キュウリの雌姓ならびに両性系統の性表現と節間伸長におよ ぼすジベレリンの影響

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Effect of gibberellin upon sex expression and internode length in gynoecious and monoecious cucumber

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Summary

Gynoecious, gynomonoecious and monoecious cucumber varieties of foreign and Japanese origins were treated with gibberellin. Promoting effect of gibberellin upon staminate flower formation was strongest in gynoecious strains, weaker in gynomonoecious varieties and weakest in monoecious plants. As the result, the application of gibberellin diminished the difference in sex expression between gynoecious and monoecious plants. It was also ob-

served in all the treated varieties that gibberellin promoted the internode elongation of cucumber in low concentration but inhibited it in high concentration. Foreign gynoecious strains which had originally shorter internodes were more strongly affected than Japanese varieties in internode elongation, but no marked difference was found among Japanese varieties.

Introduction

Sex expression in cucumber is a phenomenon of complex action of genetic constitution, environmental condition and level of auxin and gibberellin^{1,5,7,8,14,15)}. Meanwhile, gynoecious cucumbers have become convenient materials for hybridization work since the introduction of gynoecious lines from the inbred segregates of a Korean variety "Shogoin" by Peterson^{11,12)}. Gynoecism itself may be successively maintained by selfing with the pollen from gibberellin-induced male flowers^{4,7,11,12)}. In breeding work of F_1 hybrid seed production, it is necessary to know the varietal difference in the response of different cucumber lines to gibberellin treatment.

The present investigation was done as a first step to a hybridization programme of cucumber including gynoecious and monoecious varieties of foreign and Japanese origins to observe the effect of gibberellin upon the promotion of male flowers and the elongation of internode length.

Materials

Five varieties of cucumber were included in this experiment. These were (I) E 6-65020; (II) G 6-65016; (III) Higan-fushinari; (IV) Natsu-fushinari; and (V) Suyo. The first two Dutch strains⁷⁾ are materials derived from MSU 713-5¹¹⁾, an Americal gynoecious strain. Higan-fushinari and Natsu-fushinari are gynoecious or sometimes gynomonoecious cucumber of Japanese commercial varieties⁴⁾. According to Fujieda⁴⁾, Natsu-fushinari showed 80 to 90% of plants to be gynoecious when sown in May and June but monoecious plants increased when sown in July, gynoecious ones being only less than 20%, while Higan-fushinari was constantly gynoecious independently of sowing time. Suyo is monoecious. This investigation consisted of two experiments. The first experiment was tried in order to have staminate flowers on gynoecious varieties with application of gibberellin at a single concentration of 1500 ppm. The

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second experiment was similar to the first one but modified in respect of concentration of gibberellin and time of application, the varieties remaining the same. Gibberellin used here was a product of Meiji Seika & Co. Ltd.

Experimental results

Experiment I

(a) Method. Seeds of all the five varieties were germinated in the germination chamber at 28°C. Seeds having germinated were sown in the sterilized soil of the 'Jiffy' pots on the 10 th of April in 1969. The plants reaching four leaf stage were transplanted on the sand bed in a vinyl house. Three plants of each variety were treated with only one concentration of gibberellin at 1500 ppm. Two plants were kept as check in each variety. Altogether, three applications of gibberellin were made with approximately 0.3 to 0.4 cc in each spray through a hand sprayer. The first application of gibberellin at 1500 ppm was given to E 6-65020, G 6-65016 and Suyo at 8th node stage on the 30th of May and subsequent applications were given on the 14th and 21st of June. Two-week interval between the first and second sprays of gibberellin was due to some vegetative distortion developing in the plants after the first application. Natsu-fushinari and Higan-fushinari received the first treatment at 8th and 10 th node stages on the 7 th and 14 th of June, respectively. Subsequent sprays were done at weekly intervals.

Table 1. Effect of 1500 ppm gibberellin on internode length.

-			Internode length (cm)			
	Variety	Treatment	1–8 th node	9-16 th node	17-24 th node	
1.	E 6-65020	Treat. Cont.	4.62 5.01	4.12** 5.55	4.75** 6.87	
2.	G 6-65016	Treat. Cont.	4. 40 4. 10	4.30** 5.40	5.50** 6.80	
3.	Higan- fushinari	Treat. Cont.	5.62 6.84	11.69 11.63	6.26** 7.60	
4.	Natsu- fushinari	Treat. Cont.	6.78 6.97	8.75** 7.40	 5.56	
5.	Suyo	Treat. Cont.	6.10 6.06	6.54** 8.39	5.68** 9.03	

^{**} Significantly different from respective controls at 1% level.

Table 2. Sex ratio affected by the application of 1500 ppm gibberellin.

Variety	TT .	Treat- ment	Node			Flower		
	Variety		Male	Female	Male ratio	Male	Female	Male ratio
1.	E6-65020	Treat. Cont.	0.5 0.0	3.0 9.0	14.3% 0.0	0.5	3.0 9.5	14.3% 0.0
2.	G6-65016	Treat. Cont.	1.3 1.0	3.0 9.0	30.2 10.0	2.7 3.0	3.0 11.0	$\frac{47.4}{21.4}$
3.	Higan- fushinari	Treat. Cont.	0.0 0.0	3.3 3.7	0.0 0.0	0. 0 0. 0	3.3 6.0	0.0 0.0
4.	Natsu- fushinari	Treat. Cont.	0.3 1.0	7.0 5.5	4. 1 15. 4	0.3 1.0	7.3 5.5	4. 1 15. 4
5.	Suyo	Treat. Cont.	3.2 9.3	4. 5 6. 3	41.5 59.6	6.3 31.0	6.7 6.5	48.5 82.6
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- (b) Length of internode. The effect of gibberellin at 1500 ppm level in respect to the lengths of internode of treated and untreated plants is presented in Table 1. It is observed that the internode length of all the varieties showed a definite
- decrease after the application of gibberellin at 1500 ppm concentration as compared with the control plants, with the exception of Natsufushinari.
- (c) Sex ratio. Male and female flowers were counted per plant with respect to their nodes. Percentages of male nodes and male flowers were calculated from observations up to 24 nodes per plant. Table 2 reveals that Dutch strains produced larger percentage of male flowers at 1500 ppm concentration of gibberellin but Higan-fushinari remained unaffected. In contrast with this, Natsu-fushinari and Suyo

showed the decrease of male flower ratio.

Experiment II

(a) Method. The second experiment was started on the 9th of July with all five varieties of cucumber, but in this case two Dutch gynoecious strains were put together owing to the scanty number of plants. Each application of gibberellin was made with 0.1cc through a graduated pipette. Four concentrations were used, i. e., 250, 500, 1000, and 1500 ppm. The first spray was done in every variety at the first leaf stage on 19th of July. After that, gibberellin of both 250 and 500 ppm concentrations was applied at two-day intervals and 1000 and 1500 ppm at one-week intervals. Altogether four applications were made.

(b) Length of internode. All the applications of gibberellin were done within 8th node stage

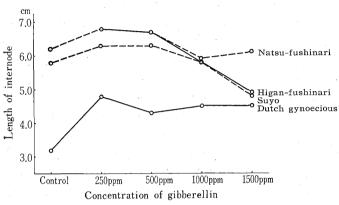


Fig. 1. Effect of various concentrations of gibberellin on internode length.

Table 3. Sex ratio affected by the application of various concentrations of gibberellin.

Variety	Treat- ment	Node			Flower		
		Male	Female	Male ratio	Male	Female	Male ratio
Dutch gynoecious	ppm 1500 1000 500 250 Control	4 1 2 0 0	0 1 2 2 0	100.0 50.0 50.0 0.0 0.0	6 1 2 0	0 1 2 2 0	100.0 50.0 50.0 0.0 0.0
Higan- fushinari	1500 1000 500 250 Control	2 5 0 0	2 2 4 4 —	50.0 71.4 0.0 0.0	3 13 0 0 -	2 2 4 4 —	60. 0 86. 7 0. 0 0. 0
Natsu- fushinari	1500 1000 500 250 Control	5 4 8 6 4	7 6 8 7 9	41.7 40.0 50.0 46.2 30.8	22 12 29 17 6	7 6 8 7 9	75. 9 66. 7 78. 4 70. 8 40. 0
Suyo	1500 1000 500 250 Control	21 21 20 20 20 20	2 1 4 3 2	91.3 95.5 83.3 87.0 90.9	123 162 119 133 125	2 1 5 3 2	98. 4 99. 4 96. 0 97. 8 98. 4

of the plant. Therefore, internode length for this experiment was considered up to 8th node and presented in Fig. 1. It would be generally noticed that internode elongation was observed in plants receiving concentration up to 500 ppm, but there was no further increase at 1000 ppm. At 1500 ppm, internode was shortened in Higanfushinari and Suyo but the effect remained the same as in 1000 ppm in Dutch strains and Natsu-fushinari.

(c) Sex ratio. Percentages of male nodes and male flowers are given in Table 3. In Dutch gynoecious strains the percentage of male flowers became higher according as the higher concentrations of gibberellin were applied, and Higan-fushinari also showed the similar tendency. The application of gibberellin slightly increased male flowers in Natsu-fushinari but had no decisive effect in Suyo.

Discussion

It is well known that the application of gibberellins promotes the formation of staminate flowers in monoecious, gynomonoecious or gynoecious cucumbers^{4,12,15)}. As to the promotion of male flowers

in the present study, gibberellin was effective only in Dutch gynoecious strains but had no effect upon other varieties (Table 2). The application of gibberellin at younger stages of plant growth, however, promoted male flower formation not only in Dutch strains but also in Japanese gynoecious or gynomonoecious varieties such as Higan-fushinari and Natsu-fushinari (Table Suyo received no effect. That is, the effect of gibberellin is strongest in gynoecious strains, weaker in gynomonoecious varieties, and weakest in monoecious plants. It could be considered that gibberellin works more strongly in the plants having originally less male flowers than in those having many male flowers. In addition to this, in foreign gynoecious plants the percentage of male flowers increases in proportion to the increase of concentration of applied gibberellin (Table 3). Peterson and Anhder 12 stated that sex expression in cucumber can be explained on the basis of response to specific chemical substances, and they suggested the possibility that chemical synthesis in the plant of a gibberellin-like growth substance does not occur in gynoecious strains. If it is true, the difference of male flower formation among various sex types may be dependent upon the amount of endogenous gibberellin. In fact, Atsmon et al.2) found that the amounts of gibberellin diffusing from seedlings as well as their amounts in root exudate are significantly higher in monoecious than gynoecious cucumber plants. When gibberellin is applied exogenously, the response of plants will differ according to the amount of their own endogenous gibberellin. In the present study, gibberellin application was most effective in the gynoecious strains which may have no or little endogenous gibberellin and least effective in Suyo variety which may be abundant in gibberellin in itself (Tables 2 and 3). It can be said that the application of exogenous gibberellin diminishes the difference in sex expression between gynoecious and monoecious plants through making their endogenous gibberellin at the similar level.

The staminate flower formation is closely related to vegetative growth such as hypocotyl and internode elongation. Atsmon¹⁾, treating various sex types of cucumbers, i.e., gynoecious, monoecious, hermaphrodite, and andromonoecious plants, found that plants with strong hereditary male tendency had relatively longer hypocotyls than those with strong female tendency and that internode length exhibited the same trend as hypocotyls. He suggested that such differences in the hypocotyl and the internode were possibly due to differences in endogenous gibberellins among different sex types. This is true of internode length in the present experiment only when untreated plants of foreign gynoecious strains are compared with those of other Japanese varieties (Table 1 and Fig. 1). But any marked difference could not be recognized among different sex types within Japanese varieties. It is reasonable to consider that the difference in internode length between Japanese and foreign varieties is not only due to gynoecism itself but also due to other genetic background of varieties. In this respect, Atsmon¹⁾ stated that direct comparisons of internode length are meaningful only between the different sex types within a given cultivar, but not between any of one cultivar and any of another one. It is possible that the effect of endogenous gibberellins varies with different cultivars.

BRIAN and Hemming⁸⁾ found hypocotyl elongation due to the application of gibberellins. MITCHELL and WITTWER¹⁰⁾ reported the increased length of first internode of gynoecious cucumber when cultured in gibberellin-added solution as the root growth medium. Atsmon¹⁾ found gibberellic effect upon internode length to be more intensive in gynoecious than monoecious

cucumbers. And Fuhleda⁴⁾ also observed the elongation of internode length by the application of gibberellin. In Experiment I, however, almost all the varieties showed shorter internode length by the application of 1500 ppm gibberellin (Table 1). This is more clearly understood by Experiment II. As shown in Fig. 1, gibberellin had promoting effect of internode elongation at 250 ppm and 500 ppm, but this effect disappeared at 1000 ppm. At 1500 ppm, on the contrary, gibberellin showed an inhibiting effect upon internode length. Therefore, it is safely assumed that gibberellin promotes the internode elongation of cucumber in low concentration but inhibits it in high concentration.

There are some chemicals which cause the decrease of staminate flowers and the increase of pistillate ones. Laibach and Kribben^{8,9)} succeeded in increasing the proportion of pistillate flowers by treatment with NAA and IAA. According to them, the sex determination of cucumber flowers depends upon the concentration of auxin in the lateral bud, and pistillate flowers require higher concentration of auxin than staminate flowers in their formation. Ito and Saito⁵⁾ observed that the application of IAA, NAA and 2,4-D on cucumber plants suppressed vegetative growth and promoted reproductive one, causing the sex reversal from staminate flowers to pistillate ones. The grade of suppression of vegetative growth was proportional to the concentration of applied chemicals. The concentration effective for the induction of pistillate flowers in IAA was above 500 ppm, and that in NAA was above 10 ppm. They considered that sex expression of cucumber is related to the amount of auxin in plant and pistillate flower formation is promoted at a high auxin level. Wittwer and Hillyer (17) regarded such a reduction of the ratio of staminate to pistillate flowers as the chemical induction of male sterility.

RHEM¹³⁾ stated that treatment with growth hormones reduced the fertility of plants. According to him, the auxins seem not only to be antagonistic to the initiation of flowering but also to reduce the number of seeds, or they may cause total sterility. This effect is used in blossom-thinning sprays and in the production of parthenocarpic fruits. Saito and Ito(14) conceived that the sex pattern in cucumber is manifested by the accumulation of the flowerforming substances. The flower-forming substances are produced in the leaf under cool shortday conditions and transported through sieve tubes into the meristem. Such substances in the low concentration induce the staminate flower at first, which are followed by the induction of the bisexual flower with the accumulation of the substances. In further high concentration, they induce the pistillate flower. In this case, they found that a low level of endogenous auxin is necessary in the meristem for the induction of the pistillate flower. The high concentration of auxin acts antagonistically to the promotion of flower formation and pistillate flower differentiation. Saito and Ito15) further considered that gibberellin application increases the content of endogenous gibberellins in the stem apex and the increased gibberellins invigorate plant growth and counteract the effect of the flower-forming substances. Gibberellin, like auxin, seems to inhibit the accumulation of the flower-forming substances in the meristem.

As stated above, there are two opposite opinions about the relation of auxin to pistillate flower initiation, that is, one is that a high concentration of auxin causes pistillate flower induction and the other is that a low concentration of auxin is necessary for the initiation of the pistillate flower. This contradiction may be explained as the following interpretation. It

is a generally accepted hypothesis that auxin in appropriate concentration has a promoting effect upon the growth of cells, but, when excessively given, it becomes suppressive [16]. The turning point of auxin concentration from promotion to suppression is different with tissues or organs. The root is more sensitive to auxin and reacts in lower concentration than the stem or the bud. As to flower formation in cucumber, the similar supposition may be possible. If endogenous auxin exists in high concentration, vegetative growth is promoted and conversely reproductive growth, hence, pistillate flower formation is suppressed. If endogenous auxin is in low concentration, it will be beneficial to pistillate flower induction. And, if exogenous auxin such as IAA or NAA is added and consequently endogenous auxin becomes excessive, vegetative growth may be suppressed and reproductive growth is promoted. With the increasing concentration of auxin, growth of cucumber may be affected as follows: reproductive —> vegetative —> reproductive.

In the present experiment, spraying with high concentration of gibberellin caused the decrease of internode length and some malformation of leaves (Table 1 and Fig. 1). Such a phenomenon may be contrary to the generally accepted fact⁶⁾ that the effect of gibberellin on stem elonga tion is proportional to the dose of applied gibberellin and even high concentration does not cause inhibiting reaction. The suppression effect of gibberellin, however, is sometimes seen in the root of various kinds of plant⁶⁾. And this effect is considered to be due to the concentration of endogenous gibberellin of the root. It is not strange to assume that the action of gibberellin in the stem changes from promotion to suppression when its concentration becomes extremely high as it acts in the root. In fact, Fujieda reported that the effect of gibberellin upon internode elongation is only temporary and followed by shortening of internodes soon after the removal of the effect, especially in high concentration (1500 ppm). Peterson and Andher¹²⁾ found that considerable vegetative distortion followed the 5000 ppm treatment but no serious vegetative injury resulted from a single application of 2000 ppm. As for the relation of gibberellin to auxin, it is sometimes assumed that the action of auxin is closely related to and controlled by gibberellin6). If it is true, it is natural that gibberellin acts in the similar way as auxin.

When the male flower ratio is compared with internode elongation, it was found that Dutch gynoecious strains had no further increase of internode length at 1500 ppm in which male flower ratio was maximum (Table 3, Fig. 1). Higan-fushinari at 1000 ppm showed a decrease in internode length. It was thus observed that maximum male flower ratio had reverse action on internode elongation in these plants. Natsu-fushinari and Suyo presented the internode elongation up to 500 ppm (Fig. 1) but did not show any difference of sex ratio according to the different concentrations of applied gibberellin up to 1500 ppm (Table 3). In Table 2, however they showed the limiting point of the promotion of male flower at 1500 ppm. In other words the limiting concentration of gibberellin to promote vegetative growth is not always the same as the limiting concentration to promote the staminate flower. The physiological action of gibberellins in promoting staminate flowers in gynoecious cucumber and its relation with vegetative character may perhaps require further research.

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キュウリの雌性ならびに両性系統の性表現と節間伸長 におよぼすジベレリンの影響

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キュウリの雌性系統,準雌性系統および両性系統を用いてジベレリン処理を行ない,ジベレリンの節間伸長および雄花誘起に及ぼす影響を調べた。

各系統を通じてジベレリンは 250 ppm および 500 ppm の低濃度で節間の伸長を促したが、1000 ppm ではその伸長を停止し、1500 ppm の高濃度では逆に抑制的に働いた。元来節間の短い外国の雌性系統は節間の長い我が国の品種に比較してジベレリンによる伸長効果は大である。

またジベレリンによる雄花誘起の作用は雌性系統において最も強く,準雌性系統がこれに次ぎ,両性系統では

はとんどその効果がなかつた。その結果,ジベレリンの 処理によつて雌性系統と両性系統との間の性表現の差が 短縮された。これは,雌性系統では両性系統にくらべて 本来内在的ジベレリンの量が少なく,そのためジベレリン処理による効果が大きく現われると考えられる。雌性 系統の雄花誘起の割合は処理したジベレリンの濃度に比 例して高まつた。

以上のことからジベレリンの節間伸長に対する限界濃度は必ずしも雄花誘起の限界濃度と同じではないと言い得る。