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Effect of Plant Regulators on Set and Berry Development in Certain Seedless and Seeded Varieties of *Vitis vinifera* L.

by

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Introduction

The three known classes of plant hormones — auxins, gibberellins, and kinins — are probably all concerned at some time with the set and growth of fruit (17). The purpose of these experiments was to study the effects of applying the auxin 4-chlorophenoxyacetic acid (4-CPA), gibberellic acid (GA_3), and a kinin (benzyladenine) to clusters of grapes at the flowering or set stage. A study of the responses obtained by the application of exogenous plant regulators should provide some insight into the mechanisms of fruit set and development.

Materials and Methods

Mature vines in an irrigated vineyard at the University of California at Davis were utilized as experimental plants. An exception was the 'Pinot Chardonnay', which grew in a nonirrigated University vineyard at Oakville, California. Varieties that normally set poorly were selected. The seedless variety, Black Corinth, was cane-pruned. The seeded varieties, 'Pinot Chardonnay', 'Muscat of Alexandria' (hereafter referred to as 'Muscat'), and 'Grenache', were head-trained and spur-pruned. Except for the dipping of clusters, defoliation, and girdling treatments, vines received normal vineyard care.

The plant regulators were obtained from commercial sources. The 4-CPA was dissolved by adding ammonia to the suspended compound. The GA_3 was dissolved in water. A formulation of benzyladenine was supplied by Dr. J. van Overbeek of Shell Oil Co.

Uniform shoots and clusters were selected for treatment; only one cluster was retained per shoot. Clusters were trimmed with scissors so that all experimental clusters within a given variety were approximately the same size. Each cluster was dipped momentarily into one of the solutions. Dreft was used as a wetting agent. Ten replicate clusters were used in each experiment.

Experiments were performed on partially defoliated and nondefoliated shoots. The defoliated shoots were girdled below the cluster to isolate the latter from the parent vine; thus, the berries were dependent on the leaves on the same shoot for elaborated food materials and plant regulators. All girdles were

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covered with cellophane tape to prevent drying. Any shoots or leaves that developed after treatment were removed. In the defoliation experiments, fruit was usually harvested soon after set, within two to three weeks after treatment — since the berries dried if left on the vine any longer. In experiments on the ungirdled nondefoliated shoots, clusters usually were not harvested until the berries were at least half the size of a normal mature berry.

Yellowish or darkened ovaries or berries that had shown no growth were not included in berry counts. Such undeveloped fruits were less than 1 1/2 mm in diameter and weighed only 1 to 2 mg each. Ordinarily there were only a few of these on each cluster.

Berries were cut open with a knife in order that the number of seeds could be counted. Only seeds that were at least half the size of a normal full-sized seed were counted.

Experimentation with 'Black Corinth'

Effect of Leaf Surface on Set and Berry Weight.

Preliminary defoliation experiments were run in 1960 to determine the amount of leaf surface necessary to maintain 50 % normal set. The effects of exogenous regulators could be ascertained more easily by using clusters with such a reduced set. The results with girdled shoots showed set was not much lessened until the leaf surface was reduced to 1/4 leaf. When the total leaf surface associated with a girdled shoot containing one cluster was reduced to about 1/16 of a leaf — approximately one square inch of leaf surface — set was found to be reduced to about 1/2 the normal set (Fig. 1). Set was nil if no leaves were retained. In subsequent experiments with defoliated 'Black Corinth', 1/16 leaf above the cluster was retained, and the shoot was cut off about 2 or 3 inches above the leaf.

Effect of GA_3 and 4-CPA on Set and Fruit Development.

Nondefoliated Shoots. Treatments were made on May 26, 1961, when from 95 to 100 % of the calyptras had fallen. Clusters selected were trimmed to a length of 6 inches, and wings were removed. One series of shoots was not girdled and not treated; a second series was girdled but not treated. Clusters in another series of ungirdled shoots were dipped in 4-CPA at 15 ppm, or GA_3 at 5 or 15 ppm.

Clusters were harvested on July 6 when controls had a high percentage set of small berries, and coloring of fruit was just beginning (Table 1). Berry set was significantly reduced by GA_3 at 5 and 15 ppm; however, there were no significant differences among the other treatments. All treatments produced heavier rachises, clusters, and berries than did the untreated, ungirdled controls. The girdling treatment resulted in the largest total weight of berries and clusters. Both the girdling and the 4-CPA treatment produced round berries, while GA_3 treatment produced elongated ones.

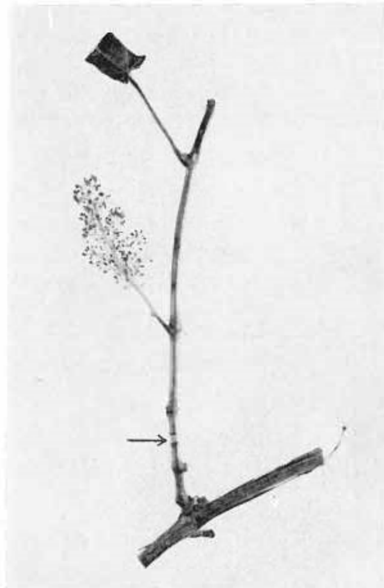

Fig. 1: Black Corinth shoot after topping and reducing leaf surface to 1/16 leaf

Arrow denotes location of girdle (photographed June 5, 1961)

Shoot with $^1/_{16}$ leaf. Clusters were treated on May 26 and harvested on June 5, after shatter was complete. The girdles had not healed. In subsequent experiments in which only a portion of a leaf was retained, girdles also had not healed by harvest.

The data (Table 2) show that 4-CPA significantly increased set, but that GA_3 markedly reduced set — as much as 85 % at 15 ppm. A solution containing both GA_3 and 4-CPA produced a mixture of small and large berries but did not alter set significantly (Fig. 2). Although the percentage set was the smallest, the largest berries were produced by GA_3 at 15 ppm.

Experimentation with Seeded Varieties

The varieties 'Pinot Chardonnay', 'Muscat', and 'Grenache' were treated in 1961. With each variety, dipping experiments with GA_3 and 4-CPA were performed on nondefoliated ungirdled shoots, and on girdled, partially defoliated shoots. About $^1/_4$ leaf was left on each partially defoliated shoot, as this treatment had been shown by Coombe (3) to result in a marked decrease in set of seeded varieties. GA_3, 4-CPA, or GA_3 plus 4-CPA were applied at full bloom. In another treatment, 4-CPA was applied at bloom to increase set, and then GA_3 applied at set time to determine whether berry size of seeded varieties could be increased.

'Pinot Chardonnay', Nondefoliated Shoots. Treatments at bloom were made on May 23. In addition on June 6, when shatter was about completed, GA_3 at 20 ppm was applied to treatment 5 (Table 3). Clusters were harvested on July 31. Many berries on control clusters were about 7/16 inch in diameter, and some shot berries ranged up to 1/4 inch in diameter. There was a marked variation in seed number and size, although the majority of berries contained none, or only one developed seed. Many berries had small, gritty seeds, but these seeds were not counted. The number of seedless berries was significantly increased by all treatments. The GA_3, and the mixture of GA_3 and 4-CPA, reduced the number of one-seeded berries. Treatment 5 in which 4-CPA was applied at bloom and then GA_3 applied at shatter, increased the total number of berries per cluster.

The weight of seedless berries was increased by all treatments except the ones in which 4-CPA was applied alone at bloom. Total weight of one-seeded

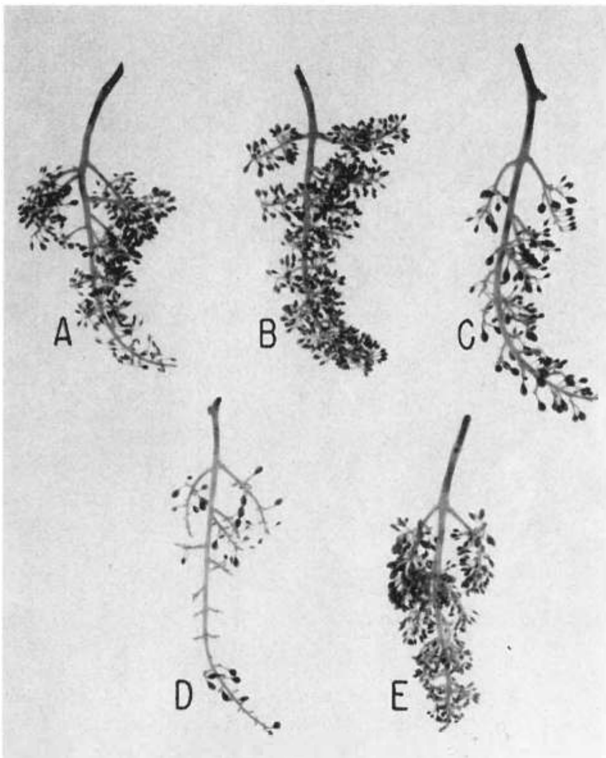

Fig. 2: Black Corinth cluster on girdled and partially defoliated shoots after treatments on May 26, 1961

(A) Control, (B) 4-CPA at 15 ppm, (C) GA_3 at 5 ppm, (D) GA_3 at 15 ppm, and (E) mixture of 4-CPA at 15 ppm and GA_3 at 15 ppm. Note that 4-CPA (B) has increased the percentage of set, but that GA_3 at 5 ppm (C) or 15 ppm (D), has sharply reduced it (photographed June 5, 1961)

Table 1

Data at harvest (July 6, 1961) for Black Corinth grapes on nondefoliated shoots after treatment at bloom with plant regulators

Treatment	No. of berries set per cluster	Weight of rachis (gm)	Total weight of berries per cluster (gm)	Weight per cluster (gm)	Weight per 100 berries (gm)
1. Control, not girdled	455	3.6	35	39	7.76
2. Girdled only	408	7.7	167	175	40.77
3. 4-CPA, 15 ppm, not girdled	468	6.2	76	83	16.33
4. GA_3, 5 ppm, not girdled	341	5.2	94	99	27.62
5. GA_3 15 ppm, not girdled	354	8.1	131	139	37.15
$d_{0.05}$	78	1.7	29	30	—

Table 2

Data at Harvest (June 5, 1961) for Black Corinth clusters on partially defoliated, girdled shoots after treatment with 4-CPA and GA_3 at bloomtime

Treatment	No. of berries per cluster	Total weight of berries per cluster (gm)	Calculated weight per 100 berries (gm)
1. Girdled only	323	2.2	0.68
2. 4-CPA, 5 ppm	544	4.4	0.81
3. GA_3, 5 ppm	153	3.0	1.96
4. GA_3, 15 ppm	48	1.2	2.50
5. GA_3, 15 ppm and 4-CPA, 15 ppm	281	3.9	1.39
$d_{0.05}$	68	0.9	—

Table 3

Data at harvest (July 31, 1961) for nondefoliated Pinot Chardonnay after treatments with plant regulators at bloom or shatter stage

Treatment	No. of seeds per berry: 0		1		2		Total No. berries*) per cluster	Weight per cluster (gm)
	No. of berries	Weight per berry (gm)	No. of berries	Weight per berry (gm)	No. of berries	Weight per berry (gm)		
1. Controls	53.1	80	36.4	437	3.3	695	93.3	29.5
2. GA_3, 5 ppm	87.6	123	20 6	441	1.8	650	110.4	27.0
3. 4-CPA, 5 ppm........	72.3	72	30.9	397	6.4	588	111.8	28.3
4. GA_3, 5 ppm and 4-CPA, 5 ppm........	83.6	150	29 0	458	3.9	580	117.0	38.7
5. 4-CPA, 5 ppm at bloom, then GA_3, 20 ppm at shatter.....	85.1	178	34.6	344	8.1	465	135.0	41.6
$d_{0.05}$	15 9	40	7.2	24	3.9	N. S.	24.5	9.3

*) A few 3- and 4-seeded berries occurred, and are included in this column of figures

berries was not significantly increased by any treatment, but it was decreased by 4-CPA applied at bloomtime (Treatments 3 and 5). The weights of two-seeded berries did not differ significantly among the various treatments.

Treatment 5 increased the weight per cluster.

'Pinot Chardonnay', Shoot with 1/4 Leaf. On May 23, clusters were trimmed to 4 inches in length, and the shoots were girdled, defoliated, and treated. About 80 to 90 % of the calyptras had fallen.

Clusters were harvested on June 5. The number of berries per cluster for clusters girdled only, treated with GA_3 at 5 ppm, 4-CPA at 5 ppm, or GA_3 at 5 ppm plus 4-CPA at 5 ppm was 88, 91, 169, and 151, respectively. The $d_{0.05}$ was 48. It is of interest that GA_3 did not reduce set in this seeded variety as it did in the seedless Black Corinth.

'Muscat', Nondefoliated Shoots. Even in years of good set many clusters of this variety are loose and straggly. Clusters were trimmed to a length of 7 1/2 inches and treated on May 26 when from 80 to 100 % of the calyptras had fallen.

All treatments, especially the GA_3 treatments applied at bloom, markedly reduced set and cluster weight (Table 4). Controls also set poorly and had many shot berries. When GA_3 was applied at shatter the weight of seedless berries was increased. No significant increase in berry weight of seeded berries occurred as a result of any treatment.

'Muscat', Shoot with 1/4 Leaf. Treatments were made on May 26, and clusters were harvested on June 12. The number of berries that set in girdled only, GA_3 at 5 ppm, 4-CPA at 5 ppm, and the mixture of GA_3 at 5 ppm and 4-CPA at 5 ppm were 45, 47, 92, and 51, respectively. The $d_{0.05}$ was 25.

'Grenache', Nondefoliated Shoots. Clusters were trimmed to 5 1/2 inches in length and treated on May 25 when 95 to 100 % of the calyptras had fallen. In addition on June 11 when shatter was about completed GA_3 at 20 ppm was applied to Treatment 5 (Table 5). Berries were just beginning to color at harvest on August 15. Controls had made a good set. There was much variation in berry size, with many small berries interspersed among the larger ones.

The set of seedless berries was significantly increased only by 4-CPA applied at bloom, followed by GA_3 at shatter (Table 5). The set or weight of seeded berries was not significantly increased by any treatment. Also, there were no significant differences among treatments in total number of berries per cluster or in total weight per cluster.

'Grenache', Shoot with 1/4 Leaf. Clusters were treated on May 25 and harvested on June 12. The average number of berries at harvest per cluster girdled only, dipped in GA_3 at 5 ppm, 4-CPA at 5 ppm, or 4-CPA at 5 ppm plus GA_3 at 5 ppm was 88, 90, 95, and 100. The differences were not significant.

Table 4

Data at harvest (August 7, 1961) for nondefoliated Muscat of Alexandria after treatments with plant regulators at bloom or shatter stage

Treatment	No. of Seeds per berry: 0		1		2		3		4		Total No.[1]) of berries set	Weight per cluster (gm)
	No. per cluster	Weight per berry (gm)	No. per cluster	Weight per berry (gm)	No. per cluster	Weight per berry (gm)	No. per cluster	Weight per berry (gm)	No. per cluster	Weight per berry (gm)		
1. Control	13.5	0.258	8.9	1.410	35.1	1.776	42.2	2.121	21.5	2.163	126.7	264
2. GA_3, 5 ppm	9.6	0.265	5.9	1.174	8.2	1.959	8.2	2.371	6.0	2.071	38.6	70
3. 4-CPA, 5 ppm ..	9.5	0.291	3.8	1.397	19.2	1.399	31.0	2.002	26.4	2.201	93.1	193
4. GA_3, 5 ppm and 4-CPA, 5 ppm ..	3.4[2]	0.306[2]	2.2[2]	0.863[2]	8.1[2]	1.515[2]	13.6[2]	1.849[2]	13.1[2]	2.321[2]	44.4[2]	92[2]
5. 4-CPA, 5 ppm bloom, then GA_3, 20 ppm at shatter	12.8	0.550	5.4	1.612	9.1	1.765	24.3	2.186	22.3	2.265	75.6	147
$d_{0.05}$	6.6	0.120	3.0	0.317	9.5	N. S.	10 3	N. S.	11.1	N. S.	20.0	50

1) A few 5- and 6-seeded berries occurred, and are included in this column of figures
2) Not included in statistics due to missing replicates

Table 5

Data at harvest (August 15, 1961) for nondefoliated Grenache shoots after treatment with plant regulators at bloom or shatter stage

Treatment	No. of seeds per berry: 0		1		2		Total No. berries*) per cluster	Total weight per cluster (gm)
	No. of berries per cluster	Weight per berry (gm)	No. of berries per cluster	Weight per berry (gm)	No. of berries per cluster	Weight per berry (gm)		
1. Control	23.9	0.258	143.8	0.551	60.3	0.763	233.4	169.8
2. GA_3, 5 ppm	36.3	0.257	139.7	0.561	33.5	0.776	211.6	137.6
3. 4-CPA, 5 ppm	33.8	0.202	184.1	0.523	54.2	0.751	278.3	190.0
4. 4-CPA, 5 ppm and GA_3, 5 ppm	48.1	0.292	158.8	0.698	41.5	0.970	251.0	201.0
5. 4-CPA, 5 ppm at bloom, then GA_3, 20 ppm at shatter	68.5	0.262	155.2	0.688	42.2	0.927	266.1	199.8
$d_{.05}$	27.7	0.051	N. S.	N. S.	17.7	N. S.	N. S.	N. S.

*) A few 3- or 4-seeded berries occurred, and are included in this column of figures

Experiments with Kinin

Kinins are best known as compounds which induce cell division (16). Since mitosis occurs during set and in some species, at least, during the early growth of the berries, it was thought that kinins may be involved in these processes (4). A kinin, benzyladenine, was applied separately and in conjunction with 4-CPA and GA_3.

Tests were made at full bloom on 'Pinot Chardonnay', 'Grenache', and 'Muscat' grapes. Clusters of each variety were dipped in a solution of benzyladenine at 0, 5, 50, or 500 ppm, or in a solution containing GA_3 at 5 ppm, 4-CPA at 5 ppm, and benzyladenine at 50 ppm. Only nondefoliated, ungirdled shoots were used.

Treatments were made on May 23, and clusters were harvested on July 31. The benzyladenine failed to increase set or size of berry. However, in the 'Chardonnay', the mixture of regulators increased set and weight of seedless berries, as well as the weight of one-seeded berries.

In 'Muscat' the kinin greatly increased the development of a purple anthocyanin pigment in the rachis.

Discussion

On ungirdled, nondefoliated shoots of 'Black Corinth', GA_3 at 15 ppm reduced the set about 13 %. However, on girdled shoots defoliated to $^1/_{16}$ leaf, GA_3 at 15 ppm reduced the set approximately 85 %. Shoots with only a leaf stub produce a relatively small amount of auxin, elaborated food materials, or some set factor while large amounts of these substances are available to a cluster on a nondefoliated shoot. Since a very small amount of leaf surface will induce set, it is unlikely that carbohydrate production alone would be the direct cause of set. That leaves of 'Black Corinth' produce a set factor was shown in the preliminary experiments in this paper. One might hypothesize from our results that, in 'Black Corinth', the ratio of this set factor to gibberellin is the controlling factor in set. The small amount of set factor that moves into the cluster from the leaf stub, and the addition of GA_3 produces a ratio unfavorable to set. Since GA_3 reduced set only a small degree in nondefoliated 'Black Corinth' shoots, it is possible that the ratio of set factor to gibberellin is more favorable in nondefoliated shoots than in defoliated shoots.

On defoliated shoots of 'Black Corinth', 4-CPA significantly increased set, while a mixture of 4-CPA and GA_3 produced no significant effect. These data might indicate that auxin enhances set, and that gibberellin opposes set. However, it has been shown previously that either auxin or GA_3 can induce set in emasculated clusters of ungirdled 'Black Corinth' as well as in 'Thompson Seedless' and 'Tokay' (19). In the seeded varieties, 4-CPA increased set in both 'Pinot' and 'Muscat', while GA_3 alone had no effect. Most of this increase, however, probably resulted from an increase of set in seedless berries.

There was a varietal difference in toxic response of seeded varieties to the plant regulators. In general, the compounds injured the 'Muscat', and the set and berry size in this variety were usually reduced.

On nondefoliated shoots of seeded varieties there was often a decrease in set of seeded berries as a result of treatment with regulators. In 'Pinot' and 'Grenache' this reduction usually occurred when GA_3 was applied at bloom (Treatments 2 and 4). Coombe (5) showed GA_3 at 18 ppm applied at bloom reduced set in 'Ruby Cabernet'. Although our results support his findings, it should be noted Coombe used a relatively high concentration of GA_3. Several investigators (1, 15, 18, 20) showed that prebloom sprays of GA_3 are also effective in reducing the set of seeded varieties of grapes.

Our finding that GA_3 increased size of seedless but not of seeded berries is not in agreement with the results of Lavee (11). He found that, in the 'Queen of the Vineyard' grape, GA_3 increased the size of one- and two-seeded grapes as well as of seedless grapes, but did not increase the size of three-seeded berries. It is well known that berry size increases with number of seeds, and Lavee reasoned that GA_3 compensated for lack of seeds.

The work of Gustafson (9) and others (6, 13, 19) on induction of parthenocarpy in various plant species demonstrated that auxin is of importance in set. Auxin probably is involved also in fruit growth (12). More recently it has been shown that GA_3 can induce set and mesocarp development in almond and apricot (7), and in peach (8). In cherry, GA_3 plus an auxin promoted parthenocarpy, while either material alone failed in this respect (14).

Our results indicate that both auxin and gibberellin are involved in set and berry development of seedless berries in both seedless and seeded grape varieties. Although GA_3 reduced set in 'Black Corinth', the development of large, elongated berries showed that GA_3 influences berry growth. Usually no increase in set or berry size of seeded berries occurred as a result of application of the plant regulators to nondefoliated shoots. This might indicate sufficient hormones for growth are produced within the berry itself once seed development has initiated.

Benzyladenine alone failed to increase set or berry size. It may be that kinins were not a limiting factor in the berry tissue. Tissue culture methods for growing berries would enable us to eliminate the leaf tissue which might be supplying sufficient kinin. Also, a quantity of the compound sufficient for physiological activity may not have entered the ovaries and berries, since benzyladenine is soluble only to about 10 ppm (van Overbeek, private communication). Whether the kinin enhances the effect of auxin and gibberellin could not be ascertained from our experiments.

In 'Muscat', benzyladenine accentuated the development of the purple anthocyanin pigment. An increase in anthocyanin formation has also been reported in *Impatiens* (10) and *Amaranthus* seedlings (2).

Summary

1. Flowering clusters on ungirdled, nondefoliated shoots of 'Black Corinth', and girdled shoots defoliated to 1/16 leaf, were dipped in 4-CPA at 15 ppm, or GA_3 at 5 or 15 ppm. In nondefoliated shoots the set was decreased about 13 % at 15 ppm, but there were no significant differences among the other

treatments. All treatments produced heavier rachises, berries, and clusters than the ungirdled, untreated controls. In defoliated shoots the set was decreased approximately 85 % by GA_3 at 15 ppm. 4-CPA significantly increased set, but a mixture of GA_3 and 4-CPA did not alter set.

2. Similar experiments were carried on with the seeded varieties 'Pinot Chardonnay', 'Muscat of Alexandria', and 'Grenache'. Clusters on ungirdled nondefoliated shoots were dipped in GA_3, 4-CPA, or a mixture of the two compounds. Like treatments were made on other clusters on shoots defoliated to 1/4 leaf. There was a varietal difference in response among the seeded varieties. The compounds injured the Muscat and reduced the set and berry size.

3. All treatments increased the set of seedless berries on nondefoliated shoots of 'Pinot'. In both 'Chardonnay' and 'Grenache' there was a shift from seeded to seedless berries. Application of 4-CPA resulted in a significantly greater set in total number of berries on defoliated shoots of 'Chardonnay' and 'Muscat'.

4. All solutions containing GA_3 increased size of seedless berries on nondefoliated shoots of 'Pinot'. GA_3 applied at shatter stage increased size of seedless 'Muscat' berries. With one exception, there was no increase in size of one-, two-, or three-seeded berries.

5. Percentage set was significantly increased in defoliated shoots of 'Muscat' by 4-CPA, and in 'Pinot' by 4-CPA or a mixture of 4-CPA and GA_3.

6. A kinin, benzyladenine, failed to increase set or berry size, but intensified the development of a purple anthocyanin pigment in 'Muscat'.

7. The possible importance of the ratio of a leaf-produced set factor to gibberellin in berry set in 'Black Corinth' is discussed.

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