Genetic Studies on *Cosmos bipinnatus*.

II. Further Studies on the Inheritance of Flower Types.*

Yoshihiko SAMATA

(Faculty of Agriculture, University of Tokyo)

1. Introduction

In the previous paper (Jap. J. Breeding., 8(2)), the present writer classified the flower-types of cosmos into the following four groups. —Single type (S type), Malformed type (M type), Double type (D type) and Malform-double mixed type (MD type), accompanied with genetic analyses of each of them. The important facts revealed by this study may be summed up as follows: (1) the Single and Non-petaled type are genetically fixed. (2) the Sub-petaled type (Ms type) seems to be the intermediate type between S and Np types. (3) the Tubular-petaled type (Mt type) and Vestigial-petaled type (Vt type) are different from Np type according to the number of modifiers. (4) Double flower-heads are usually represented by the genotype which has the single and the double factor in heterozygous condition. (5) The different degrees of doubleness may be caused by the different number of modifiers added to a major gene of doubleness.

Various combinations of crossings among these flower types, especially those between S and Np, and D and Np and the segregations of their following progenies were further examined in details, and the results of the investigation are reported in this paper. At the end of this paper, the genotypes for each of the flower types are postulated, so that each experimental result may be explained without contradiction.

2. Materials and Methods

The materials used and the methods adopted are the same as reported in the previous paper so that the treatments concerning these items are omitted in this paper.

3. Experimental Results.

1. Segregation of offsprings of the crosses $Np \times S$

In the preceding paper it was reported that the single and the non-petaled type may be both homozygous, yet differ from each other by the gene controlling the flower type. In order to determine the genetic relation between these two types, a fairly large number of crosses between them and the segregations of some of their F_1 , F_2 , F_3 , and back-cross generations were examined.

(a) Segregation of F_1 generations of the crosses $Np \times S$ From crosses of S with Np from homozygous lines, there appeared a total of 23 F_1 generations containing 389 individuals. The resultant offsprings strongly resembled the single type with some of Ms and slightly doubled types.

From the results of F_1 generations it may therefore be concluded that the single type completely or incompletely dominates over the non-petaled type, and that when the dominance is incomplete, Ms type may be represented as the intermediate type. Examination of Table 1 reveals that when the early-flowering varieties with large flower-heads were the single parents, the number of Ms types segregated was smaller than that of the S types in F_1 . If, however, the early-flowering varieties with small flower-heads or

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Table 1. Segregating F_1 generations of the crosses $Np \times S$

No.	Offspring Parent	Ms	S	D'''	D''	D'	Total	Year	No.	Offspring Parent	Ms	S	D'''	D''	D'	Total	Year
1	$Np \times LS$	8		1			9	1953	13	$Np \times ES$	1	5				6	1956
2	$Np \times ES$	1	2	1			4	1953	14	$Np \times ES$		4				4	1957
3	$Np \times S$	6	6				12	1953	15	$Np \times LS$		10				10	1957
4	$Np \times S$		4				4	1954	16	$Np \times ES$		6				6	1957
5	$Np \times S$		8				8	1954	17	$Np \times ES$	5	17				22	1957
6	$Np \times S$		4				4	1954	18	$S \times Np$		27	1	3	1	32	1954
7	$Np \times LW$	39	35				74	1956	19	$ES \times Np$	2	7				9	1954
8	$Np \times ES$	8	82	12			102	1956	20	$S \times Np$	6	6				12	1954
9	$Np \times ES^*$	8	2				10	1956	21	$S \times Np$		7				7	1954
10	$Np \times ES^*$	3	1				4	1956	22	$ES \times Np$	7	13				20	1956
11	$Np \times ES^*$	8	3				11	1956	23	$LS \times Np$			7			7	1956
12	$Np \times ES$	1	11				12	1956		Total	103	260	22	3	1	389	

* Early flowering small flowered types L : Late-flowering types E : Early-flowering types

late-flowering varieties were the single parents, the reverse was usually the case. This fact shows that whether the F_1 generation shows Ms or S type depends upon the genetic conditions of the single parents as well as upon the outward environments of the plants. The fact that slightly doubled flower-heads appeared in this generation seems to suggest that some factors causing doubleness may sometimes be in the Np type. Discussions on this point will appear later on.

(b) Segregation of F_2 generations of the crosses $Np \times S$ 11 results from F_2 generations may be divided into two groups : one showing no segregation of doubled types in the progenies, and the other showing more or less frequent appearances of them. The former group came out from F_1 generations containing no doubled plants, while the latter occurred from F_1 generations which were more or less doubled. As for the first group the numerical proportions of each flower-type in F_2 were examined and monofactorial difference between S group ($S+Ms$) and Np group ($Mt+Vt+Np$) and the dominance of S were confirmed as shown in Table 3.

Table 2. Segregating F_2 generations of the crosses $Np \times S$

No.	Parent	F_1 No.	Offspring F_1 Parent	Np	Vt	Mt	Ms	S	D'''	D''	D'	D	Total	Year
1	$Np \times LS$	5	$S \times S$	8	5		4	33					50	1955
2	$Np \times LS$	4	$S \times S$	16	2			33					51	1955
3	$Np \times ES$	—	$S \times S$	37	24	1	3	231					296	1956
4	$Np \times LS$	7	$S \times Ms$	66	8	12	101	118		2			307	1957
5	$Np \times LS$	1	$Ms \times D'''$	5	6		31	36		24	6	1	109	1954
6	$Np \times ES$	2	S, Ms, D''' (mixed)		1	2	2	12		9	4	3	33	1954
7	$Np \times S$	6	$S \times S$	37	4	1	19	160	9	2	1		233	1955
8	$Np \times ES$	8	$S \times Ms$	18	15	1	13	82	17	11	1	3*	161	1956
9	$Np \times ES$	8	$Ms \times Ms$	11		2	8	25	1				47	1957
10	$Np \times LS$	7	$Ms \times Ms$	59	3	12	68	81	4	1			228	1957
11	$LS \times Np$	23	$D''' \times D'''$	1			1	16	10	16	2	2	48	1957
	Total			258	68	31	250	827	41	65	14	9	1,563	

* MsD type

Table 3. Segregation of the offsprings in F₂ generations having no doubles

No.	Parent	Offsprings	NP	Vt	Mt	Ms	S	D	total	theoret. 3 : 1	χ^2	P	Year
		F ₁ Parent											
1	Np×LS	S×S	8	5		4	33		50	37.5 : 12.5	0.026	0.95~0.50	1955
2	Np×LS	S×S	16	2			33		51	38.25 : 12.75	2.878	0.1 ~0.05	1955
3	Np×ES	S×S	37	24	1	3	231		296	222 : 74	2.594	0.2 ~0.1	1956
4	Np×LS	S×Ms	66	8	12	101	118		305	228.75 : 76.25	1.659	0.2 ~0.1	1957

Table 4. Segregation of the offsprings in F₂ generations having double flower-heads

No.	Parent	Offsprings	NP	Vt	Mt	Ms	S	D'''	D''	D'	D	total	Year
		F ₁ Parent											
1	Np×LS	Ms, D''' mixed	5	6		31	36		24	6	1	109	1954
2	Np×ES	S, Ms, D''', mixed		1	2	2	12		9	4	3	33	1954
3	Np×S	all S	37	4	1	19	160	9	2	1		233	1955
4	Np×ES	S, Ms mixed	18	15	1	13	82	17	11	1	3	161	1957

The segregating percentage of the doubled plants in F₂ was too distributed (from about 5% to about 50%) to ascertain the numerical proportions in comparison with other types. (Table 4). That the different genotypes of F₁ generations were mixed in different ratios in the F₁ crossings, may be the main cause of this high variability of double percentage. It is supposed, however, that some factors influencing the expression of doubleness may exist in Np and exert their influence more or less in F₂ generations as well as in F₁ generations.

This assumption will be largely and perhaps more satisfactorily explained by the results of the following back-cross generations and F₃ generations. In some segregations of F₂ more highly doubled flower-heads were found than in F₁.

(c) **Segregation of offsprings of back-crosses.** segregation of the back-crosses both with recessive and dominant parents were tried and examined and the results are shown in Tables 5 and 6.

Table 5. Segregations of the offsprings of back-crosses with recessive parent

No.	Parent	Offsprings	F ₁ or F ₂ No.	Np	Vt	Mt	Ms	S	D	total	theoret. 1 : 1	χ^2	P
1	(Np×LS)S×Np		6	25	1			32		58	29 : 29	0.621	0.50~0.20
2	(Np×ES)S×Np		4	17	5			24		46	23 : 23	0.087	0.95~0.50
3	(Np×ES)S×Np	3(F ₂)	61	14	3	24	88			190	95 : 95	6.084	0.02~0.01
4	(Np×ES)S×Np	—	33	3		14	58			108	54 : 54	—	—

Table 6. Segregations of the offsprings of back-crosses with dominant parent

No.	Parent	Offsprings	F ₁ No.	Np	Vt	Mt	Ms	S	D'''	D''	D'	D	total	thoret. 1 (D) : 1 (S)	χ^2	P
1	(Np×S)D'''×S		23		1	2	34	10	29	4	1		81	40 : 40	0.800	0.50~0.20
2	(Np×S)S×S		8			1	40	6	11	11	1		70	35 : 35	2.057	0.20~0.10

Though in one case the departure from the 1 : 1 ratio was fairly large as shown in Table 5, monofactorial interpretation between Np group and S group proves to be possible.

Table 6 shows the result of the crossing between the slightly doubled individuals or the apparently single individuals of F₁ generations and the pure single individual from another population. The segregations showed a fairly good instance of the usual 1S : 1D

ratio and a considerably large number of the double were found to possess higher degrees of the original character. This observation points to the fact that the parents selected from F_1 generation, although they were single or slightly doubled in appearance, were heterozygous in double factor as is the case with the common double, yet the expression of doubleness had been more or less inhibited by some factors in F_1 generations. Taking the results of F_1 , F_2 , and back-cross generations of the crosses between S and Np into consideration, there can be little denying that there are two kinds of Np type which are different in genetic constitutions though showing little outside difference. The one has no double factor and is recessive to the single, and the other involves the D factor at least in heterozygous condition. In the latter case the expression of doubleness may be inhibited perhaps by some factors related to the Np type or more probably by [some modifiers accompanying the D factor. These are again confirmed by the segregation of F_3 progenies.

(d) **Segregation of the offsprings in F_3 generations.** The materials for the F_3 generations were not sufficiently plentiful. Various flower types in F_2 generations were selected and the segregating offsprings of intercrosses or of the crosses with other types were counted. The results, which were quite in accordance with the above, are shown in Table 7. The intercrosses of the single types produced the single type only, which means that the singles in F_2 generations in this case had already become homozygous. The intercrosses of the Ms type again yielded 3 single group (S+Ms): 1 Np group (Mt+Vt+Np), which again confirmed that there is a monofactorial scheme between S and Np and that Ms is the intermediate type between the parents. The Np types from the F_2 generations produced exclusively Np types of offsprings in F_3 generations, thus the recessive homozygosity of the Np type can hardly be doubted.

Table 7. Segregations of the offsprings in F_3 generations.

No.	Parent	F_3 offsprings F_2 Parent	F_1 or F_2 No.	Np	Vt	Mt	Ms	S	D'''	D''	D'	D	total	theoret.	χ^2	P	Year
1	Np×LS	S×S	6				1	67					68	all S		1.00	1955
2	Np×LS	S×S	6					188					188	all S		1.00	1955
3	Nd×ES	Ms×Ms	4	31	1	1	57	31					121	3 : 1	0.329	0.95~ 0.50	1957
4	Np×ES	Np×Np	3(F_2)	27									27	all Np		1.00	1957
5	Np×LS	D'''×D'''	6					4	7	1	3	1	16	3 : 1		1.00 0.50~	1955
6	Np×ES	D'×S	2				3	8		1	1	5	18	1 : 1	0.888	0.20	1955
7	Np×ES	D''×S	2					4	1		1	3	9	1 : 1	0.111	0.95~ 0.50	1955

Two differently doubled plants segregated in F_2 generation were crossed with a pure single type and the results showed 1S : 1D relations. In this generation again more highly doubled plants were obtained than in F_1 or F_2 generations. That the degree of doubleness rose higher, and the segregating ratio between S and D came nearer to 1:1 ratio as the generation advanced, seems to favor the assumption that there exists some inhibiting factors for the double in the Np parents and that the power of inhibition grows less and less strong in the course of generations, especially by the backcrosses with the singles which are free from this inhibiting action.

(2) Segregation of offsprings of the crosses D×Np.

The last of my attempts at gene analysis of flower types is of the relation between D and Np. Several highly doubled plants were selected for this purpose from the natural populations and were crossed

Table 8. segregation of offsprings of the crosses D×Np (three segregations summed up)

No.	Parent	Offsprings	Ms	S	D	MsD	total
1	D×Np		14	11	4	20	49

with Np types. The results of 3 F₁ generations are summarized in Table 8.

As expected, the segregating offsprings consisted of four types of flower-heads. As the double is usually heterozygous in S and D factor, it may produce both S and D gametes; and the S gamete, when paired with the Np gamete, may produce either the S or the Ms type according to the environments, while the D gamete paired with Np gamete may yield either D or MD type. The segregation of F₂ generations from Ms [or MsD type intercrosses were experimented and the numerical proportions of the progenies obtained were as given in Table 9.

Table 9. Segregations of offsprings of the crosses D×Np in F₂ generation.

No.	Parent	F_2 Offsprings	F_1 No.	Np	Vt	Mt	Ms	S	D'''	D''	D'	D	total
		F_1 Parent											
1	D $\times$ Np	Ms $\times$ Ms	1	3			8	11					22
2	" "	Ms $\times$ Ms	1	8			23	18					49
3	" "	Ms $\times$ Ms	1	14	1		6	12	9	4			46
4	" "	Ms $\times$ Ms	1	53	6		11	30	32	6	2	1	141
5	" "	Ms $D''' \times MsD'''$	1	6	1		7		1	2			17
6	" "	Ms $D'' \times MsD''$	1	5			4	1	1	1	1		13

An examination of this table will show that in one group the progenies of Ms intercrosses represent the three flower types, Np, Ms and S, to the exclusion of any double. This segregation may be compared with that of F₂ between S and Np involving no double individuals. The Ms parent in this case might have occurred by the pairing of the S gamete of the doubled plant with the Np gamete with no double factor.

If we adopt this assumption, despite the apparent discrepancy in the numerical proportions between the actual and the theoretical, monofactorial scheme may be supported, attributing the deficiency of Np plants to some unknown cause or causes.

In the other group, the progenies of some of the Ms intercrosses or all of the MsD intercrosses are seen to produce a large number of doubles. The double progenies from the Ms intercrosses seem to have originated from the double factor which had been concealed in the Np parent and which might have been again inhibited from expression in the Ms type of the following generation. The fact that the four distinct types were segregated in the F₁ and F₂ generation cannot be explained by the monofactorial scheme, and difactorial theory comes in to help to answer this question. More discussions on this point will be given later.

4. Discussion

In 1937 Dr. WIT, F. who had been studying the inheritance of flower types in the China aster, explained his results by assuming that different genes exist which affect the shape of ray and disk florets respectively. This theory of his seems to adopt very well to explain the results of my experiments.

In the cosmos, as in the China aster two pairs of major genes and some modifiers affecting the shape of flower-heads can be assumed, as seen in the results of my experiments, one pair controlling the development of ray florets, and the other, affecting the development of disk florets. Symbols S-s, are given to the former and D-d to the latter.

Single flower-heads with well developed rays and unlengthened disk florets can be represented as SSdd. Double flower-heads with developed rays and lengthened disk florets as SSDD. Since double plants always set seed by getting pollen from single plants, they should usually be heterozygous as regards D gene. Besides the gene D, other genes might be considered to exist influencing the degrees of doubleness.

Np flower-heads with no rays and unlengthened disk florets can be represented as ssdd

or ssDd. The first genotype is that of Np which did not segregate any doubles in the following generations in the crosses with S and which showed monofactorial difference between the Single type. The second genotype is that of Np which segregated more or less doubles in the following generations of the same crosses. It involves the double factor D, but owing to the inhibiting action of some genes involved in this type, it does

Fig 1. Np and D flower-heads found on the same plant.

not express the double flower-heads and the phenotype usually can not be distinguished from that of Np whose genotype is ssdd. An interesting fact which illustrates this theory is that two phenotypes of Np were observed on the same plant. Among Np progenies, I found two plants some branches of which bore small apparently double flower-heads while the rest of whose branches bore non-petaled flowers. (Fig 1) Strong pinching had been given to these plants just before the time of flower bud initiation.

Competitions among some environmental factors, such as water, nutrients, or the sunlight, might have taken place on the branches which sprouted just after pinching. These environmental differences might certainly have acted upon the inhibiting action of some modifiers in ssDd genotype and on some branches on which double flower-heads appeared, the action of D might be taken to have exceeded the inhibiting power of modifiers on account of environments.

POST, K. reported that the development of ray and disk florets in chrysanthemum are largely influenced by the effect of photoperiod.

OKADA, M. found in zinnia that the doubleness decreases as the day-length becomes shorter.

That the flower types of the Compositae are generally changeable due to the environmental effects, especially to day-length, seems to be beyond doubt. This phenomenon can, of course, be interpreted by the theory of bud mutation, if we assume the occurrence of dominant mutation. Whether a mutation or an environmental change should be determined in the future experiments.

The genotype of Ms may be represented as Ssdd. Owing to the incomplete dominance of S over s, this plant usually has Ms flower-heads, but depending upon environmental and perhaps upon some genetic conditions the same genotype sometimes expresses single flower-heads, as have already been discussed. When the inhibiting action is large enough, SsDd genotype may sometimes have Ms flower-heads in appearance, but when it is small the same genotype represents MD type. It is the phenomena frequently observed in F_1 or F_2 generation of crosses $Np \times S$ and $D \times Np$.

As regards the major gene, Mt and Vt types may have the same genotype as that of Np: ssdd. But the differences in the development of rays may be caused by some modifiers. The possibility of the existence of these modifiers was already suggested in the previous paper but in order to give the numerical foundations to this hypotheses, it must be admitted that the number of progenies observed was insufficiently small.

The different degrees of double flower-heads may also be caused by the presence of some modifiers. The segregating ratios of the progenies of various doubled flower-heads suggest this possibility, but in this case again the available data were so insufficient that we must await further investigations to give any definite word concerning the gene analysis and the numerical relations of the modifiers.

In the above discussion, I have tried to explain the occurrence of various grades of double flower-heads, or the existence of flower types which have the double genotype

with no double expression, by the supposed inhibiting action of modifiers on the major gene D. This can, also, be explained by the supposed existence of modifiers which exert promoting effect on the D gene, supposing the Double genotype with no modifying effect to represent the lowest type of doubleness. Whether inhibitors or intensifiers concern in the phenomenon, I have the decision to my further experiments.

In some segregations the numerical ratio of the offsprings are found to depart from the theoretical. The deficiency or the excess of any one flower-type might be the cause of this departure. Mutability of some genes, different viability of plants or gametes, competition for fertilization among different gametes, — these must be taken into account. I look forward to my further investigations to clarify all these points.

The appearance of abnormal rays or disk florets in the flower-heads seems to be the phenomenon common to the Compositae family. In the chrysanthemum, China aster, marigold, zinnia, sunflower, and several other plants in the Compositae, the malformities of flower-heads as are found in cosmos are often observed. In these cases the parallel mutation of genes concerning the flower-types might possibly be postulated.

KASAWARA, M. reports that the non-petaled type of zinnia is the double recessive type to the commonly petaled.

In 1940 Prof. J. CLAUSEN found in the serpentine soil of California a new variety of plant which in appearance looks like *Layia glandulosa* of the Compositae family, and which, however, is different from *Layia* in that it has no rays and involucres. He made a crossing between these two plants and a large number of F₁ and F₂ plants were brought under his examination. In the F₁ generation the development of rays were markedly inhibited both in length and in number, while in the F₂ generation, the development of rays was found to be more or less inhibited, not only in the degree of development, from the rayless to the fully developed, but also in number, 0, 1, 3, 5, and 8. To account for these results, his suggestion is that there may be one or two pairs of genes in determining the existence of rays and involucres, and that the number and length of rays may be decided by the action of several genes working together. In my treatise similar speculation has been forwarded as to the genetic difference between the commonly rayed and the rayless types of cosmos. The two may be different from each other by one major gene which determines the existence of rays and by several small genes which may influence the development of rays. Though the serpentine plant has no rays, it has the ability of inhibiting the development of the rays and retains the gene which determines the color of rays. Similar facts are also observed in *Cosmos*, and some space was given in the first report of the same author to the discussion that the rayless type has the ability of inhibiting the development of rays.

As the serpentine plant retains the ability of influencing the color of rays of *Layia*, so the rayless cosmos has the ability of expressing ray color peculiar to the variety. Thus the white variety (white being the character of double recessive), when crossed with the rayless type having the ability of color expression, often segregated colored variety in the following generations.

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コスモスの育種学的研究

II. 花型の遺伝について (続報)

佐 俣 淑 彦

コスモスに見られる種々の花型の分類, 及び, 基本的花型である一重型・八重型・無弁型の遺伝的構成については既に前号に報告した。引き続きこれ等花型相互の交雑により次の諸点を明にした。

(1) Np 型と S 型の交配の F_1 , F_2 , F_3 , B_1 等の分離より Np 型に異なつた二つの遺伝子型のある事が推論された。一方は八重の遺伝子を含まず, F_1 で中間型の Ms 型の表現をし, F_2 で両親型を 3:1 に分離をし, 他方は八重遺伝子を含む。この F_1 では他の要素のために八重の表現が抑制されているが, 世代を重ねるにつれ, 次第

に八重の表現率が高められて行く。

(2) Np 型と D 型の後代からも上同様の Np 型に二つの異なつた遺伝子型の存在を暗示する分離が見られた。

(3) 実験結果を総合して, コスモスの花型の表現に関与する遺伝子として, 舌状花の発達と筒状花の発達を支配する別々の遺伝子を想定し, 更にその各々にいくつかの変異遺伝子の働きを付加して考えると, 分離の結果が大体説明出来ることがわかつた。(摘要)

永年作物育種に関する資料

II. 果樹の育種に関する資料 (iv)

倍数体育種法 コルヒチンによる倍数体の誘起は我国ではまとまつた研究は見当らない。外国では梨, 桃, ぶどう, 木苺, ツルコケモモを用いた試験があるが未だ優良品種が作出されないようである。これは倍数個体が必ずしも果樹として優良な形質を備えているとは限らない面もあるが, 一面倍数体育種法が取上げられてからまだ日が浅い為でもある。ぶどう等では果房も果粒も大きくなり種子の abortion も減じて粒揃も良くなるから将来利用できよう。また育成された倍数体がそのまま利用されないでも交雑育種の材料としての利用も考えられるので, 今後はわが国でも腰をすえた試験が望ましい。ツルコケモモの細胞組織学的研究の結果によればコルヒチンで誘起された倍数体は sectorial 又は periolinal キメラになり易く, 処理細胞が mitotic phase 時にのみ有効で, nuclear phase 時には無効である。しかしこの試験では僅かではあるが, total polyploidy も出ている。又倍数体育種は自然にある倍数体の探索及びその育種への利用も研究されており, わが国でも 2~3 の発表がある。

放射線照射による突然変異の誘起 一番新しい問題で果樹の育種にはまだわが国で着手した研究は無い。

カナダの BISHOP, C. J. が第 14 回国際園芸学会で「最初に放射線が突然変異誘起に役立つ事を見出したのは MULLER, H. J. (1927) で相当前の事になる。しかしその直後リンゴ等で行つた初期の試験は顕著な効果が認められず試験は中断していた。これを再興したのはスウェーデンの GUSTAFSSON 等で, 最初穀類に X 線を用いて成功したので 1944 年にリンゴについて研究を始めた。この研究はその後 Balsgard の果樹育種研究所を中心に研究が進められており, 最近リンゴの紅色系枝変わり等も出している。カナダで 1948 年にリンゴ等の X 線照射を行つているが更に 1953 年からアメリカの Brookhaven National Laboratory と共同で熱中性子の照射も開始している。1948 年にドイツで始めた試験は既に 1938 年に始めていた SCHMIDT 等の仕事の復興である。」と経過報告した。これ等の試験はいずれも開始後日も浅い為はまだ最も突然変異の誘起に有利な照射法の探索, 誘起された変異個体の早期発見と分離法等について論じているものが多いので本当の成果は今後待つべきである。現在利用されている放射線は X 線, ガンマ線が主なものであるが, 中性子照射は 2~4 倍の効果を上げると云われている。