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

III. Role and Effects of the Prebloom Gibberellin Application on the Blossom Bud Development to Anthesis

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Summary

Studies were carried out with Delaware and Campbell Early grapes on the effects of prebloom gibberellin application upon the blossom bud development to anthesis.

As for the effectiveness of the prebloom gibberellin application, the time factor is most important (Figs. 1 and 3).

The effects varied with the time of gibberellin application as follows;

Early stage application (Period 0–I in the previous report); Blossom buds were enhanced to develope rather slowly to anthesis, yet the full bloom of the treated inflorescence was 1–3 days earlier than that of the untreated one. The final flower size was a little smaller when treated at Period 0 while slightly larger when treated at Period I, than in the untreated inflorescences. The high levels of applied gibberellin activity soon declined sharply and after about 10 days reached such a low level as in the untreated inflorescences and that low level was kept thereafter to flowering.

Middle stage application (Period II in the previous report); It was the most effective application. Blossom buds were most vigorously enhanced to develope to anthesis. Full bloom of the treated inflorescence was earlier by 4–5 days than the untreated one, and the final flower size was also greatly enlarged. Among the floral organs, that is calyptra, pistil, stamen and receptacle, this application especially promoted the development of the pistil, which was the most vigorously growing organ in this period (Figs. 7 and 8).

High gibberellin activity following application declined sharply (Fig. 9) yet maintained a higher level as compared with the untreated inflorescence, towards anthesis (Fig. 10).

Thus, in this case, gibberellin activity was kept at a considerably higher level at anthesis (Fig. 10), which seemed to be responsible for the more vigorous development of seedless fleshy berries as described in the previous report (1).

Late stage application (Period III in the previous report); Blossom buds were

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enhanced to grow vigorously to anthesis, full bloom of inflorescences being 1–3 days earlier than the untreated ones. The final flower size was a little smaller than that of the middle stage application. The high level of applied gibberellin activity declined sharply, yet at anthesis it remained more or less at a higher level than in the inflorescences treated earlier.

Introduction

In the previous reports (1, 2), the effects of the prebloom gibberellin application upon the seedlessness and the parthenocarpic berry development were described and discussed in which the importance of the time of application was accentuated. Gibberellin application at the appropriate stage results in the better development of seedless berries. The authors supposed that the changes of gibberellin activity from the blossom bud stage towards flowering may be related to the blossom bud development, the flower size at anthesis, and consequently to the final size of seedless berries in the long run.

This report presents the results of the investigations on the effects of prebloom gibberellin application with special reference to the blossom bud development to anthesis in relation to the change of applied gibberellin activity and, in addition, to the development of floral organs in the blossom bud and in the flower at anthesis.

Materials and Methods

Mature vines of Delaware and Campbell Early grapes, eight years old in 1969, growing in the vineyard of Tohoku University in Sendai, were used. Experiments were carried out over the three years from 1969 to 1971.

Gibberellin application — Inflorescences were thinned out before gibberellin application, so that two of them were borne on a current shoot.

Gibberellin solution was prepared by dissolving gibberellin crystals in a small amount of 95 percent ethanol and diluting to 100 ppm with deionized water, then Aerol OP as a wetting reagent was added at 100 ppm.

Ten inflorescences as a group received one gibberellin application by dipping and this was practiced at intervals of 5 days (2–3 days exceptionally in Fig. 3) 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.

In this paper, the day of anthesis means the day when the calyptra has disconnected from the receptacle in the individual flowers, and the day of full bloom means the day when the calyptra fell from receptacle in about 50–70 percent of the flowers in each inflorescence.

Sampling — Blossom buds were sampled and weighed every 2–3 days from 30 days before the expected full bloom of untreated inflorescences. As to the flowers, the number and weight were recorded on the day of anthesis, which was practiced

every day throughout the flowering period over three years.

For the study of the development of each floral organ, the weight of the calyptra, stamen, pistil and receptacle were measured separately and their ratios to the weight of the blossom bud as a whole or to that of the flower including the calyptra were calculated. Blossom bud weight means the total weight of the calyptra, stamen, pistil and receptacle, while that of the latter three is discriminated as the weight of the flower portion at bud stage. Flower weight means the total weight of the stamen, pistil and receptacle; the calyptra is not included for it will have fallen off at anthesis. When necessary, its weight, having been separately measured, is added to the flower weight.

Bioassay of gibberellin activity — Each sample for determination of gibberellin activity consisted of 100 blossom buds or flowers. Fresh materials were homoginized with a glass homoginizer with methanol, extracted three times over 48 hours in an ice box and divided into soluble and insoluble fractions by centrifugation. Methanol soluble fraction was stored in ice box. After methanol was evaporated under reduced pressure, the aqueous solution was adjusted to PH 2.8–3.0 with HCl, and extracted with ether for six hours continuously with an ether extractor. The ether solution in a 50 ml tall beaker was dried up under reduced pressure. The gibberellin activity was bioassayed by the rice seedling test according to the method of Murakami (3) modified by Tamura (4), and represented by the elongation of the second leaf-sheath.

Results

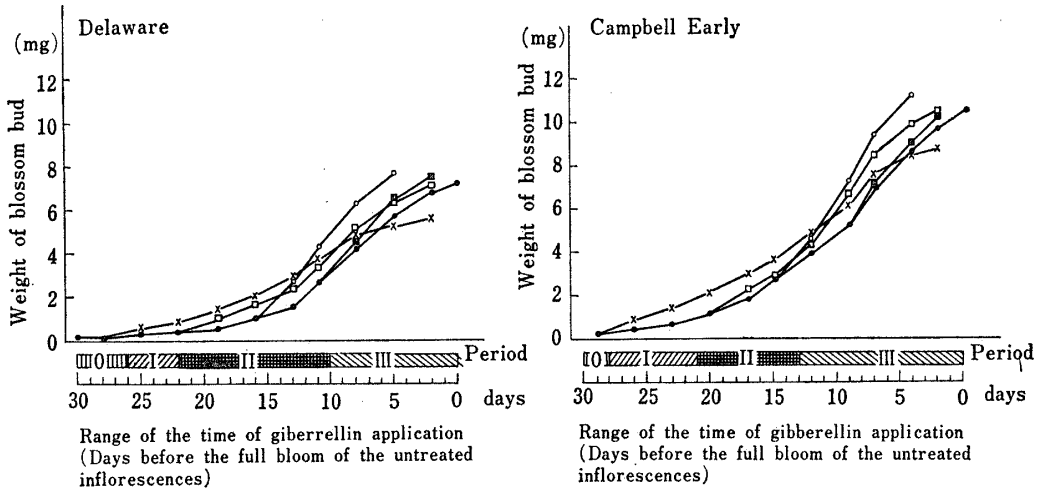
1. *Effects of the Time of Gibberellin Application.*

(1) *Development of blossom bud.*

The growth curves of blossom buds to anthesis associated with the time of gibberellin application are shown in Fig. 1.

In Fig. 1, it is obviously shown that gibberellin application accelerated and enhanced the growth of the blossom bud to anthesis. When gibberellin was applied about 15 days before the full bloom of the untreated inflorescences, the growth of the blossom buds was most remarkably promoted in both varieties. When treated earlier or later, that is 30–25 days or 10 days, respectively, before the full bloom of the untreated inflorescences, the weight of blossom buds showed a smaller increase in both varieties.

The growth rate curves of blossom bud to anthesis treated with gibberellin are shown in Fig. 2. The growth promotive effect of the applied gibberellin on the blossom bud are more clearly shown in Fig. 2 compared with Fig. 1. In Delaware, when treated 16 days before the full bloom of the untreated inflorescences, the growth rate increased most rapidly, and when treated 28 or 22 days before, it increased most slowly. In Campbell Early, when treated 15 days before, it increased most rapidly, and most slowly when treated 29 days before the full bloom



Time of gibberellin application, represented as days before the full bloom of the untreated inflorescences in both varieties.

	●	×	□	○	■
Delaware	Untreated	28	22	16	11
Campbell Early	Untreated	29	20	15	9

FIG. 1. The growth curves of the blossom bud.

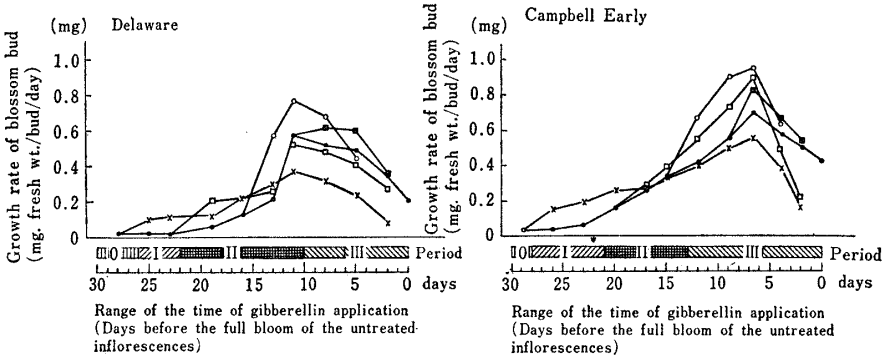


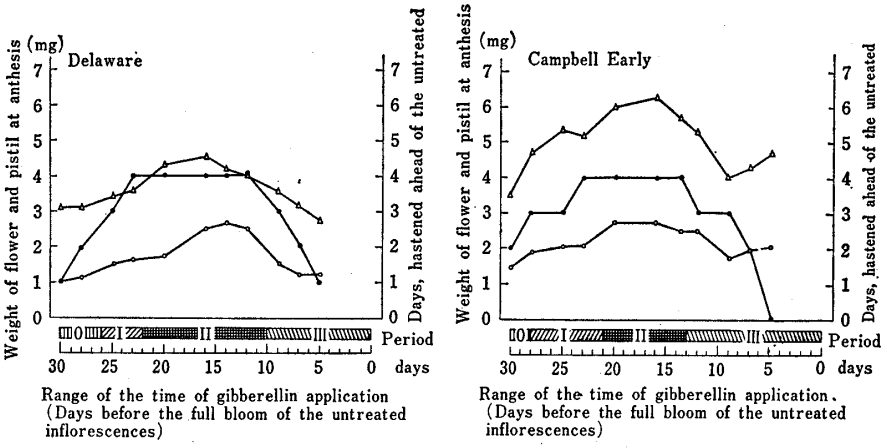
FIG. 2. The growth rate curves of the blossom bud. Growth rate was calculated from the results of Fig. 1 as the increment in fresh weight of blossom bud per day.

of the untreated inflorescences.

(2) *Flowering of inflorescences and final flower size.*

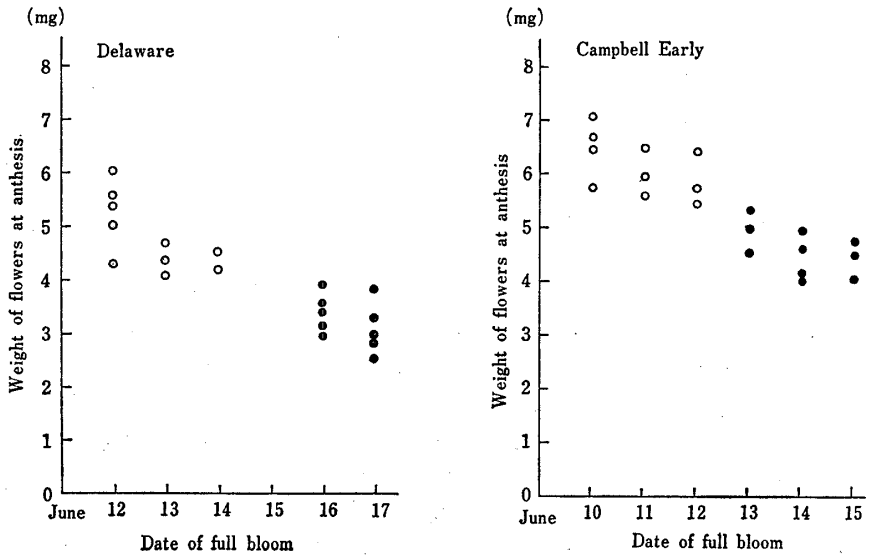
In Fig. 3, the average weight of flowers and their pistils at anthesis as well as the earliness of the full bloom of inflorescences are shown in relation to the time of gibberellin application.

It is shown in Fig. 3 that in Delaware when treated 23–12 days before and in Campbell Early 23–14 days before the full bloom of the untreated inflorescences,



●; Days, flowering hastened ahead of the untreated inflorescences. △; Weight of flowers at anthesis. ○; Weight of pistils at anthesis.

FIG. 3. Effects of the time of prebloom gibberellin application upon the hastening of flower and the average weight of flowers and its pistils at anthesis.



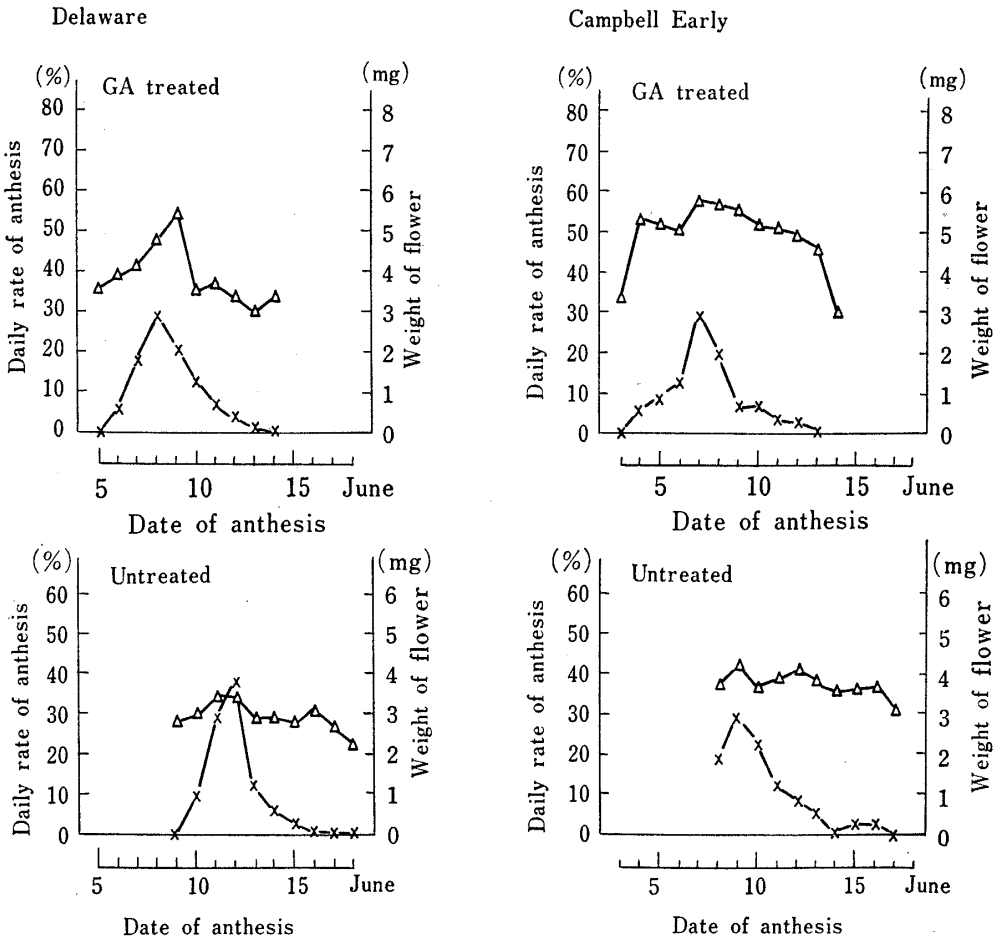
●; Untreated. ○; Gibberellin treated on June 1.

FIG. 4. Full bloom date as related to the average flower weight of the inflorescences.

the full bloom was hastened 4 days in advance of the untreated ones.

The flowers, especially the pistils, in Delaware treated 20–12 days before and in Campbell Early 20–14 days before the full bloom of the untreated inflorescences, are the greatest in weight at anthesis (Fig. 3).

Earlier or later gibberellin application promoted the blossom bud growth and accelerated the flowering of the inflorescences in less degree than the middle stage application. It is noticeable in Fig. 3 that there exists a positive correlation between the enhanced growth of floral organs and the earliness of the flowering.



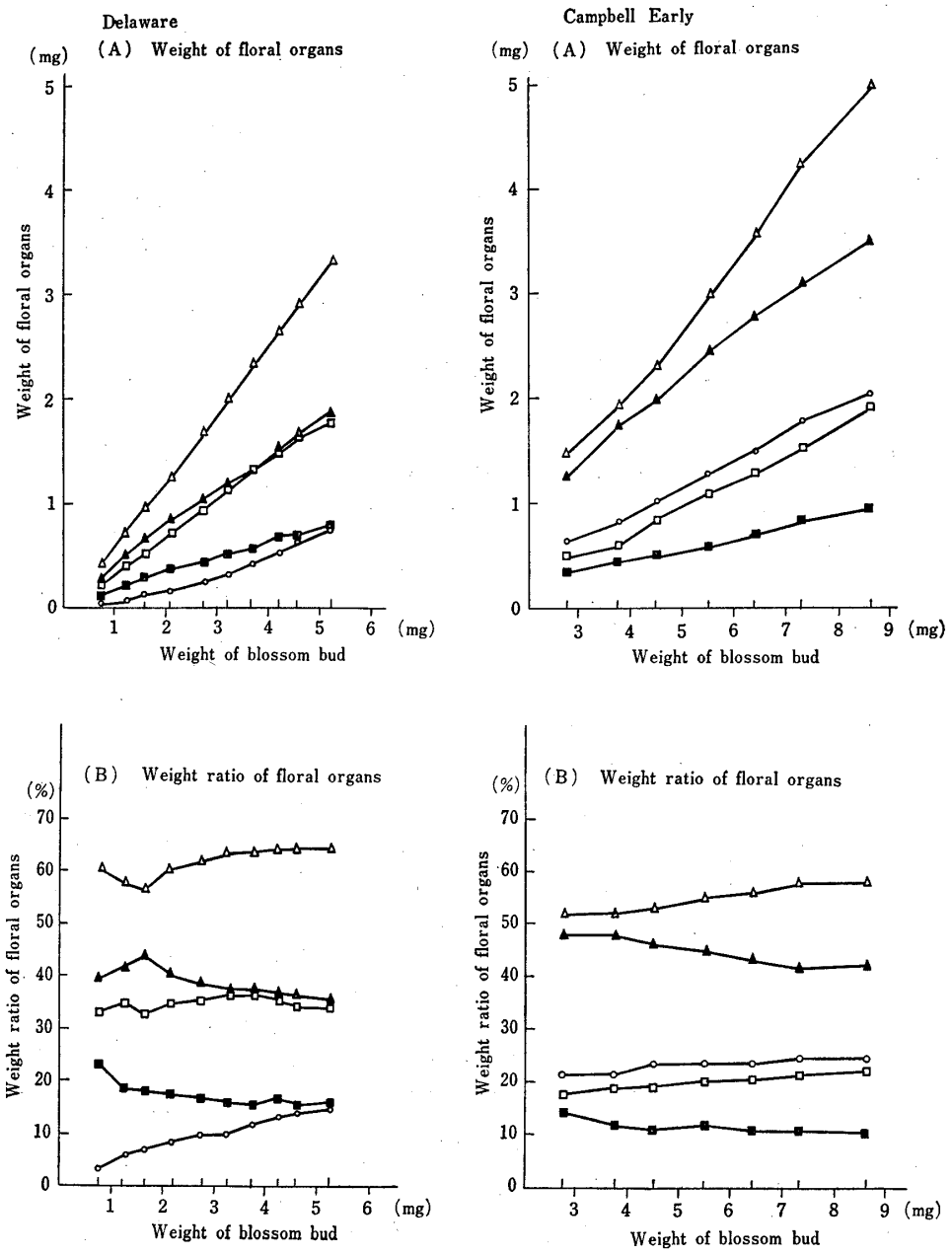
△; Weight of flowers opening each day.
×; Daily rate of anthesis per inflorescence.

FIG. 5. Relations between the daily rate of anthesis and the weight of the flower blooming each day in each inflorescence throughout flowering period. Gibberellin was treated on May 25.

2. *Flowering of Inflorescences in Relation to Flower Size at Anthesis in Each Treatment.*

Dates of full bloom of each of ten inflorescences treated about 15 days before the full bloom of untreated inflorescences together with those of ten untreated inflorescences were plotted in Fig. 4 to their average flower weight at anthesis.

As mentioned above, the effects of gibberellin were most prominent when applied about 15 days before the full bloom of the untreated inflorescences. It is evident from Fig. 4 that the average flower weight was larger in gibberellin treated inflorescences than in untreated ones and that the earlier the full bloom of inflorescences the larger the average weight of their flowers regardless of the gibberellin application and its time.



△; Stamen, pistil and receptacle (Flower portion) ▲; Calyptra ○; Pistil □; Stamen ■; Receptacle

FIG. 6. A. The weight of floral organs as related to the weight of the blossom bud.
B. The weight ratio of the floral organs as related to the weight of the blossom bud.

3. *Flower Weight and Daily Rate of Anthesis in Relation to the Day of Anthesis in Each Inflorescence.*

Flowers were nipped off from inflorescences on the day of their anthesis, which was practiced every day throughout the flowering period and their number and weight were recorded, then the average weight of the flowers which bloomed each day together with daily rate of anthesis, that is the percentage of the number of flowers that bloomed each day to their total number, were calculated. Some of

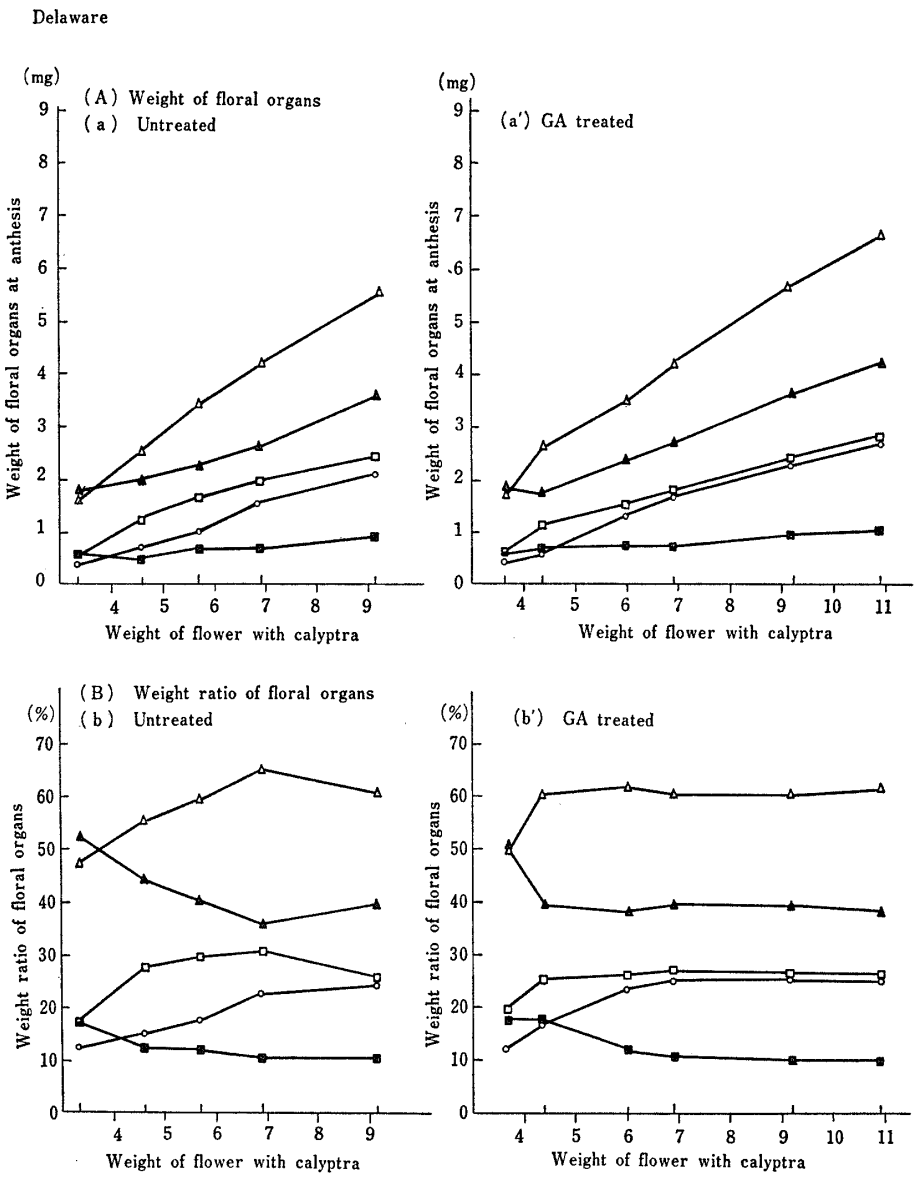
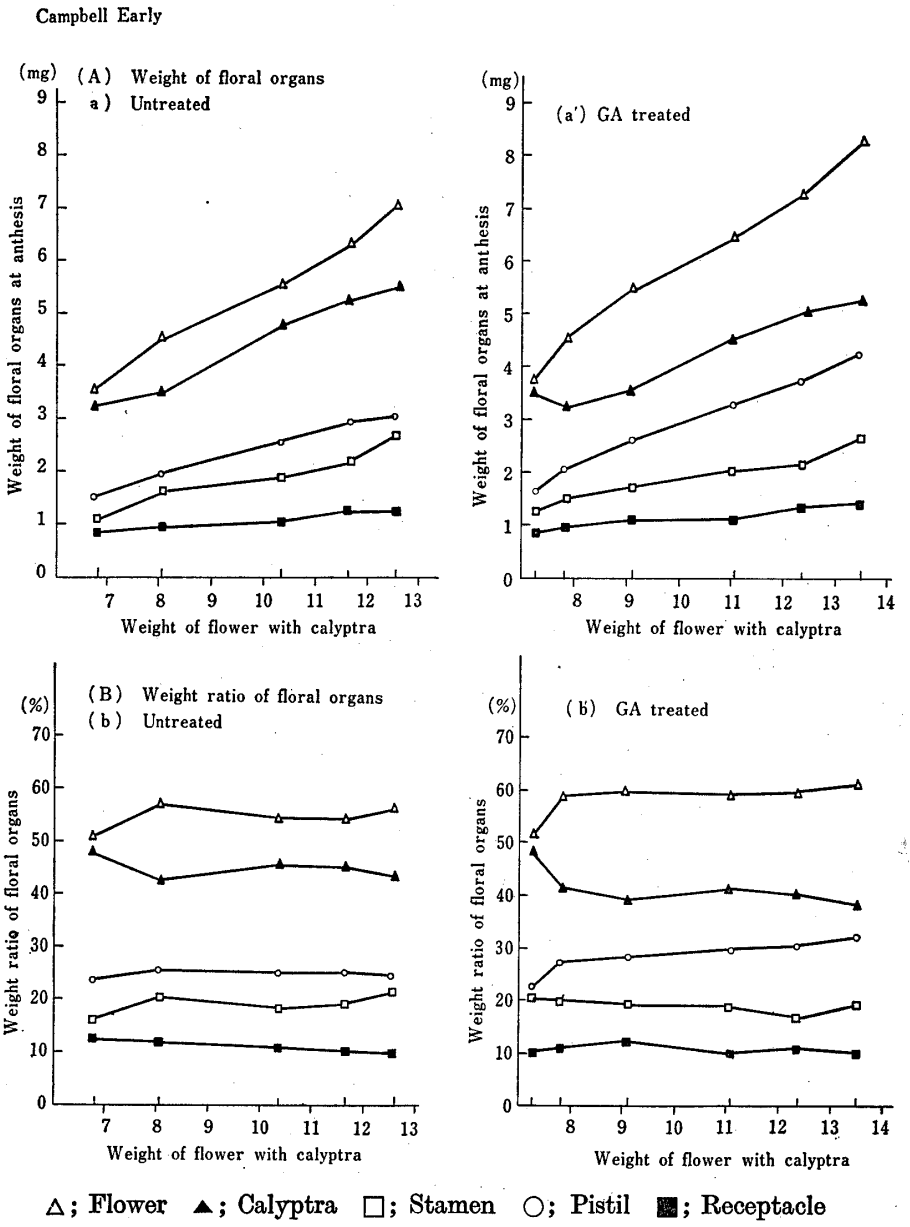


FIG. 7. A. The weight of the floral organs as related to the flower weight with calyptra at anthesis.
B. The weight ratio of the floral organs as related to the flower weight with calyptra at anthesis.

these results are shown in Fig. 5.

It is evident in Fig. 5, that regardless of gibberellin application there was found to be a clear peak in the daily rate of anthesis and the flowers which bloomed at the peak were, in general, more or less larger in their weight than those which bloomed before or after the peak in both varieties. It is also evident that gibberellin application increased the weight of the flower at anthesis as well as hastened the flowering without changing the flowering pattern mentioned above. The existence of the peak in flower weight, though it was less clear in Fig. 5, could be recognized by putting the results over the three years together.

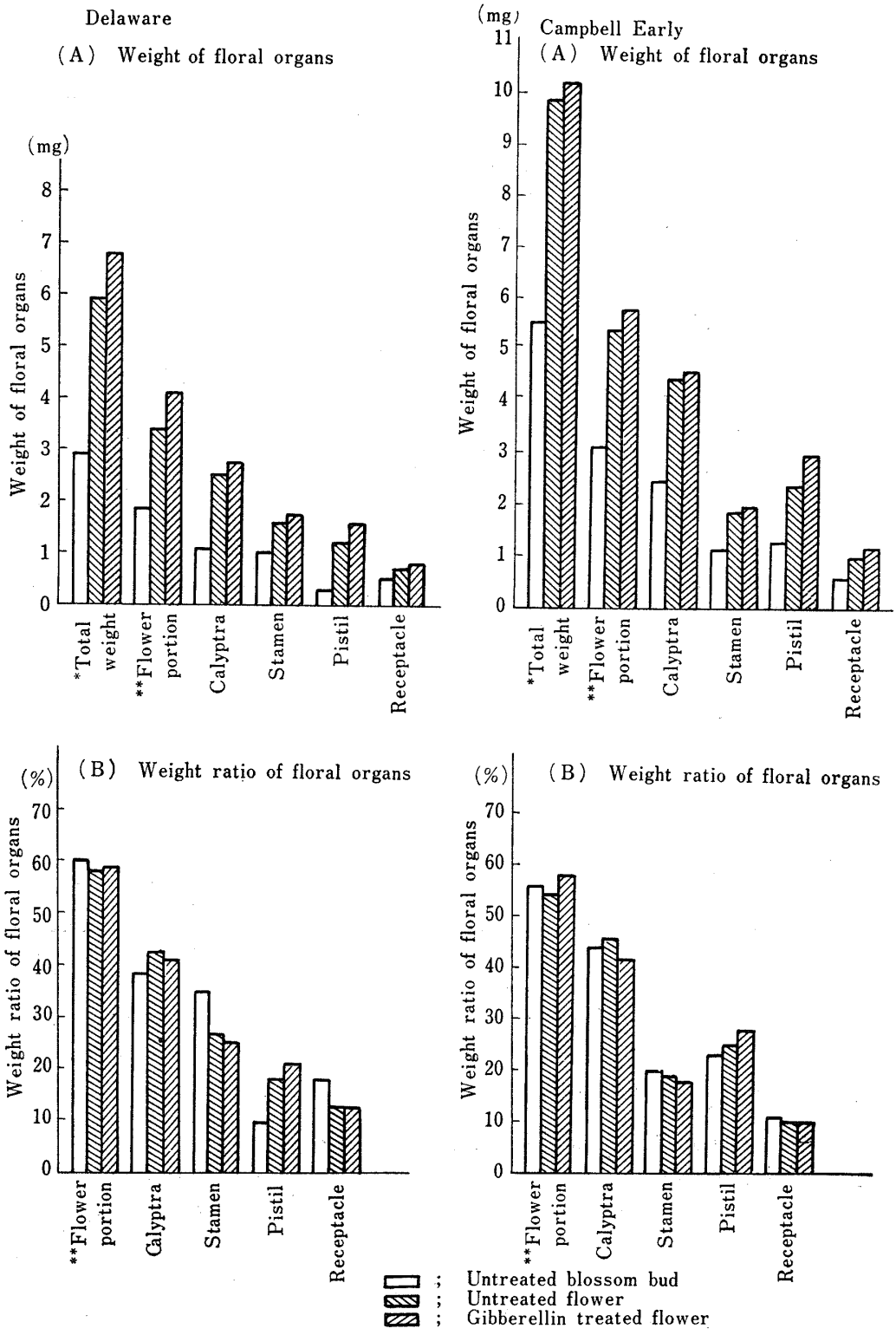


4. *Development of Floral Organs.*

(1) *Floral organs at blossom bud stage.*

All of the blossom buds on some untreated inflorescences that were expected to reach full bloom within 5 to 15 days were collected and classified by weight. Then in each weight class the weights of the floral organs were measured separately, and their ratios to the blossom bud weight were calculated and the results are shown in Fig. 6 (A, B).

In Fig. 6 it is apparent that the weight of each floral organ increased with the blossom bud weight, and that with the increase of blossom bud weight, the weight ratios of the pistil and stamen increased while those of the receptacle and calyptra decreased.



* Total weight of floral organs (calyptra, stamen, pistil and receptacle)

** Total weight of floral organs without calyptra (stamen, pistil and receptacle)

FIG. 8. Average weight and weight ratio of each floral organs as related to the weight of the blossom bud and that of flower with calyptra.

(2) *Floral organs at anthesis.*

Individual flowers, nipped off from inflorescences on the day of their anthesis, were classified by weight. In each weight class, the weight of floral organs were measured separately and their weight ratio to flower including calyptra were calculated. The results are shown in Fig. 7 (A, B). In Fig. 7, it is shown that with the increase of the weight of flower including calyptra, the floral organs increased their weight at different rates, consequently their weight ratios to that of flower including the calyptra increased remarkably in the pistil and less remarkably in the stamen, while it remained constant or decreased in the receptacle and calyptra.

(3) *Development of floral organs as influenced by gibberellin application.*

The average weight of each floral organ and its ratio to that of blossom bud or flower including calyptra were calculated with all the flowers in Figs. 6 or 7 and shown in Fig. 8.

It is evident in Fig. 8 that the average weight of each floral organ was larger at anthesis than at blossom bud stage and also larger in gibberellin treated flowers than in untreated ones. Regarding the weight ratio, however, a clear increase was found especially in the pistil towards anthesis as well as in gibberellin treated flowers.

5. *Gibberellin Activity.*

(1) *The change of gibberellin activity in the blossom bud as influenced by gibberellin application.*

The change of gibberellin activity in the blossom buds as related to the time of the prebloom gibberellin application were plotted in Fig. 9.

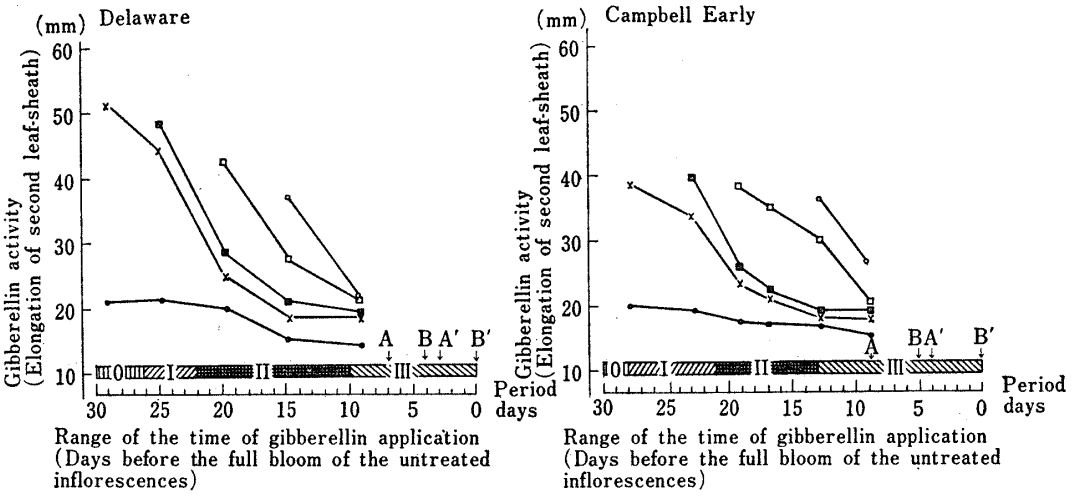
In the untreated blossom buds, the gibberellin activity was low and slowly decreased towards anthesis. While in the gibberellin treated blossom buds, regardless of application time, the gibberellin activity was raised remarkably following application. It soon sharply declined, however, yet thereafter to anthesis it remained a little higher than in the untreated blossom buds.

(2) *Gibberellin activity in flower at anthesis.*

Using the daily flower samples in Fig. 5 the gibberellin activity was bioassayed throughout the flowering period. The results, together with the average weight of the flowers, are shown in Fig. 10.

In gibberellin treated inflorescences, as shown in Fig. 5, there was found to be a clear peak in flower weight as well as in the daily rate of anthesis in relation to the day of anthesis.

In addition, Fig. 10 indicates the existence of a clear peak in gibberellin activity in relation to the day of anthesis as well as a similar tendency among the



Time of gibberellin application, represented as days before the full bloom of the untreated inflorescences in both varieties.

	●	×	■	□	○
Delaware	Untreated	29	25	20	15
Campbell Early	Untreated	28	23	19	13

A ; Beginning of anthesis of gibberellin treated group.
A′; Beginning of anthesis of untreated group.
B ; Full bloom of gibberellin treated group.
B′; Full bloom of untreated group.

FIG. 9. The changes of the gibberellin activity as related to the time of the prebloom gibberellin application. Gibberellin activity was bioassayed by rice seedling test and represented by the elongation of second leaf-sheath.

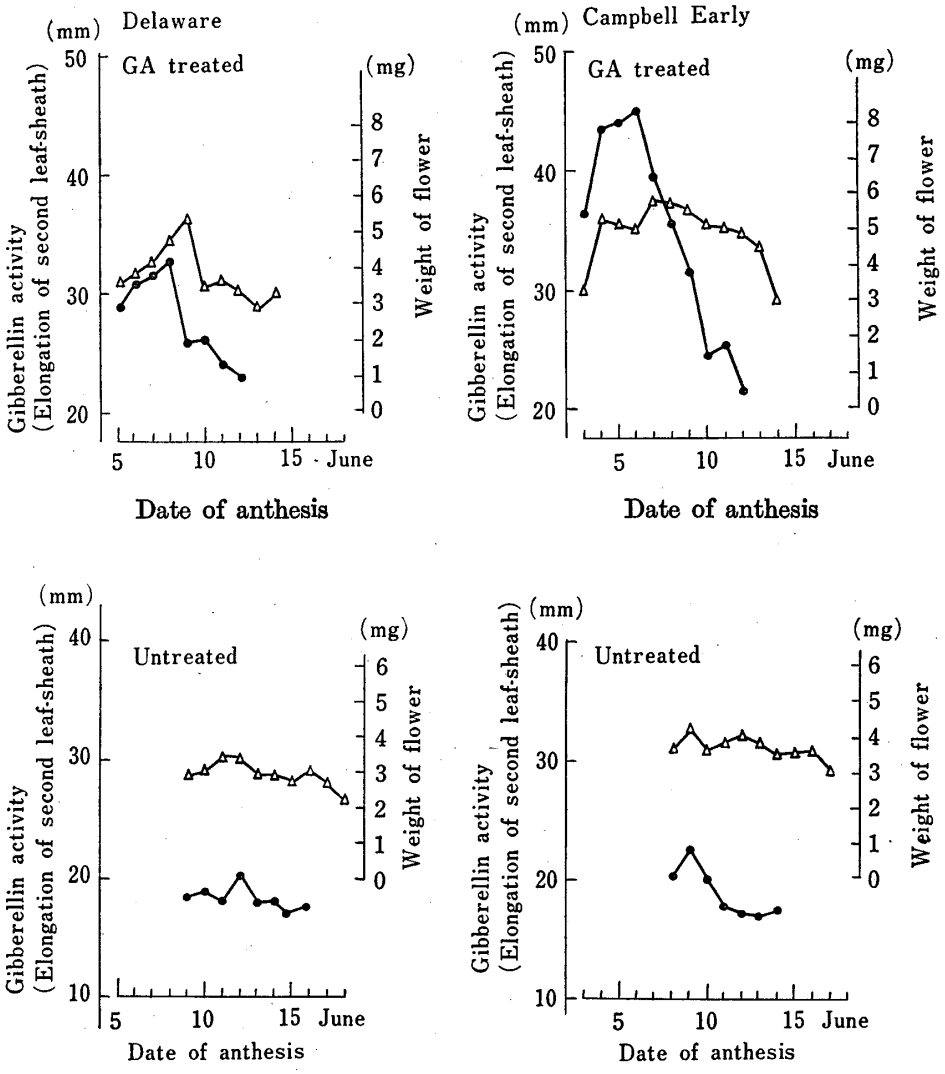
change of gibberellin activity, flower weight and daily rate of anthesis.

The same tendency was found, though less clearly in untreated inflorescences.

Discussion

In grapes, blossom buds arise in the primordial inflorescence. Initiation of inflorescence occurs in midsummer and continues in the newly forming buds throughout the growing season. Primordia of inflorescence appear as blunt, rather broad outgrowths of the growing points of the bud. Primordial inflorescences in the bud of the middle of the shoot become larger than those in the basal or apical bud which may be due to a good supply of food materials.

The number of blossom buds that develop on an inflorescence largely depends upon the growing conditions in the spring, which determine how the stored food is to be used and also how much carbohydrates may be produced in the young leaves. There is a positive correlation between the vigour or length of shoots and the number of blossom buds differentiated on the inflorescence, under such conditions which do not permit enough growth of shoot, the inflorescences will not reach full size.



△; Weight of flowers blooming each day
●; Gibberellin activity in flowers blooming each day

FIG. 10. Gibberellin activity and the weight of the flowers blooming each day throughout the flowering period. Gibberellin was treated on May 25, and its activity was represented by the elongation of second leaf-sheath.

1. *Blossom Bud Development to Anthesis as Influenced by Prebloom Gibberellin Application.*

Figs. 1–3 reveal that the growth of the blossom bud was promoted by applied gibberellin regardless of the application time. Blossom buds growth was most marked when gibberellin was applied about 15 days before the full bloom of the untreated inflorescences, which resulted in an earlier full bloom compared with the earlier or later application and in a greater weight of flower with a high ratio for the pistil (Fig. 3).

It may be reasonably concluded that the exogenous gibberellin is most effective

in attracting nutrients when applied about 15 days before the full bloom of the untreated inflorescences.

In addition, among inflorescences, the ealier the full bloom, the larger the average weight of their flowers. This is regardless of gibberellin application (Fig. 4).

Fig. 5 shows that regardless of gibberellin application, there exists a peak in the daily rate of anthesis of each inflorescence and that the full bloom day of inflorescence usually agrees with that peak or is delayed a few day.

It seems that flowers which bloomed at the peak are favoured with a sufficient supply of nutrients and show a steady growth reaching a larger final size. Earlier and/or later flowers, being more or less inferior in attracting of nutrients, reach a smaller final size.

2. *Development of Floral Organ of Blossom bud and Flower.*

In Fig. 6 which shows the weight ratios of floral organs of the blossom buds of different weights, the weight class of blossom buds may be assumed, with some reservations, to correspond with the difference of their growth stage, then it may be realized that the growth of the blossom buds is greatest about 15 days before the full bloom of inflorescence (which corresponds with the bud stage of 1 and 3 mg in weight, respectively, in Delaware and Campbell Early from Figs. 1 and 6) to anthesis and that the growth rate is largest in the pistil. In the other words, among floral organs, it is the pistil that shows the most vigorous growth in this period and when the growth of buds is enhanced in this period by any factor, there develop flowers of a greater weight and with a higher ratio for the pistil. Thus, for example, in Delaware, flowers with calyptra less than 4 mg in weight show the following order in weight of their floral organs, stamen>receptacle>pistil, while in the flowers with calyptra above 4 mg in weight the order is stemen>pistil> receptacle and occasionally pistil>stamen>receptacle.

In general, it is evident that exogenous gibberellin enhances the growth of the floral organ and especially of the vigorously growing organ i.e. the pistil in the blossom bud 15 days before the full bloom of inflorescences to anthesis (Figs 6 – 8).

3. *Growth of Blossom Buds in Relation to Gibberellin Activity.*

As is evident in the previous reports, prebloom gibberellin application induces seedlessness and in consequence, seedless berry development. In addition this report shows that gibberellin applied at any stage of blossom bud development promotes the growth of blossom buds to anthesis. These effects, however, are somewhat different among the developmental stages of gibberellin application, and are especially remarkable when treated at Period II (Fig. 9).

The growth of blossom buds in relation to gibberellin activity may be explained as follows.

In untreated blossom buds, endogenous gibberellin activity decreases gradually throughout their development to anthesis, which seems to be sufficient for their normal growth. While gibberellin treated blossom buds seem to make some gain in their growth over the untreated ones due to the high level of gibberellin activity following gibberellin application.

When treated at an early stage of inflorescences, the incipient high gibberellin activity somewhat hastenes thier early growth of blossom buds, but it declines rapidly and remaines as low as in the untreated buds for about 15 days preceding the full bloom of the inflorescences, which is ineffective for surplus growth promotion and results in comparatively small flowers and in consequence, in a low percentage as well as inferior growth of seedless fleshy berries, although anthesis is somewhat hastened.

In the application at the appropriate stage, gibberellin activity decreases rapidly but yet maintains a considerably higher level towards anthesis than in the earlier application (at anthesis it again increases a little, although the process is unknown) and it seems to results in the earliest anthesis, the largest flowers and more vigorous development of many seedless berries.

The later application is too late in time to induce sufficient seedlessness, and a gain in the bud growth can not be expected because of the short duration of high gibberellin activity from treatment to anthesis, although anthesis is hastened a little.

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