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Postharvest Berry Drop of Seedless Berries Produced by GA Treatment in Grape Cultivar 'Kyoho'

II. Relationship between Rachis Hardness and Differentiation of Rachis Xylem

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Summary

In 'Kyoho', rachis hardening was hastened in GA-treated rachis especially at its early developing stage, while it occurred slowly in the control rachis, and the difference in hardness between the two rachises was kept till harvest time. In 'Delaware', one of the difficult-to-drop cultivars, however, the hardening was generally less severe than in 'Kyoho' and there was found little difference between the GA-treated and control rachises, because in the former hardening was discontinued at its later developing stage.

When GA was applied at different times to 'Kyoho', 'Campbell Early' and 'Muscat Bailey A', rachis elongation was larger after earlier applications of GA in the former two, while in 'Muscat Bailey A' it was comparatively smaller. Rachis hardening occurred markedly after GA treatment up to mid-July in 'Kyoho' and 'Campbell Early' but barely occurred in 'Muscat Bailey A'. Increase in the rachis hardness was always accompanied with increases in the diameters of rachis and rachis xylem, which, in turn, corresponded to the increase in the number of cell layers of the secondary xylem. However, cell size and cell wall thickness, together with widths of the phloem and primary xylem, were not affected by GA treatment.

Rachis hardening was more marked after GA_3 than GA_{4+7} treatments. Increases in the rachis diameter and the number of cell layers of the secondary xylem were also larger in GA_3-treated rachis, but the cell size and cell wall thickness were not affected by GA_3 nor GA_{4+7}.

Thus, it appeared that rachis hardening following GA treatment was caused by the increase in the number of secondary xylem cells, although the extent of lignification of the cells seemed also to be involved in rachis hardening.

In the previous paper (1), we reported that the postharvest berry drop in 'Kyoho' hastened by GA treatment was caused by rachis hardening rather than

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advanced berry maturity and the increase in rachis hardness was accompanied with increase in the rachis diameter.

The objectives of this report were to elucidate 1) changes with time in rachis hardness and diameter affected by GA treatment and 2) changes in hardness, length, diameter and internal anatomy of the rachis with the time of GA treatment. In addition, the effects of GA_3 on the hardening and internal anatomy of rachis were compared with those of GA_{4+7}.

Materials and Methods

1. *Hardening of Rachis Following GA Treatment.*

Eleven-year-old 'Kyoho' and 9-year-old 'Delaware' grapevines grown in the orchard of Chiba University were used. 'Delaware' is a difficult-to-drop cultivar and was used to compare with 'Kyoho'. Flower clusters of 'Kyoho' and 'Delaware' were dipped twice into GA_{4+7} and GA_3 solutions, respectively, at 100 ppm with 100 ppm Aerol OP as a wetting agent, 3 and 19 days after full bloom (June 8 and 24) in 'Kyoho' and 18 days before and 10 days after full bloom (May 11 and June 8) in 'Delaware'. GA-treated clusters together with control ones were sampled 6 times during the period from June 8 to August 17 in 'Kyoho' and 6 times during the period from May 11 to August 7 in 'Delaware'. Control clusters of 'Delaware' were sampled further 2 times on August 14 and 26 because they were delayed in ripening. Deflection angle of rachis and diameters of rachis and rachis xylem at the fulcrum were determined as described previously (1). For the determination of deflection angle of rachis, weights of 20 and 5 g were used in 'Kyoho' and 'Delaware', respectively. Immediately after the determinations, the rachises were stored at –25°C for further investigations.

2. *Elongation, Hardening and Thickening of Rachis as Affected by the Time of GA Treatment.*

Six-year-old 'Kyoho' and 16-year-old 'Campbell Early' and 'Muscat Bailey A' grown in the orchard of Tohoku University were used. The former two are easy-to-drop cultivars and the latter one is a difficult-to-drop cultivar. The latter is also late in sprouting and flowering. Clusters uniform in size were selected. Four clusters each were dipped into GA_3 solution at 100 ppm with 100 ppm Aerol OP 10 times during the period from May 23 to August 3 in 'Kyoho' and 'Campbell Early' and 8 times during the priod from June 9 to August 3 in 'Muscat Bailey A'. Elongation of clusters treated with GA earlier was measured successively until June 27 in 'Kyoho' and 'Campbell Early' and July 24 in 'Muscat Bailey A', because the elongation was found to be marked after the earlier treatments. On September 18, all GA-treated clusters were harvested, and rachis length, deflection angle of rachis (a weight of 50 g was used for the 3 cultivars) and diameters of rachis and rachis xylem were determined. The deflection angle was expressed in percentages of that of the control. After the determinations, rachises were fixed in 50% alcohol. The fixed rachises of 'Campbell Early' and 'Muscat Bailey A' were sectioned transversely by hand at their proximal ends and xylem tissues were stained with 1% phloroglucinol and concentrated HCl. From their photomicrographs, the number of cells along the radial diameter of secondary xylem was counted in 5 replications. Width of the secondary xylem, cell width and cell wall thickness of the secondary xylem and widths of the primary xylem and phloem were measured in 5 replications using an ocular micrometer.

3. *Rachis Hardening as Affected by the Treatments of GA_3 and GA_{4+7}.*

Six-year-old 'Kyoho' grapevines grown in 45-cm pots in Tohoku University were used. Flower clusters were dipped into GA_3 and GA_{4+7} solutions at the concentrations of 10, 25, 50, 75 and 100 ppm 2 days after full bloom (June 26) and harvested on August 30. The measurements were the same as in Experiment 1.

Results

1. *Rachis Hardening Following GA Treatment.*

As shown by their deflection angle, the GA-treated rachises in 'Kyoho' hardened more rapidly than the control ones until June 21, 13 days after the first treatment. Thereafter, the increase in hardness continued until July 30, although it stopped for a time late in June in the treated rachises. Thus, the control rachises were always kept more flexible than the treated ones and showed a deflection angle 2 times as large as that of the latter at harvest time. Also in 'Delaware', the GA-treated rachises hardened more rapidly than the control ones until June 30. The second increase began on July 16 in the control rachises, while in the treated ones it began on July 30, just before the harvest time. Thus, the difference in hardness was rather great during mid-June to mid-July, but it was much diminished when compared at harvest in August (Fig. 1).

Rachis diameter was 2 times larger in 'Kyoho' than 'Delaware' at flowering. In 'Kyoho', it increased with time in inverse proportion to the deflection angle in the treated rachises. In the control rachises, however, the increase was small and it was especially true late in July. Thus, at harvest, the GA-treated rachises were 1.22 times larger in diameter than the control ones. In 'Delaware', the diameter increased also with time and more so in the treated rachises, but the increase was comparatively small as compared with 'Kyoho', and there was little difference between the treated and control rachises at harvest time (Fig. 2).

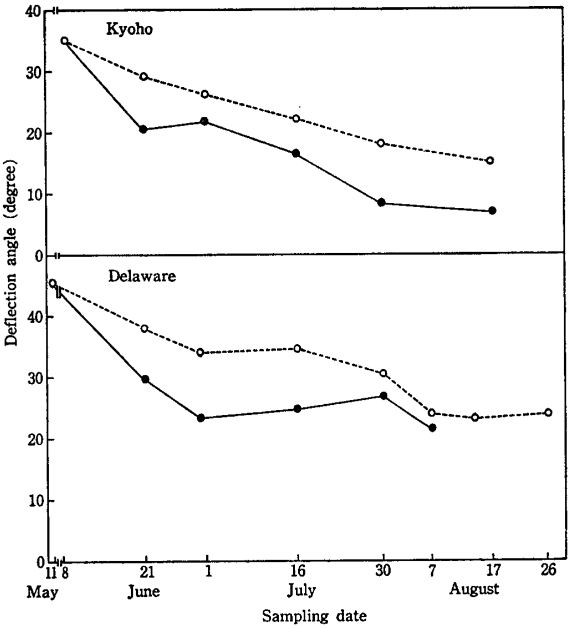

FIG. 1. Changes in hardnesss of GA-treated and control rachises as measured in deflection when weights of 20 and 5 g were hung at the distance of 10 cm from fulcrum in 'Kyoho' and 'Delaware', respectively. Clusters were dipped in GA$_{4+7}$ solution at 100 ppm twice, 3 days (June 8) and 19 days (June 24) after full bloom in 'Kyoho' and in GA$_3$ solution at 100 ppm twice, 18 days before (May 11) and 10 days after (June 8) full bloom in 'Delaware', respectively. GA-treated: ●—●. Control: o---o.

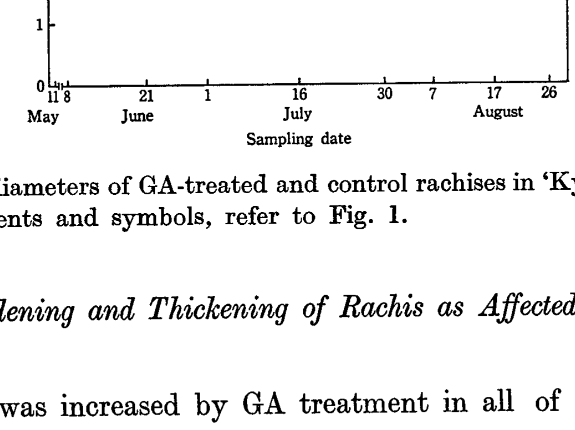

FIG. 2. Changes in diameters of GA-treated and control rachises in 'Kyoho' and 'Delaware'. For GA treatments and symbols, refer to Fig. 1.

2. *Elongation, hardening and Thickening of Rachis as Affected by the Time of GA Treatment.*

Rachis length was increased by GA treatment in all of the three cultivars used, although the increase was considerably smaller in 'Muscat Bailey A', which showed almost no hardening of rachis following GA treatment. In addition, the earlier the GA treatment, the larger the rachis elongation immediately after the treatment and in consequence, the larger the rachis length at harvest (Fig. 3). When GA was applied on and after June 27 to 'Kyoho' and 'Campbell Early' and

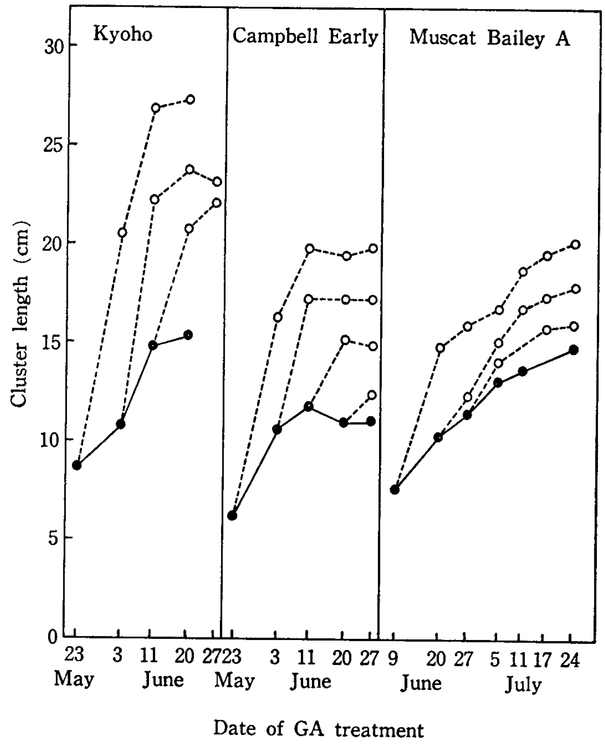

FIG. 3. Effects of time of GA treatment on cluster elongation in 'Kyoho', 'Campbell Early' and 'Muscat Bailey A'. GA-treated: o---o. Control: ●—●.

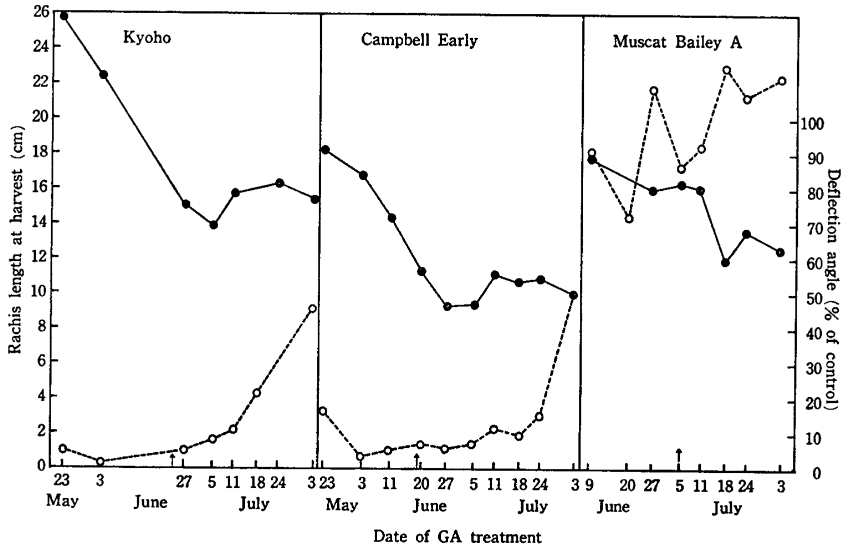

FIG. 4. Effects of time of GA treatment on rachis length and deflection of rachis when a weight of 50 g was hung at the distance of 10 cm from fulcrum in 'Kyoho', 'Campbell Early' and 'Muscat Bailey A'. Arrows designate dates of full bloom. Rachis length: ●—●. Deflection angle: o---o.

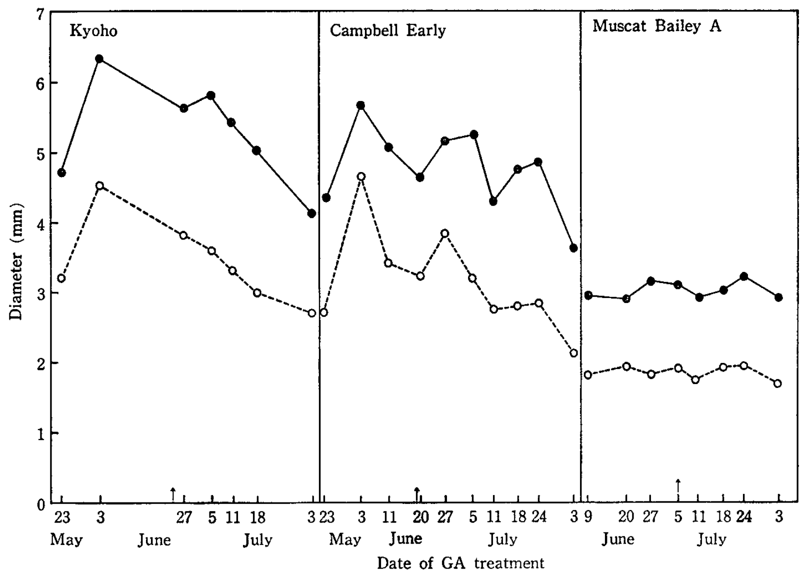

FIG. 5. Effects of time of GA treatment on diameters of rachis and its xylem in 'Kyoho', 'Campbell Early' and 'Muscat Bailey A'. Arrows designate dates of full bloom. Rachis diameter: ●—●. Xylem diameter of rachis: o---o.

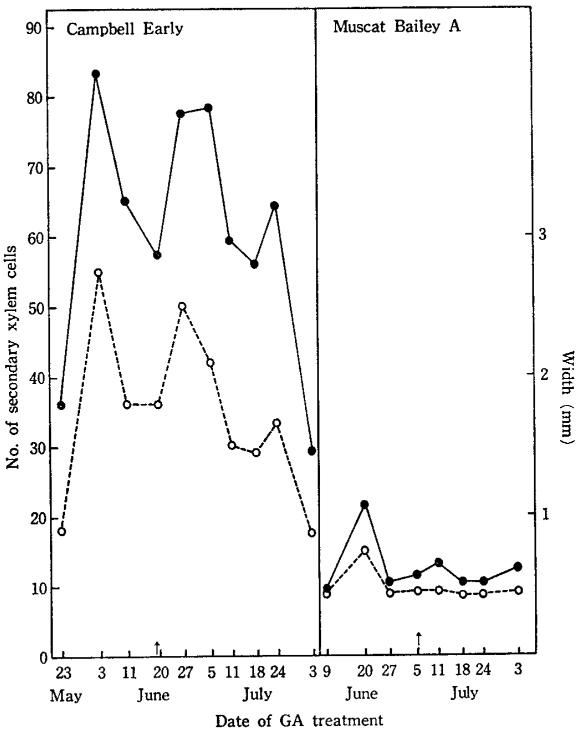

FIG. 6. Effects of time of GA treatment on number of cells and width of secondary xylem along radial diameter of rachis in 'Campbell Early' and 'Muscat Bailey A'. Arrows designate dates of full bloom. Number of secondary xylem cells: ●—●. Secondary xylem width: o---o.

July 18 'Muscat Bailey A', there was found little effect of GA on rachis elongation.

In 'Kyoho' and 'Campbell Early', rachis hardness at harvest time was larger when GA was applied during the period from May 23 to July 11 or 24 and largest when applied on June 3. In 'Muscat Bailey A', however, the deflection angle of rachis was larger than in 'Kyoho' and 'Campbell Early' and its hardness seemed little affected by GA treatment, although it varied considerably with the time of GA treatment (Fig. 4).

In 'Muscat Bailey A', the rachis diameter was comparatively small and not affected by GA treatment. While in 'Kyoho' and 'Campbell Early', the rachis diameter at harvest was largest when GA was applied on June 3. The increase became smaller when GA was applied later, although there were small increases when it was applied around July 5 and July 24, but only in 'Campbell Early'.

The diameter of rachis xylem occupied about 60 ('Muscat Bailey A') to 70 ('Kyoho' and 'Campbell Early') percent of that of rachis and varied with the time of GA treatment and almost paralleling the rachis diameter (Fig. 5). The number of cells and width of the secondary xylem of rachis were measured for 'Campbell Early' and 'Muscat Bailey A'. The two items varied also with the time of GA treatment almost paralleling the rachis and rachis xylem diameters in 'Campbell Early', while in 'Muscat Bailey A' they were little affected by GA treatment although small increases were found following the treatment on June 20 (Fig. 6).

Cell size and cell wall thickness of the secondary xylem of rachis and the widths of primary xylem and phloem, however, varied little with the time of GA treatment in both cultivars (Fig. 7, 8).

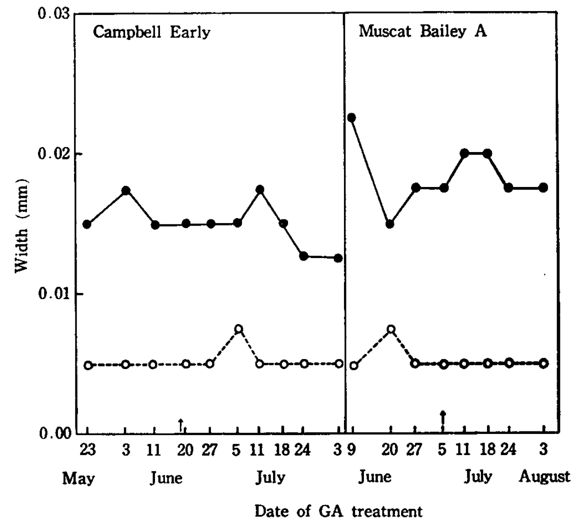

FIG. 7. Effects of time of GA treatment on cell size and cell wall thickness of the secondary xylem of rachis in 'Campbell Early' and 'Muscat Bailey A'. Arrows designate datas of full bloom. Cell size: ●—●. Cell wall thickness: o---o.

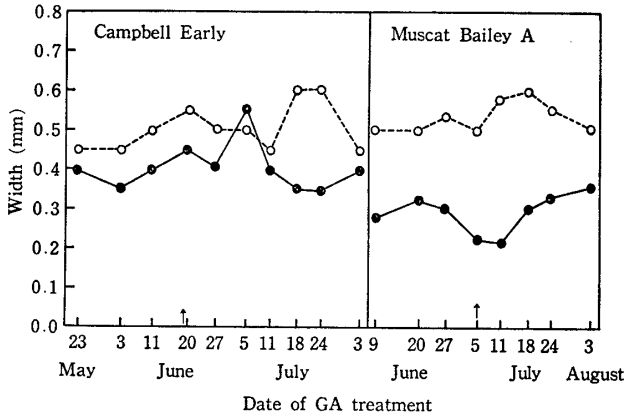

FIG. 8. Effects of time of GA treatment on widths of primary xylem and phloem along radial diameter of rachis in 'Campbell Early' and 'Muscat Bailey A'. Arrows designate dates of full bloom. Primary xylem: ●—●. Phloem: o---o.

3. *Hardening and Thickening of Rachis as Affected by GA_3 and GA_{4+7}.*

Rachis hardness increased with the concentrations not only of GA_3 but also GA_{4+7} but slowly at concentrations higher than 50 ppm. Diameters of rachis and rachis xylem also increased up to 100 ppm with GA_3 and 75 ppm with GA_{4+7}. The effects of GA_3 were always larger than those of GA_{4+7} (Fig. 9), and it was evidently shown in the number of cells and width of the secondary xylem, both of which increased more markedly with GA concentrations in GA_3-treated rachises (Fig. 10). The cell size and cell wall thickness of the secondary xylem, however, were little affected by GA_3 or GA_{4+7}. The microscopical observation was not done for 'Kyoho' in experiment 2. From this experiment, however, it was shown that also in 'Kyoho', the number of cells in the secondary xylem increased following GA treatment, though it was not so marked as in 'Campbell Early' in Experiment 2.

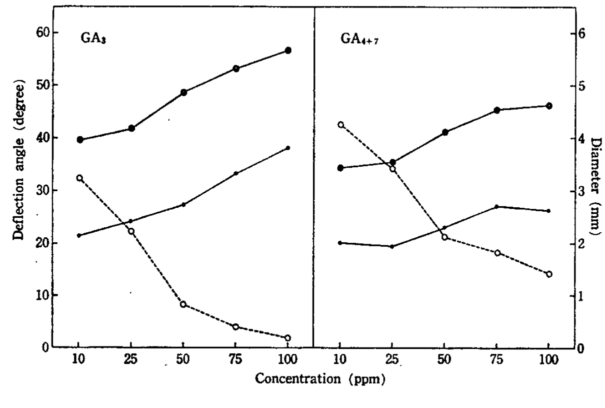

FIG. 9. Effects of GA_3 and GA_{4+7} and their concentrations on diameters of rachis and its xylem and deflection of rachis when a weight of 50 g was hung at the distance of 10 cm from fulcrum. Clusters were dipped in 10, 25, 50, 75 and 100 ppm solutions of GA_3 or GA_{4+7} on June 26, 2 days after full bloom. Rachis diameter: ●—●. Xylem diameter of rachis: ·—·. Deflection angle: o---o.

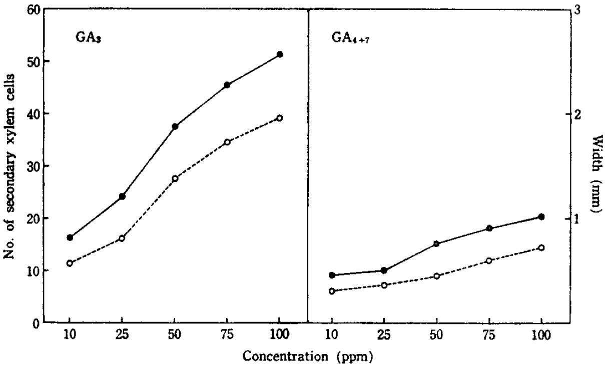

FIG. 10. Effects of GA_3 and GA_{4+7} and their concentrations on number of cells and width of secondary xylem along radial diameter of rachis. Clusters were dipped in 10, 25, 50, 75 and 100 ppm solutions of GA_3 or GA_{4+7} on June 26, 2 days after full bloom. Number of secondary xylem cells: ●—●. Secondary xylem width: o---o.

Discussion

In both easy-to-drop and difficult-to-drop cultivars, rachises hardened with their development. The hardening was more marked in easy-to-drop cultivars although the deflection angle as an index of rachis hardness could not be directly compared between cultivars because of different rachis diameters and different weights used for measurement. In addition, the hardening was hastened by GA especially immediately after its application. The differences in hardness between the GA-treated and control rachises were noticeable until harvest in easy-to-drop cultivars, while in difficult-to-drop cultivars, the differences had disappeared at harvest time because the hardening of GA-treated rachises discontinued at the later developing stages. In easy-to-drop cultivars, rachis hardening was recognized after GA treatments as late as mid-July, and was most marked after GA treatment on June 3. While rachis length was larger after earlier GA treatments but was not affected by GA treatments on and after June 30. Thus, rachis hardening and elongation hastened by GA seemed to be induced by different mechanisms. However, the fact that rachis elongation was larger in easy-to-drop cultivars and smaller in difficult-to-drop cultivars may suggest some relation between hardening and elongation, so far as the cultivars used were concerned.

As already shown, it was evident that rachis hardening was accompanied with the increase in diameters of rachis and rachis xylem. Furthermore, rachis diameter varied almost in parallel with the number of cell layers of the secondary xylem in relation to the time of GA treatment. Cell size and cell wall thickness of the secondary xylem together with the widths of the phloem and primary xylem, however, did not differ from those of the control. In this respect, Itakura (2) reported that GA treatment hastened development of secondary xylem more markedly in 'Campbell Early' than 'Delaware', though he did not count the number of cells. These facts may indicate that the increase in the number of cells of the secondary xylem participates in the increase in rachis diameter, and hence, rachis hardening. However, this is not always true of 'Kyoho'. In 'Kyoho', the number of the cells increases though not so markedly as in 'Campbell Early', while lignification of the cells proceeds markedly to hasten rachis hardening as will be shown later.

Promotion of xylem differentiation by exogenous GA has been reported in apricot (3), Adzuki beans (4), some woody plants (5), *Solanum nigrum* (6), grapefruit (7), tomato (8), olive (9), etc. and in these plants, exogenous GA is considered to work with the endogenous auxin present in adequate amount in their tissues. However, in disbudded or defoliated sycamore (10), *Populus* (11) and *Xanthium* (12), GA promotes the normal xylem differentiation only when auxin is added to GA.

It is generally stated that GA and auxin play important roles in xylem differentiation and at a certain balance between them the newly formed xylem cells are normally lignified, differing little from those of control. Excepting grapevines reported here, varietal difference in xylem differentiation following GA treatment, however, is reported only in tomato (8), in which GA is known to stimulate the production and differentiation of xylem in a cultivar, vascularization of which is genetically limited. In the case of grapevines, the varietal difference seems to be due to the intrinsic balance between endogenous GA and auxin or the rate of inactivation of exogenous GA, varying with cultivars.

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