Effects of Exogenous Plant Growth Regulators on Yield, Fruit Growth, and Concentration of Endogenous Hormones in Gynoecious Parthenocarpic Cucumber (*Cucumis sativus* L.)

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It has been reported that parthenocarpic cucumbers with many female flowers and heavy fruit load often show fruit abortion and reduced fruit yield. To achieve the stable fruit production, it is necessary to elucidate the mechanism involved in fruit abortion in cucumbers via fruit load and endogenous plant hormones. In Exp. 1, the effects of exogenous plant growth regulators (PGRs) on yield and fruit growth were examined in a gynoecious, parthenocarpic cucumber (*Cucumis sativus* L.). Four types of PGR [indole-3-acetic acid (IAA), 2,3,5-triiodobenzoic acid (TIBA), benzyl adenine (BA), and gibberellic acid (GA₃)], which have been shown to enhance fruit growth in non-parthenocarpic cucumbers, were applied using lanolin paste to the peduncles at each node (6–25) of cucumber plants at anthesis. TIBA and BA applications significantly decreased the rate of fruit abortion, thereby increasing yield. IAA and GA₃ treatments increased the rate of fruit abortion at the middle and upper nodes, thereby reducing fruit yield. In Exp. 2, to clarify whether PGRs affected the concentrations of endogenous plant hormones, and whether IAA of high concentration increased fruit abortion under low-fruit-load conditions, we applied these PGRs (two concentrations of IAA, BA, and TIBA) to cucumber plants bearing only one fruit at node 11 or 12. No fruit abortion occurred following any PGR or control treatment, although both IAA and BA treatments inhibited fruit growth. BA application increased the production of cytokinins (Z, ZR, iP, and iPR) to a level similar to that after TIBA application one day after anthesis. However, compared with the response to TIBA treatment, after BA treatment, the peak in endogenous cytokinin production occurred at an earlier stage of fruit development. Additionally, both IAA and TIBA treatments increased endogenous IAA and cytokinin concentrations in fruit. These results suggest that exogenous PGRs affect the overall concentration of PGRs, as well as that of other endogenous plant hormones. However, PGRs may not be associated with fruit abortion when the fruit load is low. In conclusion, fruit load may have a greater influence on fruit abortion than that of PGRs.

Key Words: cytokinin, fruit abortion, fruit load, IAA, TIBA.

Introduction

High labor and supply costs are involved in vine training and disease control during long-term cucumber cultivation. The utilization of cultivars with many female flowers, such as cucumbers with several pistillate flowers per node (multi-pistillate type) or gynoecious and parthenocarpic fruit, increases the rate at which cucumbers can be harvested within a short period (Denna, 1973; Fujieda et al., 1982; Hikosaka and Sugiyama,

2004; Nandgaonkar and Baker, 1981; Uzcategui and Baker, 1979). Although the female flowers of multi-pistillate or gynoecious-type cucumbers often open successively, some types of fruit temporarily stop growing or abort (Hikosaka and Sugiyama, 2003). It has been reported that parthenocarpic cucumbers with many female flowers exhibit large periodic fluctuations in yield (Hikosaka and Sugiyama, 2003; Marcelis, 1992; Schapendonk and Brouwer, 1984), leading to unpredictable employment and labor management needs at harvest. Therefore, it is necessary to reduce the occurrence of fruit abortion in these cucumbers.

Fruit abortion in cucumbers can result from the unequal distribution of photoassimilates among fruit and

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vegetative organs (Marcelis, 1992; Schapendonk and Brouwer, 1984) due to changes in sugar metabolism related to variations in fruit load (Boonkorkaew et al., 2011). The distribution of photoassimilates can be attributed to differences in the plant hormone concentrations in fruits (Bangerth, 1989, 2000; Bangerth et al., 2000; Bertin, 1995; Schapendonk and Brouwer, 1984), sink sizes (i.e., the number of cells per fruit) (Bertin et al., 2002; Jullien et al., 2001), or the ontogenetic order of fruit (Egli and Bruening, 2002; Marcelis, 1996). Ganeshaiah and Shaanker (1994) suggest that the autocatalytic or feedback regulation of photoassimilate flow to developing sinks also plays a role in their distribution.

Studies have investigated the effect of plant growth regulators (PGRs) and exogenous plant hormones on fruit growth, in order to elucidate its driving mechanisms. In particular, indole-3-acetic acid (IAA) (Hayashi et al., 1970), 2,3,5-triiodobenzoic acid (TIBA) (Hamamoto et al., 1998; Kim et al., 1992), benzyl adenine (BA) (Shishido et al., 1990), N-(2-chloro-4-pyridyl)-N'-phenylurea (CPPU) (Li et al., 2014), and gibberellic acid (GA₃) (Ogawa et al., 1989; Shimizu, 1967) have been reported to induce parthenocarpic fruit growth in cucumbers and tomatoes. However, these studies applied PGRs to only one fruit per plant. Therefore, it is unclear whether the application of PGRs to multiple fruits per plant would decrease fruit abortion.

Although the application of PGRs to parthenocarpic fruit growth has been studied and transcriptional hormone analyses have been conducted (Li et al., 2014), there have been few studies (Ogawa et al., 1989, 1990) quantifying the concentration of endogenous plant hormones after PGR application. Ogawa et al. (1989, 1990) studied the effects of PGR application using a paper chromatographic bioassay to measure endogenous gibberellins and cytokinins in fruit of non-parthenocarpic cucumber cultivars.

To determine the effects of plant hormone application on fruit abortion, we studied the effect of various exogenous PGRs on fruit yield and individual fruit growth in a gynoeocious cucumber cultivar, which produces a higher fruit load than monoecious cultivars. Additionally, we studied whether exogenous PGRs affected the concentration of endogenous plant hormones in cucumber fruit, and whether the PGRs could be a predisposing factor triggering fruit abortion even under low-fruit-load conditions (one fruit per plant).

Materials and Methods

Experiment 1. Effects of PGR application on fruit yield and growth

Gynoeocious and parthenocarpic cucumbers (*Cucumis sativus* L. 'NK × AN8'), which bear 1 to 2 fruit per node, were sown in 10.5 cm pots. Seeds were obtained from Institute for Horticultural Plant Breeding (Matsudo, Chiba, Japan). Twenty-nine days after sow-

ing, 30 plants with three fully expanded leaves each were transplanted individually into plastic containers (20 L) filled with growth medium containing starter fertilizer (N, P, and K levels were 0.4, 0.9, and 0.5 g·kg⁻¹ soil, respectively) and cultivated in a greenhouse.

Nodes were numbered acropetally with the cotyledonary node designated as "node 0". Lanolin paste (1 g) containing four different PGRs, specifically, IAA (0.1 g·kg⁻¹), 2,3,5-triiodobenzoic acid (TIBA) (an inhibitor of auxin transportation, 0.1 g·kg⁻¹), BA (2 g·kg⁻¹), and GA₃ (1 g·kg⁻¹), was applied to the peduncle of each flower at nodes 6 to 25, at anthesis. These PGR concentrations have been shown to induce parthenocarp in cucumbers (Hayashi et al., 1970; Shimizu, 1967; Shishido et al., 1990) and tomato (Hamamoto et al., 1998). As a control, lanolin paste without a PGR was applied to flower peduncles at nodes 6 to 25, at anthesis. Six plants per treatment were placed in randomized blocks with one replicate per greenhouse. Lateral shoots at all nodes and flower buds at nodes 1 to 5 were removed, leaving the apical portions of the main vines untouched.

Each fruit (ovary) length (FL, in mm) and diameter (D, in mm) was non-invasively measured every 3 days from anthesis to harvest, to estimate fruit fresh weight (FW, in g). A preliminary experiment showed that the FW of 'NK × AN8' fruit could be estimated precisely from FL and D, as follows (Hikosaka and Sugiyama, 2005):

$$FW = 8.09 \times 10^{-4} \times (D/2)^2 \pi \times (FL) + 7.32 \times 10^{-1} \\ (n = 241, R^2 = 0.993)$$

Hikosaka and Sugiyama (2003) monitored the changes in the logarithms of fruit FW over time, in which the slope represented the relative growth rate, and cucumber fruit growth was divided into three phases. The first phase (Phase 1) lasts several days after the appearance of flower buds (longer than 20 mm in length) until a few days after anthesis; fruit (ovary) growth continues during this phase. The second phase (Phase 2), which starts from a few days after anthesis and varies in duration depending on the fruit, was defined as the stagnant growth phase. In this phase, the relative growth rate (RGR) was quite low (< 0.3 g·g⁻¹·d⁻¹) and ovary length was less than 40 mm. The third phase (Phase 3) corresponds to the rapid growth stage of fruit. The standard growth pattern of cucumber fruit under low-fruit-load conditions was established by combining with Phase 1 and Phase 3, without the stagnant growth phase (Phase 2).

In Exp. 1, we divided the stems into three sections: low (nodes 6 to 13), middle (nodes 14 to 20), and upper (nodes 21 to 25), according to the fruit growth patterns shown in the control. When fruit reached approximately 100 g in weight (commercial size in Japan), they were harvested regardless of the duration of phase 2, and the actual fresh weight was measured. Harvested fruit that

were slow to reach 100 g (later than 10 to 12 days after anthesis) were classified as stagnant. Fruit that failed to reach 100 g by 20 days after anthesis were usually yellowing and wilted, and were considered to be aborted. The ratio of aborted fruit was calculated as a comparison of the number of aborted fruit and the total number (aborted and harvested) of fruit.

Leaf area (LA, cm²) of 'NK × AN8' was estimated using leaf length (L, cm) and breadth (B, cm), with the following equation:

$$LA = 8.33 \times 10^{-1} \times (L \times B) - 2.52$$

(n = 162, R² = 0.982)

This equation was generated for 'NK × AN8' in a preliminary experiment (Hikosaka and Sugiyama, 2004), according to the method used by Robbins and Pharr (1987). L and B were measured at 7-day intervals.

Plants were irrigated daily with water or a nutrient solution (1–2 L·d⁻¹ per plant) (16 mM NO₃⁻, 4 mM H₂PO₄⁻, 4 mM Ca²⁺, 2 mM Mg²⁺, 8 mM K⁺, and 1.3 mM NH₄⁺).

Experiment 2. Effects of exogenous IAA, TIBA, and BA on fruit growth, and endogenous IAA and cytokinins of cucumber fruit under low-fruit-load conditions

Seeds of *C. sativus* L. 'NK × AN8' were sown in 10.5 cm pots and transplanted into plastic containers (20 L) filled with the same growth media used in Experiment 1 34 days after sowing, and cultivated in a greenhouse. All flower buds, except those at node 11 or 12, and lateral shoots were removed; that is, each plant bore a single fruit. Lanolin paste (1 g) containing IAA (0.1 g·kg⁻¹ or 2 g·kg⁻¹, IAA 100 or IAA 2000), TIBA (0.1 g·kg⁻¹), or BA (2 g·kg⁻¹) was applied to flower peduncles at node 11 or 12, at anthesis. As a control, lanolin paste without a PGR was applied to flower peduncles at node 11 or 12.

Endogenous hormone analysis

Four fruit at node 11 or 12 were harvested at 0, 1, 2, 4, and 8 days after anthesis, from each treatment group. Fruit were weighed, frozen in liquid nitrogen, and then the concentrations of trans-zeatin (Z), trans-zeatin riboside (ZR), isopentenyladenine (iP), isopentenyladenosine (iPR), and IAA were determined. These hormones are active forms of auxin and cytokinin that function as primary inducers of fruit growth in cucumber plants (Kim et al., 1992; Ogawa et al., 1989, 1990). The extraction and purification of hormones were performed as described by Yu et al. (2001) and Ito et al. (1999), with some modifications (Boonkorkaew et al., 2008). The extraction steps (except evaporation) were carried out at 4°C. Lyophilized samples were ground with 80% methanol containing 0.1% butylated hydroxytoluene (BHT), 0.06% polyvinyl-pyrrolidone, and 5% ascorbic acid. The homogenate was filtered and evaporated to an

aqueous phase under a vacuum. Hexane was added three times to remove impurities, and was discarded each time by partitioning with an equal volume of the aqueous phase. The aqueous phase was partitioned against an equal volume of n-butanol, after adjusting the pH to 8.0 with NaOH. The remaining aqueous phase was partitioned three times against equal volumes of ethyl acetate, after adjusting the pH to 3.0 via the addition of HCl.

The n-butanol soluble (n-BuOH) fraction was used to quantify cytokinin content, and the acidic ethyl acetate soluble (AE) fraction was used to quantify IAA. Each was evaporated to dryness under a vacuum and then dissolved in a small amount of solvent: water for the n-BuOH fraction and 80% methanol for the AE fraction. These fractions were loaded on a C18 Sep-Pak Plus cartridge (Waters Associates, Milford, MA, USA) and eluted with 80% methanol. To decrease the impurity of the n-BuOH fraction, the cartridge was washed with 5% methanol before elution. Each eluate was dried under a vacuum, dissolved in a small volume of methanol, and loaded into an ODS HPLC column (4.6 mm i.d. × 250 mm; Senshu Scientific Co., Tokyo, Japan) equilibrated with 5% acetonitrile. The column was then eluted with a water-acetonitrile gradient containing 0.5% acetic acid. The methods used to elute cytokinins from the n-BuOH fraction and IAA from the AE fraction were the same as those used in studies of Japanese pear shoots, described by Ito et al. (1999). Briefly, the elution conditions were as follows: 0–5 min with 5% acetonitrile, 5–50 min with a linear gradient from 5% to 30%, 50–60 min with a linear gradient from 30% to 80%, and 5 min with 80% acetonitrile. The flow rate was 1.5 mL·min⁻¹ and the column temperature was maintained at 40°C. The retention times of Z (12 min), ZR (18 min), iP (28 min), iPR (31 min), and IAA (40 min) were determined by running authentic standards under the same conditions.

Cytokinins and IAA were analyzed by enzyme-linked immunosorbent assay (ELISA) with polyclonal antibodies, as described by Weiler (1980) and Ito et al. (1999). Prior to the analysis of IAA, methylation with diazomethane was conducted. Although the recovery ratio of IAA in each sample was measured using indole propionic acid (IPA) as an internal standard (45 to 60%), we did not check the recovery ratios for cytokinins, and we presented the direct ELISA data collected during this experiment. These antibodies and cytokinin tracers were bought from OIChemIm Ltd., Olomouc, Czech Republic. The ratios of cross-reacting antibody between Z and ZR, and between iP and iPR were 5% and 20%, respectively.

Results

Experiment 1

Fruit yield in the TIBA and BA treatment groups was significantly higher than in the control group, while that

in the IAA and GA₃ treatment groups was significantly lower than in the control group (Fig. 1). No differences were observed in the number of pistillate flowers (Table 1), fruit shape, or fruit color among the different treatments (data not shown). The time elapsed between anthesis and harvest (days to harvest) in the TIBA treatment at both the lower (nodes 6 to 13) and the upper nodes (nodes 21 to 25) was shorter than in the control, and longer in the IAA treatment group at the middle nodes (nodes 14 to 20). Fruit abortion at nodes 14 to 20 was more frequent than at nodes 6 to 13 and 21 to 25 in all treatment groups. In fruits at nodes 14 to 20, the rate of fruit abortion in the IAA and GA₃ treatment was >90%, while in the TIBA and BA treatment groups it was <65%. There was a >60% incidence of fruit abortion at nodes 21 to 25 in IAA and GA₃ treatments, compared with <20% in TIBA and BA treatments. Even if fruit at nodes 14 to 20 did not abort in IAA treatment, most of these fruit exhibited stagnant growth, and thus the period from anthesis to harvest was longer. Conversely, the number of stagnant fruit at nodes 6 to 13 and 21 to 25 in all treatments was low, and did not differ among the treatments (data not shown).

The typical growth pattern of fruit on individual plants varied among the treatments (Fig. 2). At nodes 6

Fig. 1. Effects of application of plant growth regulators (PGRs) on yield of gynoecious cucumber (Exp. 1). Vertical bars represent standard error ($n = 6$). Different letters indicate significant differences among the treatments at $P < 0.05$ by Tukey-Kramer's test.

to 13, the control and IAA- and GA₃-treated fruit grew and were harvested almost simultaneously, while in the

Fig. 2. Effects of application of PGRs on individual fruit (nodes 6 to 25) growth in a single plant of gynoecious cucumber (Exp. 1). Similar patterns were obtained in the other 5 plants. Plots are shown after anthesis.

Table 1. Effects of application of plant growth regulators (PGRs) on the number of pistillate flowers, period from anthesis to harvest, and ratio of aborted fruit number to flower number in gynoecious cucumber (Exp. 1).

	No. of pistillate flowers from nodes 6 to 25	Nodes 6 to 13		Nodes 14 to 20			Nodes 21 to 25	
		Days to harvest	Rate of aborted fruit (%) ^z	Days to harvest	Rate of aborted fruit (%) ^z	Rate of stagnant fruit (%) ^y	Days to harvest	Rate of aborted fruit (%) ^z
Control	19.0 a ^x	12.5 ab ^x	4 a ^w	11.3 b ^x	81 ab ^w	40.0 b ^w	10.0 a ^x	37 bc ^w
IAA	19.7 a	13.1 a	6 a	20.0 a	95 a	100.0 a	10.0 a	67 a
TIBA	19.7 a	11.1 c	0 a	10.5 b	64 bc	13.3 c	8.9 b	17 c
BA	19.5 a	11.7 bc	2 a	11.0 b	43 c	15.4 c	10.0 a	10 c
GA ₃	19.2 a	12.7 ab	2 a	12.3 b	90 a	25.0 bc	9.8 ab	63 ab

^z Aborted fruit number/(harvested fruit number + aborted fruit number) × 100 (%). Harvested fruit included both stagnant and non-stagnant fruits.

^y (Stagnant fruit number/harvested fruit number) × 100 (%).

^x Different letters indicate significant differences among the treatments at $P < 0.05$ by Tukey-Kramer's test.

^w Arcsin of the rates was tested at $P < 0.05$ by Tukey-Kramer's test.

TIBA- and BA-treated groups, this occurred at distinct intervals. Although many fruit at nodes 14 to 20 aborted in all treatments, some fruit in the TIBA treatment group grew in the same manner as those at nodes 6 to 13, and the development of some fruit in the BA treatment group paused before the start of growth. The fruit at nodes 21 to 25 in the control, TIBA, and BA treatment groups grew at distinct intervals, while few fruit grew in the IAA and GA₃ treatments. There were no significant differences in leaf area among treatments (Fig. 3).

Experiment 2

When only one fruit was borne per plant, no fruit were aborted in any of the treatment groups (data not shown). The rate of fruit growth was slightly, but not significantly, higher in the TIBA treatment group, while being significantly lower in the IAA (0.1 g and 2 g·kg⁻¹) and BA treatment groups than in the control (Fig. 4).

Endogenous IAA expression was considerably higher at 1 and 2 days after anthesis, when 0.1 g and 2 g·kg⁻¹

Fig. 3. Effects of application of PGRs on leaf area of gynocarpic cucumber (Exp. 1). Vertical bars represent standard error ($n = 6$).

Fig. 4. Effects of application of PGRs to a single fruit per plant on fruit growth of cucumber (Exp. 2). Vertical bars represent standard error ($n = 6$ to 10). Different letters indicate significant differences among the treatments at $P < 0.05$ by Tukey-Kramer's test.

IAA was applied to peduncles, respectively (Fig. 5). Although the concentrations of endogenous IAA differed among treatments, endogenous IAA in all treatments increased until 1 or 2 days after anthesis, and then decreased. Between 1 and 4 days after anthesis, endogenous IAA concentrations in the TIBA treatment were intermediate between those in the IAA treatment and control groups.

The application of IAA at a concentration of 2 g·kg⁻¹ increased the production of endogenous cytokinins (Z, ZR, iP, and iPR), but the time course of these changes differed among cytokinin species (Fig. 6). Z, ZR, iP, and iPR showed peak levels at 1, 4, 2, and 4 days after anthesis, respectively. In contrast, the application of IAA at a concentration of 0.1 g·kg⁻¹ did not affect cytokinin concentrations.

The application of TIBA increased endogenous ZR and iPR to similar degrees as IAA application at 2 g·kg⁻¹, at least during the early stage of fruit development. On the other hand, during the early stage of fruit development, the effects of TIBA on Z and iP concentrations were weaker than those of IAA at 2 g·kg⁻¹.

The application of BA increased cytokinins (Z, ZR, iP, and iPR) in a manner similar to TIBA application, one day after anthesis. However, the concentrations of endogenous cytokinins, excluding ZR, continued to increase up to 2 days after anthesis in the TIBA treatment.

Discussion

Our results show that the application of TIBA and BA reduced fruit abortion in a gynocarpic parthenocarpic cucumber cultivar in Exp. 1. Evidently, TIBA and BA decreased the rate of abortion and fruit growth stagnation at the middle (14 to 20) and upper nodes (21 to 25) when fruit load was high. This is consistent with studies conducted by Kim et al. (1992) and Shishido et al. (1990), who reported that the application of TIBA and BA to a single fruit per plant enhanced fruit growth

Fig. 5. Effects of application of PGRs to a single fruit per plant on endogenous IAA in cucumber fruit (Exp. 2). Vertical bars represent standard error ($n = 6$ to 10). Different letters indicate significant differences among the treatments at $P < 0.05$ by Tukey-Kramer's test.

Fig. 6. Effects of application of PGRs to a single fruit per plant on endogenous cytokinins (zeatin, zeatin riboside, isopentenyl adenine, and isopentenyl adenine riboside) in cucumber fruit (Exp. 2). Vertical bars represent standard error ($n = 6$ to 10). Different letters indicate significant differences among the treatments at $P < 0.05$ by Tukey-Kramer's test.

without pollination in non-parthenocarpic cultivars, leading to increased yield. However, the application of IAA and GA_3 to a parthenocarpic cultivar led to the inhibition of fruit growth at the middle and upper nodes in our study. Conversely, Shimizu (1967), Ogawa et al. (1989), and Hayashi et al. (1970) found that the IAA and GA_3 treatments of a single fruit per plant induced parthenocarpic fruit growth in non-parthenocarpic cultivars.

Comparing both fruit growth patterns and abortion rates among PGR treatments in Exp. 1, PGRs can be classified into three types. First, IAA and GA_3 induce the simultaneous growth of fruit at the lower nodes, with high numbers of aborted fruit at the middle and upper nodes. Second, TIBA induces consecutive fruit growth at certain intervals, from the lower to the upper nodes. Third, BA induces consecutive fruit growth at the lower nodes, but with a short pause (Phase 2) before the start of fruit growth at the middle nodes. In the control treatment, the fruit growth pattern is consistent with that observed following IAA and GA_3 treatment at the lower nodes, and TIBA and BA treatments at the upper nodes. In parthenocarpic cucumber plants with high fruit loads, some fruit temporarily cease to grow after anthesis, finally aborting after a long growth pause (Hikosaka and Sugiyama, 2005). When the fruit load is larger than the carbon assimilation ability of the leaves is capable of supporting, the amount of photoassimilates available during the early stages of fruit growth may limit the number of growing fruit (Marcelis, 1992; Murakami et al., 1982). Therefore, it is possible that the

nearly simultaneous growth of fruit at the lower nodes increases fruit load relative to that observed to occur following TIBA and BA treatments, leading to increased fruit abortion at the middle and upper nodes in plants treated with IAA and GA_3 .

Hikosaka and Sugiyama (2005) reported that high fruit load depressed leaf area only slightly in the same gynoeceous cucumber cultivar used in this study. It has been reported that carbon assimilation by leaves is stimulated by the presence of developing fruits on cucumber plants (Barret and Amling, 1978; Marcelis, 1991). In accordance with these results, there were no significant differences in leaf area among treatments in Exp. 1. This suggests that high fruit production in the TIBA and BA treatment groups can be supported by the same leaf area as that observed in the IAA and GA_3 treatment groups. It is possible that fruit abortion in IAA and GA_3 treatments may not be due to a shortage of photoassimilates, but caused by an interaction with a high fruit load.

Following IAA and GA_3 treatments in Exp. 1, the rates of fruit abortion remained high at the upper nodes, although many fruit at the middle nodes also aborted. This suggests that the application of exogenous IAA or GA_3 at the lower nodes may increase the concentrations of endogenous IAA or GA_3 in fruit at middle and upper nodes, leading to fruit abortion. Additionally, there are two other possible explanations for the high rates of fruit abortion at the middle and upper nodes in IAA and GA_3 treatments. First, the simultaneous application of IAA and GA_3 to multiple flowers may cause an im-

balance in the levels of endogenous hormones in the plant, especially at the middle and upper nodes, leading to fruit abortion. Second, some PGRs such as IAA and GA₃ may weaken the sink strength of fruit at the upper nodes, leading to fruit abortion, as fruit with low sink strength frequently abort regardless of fruit load.

To clarify which parameter, fruit load or PGR, is a prior factor of fruit abortion (or to clarify whether IAA accelerates fruit abortion even under low-fruit-load conditions), and whether PGRs (the high concentrations of IAA alongside those of IAA, TIBA, and BA used in Exp. 1) affect the concentration of endogenous plant hormones, we applied PGRs to cucumber plants bearing only one remaining fruit at node 11 or 12 in Exp. 2 (low-fruit-load conditions). The results suggest that IAA and BA weakened sink strength and inhibited fruit growth, but did not promote abortion. Because high rates of fruit abortion at the upper nodes were found to occur in the IAA treatment, but not in the BA treatment, it appears that weak sink strength does not necessarily increase abortion rates at the upper nodes. Furthermore, it is unlikely that application of a large amount of IAA would trigger fruit abortion at the upper nodes because this did not occur following treatment with 2 g·kg⁻¹ of IAA in Exp. 2.

It is well known that PGR application to a single fruit per plant improves fruit growth and prevents fruit abortion (Hayashi et al., 1970; Kim et al., 1992; Ogawa et al., 1989; Shimizu, 1967; Shishido et al., 1990). Kim et al. (1992) reported that the application of either N-1-naphthylphthylamic acid (naptalam, an auxin transport inhibitor) or TIBA to the peduncles of non-parthenocarpic single cucumber fruits doubled their IAA content compared with that of unpollinated ovaries, and decreased fruit abortion. This was also the case with pollinated ovaries. The authors suggested that TIBA prevented IAA from being exported from the fruit to the plant via the peduncle, leading to increased IAA levels in fruit. Consistent with this, IAA and TIBA application to the peduncles also increased endogenous IAA concentrations in fruits in this study, but the effect on endogenous IAA concentration was more evident when comparing IAA and TIBA treatments.

The effects of IAA application on endogenous cytokinins differed depending on the concentration applied in Exp. 2, but the fruit growth restriction was comparable at both IAA concentrations. Conversely, TIBA application increased endogenous IAA production to a level between those observed in the IAA treatment and the control, but showed slightly increased fruit growth compared with the control. Therefore, it is possible that fruit growth was stimulated at optimal concentrations of endogenous IAA, independently of endogenous cytokinin concentrations.

BA application to the peduncle slightly but non-significantly increased endogenous cytokinin concentrations in fruit compared with the control, while TIBA

application significantly increased cytokinin concentrations. However, it is possible that, in Exp. 1, the effects of exogenous PGRs on IAA and cytokinin concentrations in fruit at the lower nodes were similar to those found in Exp. 2 because fruit load was low at the lower nodes and nodes 11 and 12 in Exp. 1 and 2, respectively. If this is the case, very low rates of fruit abortion at the lower nodes in all treatments in Exp. 1 are consistent with the hypothesis that endogenous IAA and cytokinins do not affect fruit abortion when fruit load is low.

In conclusion, exogenous PGRs affected the concentrations of some endogenous plant hormones in cucumber fruit. Additionally, the concentrations of endogenous plant hormones were not necessarily related to fruit abortion when the fruit load of the plant was low. Although other plant hormones should be analyzed for a more complete understanding of the mechanics involved, fruit load (existence of other growing fruit) may play a more significant role in fruit abortion than the PGRs measured in this study. Further studies are required to determine how and which PGRs or endogenous hormones affect simultaneous fruit growth or abortion in parthenocarpic cucumber plants with high fruit loads.

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