Hereditary dwarfism in yellow lupin (*Lupinus luteus* L.)

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(Received: January 2, 1976)

Abstract

A dwarf plant was found in the F_4 generation of a hybrid between two yellow lupin subspecies. Genetic analysis demonstrated that the dwarf growth is conditioned by one recessive factor which was named nanus. This factor acts pleiotropically since it reduces the height, changes the morphological structure and some anatomical traits and reduces fertility in the dwarf plants. It is believed that in the chromosome with translocation a gene block arose in the F_4 plant. These genes acting as a compact system cause dwarfism, changes in the anatomical structure and reduce fertility.

INTRODUCTION

In the 4th generation of a hybrid between *Lupinus luteus* ssp. *luteus*, cv. Ekspress and *L. luteus* ssp. *orientalis* — a primitive form originating from Israel (Kazimierski and Kazimierska, 1975a), a plant was found differing in habitus both from the parent plants and the remaining F_4 ones.

Plants of the cv. Ekspres grow rapidly, they are tall, but little branched with large green leaves; plants of the other parent form grow slowly, they are low (up to 40 cm high), profusely branched at the base of the shoot, the leaves are small dark green. Both parent forms exhibit normal fertility.

The different F_4 plant was low, it grew very slowly, the leaves were intensely dark green and it branched in the upper part of the shoot. The scarce flowers were mostly shed after overblowing and seeds were found only in a single ripe pod and proved underdeveloped. Plants with a typical habitus were pollinated with pollen from the above described plant and bore seeds.

The low plant with habitus not typical for the yellow lupin forms known to the authors or described by others (Atabiekova and May-

surian, 1974; Hackbarth and Troll, 1959; Hanelt, 1960; Zhukovski, 1928, 1929, 1964), was considered to be a dwarf. Results of comparative analysis of its morphological traits are given together with some anatomical features of tall and low plants appearing among the hybrids obtained from the cross between a tall plant and the dwarf one, and the mode of inheritance of dwarf stature and causes of low fertility of this plant are discussed.

MATERIAL AND METHODS

For investigation F_1 to F_4 plants of the hybrid between tall plants and the dwarf one were used. For characterizing the dwarf plants and comparing them with the high ones the following measurements were performed: height of flowering and mature plants, length and breadth of leaf blade, vexillum and bracteole length of flower, calyx, petiole and stipules. The flowers on the shoot, and in ripening plants, pods and leaves were counted. The length and breadth of stomatal cells of the epidermis taken from the lower side of the leaf blade were measured.

After harvesting the pods the ovules and mature seeds in the pod were counted, on the tall plants in 10 pods, on the dwarfs in all ripe pods of each plant.

During the vegetation season the date of anthesis was noted. Pollen was collected from flowering plants, stained with carmine and the pollen grains with and without plasma were counted. The fertility of the dwarf plants was low, indicating that this may be caused by deviations in the process of meiosis. Young buds used for analysis of the course of meiosis were immersed in Carnoy solution, and pollen mother cells were then pressed out of the anthers onto a cover slip, stained with propionocarmine and analysed in a microscope.

RESULTS

Morphological traits

The results of measurements of some morphological features of high and dwarf plants are listed in Tables 1—3. The dwarf plants are on the average one half smaller than the tall ones. The largest dwarfs are smaller than the lowest high plants. Shoot length of the dwarf plants is 46 per cent of that of the tall ones, and the number of leaves is the same in both forms (Table 1). Therefore the distribution of leaves on the shoot is denser in the dwarf forms than in the tall ones. The same number of leaves on a short shoot and on a twice longer one gives a two times greater density on the former.

Table 1

Some morphological characters of tall and dwarf yellow lupin plants

Character	Plants						As compared to tall plants, %
	tall			dwarf			
	mini- mal	maxi- mal	mean	mini- mal	maxi- mal	mean	
Height of plant, cm	43	71	56.3	18	34	23.8	42.3
Shoot length, cm	32	60	46.5	18	27	21.4	46.0
Number of leaves on shoot	14	23	18.5	16	24	18.0	97.3
Number of side branchings							
at base of shoot	2	6	3.1	0	2	1.5	48.4
in upper part	2	4	3.0	2	6	3.7	125.0
Length of inflorescence, cm	11	22	16.0	2	10	5.8	36.2
Number of flowers in main inflorescence	25	45	36.5	20	30	25.0	68.5
Number of pods on main shoot	9	29	18.7	6	18	10.7	57.2
Number of pods on plant	13	75	42.1	6	18	10.8	25.6
Number of plants without pods	—	—	0	—	—	4	—

The leaves on the dwarf plants grow on short stiff petioles (Photo. 1) and the angle between the shoot axis and the petiole is about 30° . In tall plants the leaves grow on twice longer petioles which under the weight of the blades bend downwards (Photo. 2), thus the angle between the petiole and the shoot axis is wider reaching 80° .

Fig. 1. Variability of pollen grain diameter in dwarf and tall yellow lupin plants
Y axis — per cent of pollen grains to given diameter, X axis — pollen grain diameter in microns. Continuous line — dwarf plants, broken line — tall plants

Phot. 1—9. Plants, leaves, leaflets and shoot with pods of the high and dwarf yellow lupin plants

1 and 2. Flowering plants: 1 — dwarf; 2 — high; 3 and 4. Ripe plants: 3 — dwarf; 4 — high; 5—7. Leaves of the plants: 5 — high; 6 — F_1 ; 7 — dwarf; 8 — Leaflets: in the upper row from the high plant, in the lower row from the dwarf plant; 9 — Shoot with pods

The leaves of the dwarf plants do not dry up and are not shed, they remain on the plant till late autumn (Photo. 3), whereas the tall plants mature towards the end of summer and lose their leaves (Photo. 4). The stipules also differ in the two groups — in the dwarf plants they are by one half shorter than in the tall ones (Table. 2).

Table 2

Length and breadth of leaf blade, length of petiole and stipule, number of leaflets in leaf of tall and dwarf yellow lupin plants

	Plants						As compared to tall plants, %
	tall			dwarf			
	mini- mum	maxi- mum	mean	mini- mum	maxi- mum	mean	
Length of leaf blade, cm	4.0	7.6	5.6	2.1	4.3	3.5	62.5
Breadth of leaf blade, cm	0.9	1.8	1.3	0.6	1.5	1.1	83.4
Length/breadth ratio	—	—	4.4	—	—	3.3	—
Length of petiole, cm	11.5	16.5	13.6	6.5	8.5	7.5	55.1
Length of stipule, cm	2.5	4.1	3.2	1.6	2.0	1.8	56.2
Number of leaflets in leaf	10.0	11.1	10.1	9.0	12.0	10.6	104.9

The number of leaflets in the leaf of tall plants, dwarf ones and F_1 ones (tall x dwarf and vice versa) is similar (Table 2, Photos. 5—7), but the dimensions and shapes of the leaf blades differ. The leaf blades of tall plants are twice the length of the dwarf ones, while they do not differ much in breadth (Table 2, Photo. 8). In tall plants the leaflets are barely 0.2 mm wider than those of the dwarf forms, thus their shape expressed by the length-to-breadth ratio is different (Table 2). The leaf end is also different: in the tall plants the blade tapers uniformly ending in a sharp tip, and in the dwarf plants at mid length or at 1/3 of its length from the tip it is bent downwards and twisted to the left. At the tip it is ends by a slight rounded convexity (Photos. 5—8).

Both the tall and dwarf plants branch but little. The tall plants form more branchings at the base of the shoot than the low ones (Table 1). The difference between the lateral branches formed at the base of the main shoot in tall and dwarf plants consists in that the former mostly produce long branchings ending in an inflorescence and later pods, whereas in the dwarf plants the lateral shoots are short, underdeveloped and bear no flowers.

The branchings in the upper part of the main shoot, growing from under the apical inflorescence constituting the ending of the main shoot are more numerous in dwarf plants than in the tall ones (Table 1). These shoots in both groups of plants end by inflorescences.

The inflorescence on the main shoot of tall plants is about 10.2 cm longer than in the dwarfs (Table 1), and the number of flowers in it in the former is on the average larger by 11 than in the latter. Hence the distribution of the flowers on the inflorescence axis is much looser in the tall plants than in the dwarf ones. This dense accumulation of flowers on a small area of the inflorescence stem is one of the causes of poor setting of seeds by the dwarf plants. Observations showed that the pods contact one another after 3—4 weeks, forming a compact ring around the stem and part of them, probably the weaker ones, are shed.

Phot. 10—14. Shoot with pods, flowers, pods and seeds of the high and dwarf yellow lupin plants

10 — top of shoot of the sterile dwarf plant; 11 — shoot with pods of the high plant; 12 — flowers: on the left — high plant, on the right — dwarf plant; 13 — pods: on the left — high plant, on the right — dwarf plant; 14 — seeds: on the left — dwarf plant, on the right — high plant

Not all dwarf plants had pods on the main shoot (Photo. 9) at the period of ripening, and on the lateral branches there were none (Table 1, photo 3), whereas the tall plants all bore seeds (Photo. 11).

The flowers and bracteoles of the dwarf plants are shorter and the wings and vexillum narrower than in the tall plants (Table 3, Photo 12). The upper part of the keel containing the anthers and the pistil style with

Table 3

Flowers and bracteoles of tall and dwarf yellow lupin plants

	Plants		As compared with tall plants, %
	tall	dwarf	
Length of flower, mm	15.6	12.4	79.5
Breadth of wings, mm	7.0	5.9	84.3
Breadth of vexillum, mm	10.4	8.1	77.8
Length of lower lip of calyx, mm	9.3	6.0	64.5
Bracteoles — length, mm	6.2	5.1	82.2
breadth, mm	4.9	3.7	75.5

the stigma is fused in the tall plants, while in the dwarf ones it is open and in the fully developed flower the anthers and pistil are exposed.

The stomatal cells on the lower side of the leaves of tall and dwarf plants are of almost the same length, in the dwarfs they are by 4 μ narrower. The number of stomata per surface area unit of the leaf is in the dwarf plants by 30 per cent higher. The mean surface area of leaf epidermis cells, on the other hand, is by 34.2 per cent smaller in the dwarf plants than in the tall ones (Table 4).

Table 4

Length and breadth of stomatal cells (μ), their number per surface area unit of leaf, surface area of epidermal cells on lower side of leaf blade in tall and dwarf yellow lupin plants

	Plants						In comparision with tall plants, %
	tall			dwarf			
	mini- mal	maxi- mal	mean	mini- mal	maxi- mal	mean	
Stomatal cells: length	34.0	44.2	39.8	34.0	44.2	38.2	95.9
breadth	23.8	30.6	27.8	23.8	30.6	23.8	85.6
number in microscope field of vision	3	12	6.7	3	16	8.7	129.8
Surface area of epidermal cells	5.0	31.0	12.6	3.9	18.9	8.3	65.8

The period from seeding to anthesis on the main shoot in the tall plants was in various years 66—88 days and in dwarf plants 70—93 days (Table 5). Thus, the tall plants began flowering 4 to 6 days earlier.

The mean pollen grain diameter is the same in both groups of plants amounting to 38.85 μ . The curves of variability of the pollen grain diame-

Table 5

Date of anthesis of tall and dwarf yellow lupin plants

Generation	Plants	Dates of anthesis		Number of days from seeding to flowering
		11—20.VI.	21—30.VI.	
F ₂	tall		12	88
	dwarf		4	93
F ₃	tall		10	87
	dwarf		10	91
F ₄	tall	32	9	64
	dwarf		15	70

ter are of the same shape and run almost parallelly to one another. The largest per cent of pollen grains fall within the range of 37.4—40.8 μ . Pollen grains with a smaller or larger diameter are seldom found in both groups (Diagram 1).

INHERITANCE OF DWARFISM

F₁ plants of the hybrid tall x dwarf and vice versa are tall and fertile, they show no noticeable changes in the structure of vegetative organs and flowers. The heterozygotic F₂ and F₃ and F₄ plants are tall and they segregate into tall and dwarf forms in a 3 : 1 ratio (Table 6). The progeny

Table 6

Inheritance of dwarfism in yellow lupin

Generation	Number of plants		Total	χ^2
	tall	dwarf		
F ₂	12	4	16	
F ₃	10	2	12	
F ₄	41	13	54	
Total	63	19	82	0.1462
F ₃	—	8	8	
F ₄	—	2	2	
Total	—	10	10	

of the dwarf plants in F₃ and F₄ generations consisted of a small number of plants which all were dwarfs (Table 6). Thus it may be assumed that the dwarf type of growth, studied in yellow lupin, is conditioned by one recessive factor which occurs in the homozygotic state.

Fertility

Not all dwarf plants set pods, and those which did had but few. Among the tall plants there were no individuals without pods (Table 1). The pods of the dwarf plants were shorter and narrower and contained fewer seeds than the tall ones (Photo. 13). The number of ovules in the ovary and the number of ripe seeds in the pod were similar in both groups (Table 7). The per cent of ovules developed to seeds and the mean yield of seeds from one plant were lower in the dwarf plants than in the tall ones (Table 7). The 1000-grain weight was also smaller for the former (Table 7). It should be mentioned that the seeds from the tall plants did not differ from one another in shape and size, whereas each dwarf plant produced large and tiny seeds, well filled ones and meagre ones (Photo. 14).

Table 7

Number of ovules in ovary, seeds in pod, seed yield of plant and 1000-seed weight (g) in tall and dwarf yellow lupin plants

	Plants					
	tall			dwarf		
	from	to	mean	from	to	mean
Number of ovules in ovary	5	6	5.59	5	6	5.16
Number of seeds in pod	2	6	4.15	0	3	2.21
Ovules transformed to seeds, %	—	—	74.2	—	—	42.7
Number of seeds from 1 plant	22	254	120.6	0	15	5.1
1000-seed weight, g	115.0	197.4	166.8	50.0	138.7	118.0

The, in general, poor fertility of the dwarf plants is in some extent connected with the reduced number of flowers on the shoot, deficient development of side branches in the lower part of the shoot and shedding of flowers. It may, however, also be the result of an abnormal course of meiosis and microsporogenesis.

Meiosis and microsporogenesis

During diakinesis and the first metaphase 26 bivalents were found in most of the analysed pollen mother cells of tallplants (Table 8, Photo 15). In some few cells, 12.0 per cent of the total number analysed, 2 to 4 univalents were present and seldom 1—2 tetravalents. In the pachytene and diakinesis phases there were no univalents, thus they arose as the result of premature movement of chromosomes towards the poles during the first metaphase. The tetravalents indicate a structural difference in the chromosomes of the studied plant group. Anaphase I in most pollen

mother cells runs a typical course, 26 chromosomes translocate to each pole. In the few cells analysed in this division phase a single lagging chromosome, and in one cell a chromosome bridge were seen. The second metaphase and anaphase occurred without disturbance and the microsporocytes transformed to regular microspore tetrads.

In pollen mother cells from the dwarf plant chromosomes joined to form bivalents and tetravalents were found during pachytene and diakinesis (Photos 16 and 17). In 69.8 per cent of the pollen mother cells in the stage of metaphase I 1 to 2 tetravalents were present. Univalents (2—10) were found in 26 pollen mother cells (Photos. 20 and 21) and in 32 of the total number of 106 examined cells in metaphase I there were only 26 biavalents in each (Table 8, Photo. 18). On the average, to one examined pollen mother cell in the stage of first metaphase there fell

Table 8

Meiosis and microsporogenesis in tall and dwarf yellow lupin plants

Division phases	Plants	Number of analysed PMC			Kind of disturbance
		Total	with disturbances	with disturbances, %	
Metaphase I	tall	125	11	12.0	univalents 2-4; tetravalents 1-2
	dwarf	106	74	69.8	univalents 2-10; tetravalents 1-2
Anaphase I	tall	104	8	7.7	lagging chromosome 1; bridge 1
	dwarf	45	17	37.7	lagging chromosomes 1-20
Metaphase II	tall	70	0	0.0	
	dwarf	62	1	1.5	lagging chromosomes 2
Anaphase II	tall	61	0	0.0	
	dwarf	23	4	17.4	lagging chromosomes 1-3
Tetrads	tall	405	0	0.0	
	dwarf	966	29	3.0	microspore diads and triads

23.84_{II}, 0.78_{IV}, 1.24_I. In the pollen mother cells of the dwarf plants, like in the tall ones, there were no univalents in the pachytene phase and diakinesis. Thus they arose from premature tearing of the terminal chiasmata. There also were cells in which the bivalents did not divide simultaneously. In such cells simple bivalents with one chiasma divided earlier as a rule than ring bivalents with two chiasmata (Photo. 19). Sometimes the chiasmata also burst difficultly in simple bivalents, and when the chromosomes were close to the cell poles thin chromatin junctions between them persisted (Photo. 19).

Separation of chromosomes to the division spindle poles during the anaphase I occurs normally in 62.3 per cent of the analysed pollen mother cells of dwarf plants. To each of the opposite poles 26 chromosomes were translocated (Photo. 22). In the remaining cells retarded chromosomes were seen. Cells containing them could be divided into two groups: the

first — of 13 cells — for which the number of lagging chromosomes varied from 1 to 4, and the second with 5 to 20 chromosomes in the cell.

In the pollen mother cells of group one the lagging chromosomes joined the polar groups, since at telophase and interphase there were no chromosomes or micronuclei in the cell cytoplasm, and the number of chromosomes in the interphase nuclei and in the groups during prophase of the second division and the second metaphase was 26.

In 4 cells of group two, the chromosome arrangement in anaphase I was as follows: 25—5—22, 22—8—22, 21—12—19 and 16—20—16. As seen, in two cells the chromosome number at the poles was the same and in two it was different. The chromosomes which remained in the equatorial plane of the cells showed no tendency to translocation towards the poles, they rather gave the impression of dividing into chromatides (Photo. 23).

The second division, with the exception of some few cells with 1—3 lagging chromosomes, showed an undisturbed course leading to the formation of four-nucleate microsporocytes. After the second division 97.0 per cent of the 4-nucleate microsporocytes transformed to microspore tetrads, and the remaining ones to triads and diads (Table 8). In the triads two small microspores are mononuclear and one large has two nuclei. In the diads both microspores are binuclear. The binuclear microspore in the triads arises in the following way: after the second division two nuclei of the microsporocyte remain close to one another and the two other ones at a certain distance (Photo. 24). The forming plasmatic membranes divide the 4-nuclear microsporocyte so that each of the nuclei lying further from one another are surrounded by a separate plasmatic membrane, while the close-lying ones have one common membrane (Photo. 25). Thus, from a 4-nucleate microsporocyte there arises a microspore triad in which two microspores are mononuclear and one is binuclear. When after the second division the nuclei lie in pairs close to one another, the wall dividing the microsporocyte forms between the pairs of nuclei which lie at a distance from each other, and from the 4-nucleate microsporocyte there arise two 2-nucleate microspores.

In the tall and dwarf plants the per cent of fertile pollen grains is 42.0 to 99.0 per cent (Table 9). Plants with a low and high per cent of fertile pollen grains are found in both types of plants. Among the tall plants, however, the number of plants with more than 90.0 per cent of fertile pollen was higher than among the dwarf plants. This phenomenon may be explained by the fact that in the dwarf plants the processes leading to degeneration of the microspores start as early as the tetrad phase, where the dying microspore is shapeless and contains numerous vacuoles. The advancing process of vacuolization in the developing pollen grains (Photo 26), particularly in the flowers on the side branchings results in that all the grains filling the pollen sacs do not contain nuclei and plasma and are lifeless (Photo 27).

Phot. 15—27. Meiosis and microsporogenesis in high and dwarf yellow lupin plants
 15 — metaphase I in high plant, 26_{II}, polar view; 16—27. Meiosis and microsporogenesis in dwarf plants; 16 — pachytene, tetravalent; 17 — diakinesis, 24_{II}1_{IV}; 18—21. metaphase I: 18 — 26_{II}; 19 — 22_I8_I, bivalents rod and ring, in rod bivalents the ends of chromosome arms with a chiasma are thin and very long; 20 — 18_{II}1_{IV}12_I; 21 — 19_{II}2_{IV}6_I (on the Phot. 17, 20 and 21 tetravalents are marked with arrow); 22—23. anaphase II: 22 — both groups with 26 chromosomes; 23 — 22 chromosomes at the poles, 8 chromosomes into the middle of them; 24 — tetrad — to nuclei close to each other and two in some distance; 25 — triad of microspores, one of them 2-nucleated; 26 — one nucleated microspores with formed egzine die off; 27 — anther from flower of lateral branche with dead pollen grains

Table 9

Pollen viability in tall and dwarf yellow lupin plants

Generation	Plants	Viable pollen grains, %						Number of plants examined*
		41.0— 50.0	51.0— 60.0	61.0— 70.0	71.0— 80.0	81.0— 90.0	91.0— 100.0	
F ₃	tall			2		1	19	22
	dwarf			1	2		5	8
F ₄	tall	2	2	1	2	1	14	22
	dwarf	1	1		1	2	7	12

DISCUSSION

The dwarf type of yellow lupin here described is conditioned by one recessive factor, since in F₂ and the heterozygotic daughter plants of the tall F₃ and F₄ generations the ratio of tall to dwarf plants is 3 : 1. The factor causing dwarfism was named nanus.

The dwarf plants differ from the tall homozygotic and heterozygotic ones in height and numerous morphological and anatomical characters, fertility and fecundity. The factor conditioning dwarfism shortens the stem by more than 50 per cent without reducing the number of leaves. Hence in the dwarf plants the distribution of leaves on the stem is denser than on the tall ones. Together with shortening of the shoots reduction of the length of the petioles stipules and leaf blades occurs in the dwarf

plants. The width of the leaf blades is only slightly reduced so that the ratio of length to breadth of the blade is changed, thus its shape. The tip of the leaf blade is also different than in the tall plants. In the latter it is curved downwards and sharp at the end, whereas in the dwarfs it is softly rounded, strongly curved downwards and twisted to the left.

The inflorescence on the main shoot is also shortened. The flowers on the stem are distributed densely, on the average they are by 20 (31.5%) less numerous than on tall plants.

At the base of the leader stem the dwarf plants produce as a rule less side branchings than the tall ones. The branchings, if any, are usually short without flowers at the tip. Somewhat more numerous are branchings in the upper part of the main stem of dwarf plants and some of these end in inflorescences. However, the dwarfs produced no pods on the lateral ramifications,

The side branchings at the base of leader stem of tall plants form with the stem axis an angle of 30° , and in the upper part of the shoot of 20° . In the dwarf plants the ramifications grow almost parallelly to the stem axis. This has no doubt a certain influence on the fructification of the plants since the leaves on the side branches are so densely distributed that they adhere to the inflorescence so that within it a specific moist microclimate develops. Since in the dwarf plants the keels are not coalesced, the pistils and stamens are exposed to the direct action of external factors and the compact ring of leaves surrounding them does not favour pollination (more difficult dehiscence of moist anthers coalescence of pollen grains).

The dwarf plants are less fertile than the tall ones and some of the individuals bear no seeds. The lower fertility of the dwarfs cannot be attributed solely to the lower per cent of individuals with pollen fertility above 90.0 per cent, the lower number of ovules in the ovary — the difference is only slight amounting to 0.43 ovule, this giving 7.6 per cent in favour of the tall plants — and the smaller number of flowers on the leader stem. Some of the tall plants with pollen fertility below 90.0 per cent set seeds not less numerous than those with fertility above 90.0 per cent. The number and per cent of ovules transformed to seeds in the pods of tall and dwarf plants reveal better the causes of low fertility of the dwarfs. The mean number of seeds per pod for tall and dwarf plants was 4.15 and 2.2, respectively and the per cent of ovules transformed to seeds was for the former 72.2 and the latter 42.7 per cent. These 42.7 per cent of ovules transformed to seeds include those which gave meagre seeds incapable of germination. If we eliminate the latter, the dwarfs produced as few as 8.3 per cent of ovules which transformed to seeds.

The yield of seeds from the dwarf plants was lower than that from the tall ones. The lower fecundity of the former (mean 5.1 seeds per plant)

as compared with the tall ones (mean 120.6 seeds per plant) results from the lower number of ovules transformed to seeds, the smaller number of flowers on the stem, the poor development of the lateral branchings at the base of the stem, and the sterility of the branchings in the upper part of the stem.

Chromosome reduction and the course of meiosis in the dwarf plants show certain anomalies. In pachytene, diakinesis and metaphase I tetravalents appear, and during metaphase I also univalents. The presence of tetravalents shows that the dwarfs are structural hybrids. This property arose from the combination of the *L. luteus* ssp. *orientalis* genome with the ssp. *luteus* genome since the genomes of these subspecies differ in translocation (Kazimierski and Kazimierska, 1975b). The univalents noted in metaphase I arose owing to premature tearing of the terminal chiasmata.

Among other traits in which the course of metaphase I differed in the tall and dwarf plants may be quoted the late division of part of the bivalents and excessive elongation of the chromosome arms connected with a chiasm in the latter as well as appearance of bivalents of ring-like type with two chiasmata, which in general divide later than simple bivalents. During diakinesis and metaphase I 23.83_{II} , 0.78_{IV} and 1.24_I were present on the average in the pollen mother cells of dwarf plants and 25.84_{II} , 0.06_{IV} and 0.06_I in those of the tall plants.

At the stage of anaphase I lagging chromosomes appeared more frequently in the pollen mother cells of dwarf plants than in the tall ones. They joined, however, with the polar groups since in interphase, prophase and, metaphase II the nuclei and metaphase groups contained 26 chromosomes each.

The second division in both groups of plants occurred without major disturbances and the 4-nucleate microsporocyte of tall plants transformed to microspore tetrads. In the dwarf plants also mostly tetrads formed, although microspore triads and diads could sometimes also be found. In the case of triads the two microspores formed were mononucleate, one was binucleate and in diads both cells were binucleate. Microspore triads and diads arose owing to anomalies in the process of formation of the cytoplasmic membranes in the 4-nucleate microsporocyte.

In the dwarf plants rather frequently dying of whole tetrads or of single microspores in the tetrad was observed. In the buds on the side branchings anthers were seen in which the pollen sacs were filled with grains deprived of nuclei and plasma.

Thus, the nanus factor conditioning dwarfism in yellow lupin acts pleiotropically. It changes the habitus, the height of the plants, the shape of many organs, the anatomical structure of the stomatal and epidermal cells, it affects the process of meiosis and microsporogenesis and reduces the fertility of the plants. The above listed characters are heritable and

are inherited coupled. It would seem therefore, that in the F_4 generation of the hybrid *ssp. orientalis* x *ssp. luteus* a block of genes formed in the chromosome with translocation, acting jointly, and in such form it is transmitted from generation to generation.

CONCLUSION

1. The described dwarf type of yellow lupin is conditioned by one recessive factor since in F_2 and the progeny of heterozygotic F_3 and F_4 plants of hybrids between dwarf and tall plants the ratio of tall to dwarf plants is 3:1 and dwarfs produce only dwarfs. The factor conditioning dwarfism was named *nanus*. Dwarfism is associated with differences in habitus of the plants, shape of some organs (leaves, stipules, flowers, side branchings) and anatomical structure of the leaf blade.

2. The smaller number of flowers in the inflorescence, densely distributed on the short axis, the poor development of lateral branchings and their situation on the plant as well as deviations in the process of meiosis are the causes of low fertility or even sterility of the dwarfs.

3. In the process of meiosis, at the stage of metaphase I there were on the average in the pollen mother cells of dwarf plants 23.84_{II}, 0.78_{IV} and 1.24_I and in the tall ones 25.84_{II}, 0.06_{IV} and 0.06_I. Tetravalents and univalents in metaphase I were more frequent in the dwarfs than in the tall plants. In the process of microsporogenesis only tetrads formed in the tall plants, whereas in the dwarf ones triads and diads could be found.

4. The presence of tetravalents in meiosis prophase and metaphase I indicates that the plants were structural hybrids. This property arose owing to combination of the *L. luteus ssp. orientalis* genome with the *ssp. luteus* genome, since the genomes of these subspecies differ in translocation.

5. Dwarfism and other characters associated with it are inherited coupled. It would seem that the block of genes conditioning these characters formed in the F_4 generation of the hybrid *ssp. orientalis* x *ssp. luteus* in the chromosome with translocation, since in the pollen mother cells of dwarf plants tetravalents were frequently noted in the phases of pachytene, diakinesis and metaphase I.

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Dziedziczenie karłowatości u łubinu żółtego (Lupinus luteus)

Streszczenie

W F_4 mieszańca między *Lupinus luteus* ssp. *orientalis* i *L. luteus* ssp. *luteus* znaleziono niską roślinę, która wyglądem zewnętrznym różniła się od roślin wszystkich znanych nam form łubinu żółtego. Roślinę niską skrzyżowano z wysokimi o pokroju typowym. W F_2 oraz w potomstwie roślin heterozygotycznych F_3 i F_4 stosunek roślin wysokich do karłowatych wynosił 3:1. Karłowaty wzrost jest zatem warunkowany przez jeden czynnik recesywny, który nazwano *nanus*. Rośliny karłowe od wysokich różnią się także tym, że mają one krótsze ogonki liściowe, blaszki listkowe, przylistki i podkwiatki oraz krótsze kwiatostany z mniejszą liczbą kwiatów. Rozgałęzienia boczne u roślin karłowatych są często niedorozwinięte i bez kwiatów. Rośliny wysokie są płodne, u karłowatych płodność jest niska, a zdarzają się także osobniki bezpłodne. Przyczyną niskiej płodności roślin karłowatych są pewne odchylenia w ich budowie morfologicznej (usytuowanie na pędzie rozgałęzień bocznych, niezrośnięcie łódeczki, skrócenie osi kwiatostanu) oraz anomalie w procesie mejozy (częste występowanie tetrawalentów i uniwalentów). Cechy typowe dla roślin karłowatych dziedziczą się jako sprzężone. Przypuszcza się, że w F_4 mieszańca między dwoma podgatunkami łubinu żółtego w chromosomie z translokacją powstał blok genów działających jako jeden układ, który jest przekazywany z pokolenia na pokolenie.