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Inheritance and cytogenetics of sterility in yellow lupin (*Lupinus luteus* L.)

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Abstract

Among the hybrids of the cultivated form named 'Batavo', originating from Holland, and 6 primitive forms of the yellow lupin was one hybrid combination found (Batavo × primitive No. 5), which in F_2 and F_3 gives fertile and sterile plants with the ratio 3 : 1. The gene causing sterility was appeared as a result of crossing over at the time of prophase of meiosis in the sporogenic cells of F_1 plants. This gene in homozygotic condition in F_2 and F_3 plants causes the coalescence of chromosomes, disturbances in the process of meiosis and microsporogenesis what leads to forms with non viable microspores. The sterile plants blossom abundantly but they give not pods and seeds.

INTRODUCTION

The dependence between the chromosome behaviour in meiosis and fertility in yellow lupin is but little known. This results from the fact that until recently investigations were performed on material genetically differing but little, originating from Germany (Barbacki, 1959). Moreover, hybrids between the forms and varieties derived from this material were not analysed cytologically (Hackbarth and Troll, 1959; Barbacki, 1959; Hanelt, 1960; Atabiekova and Maysurian, 1974). The normal fertility of such hybrids seems to indicate that the central European yellow lupin is cytologically homogenous. Hybrids between the cultivated varieties derived from central-European material (Germany) and primitive forms from Portugal do not show any disturbance in chromosome reduction and are normally fertile (Kazimierski and Nowacki, 1964; Kazimierski and Nowacki, 1971; Nowacki and Kazimierski, 1971). On the other hand F_1 crosses between the cultivated central-European foms and the wild yellow

lupin from Israel are partly sterile because the plants from Israel (ssp. *orientalis*, Kazimierski and Kazimierska, 1975a) differ from the central-European ones in translocation (Kazimierski and Kazimierska, 1975b). The present investigations were performed on hybrids between various geographical yellow lupin forms. They led to the detection of the gene causing sterility of the plants. The way this sterility is inherited in yellow lupin, the moment of activation of the gene causing sterility in the ontogenesis of generative cells and its mode of action are discussed in the present paper.

MATERIAL AND METHODS

The studies were carried out in field conditions on F_1, F_2, and F_3 hybrids between the cultivated form originating from Holland named Batavo and the wild form from Portugal denoted No. 5 as well as on crosses between Batavo and wild forms from Anatolia (Nos 3 and 4) Spain (No. 6) and Portugal (Nos 1 and 2).

For protection against allogamous pollination the inflorescences of F_1 and part of the F_2 plants were covered with cheesecloth.

Pollen was collected from the flowering plants, stained with carmine and the plasma-containing and plasma-free grans were counted and hence the per cent of fertile pollen grains was calculated.

Young flower buds were fixed in Carnoy fluid for analysis of the course of meiosis. Then the pollen mother cells were pressed out of the anthers, stained with propionocarmine and examined under the microscope.

When the plants maturated their height was measured, the lateral branchings and the flowers on the main stem were counted. The pods were counted separately on the main stem and on the whole plant. Fertility was determined as follows: in 10 pods on each plant the ovules and seeds were counted and the per cent of ovules transformed to seeds was calculated.

RESULTS

Table 1 gives the mean number of flowers, and mature pods and the per cent of pods set in relation to the number of flowers on the main stem in F_1 and F_2 hybrids between Batavo and primitive yellow lupin forms. As seen the F_1 hybrids of Batavo $\times$ wild forms are fertile. On the average pods were most numerous on the main stem of the hybrid Batavo $\times$ primitive lupin No. 6 and least numerous on F_1 plants of the cross Batavo $\times$ primitive form No. 5. The highest per cent of pods on the main

stem, as compared with the number of flowers, was found in F_1 plants of crosses Batavo × primitive form No. 6, and lowest on the crosses Batavo × primitive from No. 4.

Fertile F_2 plants do not differ much between themselves in the number of flowers and ripe pods on the main inflorescence (Table 1). In general

Table 1

Average number of flowers and mature pods and per cent of pods set on main stem in F_1 and F_2 plants of Batavo × primitive yellow lupin forms

Hybrids	Generation							
	F_1				F_2			
	number of plants	average number on main stem of:			number of plants	average namber on main stem of:		
		flowers	pods	pods set %		flowers	pods	pods set, %
Batavo × primitive No. 1	19	32.3	12.2	37.7	84	39.5	18.2	46.0
Batavo × primitive No. 2	10	41.0	14.5	35.3	71	38.0	19.1	50.2
Batavo × primitive No. 3	17	38.0	13.0	34.2	45	38.4	19.7	51.2
Batavo × primitive No. 4	15	41.0	12.5	30.5	82	36.9	19.3	52.3
Batawo × primitive No. 5	15	33.7	10.7	31.7	169	37.6	20.1	53.4*
Batavo × primitive No. 6	12	35.8	15.6	43.5	59	36.2	19.9	54.9

* = only for fertile plants

the per cent of mature pods on F_2 plants, as compared with the number of flowers on the main stem, is higher than in the F_1 generation; it was highest in F_2 plants of the cross Batavo × primitive form No. 6 and Batavo × No. 5, and lowest in the cross with the primitive form No. 1.

The per cent of ovules in the pod which transformed to seeds varied in F_1 plants from 74 to 85, in fertile F_2 plants from 83 to 90 (Table 2). In each of the combinations this per cent was lower in F_1 than in the corresponding F_2 plants.

Sterile plants appeared in the F_2 generation of the cross Batavo × primitive form No. 5. As seen from the data in tables 1 and 2, the F_1 and fertile F_2 plants of this cross did not differ much as regards: the number of flowers and ripe pods on the main stem, the per cent of flowers which developed pods and the per cent of ovules in the pods which transformed

to seeds, or were the same as in the F_2 plants among which sterile plants did not appear (Tables 1 and 2).

Table 2

Fertility of F_1 and F_2 hybrids from cross Batavo × primitive yellow lupin forms

Hybrids	Fertility (per cent of seeds set as compared with number of ovules in ovary)			
	Generation			
	F_1		F_2	
	number of plants analysed	%	number of plants analysed	%
Batavo × primitive No. 1	19	73.9	84	83.9
Batavo × primitive No. 2	10	84.9	71	89.6
Batavo × primitive No. 3	17	82.3	45	88.7
Batavo × primitive No. 4	15	80.2	82	85.6
Batavo × primitive No. 5	15	75.9	169	0.0 and 83.1
Batavo × primitive No. 6	12	82.5	59	90.1

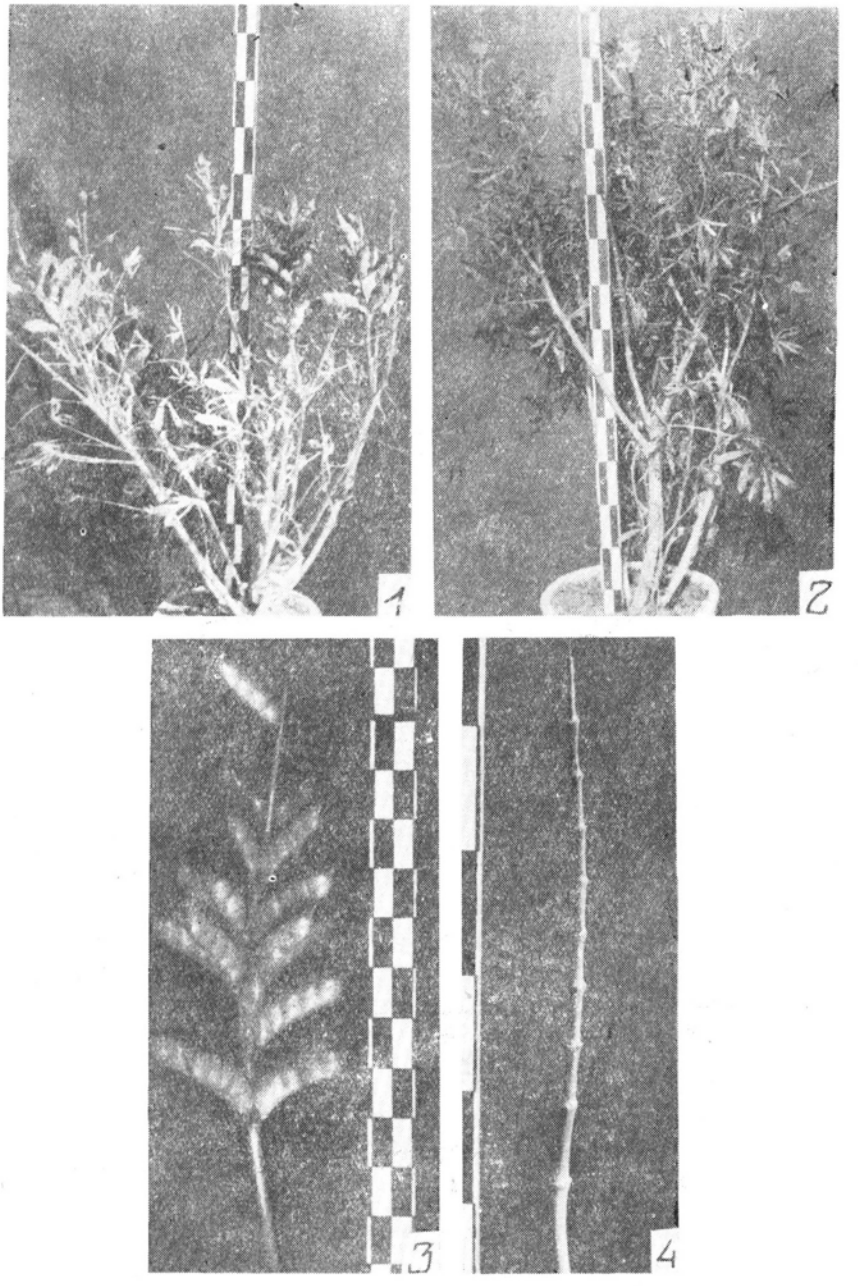
Some characters of the F_1 to F_3 plants of the hybrid Batavo × primitive form No. 5 are given in Table 3. As seen the fertile plants did not differ from the sterile ones in shoot length, number of side branchings and number of flowers on main inflorescence, they were, however, lower than the sterile plants. The difference in their height is due to the fact that

Table 3

Mean height, stem length, number of side branchings and number of flowers in main inflorescence of F_1, F_2 and F_3 fertile and sterile plants of hybrid Batavo × primitive No. 5

Generation	Plants	Number of plants analysed	Height of plant cm	Length od stem cm	Number of side branchings		Number of flowers in main inflorescence
					at base of shoot	in upper part of shoot	
F_1	fertile	15	53.6	46.8	1.8	4.0	33.7
F_2	fertile	131	50.2	47.1	3.1	2.2	43.1
	sterile	38	63.1	47.6	3.0	2.4	44.0
F_3	fertile	446	49.3	48.3	3.5	2.7	45.0
	sterile	90	62.9	48.5	3.6	3.0	45.0

the fertile plants after setting pods on the first order lateral branches did not form higher order branchings (Photo. 1). The sterile forms produced side branchings of first order on which secondary branches developed and



Phot. 1—4. Plants and stem with fruits, date of harvested: 31.VIII.
Plants: 1 — fertile; 2 — sterile; 3 stem with pods from fertile plant; 4 — fruitless stem from sterile plant.

from these in turn of 3rd order or even 4th order (Photo. 2). Hence the sterile plants were higher than the fertile ones. The flowers of the sterile plants were all shed 8—10 days from the moment of blossoming.

As shown by analysis of pollen fertility in the fertile plants, the per cent of fertile grains was 70.0—99.8 per cent, and in the sterile ones all the microspores were deprived of plasma — univable (Table 4).

Table 4

Pollen fertility in F_1, F_2 and F_3 plants of hybrid Batavo × primitive No. 5

Generation	Number of plants analysed	Pollen viability, %				
		0.0	60.1—70.0	70.1—80.0	80.1—90.0	90.1—100.0
F_1	15				2	13
F_2	172	39		4	5	124
F_3	536	90	7	15	28	396

It was easy to separate the F_2 and F_3 plants of the hybrid Batavo × primitive lupin No. 5 into fertile and sterile, since the pollen of the sterile ones was not fertile and the flowers were shed after overblooming (Photos 3 and 4). All the 25 flowers of the sterile plant pollinated with pollen of fertile plants were shed after 10—12 days.

Inheritance of sterility

F_1 plants of the cross Batavo × primitive No. 5 are fertile. In the F_2 generation the per cent of sterile plants in the progeny of the particular F_1 plants varied from 19.44 to 33.33, and the mean for the whole generation was 22.67 per cent. That is the ratio of fertile to sterile plants was close to 3 : 1 (Table 5). Thus, it may be assumed that the described sterility in yellow lupin is determined by one recessive gene. The heterozygotic plants in F_3 also segregated into fertile and sterile (Table 5). The per cent of sterile ones in the progeny of the particular F_2 plants varied from 6.89 to 28.57 per cent, mean 16.78. The somewhat lower number of sterile plants in the F_3 generation may be explained by the fact that not all F_2 plants were isolated, so a certain part of the zygotes in F_2 plants arose from pollination with foreign pollen with a dominating gene which prevented the activation of the recessive gene in F_3.

Meiosis

At prophase of meiosis there is only one nucleolus with homogeneous structure in the nucleaus of pollen mother cells of fertile plants. The particular stages of meiosis prophase are distinct (Photo 5). In diakinesis

Table 5

Inheritance of sterility

No. of plant	Generation	Number of plants		Total	Sterile plants, %	X^2
		fertile	sterile			
1	F_2	2	1	3	33.33	
2		36	13	49	26.53	
3		20	6	26	23.07	
4		19	5	24	20.83	
5		27	7	34	20.58	
6		29	7	36	19.44	
Total F_2		133	39	172	22.67	0.496
No. of plant F_2	F_3					
1		30	12	42	28.57	
2		32	11	43	25.58	
3		36	10	46	21.74	
4		37	9	46	19.56	
5		25	5	30	16.66	
6		37	7	44	15.90	
7		38	7	45	15.55	
8		36	6	42	14.28	
9		39	6	45	13.33	
10		33	5	38	13.15	
11		42	6	48	12.50	
12		34	4	38	10.52	
13		27	2	29	6.89	
Total F_3		446	90	536	16.78	19.262

and the first metaphase there are 26 bivalents in the cells (Photo 6). The first and second divisions are normal (Table 7) and after the second one the microsporocytes transform to microspore tetrads.

In sterile plants the per cent of pollen mother cells with one nucleolus in the nucleus at meiosis prophase varies from 4.2 to 23.9, mean 11.9 per cent (Table 6). From among the polynucleolar cells most numerous are those with 2 and 3 nucleoli, less so cells with 4 and 5 nucleoli. The nucleolus structure is homogeneous, although in the nuclei of part of the pollen mother cells nucleoli with „vacuoles" are present (Photo 7).

During meiotic prophase the chromosomes form a compact poorly differentiated uniformly staining mass adjoining the nucleolus or else this mass lies at a certain distance from it (Photos 8—10). In the multinucleolar cells all nucleoli may be bound with the chromosomes (Phtoto. 9) or some are joined and some lie at the periphery of the nucleus (Photo 8). The coalesced chromosomes form a more or less regular ring which may be closed around the nucleolus (Photo 9) or they form a ring at the nucleus with a small luminous in the middle.

Table 6

Number of nucleoli in nucleus of pollen mother cell at stage of meiosis prophase in sterile yellow lupin plants

No. of plant	Number of analysed PMC	Number of nucleoli in nucleus of pollen mother cells					PMC with one nucleolus in nucleus, %
		1	2	3	4	5	
1	138	33	72	26	7	0	23.9
2	133	8	65	46	11	3	6.0
3	226	25	112	80	8	1	11.0
4	71	3	43	21	4	0	4.2
5	151	14	76	50	11	0	9.2
6	144	20	77	42	5	0	13.8
Total	863	103	445	265	46	4	11.9

In some few pollen mother cells a more distinct transition could be found between diplotene and metaphase I, it was more distinct since at least part of the bivalents were visible (Photo 11). Most frequently, however, the chromosomes coalesced into one ring-shaped group as early as in diakinesis (Photos 12, 13) or they formed a figure of indefinite shape. During metaphase I the chromosomes also formed an amorphous strongly staining mass (photo 14), beyond which lay sometimes a single bivalent and univalents (Photo 15). In the cells in which during metaphase I the particular chromosome figures could be distinguished (as a rule 26_{II}) the chromosomes also coalesced ring-like (photo. 16, Table 7). The chromo-

Table 7

Meiosis and microsporogenesis in pollen mother cells of fertile and sterile F_2 and F_3 plants of hybrids Batavo × primative No. 5

Division stage of PMC	Plants	Number of analysed:				Kind of disturbances
		plants	PMC	cells with disturbances:		
				number	%	
First metaphase	fertile	4	201	0	0.0	No disturbances
	sterile	6	450	450	100.0	Chromosomes coalesced into chain
First anaphase	fertile	3	61	0	0.0	No disturbances
	sterile	6	212	212	100.0	Lagging chromosomes 1-15
Second metaphase	fertile	4	105	0	0.0	No disturbances
	sterile	5	101	101	100.0	Accelerated chromosomes 4-16
Second anaphase	fertile	3	45	0	0.0	No disturbances
	sterile	5	136	136	100.0	Lagging chromosomes 1—9
Tetrads	fertile	4	803	0	0.0	No disturbances
	sterile	6	1073	842	78.5	Monads and other than tatrad microspore polyads
Microspores	fertile	4	736	0	0.0	No disturbaces
	sterile	6	1333	454	34.0	1-4 micronuclei in microspore

some figures were counted in 9 of the 450 analysed pollen mother cells in the stage of metaphase I. In seven of these cells 26_{II} in one $25_{II}2_{I}$ and in one $24_{II}4_{I}$ were present, in the remaining cells the chromosomes were coalesced (Table 6).

During the first anaphase and telophase the chromosomes migrated to the poles unevenly and not synchronously. Separation was frequently untypical, between the polar groups there remained up to 15 chromosomes and fragments (Table 7, Photos 17—20). The chromosomes remaining between the polar groups separated into chromatides or else, beginning with late anaphase, formed micronuclei (Photos 19 and 20). Owing to the nonsimultaneous separation and uneven migration of the chromosomes to the poles during the first anaphase—telophase, diads formed with nuclei of various diameter, between which lagging chromosomes or micronuclei could be seen. There also were pollen mother cells in which the chromosomes in anaphase did not translocate to the poles. In such cells a restitution nucleus formed (Photo 21).

During prophase II chromosomes and micronuclei were found in the cytoplasm of pollen mother cells.

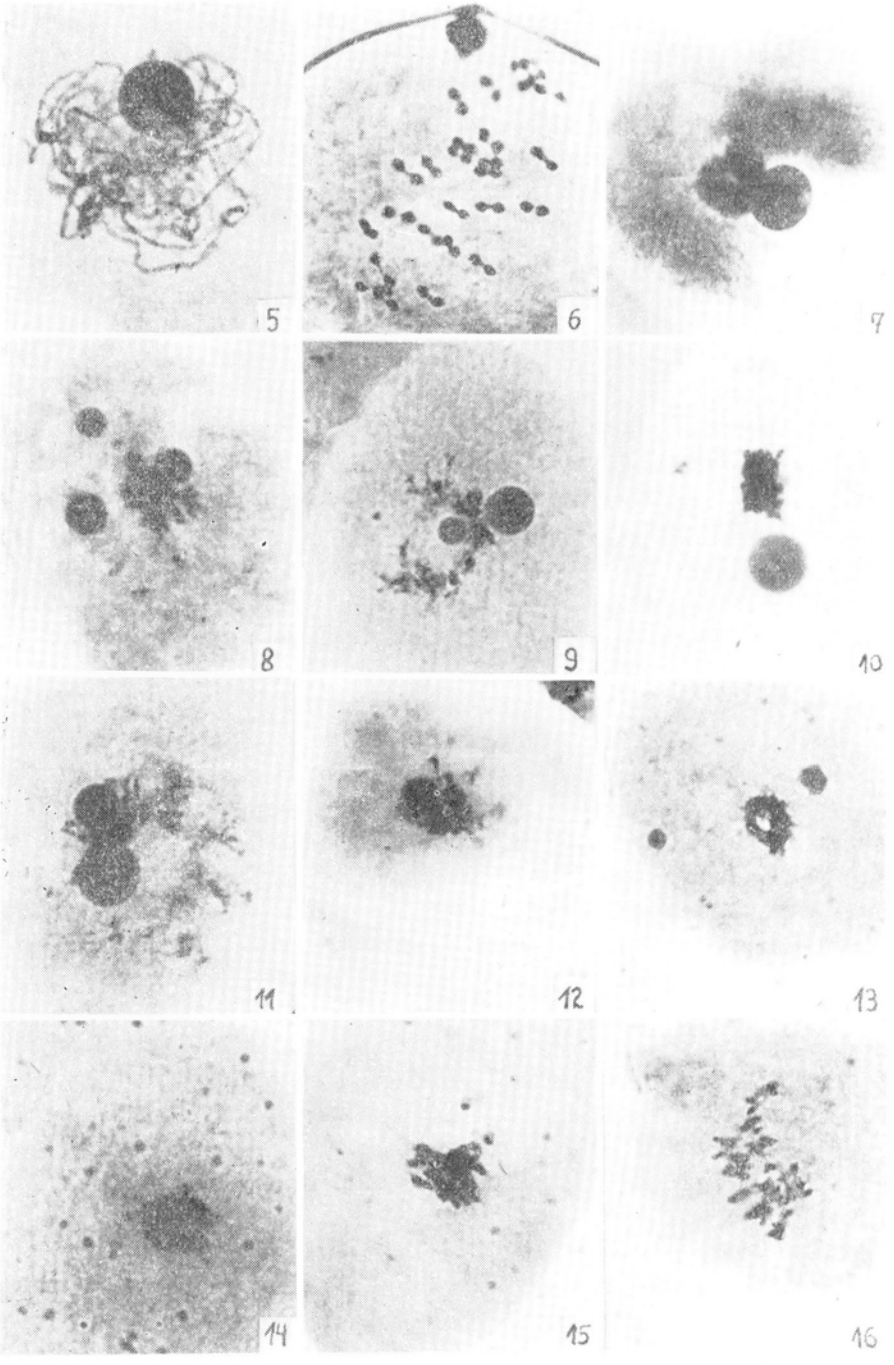
During metaphase II chromosomes as a rule did not form the typical equatorial plate (Table 7). Part of them divided in the cell at the site where they had remained after the first separation (Photos 22—24).

The second separation occurred as irregularly as did the first (Photo 25). During this separation 1 to 9 lagging chromosomes were found. Frequently, during metaphase II the equatorial plates were close to one another, and in such cells at telophase the non-sister nuclei combined (Photo 26), and diads could form from the microsporocyte (Photo 27) as well as a microspore triad (Photo 28) with one or more micronuclei. The presence or absence of micronuclei is connected with the number of chromosomes which remained in the cytoplasm after the second telophase.

Disturbances associated with the first and second division of the nuclei in pollen mother cells of sterile plants exert an important influence on microsporogenesis. As few as 21.5 per cent of microsporocytes transformed after the second division to microspore tetrads, and from the remaining ones there formed polyads of microspores other than tetrads. Some few pollen mother cells in which the nucleus was restituted yielded monads.

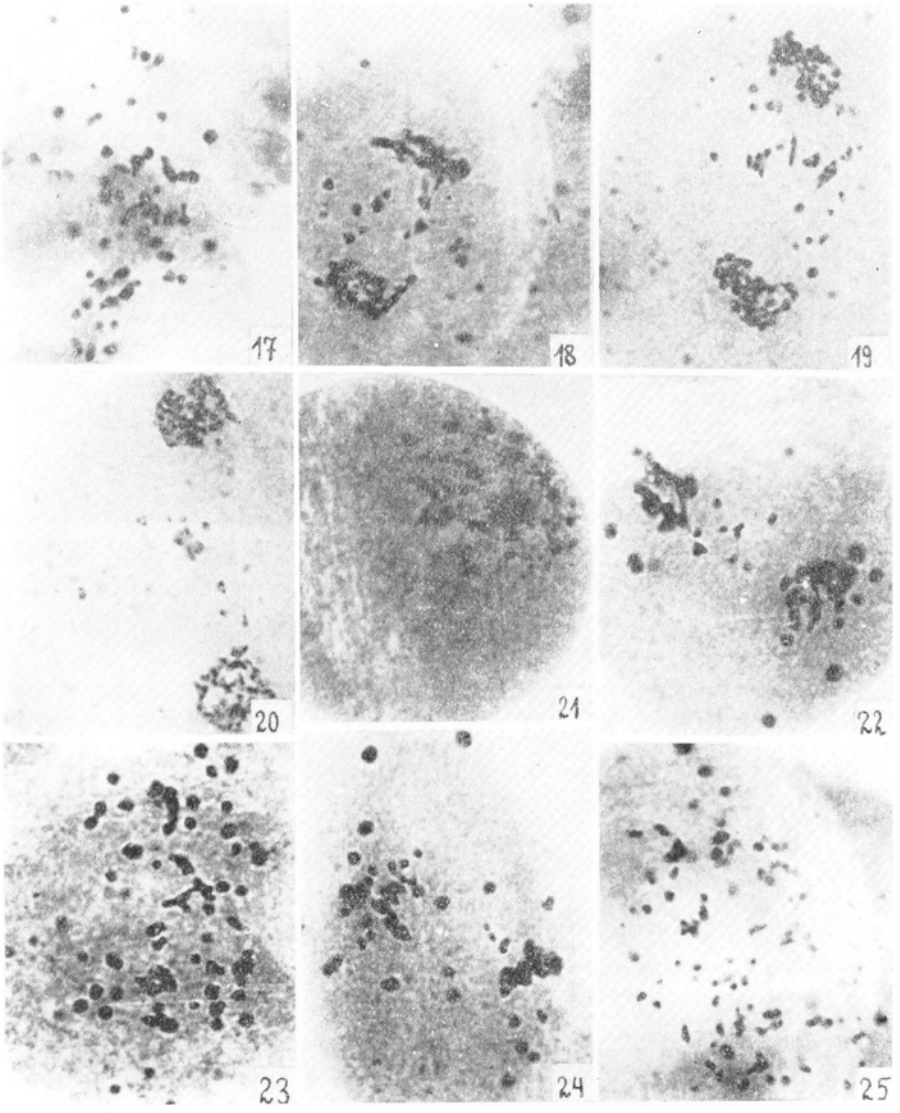
In 1/3 of the microspores analysed, beside the nucleus, micronuclei were present (Table 7, Photo 29). In the cytoplasm of pollen grains with developed exin, in which the nucleus divided into a pollen cell nucleus and a generative one, single chromosomes were found outside the metaphase group (Photo 30).

The nucleus of the microspores analysed had one nucleolus. Sporocytes were also found in which 3 microspores had one nucleolus in the nucleus, and in the fourth nucleus it was absent (Photo 31). This may be



Phot. 5—16. Meiosis in PMC's of fertile and sterile plants

5—6 fertile plants; 5 — pachytene; 6 — metaphase I, 26_{II}; 7—16 sterile plants; 7—10 prophase of meiosis; 7 — nucleoli with "vacuoles", chromosomes stick together forms a ring with a luminous in the middle; 8 — three nucleoli into nucleus, larger part of chromosomes stick together; 9 — two uncleoli into nucleus, stick chromosomes forms not closing ring; 10 — one



Phot. 17—25. Meiosis in PMC's of sterile plants

17—20 anaphase—telpohase I, lagging and accelerated chromosomes, fragments and micronuclei; 21 — restitution nucleus; 22 — metaphase II, plates ill-shaped, lagging and retarded chromosomes, micronucleoi; 23 — mataphase II, kariokinetical spindles lay close to one another; 24 — metaphase II two groups and the remaining chromosomes scattered in cell; 25 — anaphase—telophase II, irregular division.

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nucleolus into nucleus, one chromosome beyond the group the remeining stick together; 11 — diplotene, tow nucleoli in the nucleus, part of the chromosomes sticked a single of them are situated beyond the compact group; 12—13 diakinesis; 12 — sticked chromosomes forms a ring at the nucleolus; 13 — sticked chromosomes forms ring, two nucleoli; 14—16 metaphase I; 14 — sticked chromosomes and many spherical chromatin bodies; 15 — sticked chromosomes, there are visible 1_{II} and 2_{I} laying beyond compact mass and spherical chromatin bodies; 16 — 26_{II}, bivalents sticked into one ring.

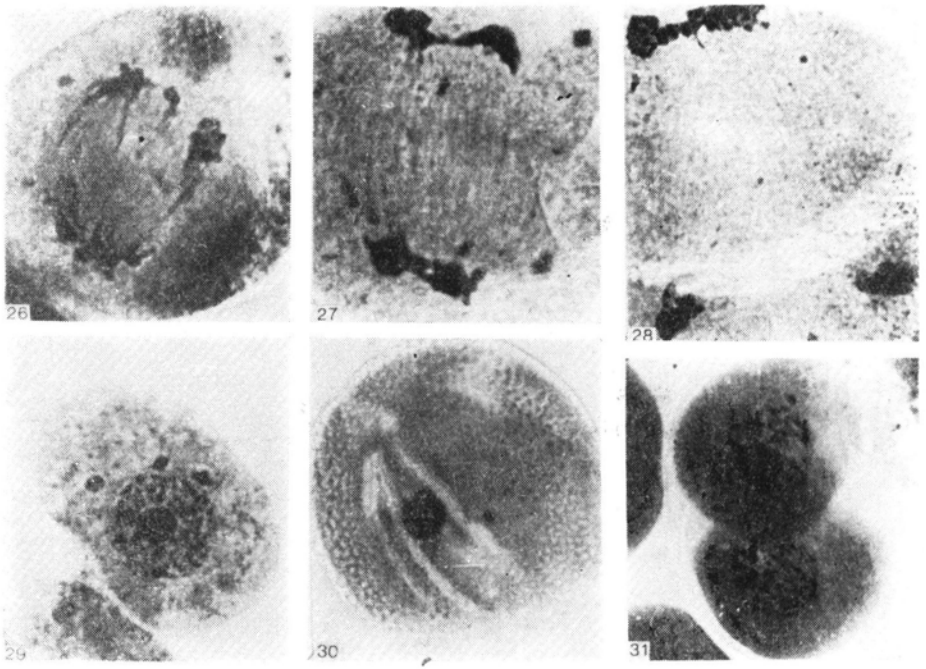

Photo. 26—31. Meiosis and microsporogenesis in PMC's of sterile plants

26—28 anaphase—telophase II; 26 — pulling chromatid arms; 27—28 connexion of non-sister nuclei, lagging chromosomes; 29 — three micronuclei in microsport; 30 — mitosis in pollen grain, one chromosome beyond metaphase group; 31 — microspores, one of them without nucleoli.

evidence that in the nucleus deprived of the nucleolus the organizer chromosome of the nucleolus is lacking. Probably in the process of division with the associated disturbances this chromosome wandered to another microspore of the tetrad. The absence of a nucleolus in the microspore nucleus may also result from a deficit in it of some compound which stimulates on the chromosome the inactive centre conditioning organization of the nucleolus.

DISCUSSION

Tedin and Hagberg (1952) obtained sterile yellow lupin plants after irradiating the seeds with X-rays. These plants exhibited also changes in other characters. The authors believe that the infertility described by them was conditioned by one recessive gene, since among 388 X_2 plants 55 were sterile. Within other wild and cultivated species of the genus *Lupinus such* a gene(s) have not been described (Hackbarth and Troll 1959; Francis and Gladstones, 1973; Barbacki, 1959; Atabiekova and Maysurian, 1974). In the present case the steri-

lity is conditioned by one recessive gene, since the ratio of fertile to sterile plants in F_2 is 3 : 1, and among the segregating F_3 lines this ratio is similar to that in F_2. Thus, the sterility described by us in yellow lupin is conditioned by one recessive gene for which we suggest the name sterilis femines et masculinus (*sfm*).

This gene appeared in F_2 of the hybrid between Batavo and the primitive No. 5. In the F_2 generation of crosses between Batavo and other prymitive forms as well as between primitive No. 5 and other primitive or cultivated yellow lupin forms no signs of activity of this sterility gene could be traced (K a z i m i e r s k i and K a z i m i e r s k a in preparation). Thus, the forms Batavo and the primitive No. 5 differ in the set of genes conditioning fertility. There formed in F_1 plants as the result of crossing-over between homologous chromosomes a new combination which made possible the manifestation of the *sfm* gene. Analysis of the segregations allows the following hypothesis. In both the studied forms fertility is conditioned by two coupled genes. In one form the latter are equivalents $\frac{SFM}{SFM}$, while in the other one gene is epistatic in relation to the other $\frac{SFMe}{sfm}$. The breaking of the coupling in the process of meiosis, translocation of the hypostatic gene (*sfm*) to the site of the equivalents one (*SFM*) and vice versa, made possible the manifestation of gene *sfm*, since it came into the neighbourhood of a gene which does not overlap its activity $\frac{SFM}{sfm}$. As regards the action of gene *SFM* which after double crossing-over was situated in the neighbourhood of the epistatic gene $\frac{SFMe}{SFM}$, it is difficult to say anything about it.

Analysis of the morphological features, the structure of the flower and inflorescence, of fertile and sterile F_2 and F_3 plants demonstrated that the *sfm* gene does not affect the morphological features. The greater height of the sterile plants results from the utilization of assimilates for development of the nonfructifying side branchings of 1st, 2nd, 3rd and 4th order. In fertile plants the assimilates produced are used for development of the seeds set on the main stem and side branchings of 1st order.

It was demonstrated in the analysis of the course of meiosis and microsporogenesis that the *sfm* gene acts on generative cells beginning with meiosis prophase. In sterile plants 2 to 5 nucleoli formed in the nucleus of most analysed pollen mother cells, whereas in the nucleus of pollen mother cells of fertile plants there was only one. The formation of additional nucleoli may be indicative of a certain excess in the nucleus of substances which are constituents of the nucleolus (B i e l a y e v a, 1971). Probably this excess causes among other things the coalescence of chro-

mosomes and of bivalents in turn. Beginning with leptotene, namely, up to the first metaphase all chromosomes or their majority are coalesced. It is. therefore, difficult in sterile plants to distinguish the stages of meiosis prophase and the chromosome figures. In some few pollen mother cells, inwhich the chromosomes lay loosely during first metaphase, it was found that they occurred in the form of bivalents the number of which was 26_{II}. Thus, the chromosome figures and their number during metaphase I were the same in sterile and in fertile plants. This would indicate that the gene *sfm* probably does not interfere with chromosome conjugation. Univalents were seldom found in pollen mother cells in the number of 2 to 4, they probably formed owing to premature breaking of the chiasmata.

Chromosomes in anaphase I were scattered between the poles. In telophase part of the chromosomes aggregated at the poles, the remaining ones divided into chromatides or formed micronuclei. The chromosomes moving towards the poles during anaphase I were coalesced and it was difficult to count them accurately. Those, however, which remained between the telophase groups (up to 15) as well as the diameter of the interphase nuclei and micronucleus allow the supposition that in the nuclei of both diads the number of chromosomes was unequal and smaller than 26.

In the examined pollen mother cells part of the chromosomes during second metaphase were outside the irregular division plates. During anaphase II the chromosomes were scattered between the poles of the karyokinetic spindles. Quite frequently the spindles in the cell lay close to one another, and in late anaphase-telophase the nonsister nuclei combined with one another.

Most microsporocytes, after the second division, transformed to microspore polyads other than tetrads, with usually one nucleolus in the nucleus. There were also microspores without any nucleolus and others in which beside the nucleolus there were 1—4 micronuclei. The absence of the nucleolus in the microspore nucleus may be evidence that among the chromosomes the nucleolus organizer is missing; owing to disturbances in division and migration of the chromosomes to the poles it wandered to the nucleus of some other microspore. Another cause may be the absence in such a microspore of trace amounts of some compounds indispensable for activation of the chromosome segment in which the nucleolus organizer is present, thus this segment remained inactive (B i e l a y e v a, 1971). In both cases the result is the same — absence of the nucleolus in the nucleus — although the causes may vary.

Micronuclei in microspores are the result of disturbances in the meiotic divisions. Lagging chromosomes were found in nearly all analysed pollen mother cells, and micronuclei in 1/3 of the examined microspores. It would seem, therefore, that in part of the microspores the lagging chromosomes combined with the polar groups before formation of the nuclear

membranes, otherwise the number of microspores with micronuclei would have been higher.

In the process of pollen mother cell division there also occurred restitution of the nucleus and the microsporocyte transformed either into one microspore, or one large and additionally one or sometimes two small microspores. In the former case the restitution may be considered as complete, in the latter — incomplete since several chromosomes are present in the small microspore.

The sterile plants produced no seeds. It is possible that the sfm gene caused disturbance in the process of meiosis in the megasporocytes not less severe than in the microsporocytes, leading to complete sterility.

CONCLUSIONS

1. F_1 hybrids between the cultivated form of yellow lupine originating from Holland and named Batavo and 6 primitive forms: 3 from Portugal (Nos 1, 2 and 5), 2 from Anatolia (Nos 3 and 4) and one from Spain (No. 6) are fertile. The F_2 plants of crosses Batavo $\times$ the primitive forms Nos 1, 2, 3, 4 and 6 are also fertile, and among the F_2 and F_3 plants of the hybrid Batavo $\times$ primitive form No. 5 fertile and sterile plants were found.

2. From among the 172 F_2 plants of the cross Batavo $\times$ primitive No. 5, 133 were fertile and 39 sterile. In the F_3 generation of the total number of 536 plants 446 were fertile and 90 sterile. In both the generations studied the ratio of fertile to sterile plants was close to 3 : 1. Thus, sterility is conditioned by one recessive gene which was named sterilis femines et masculinus *(sfm)*.

3. The *sfm* gene appeared in the F_2 generation of the hybrid between Batavo and the primitive form No. 5, thus these forms differ in their set of genes conditioning fertility. The segregations allow the supposition that in both studied forms fertility depends on two coupled genes. In one form these genes are equivalent and in the other one gene is epistatic in relation to the second one. After double crossing over the hypostatic gene *(sfm)* was brought to the neighbourhood of the equivalent gene *(SFM)* and manifested itself as the gene of female and male sterility *(sfm)*.

4. The *sfm* gene causes an increase in the number of nucleoli in the nucleus of the pollen mother cell in meiosis prophase and coalescence of chromosomes from meiose prophase up to anaphase II. The course of meiosis is irregular, lagging and accelerated chromosome fragments and micronuclei, may be found in the cell. After the second division 78.5 per centof the microsporocytes transform to various polyads beginning with tetrads. In 1/3 of the microspores micronuclei are present, some microspores have nuclei without nucleoli.

5. The sterile plants have shrivelled pollen grains without plasma, they are unfertile. When pollinated with pollen of fertile plants they do not set pods and seeds. On these sterile plants all flowers are shed 8—10 days after blossoming.

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Dziedziczenie i cytogenetyka niepłodności u łubinu żółtego (Lupinus luteus L.)

Streszczenie

Krzyżowano formę uprawną łubinu żółtego, pochodzącą z Holandii o nazwie Batavo, z sześcioma formami prymitywnymi, z których trzy pochodziły z Portugalii (Nr. 1, 2 i 5), dwie z Anatolii (Nr 3 i 4) oraz jedna z Hiszpanii (Nr 6). Wszystkie

rośliny F_1 były płodne; w F_2 mieszańca Batavo × prymitywny Nr 5 znajdowano rośliny płodne i niepłodne, drugie pokolenie pozostałych mieszańców okazało się płodne.

W F_2 i dla rozszczepiających się linii F_3 mieszańca Batavo × prymitywny Nr 5 stosunek roślin płodnych do niepłodnych był bliski 3 : 1, co wskazuje, że niepłodność jest warunkowana przez jeden gen recesywny. Wspomniany gen wywołuje jednocześnie niepłodność męską i żeńską i nazwano go *sterilis femines et masculinus* (*sfm*).

Analiza rozszczepień pozwala przypuszczać, że u obu badanych form (Batavo i prymitywny Nr 5) płodność zależy od dwóch sprzężonych genów. Przy czym u jednej z nich geny te są równoznaczne, u drugiej — jeden jest epistatyczny w stosunku do drugiego. Po podwójnej wymianie, w profazie mejozy u roślin F_1 gen hypostatyczny (*sfm*) znalazł się w sąsiedztwie genu równoznacznego (*SFM*) i ujawnił się jako gen niepłodności żeńskiej i męskiej (*sfm*). Działanie genu niepłodności, w stanie homozygotycznym u roślin F_2 i F_3, powoduje sklejanie się chromosomów, co pociąga za sobą nieregularny przebieg mejozy, mikrosporogenezy i prowadzi do powstania nieżywotnego pyłku.

Rośliny niepłodne obficie kwitną, nie wiążą jednak strąków i nie dają nasion.