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The Chemical Induction of Parthenocarpy in the Calimyrna Fig and its Physiological Significance[1]

Julian C. Crane

Department of Pomology, University of California, Davis, California

Several auxins (1, 4, 5, 6) and a gibberellin (8) have been found to be effective for inducing parthenocarpy in the *Calimyrna* fig. None of the chemicals, however, has been adopted by the industry for commercial application because of the inferior quality of the figs produced. In contrast to pollinated fruits that contain numerous drupelets with lignified endocarp tissue which imparts a seedy texture, no lignification of this tissue occurs in chemically induced parthenocarpic fruits, except those treated with benzothiazol-2-oxyacetic acid (6). The percent parthenocarpic fruit set with the latter chemical, however, is so erratic from year to year that it cannot be relied upon. Consequently, the search has continued for a growth regulator that consistently induces the production of large quantities of parthenocarpic figs containing drupelets with lignified endocarp. Preliminary tests in 1963 indicated that the herbicide Tordon[2] (4-amino-3, 5, 6-trichloropicolinic acid) offered considerable promise in this respect. The results obtained with this auxin in 1964, together with those of a kinin compound are presented here.

Materials and Methods

The investigation was conducted at the University's Wolfskill Experimental Orchards, Winters, California, and the methods used were essentially the same as those previously reported (1, 4). The growth regulators were applied as aqueous solutions on June 25, 1964, by spraying the young syconia and foliage to the point of slight drip. Each solution also contained 0.05 % Tween 20 (polyoxyethylene sorbitan monolaurate) as the surfactant. Tordon concentrations of 20 mg/liter and below were used, as severe leaf and wood damage resulted from higher concentrations in 1963. SD 8339[3], a benzyladenine in which the hydrogen on carbon atom 9 is substituted with the nonpolar ring structure of tetrahydropyran, was tested

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[1] Received November 27, 1964.

[2] Supplied by the Dow Chemical Company. Tordon is classified here as an auxin because of its similarity in biological activity to that of the substituted phenoxyacetic acids.

[3] 6-(benzylamino)-9-(2-tetrahydropyranyl)-9H-purine, produced in the laboratories of Shell Development Company and supplied by Dr. J. van Overbeek, Modesto, California.

at concentrations of 500 and 1000 mg/liter. This new synthetic kinin was not only applied as a spray but it was also injected with a hypodermic syringe through the ostiole and into the central cavity of the young fruit. The cavity was filled with 1 to 2 ml of the solution. As a basis for comparison, GA_3 (potassium salt of gibberellic acid) and the auxin PCPA (para-chlorophenoxyacetic acid), regulators proven to be effective for inducing parthenocarpy in the fig (1, 8), were used at acid equivalent concentrations of 25 and 75 mg/liter, respectively. Fifteen to 20 fruits were used for each treatment.

At the time of treatment, the female flowers within the syconia were receptive to pollination. Cross-pollination with the male fig, however, was prevented by covering the branches bearing the fruits to be treated with muslin bags. The bags enclosed the branches for about 2 weeks, the period during which pollination of unbagged fruits was accomplished by the insect *Blastophaga psenes*. Bagged but untreated fruits served as controls. Since previous tests with the surfactant Tween 20 showed it to have no effect on the fig, it was not applied in aqueous solution to the control fruits. Unless cross-pollination occurs or the syconia are treated with certain growth regulators, they cease growth, wither and absciss in about 2 weeks.

Results

Tordon is a very effective compound for inducing parthenocarpy in the fig (table I). This chemical at a concentration of 8 mg/liter was just as effective as 75 mg/liter of PCPA, the concentration of the latter that has been shown to be optimum (5). Although concentrations of 6 mg/liter and below produced parthenocarpic fruit sets of only 88 to 94 %, these were considerably greater than those generally obtained by cross-pollination under commercial orchard conditions (1, 4, 5, 6). The percent fruit set resulting from cross-pollination in the orchard where this investigation was conducted was not determined because the commercial procedure for pollination was not followed.

Maturity of the parthenocarpic fruits, as judged by color, firmness, and taste, occurred about a week earlier than that of pollinated ones. Externally, they appeared identical to fruits that had been pollinated; internally, however, the pulp was amber as contrasted to the strawberry red that characterized pollinated fruits. In contrast to parthenocarpic fruits produced with PCPA in which lignification of the endocarp in the individual drupelets does not occur, this tissue in fruits produced with Tordon was definitely lignified (fig 1). The degree of lignification, however, was not as great as that in pollinated fruits, as determined by mastication, but progressively increased as concentration of Tordon increased. The fruits had a seedy texture similar to pollinated ones; there was no evidence of embryos within the individual drupelets.

No vegetative damage whatsoever was noted from concentrations of Tordon of 6 mg/liter or less. A concentration of 8 mg/liter produced slight chlorosis of the younger leaves; leaf chlorosis and necrotic areas on current-season's shoots increased progressively as concentration was increased above 8 mg/liter. Slight leaf chlorosis developed following the application of PCPA. This symptom did not occur in previous experimentation with PCPA, perhaps because

Table I. *The Comparative Effectiveness of 2 Auxins, a Gibberellin, and a Kinin for Inducing Parthenocarpy in the* Calimyrna *Fig*

Treatment mg/liter	Parthenocarpic fruit set %	Observations on vegetative growth
Control (unpollinated)	0	
Auxins:		
Tordon 2	94	Like control
4	90	Like control
6	88	Like control
8	100	Slight leaf chlorosis
10	93	Moderate leaf chlorosis and slight shoot injury
20	100	Severe leaf chlorosis and severe shoot injury
PCPA 75	100	Slight leaf chlorosis
Gibberellin:		
GA_3 25	100	Rest period of 33 % of terminal vegetative buds was broken with subsequent shoot growth
Kinin:		
SD 8339–sprayed		
100	18	Abscission of youngest leaves
500	57	Abscission of youngest leaves
SD 8339–injected		
100	100	Like control
500	100	Like control

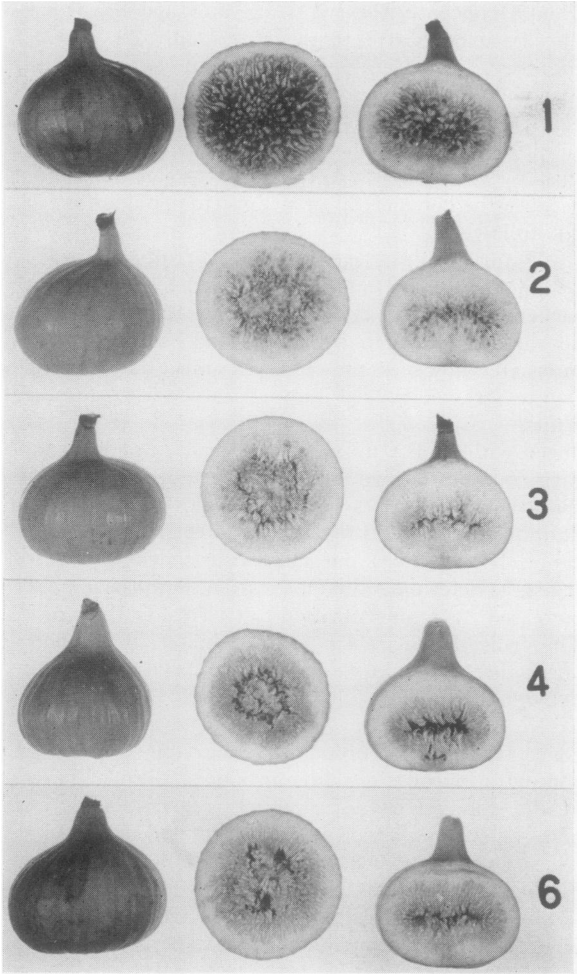

FIG. 1. 1) *Calimyrna* figs produced by cross-pollination and those produced parthenocarpically by aqueous spray application of 2) 6 mg/liter of Tordon (4-amino-3, 5, 6-trichloropicolinic acid), 3) para-chlorophenoxyacetic acid, 4) potassium salt of gibberellic acid, and 6) by injection of 500 mg/liter of SD 8339, a kinin.

a surfactant was not included in the spray solution (1, 5).

GA_3, as reported previously (8), was also very effective for inducing parthenocarpy (table I). As in the case of fruits produced with Tordon or PCPA, maturity of those produced with GA_3 also occurred about a week earlier than that of pollinated fruits. The skin of the fruits was considerably more tender than that of pollinated fruits or those induced by PCPA or Tordon and the necks were somewhat enlarged (fig 1). The internal color was amber and no lignification of the endocarp tissue occurred.

An undesirable effect of GA_3 on the fig is the breaking of the rest period of the terminal vegetative buds with subsequent shoot growth in proportion to the concentration of GA_3 applied (8). A concentration of 25 mg/liter is about the lowest effective one for inducing parthenocarpy but, as shown in table I, the rest period of 33 % of the buds was broken and an average of 4.5 cm of new shoot growth resulted.

SD 8339 was also very effective for inducing parthenocarpy, particularly when injected into the young syconia (table I). Injection of either concentration resulted in 100 % parthenocarpic set and development to maturity about a week earlier than maturity of pollinated fruits. When applied as a spray at concentrations of 100 and 500 mg/liter, SD 8339 set only 18 and 57 % of the fruits, respectively. These results indicate that the compound is not readily absorbed by fig leaves or that it may not be easily translocated. Externally, the fruits appeared as pollinated ones, but internally they were similar to fruits produced with PCPA or GA_3 (fig 1).

Abscission of the youngest leaf on shoots that were sprayed with either concentration of SD 8339 was the only vegetative response noted.

Discussion

Various auxins, gibberellin-like, and kinetin-like substances have been found to occur in fruits; the seeds are particularly rich sources of these materials (9). This information, together with the fact that fruit size and shape are positively correlated in several instances with seed number and distribution, led to the commonly accepted view that fruit growth and development are controlled by hormones emanating from the seeds. However, studies of auxins in general have revealed positive correlations between their levels and the development of the endosperm and embryo in the seed but little or no relationship has been shown between their levels and fruit growth. Similarly, relatively large quantities of gibberellin-like substances have been extracted from young seeds. In general, a positive correlation was found between growth of the seed and increase in amount of gibberellin-like substances but, as in the case of auxins, no relationship between levels of these substances and fruit growth has been demonstrated. Kinetin-like activity also has been detected in extracts of various fruits and particularly their seeds. In most cases, the highest levels of these substances have been found to occur in young fruits and it has been suggested that they may be associated with the period of cell division (14). Extracts of unfertilized apples prior to drop, as well as those of flower petals and leaves, also have been shown to contain substances that exhibit kinetin-like activity, indicating that these substances are not necessarily products of the seeds but may be synthesized in parts of the plant other than the fruit. In fact, Goldacre (10) presented evidence for a kinetin-like substance originating in root meristems and Loeffler and van Overbeek (15) have demonstrated the presence of 5 kinetin-like materials in bleeding sap of the grape, which indicates that they may have been synthesized in the roots. Thus, considerable experimental evidence casts doubt on the concept of fruit growth being stimulated by hormones moving out of the seeds via the vascular system or by diffusion through the testa.

A lack of precise information on the identity of the hormones that occur in seeds and fruits, their distribution within these organs, and the sites from which they originate enables only speculation in regard to the physiological role they play in fruit growth. In view of the ability of auxins, GA_3, and a kinin to induce parthenocarpy in the fig, together with evidence reported concerning the action of these substances individually in other connections, the physiological role of hormones in fruit growth could very well be that of mobilizing metabolites into the fruits from other parts of the plant where they are produced. The fact that parthenocarpic figs similar in gross morphology can be produced by the application of an auxin, a gibberellin, or a kinin, demonstrates indirectly that each of these hormones, should they be essential for fruit growth and development, can be supplied by some part of the plant other than the seeds. This suggests that, although seeds may contain relatively large quantities of one or more of the 3 types of hormone at some time during their development, any individual one can initiate the mobilization of essential metabolites including other hormones. This property of bringing about mobilization apparently is not unique with hormones that normally stimulate growth but chemicals classed as growth retardants apparently can do the same. Coombe (3) recently reported significant increases in berry set of both parthenocarpic and nonparthenocarpic grape cultivars as a result of dipping the clusters 3 weeks before anthesis in solutions of either 2-chloroethyltrimethylammonium chloride (CCC) or tributyl-2, 4-dichlorobenzylphosphonium chloride (Phosfon-D).

A mass of evidence showing the ability of fruits to mobilize organic and inorganic substances even at the expense of vegetative growth has been reviewed by Leonard (11). While the details of the processes of mobilization into the fruit remain obscure, there is a growing body of evidence that hormone-directed transport may be important in the redistribution of nutrient reserves from various parts of the plant to growing organs (14). That mobilization of metabolites may be a general feature of hormone effect is suggested by evidence of this role of hormones in barley seed germination (17) and such phenomena as apical dominance (2), senescence (12), abscission (16), and fruit growth (18).

Seeds are relatively rich in hormones and by virtue of this fact apparently act as mobilization centers with the surrounding fruit tissues utilizing and storing some of the metabolites that are attracted from other parts of the plant. Thus, the asymmetrical growth associated with partial fertilization or with ovule abortion in fruits that contain many potential seeds may be ascribed to the lack of centers of mobilization in the underdeveloped portions. Conversely, the larger the number of developing seeds the larger the number of mobilizing centers and the greater is growth and development of the fruit.

The results presented show that different degrees of drupelet development occur in parthenocarpic fig fruits depending upon the regulator applied to induce parthenocarpy. Of the 7 auxins that have been found to be effective for inducing parthenocarpy (1, 4, 5, 6), only benzothiazol-2-oxyacetic acid (6) and Tordon, as reported here, produce figs in which lignification of the drupelet endocarp is similar to that in pollinated fruits. The fruits produced with the other auxins, as well as GA_3, and the kinin SD 8339, contain drupelets in which lignification of the endocarp does not occur. Obviously, the effect of benzothiazol-2-oxyacetic acid or Tordon more closely duplicates that of the endogenous auxins in pollinated figs (7). Various factors might contribute to the differential development of the drupelets. As examples, time of regulator application in relation to stage of ovary development, whether or not translocation of the regulator into the ovary occurs, or its effect on vascular development or on enzyme activity associated with lignification might be involved.

Summary

Since parthenocarpic *Calimyrna* figs similar in gross morphology were produced by the application of either an auxin, a gibberellin, or a kinin, it was demonstrated indirectly that each of these endogenous hormones, should they be required for fruit growth, can be supplied by some part of the plant other than the seeds. It is proposed that fruit growth is not controlled by the hormones emanating from the seeds but, on the contrary, by their capacity to attract metabolites from other regions of the plant with the fruit tissues surrounding the seeds tapping the metabolite supply and acting as storage organs. The herbicide Tordon appears to offer promise for commercially producing parthenocarpic figs of acceptable quality.

Acknowledgments

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