The significance of Vavilov's scientific expeditions and ideas for development and use of legume genetic resources

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Summary

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This article is a synopsis of the principal expeditions of N.I. Vavilov and their significance for scientific research and practice. It also presents a discussion of Vavilov's law of homologous series in hereditary variation, studies on the problem of the Linnaean species concept, the botanical and geographical aspects of plant breeding, and the theory of the centres of origin of cultivated plants. The practical applications of the characteristics of accessions of leguminous crops assembled by Vavilov are described, as is the impact of modern research on development of Vavilov's ideas.

Key words: Ecogeographical approach, expeditions, genetic resources, legumes, plant breeding, preservation, resistance, transgression

Résumé

Importance des expéditions scientifiques de Vavilof et perspectives pour le développement et l'utilisation des ressources génétiques de légumineuses

Cet article résume les principales expéditions de N.I. Vavilov et leur importance pour la recherche scientifique et l'expérimentation. Il discute aussi de la loi de Vavilov sur les séries homologues dans la variation héréditaire, des études sur le problème du concept d'espèces de Linné, des aspects botaniques et géographiques de l'amélioration des plantes et de la théorie des centres d'origine des plantes cultivées. Les applications pratiques des caractéristiques des accessions de légumineuses rassemblées par Vavilov sont décrites ainsi que l'impact de la recherche moderne sur le développement des idées de Vavilov.

Resumen

El significado de las expediciones científicas y las ideas de Vavilov para el desarrollo y uso de los recursos genéticos de las leguminosas

Este artículo es un resumen de las principales expediciones de N.I. Vavilov y lo que significa para la investigación y la práctica científica. Presenta también un análisis de la ley de Vavilov de series homólogas en la variación hereditaria, estudios sobre el problema del concepto de especie en Linneo, los aspectos botánicos y geográficos de la mejora fitogenética y la teoría de los centros de origen de las plantas cultivadas. Se describen las aplicaciones prácticas de las características de las accesiones de leguminosas cultivadas reunidas por Vavilov, así como los efectos de la investigación moderna sobre el desarrollo de las ideas de Vavilov.

Introduction

Nikolai I. Vavilov (1887–1943) is recognized as the foremost plant geographer, botanist and geneticist of contemporary times. In the early 20th century, the world did not appreciate the urgency of protecting the environment and scientists thought little about the gradual disappearance of valuable plant species. Vavilov was among the first to recognize the need for intensive plant collecting, research and preservation. He organized and took part in over 100 collecting missions in the major agricultural areas of the world. During these expeditions, Vavilov paid special attention to leguminous crops as sources of protein and as means of increasing soil fertility (Sinskaja 1991). He considered these issues to be of the highest priority in biological and agricultural sciences for developing sustainable agricultural production.

The books and articles dedicated to the life and scientific activity of Vavilov (e.g. Sinskaja 1991; Pistorius 1997; Loskutov 1999) mention his many research studies on legumes. Many close colleagues of Vavilov (e.g. Barulina, Govorov, Zhukovsky) further developed his ideas, selecting legumes as the subject of their research. Vavilov and his colleagues revealed a number of important findings in plant biology through such research. However, this vast body of work has not been brought together in a single report. We have concentrated our attention on the results of detailed analysis of legume genetic resources at The Vavilov Institute of Plant Industry (VIR), named after Vavilov in 1967.

Vavilov's expeditions and their outcomes

Vavilov was particularly interested in the sites of ancient agricultural civilizations and of mountainous regions. In 1916, he was sent to Iran and Pamir by the Ministry of Agriculture to determine the reasons for disease epidemics among the resident Russian garrisons. Vavilov discovered that the wheat used for bread flour was contaminated with seeds of the poisonous grass species *Lolium temulentum*. Vavilov continued his travels in the northern and central regions of Iran, in Pamir and other regions of Central Asia. His main purpose was to collect early varieties of agricultural plants for testing in northern and droughty areas of Russia, and to determine the high-altitude limits of agriculture (Vavilov 1987a, 1991). He was also searching for "Persian wheat", reported to be resistant to many diseases (Bazilevskaya and Bakhareva 1991).

Despite a careful search, Vavilov did not find "Persian wheat" in Iran. However, he did collect many other valuable accessions, among them leguminous crops including mung bean, chickpea, lentil, everlasting pea, pea, beans and species of clover, not known at that time in Russia. The materials collected by Vavilov in Iran and in Pamir formed the foundation of the collection of leguminous grain crops of the VIR. As a result of his first expedition, 171 grain legumes samples were collected. Subsequent collecting missions increased the number of legume accessions from Central Asia to 1373 (Table 1). The results of a detailed investigation of these were a starting-point for developing a number of important theoretical and practical generalizations on the origin, geography, genetics, disease resistance and evolution of cultivated plants.

Vavilov's travels in Iran indicated that there were sources of ancient agriculture in southwest Asia. He also detected particular ecotypes in Pamir, which suggested their origin was in those mountains. He concluded that southwestern Asia was a centre of origin of a many legume species (Vavilov 1965b). The majority of the legumes samples from this centre were small-seeded with specific flower colours determined by recessive genes (Zhukovsky 1971). Cross-pollinated species from southwest Asia (everlasting pea, fodder beans) have a propensity for self-fertilization. In the law of homologous series (Vavilov 1920), which was largely formulated following the expedition to Iran and Pamir, Vavilov noted that variability characterized the entire Leguminosae (Vavilov 1920, 1987b). E.I. Barulina (Vavilov's wife and the principal lentil expert, Fig. 1) established a precise parallelism in variability of vetch and lentil samples that originated from Iran (Barulina 1930). Their similarity is such that even an expert finds it difficult to distinguish between seeds of these species. This example has become a classic illustration of Vavilov's law of homologous series in hereditary variability (Sinskaja 1969; Makasheva 1973, 1979; Vavilov 1987a, 1987b). Forms of legumes with various seed and flower colours, obeying the law of homologous series, are demonstrated by many species of lupin, peas, mung bean, string bean and fodder beans.

In 1924, Vavilov organized an expedition to Afghanistan together with V.N. Lebedev and D.D. Bukinich (to Herat, Afghan Turkestan, Gaimag, Bamian, Hindu Kush, Ba Kafiristan, Jalalabad, Kabul, Kandahar, Baquia, Helmang, Farakh and Sehistan). The findings from this expedition supported the conclusions about southwest Asia as a centre of origin of many plants. It was established that Afghanistan was a major primary focus of formation where there existed a large diversity of many major Eurasian crops, representing an inexhaustible source of initial material for selection (especially for drought resistance). Following this hazardous and very fruitful expedition to Afghanistan, Vavilov was awarded the N.M. Przevalski Gold Medal of the Russian Geographic Society, of which Vavilov was president from 1931 to 1940.

Vavilov had a special interest in the Khoresm oasis, whose proximity to Afghanistan and Iran supported the hypothesis that this territory was also a focus of formation. Vavilov inspected area around the Amu Darya River (Khiva, Urgench, Gurlen and Tashauz) in 1925. Whereas there were signs in Iran and Afghanistan that cultivated plants had developed locally, Khoresm showed signs of connections with northeast Africa and Egypt that influenced the features of cultivated plants. White-seeded forms of peas, haricot bean and fodder bean were found in Khoresm, together with particular forms of groundnuts and alfalfa. Khoresm oasis was characterized by an abundance of many recessive forms of cultivated plants (Vavilov 1926; Bazilevskaya and Bakhareva 1991).

Table 1. Accessions of grain legume crops collected from Central Asia

Crops	Quantity of the collected accessions	
	Personally by N.I. Vavilov in 1916	As a result of the consequent expeditions
Mung bean	115	680
Chickpea	18	434
Lentil	16	52
Everlasting pea	12	39
Pea	8	56
Fodder beans	2	112
Total	171	1373

Fig. 1. N.I. Vavilov with his wife E.I. Barulina, 1926 (before their expedition to the Mediterranean).

In 1921 Vavilov organized a trip to Canada (Ontario) and the USA. The official purpose was to search for sources of resistance to drought, necessary for restoring Russian agriculture after a severe drought in 1921. Vavilov understood from his first visit to North America that the continent was not a focus of intensive formation of plants and agriculture (Vavilov 1965b, 1987b). The main foci of plant diversity were to the south, in southern Mexico, and Central and South America. Vavilov visited a number of European countries (Britain, France, Germany, Poland, Holland and Sweden) on his return from America in 1922. As a result of these and his subsequent travels to Germany in 1927, the USA in 1930, Canada and other American countries in 1932–33, he added commercial varieties and a selection of legumes from many countries to the collection of VIR.

Vavilov visited Mediterranean countries in 1926: northern Africa, the islands of Cyprus, Crete, Sicily and Sardinia, and southern Europe (Portugal, Spain, France and Greece). He noted the role of leguminous crops (particularly chickpea) in supplying both people and livestock with protein and as a means of increasing soil fertility (especially lupin) (Vavilov 1997; Loskutov 1999). He found that the activities of people had little effect on plant diversity in any of the coastal zones of the Mediterranean. However, a different picture emerged in inland areas, oases and southern slopes of mountains, where the influence of European civilization was apparent (Vavilov 1997). Vavilov's special interest in early agrarian cultures led to an expedition to Syria, Palestine and Jordan, where there were traces of ancient agriculture. In Palestine in particular, he found useful forms of white lupins (going under the local name Tel Karam). These are distinguished by early maturity and are now widely used in breeding (Golovchenko *et al.* 1984). Plant collection in Sudan and Ethiopia yielded about 2000 accessions of local varieties. In Sudan, Vavilov found valuable forms of white lupin, and in Ethiopia found endemic forms of everlasting pea, chickpea, lentil and beans. The flora of Ethiopia is in many respects unique and Vavilov considered it to be an independent primary Abyssinian focus (Vavilov 1926), and later the Abyssinian Centre of diversity (Vavilov 1962).

In 1929 Vavilov organized an expedition to China (Xinjiang–Kashgar, Uch Turfan, Aksu, Kucha, Urumchi, Kulja and Hotan), Japan (Honshu, Kyushu and Hokkaido) and Korea. The purpose of his trip to northern and western China was to determine the role of Central Asia (within the limits of China) in the origin of cultivated plants of eastern Asia. Returning from northern and western China, he inspected the area close to the Chinese border around Lake Issyk-Kul and the Syr Darya river basin. Vavilov concluded from the results of this trip that Central Asia does not have the features of an independent focus of ancient agriculture: all that was cultivated there had been introduced from the east. His investigations in Japan, however, confirmed it as one of the centres of cultivated plants (the East Asiatic centre). He found that, while Japan had 'borrowed' some cultivated plants from China, its geographical isolation, its span in latitude, and its diversity of climate and ecology generated unique features in the cultivated flora. Wild species and cultivated forms of soybean were added to the collection following these expeditions.

Vavilov was interested for a long time in plant genetic resources of Latin America. In 1932, an invitation to the VI International Genetic Congress in the USA gave him an opportunity to inspect these regions. Vavilov visited Cuba, Mexico, Ecuador, Peru, Bolivia, Chile, Brazil, Argentina and Uruguay after the congress. Vavilov detected specific and varietal structures in cultivated plants, and received information about their history, origin and wild relatives. He collected valuable forms of kidney bean, peanuts and American species of lupin. This was Vavilov's last overseas trip.

Vavilov also traveled widely in the territory of the former Soviet Union. He paid special attention to the mountain regions of the Caucasus and Central Asia, in which there were unique cultures and wild species, whose role in the creation of cultivated plants is not doubted. The direct connection of the Caucasus with Iran, Central Asia and Turkmenistan has resulted in some similarities with the Southwest Asiatic Centre of origin of cultivated plants. Vavilov personally participated in expeditions to more than 50 countries. In 1938–1940, he wrote essays on his journeys under the title "Five Continents". The existing pages of this manuscript were published in 1962 and 1987 in Russian (Vavilov 1962, 1987a), and later in English by IPGRI (Vavilov 1997).

The characteristics of the principal legume accessions collected by Vavilov

*Mung bean (*Vigna radiata *(L.) R.Wilczek)*

Vavilov collected 115 accessions of mung bean during his first expedition in 1916. Mung bean is an ancient food crop of southwest Asia. It has a high seed protein content (23.0–32.1%), high lysine, tryptophane and vitamin contents, and good flavour and cooks quickly (20–40 min). These properties have made it a favourite food of the local population. Its foliage is useful as forage for cattle and as a green manure.

Vavilov's accessions of this crop were studied at the Central Asian branch of VIR (Popova 1937; Pavlova 1952; Ivanov 1961). From a detailed study of the assembled diversity of mung bean, G.M. Popova developed an intraspecific classification of this crop, differentiating three subspecies: Indian (*indicus*), Chinese (*chinensis*) and Iranian (*iranicus*). She also described 63 varieties of mung bean (Popova 1937). Subspecies *iranicus* are characterized by a twisted form of bush, a stalk height of 86-128 cm, 50-180 pods per plant (7-8 cm long), seeds of various colours (yellow, green, grey, brown) and 1000-seed weight of 32.8-49.8 g. Most accessions are early maturing, but late-maturing accessions also exist. The growing period in Central Asia is 91-122 days. The seed yield per plant ranges between 7.3 and 17.0 g (Table 2). Two accessions from Afghanistan (k-2209, k-2216) are highly resistant to drought and are of particular interest. Accessions of Iranian origin differ by having large above-ground biomass and are potentially useful for creating cultivars intended for fodder and green manure.

*Chickpea (*Cicer arietinum *L.)*

This is an ancient crop of Iran and Central Asia and is represented by numerous local races with small seeds. Plants are

Table 2. Characteristics of mung bean accessions collected by Vavilov in Central Asia in 1916 and 1924

VIR catalogue No.	Origin	Growth duration (days)	Plant height (cm)	1000 seed wt. (g)	Seed colour	Seed mass/ plant (g)
1826	Iran	122	128	40.0	Green	17.0
2124	Uzbekistan	91	100	41.5	Green	7.3
2125	Uzbekistan	91	94	49.8	Grey	8.0
2133	Uzbekistan	91	94	38.2	Dark green	11.0
2136	Uzbekistan	96	93	45.0	Dark green	12.1
2164	Uzbekistan	119	100	32.8	Yellow	13.3
2180	Afghanistan	117	93	46.3	Green	17.2
2183	Afghanistan	96	86	39.9	Brown	10.0
2209	Afghanistan	118	88	41.7	Green	10.4
2216	Afghanistan	91	95.0	39.4	Green	11.7

small and suited only to manual harvesting. However, they are widely used in breeding. The variety 'Tadzhiksky 10' was created by individual selection from Vavilov's Tadzhikistan samples. It matures early and is resistant to fusarium wilt. This variety was used to breed the variety 'Zimistony', which is also characterized by early maturity and high productivity in Tadzhikistan. 'Milutincky' was developed from the Iranian sample k-327 by individual selection for Uzbekistan conditions. This cultivar is drought and disease resistant. 'Tashkent 511' was created from Afghan sample k-223 through mass selection. It has enhanced protein content and disease resistance. 'Kubansky 16' was developed for conditions of the Kuban region from Uzbek sample k-16. 'Volga-5' has shown itself highly productive in central Russia. It was bred using accession k-249 from Afghanistan.

*Lentil (*Lens esculenta *Moench)*

Vavilov's lentil accessions are mainly dwarf forms with small seeds belonging to a large number of varieties: *persica*, *grisea*, *violascens* and others. There are many endemic forms of early and semi-early varieties that are drought resistant and have good cooking properties (Table 3). Pamir sample k-194 matures later than all others (growth period 86-102 days). Accessions k-5, k-196, k-434, k-435 have light-blue flowers. Material assembled by Vavilov was used as the basis for creating the commercial cultivar 'Tadzhik 95', which matures early, has good cooking properties and is drought resistant. 'Azer', now cultivated in Azerbaijan, was created using sample k-373 from northern Afghanistan. It is characteristically tall and has rhomboid beans. Its growth period is 81-95 days and it has a seed protein content of 29-30% and a 1000-seed weight of 34-37 g.

*Pea (*Pisum sativum *L.)*

Accessions of pea from Pamir have good winter-hardiness, dark seeds and a specific interaction with *Rhizobium* bacteria. Many accessions of Afghan origin do not produce nodules and have low nitrogen-fixing ability, even when artificially inoculated with *Rhizobium*. This feature is widely used for control and matching in genetic research. New varieties of peas with enhanced biological nitrogen-fixing ability have been bred from this material (Tchetkova and Tikhonovich 1986). Currently there is considerable interest in genetic studies of multimarker lines containing the sym-locus from a non-nodulating gene of Afghan origin.

Pea lines under the common name Mushung (k-181, k-182, k-184 and k-190) were the basis of the commercial cultivar of winter peas 'Mushung mestny', which was extensively cultivated in Tadzhikistan. 'Wostok 55' was bred for Uzbekistan conditions.

*Lupin (*Lupinus albus *L.)*

Valuable accessions of white lupin were collected by Vavilov during his trip to the Mediterranean in 1926 (Table 4). In Palestine, he identified very early, thermally neutral and small-seeded forms of the Jordanian ecotype. In particular, the sample Tel Karam k-290 has a growth period in Ukraine of only 105

Table 3. Characteristics of best lentil accessions collected by Vavilov in Central Asia in 1916

VIR catalogue No.	Origin	Growth duration (days)	Plant height (cm)	1000 seed wt. (g)	Cooking properties	Drought resistance
5	Iran	76-80†	25-30	69-72	Good	Average
6	Iran	76-80†	25-30	32-42	Good	Above average
7	Iran	76-80†	35-40	20-25	Good	Above average
8	Iran	76-80†	25-30	30-43	Good	Above average
10	Iran	76-80†	35-40	57-70	Average	Above average
13	Iran	76-80†	25-30	24-29	Good	Average
14	Iran	76-80†	35-40	56-63	Average	Average
194	Pamir	76-80†	35-40	34-40	Average	Average
196	Uzbekistan	86-102‡	21-31	28-30	Average	Average

† Average ripening duration.
‡ Late ripening.

Table 4. Characteristics of white lupin accessions (*Lupinus albus* L.) collected by Vavilov in Palestine and Sudan in 1926

Ecotypes	Accessions (name, VIR catalogue no.)	Characters					
		Growth duration for spring sowing (days)	Mass/plant (g)		1000-seed wt. (g)	Seed protein content (%)	Oil content (%)
			Green mass	Seed mass			
Jordanian	Tel Karam (k-290)	105	16.2	31.3	300	41.6	10.9
Jordanian	k-294	111	28.2	33.6	380	42.5	11.5
Jordanian	k-295	113	34.6	35.0	350	42.8	11.5
Jordanian	k-298	113	27.5	34.2	340	44.1	11.5
Sudanese	k-486	140	99.5	40.0	500	41.2	11.3
Sudanese	k-495	122	82.6	39.5	480	40.5	11.6

days. In contrast, lupin accessions from Sudan are very late, but highly productive and large-seeded (k-486, k-495). Samples of the Jordanian ecotype from Palestine have special value as source material for lupins bred for Russian, Polish and Ukrainian conditions. Their use in hybridization with lines of the Georgian ecotype, following mutagenesis, allowed V.I. Golovchenko to create early and highly productive cultivars, 'Kievsky mutant', 'Horizont' and 'Druzba' for Russia and the Ukraine (Golovchenko *et al.* 1984).

Vavilov not only collected and organized research on the assembled material, but also attempted to establish new methodologies. He was particularly keen to develop simpler and more accessible methods for determining alkaloid content in lupin. This was important in 1928-1929 as von Sengbusch, in Germany, had developed such a method but it was kept secret and the sweet strains of lupin were sold to a private firm. Under the management of N.N. Ivanov, and further elaborated by M. I. Smirnova and others, an efficient expression method was developed and adopted in VIR. In 1932, Vavilov wrote the foreword to a work by Ivanov *et al.* (1932) that was central to the initiation of breeding fodder (sweet) low alkaloid lupin.

Vavilov's contributions to theory and their further development

Vavilov worked on global genetic diversity of cultivated plants throughout his life, from which he developed several major theories that have played an important role in the development of botany, genetics and plant breeding. Cornerstones of this work include the law of homologous series in hereditary variability, studies on the problem of speciation, differential systematic-geographical methods for studying crops, botanical and geographical aspects of plant breeding, and the theory of the centres of origin of cultivated plants (Vavilov 1920, 1926, 1935, 1940, 1997).

Centres of origin

Vavilov's theory of introduction was based on his understanding of the nature of variation of the earth's vegetation, having identified a number of areas characterized by particular diversity and richness of species and types (Vavilov 1965b). More than 70 years ago Vavilov selected five ancient foci for the origin of cultivated plants from local flora (Vavilov 1926). Subsequently (Vavilov 1935), he introduced methods for better determining these foci and identified six foci and two centres of origin of cultivated plants. Vavilov constantly developed and deepened his main thoughts in subsequent publications. He eventually settled on seven primary centres of diversity: Tropical, East Asiatic, Southwest Asiatic, Mediterranean, Abyssinian, Central American and Andean (Vavilov 1940, 1962, 1987a, 1997) (Fig. 2). He also established specific foci for some of these centres.

The localization of centres and foci of origin of cultivated plants has been further developed by Sinskaja (1969) and Zhukovsky (1971) in Russia and by scientists from many other countries. Sinskaja (1969) revealed broader geographical connections and mutual interaction of floras. She distinguished five principal areas and updated the list of cultivated crops in each. Zhukovsky (1971) accepted Vavilov's definition of centres of diversity but increased the number to 12 and renamed them gene-centres. In our opinion (Kurlovich 1998), there are centres of formation for wild species, where they originated after the last ice-age, and also centres of origin (diversity) for cultivated plants, where these plants were domesticated.

Vavilov has received considerable support for his determination of centres of diversity (Kurth 1957; Harris 1967; Harlan 1971; Brezhnev and Korovina 1981; Mathon 1981). However, some critics believe that it is very difficult to determine the initial geographical origin of species and prefer the term "centres of diversity" instead of Vavilov's "centres of origin". Pistorius (1997) considers the term "centres of diversity" safer. Even in a modified form, Vavilov's theory of centres is used as a theoretical basis for collecting, studying and using genetic resources of cultivated plants.

Vavilov considered the Mediterranean region and mountainous areas of Mexico and the Andes to be centres of origin of the genus *Lupinus* (Vavilov 1926). This has allowed more precise determination of the centres of formation and origin (diversity) for specific lupin species (*L. albus* L., *L. luteus* L. and *L. angustifolius* L.). Our data (Kurlovich 1989), however, indicate that the centre of formation of wild white lupin (*L. albus* L.) and the primary centre of origin (diversity) of its initial cultivated forms is the Balkans, where there exists a wide diversity of wild, feral and local forms. All three white lupin subspecies (*graecus, termis* and *albus*) are grown in the Balkans. Wild forms with dotted dark brown seeds and dark blue flowers are found there. The centres of diversity of cultivated white lupins include the Apennines and Egypt, where cultivated forms of white lupin originated in

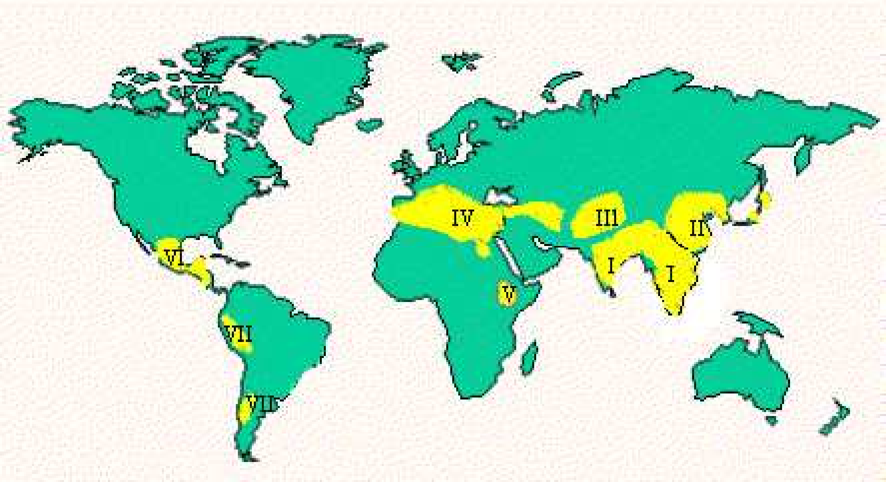

Fig. 2. Centres of origin of cultivated plants (Vavilov 1962, 1987a). I – The Tropical Centre, II – The East Asiatic Centre, III – The Southwest Asiatic Centre, IV – The Mediterranean Centre, V – Abyssinian Centre, VI – The Central American Centre, VII – The Andean Centre.

ancient times. In Egypt, forms with pink-and-blue or light pink flowers exist; in the Apennines, there are forms with greyish-and-light blue or white flowers.

Two close *Lupinus* species exist in the Pyrenees (*L. luteus* L. *and L. hispanicus* Boiss. et Reut.). They have the same number of chromosomes (2n=52) and there is a wide diversity of wild and cultivated forms of yellow lupin (*L. luteus* L.) and a long historical record of their growing there. This indicates that the Pyrenees was a centre of formation of the wild forms of yellow lupin (*L. luteus* L.) and the centre of diversity of cultivated plants (Kurlovich 1998). For similar reasons, we consider the Pyrenees to be a centre of diversity for narrow-leafed lupin (*L. angustifolius* L.).

The agricultural area devoted to lupins has gradually increased as a result of varietal development. Consequently, secondary macro and micro centres of diversity of cultivated forms have developed on different continents. These correspond to many geotypes and ecotypes described by Kurlovich (1998). Secondary centres of diversity of cultivated white lupin occur in Belarus, Chile, France, Germany, Poland and Russia. Secondary centres of diversity of blue lupin exist in Australia, Belarus, Poland South Africa and southeastern USA. Secondary centres of diversity of yellow lupin occur in Belarus, Germany, Poland, Russia and Ukraine. Results of these studies make it possible, to a certain extent, to provide answers to the most important questions of plant introduction and breeding regarding the type and location of material that should be collected and the purpose to which it should be put.

Vavilov's law of homologous series

When studied under different geographical conditions, any plant species segregates into a wide range of hereditary forms, which is initially difficult to understand. However, according Vavilov's law of homologous series in hereditary variability, intraspecific diversity does have some regularity. The essence of the law is that closely related species and genera are characterized by similar series of variation. Knowing the nature of succession of varieties in one species, one can forecast the existence of similar forms in other species and genera. Whole plant families in general are characterized by a definite cycle of variability, which exists similarly in all genera and species of that family.

Vavilov described variability in the Fabaceae (Leguminosae) and established regularity in its differentiation in separate genera and cultivars, by monitoring characters of seeds, fruits, and flowers, and vegetative organs. He analyzed variability of characters in accessions of Vicieae, Trifolieae, Loteae, Galegeae and Phaseoleae (Vavilov 1920; 1987b). It became clear that, despite differences between these sections, the variability of characters was similar for all genera within a given family. The genus *Lupinus* is more variable than any other genus of the Fabaceae and illustrates Vavilov's law of homologous series in hereditary variability (Maissurjan and Atabekova 1974, Kurlovich *et al.* 1995). The law of homologous series in hereditary variability indicates which material should be sought and underlies the theory for the centres of origin of cultivated plants. It also indicates where such centres should be located.

Differential systematic-geographical methods

Vavilov and his followers used a differential systematic-geographical method to study intraspecific diversity and to determine the centres of origin of cultivated plants (Vavilov 1931). This method consisted of the following:

- differentiation of a genus into species and intraspecific diversity using morphological, hybridisation, cytological and other characters
- determination of the genotypical composition of a species
- geographical localization of hereditary forms of a species and the centres of their diversity

The large body of theoretical and practical work involved in these studies allowed Vavilov to comment on the nature and role of species as a system (Vavilov 1931, 1965a). Previously the prevailing ideas were those of Komarov (1931, 1944), based on monotypic species, according to which species cannot include a systematic unit of a lower rank. The concept of a biological species based on no crossing between species was also widely accepted (Grant 1981, 1984). Vavilov, however, in a study of several hundred species showed the absence of monotypic species, i.e. species represented by a sole race or form. All the species studied appeared to incorporate a number of forms (genotypes). He considered a species to be a flexible, isolated, complex, morphophysiological system linked to a particular environment and area (Vavilov 1931, 1965a). This led to the understanding of the Linnaean species concept, an integral entity consisting of closely interlinked components where the whole and the parts are merged (Vavilov 1965a; Agaev 1987; Korovona 1987).

Geographical and ecological differentiation

Vavilov not only paid attention to morphological traits, but also took into account geographical and ecological differentiation of plants. Such an approach based on development of various intraspecific classifications allowed detailed study of intraspecific and varietal diversity of cultivated plants, and developments for their effective use. In the international code for botanical nomenclature there exist fixed categories for intraspecific classification, including subspecies, varieties, sub-varieties and forms.

Vavilov paid particular attention to ecogeographical differentiation of a species into ecotypes, genotypes, concultivars etc. (Vavilov 1931, 1965a). For classification purposes, VIR's scientists routinely use anatomical, cytological, paleobotanical, ontogenetic, biochemical, physiological, geographical, genetic and other criteria in addition to the more usual traits. Such a comprehensive approach is particularly effective for the study of intraspecific diversity in cultivated leguminous crops. Vavilov's theories are all interconnected and represent a complex doctrine about global genetic diversity of cultivated plants. They have allowed scientists from VIR to develop intraspecific classifications for practically all leguminous crops, particularly peas (Govorov 1937; Makasheva 1979), mung bean (Popova 1937), soya bean (Korsakov 1971; Teplyakova 1997), lupin (Kurlovich and Stankevich 1990), chickpea (Seferova 1997) and vetch.

Continuing Vavilov's work

Vavilov's work in collecting and studying genetic resources of leguminous plants has been continued by VIR scientists. The department of leguminous crops of VIR was established in 1924. Vavilov invited his friend L.I. Govorov to manage the department, and he recruited experts in leguminous plants to the staff. Govorov developed intraspecific classification for peas (Govorov 1937), organized breeding work with leguminous crops in the former USSR and created many pea cultivars. Like Vavilov, Govorov had a tragic destiny; he was arrested and disappeared.

P.M. Zhukovsky was invited to manage the lupin collection. He developed and published important works on interspecific and intraspecific diversity (Zhukovsky 1929). Research on the genetic resources of lentil was done by E.I. Barulina (Vavilov's wife). She took part in many expeditions, e.g. to Crimea, Georgia and other regions (Barulina 1930). During the Second World War the department of leguminous crops was managed by N.R. Ivanov, who made a substantial contribution to preserving the collection during the seige of Leningrad. He carried out important research on the genetic resources of kidney bean (Ivanov 1961). After the Second World War, under the direction of Korsakov, ecological and geographical research at VIR was modified and databases on genetic resources were created. Korsakov also contributed to the clarification of centres of origin of various soya bean species (Korsakov 1971).

Recent activities at VIR

Currently, VIR has 43 000 accessions belonging to 15 genera and 160 species of the Fabaceae, including pea, soya bean, vetch, lupin, faba bean, lentil, everlasting pea, chickpea, cowpea, mung bean and kidney bean. The collection contains genetic resources from five continents, but most of the accessions were collected from the former USSR and Europe. The staff of the department of leguminous crops selects new, valuable lines, works out advanced methods for breeding and performs research on taxonomy and evolution. Considerable effort is directed at evaluating agronomic traits, including yield factors and tolerance of biotic and abiotic stresses, and at ecogeographic research in various regions of Russia. For the first time in Russia, selection for new characters in peas is beginning to produce stipulate lines with non-dehiscent pods, polyembryonic types and determinate types. During recent years, experiments were conducted to determine resistance in pea to *Aphanomyces* root rot, bruchids and lima bean pod borer. Lupin lines with horizontal resistance to fusarium wilt are sought along with sources of high nitrogen fixing ability. Genetic research includes that on analysis of genetic diversity and determination of the genetic control of important agronomic traits, including disease and stress resistances and genetic adaptation (Chekalin and Alpatiev 1988). The work of R. Makasheva on selection characters of peas based on Makasheva (1973) was translated into English and others languages. Breeding low-alkaloid, perennial lupin forms (*Lupinus polyphyllus* Lindl.) was also developed (Chekalin and Kurlovich 1989).

Ecogeographical investigations initiated by Vavilov have made it possible to create valuable materials through hybridization of forms with different characters under different conditions. One example is a method for obtaining transgressive forms of lupin based on an ecogeographical approach (Kurlovich *et al.* 1995; Rep'ev and Barulin 1998). We have shown that each quantitative character has from two to five or more types of variability (Rep'ev 1988). It was not always appreciated that, for a majority of accessions, plant characters change under different conditions. Hybrid progeny can behave similarly to the parental forms when crosses have involved parents with identical types of variability for a character. However, hybrid progeny include transgressive forms when the result of crosses between parents with different types of variability. The distinctions in variability of characters in parental forms can be based on testing under different conditions. Investigations of this phenomenon can lead to identification of valuable transgressive forms for many characters, including chemical composition and disease resistance (Kurlovich *et al.* 1995). Increased resistance of lupin to fusarium wilt is an example (Figs. 3 and 4). Lupin cultivars and lines (547 accessions) were tested for fusarium resistance under different environmental conditions in two regions in Russia (near Bryansk and St. Petersburg) and in Ukraine (near Kiev) on plots with artificially infected soil. A large num-

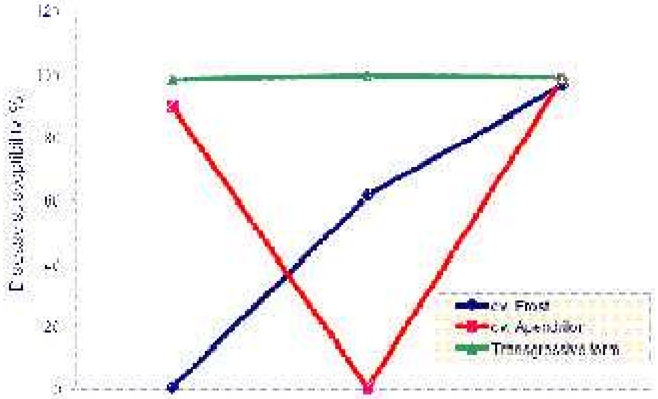

Fig. 3. Variation in the degree of fusarium wilt susceptibility of two cultivars of *Lupinus angustifolius* and their transgressive form on plots with artificially infected soil in different regions of Russia and Ukraine.

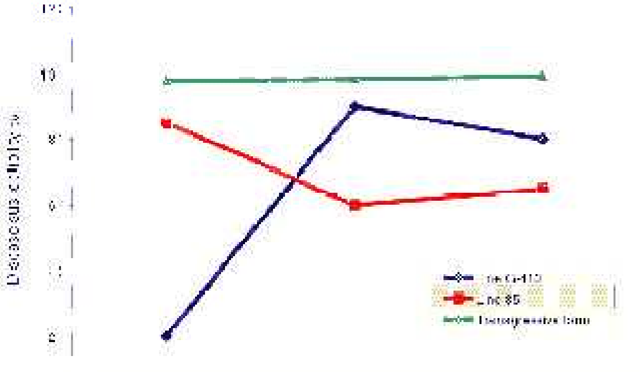

Fig. 4. Variation in the degree of fusarium wilt susceptibility of two lines of *Lupinus luteus* and their transgressive form on plots with artificially infected soil in different regions of Russia and Ukraine.

ber of accessions of different lupin species were selected for their resistance based on results from a single plot with infected soil. Yet on two other plots they were susceptible. Differences in the disease susceptibility of the same accessions were thus found in contrasting environments. Resistant forms from one region were crossed with accessions resistant in two other regions. This resulted in two transgressive resistant forms in the F_4. Crosses were 'Frost' x 'Apendrilon' (*L. angustifolius*) and line G-413 x line 85 (*L. luteus*). Their resistance in all three regions appeared to be higher than that of their parental forms (Fig. 3 and 4). These two transgressive forms with increased resistance to fusarium wilt were found suitable for inclusion in the breeding program of fusarium resistant forms in Russia, Belarus and Ukraine.

This interesting phenomenon was commented on by Ride (1992), in which the author summarized what was known about the recognition and response mechanisms of higher plants to fungi. Study of the specific incompatibility between races of pathogens and certain host cultivars has allowed rapid progress to be made in understanding the mechanism underlying successful infection (compatibility) and resistance (incompatibility).

Results from our experiments indicate why transgressive forms occur in the breeding process only very seldom, accidentally, and among large numbers of hybrid materials. Our approach to breeding makes the process of obtaining transgressives more controlled and effective. We have also tested Dragavtsev's ideas about limiting environmental factors on leguminous crops (Dragavtsev 1997) for transgressive selection. Using our ecogeographical approach, transgressive forms of vetch, pea and chickpea were also obtained (Rep'ev 1988). Vavilov's geographical and ecological approaches have been widely used and developed by other scientists (Korsakov 1971; Chekalin and Alpatiev 1988; Tigerstedt 1994; Hill *et al.* 1998).

Vavilov foresaw the disappearance of many valuable forms of plants under the influence of human activity. Luckily, many species and forms were saved following the expeditions of Vavilov and his colleagues. Many scientists from Brazil, Ethiopia, Israel, Portugal and elsewhere have asked VIR for accessions of leguminous crops Vavilov collected in their countries. These genetic resources only existed in the collection of VIR thanks to Vavilov, and are now accessible for all to use. The traditions and methods of Vavilov are continued by numerous scientists in many countries. In the field of leguminous crops, the ideas of Vavilov have been further developed in Australia (Gladstones 1974, 1998; Sweetingham 1986, 1989; Cowling 1994), Finland (Koskenmäki 1994; Hovinen 1994; Tigerstedt 1994), Germany (Diederichsen and Hammer 1996), Italy (Laghetti *et al.* 1996; Saccardo 1996), Poland (Sw cicki 1988; Kazimierski and Kazimierska 1992, 1994), Portugal (Mota 1984; Tavares de Sousa *et al.* 1992; Neves Martins 1994), Sweden (Blixt 1970, 1996), UK (Polhill 1976; Bisby 1981; Ambrose 1996) and many other countries.

Conclusions

Vavilov was the first to recognize the necessity for intensive plant collecting and preservation. He was a highly qualified collector of plant genetic resources and manager of collecting missions, and an author of many theoretical and practical ideas in the field of the global genetic diversity of cultivated plants. A major contribution of Vavilov was his ability to translate his rapidly growing scientific knowledge in genetic resources into economic use. Vavilov's plant collecting expeditions served as the basis for the leguminous crop collection in VIR, which provided the initial materials for over 75% of new grain legume cultivars created in Russia and other countries of the former USSR (Kurlovich 1996).

It is very difficult to do justice to Vavilov in this short article. The scope of Vavilov's interests was extraordinarily wide and included practically all agricultural crops and disciplines of plant science. The memory of Vavilov has been preserved through his collections of plant genetic resources, ideas, books and followers. These are an important legacy of N.I. Vavilov, and were recently documented posthumously in his book 'Five Continents' (Vavilov 1962, 1987a, 1997).

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References

Agaev, M.G. 1987. Vavilov's conception of species and it development. Genetica XXIII(11):1949–1960.

Ambrose, M. 1996. Grain legume collections and activities in the UK. Pp.100-102 *in* Report of a Working Group on Grain Legumes (T. Gass, M. Ambrose, J. Le Guen, A. Hadjichristodoulou and S. Blixt, compilers). ECP/GR-Grain Legumes Network, IPGRI, Rome, Italy.

Barulina, E.I. 1930. Lentil in USSR and other countries. Bull. Appl. Bot. Genet. Plant Breed. (Leningrad), Supplement 40:1–319.

Bazilevskaya, N. I. and S.N. Bakhareva. 1991. N.I. Vavilov's exploring expeditions and their importance. Bull. Appl. Bot. Genet. Plant Breed. 140:12–23.

Bisby, F.A. 1981. *Genisteae*. Pp. 409-425 *in* Advances in Legume Systematics, Part 1 (R.H. Polhill and P.H. Raven eds.). Royal Botanic Gardens, Kew, UK.

Blixt, S. 1970. Studies of induced mutations in peas. XXVI. Genetically conditioned differences in radiation sensitivity. Agr. Hort. Genet., Bd. 28:55-116.

Blixt, S. 1996. Status of legume collections in the Nordic countries. Pp. 61-62 *in* Report of a Working Group on Grain Legumes (T. Gass, M. Ambrose, J. Le Guen, A. Hadjichristodoulou and S. Blixt, comps). ECP/GR-Grain Legumes Network, IPGRI, Rome, Italy.

Brezhnev, D.D. and O.N. Korovina. 1981. Wild relatives of cultivated plants from flora USSR. Kolos, Leningrad, USSR. 375 pp.

Chekalin, N.M. and B.S. Kurlovich. 1989. Author's certificate 1499737. Moscow, USSR.

Chekalin, N.M. and V.N. Alpatiev 1988. Valuation of the world collection of soybean on parameters of attraction ability and micro distributions. Bull. Appl. Bot. Genet. Plant Breed. 117:20-24.

Cowling, W.A. 1994. Use of lupin genetic resources in Australia. Pp. 9-18, *in* Advances in Lupin Research (J.M. Neves Martins and M.L. Beirao da Costa, eds.). Proceeding of the 7th International Lupin Conference, Evora, Portugal. ISA Press, Lisbon, Portugal.

Diederichsen, A. and K. Hammer. 1996. Status of plant genetic resources and research on grain legumes in Germany. Pp.45-50 *in* Report of a Working Group on Grain Legumes (T. Gass, M. Ambrose, J. Le Guen, A. Hadjichristodoulou and S. Blixt, comps). ECP/GR-Grain Legumes Network, IPGRI, Rome, Italy.

Dragavtsev, V.A. 1997. Genetic and physiological mechanisms of plant adaptation. Pp. 59-67 *in* Adaptation in Plant Breeding (P.M.A. Tigerstedt, ed.). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Gladstones, J.S. 1974. Lupin of the Mediterranean region and Africa. W. Aust. Dept. Agr. Tech. Bull. 26. 48 pp.

Gladstones, J.S. 1998. Distribution, origin, taxonomy, history and importance. Pp. 1-39 *in* Lupin as Crop Plants. Biology, Production and Utilization (J.S. Gladstones, C. A. Atkins and J. Hamblin, eds.). Cambridge University Press, Cambridge, UK.

Golovchenko, V.I., N.S. Kucherenko, N.G. Lesunova and A.S. Porokonnyij. 1984. Genefund and the result of breeding fodder lupine. Res. Bull., N.I. Vavilov Inst. Plant Ind., Leningrad, USSR 139:7-12.

Govorov, L.I. 1937. Pea. Pp. 229-336 *in* Flora of Cultivated Plants. State Printing Office, Moscow and Leningrad, USSR.

Grant, V. 1981. Plant Speciation. Columbia University Press, New York, USA. 528 pp.

Grant, V. 1984. Plant Speciation. Transfer with English. Publishing House – World, Moscow, USSR. 528 pp.

Harlan, J.R. 1971. Agricultural origins; centers and noncenters. Science 174:468-474.

Harris, D. R. 1967. New light on plant domestication and the origins of agriculture. Geogr. Rev. 57:90-107.

Hill, J., H.C. Becker and P.M.A. Tigerstedt. 1998. Quantitative and Ecological Aspects of Plant Breeding. Chapman & Hall, London, UK. 275 pp.

Hovinen, S. 1994. Tiina – uusi herneen yleislajike. Koetoiminta ja Käytäntö 51:35.

Ivanov, N.N., M.I., Smirnova, N.I. Sharapov *et al.* 1932. Problem of alkaloid-free lupin. Exhibit 54 to Bull. Appl. Bot. Genet. Plant Breed. 63 pp.

Ivanov, N.R. 1961. Kidney bean. State Printing Office, Moscow and Leningrad, USSR. 280 pp.

Kazimierski, T. and E.M. Kazimierska. 1992. Natutalne tetraploidy lubinu bialego (*Lupinus albus* L.). Materialy konferencji "Genetika 2000". Kraków, Poland.

Kazimierski, T. and E.M. Kazimierska. 1994. The course of meiosis and microsporogenesis in dihaploid plants of white lupin (*L. albus* L.). Genet. Pol. 35(3):153-160.

Komarov, V.L. 1931. Origin of cultivated plants. State Printing Office, Moscow and Leningrad, USSR. 200 pp.

Komarov, V.L. 1944. The doctrine about a species at plants. Leningrad, USSR. 285 pp.

Korovina, O.N. 1987. N.I. Vavilov on the primary centres of cultivated plant origin. Bot. Journal, St. Petersburg 6:721-729.

Korsakov, N.I. 1971. Geographical seats of soybean formation. Bull. Appl. Bot. Genet. Plant Breed. 45:189-193.

Koskenmäki, V. 1994. Integraatio syvenee – laskeeko huoltovarmuus? Maaseudun Tulevaisuus 78(140):2.

Kurlovich, B.S. 1989. On the centers of species formation of the genus *Lupinus* L. Bull. VIR 193:20-24.

Kurlovich, B.S. 1996. Genetic resources of grain legume crops in N.I. Vavilov All-Russian Research Institute of Plant Industry. Pp.77-81 *in* Report of a Working Group on Grain Legumes (T. Gass, M. Ambrose, J. Le Guen, A. Hadjichristodoulou and S. Blixt, comps). ECP/GR-Grain Legumes Network, IPGRI, Rome, Italy.

Kurlovich, B.S. 1998. Species and intraspecific diversity of white blue and yellow lupins. Plant Genet. Resources Newsl. 115:1-10.

Kurlovich, B.S. and A.K. Stankevich. 1990. Intraspecific diversity of three annual lupine species (*Lupinus* L.). Bull. Appl. Bot. Genet. Plant Breed. 135:19-34.

Kurlovich, B.S., S.I. Rep'ev, L.G. Shchelko, V.I. Budanova, M.V. Petrova, T.V. Buravtseva, A.K. Stankevich, L.T. Kartuzova, T.G. Alexandrova, T.E. Teplyakova and L.K. Malysh. 1995. Theoretical basis of plant breeding. Vol. III. The gene bank and breeding of grain legumes (lupine, vetch, soya and bean). VIR, St. Petersburg, Russia. 438 pp.

Kurth, H. 1957. Vom Wildgewächs zur Kulturpflanzensorte. Ziemsen Verlag, Wittenberg, Lutherstadt, Germany. 142 pp.

Laghetti, G., K. Hammer and P. Perrino. 1996. Plant genetic resources in Pantelleria and Pelagie archipelago, Italy: collecting and conservation of local crop germplasm. Plant Genet. Resources Newsl. 108:17-25.

Loskutov, I.G. 1999. Vavilov and his institute. A history of the world collection of plant genetic resources in Russia. IPGRI, Rome, Italy. 188 pp.

Maissurjan, N.A. and A.I. Atabekova. 1974. Lupine. Kolos, Leningrad, USSR. 463 pp.

Makasheva, R. Kh. 1973. Pea. Kolos, Leningrad, USSR. 311 pp.

Makasheva, R. Kh. 1979. Pea. Flora of cultivated plants. V. IV, part 1. Kolos, Leningrad, USSR. 322 pp.

Marhon, Cl.Ch. 1981. Phytogeographie appliquée a l'origine des plantes. Masson, Paris, France. 182 pp.

Mota, M. 1984. Lupin germplasm resources in Portugal. p. 8 *in* Abstracts of the IIIrd International Lupin Conference, La Rochelle, France.

Neves Martins, J.M. 1994. Numerical taxonomy on the study of *Lupinus albus* accessions. Pp. 84-89 *in* Advances in Lupin Research: Proceedings of the 7th International Lupin Conference, Evora, Portugal, 1993 (J.M. Neves Martins and L.M. Berão da Costa, eds.). ISA Press, Lisbon, Portugal.

Pavlova, A.M. 1952. Varieties of mung bean for new regions of irrigation. Bull. Appl. Bot. Genet. Plant Breed. 29(3):67-70.

Pistorius, R. 1997. Scientists, Plants and Politics—A history of the Plant Genetic Resources Movement. IPGRI, Rome, Italy. 134 pp.

Polhill, R.M. 1976. *Genisteae* (Adans.) Benth. and related tribes (Leguminosae). Bot. Systematics 1:143-368.

Popova, G.M. 1937. *Phaseolus aureus* (Roxb.). Piper – Mung pea. Pp. 573-601 *in* Flora of cultivated plants. VIR, Leningrad, USSR.

Rep'ev, S.I. 1988. Principles governing selection of parental pairs in the transgressive breeding of common vetch. Bull. Appl. Bot. Genet. Plant Breed. 117:69-76.

Rep'ev, S.I. and V.N. Barulin. 1998. Human Being: Information, Systems of Interaction, Heredity. Theory and Practice. Intan, St. Petersburg, Russia. 116 pp. (in Russian).

Ride, J.P. 1992. Recognition signals and initiation of host responses controlling basis incompatibility between fungi and plants. Pp. 213-37 *in* Perspectives in Plant Cell Recognition (J.A. Collow and J.R. Green, eds.). Society for Experimental Biology Seminar Series 48. Cambridge University Press, Cambridge, UK.

Saccardo, F. 1996. Status of grain legume collection in Italy. Pp. 53-56 *in* Report of a Working Group on Grain Legumes (T. Gass, M. Ambrose, J. Le Guen, A. Hadjichristodoulou and S. Blixt, comps). ECP/GR-Grain Legumes Network, IPGRI, Rome, Italy.

Seferova, I.V. 1997. Varieties of chickpea –*Cicer arietinum* L. Bull. Appl. Bot. Genet. Plant Breed. 152:9-18.

Sinskaja, E.N. 1969. The historical geography of flora of cultivated plants. Leningrad, USSR. 480 pp.

Sinskaja, E.N. 1991. Memoirs about Vavilov. Scientific Thought, Kiev, Ukraine. 203 pp.

Sw cicki, W. 1988. Lupin gene resources in the Old World. Pp.2-11 *in* Proceedings of the 5th International Lupin Conference (T. Twardowsky, ed.). PWRiL, Poznan, Poland.

Sweetingham, M.W. 1986. Research into lupin root diseases. West. Aust. J. Agr. 27:49-52.

Sweetingham, M.W. 1989. Fungi associated with root and hypocotyl diseases of seedling lupin. Research into lupin root diseases. West. Aust. J. Agr. 40:781-789.

Tavares de Sousa, M.M., I. M. Duarte and M.G. Pereira. 1992. Potential production of winter chickpea in southern Portugal. *In* Proceedings of the International Food Legume Research Conference II, Cairo, Egypt, 12-16 April.

Tchetkova, S.A. and I.A. Tikhonovich. 1986. Selection and use of the strains, effective on peas of the Afghani origin. Microbiology (Moscow) 55:143-146.

Teplyakova, T.E. 1997. Nomenclature analysis of the basis taxonomic systems in soya (*Glycine max* (L.) Merr.). Bull. Appl. Bot. Genet. Plant Breed. 152:111-118.

Tigerstedt, P.M.A. 1994. Adaptation, variation and selection in marginal areas. Pp. 13-19 *in* Breeding Fodder Crops for Marginal conditions (O.A. Rongli, E. Solberg and I. Schjelderup, eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Vavilov, N.I. 1920. The Law of Homologous Series in Hereditary

Variation. Pp. 3-20 *in* Proceedings of the III All-Russian Plant Breeding Congress, Saratov, Russia.

Vavilov, N.I. 1926. Centres of origin of cultivated plants. Bull. Appl. Bot. Genet. Plant Breed. 16(2). 248 pp.

Vavilov, N.I. 1931. Linnaeus species as a system. Bull. Appl. Bot. Genet. Plant Breed. 26(3):109-134.

Vavilov, N.I. 1935. Theoretical basis of plant breeding. VIR, St. Petersburg, USSR.

Vavilov, N.I. 1940. The doctrine about an origin of cultural plants after Darwin. Sov. Sci. 2:55-75.

Vavilov, N.I. 1962. Five Continents. State Publishing House of the Geographical Literature, Moscow, USSR. 225 pp.

Vavilov, N.I. 1965a. Linnaeus species as a system. pp. 223-250 *in* The selected works. 5 vols. State Printing Office, Moscow and Leningrad, USSR.

Vavilov, N.I. 1965b. Origin and geography of cultural plants. p. 179 *in* The selected works. 5 vols. State Printing Office, Moscow and Leningrad, USSR.

Vavilov, N.I. 1987a. Five Continents. Science Publishing House, Leningrad, USSR. 213 pp.

Vavilov, N.I. 1987b. Origin and geography of cultivated plants. VIR, St. Petersburg, USSR.

Vavilov, N.I. 1991. Near the Pamirs (Darvaz, Roshan, Shugnan). Agricultural essay. Bull. Appl. Bot. Genet. Plant Breed. 140:1-12.

Vavilov, N.I. 1997. Five Continents (L.E. Rodin, S. Reznik and P. Stapleton, eds.). IPGRI, Rome, Italy. 198 pp.

Zhukovsky, P.M. 1929. A contribution to the knowledge of genus *Lupinus* Tourn. Bull. Appl. Bot. Genet. Plant Breed. 21(1):16-294.

Zhukovsky, P.M. 1971. Cultivated plants and their relatives. Kolos, Leningrad, USSR. 751 pp.