キュウリ果実の肥大の機械的な抑制が水と乾物の蓄積に及ぼす影響

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Effects of Mechanically Restricting Enlargement of Cucumber Fruits on Water and Dry Matter Accumulation

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Summary

The control of soluble sugar concentration during a rapidly growing stage was investigated in relation to water content in cucumber fruits. To evaluate the influences of the rate of water accumulation on the concentration of soluble sugars, the enlargement of the fruits was restricted by enclosing the fruits within acrylic sleeves to prevent mechanically the further accumulation of water for 3 to 4 days. The treatment restricted fruit enlargement by 40% to 72% of control fruits on a fresh weight basis, whereas dry matter and hexose contents increased from 127% to 138% and from 134% to 173%, respectively. Although sucrose constitutes a small percentage of total sugars, it increased significantly during the treatment. The activity of acid invertase was negatively correlated to the concentration of sucrose, suggesting that the significant accumulation of sucrose was related to the reduced activity of acid invertase. Whereas the concentration of soluble sugars consistently increased with time, the concentration of dry matter remained constant during the treatment, indicating that the accumulation of soluble sugars was not due to excessive import of carbohydrates relative to water inflow. The relationship between the concentration of soluble sugars and the rate of water accumulation is discussed.

Key Words: sugar content, water accumulation, dry matter accumulation, enlargement, *Cucumis sativus*.

Introduction

Soluble sugar concentration is important in determining fruit quality in many horticultural crops. Although cucumber fruits contain only 1% to 1.5% glucose and fructose and a smaller concentration of sucrose (Davies and Kempton, 1976; McCreight et al., 1978), sugars at such low concentrations affect the taste of the fresh fruits (Robinson, 1987).

The cucumber fruits grow very rapidly during the harvesting stage, e.g. fruits of 9 to 20 cm in length enlarge at the rate of 2% to 6% per hour (Tazuke and Sakiyama, 1984). The high rate of enlargement is accompanied by a rapid import of water and carbohydrates into the fruits. In cucumber, about 90% of the fresh weight consists of water (Davies and Kempton, 1976), so that the high rate of fruit enlargement indicates a high rate of water accumulation. The import of carbohydrates is necessary to maintain rapid growth, respiration, and assimilation of structural material and storage carbohydrates, including starch, and to accumulate soluble sugars. Therefore, the fruits quickly accumulate both carbohydrates and water at the same time during the rapid growth stage. In this context, the concentration of carbohydrates and, thus, that of soluble sugars seem to be determined by the balance between the import rates of carbohydrates and water. This concept is supported by the well-known phenomenon that, in many crops, excessive irrigation results in large fruits with a lower concentration of soluble sugars (Prashar et al., 1976). On the other hand, some metabolic controls govern the levels of soluble sugars. To understand the regulation of soluble sugar concentration in enlarging tissues such as cucumber fruits, the relative contribution of water accumulation and metabolic control needs to be evaluated.

In this study, we attempted to evaluate the effect of the fluctuation in water accumulation on the concentration of soluble sugars in cucumber fruits by manipulating the accumulation of water with plastic sleeves to restrict fruit enlargement.

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Materials and Methods

Seedlings of cucumber (*Cucumis sativus* L. cv. Tachibana) were planted on March 6 and on September 18 in rockwool beds and irrigated several times a day with 1/2 strength Hoagland nutrient solution in a greenhouse kept above 13 °C.

Experiment 1: Effects of initial size and mechanical restriction on cucumber fruits

Six fruits, 10 cm long, were selected from different plants. Half of them were used as controls and the others were enclosed within acrylic sleeves, 16 mm inside diameter (I. D.) and 12 cm long (Fig. 1). Four days after fitting the acrylic sleeves, both treated and

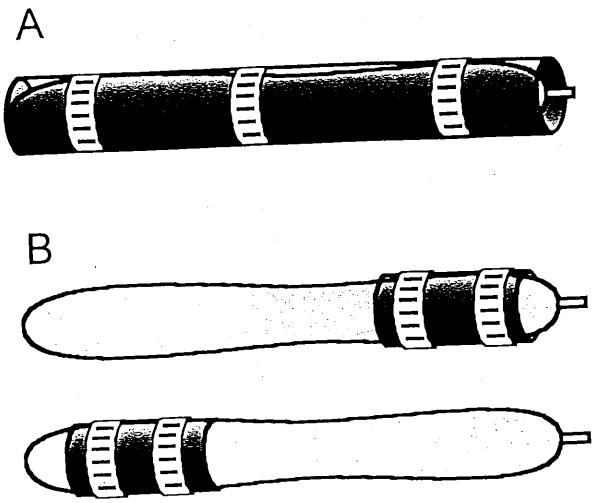

Fig. 1. Illustration showing mechanical restriction of fruit enlargement in cucumber. Acrylic sleeves were longitudinally cut into halves, set around the fruits and then fixed using iron bands. A: A whole fruit was enclosed within the sleeves of 16 mm in inside diameter and 12 cm long or within the sleeves of 24 mm in inside diameter and 25 cm long. B: A part of basipetal or acropetal halves of the fruits was enclosed within the sleeves of 16 mm in inside diameter and 4 cm long.

control fruits were sampled. The length of the control fruits at the sampling day was about 20 cm. Similarly, 6 fruits, 20 cm long, were selected and half of them were enclosed within acrylic sleeves of 24 mm I. D. and 25 cm long. Three days after fitting the sleeves, when the length of the control fruits was 25 cm, both treated and control fruits were sampled. Other fruits, 10 cm long, were similarly selected and the acropetal or basipetal halves of the fruits were enclosed within acrylic sleeves of 16 mm I. D. and 4 cm long (Fig. 1). After 4 days, both treated and untreated halves of the fruits were sampled. Samples were cut into slices and stored at -20 °C.

Experiment 2: Effects of the duration of mechanical restriction on fruits

Nine fruits, 10 cm long, were selected and their acropetal halves were enclosed within acrylic sleeves of 16 mm I. D. and 4 cm long. Since it took about one day before the fruit to contact the walls of the acrylic sleeves, the day after enclosure was regarded as the start of the restriction and stated as Day 0. Treated acropetal halves and untreated basipetal halves which were sampled 2 or 4 days after Day 0 are designated as Day 2 and Day 4, respectively. The samples were sliced into sections and frozen immediately in liquid N_2 and stored at -70 °C.

Experiment 3: Effects of releasing fruits from mechanical restriction

The enlargement of the acropetal halves of 16 fruits was restricted as in Experiment 2. Four days after the setting of acrylic sleeves (i. e. three days of restriction treatment), the acrylic sleeves were removed. Fruits were analyzed immediately or 1, 2, and 3 days later. Samples were sliced into cross sections, photocopied, and then stored at -20 °C. The cross-sectional area of the fruits was measured from the photocopies.

In this experiment, the accumulation of water (ΔW), dry matter (ΔD), and soluble sugars (ΔS) per day per volume ($g \cdot day^{-1} \cdot cm^{-3}$) were calculated. Grams of water (W_i), dry matter (D_i), and soluble sugars (S_i) contained in 1 cm^3 volume of fruit tissue on Day i are expressed as:

$$W_i = k_i \times 1$$
$$D_i = k_i \times d_i \times 1$$
$$S_i = k_i \times s_i \times 1$$

where k_i are content of water per volume ($g \cdot cm^{-3}$); d_i and s_i are concentrations of dry matter and soluble sugars expressed on a water content basis ($g \cdot g^{-1}$ water), respectively. It was assumed that 1 cm^3 of fruit tissue on Day i enlarged to $(A_{i+1}/A_i)^{3/2}$ cm^3 on Day i+1, where A_i and A_{i+1} are cross-sectional area (cm^2) on Day i and Day i+1, respectively. The content of water (W_{i+1}), dry matter (D_{i+1}), and soluble sugars (S_{i+1}) in $(A_{i+1}/A_i)^{3/2}$ cm^3 volume of fruit tissue on Day i+1 are similarly expressed as:

$$W_{i+1} = k_{i+1} \times (A_{i+1}/A_i)^{3/2}$$
$$D_{i+1} = k_{i+1} \times d_{i+1} \times (A_{i+1}/A_i)^{3/2}$$
$$S_{i+1} = k_{i+1} \times s_{i+1} \times (A_{i+1}/A_i)^{3/2}$$

Since the volume is highly correlated to water content rather than fresh weight, the volume was estimated as a linear function of water content. Thus, k_i and k_{i+1} were regarded as constant value. If k_i and k_{i+1} are approximated as 1, then ΔW, ΔD, and ΔS are calculated by the following equation:

$$\Delta W\ (=W_{i+1}-W_i) = (A_{i+1}/A_i)^{3/2} - 1$$
$$\Delta D\ (=D_{i+1}-D_i) = d_{i+1} \times (A_{i+1}/A_i)^{3/2} - d_i$$
$$\Delta S\ (=S_{i+1}-S_i) = s_{i+1} \times (A_{i+1}/A_i)^{3/2} - s_i$$

Carbohydrate analysis

Freeze-dried materials were ground into powder, using a mortar and pestle, and extracted with 80% ethanol at 80 °C for 1.5 hours. The extract was centrifuged at 1,000×g for 30 min. The supernatant was dried in a rotary evaporator and re-dissolved in water. The solution was centrifuged at 19,500×g for 10 minutes. The supernatant was deionized by passing it through a small column of Amberlite MB3. The eluate was loaded on a Cosmosil 5NH_2 (Nakarai) column and eluted with 80% acetonitrile-water (80 : 20) at the rate of 1 ml $\cdot$ min^{-1} at 33 °C, using Shimadzu 6A HPLC system fitted with a refractive index detector (RI-2, Japan Analytical Industry).

Assay of acid invertase

The frozen tissue, sampled in Experiment 2, was ground into powder with a mortar and pestle in liquid N_2. The mortar was kept on ice until the mortar approached 0 °C. The powder was homogenized then with 8 to 15 ml of extraction buffer (80 mM HEPES pH 7.5, 0.4 M NaCl, 15 mM EDTA, 0.08% dithiothreitol, 1.5% insoluble polyvinylpyrrolidone) for 5 minutes. The homogenate was centrifuged at 1,500×g for 5 minutes at 4 °C and a 1-ml aliquot of the supernatant was desalted by passing it through a SephadexG-25 (Pharmacia) column pre-equilibrated with an elution buffer (10 mM HEPES, pH 7.0). This crude enzyme fraction was assayed for acid invertase. The assay mixture included 70 μl of crude enzyme solution, 140 mM sucrose, and 14 mM citrate-23 mM Na_2HPO_4 (pH 4.5). The reaction was performed at 30 °C for 30 minutes and terminated by boiling for 3 minutes after adding 0.5 ml of 200 mM Na_2HPO_4. The concentrations of glucose in the assay mixture before and after the reaction were determined by an enzymatic method (F-kit glucose, Boehringer Mannheim). Protein content was determined according to Lowry et al. (1951) with a modification of Bensadoun and Weinstein (1976). Bovine serum albumin was used as standard for the calibration of the protein content. The extraction of crude enzyme and acid invertase assay were conducted in duplicate for each sample.

Results

Experiment 1

Enclosing the whole fruits in acrylic sleeves significantly prevented the enlargement as expressed in fresh weight (Table 1). The treatment also restricted the dry weight accumulation by the fruits, but increased the concentrations of dry matter, ethanol soluble solids, ethanol insoluble solids, and soluble sugars. Although the treated and control cucumber fruits contained mainly fructose and glucose and a smaller concentration of sucrose, the concentration of sucrose in the restriction treatment was several times higher than that in the control. Restricting the enlargement of acropetal or basipetal halves of cucumber fruits increased the concentrations of all the constituents measured in this experiment (Table 2). The concentration of each constituent was similar between acropetal treatment and basipetal treatment in both treated and untreated halves of the fruits.

Experiment 2

Since no difference was found in the effects on the fruit constituents between acropetal and basipetal treatments, only the acropetal halves of fruits were restricted by acrylic sleeves in this experiment and the untreated basipetal halves were used as the control. At Day 0 (one day after the enclosure of the fruits), the concentration of dry matter (Fig. 2) in the treated segment was already higher than that in the control, indicating that the concentration of dry matter increased immediately after the surface of the fruits contacted the sleeve, whereas no difference in the concentration of soluble sugars was found between treated and untreated halves of the fruits at Day 0 (Fig. 2).

Whereas the concentration of soluble sugars increased with time from Day 0 to Day 4, the concentration of dry matter in the treated halves of fruits remained constant during the experiment. The concentration of hexose (Fig. 2) increased by 1.37 times in the first 2 days and by 1.07 times in the subsequent 2 days of the treatment. The concentration of sucrose continuously increased during the experimental period. The activities of acid invertase, expressed on a fresh weight basis, were higher in the treated acropetal halves of the fruits than in the untreated basipetal halves at Day 0, 2,

Table 1. Effects of restricting the enlargement of cucumber fruits on the fresh weight, the dry weight, and the concentrations of dry matter, ethanol insoluble (EIS), ethanol soluble solids (ESS), and soluble sugars. A part of basipetal halves was enclosed in acrylic sleeves (16 mm or 24 mm in inside diameter, 4 cm long) to restrict further enlargement. After 4 days, both treated acropetal and untreated basipetal parts of the fruits were analyzed.

Variable	Sleeve size				ANOVA		
	16 mm		24 mm		Factor		
	Untreated	Treated	Untreated	Treated	Treatment	Sleeve size	Interaction
Fresh weight (g)	81.6	35.1	167	121	**	***	ns
Dry weight (g)	4.33	2.51	8.16	7.60	*	***	ns
Dry matter (% FW)	5.35	7.17	4.91	6.26	**	ns	ns
EIS (% FW)	2.15	2.65	1.74	2.11	*	ns	ns
ESS (% FW)	3.20	4.52	3.17	4.15	**	ns	ns
Fructose (% FW)	1.06	1.41	0.85	1.33	*	ns	ns
Glucose (% FW)	1.01	1.37	0.80	1.34	*	ns	ns
Sucrose (% FW)	0.01	0.20	0.00	0.06	***	**	**

ns, *, **, ***: nonsignificant and significant at $P < 0.05$, 0.01, and 0.001, respectively.

Table 2. Effects of restricting the enlargement of cucumber fruits on the concentrations of dry matter, ethanol insoluble (EIS), ethanol soluble solids (ESS), and soluble sugars. A part of acropetal or basipetal halves of fruits was enclosed within acrylic sleeves (16 mm in inside diameter, 4 cm long) to restrict further enlargement. After 4 days, both treated and untreated halves of fruits were analyzed.

Variable	Treated part fruits				ANOVA		
	Acropetal		Basipetal		Factor		
	Untreated	Treated	Untreated	Treated	Treatment	Treated Part	Interaction
Dry matter (% FW)	5.66	7.81	5.70	7.62	**	ns	ns
EIS (% FW)	2.15	3.03	2.19	2.99	**	ns	ns
ESS (% FW)	3.51	4.78	3.51	4.63	***	ns	ns
Fructose (% FW)	1.23	1.66	1.06	1.80	**	ns	ns
Glucose (% FW)	1.14	1.62	1.01	1.79	**	ns	ns
Sucrose (% FW)	0.01	0.23	0.02	0.18	**	ns	ns

ns, **, ***: nonsignificant and significant at $P < 0.01$ and 0.001, respectively.

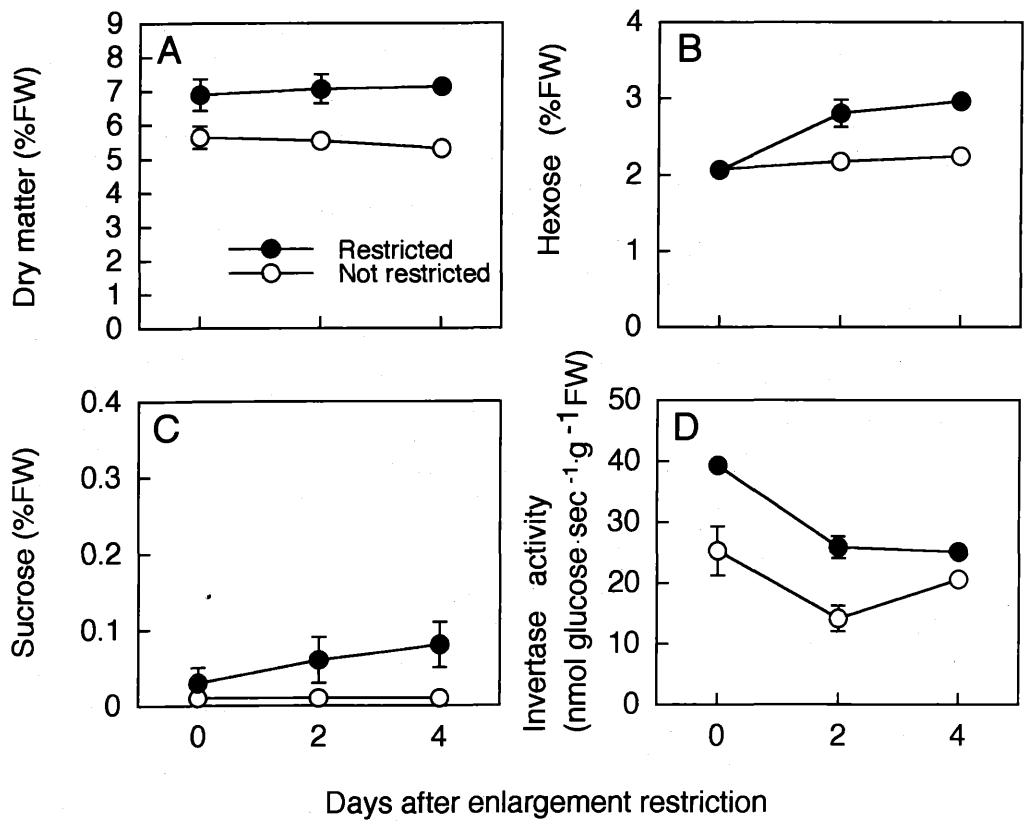

Fig. 2. Changes in the concentrations of dry matter (A), hexose (B), and sucrose (C), and the activity of acid invertase (D) during the mechanical restriction of fruit enlargement in cucumber. Vertical bars represent standard errors.

and 4, but its activity tended to decrease with time in the treated fruit. A correlation between sucrose concentration and acid invertase activity among different sampling days was sought by an analysis of variance; the sucrose concentration and acid invertase activity were transformed by subtracting the mean value for each sampling day. When the activities of acid invertase were plotted against the concentrations of sucrose, using the transformed data set, a significant negative correlation was found (Fig. 3).

Experiment 3

When the restriction was alleviated, the cross-sectional areas of the fruits increased at the same rate in treated and untreated halves (Fig. 4). The concentrations of dry matter, hexose, and sucrose (Fig. 4) in the treated

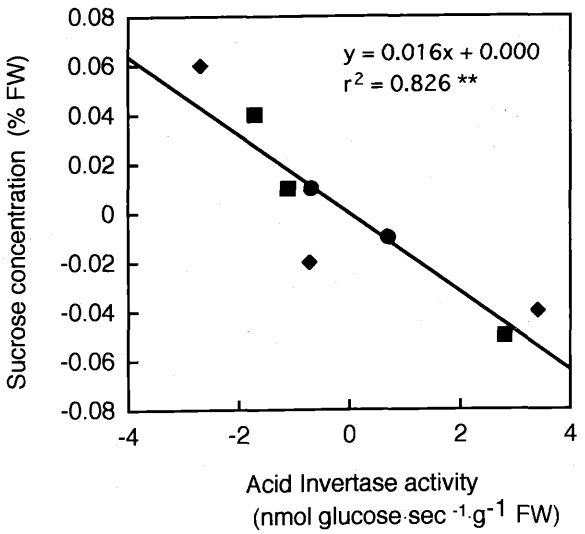

Fig. 3. Relationship between sucrose concentration and acid invertase activity of cucumber fruits during mechanically restricting the enlargement for 0 (●), 2(▲), and 4(■) days. The data was transformed by subtracting the mean for the corresponding treatment days from each measurement.
** : Significant at $P<0.01$

halves of the fruits decreased to the same levels as those in the untreated parts of the fruits within a day. The calculated accumulation rate of water, dry matter, and total sugars after the release from the restriction treatment reveals that the rate of dry matter accumulation varied but was positive during the whole experiment, whereas the rate of total sugar accumulation started 1 day after the release (Table 3). The ratio of accumulated dry matter to accumulated water increased during the experimental period.

Discussion

Control of carbohydrate concentration

The enlargement of fruits is a process of volumetric increase due to water accumulation. If water accumulation and carbohydrate accumulation fluctuate independently during the enlargement, a decrease in water accumulation would lead to a higher concentration of carbohydrates. In our study with cucumber, in which the accumulation of water was reduced by mechanically restricting the enlargement, the concentration of carbohydrates increased, followed by a marked inhibition

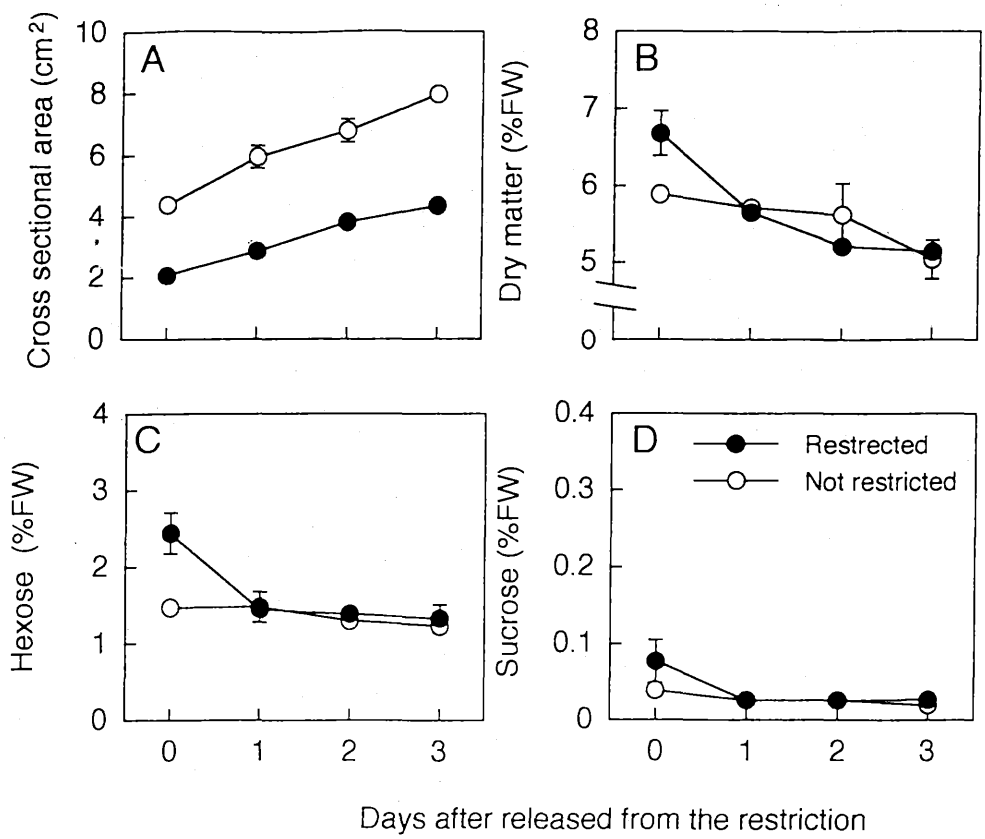

Fig. 4. Changes in fruit cross-sectional area (A) and concentrations of dry matter (B), hexose (C), and sucrose (D) of cucumber fruits after their release from the mechanical restriction of enlargement. Vertical bars represent standard errors.

Table 3. Estimated import of water (Δ W), dry matter (Δ S), and soluble sugars (Δ W) per volume in cucumber fruits after released from the mechanical restriction.

Days after the release from the restriction	Δ W ($g \cdot cm^{-3}$)	Δ D ($mg \cdot cm^{-3}$)	Δ S ($mg \cdot cm^{-3}$)	ΔD/ΔW (%)	ΔS/ΔW (%)
0 ~ 1	0.627	10.2	−20.5	1.62	−3.27
1 ~ 2	0.546	38.2	11.8	7.01	2.16
2 ~ 3	0.220	20.3	4.5	9.21	2.04

of carbohydrate import. Thus, when the enlargement of the whole fruits was restricted in Experiment 1, the concentration of dry matter on a fresh weight basis increased, but the total dry matter on a per fruit basis (i. e. fruit dry weight) decreased by 42%. In Experiment 2, although the concentration of dry matter increased during the early period of the treatment (i. e. within 24 hours), it remained constant thereafter, indicating that the import of carbohydrates was restricted completely.

It is not evident how the importation of water was restricted more severely than that of carbohydrates during the early period of the treatment, and how the latter was almost completely restricted during the later period of the treatment. There is a possibility that the accumulation of carbohydrates is controlled by biochemical mechanisms, whereas the import of water is controlled passively so that it is more susceptible to changes in the physical environment. It has been suggested that the sucrose synthase is involved in the determination of sink strength in tomato fruits (Balibrea et al., 1996; Sun et al., 1992; Wang et al., 1993), potato tubers (Sonnewald et al., 1994; Sung et al., 1989; Zrenner et al., 1995), and sugarcane internodes (Lingle and Smith, 1991). In addition, Maas et al. (1990) reported that an inhibitor of cellulose synthesis blocked the transcription of sucrose synthase in protoplasts of maize grown in suspension culture. Therefore, the changes in dry matter concentration with time in this experiment may be explained as follows: (1) the importation of carbohydrates driven by sucrose synthase continued even after the inflow of water was restricted physically; (2) a decline in cell wall synthesis, which accompanied fruit enlargement, inhibited the expression of sucrose synthase; and (3) the import of carbohydrates was prevented by the inactivation of sucrose synthase. To understand the control of carbohydrate concentrations in the expanding tissues, one would need to study the biochemical linkage between cell wall synthesis and phloem unloading of carbohydrates.

Control of soluble sugar concentration

The restriction treatment increased the concentration of soluble sugars by 27% to 73%. The comparison between the changes in the concentration of dry matter and soluble sugars during the treatment (Fig. 2) revealed that the increase in soluble sugar concentration was not associated with the import of carbohydrates. On Day 0, the concentration of dry matter was already higher in the treatment than in the control, but that of soluble sugars was the same (Fig. 2). While the concentration of soluble sugars increased persistently from Day 0 to Day 4, the concentration of dry matter remained constant during that period.

Therefore, it is unlikely that the increase in the concentration of soluble sugars was due to their preferential import with respect to water. Instead, it is more likely that the metabolic process of soluble sugar accumulation continued even after the importation of carbohydrates had been interrupted. Thus we speculate that the import of carbohydrates and the accumulation of soluble sugars are two independent processes.

In addition, in Experiment 3, the rapid decline in soluble sugar concentration after the pressure was released could not be explained by a sudden, rapid import of water in relation to carbohydrates. While the concentration of total sugars decreased by 41% within one day after the release, the dry matter concentration decreased by only 15%. Estimating the daily accumulation of dry matter and soluble sugars per volume (Table 3) showed that, even though the accumulation of carbohydrates started immediately after the release from the restriction, that of soluble sugars started with a lag time of one day.

The metabolic control of soluble sugar content in growing tissues is not well understood yet. However, acid invertase, which hydrolyzes sucrose to glucose and fructose, has been suggested as the key controlling enzyme. Its activity correlated positively with the concentration of hexose in bean (Morris and Arthur, 1984, 1985), tomato (Russel and Morris, 1982), strawberry (Ranwala et al., 1992), sweet pepper (Nielsen et al., 1991), and transgenic tobacco plant (yeast-derived acid invertase, Heineke et al., 1994); but negatively with the concentration of sucrose in sugarbeet (Giaquinta, 1979), citrus (Kato and Kubota, 1978), sugarcane (Gayler and Glasziou, 1972), carrot (Ricardo and apRees, 1970), and sucrose accumulating and non-accumulating genotypes of *Cucumis* (Schaffer et al., 1987).

In our experiment, the acid invertase activity was high on Day 0 when the accumulation of hexose started, and it declined, thereafter, concomitantly with an increase in sucrose concentration and deceleration in the rate of hexose accumulation. Thus, it may be assumed that hydrolysis of sucrose by acid invertase continued during the earlier part of the experiment, which caused the increase in hexose concentration; whereas the inhibition of acid invertase activity during the later period of the treatment caused a decrease in hexose accumulation and an increase in sucrose concentration. The observed correlation between acid invertase activity and sucrose concentration supports the idea that acid invertase plays an important role in the hydrolysis of sucrose.

Limitation of using acrylic sleeves for the restriction treatment

Our experiment showed that restricting the accumulation of water caused the increase in the concentration of soluble sugars. It is tempting to conclude that the rate of water accumulation is a determinant of soluble sugar concentration in cucumber fruits but the mechanical restriction, using the acrylic sleeves, restricted water accumulation almost completely and prevented further uptake of water by cells. Therefore, once the concentration of soluble sugars increased, it would not be diluted by water inflow, and thus, the concentration would not decline even though the accumulation of soluble sugars was inhibited. If the fruits had been treated such that they would continuously enlarge at a slow rate, the concentration of soluble sugars might increase temporally and then decrease to the original level. In our previous study with turnip (Kawabata et al., 1992), when the enlargement of the roots was restricted mechanically by acrylic sleeves, restricting lateral growth completely but which allowed continuous growth in length, the treatment caused a slight decrease in the concentration of hexose, unlike the results we obtained with cucumber fruits.

The second problem encountered was that the time when the restriction started could not be determined precisely. In Experiment 2, the day after the set was regarded as the start of the treatment. However, on Day 0, differences in dry matter concentration and acid invertase activity already existed between treated and untreated halves of the fruits. It may be that fruit enlargement had already been restricted to a sufficient level to influence the concentration and to induce the physiological responses, albeit, the enlargement was very small.

To solve these problems, it would be necessary to develop a device that would inhibit enlargement but would enable the fruits to enlarge at a low rate; such a device will need to restrict fruit enlargement immediately after its installation.

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キュウリ果実の肥大の機械的な抑制が水と乾物の蓄積に及ぼす影響

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摘　要

肥大生長期にあるキュウリ果実の糖濃度の決定機構について水分蓄積との関係から調べた．水分蓄積が糖濃度に与える影響を評価するため，キュウリ果実をアクリルパイプで覆って肥大成長を抑制し水分の蓄積を機械的に抑制した．この処理は，果実肥大を新鮮重で対照果実の 40 から 72%に抑制した．乾物率とヘキソース濃度はそれぞれ対照の 127%から 138%および 134%から 173%に増加した．スクロースは，全糖濃度に占める割合は小さかったが，処理後顕著に増加した．酸性インベルターゼ活性はスクロース濃度と負の相関があり，スクロースの蓄積は酸性インベルターゼ活性の低下と関係していることが示唆された．経時的に処理効果をみると，乾物率が一定に推移したのに対し，可溶性糖濃度は全処理期間を通じて増加し続けた．従って，可溶性糖濃度が増加したのは，炭水化物の流入が相対的に水の流入を上回ったためではないことを示した．可溶性糖濃度と水分蓄積との関係について考察した．