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journal or publication title	Tohoku journal of agricultural research
volume	23
number	1
page range	15-32
year	1972-06-20
URL	http://hdl.handle.net/10097/29626

Tohoku Journal of Agricultural Research
Vol. 23, No. 1, April 1972
Printed in Japan

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

II. Role and Effects of the Prebloom Gibberellin Application as Concerned with the Flowering, Seedlessness and Seedless Berry Development of Delaware and Campbell Early Grapes.

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(Received December 28, 1971)

Summary

Studies were carried out with Delaware and Campbell Early grapes on the role and effects of prebloom gibberellin application upon the flowering, the seedlessness and the seedless berry development throughout the three years from 1967 to 1969.

As for the efficiency of the prebloom gibberellin application, the time factor is most important. The time of prebloom gibbrellin application in relation to the state of the ovule was shifted as follows;

The range of the time of gibberellin application (period: 0–I–II–III).

Period O; 30–26 days before the full bloom of the untreated inflorescences in Delaware and 30–28 days before that in Campbell Early. Gibberellin hastened the full bloom by 2–3 days ahead of the controls (Fig. 1). Many seeded berries were produced and the rest remained as shot berries (Fig. 2). Most ovules might not be sensitive to gibberellin, so with pollination they induced seeded berry development. Clusters appear to be filled with seeded full-sized berries, many shot berries being hidden among them (Plate 1).

Period I: 26–22 days before the full bloom of untreated inflorescences in Delaware and 28–21 days before that in Campbell Early. Gibberellin hastened the full bloom 3–4 days ahead of the controls (Fig. 1). Clusters were occupied with many shot berries, a few small seedless fleshy berreis and a few seeded berries (Plate 1). Most ovules might have grown to be sensitive and killed by gibberellin, so seedless berry development was induced. A few ovules, remained alive, induced seeded berry development with pollination.

Period II: 22–10 days before the full bloom of the untreated inflorescences in Delaware and 21–13 days before that in Campbell Early. Gibberellin hastened the full bloom 4–5 days ahead of the controls (Fig. 1). A few seeded berries and a considerable amounts of seedless fleshy berries were formed (Plate 1), and the

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rate of shot berries was comparatively lower as compared with that of the other period (Fig. 2). A considerable amount of ovules may be sensitive to gibberellin, and parthenocarpic berry development was induced. Applied dose of gibberellin was capable of killing ovules and favoured in its turn the seedless berry development. In this period, as concerned with flowering and the seedless berry development, the effects of the prebloom application of gibberellin was most remarkably and successfully exerted.

Period III; 10–0 days before the full bloom of the untreated inflorescences in Delaware and 13–0 days before that in Campbell Early. Gibberellin hastened the full bloom 3–0 days ahead of the controls (Fig. 1). Many seeded berries and a few seedless fleshy berries with a few shot berries were produced per cluster (Plate 1). Ovules might have grown enough to be resistant to gibberellin and a few of them may yet remain sensitive to gibberellin. The prebloom treatment so neared the full bloom that the effect of gibberellin was inevitably minified.

Dipping of inflorescences of Delaware into 100 ppm solution of gibberellin about 15 days before and 10 days after the full bloom results in seedless berry formation of marketable size. This technique has become a commercial practice in Japan for the production of seedless Delaware grapes. With other varieties, however, especially with Campbell Early, it is very difficult to induce the seedless berry development in practice.

It has been explained that prebloom application kills the ovules and postbloom application stimulates the parthenocarpic seedless berry development to attain the marketable size in Delaware. About 15 days before the full bloom was appointed for the prebloom gibberellin application with Delaware grapes and in case of the miss of the time, it fails to induce the seedlessness.

The experiments reported in this paper were designed to gain information which may explain the nature and the role of the prebloom gibberellin application. The prebloom application of gibberellin was shifted over the range of about thirty days before the full bloom. The effects on the flowering, the seedlessness and the seedless berry enlargement of Delaware and Campbell Early grapes were studied.

Materials and Methods

Mature vines of Delaware and Campbell Early grapes (about six years old in 1967), growing in vineyard at Tohoku University in Sendai, were used. Experiments were carried out during the three years from 1967 to 1969.

Inflorescences were thinned out before anthesis, so that two inflorescences were borne on a current shoot.

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

Ten clusters were used as one group. Gibberellin application was carried out every day except on rainy days, from 30 days before the expected full bloom to the actual full bloom of the untreated inflorescences.

The number of blooming flowers in each inflorescences were counted each day.

In this paper, the day of flowering appoints the day when caryptras was disconnected from receptacle. And the day of full bloom appoints the day when caryptras has fallen from about 50–70 percent of flowers in inflorescences. Actual number of days were counted back starting from the actual day of the full bloom of the untreated inflorescences. The first day of flowering, the day of full bloom, the last day of flowering and flowering period of treated versus control were recorded and compared respectively.

Clusters were harvested when the seedless fleshy berries ripened and the seeded berries were still green.

In this report, a seeded berry means the fruit which contains seeds against the gibberellin application, a seedless fleshy berry means the fruit which developed above 4 mm in diameter, and a shot berry means the parthenocarpic fruit that stuck to the vine and remained below 4 mm in diameter.

Seeded, seedless fleshy and shot berries were identified and berry diameter and weight were measured per cluster.

Proportion of these three types of berries were calculated and seedlessness ratio, rate of seedless fleshy berries were represented as follows;

$$\text{Seedlessness ratio}(\%)=\frac{\text{Number of seedless fleshy berries}+\text{shot berries}}{\text{Number of (seeded}+\text{seedless fleshy}+\text{shot) berries}}\times 100$$

Rate of seedless fleshy berries(%)

$$=\frac{\text{Number of seedless fleshy berries}}{\text{Number of (seeded}+\text{seedless fleshy}+\text{shot) berries}}\times 100$$

It follows that:

Percent of seeded berries: 100−Seedlessness ratio
Percent of seedless fleshy berries: Rate of seedless fleshy berries
Percent of shot berries: Seedlessness ratio−Rate of seedless fleshy berries

Results

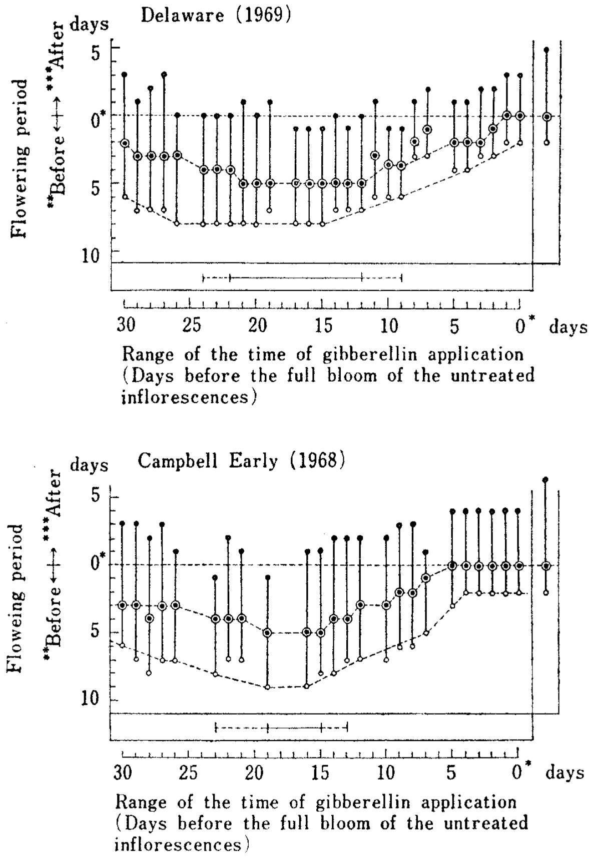
1. *Effects on Flowering*

(1) *First flowering*

When the prebloom dipping treatment was carried out 30 days before the full bloom of the untreated inflorescences, the treated inflorescences of Delaware and Campbell Early grapes flowered 4 days earlier than the controls. Later the prebloom dipping applied, earlier the inflorescences flowered (Fig. 1).

With Delaware, when treated 26 to 15 days before the full bloom of the untreated inflorescences (Period I-II), flowering was hastened 6 days earlier than the control. With Campbell Early, when treated 19 to 16 days before the full bloom of the untreated inflorescences (Period II), flowering was hastened 7 days earlier than the control. When treated later than these days, flowering was less hastened. With Campbell Early, when treated within 4 days before (Period III), and with Delaware, when treated a day before the full bloom of the untreated inflorescences (Period III), flowering was no more hastened (Fig. 1).

The same tendency was observed throughout the three years of experimentation from 1967 to 1969, though there were some fluctuations among the years.



*0: The day of the full bloom of the untreated inflorescences
** Before: Days before the full bloom of the untreated inflorescences
*** After: Days after the full bloom of the untreated inflorescences
○: The first day of flowering
⊙: The day of full bloom
●: The last day of flowering

FIG. 1. Effects of the shift of the time of prebloom gibberllin application upon the flowering and flowering period in a cluster.

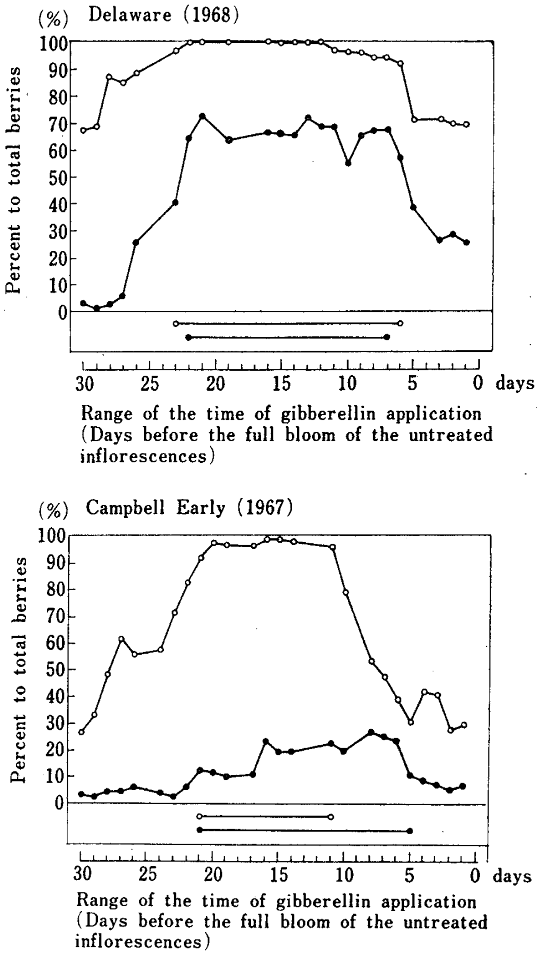
(2) *Full bloom*

In Fig. 1, with Delaware, it is shown that when the prebloom dipping was treated 21 to 12 days before (Period II), the full bloom was hastened 5 days ahead, and when treated 24 to 22 (Period I-II) or 10 to 9 (Period III) days before, it was hastened 4 days earlier than that of the control. The period, at which the prebloom treatment hastened the full bloom over 4 days, was 24–9 (Period II) days in Delaware and in Campbell Early 23–13 (Period II) days prior to the full bloom of the untreated inflorescences.

In both verieties, when the treatment was applied earlier or later than the period described above, the hastening effect on the full bloom declined. The same tendency was observed throughout the three years of experimentation from 1967 to 1969 (Fig. 4). During these three years, it was shown that the period at which the prebloom dipping hastened the full bloom over 4 days was with Delaware 21–12 days (Period II), and with Campbell Early 19–13 days (Period II) prior to the full bloom of the untreated inflorescences (Fig. 4).

(3) *Flowering period*

The flowering period was represented as intervals from the first day to the last day of flowering (Fig. 1). In both varieties, the earlier the prebloom dipping was treated, the longer the flowering endured, and the later the dipping was treated, the shorter the flowering endured. The flowering period was shortened when the



○——○: Seedlessness ratio (Rate of seedless fleshy berries+shot berries)
●——●: Rate of seedless fleshy berries

FIG. 2. Effects of the shift of the time of prebloom gibberellin application upon the seedlessness ratio and the rate of seedless fleshy berries.

treatment neared the date of the untreated inflorescences.

The length of the intervals from the first flowering to the full bloom showed the same tendency in Delaware as with the flowering period, and in Campbell Early the tendency was obscure. The same tendencies were observed throughout the three years of experimentation from 1967 to 1969.

2. *Effects on Seedlessness*

The ratio of seeded, seedless fleshy and shot berries per cluster produced by prebloom gibberellin application are shown in Fig. 2.

With Delaware, in 1968, seedlessness ratio reached above 90 percent when the prebloom dippings were treated 23–6 days before (Period II), and with Campbell Early, in 1967, 21–11 days before (Period II) the full bloom of the untreated inflorescences (Fig. 2).

When the treatment was applied earlier or later than the date, as above related, the seedlessness ratio declined.

It is shown in Fig. 4 that throughout these three years experiments, the period at which the prebloom dipping enabled the seedlessness ratio to reach above 90 percent was with Delaware 22–8 days before (Period II), and with Campbell Early 21–12 days before (Period II) the full bloom of the untreated inflorescences.

3. *Effects on the Development of the Seedless Berries*

(1) *Ratio of seedless fleshy berries*

In Fig. 2, it is shown that the ratio of seedless fleshy berries with Delaware reached above 60 percent when the prebloom dippings were treated 22–7 days before (Period II-III) and with Campbell Early it reached above 10 percent (30 percent at the most) when treated 21–5 days before (Period II-III) the full bloom of the untreated inflorescences. Throughout the three years of experimentation from 1967 to 1969, with Delaware it reached above 60 percent when treated 22–10 days before (Period II), and with Campbell Early above 10 percent when treated 21–13 days before (Period II) the full bloom of the untreated inflorescences (Fig. 4). In both varieties, the ratio of seedless fleshy berries declined remarkably when treated ealier or later than the above appointed period. With the earlier application much more shot berries were produced (Period I).

In examining the results of Fig. 2, it was apparent that much more seedless fleshy berries were produced than the shot berries in Delaware, and in Campbell Early less fleshy seedless berries and many shot berries were produced per cluster.

(2) *Size of seedless fleshy berries*

Diameter and weight of seedless fleshy berries in 1968 are shown in Fig. 3.

In Delaware, the size of seedless berries were smaller when the prebloom treatment was earlier, and got larger when treated later, but when treatment neared within 10 days before the full bloom of the untreated inflorescences, the berry

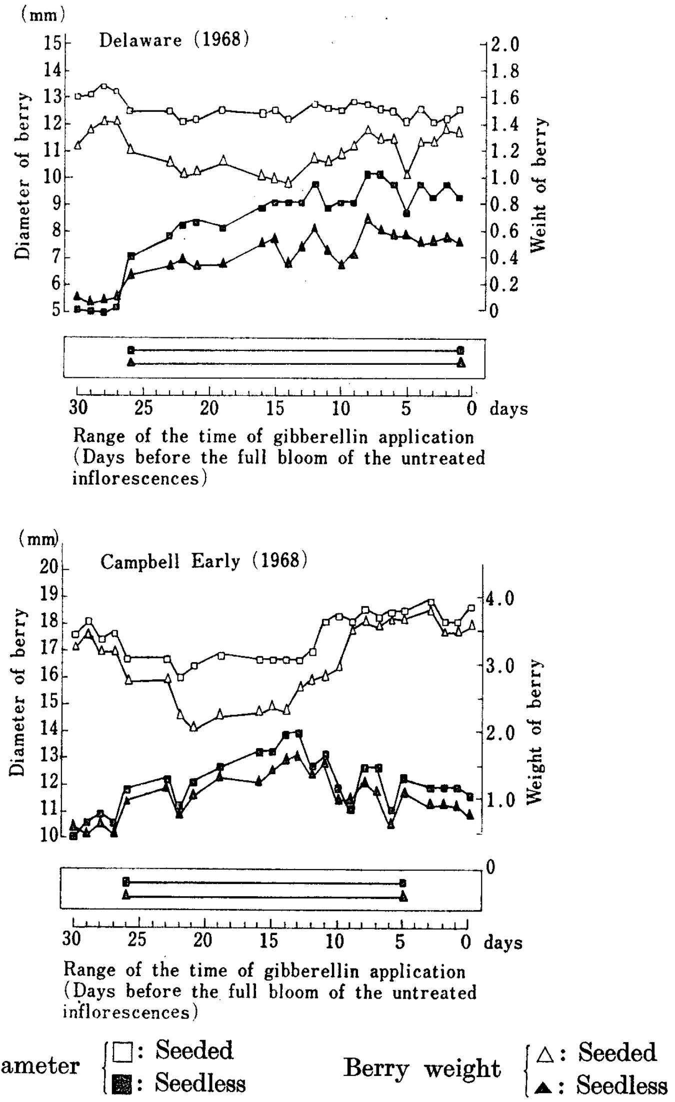


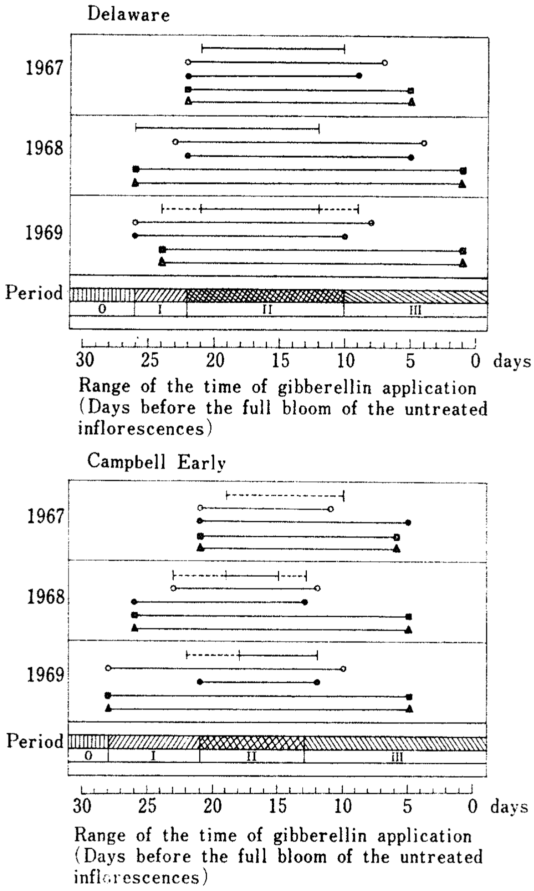
FIG. 3. Effects of the shift of the time of prebloom gibberellin application upon the berry growth in size and weight.

size increased no more. In Campbell Early, the same tendency was observed, but when treatment neared within 10 days before the full bloom of the untreated inflorescences, the berry size tended to decrease gradually.

The period at which the prebloom dipping enabled the berries to grow remarkably was in Delaware 26–1 days before (Period I-III), and in Campbell Early 26–5 days before (Period I-III) the full bloom of the untreated inflorescences (Fig. 3). Throughout the three years of experimentation, the effective period was in Delaware 22–5 days before (Period II-III) and in Campbell Early 21–6 days before (Period II-III) the full bloom of the untreated inflorescences (Fig. 4).

4. *The Most Effective Successful Period for the Prebloom Gibberellin Application*

As for the flowering advancement, seedlessness and seedless berry growth, the time range for the prebloom gibberellin application can be considered in four



Period	at which
|- - -|	The full bloom was advanced 4 days ahead of the untreated inflorescences
|——|	The full bloom was advanced 5 days ahead of the untreated inflorescences
○——○	The seedlessness ratio reached above 90%
●——●	The rate of seedless berries reached above 60% in Delaware and above 10% in Campbell Early
■——■	The diameter of seedless berries reached favorable size
▲——▲	The weight of seedless berries reached favorable size

Fig. 4. The most successfull period (Period II) for the prebloom gibberellin application.

periods (Fig. 4 and Plate 1 and 2).

Period 0 (30–26 days before the full bloom of the untreated inflorescences in Delaware, 30–28 days before that in Campbell Early): Nonsensitive to gibberellin, and many seeded berry formation per cluster (Plate 2-C,D,E and F).

Period I (26–22 days before the full bloom of the untreated inflorescences in Delaware, 28–21 days before that in Campbell Early): Sensitive to gibberellin, and a few seedless fleshy berry formation with too much shot berry formation (Plate 2-E,F,G and H).

Period II (22–10 days before the full bloom of the untreated inflorescences in Delaware, 21–13 days before that in Campbell Early): Sensitive to gibberellin, and abundant seedless fleshy berry formation (Plate 2-G, H, I, J and K).

Period III (10–0 days before the full bloom of the untreated inflorescences in

Delaware, 13–0 days before that in Campbell Early): Resistant to gibberellin, and abundant seeded berry formation (Plate 2-I, J, K and L).

The most effective, successful period for the prebloom gibberellin application was shown in Fig. 4 (Period II).

It may be concluded that the most successful period for the prebloom gibberellin application is from 22 days to 10 days in Delaware and in Campbell Early from 21 days to 13 days prior to the full bloom of the untreated inflorescences.

Discussion

The details of the effects of the prebloom application of exogenous gibberellin are described and discussed under separate headings below.

1. *Effects on Flowering*

With Delaware, Campbell Early, Muscat of Alexandria, Muscat Hamburg and other varieties of grapes, Kishi et al. (1), Muranishi (2) and other workers (3, 4) reported that the earlier the gibberellin treatment was applied, the more hastened the flowering took place.

In this report, it is shown that flowering was hastened by the prebloom gibberellin dipping treated during a certain range of prebloom period (Fig. 1 and 4). It seems to be due to the growth acceleration of gibberellin for the flowers just becoming sensitive to gibberellin. So the effect was gradually diminished as the treatment neared the full bloom of the untreated inflorescences. On the other hand, a lesser sign of response was shown to the earlier dipping treatment.

2. *Effects on the Seedlessness*

Kishi et al. (1) pointed out the importance of the time of prebloom treatment with Delaware. Christodoulou et al. (5) reported that the timing of gibberellin application influences cluster looseness, primarily by its effect on berry set and on berry size and shape.

As ovules mature, they grow to be less sensitive to auxins and gibberellin. It is shown that the young ovules which are very sensitive to auxins are actually killed by the exogenous auxin (Luckwill (6), Murneek and Teubner (7), Teubner and Murneek (8)) and it will be reasonably assumed that the exogenous gibberellin also killed the very sensitive ovules and produced seedless berries (Figs. 2 and 4).

3. *Effects on the Development of Parthenocarpic Seedless Berry*

(1) *Effects of growth substances in parthenocarpy and the critical time for efficiency*

Comparison of the endogenous levels of native growth regulators in seeded and seedless strains have been made by several workers, for example, by Gustafson (9) in oranges, lemons and grapes, Crane et al. (10) in figs, Nitsch et al. (11) in

Vitis labrusca, Coombe (12) in *Vitis vinifera*. In all these cases, it was found that the seedless variety, while having generally a lower level of auxins and gibberellins in the developing fruits, had a "head start" over the seeded strains. Thus what seems to be important is the ability to create a certain threshold concentration at the critical time of anthesis.

It follows that a single application of gibberellin made timely prior to the full bloom can suffice to obtain fruits approximately in full size (Figs. 2, 3, 4, 8 and 9). A too early application (Period I, 26–22 days before in Delaware and 28–21 days before in Campbell Early) failed to induce seedless fleshy berry formation and berries remained as shot berries. A too late application (Period III, 10–0 days before in Delaware and 13–0 days before in Campbell Early) failed to induce seedless berry formation, being presumably due to the increasing resistance to gibberellin.

The fruit itself is a composite organ in which the development of the seeds and that of the various fruit tissues have to occur harmoniously. These various components grow in a certain sequence. The supply of gibberellin may become critical very early, before or immediately after anthesis.

(2) *Role and effects of postbloom versus prebloom gibberellin application*

It is shown in Fig. 5 that the seedless fleshy berries induced by a single prebloom application of gibberellin are more or less inferior in growth to those induced by the prebloom application accompanied by the postbloom application of gibberellin.

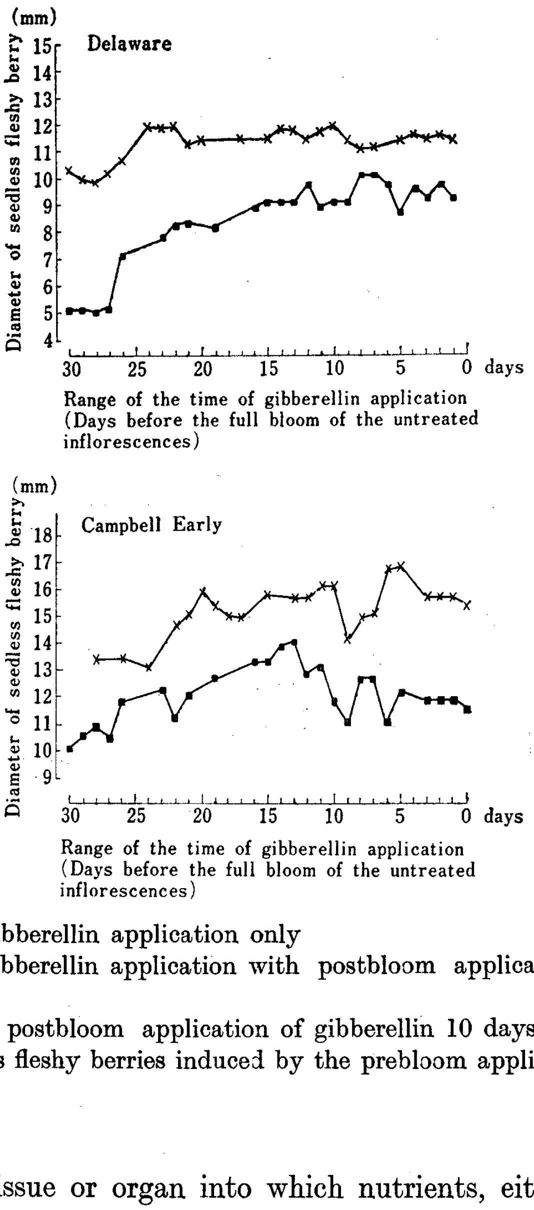
Postbloom application stimulates the growth of the seedless fleshy berries to the level of 10–12 mm in Delaware and to the level of 13–16 mm in Campbell Early. It is clearly shown that especially the far inferior berry growth induced by the earlier prebloom application was remarkably enhanced (Fig. 5).

It may be due to the restored increased gibberellin and auxin activities, being supplemented by the postbloom application of gibberellin. In the previous report (13), it is shown that the auxin and gibberellin activities rise rapidly in response to the exogenous gibberellin application.

(3) *Mode of action of hormones in fruit-set and growth*

While berries develop, seeded berries and seedless berries vary in intensity and so does the demand they exert on the nutrients available. It is suggested that carbohydrate nutrition of the inflorescences is of prime importance in fruit-set and that the limiting factor to fruit-set may be the ability of the developing cluster to command nutrients.

Fruit-set is almost certainly a correlative phenomenon. It has been known for many years that fruit-set is stimulated by such practices as pinching or topping of elongating shoots. Such pruning treatments reduce the number of competing sinks and make assimilates more readily available for inflorescences growth. A



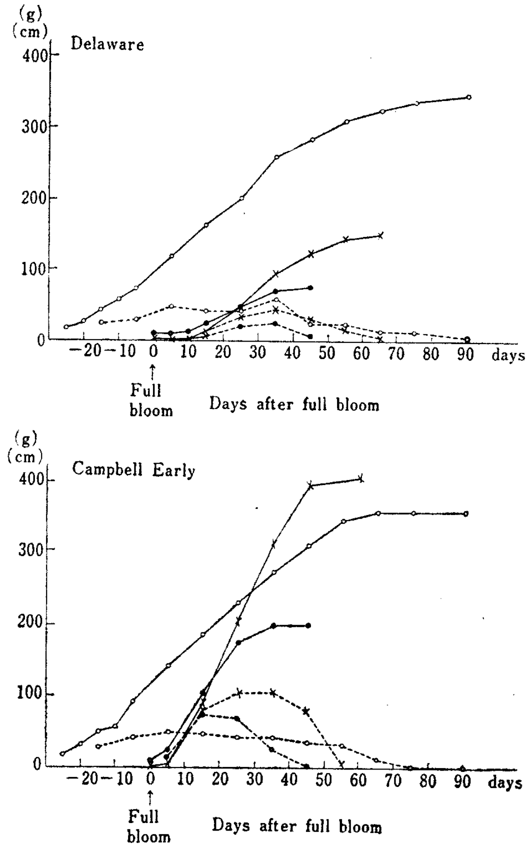
■——■ Prebloom gibberellin application only
×——× Prebloom gibberellin application with postbloom application 10 days after full bloom

FIG. 5 Effects of the postbloom application of gibberellin 10 days after full bloom upon the size of seedless fleshy berries induced by the prebloom application made at diverse times.

sink is a region of tissue or organ into which nutrients, either inorganic ions or organic metabolites, appear to move preferentially. An important factor in regulation of fruit-set would appear to be the relative rates of growth substance produced by apices, expanding leaves and perhaps by roots, since these relationships may decline the relative abilities of the individual organs to attract organic nutrients (Fig. 6).

The idea that the ability of developing fruit to attract nutrients was under some sort of hormonal control appeared to have been first started by Murneek (14) before the nature of any plant hormones was known. Recent work clearly suggests that translocation is under some sort of control. In intact plants there have been demonstrations that applications of either auxin, gibberellin, or cytokinin can increase the movement of phosphate and other inorganic ions.

When either cytokinis or gibberellic acid were applied to grape shoots or



Growth curve o——o Shoot length (cm)
×——× Seeded } Berry-weight per cluster (g)
●——● Seedless
Growth rate o- - -o Shoot length
×- - -× Seeded } Berry-weight per cluster
●- - -● Seedless

Fig. 6. Growth curve and growth rate of shoots length and berry-weight per cluster.

portions of shoots the normal pattern of labelled assimilate was altered in that there was augmented movement into the treated regions (Shindy (15)).

It has been shown that applications of gibberellic acid to developing grapes increase the movement of ^{14}C-labelled assimilates into fruits from leaves exposed to $^{14}CO_2$ (Kriedermann (16), Weaver et al. (17)).

(4) *Metabolites and fruit-set and growth*

It was found by Mullins (18) that inflorescences continued to grow and that they subsequently flowered and set fruit on the vine cuttings. Growth of inflorescences and fruits was accompanied by a disappearance of reserve starch from the cane and where the size of the reservoir of reserve material was larger relative to the size of the inflorescences there was a proportionate increase in the numbers of the fruitlets retained.

4. *The Attraction of Nutrients*

(1) *Competition phenomenon*

It has long been recognized that fruits exhibit a relative stability in chemical composition under the changing conditions of nutrition. This implies that available nutrients move preferentially to developing fruits at the expense of other plant organs.

Many studies of the movement of ^{14}C-assimilates from leaves treated with $^{14}CO_2$ to developing fruits, have illustrated the capacity of these latter to act as sinks.

It is clear that active competition exists between developing fruits and developing leaves and shoots and that the situation is constantly changing.

Coombe (19) found that removal of immature leaves and shoot tips from ringed branches increased fruit-set in grapes. He attributed these results to the superior ability of immature leaves and shoot apices to procure nutrients at the expense of the developing fruit. If branches were not girdled, leaf removal had no effect on fruit-set; presumably under these conditions, nutrients moved to elsewhere (Coombe (20)).

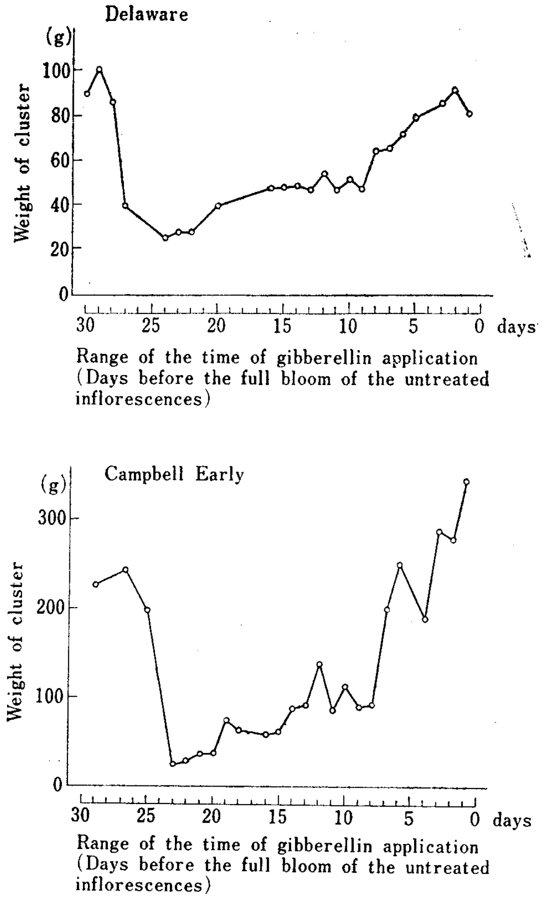


FIG. 7. Effects of the shift of the time of prebloom gibberellin application upon the weight of cluster with equal number of berries.

(2) *Competition between fruits*

Competition between individual fruits developing at the same time also occurred. The first set fruit commenced growth and although the other fruits may be fertilized in quick succession, it appears that the first fruit monopolizes the available nutrients to the extent that the remaining fruits grow less quickly.

It is shown in Fig. 6 that growth of shoots and berries most progressively proceed at the same period from 10 days before to 30–40 days after the full bloom of the untreated inflorescences.

It is shown in Figs. 2, 3 and 7 that the seedlessness reaches a high level and the weight of the cluster drops to a low level in the case of the prebloom gibberellin application from 26 to 5 days before the full bloom of the untreated inflorescences (Period I-III), and at the same time the diameter and the weight of the seedless berries reach high levels.

It seems that less nutrients move into these clusters mostly occupied with the seedless berries, being suppressed by the superior nutrient demand for the growth

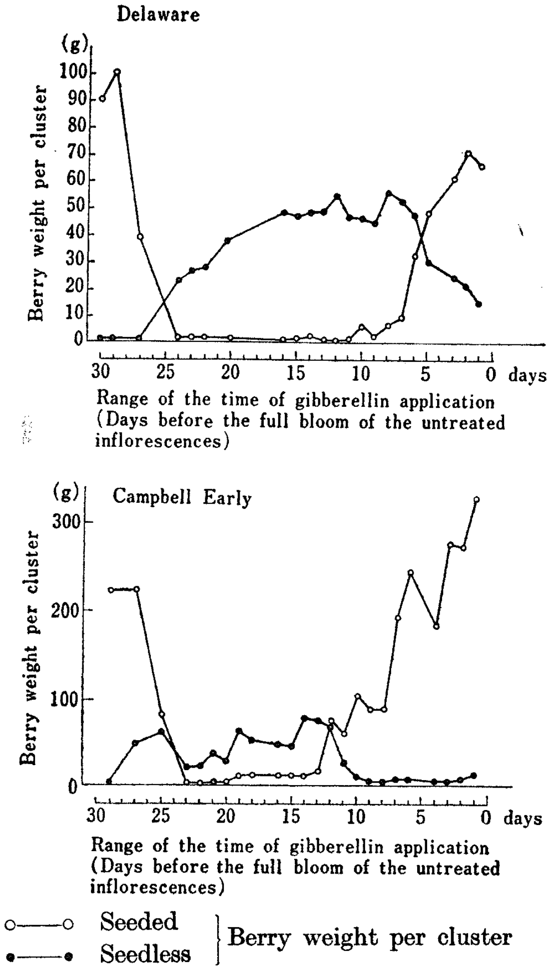


FIG. 8. Effects of the shift of the time of prebloom gibberellin application upon the weight of seedless-berries versus seeded-berries per cluster.

of shoots and leaves (Figs. 2 and 7). On the other hand, each seedless berry reaches a higher level in size and weight, being favoured by a less seeded berry set per cluster (Figs. 2,3,8 and 9). Seeded berries have the superior ability to procure nutrients at the expense of seedless berries in the same cluster.

It is shown in Figs. 2, 8 and 9 that gibberellin application earlier than 25 days before or later than 10 days after the full bloom of the untreated inflorescences induced a higher set and growth of the seeded berries than the seedless, and the growth in the size and weight of the seedless berries were much suppressed by the superior growth of the seeded berries in the same cluster (Fig. 3).

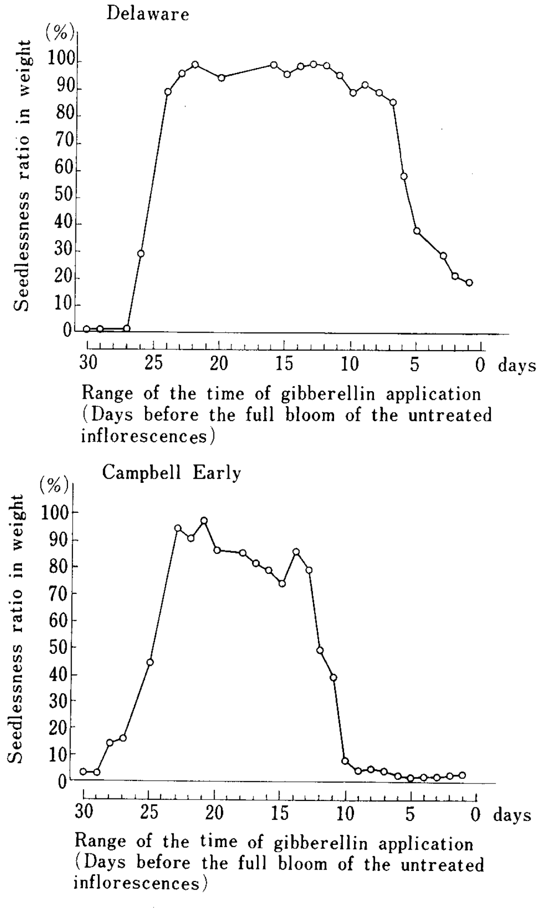
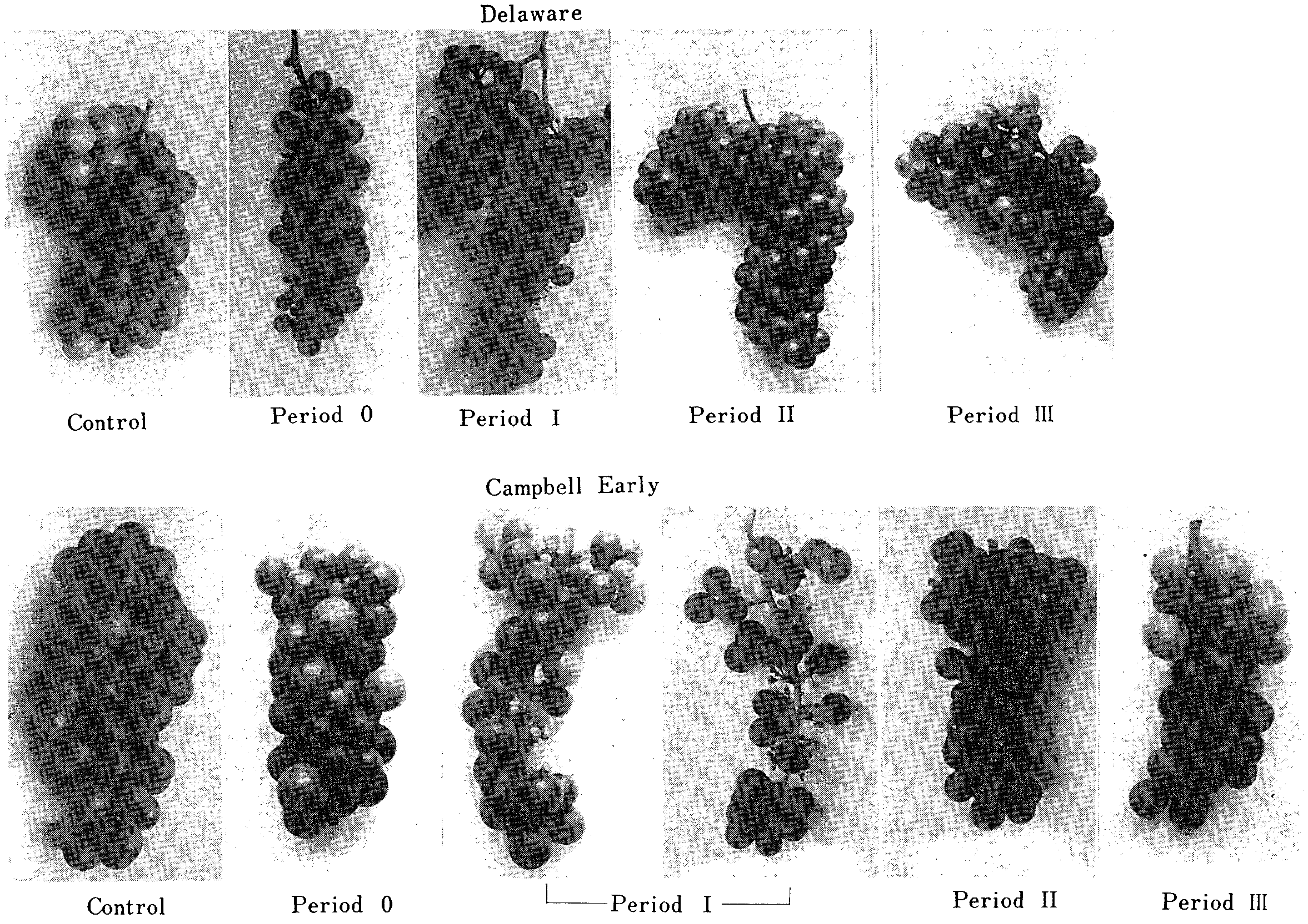


Fig. 9. Effects of the shift of the time of prebloom gibberellin application upon the sum of seedless berry weight represented as percent to the total berry weight per cluster

5. *Varietal Difference Between Delaware and Campbell Early Grapes*

It is shown in Fig. 2 that with Campbell Early the range of gibberellin application period at which the seedless berry formation reaches above 60 percent is much narrower than with Delaware. It may be presumably due to the varietal difference in the ovule sensitivity to gibberellin changing with maturation process.

In Campbell Early the seeded berries as compared with the seedless berries have much more superiority in attracting nutrients than in Delaware, so in the



Delaware

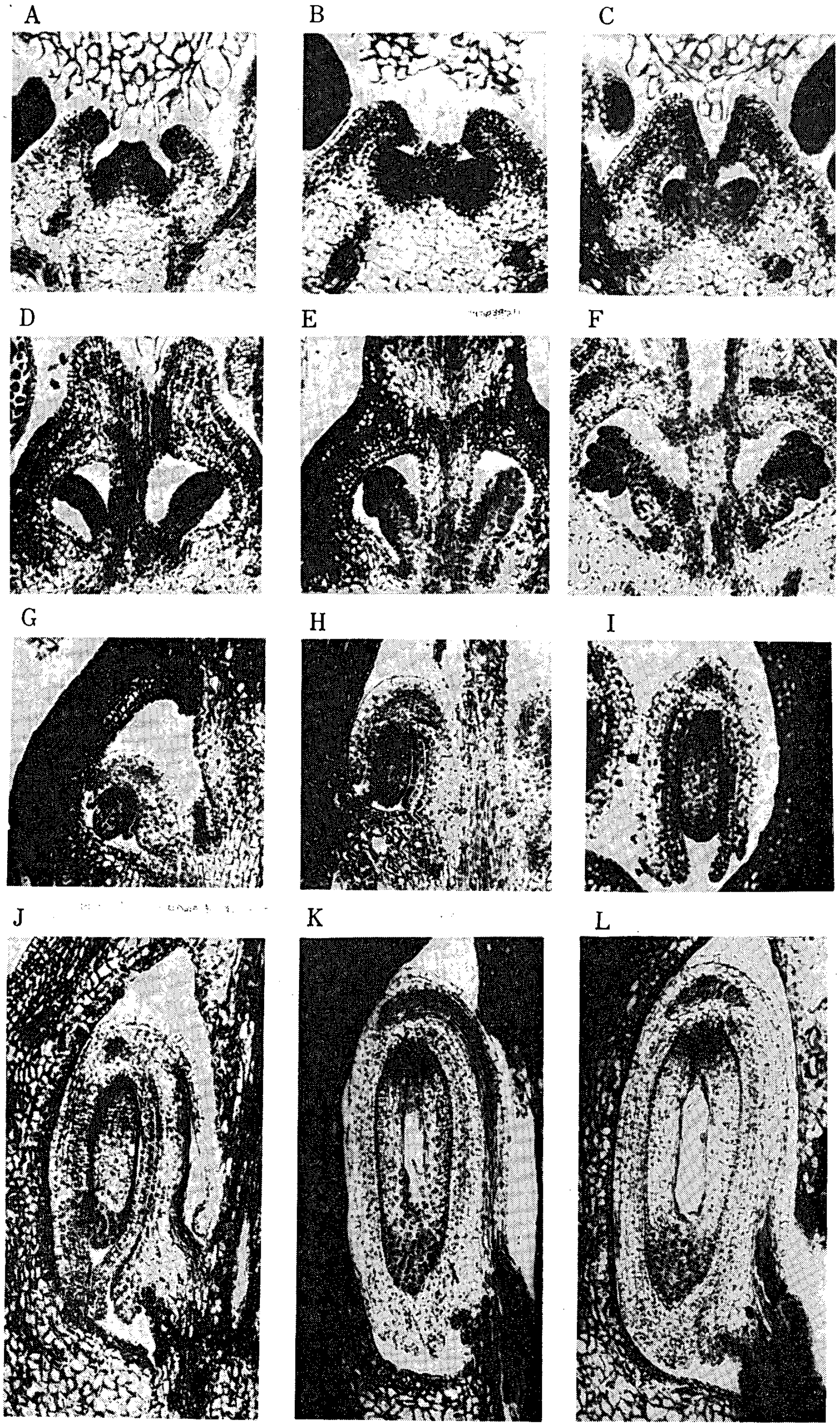
Control Period 0 Period I Period II Period III

Campbell Early

Control Period 0 Period I Period II Period III

Period O : Much many seeded berries with many shot berries hidden among the former
Period I : Many shot berries with a few seeded and seedless fleshy berries
Period II : Many seedless fleshy berries formed
Period III: Many seeded berries with a few seedless fleshy berries

Plate 1. Effects of the shift of the time of prebloom gibberellin application. (Period appoints the time of prebloom application).



A: 45–40 days, B: 40–35 days, C: 35–30 days, D: 35–30 days, E: 30–25 days, F: 30–25 days, G: 25–20 days, H: 25–20 days, I: 20–15 days, J: 20–15 days, K: 15–10 days, L: 10–5 days before the expected full bloom of the untreated inflorescences.

PLATE 2. Development of the ovules of Delaware grape.

former the growth of the seedless berries are suppressed more detrimentally than in the latter (Figs. 3, 8 and 9).

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