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Genetic and Hormonal Control of Parthenocarpy in Cucumber (*Cucumis sativus* L.)

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Inheritance of parthenocarpy in cucumber was controlled by a single dominant gene expressing incomplete dominance. A genetic factor for parthenocarpy was associated with high content of indoleacetic acid (IAA) in the ovary; content of IAA in unpollinated ovaries was higher in genetically parthenocarpic 'Pandex' than in non-parthenocarpic 'Khira'. Pollination or 4-chlorophenoxyacetic acid (4-CPA) treatment caused an increase of IAA content in both the cultivars and their F_1, whereas there seemed no relationship between abscisic acid (ABA) content and parthenocarpic fruit set.

INTRODUCTION

Natural parthenocarpy occurs in many plant families, particularly in the species which have large number of ovules per fruit, such as bananas, pineapples, figs tomatoes, cucumbers, etc. Gustafson (1939) suggested that the auxin content was higher in the ovaries of parthenocarpic cultivars of lemons, oranges and grapes than in the corresponding non-parthenocarpic ones, and proposed a hypothesis that the high auxin content in the ovaries at the time of blossoming is responsible for the development of parthenocarpic fruits. In cucumber, genetic of parthenocarpic fruiting was hypothesized that it is controlled by one incompletely dominant gene (Pike and Peterson, 1969), that one recessive gene might be responsible for the expression of parthenocarpy (Juldasheva, 1973) or that many incompletely recessive genes also control parthenocarpy (Kvasnikov et *al.*, 1970). However, physiological action of the gene(s) is not known, and detail studies on the changes of endogenous auxin were not conducted.

Reports available on the role of abscisic acid (ABA) in parthenocarpy are also very limited. Jackson and Blundell (1966) observed parthenocarpic development in *Rosa* by ABA. Endogenous studies on ABA content in reference to parthenocarpy are also few.

The purpose of this study was to investigate the inheritance of parthenocarpy in cucumber, and to clarify the role of endogenous indoleacetic acid (IAA) and ABA in parthenocarpy.

MATERIALS AND METHODS

'Pandex', a gynoecious parthenocarpic cultivar, and 'Khira', a monoecious non-parthenocarpic cultivar, were used in these experiments.

Experiment 1. Inheritance of parthenocarpy

The two cultivars, their F_1, F_2 and backcrossed progenies which were established during September, 1988 to June, 1989 in a plastic-film greenhouse were used in the gene analysis of the inheritance of parthenocarpy. Seeds were sown on August 11, 1989 and the seedlings were transplanted and grown in a sand culture system in the plastic-film greenhouse on September 6. The plants were irrigated with a solution of $1 g l^{-1}$ compound fertilizer OK-F-1 ($N:P_2O_5:K_2O = 15:8:17$, Otsuka Chemical Co.). Pistillate flowers were bagged one day before anthesis for isolation. The plants which produced at least one parthenocarpic fruits on the main stem up to the 25th node were determined as parthenocarpic plants.

Experiment 2. Role of endogenous IAA and ABA in parthenocarpy

Seeds of 'Pandex', 'Khira' and their F_1 were sown on February 27, 1990. The seedlings were transplanted on March 26 and grown in the plastic-film greenhouse. The pistillate flowers developed at the 7th to 25th nodes on the main stem were unpollinated (control), pollinated or unpollinated but sprayed with 100 $mg l^{-1}$ of 4-chlorophenoxyacetic acid (4-CPA) at anthesis. Self-pollination was done in 'Khira' and the F_1. 'Pandex' was pollinated with 'Khira' since 'Pandex' had no male flower during pistillate flower production. For hormone analysis, unpollinated ovaries were collected one day before anthesis to three days after anthesis at 24 hr intervals, and the ovaries pollinated or treated with 4-CPA were collected one, two, three and five days after pollination or treatment. They were weighed, frozen immediately in liquid nitrogen, freeze-dried and stored at -40°C until analysis.

Lyophilized materials were extracted with 80% cold methanol containing 100 $mg l^{-1}$ butylated hydroxytoluene (BHT) as an antioxidant for 24 hr at 5°C. Purification of the extract followed the procedure of Okubo et *al.* (1988). The methanol extract was concentrated under reduced pressure to the aqueous phase, acidified to pH 3.0 with 6 N HCl and extracted three times with 50 ml ethyl acetate. The ethyl acetate phase was extracted three times with 50 ml of 2 % sodium bicarbonate and the aqueous phase was readjusted to pH 3.0. Then it was extracted again three times with 50 ml ethyl acetate. The ethyl acetate fraction was evaporated to dryness under reduced pressure to store at -40°C until an HPLC analysis.

Quantification of IAA was undertaken using indolo-a-pyrone fluorescence method. Conversion of IAA into indolo-a-pyrone was carried out basically according to the method of Stoessl and Venis (1970), with the modifications suggested by Blakesley et *al.* (1983). Dried sample in a test tube was dissolved in 0.4 ml of a 1:1 mixture of acetic anhydride (AA) and trifluoroacetic acid (TFA) at 0°C for 60 sec. The mixture was immediately injected into HPLC (Simadzu, LC6-A) with shimpack-clc-ODS column (15cm *x* 6mm in diameter). The solvent was programmed from 30 to 70 % methanol in water (adjusted to pH 3.5 with acetic acid) with a flow rate of 1

$ml min^{-1}$.

Fluorescence was measured using a fluorescence HPLC monitor (Simadzu, RF-535) adjusted to an excitation wavelength of 440 nm and an emission wavelength of 490 nm.

Quantification of ABA was determined using HPLC equipped with Inertsil ODS-2 column (25 cm *x* 4.6 mm in diameter) and UV spectrophotometric detector (Simadzu, SPD-GA) set at '254 nm. Elution was performed by a gradient of 22-35 % acetonitrile in 0.2 M acetic acid at flow rate of 1 $ml min^{-1}$.

RESULTS AND DISCUSSION

Inheritance of parthenocarpy

Parthenocarpic fruit development in 'Pandex' started from the very beginnig of the fruit bearing at the lower nodes from the plant base (early parthenocarpy)(Table 1). Therefore, 'Pandex' was considered homozygous genotype for parthenocarpy. 'Khira' produced no parthenocarpic fruit (non-parthenocarpy), and was considered to be homozygous for non-parthenocarpy. Their F_1 hybrid with heterozygous genotype, produced some parthenocarpic fruits on the 8th node and above (late parthenocarpy).

In segregating generations, early, late and non-parthenocarpy were observed. Chi-square values for segregation of parthenocarpy in the F_2 and backcrossed populations agreed with the expected ratio of 1:2:1 and 1:1, respectively. Therefore, the genotypes

Table 1. Segregation for parthenocarpic fruiting in cucumber.

Entry	Genotype	Number of plants	Fruiting habit: Early parthenocarpy[z] (*PP*) Observed	Early parthenocarpy[z] (*PP*) Expected	Late parthenocarpy[y] (*Pp*) Observed	Late parthenocarpy[y] (*Pp*) Expected	Non-parthenocarpy (*pp*) Observed	Non-parthenocarpy (*pp*) Expected	x^2	P
Pandex(A)	*pp*	40	40	40	0	0	0	0	0	
Khira (B)	*pp* ×	20	0	0	0	0	20	20	0	
F_1(B × A)	***PP***	40	2	0	37	40	1	0	0.225	0.5<P<0.75
F_1(A × B)	*PP* × *pp*	18	1:	0	16	18	1	0	0.222	0.5<P<0.75
F_2(B × A)	***pp x P P***	46		11.5	26	23	9	11.5	0.956	0.5<P<0.75
BC_1(B x A) x A	*Pp* × *PP*	39	21	19.5	18	19.5	0	0	0.230	0.5<P<0.75
BC_1 B x (B x A)	*pp* × *Pp*	18	0	0	10	9	8	9	0.222	0.5<P<0.75

[z] Parthenocarpic fruit development from the 1st to 7th node. [y] Parthenocarpic fruit development at the 8th and above nodes.

Table 2. Number of fruits and range of nodes at which parthenocarpic fruits were produced.

Entry	Range of 1st fruiting node *PP*	Range of 1st fruiting node *Pp*	Average node of 1st fruiting *PP*	Average node of 1st fruiting *Pp*	Range of fruit No. *PP*	Range of fruit No. *Pp*	Average No. of fruits *PP*	Average No. of fruits *Pp*
F_1(B × A)	-	8-20		16.48±3.31[z]		1-5		2.51±1.20
F_1(A × B)	-	9-17		14.29±2.54		1-5		2.35fl.03
F_2(B × A)	8-19	5.55±1.50	13.13f3.33		2-6	2-5	3.54±1.44	2.64il.13
BC_1(B x A) x A	3-7	7-19 5.05±0.64	9.53k3.65		2-7	1-6	3.45±1.53	3.29i1.27
BC_1 B x (B x A)	4-6	9-20 -		17.09±3.53	-	*1-3*		*1.7320.62*

A:'Pandex', B:'Khira,' [z]Means±SD.

for parthenocarpy, non-parthenocarpy and late parthenocarpy were determined as *PP*, *pp* and *Pp*, respectively.

These data reinforce that parthenocarpic trait in cucumber is controlled by single incompletely dominant gene, as suggested by Pike and Peterson (1969). They used a parthenocarpic monoecious cultivar and a non-parthenocarpic gynoecious line as parents, whereas our materials were gynoecious parthenocarpic and monoecious non -parthenocarpic cultivars.

Average first fruiting node in segregated generation was observed at the 5th in homozygous plants and at the 10th to 17th in heterozygous plants (Table 2). The homozygous plants produced larger number of fruits than the heterozygous plants. Rudish et *al.* (1977) also suggested that the degree or intensity of parthenocarpy could be measured by both the earliness of fruiting and the total number of parthenocarpic fruits.

Role of endogenous IAA and ABA in parthenocarpy

Fresh weight of the ovary throughout the early fruit set period is shown in Fig. 1. In 'Pandex', the increase in ovary weight was similar in all the treatments. In 'Khira' and F_1, however, the unpollinated ovaries lost their growth activity after anthesis. Threr were no significant difference of weight between pollinated and 4-CPA treated ovaries in all the genotypes.

Content of IAA in the unpollinated ovaries of 'Pandex' reached a maximum peak at anthesis, then declined gradually (Fig. 2). In the F_1, a similar changing pattern of IAA was observed, but the content was less than 50 % of that in 'Pandex'. Parthenocarpy occurred only on the upper nodes in the F_1, and the ovaries at the 7th to 25th nodes were collected for IAA analysis irrespective of parthenocarpy. These might be the reason for low IAA content in the F,. Content of IAA in the ovaries of 'Khira' one day before anthesis was almost the same as that of 'Pandex', but did not increase at anthesis.

It appears that the high IAA content of parthenocarpic 'Pandex' ovaries induced fruit set without pollination. For non-parthenocarpic 'Khira', on the contrary, pollination is essential for further fruit development because the IAA content of the ovary probably does not reach the optimum level before pollen tube penetration. These results thus suggest that the occurrence of parthenocarpy in cucumber might be controlled by the genetic factor (P^-) producing a high amount of IAA in the ovaries at anthesis. This hypothesis is supported by the results that the IAA content was higher in the ovaries on the upper nodes than in those on the lower nodes in the F_1 plants (Kim et al., 1991). Mapelli et al. (1978) also reported that auxin concentration in tomato at anthesis was about three times higher in the ovary of the parthenocarpic line than in the non-parthenocarpic line. Similar observations have been reported in guava (Nagar and Raja Rao, 1983), fig (Lodhi et *al.*, 1969) and clementine mandarin (Garcia-Papi and Garcia-Martinez, 1984).

Pollination caused an increase of IAA content in all the genotypes. The first peak was observed one day after pollination in 'Khira' and F_1, while it was two days after pollination in 'Pandex'. Pollen tube growth and the developing seeds have been recognized as the center for the production of growth-promoting substances needed for fruit development (Nitsch, 1950). Therefore, it is reasonable to assume that the increase of

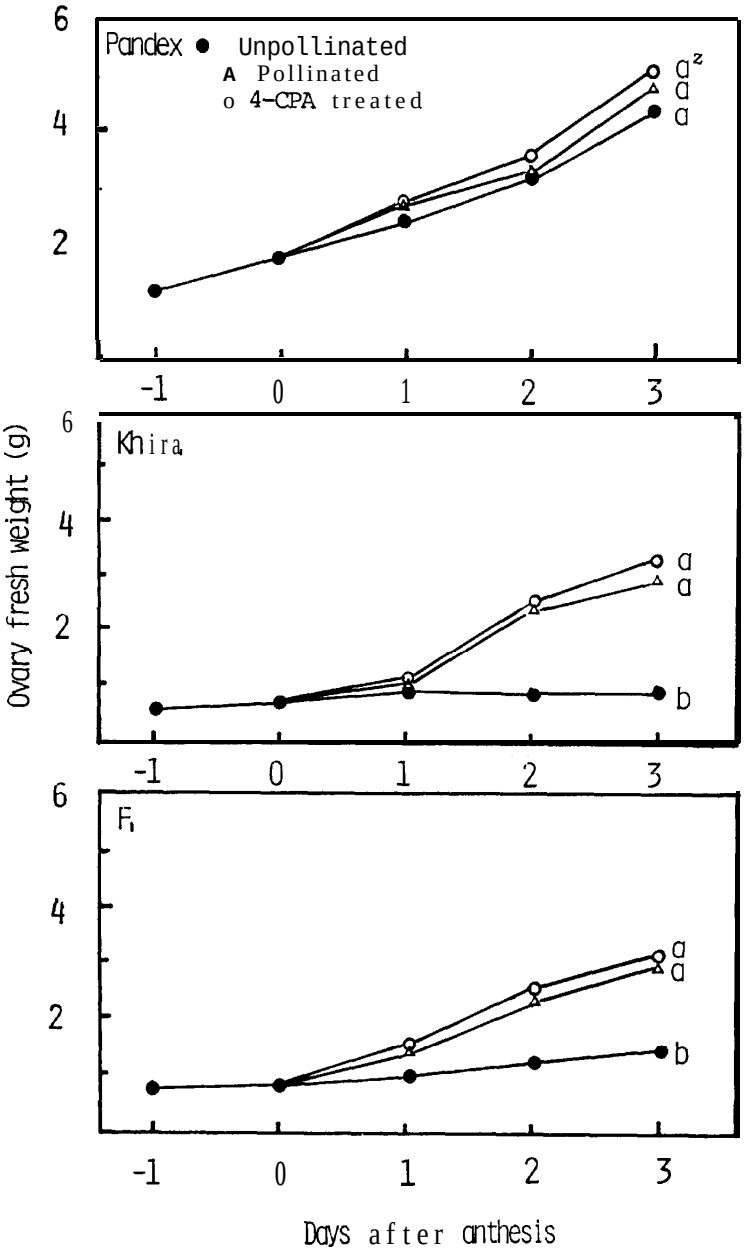

Fig. 1. Effect of pollination, unpollination or 4-CPA treatment on fresh weight of cucumber ovaries. 'Mean separation within treatments by Duncan's multiple range test, 5% level.

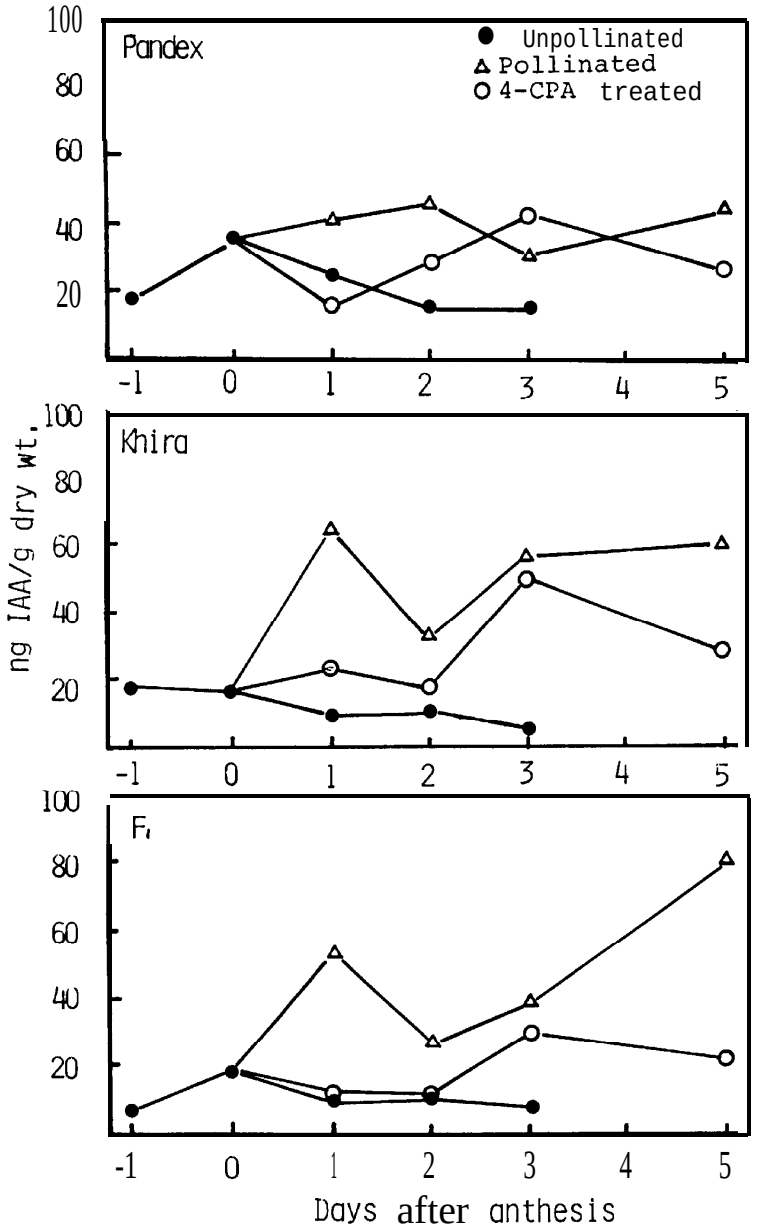

Fig. 2. Changes in IAA content in cucumber ovaries.

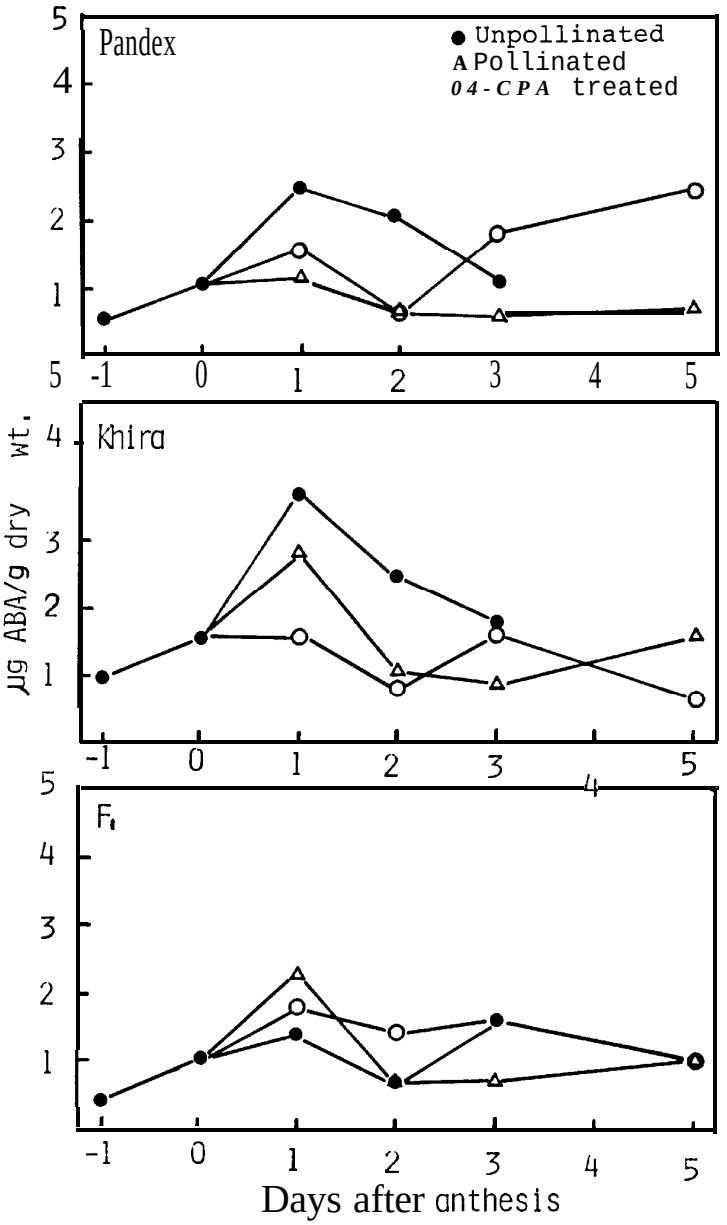

Fig. 3. Changes in ABA content in cucumber ovaries.

IAA content in cucumber ovaries following pollination might have associated with the presence of pollen tubes. In cucumber, histological examinations showed that pollen tubes penetrated beyond the base of the style into the ovary 12 hr after pollination, and accomplished fertilization 30 to 36 hr after pollination (Fuller and Leopold, 1975). Similar patterns of auxin-like activity with fertilization and endosperm development were demonstrated in other works (Luckwill, 1948; Murneek, 1952; Lund, 1956).

In 4-CPA treated ovaries, the IAA content reached the highest level three days after treatment and decreased thereafter in all the genotypes. But it was considerably low in comparison with the content in the pollinated ovaries, the exception being at three days after pollination in 'Pandex', although no significant difference in fruit size was observed (Fig. 1). Sjut and Bangerth (1981) also reported that 4-CPA treated parthenocarpic tomato fruit contained less extractable IAA than pollinated fruit.

As shown in Fig. 3, ABA levels in pollinated and unpollinated ovaries increased until one day after anthesis, and declined thereafter. Unpollinated ovaries contained higher ABA levels than pollinated ones both in 'Pandex' and 'Khira', and the ABA content was not significant in all the genotypes treated with 4-CPA. The changes of ABA, however, did not show clear relation to the parthenocarpic fruit set in cucumber.

The results of the present study show that genetic factor for parthenocarpy in cucumber may be associated with high content of IAA in the ovaries at anthesis, but probably not with the changes of ABA.

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