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The interaction of gibberellic acid and 2-(chloroethyl) trimethyl ammonium chloride on fruit cluster development in Vitis vinifera L.

by

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Der Einfluß von Gibberellinsäure und CCC auf die Traubenentwicklung bei Vitis vinifera L.

Zusammenfassung. — Der Einfluß von Gibberellinsäure (GS)- und CCC-Gaben in faktorieller Kombination und in verschiedenen Entwicklungsphasen auf die generative Entwicklung der fünf Vitis vinifera-Sorten Doradillo und Muskat (samenhaltig), Sultana (stenospermokarp), Cape Currant und Zante Currant (parthenokarp) wurde gemessen.

Der Einfluß der GS auf den Fruchtansatz hing von der Konzentration, dem Entwicklungsstadium zur Zeit der Applikation und von der Sorte ab, d. h. ob samenhaltig, stenospermokarp oder parthenokarp. Vor der Anthesis angewendet, verminderte GS den Fruchtansatz; spätere Anwendungen waren ohne Wirkung. Bei Sultana verminderte GS den Fruchtansatz, wenn sie zur Blütezeit, und erhöhte ihn, wenn sie vorher oder nachher appliziert wurde. Bei den samenhaltigen Sorten verminderte GS die Zahl der samenhaltigen und erhöhte die der samenlosen Beeren; die Gesamtzahl der Beeren war gewöhnlich vergrößert. Die Anwendung von CCC zwei Wochen vor dem Blühen erhöhte allgemein den Fruchtansatz.

Über die Samenentwicklung beeinflußte GS auch das Frischgewicht der Beeren; samenhaltige Beeren ließen keine Wirkung erkennen, während samenlose meistens vergrößert waren, und zwar am stärksten bei parthenokarpen Beeren, besonders nach Behandlung während der Anthesis. Bei stenospermokarpen Beeren hatte die zwei Wochen nach der Blütezeit applizierte GS die größte Wirkung. CCC, vor oder nach dem Aufblühen angewendet, verminderte die Beerengröße; der Rückgang betrug 2—20%.

Durch GS wurde — sortenabhängig — das Verhältnis Länge/Breite der Beeren vergrößert, besonders bei Anwendung während der Anthesis. CCC verminderte dieses Verhältnis bei Sultana-Beeren. Auch das Wachstum des Traubenstieles wurde durch GS und CCC gegensätzlich beeinflußt; GS förderte das Längenwachstum von Trauben- und Beerenstielen, besonders bei Anwendung vor der Blüte; CCC verminderte es.

In einigen Fällen beeinflußten sich GS und CCC gegenseitig signifikant; im allgemeinen wurden hierdurch bei den verwendeten Konzentrationen ihre Wirkungen gesteigert.

Introduction

The literature describing experiments in which gibberellic acid (GA) and 2-chloroethyl) trimethyl ammonium chloride (CCC) have been applied separately to grape clusters suggests that the relationship between GA and CCC is antipodal: in general, the application of GA results in increased berry size and decreased berry set (e. g. Weaver and McCune 1959 a, b, c; Coombe 1959), while the application of CCC results in decreased berry size and increased berry set (Coombe 1965 a, 1967, 1970; Claus 1965). These facts are consistent with the deduction made from other work (e. g. Reid and Carr 1967; Radley 1967), that CCC may have its effect by inhibiting the production of some physiologically active gibberellins within the plant.

The ability of a grape berry to increase in size in response to the application of GA is influenced to a marked degree by the extent of seed development within

that berry; the less the seed development the greater the response (Weaver and McCune 1959 a, b; Lavee 1960; Smirnov and Perepelitsyna 1965). The reduction in berry size in response to CCC is independent of the presence of seed in a berry (Coombe 1965 a, 1967).

In view of these observations it was decided to examine how applications of GA and CCC interacted in terms of cluster development, and how this interaction was influenced by the type and amount of seed development in the berry. Accordingly, tests were carried out on five grape cultivars differing in amount of seed development. The experiments were also designed to test the interaction of GA and CCC when applied at different times, because it is clear that the concentrations of endogenous gibberellin-like compounds vary during the development of the berry (Coombe 1960; Iwahori, Weaver and Pool 1968).

Material and Methods

The five cultivars chosen were:

(i) Doradillo — seeded;
(ii) Muscat Gordo Blanco (syn. Muscat of Alexandria; hereafter referred to as Muscat) — seeded;
(iii) Sultana (syn. Sultanina, Thompson Seedless) — stenospermocarpic;
(iv) Cape Currant (known locally as Tunn Currant) — parthenocarpic;
(v) Zante Currant (syn. Black Corinth) — parthenocarpic.

The experimental unit chosen was a single shoot with one cluster attached. Besides being expedient, this had the merit of reducing the interaction of treatment effects with whole vine yield.

The design of the 1966—67 (year 1) experiment was a 3×4 factorial in a randomised block, replicated 10 times. CCC was applied at rates of 0, 100, and 1000 mg/l, in combination with GA at 0, 0.2, 2.0 and 20.0 mg/l. All treatments included 0.075 per cent (v/v) "Agral 60" as a wetting agent, and were applied to clusters as a dip at the one time, about two weeks before anthesis. The vines, which were trained to four arms on a "T" trellis system, were divided into quarters, one per cordon. One cluster was selected per cordon and the twelve treatments were randomized between three adjacent vines which were selected to minimise between-vine variation. Muscat, Cape and Zante Currant were used.

The 1967—68 (year 2) experiments were more comprehensive and included a comparison of time of treatment. CCC at concentrations of 0, 50 and 2000 mg/l was applied in factorial combination with GA at 0, 0.5 and 20 mg/l. "Tween 20" 0.05 per cent (v/v) was included as a wetting agent. The treatments were applied as a dip to single clusters, nine of which were randomly selected on a single vine. The treatments were applied at the following five combinations of application times:

(i) CCC early, GA early;
(ii) CCC early, GA at anthesis;
(iii) CCC early, GA late;
(iv) CCC late, GA early;
(v) CCC late, GA late.

"Early" and "late" mean approximately two weeks before and after anthesis respectively, the latter being when berry setting occurs. Each time-combination was allotted to single vines and the whole was replicated in a randomised block design (10 times on Muscat, Sultana, Cape and Zante Currant; 8 times on Doradillo).

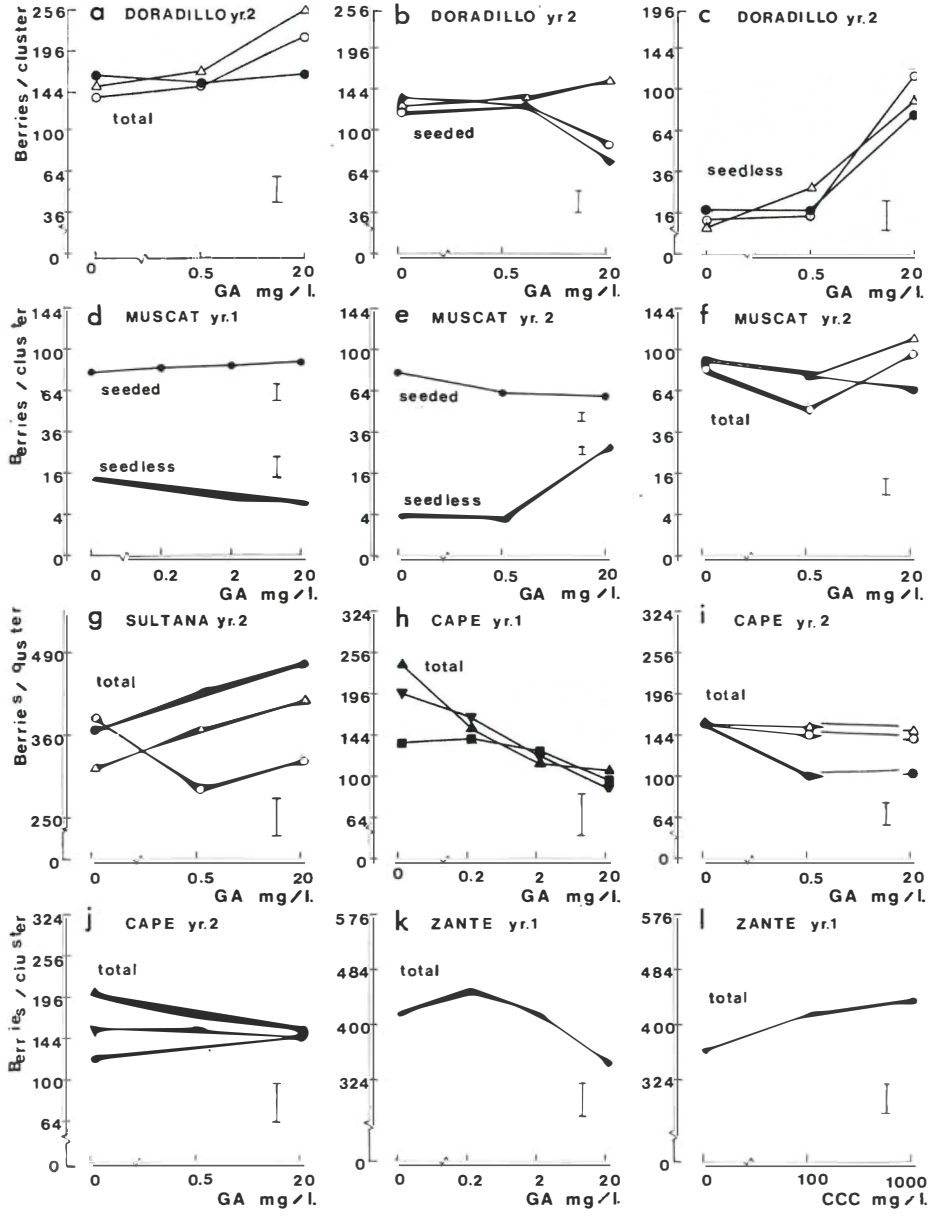

Fig. 1: The effect of GA and CCC on the number of berries set in five cultivars.
a, b, c, f, g, and i. Effect of GA applied two weeks before anthesis (●), at anthesis (o) or two weeks after anthesis (△). Each point is the average of the three concentrations of CCC, applied pre-anthesis.
d, k. Effect of GA applied two weeks before anthesis. Each point is the average of the three concentrations of CCC used.
e. Effect of GA. Each point is the average of the three times of application of GA and the three concentrations of CCC, applied pre-anthesis.

The clusters were harvested at maturity or a little before, and were placed in a cool store until they were measured, generally within the next ten days.

Fresh weight and length of each cluster were measured, and then the seeded and seedless berries were counted; the presence of seeds was determined by candling the berries, and was checked occasionally by opening. The presence of any hardened structures was used as the criterion for seedness, and thus the term, as used here, does not mean that the seeds were viable. Pedicel length was measured on five or ten randomly chosen pedicels. Berry length and width were obtained from a random sample of ten berries. Refraction of the juice squeezed from these ten berries was used to measure sugar content; it was determined at room temperature and expressed as degrees Brix.

The 1966—67 results were analysed as a two-way factorial with 119 degrees of freedom. The 1967—68 analysis was carried out using an extended version of the Wellesbourne-Waite "Genstat" computer programme. The results were analysed as a split-plot with the differences between the major plots (vines) being removed first to assess differences between the time-combinations. A factorial analysis of GA × CCC was carried out within the major plots; because of limitations imposed by the computer programme, main effects and the interaction of each with time of application are confounded and thus the F ratios are based on the sum of the main effect and the interaction, that is, a significant F ratio may be caused by significance of the effect of GA and CCC and/or a significance of their interaction with time of treatment. These have been discriminated by Least Significant Difference (L.S.D.) values. The total number of degrees of freedom was 499 except for Doradillo, 359. Transformations were used where they improved the homogeneity of the data and it will be noted that the ordinate scale in the figures is sometimes non-linear.

In presenting these data, preference has been given to averages rather than individual values where the interaction was not significant. This applies wherever the three concentrations had an equal tendency as was often the case with CCC.

Results

a) Fruit set

Pre-anthesis application of GA increased the total number of berries set in the stenospermocarpic Sultana (Fig. 1g), decreased set in the parthenocarpic Cape and Zante Currant (Figs. 1h, 1i, 1k, Table 1), and had no effect on the two seeded cultivars (Figs. 1a, 1f). Anthesis application of GA increased the set of berries in Doradillo (Fig. 1a), had no effect on Muscat (Fig. 1f), Cape Currant (Fig. 1i), or Zante Currant (Table 1), and decreased set in Sultana (Fig. 1g). Post-anthesis applications of GA increased set in cultivars other than the wholly parthenocarpic (Fig. 1a, 1f, 1g, 1i, and Table 1).

With the seeded cultivars in the 1967-8 experiments the number of seedless berries set was increased by GA at any of the application times (Figs. 1c and 1e). At the same time, the set of seeded berries was decreased except in the case of the post-anthesis GA on Doradillo (Figs. 1b, 1c, Table 1).

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h. Effect of GA and CCC both applied two weeks before anthesis; CCC nil (■), CCC 100 mg/l (▼) and CCC 1000 mg/l (▲).

j. Effect of CCC applied two weeks before anthesis on the response to GA applied two weeks after anthesis; CCC nil (■), CCC 50 mg/l (▼) and CCC 2000 mg/l (▲).

l. Effect of CCC. Each point is the average of the three concentrations of GA used.

Table 1

The general effect, relative to untreated, of GA applied early (E, 2 weeks before anthesis), mid (M, at anthesis) and late (L, 2 weeks after anthesis) and of CCC applied early and late. 1967-8 experiments

Parameter		Doradillo					Muscat					Sultana				
		GA			CCC		GA			CCC		GA			CCC	
		E	M	L	E	L	E	M	L	E	L	E	M	L	E	L
Fruit set	— Seeded	−−	−	+	+	0	−−	−−	−	+	0					
	— Seedless	++	++	++	0	0	++	++	++	0	0	+	−	+	+	0
	— % Seedless	++	++	++	0	0	++[1]	++	++	0[1]	0					
	— Total	0	+	++	(+)	(+)	0	(−)	+	+	0					
Fresh weight	— Seeded	0	0	0	−	−	0[1]	0	0	−−	−−					
	— Seedless						0[1]	0	+	0[1]	−	0	+	++	−	0
Length	— Seeded	0	0	0	−	−	+[1]	++	+	−−	−−					
Width	— Seeded	0	0	0	−	−	−−	−	0	−−	−−					
Length/width	— Seeded	+	+	0	0	0	++	++	+	−	0					
Length	— Seedless						+[1]	+	++	(−)	−	0	++	++	−−	0
Width	— Seedless						0[1]	0	++	0	−	0	+	++	0	0
Length/width	— Seedless						+	++	0	0	0	0	++	+	−	0
Sugar (refract.)	— Seedless											0	0	−	0	0
Rachis length		0	+	+	0	0	+	+	0	0[1]	0	++	+	+	(−)	(−)
Pedicel length																
Cluster weight		−−	−	++	0	0	−	0	0	0	−	0	0	++	0	0

+, —, 0: Indicates the direction of the response, that is, whether the parameter increased (+), decreased (—) or was unaffected (0) by increasing concentrations of GA and CCC. Single signs denote significant effects and double signs indicate large and highly significant effects.
( ): Indicates uncertainty in the assessment due to different effects of high and low concentrations:
1, 2, 3: 1966-7 experiments show different trends: negative (1), nil (2) or positive (3).
Open spaces: Not measured.

(Continued from Table 1)

Parameter		Cape Currant GA E	GA M	GA L	CCC E	CCC L	Zante Currant GA E	GA M	GA L	CCC E	CCC L
Fruit set	– Seeded	–	–	–	+	–					
	– Seedless	–	0	0	++	0	0[1]	0	0	0[3]	0
	– % Seedless	+	+	0	–	–					
	– Total	–	0	0	++	0					
Fresh weight	– Seeded										
	– Seedless	++	++	++	0	0	+	++	++	0	0
Length	– Seeded										
Width	– Seeded										
Length/width	– Seeded										
Length	– Seedless	++	++	+	0	0	+	++	+	–	–
Width	– Seedless	+	+	+	0	0	+	++	+	–	–
Length/width	– Seedless	++	++	0	0	0	0	++	+	0	0
Sugar (refract.)	– Seedless						+	0	–	(+)	–
Rachis length		++	++	0	–	0	++	++	+	0	0
Pedicel length							+	++	+	0	0
Cluster weight		+	++	+	(+)	0	0[3]	++	++	0	0

The application of CCC prior to anthesis generally increased set (Figs. 1h, 1j, 1l, and Table 1), while post-anthesis application did not. The increase in setting of Cape Currant following pre-anthesis CCC was associated with a lower proportion of seedless berries: the converse was true with GA (Table 1).

A significant interaction between CCC and GA was found on Cape Currant in 1966-7. This was due to the domination by GA of the CCC response (Fig. 1h). A similar result was obtained in 1967-8 in the same cultivar, but only when the GA was applied post-anthesis to a cluster that had received a pre-anthesis application of CCC (Fig. 1j).

b) Berry growth

In general, the two growth substances exerted opposite effects on berry size. GA had a large effect on the final weight of those berries in which seed development

Table 2

The effect of stage of development on the response of berry fresh weight (g) to the application of GA (20 mg/l, 1967—68)[1])

Type of berry	Nil	GA applied:			L.S.D. $P < 0.05$
		Pre-anthesis	Anthesis	Post-anthesis	
Doradillo, seeded	3.77	3.82 (+1)	3.82 (+1)	3.69 (—2)	0.25
Muscat, seeded	4.48	4.55 (+2)	4.72 (+5)	4.36 (—3)	0.38
Muscat, seedless	1.68	1.60 (—5)	1.80 (+7)	2.47 (+47)	0.30
Sultana, stenospermocarpic	1.98	1.90 (—4)	2.89 (+46)	3.43 (+73)	0.19
Cape Currant, parthenocarpic	0.60	1.51 (+151)	1.89 (+215)	1.37 (+128)	0.13
Zante Currant, parthenocarpic	0.32	0.48 (+50)	1.40 (+337)	0.94 (+194)	0.07

[1]) All values are averages of the CCC pre-anthesis results only.
( ) Percentage change from nil.

was imperfect. The magnitude of this effect depended on concentration, cultivar, and the time of application: in the parthenocarpic cultivars the response was greatest to an anthesis application, but in the berries in which some seed development occurred (the stenospermocarpic Sultana and the seedless Muscat berries) the greatest response was from an application of GA after anthesis (Table 2). GA had no effect on berry weight in cases where it did not prevent complete seed development (Table 1) though in one instance it did reduce the average weight of seeded berries significantly (Muscat 1966-7, see Fig. 2a).

CCC reduced berry weight in all cases, the effect being highly significant on seeded berries (Table 3). Both times of application showed this reduction though on seedless cultivars the effect of pre-anthesis application was slightly greater than at post-anthesis.

GA significantly increased the length/width ratios of berries, especially when applied at anthesis (Table 4). The degree of response was unrelated to seed development. Cape Currant was the most responsive while Muscat, Sultana, and Zante

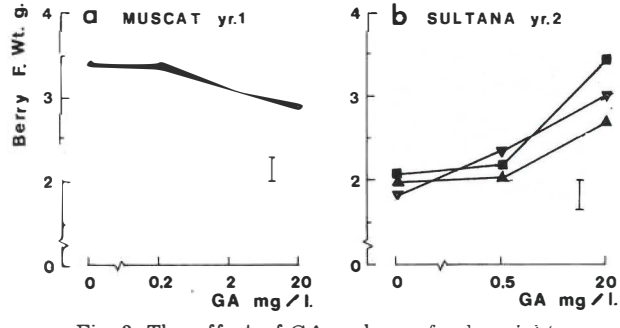

Fig. 2: The effect of GA on berry fresh weight.
a. Effect of GA applied two weeks before anthesis. Each point is the average of three concentrations of CCC used.
b. Effect of CCC applied two weeks before anthesis on the response to GA applied two weeks after anthesis; CCC nil (■), CCC 50 mg/l (▼) and CCC 2000 mg/l (▲).

Table 3

The effect of stage of development on the response of berry fresh weight (g) to the application of CCC (2000 mg/l, 1967—68)[1])

Type of berry	Pre-anthesis		Post-anthesis		L.S.D. $P < 0.05$
	Nil	CCC	Nil	CCC	
Doradillo, seeded	3.68	3.28 (—11)	3.78	3.25 (—14)	0.17
Muscat, seeded	4.46	3.61 (—19)	4.39	3.66 (—17)	0.27
Muscat, seedless	1.75	1.60 (—9)	1.84	1.47 (—20)	0.24
Sultana, stenospermocarpic	2.23	1.95 (—13)	2.46	2.36 (—4)	0.14
Cape Currant, parthenocarpic	0.97	0.91 (—6)	1.05	0.99 (—6)	0.09
Zante Currant, parthenocarpic	0.48	0.41 (—15)	0.51	0.50 (—2)	0.05

[1]) All values are averages of both pre- and post-anthesis GA applications.
( ) Percentage change from nil.

Table 4

The effect of GA (20 mg/l) applied at anthesis and CCC (2000 mg/l) applied pre-anthesis on length/width ratio of berries

Type of berry	Nil	GA	CCC	L.S.D. $P < 0.05$
Doradillo, seeded	0.97	0.99 (+2)	0.97 (0)	0.01
Muscat, seeded	1.11	1.28 (+15)	1.09 (—2)	0.03
Muscat, seedless	1.11	1.25 (+12)	1.13 (+2)	0.04
Sultana, stenospermocarpic	1.23	1.43 (+16)	1.18 (—4)	0.03
Cape Currant, parthenocarpic	1.05	1.45 (+38)	1.02 (—3)	0.04
Zante Currant, parthenocarpic	1.02	1.18 (+16)	1.01 (—1)	0.02

( ) Percentage change from nil.

were less so. Doradillo was the least affected, although the small effect was highly significant. The elongation of seeded Muscat berries was not accompanied by a change in berry weight (Table 1). The similarity between the responses of Sultana and seedless Muscat berries shown in Table 1 is noteworthy. These data also show that post-anthesis application of GA had as large an effect on berry length as did anthesis treatment but berry width was also increased so that the length/width ratios were influenced less.

CCC significantly reduced the length/width ratio of Sultana berries but only when applied before anthesis (Table 4).

The effects of treatments on the "sugar" concentration of juice were various: With Sultana, GA 20 mg/l applied post-anthesis decreased berry sugar significantly (13.7° Brix to 12.9° in one instance and 14.6° to 12.5° in the other). A pre-anthesis application of GA significantly increased the sugar concentration of Cape Currant berries (Fig. 3a). With Zante Currant, GA treated berries had an increased con-

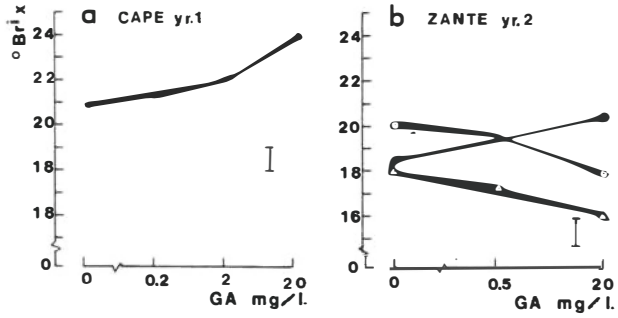

Fig. 3: The effect of GA on the refractive index of the juice (expressed as °Brix).
a. Cape Currant and b. Zante Currant.
GA was applied two weeks before anthesis (●), at anthesis (0) or two weeks after anthesis (△).
Each point is the average of the three concentrations of CCC, applied pre-anthesis.

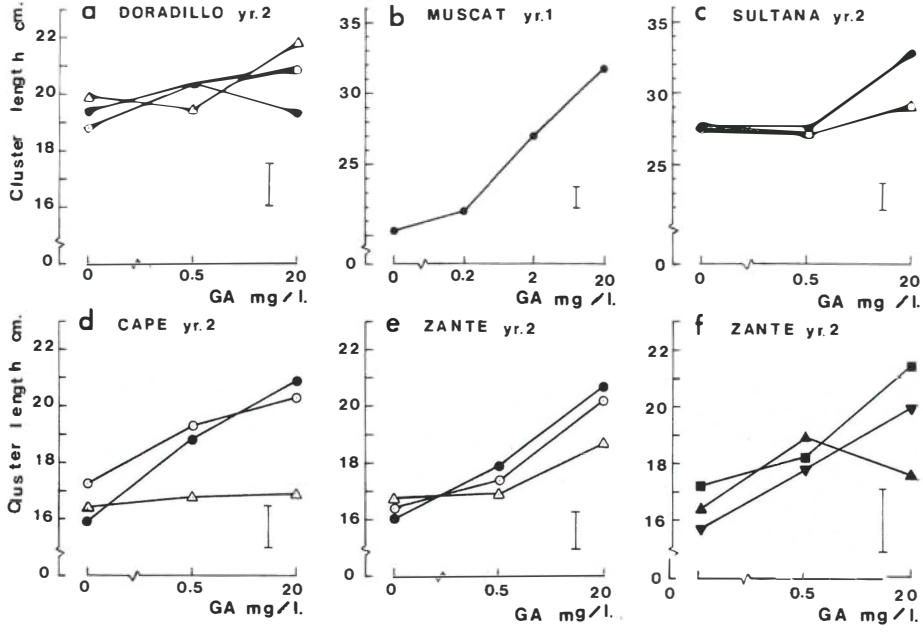

Fig. 4: The effect of GA and CCC on cluster length.
a to e. Effect of GA applied two weeks before anthesis (●), at anthesis (0) or two weeks after anthesis (△). Each point is the average of the three concentrations of CCC, applied pre-anthesis.
f. Effect of GA and CCC both applied two weeks before anthesis; CCC nil (■), CCC 50 mg/l(▼) and CCC 2000 mg/l (▲).

centration of sugar if the treatment was applied pre-anthesis but a decreased level if applied post-anthesis (Fig. 3b). A similar trend was apparent for CCC treatments (Table 1).

c) Rachis and pedicel length

The lengths of the rachis and pedicel were often increased by GA, especially when applied pre-anthesis (Table 1 and Fig. 4a, 4b, 4c, 4d, and 4e). There was a

trend, sometimes significant, for CCC to retard the elongation of the rachis and pedicel (Table 1). In one instance (Zante Currant 1967-8) the response of rachis elongation to a pre-anthesis application of GA was offset by a post-anthesis application of CCC (Fig. 4f).

d) Cluster weight

Of the factors contributing to cluster weight, berry weight had the chief influence. GA increased cluster weight in the seedless cultivars; anthesis applications were the most effective for Cape and Zante Currant (Figs. 5d and 5e); post-anthesis treatment of Sultana gave the heaviest clusters (Fig. 5c). Pre-anthesis application of GA to seeded cultivars resulted in lowered cluster weights (Figs. 5a and 5b); this was due to an increased proportion of berries with inhibited seed development which weigh less. Later applications of GA to seeded cultivars did not reduce cluster weight (Fig. 5a and 5b); in fact, post-anthesis GA on Doradillo increased it. This was due to an increased set of berries (Fig. 1a), and presumably, to an increase in the weight of seedless berries (the latter was not measured but the presumption is based on the effect of GA on seedless Muscat berries — Table 2).

Discussion

In many perennial fruit plants, fruit setting is limited by the events leading to syngamy, namely, ovule development, ovule receptivity, pollination, pollen viability, and pollen tube growth (compatibility). This is not true in most cultivars of *Vitis vinifera* since fertilization is adequate; rather, it is suggested that the supply of

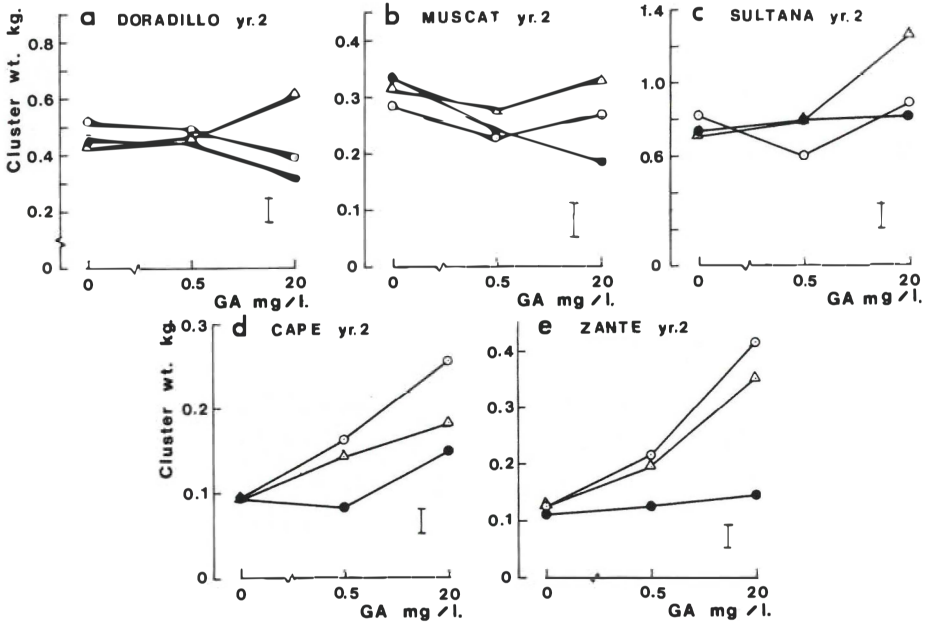

Fig. 5: The effect of GA on cluster weight.
GA was applied two weeks before anthesis (●), at anthesis (o) or two weeks after anthesis (△). Each point is the average of the three concentrations of CCC, applied pre-anthesis.

organic nutrients to the flowers is the prime determinant of set (Coombe 1959, 1962, 1965 b, 1970; Hale and Weaver 1962; Mullins 1967; Skene 1969). On this basis, factors affecting the source of organic nutrients (area of illuminated mature leaves, etc.) and the demands by competing sinks will affect setting. The chief competitor to flowers is the shoot tip since grape vines, unlike most deciduous fruits, bloom when the shoots are growing actively. However, all active meristems and regions of growth contribute to competition; hence the degree of cell division and enlargement within the berries themselves would influence the average demand per berry.

Within the framework of the foregoing ideas, is it possible to explain the effects of GA and CCC treatment on grape setting?

The following reactions can be explained on the basis of competition:

(1) Increases in set associated with a decrease in flesh growth and no apparent change in seed number and growth (and undoubtedly contributed to by a decrease in shoot growth; Coombe 1970): — Three of the five cultivars treated with CCC (Table 1).
(2) Decreases in set associated with an increase in flesh growth: — Cape Currant treated pre-anthesis with GA and Sultana treated at anthesis with GA (Table 1).

However, there were many setting reactions which can be regarded as anomalous to the concept of competition, for example:
(1) No change in set but an increase in berry size — Cape and Zante Currant treated with GA at or after anthesis (Table 1).
(2) Increased set but no decrease in seed or flesh growth — Doradillo treated with GA after anthesis (Table 1).
(3) Increased set but also an increased berry size — Sultana treated with GA after anthesis (Table 1).
(4) Disproportionate changes in berry set and size — Sultana treated with GA 0.5 mg/l at anthesis; similarly for Muscat compared with its response to 20 mg/l (Figs. 1f, 1g, Table 1).
All of these examples are associated with GA effects (see also Lynn and Jensen 1966; Mosesian and Nelson 1968; Christodoulou *et al.* 1968). They establish that GA has many effects on setting which are not inversely correlated with seed or pericarp growth. Moreover, any interaction with shoot growth is unlikely since GA treatment of inflorescences does not affect the growth of shoots (Weaver and McCune 1959 b, c).

Decreases in fruit set following GA treatment have been ascribed to reductions in pollen viability (Weaver and McCune 1960) and to interference with ovule development (Smirnov and Perepelitsyna 1965). Neither pollen viability nor ovule development was measured in the present experiments but both may have been affected since there was an increase in the percentage of seedless berries (Table 1).

How then can increases in setting by GA treatment be explained? Unlike CCC, GA rarely increased the set of seeded berries; most increases in the total number of berries set were attributable to seedless berries (Table 1). Weaver, McCune and Hale (1962) concluded that the control of set resides in a ratio between gibberellin and a fruit setting factor synthesised in the leaves. The latter may be the supply of photosynthate (Coombe 1965 b; Mullins 1967) though the possibility of a specific metabolite proportional in amount to total photosynthate cannot be eliminated. In any case, gibberellin's role is unexplained.

Crane (1964) concluded that hormones set parthenocarpic fruit by initiating an active gradient along which metabolites move to the fruit, thus stimulating growth. The movement of metabolites in response to the presence of growth substance has

been amply demonstrated (see for example MULLINS 1970); whether the movement is a direct effect of the growth substance and/or the result of the creation of a metabolic sink is, however, unresolved.

The degree of development of the seed has a pronounced effect on the responsiveness of the pericarp to GA. As shown in Table 2, berry size response is of three types: (1) No response to GA at any time of application, e. g. seeded berries of Muscat and Doradillo; (2) Berries enlarged most by GA applied after anthesis, e. g. stenospermocarpic berries of Muscat and Sultana; (3) Berries enlarged most by GA applied at anthesis, e. g. parthenocarpic berries of Cape and Zante Currants. Treatments made before anthesis had little effect on berry size except with parthenocarpic berries, as has been noted also by WEAVER and MCCUNE (1959 a, c) and ZULUAGA *et al.* (1968). Responsiveness of the pericarp seems to be connected with anthesis and the development of the seed. In parthenocarpic berries pollination enhances the response to growth regulators (WEAVER and MCCUNE 1960) while in stenospermocarpic berries maximum responsiveness appears to coincide with the cessation of embryo development.

There are varietal differences in the amount of seed development required to offset the stimulus of a post-anthesis application of GA; thus Queen of the Vineyard berries respond if one or no seeds are present (LAVEE 1960), but in Muscat only one seed is required to offset the effect of GA (WEAVER, MCCUNE and HALE 1962). No attempt was made in the present experiments to separate berries into groups based on the number of seeds.

A simple explanation for the unresponsiveness to GA of berries in which seeds are developing is that sufficient gibberellin is synthesised endogenously after syngamy so that it does not limit pericarp growth. Recent measurements of endogenous gibberellin-like activity in cultivars of *Vitis* (IWAHORI *et al.* 1968; ITO *et al.* 1969; CONSIDINE 1970) have demonstrated that activity is greatest in seeded cultivars. ITO *et al.* (1969) were able to demonstrate that the amount of gibberellin-like activity in seedless berries treated externally with GA more nearly equalled that in seeded berries, particularly if the GA was applied after anthesis.

COOMBE (1965 a, 1967) observed that berry size is reduced by early application of CCC. In the present experiment, CCC treatment of the seeded cultivars reduced berry size in every case, that is, the effect was independent of the time of application used (Table 1). It seems inconsistent that no response can be obtained from the application of a promoter (GA) while size is reduced by a supposed inhibitor of the synthesis of that promoter (RADLEY 1967; REID and CARR 1967). Thus either gibberellins do not limit growth in seeded cultivars but are none the less essential, or CCC acts in some other way. It is suggested that abscisic acid (ABA) is the important additional factor in the hormonal control of pericarp growth.

There are three reasons for suggesting that ABA has this role in grape berries; (1) ABA has been shown to occur in grape berries (LOTT 1968; CONSIDINE 1970); (2) ABA concentration of berries is high at anthesis and gradually declines as berries develop (CONSIDINE 1970), and (3) treatment of grape flowers with CCC reduces the decline in ABA concentration but has no effect on the levels of gibberellins (CONSIDINE 1970). ABA inhibits cell expansion (THOMAS *et al.* 1964). It is quite conceivable that the control of pericarp cell expansion resides in an interaction between promoters (e. g. GA) and inhibitors (e. g. ABA) and that CCC affects only the latter.

All seedless berries were elongated by GA treatment (Table 4). However, only one seeded cultivar has been documented as responding; WEAVER and MCCUNE (1959 a) observed that Muscat berries treated with GA were elongated and this has

been confirmed by the present investigation. The effect of GA was to cause a redistribution of growth — the longitudinal axis was expanded and the equatorial axis was decreased. A supplement to this information is the observation that seedless Muscat berries show essentially the same qualitative response as Sultana berries (Table 4). In all cases where increases in length/width ratio were noted they were greatest when the GA was applied at anthesis (Table 1).

The degree of elongation caused by an anthesis application of GA bears no relation to the presence of seed or the normal length/width ratio (Table 4). The responses fall into three groups: (1) seeded Doradillo berries — a small but significant increase; (2) Muscat seeded and seedless, Sultana and Zante Currant, — approximately a 15 per cent increase; and (3) Cape Currant — a 38 per cent increase in length/width ratio in response to 20 mg/l GA. It can be seen that these groups are unrelated to the berry weight groups in Table 2.

Coombe (1960) and Harris *et al.* (1968) noted that cell division occurred in the pericarp mainly during the first two weeks after anthesis. That GA is most effective when applied before or concurrently with this cell division suggests that GA may affect berry shape by increasing cell division in the polar regions of the berry more than in the equatorial regions. Data supporting this hypothesis were obtained by Weaver and Sachs (1968). They demonstrated that in both Sultana and Zante Currant GA treatment resulted in an increase in both cell number and cell size. Examination of Zante Currant berries revealed that the stimulus was greatest to distal pericarp cells, thus the increase in berry length. Their study also indicates that berry shape is determined by the balance between applied gibberellin and applied auxin. As well, this offers an explanation for the effect of GA on berry shape in the seeded cultivars, since the balance between endogenous auxins and gibberellins would presumably be altered.

Clusters treated with GA two weeks prior to anthesis were elongated (Table 1, Fig. 4). Other authors have described this (Alleweldt 1959; Rives et Pouget 1959; Weaver and McCune 1959 a, b, c, 1962) and have referred to its practical implications since elongation of the rachis and pedicels should permit better aeration of the clusters and thus reduce the likelihood of damage due to moulds. However, the treatment has proved impractical due to the deleterious effect of GA on flower initiation on many cultivars (Weaver 1960, Julliard et Balthazard 1965). Sultana does not display this GA reduction of flower initiation but cluster compactness is not as serious a problem in this cultivar as in some of the seeded cultivars.

The observations in this investigation demonstrate that in all of the cultivars tested, GA application resulted in increased rachis elongation, but in only some instances were rachises significantly shortened by the application of CCC preanthesis (Table 1). An interesting observation (also noted by Weaver and McCune 1959 a, Coombe 1965 a) was that the application of GA in quantities greater than 20 mg/l tended to produce rachises that were coiled, toughened and thigmotropic. Since tendrils and reproductive clusters of *Vitis* originate by divergent development of the same structure this result may have bearing on the physiology of tendril growth.

In general GA dominated the CCC effect though not always completely. Recently, El-Zeftawi and Weste (1970) demonstrated that GA and CCC can be usefully employed together to increase the yield of Zante Currant vines. In this instance the concentrations and time chosen have produced only partial domination of the set effect of CCC by GA (Considine and El-Zeftawi 1971; El-Zeftawi and Weste, unpublished data). The joint use of these two compounds in practical viticulture will

require the careful examination of the generally dominant effect of GA and the observation that in some instances CCC treated clusters were less responsive to GA.

Summary

The effects of applications of GA and CCC in factorial combinations and at different stages of development were measured on reproductive development of five cultivars of *Vitis vinifera:* Doradillo and Muscat (seeded), Sultana (stenospermocarpic), and Cape Currant and Zante Currant (parthenocarpic).

The effect of GA on fruit set varied with concentration, stage of development when applied, and the cultivar, that is whether seeded, stenospermocarpic, or parthenocarpic. Set was decreased in the parthenocarpic cultivars by GA applied before anthesis; other timings were without effect. On Sultana, set was decreased by GA applied at anthesis but was increased by earlier or later applications. With the seeded cultivars, GA reduced the number of seeded berries but increased the number of seedless berries, the net effect being usually an increase. The application of CCC two weeks before anthesis generally increased set.

The amount of seed development also influenced the effect of GA on berry fresh weight; seeded berries were unaffected but seedless berries were usually enlarged. The enlargement was greatest in parthenocarpic berries especially when treated at anthesis. On stenospermocarpic berries, treatment two weeks after anthesis had the greatest effect. CCC reduced berry size whether applied before or after anthesis; the reductions ranged from 2 to 20 per cent.

GA increased the length/width ratio of berries, particularly when applied at anthesis, but the amount of change depended on the cultivar. CCC reduced the length/width ratio of Sultana berries. The effects of GA and CCC on rachis elongation were also opposite: GA increased the length of the rachis and pedicel, particularly if applied before anthesis; CCC reduced their length.

There were few instances where GA and CCC interacted significantly; their effects within the concentration ranges chosen were generally additive.

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