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Effects of Fruit Detachment on Ethylene Biosynthesis and Loss of Flesh Firmness, Skin Color, and Starch in Ripening 'Golden Delicious' Apples

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Abstract. **Prior to 25 Oct., about 4–6 weeks (1983) or 3–5 weeks (1984) after the normal commercial harvest period, 1-aminocyclopropane-1-carboxylic acid (ACC), ethylene-forming enzyme (EFE), and internal ethylene concentration (IEC) in 'Golden Delicious' (*Malus domestica* Borkh.) apples attached to the tree were low. Thereafter, they began to increase rapidly. The increase in both ACC and IEC was earlier in detached preclimacteric fruit than in fruit attached to the tree. The increase of EFE coincided with that of IEC in detached fruit kept at 20°C. Attached fruit subsequently attained a higher level of ACC but a lower level of IEC as compared to the detached fruit. The results suggest that inhibitor(s) supplied from the tree not only delayed the accumulation of ACC in the fruit but also greatly inhibited its subsequent conversion to ethylene. Once the ripening process is initiated, the development of EFE precedes the development of ACC synthesis in both attached and detached fruit. Since attached fruit showed a steady loss of flesh firmness, green skin color, and starch, these changes did not appear to be related directly to the levels of ACC and internal ethylene. Detached fruit stored at 0° accumulated ACC and increased IEC slightly earlier than those stored at 20°. The magnitudes of these increases during subsequent storage at 0° were, however, smaller than those at 20°.**

Many fruit undergo climacteric changes soon after harvest, whereas they might not ripen for weeks if left on the tree (4, 5, 12, 15). Several reports have provided physiological evidence for the existence of such "tree factor(s)" that suppresses ripening, but none has been identified chemically (3, 7, 15, 17).

Ethylene is synthesized in apple tissue by the following pathway: methionine → S-adenosylmethionine → 1-aminocyclopropane-1-carboxylic acid (ACC) → ethylene (2). Biogenesis of ethylene in both fruit and vegetative tissues was influenced by various developmental and external factors, including ripening, senescence, growth regulators, mineral ions, anaerobiosis, and stresses from cold, heat, wounding, drought, and flooding (19). The ethylene production rates in ripening fruit are controlled by the tissue's capability to synthesize ACC (ACC synthase) and to convert ACC to ethylene (EFE) (8, 19). In this study we investigated the effect of fruit attachment and detachment on the accumulation of ACC and production of ethylene in relation to fruit softening, color change, and starch hydrolysis in 'Golden Delicious' apples during subsequent storage at 20° or 0°C.

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Materials and Methods

Fruit. Samples of 'Golden Delicious' apple fruit on M 26 rootstock (5 replicates of single fruit per treatment per examination date) were harvested at a preclimacteric stage on 6 Sept. (1983), or 31 Aug. and 10 Sept. (1984), from the mid-third of 3 (1983) and 6 (1984) trees in an orchard near Summerland, B.C., in a spiral fashion (picking at the outside perimeter and then spirally inward to the center of the tree). Upon harvest, the samples were kept continuously at 0°C (1983) or at 20° (1983 and 1984). The remaining apples attached to the trees were left unpicked at ambient temperatures.

Determinations of IEC, EFE, ACC, firmness, starch, and skin color. Samples of attached and detached fruit were assessed at 2- to 14-day intervals for flesh firmness and internal ethylene concentration according to methods described previously (11). Skin color was measured with a 'Golden Delicious Color Meter' [Model GD, Techwest Enterprises Ltd., Vancouver, B.C. (high values indicate little green color)]. ACC was extracted from 2 opposite sectors (50 g) of cortical tissue from each apple with 150 ml of 2% HCl in 1983 or from 3 plugs (4 g; described below) with 12 ml of 95% ethanol. ACC content in the extract was assayed according to the method of Lizada and Yang (14). The 3 plugs (1 cm in diameter × 12 cm in length) were obtained longitudinally and around the apple through the mid-third of each fruit, half-way between the outer cortex and core. Two additional plugs were obtained from the opposite side of the same apple for EFE determination. The 2 plugs were placed in a test tube, soaked for 1 hr in 4 ml of 1 mM ACC in 2% KCl, blotted dry, and then placed under partial vacuum (5.7 kPa) to remove any trapped ethylene before sealing in a 25-ml test tube with a serum cap. The amount of ethylene produced during the next 60-min incubation at 20°C was regarded as the activity of EFE, expressed as nanoliters of C_2H_4 produced per gram per hour. The extent of starch hydrolysis in the cortical tissue (starch index) was determined by dipping the cut surface of the top third of each fruit in an I_2-KI solution and comparing with a 'Golden Delicious' starch chart (16); high values indicate low starch (0 = whole fruit, including core area, filled solidly with starch; 9 = cortex devoid of starch).

Results and Discussion

Detached fruit stored at 20° or 0°C. In both 1983 and 1984, apples harvested at a preclimacteric stage (6 Sept. 1983 and 31 Aug. 1984) and stored at 20° increased rapidly in IEC and ACC content after about one and 3 weeks of storage, respectively. They also showed a rapid loss of starch and a steady loss of green skin color, but only a small decrease in flesh firmness (Figs. 1 and 2) during the early stage of storage. The rise in IEC corresponded precisely to the rise in EFE (Fig. 2). Fruit picked 10 days later (10 Sept. 1984) showed a pattern of ACC accumulation, EFE activity, and ethylene production similar to those picked on 31 Aug. 1984, except with a much (2 to 3 times) shorter lag period (data not shown).

Accumulation of ACC in fruit stored at 0°C was initiated about one week earlier than in fruit stored at 20°, although the

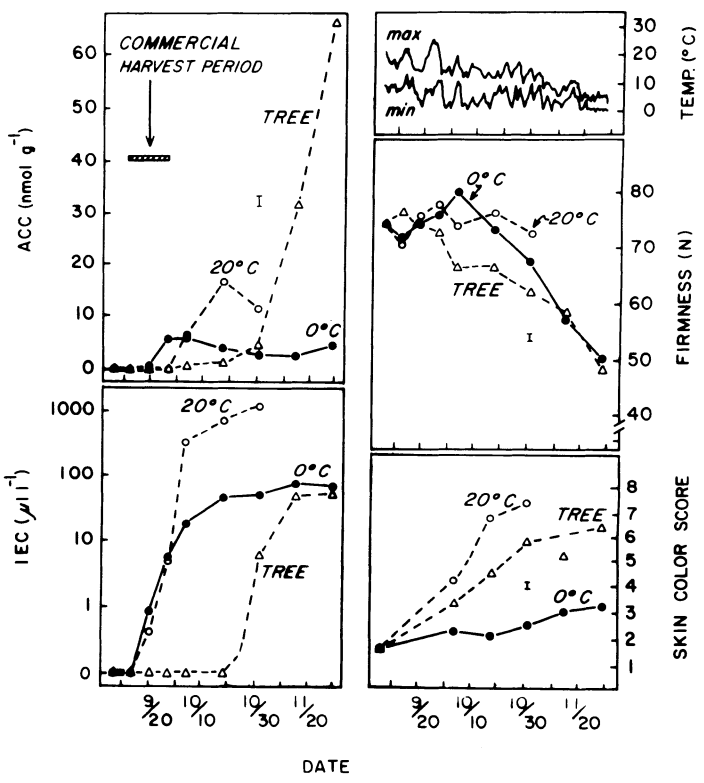

Fig. 1. Changes of 1-aminocyclopropane-1-carboxylic acid (ACC), internal ethylene concentration (IEC), flesh firmness, and skin color in 'Golden Delicious' apple fruit attached to the tree at ambient orchard temperatures or detached from the tree and kept at 20°C or 0° (1983). Vertical bars represent the pooled (13 Sept.–1 Nov.) SE; SE_{IEC} = 37.

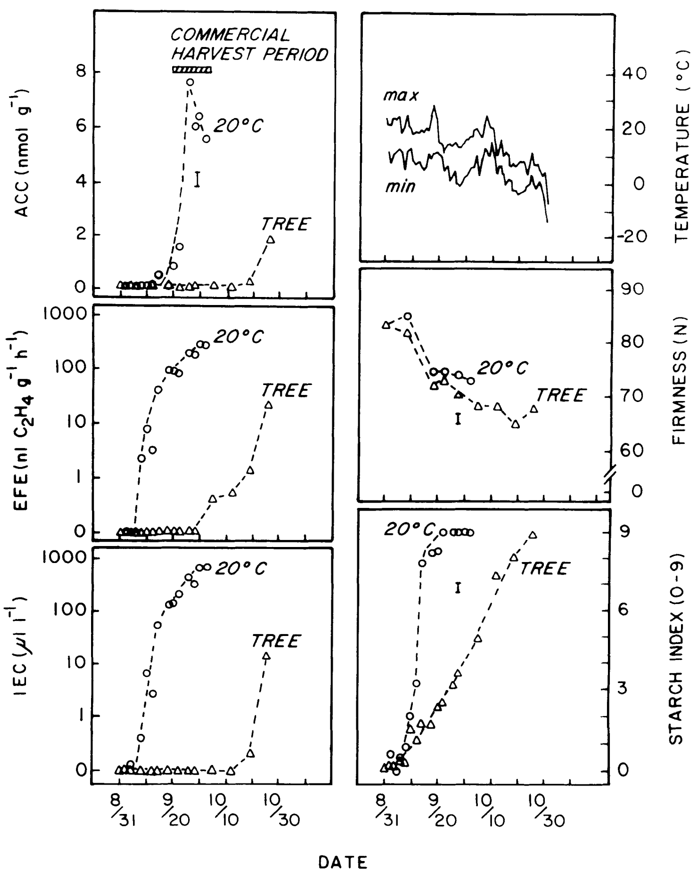

Fig. 2. Changes of 1-aminocyclopropane-1-carboxylic acid (ACC), ethylene-forming enzyme (EFE), internal ethylene concentration (IEC), flesh firmness, and starch in attached (at ambient temperatures) and detached (at 20°C) 'Golden Delicious' apple fruit (1984). Vertical bars represent the pooled (2–28 Sept.) SE; SE_{EFE} = 33 and SE_{IEC} = 53.

magnitude of its subsequent accumulation and the rate of ethylene production were reduced (Fig. 1). These results indicate that storage at 0°C enhances the onset of ACC and ethylene synthesis. However, the disappearance of green skin color was slower at 0° than at 20°. Flesh firmness was not affected by storage temperature during a 56-day storage period (Fig. 1). Using a flow-through system and slightly delayed picking of 'Golden Delicious' fruit, Knee et al. (10) reported that the onset of rapid ethylene production began earlier and more uniformly at 3° than at 18°–20°. Acceleration of the onset of ethylene production by low temperature appeared to be cultivar-dependent, because they did not observe this phenomenon in 'Cox's Orange Pippin' apples (10).

Attached fruit at ambient orchard temperatures. The IEC of fruit attached to the tree at ambient orchard temperatures was low initially (<0.1 μl·liter^{-1} before 11 Oct. in both 1983 and 1984) and finally reached a high level [>1 μl·liter^{-1} on 1 Nov. 1983, about 5–7 weeks after normal commercial harvest and 45 μl·liter^{-1} on 15 Nov. 1983 (Fig. 1), and 13 μl·liter^{-1} on 26 Oct. 1984, about 3–5 weeks after normal commercial harvest (Fig. 2)]. In 1983, ACC accumulated rapidly after 18 Oct. and reached a high level (66 nmol·g^{-1}) on 29 Nov. (Fig. 1). In 1984, ACC also began to increase after 19 Oct. and reached a level of 2 nmol·g^{-1} on 26 Oct. (Fig. 2). Further measurements were not made because the remaining fruit were frozen solidly on the trees as the ambient orchard temperatures dropped to −14°C on 30 Oct.

The pattern of ethylene production in attached 'Golden Delicious' apples as related to harvest dates (Figs. 1 and 2) was different from other apple cultivars such as 'King', 'McIntosh', 'Spartan', and 'Delicious', in which initiation of commercial fruit harvesting coincides with or shortly precedes the onset of IEC increase (ref. 6; O.L. Lau, unpublished data). 'Golden Delicious' apples are harvested considerably before the onset of IEC increase. Thus, unlike other cultivars, IEC in attached fruits of 'Golden Delicious' does not serve as a useful maturity indicator, particularly for those destined for long-term storage. On the other hand, definite changes in starch index were observed in attached fruit well before the onset of ethylene production, and also occurred slightly prior to the dates for commercial harvest (Fig. 2). This result suggests that the use of starch index, when used along with other measurements such as firmness, soluble solids, and titratable acidity, might be a more practical means than IEC for determining the harvest dates for this cultivar. There was, however, a very good correlation between IEC and the rates of ethylene production by apple cortical tissues [$r = 0.963$, $P < 0.001$, n = 245; the ratio of IEC (μl·liter^{-1}) to the rate of ethylene production (nl·g^{-1}·hr^{-1}) is 3.27 to 1], indicating that IEC is indicative of the ethylene production rate in apple.

Attached fruit appeared to soften faster than detached fruit stored either at 20° or 0°C, and they lost the green skin color faster than detached fruit stored at 0°, but slower than those at 20° (Fig. 1). These data indicate that softening and the change in skin color do not correlate with IEC when fruit, under different conditions, are compared.

The results of Figs. 1 and 2 indicate that the delay in the onset of ACC accumulation and of IEC increase in attached fruit cannot be attributed to a difference in temperature. Such an inhibition of ethylene synthesis in attached fruit has been recognized in many fruit, including apples (17). It generally is assumed that trees produce an inhibitor or inhibitors that are translocated to the attached fruit. This tree factor inhibited not only the accumulation of ACC but also the development of EFE. However, other ripening processes such as flesh softening, color change, and starch hydrolysis in 'Golden Delicious' apples did not appear to be suppressed effectively by the inhibitor(s). It has been suggested that the "tree factor" entering the fruit from the tree via the phloem either inhibits ethylene production or reduces fruit tissue sensitivity to ethylene (3, 4, 7, 15, 17). When the fruit are detached from the tree, the inhibitor presumably disappears gradually, and eventually, the ripening process ensues (4).

Although preclimacteric fruit convert methionine to S-adenosylmethionine (1, 2), they convert little S-adenosylmethione to ACC and ACC to ethylene (19). Thus, the onset of the ripening process, which is accompanied by a massive increase in ethylene production (17, 18), requires both the rapid synthesis of ACC and the rapid conversion of ACC to ethylene (Figs. 1 and 2).

In both detached and attached fruit the rise in ACC level followed the rise in IEC (Figs. 1 and 2). Knee (9) also observed that the rise of ethylene production preceded the rise in ACC level in ripening apple fruit. These observations are consistent with the view that the development of EFE precedes the development of ACC synthase during the ripening process. Such a view is confirmed fully by the results of Fig. 2. In detached fruit kept at 20°C, the rise in EFE preceded the rise in ACC, although the former coincided with the rise in IEC. Recently Liu et al. (13) have treated mature but preclimacteric muskmelon and tomato fruit with exogenous ethylene for short periods (16 hr), and examined the synthesis of ACC and the capability to convert ACC to ethylene (EFE) in these fruit tissues. With such a short treatment, ethylene did not cause an increase in ACC synthesis but markedly increased conversion of ACC to ethylene (EFE) in the tissue.

In attached fruit the onset of massive increase in ACC and EFE were both delayed, but, as in detached fruit, the rise in EFE preceded the rise in ACC (Fig. 2). Thus, the "tree factor" delayed the onset of not only ACC synthesis but also ACC-to-ethylene conversion. However, it should be noted that the rapid accumulation of ACC in attached apples after 1 Nov. 1983 (Fig. 1) or 19 Oct. 1984 (Fig. 2) was accompanied by a smaller increase in IEC (Figs. 1 and 2) or EFE (Fig. 2) as compared to detached fruit. These results indicate that the conversion of ACC to ethylene (EFE) was more sensitive to inhibition by the "tree factor" than the conversion of S-adenosylmethionine to ACC (ACC synthase).

Our data support the contention that there is a "tree factor" that delays the onset of ethylene production. This factor was exerted not only by the inhibition of ACC synthesis but also by the suppression of the conversion of ACC to ethylene. Once the ripening process is initiated, the development of EFE precedes the development of ACC synthesis.

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Carbohydrate Composition and Sensory Quality of Fresh and Stored Sweet Corn

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Abstract. **Sweet corn (*Zea mays* L.) was evaluated for sensory quality and carbohydrate composition at harvest and after storage at 0° or 10°C for 2 weeks. Total sugar (reducing sugar plus sucrose) declined more quickly during storage at 10° than at 0° in all cultivars, but the relative changes in sucrose and reducing sugars during storage were often complex. Hedonic (like/dislike) and sweetness scores awarded by taste panelists were significantly correlated with each other and with reducing sugar, sucrose, and total sugar concentrations only after storage. The highest correlations were between sucrose concentration and hedonic taste scores ($r = 0.76$, $P < 0.01$) and between sucrose concentration and sensory sweetness scores ($r = 0.73$, $P < 0.01$). Starch concentration varied with cultivar, but was not correlated with sensory quality. Water-soluble polysaccharide concentration varied with cultivar, storage time, and storage temperature, but did not correlate with sensory quality.**

Consumer quality of fresh sweet corn is affected greatly by the sugar and soluble carbohydrate content of the kernels. Sugar depletion after harvest may be reduced by prompt cooling, storage at low temperatures, and by the use of cultivars with genetic modifications of carbohydrate metabolism. Standard sweet corn is homozygous for the recessive allele *sugary (su),* which results in greatly increased levels of water-soluble polysaccharides (primarily phytoglycogen) and twice the sugar content of field corn (11). Other mutants affecting carbohydrate metabolism include *shrunken-2 (sh2), amylose extender (ae), dull (du), waxy (wx),* and *sugary enhancer (se)*; these mutants have been incorporated into commercial cultivars in various ways. 'Extra Sweet' and 'Super Sweet' cultivars are homozygous for the recessive allele *sh2*. Recently, sweet corn hybrids that are homozygous *su* but heterozygous *sh2* (the ear segregates for *sh2*) have been produced to combine the quality of *sugary* and the increased sweetness produced by *shrunken-2*. Similarly, 'sugary extender', 'sugary enhanced', or EH ('Everlasting Heritage', trademark of Musser Seed Co.) use the modifier gene *se* (either homozygous or heterozygous) to enhance *sugary* cultivars. Finally, the 3 genes *ae, du,* and *wx* have been combined (2).

Since the introduction of new cultivars with genetic modifications of carbohydrate metabolism, little work has been done on the relation between carbohydrate composition of the endosperm and sensory quality. The supposition that high sugar content improves consumer satisfaction has proven true in studies by Wann et al. (11) on fresh, stored, and canned *ae du wx* corn, and by Showalter and Miller (9) on *sh2* corn compared with standard corn at retail outlets. Garwood et al. (4) found that *ae du wx* and *sh2* corn lost sugar during storage, but the initial sugar content was so high that even after 4 days at 27°C the level was equal to freshly harvested *su*.

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