Species and intraspecific diversity of white, blue and yellow lupins

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Summary

The lupin collection of the N.I. Vavilov Institute holds more than 2500 accessions. Many years of study in various geographic regions, and generalization of the data obtained by other researchers, have revealed intraspecific taxonomic and ecogeographic classifications. A series of patterns in the genepool variation has been identified that depends on the degree of cultivation, environment and soil condition. These patterns more accurately define the centres of origin of cultivated lupin species. This foundation will allow more targeted collecting and permit development of recommendations for breeding practice.

Introduction

The fundamental objective of the scientific activities of VIR is to accumulate specific and varietal diversity of cultivated plants and their wild relatives in the genebank. The VIR lupin collection includes local and breeding varieties, breeding lines that have become wild and wild-growing forms. VIR organizes exploration trips with the purpose of collecting wild and cultivated germplasm of lupin. It is responsible also for the exchange of collection accessions and their availability to scientific institutions, seed companies and individual researchers from all over the world. The institute includes a herbarium that studies the phylogeny, systematic status, taxonomy and geography of cultivated lupin plants and their wild relatives.

The present work has been developed using the VIR lupin collection, which has accumulated more than 2500 accessions from 50 countries. Generalized data offer an opportunity of answering three of the most important questions of plant introduction and plant breeding. When should collecting take place? What genepool is to be collected? What may be utilized and for what purposes?

Up to now we have published only part of our experimental results on the diversity of lupin's genepool, and mainly in Russian. Data on VIR collecting of lupins and guidelines for breeding were published in 1988 (Kurlovich 1988). Intraspecific taxa of lupin were reported by Kurlovich and Stankevich (1990). Kurlovich (1991) describes, in Russian, the full-scale characterization of lupin accessions of different genotypes, ecotypes and concultivars. Kurlovich *et al.* (1995) reviewed the theory of breeding of four leguminous crops, including lupin. This article refines previous work and draws general conclusions from earlier data.

Materials and methods

Research materials were assembled from the lupin collection of the Vavilov Institute, which represents all the world diversity of lupin. Many years (1973-96) of observing the plants sown in various regions of Russia (St. Petersburg, Moscow and Tambov provinces), Ukraine (near Kiev) and Abkhazia (near Sukhumi), using VIR methodologies (Kurlovich and Nazarova 1990) have revealed new characters and combinations that are taxonomically significant and genetically determined. These data and those of other researchers (Zhukovsky 1929; Kazimierski and Novacki 1961; Gladstones 1974; Maissurian and Atabekova 1974; Kazimierski and Kazimierska 1975) allow corrections in the intraspecific taxonomic classifications of white, blue and yellow lupins. Maissurian and Atabekova (1974) described intraspecific classifications of lupins. However, this work did not follow the International Plant Nomenclature Code rules, so the majority of the names of the variants were not valid. This article presents a revised classification, with every form of lupin assigned a rank (Table 1).

Allelism and character complementarity tests have shown that the colour of seed is correlated with the corolla colour. This linkage reflects the stability of a genetic system which corresponds to the rank of variant (varietas). A good diagnostic character is the colour of the vegetative parts, and the absence or presence of anthocyaninin in particular. Being less stable this character could be used in detecting subvariants (subvarietas). Plants with determined branching, fascicular stems and other characters of breeding value would be of considerable practical interest to breeders. Such forms are theoretically possible in all the variants and subvariants systematized by us. Therefore, it would be justified to regard them in the rank of forms (forma).

Table 1. The essential characters of the lupin species and the interspecific taxa

Taxa	Characters
Species (sp.)	Area, liable to cross, ability to produce fertile progeny with constant inheritance of the characters of both parents, identity of karyotype
Subspecies (subsp.)	Growing or natural area, concrete range variability of vegetative and generative organ's form and colour, characters of pubescence, form and colour of seeds
Varietas (Var.)	Colour of the seed cover in correlation with the colour of the corolla
Subvarietas (Subvar.)	Colouration of the cotyledons, vegetative organs, carina's edge and the presence or the absence of anthocyan
Forma (f.)	Determined branching, fascicular stem and other characters of breeding value

Cultivated annual lupin is one of the species that has preserved a close connection with wild relatives. These species usually show regional geotypes and ecotypes that correspond to the subspecies (Sinskaja 1969). There is a homologous series in the hereditary variation of seeds, flowers and vegetative organs, beginning with the wild types, with motley seeds and intensively coloured flowers, then follows the series with the medium colouring and finally the form with white flowers and seeds. Each variation is seen in cultivated and wild forms, since the distinction between the forms is only quantitative.

Samples of different origin with ecologically and geographically influenced differences in biological, physiological, biochemical and other properties can also be arranged into geotypes, ecogeographic groups of ecotypes, separate ecotypes and concultivars (varieties types). The samples of each lupin species adapted to a definite and sufficiently vast habitat or geographic area of cultivation were grouped into geotypes, typical of the species with wide areas of distribution. The term 'geotype' was defined by Agaev (1987) as: "morphological weakly differentiate, genetic deterministic race appears in the composition of species as a result of its settlement and evolution". This definition has allowed us to develop a more detailed ecogeographical classification and reveal efficient ways of using the lupin genetic resources in breeding.

Geotypes were divided into separate ecotypes or ecogeographic groups of ecotypes (if it is difficult to select separate ecotypes). The ecotype groups showed plants adapted to specific niches in the wild, e.g. mountains, littoral, close to villages or roads) or in agriculture (e.g. different local forms). Breeding varieties were classified into concultivars (varieties types) on the basis of similar biological and economical properties. Passport information about the VIR lupin collection, primary and secondary evolution was computerized; dBASE4F was used to classify and distribute the accessions through the taxa, geotypes, groups of ecotypes, separate ecotypes and concultivars.

Results

Key to the lupin species

1. Flowers verticillate. Colour of corolla-yellow,lemon-yellow, orange or whitish. Flowers scented ..... 3. *L. luteus* L.
\+ Verticillate only upper flowers. Lower flowers of inflorescences alternate. Colour of corolla blue, pale violet, pink or white. Flowers not scented ..... 2.
2. Lower lip of calyx entire, upper lip deeply bipartite. Colour of corolla from blue to white ..... 2. *L. angustifolius* L.
\+ Lower lip of calyx with 3 teeth, upper entire. Colour of corolla white to violet-blue ..... 1. *L. albus* L.

1. *L. albus* L. 1753, Sp. Pl. :721; Willd. 1803, Sp. Pl. ed. 4, 3:1022; DC. 1825, Prodr. 2:407; Boiss. 1872, Fl. Or. 2:29; Willk. et Lange 1880, Prodr. Fl. Hisp. 3:466; Halacsy 1901, Consp. Fl. Graec. 1:341; Fiori 1925, Nuov. Fl. Anal. Ital. 1:804;Franco et Silva 1968, in Fl. Europ. 2:105; Chamberlain in Davis 1970, Fl. Turkey 3:38; Zohary 1972, Fl. Palaest. 2:42; Gladstones 1974, W. Austral. Dep. Agric. Tech. Bull. 26:5.
Typus : Herb. Linn. No. 898-2 (LINN).

Annual plants 30-120 cm high. Stems and petioles sparsely sericeous. Stipules subulate, concrescent with the petioles over 1/3 of their length. Leaflets 5-11, 20-60 x 10-20 mm, villous below, margins ciliate. Colour of corolla white, greyish and light blue, rare pink blue, dark blue or violet blue. Lower flowers of inflorescences alternate. Lower lip of calyx lobed with 3 teeth, upper entire. Pods 70-160 x 10-20 mm, 3-6 seeded, seeds square, compressed, white variably tinged salmon pink, or dotted, dark brown. $2n = 50$ (Fig. 1). Distributed as wild plants on the Balkan peninsula, cultivated throughout the Mediterranean and elsewhere. *Lupinus albus* has been selected as the type genus *Lupinus* L.

The closest neighbours to this species are *L. graecus* Boiss. et Sprun. and *L. termis* Forsk. The former is a wild plant on the Balkan peninsula, the latter grows in Egypt, Libya, Sudan, Ethiopia, Israel, Palestine and Syria. All three species differ only in colour of flowers and seeds. The species was domesticated by the ancient Greeks (Gladstones 1974). From Greece it spread throughout the Mediterranean and elsewhere. Forms with white seeds and pink and blue or light pink flowers (*L. termis*) spread to the south, and to the west (Apennine peninsula and farther) mainly the forms with white seeds and greyish-blue or white seeds (*L. albus*). White lupin (*L. albus*) is still grown in Greece, where the wild *L. graecus* can also be found. The absence of clear specific characters makes it possible to consider all three species within the one Linnean species *L. albus*. The existence of geographical and physiological differentiation is enough to recognize the subspecies: subsp. *albus*, subsp. *graecus* (Boiss. et Sprun.) Franco et Silva and subsp. *termis* (Forsk.) Ponert.

Small species such as *L. vavilovii* Atab. et Maiss. and *L. jugoslavicus* Kazim. et Nowacki, recognized by some plant growers of the former USSR and Poland, are only nomenclatural synonyms of the Balkan subspecies *graecus*.

Key to the subspecies of Lupinus albus *L.*

1. Rosettes form first from the leaves, stalks appear at the time of flowering. Corolla is dark-blue with white centrobasal spots as standard. Pods 60-80 x 11-14 mm, shattering at maturity, seeds 7-10 x 6-8 x 2-3 mm, dark brown, dotted with impermeable testa. Native to the Balkan peninsula ..... subsp. *graecus*

Fig. 1. *Lupinus albus* L. (holotype).

+ Rosette is lacking. The colour of the corolla pink, blue, greyish, light blue and white. Pods 80-150 x 16-20 mm, non-shattering at maturity, seeds pinkish white or white with permeable testa 2
2. Plants shaggy, sericeous. Inflorescence stretched, crumbly. Flowers pink or blue, calyx with bract. Found in Egypt, Libya, Sudan, Ethiopia, Israel ..... 2. subsp. *termis*
+ Plants softly villous. Inflorescence short, more or less compact. Flowers greyish, light blue, white. Calyx without bract (it falls early). Cultivated in the Mediterranean area, in Europe, North and South America, Asia ..... 3. subsp. *albus*

1. Subsp. ***graecus*** (Boiss. et Sprun.) Franco et Silva 1968, Feddes Repert. 79 :52; *idem* 1968, in Fl. Eur. 2 : 105; Chamberlain in Davis 1970, Fl. Turk. 3 :39

(Descriptions are given in the key to the subspecies of *Lupinus albus* L.).

Typus: In cultis Graeciae, inter Spartam et Mistra, E. Boisser et W. Spruner, April 1842 (G).

This subspecies is widespread in Greece, on Crete and on other Aegean islands, Albania, western Turkey (Gladstones 1974), and can also be found in Italy (Hammer *et al.* 1992). Occurs as an annual, winter and perennial crop.

2. Subsp. *termis* (Forsk.) Ponert 1973, Feddes Rep. 83 (9-10) :619.

Typus : In Delta ad pagum Nedjel. Copiose in agris, an spontaneus, nestio (C?).

Spread and cultivated in Egypt, Libya, Sudan, Ethiopia, Israel. Slightly wild. Name of subspecies originated from Greek word '*thermos*' (hot). Subsp. *termis* differ from typical (standard) subspecies (subsp. *albus*) more early flowering, fine stems and more small flowers and seeds. The flowers have another colour.

We have at our disposal accessions from Libya, Egypt and Ethiopia. Libkind (in 1932) described them as varieties but she did not indicate the types.

1. Var. *abissinicus* Libk. 1931, Lupin:59, sine typo. Flowers pink and blue. Vegetative parts with anthocyanin.

Neotypus: 'B-5', received from Bielorussia, k-2237, reproduction of Pushkin's laboratories of VIR, 28. 07. 1989, L.T. Kartuzova (WIR).

Distribution - the upper reaches of the Nile.

2. Var. *subroseus* Libk. 1931, l. c. :59, sine typo. Flowers light pink. Vegetative parts green.

Neotypus: Libya, k-2094, reproduction of Pushkin's laboratories of VIR, 28. 08. 1989, L.T. Kartuzova (WIR).

Distribution - Libya, Egypt, Israel, Syria, Greece.

3. Subsp. *albus*. Differ by thick meaty stalks, large leaves and seeds. The genepool of subsp. *albus* has large variations in physiological properties of plants. Cultivated in many countries of Europe, Asia, America.

3. Var. *albus*. Kurl et Stankev. 1990, Bull. Appl. Bot. Gen. Plant Breed., Leningrad 135:33. Flowers white, carina's edge without anthocyanin.

We put the accession 'Mutant 47' down to this variety.

4. Var. *vavilovii* Kurl. et Stankev 1990, Bull. Appl. Bot. Gen. Plant Breed., Leningrad 135:33. Flowers white, carina's edge with anthocyanin.

Typus: 'Bialy-1', Poland, k-1602, reproduction of Pushkin's laboratories of VIR, 9. 08. 1986, A. K. Stankevich (WIR).

5. Var. *vulgaris* Libk. 1931, l. c. :59, sine typo. Flowers greyish-blue, carina's edge with anthocyanin.

Neotypes: 'Kievsky mutant', Ukraine, k-1904, reproduction of Pushkin's laboratories of VIR, 9. 08. 1989, B. S. Kurlovich (WIR).

This variety is the most widespread.

1. f. *libkindae* Kurl. et Stankev. 1990, Bull. Appl. Bot. Gen. Plant Breed., Leningrad 135:33. Side shoots absent or shortened. Flowers axillary.

Typus: 'EP-1', Poland, k-2890, reproduction of Pushkin's laboratories of VIR, 24. 08. 1989, B. S. Kurlovich (WIR).

The genepool of *Lupinus albus* L. has large intraspecific variation in physiological properties of plants: duration of the period of vernalization and growth rate, photoperiodic sensitivity, shape tolerance, drought resistance, cold- and winterhardiness. There are winter and spring forms. The lupin collection also has wild, turned wild, local forms and modern breeding varieties and genetic resources, which have a wide degree of diversity. We have developed a new ecogeographic classification of *L. albus* by grouping the genepool of white lupin into 11 geotypes and agrogeotypes, 4 ecogeographic groups of ecotypes, 17 separate ecotypes and 10 concultivars (Kurlovich 1994). The list and characteristics of different geotypes, ecotypes and concultivars are presented in Table 2. Ecogeographical research revealed the ranges of changeability of different characters of lupin forms. Duration of growing period under spring sowing changes from 106 to 180 days, weight of seeds from plants changes from 2.2 to 40 g, green mass from plant varies from 9 to 250 g, protein content from 35.0 to 53.7%, and oil content from 6.2 to 12.0%. Full-scale characteristics of white lupin samples of different geotypes, ecotypes and concultivars together with the possible ways of their utilization in breeding practice are presented in Russian in Kurlovich (1991) and Kurlovich *et al.* (1995).

2. ***L. angustifolius*** **L.** 1753, Sp. Pl. :721; Willd. 1803, Sp. Pl. ed. 4, 3;124; DC. 1825, Prodr. 2:407; Boiss. 1872, Fl. Or. 2:28; Willk. et Lange 1880, Prodr. Fl. Hisp. 3:466; Halacsy 1901, Consp. Fl. Graec. 1:340; Aschers. et Graebn. 1907, Syn. Mitteleur. Fl. 6 (2) :231; Fiori 1925, Nuov. Fl. Anal. Ital. 1:804; Plitmann 1966, Israel J. Bot. 15:26; Chamberlain in Davis 1970, Fl. Turkey 3:39; Zohary 1972, Fl. Palaest. 2:43; t. 57; Gladstones 1974, W. Austral. Dep. Agric. Tech. Bull. 26:9; Vass. 1987, in Fl. Part. Eur. URSS, 6:214.

Typus : Herb. Linn. [1]. 898-7 (LINN).

Table 2. Biodiversity of white lupin (*L. albus* L.)

Geotypes (agrogeotypes), ecogeographic group of ecotypes, ecotypes, concultivars	Characters									
	Status of accessions	Growth habit	Alkaloid-ness	Duration of growing period under spring sowing (days)	Mass/plant (g)		1000-seed weight (g)	Protein content in mature seeds (%)	Oil content (%)	Typical samples (name or indication number in the VIR catalogue)
					Green mass at flowering stage	Seed mass				
IBALKAN-ASIAN GEOTYPE										
winter mottled seed	wild	winter	bitter	rosette	9.0-20.4	30-40	250-270	35.0-36.2	8.3-9.2	*Lupinus vavilovi*
semi-winter mottled seed	wild	intermediate	bitter	rosette	9.1-30.2	26-30	250-270	31.5-36.9	8.5-9.6	k-3018,3118
Balkan early-ripening	turned wild	winter,intermediate	bitter	140-150	29-40	25-27	250-280	37.6-39.2	9.6-11.2	k-3117,3339
Peloponnesus	turned wild	intermediate,spring	bitter	140-150	31-44	28-30	300-380	37.8-41.2	9.8-11.4	k-1440,1441
Macedonian	local	intermediate,spring	bitter	120-140	150-200	32-38	380-500	35.0-36.7	10.9-11.6	k-1432,1435,3115
Turkish	local	intermediate,spring	bitter	115-140	200-250	36-39	400-450	35.0-35.9	10.8-11.7	k-529,530,532
Georgian	local	winter	bitter	rosette	200-250	39-41	285-300	39.2-40.1	10.5-11.1	k-1423,2910,3292
PALESTINIAN GEOTYPE										
Palestinian wild	wild,turned wild	intermediate	bitter	105-115	9.0-25.0	26-31	280-300	31.5-36.2	10.5-12.0	k-3293,3244
Jordan	local	spring,intermediate	bitter	105-113	16-35	31-35	300-380	41.0-44.3	9.8-11.5	k-290,298
Israeli	local	intermediate	bitter	110-125	12-30	48-40	420-480	36.8-37.9	11.3-12.0	k-3225,3226
ABYSSINIAN GEOTYPE										
Nile wild	wild,turned wild	intermediate	bitter	105-140	15-35	27-31	280-380	38.1-38.9	10.5-11.9	k-484,507,509
Egiptian	local	intermediate,spring	bitter	108-130	50-75	35-38	300-350	39.6-40.7	10.6-12.0	k-510,3105
Sudanese	local	winter,intermediate	bitter	110-140	80-100	38-40	450-500	39.9-41.2	11.2-12.0	k-1930,1931
ALGERIAN GEOTYPE†	local	intermediate,spring	bitter	130-180	190-240	30-35	350-400	39.6-40.2	10.2-11.4	k-2002,2005,3110
IBERIAN GEOTYPE										
Iberian wild -grown	turned wild	winter,intermediate	bitter	rosette	150-250	2.2-8.5	250-320	46.2-50.0	6.2-9.4	k-201,210,516,2356
Algarvian ecogeographic group of ecotypes	local	winter,intermediate	bitter	150-180	200-250	20-25	400-450	47.4-53.6	8.6-9.5	k-2625,2626,3261
Santarem ecogeographic group of ecotypes	local	intermediate,spring	bitter	140-180	180-250	3.7-20.0	250-280	48.2-53.7	7.5-10.0	k-2627,2628,3263
APPENINEN GEOTYPE										
Neapolitan ecogeographic group of ecotypes	wild,turned wild	intermediate,spring	bitter	130-160	100-140	10-40	280-350	40.0-43.6	8.6-9.6	k-218,314,2861
Calabrian ecogeographic group of ecotypes	local	intermediate,spring	bitter	140-160	190-240	23-30	400-450	42.0-44.3	8.8-10.0	k-313,1600,1661
WEST-EUROPEAN AGROGEOTYPE†										
Swiss	local	spring	bitter	130-150	60-80	30-35	300-360	45.6-49.2	9.6-10.0	k-94,124,240
Toulon	local	winter	bitter	rosette	200-250	25-35	280-360	41.6-41.9	9.9-10.2	k-3340
Nothern France	local	spring	bitter	130-140	91-105	10-15	280-350	41.9-42.6	9.5-10.8	k-223,1547
concultivar Lucku	br‡	winter,intermediate	sweet	130-140	91-105	20-30	380-400	45.6-49.2	9.9-11.0	Lucku,LA-99,ITA-30
concultivar Leblane	br	spring	sweet	130-150	50-60	15-18	340-350	43.1-44.2	9.8-10.5	Lublanc,Lutop,Lukrop
GERMAN AGROGEOTYPE										
concultivar Snezhinca	br	spring	bitter	130-170	230-245	10-16	300-320	38.5-45.1	8.8-10.5	Snezhinka,k-1426
concultivar Kraftquell	br	spring	sweet	140-175	60-90	10-15	320-380	47.3-52.8	8.2-10.5	Kraftquell,Hansa,Ultra
POLISH AGROGEOTYPE										
concultivar Gorzki	br	spring	bitter	120-180	180-210	25-32	280-320	36.0-39.0	7.0-8.7	Gorzki, Wielkopolski
concultivar Kalina	br	spring	sweet	130-160	150-180	20-26	350-400	38.8-40.2	9.5-9.9	Kalina,Kali,Bialy
concultivar Wat	br	spring	sweet	120-140	40-50	30-35	260-320	39.6-41.1	9.3-9.8	Wat,Hetman
EAST-EUROPEAN AGROGEOTYPE										
concultivar Chemigovsky	br	spring	bitter	135-165	210-250	18-25	350-420	37.1-41.2	8.4-9.7	Chernigovsky
concultivar Kievsky mutant	br	spring	sweet	115-130	180-220	22.3-25.1	300-320	35.6-42.6	10.9-11.0	Kievsky mutant,Dnepr
concultivar Ctart	br	spring	sweet	106-115	80-90	20.0-22.1	200-250	39.2-44.3	8.9-11.0	Start,Tambovsky
CHILEAN AGRO GEOTYPE†	br	winter	sweet	rosette	190-230	20.3-21.6	400-500			Amiga ,Prima,Victoria

†Not divided into ecotypes or concultivars because accessions insufficiently studied.

‡Breedibng resources.

Annual plants 20-160 cm height. Stems sparsely sericeous. Stipules linear-subulate. Leaflets 5-9, 38-56 x 3-7, 5 mm, linear to linear-sparthulate, upper surface glabrous, lower sparsely sericeous. Colour of corolla blue, pink, pale violet or white. Only upper flowers verticulate. Lower flowers on inflorescences alternate. Flowers not scented. Lower lip of calyx entire, upper lip of calyx deeply bipartite. Pods 30-50 x 7-10 mm with 4-7 seeds. Seeds 4-8 x 3-7 x 3-6 mm, globular, testa smooth, variously coloured and patterned with cream spots and pale, dark brown or black reticulations on a cream, greenish brown or grey background. $2n = 40$ (Fig. 2).

Distributed as wild plants everywhere around the Mediterranean, mainly coastal, occurring as a weed at roadsides and cultivated fields. Naturalized in South Africa and Australia, cultivated in Australia, North America and in many countries of Europe.

Lupinus angustifolius is an extremely polymorphic species (Table 3). Characters change depending on ecogeographic conditions (see Table 4). Wild ecotypes have as a rule more, smaller seeds, narrower pods and smaller and finer leaflets. Seed size and colour are very valuable characters. Plants with large seeds usually occur near arable land, close to villages and roads (probably turned wild). Plants with smaller seeds occur on coastal and mountain sand and rocky soils. The Linnaean specimen is clearly of the larger cultivated type (Fig. 2).

Seed colour varies from almost black, with small white specks and spots, motley, grey, with unclear spotting to beige (hazel) with brown spots, white with sparse brown and grey spots, and sheer white, glossy.

Usually seeds with coloured spotted surfaces are combined with blue and pink flowers. There is considerable variability in these two characters. Plants with white or pale-violet flowers usually also have beige or white seeds. But specific combinations of these and other characters do not demonstrate geographical or ecogeographical arrangements.

Fig. 2. *Lupinus angustifolius* L. (holotype).

These is no sharp gap between wild and cultivated forms. On the contrary, the transitions are very fluent. The two species *L. linifolius* Roth and *L. opsianthus* Atab. et Maiss., and also the two subspecies *angustifolius* and *reticulatus* (Desv.) Franco et Silva, are distinguished only on the difference in the width of leaflets and size of seeds (quantitative characters). We think that these species are more correctly subdivided as variants.

Using the developed criteria of intraspecific taxa on VIR's blue lupin collection disclosed 13 variants of *L. angustifolius* distinct from each other by seed and corolla colour. Variations in the colour of cotyledons, vegetative parts and carinae have been used for identification of 12 subvariants. In addition, the plants with determined branching and fascicular stems are described as 9 separate forms. The more distributed intraspecific taxa of *L. angustifolius* are presented in Table 3.

Diagnoses, citations and descriptions of the all intraspecific taxa in accordance with the regulations of the International Plant Nomenclature Code have been published in Kurlovich and Stankevich (1990).

The biodiversity of *L. angustifolius* in accordance with our ecogeographic classification is presented in Table 4. The genepool of blue lupin has been divided into 12 geotypes, 3 ecogeographic group of ecotypes, 16 separate ecotypes and 13 concultivars. We have revealed the ranges of changeability of different characters in lupins' forms. Duration of growing period under spring sowing in blue lupin change from 72 to 170 days, mass of seeds from plant from 1.1 to 30.6 g, green mass from 5.0 to 120 g, protein content from 18.0 to 39.2%, oil content from 3.2 to 8.5%, length of leaflets from 38.0 to 56.0 mm and width from 3.0 to 7.5 mm. Full-scale characteristics of different geotypes, ecotypes and concultivars, together with possible ways of their utilization in breeding practice, are presented in Kurlovich *et al.* (1995)

Table 3. The most widespread intraspecific taxa of *L. angustifolius* L.

Taxa (Var., Subvar., f.)	Characters	
Var. *angustifolius*	Flowers blue.Seeds motley, grey with unclear spotting	
	Subvar. *angustifolius*	Cotyledons and the carina's edge anthocyan - coloured
	f. *angustifolius*	Side shoots absent or shortened, flowers axillary
	Subvar. *viridulus* Kurl.et Stankev.	Cotyledons and the carina's edge green
Var. *albopunctatus* Kurl.et Stankev.	Flowers blue. Seeds almost black with tiny white dots and spots	
Var. *grisemaculatus* Kurl.et Stankev.	Flowers blue. Seeds grey with white spots	
	f. *belorussicus* Kurl.et Stankev.	Side shoots shortened, flowers axillary
Var. *chalubeus* Kurl.et Stankev.	Flowers blue. Seeds white with sparse dark-brown and grey spots	
Var. *corylinus* Kurl.et Stankev.	Flowers blue. Seeds beige with brown spots	
	f. *zhukovskii* Kurl.et Stankev.	Side shoots absent or shortened, flowers axillary
Var. *purpureus* Kurl.et Stankev.	Flowers pink. Seeds motley or grey with unclear spotting	
	Subvar. *purpureus* Kurl.et Stankev.	Cotyledons anthocyan - coloured, vegetative parts dark-violet
	Subvar. *rhodantus* Kurl.et Stankev.	Cotyledons and vegetative parts green
Var. *rubidus* Kurl.et Stankev.	Flowers pink. Seeds almost black with tiny white dots and spots	
	Subvar. *rubidus* Kurl.et Stankev.	Cotyledons anthocyan-coloured, vegetative parts dark-green
	Subvar. *maissurianii* Kurl.et Stankev.	Cotyledons and vegetative parts anthocyan-coloured
Var. *atabekovae* Kurl.et Stankev.	Flowers pink. Seeds with white spots	
Var. *sparsiusculus* Kurl.et Stankev.	Flowers pink. Seeds white with sparse dark-brown and grey spots	
Var. *brunneus* Kurl.et Stankev.	Flowers pink. Seeds beige with brown spots	
Var. *albosyringeus* Taran.	Flowers pale-violet. Seeds white, dull at the scar,without a triangular spot or strip	
	Subvar. *albosyringeus* Taran.	Cotyledons without anthocyan, vegetative parts dark-green
	f. *kloczkovii* Kurl.et Stankev.	Side shoots absent or shortened, flowers axillary
	f. *confertus* Kloczko et Kurl.	Stem fascicular. Flowers,pods and side shoots clustered at the top of the stem
	Subvar. *polonicus* Kurl.et Stankev.	Cotyledons and vegetative parts anthocyan–coloured
	Subvar. *lilacinus* Kurl.et Stankev.	Cotyledons and vegetative parts light-green
Var. *albidus* Kurl.et Stankev.	Flowers white. Seeds white with sparse brown spots	
	f. *kuptzovii* Kurl.et Stankev.	Side shoots absent or shortened, flowers axillary
Var. *candidus* Kurl.et Stankev.	Flowers white. Seeds green-white, glossy	
	Subvar. *candidus* Kurl.et Stankev.	Cotyledons and and vegetative parts without anthocyan
	Subvar. *virescens* Kuptzov et Kurl.	Cotyledons anthocyan-coloured
	Subvar. *violaceus* Kuptzov et Kurl.	Cotyledons and vegetative parts anthocyan-coloured

Table 4. Biodiversity of blue lupin (*L. angustifolius* L.)

Geotypes (agrogeotypes), ecogeographic group of ecotypes, ecotypes, concultivars	Characters											
	Status of accessions	Growth habit	Alkaloid-ness	Length of leaflets (mm)	Width of leaflets (mm)	Duration of growing period under spring sowing (days)	Mass/plant (g)		1000-seed weight (g)	Protein content in mature seeds (%)	Oil content (%)	Typical samples (name or indication number in the VIR catalogue)
							Green mass at flowering stage	Seed mass				
IBERIAN GEOTYPE												
Iberian waterside ecotype	wild	winter	bitter	40-42	3.0-4.0	no ripening	16-20	2.0-4.5	30-70	31.5-37.2	3.2-3.5	k-2969
Iberian rock	wild	winter	bitter	38-43	3.0-4.0	no ripening	18-22	1.5-5.0	30-80	30.2-36.8	3.4-3.8	k-2979
Iberian roadside	turned wild	winter	bitter	48-52	6.0-6.3	no ripening	80-100	8.0-12.0	81-120	30.0-30.7	3.2-3.9	k-3080,3081
Iberian green manure	local	intermediate	bitter	50-53	6.1-6.4	140-160	80-120	9.2-14.5	85-120	36.5-39.2	4.1-4.5	k-511,3275
MAROCCO GEOTYPE												
Marocco waterside	wild	intermediate	bitter	41-44	3.5-4.0	140-160	18-21	3.0-5.0	45-85	38.0-39.9	3.3-3.6	I-494161
Marocco rock	wild	winter	bitter	40-43	3.5-4.5	no ripening	15-25	2.5-6.0	50-90	36.6-39.0	3.4-3.9	k-3092
Marocco roadside	turned wild	spring	bitter	50-54	6.2-6.7	140-160	75-115	5.6-11.3	100-180	32.1-37.5	3.3-4.0	k-2003,3091
ALGERIAN GEOTYPE†	wild	intermediate	bitter	45-48	7.3-7.5	130-165	80-120	20-25	130-210	29.0-36.2	4.0-6.2	k-91,1939
APENNINE GEOTYPE												
Neopolitan ecogeographic group	wild	intermediate	bitter	45-50	4.5-5.0	130-145	14-18	8-10	90-120	23.2-27.0	5.0-6.1	I-494076
Apennine roadside ecogeographic group	turned wild	intermediate	bitter	52-55	6.4-6.8	125-160	60-90	10-14	110-120	25.0-27.8	6.2-6.4	I-494073
Apennine green manure ecogeographic group	local	intermediate	bitter	53-55	6.5-7.0	120-130	80-110	16-25	130-200	26.5-35.6	6.3-6.5	k-169,2868
BALKAN - ASIAN GEOTYPE												
Balkan wild	wild	intermediate	bitter	46.2-55.5	4.8-5.2	120-140	7-20	10-13	100-130	18.0-31.5	5.2-5.6	k-3346
Izmir	wild	intermediate	bitter	46.0-51.2	5.0-5.3	115-135	6-19	11-14	110-140	18.0-31.3	5.4-5.7	Izmir-1,Anatolia 30
Balkan roadside	turned wild	intermediate	bitter	51.0-54.1	5.0-5.4	110-130	50-80	15-26	120-145	25.0-29.8	6.1-6.3	Apendrilon
Balkan green manure	local	spring	bitter	53.0-55.0	6.5-7.0	100-120	60-90	18-27	140-200	31.0-32.0	6.5-8.0	k-3345
PALESTINIAN GEOTYPE												
Palestinian narrow-lived	wild	intermediate	bitter	48.5-53.0	5.0-5.3	95-120	5-15	15-20	100-130	18.0-29.6	5.5-7.4	I-494069
Palestinian broad-leaved	local	intermediate	bitter	54.0-56.0	6.4-7.5	90-110	45-53	25-30	140-210	19.6-31.2	6.9-8.5	k-288
SOUTH-AFRICAN GEOTYPE†	naturalized or turned wild	intermediate	bitter	50.0-54.0	6.0-6.4	130-150	71-80	20-28	150-180	21.5-36.3	6.2-8.4	k-1992
AUSTRALIAN AGROGEOTYPE												
West-Australian ecotype	naturalized	winter	bitter	43.0-49.0	5.2-5.8	106-125	70-120	14-18	155-165	33.4-36.1	6.7-6.9	I-521061
concultivar New Zealand Blue	br*	intermediate	bitter	43.0-49.0	5.2-5.8	106-125	70-120	14-18	155-165	33.4-36.1	6.7-6.9	New Zealand Blue
concultivar Unicrop	br	intermediate	sweet	49.1-55.0	6.1-6.3	78-110	115-120	17-25	150-160	36.8-39.1	6.8-7.1	Unicrop,Yorrel
NORTH-AMERICAN AGROGEOTYPE												
concultivar Rancher	br	winter	sweet			140-170	100-120	8-15	140-160	22.4-29.5	6.0-6.3	Rancher,Blanco L.
concultivar Frost	br	winter	sweet				140-170	115-120	21-30	108-110	26.2-31.3	5.8-6.2 Frost,Tifblue
GERMAN AGROGEOTYPE												
concultivar Pflug	br	spring	bitter			140-160	80-115	18-21	150-160	30.0-32.6	5.2-6.1	Pflug,Bismark
concultivar Munheberg	br	spring	sweet			130-155	45-58	15-18	160-180	30.8-31.6	5.4-6.3	Munheberg Sweet
POLISH AGROGEOTYPE												
concultivar Pulavski	br	spring	bitter			120-140	75-110	16-20	160-180	29.5-31.6	5.6-7.2	Pulavski,Wielkopolski
concultivar Mirela	br	spring	bitter			85-110	60-71	26-30	140-150	32.5-33.8	6.2-7.4	Mirela,Turkus
concultivar Emir	br	spring	sweet			90-115	50-60	20-25	120-130	30.0-34.2	6.5-7.3	Emir,Kazan,Ignis
EAST-EUROPEAN AGROGEOTYPE												
concultivar Bieniakonsky	br	spring	bitter			100-130	95-120	25-29	150-155	32.0-34.0	6.2-7.5	Bienniaconsky
concultivar Niemchinovsky	br	spring	sweet			95-105	80-100	23-26	120-130	31.0-31.4	6.3-6.4	Niemchinovsky 846
concultivar Danko	br	spring	sweet			96-119	60-80	25-30	130-140	36.0-39.0	6.3-8.5	Danko,Rezerv
concultivar Ladny	br	spring	sweet			72-90	30-40	20-22	120-130	32.5-33.6	6.4-6.9	Ladny,Lanedex

†Not divided into ecotypes or concultivars because were not found essential differences between accessions.

*Breeding resources

3. *L. luteus* L. 1753, l. c. :722; Willd. 1803, l. c. :1024; DC. 1825, l. c. :407; Willk. et Lange 1880, l. c. :468; Franco et Silva 1968, l. c. :105; Zohary 1972, l. c. :44; Gladstones 1974, l. c. :17; Vass. 1987, l. c. :214.

Typus : Herb. Linn. No.. 898-8 (LINN).

Protologus : < In Siciliae arenosis >.

Plants 20-80 cm high, rosetted at first, becoming erect with basal branching. Stems short, hirsute, bushy. Leaflets 7-9, ovate-oblong, 30-60 x 8-15 cm mucronate, villous above, sparsely sericeous below. Inflorescence 5-15 cm long. Flowers verticulare. Colour of corolla yellow, lemon yellow, orange or whitish. Corolla 14-16 mm long and high. Flowers scented. Upper lip of calyx very deeply bipartite, lower lip shallowly 3-toothed. Pods 40-60 x 10-15 mm, densely villous, 4-6 seeded. Seeds 5.5-6.5 mm in diameter with semilunate, punctate or marbling type of pattern. Colour of seeds from black to white with different spotting. $2n$=52 (Fig. 3).

Distributed as wild, turned wild or naturalized plants on the Western coastal part of the Iberian Peninsula, coastal Morocco, southern Sicily, Sardinia, Corsica, Greece, Israel, cultivated in many countries of Europe, and to smaller extents in South Africa and Australia.

Variation in the degree of morphological characters in this species is rather poor but the colour of the seeds make it possible to form homologous series similar to *L.angustifolius*. Most of the corolla in *L. luteus* is yellow, rarely lemon-yellow, orange or whitish. According to the developed criteria of intraspecific taxa, there have been disclosed 18 variants of *L. luteus* distinctly differing from each other by the seed corolla colour. Variation in the colour of vegetative parts and carinae have been used for identification of 4 subvariants. Besides, the plants with determined branching and fascicular stems are described as 6 separate forms (Kurlovich and Stankevich 1990). The most distributed intraspecific taxa of *L. luteus* are presented in Table 5.

According to the developed criteria of ecogeographic classification the genepool of yellow lupin has been classified into 8 geotypes, 2 ecogeographic groups of ecotypes, 10

Table 5. The most widespread intraspecific taxa of *Lupinus luteus* L.

Taxa (Var., Subvar., f.)	Characters	
Var. *luteus*	Flowers yellow. Seeds white with black dots without arcs (dotted)	
	f. *volovnenkoae* Kurl.et Stankev.	Side shoots absent or shortened, flowers axillary
	f. *compactus* Kazim.et Kaz.	Flowers and pods clustered at the top of the stem
Var. *maculosus* Kurl.et Stankev.	Flowers yellow. Seeds white with black spots and two light arcs	
Var. *kazimierski* Kurl.et Stankev.	Flowers yellow. Seeds white with brown spots without arcs	
Var. *arcellus* Kurl.et Stankev.	Flowers yellow. Seeds white with brown spots and two dark arcs	
Var. *sempolovskii* Kurl.et Stankev.	Flovers yellow. Seeds white with black spots and wide clear space round the scar	
Var. *melanospermus* Kurl.et Stankev.	Flower yellow. Seeds brown-and-black with light arcs	
Var. *niger* Kurl.et Stankev.	Flowers yellow. Seeds black,without arcs	
Var. *leucospermus* Kurl.et Stankev.	Flowers yellow. Seeds white	
Var. *citrinus* Kurl.et Stankev.	Flowers lemon-yellow. Seeds white with black dots without arcs (dotted)	
	f. *lukasheviczii* Kurl.et Stankev.	Side shoots absent or shortened, flowers axillary
Var. *sulphyreus* Kurl.et Stankev.	Flowers lemon-yellow. Seerds white with black spots and two light arcs	
Var. *stepanovae* Kurl.et Stankev.	Flowers lemon-yellow. Seeds creme-coloured with two white arcs	
Var. *ochroleucus* Kurl.et Stankev.	Flowers lemon-yellow. Seeds white	
	Subvar. *ochroleucus* Kurl.et Stankev.	Carina's edge with anthocyan
	Subvar. *chloroticus* Kurl.et Stankev.	Carina's edge without anthocyan
	f. *bernatzkayae* Kurl.et Stankev.	Side shoots absent or shortened, flowers axillary
Var. *aurantiacus* Kurl.et Stankev.	Flowers orange. Seeds white with black dots without arcs	
Var. *aureus* Kurl.et Stankev.	Flowers orange. Seeds white	
	f. *golovczenkoi* Kurl.et Stankev.	Side shoots absent or shortened, flowers axillary
Var. *albicans* Kurl.et Stankev.	Flowers whitish. Seeds white with black spots and two light arcs	
Var. *sinskayae* Kurl.et Stankev.	Flowers whitish. Seeds white	

separate ecotypes and 10 concultivars (Table 6). Ecogeographical research has revealed the range of changeability of different characters. Duration of growing period under spring sowing changes from 90 to 175 days, mass of seeds from plant from 2.0 to 24.6 g, green mass from 8.0 to 245.0 g, protein content from 34.0 to 55.0%. The comprehensive characteristics of yellow lupin samples of different geotypes, ecotypes and concultivars, together with the possible ways of their utilization in breeding practice, are presented in (Kurlovich *et al.* 1995).

Neighbouring but isolated from *L. luteus* is *L. hispanicus* Boiss. et Reuther. It has not yellow but violet or cream flowers. The surface of the seeds is uneven (specific character). Both species have the same number of chromosomes but serologically are different. *Lupinus luteus* is distributed on the coastal region of the Iberian Peninsula and *L. hispanicus* on the central part of the peninsula on granite mountains. Both species may have had the same initial forms but the divided a long time ago. More detailed investigations are needed into the breeding potential of these two species of lupin.

Fig. 3. *Lupinus luteus* L. (holotype).

Discussion

Variability of characters and diversity of forms of several lupin species have been studied by many botanists and plant scientists (Zhukovsky 1929; Gladstones 1974; Kazimierski and Kazimierska 1975). The most detailed research was conducted by Maissurian and Atabiekova (1974). In their classification of intraspecific diversity of lupin forms they used flower and seed coat colour following the interrelation of these characters originally outlined by Vavilov (1920). However, their classification did not involve genetic determination of the degree of character expression. In a number of cases the composed determinant tables contained "overlapping" characters, therefore in the process of classifying one and the same plant may be systematized into different classes. This work is aimed at removing these ambiguities. Many years of observing the plants in various regions have provided the knowledge to make essential corrections in the classifications of lupin. During our research (1973-96) we have studied and described 50 new intraspecific taxa of *L. albus*, *L. angustifolius* and *L. luteus* in accordance with the regulations of the International Plant Nomenclature Code (Kurlovich and Stankevich 1990). Further study of the biodiversity of lupin will probably reveal new intraspecific taxa, particularly subvariants and forms.

Table 6. Biodiversity of yellow lupin (*L. luteus* L.)

Geotypes (agrogeotypes), ecogeographic group of ecotypes, ecotypes, concultivars	Characters								
	Status of accessions	Growth habit	Alkaloid-ness	Duration of growing period under spring sowing (days)	Mass/plant (g)		1000-seed weight (g)	Protein content in mature seeds (%)	Typical samples (name or indication number in the VIR catalogue)
					Green mass at flowering stage	Seed mass			
IBERIAN GEOTYPE									
Lisbon ecotype	wild	winter	bitter	no ripening	110-120	2-5	75-90	46.9-51.3	k-3099
Madrid	wild	intermediate	bitter	no ripening	80-90	3-6	70-100	46.2-49.4	k-3072
Galician	turned wild	intermediate	bitter	150-175	200-210	10-12	90-120	48.2-55.0	k-2290,2292
Seville	local	intermediate	bitter	140-180	235-245	10-12	100-120	47.9-53.8	k-2865,2992
MAROCCO GEOTYPE									
Tangier	wild	intermediate	bitter	140-180	78-85	4-7	80-120	42.6-50.1	Anamoro
Rabat	turned wild	intermediate	bitter	130-160	190-200	12-13	110-130	44.9-52.3	k-2004
APENNINE GEOTYPE									
Messina ecogeographic group of ecotypes	wild	intermediate	bitter	120-150	50-85	6-18	90-135	40.2-43.6	Sicilia KI -1
Italian green manure ecogeographic group of ecotypes	local	intermediate	bitter	135-155	100-130	10-12	140-150	42.4-45.5	k-3341,2074
BALKAN-ASIAN GEOTYPE									
Greek	wild	intermediate	bitter	120-130	45-50	18-22	110-150	34.5-38.2	k-1456,3342
Anatolian	wild	intermediate	bitter	115-128	30-40	19-23	130-160	34.3-36.9	k-2075,2081
PALESTINIAN GEOTYPE									
Oriental	wild	intermediate	bitter	115-120	20-30	19-24	95-125	34.0-36.0	Izrael 8a
Jerusalem	local	intermediate	bitter	108-120	40-45	20-24	10-160	35.5-40.1	Palestina 1
GERMAN AGROGEOTYPE									
concultivar Luneburger	br†	spring	bitter	125-135	200-250	10-15	120-160	43.3-44.5	Luneburger,Paulse
concultivar Weiko	br	spring	sweet	120-135	80-90	20-24	140-170	42.2-46.8	Weiko 1,2,3,4
concultivar Borluta	br	spring	sweet	120-140	130-140	20-24	140-160	45.2-46.8	Borluta,Bornova
POLISH AGROGEOTYPE									
concultivar Express	br	spring	sweet	120-130	200-210	15-19	110-120	45.3-46.9	
concultivar Afus	br	spring	sweet	130-135	230-250	22-24	110-125	41.9-49.5	Afus,Cyt,Tomik
concultivar Iryd	br	spring	sweet	110-120	180-220	20-22	120-130	44.2-46.5	Iryd,Baltyk,Ventus
EAST-EUROPEAN AGROGEOTYPE									
concultivar Akademichesky	br	spring	sweet	95-120	180-200	20-25	120-130	42.3-47.5	Akademichesky
concultivar Kastrychnik	br	spring	sweet	90-115	200-250	23-25	115-120	42.3-48.4	Kastrychnik
concultivar Kopylovsky	br	spring	sweet	105-130	240-250	24-26	105-120	46.2-47.5	Kopylovsky
concultivar Zhitomirsky	br	spring	sweet	90-105	40-45	12-15	120-135	41.3-46.6	Zhitomirsky

†Breeding resources

More efficient utilization of the potential of the crop in plant breeding, beyond recording morphological characters, requires detailed information on biological, physiological, biochemical and other properties of the plants. Ecogeographic classification reflects the patterns of variability of these properties, based on the specific nature of the geographic, historic, ecological and agronomic conditions. It cannot replace the botanical classification of the species, but supplements it. Taken together they provide for purposeful and conscious utilization of plant genetic diversity in breeding practice, as Vavilov repeatedly noted(Vavilov 1920, 1935, 1987).

In our research we were guided by Vavilov's differential systemogeographic method of crop studies (Vavilov 1935), which provided a possibility to perform targeted searching for valuable breeding materials in various regions and solve the problems of phylogeny, taxonomy and evolution. This enabled us not only to disclose the diversity of forms, but also to reveal a series of regularities in their variation depending on the degree of cultivation, geographic environments and soil conditions. All the species within the limits of different geotypes showed similar ecotypes, with variability governed by Vavilov's Law of Homologous Series in Variation (Vavilov 1920) and the Law of Spiral Series (Sinskaja 1969). Thus, different geotypes of the Mediterranean area had large-seed and small-seed ecotypes, and *L. angustifolius* ecotypes with very narrow leaflets and broader ones (Table 4). However, perfect similarity of ecotypes does not exist. Geographic regularities were identified in the variability of a series of characters and properties in similar ecotypes (Tables 7-9). From the west of the Mediterranean to the east, seed productivity, seed weight and oil content increased in seeds in all three species. In addition, the length and width of leaflets of the narrow blue lupin increased (Table 8). Correspondingly the duration of the growing period, the green mass of plants and the protein content in mature seeds decreased. As examples, Table 7 presents variation in the degree of characters at the local forms of *L. albus*, Table 8 variation in wild forms of *L. angustifolius* and Table 9 in the wild forms of *L. luteus*. Moreover, we have found a negative connection between protein and oil content. Variation in the degree of protein and oil content in seeds of local white lupin forms from different geotypes are presented in Figure 4. These data were confirmed to a considerable extent by other researchers (Mota *et al.* 1982; Simpson and Martins 1984; Swecicki 1988; Cowling 1994).

The differential systemogeographic method of crop studies allows more accurate distinguishing of the centres of formation and origin of different lupins' forms. The centre of formation of wild white lupin *(L. albus)* and the primary centre of origin of its initial cultivated forms is Balkan, where an exceptionally wide diversity of wild, turned wild and local forms is concentrated. Three subspecies of white lupin (subsp. *graecus* Franko et Silva, subsp. *termis* Ponert., subsp. *albus)* grow in the Balkans. This region also has wild forms with dotted dark brown seeds and dark blue flowers (subsp. *graecus*).

The Apennines and Egypt are also centres of origin of forms of cultivated white lupin, having been cultivated since the earliest recorded history. Moreover, ancient Egypt had widespread forms with pink and blue or light pink flowers

Table 7. Variation in the degree of characters in local forms of *L. albus* L.

Ecotypes, ecogeographical group of ecotypes	Characters						
	Status of accessions	Duration of growing period under spring sowing (days)	Mass/plant (g)		1000-seed weight (g)	Protein content in mature seeds	Oil content (%)
			Green mass at flowering	Seed mass			
Algarvian ecogeographic group of ecotypes	local	150-180	200-250	20-25	400-450	47.4-53.6	8.6-9.5
Calabrian ecogeographic group of ecotypes	local	140-160	190-240	23-30	400-450	42.0-44.3	8.8-10.0
Macedonian ecotype	local	120-140	150-200	32-38	380-500	35.0-36.7	10.9-11.6
Turkish ecotype	local	115-140	200-250	36-39	400-450	35.0-35.9	10.8-11.7
Egiptian ecotype	local	108-130	50-75	35-38	300-350	39.6-40.7	10.6-12.0
Israeli ecotype	local	110-125	12-30	48-40	420-480	36.8-37.9	11.3-12.0

Table 8. Variation in the degree of characters in the wild forms of *L. angustifolius* L.

Ecotypes, ecogeographical group of ecotypes	Characters								
	Status of accessions	Length of leaflets (mm)	Width of leaflets (mm)	Duration of growing period under spring sowing (days)	Mass/plant (g)		1000-seed weight (g)	Protein content in mature seeds	Oil content (%)
					Green mass at flowering	Seed mass			
Iberian waterside	wild	40-42	3.0-4.0	no ripening	16-20	2.0-4.5	30-70	31.5-37.2	3.2-3.5
Marocco waterside	wild	41-44	3.5-4.0	140-160	18-21	3.0-5.0	45-85	38.0-39.9	3.3-3.6
Neopolitan ecogeographic group of ecotypes	wild	45-50	4.5-5.0	130-145	14-18	8-10	90-120	23.2-27.0	5.0-6.1
Balkan wild	wild	46.2-55.5	4.8-5.2	120-140	7-20	10-13	100-130	18.0-31.5	5.2-5.6
Izmir	wild	46.0-51.2	5.0-5.3	115-135	6-19	11-14	110-140	18.0-31.3	5.4-5.7
Palestinian narrow-lived	wild	48.5-53.0	5.0-5.3	95-120	5-15	15-20	100-130	18.0-29.6	5.5-7.4

Table 9. Variation in the degree of characters in wild forms of *L. luteus* L.

Ecotypes, ecogeographical group of ecotypes	Characters					
	Status of accessions	Duration of growing period under spring sowing (days)	Mass/plant (g)		1000-seed weight (g)	Protein content in mature seeds
			Green mass at flowering	Seed mass		
Lisbon ecotype	wild	no ripening	110-120	2-5	75-90	46.9-51.3
Madrid ecotype	wild	no ripening	80-90	3-6	70-100	46.2-49.4
Tangier ecotype	wild	140-180	78-85	4-7	80-120	42.6-50.1
Messina ecogeographic group of ecotypes	wild	120-150	50-85	6-18	90-135	40.2-43.6
Greek ecotype	wild	120-130	45-50	18-22	110-150	34.5-38.2
Anatolian ecotype	wild	115-128	30-40	19-23	130-160	34.3-36.9
Oriental ecotype	wild	115-120	20-30	19-24	95-125	34.0-36.0

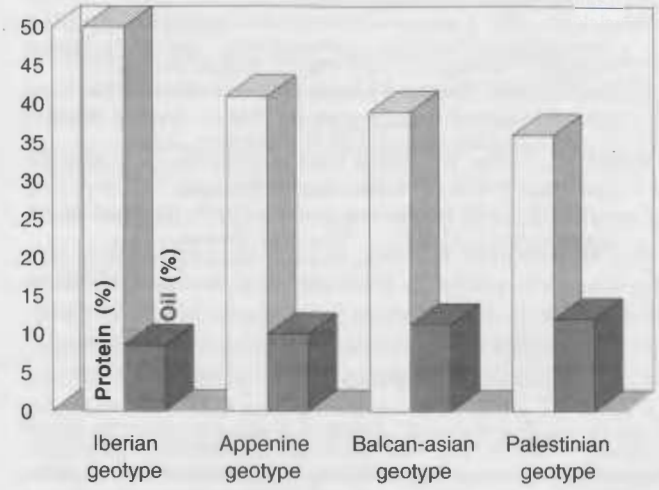

Fig. 4. Variation in the degree of protein and oil content in seeds (local forms of *Lupinus albus* L. from different genotypes).

(subsp. *termis*). The Apennines showed widespread forms with greyish and light blue or white flowers (subsp. *albus*).

Two close species (*L. luteus* and *L. hispanicus* Boiss. et Reut.) exist in the Pyrenees with the same number of chromosome ($2n$=52), a wide diversity of wild and cultivated forms of yellow lupin (*L. luteus*) and a long historical period of growing there. Together, these suggest that the Pyrenees was the centre of formation of the wild forms of yellow lupin and the centre of origin of the cultivated plants. The Pyrenees are probably also the centre of formation and origin of the blue lupin (*L. angustifolius*), because this peninsula shows the highest concentration and the widest diversity of forms with very primitive dominant characters (mostly small seeds, mostly narrow leaflets, monopodial branching) and forms with characters of cultivated plants (more large seeds and leaflets, simpodial branching).

As a result of increased use of the lupin in agriculture, its area of cultivation gradually increased, leading to the formation of secondary macro- and microcentres of origin of cultivated lupin forms. These correspond to the many geotypes we have described. We think, at present, that the secondary centres of origin of cultivated white lupin (*L. albus*) are in France, Germany, Poland, Bielorussia, Russia and Chile. The secondary centre of origin of the blue lupin (*L. angustifolius*) is first Australia, then South Africa, the southeastern United States, Poland and Bielorussia. The secondary centres of origin of yellow lupin (*L. luteus*)are in Germany, Poland, Bielorussia, Russia and the Ukraine.

Conclusions

The results indicate that the lupin samples of Iberian geotype were the most efficient in breeding for resistance to disease or for fresh green mass. Specimens from the Balkan-Asian and Palestinian geotypes are more efficient in creating cultivars for grain yield breeding for earlyness, large seed, drought resistance and increased oil content. Wild-growing forms of all the above lupin species undoubtedly bear numerous valuable characters: small seed, drought tolerance, resistance to low temperatures and diseases. Among the forms most adapted for cultivation and breeding in Russia are those that have escaped from domestication, or turned wild, as well as local varieties from the Mediterranean countries.

The breeding programmes of most lupin-growing countries use the most diverse initial material, mainly because of geography. The countries of the Mediterranean region, Australia, New Zealand, Chile and the USA have favourable conditions to utilize the great diversity found in Mediterranean forms, particularly that from the western coastal area of the Mediterranean.

Russia and other countries of the former USSR as well as Poland and Germany are situated in more northern latitudes, and there are limited possibilities to use the wild-growing Mediterranean forms. Many of them can be cultivated only in greenhouses or climate chambers, although some are suitable for autumn sowing under Transcaucasian conditions. Of more broad application here are the genetic resources from the eastern coastal area of the Mediterranean, distinguished by their greater scope of modification, variability, earliness and large seeds. Plant breeders in Russia and Poland have used induced mutagenesis widely in recent years. However, the best results might be realized with an optimum combination of mutagenesis and hybridization of both mutants and wild-growing or domesticated forms of various ecogeographical origin.

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Résumé

Espèces et diversité intraspécifique chez les lupins blancs, bleus et jaunes

La collection de lupins de l'Institut N.I. Vavilov contient plus de 2500 accessions. De nombreuses années d'études dans diverses régions géographiques, et la généralisation des données obtenues par d'autres chercheurs ont révélé des classifications taxonomiques et géographiques intraspécifiques. On a identifié une série de patterns dans la variation des pools géniques qui dépend du degré de culture et des conditions d'environnement et de sol. Ces patterns définissent de manière plus précise les centres d'origine des espèces cultivées de lupin. Cette base de connaissances permettra des collectes mieux ciblées ainsi que le développement de recommendations pour les pratiques d'amélioration.

Resumen

Especies y diversidad de lupinos blanco, azul y amarillo

La colección de lupinos del Instituto N.I. Vavilov posee más de 2.500 accesiones. Muchos años de estudios en distintas regiones geográficas y la generalización de los datos obtenidos por otros investigadores, han puesto de manifiesto una taxonomía intraespecífica y clasificaciones ecogeográficas. Se ha identificado una serie de imágenes en la variación del acervo genético que depende del grado de cultivo, medio ambiente y condiciones del suelo. Estas imágenes definen más exactamente los centros de origen de las especies cultivadas de lupinos. Esta fundación ayudará a realizar una recolección más específica y permitirá el desarrollo de recomendaciones para fitomejoramiento.