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Exogenous Gibberellin as Responsible for the Seedless Berry Development of Grapes.

V. Effects of 6-Benzyl Adenine Applied with Gibberellin on the Induction of Seedless Fleshy Berries in Delaware and Campbell Early Grapes.

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Summary

Recently in Japan, 6-benzyl adenine (BA) has been put to practical use for the production of seedless Delaware berries as an adjuvant to gibberellin (GA). In this paper, the effects of BA added to GA on the induction of seedlessness and seedless berry development in grapes were investigated. The addition of BA to the prebloom application, was effective not only on the induction and development of seedless fleshy berries, but also on the increase of their average weight. These effects were recognized in both cultivars of Delaware and Campbell Early, and seemed to be due to the delay of the lowering of applied GA activity on blossom buds and flowers and to be associated with the promotion of the development of flowers, and especially of the pistils.

The effects of BA on the accumulation of assimilates and the development of pistils are discussed in relation to GA from a physiological viewpoint.

The addition of 6-benzyl adenine (BA) to the prebloom application of GA was explained as being used to stabilize the effects of GA and increase the berry set and the berry development.

In Muscat Bailey A (6), perfect- and imperfect-hermaphroditic flowers and male flowers develop under field conditions. BA application 2-3 weeks before anthesis promoted the pistil development and increased the frequency of perfect-hermaphroditic flowers and in addition the subsequent application of GA increased the rate of seedless (fleshy) berries at harvest as compared with the application of GA alone.

Also in the male type wild strains of *Vitis*, BA was reported to be able to induce the pistil development (9-15).

Moreover, as an effect of BA, an increase of the movement of 14-C assimilates into the BA treated portion were demonstrated in the grapes by some workers (22-26).

In the previous papers (2, 3), the authors reported that the change of the GA activity as its application had an influence on the blossom bud development, and consequently the flower size at anthesis, which seemed to be related to the seedless berry development.

In this paper, we attempted to elucidate the effects of the addition of BA to GA on the induction of seedlessness and the development of seedless fleshy berries through its effect on the change of applied GA activity, the growth of pistils and the sugar contents of the flowers.

Materials and Methods

Two cultivars, Delaware and Campbell Early, were used. The vines were grown in the vineyard of Tohoku University in Sendai, and were 11 years old on the first year of the experiments, which were carried out over three years from 1972 to 1974. Inflorescences were thinned out before GA and/ or BA application, so that one inflorescence was borne on a current shoot in Campbell Early and two inflorescences in Delaware.

GA solution was prepared as described in the previous papers (1, 2). BA solution provided by the Kumiai Kagaku Co., Ltd. (3 per cent in net contents) was diluted with deionized water to the desired concentrations. Aerol OP was added in 100 ppm as a wetting agent.

In each experiment four treatments were made as follows; 1. GA 100 ppm, 2. GA 100 ppm+BA 100 ppm, 3. BA 100 ppm. 4. Untreated (the control). In each treatment ten inflorescences as a group were used. The test solutions were applied by dipping to the separate groups at intervals of 2-5 days starting from 30 days before the expected full bloom day of the untreated inflorescences. Application dates, however, are expressed hereafter by the number of days counted back from the actual full bloom day of the untreated inflorescences.

Percentage distribution of seeded berries, seedless fleshy berries and shot berries in each harvested inflorescences were calculated as described in the previous paper (1).

The effects of the addition of BA on the weight of blossom buds and flowers, and GA activity in them were most conspicuous when applied 2-4 days earlier than the most suitable time of the application of GA alone (about two weeks before full bloom), then, they are represented for the inflorescences treated 18-20 days before the full bloom day of untreated inflorescences.

Blossom buds were sampled every two or three days, from immediately after the treatment to the beginning of flowering. Average flower weights were recorded on the day of anthesis in each inflorescence throughout the flowering period. The weight of blossom buds or flowers and the GA activity of them are expressed per 100 blossom buds or flowers.

In Campbell Early, 500 blossom buds and 500 flowers were sampled on May 31

and June 3, respectively, from the inflorescences treated on May 24, 1973. The weight of floral organs (calyptra, stamens, pistil and receptacle) was measured separately, and the GA activity of each of them was bioassayed.

The bioassay of GA activity in blossom buds, flowers and each floral organ was carried out with the same method as described in the previous paper (2).

On the flowers at anthesis of Campbell Early, soluble solid in 80 per cent ethanol, insoluble solid and total solid were determined. In addition, on the 80 per cent ethanol soluble fraction total invert sugar, reducing sugar and non-reducing sugar were determined. Sugar determinations were carried out with the same method as described in the previous paper (3).

Results

1. Development of Seedless Berries as Affected by Application Dates.

As shown in Fig. 1 and 2, GA+BA, as compared with GA alone, increased the ratio of seedless fleshy berries in Delaware when applied earlier than the most suitable time for the application of GA alone. Thus, in GA+BA, the ratio was 8–14 per cent higher when applied earlier than 18 days before the full bloom of the untreated inflorescences. Also it exceeded 50 per cent when applied 20 to 12 days before the full bloom day, as compared with 18 to 10 days in GA alone. The highest value of the ratio, however, differed only a little between the two treatments.

In Campbell Early the seedlessness can be induced easily by GA, but most of the seedless berries remain as shot (berries), though some of them become fleshy.

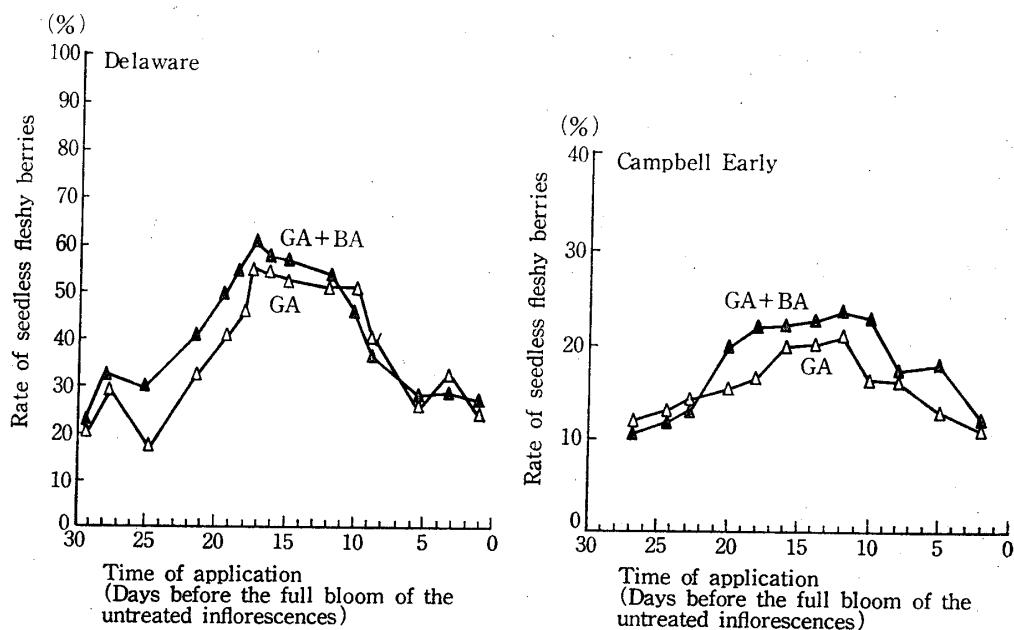


FIG. 1. Effects of the time of prebloom application of BA with GA on the rate of seedless fleshy berries.

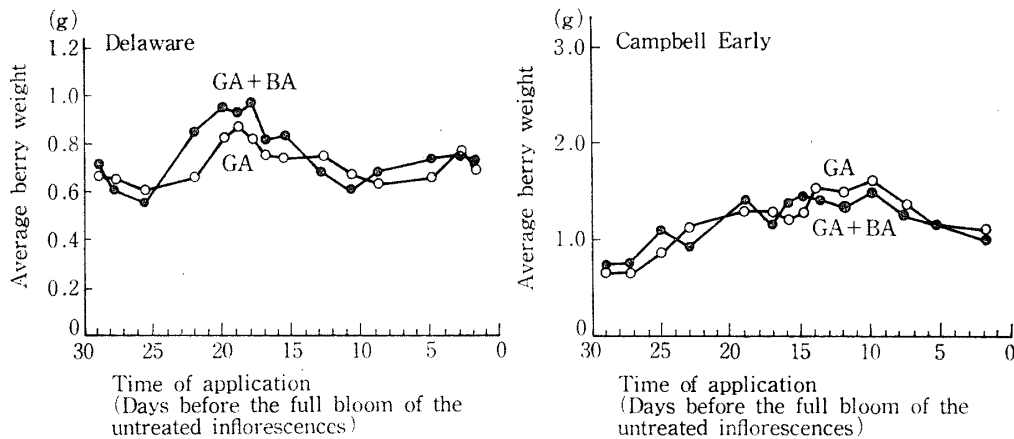


FIG. 2 Effects of the time of prebloom application of BA with GA on the average weight of seedless fleshy berry.

In this cultivar, the addition of BA increased the ratio of the seedless berries except for very early application. Contrary to Delaware, however, the average weight of the seedless fleshy berries, was not affected by the addition of BA.

The application of BA alone was not effective in inducing seedlessness in both cultivars.

2. Development of Blossom Buds, Flowers and Floral Organs.

The growth of blossom buds towards anthesis affected by GA and/or BA application is shown in Fig. 3.

As is shown most evidently when applied 20 days before the full bloom, GA+BA increased the blossom bud growth more remarkably and consequently resulted in larger flowers than GA alone. But the effects of GA on the prolongation of the flowering period and on the hastening of the flowering, which had been shown in the previous paper (1), were not increased by the addition of BA in our experiment. The application of BA alone increased the blossom bud growth slightly compared with the control.

Average daily flower weight at anthesis throughout the flowering period of each inflorescence is shown in Fig. 4, and in Fig. 5 their total average is shown. It is evident from Fig. 4, that daily flower weight had a clear peak early in the flowering period, especially following GA or GA+BA application.

It is also evident that the application of GA alone or GA+BA increased the weight of the flower at anthesis (Fig. 4) as well as hastened the flowering without changing the flowering pattern. Daily and the total average flower weight (Fig. 5) were larger when applied with GA+BA compared with GA alone. Application of BA alone increased the flower weight slightly.

Weight of each floral organ (calyptra, stamens, pistil and receptacle) of blossom buds and flowers of Campbell Early and their relative values are shown in

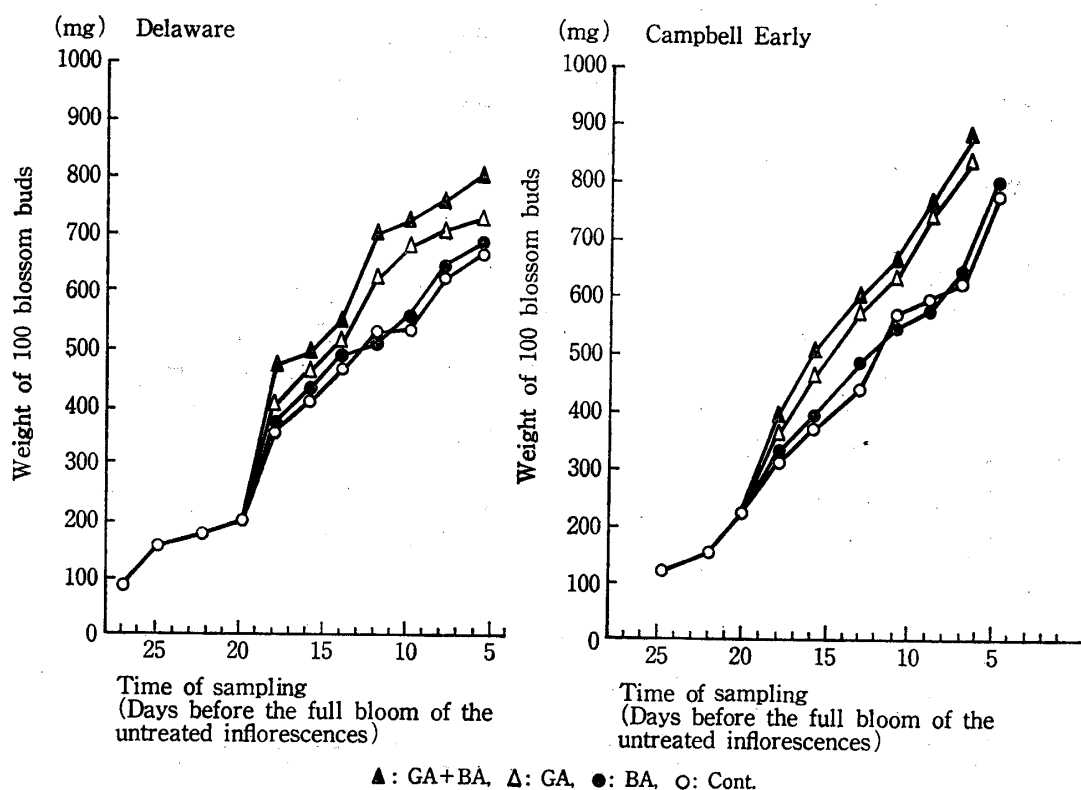


Fig. 3. Effects of BA and/or GA on the blossom bud development. (GA and/or BA was applied 20 days before the full bloom of the untreated inflorescences)

Fig. 6 and Table 1, the growth of pistil and next of the calyptra were promoted remarkably by the application of GA and/or BA, while stamens and receptacle were less affected. In consequence, a clear increase was found especially in the weight of the pistil of the flowers applied with BA and/or GA.

3. Activity of GA in Blossom Buds and Flowers Affected by the Addition of BA.

Fig. 7 shows the change with time of the biological activity of applied GA affected by the addition of BA in the blossom buds. It is evident from Fig. 7 that the GA activity in GA treated blossom buds decreased with time after its application towards flowering but the decrease was delayed considerably when BA was added to GA. In the blossom buds applied with BA alone and those untreated, GA activity was low and almost constant towards flowering.

Using the daily flower samples in Fig. 4, GA activity was bioassayed throughout the flowering period. The results are shown in Fig. 8. GA activity in the flowers applied with GA or GA+BA, changed with the day of anthesis, and showed a peak corresponding to that in their average weight in Fig. 4. In addition, GA activity was kept always higher in the flowers applied with GA+BA than with GA

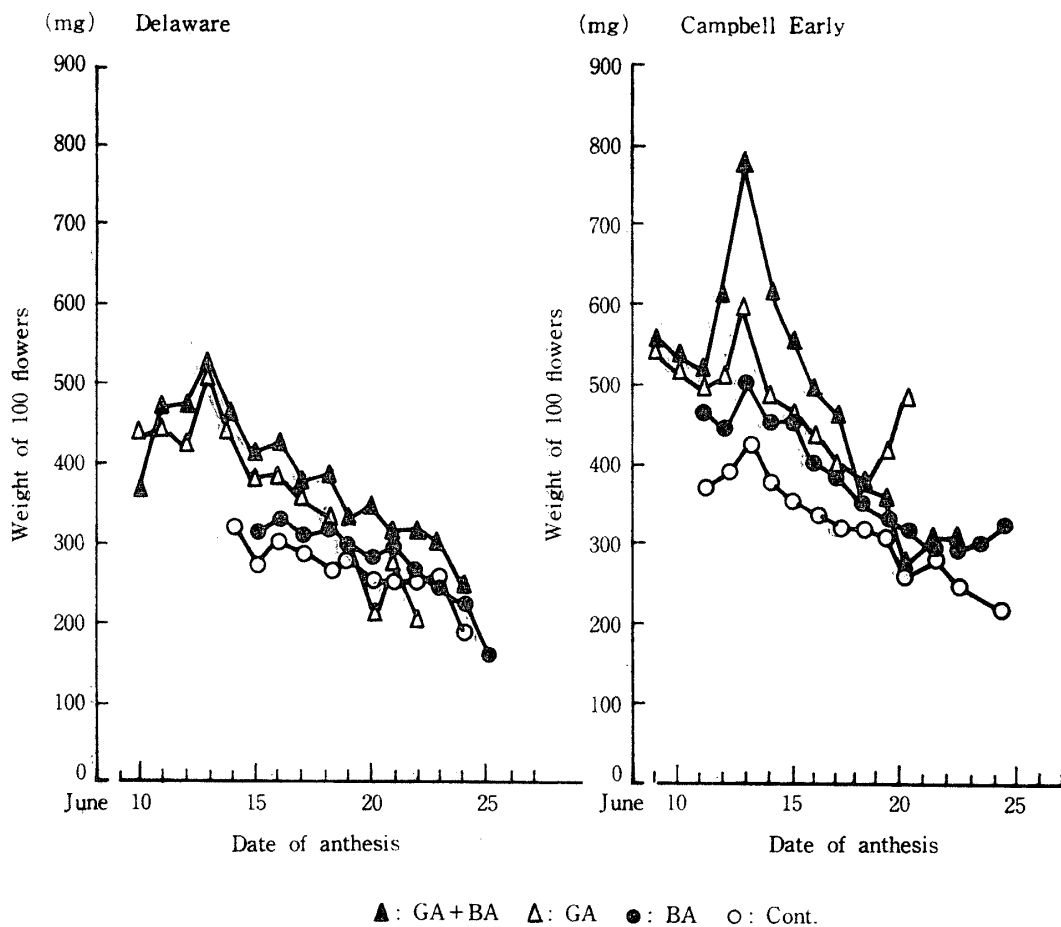


FIG. 4. Effects of BA and/or GA on the daily flower weight throughout the flowering period within an inflorescence.

alone in both cultivars, while in the flowers treated with BA alone and in untreated flowers, it was kept low throughout the flowering period.

GA activity in each floral organ in Campbell Early is shown in Fig. 9 and Table 1. Among floral organs, the activity was higher in the pistil and calyptra, and also higher when treated with GA+BA than with GA alone.

GA activity, when examined per unit weight, was the highest in the pistil as is shown in Table 2.

4. Solid and Sugar Contents of Flowers.

As is shown in Fig. 10, concentrations of solids and sugars in flowers applied with GA were inferior to those in the untreated control.

It is notable that the addition of BA increased the solids and sugars concentrations in the flowers, although their concentrations were inferior to (for sugars) or no more than (for solids) those in the untreated control. But the fresh weight of the flowers applied with GA or GA+BA was so high that the amounts of solids and sugars contained in them were greater than those in the untreated flowers.

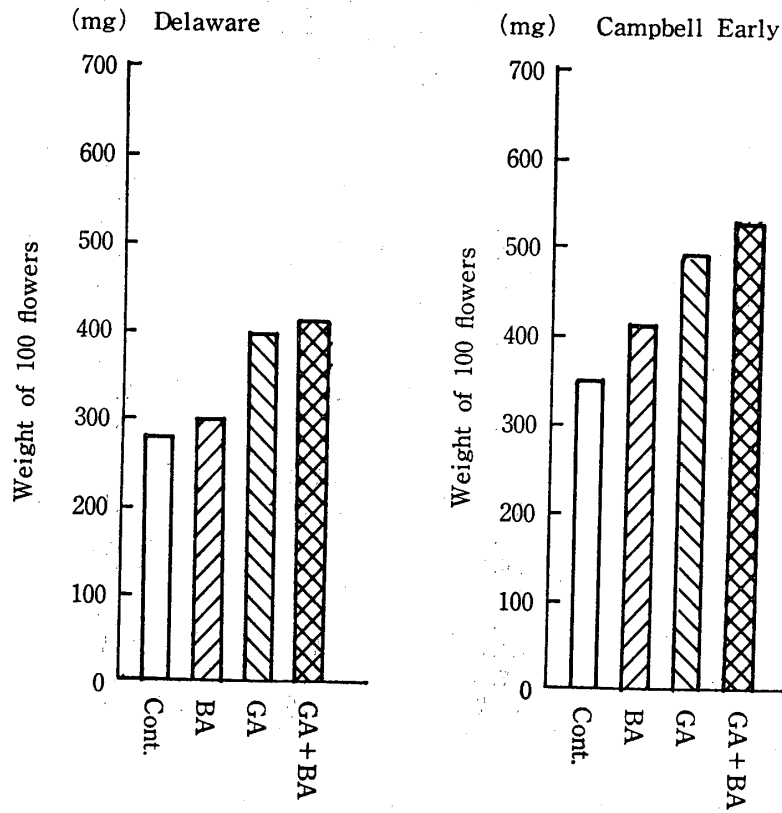


FIG. 5. Effects of BA and/or GA on the total average of flower weight.

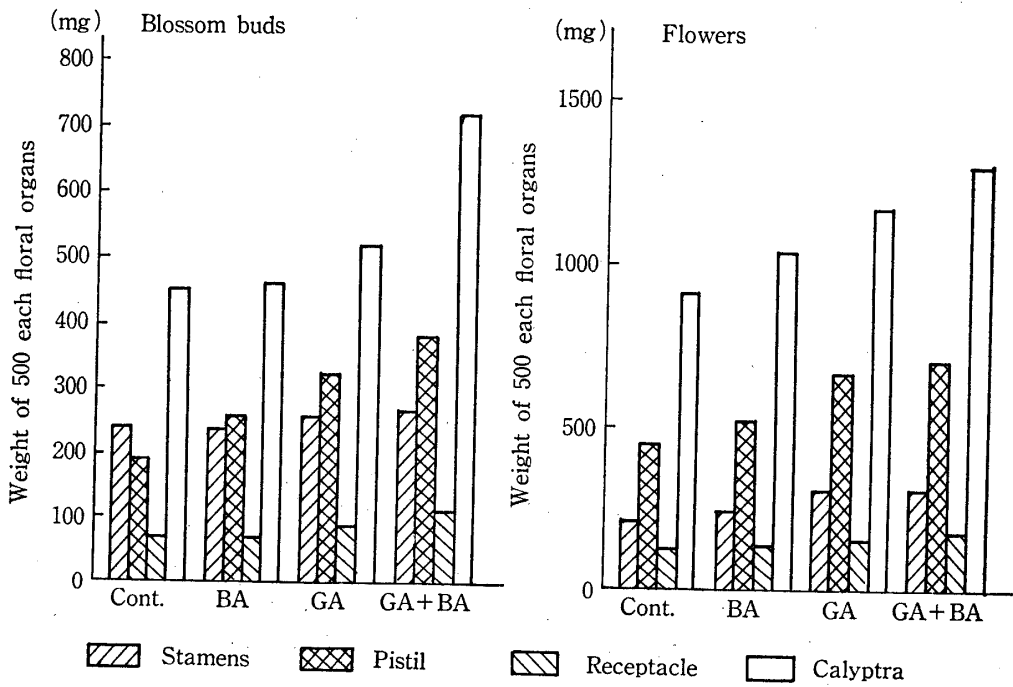


FIG. 6. Effects of BA and/or GA on the weight of floral organs in Campbell Early.

TABLE 1. *Relative Weight and Relative GA Activity of Each Floral Organ in Blossom Buds and Flowers as Affected by BA and/ or GA.*

Treatment	Flower Organs	Weight		GA activity	
		Blossom bud	Flower	Blossom bud	Flower
Untreated	Stamens	100.0	100.0	100.0	100.0
	Pistil	100.0	100.0	100.0	100.0
	Receptacle	100.0	100.0	100.0	100.0
	Calyptra	100.0	100.0	100.0	100.0
BA	Stamens	95.8	104.8	100.0	88.0
	Pistil	132.4	115.9	100.0	100.0
	Receptacle	100.0	108.3	107.1	86.3
	Calyptra	103.4	114.4	113.6	102.1
GA	Stamens	106.3	157.6	140.0	88.0
	Pistil	173.0	150.0	191.7	217.4
	Receptacle	121.4	133.3	138.1	127.3
	Calyptra	116.9	130.0	322.7	202.1
GA+BA	Stamens	112.5	151.9	200.0	88.0
	Pistil	204.3	157.0	166.7	226.1
	Receptacle	157.1	150.0	261.9	118.2
	Calyptra	160.7	145.6	213.6	202.1

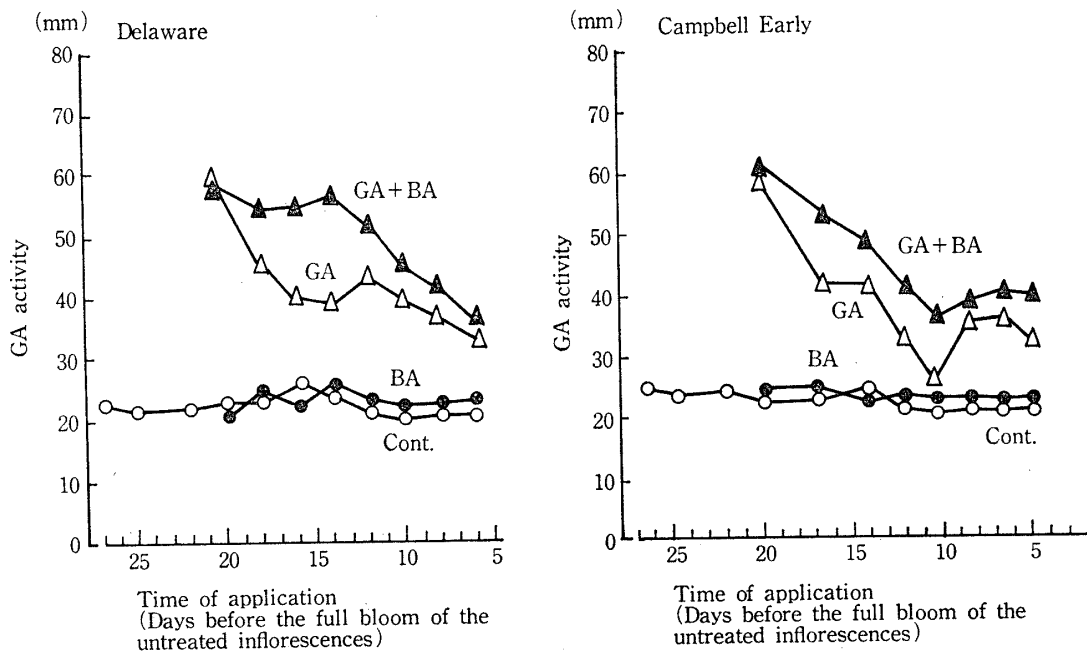


FIG. 7. Effects of BA and/or GA on the change of GA activity with time in blossom buds. (GA activity was shown by the length of the second leaf sheath of rice seedling.)

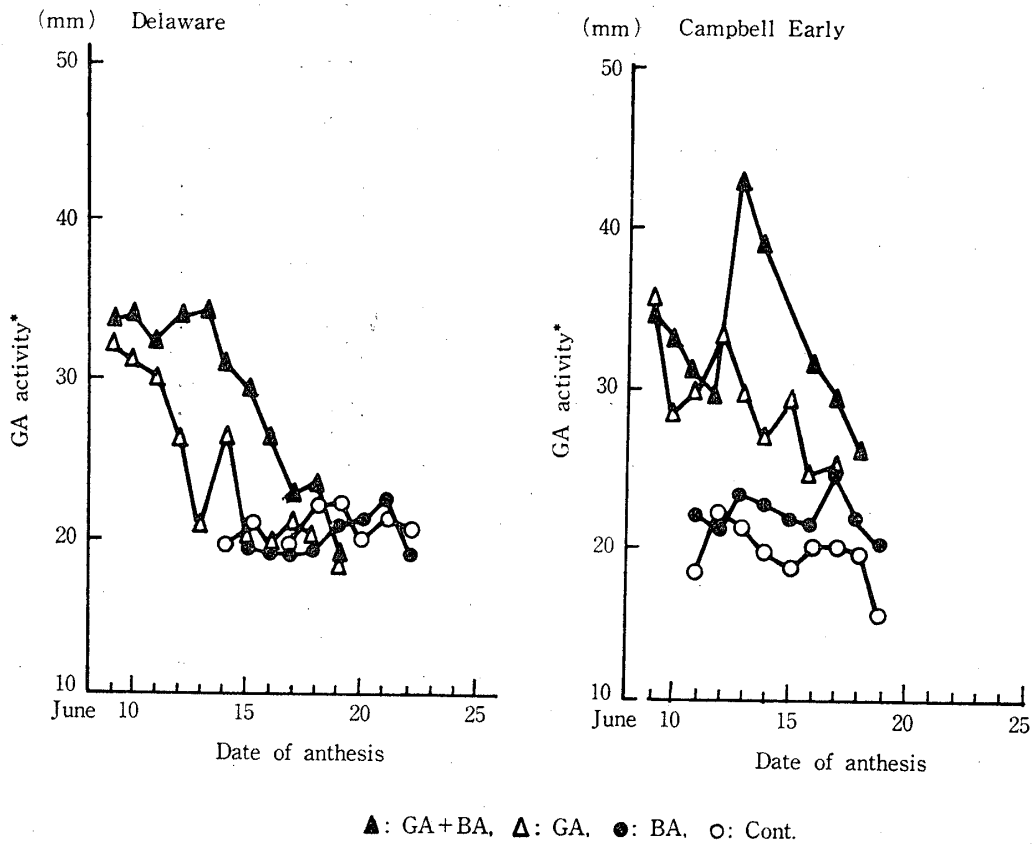


Fig. 8. Effects of BA and/or GA on GA activity in flowers throughout the flowering period. (* shown in the same way as in Fig. 7)

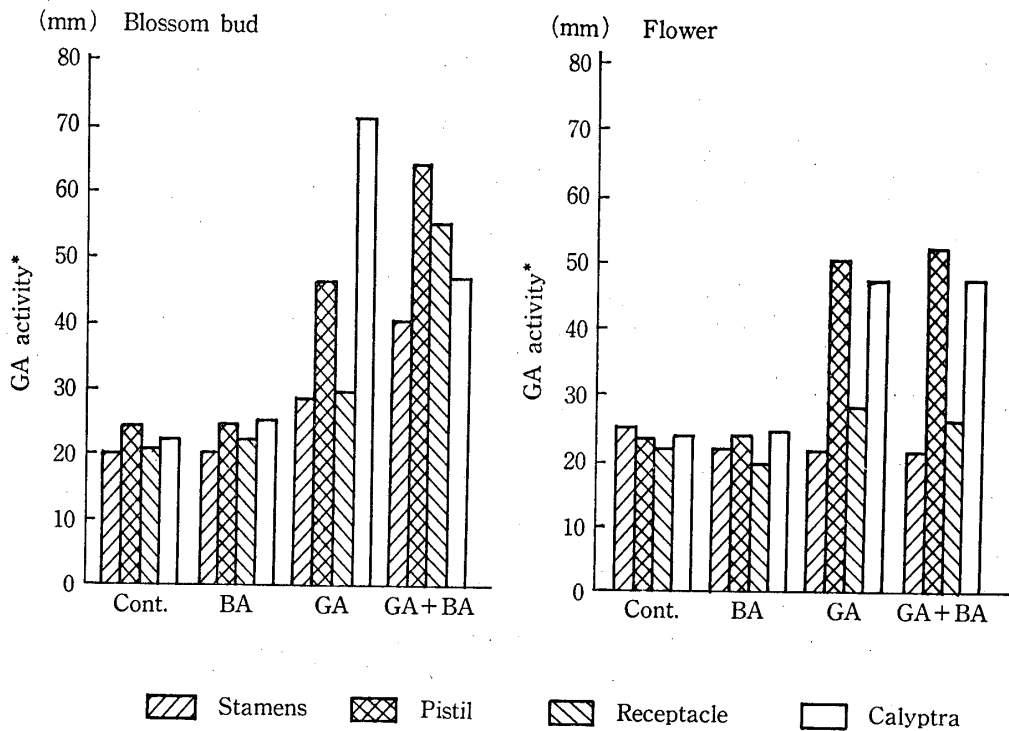


Fig. 9. Effects of BA and/or GA on the GA activity of floral organs in Campbell Early. (* shown in the same way as in Fig. 7)

TABLE 2. GA Activity per Unit Weight of Floral Organs as Affected by GA added to BA

Treatments	Flower Organs	GA activity per unit weight*	
		Blossom bud	Flower
GA	Stamens	0.31	0.65
	Pistil	8.13	4.55
	Receptacle	10.59	0.50
	Calyptra	9.81	2.35
GA+BA	Stamens	7.41	0.63
	Pistil	11.64	4.63
	Receptacle	31.82	3.33
	Calyptra	3.78	2.10

* [Increase of the length of the second leaf sheath of rice seedling (mm)/Fresh weight of each floral organ (mg)] \times 100

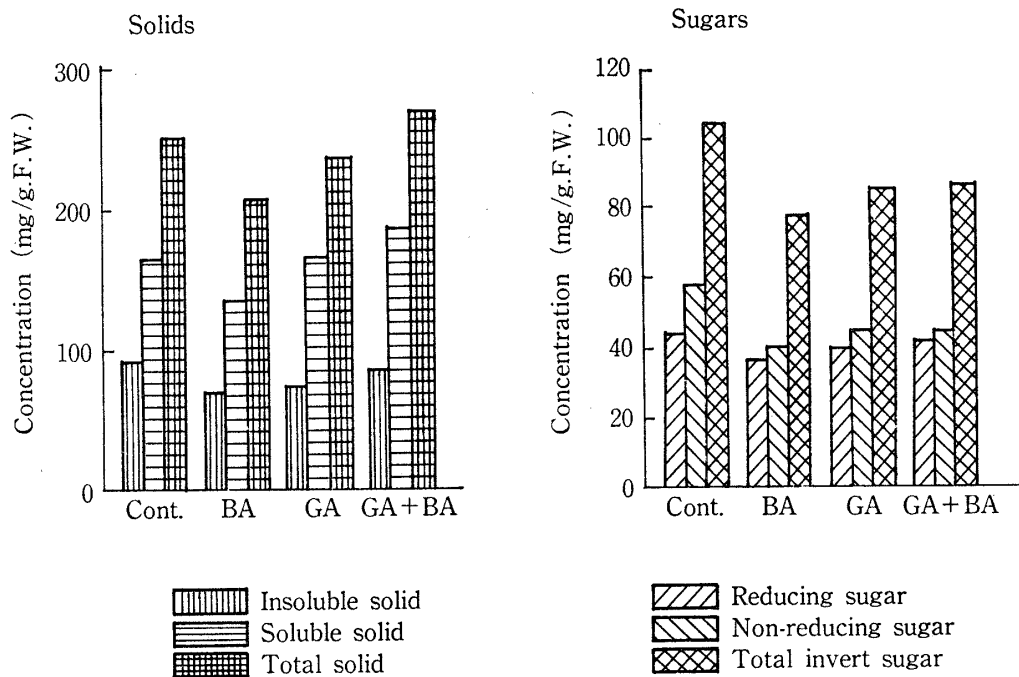


FIG. 10. Effects of prebloom application of BA and/or GA on the solid and sugar concentrations of flowers in Campbell Early.

Discussion

In Muscat Bailey A, which produced perfect- and imperfect-hermaphroditic flowers and male flowers under field conditions BA was reported to promote the development of the pistil and in consequence, to increase the ratio of perfect-hermaphroditic flowers, when applied 2-3 weeks before anthesis. In addition, the application of GA following that of BA increased the ratio of seedless fleshy

berries, as compared with the application of GA alone, which was explained to be associated with the increase of the occurrence of hermaphroditic flowers (5-8). In some male type wild strains of *Vitaceae*, cytokinins including BA were reported also to induce sex conversion, that is, to increase the occurrence of female organs in male type vines (9-15).

In the previous paper (2) we reported in Delaware and Campbell Early that the growth of blossom buds and flowers and, among floral organs, that of the pistil were increased remarkably by GA application. The results presented here (Fig. 3-6) indicated that such an increase of the growth was much accentuated by the addition of BA to GA, although the application of BA alone had almost no effect as compared with the control. BA added to GA increased also the ratio as well as the average weight of seedless fleshy berries as compared with GA alone (Fig. 1, 2). These effects would be probably due to the fact that the decrease of applied GA activity in blossom buds and flowers was considerably delayed by the addition of BA (Fig. 7-9). As previously suggested (1-3), the seedlessness and the development of the seedless berries were increased by the high GA activity about 2 weeks before the full bloom and the high GA activity kept till flowering and thereafter, respectively (3).

Why BA delayed the decrease of GA activity was not known, but Reid *et al.* (27) described that the foliar spray of BA restored GA content of tomato plants. BA addition increased the seedlessness when applied earlier than the most suitable time in case of GA alone. This is perhaps due to the effects of BA on hastening and extending the bud stage at which seedlessness can be induced by GA, and may be one of the reasons why BA has been appraised to be a stabilizer of GA effects.

BA addition to GA increased also the sugar content of flowers and the average weight of seedless fleshy berries (Fig. 10). In grapes the inflorescence (seeded berries) can be a strong sink for assimilates due to being the production site of some endogenous growth regulators although their working mechanism is not necessarily clear. In the seedless berries exogenous growth regulators can work in place of the endogenous ones and increase the rate of development and the final size of berries, as is shown by GA, auxins and cytokinins in seedless Black Corinth and by GA in some cultivars including Delaware (16-21). Cytokinins were reported, in Delaware, to be found high in the inflorescence till flowering (28). In addition, in the leaves of grapes, BA was known to cause a marked movement of 14-C assimilates into the treated leaves (22-26).

Thus, it can be argued that BA itself, together with GA activity the decrease of which is delayed by BA addition, increase effectively the movement of the assimilates into the berries.

Previously we reported the effects of cyclic 3',5'-adenosine monophosphate (cAMP) applied with GA on the induction of seedlessness and seedless berry development in Delaware and Campbell Early grapes (4). Cyclic AMP, alike BA

described in this paper, increased the ratio as well as the average weight of seedless fleshy berries when applied with GA, and it was remarkably so in Campbell Early. The effects of cAMP and BA, however, are not necessarily the same. Thus, cAMP like BA, showed no effects in preserving the green color of the curd of Italian broccoli nor in hastening the fruit growth in the cucurbits (unpublished).

In addition, we investigated benzoyl adenine (BOA) on the same purpose with BA, but its additive effects to GA on the prolongation of GA activity and the development of seedless fleshy berries could not be recognized. From the fact that BA, BOA and cAMP have an adenyl group in common in their chemical structure, but are not always the same in their effects, it may be deduced that the effective group in their structure is located in the residuals instead of being confined to the adenyl group.

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