トマトの乱形果発生に及ぼす植物生長調節物質の影響

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Regulation of Low Temperature-induced Malformation of Tomato Fruit by Plant Growth Regulators

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Summary

Low temperature-induced fruit malformation in tomato was studied from plant hormonal view point. Treatment of TIBA (2, 3, 5-triiodobenzoic acid) and NAP (sodium N-1-naphthylphthalamic acid), auxin-transport inhibitors, increased locule numbers and induced severe malformation including catfaced and strawberry fruits with ovary splits, and oblate and fasciated fruits. Bendroquinone (2-benzimidoyl-3-hydroxyl-1, 4-napthoquinone), which is considered to have the similar action mechanism to TIBA and NPA, also showed the same effects. Auxins, PCPA (*p*-chlorophenoxyacetic acid), 2, 4-D (2, 4-dichlorophenoxyacetic acid) and 2, 4, 5-T (2, 4, 5-trichlorophenoxyacetic acid) reduced oblate and triangular types of malformation by decreasing locule numbers. Gibberellin (GA_3) induced ovary split but CCC [(2-chloroethyl) trimethylammonium chloride] and SADH (succinic acid-2, 2-dimethylhydrazide), which are considered to inhibit gibberellin synthesis, could not reduce low temperature-induced fruit malformation.

Introduction

In forcing culture of tomato, irregularly shaped fruits frequently occur through abnormal development of carpels. These deformed fruits comprise catfaced fruits due to incomplete development of the ovary wall near the base of the style, strawberry fruits with split ovary by incomplete fusion of carpels, and oblate or triangular fruits due to the development of multilocular ovary, and so on. It is well known that these abnormal developments of ovary are caused by exposure of pre-floral plants to low temperatures (4, 9, 16, 14). Excessive fertilizing and frequent watering intensify the degree of irregularities of fruit shape (8, 17, 23). As for effects of growth regulators on the occurrence of fruit malformation in tomato, Sawhney and Greyson (20) reported that gibberellin applied to pre-floral plants stimulated the occurrence of multilocular fruits, and Ito and Fujimoto (7) reported that the application of N-arylphthalamic acids induced large deformed flowers with multicarpels. However, the relationship of fruit malformation induced by low temperature through the aberration of hormonal balance have not been clarified. Therefore, we investigated possible role of hormonal balance on the occurrence of fruit malformation and tried to reduce low temperature-induced malformation of fruits by the treatments of auxins and gibberellin synthesis inhibitors.

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Materials and Methods

Tomato cultivar 'Ogata-fukuju' was used for all the experiments, since this cultivar showed typical fruit malfomation when exposed to low temperature at the seedling stage.

Seedlings were planted in small plastic pots filled with gravel and cultured in Mie University nutrient solution of half strength (24.6 g $MgSO_4 \cdot 7H_2O$, 7.6 g NH_4PO_4, 26.1 g K_2SO_4, 59 g $Ca(NO_3)_2 \cdot 4H_2O$, 1.2 g Fe EDTA, 0.0188 g CuEDTA, 0.0075 g Zn EDTA, 0.22 g MnEDTA, 0.001 g $Na_2MoO_4 \cdot 2H_2O$, 0.225 g $Na_2B_4O_7 \cdot 10H_2O$ /100 l) in hydroponic beds (Kubota Co. Ltd.). After 2-leaf stage they were grown for 16 to 25 days under the condition where most of daily minimum temperatures were below 10 °C, and then transferred to the temperature

Fig. 1. Degree of fruit malformation.
0……normal, 1……slight, 2……intermediate, 3……strong, 4……severe.

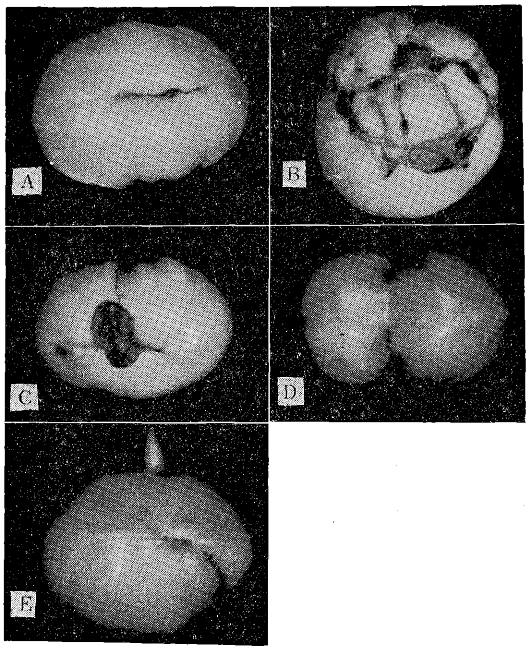

Fig. 2. Types of fruit malformation.
A : Oblate, B : Catfaced, C : Strawberry,
D : Fasciated, E : Carpel protrudent.
B and C are classified as ovary split in the present experiment.

condition above 10°C. Chemical treatments were conducted with foliar spray or pot immersion at 2.5- to 3-leaf stage during the period of low temperature exposure.

The node number to the first truss and the flower number of the first truss were recorded at anthesis, and the sepal and locule numbers of the first and second fruits of the first truss at harvest (green mature stage). The degree of fruit malformation was determined according to the criterion shown in Fig. 1. The types of fruit malformation were classified to five groups (normal, oblate or triangular, ovary split, fasciated and protrudent carpel) (Fig. 2).

Ten to fifteen plants were replicated for each treatment and most of the experiments were carried out from fall to spring.

Results

Experiment 1. Effect of TIBA, NPA and bendroquinone on occurrence of fruit malformation.

Ten ppm TIBA, 10 ppm NPA and 50 ppm bendroquinone were sprayed twice at 2.5- and 3-leaf stages. Mean minimum temperature for 16 days after 2-leaf stage was 6.6°C.

The node number to the first truss did not change, while the flower numbers considerably increased following the chemical treatments (Table 1). The treated plants increased in the flower number of the first truss, produced extra inflorescence in the position of the terminal bud, and became self-topping.

The chemical treatments induced a variety of fruit malformation from oblate to extreme fasciation (Figs. 3 and 4). Some oblate fruits were accompanied by ovary splits. The degree of malformation was greatly intensified by the treatments (Fig. 5), and the sepal and locule numbers also increased remarkably in fruits of the treated plants (Table 1). TIBA treatment induced fruit malformation even when the seedlings were grown at high temperatures of 20°C and above (Fig. 6).

Experiment 2. Effect of gibberellin on occurrence of fruit malformation.

Five and ten ppm GA_3 was sprayed once at 2.5-leaf stage. Mean minimum temperature for 25 days after 2-leaf stage was 6.6°C.

The node number to the first truss was not decreased by 10 ppm GA_3 treatment, and the flower number was decreased (Table 2). The locule number increased considerably and the sepal number, slightly. The degree of

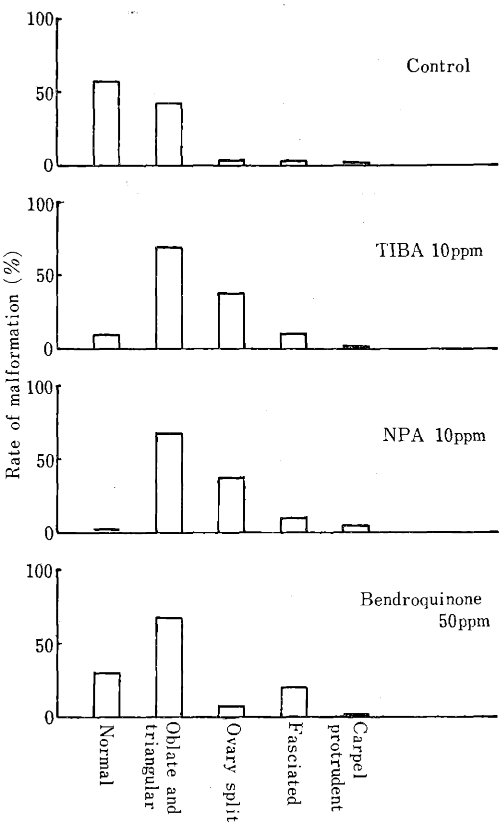

Fig. 3. Types of malformation in the 1st and 2nd fruits in TIBA-, NPA- and bendroquinone-treated plants. Some fruits share two malformation types.

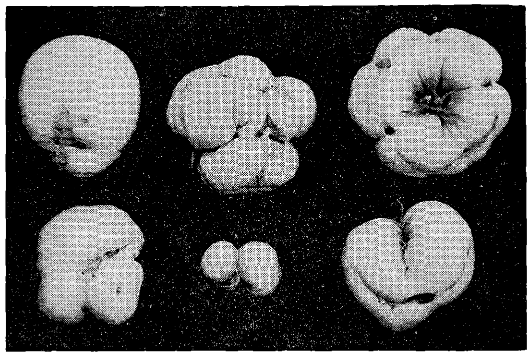

Fig. 4. A variety of fruit malformations induced by NPA treatment.

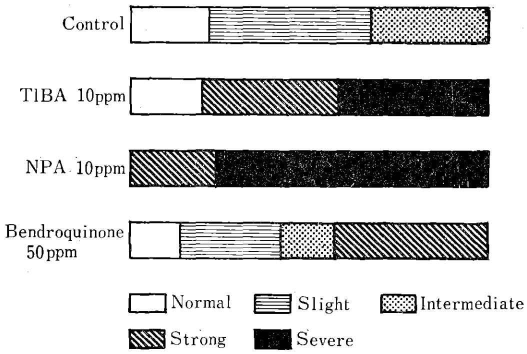

Fig. 5. Effect of TIBA, NPA and bendroquinone on degree of malformation in the 1st fruit.

malformation was higher in fruits of gibberellin treated plants than in those of the control, and all fruits of the treated plants had ovary splits. GA_3 intensified the degree of malformation even when the seedlings were grown above 12°C and fruit malformation was very little in the control (Fig. 6).

Table 1. Effect of TIBA, NPA and bendroquinone on development of flower and fruit.

Treatment	Nodes to 1st truss	Flower number of 1st truss	Sepal number		Locule number	
			1st fruit	2nd fruit	1st fruit	2nd fruit
Control	6.9	7.9	8.9	6.8	11.8	7.2
TIBA 10 ppm	7.1	28.6	18.8	12.9	20.0	18.0
NPA 10 ppm	7.3	26.2	23.3	14.8	24.3	10.6
Bendroquinone 50 ppm	7.8	11.1	11.9	8.9	17.9	13.2

Table 2. Effect of gibberellin on development of flower and occurrence of fruit malformation in the 1st fruit.

Treatment	Nodes to 1st truss	Flower number of 1st truss	Of 1st fruit		Rate of malformed fruits (%)	
			Sepal number	Locule number	Intermediate and over	Slight
Control	6.7	5.3	7.3	14.1	32.5	67.5
GA_3 5 ppm	6.5	5.1	7.8	25.3	100.0	0
GA_3 10 ppm	6.6	3.2	8.4	22.6	86.0	14.0

Table 3. Effect of auxins on development of flower and fruit.

Treatment	Nodes to 1st truss	Flower number of 1st truss	Sepal number		Locule number	
			1st fruit	2nd fruit	1st fruit	2nd fruit
Control	7.3	4.8	9.4	8.0	16.1	11.2
2,4-D 1 ppm	7.2	5.9	9.1	6.9	12.3	7.5
2,4,5-T 1 ppm	7.1	6.0	9.1	6.4	12.7	8.7
PCPA 10 ppm	7.0	5.8	6.7	6.4	9.3	10.8

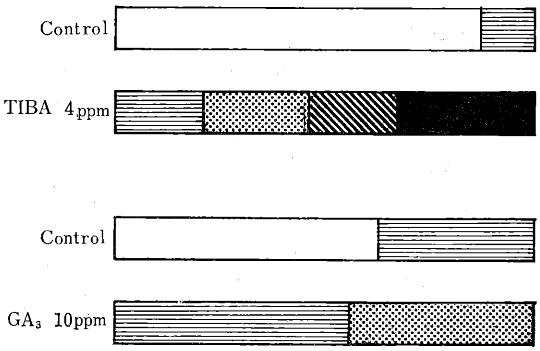

Fig. 6. Effect of TIBA and GA_3 on degree of malformation in the 1st and 2nd fruits. TIBA-treated seedlings were grown above 20°C and GA_3-treated ones above 12°C.

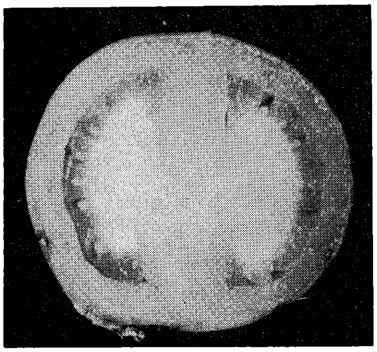

Fig. 7. Fruit with only two locules which developed in PCPA-treated plant.

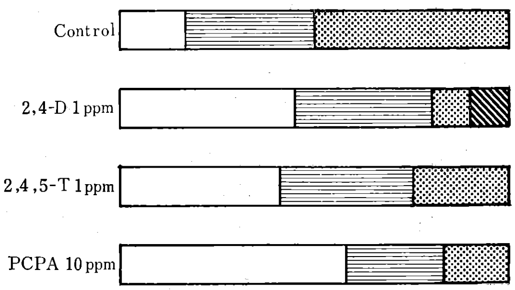

Fig. 8. Effect of auxins on degree of malformation in the 1st fruit.

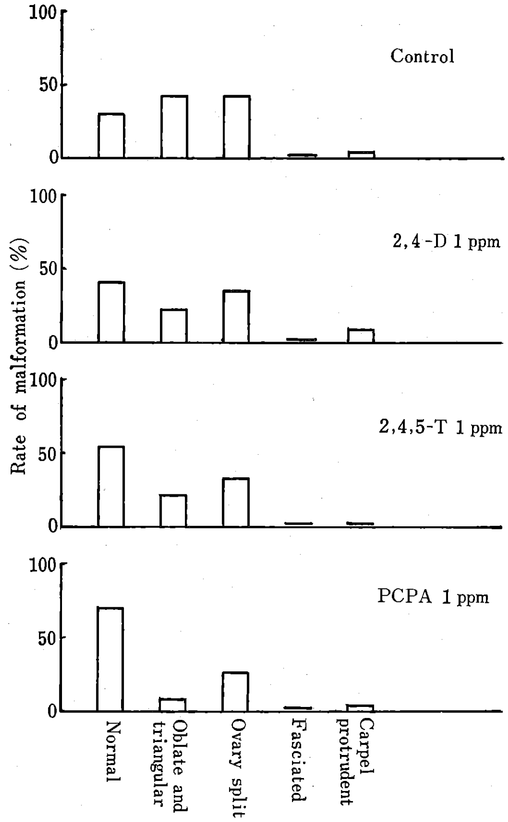

Fig. 9. Types of malformation in the 1st and 2nd fruits in auxin-treated plants. Some fruits share two malformation types.

Experiment 3. Effect of auxins on occurrence of fruit malformation.

One ppm 2,4-D, 1 ppm 2,4,5-T and 10 ppm PCPA were sprayed once at 3-leaf stage. Mean minimum temperature for 25 days after 2-leaf stage was 6.1°C.

Auxin spray induced slight curling of young leaves and delayed flowering a few days. The node number to the first truss and the flower number did not differ so much from those of the control (Table 3). The

Table 4. Effect of gibberellin synthesis inhibitors on development of flower and occurrence of fruit malformation.

Treatment	Nodes to 1st truss	Flower number of 1st truss	Sepal number		Locule number		Degree of malformation*	
			1st fruit	2nd fruit	1st fruit	2nd fruit	1st fruit	2nd fruit
Control	7.2	10.7	9.5	7.4	22.8	10.6	2.1	1.4
CCC 100 ppm	7.3	9.6	8.5	7.8	19.1	10.6	1.8	1.6
SADH 1000 ppm	7.5	11.9	9.0	6.4	32.0	11.3	2.3	1.0

* Refer to Fig.1

sepal number of fruits was decreased by PCPA treatment. The locule number in auxin-treated fruits decreased to 60~90% of the control in the first fruit and 70~80% in the second fruit. In the extreme case, one of PCPA-treated fruits had only two locules (Fig. 7).

The degree of malformation was decreased by all of the auxins with maximum effect of PCPA (Fig. 8). Particularly, reduction of triangular and oblate fruits was considerable (Fig. 9). Fruits with split ovaries were not decreased so much by 2, 4-D and 2, 4, 5-T but was decreased to 40% by PCPA.

Experiment 4. Effect of gibberellin synthesis inhibitors on occurrence of fruit malformation.

The roots of seedlings at 2.5-leaf stage were immersed in 100 ppm CCC solution free of nutrients for 24 hours and then the seedlings were returned to CCC-free culture solution. 1000 ppm SADH was sprayed to the other seedlings at 2.5-leaf stage. Mean minimum temperature for 21 days after 2-leaf stage was 10.4°C.

The node number to the first truss and the flower number were not influenced by the treatments (Table 4). The locule number of fruits was increased by SADH. The degree of malfomation was not decreased by CCC and SADH.

Discussion

It has been reported in eggplant that irregulary shaped multistyled ovaries often developed in the cool cultural season(12). Hartsema(6) mentioned the phenomenon that the number of floral parts increased when flower formation proceeded at low temperature. Especially, in large-fruited cultivars of tomato which have been bred through accumulation of genes increasing carpel numbers, the increase of carpel numbers and the following abnormal development of ovary seem liable to occur at low temperature.

Fujimura et al. (5), and Saito and Ito(18) observed the phenomenon that ample fertilization intensified fruit malformation, and suggested on the mechanism of occurrence of fruit malformation in tomato that development of extralocules and split ovaries were induced by nutrient accumlation in the flower bud which developed at low temperature.

Zimmerman(24) found that TIBA induced fruit malformation in tomato. Saito(15) also recognized that TIBA treatment promoted an increase of carpel numbers. In the present experiment, most of fruits affected by TIBA resembled severe ones of low tempereture-induced malformed fruits. It is well known that TIBA treatment increases the number of flowers in tomato plants(25), and there are some evidences to suggest that promotion of flowering response by TIBA is correlated with a lowered auxin level in the plant. In fact, it is well known that TIBA is one of auxin-transport inhibitors(2, 11).

From these facts, it is considered that low temperature lowers endogenous auxin level in the shoot apex, resulting in malformation of fruits. NPA, which is another auxin-transport inhibitor(3, 10, 13), also increased flower numbers and induced severe fruit malformation in the present experiment. We observed in the preliminary experiment that bendroquinone, which is a new type of plant growth regulator(21, 22), had the similar flowering effect to TIBA in tomato. This chemical induced fruit malformation as TIBA and NPA in Experiment 1. Therefore, bendroquinone would also affect ovary development of tomato through lowering auxin level.

Based on this supposition, synthetic auxins were tested to elevate auxin level in the shoot apex of the seedlings exposed to low temperature. All the auxins tested reduced the degree of fruit malformation, especially in oblate or triangular type, but NAA (α-naphthaleneacetic acid)and HCPA(2-hydroxy-methyl, 4-chlorophenoxyacetic acid) were less effective (data not shown). Since fruits with split ovary (catfaced and strawberry fruits) were not decreased so much by 2·4-D and 2·4·5-T, another factor such as nutrient accumlation might be involved in occurrence of this type of abnormality. Slight decrease of fruits with ovary splits by PCPA may be due to ease of carpel envelopment, since ovary diameter decreased with reduction of carpel numbers. Audus(1) referred to an example of reduction in sepal numbers by fusion with α-phenoxypropionic acid treatment, but did not mention its effect on carpel numbers. Since we recognized a high correlation between sepal numbers and locule numbers ($r=0.90$, significant at 5%) in the fruit which developed at low temperature, locule numbers in Audus' example might have been reduced by the auxin treatment.

As for effect of gibberellin on ovary development, many reports show that multilocular or multistyled ovaries are induced by gibberellin treatment ([eggplant(12), pepper (19), tomato(20)]). In the present study also, GA_3 promoted the occurrence of multilocule as well as ovary split. However, the flower number decreased, contrary to the case of low temperature-experienced seedlings. Moreover, CCC and SADH, gibberellin-synthesis inhibitors could not alleviate fruit malformation induced by low temperature. Therefore, rise of endogenous gibberellin level by low temperature would not be so great as decline of endogenous auxin level. This supposition should be testified by analyses of endogenous auxin and gibberellin levels in the shoot apex exposed to low temperature.

Auxin treatment could alleviate fruit malformation of multilocular type, but for practical use, reduction of fruit size and delay of flowering must be counteracted effectively.

Acknowledgement

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トマトの乱形果発生に及ぼす植物生長調節物質の影響

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摘　要

低温により誘起されるトマトの乱形果に関して，植物生長調節物質の影響を検討した．オーキシン移動阻害剤であるTIBAおよびNPAは心室数を増し，果頂部が融合しない果実 (catfaced fruit)，果皮に裂け目が入り胎座部が見える果実 (strawberry fruit)，偏平果および重合果の発生を促進した．TIBAおよびNPAと同様な作用をもつと考えられる bendroquinone も同じ効果を示した．オーキシン類の PCPA, 2, 4-D および 2, 4, 5-T は心室数を減少させ，偏平果および三角果の発生を抑制した．ジベレリン (GA_3) は頂裂果の発生を促進したが，ジベレリンの合成を阻害すると考えられる SADH や CCC は低温下での乱形果発生を防止できなかった．