharvest ripening. Data, expressed in terms of deformation under a force of 3 N, are the means of 10 fruits, the same fruits for all the experimental period. Vertical bars indicate SD.**Figure 4.** Changes in glycosidases activities (\circ α -L-arabinofuranosidase; \triangle α -D-galactosidase; \diamond β -D-galactosidase; \square α -D-mannosidase) in apricots during postharvest ripening in air. Data are the means of 5 samples. Vertical bars indicate SD.**Figure 5.** Changes in glycosidases activities (\blacksquare α -D-glucosidase; \blacktriangle β -D-glucosidase; \bullet β -D-xylosidase) in apricot during postharvest ripening in air. Data are the means of 5 samples. Vertical bars indicate SD.

binofuranosidase (**Table 2**). After 24 or 48 h of propylene treatment, α -L-arabinofuranosidase activity increased as compared to the initial value and to a greater extent than in air-treated fruit. After 3 days in air following propylene treatment,

Table 2. Enzyme Activity (nkat/g of fresh weight) of Apricots after Propylene Treatments (500 $\mu\text{L L}^{-1}$) and Increase (%) in Activity over Control Fruit Ripened in Air^a

	1 day propylene	2 days propylene	1 day propylene +3 days in air	2 days propylene +3 days in air
β -D-xylosidase	0.27 \pm 0.05	0.49 \pm 0.05	0.50 \pm 0.02	0.72 \pm 0.01
(% increase)	+8	+44	+16	+33
β -D-galactosidase	1.66 \pm 0.2	2.04 \pm 0.1	2.06 \pm 0.1	3.10 \pm 0.3
(% increase)	+39	+22	+15	+30
α -D-mannosidase	3.20 \pm 0.2	4.05 \pm 0.2	4.15 \pm 0.3	5.20 \pm 0.1
(% increase)	+15	+28	+14	+33
α -L-arabinofuranosidase	3.09 \pm 0.2	5.00 \pm 0.2	5.31 \pm 0.4	9.60 \pm 0.6
(% increase)	+52	+43	+6	+41

^a Initial value: β -D-xylosidase 0.2 \pm 0.05; β -D-galactosidase 1.06 \pm 0.16; α -D-mannosidase 2.05 \pm 0.4; and α -L-arabinofuranosidase 1.7 \pm 0.2. Data are the means of five samples \pm SD.

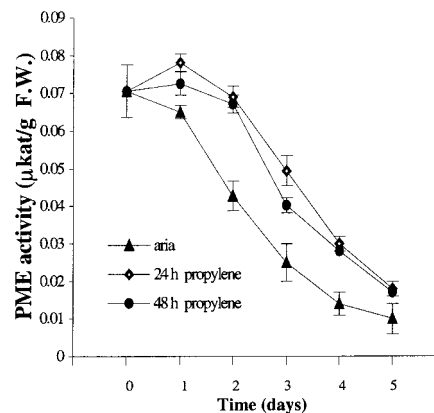
**Figure 6.** Changes in PME activity in apricots during postharvest ripening in air. Data are the means of 5 samples. Vertical bars indicate SD.

the activity continued to rise but the percentage of increase over the air-treated fruit decreased, especially for 24 h treated samples, indicating a continuous increase in activity in air-treated fruit. α -D-Mannosidase activity rose in propylene- and air-treated samples without a difference after 24 h of propylene treatment (15% increase) and slightly significant after 48 h (28%); after 3 days in air the activity was still increasing but with the same percentage increase over the control in air. β -D-Galactosidase increased in propylene-treated fruit both after 24 and 48 h, and the increase percentage over the air-treated fruit was higher after 24 h than after 48 h as observed for α -L-arabinofuranosidase. After 3 days in air, activity of 24 h-treated fruit remained constant and the percentage increase over the air-treated fruit decreased, while in the 48 h-treated fruits the activity and the increase percentage still rose. After 48 h of treatment, β -D-xylosidase activity, even though at a much lower level than the other glycosidases, increased. In the 3 days following propylene treatment, the activity of both propylene-treated samples increased, but the difference over the air-treated fruits was only higher for the 48 h-treated fruits.

PME Activity in Control and Propylene-Treated Fruits during Postharvest Ripening. PME activity greatly decreased during the ripening out of tree with an opposite trend as compared to α -D-mannosidase and β -D-xylosidase (Figure 6). Propylene accelerated the activity of PME, but the declining pattern was similar to the untreated fruit; no effect was observed between 24 and 48 h of treatment (Figure 7).

DISCUSSION

SSC and titratable acidity measurements of apricots correspond to total sugar content and free organic acids (22). Kader

**Figure 7.** Changes in PME activity in apricots during propylene treatment (24 and 48 h) and maintenance at 20 °C. Data are the means of 5 samples. Vertical bars indicate SD.

(24) has reported that an acceptable quality of apricots is reached with a minimum SSC of 10% and an acidity of 0.8%. *Boccuccia spinosa* apricots harvested at the beginning of the ripening process, with firm flesh, exhibited greater than 12% SSC but were not edible due to high acidity, after a subjective taste evaluation carried out in the laboratory. As reported by Audergon et al. (22) acidity of apricots greatly modifies consumer's reaction. We have defined a ripening index comprised of the ratio between acidity and SSC. For *B. spinosa* apricots, a ratio between 0.09 and 0.075 indicates the best eating quality (Table 1).

Fruit firmness decreased during 10 days of postharvest ripening in air even though ethylene increase was not so marked. The softening was paralleled by large increases in the activity of α -L-arabinofuranosidase and, at much lower rate, of β -D-xylosidase, as well as a rapid decrease of PME. Polygalacturonase (PG) and endoglucanase (Cx) was also tested, but no activity was found.

The increase in activities of α -L-arabinofuranosidase and β -D-xylosidase was expected since Gross and Sams (25) reported that arabinose, an important sugar component of pectin polysaccharides, increased during apricot ripening as pectins degraded, and xylose was the predominant neutral monosaccharide lost from cell walls. The high initial activity and the consequent dramatic decrease of PME indicated the initial involvement of the deesterification on the cell wall degradation (5). Even in other fruits such as peach, banana, and melon, the activity of PME was decreasing during the ripening (8, 26, 27).

Significant increase of activity was also observed for α -D-galactosidase, α -D-mannosidase, and β -D-glucosidase. β -D-Galactosidase activity did not increase to as great an extent as

the other enzymes during the ripening, and its activity was lower than α -D-galactosidase, similar to observations in tomato (28).

When propylene was applied for even 1 day, β -D-galactosidase and α -L-arabinofuranosidase activities increased with the greater fruit softening and ethylene production. β -D-Xylosidase and α -D-mannosidase activities also increased in response to propylene treatment, especially after a 48 h treatment. Activities of all these glycosidases continued to rise during the 3 days in air following propylene treatment, in parallel with accelerated softening of the fruit.

This activation of β -D-galactosidase in response to propylene treatment suggests a differential sensitivity to ethylene concentration as compared to α -L-arabinofuranosidase. Galactose together with arabinose is a major sugar component of pectin polysaccharides, existing primarily as the side chains on the rhamnogalacturonane backbone (29). Release of galactose and arabinose appears to be a ubiquitous feature of ethylene-regulated fruit softening. Exogenous ethylene applied to transgenic ethylene-suppressed tomato fruit (antisense ACC synthase) reduced flesh firmness and increased total α -D-galactosidase and β -D-galactosidase activities (30). Similarly, in transgenic ethylene-suppressed melons (antisense ACO), exogenous ethylene treatment increased the activity of exo and endo-polygalacturonase, β -D-galactosidase, and α -L-arabinofuranosidase (8). In olives, cell wall enzymes including glycosidases were induced by exogenous ethylene at the black stage (31).

Finally, propylene increased the activity of PME; 24 h treatment was effective as well as the 48 h treatment. Differently from glycosidases, the activity remained high during the treatment, but, after the removal to air, the decline was at the same rate as untreated apricots, although significantly higher.

This result suggests that ethylene affects PME of apricots, but the activity of the enzyme is already high in untreated fruits, when ethylene production is very low at the beginning of ripening; likely the sensitivity of this enzyme to ethylene is very high confirming that observed by Botondi et al. (8) on ethylene-inhibited melon.

CONCLUSION

Ripening of apricots is significantly characterized by the loss of firmness. Softening of apricots starts when ethylene production is undetectable, revealing that the sensitivity of the tissue to the hormone is very high (32). Glycosidase activities increased in concert with the increase of ethylene production and softening during postharvest ripening, while PME declined. Exogenous propylene treatment stimulates both ethylene production and fruit softening in parallel with the stimulation of β -D-galactosidase, α -L-arabinofuranosidase, β -D-xylosidase, α -D-mannosidase, and PME activity.

In conclusion, PME and glycosidases play an important role in apricots softening via ethylene tissue sensitivity, but it is clear that the cell wall degradation system is more complex, involving a pool of enzymes as well as expansin (4).

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