Studies on the Flower Initiation in *Pharbitis* Seedlings II. Influences of Gamma-ray Irradiation

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Abstract

In the present experiment, it was found that *Pharbitis* plant is very radio-sensitive in the early stage, especially for initiation and development of flower primordia. At the irradiation doses below 1000 R, especially those ranging from 450 to 660 R, gamma-rays inhibited the flower initiation considerably. On the other hand, the growth of seedlings were scarcely affected. Furthermore, acute irradiations with low doses of gamma-rays (below 330 R) promoted the flower initiation, when the seedlings were irradiated before a single flower-inductive dark period.

The influence of gamma-rays on the flower initiation was different depending mainly on the time when the seedlings were irradiated: the reversion of flower-buds to vegetative ones, and the appearance of various malformed types of flower-buds were observed. And a definite relationship between the occurrence of the malformation and the time of irradiation was found.

Introduction

The detailed observations of the initiation of flower primordia in the *Pharbitis* seedlings indicated that bract primordia appeared three to four days after the end of a 16-hour dark period at the second or the third axillary bud^{1,2)}. In the previous paper³⁾, it was shown that the inductive amount of flowering stimulus had arrived at the plumule 14-16 hours after the start of the dark period. Although no visible morphological changes are observed during the first three to four days, certain cryptic changes accompanied by cell multiplication should have occurred in this period (Wada, unpublished).

It is a well-known fact that cell multiplication is affected, either directly or indirectly, by ionizing radiations, and that the meristem, vigorously dividing tissue, is the most radio-sensitive tissue⁴⁾. Since the beginning of the twentieth century, many morphological investigations on plants exposed to ionizing radiations have been carried out. Attention has also paid to the influences of ionizing radiations on flower development⁵⁻¹²⁾. However, little is known about the effects of ionizing radiations on the initiation and development of flower primordia in the seedling.

In order to analyze the early stage of the initiation and development of flower primordia in the *Pharbitis* seedlings, the present experiment was carried out by irradiating the seedlings with acute gamma-rays at different ages, i. e., before and after the flower-inductive dark period.

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Material and Methods

The material used was the Japanese morning glory, *Pharbitis nil* Chois., strain VIOLET. All experiments were performed with the seedlings, photoperiodic behaviours of which were reported by Kujirai and Imamura¹³⁾. And the procedures of the experiments were similar to those already described^{2,3)}.

Gamma-ray irradiation was performed at the Radiochemistry Research Laboratory of Shizuoka University. A gamma-ray source was about 1 k Ci of Cobalt-60. The distribution of the dose intensity around the source and some other characteristics of the source were estimated by Hasegawa¹⁴⁾. The details of the radiation treatments will be described in the Tables referred to in the following sections.

Results and Discussion

1) *Growth and flowering of the seedlings irradiated with varying dosages of gamma-rays*: Five to six days after the H_2SO_4 -treatment the seedlings were subjected to a single 16-hour dark period. At the end of the dark period they were exposed to varying doses of gamma-rays at the same dose rate of 340 R per minute for different lengths of time; 0, 2500, 5000, 10000, and 15000 R.

As shown in Fig. 1 and Table 1, the acute gamma-irradiations with higher dosages severely affected not only the growth of plumule and cotyledons, but also flower initiation. When the seedlings were exposed to 2500 R of gamma-ray, all buds, terminal and axillary, which were present at the time of irradiation, died, and later subsidiary buds developed. The leaf primordia, which were present at the time of irradiation, survived, and developed into abnormal leaves. The margins of these three or four leaves became irregular, and the leaf-blades became variegated with a number of small white dots due to chlorophyll-deficiency. Flower initiation was destroyed in all lots irradiated with dosages over 2500 R.

Tables 2 and 3 show that the seedlings exposed to lower dosages than 2600 R continued to grow to some extent. When the seedlings were irradiated with 2600 R of gamma-ray, the growth of stem and hypocotyl was depressed slightly, but with 1300 R or less there was no difference in appearance between the lots of irradiated

Fig. 1. *Pharbitis nil*, "VIOLET" exposed to gamma-ray at the seedling stage. From left to right, the plants received 0 R, 2500 R, 5000 R, 10000 R, and 15000 R acute gamma-ray.

Table 1. A summarized description of morphological observations of the plants exposed to various dosages of gamma-rays.

Dosage of gamma-ray	Dead plants	Morphological observations			
		Dead cotyledons	Chlorosis in cotyledon	Plumule growth	Flowering
0 R	Non	Non	Non	Normal	*
2,500 R	Non	Non	Partially	Abnormal	C. I.**
5,000 R	Non	Non	Almost	No growth, but alive	C. I.**
10,000 R	A part	Almost all	Whole	Completely inhibited	C. I.**
15,000 R	All	All	Early occurred	Lethal	C. I.**

Seedlings of six-day old were subjected to a 16-hour dark period at the end of which they were exposed to various dosages of gamma-rays, and grown in greenhouse under continuous illumination for 50 days before observation.

....* In this experiment seedlings in the control lot were not subjected to a 16-hour dark period.

C. I.** Completely inhibited.

Fig. 2. *Pharbitis* plants received acute gamma-rays (650 R) at the seedling stage. B and D were exposed to gamma-rays before and after a 16-hour dark period, respectively. A and C were not exposed to gamma-rays. A, control plants grown under continuous illumination; C, flower-induced plants.

seedlings and non-irradiated ones (Table 2, Table 3-b, and Fig. 2). Flowering feature, however, was affected strikingly: e. g., in the seedlings irradiated with 1300 R the flowering percentage was as low as 5.0%, while that of the control plants as high as 45% up to 100% (Table 2-a). The flowering was suppressed to some extent (64%) even by the dosage of 330 R (Table 3-a). Both growth and flowering were slightly promoted by gamma-rays below 330 R, though the data are not shown here. Such enhancement caused by low dose gamma-rays will be described in later paper coupled with X-irradiation experiments.

2) *Relation between gamma-ray irradiation and shoot apex age*: It was shown in the previous paper²⁾ that the advancement of shoot apex age, a numerical indicator of shoot development, was accelerated by flower-inductive dark treatment. In the present experiments, the effect of gamma-ray irradiation on the advancement of shoot apex age was examined in relation to flower initiation.

Seedlings were subjected to a single dark period of 16 hours and irradiated with gamma-rays immediately, 11 hours, and 24 hours, respectively, after the end of the dark period. Shoot apex ages at the terminal and the axillary buds were examined about two weeks after the dark treatment (Table 4). Without the irradiation, a

single 16-hour dark period greatly advanced the shoot apex ages of terminal and axillary buds. But gamma-ray irradiation given within 24 hours after the 16-hour dark period depressed the advancement of the shoot apex ages to the same level as those in the control seedlings which were illuminated continuously. On the other hand, the shoot apex ages in the seedlings which were subjected to continuous illumination were scarcely affected by gamma-ray irradiations (660–1300 R). Similar results are shown in Table 5. These facts indicate that an acute gamma-ray irradiation nullified the effect of a single 16-hour dark period on the advancement of shoot apex age, though the elongation of seedlings was not affected by the irradiation.

3) *Effect of gamma-ray irradiation given at different times*: Table 6 shows the results when *Pharbitis* seedlings were exposed to gamma-rays (660 R) at different times before or after a flower-inductive dark period. Application of an acute gamma-ray (660 R) before a single 16-hour dark period lowered the flowering percentage slightly (see total FL% in Table 6). When the gamma-rays were given after the dark period, however, flower initiation was strongly inhibited. The greatest inhibition was observed when gamma-ray irradiation was applied immediately or 8 hours after the end of a 16-hour dark period. It is interesting that flower initiation from the second to the fourth axillary buds was inhibited by gamma-ray irradiation applied 24 and 8 hours before the dark period, but flower initiation at the fifth axillary bud and terminal

Table 2. Influences of gamma-rays given at various dosages on flower initiation and stem elongation of *Pharbitis nil* (The seedlings were irradiated immediately after a 16-hour dark period).

a. Flowering percentages in axillary and terminal buds.

Dosage	Continuous illumination	A 16 ^h dark period		
	0 R	0 R	1,300 R	2,600 R
Axillary bud				
1st	0	45.0	0	0
2nd	0	100.0	5.0	0
3rd	0	76.2	0	0
Terminal bud	0	47.6	0	0

b. Lengths of stem internode and hypocotyl (cm).

Dosage	Continuous illumination	A 16 ^h dark period		
	0 R	0 R	1,300 R	2,600 R
Hypocotyl	11.9	11.1	11.8	10.5
1st internode	6.4	6.1	6.9	4.8
2nd internode	5.3	7.4	5.8	2.1
3rd internode	5.8	7.4	5.3	1.9
Plants observed	18	21	20	34

Growth condition: Air-conditioned room kept at 30° and illuminated continuously with artificial light.

Gamma-rays: 100 R/min × 13 min = 1,300 R

100 R/min × 26 min = 2,600 R

bud was promoted. This implies that the buds responded differently to flowering stimulus and to gamma-ray irradiation according to their physiological ages.

No external-morphological changes were observed during the first three to four days after the end of a flower-inductive dark period. To study the effect of gamma-ray irradiation given during this early stage, an acute gamma-ray (660 R) was given at the beginning or 0, 24, 48, 72, 102, or 120 hours after the end of a single 16-hour dark period (Tables 7 and 8).

Total flowering percentages in Table 7 show that the flower initiation was inhibited as a whole by the gamma-ray irradiation which was given at the beginning or within 24 hours after the end of the dark period. Here, it must be noted that the response to irradiation differs in each bud. As shown in Fig. 6 of the previous paper²⁾, it was found that the initiation and development of flower primordia of the first, the second, the third, and the fourth axillary buds take place one after another

Table 3. Influence of various dosages of gamma-rays on flower initiation and stem elongation of *Pharbitis nil* (Plants were irradiated 24 hours after the end of a 16-hour dark period).

a. Flowering percentages in axillary and terminal buds.

Dosage	0 R		330 R		660 R		1, 215 R	
	CL*	16 ^h d**	CL*	16 ^h d**	CL*	16 ^h d**	CL*	16 ^h d**
Axillary bud								
1st	0	95.0	...	4.0	0	3.3	0	0
2nd	0	95.0	...	28.0	0	20.3	0	0
3rd	0	90.0	...	20.0	0	3.3	0	0
4th	0	60.0	...	8.0	0	6.7	0	0
Terminal bud	0	95.0	...	40.0	0	33.3	0	0
Total FL %	0	95.0	...	64.0	0	36.7	0	0

b. Stem elongation (cm).

Dosage	0 R		330 R		660 R		1, 215 R	
	CL*	16 ^h d**	CL*	16 ^h d**	CL*	16 ^h d**	CL*	16 ^h d**
Hypocotyl	11.5	10.4	...	10.1	11.0	11.1	10.7	10.4
1st internode	8.3	8.8	...	8.2	8.8	8.8	7.3	7.4
2nd internode	9.3	11.3	...	10.0	9.6	9.9	7.0	8.2
3rd internode	9.0	12.0	...	13.4	11.5	10.3	7.6	8.2
Total length	38.1	42.5	...	41.7	40.9	40.1	32.6	34.2
±	±	±	...	±	±	±	±	±
Standard error	0.88	1.16	...	1.07	0.86	0.76	0.68	0.62
No. of plants observed	30	20	...	25	30	30	30	30

Gamma-rays : 44 R/min × 7.5 min = 330 R
 44 R/min × 15 min = 660 R
 81 R/min × 15 min = 1,215 R

* Continuous illumination
** A 16-hour dark period

at fairly regular intervals of 24-31 hours. In the present experiment (Table 7), maximum inhibition of flower initiation in each axillary bud also occurred over a time-interval of about 24 hours. Minimum values of flowering percentages in each axillary bud were underlined in Table 7. Thus, at a certain developmental stage the axillary flower bud seems to be very sensitive to gamma-ray irradiation. Even the

Table 4. Influences of gamma-ray irradiation on shoot apex age (I).

(Experiment 1)		Continuous illumination		A singl 16-hour dark period	
		Non-irradiated		Irradiated immediately after the end of a 16 ^{hd} **	
		0 R		0 R 1300 R 2600 R	
Axillary bud					
1st		13		20	11 6
2nd		14		27	14 3
3rd		11		24	11 3
Terminal bud		32		37	33 8

(Experiment 2)		Non-irradiated		Irradiated 24 ^h after the end of a 16 ^{hd} **					
		0 R		330 R		660 R		1215 R	
		CL*	16 ^{hd} **	CL*	16 ^{hd} **	CL*	16 ^{hd} **	CL*	16 ^{hd} **
Axillary bud									
1st		15	26	...	18	12	9	8	4
2nd		14	27	...	23	14	18	8	8
3rd		13	26	...	18	14	15	12	12
4th		10	21	...	14	11	13	11	12
Terminal bud		34	45	...	44	36	41	35	46

(Experiment 3)		Non-irradiated		Irradiated (660 R)			
				11 ^h after the end of a 16 ^{hd} **		24 ^h after the end of a 16 ^{hd} **	
		CL*	16 ^{hd} **	CL*	16 ^{hd} **	CL*	16 ^{hd} **
Axillary bud							
1st		15	26	13	13	12	9
2nd		14	27	14	17	14	18
3rd		13	26	14	16	14	15
4th		10	21	11	13	11	13
Terminal bud		34	45	37	38	36	41

* Continuous illumination.

** A single 16-hour dark period.

gamma-ray irradiation given at the beginning of the inductive dark period was very inhibitory for flower initiation at the first axillary bud (Table 7). This suggests that the gamma-ray irradiation produces some effects which make the apical meristem incapable of responding to flowering stimulus. As gamma-ray irradiation inhibits cell division, it is highly probable that this effect is due to the low activity of irradiated apical meristem.

As to the terminal bud, the position of the node at which the terminal flower was initiated was used as a measure of readiness to enter into the reproductive phase. We may assume that the earlier the terminal flower bud appeared, the more rapidly the plant responded to flowering stimulus. The position of the terminal flower bud was indicated by the average node-numbers in Table 7. The average node-number was largest in the seedlings irradiated with gamma-ray 24 hours after the end of a

Table 5. Influence of gamma-ray irradiation (700 R) on shoot apex age (II).
(Mean $\pm$ Standard error)

Position of bud	Non-irradiated	Irradiated	
	Control	at the middle of a 16 ^h d**	4 ^h after the end of a 16 ^h d**
	CL* (30)	CL* (30)	CL* (30)
Axillary bud			
1st	12.9 $\pm$ 0.23	11.8 $\pm$ 0.25	11.6 $\pm$ 0.57
2nd	14.7 $\pm$ 0.32	13.6 $\pm$ 0.32	13.2 $\pm$ 0.22
3rd	14.4 $\pm$ 0.32	14.8 $\pm$ 0.43	14.2 $\pm$ 0.34
4th	12.4 $\pm$ 0.29	11.4 $\pm$ 0.22	12.1 $\pm$ 0.21
Terminal bud	36.9 $\pm$ 0.49	36.4 $\pm$ 0.32	37.9 $\pm$ 0.34

The numbers of plants observed are indicated in parentheses.

* Continuous illumination.

** A single 16-hour dark period.

Table 6. Flowering response of *Pharbitis* seedlings exposed to gamma-rays (44 R/min $\times$ 15 min = 660 R) at different times before and after a flower-inductive 16-hour dark period (I).

Position of buds	Flowering percentage (FL%)						
	Non-irradiated control	Time of irradiation after the beginning of a 16-hour dark period					
		−24h	−8h	0h	+16h	+24h	+40h
Axillary bud							
1st	0	0	0	0	0	0	0
2nd	43.3	10.0	16.7	66.7	9.5	6.7	30.0
3rd	96.7	86.7	63.3	16.7	0	0	16.7
4th	36.7	26.7	23.3	0	0	0	0
5th	0	13.3	13.3	0	0	0	0
Terminal bud	0	53.3	30.0	0	0	0	0
Total FL%	100.0	86.7	70.0	76.7	9.5	6.7	46.7
No. of plants observed	30	30	30	30	21	30	30

16-hour dark period. The above-mentioned results are interest in relation to the following fact: Wada¹⁵⁾ found that the number of mitotic figures at the flower-induced shoot apex of terminal bud begins to increase 24 hours after the end of a 16- or 24-hour dark period as compared to that at non-induced apex.

Some interesting observations were made in the experiments mentioned above; various types of abnormalities of flowers were observed (Table 8). Fig. 3 shows the abortive flower bud having two to four bract-like leaves without any other floral organs, or abnormal flower buds which have normal floral organs but three to four bracts. As shown in Table 8, when a gamma-ray irradiation (660 R) was applied 24, 48 or 72 hours after the end of the dark period, the abortive flower buds were observed most frequently in the second, the third, and the fourth axillary buds, respectively.

The abnormal flower buds with three to four bracts were observed mainly in the second and the third axillary buds when gamma-ray treatment was given to two

Table 7. Flowering response of *Pharbitis* seedlings exposed to gamma-ray (660 R) at different times before and after an inductive 16-hour dark period (II).

Flowering percentage** (FL %)	Non-irradiated		Irradiated (660 R=44 R/min×15 min)						
	Continuous illumination	16 ^h d*	Before 16 ^h d*		After 16 ^h d*				
			0h	0h	24h	48h	72h	102h	120h
Axillary bud									
1st	0	80.7	0	0	3.3	16.7	33.3	13.3	75.0
2nd	0	100.0	56.7	57.7	26.7	96.7	100.0	100.0	100.0
3rd	0	100.0	93.3	80.8	56.7	55.7	46.7	100.0	100.0
4th	0	100.0	90.0	63.6	50.0	40.0	6.7	53.3	100.0
Terminal bud	0	100.0	86.7	48.0	66.7	93.3	50.0	46.7	100.0
Total FL %	0	100.0	96.7	88.0	83.3	100.0	100.0	100.0	100.0
No. of plants	30	27	30	25	30	30	30	30	12
Position of terminal flower buds	Non-irradiated		Irradiated (660 R=44 R/min×15 min)						
	Continuous illumination	16 ^h d*	Before 16 ^h d*		After 16 ^h d*				
			0h	0h	24h	48h	72h	102h	120h
5th node	...	19/27	5/26	1/12	...	8/28	4/15	1/14	6/12
6th node	...	8/27	16/26	6/12	4/20	13/28	6/15	10/14	6/12
7th node	...	...	5/26	4/12	10/20	5/28	5/15	2/14	...
8th node	...	...	...	1/12	6/20	1/28	...	1/14	...
9th node	...	...	...	...	...	1/28	...	...	...
Av. node number of terminal flowers	...	5.3	6.0	6.4	7.1	6.1	6.1	6.2	5.5

* A single 16-hour dark period.

Numerator: number of terminal flower buds at each node.

Denominator: number of terminal flower buds.

** Abnormal flower buds having 3-4 bracts and other floral organs were included in flowering percentages, but abortive flower buds which have 1-4 bracts and no other floral organs were excluded (cf. Table 8).

groups of seedlings 48 and 72 hours respectively, after the dark period.

The reversal of the buds, which were once flower-induced, to the vegetative types was also observed, especially in terminal buds. As shown in Fig. 4, some plants developed only bracts but no other floral organs, and returned again to the vegetative phase. Such reversal was caused by gamma-ray irradiation given earlier than the stages at which gamma-rays induced abortive or malformed flower buds; e. g., by gamma-ray irradiation applied from 0 to 24 hours after a 16-hour dark period in the third axillary buds, and 24 hours after the dark period in terminal buds (Table 9). The above-mentioned results will be summarized diagrammatically in the continued paper.

Fig. 3. Various types of abnormal flowers in axillary buds of seedlings exposed to gamma-rays (660 R). A, normal flower bud; B-E, abortive flower buds having 1-4 bract-like leaves; F and G, abnormal flower buds having 3-4 bracts with other normal floral organs.

Table 8. Flowering response of *Pharbitis* seedlings exposed to gamma-ray (660 R) at different times before and after an inductive 16-hour dark period (III).

Percentage of abortive flower buds having only 1-4 bracts (per total plants)									
Non-irradiated			Irradiated (660 R=44 R/min×15 min)						
Continuous illumination	16hd*		Before 0h	16hd* 0h	24h	After 48h	16hd* 72h	102h	120h
Axillary buds									
1st	0	0	0	4	7	3	0	0	0
2nd	0	0	0	8	70	3	0	0	0
3rd	0	0	0	0	3	30	17	0	0
4th	0	0	0	0	0	0	7	3	0

Percentage of abnormal flower buds having 3-4 bracts and other normal floral organs (per plants)									
Non-irradiated			Irradiated (660 R=44 R/min×15 min)						
Continuous illumination	16hd*		Before 0h	16hd* 0h	24h	After 48h	16hd* 72h	102h	120h
Axillary buds									
1st	0	0	0	4	0	0	0	0	0
2nd	0	0	0	0	0	50	10	0	0
3rd	0	0	0	0	0	10	27	3	0
4th	0	0	0	0	0	0	0	0	0
No. of plants observed	30	27	30	25	30	30	30	30	12

* A single 16-hour dark period.

Table 9. Reversal of the buds, which were once flower-induced, to vegetative ones.

	Non-irradiated			Time of irradiation after a 16-hour dark period			
	Control			0h	12h		24h
	0 R	500 R	1000 R	500 R	1000 R	500 R	1000 R
Axillary bud							
1st	0	0	0	0	0	0	0
2nd	0	0	0	0	1/20	0	1/25
3rd	0	2/15	1/24	1/18	3/20	0	1/25
4th	0	0	0	0	0	0	0
Terminal bud	0	0	0	0	0	1/18	3/25

Gamma-rays: 500 R=44. 3 R/min×11 min

1000 R=44. 3 R/min×23 min

Numerator: Number of buds which were flower-induced but reversed to vegetative shoot.

Denominator: Number of buds observed.

The seedlings in each lot were flower-induced by a single 16-hour dark periop.

Fig. 4. Reversal of *Pharbitis* shoots from reproductive phase to vegetative one. From left to right, 1) the reproductive shoot developed from flower-induced but non-irradiated seedling, 2) flower-induced and irradiated with an acute X-ray (645 R) 12 hours after a 16-hour dark period, 3) similar shoot reversed from reproductive phase to vegetative one, 4) non-flower-induced and non-irradiated control.

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摘 要

和田清美：アサガオの花芽分化についての研究 II.

ガンマー線照射の影響

アサガオ（紫）の芽ばえを用い、花芽分化にたいする電離放射線の影響をしらべる一連の研究の一部として、コバルト 60（約 1 キロ Ci）よりのガンマー線を用いて実験をおこなった。照射は長期にわたる緩照射（chronic irradiation）はおこなわず、短時間の急照射（acute irradiation）のみとした。尚、照射は幼植物全体にたいするもので、その線量は幼芽の位置で測定した。

結果は次のようであった。1) このアサガオは、花芽分化に関してとくに放射線感受性が高い。すなわち、1000 R 以上の線量では勿論、450～660 R の範囲の線量で花芽分化は甚大な影響を受ける。一方、同一線量で茎の伸長、葉芽での葉原基形成はほとんど影響を受けなかった。2) 低線量（300 R 以下）を、花成誘導に必要な暗期前に照射した場合、幼芽に存在する各腋芽および頂芽で花芽分化の促進・抑制がみられた。このことは、前報²⁾で報告したごとく、幼芽に存在するそれぞれの生長点分裂組織の生理的令（physiological age）に差異があることをはっきりと示す。この差は、暗期後の照射の場合にもはっきりと示された。3) 花成誘導に必要な暗期の前後（24 時間前から 120 時間後まで）のいろいろな時間に短かい照射をおこなったところ、その時期により、(a) 一旦花芽分化を開始したが再び葉芽へと完全に逆戻りする。(b) 一對の苞葉だけが形成されたのち葉芽へ逆戻りする。(c) 3-4 枚の苞葉に似た形態の葉が形成され、それ以外の花葉はすべて欠損する。(d) 苞葉が 3-4 枚のほかは、正常な花芽といったように、いろいろな奇形花芽が生じた。これらの奇形花芽の発生とガンマー線照射の時期とを合わせ考えることにより、暗期後での花芽分化の初期段階（暗期開始後 14-16 時間から 3-4 日までの期間）をその放射線感受性の差によって細分することができる。この点についての詳細は、X 線についての続報および X 線とガンマー線の局部照射についての続々報で報告する。（静岡大学理学部生物学教室）