THE ROLE OF HORMONES IN FRUIT SET AND DEVELOPMENT

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This subject has been reviewed periodically by Nitsch (60) in 1953, Luckwill (53) in 1959, Leopold (47) in 1962, and lastly by Crane (19) in 1964. It has been pointed out repeatedly that the seeds in fruits are rich sources particularly of auxins, but also of gibberellins and cytokinins as well. Various types of evidence would indicate that these hormones emanating from the seeds stimulate growth of the fruit tissues surrounding them and also control fruit abscission. For example, in many fruits marked correlations exist between seed number and ultimate fruit size and also between seed distribution and fruit shape. Fruits that absciss prematurely are usually multi-seeded ones with a lower seed content than normal, or are single or multi-seeded fruits in which the seeds abort.

In a comprehensive review of the literature Crane (19) pointed out that in general no relationship has been proven between the changing levels of any of the endogenous hormones in seeds and fruit growth. Similarly, evidence was presented which indicated that the hormones shown to be present in seeds do not necessarily have a direct effect on abscission of the fruit. In view of the varied chemical and physical properties of the different hormones, together with the results of radioactive tracer studies of the movement and distribution of organic materials in plants, Crane proposed that the developing seeds with their attendant high levels of hormones act as mobilization centers of nutrients required for their growth and that of the surrounding fruit tissues. Thus, the relatively high concentrations of these substances in the seeds attract metabolites to the fruit and enable it to compete with other growing organs of the plant.

pertinent literature that has appeared principally during the past 5 years with regard to growth substances in relation to fruit set and development and to the concept of mobilization mentioned above.

INDUCTION OF PARTHENOCARPY AND INCREASED FRUIT SET

Work has continued towards the induction of parthenocarpy in several fruit species or in attempts to increase the percentages of fruit set under conditions unfavorable for pollination. Crane (20), using 4-amino-3, 5, 6-trichloropicolinic acid, described by Kefford and Caso (39) as a strong auxin with unique chemical structure, produced parthenocarpic 'Calimyrna' figs that were remarkably similar to those resulting from cross-pollination. Parthenocarpic fruits of the same cultivar, identical morphologically to those previously induced by auxin or gibberellin, were also induced by the application of a cytokinin (21). Thus, it was demonstrated indirectly that each of the 3 types of endogenous growth promoting hormones, should they be required for fruit growth, can be supplied by some part of the plant other than the seeds.

The grape is the only other fruit that has been produced parthenocarpically by application of a cytokinin (84), although fruit set of open-pollinated muskmelons is enhanced by cytokinin treatment (38). Grape clusters of certain cultivars dipped in a cytokinin solution at time of bloom produced berries that were larger than untreated ones (85). An interesting side light in this connection was the finding by Negi and Olmo (59) that a cytokinin applied to flower clusters of a male grapevine 3 weeks before anthesis completely converted the flower sex from male to hermaphroditic. It was difficult for Coombe (13) to rationalize the significant increase in set of berries of 3 grape cultivars following treatment 2 to 3 weeks before anthesis with the growth retardant chemicals (2-chloroethyl) trimethylammonium chloride (CCC) or tributyl-2, 4-dichlorobenzylphosphonium chloride (Phosfon-D). However, Skene (73) has shown recently that sap from CCC-treated grape plants contained 20 times the kinetin equivalent that was detected in sap from untreated plants. N-dimethylaminosuccinamic acid (Alar) (80) and other materials such as N-1-naphthyl phthalamic acid (57) and 4-phthalimido-2, 6-dimethylpyrimidine (68) and abscisic acid (37) have increased fruit set in grapes, tomatoes, and *Rosa*. The effects of these chemicals on changes in plant composition and their possible relationship to fruit set and development remain to be demonstrated.

The blueberry was added in 1965 to the list of fruits that may be produced parthenocarpically (5). Gibberellic acid (GA3) proved to be far more effective for this purpose than several auxins tested. Dipping Delaware[1] grape clusters at pre-bloom and again at post-bloom in a solution of GA3 was found under Washington conditions to produce

from 88 to 96% seedless berries that matured 28 or more days early with lower sugar-acid ratios than controls (11). The cranberry (25) and a particular pear (56) cultivar were also found to respond to GA3 application by increased fruit set and yield. In the case of 5 apple cultivars, however, Dennis and Edgerton (23) found set of open-pollinated flowers was not significantly affected by GA3 application, although the higher concentrations tended to reduce set and inhibit flower bud formation. The application of potassium gibberellate delayed maturity and increased total weight of pecan nuts, but inhibited catkin formation (74). Thompson (78), in Scotland, has continued his provocative work with the strawberry and produced parthenocarpic fruits similar in size to pollinated ones when a combination of GA3 and an auxin were used. While auxin alone was effective in this respect, the inclusion of GA3 shortened the period of fruit development.

ENDOGENOUS HORMONES IN FRUITS

Auxins, Gibberellins, and Cytokinins:

Before the relationship between hormones and fruit set and development can be clearly defined, it is necessary to isolate, chemically identify, and establish their patterns in fruits. Known and unknown auxins have been isolated from apple fruits and seeds (19) and Dennis and Nitsch (22) isolated GA4 and GA 7 from immature 'Golden Delicious' seeds. These 2 gibberellins were found subsequently by Bukovac and Nakagawa (6) to be the most effective of several tested for the promotion of parthenocarpic development of 'Wealthy' apple fruits. In view of the fact that an extract of young 'Wealthy' apple seeds was very effective for inducing parthenocarpy when applied in lanolin to unpollinated 'Wealthy' flowers, Dennis (24) concluded that gibberellins synthesized in the seeds are responsible for fruit set. However, Hayashi, *et al.* (31) demonstrated the presence of GA3 in "...parthenocarpic..." apple fruit tissue which suggested that tissues of the fruit other than those in seeds may participate in the biosynthesis of gibberellin.

Fruit set in the parthenocarpic navel orange was found by Lewis *et al.* (50) to be correlated with a high level of citrus auxin, a compound distinct from indoleacetic acid (41). The period of maximum fruit drop coincided with a change in pattern of accumulation of this auxin and the initial detection of an inhibitor. They cautioned, however, that before these correlations may be meaningful, the picture as regards gibberellins (40) and cytokinins (44) must be developed and integrated.

While Steward and Simmonds (75) demonstrated the presence of a cytokinin-like material in young banana fruits as early as 1954, it was not until 1966 that indoleacetic acid (42) and gibberellin-like (43) substances were also detected.

The pattern of auxin in the developing blueberry fruit, determined by Collins *et al.* (12), was found to be similar to that of several other fruits (19). They found no correlation between growth of the fruit and concentration of auxin in the fruit tissues.

A comparison of the levels of gibberellin-like substances during development of seeded and seedless (a mutant of the seeded type) 'Tokay' grape berries revealed similar patterns (33). Peak levels of activity were detected at time of fruit set, followed by a more rapid decline in seedless than in seeded berries. This was thought to be the result of embryo abortion in the former. Second, but much lower, peaks in activity occurred in June and August in seedless and seeded berries, respectively. Fluctuations in activity generally did not correlate with berry growth.

A very detailed and significant study was made by Powell and Pratt (67) of the "total" growth-promoting substances in developing ovules and fruits of early-, midseason-, and late-maturing peaches. While cytokinins (46, 66) and gibberellins (61) have been isolated from ovules and young fruits of this species, the ability of the bioassay used by Powell and Pratt to detect gibberellins was unknown. Furthermore, it was not one that is recognized as being suitable for measuring cytokinin activity. Consequently, the "total" growth substances measured presumably were primarily of auxin type. No more than trace amounts of growth substances were detected in the fleshy pericarp at various stages of development, including periods when maximum levels were present in the ovules. Failure to detect greater amounts was acknowledged as possibly being due to interference in the bioassay by inhibitors. The seeds of each cultivar exhibited similar peaks in growth substance content that accompanied

either nucellus or endosperm development; second and major peaks accompanied rapid embryo growth and maximum endosperm development. The mid season- and late-maturing cultivars produced third and minor peaks after completion of embryo growth. Mature fruit abscission in the early and midseason cultivars began when the growth substances in the seeds dropped to low levels, but it did not occur in the late-season cultivar until nearly 3 weeks after disappearance of growth substances in the seeds. Powell and Pratt (67) concluded that no clear relationship was apparent between growth substances in the seeds in either the growth of the pericarp or abscission of the fruit.
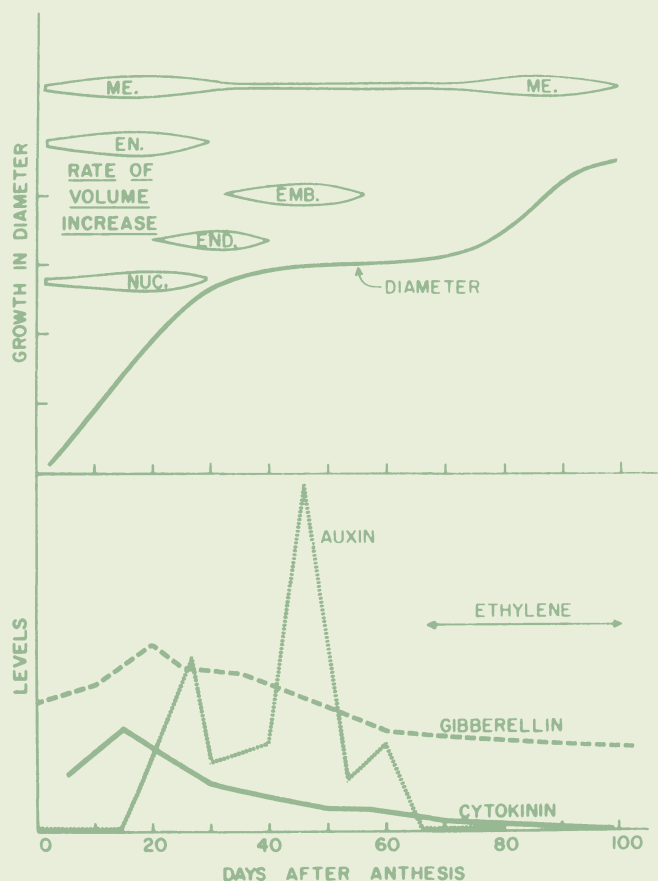

Fig. 1. Fruit growth as related to rate of volume increase of its component parts and to levels of hormones, based on data contained in (34), (49), (55), and (67). The levels of hormones bear no relationship to one another but only to time after anthesis. ME., mesocarp; EN., endocarp; NUC., nucellus; END., endosperm; EMB., embryo.

Levels of gibberellin-like activity in seeds and pericarp of apricot (34) and peach (36) have been determined; the activity in the latter fruit was found to be due to the presence of more than one compound (35). In both kinds of fruit, gibberellin-like activity at times was higher in the pericarp than in the seed, which suggested that the former may be self-sufficient for this hormone. Since the levels of gibberellin-like activity were more closely correlated with growth of the tissues from which the materials were extracted than they were with growth of the fruit as a whole, Jackson (36) concluded that gibberellins in a given tissue are intimately associated with cell expansion in that tissue. The very high levels of gibberellin-like activity found in apricot fruits (34) may be related to the negligible growth response of fruits of this species to exogenous gibberellin application (Crane, unpublished), whereas marked growth stimulation results from exogenous auxin application (17).

Abscisic Acid:

Although we have been cognizant for many years of a number of growth-inhibiting substances in fruits and seeds (19), progress in their isolation and chemical identification has been relatively slow. However, Ohkuma *et al.* (62) reported in 1963 the isolation and some of the chemical and physiological properties of a compound they obtained from young cotton fruits and named "abscisin II". Its chemical structure was revealed in 1965 (63). A parallel investigation by Eagles and Wareing (26) showed the presence of an inhibitory substance in the leaves and buds of *Acer* and *Betula* which they termed "dormin". Cornforth *et al* (14), in 1965, reported dormin to be chemically identical with abscisin II, and subsequently described its synthesis (15). To avoid further confusion from the use of the 2 names, abscisin II and dormin, the term abscisic acid was proposed in 1968 (3).

The experiments of Addicott *et al.* (2) and others (27, 28, 37) have shown that application of exogenous absisic acid promotes abscission of young fruits, causes the cessation of extension growth and onset of dormancy in buds, promotes parthenocarpy, accelerates senescence, and inhibits or promotes flower induction in different species. While it cannot be concluded that these responses are controlled by endogenous abscisic acid, it is probable that in some of them at least abscisic acid is functioning as a hormone. Little is known with regard to its role, if any, in fruit set and development. It is interesting to note, however, that Thompson (77) in 1961 suggested that growth of strawberry fruit tissues ceases at anthesis because of an inhibitory factor produced by the carpels and which is overcome by pollination and fertilization. Abscisic acid has been found since to be a component of strawberry leaves and fruits (29, 69). It has been isolated from apple leaves and fruit juice (65), and its disappearance in peach seeds during stratification has been correlated with ability of the seeds to germinate (51). Abscisic acid has been shown to inhibit auxin-mediated *Avena* coleoptile growth (2), to inhibit gibberellin-controlled responses (76), and to interact with cytokinins (4, 82).

Ethylene:

The advent of gas chromatography has enabled the detection of quantities of ethylene in fruits previously thought to contain none or insignificant amounts. In fact, the data tabulated by Burg and Burg (8) show that ethylene concentrations (0.04 to 0.2 ppm), nearly stimulatory of the climacteric, are present in various fruits throughout their development. Convincing evidence that this gas is a fruit ripening hormone may be found in the reviews of Burg (7) and Burg and Burg (8).

Auxins stimulate markedly the production of ethylene by roots, stems, leaves, and fruits (1, 10). The application of 2, 4, 5-trichlorophenoxyacetic acid was found several years ago to hasten growth and maturation of fig fruits as much as 60 days (16). Stimulated by the fact that auxin application promoted ethylene formation and subsequent flowering in pineapple plants (9), Maxie and Crane (54) found production of ethylene by leaves and fruits of the fig tree to be increased greatly following their treatment with 2, 4, 5-trichlorophenoxyacetic acid. Thus, what was thought originally to be an auxin response now appeared to be attributable to the action of ethylene. This was confirmed recently by Maxie and Crane (55) who found that immature fig fruits, attached to the tree and subjected to an atmosphere containing 5 ppm of ethylene, grew rapidly and matured in 6 to 10 days, depending upon stage of fruit development at the time of treatment. Because of this response and the determinations by Hirai (32) of endogenous ethylene in fig fruits, it was proposed that ethylene initiates growth period III (final swell to maturity) in fig fruits and perhaps in others that exhibit the double-sigmoid type of growth curve as well.

MOBILIZATION

From the evidence that was available at the time Crane (19) completed his review in 1964, it was folly to ascribe specific roles played by auxins, gibberellins, and cytokinins individually or in concert in fruit set and development. While considerable progress has been made in the past 5 years, the roles of the endogenous hormones in this connection have become even more nebulous, particularly in view of the implication that abscisic acid and ethylene are also intimately involved. The interactions and interrelationships among the growth-promoting substances are obscure to say the least, not to mention the involvement of growth-inhibiting substances (64, 81). Consequently, the action of these substances in fruit set and development may be interpreted only in general terms at the present time.

Although we seem to be further away from pinpointing the coordinated action of hormones in fruit set and development,

evidence increasingly indicates the significance of mobilization in these respects. Dominance of reproductive over vegetative organs as illustrated by patterns of assimilate distribution and changes in them following leaf or fruit removal is documented in the review of Wardlaw (83). It is well-established that reproductive organs, acting as mobilization centers, divert the flow of nutrients from vegetative organs to the extent that growth of the latter may be greatly depressed (45). Much evidence (19, 48, 72) has accumulated that mobilization of metabolites and other materials into developing fruits is mediated by their hormone-directed transport from other organs, strong synergistic interaction among the hormones in this respect having been demonstrated (71). It is significant that such processes as abscission (70), senescence (48, 58), and polar transport (86) have also been related to the phenomenon of mobilization of plant constituents.

It has been established clearly that developing seeds contain large quantities of the known as well as unknown hormones, the evidence indicating that they are the richest source of these materials and thereby enable the fruit to compete dominately with vegetative structures. As shown in Fig. l, peak levels of the various hormones are not attained simultaneously but are correlated with development of structures in the ovules and occur one after another during the major portion of the fruit-growth period. Thus, high levels of hormone activity are present for the fruit to compete successfully with other developing organs of the tree. In cases of natural parthenocarpy, the development of specialized structures within the ovules has been correlated with high auxin levels (18, 52). When cytokinins gibberellins, and auxins decline to low levels, the work of Maxie and Crane (55), who showed that ethylene also has a strong mobilizing capacity, at least in fig fruits, suggests that it may bring about continued flow of nutrients into the fruit during the final stage of growth to maturity. Growth of the fruit during this period is by cell enlargement exclusively and it has been demonstrated that ethylene promotes expansion of cells (10, 30). Thus, the results of Tukey (79), where growth and early maturity occurred in peach and cherry fruits in which the ovules were destroyed upon completion of embryo development, may be explained by the production and action of ethylene.

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HORMONAL CONTROL OF FRUIT RIPENING

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Ripening is the process by which physiologically mature fruits are transformed from a relatively unfavorable to a favorable condition with respect to texture, color, flavor, and aroma. In many fruits ripening occurs while the fruit is still attached to the parent plant, while in others such as the avocado, ripening takes place only following harvest. The complex physical and chemical changes of ripening have been studied extensively and techniques of handling and storage have evolved which can be satisfactorily applied to control the rate of ripening in the post-harvest period. While ripening normally occurs in fruit after growth ceases, it is a natural consequence of developmental changes during growth. This is evident from the fact that the time period from bloom to physiological maturity can be manipulated. A fruit is physiologically mature when the stage is set for ripening to ensue. The stage is set by the genetic makeup of the cultivar and the actors are the environmental conditions and chemical stimuli interacting during growth and development. Naturally occurring plant growth substances, their chemical analogs and antidotes, most certainly play a role in growth and development, and therefore must in some way influence the development of ripening capacity. However, the mechanism of their action has not been resolved, but this does not curtail speculation based on numerous observations which have been made. My purpose will be to briefly review the effects of certain plant growth substances on fruit ripening and suggest a possible role they may play in the process.

Auxins

It is well established that auxins stimulate growth and hasten maturation of several fruits. Maxie and Crane (22) provided evidence that 2, 4, 5-trichlorophenoxyacetic acid (an auxin analog) hastened maturity of fig fruit indirectly through stimulation of ethylene synthesis. Previous studies by these and other investigators working on auxin stimulated ripening of a wide range of fruits can now be interpreted in a similar way. Studies currently underway confirm that this auxin response works through ethylene. The stage of fruit development at the time of auxin application apparently has a pronounced effect upon the response. For example, treatment of apricots with 2, 4, 5-T at the initiation of pit hardening controlled fruit drop, increased fruit size and hastened maturity while applications made several weeks after pit hardening had begun were much less effective (Crane 11). Auxin stimulated synthesis of ethylene by tomato fruits is also dependent upon the stage of maturity at the time of treatment. Abeles and Rubenstein (2) found that immature tomato fruits produced more ethylene after auxin treatment, but that fruits at the pink stage did not. They further mentioned (no data given) that ethylene evolution of mature apple and pear fruits was inhibited by auxin treatment.

An interesting aspect of the study by Maxie and Crane was that normal ripening was achieved in figs which were not fully grown indicating that a rapid transition (nearly two months) from an immature to a mature condition was brought about through the action of ethylene. Analogous to this is the ripening of banana and other fruits at an "immature" stage following treatment with ethylene or other unsaturated hydrocarbons or substances that either stimulate ethylene synthesis or breakdown to ethylene, such as Ethrel (2-chloroethane phosphonic acid).

The effects of exogenously applied auxin or auxin analogs on