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# Some observations on male sterility in *Geranium sylvaticum* L. var. *alpestre* Schur.

A. PUTRAMENT

## INTRODUCTION

Studies on genetic mechanism of male sterility have been started by Correns some decades ago and since then they are the object of many investigations. Mutations towards male sterility seem to be relatively frequent. In tomato, for example, at least 17 independent male-sterile mutants are known (Rick 1956), in maize — still more. Many examples of male sterility are known appearing in progenies of interspecific crosses, when genes present in one species have been introduced into the cytoplasm of another (e.g. *Geranium* — Sansome 1936; *Linum* — Gajewski 1937; *Epilobium* — Michaelis and Bakker 1948; *Medicago* — Childers 1958; *Solanum* — Buck 1960; *Nicotiana* — Burk 1960, and others).

The most common genetic determination of male sterility seems to be a "plasmon-sensitive" gene interacting with certain types of cytoplasm (cf. Edwardson 1956). However, more complicated cases are known as well, for example in *Lolium* (Fejer 1958), *Capsicum* (Peterson 1958), *Nicotiana* (Radakrishna and Bhat 1958), maize (Schwartz 1951).

On the other hand, in wild populations there is strong selection against male sterility factors, and they are maintained and become a part of the breeding system in a species (gynodioecy) only in certain special conditions. Indeed, as Lewis and Crowe (1956) had pointed out, if male sterility is determined by one gene, a hermaphrodite plant contributes to each new generation three times as many genes as does a female, the former supplying eggs and pollen as well as pollen for the females. If female plants are to occure more frequently in a population than the mutation rate towards male sterility they must have at least a two-fold initial selective advantage over the hermaphrodites.

Watson and Caspari (1960) have calculated that in a population of plants in which pollen sterility is dependent on a cytoplasmic factor and one pair of Mendelian alleles the ratio of the two cytoplasms remains constant. Yet the genic factor involved in the production of pollen sterility will be selected against and be eliminated unless the process of elimination is counteracted by mutation to the plasmon--sensitive allele or male sterile plants have a high selective advantage over male-fertile individuals.

A perfect example of very complicated genetic mechanism of gynodioecy is that found by Lewis and Crowe (1956) in *Origanum vulgare*. A dominant gene F is responsible for pollen degeneration, another dominant factor H suppresses gene F. Plants with F-hh genotype are female, plants ffH- or F-H- are hermaphrodite. Bottom recessive homozygotes ffhh are apparently lethal; viability of homozygotes HH is in natural conditions much lowered. Besides, seed setting in females is higher than that in hermaphrodites. Such a complicated breeding system enables female plants to maintain rather high (apparently up to 50%) frequency in wild populations.

Table 1

Three types of plants of *G. sylvaticum* var. *alpestre* found in different populations in Tatra Mountains

| Locality | Altitude m.ab.s.l. | Types of plants | | | | | | Total |
|---|---|---|---|---|---|---|---|---|
| | | Male-fertile | | Partially fert. | | Male-sterile | | |
| | | Number | % | Number | % | Number | % | |
| Velicka dolina | 1700 | 176 | 81.5 | 26 | 12 | 17 | 6.5 | 216 |
| Velicka dolina | 1750 | 339 | 65.6 | 68 | 13.1 | 110 | 21.3 | 517 |
| Velicka dolina | 1800 | 310 | 59.6 | 81 | 15.6 | 129 | 24.8 | 520 |
| Velicka dolina | 1700 | 148 | 61.4 | 37 | 15.4 | 56 | 23.2 | 241 |
| Hincove Pleso | 1700 | 420 | 71.1 | 47 | 7.9 | 124 | 21.0 | 591 |
| Mlynicka dolina | 1600 | 291 | 88.2 | 14 | 4.2 | 25 | 7.6 | 330 |
| Mlynicka dolina | 1650 | 154 | 92.2 | 7 | 4.2 | 6 | 3.6 | 167 |
| Furkota dolina | 1600 | 99 | 79.8 | 5 | 4.1 | 20 | 16.1 | 124 |
| Furkota dolina | 1800 | 131 | 83.4 | 14 | 8.9 | 12 | 7.7 | 157 |
| Morskie Oko | 1600 | 134 | 80.2 | 14 | 8.4 | 19 | 11.4 | 167 |
| Morskie Oko | 1650 | 308 | 86.7 | 28 | 7.9 | 19 | 5.4 | 355 |
| Morskie Oko | 1700 | 197 | 92.0 | 10 | 4.7 | 7 | 3.3 | 214 |
| Total | | 2707 | 75.2 | 351 | 9.7 | 544 | 15.1 | 3602 |

Gynodioecy is rather common in natural populations of *Geranium sylvaticum* L. var. *alpestre* Schur. in the Tatra Mountains. In fact there are three types of plants: hermaphrodite (male-fertile, MF), female (male-sterile, MS), and intermediate, with some flowers fully fertile, others fully sterile and still others having some anthers with normal,

fertile pollen and some with degenerated pollen grains (partially sterile, PS plants). MS plants can be easily distinguished owing to much smaller corolla size than that of MF plants. PS individuals, however, can not be always distinguished unambiguously, because at the time of examination only MS or only MF flowers can be opened. So one can suppose that the frequency of PS plants is in fact higher than that shown in Table 1. One can see that although there are some differences in frequencies of the three classes of plants, the most frequent are always MF. On the other hand, MS plants are frequent enough in all populations examined to suppose them to be an important part of the breeding system in the populations.

Some plants (picked up when they did not flower) were brought to Warsaw and subjected to cytological observations as well as breeding experiments.

## Description of the original plants

All plants studied cytologically had chromosome number $2n = 28$ *

Plant No. 1. Male-fertile. Petals 16 mm in length, 10 mm width. Colour Amethyst violet 35/1 **. Meiosis normal (Fig. 1, *A*—*D*). Further course of microsporogenesis normal. When the diameter of pollen grains is about 56 microns, the division of the pollen nucleus into vegetative and generative takes place. Soon afterwards, when the diameter of the pollen grains is about 61 microns, the generative nucleus divides to form two sperm nuclei. Mature pollen is about 80 microns in diameter. Pollen fertility (determined by staining in aceto-carmine) is 86—96%. Seed setting when uncontrolled pollinated 1.76 seeds per flower. (Maximum possible — 5 seeds per flower.) When selfed no seed setting was observed although the flowers (covered with cellophane bags) were each day hand pollinated.

Plants No. 2, and 6 to 19 did not differ from the one described above.

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* For cytological examination the best fixative proved to be Randolph's modified Navashin fluid after 3—5 min. pretreatment in Carnoy's solution. The preparations were stained according to Newton's gentian violet-iodine method.

For pollen fertility examinations whole anthers were squashed in aceto-carmine.

** According to Horticultural Colour Chart, issued by The British Colour Council in collaboration with The Royal Horticultural Society.

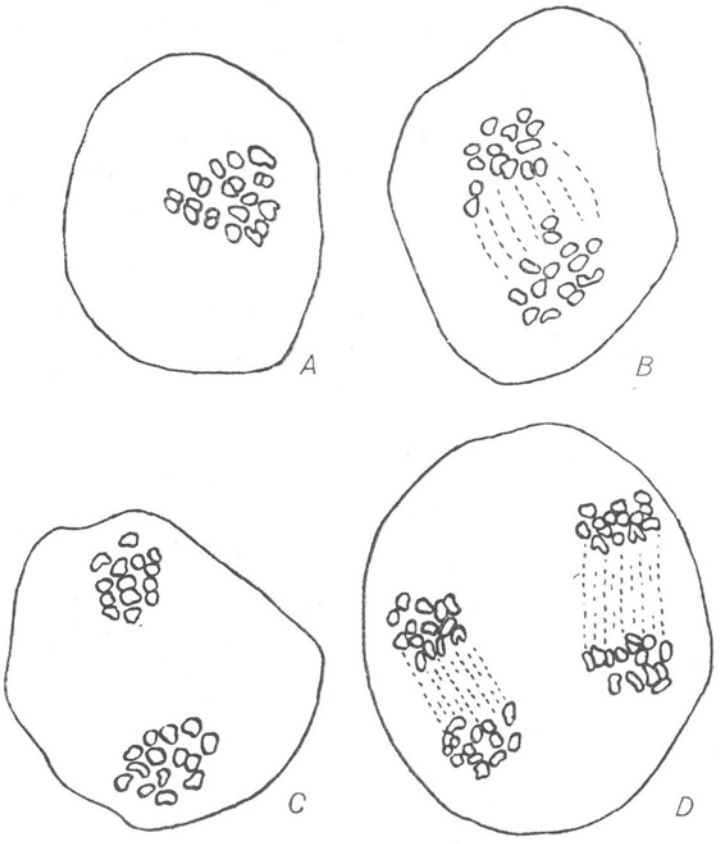


Fig. 1. *A—D.* Normal course of meiotic division in *G. sylvaticum* var. *alpestre*

Plant No. 3. There were in fact two plants, or a chimera due to somatic mutation, because during several years when observations were made there were two kinds of shoots: some with MF flowers similar to those described above and with seed setting 1.59 per flower, and others with small, completely MS flowers. Mean length of petals of the last type of flower was 9.8 mm, width — 5.5 mm, colour — Amethyst violet 35. Meiosis normal. Later in microsporogenesis pollen grains shrink and collapse. In mature flowers the anthers are completely devoid of any traces of pollen grains, or sometimes — there are small pollen grains completely devoid of any protoplasmic structures. Mean seed setting — 3.31 per flower.

Plant No. 4. Completely male-sterile. Petals 8.44 mm in length and 5.52 mm in width. Colour: Amethyst violet 35. Meiosis normal.

The release of young microspores from the tetrads normal. Soon afterwards, degeneration of pollen grains begins, and at the time when flowers open the anthers are completely or almost completely empty (out of 106 anthers examined 98 were completely empty, and eight contained the remains of pollen cell walls). Seed setting — 2.29 seeds per flower. Observations on the plant lasted five seasons, and one year two shoots have been observed with several flowers having normally developed pollen. The size of the flowers was approximately as that of usual MF flowers. The exceptional flowers were selfed and some seeds obtained.

Table 2

Numbers of bivalents per PMC at the end of MI in Plant No. 5

| | Numbers of bivalents | | | | | Total | | Bival. per 100 cells |
|---|---|---|---|---|---|---|---|---|
| | 0 | 1 | 2 | 3 | 4 | Bival. | Cells | |
| No. of cells | 86 | 139 | 63 | 13 | 8 | 336 | 309 | 109 |

Plant No. 5. Completely male-sterile. Petals 9.9 mm in length and 6.9 mm in width. Colour: Amethyst violet 35. The course of meiosis highly abnormal: In diakinesis $14_{II}$ or $13_{II}+ 2_{I}$ can be distinguished, so that initial chromosome conjugation seems to be normal or nearly normal. But soon desynapsis takes place and at the very beginning of anaphase only a few if any bivalents can be observed (Table 2). The univalents are scattered and their groupping in telophase is nearly random (Figure 2, *A—E*). In second division anaphase the chromatid separation seems to be normal and the total number of chromosomes is doubled after second meiotic division (Fig. 2). It is difficult to estimate the smallest numbers of chromosomes necessary to form separate spores; but the smallest spores seem to contain not more than 4 chromosomes. The numbers of sporads range from 2 to 9, with hexades as the most frequent (Table 3, Fig. 2 *F*).

Table 3

Numbers of sporads per one PMC in Plant No. 5

| No. of sporads per 1 PMC | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| No. of PMCs | 0 | 2 | 2 | 86 | 49 | 129 | 29 | 9 | 1 | 304 |
| % of total PMCs scored | 0 | 0.66 | 0.66 | 28.29 | 16.12 | 42.43 | 8.55 | 2.96 | 0.33 | 100.00 |

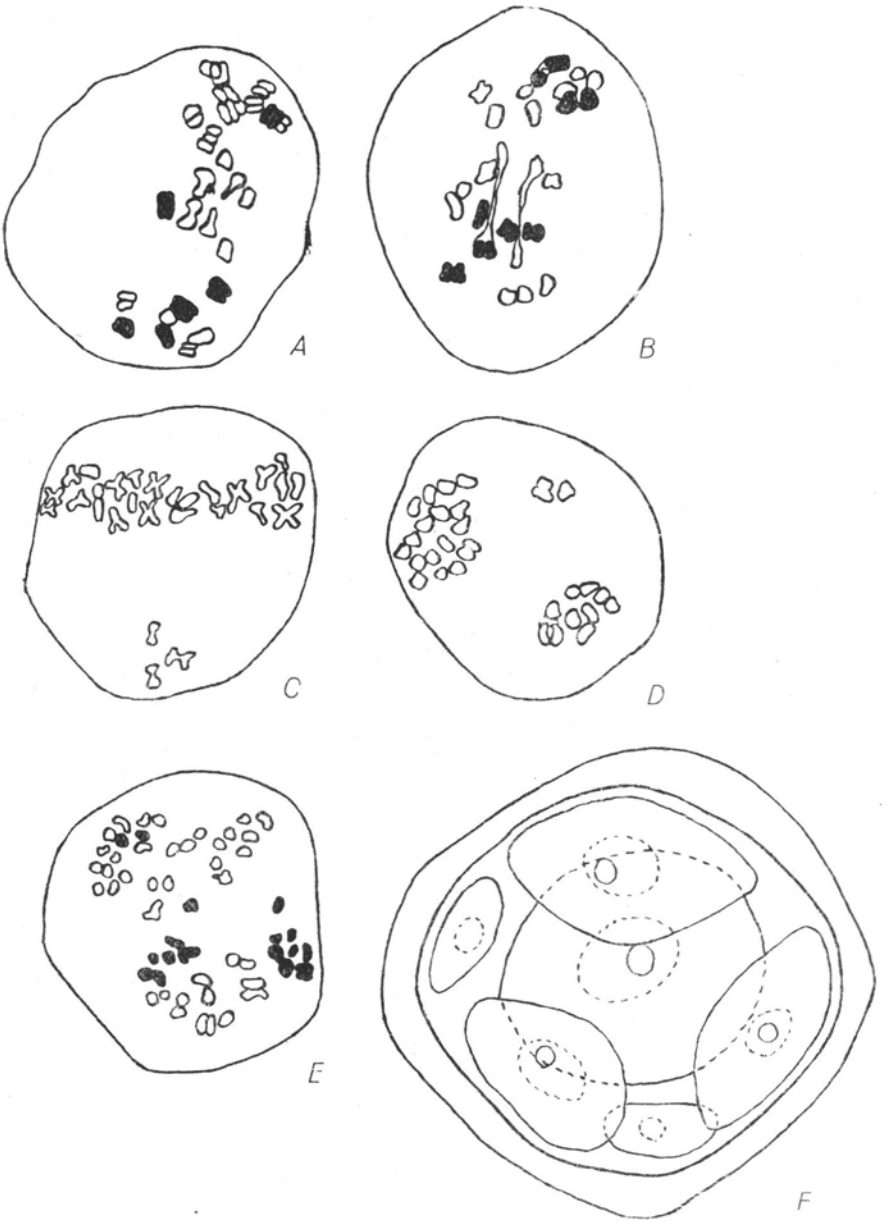


Fig. 2. *A—F*. Abnormal meiotic divisions in Plant No. 5
*A*. Meta-anaphase I with no bivalents. Univalents are scattered all over the spindle. *B*. Meta-anaphase I. Two bivalents can be observed. *C*. Telophase I. Extremely unequal chromosome segregation, most of the chromosomes are grouped at one pole of the PMC. *D*. Metaphase II. Three groups of chromosomes can be observed. *E*. Anaphase II. Total number of chromosomes is doubled in one PMC, indicating normale chromatid separation. *F*. A hexade. Striking differences in sizes of spores can be observed

Further pollen development in most anthers examined seems to proceed normally for some time. The pollen grains are extremely variable in size the biggest being as much as 4 times larger than the smallest. Divisions of pollen nuclei have not been observed although out of 2500 pollen grains examined, in 6 cases nuclei seemed to be in prophase. Shortly before anthesis the protoplasm in pollen grains shrinks and collapses. When flowers open pollen grains are completely or almost completely devoid of protoplasm, but they remain easily distinguishable because of very well developed cell walls characteristic for *G. sylvaticum* pollen grains. In some anthers complete degeneration of pollen occurs and the anthers are completely empty.

Seed setting in the plant is lowered, mean number of seeds per flower being 0.69 when uncontrolled pollinated.

Plant No. 20. was of different origin. It was *G. sylvaticum* var. *sylvaticum* from Puszcza Piska (lowland). It was fully male-fertile, and was not examined cytologically.

## Selfed and crossed progenies

The seed setting under cellophane bags is very poor in *G. sylvaticum* when crossed and especially when selfed. The seed germination is rather poor too, the seeds being hard. In the experiments the seeds germinated only after treating them with concentrated sulphuric acid for 3—5 minutes. The seedlings are rather weak at the beginning of their growth. Thus the progenies (especially selfed ones which were extremely weak) were not numerous.

Family No. 22. ($S_1$ of Plant No. 3, MF shoots) segregated giving 3 PS (Table 4) and 2 MF plants. The course of meiosis normal in all of them.

Family No. 24. ($S_1$ of Plant No. 4 obtained from exceptional shoots with MF flowers) consisted of 2 MS, 2 PS and 1 MF plants. Meiosis normal. Pollen degeneration in MS plants takes place early in their development and at the time when flowers open as a rule the anthers are devoid of any pollen traces. Two PS plants differ from each other strikingly. One (No. 24—3, Table 4) is almost completely male-sterile having 98.11% of MS flowers. In most anthers examined no pollen grains can be distinguished, which indicates that degeneration begins early in pollen development. The other PS plant (No. 24—2, Table 4) has 20.50% of MS flowers. The anthers of completely MS flowers are entirely devoid of any traces of pollen. Sterile anthers of PS flowers are

Table 4

Various degrees of male sterility in some plants classified as PS

| Plant No. | Male-sterile flowers | | Partially sterile flowers | | Male-fertile flowers | | Total |
|---|---|---|---|---|---|---|---|
| | Number | Per cent | Number | Per cent | Number | Per cent | |
| 20—2 | 57 | 96.66 | 2 | 3.44 | — | — | 59 |
| 20—12 | 73 | 96.05 | 3 | 3.95 | — | — | 76 |
| 20—8 | 65 | 90.28 | 4 | 5.55 | 3 | 4.17 | 72 |
| 20—10 | 51 | 82.26 | 5 | 8.06 | 6 | 9.68 | 62 |
| 20—1 | 113 | 58.55 | 68 | 35.23 | 12 | 6.22 | 193 |
| 20—5 | 32 | 21.19 | 62 | 41.06 | 57 | 37.75 | 151 |
| 20—3 | 6 | 5.31 | 58 | 51.33 | 49 | 43.36 | 113 |
| 20—7 | 2 | 1.13 | 12 | 6.78 | 163 | 92.09 | 177 |
| 21—6 | 1 | 0.35 | 104 | 36.49 | 180 | 63.16 | 285 |
| 21—1 | — | — | 9 | 11.39 | 70 | 88.61 | 79 |
| 22—2 | 40 | 76.92 | 10 | 19.23 | 2 | 3.85 | 52 |
| 22—3 | 2 | 0.43 | 40 | 8.60 | 423 | 90.97 | 465 |
| 22—1 | — | — | 9 | 10.70 | 75 | 89.30 | 84 |
| 22—4 | — | — | 11 | 3.97 | 266 | 96.03 | 277 |
| 24—3 | 52 | 98.11 | 1 | 1.99 | — | — | 53 |
| 24—2 | 49 | 20.50 | 117 | 48.95 | 73 | 30.55 | 239 |

either completely empty, or contain small pollen grains without any protoplasmic structures, but in some of them one or two pollen sacs can be completely empty and the others contain pollen grains inviable and devoid of protoplasm. The viability of pollen in fertile anthers is 94.6%.

Family No. 20. $F_1$ of cross: Plant No. 4 × Plant No. 1). 12 MS, 15 PS and 16 MF plants were obtained. In all three groups of plants meiosis normal with the exception of Plant No. 20—1. In this plant out of 32 PMCs studied in anaphase I, 14 showed various degrees of desynapsis. In some anthers pollen grains of very variable sizes could be observed, indicating that some kind of desynaptic divisions similar to that observed in Plant No. 5 could operate here. In MS plants, as a rule anthers are completely empty at the time of flowering. In PS plants pollen degeneration takes place at various times of development, and when buds open some anthers are completely empty, others contain small pollen grains without protoplasm, and in still others pollen grains contain some shrunken protoplasm. It looks as though degeneration started just before anthesis. Some anthers, sometimes all anthers in a single flower, contain normal pollen.

As it is apparent from the data in Table 4 the group of plants classified as PS, is in fact highly heterogenous. Plants

No. 20—2 and 20—12 have only very few PS flowers, the great majority of them being MS. In plant 20—7 however, the majority of flowers are with normally developed pollen. Other plants are intermediate between these two extremes. It seems that there are differences in the time of the onset of pollen degeneration. Even within the same plant, in some flowers degeneration can begin much earlier than in others. The distribution of the three types of flowers has been observed on some shoots of PS plants (Fig. 3). It is difficult to distinguish any regularity in the

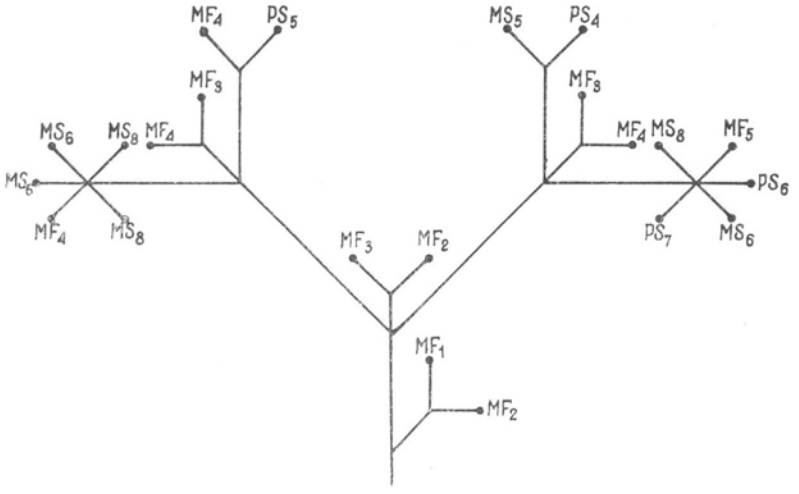


Fig. 3. Plant No. 20—5. Distribution of the three types of flowers on a shoot. Numbers indicate succesive days of flowering

pattern of distribution of the three types of flowers. It seems that at the beginning of flowering, among the first flowers to open there are more MF than later on, but among the last flowers on a shoot sometimes there can be again more MF. One can not distinguish sectors with one of the three types of flowers.

Family No. 25 ($S_1$ of PS plant No. 20—5) consists of 6 PS and 1 MF plant.

Family No. 21 ($F_1$ of cross: Plant No. 5 × Plant No. 1) consists of 4 MS and 2 PS individuals. Meiosis normal in all of them. Pollen degeneration in MS plants begins early and at the time of flowering the anthers are completely empty, without any traces of pollen grains. In PS plants pollen degeneration can begin at different times not only in different flowers or in different anthers of the same flower, but also in different pollen sacs within one anther. So some anthers are completely empty at the

time of flowering, others contain pollen grains devoid of protoplasm or with protoplasm shrunken and collapsed, and in some anthers there are normal, fully viable pollen grains. In normal anthers from PS flowers 93% of pollen is fertile, and from MF flowers 95% of pollen is fertile.

Family No. 26 ($F_1$ of cross: MS Plant No. 21—7 × Plant No. 1) consists of 14 MS, 4 PS, and 9 MF plants.

Family No. 27 ($F_1$ of cross: MS Plant No. 21—5 × Plant No. 2) consists of 9 PS and 17 MF individuals.

Family No. 28 ($F_1$ of cross: MS Plant No. 21—5 × MF Plant No. 10) shows segregation into 3 MS, 4 PS and 16 MF plants.

Family No. 29 ($F_1$ of cross: MS Plant No. 21—5 × MF Plant No. 20) consists of 10 MF plants, very vigorous, showing a striking heterosis.

Family No. 30 (progeny of MF Plant No. 18, uncontrolled pollination) shows segregation into 1 MS, 1 PS and 51 MF plants.

## DISCUSSION

As it has been pointed out by Warburg (1938) and Sansome (1936) Geraniums are not easy both for cytological studies and breeding experiments, and it is extremely difficult to collect material sufficient for any conclusive explanation of genetical background of gynodioecy in the taxon studied.

Desynapsis found in Plant No. 5 and to some extent in Plant No. 20—1 seems to be the exception rather than rule in MS plants of *G. sylvaticum:* First, progeny of Plant No. 5 showed completely normal meiosis. Second, when desynapsis occurs resulting pollen grains are of very variable sizes, so that it is enough to examine the pollen grains to determine whether meiosis was normal or not. In this manner 16 MS and 10 PS plants from a wild population of *G. sylvaticum* were examined. In 7 (MS) plants the anthers contained no pollen. In all others the anthers contained pollen showing varying degrees of degeneration (in some anthers from PS plants pollen was of course normal), but always within one anther all pollen grains were of equal sizes. This indicated that there were probably no disturbances during meiosis.

Third, is seems as if desynapsis only were responsible for abnormal pollen formation one would expect that in some microspores at least there would be the full haploid chromosome complement and some pollen grains would be fully viable (c.f. e.g. Koller 1938; Gajewski 1949; Rick 1945, 1956; Swaminathan and Murty 1959). But in Plant No. 5 all pollen was inviable and at the time of flowering —

devoid of protoplasm. So apart from abnormal meiosis there was probably another factor (or factors) responsible for pollen degeneration and operating at some time after meiosis and before flowering.

On the basis of present cytological evidence no hypothesis as to the real causes of pollen degeneration in *G. sylvaticum* can be worked out. No obvious differences in tapetum between MS and MF plants were observed. The cytological picture of pollen degeneration can be summed up as follows:

1. Degeneration can begin at any moment after the liberation of young pollen grains from tetrads and before anthesis.

2. First symptom of pollen degeneration is cytoplasm shrinking and collapsing of pollen grains walls. If this process begins early (soon after young spores liberate from tetrads) the anthers remain small and sometimes they are dry at the time of flowering, or if not dry they are completely empty. If pollen degeneration begins late, just before flowering, the anthers can be of nearly normal size, but colourless. The pollen grains are then large but either completely devoid of protoplasm or it is shrunken.

3. Pollen degeneration can occur either in the whole anther, or in part of it (one or two pollen sacs, or even a half of one pollen sac can degenerate), but always in a given part of an anther all pollen grains are affected.

*G. sylvaticum* seems to be a perfect example of dependence between pollen development and corolla dimensions (c.f. S a n s o m e 1936). The petals of MS plants were nearly half the size of MF flowers. Besides, the former were more intensely coloured than the latter (total amount of pigment per flower unchanged?). When one or two anthers in a flower were non-degenerated the petals opposite to them were distinctly bigger than the others (Fig. 4).

The most characteristic feature of male sterility in *G. sylvaticum* is the presence of three types of plants, MF, MS an intermediate — PS. The last class contained plants with all possible degrees of male sterility, from individuals with only some anthers in a few flowers being degenerated, to those in which only some anthers in a few flowers contained normal pollen. This suggests that there can exist some sub-threshold physiological condition which can be shifted towards pollen degeneration at different times of pollen development. This situation can be interpreted from the point of view of its genetical background in two ways.

First, male sterility is determined by several genes whose common effects result in pollen degeneration. Small doses of the genes remain without effect or the effect is delayed — then pollen does not degene-

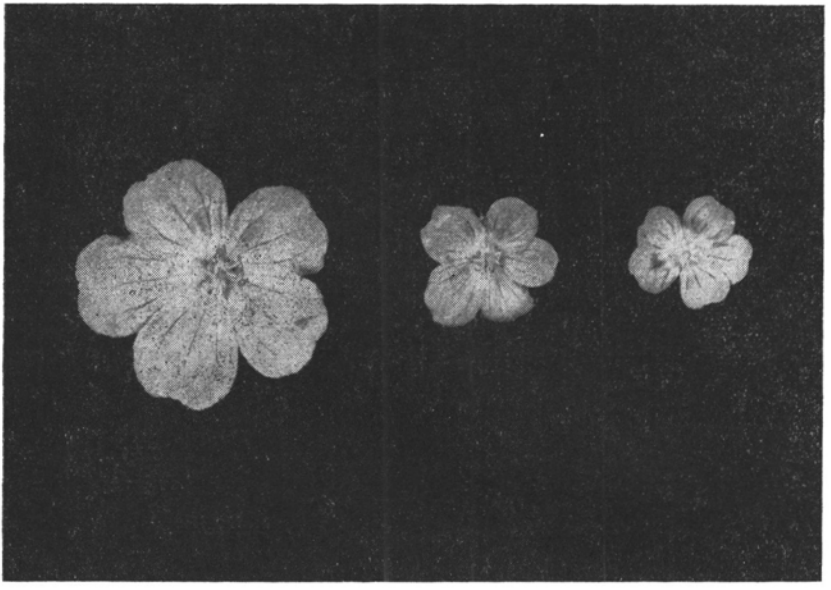

Fig. 4. Three types of flowers of *G. sylvaticum* var. *alpestre*. Left — MS flower; centre — PS flower with two fertile anthers and distinctly bigger adjacent petals; right — MF flower

rate or only some anthers degenerate. When the doses of the genes are higher the equilibrium is shifted towards earlier pollen degeneration. Then there are more PS or MS flowers. Lastly if the doses of male-sterility genes are still higher, all pollen degenerates, the plants being completely male-sterile (c.f. M e y e r s 1946). On this assumption both MS and MF plants can be heterozygous and show segregation. This is in full agreement with the following observations: In "exceptional", selfed progeny of Plant No. 4 there were MS, PS and MF plants. The selfed MF sector of Plant No. 3 gave both MF and PS plants. Among progeny of MF Plant No. 18 there were the three types of plants, MS, PS and MF.

Alternatively, there are two major genes determining male-sterility, but their phenotypic expression is modified by minor factors which gives in effect the whole range from complete male-sterility to complete male fertility. *G. sylvaticum* is a typical cross-pollinating species with protandry and partial selfincompatibility. Plants in wild populations must be highly heterozygous and many factors can segregate both in wild populations and in progeny of controlled crosses. The facts stated above (both, MS and MF plants can show segregation) could be explained by analogy with the situation stated in *Origanum vulgare:* MF plants with FfHh genotypes segregate MF and MS progeny. MS

plants can be either homozygous (FFhh) or heterozygous (Ffhh). If it were possible to obtain selfed progeny of the heterozygotes and if bottom recessive homozygotes (ffhh) were viable, the segregation of heterozygous female plants (Ffhh) would be detected.

The data presented here are not sufficient for explanation of genetic mechanism of gynodioecy in the species studied. In *G. sylvaticum* there is no clear-cut difference between MF and MS plants, which suggests a very delicate balance in the physiological state of the developing anthers. Maybe the cytochemical examination of different parts of anthers e.g. tapetum, in different plants could help to understand the process of pollen degeneration in male sterile plants.

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