GIBBERELLIN AND THE GROWTH OF PEACH AND APRICOT FRUITS

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Summary

Levels of gibberellin in purified extracts from developing peach fruits were compared with rates of cell division and cell expansion in the fruit tissues. No gibberellin was found in the ovary before full bloom. Immediately after full bloom gibberellin activity was found in the seed, and later in the mesocarp and endocarp as well. Gibberellin concentration was closely correlated with the rate of cell expansion in each tissue, but not with cell division. Until the final growth phase, when activity was found only in the mesocarp, the highest gibberellin level was always found in the seed.

Application of gibberellic acid at the beginning of pit-hardening to individual apricot or peach fruits increased growth rate. It is suggested that presence of gibberellin increases the ability of a tissue to compete for metabolites.

I. Introduction

Although the presence and effects of hormones on fruits have often been reported, the role of these compounds in fruit growth is not fully understood. Indirect evidence suggests that the seed controls fruit growth via its production of hormones. Unfertilized seedless fruits will normally drop but the application of hormones will sometimes counter this. Also, fruit size is often related to seed number and seeds are rich sources of hormones (Crane 1964). Hormone concentration in the seed, however, seldom correlates with fruit growth (Leopold 1962; Powell and Pratt 1966) and the seed can be destroyed or removed after a certain stage of development without seriously affecting fruit growth (Tukey 1936; Abbott 1959).

Removal of developing leaves which may compete for reserve metabolites can enable limited parthenocarpic development of apples (Abbott 1965) and promote fruiting in grape cuttings (Mullins 1966). Crane and Van Overbeek (1965) suggest that hormone-rich seeds actively attract metabolites to the fruits. In this way developing fruits may compete successfully for nutrients.

In addition to the induction of parthenocarpic development, other effects of hormones on fruits are known. Thus the auxin 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) will increase growth of apricots when applied at the beginning of pit-hardening (Crane 1953) and both 2,4,5-T and gibberellic acid (GA₃) can increase growth rate of peaches when applied at a similar stage, though the effect of the latter is short-lived (Carlone 1962). On the other hand, GA₃ applied to apricots just before full bloom will depress growth by reducing cell division (Jackson and Coombe 1967).

An attempt has been made in the present study to elucidate further the role of gibberellin in fruit growth of peach and apricot. Two approaches have been made: first, to determine the effect of exogenous GA₃ on fruit growth; and second, in peaches only, to relate gibberellin levels to cell division and expansion in each tissue.

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II. MATERIALS AND METHODS

Treatment and Measurement of Fruits on Trees

Mature peach (cv. Golden Queen) and two-year-old apricot (cv. Moorpark) trees growing in Auckland were used. Hormone solutions were applied to selected fruits by spraying. Surrounding leaves and other fruits were carefully shielded. Flowers were emasculated and pollination prevented by cutting away, before the flowers opened, the distal end containing stigma and anthers. "Mean fruit diameter" in apricots refers to the mean of the suture and cheek diameter of each fruit. Apricots were measured with vernier calipers, and peaches with a circummeter (Batjer *et al.* 1957).

Extraction and Bioassay of Gibberellin-like Compounds

Fruits were collected from mature peach trees in the 1965–66 season, quick-frozen, and stored at $-17°C$ before being lyophilized. Extracts were prepared and subjected to thin-layer electrophoresis by methods already described (Jackson 1967), except that six extracts were separately spotted on each plate. After electrophoresis (20 min, 870 V, pH 5·7), the regions $0·5-2·5$ cm and $2·5-4·5$ cm from the origin in the anode direction were taken for bioassay. Most activity in extracts was found in the second band, but occasionally some activity was also recovered in the first. Authentic GA_3 marker moved about 3 cm towards the anode under these conditions. Monocarboxylic gibberellins and compounds with similar electrophoretic properties account for most of the activity in peach tissue (Jackson 1967).

The barley-endosperm (Coombe, Cohen, and Paleg 1967) and the d-5 dwarf-maize (Phinney and West 1961) bioassays were used to test for gibberellin activity. Treatment of the thin layer before barley-endosperm bioassays has already been described (Jackson 1967). For the dwarf-maize bioassay the water extract so prepared was lyophilized, then taken up in a smaller quantity of water containing $0·1\%$ Tween 20. Each plant was treated with $0·1$ ml of this extract. Eluates from thin-layer electrophoresis were replicated three times in each bioassay and, in addition, another replicate was subjected to the barley-endosperm procedure without the addition of endosperm halves. Lack of activity in the latter indicated that reducing compounds had been excluded by this method of electrophoresis. These compounds interfere in this bioassay and, in peach mesocarp, can show a response equivalent to 10^4 pg GA_3/10 mg tissue. They move $0-0·5$ cm towards the cathode.

Equivalents of GA_3 were estimated from dosage-response curves and total gibberellin activity is the sum of activity from the two bands obtained by thin-layer electrophoresis and already described. In the barley-endosperm test any response falling below 100 pg on the standard curve was recorded as zero.

Cell Size and Cell Number

Cell size and number were determined on fruits harvested together with those which were used for extraction and bioassay of gibberellin-like compounds. Fruits were stored in standard formalin-aceto-alcohol fixative. Cell number was estimated by the method of Jackson and Coombe (1967) and radial cell diameter by direct measurement of cells in the middle of each tissue. Three average-sized fruits were measured at each date. Wax embedding was used for fruits younger than 9 days after full bloom, and a freezing microtome for older fruits.

III. RESULTS

(a) *Response of Apricots to Chemicals and other Treatments*

Each of the following treatments was applied to three apricot trees:

(1) Control, trees left untreated.

(2) All developing leaves and shoots removed every 3 days until 14 days after full bloom (full bloom occurred on September 21, 1966).

(3) Flowers emasculated.

(4) Flowers emasculated; developing leaves and shoots removed until 14 days after full bloom.

Diameters of all fruits on a tree were measured at intervals after full bloom and mean diameter per treatment was calculated. Growth rate in fruits from emasculated flowers [treatment (3)] was equivalent to that of control for about 6 days after full bloom, but soon after this emasculated fruits dropped. Leaf removal caused fruits from emasculated and non-emasculated flowers [treatments (2) and (4)] to grow more
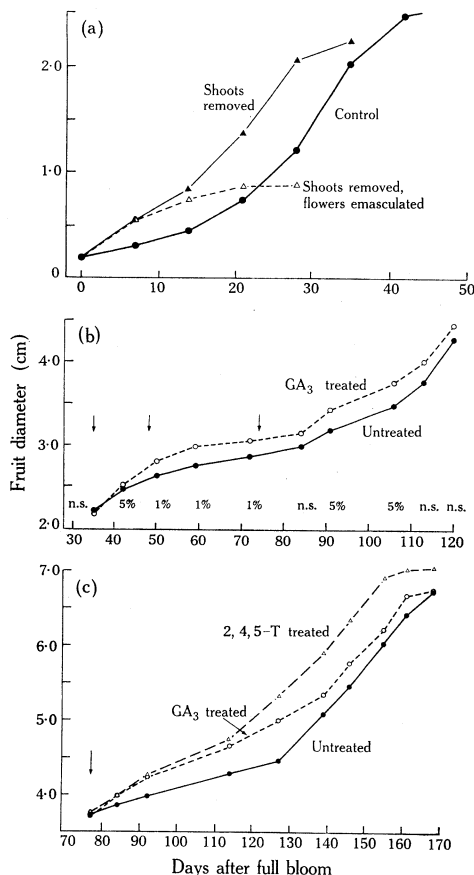

Fig. 1.—(a) Effect upon apricot fruit growth of emasculating flowers and removing, for 14 days after full bloom, developing shoots. (b) Effect of GA₃ (500 p.p.m.) on the growth of apricots. Times of application indicated by arrows. Significance of difference between values for treated and untreated fruits are indicated. (c) Effect of 500 p.p.m. GA₃ and 100 p.p.m. 2,4,5-T on growth of peach fruits. Time of application indicated by vertical arrow. Differences between control and 2,4,5-T treatments between 92 and 155 days after full bloom (inclusive) and also between control and GA₃ treatments between 92 and 127 days after full bloom (inclusive) are significant at the 1% level. Differences are significant at 5% level between GA₃ and 2,4,5-T treatments at 127 days after full bloom and at 1% level at days 139–155 after full bloom. Other differences are not significant.

rapidly than control for 10–20 days after full bloom [Fig. 1(a)]. Growth rate, however, soon decreased below control, and between 25 and 34 days after full bloom all these fruits dropped. Growth rate decreased and fruits dropped sooner in emasculated fruit. Although in the first month after full bloom considerable drop of control fruits occurred, four to five fruits per tree (from an average of 40 at full bloom) remained until maturity.

Ten pairs of equal-sized fruits were selected on apricot trees in 1966 at the beginning of pit-hardening (35 days after full bloom). Gibberellic acid (500 p.p.m.) was applied to one fruit of each pair on three occasions. A statistically significant

increase in size due to GA$_3$ was noted 7 days after the first treatment and size differences were maintained until maturity [Fig. 1(b)].

(b) Response of Peaches to Chemicals

The following treatments were applied to three fruits on each of five trees at the beginning of pit-hardening:

(1) Control, trees left untreated.

(2) GA$_3$, 500 p.p.m.

(3) 2,4,5-T, 100 p.p.m.

(4) 2,3,5-triiodobenzoic acid (TIBA), 75 p.p.m.

(5) 2-Isopropyl-4-dimethylamino-5-methylphenyl-1-piperidenecarboxylate methyl chloride (AMO-1618), 100 p.p.m.

(6) 2,4-Dichlorobenzyltributylphosphonium chloride (Phosphon D), 100 p.p.m.

(7) N-Dimethylaminosuccinamic acid (B-995), 1000 p.p.m.

(8) B-995, 10,000 p.p.m.

Full bloom occurred on September 20, 1966, and pit-hardening began 78 days later.

No significant response in terms of fruit size occurred after treatments (4)–(8). Both GA$_3$ and 2,4,5-T significantly increased growth rate of fruits over control [Fig. 1(c)] but the effect of 2,4,5-T was greater, particularly in the final stages of growth. Fruits treated with 2,4,5-T were somewhat angular and distorted, they matured and dropped sooner, and had very poor flavour. The skin of fruits treated with Phosphon D was slightly mottled. Otherwise no effect of chemicals on fruit appearance and drop was noted.

(c) Endogenous Gibberellin in Peaches and its Relation to Tissue Development

Growth of peach fruits followed the expected double-sigmoid growth curve (Conners 1920). The first growth period lasted 80 days. It was followed by a slow growth phase of 40 days (pit-hardening), during which the endocarp hardened, the endosperm grew to its maximum volume, and the embryo began to develop rapidly. The second period of active growth lasted 60 days. The embryo continued its growth and by 13 days after the commencement of this final growth phase it occupied the full volume within the integuments. These findings confirm the growth studies made by other workers (Conners 1920; Ragland 1934; Stahly and Thompson 1959).

Gibberellin activity in the seed is shown in Figure 2(b) and data for cell expansion in component tissues in Figure 2(a). Observations on cell division activity were also made. Cell number along the integuments increased threefold during the 40 days before full bloom, but cell size increased very little. Cell division in the embryo continued up to 133 days after full bloom when the embryo reached full size. Cell division was not seen in either endosperm or nucellar tissue, so all cell division must have occurred early in their development. Gibberellin concentration in the seed was the highest during the period of rapid cell expansion in nucellus, endosperm, and embryo [Figs. 2(a), 2(b)], but no association with cell division in the integuments

or embryo was apparent. Similarly, gibberellin activity was absent during the main cell division phase in pericarp, mesocarp, and endocarp, but appeared during periods of rapid cell expansion [Figs. 2(c), 2(d)].

Gibberellin activity in the seed 63 days after full bloom and in the mesocarp 42 days after full bloom were also tested using the d-5 dwarf-maize bioassay. Activity in the seed was equivalent to 1×10^5 pg GA_3/100 mg tissue and in the mesocarp to 2×10^3 pg GA_3/100 mg. In the barley-endosperm test [Figs. 2(b), 2(d)], gibberellin
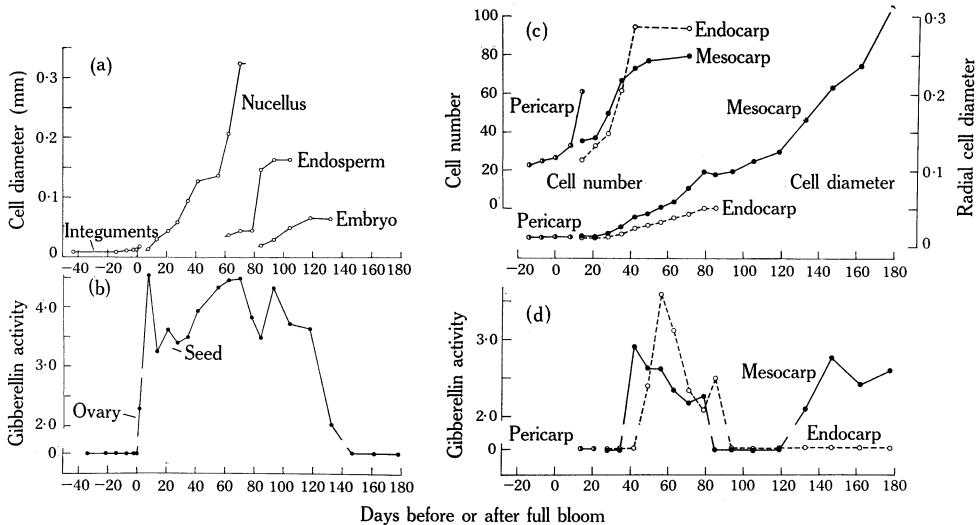

Fig. 2.—(a) and (b) Gibberellin levels in developing peach seeds in relation to size of cells in component tissues. (c) and (d) Gibberellin levels in the developing endocarp and mesocarp of peach fruits in relation to growth of these tissues by cell expansion and cell division. Gibberellin activity expressed as the logarithm of GA_3 equivalents (in picograms) per 10 mg tissue.

activity (measured from 10 mg of tissue) was equivalent to 3×10^5 pg GA_3/100 mg and to 8×10^3 pg GA_3/100 mg for the seed and mesocarp respectively. Thus activity measured in the two tests was of the same order, although slightly less in the dwarf-maize bioassay.

IV. DISCUSSION

More than one compound has been shown to contribute to gibberellin-like activity in seeds, mesocarp, and young shoots of peach 63 days after full bloom (Jackson 1967). In the present experiments only compounds with electrophoretic properties similar to monocarboxylic gibberellins were bioassayed. Other compounds which probably have less gibberellin activity (Jackson 1967) may not vary in the same way as those shown in Figures 2(b) and 2(d).

Hormone levels in seeds rarely correlate with the growth of the whole fruit (see Introduction). More commonly high levels of hormone correspond to periods of rapid seed growth (Ogawa 1965; Powell and Pratt 1966). This suggests that growth of other fruit tissue is not directly dependent on supplies of hormone synthesized by the seed. In apricots the gibberellin concentration may at times be higher in the flesh

than in the seed and these fruit tissues may be self-sufficient for this hormone (Jackson and Coombe 1966). The present work with peach supports this view and further suggests that gibberellin levels in a given tissue are intimately associated with cell expansion in that tissue.

It is generally accepted that there is considerable competition for food reserves by young fruits and developing shoots (Abbott 1960; Coombe 1962), and a stimulation to early fruit growth obtained by removing competing shoots and leaves has been demonstrated here and elsewhere (Abbott 1965; Mullins 1966). It has been suggested that auxins (Davies and Wareing 1965), cytokinins (Müller and Leopold 1966), and gibberellins (Denisova and Lupinovich 1962) can direct the flow of minerals or metabolites to sites of synthesis or application of these hormones. For example, the presence of hormone in an organ like a fruit may attract metabolites, minerals, and water, and the strength of this attraction may determine the ability of this organ to compete for these materials. Crane and Van Overbeek (1965) also suggest that the seed, by synthesizing hormones, particularly is responsible for attracting metabolites to the fruit. Failing fertilization, the seed does not develop and the most potent gibberellin source in the fruit at this stage is therefore lacking. Nutrients may then be diverted to organs such as the developing shoots which have been shown to contain a high concentration of gibberellin (Jackson 1967). The balance, however, may be restored by hormone application. It now seems possible that fruit tissues other than the seed may synthesize hormones (e.g. gibberellin). In both peach and apricot the gibberellin concentration of seed, high initially, subsequently declines and eventually falls below that in the mesocarp [Figs. 2(b), 2(d); Jackson and Coombe 1966]. At this stage the role of the seed in fruit growth is much reduced and it may even be destroyed without affecting growth (Tukey 1936). The leaves are now exporters of food materials and growth of shoot tips is much reduced. Under these less competitive conditions gibberellin in the mesocarp is probably adequate to maintain the fruit on the tree.

Growth may occur because nutrients are attracted to an organ which contains an optimal level of hormone, but the growth produced may differ markedly according to other factors, such as the type of hormone or its concentration. Thus both 2,4,5-T and GA_3 stimulated growth of peach, but fruits treated with 2,4,5-T were distorted and had poor flavour. The period of stimulation also differed [Fig. 1(c)], possibly because of different modes of action or because of more rapid breakdown of GA_3. Auxin, cytokinin, and gibberellin all stimulate parthenocarpic development of the fig but the resultant morphology differs markedly (Crane 1965). Thus while a similar effect or result may be produced by different types of hormone, it is possible that their mechanism of action may be quite dissimilar.

V. Acknowledgment

VI. References

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