

***Modified Characterizations of the Gene-controlled
Peloric Flower by the Female-cytoplasm
in Digitalis purpurea L.***

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Abstract

1. Reciprocal crosses were made between two peloric strains of the common foxglove, *Digitalis purpurea* L. The one had proved to breed true for this anomalous flower character in pedigree cultures while the other had its origin in the seed in the market.
2. When the former plants were female parents resulting offsprings were exclusively peloric plants, while in the reciprocal crosses the populations covered a wide range of plants from seeming normals through remarkably peloric plants. This variation in the flower form among genotypically peloric plants could be observed repeatedly in subsequent inbred generations as a whole regardless of their parental phenotypic appearances.
3. The dissimilarity in the flower form in reciprocal crosses was found to be consistent for three consecutive generations.
4. The plants homozygous for normal flower, however, irrespective of their maternal strains, were found to behave consistently as normal plants in subsequent successive generations.
5. In conclusion, it can be said that in the foxglove a cytoplasm derived probably from a seed of obscure origin in the market could so interfere with or modify the characterization of gene-controlled peloric flower that there was observed a more or less continuous variation which covers the plants bearing flowers of seeming normality through the plants of apparent peloric flowers.

1 Introduction

We have considerable reports available of the occurrence of heritable flower misbuildings in flowering plants. Some of them seem to be induced typically by a gene or genes alone, while others occur by a possible interaction of genes and plasmon or some environmental factors.

In the latter cases, gene-manifestating processes which produce ultimately anomalous character often tend to be more or less unstable, and there are found some variations in segregating ratios in the hybrids or in the manifestation of genes concerned.

With the common foxglove, *Digitalis purpurea* L., several authors (SAUNDERS, 1911; KEEBLE et al, 1910; WARREN, 1915; MIYAKE et al, 1919, 1920; HAASE-BESSELL, 1926, 1927) have studied genetically the morphological characters of vegetative parts, flower-colouring and some abnormalities. Especially, in this species several kinds of flower-misbuilding were described and their genetical behaviors were traced.

On the progress of the breeding of *Digitalis* in our field, there occurred three kinds of abnormal growth of organ: fasciated stem and flower axis, heptandric flower and peloric flower.* They were found to be profitable and attractive materials to study the possible relations of gene-actions with plasmon-effect and physiological or ecological conditions of the plant.

It has been suggested that in the foxglove some kinds of complexity in genetical behaviors of certain characters may often occur owing to its polyploidal construction.

The peloric flower* which has been observed in our *Digitalis* fields is of rather a unique nature in that not only it matures prior to the other ordinary irregular flowers, otherwise it has acropetal flowering habit characteristic of this species, but also it is conspicuous large and of a monstrous cup-shaped appearance.

This type of flower may be regarded as arising from the suppression of certain internodes of the flower-axis and the concurrent fusion of the flower-buds resulting in a more or less regular cup- or saucer-shaped flower at the top of the axis.

The inheritance of this monstrous type of flower was studied formerly by KEEBLE et al (1910), WARREN (1915) and SAUNDERS (1917). They reported that the peloric character in this species is monogenic recessive to normal non-peloric condition. The present author also obtained the similar results in this respect of his genetical studies on this plant.

By more extensive observations subsequent to above mentioned studies, it was found that the manifestation of genes concerned could be modified by or interfered with a combination with a certain cytoplasm derived from female parent. The results presented here might furnish additional evidence for the plasmic interference with gene-controlled flower anomaly.

* The peloria is an abnormal regularity of flower structure occurring in normally irregular flowers.

2 Materials and Their Origins

In the course of our genetical work on the foxglove, the peloric nature of flower proved to behave as monogenic recessive to normal non-peloric condition, though there was very often observed perceptible variation in the flower shape.

In 1955, we made reciprocal crosses between a peloric plant p-III from a strain p(11-13), which had proved to breed true for this deformity, and a peloric plant p-X as well, which was a segregant of a selfed plant raised from the seed in the market.

In 1957, unexpectedly, a definite distinction was so recognized between above two crosses that; with a cross p-III \times p-X the resulted offsprings bred true for the peloric condition, while the hybrids from a reciprocal cross p-X \times p-III gave a wide variation in flower form from phenotypically near normal to distinct peloric plant without any sign of monogenic segregation. Furthermore, the same was true of their three consecutive selfed generations respectively.

Concerning to the origin of the seeds in the market used on crossing, we could not trace to their source.

3 Results from Inbreedings and Crossings*.

1 Inbreedings

i) Inbreedings of (PP)

A normal-flowered plant was obtained in a segregating F₂ population from a cross [pp] \times (PP) in 1959. This plant proved to be homozygous for normal flower carrying cytoplasm from the original [pp] plant.

The plant was characterized by perfectly normal flowers, without any tendency towards the peloric condition. When selfed, the same was true of two

* Signs and Symbols adopted

In this paper, following signs and genic symbols are used to make description as short as possible.

Genic symbol PP : normal non-peloric flower.

pp : peloric flower.

() : a plant with cytoplasm derived from the plant p-III.

[] : a plant with cytoplasm derived from the plant p-X.

Among peloric plants carrying the cytoplasm derived from p-X, following three phenotypic classes were made.

[pp]-N : a plant near normal.

[pp]-M : a plant medial peloric.

[pp]-R : a plant remarkably peloric.

That is, for example, a sign [pp]-R \times (PP) stands for a hybrid between a homozygous peloric plant carrying a cytoplasm from an original plant p-X and a plant homozygous for normality carrying a cytoplasm from the other original plant p-III.

subsequent consecutive generations.

Accordingly, it seems to be no doubt that the cytoplasm concerned had no effect on the flower development in the presence of homozygous dominant genotype PP in this respect.

ii) *Inbreedings of [pp]-N, [pp]-M, or [pp]-R*

These three types of plant, when inbred gave the populations in three consecutive generations as shown in Tab. 1.

Table 1 Seemingly normal plant percentage in inbred offsprings of three different phenotypes of [pp] plant.

Inbred generations	Phenotypical classes		
	[pp]-N	[pp]-M	[pp]-R
1st generation	55	17	34
2nd generation	27	51	27
3rd generation	34	22	53
Mean percentage	39	30	38

Above classification of flower types in each generation was made as impartially and carefully as possible according to the grade towards anomaly.

Now, it was found that the numerical proportions of these classes in any generation showed no definite different patterns of segregation though perceptible annual fluctuations were observed.

2 Crossings

i) *Crossing of [pp]-N × [pp]-R*

“ of [pp]-R × [pp]-N

These reciprocal crosses fall under those which are made between two plants having a common genotype for peloric character and the same cytoplasm but showing different external appearances.

The results obtained are shown in Table 2.

From the data obtained, it is assumed that these two crosses gave essentially the equal offsprings which exhibited practically continuous variation as to this monstrosity.

ii) *Crossing of [pp]-N × (pp)*

“ of [pp]-R × (pp)

These two crosses were made to confirm the genotypical identification of plants assumed to correspond to [pp]-N and [pp]-R respectively. The distribution of variants over the above three classes was presented in Table 3.

Table 2 Reciprocal matings and their progenies between plants having the identical genotype and cytoplasm but different in phenotypical appearance.

Crosses	Classes in Populations			
	[pp]-N	[pp]-M	[pp]-R	Total
[pp]-N × [pp]-R	19	35	11	65
1st inbred. population	27	31	50	108
2nd inbred. population	37	17	28	82
Total	83	93	89	256
[pp]-R × [pp]-N	30	23	10	63
1st inbred. population	42	35	40	117
2nd inbred. population	18	22	30	70
Total	90	70	95	255

Table 3 Phenotypic variation of inbred offsprings from crossings [pp] plant ♀ × (pp) plant ♂

Crossing	Classes in Populations			
	[pp]-N	[pp]-M	[pp]-R	Total
[pp]-N × (pp)	31	29	40	100
F ₁	18	15	25	58
F ₂	27	22	31	80
Total	76	66	96	238
[pp]-R × (pp)	43	49	19	111
F ₁	53	29	38	120
F ₂	19	40	31	90
Total	115	118	88	321

From Table 3, it may be seen that between two types of hybrid population we can find no significant difference in the distribution of variants in this regard.

iii) *Crossing of (pp) × [pp]-N*

“ *of (pp) × [pp]-R*

Lastly, in order to confirm a lack of participation of male-cytoplasm in the manifestation of genes concerned, above two types of crossing were undertaken.

These crossings, as expected, gave families which were classed together by common malformation, and this was true of subsequent selfed-generations.

Consequently, in light of the results obtained here, it seems highly improbable that the cytoplasm of male parent contributes to the hybrid in the manifestation of genes concerned.

4 Discussion

Several works have been done on the inheritance of peloric flower in some plant species.

SIRKS (1925) crossed an abnormal form of *Lamium album* bearing peloric top flowers with a normal form. All F_1 plants had exclusively normal flowers.

From the results of F_2 generations and backcrosses, he concluded that pelorism of flower in this species behaves as multiple-genic recessive.

It was supposed that in this case, at least four, possibly five or more genes are responsible for the character.

On the contrary, a dominant peloric feature was also observed with *Mimulus* species by BROZEK (1923). A pure line of *M. tigrinus* bearing peloric top flowers was crossed with a pure line of *M. quinquevulnerus* lacking it, producing F_1 plants with peloric flowers, and a monogenic segregating ratio of 3 : 1 in F_2 was obtained.

RANT (1922) observed a similar condition of dominance in *Clitoria ternata*.

With *Antirrhinum* species we had an abnormal form named *radialis* (*ee*), the flower of which being radial instead of normal zygomorphic form. (BAUR, 1924)

On the other hand, there was found in this species another type, *variabilis* (*pp* and *qq*), which is characterized by a conspicuous variation in the flower form, bearing in each plant various types of flower, namely, radial, zygomorphous and several gradations of intermediacy between them.

Though the effects of these two genes are slightly different from each other, the heterozygote *Pp Qq* was normal-flowered, giving a segregation in F_2 into *normal* and *variabilis* in a ratio of 9 : 7.

On the early stage of the genetical investigation on the foxglove, we have several papers dealing with the inheritance of peloric character of the flower. (KEEBLE et al, 1910; MIYAKE et al. 1919)

According to them, the formation of peloric flower at the top of the axis was found to behave as a monogenic recessive to normal non-peloric condition.

On the contrary, however, much more complicated segregating ratios were also obtained by HAASE-BESSELL (1926), in which peloric plants were sometimes segregated out as a dominant, sometimes however as a recessive character, probably ascribing to the cytological complicated nature of tetraploidy of this plant.

Consequently, there can be two cases in which the peloric condition behaves as a dominant character or as a recessive one.

Furthermore, the number of genes responsible for the development of peloric flower was found sometimes to be one, but sometimes to be two or more. But the actual distribution of variants which apparently deviate from the typical

recessive within a recessive population may suggest much more intricate relations among them.

In fact, it was found by WARREN (1915) that, imperfect crowns or peloric flowers of different degrees of incompleteness could occur if it is assumed that the cross between a peloric plant and an ordinary non-peloric one would give the offspring of more or less intermediate characters.

He adopted conventionally an empirical grading of the character in which the variants were placed in the following four grades according to their capacity to form the typical peloric flowers.

100, 75, 50, and 25% grades

His paper, however, contains no mention of the genetic behaviour of this anomalous character.

In light of the results reported by WARREN and HAASE-BESSELL, it seems likely that this more or less continuous variation of peloric nature is induced by some complicated genetical construction which is attributed to the original formation of this species.

Be the matter as it may, in order to obtain an actual Mendelian relationship, it is necessary to include in the peloric category all plants which exhibit any distinct tendency towards the peloric condition.

Concerning the participation of the cytoplasm of female parent in the manifestation of genes in the hybrids, we have several reports regarding the pollen-fertility and other characters.

A number of studies are available in which a gene or genes are involved in the plasmic male-sterility.

For instance, JONES and CLARKE (1943) found that male-sterility in *Allium cepa* occurred exclusively in a combination of a genotype *msms* with a sterile-cytoplasm (S). However, plants of all other genotypes with normal-fertile cytoplasm (N), were fertile.

A classic work with flax by BATESON et al (1921) and that with *Dactylis* species by MYERS (1946) yielded also similar conclusion.

According to the data obtained by the present author, the peloric flower of *Digitalis* plants was found to behave as a monogenic recessive character, if all plants that have the flowers which show any indication of pelorism were included into the peloric class.

In general, the genetical effect of plasmons seems to work only when an interspecific cross is performed.

Concerning to it's mechanism, a number of explanations have been given, one of which is the classic theory of plasm-sensible genes by RENNER and KUPPER (1921).

Their theory suggests that, some unstable substance produced by the cytoplasm of female parent can affect the action of certain genes of the male parent.

With our initial test plant, whose offsprings were available in this study, it was not yet confirmed whether it was an offspring of any possible interspecific hybrid ever occurred naturally, or had originally some modified cytoplasm owing to a mutation-like phenomenon.

Explanation of Plates

- Pl. 1; Fig. 1 A peloric flower of the plant p-III : (pp)
Fig. 2 A peloric flower of the plant p-X : [pp]-R
- Pl. 2; Fig. 3 The sequence of flower development on the inflorescence of peloric plants.
Fig. 4 A monstrous peloric flower on a plant derived from a cross p-X × p-III : [pp]-R
- Pl. 3; Fig. 5 A plant genotypically homozygous dominant : Normal, (PP)
Fig. 6 A seemingly normal appearance of a peloric segregant carrying the modifying cytoplasm : [pp]-N
- Pl. 4; Fig. 7 ditto
Fig. 8 ditto

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Plate 1

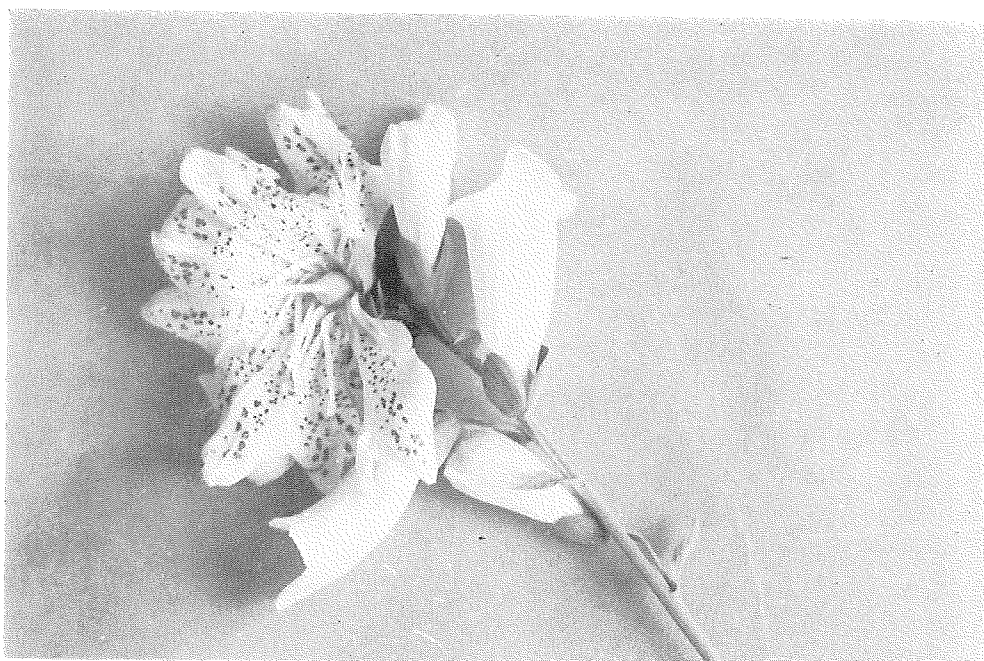


Fig. 1

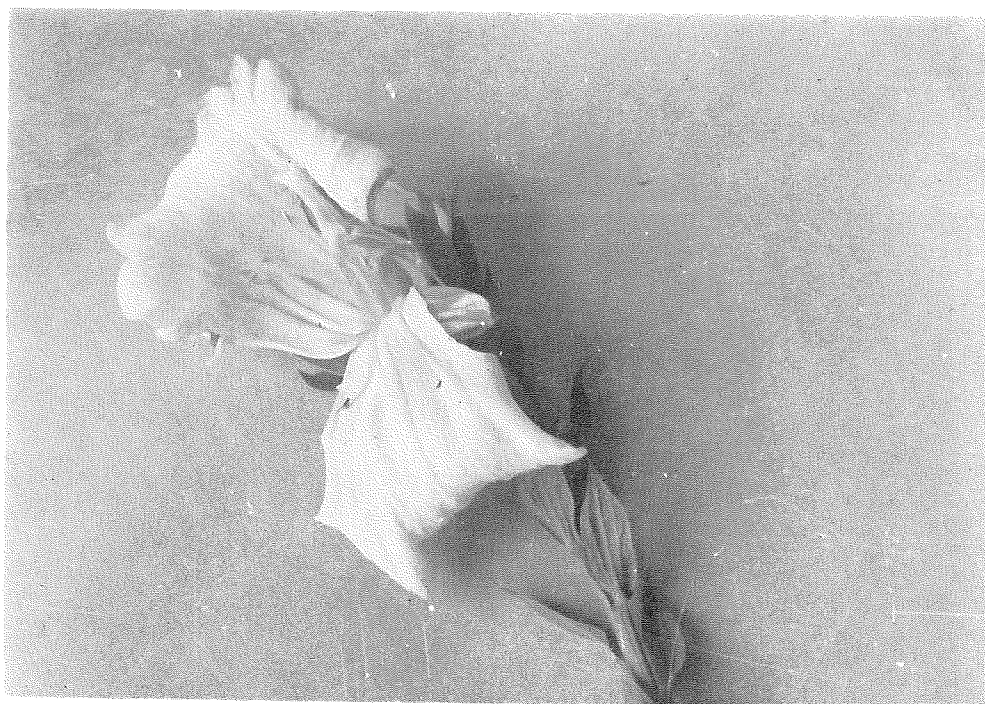


Fig. 2

Plate 2

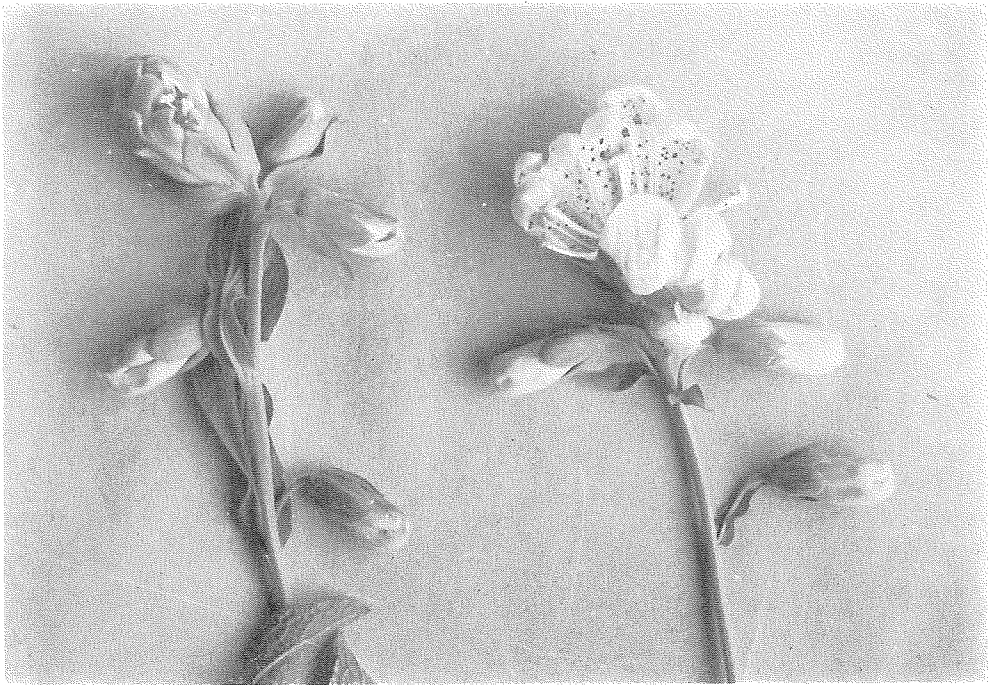


Fig. 3

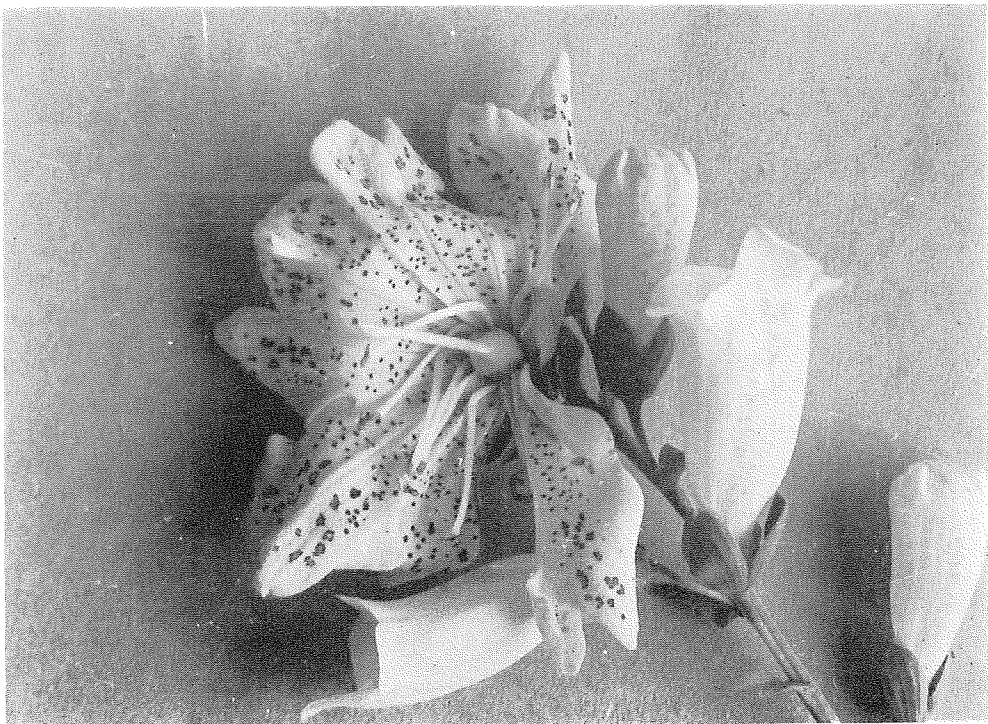


Fig. 4

Plate 3



Fig. 5



Fig. 6

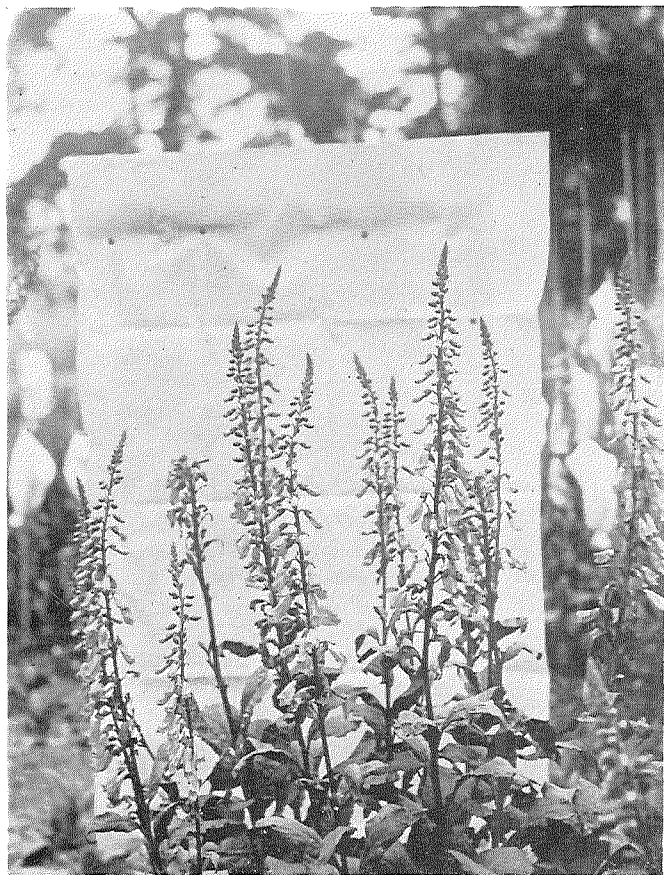


Fig. 7



Fig. 8