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Inheritance of changes conditioned by the leaf-reducing gene in Swedish clover (*Trifolium hybridum* L.)

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Abstract

A description of a new mutant of *Trifolium hybridum* with reduced leaf blades is given. The mutants are female sterile due to deficient ovary development. The genetic analysis showed that morphological changes and lowered fertility are caused by one recessive allele of the gene called *reductivus*.

Male infertility in B_1 plants depends also on one recessive gene, but located on a different chromosome than is the *reductivus* gene.

INTRODUCTION

In the progeny of Swedish clover plants originating from a population from the environs of Poznań one plant was found with different leaflets. Particularly the lateral leaflets with deeply serrated edges were greatly reduced. No plants with such leaf structure have been found in other examined Polish and foreign populations. Neither is there mention, in systematic descriptions, breeding and genetic studies devoted to Swedish clover, of occurrence within this species of plants with a similar leaf structure (Hegi, 1954; Szafer and Pawłowski, 1959; Bobrov, 1947; Coombe, 1976; Kozhukharov, 1976; Vavilov, 1922; Zhelenina, 1932; Williams, 1951; Julen, 1959; Mackiewicz, 1965).

The plant with reduced leaves proved to be but little fertile. The question arises whether leaflets blade reduction has any connection with fertility.

The present investigations revealed how this discovered trait is manifested and inherited.

MATERIAL AND METHODS

Some morphological traits were measured: length and width of leaflet blades, length of petiole, length of shoots, length of flower and width of vexillum, on normal and reduced leaves of the initial plants and those of the F_1, F_2 and B_1 generations. The inflorescences were also counted on each plant and flowers in the head. The epidermis was removed from the lower side of the leaf blade and placed in glycerin. Then the length and width of the stomata was measured under the microscope and their number per leaf surface area unit. Pollen was collected from the opened flowers, stained with an aceto-carmine--glycerin mixture, and the number of stained and unstained grains was counted and the diametre of stained grains was measured.

In the flowers chosen for crossing the anthers were removed, and on the next day they were pollinated with pollen from related and unrelated plants.

The ovary was analysed under a stereoscopic microscope for establishing its structure after removal of the calyx and perianth. Particular attention was devoted to the degree of coalescence of the ventral suture and the position of the ovules.

The crosses and measurements were done on material growing in a greenhouse. For genetic analysis material from an experimental plot and from a greenhouse was used.

RESULTS

The plant with reduced leaflet blades was found among 5086 specimens in one of 39 Swedish clover populations. The origins of the studied populations were as follows: 35 of them belonged to native populations collected from natural sites in Poland in the period 1966—1968, 4 populations were foreign, they came from Bulgaria, Czechoslovakia, France and Portugal. The plant with different leaflet structure was found in one of three populations from the environs of Poznań.

The plant with different leaflets was reciprocal-crossed with plants having typical leaflets. A total of 128 flowers were pollinated from which 59 seeds were obtained. The plant with reduced leaf blades set but few seeds — from 88 pollinated flowers only 5 seeds were collected. In reciprocal crossing, from 40 flowers 54 seeds were obtained. In the former case 0.06 and in the latter 1.35 seeds to one pollinated flower were obtained on the average.

Table 1

Average length of petioles and length and breadth of leaflets in F_1 and F_2 hybrids between Swedish clover plants with normal and reduced leaflets

Generation	Leaflets	Length of petioles (cm)	Length of leaflets (mm)			Width of leaflets (mm)			Length to breadth ratio		
			middle	lateral		middle	lateral		middle	lateral	
				1	2		1	2		1	2
F_1	normal	12.7	31.8	29.4	29.2	23.4	23.7	20.7	1.35	1.24	1.41
F_2	normal	10.2	25.5	24.4	24.1	20.5	18.1	17.9	1.24	1.35	1.34
	reduced	11.1	23.6	16.0	14.7	15.4	7.0	6.0	1.53	2.27	2.44

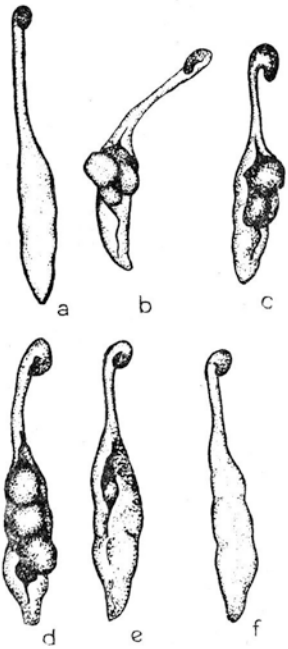


Fig. 1. Ovary from the plants with normal and reduced leaves:

a — from the plant with normal leaves; b, c, d, e, f, — from the plant with reduced leaflets; b, c, d, e, — non-fused ovary, ovules outside the ovary; f — fused ovary

F_1 sedlings in reciprocal-crosses did not differ from one another. They had wide obovate leaflets (Table 1) finely serrated on the edges. The F_1 plants were tall and formed numerous shoots and flower heads (Table 2). There were few heads with less than 50 and more than 90 flowers. Most frequently their number varied between 51 and 90.

Table 2

Height of plants, number of shoots and heads in F_1 and F_2 hybrids between Swedish clover plants with the normal and reduced leaflets

Generation	Leaflets	Height of plants (cm)			Number of:									analysed plants
					stems			heads per plant			heads per stem			
		from	to	average	from	to	average	from	to	average	from	to	average	
F_1	normal	45	89	63.4	21	55	33.5	35	132	90.0	3	17	6.2	43
F_2	normal	29	88	54.2	9	26	15.9	29	155	67.6	2	15	5.3	64
	reduced	15	63	40.6	5	20	10.7	10	91	33.2	1	5	3.2	28

Table 3

Variability of the beginning of flowering in Swedish clover hybrids between plants with normal and reduced leaflets

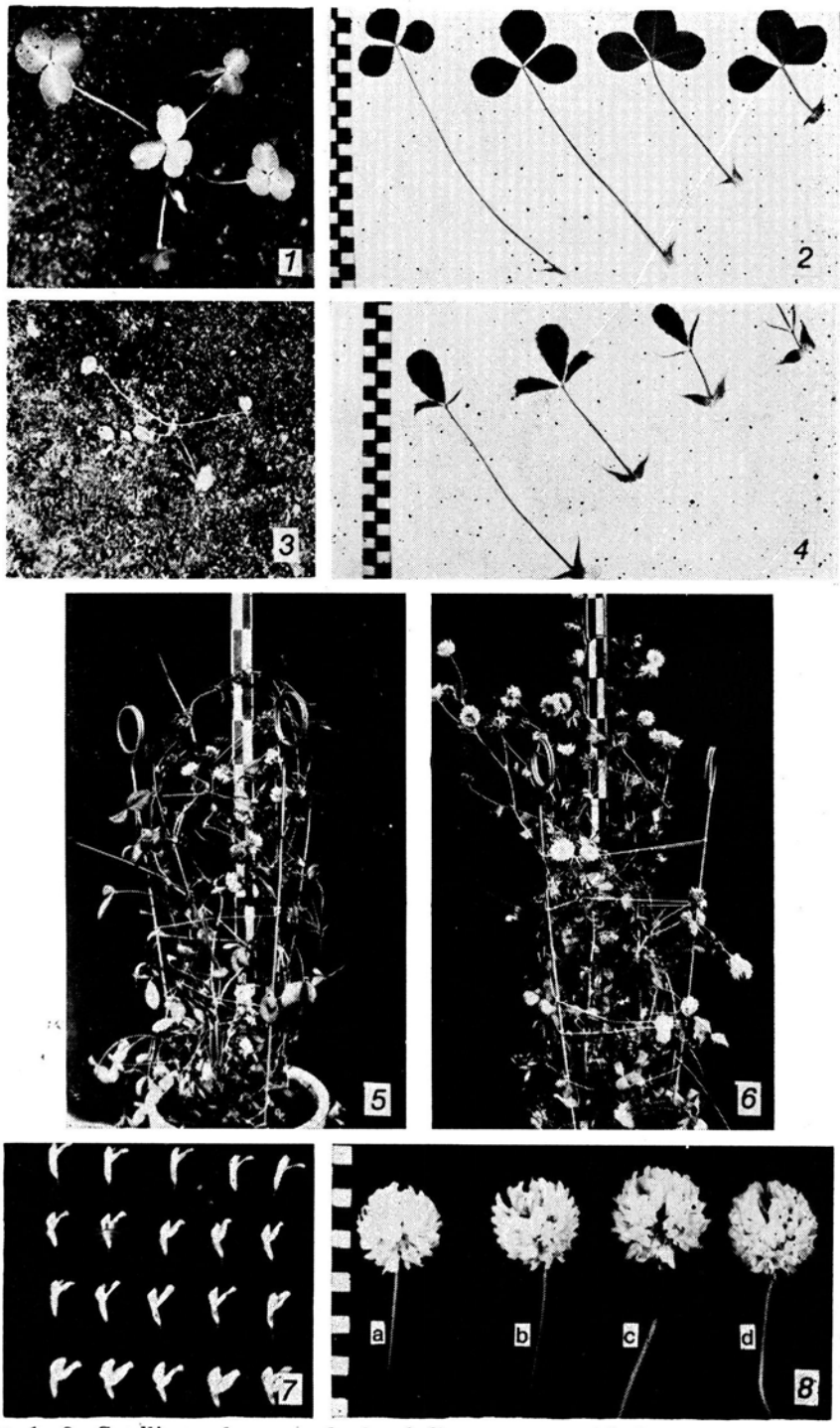
Generation	Leaflets	Date of flowering:							Number of analysed plants
		1—10.III.	11—20.III.	21—30.III.	31.III.—9.IV.	10—19.IV.	20—29.IV.	30.IV.—9.V.	
F_1	normal	4	8	14	9	5	2	1	43
		11—20.V.	21—30.V.	31.V.—9.VI.	10—19.VI.	20—29.VI.	30.VI.—9.VII.	10—19.VII.	
F_2	normal	3	13	25	23	11	3		78
	reduced		6	16	6	3	1	1	33

F_1 plants started to flower in March and continued to the beginning of May (Table 3). When intercrossed and back-crossed with the plant exhibiting reduced leaflets, they set seeds abundantly. The F_2 and B_1 seedlings differed from one another by the shape of their leaflets. After emergence the first developed single leaf was oval in most seedlings, somewhat elongated with smooth unserrated edges. The remaining seedlings showed a first leaf reduced almost to the main vein, its edges constituting the remnants of the leaf blade were deeply serrated. In seedlings with a typical first leaf the following ones are trilobate (Photo 1). They do not differ much from one another in shape and dimensions and their edges are shallowly serrated (Table 1, Photo 2). The ratio of the leaflet blade length to the width of the middle and two lateral lobes was 1.2 and 1.3.

In plants with reduced leaf blade in the first leaf (Photo 3) the following developing leaves grew on a petiole longer on the evarage than in the plants with normal leaves. These leaves consisted of 3 lobes of different length (Table 1). The differences between the width of the middle and lateral leaflet blades proved wider than those in length. The edges of these leaflets were deeply serrated (Photo 4). The length to width ratio in the middle and lateral leaflets (Table 1) indicates a greatly advanced reduction, particularly of the side leaflets. This reduction was not equal, one side leaflet being larger than the other. In leaves on the shoots, particularly those growing from the nodes at the tip of the shoot, the blades were almost nonexistent (Photo 4). They consisted of 3 midveins and remains of the blade in the form of serration. Thus, the leaflets of plants with reduced blades were shorter and narrower than those of normal plants and differed from them in shape.

The plants with reduced leaflets were on the average 14 cm lower, they developed less shoots and flower heads than those with normal leaflets (Table 2, Photos 5 and 6). The number of internodes on the shoot in plants with normal leaflets was higher than in those with reduced leaflets. In the former plants it was never below 5 and amounted on the average to 9.2, in the latter the lowest number of internodes was 3, and the average 6.9. The successive internodes on the shoot of plants with normal leaflets were longer than on those with reduced leaflets. The number of heads on the shoot of plants with normal leaflets was on the average higher than on the plants with reduced leaves (Table 2).

Plants with normal leaf blades started to flower earlier, those with reduced leaflets came into flower about 10 days later. The latest to flower was one of the plants with reduced leaflets which bloomed 10 days later than the latest plants with normal leaflets (Table 3).



Photos 1—8. Seedlings, leaves, plants, inflorescences and flowers of *Trifolium hybridum* plants with the normal and reduced leaflets

Photo 1 — Seedling with normal leaves; Photo 2 — Leaves with normal leaflets; Photo 3 — Seedling with reduced leaflets; Photo 4 — Leaves with reduced leaflets; Photo 5 — Plant with reduced leaflets; Photo 6 — Plant with normal leaflets; Photo 7 — Flowers: lines 1 and 3 — from the plants with reduced leaflets, lines 2 and 4 — from the plants with normal leaflets; Photo 8 — Inflorescences: a and c from the plants with reduced leaflets, b and d from the plants with normal leaves

In the period of flowering the length of the inflorescence peduncles and flowers was measured, the flowers in heads were counted and pollen was taken for calculating the percentage of viable grains and measuring the grain diametre.

Table 4

Length of inflorescence peduncles, flowers and the vexillum breadth in Swedish clover plants with normal and reduced leaflets

Generation	Leaflets	Length of: inflorescence peduncle (cm)			flower (mm)			Breadth of vexillum (mm)		
		from	to	average	from	to	average	from	to	average
F_1	normal	5.2	10.9	6.8	8.1	10.6	9.4	3.8	5.6	4.6
F_2	normal	4.3	10.1	6.1	8.0	10.3	9.2	3.9	5.5	4.7
	reduced	4.7	10.6	6.0	8.0	9.9	8.8	2.9	4.1	3.5

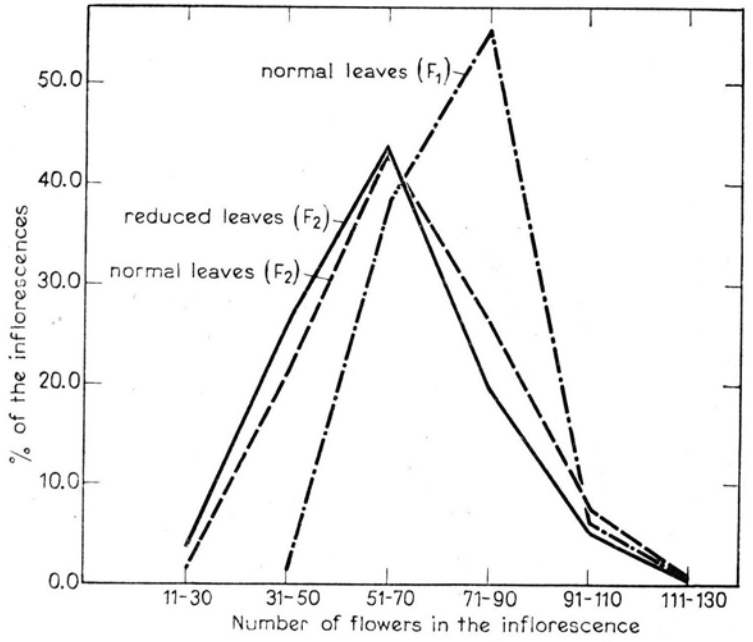


Diagram 1. Flowers number variability in the inflorescences of F_1 and F_2 hybrids between *Trifolium hybridum* plants with the normal and reduced leaflets

The inflorescence peduncles of plants with normal and reduced leaflets proved almost equal in length (Table 4). The flowers of normal plants were by 0.4 mm longer and their vexilla by 1.2 mm broader than in the plants with reduced leaflets (Table 4, Photo. 7).

The number of flowers in the head varied for both plant groups from 18 to 124 (Photo. 8). The curves of frequency of heads with a given number of flowers for both groups of plants were characterized by one peak and their shapes were similar (Diagram 1). For F_2 plants the curves differ from those for the F_1 ones. The latter have a somewhat different range of variability and do not descend below 36 flowers in the head (Diagram 1).

Pollen viability in the initial and F_1 plants was high (Table 5) in some specimens it was lower than 80.0 per cent. For the F_2 plants the percentage of viable pollen grains is given separately for the group with normal and that with reduced blades (Table 5). As seen, the plants can be classified as those which contain in the anthers viable grains and those in which such grains are absent — the anthers are dried up. Of the former there was 92.8 per cent among the F_2 plants and of the latter 7.8 per cent. The per cent of specimens with viable pollen and those with dry anthers for normal plants and those with reduced leaflets was 92.3 and 7.7 and 93.9 and 6.1 per cent, respectively. Thus, the ratio of plants with viable pollen to those with dried anthers was similar in both groups.

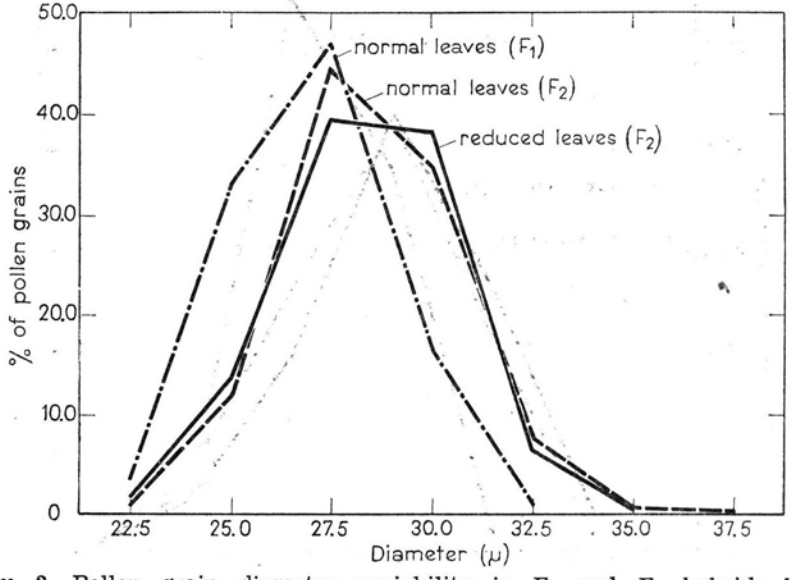


Diagram 2. Pollen grain diameter variability in F_1 and F_2 hybrids between *Trifolium hybridum* plants with the normal and reduced leaflets

Among the plants with reduced leaflets there were no specimens with a percentage of viable pollen grains lower than 50.0 per cent. In the group with normal leaves single plants could be found with a percent of viable pollen grains below 50. For most plants of both groups the percent of viable pollen grains was higher than 90.0.

Table 5

Pollen viability in parental and hybrid plants of Swedish clover

Plants	Percent of viable pollen grains in plants with leaflets: normal									reduced							Total
	0.0	31.0—40.0	41.0—50.0	51.0—60.0	61.0—70 0	71.0—80.0	81.0—90.0	91.0—100.0	Number of analysed plants	0.0	51.0—60.0	61.0—70.0	71.0—80.0	81.0—90.0	91.0—100.0	Number of analysed plants	
Parental:																	
normal leaflets								4	4								4
reduced leaflets															1	1	1
F_1 leaflets: normal × reduced						7	4	25	36								36
F_1 leaflets: reduced × normal							1	3	4								4
F_2		1		4	1		3	23	32				1	2	5	8	40
B_1 (F_1 × leaflets reduced)	6		1	2	3	2	4	28	46	2	3	1		3	16	25	71

Plants with dried up anthers appeared in the F_2 generation when the F_1 plants were pollinated with pollen from the initial plant with reduced leaflets. The direction of the cross played no role here, since in the combination plants with reduced leaves × those with normal ones and in the reverse combination specimens with dry anthers were found. Among the F_2 plants from crosses between F_1 specimens there were none with dry anthers (Table 5).

The average pollen grain diametre was: for F_1 plants 27.5 μ, For F_2 with normal leaflets 28.3 μ, those with reduced leaflets 28.4 μ. The F_1 and F_2 plants did not show any major differences in the average pollen grain diametre. There are, however, certain differences in the variability of pollen grains (Diagram 2). The shape of the curves shows the differences in the grain diametre. Although these curves reach their peaks at 27.5 μ, these peaks are not superposed. The curve of grain diametre for plants with reduced leaflets has a somewhat different range of variability than that for plants with normal leaflets. The latter is similar to the curve for F_1 plants.

Table 6

Length and breadth of stomatal cells in μ and their number on surface of leaves in Swedish clover plants with normal and reduced leaflets

Plants with leaflets	Stomatal cells: length			Stomatal cells: breadth			Number of cells per surface unit			Length to breadth ratio
	from	to	average	from	to	average	from	to	average	
Normal	17.22	21.90	18.80	11.38	15.76	13.87	3	6	4.3	1.35
Reduced	18.98	26.28	21.30	14.30	23.36	17.84	1	6	3.2	1.19

The structure of the epidermis differs in plants with normal and reduced leaflets (Table 6). The stomatas in plants with reduced leaflets are on the average 2.50 μ longer and 3.97 μ wider than in those with normal leaflets. The shape of the cells is also changed: in the plants with reduced leaflets they are rounded, in those with normal leaflets ellipsoidal. Per surface unit of one leaf there are on the average 1.1. more stomata in the plants with normal leaflets than in those with the reduced ones. It should be added that in the plants with reduced leaflets the variations between the minimal and maximal number of stomata per surface unit of the leaf were wider than in the plants with normal leaflets.

As already mentioned, the initial plant with reduced leaflets, when pollinated with pollen from plants with normal leaflets, produced seeds only sporadically. The F_1 plant when intercrossed and reciprocal — crossed with the plants with reduced leaflets gave on the average more

than 1 seed from the pollinated flower. From the F_2 plants with reduced leaflets, after intercrossing and pollination with pollen from plants with normal leaflets, only few seeds were collected (Table 7).

Table 7

Number of pollinated flowers and collected seeds after crosses of Swedish clover plants with normal and reduced leaflets

Year	Leaflets in crossed plants ♀ ♂	Number of: pollinated flowers	Number of: collected seeds	Average number of seeds
1975	reduced × normal	88	5	0.05
	normal × reduced	40	54	1.35
1976	normal × normal	310	356	1.15
	normal × reduced	98	139	1.42
	reduced × normal	80	2	0.02
1977	reduced × reduced	295	31	0.10
	reduced × normal	499	22	0.04
	normal × reduced	110	240	2.18
	normal × normal	50	105	2.10

The number of fertilised flowers which developed pods with seeds, the percentage of pods and the number of seeds in each of them in crosses of two groups of F_2 plants is shown in table 8. When plants with reduced leaflets were intercrossed, or when they were pollinated with pollen from plants with normal leaflets, the percentage of flowers from which pods with seeds developed was low. The pods usually contained 1 and seldom 2 seeds (Table 8). The percentage of flowers with pods and seeds after crossing of normal plants and after pollination of such plants with pollen from plants with reduced leaflets proved high. The most frequently found number of seeds was 2—3 and in some as much as 4. There were but few pods with 1 seed or none (Table 8).

The poor setting of seeds by plants with reduced leaflets may have been due to some changes in the structure of the ovary. Morphological analysis of the ovaries demonstrated that only some of them were typical — the ovules were inside the ovary, the walls of which were coalesced (Fig. 1, Table 9). The percentage of such ovaries varied from 2.4 to 51.3, on the average it was 21.1. The remaining ovaries were not fused, with ovules which lay outside the ovary or in it. It is also possible that the lack of coalescence of the ovary in the plants with reduced leaflets may be influenced by the phase of the vegetation period. In order to confirm or reject this supposition the analyses were repeated for two plants (55/1 and 67/3). It appeared that the percentage of uncoalesced ovaries was similar in the first and second analysis (Table 9).

Table 8

Number of mature seeds per pod after crosses of Swedlish clover plants with normal and reduced leaflets

Leaflets in crossed plants: ♀ ♂	Number of pollinated flowers	Number of seeds per pod: 0	1	2	3	4	Pod with seeds (percent)
Reduced × reduced	140	123	12	5	—	—	12.1
Reduced × normal	162	133	23	6	—	—	17,9
Normal × reduced	91	6	10	48	23	4	93.4
Normal × normal	70	4	9	28	22	7	94.2

Table 9

Structure of ovary in Swedish clover plants with reduced leaflets

No. of plant	Non-fused ovaries: number of ovules outside the ovary 1	2	3	4	all ovules inside the ovary	Fused ovary	Number of examined ovaries	Percent of fused ovaries
53/1	10	16	4	1	7	5	43	11.6
53/2	8	4	6	1	1	2	22	9.1
54/1	8	17	6	3	6	11	51	21.5
55/1	12	11	1		11	37	72	51.3
55/1 *	13	3	1		16	28	61	45.9
60/2	4	9	19	6	2	1	41	2.4
60/3	8	20	8	1	8	3	48	6.2
62/1	10	17		1	9	10	47	21.2
62/4	24	11	2		3	14	54	25.9
63/1	9	13	1	5	10	5	43	11.6
65/12	9	8	8	2	3	4	34	11.8
66/2	11	6	1		9	11	38	28.7
67/3	12	16	7	2	6	3	46	6.5
67/3 *	10	16	9	3	3	2	43	4.6
Total	148	167	73	25	94	136	643	21.1

* = analyses were repeated about the end of vegetation period.

Plants with normal leaves, when crossed with those having reduced leaves and vice versa, gave plants with normal leaves. In F_2 the ratio of plants with normal leaflets to those with reduced ones was close to 3 : 1 with a small excess of normal plants (Table 10). In B_1 this ratio was close to 1 : 1 with a rather large excess of plants with normal leaflets. The plants with reduced leaflets when intercrossed gave a progeny with reduced leaflets. It may, therefore, be considered that the trait studied — leaf reduction in Swedish clover is recessive and conditioned by one Mendelian factor.

Table 10

Inheritance of the reduced leaflet blade in Swedish clover

Leaflet blade in crossed plants ♀ ♂	Number of plants: total	with leaflet blade: normal	with leaflet blade: reduced	Ratio of plants with normal to plants with reduced leaflet blade	X^2
Normal × reduced	36	36	0		
Reduced × normal	4	4	0		
$F_1 \times F_1$	289	221	68	3.25 : 1.00	0.333
F_1 × reduced	79	49	30	1.63 : 1.00	4.682
Reduced × reduced	16	0	16		

DISCUSSION

The reduction of the surface of leaflet blades in dwarf Swedish clover plants conditioned by one gene, was associated with a change of numerous morphological and anatomical traits and a slight dominution of fertility. The shape of the particular organs, however, showed no major changes, and the dwarf plants were a miniature of the normal ones (Kazimierski and Kazimierska, 1975). In red clover the atrophy of the lateral blades did not cause changes in the shape of the central leaflet, and sterility of such plants was due to the lack of development of normal flowers in the heads (Strzyżewska, 1974). These traits — one leaflet and lack of flowers were dependent on two interacting genes.

The leaflet reduction in Swedish clover, like dwarfism depend on one recessive gene in the homozygotic state. This gene, however, not only causes a reduction of the leaflet surface, but changes their shape, shortens the internodes and reduces their number, retards flowering, changes the shape, dimensions and number of stomata in the epidermis of the lower leaf surface. The action of this gene on generative organs appears in a certain diminution of the flower length and considerable narrowing of the vexillum as well as in disturbances in the ovary development, this probably affecting unfavourably fertility. The above named changes in the morphological and anatomical structure and in the fertility of plants with reduced leaflets indicate that the investigated genetic factor exerts a pleiotropic action. Since its action is manifested in a reduction of the size of organs and of fertility and changes in their structure, it has been named *reductivus*.

Hereditary infertility or low female fertility conditioned by the nontypical morphological structure of the ovary is known to occur in *Trifolium repens* and *Nicotiana* hybrids (Kazimierski, 1978;

Tsikov, Tsikova and Nikova, 1977). In dwarf yellow lupin it depends on changes in the flower and inflorescence structure. (Kazimierski, Kazimierska, 1976). It is, therefore possible that the low fertility of the investigated Swedish clover plants with reduced leaflets is caused by the lack of coalescence of the ovary. In such plants, however, part of the ovary is grown together, nevertheless the number of seeds collected after cross pollination proved very low (Table 7). Analysis of the percentage of viable pollen grains on plants with reduced leaflets did not indicate that the low fertility might be attributed to a poor viability of the pollen. Thus, there must be some-other causes limiting the fertility of plants with reduced leaflets. Perhaps further investigations will reveal them.

The smaller than expected number of plants with reduced leaflets in the F_2 and B_1 generations might be explained by the weaker germinating power of seeds from back-crosses (60.0%) than in the crosses between F_1 plants (73.0%). It would seem that the *reductivus* gene depresses in homozygotic state the viability of seeds, hence the small number of seedlings and plants with the recessive trait.

Male infertility in the progeny of back-crosses with the plant having reduced leaflets (appearance of plants with dried up anthers) is probably an infertility of Mendelian type. Such an interpretation seems correct since the plants with dried anthers were found in the progeny of back-crosses with the plant showing reduced leaflets, both when this plant was used as female and male partner for breeding F_1 plants. The number of plants from back-crosses, including individuals with viable pollen and with dried anthers was 33. This group contained 25 plants with viable pollen and 8 with dried anthers. The ratio of plants with viable pollen to those with dried anthers was 3 : 1. Thus male--infertility in the examined plant group depended on one recessive factor. Besides, this trait is not linked with the *reductivus* gene, since in appears with equal frequency among individuals with reduced and with normal leaflets.

CONCLUSIONS

1. Plants with reduced leaflet blades are on the average lower, they form less shoots and flower heads on the shoot than plants with normal leaflets; their internodes are shorter and the number of nodes on the shoot is smaller; the flowers are shorter and the vexillae narrower than on plants with normal leaflets.

2. The number of flowers in the head of plants with reduced leaflets does not differ much from that on normal ones. The pollen grain viability is similar in both these groups.

3. The stomata in the epidermis are longer and wider, and their number per surface unit of the leaf is lower in plants with reduced leaflets than in normal plants.

4. Plants with reduced leaflets when intercrossed and pollinated with pollen from normal plants set but few single seeds. It would seem that the very low fertility of these plants is due to the faulty coalescence of the ovary.

5. All the traits of plants with reduced leaflets, including low fertility are caused by one recessive factor acting pleiotropically and termed *reductivus*.

6. Male sterility in B_1 plants (with dried anthers) is probably a sterility of Mendelian type, dependent on the recessive gene. This trait is unlinked with the trait of reduced leaves.

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Dziedziczenie zmian warunkowanych genem redukującym liście u koniczyny szwedzkiej (Trifolium hybridum L.)

Streszczenie

Z jednej z krajowych populacji koniczyny szwedzkiej wyodrębniono roślinę o zredukowanych listkach i skrzyżowano ją zwrotnie z roślinami o listkach normalnych. Otrzymane mieszańce krzyżowano między sobą oraz wstecznie z rośliną o listkach zredukowanych. Rośliny o listkach zredukowanych, z F_2 i B_1, krzyżowano między sobą oraz z roślinami o listkach normalnych.

Rośliny F_1 miały listki normalne, w F_2 stosunek roślin o listkach normalnych do roślin o listkach zredukowanych był bliski 3 : 1, a w B_1 zbliżony do 1 : 1. Rośliny o zredukowanych listkach były niższe, miały mniej pędów i główek na pędzie, ich międzywęźla były krótsze a liczba węzłów na pędzie mniejsza niż u roślin o listkach normalnych. Dwie badane grupy roślin różniły się między sobą także kształtem, wielkością i liczbą komórek szparkowych przypadającą na jednostkę powierzchni liścia. Natomiast liczbę kwiatów w główce, długość szypuł kwiatostanowych, średnicę ziarn pyłku i odsetek ziarn żywotnych obie grupy roślin miały podobne.

Rośliny o listkach zredukowanych okazały się słabo płodne. Przypuszcza się, że słaba płodność tych roślin była w dużej mierze powodowana niezrośnięciem się zalążni.

Cechy roślin o listkach zredukowanych, łącznie ze słabą płodnością, zależą od jednego działającego plejotropowo genu recesywnego, który nazwano redukującym — *reductivus*. Męska bezpłodność, stwierdzona wśród roślin B_1, jest bezpłodnością typu mendlującego i dziedziczy się niezależnie od cechy zredukowanych listków.