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Endogenous Plant Growth Substances in Developing Fruit of *Prunus cerasus* L. II. Levels of Extractable *para* Coumaric Acid in the Pericarp[1]

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Abstract. An inhibitor of wheat coleoptile elongation and cress seed germination was isolated from the pericarp of sour cherry (*Prunus cerasus* L.) fruit and identified as *para* coumaric acid (PCA). PCA was present in the free acid and bound forms. The concentration of PCA remained relatively constant (10 to 16 μg g dry weight^{-1}) during fruit development. The bound form, with one exception, was present at the highest concentration during Stage II. On a per fruit basis, the free and bound PCA increased progressively with fruit development. PCA was an effective activator of IAA-oxidase also isolated from the cherry fruit pericarp. The possible role of PCA in fruit growth is discussed.

Phenolic substances are second only to the carbohydrates in abundance in plants (22). Many are important intermediates in secondary metabolism, and in particular, in the biosynthesis of lignin (2, 22). Some naturally occurring phenols are important inhibitors of seed germination (15, 31) and plant growth (1, 3, 12). Phenols are also implicated (21, 23, 29, 33) in regulation of growth processes as enzyme cofactors or inhibitors in the oxidation of indole-3-acetic acid (IAA).

Data on the occurrence and role of biologically active phenolic compounds in fruit tissue are limited. Ryugo (24, 25) has shown the presence of vanillin and structurally related aldehydes in the endocarp of several *Prunus* species. These compounds were intermediates in lignification of the endocarp. To what extent phenolic compounds may constitute important regulators of fruit growth is not known.

In our studies of endogenous growth substances in the sour cherry we isolated an inhibitor of seed germination and wheat coleoptile extension, and identified it as *para* coumaric acid (4-hydroxy cinnamic acid). Further, we report on levels of the free and bound acid in relation to fruit development and suggest that it can serve as a cofactor for an enzyme isolated from the pericarp capable of oxidizing IAA.

Materials and Methods

Plant material. Sour cherry (*Prunus cerasus* L. cv. Montmorency) fruits were collected from 7-year-old trees at 7-day intervals from 1 week after anthesis to maturity. The fruits were immediately frozen with dry ice and lyophilized. After constructing a fruit growth curve (based on dry wt),

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samples collected on 21 and 28, 35 and 42, and 56 and 70 days after anthesis were selected as representing Stages I, II, and III, respectively, of fruit growth (16). The seed was removed from the fruit and the pericarp was ground to pass through a 20 mesh screen and stored at -25°C.

Extraction and fractionation. Thirty g of ground pericarp were extracted with 200 ml of 80% methyl alcohol on a rotary shaker at 21°C for 8 hr. The methanol was decanted and the residue was re-extracted 2 times. The extracts were combined and the methanol was evaporated under vacuum at 40°C. The remaining water phase was centrifuged at 10,000 rpm for 30 min to remove suspended materials. The supernatant was recovered, adjusted to pH 9.0 with 4% sodium bicarbonate and extracted with diethyl ether (1:1 v/v) until the ether phase was clear. The ether extracts were then combined and washed with 4% sodium bicarbonate. Any water present was frozen at -25°C, the ice pellet removed, and the ether evaporated to dryness yielding the basic-ether fraction (F-1).

The sodium bicarbonate fraction was then adjusted to pH 2.5 with 5% sulfuric acid and extracted several times with diethyl ether. The ether extract was washed with 1% sulfuric acid, the water was frozen out, and the ether evaporated under vacuum to dryness yielding the acidic-ether fraction (F-2).

The remaining aqueous phase was hydrolyzed by adjusting the pH to 11 with 5% sodium hydroxide and incubating at 60°C for 60 min. The hydrolysate was cooled and extracted with ether yielding the basic-ether fraction (F-3). The aqueous phase was then adjusted to pH 2.5 with 5% sulfuric acid and extracted with ether yielding the acidic-ether fraction (F-4).

Thin-layer chromatography (TLC). Each of the above fractions was further purified using 20 x 20 cm glass plates precoated with Silica Gel G or GF_{254} (250 μm thick). The ether residue, dissolved in 0.25 ml of methanol, was streaked on the plate and developed as follows: (a) acidic-ether fractions (F-2, F-4) with hexane:ethyl acetate:formic acid (80:20:1 v/v) and (b) basic-ether fractions (F-1, F-3) with hexane (saturated with water):ethyl acetate (80:20 v/v). Each plate was subdivided into 11 equal horizontal zones (1 representing the starting line only), and the silica gel was scraped from the plate and eluted with 5 ml of 1% formic acid in methanol. The eluate was evaporated to dryness under vacuum until traces of formic acid were removed, and the residue redissolved in 5 ml of methanol. Aliquots were evaporated to dryness, dissolved in water or buffer, according to need, and bioassayed.

Bioassay. The wheat coleoptile straight growth assay as described by Nitsch and Nitsch (19), and cress seed germination bioassay according to Taylor (28) were employed.

(a) *Wheat coleoptile.* Wheat coleoptiles, 4.5 mm initial length, were incubated with appropriate aliquots of each fraction in 0.5 ml of phosphate-citrate buffer at pH 5.0 for 24 hr at 25°C. Tubes were rotated at 1 rpm. At least 3 replicates of 8 coleoptiles each were used for each treatment. Net elongation (final length-initial length) was determined and data were expressed as percent of control.

(b) *Cress seed germination.* Twenty-five cress seeds were placed on Whatman No. 1 filter paper in Petri dishes in the presence of water (control) or in solutions of the appropriate fractions at 24 to 26°C. Three replications were used. The number of seeds germinated was determined after 40 hr. The data were expressed in percent of control.

Combined gas chromatography-mass spectrometry. The mass spectrum of the unknown was obtained using the LKB 9000 GC/MS. The underivatized unknown was introduced via the direct inlet system to the ion source. The methyl ester was introduced after fractionation on an SE-30 column isothermal at 160° with a helium flow rate of 35 ml min^{-1}. Instrument conditions were: electron energy 70 eV, ion source temperature 290°C and molecular separator temperature 235°C.

Quantitative determination. Methanolic eluates from zones showing inhibition of wheat coleoptile extension and cress seed germination were further purified by TLC using benzene:ethyl acetate:formic acid (70:30:1 v/v) as the developing solvent. The inhibitory zone (cress seed assay), was removed and eluted as described above. The eluates were evaporated to dryness and the residue dissolved in ethanol. Aliquots were diluted with ethanol as needed and acidified with 0.1 N sulfuric acid, and UV absorption curves were determined with a recording spectrophotometer (Cary 15). Maximum absorption occurred at 312 nm and the concentration was calculated based on absorbance at this wavelength.

IAA-oxidase activity. (a) Extraction and purification of enzyme. A 5 g sample of ground pericarp from each harvest date was combined into a composite 30 g sample. The pericarp was homogenized with cold (-20°C) acetone in a -25°C ethanol bath. The acetone was filtered under vacuum and the residue homogenized repeatedly until the acetone was free of color. The remaining acetone powder was dried under vacuum and used for enzyme extraction.

The acetone powder was extracted with 0.1 M phosphate buffer, pH 6.0, in the ratio of 1 g of powder to 4 ml of buffer. Tween 80 (polyoxyethylene sorbitan monooleate) was added (0. 1 ml) to minimize formation of protein-tannin complexes. The mixture was stirred for 1 hr in an ice bath and then centrifuged at 2000 rpm for 45 min. The precipitate was discarded and the supernatant mixed in an ice bath for 60 min with insoluble polyvinylpyrrolidone (PVP) in the ratio of 1 g of powder to 0.4 g of PVP. The suspension was then centrifuged at 20,000 rpm and the supernatant was dialyzed overnight against demineralized water. The dialyzed protein solution was then used for determination of IAA-oxidase activity.

(b) *Enzyme activity.* Preliminary experiments established that optimum activity was obtained at pH 4.0 with phosphate (0.06M) - citrate (0.05M) buffer and that Mn^{2+} had no effect. IAA-oxidase activity was determined colorimetrically by measuring the unreacted IAA at 530 nm by means of a modified Salkowski reagent (20).

The reaction mixture consisted of 1 ml of enzyme solution, 250 μg of IAA and 1 ml of cofactor solution, (2,4-dichlorophenol or PCA) at the desired concn, and phosphate-citrate buffer (pH 4.0), in a total volume of 10 ml. The reaction mixture was incubated for 30 min at 30°C, after which 1 ml aliquots were transferred to colorimeter tubes containing 4.0 ml of Salkowski reagent. The tubes were held in the dark for 20 min and absorbance (A_{530}) read on a colorimeter (Bausch and Lomb, Spectronic 20).

The reaction mixture for the control contained the same components, except no IAA was added, and was incubated as described above. After the incubation period 0.9 ml of this mixture was transferred to the Salkowski reagent and then 0.1 ml (25 μg) of IAA solution was added and absorbance determined as above. IAA (25 μg) was also added to appropriate blanks (reaction mixture minus enzyme) and corrections for IAA content in the reaction mixture were made if necessary (8).

Enzyme activity in the absence and presence of added cofactors (2,4-dichlorophenol and PCA) was determined as described above. Reagent controls (reaction mixture minus enzyme and IAA) were used for each concn of cofactor tested.

Results

The basic-ether extracts before (F-1) or after (F-3) hydrolysis did not inhibit wheat coleoptile elongation or cress seed germination. By contrast, 2 zones of inhibition of wheat coleoptile elongation (Fig. 1A) were found after TLC of the acidic-ether extracts (F-2 and F-4). One zone of inhibition occurred at Rf 0.0 to 0.2, which corresponded to synthetic RS-abscisic acid (ABA), and the other at Rf 0.5 to 0.9 (Fig. 1A).

When the active components of these 2 zones were eluted

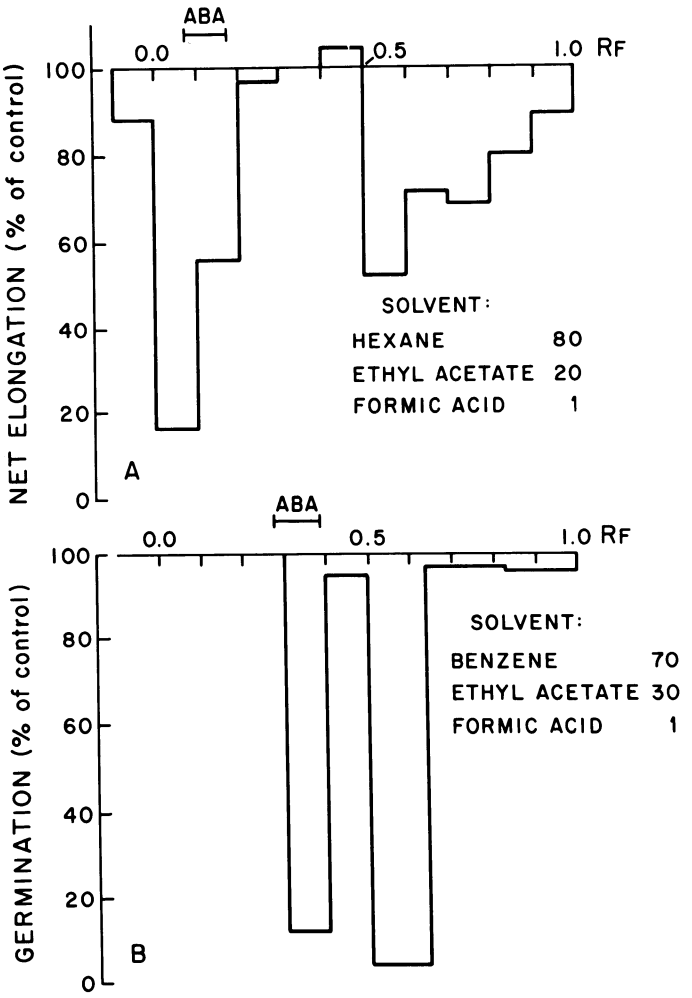

Fig. 1. Histograms depicting the presence of inhibitory substances in the acidic-ether fraction after hydrolysis of a methanol extract of cherry pericarp tissue (42 days after anthesis). A. Growth response of wheat coleoptiles; TLC with hexane:ethyl acetate:formic acid (80:20:1 v/v). B. Germination of cress seed. Inhibitory zones Rf 0.0-0.2 and 0.5-0.8 eluted from A and rechromatographed with benzene:ethyl acetate:formic acid (70:30:1 v/v).

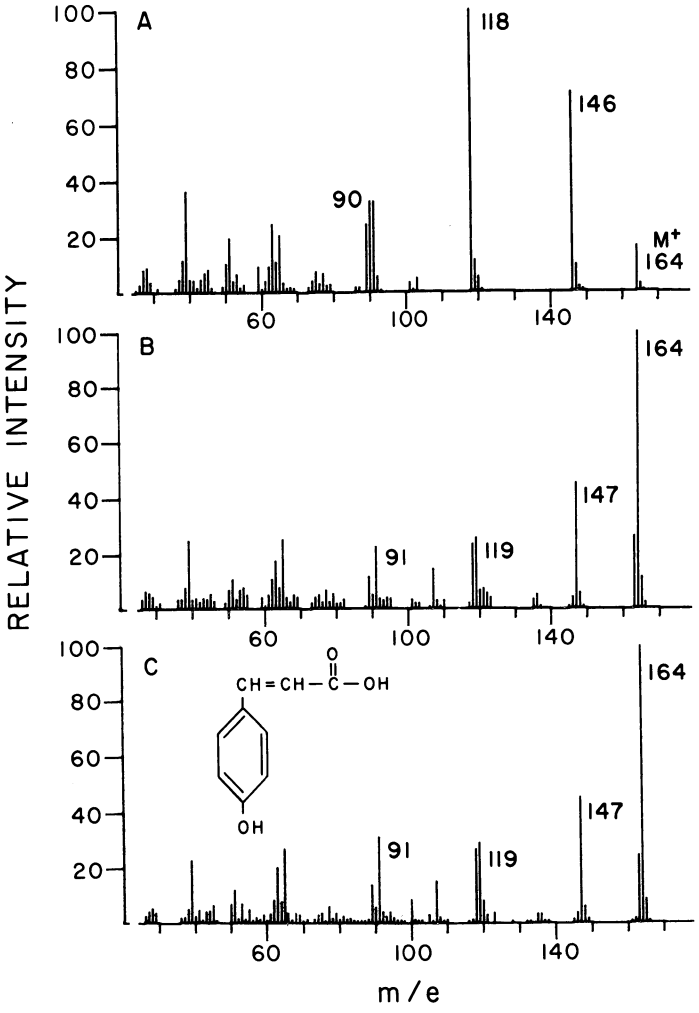

Fig. 2. Mass spectra of *ortho* coumaric acid (A), *para* coumaric acid (B) and the inhibitor (C) isolated from the cherry pericarp.

from duplicate chromatograms, combined and rechromatographed in a different solvent, 2 zones were detected which inhibited cress seed germination (Fig. 1B). The inhibitory component present at Rf 0.3 to 0.4 was investigated separately and will be the subject of another paper. The subsequent data and discussion will deal only with the nature of the inhibitory component at Rf 0.5 to 0.64 (Fig. 1B).

The unknown present at Rf 0.5 to 0.64, after further purification by TLC, was successfully crystallized from ethyl acetate on addition of petroleum ether and cooling. These crystals resulted in marked inhibition of wheat coleoptile elongation and cress seed germination.

Identification. The mass spectrum of the underivatized unknown (Fig. 2C) was indistinguishable from that of the *para* coumaric acid (Fig. 2B) obtained under the same conditions. The spectra of the unknown and the *para* isomer differ from the spectrum of the *ortho* isomer (Fig. 2A) mainly in: (a) the intensities of the molecular ion at m/e 164; (b) the molecular ion of the *ortho* isomer loses a molecule of water to yield an ion at m/e 146, while the molecular ions of the *para* isomer and the unknown each lose a hydroxyl radical to yield ions at m/e 147; (c) the m/e 146 ion of the *ortho* isomer further loses a molecule of carbon monoxide to form an ion at m/e 118, while the same fragmentation of the m/e 147 ions of the *para* isomer and the unknown yield ions at m/e 119; (d) finally, the m/e 118 ion of the *ortho* isomer loses an additional carbon monoxide molecule to yield an ion at m/e 90, while the m/e 119 ions of the *para* isomer and the unknown rearrange to form typical tropylium ions at m/e 91. Further, identical mass spectra were recorded for the methyl esters of the *para* isomer and the unknown. These data provide conclusive evidence that the unknown is *para* coumaric acid (PCA).

Changes in levels of free and bound PCA during fruit development. PCA was present as the free acid and in a bound form in the pericarp (Table 1). The levels of the free acid were low, ranging from 10 to 16 μg g dry wt^{-1}. Levels of PCA present in a bound form in the ethanol extract and released on base hydrolysis were 8 to 48 times greater.

The concn of PCA, as a free acid, was relatively constant during development of the fruit (Table 1). However, on a per fruit basis the amount doubled between 21 to 28 days after anthesis (Stage I), remained constant during Stage II and increased approximately 4-fold during Stage III. The bound fraction was lowest during Stage I and then increased progressively with continued fruit development (Table 1). With the exception of 21 days after anthesis, the ratio of the bound to free PCA was highest during Stage II (Table 1).

Comparative biological activity of PCA and ABA. PCA was less inhibitory to wheat coleoptile extension and cress seed germination than ABA (Fig. 3). PCA at 10^{-4}M resulted in 15 to 20% inhibition, whereas, ABA almost completely inhibited both seed germination and coleoptile extension at this concn. Cress seed was less sensitive to ABA than wheat coleoptiles; however,

Table 1. Changes in levels of free and bound *para* coumaric acid in the pericarp of sour cherry fruit during development.

Days after anthesis[z]	Free		Bound		Ratio
	μg g dry wt^{-1}	μg fruit^{-1}	μg g dry wt^{-1}	μg fruit^{-1}	Bound:free
21	15.4	0.9	434.0	25.2	28.2
28	12.9	1.8	104.9	14.5	8.1
35	11.7	2.2	299.6	56.0	25.6
42	10.3	2.1	492.4	101.9	47.8
56	15.9	8.3	219.3	114.2	13.8
70	12.3	8.0	189.0	123.5	15.4

[z]Days 21 and 28 represent Stage I, 35 and 42 Stage II, and 56 and 70 Stage III of fruit growth.

they were equally sensitive to PCA. We found the cress seed assay useful for determining the presence of inhibitory compounds, including ABA, during fractionation and purification.

Presence of IAA-oxidase activity in the pericarp and effectiveness of PCA as a cofactor. IAA-oxidase activity was present in the pericarp. 2,4-Dichlorophenol (DCP), commonly used as a cofactor for IAA-oxidase from other tissues, stimulated enzyme activity at 10^{-3}M (Fig. 4). PCA was more effective than DCP as a cofactor for the sour cherry enzyme (Fig. 4). PCA at 10^{-4}M equaled the activity of DCP at 10^{-3}M. The IAA-oxidase activity was approximately 45% greater with 10^{-3}M PCA than with 10^{-3}M DCP (Fig. 4).

Discussion

The physiological role of phenolic acids and bound phenolic compounds in fruit growth is not clear (22). They are wide-spread in higher plants and appear to be active intermediates in secondary metabolism (2, 17). PCA may be enzymatically formed from the corresponding amino acid, tyrosine (18), and enzymes are present which readily convert PCA to hydroxybenzoic acid (4, 22) and to caffeic acid (26), and to other known plant growth inhibitors (1, 14, 21).

Two physiological roles can be envisaged for PCA in the cherry. First, PCA may serve as an intermediate in lignin synthesis during development of the endocarp. PCA is known to be incorporated into lignins of higher plants (2, 6, 17). Specifically, vanillin and other related aldehydes, for which PCA may serve as an intermediate, have been isolated from the endocarp of 7 *Prunus* species by Ryugo (25). There does not appear to be a relationship between the concn of free PCA found in this study and hardening of the endocarp; however, the concn of bound PCA was highest, with one exception, during lignification of the endocarp (Table 1). Unfortunately we did not analyze the endocarp separately and thus, in this respect, our data are not conclusive. It is interesting to note that the alcohol-soluble esters of PCA show marked incorporation into lignins of wheat (5). A similar lack of correlation between PCA concn and lignin formation was observed for wheat (6).

Secondly, PCA may also play a role in cherry fruit development by action on growth of the pericarp. PCA, or compounds readily derived from PCA, e.g., hydroxybenzoic acid or caffeic acid, may act directly *in vivo* as an inhibitor of pericarp growth. Experimental evidence for such a role is lacking.

There are considerable data from higher plants indicating that PCA may function in regulating growth through the oxidation of IAA. PCA in the acid or ester form serves as a coenzyme for pineapple IAA-oxidase (9). Numerous other studies (1, 7, 10, 11, 23, 27, 32) indicate that PCA functions as a cofactor for enzymatic degradation of IAA *in vitro*. More importantly, evidence is now available that PCA can enhance

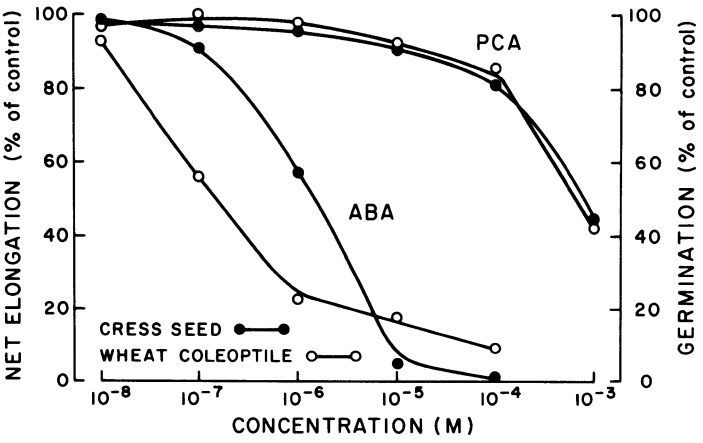

Fig. 3. Comparative biological activity of abscisic acid (ABA) and *para* coumaric acid (PCA) in cress seed germination and wheat coleoptile elongation bioassays.

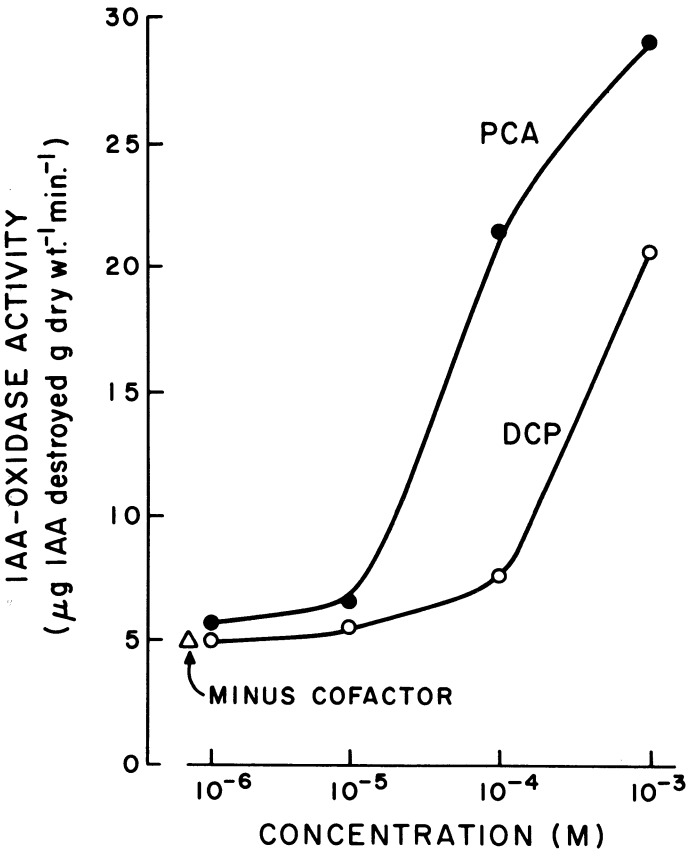

Fig. 4. Activity of IAA-oxidase isolated from cherry pericarp in the absence (minus cofactor) and presence of various concentrations of *para* coumaric acid (PCA) or 2,4-dichlorophenol (DCP).

IAA-oxidase activity *in vivo* and thus promote the destruction of endogenous IAA (13, 33). The involvement of PCA in regulating growth is further supported by data showing that growth responses can be altered with PCA (1, 29, 30), and that endogenous IAA levels can be depressed by treatment of tissue with PCA (13) or *para* hydroxybenzoic acid (21), which can be formed in plants from PCA.

It is important to recognize that in the pericarp of the sour cherry we have 3 components of a potential growth regulating system. Hopping[4] recently established the presence of IAA in cherry pericarp, and we have demonstrated in this study the presence of (a) IAA-oxidase activity, and (b) a substance capable of inhibiting growth and activating IAA-oxidase. Thus, 3 components of a potential growth regulating system coexist. The degree of interaction among these components in the cherry fruit remains to be documented; however, their coexistence in the same tissues becomes an important consideration.

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