

Some Remarks on Fasciation of *Pharbitis Nil*.

By

Yoshitaka Imai and Benso Kanna.

With one Text-figure.

CONTENTS.

	Page.
Introduction	409
Occurrence of temporary fasciation	409
The polymeric genes	410
Crypto-fasciation	413
The non-pear fasciated segregates	414
Summary	417
Literature cited	418

Introduction.

Fasciated strain in the Japanese morning glory, *Pharbitis Nil*, has long been known in Japan, where it was described and pictured about 120 years ago (cf. IMAI 1927). The genetics of fasciation in this plant was investigated by HAGIWARA (1924, 1926), IMAI (1926, 1927, 1930b), and YAMAGUCHI (1926a, 1926b). According to IMAI, this stem abnormality is expressed by three polymeric recessive genes, fasciated-1, fasciated-2, and fasciated-3. The locations of the genes are as follows: both fasciated-1 and fasciated-2 in the pear chromosome and fasciated-3 in the variegated chromosome (IMAI 1927, 1933).

Occurrence of Temporary Fasciation.

Fasciation occurs widely in many plants, including herbs, shrubs, trees, and even in some fungi (MASTERS 1869, PENZIG 1890-4,

[Jour. Coll. Agric., Vol. XII, No. 3, 1934.]

WORSDELL 1915-6, WHITE 1916, SHIRAI 1925). Its existence is generally temporary, having been caused either by certain environmental influences or by accident. Under certain environmental conditions, the various plant species or strains are predisposed to fasciation in response to these influences.

Physiological or temporary fasciation does not transmit the abnormality to their progeny. Such fasciation has not yet been observed in the Japanese morning glory (IMAI 1927), all fasciation so far observed being hereditary. The writers recently obtained two specimens showing fasciation to a considerable degree in a pedigree culture originally unconnected with heritable fasciation. These fasciated plants bred true to normal in the offspring. Two similar non-hereditary cases have been reported to the writers by cultivators. The writers sowed seeds, both of a fasciated branch and of normal branches of a normal plant, sent by another cultivator, but the flattened stem character did not transmit to the offspring. These physiological forms bore normal leaves. In this plant therefore we have temporary fasciation due to stimulation from certain environmental factors. The occurrence however being rare, the tendency to fasciation is relatively speaking very weak in this plant.

The Polymeric Genes.

In the Japanese morning glory, IMAI (1927) analyzed three polymeric recessive genes for fasciation. New F_2 data obtained by crossing fasciated with normal are presented in Table I.

TABLE I.
 F_2 from crossing of pear fasciated with normal.

Cross	Normal	Pear	Fasciated	Pear fasciated	Total	% of fasciated
SW×NF	268	84	0	12	364	3.30
415×NF	170	47	3	11	231	6.06
SU×NF	254	45	1	8	308	2.92
356×NF	141	40	0	7	188	3.72
9T×NF	154	41	1	4	180	2.78
190×NF	132	32	0	5	169	2.96
220×NF	59	17	0	3	79	3.80
M3×NF	130	31	0	4	165	2.42
ID×NF	108	29	0	4	141	2.84
SK6×NF	116	26	0	3	145	2.07
N2×WF	94	38	0	2	134	1.49
RF×IF	43	18	0	6	67	8.96
RF×WF	204	44	0	13	261	4.98
435×IF	41	11	0	4	56	7.14
Total	1894	503	5	86	2488	3.66

The frequency of fasciated segregates runs from 1.49 to 8.96 percent. In a previous paper, IMAI gave the F_2 results of six crosses, in which the fasciated segregates varied from zero to 2.97 percent. From progeny tests of a cross, in F_2 of which 2.97 percent of the fasciated segregates were obtained, IMAI analyzed three polymeric genes for fasciation. The segregating ratio is modified by the linkage between fasciated genes and by the fluctuation in the manifestation of fasciation. Since the extent of the fluctuation differs in the different strains, it is difficult to know from the segregating ratio in F_2 the number of genes responsible for fasciation in a given cross. In some cases with a low percentage of fasciated segregates, the number of genes responsible for the fasciation complex seems to be more than three, or there are one or more modifiers at work (IMAI 1927). There exist, of course, normals having one or two sets of normal (non-fasciated) allelomorphs. When such normals are crossed with fasciated we should obtain monogenic or digenic segregation in the hybrid progeny. The data obtained by HAGIWARA (1924, 1926) and YAMAGUCHI (1926a) include duplicate genes in the production of fasciation. In a backcross experiment, IMAI (1933) detected two fasciated genes (fasciated-1 and fasciated-3). By backcrossing parental fasciated with an F_1 , the segregation that occurred in the offspring was 215 normal and 74 fasciated, or 25.6 percent fasciated. In crossing fasciated with pear-leaved normal, the writers obtained the simple results as shown in Table II.

TABLE II.

F_2 from crossing of pear fasciated with pear.

Cross	Pear	Pear fasciated	Total	% of fasciated
SK × WF	59	21	80	26.25
SK × DF	82	32	114	28.07
Total	141	53	194	27.32

The segregation is monogenic for fasciation. In Table III are indicated new backcross data proving digenic segregation.

TABLE III.

Backcross: (normal \times pear fasciated) \times pear fasciated.

Backcross	Normal	Pear	Fasciated	Pear fasciated	Total	% of fasciated
(RF \times IF) \times IF	60	36	0	31	127	24.41
(RF \times WF) \times IF	120	70	0	46	236	19.49
(435 \times IF) \times IF	47	23	0	11	81	13.58
Total	227	129	0	88	444	19.82

The backcross experiments revealed the fact that the normal parents in these crosses have two sets of normal allelomorphs for fasciated-1 and fasciated-3. The corresponding F_2 shown in Table I gave for fasciated segregates 8.96 percent, 4.98 percent, and 7.14 percent respectively. These figures are much higher than the 2.89 percent for cross 326 \times A5, in which segregation was trigenic.

The subject of hereditary fasciation of plants is fortunate in the abundance of genetic literature. The main genetic literature on fasciation are the works of MENDEL (1865) and others (cf. WELLSIEK 1925) on *Pisum*; EAST and HAYES (1911), and EMERSON (1912) on *Zea*; WHITE (1916) on *Nicotiana*; STOUT (1918) on *Cichorium*; LLOYD (1918) on *Gossypium*; BAUR (1924) on *Antirrhinum*; COLLINS (1924) on *Crepis*; NAGAI (1926) and TAKAGI (1929) on *Glycine*; KELLY (1927) on *Phlox*; SHULL (1929) on *Capsella*; NOHARA (1933) on *Sesamum*; KANNA (unpublished data) on *Impatiens*; and others. Generally, fasciation is monogenically recessive to normal, but in a few cases such as EAST and HAYES' *Zea*, WHITE's *Nicotiana*, STOUT's *Cichorium*, and LLOYD's *Gossypium*, the abnormality is transmitted as dominant. In some cases, the genetics is of a more complicated nature, not yet fully worked out. SHULL however identified two recessive genes responsible for fasciation. NOHARA, in studying *Sesamum*, came to the conclusion that in his first series of experiments, duplicate recessive genes were concerned in the manifestation of monstrosity. His data, however, on the basis of which he drew the above conclusion, may not be sufficient to be conclusive. In the writers' opinion, the deficit of fasciated segregates in the hybrid progeny may be attributed to manifestation of fluctuation in the fasciation, seeing that his fasciated stocks frequently give normal atavists.

Crypto-fasciation.

In some cases the fasciation bred true or almost true to type in the offspring, but in others it was mixed with a few or many normals. Such normals, when selfed, give rise to many fasciations, showing the normals to be false or crypto-fasciated. DE VRIES (1901-3) and other investigators were fully aware of the occurrence of such normal atavists in certain fasciated plants. This means that the fasciation at times fails in its manifestation through environmental influences. In *Pharbitis*, the fasciation is affected in its expression by environmental factors, frequently giving rise to crypto-fasciated (IMAI 1927, 1930b). Fasciated *Sesamum* (NOHARA 1933) also throws out many normal atavists. For such normals, NOHARA, while partly admitting his failure in correctly diagnosing fasciation, still attributed some of the cases to "Rückmutation" from fasciated to normal, without any reliable genetic basis. It seems more natural to regard them as crypto-fasciated or false normals.

Although frequency in the occurrence of the crypto-fasciated in the fasciated *Pharbitis* may be influenced by environmental factors, yet the stocks show roughly definite average proportions, which differ in different pedigrees (IMAI 1927). These two fasciated strains of different origin were observed for three successive years in order to examine the rate of occurrence of crypto-fasciated. Table IV summarizes the data obtained.

TABLE IV.

Proportion of crypto-fasciated in two fasciated strains.

Year	Strain DF				Strain WF			
	Normal	Fasciated	Total	% of fasciated	Normal	Fasciated	Total	% of fasciated
1930	3	66	69	4.35	17	100	117	14.53
1931	13	151	164	7.93	18	82	100	18.00
1932	10	182	192	5.21	20	136	156	12.82
Total	26	399	425	6.12	55	318	373	14.75

These two strains of commercial origin have been bred by pedigree culture for several years before we made tests. Strain DF produced a smaller percentage (6.12%) of the crypto-fasciated than

strain WF (14.75%), that is, the latter is more unstable in the manifestation of the fasciated character than the former. The degree of stem flattening is more conspicuous in strain DF. Thus the two strains have nearly definite but somewhat variable rates for producing crypto-fasciated. There are more fluctuating strains in which the extent to which false manifestation may occur has a much wider variation. Fasciated strain A5 that was used in IMAI's experiments (1927) bred almost true to fasciated. This strain was lost before further tests could be made. YAMAGUCHI's stock (1926a) also had a high constancy. The difference in rate of occurrence of the crypto-fasciated implies the presence of certain genic modifiers that qualify the frequency and possibly also the average degree of stem flattening.

The crypto-fasciated, when selfed, gave rise to many fasciated in the offspring, with reappearance of some normal atavists (IMAI 1927, 1930b). The four crypto-fasciated that appeared in strain WF produced 10 normal and 52 fasciated; that is, the frequency of normals is 16.13 percent, nearly agreeing with that obtained by selfing the fasciated (14.75%).

The fasciated *Pharbitis* frequently put forth normal branches. These branches are also produced by mere fluctuation. Tests made by the writers showed the following results: The seeds collected from the normal branches gave 10 normal and 40 fasciated, whereas those from fasciated stems of the same individuals produced 6 normal and 24 fasciated, the frequency of normal being 20 percent in both cases, thus proving the manifestation of fluctuation.

The Non-pear Fasciated Segregates.

Heritable fasciation of *Pharbitis* always accompanies pear leaves. Pear is a simple recessive leaf character (cf. IMAI 1930a). YAMAGUCHI (1926a, 1926b) observed the break in the combination between pear and fasciated, and estimated the recombination frequency to be about 4 or 5 percent. From his own data, IMAI (1927) calculated the recombination for pear and fasciated-1 to be about 2.5 percent. Neither author made any attempts to breed the non-pear fasciated that were regarded as crossovers. The writers made good this gap with experiments. They selfed three non-pear fasciated segregates (Fig. 1) but obtained practically no non-pear fasciated

in the offspring. One of them gave only normals for two genera-

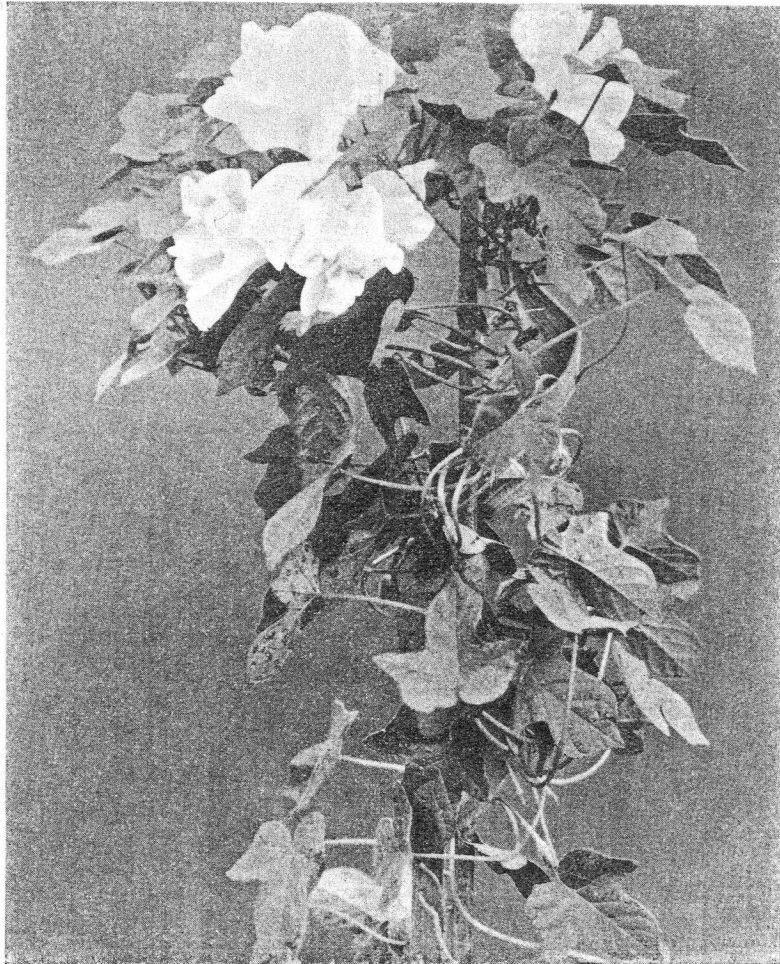


Fig. 1. Non-pear fasciated segregate.

tions. The other two segregated out some pear fasciated, but with the exception of one individual which was non-pear fasciated like the grand-mother, gave no non-pear fasciated during two generations. What is the criteria of these breeding results? It seems probable that these non-pear fasciated segregates are not crossovers between pear and fasciated-1, but only temporary fasciation with normal leaves, caused by environmental influences. If we sum up

all the non-pear fasciated segregates in the data available for F_2 , including those published by IMAI (1927), the frequency in the total normal (non-fasciated) is 0.24 percent. This figure, though very small, seems much greater when it is compared with frequency in the occurrence of false fasciated in the pure normal pedigrees. This difference may be due partly to the genic modifiers and partly to the condition heterozygous for fasciation.

For the writers to draw final conclusions after having examined only three non-pear fasciated segregates might seem somewhat premature, but from all that is known at present they feel it permissible to say that the pear-fasciated characters are either linked together by a very rare recombination (less than 2.5 percent) or that they are due to the manifold effects of one and the same gene. HAGIWARA (1924, 1926) held the latter view, because he failed to obtain such segregates in his hybrid progeny owing to the small number tested. In backcrossing the fasciated parent to F_1 , IMAI obtained 134 normal, 81 pear, and 74 pear fasciated, without any non-pear fasciated, or a ratio of 2:1:1. This shows the strong combination of the two characters (pear and fasciated-1).

YAMAGUCHI (1926a) and IMAI (1927) gave instances of families in which the segregation was simplified to monogenic in the hybrid progeny. In Table V are presented new F_3 data showing such a segregation from cross 220×DF, in which two genes are responsible for fasciation (IMAI 1933).

TABLE V.

F_3 from cross 220×DF, showing monogenic segregation for fasciation.

Number of pedigrees	Normal	Pear	Fasciated	Pear fasciated	Total	% of fasciated
16	454	17	2	153	625	24.80

In these pedigrees the segregation is greatly simplified, giving monogenic segregation for fasciation (24.80 percent of recessives). Of these segregates, pear and non-pear fasciated may, at least partly, or mostly, be temporary manifestations of pear fasciated (in the former) and normal (in the latter). By backcrossing double recessive with F_1 , obtained by the cross between fasciated with polycelled ovary (double recessive) and normal (double dominant) of

Sesamum, NOHARA (1933) raised 143 normal, 59 polycelled, and 103 polycelled fasciated segregates. From these data he made an attempt to calculate the recombination frequency. In this backcross experiment, he however had no two-celled fasciated. With this exception, the case is apparently similar to that of *Pharbitis*. If any recombination were expected in *Sesamum*, the frequency would probably be very low. NOHARA made his estimate however by treating the data too arbitrarily and calculated a 16.07 percent recombination. In his backcross data, 59 polycelled segregates, at least the majority of them, may be considered to be genotypically polycelled fasciated. If all of them are so, the frequency in occurrence of the false normals in these fasciated segregates amounts to 36.42 percent!

Summary.

1. Temporary fasciation of the Japanese morning glory, caused by certain environmental influences, occurs in cultures unconnected with heritable fasciation. On selfing, they back to normal in their offspring.

2. Segregation of the fasciated in the hybrid progeny is either monogenic, digenic, or trigenic, according to differences in genotypes of their normal parents or of their heterozygous mother plants.

3. Crypto-fasciated occur in the pure fasciated pedigrees. They give rise to many fasciated in the offspring.

4. Thus mismanifestation occurs reversibly between normal and fasciation, the frequency being probably affected by genic modifiers.

5. So far as tested, the non-pear fasciated segregates in the hybrid progeny proved to be normal in their genotype. Therefore, the characters, pear and fasciated-1, are either linked together closely than hitherto supposed or they are manifested by one and the same gene.

LITERATURE CITED.

- BAUR, E. (1924): Untersuchungen über das Wesen, die Entstehung und die Vererbung von Rassenunterschieden bei *Antirrhinum majus*. Bibliotheca Genetica, 4: 1—170.
- COLLINS, J. L. (1924): Inheritance of *Crepis capillaris* (L.) WALLR. III. Nineteen morphological and three physiological characters. Univ. Calif. Publ. Agr. Sci., 2: 249—296.
- EAST, E. M. and H. K. HAYES (1911): Inheritance of maize. Conn. Agri. Exp. Sta. Bull., 167: 1—142.
- EMERSON, R. A. (1912): Inheritance of certain "abnormalities" in maize. Rpt. Amer. Breed. Assn., 8: 385—399.
- HAGIWARA, T. (1924): Preliminary note on the inheritance of the fasciation in the Japanese morning glory. Jour. Sci. Agri. Soc., 255: 54—63. In Japanese.
- (1926): Genetic studies of the fasciation in morning glories. Bot. Magazine, Tokyo, 40: 281—294. In Japanese with English résumé.
- IMAI, Y. (1926): Genetic studies on morning glories. XVIII. Bot. Magazine, Tokyo, 40: 655—657. In Japanese with English résumé.
- (1927): Experiments with a pear-leafed and fasciated strain of the Japanese morning glory. Jour. Genetics, 18: 275—314.
- (1930 a): A genetic monograph on the leaf form of *Pharbitis Nil*. Zeitschr. f. ind. Abst.- u. Vererbungsl., 55: 1—107.
- (1930 b): Is fasciated a frequently mutating character? Bot. Gazette, 90: 116—118.
- (1933): Linkage studies in *Pharbitis Nil*. Zeitschr. f. ind. Abst.- u. Vererbungsl., 66: 219—235.
- KELLY, J. P. (1927): Fasciation in *Phlox Drummondii*. Jour. Heredity, 18: 323—327.
- LLOYD, F. E. (1918): The origination of ascidia under quasi-experimental conditions. Trans. Roy. Soc. Canada, 1: 71—80.
- MASTERS, M. T. (1869): Vegetable teratology. London.
- MENDEL, G. J. (1865): Versuche über Pflanzen-Hybriden. Verh. d. Naturf. Vereins in Brünn, 4 (Reprinted in Flora, 89: 364—403, 1901).
- NAGAI, I. (1926): On the inheritance of soy-beans. I. Agriculture and Horticulture, Tokyo, 1: 4—14. In Japanese.
- NOHARA, S. (1933): Genetical studies on *Sesamum indicum*, L. Jour. Coll. Agri., Tokyo Imp. Univ., 12: 227—386.
- PENZIG, O. (1890—4): Pflanzen-Teratologie. 2 Bd. Genua.
- SHIRAI, M. (1925): Plant teratology. Tokyo. In Japanese.
- SHULL, G. H. (1929): Species hybridizations among old and new species of shepherd's purse. Internat. Congr. Plant Sci., 1: 837—888.
- STOUT, A. B. (1918): Duplication and cohesion in the main axis in *Cichorium Inthybus*. Brooklyn Bot. Gard. Mem., 1: 480—485.
- TAKAGI, F. (1929): On the inheritance of some characters in *Glycine Soja*, BENTHAM (Soy-bean). Sci. Rpt. Tôhoku Imp. Univ., IV, Ser. (Biol.) 4: 577—539.

- VRIES, H. DE (1901—3): Die Mutationstheorie. 2 Bd. Leipzig.
- WELLENSIEK, S. J. (1925): Genetic monograph on *Pisum*. Bibliographia Genetica, **2**: 343—476.
- WHITE, O. E. (1916): Studies of teratological phenomena in their relation to evolution and the problem of heredity. II. The nature, causes, distribution and inheritance of fasciation with special reference to its occurrence in *Nicotiana*. Zeitschr. f. ind. Abst.- u. Vererbungsl., **16**: 49—185.
- WORSDELL, W. C. (1915—6): The principles of plant-teratology. 2 Vols. London.
- YAMAGUCHI, Y. (1926 a): On the inheritance of fasciation in *Pharbitis Nil*. Proc. Jap. Assn. Adv. Sci., **2**: 264—273. In Japanese.
- (1926 b): Notiz über die Vererbung der Fasziation bei *Pharbitis Nil*. Bot. Magazine, Tokyo, **40**: 535—537.
-