Journal
Appl Hort

Factors affecting fruit abortion in a gynoecious cucumber cultivar

A. Tazuke[1], P. Boonkorkaew[2], S. Hikosaka[2] and N. Sugiyama[2]

[1]*College of Agriculture, Ibaraki University, Ami, Ibaraki, 300-0393, Japan,* [2]*Graduate School of Agricultural and Life Sciences, Bunkyo-ku, Tokyo, 113-8657, Japan. E-mail: tazuke@mx.ibaraki.ac.jp*

Abstract

Fruit growth of the gynoecious cucumber 'NK × AN8' was measured non-destructively to clarify whether the presence of fruit at lower nodes caused the abortion of fruit at upper nodes. When only one fruit per plant was allowed to grow, fruit growth could be divided into two phases: slow exponential and fast exponential. Phase change from slow to fast occurred when cumulative temperatures (CTs) after anthesis reached 38 and 54ºC d for pollinated and parthenocarpic fruit, respectively. The CT was calculated as the sum of the differences between daily temperatures and 5ºC. When fruit at nodes 4 and above were allowed to grow, the first growth phase was prolonged. Furthermore, parthenocarpic fruit aborted frequently when the sum of the relative growth rate (RGR) with respect to the CT (the sum of RGRs) for fruit at lower nodes exceeded 0.1 g g^{-1} (ºC d)$^{-1}$. Pollination with pollen of the monoecious cucumber '028' strongly suppressed fruit abortion; a large number of fruits could develop to a commercial size even when the sum of RGRs for fruit at lower nodes exceeded 0.1 g g^{-1} (ºC d)$^{-1}$. These results suggested that fruit abortion is more related to the existence of actively growing fruit than to the absolute amount of dry mass accumulation in the fruit.

Key words: Cucumber, gynoecious cultivar, fruit growth, fruit abortion, pollination, relative growth rate

Introduction

A large number of pistillate flowers are formed within a short period in gynoecious cucumber cultivars. Although the number of pistillate flowers is about two times greater in gynoecious cultivars than in monoecious cultivars, the yield is only 10-20% higher in the former than in the latter cultivars. A higher percentage of flowers abort in gynoecious cultivars compared with monoecious cultivars, leading to a lower yield than expected from the number of flowers (Hikosaka and Sugiyama, 2004). Marcelis (1994) proposed a simulation model of cucumber fruit growth, but his model is not satisfactory for the precise estimation of fruit abortion.

Fruit abortion being an important factor determining fruit production, it has been studied extensively in many crops. However, an unequivocal conclusion has not yet been attained. Some authors have considered that the abortion of reproductive organs was affected by plant hormones. For example, ethylene production is suggested to cause the abortion of *Hibiscus* flower buds (Van Meeteren and Van Gelder, 1995) and pepper fruit and flower buds (Huberman *et al.*, 1997; Wien *et al.*, 1989). On the other hand, the inhibition of auxin transport is related to the abortion of pepper fruit and flower buds under high temperature (Huberman *et al.*, 1997). Bangerth (1989) hypothesized that auxin exported from early-developed fruit inhibits auxin exported from later-developed fruit, causing fruit abortion.

In contrast, Marcelis *et al.* (2004) emphasized the importance of the source–sink relationship in the fruit abortion of sweet pepper. In tomato, fruit set was related to the source–sink ratio (Bertin, 1995). Guinn (1974) pointed out the importance of photoassimilate supply in preventing fruit abortion in cotton. Turner and Wien (1994a, b) considered that cultivar differences

in the abortion of pepper fruit and flower buds can be ascribed to differences in photosynthetic activity, respiratory activity, and photoassimilate partitioning.

In monoecious cucumber cultivars, nodes with pistillate flowers are distributed at random on vines, while pistillate flowers are formed regularly at each node in gynoecious cultivars. Therefore, it is possible that the rate of flower formation and increases in the fresh mass of the fruit (crop load) can be estimated precisely in gynoecious cultivars, but not in monoecious cultivars. In the present experiment, we grew gynoecious parthenocarpic cucumbers to conduct a systematic growth analysis of the fruit. From the analysis of growth data, we tried to clarify the factor that was dominant in fruit abortion, that is, the existence of fruit or the crop load.

Materials and methods

Gynoecious parthenocarpic 'NK × AN8' cucumbers were sown on 5 April, 2004. Seeds were obtained from the Nihon Horticultural Production Institute (Matsudo, Chiba, Japan). On 30 April, plants with three fully expanded leaves were transplanted individually into plastic containers (20 L) filled with a growth medium (Soil Mix, Sakata Co., Yokohama, Japan) containing starter fertilizer (0.4 g kg^{-1} N, 0.9 g kg^{-1} P, and 0.5 g kg^{-1} K). Nodes were numbered acropetally, with the cotyledonary node designated as node 0. All lateral shoots were removed, while the apical portions of the main vines were not pinched. For all experiments, ten plants were used; five plants were allocated to the parthenocarpic treatment and the other five to the pollination treatment. In the parthenocarpic treatment, petals were clipped before anthesis to prevent pollination. In the pollination treatment, hand pollination was carried out using pollen from staminate

flowers of the monoecious cultivar '028'. In Experiment 1, only one fruit per plant was allowed to grow (node 10) and the diameter and length of the fruit were measured every day. Flower buds at nodes 4–9 and above 11 were removed just after their appearance. In Experiment 2, fruit at nodes 4 and above were allowed to grow. The length and diameter of all fruit (ovaries) at nodes 4–15 were measured daily from anthesis to harvest using a digital calliper. In both experiments, the fresh weight (FW) of an 'NK × AN8' fruit (g) could be estimated precisely from fruit (ovary) length (FL, mm) and diameter (D, mm) as follows: $FW = 8.09 \times 10^{-4} \times (D/2)^2 \pi \times (FL) + 0.732$ ($n = 241$, $r^2 = 0.993$) (Hikosaka and Sugiyama, 2004). All fruit were harvested when they reached a commercial size, *i.e.*, 150 mm in length.

The maximum and minimum temperatures in the glasshouse were controlled at 28/15ºC. Temperature and photosynthetically active radiation inside the greenhouse were monitored every minute with a datalogger (CR10X; Campbell Scientific Inc., Logan, UT, USA). Plants were irrigated with 1-2 L of nutrient solution every day to maintain sufficient water and nutrient supply. The concentrations of ions in the nutrient solution were as follows: NO_3^-, 16 mM; $H_2PO_4^-$, 4 mM; Ca^{2+}, 4 mM; Mg^{2+}, 2 mM; K^+, 8 mM; and NH_4^+, 1.3 mM. The CT after anthesis was calculated as the sum of the differences between daily temperatures and 5ºC. This was because the RGR of the fruit of a typical Japanese cucumber cultivar is almost zero at 5ºC and increases linearly to 30ºC (Tazuke and Sakiyama, 1986). The RGR with respect to the CT ($g\,g^{-1}\,(ºC\,d)^{-1}$) and the growth rate (GR, $g\,d^{-1}$) of a fruit between n and n+1 days after anthesis (DAA) was calculated as:

$$RGR = (\ln FW_{n+1} - \ln FW_n) / (T_n - 5)$$

and

$$GR = FW_{n+1} - FW_n,$$

where, FW_n and FW_{n+1} are the estimated FWs of fruit at n and n+1 DAA, respectively, and T_n is the daily average temperature at n DAA.

Results

Fruit growth in abscence of competing fruit (Experiment 1): When only one parthenocarpic fruit was allowed to grow on a plant, increases in the logarithms of fruit FW ($\ln FW_n - \ln FW_0$, where FW_n and FW_0 are the FWs of fruit at n and 0 DAA, respectively) against the CT after anthesis can be depicted by two lines (Fig. 1a). These two lines intersected at 54ºC d, where FW reached about 3 g. In pollinated fruit, it appears that increases in the logarithm of fruit FW increased linearly with an increase in the CT. An exception was for fruit smaller than 3 g (fruit at 0-38ºC DAA). When the relationship between increases in the logarithm of fruit weight and the CT was calculated after fruit FW reached 3 g, no difference was found in the slopes between pollinated and parthenocarpic fruit. Therefore, the regression line in Fig. 2 was calculated for pooled data of both pollinated and parthenocarpic fruit. The relationships between increases in the logarithm of fruit FW and the number of days were diverse among fruit (data not shown), suggesting the rationality of expressing RGR based on CT.

Growth of parthenocarpic fruit in presence of competing fruit (Experiment 2): An example of the growth of parthenocarpic
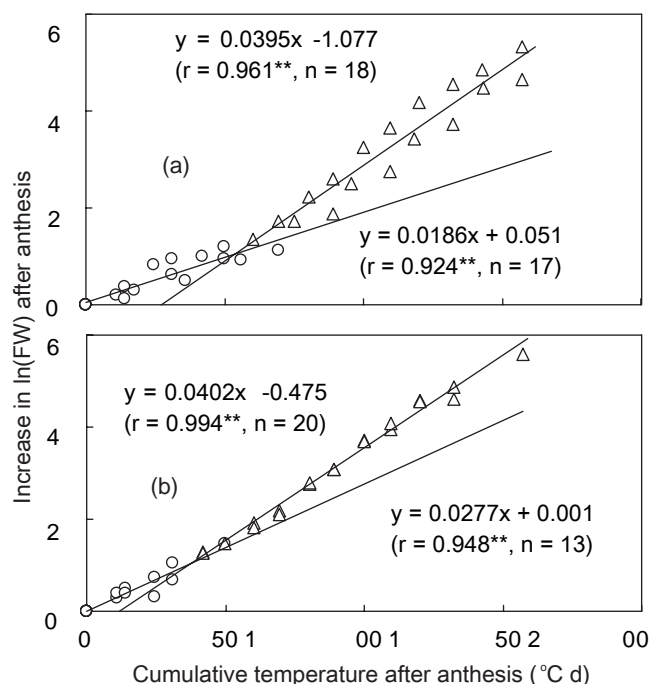

Fig. 1. Growth of cucumber 'NK × AN8' fruit in absence of competing fruit. Increases in the logarithm of fruit fresh weight (FW) after anthesis were plotted against cumulative temperature after anthesis. The cumulative temperature was calculated as the sum of the differences between daily average temperatures and 5ºC. Circles, fruit whose FW is less than 3 g; triangles, fruit whose FW weight is greater than 3 g. (a) parthenocarpic fruit, (b) pollinated fruit.
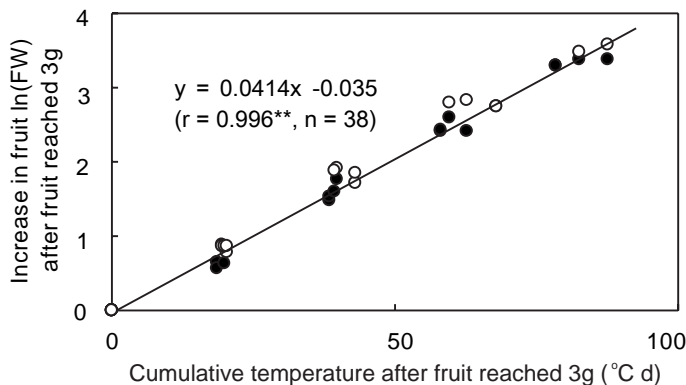

Fig. 2. Growth of cucumber 'NK × AN8' fruit in absence of competing fruit after the onset of rapid exponential growth. Increases in the logarithm of fruit fresh weight (FW) were plotted against cumulative temperature after fruit reached 3 g. Closed circles, pollinated fruit; open circles, parthenocarpic fruit. The regression line was calculated by pooling the data of both pollinated and parthenocarpic fruits.

fruit on a plant is shown in Fig. 3a, along with the sum of RGRs (Fig. 3b), GRs (Fig. 3c), and the number of fruit per plant (Fig. 3d). Fruit at node 4 usually grew almost exponentially, but several fruit at nodes 5 and above did not grow immediately. Fruit growth usually resumed thereafter. In severe cases, however, fruit growth did not resume, leading to fruit abortion. When the growth of fruits at nodes above 9 was completely suppressed at 130ºC d, the sum of RGRs and the number of fruit were very high: 0.1 g $g^{-1}\,(ºC\,d)^{-1}$ and six fruits, respectively. However, the sum of GRs remained quite low.

Growth of pollinated fruit in presence of competing fruit (Experiment 2): When the pistillate flowers were pollinated, the growth pattern of fruit changed markedly (Fig. 4a). A few fruit ceased growing for a while after anthesis. When fruit at nodes 5
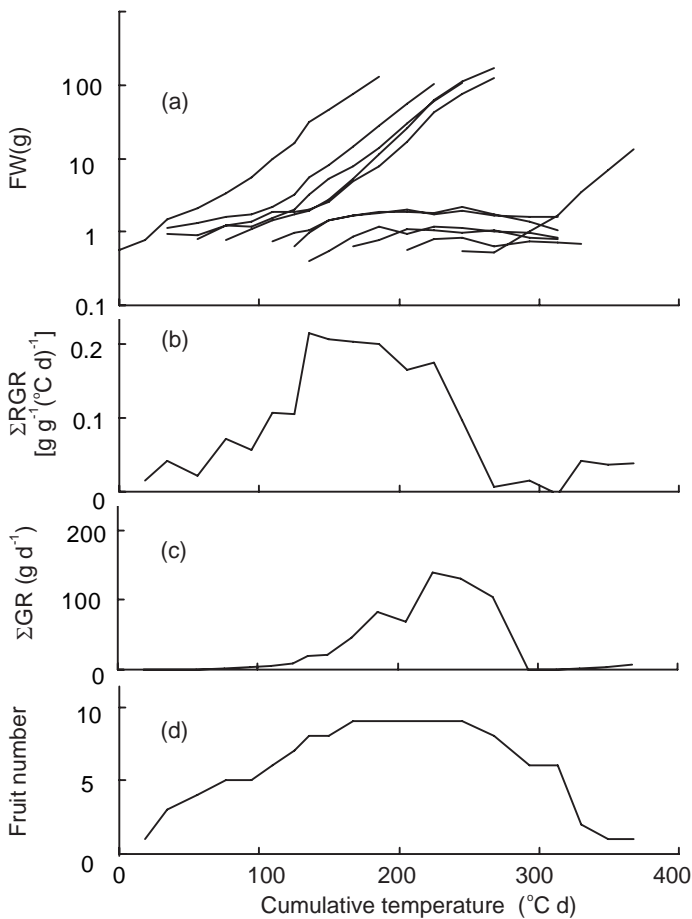
Fig. 3. Relationship between fruit growth and the sum of relative growth rates ($\sum$RGRs), the sum of growth rates ($\sum$GRs), and the number of fruit summed for all fruit from plants of the parthenocarpic cucumber 'NK × AN8'. Data of a plant are shown. All fruits at nodes 4-15 were allowed to grow and were harvested once they reached a marketable size. The data for the 14th node are missing because as a very rare case, male flower flowered on the 14th node. The sum of RGRs was calculated based on cumulative temperatures. Data from one plant are shown as an example.

and above were compared, the period from anthesis to harvest was found to be shorter in pollinated fruit than in parthenocarpic fruit (Figs. 3 and 4). The competing potential of fruit at lower nodes against fruit at upper nodes, *i.e.*, the sum of RGRs, the sum of GRs, and the number of fruit, did not differ between plants with pollinated fruit and those with parthenocarpic fruit until CT reached 250ºC d (Figs. 4b-d *vs*. Figs. 3b-d, respectively).

Evaluation of the initial period of slow growth (Experiment 2): To evaluate the effect of the sum of RGRs, the sum of GRs, and the number of competing fruit on the period of initial slow growth, these values were plotted against the reciprocal of the CT (1/CT) necessary for the development of fruit weighing 2, 3, 4, or 5 g. The CT was infinite (1/CT = 0) for fruit that did not reach 2, 3, 4, or 5 g. In the parthenocarpic treatment, some fruits reached 2-4 g despite the sum of RGRs being greater than 0.1 g g^{-1} (ºC d)$^{-1}$ (Fig. 5). On the other hand, all fruits reached 5 g when the sum of RGRs was smaller than 0.1 g g^{-1} (ºC d)$^{-1}$, but no fruit reached 5 g when the sum of RGRs was 0.1 g g^{-1} (ºC d)$^{-1}$ or higher (Fig. 6a). In many pollinated fruits, however, the values of 1/CT were maintained at about 0.01 (ºC d)$^{-1}$ even when the sum of RGRs was greater than 0.1 g g^{-1} (ºC d)$^{-1}$ (Fig. 6a). In contrast, there was no relationship between 1/CT and the sum of GRs for parthenocarpic
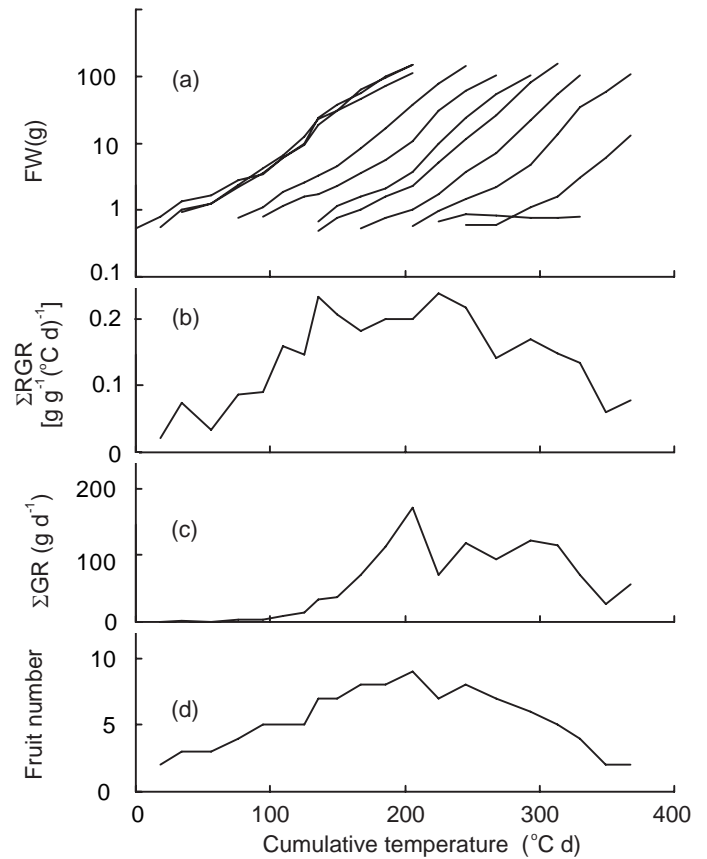

Fig. 4. Relationship between fruit growth and the sum of relative growth rates ($\sum$RGRs), the sum of growth rates ($\sum$GRs), and the number of fruit summed for all fruit from plants of the pollinated cucumber 'NK × AN8'. Data of a plant are shown. All fruits at nodes 4-15 were allowed to grow and were harvested once they reached a marketable size. Pollen was obtained from plants of the monoecious cultivar '028'. $\sum$RGRs was calculated based on cumulative temperatures. Data from one plant are shown as an example.

fruits (Fig. 6b). Relationships between 1/CT and the number of competing fruit were similar to those between 1/CT and the sum of RGRs, although they were not as clear (Fig. 6c).

Discussion

Potential growth curve of a fruit: Marcelis (1994) estimated the 'potential growth rate' of a fruit by monitoring fruit growth when there was no competition for assimilates from other fruit. He found that fruit growth fitted a Richards' equation and that the potential growth rate could be estimated from this equation. We also assumed that potential fruit growth could be attained when only one fruit was left on a plant to avoid competition from other fruit. In the present experiment, pollinated and parthenocarpic fruit grew exponentially at the same RGR, which started from 38ºC d and 54 ºC d of CT after anthesis, respectively (Figs. 1 and 2). This result suggests that potential fruit growth is independent of pollination, but that pollination hastens the start of rapid exponential growth. It is interesting to note that fruit cells began to enlarge 2 DAA in pollinated fruit and 4 DAA in parthenocarpic fruit of this cultivar (Boonkorkaew, pers. comm.). As 2 and 4 d roughly corresponded to 35 and 70ºC d, respectively, it is likely that the potential growth rate could be accomplished in both parthenocarpic and pollinated fruit when fruit cells begin to enlarge. Furthermore, an initial slow growth period exists after anthesis even when only one fruit is allowed to grow on a
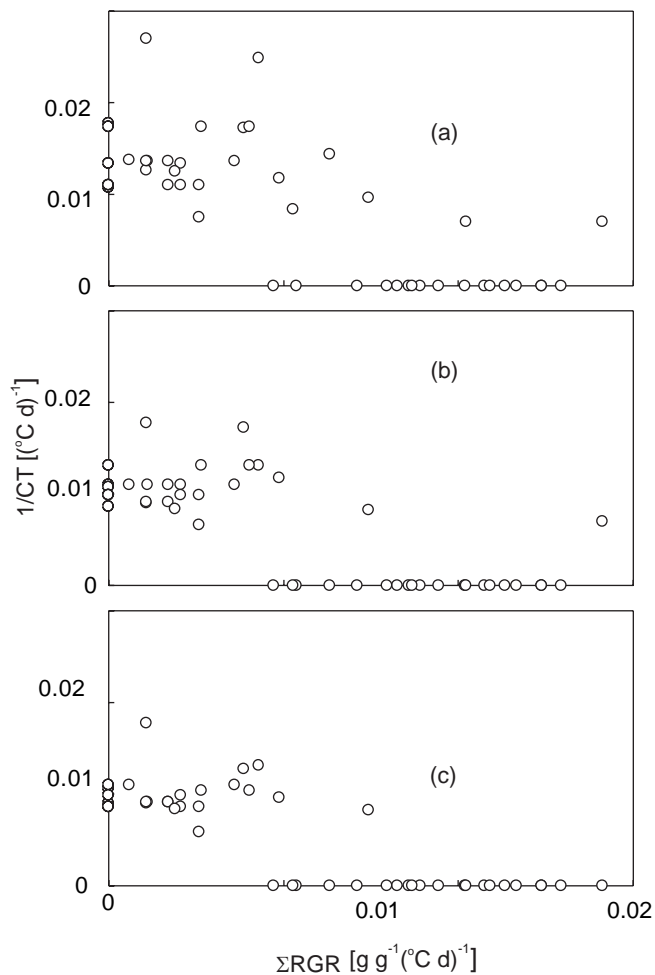
Fig. 5. Relationships between the reciprocal of the cumulative temperatures (1/CT) necessary for the development of fruit weighing (a) 2, (b) 3, and (c) 4 g and the sum of relative growth rates ($\sum$RGRs) of fruit at lower nodes of the parthenocarpic cucumber 'NK × AN8'. $\sum$RGR was calculated on the day of anthesis of the fruit for which 1/CT was calculated.

Fig. 6. Relationships between the reciprocal of the cumulative temperatures (1/CT) necessary for the development of fruit weighing 5 g and (a) the sum of relative growth rates ($\sum$RGR), (b) the sum of growth rates ($\sum$GR), and (c) the number of fruit at lower nodes of both the parthenocarpic and the pollinated cucumber 'NK × AN8'. In pollinated fruit, pollen was obtained from plants of the monoecious cultivar '028'. $\sum$RGR, $\sum$GR, and the number of fruit were calculated on the day of anthesis of the fruit for which 1/CT was calculated. Open circles, parthenocarpic fruit; closed circles, pollinated fruit. $\sum$RGRs was calculated based on cumulative temperature.

plant. The discrepancy from the sigmoidal Richards' equation in the present experiment can be ascribed to the fact that fruit was harvested much earlier in the present experiment than in the experiment of Marcelis (1994).

Fruit abortion and competition between fruits: In absence of competing fruits, fruit FW reached 3 g at 54ºC d of the CT. However, the existence of competing fruits extended the initial slow growth period of parthenocarpic fruit from 54 to more than 100ºC d (Fig. 3). Furthermore, it appears that fruit FW at the end of the initial slow growth phase varied from 2 to 5 g when there was competing fruit. This makes the relationship between 1/CT and the sum of RGRs unclear if we assume that fruit FW reached 2-4 g at the end of the slow growth phase (Fig. 5). When the sum of RGRs was smaller than 0.1 g g^{-1} (ºC d)$^{-1}$, all fruits reached 5 g by about 100ºC d. However, all fruits aborted when the sum of RGRs was larger than 0.1 g g^{-1} (ºC d)$^{-1}$. These results suggested that (1) fruits that are not exposed to severe competition can complete the slow growth phase, (2) fruit FW at the end of the slow growth phase differs between individual fruits (2-5 g) and (3) fruits of which FW at the end of the slow growth phase was 2-4 g cease to growth and finally abort (1/CT=0). On the other hand, it is likely that fruit that can enter the fast growth phase do not abort because all fruit larger than 5 g would develop to
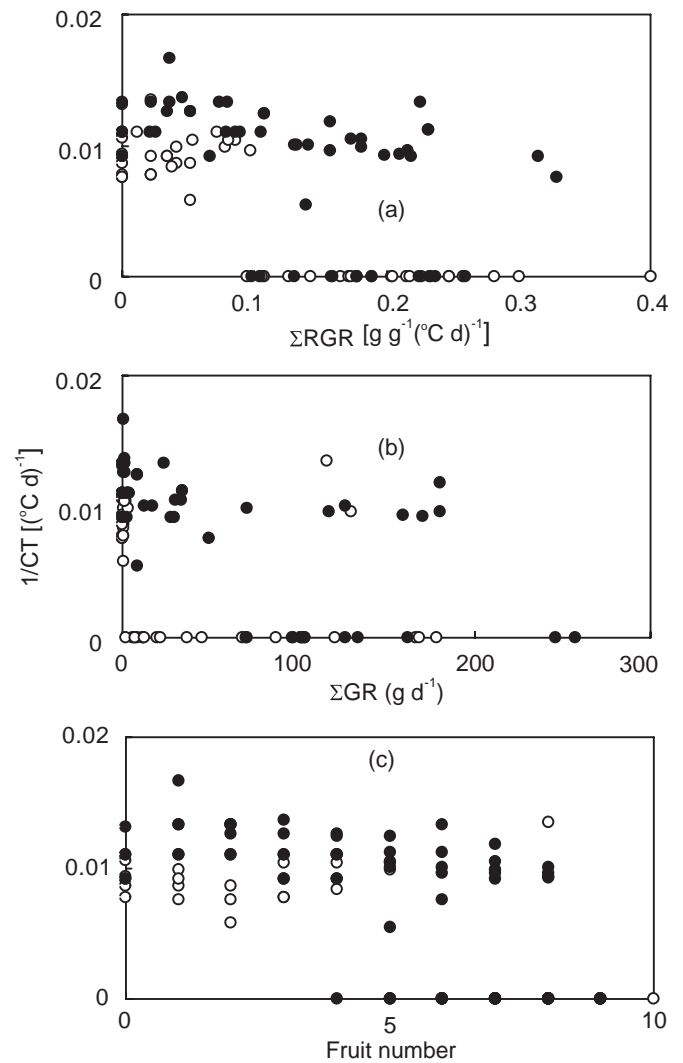
a commercial size. Takeno and Ise (1992) reported that in a gynoecious cucumber cultivar, fruit that reached 6 cm in length never aborted.

In cucumber fruits, RGRs were almost the same from the start of rapid exponential growth to harvest. Therefore, the sum of RGRs would be proportional to the total number of growing fruits, whereas the sum of GRs would be dependent on the number of large fruits. In the present study, the sum of GRs and the number of fruit did not relate closely with 1/CT; fruit FW did not reach 5 g even when the sum of GRs was very low. This suggests that growth suppression or fruit abortion is determined by the existence of the actively growing fruit, not by the size of the competing sink. Schapendonk and Brouwer (1984) reported that severe defoliation did not inhibit the normal development of cucumber fruit when only one fruit was allowed to grow. Thus, they hypothesized that factors other than the shortage of photoassimilates could cause fruit abortion. Stephenson *et al.* (1988) reported that seed number

in the first fruit determines whether later-developed zucchini fruit abort or not. The removal of old fruit decreased the abortion of young fruit by decreasing the ABA content of young fruit (Tamas *et al.*, 1979). Unlike parthenocarpic fruits, many pollinated fruit reached 5 g even when the sum of RGRs was larger than 0.1 g g^{-1} (ºC d)$^{-1}$. This suggests that pollination nullified the effect of the sum of RGRs on fruit abortion. It is well known that pollination stimulates the synthesis of plant hormones such as auxin.

Although Marcelis *et al.* (2004) emphasized the importance of the source–sink relationship in the abortion of flowers or fruit of sweet pepper, they also admitted the involvement of some dominance effect. It is well known that actively growing fruit produce plant hormones that might be involved in fruit retention (Huberman *et al.*, 1997; Takeno and Ise, 1992; Wien *et al.*, 1989). It is reported, however, that the availability of photoassimilates is associated with the occurrence of fruit abortion in plants other than cucumber (Aloni *et al.*, 1996; Guinn, 1974; Kinet, 1977; Marcelis *et al.*, 2004; Wien *et al.*, 1989). Therefore, although the relationship between 1/CT and the sum of the GR was not clear, the possibility that fruit abortion is determined by the availability of photoassimilates could not be ruled out.

In parthenocarpic fruit that reached 5 g, 1/CT ranged from 0.0058 to 0.0134 (Fig. 6a). This indicates that fruit that did not reach 5 g by 74-171ºC d of the CT, aborted in the parthenocarpic treatment. Hikosaka and Sugiyama (2005) reported that parthenocarpic fruit whose growth was suppressed by up to 10 d (ca. 175ºC d) usually aborts. As such, it is likely that the value of 1/CT changed abruptly from 0.0058 to zero in the present experiment.

In conclusion, the initial slow growing period of cucumber can be completed if the competing potential of fruit that flowered early was low. Also, the competing potential can be evaluated by the sum of RGRs of fruit at lower nodes, not by the sum of fruit weight.

References

Aloni, B., L. Karni, Z. Zaidman and A.A. Schaffer, 1996. Changes of carbohydrates in pepper (*Capsicum annuum* L.) flowers in relation to their abscission under different shading regimes. *Ann. Bot.*, 78: 163-168.

Bangerth, F. 1989. Dominance among fruits/sinks and the search for a correlative signal. *Physiol. Plant.*, 76: 608-614.

Bertin, N. 1995. Competition for assimilates and fruit position affect fruit set in indeterminate greenhouse tomato. *Ann. Bot.*, 75: 55-65.

Guinn, G. 1974. Abscission of cotton floral buds and bolls as influenced by factors affecting photosynthesis and respiration. *Crop Sci.*, 14: 291-293.

Hikosaka, S. and N. Sugiyama, 2004. Characteristics of flower and fruit development of multi-pistillate type cucumbers. *J. Hortic. Sci. & Biotech.*, 79: 219-222.

Hikosaka, S. and N. Sugiyama, 2005. Effect of fruit-load on growth patterns of fruit at the middle node of gynoecious-type cucumbers. *J. Hortic. Sci. & Biotech.*, 80: 130-134.

Huberman, M., J. Riov, B. Aloni and R. Goren, 1997. Role of ethylene biosynthesis and auxin content and transport in high temperature-induced abscission of pepper reproductive organs. *J. Plant Growth Regul.*, 16: 129-135.

Kinet, J.M. 1977. Effect of light conditions on the development of the inflorescence in tomato. *Sci. Hortic.*, 6: 15-26.

Marcelis, L.F.M. 1994. A simulation model for dry matter partitioning in cucumber. *Ann. Bot.*, 74: 43-52.

Marcelis, L.F.M., E. Heuvelink, L.R. Baan Hofman-Eijer, J. Den Bakker and L.B.Xue, 2004. Flower and fruit abortion in sweet pepper in relation to source and sink strength. *J. Exp. Bot.*, 55: 2261-2268.

Schapendonk, A.H.C.M. and P. Brouwer, 1984. Fruit growth of cucumber in relation to assimilate supply and sink activity. *Sci. Hortic.*, 23: 21-33.

Stephenson, A.G., B. Devlin and J.B. Horton, 1988. The effects of seed number and prior fruit dominance on the pattern of fruit production in *Cucurbita pepo* (Zucchini squash). *Ann. Bot.*, 62: 653-661.

Takeno, K. and H. Ise, 1992. Parthenocarpic fruit set and endogenous indole-3-acetic acid content in the ovary of *Cucumis sativus* L. *J. Japan. Soc. Hort. Sci.*, 60: 941-946.

Tamas, I.A., D.H. Wallace, P.M. Ludford and J.L. Ozbun, 1979. Effect of older fruits on abortion and abscisic acid concentration of younger fruits in *Phaseolus vulgaris* L. *Plant Physiol.*, 64: 620-622.

Tazuke, A. and R. Sakiyama, 1986. Effect of fruit temperature on the growth of cucumber fruits. *J. Japan. Soc. Hort. Sci.*, 59: 745-750.

Turner, A.D. and H.C. Wien, 1994a. Dry matter assimilation and partitioning in pepper cultivars differing in susceptibility to stress-induced bud and flower abscission. *Ann. Bot.*, 73: 617-622.

Turner, A.D. and H.C. Wien, 1994b. Photosynthesis, dark respiration and bud sugar concentrations in pepper cultivars differing in susceptibility to stress-induced bud abscission. *Ann. Bot.*, 73: 623-628.

Van Meeteren, U. and H. Van Gelder, 1995. Role of flower buds in flower bud abscission in *Hibiscus*. *Acta Hortic.*, 405: 284-289.

Wien, H.C., A.D. Turner and S.F. Yang, 1989. Hormonal basis for low light intensity induced flower bud abscission of pepper. *J. Amer. Soc. Hort. Sci.*, 114: 981-985.