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PLANT GENETICS

Molecular Genetic Diversity of the Pea (*Pisum sativum* L.) from the Vavilov Research Institute Collection Detected by the AFLP Analysis

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Abstract—In this work, a set of pea accessions obtained from the Vavilov Research Institute (VIR) collection comprising 83 *P. sativum* samples, including representatives of three subspecies, was studied using the AFLP method. Local cultivars for different uses with maximum ecological and geographical diversity (including those from the centers of origin of the species) were predominantly chosen for the study; a number of their morphological and biological characteristics were evaluated. We obtained 382 polymorphic AFLP fragments; each sample was characterized by a unique set of fragments. The genetic diversity of the studied material was evaluated, and a wide range of genetic differences in the investigated samples (0.07–0.27) was demonstrated. The affiliation of the samples to the certain subspecies was not confirmed by the obtained data; the ecogeographical differentiation of the samples was not reflected by the data. Factor analysis allowed us to identify the sample groups of European and Asian origin and the intermediate nature of most of the samples from the studied set of pea accessions.

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INTRODUCTION

Pisum sativum L. pea (Fabaceae) is the major leguminous crop of our country. N.I. Vavilov assumed that Ethiopia and mountainous areas of the Near East and Central Asia were the primary centers of origin for pea and that the Mediterranean was the secondary center [1]. Modern research has somewhat corrected the understanding of the primary center, expanding it to the countries of Western Asia (Iran, Afghanistan, Pakistan, and Turkmenistan) and the entire Mediterranean (Greece, Italy, Spain, and Morocco) [2]. Ethiopia is now considered a secondary center of pea diversity and origin [3, 4].

Great morphological and biological diversity, together with the existence of a continuum of morphological forms, complicate the classification of the genus *Pisum* L., particularly analysis of the *P. sativum* composition and species boundaries [5–7].

For instance, certain researchers recognize not only *P. sativum* but also the *P. abyssinicum* A. Br., *P. elatius* Bieb., and *P. fulvum* Sibth. et Smith species [7], while the other researchers limit the scope of the genus to three (*P. sativum*, *R. abyssinicum*, and *P. fulvum*) [2, 8, 9] or even two (*P. sativum* and *P. fulvum*) species [3, 10]. Based on an analysis of global diversity (presented by the Vavilov Research Institute (VIR) collection), morphological and cytological data, and data on the hybridization and composition of the storage proteins, there was a proposal to distinguish six subspecies within the *P. sativum* species: *abyssinicum* (A. Br.) Berger, *asiaticum* Govorov, *elatius* (Bieb.) Schmalh., *sativum*, *syriacum* (Boiss. et Noé Berger), and *transcaucasicum* Makash. [3].

Recent studies of pea genetic diversity were focused either on the polymorphism evaluation of different biochemical and molecular markers [11, 12] or on analysis of the individual world collections of pea [13–15]. However, in these studies, the VIR collection—one of the world's largest collections (over 7000 specimens)—was represented only by individual selections. The polymorphism of 95 Eastern European cultivars from the VIR collection was previously studied using the RAPD method [16]. Since the cultivars represent only a part of the pea collection, the data on the genome polymorphism of the pea samples from the VIR collection can be considered fragmented, and the question of its genetic diversity range remains unanswered. In this work, the polymorphism of *P. sativum* from the VIR collection was studied using the AFLP system of multilocus molecular analysis.

The efficiency of the AFLP method has been demonstrated repeatedly for assessing the genetic diversity of gene bank collections, identifying the genetic structure of populations, delimiting taxa, and separating taxonomically complex species, subspecies, and varieties [14, 15, 17, 18].

Thus, the aim of this study was to perform a molecular AFLP analysis of *P. sativum* samples in order to explore the relationship between the genetic diversity of the samples, their ecogeographical origin, and the species/subspecies taxonomic affiliation. The samples were obtained from the VIR gene bank collection, characterized by a complex of biological, morphological, and agronomic traits, and chosen to represent different subspecies, local and modern pea cultivars from all of the agricultural areas of the world.

MATERIALS AND METHODS

For this study, 83 samples of cultivated pea *P. sativum* were selected from the collection of the Vavilov Research Institute of Plant Industry (St. Petersburg). The basic selection criterion was that of the maximum ecological and geographical diversity of the samples adapted for different uses: grain, forage, and vegetable. A significant part of the selection comprised specimens from the centers of origin for the genus *Pisum*. All samples were preliminarily characterized by a complex of biological, morphological, and agronomic traits [19]. A specimen of the wild-type *P. fulvum* was used as an outgroup as outgroup (see table).

Total plant DNA was isolated using a standard technique [20]. The AFLP analysis was also performed by a standard method [21]. Genomic DNA from each sample was digested by the restriction enzymes *Eco*RI/*Tru*I. Standard adapter primers *Eco+1* and *Tru+1* with one selective nucleotide at the 3'-end were used for the first round of amplification. For the second round of amplification, different combinations of *Eco*RI/*Tru*I primers with three selective nucleotides on the 3'-terminus of each primer were used. Twelve primer/enzyme combinations were tested.

Amplification products were separated in 6.5% denaturing polyacrylamide gel using a LI-COR 4300 DNA Analyzer (United States) fragment analysis system.

Based on the obtained AFLP spectra, genetic distance values and genetic similarity coefficients were calculated for the analyzed samples, a dendrogram was constructed using the UPGMA method [22], and a principal coordinate analysis (PCA) was performed. Statistical data processing was performed using a STATISTICA-6.0 software package (Microsoft Corporation, 1990–1995, United States).

The population structure was analyzed using the Bayesian algorithm and STRUCTURE 2.3.1 software [23]. A model implying the mixture of genetic material (admixture model) and models implying allele inheritance from a common ancestor through genetic drift were used in the analysis. Analysis was performed in triplicate for the subpopulation number $k = 2, 3, 4, 5,$ and 6 at the number of repetitions of 10^6 and the "burn in" of 5×10^5.

RESULTS AND DISCUSSION

In order to analyze 84 pea samples, 12 AFLP primer/enzyme combinations were tested; among them, two primer/enzyme pairs E-ACA/M-CGA and E-ACA/M-CTG were most informative, i.e. allowed the identification of the optimal number of fragments (50–250) on the polyacrylamide gel and to detect intraspecific polymorphism.

As a result of the AFLP analysis, 405 fragments of the pea genome were identified. The fragment length ranged from 80 to 650 bp. The number of the markers available for analysis was 186 for E-ACA/M-CGA and 219 for E-ACA/M-CTG.

The obtained spectra were characterized by a significant level of polymorphism. For instance, 382 of 405 amplified AFLP fragments were polymorphic (94.3%). The percentage of detected polymorphic fragments for the E-ACA/M-CGA primer pair was 96.8; for the E-ACA/M-CTG pair, it was 92.2.

The number of unique sample-specific DNA fragments identified using selected primer pairs was high: 56 fragments. As a result of the molecular labeling, each of the 84 pea samples was characterized by a specific range of AFLP fragments.

Based on the AFLP spectra, the genetic diversity levels of the pea samples were estimated. Maximal genetic differences—0.32 (0.25–0.32)—were detected between the *P. sativum* and *P. fulvum* specimens. The levels of intraspecific diversity of the *P. sativum* samples varied within a wide range (0.07–0.27), which can apparently be explained by the prevalence of local cultivars in the studied material. The highest value of the interpopulation genetic distances for *P. sativum* ssp. *sativum*—0.27—was detected for samples with a remote habitat: k-40 (Manchuria)–k-59 (Czech Republic). The lowest value of the interpopulation genetic distances—0.07—was determined for the geographically close samples of Asian origin: k-40 (Manchuria)–k-44 (Mongolia) and k-40 (Manchuria)–k-32 (Afghanistan).

In the context of the available data on pea genetic polymorphism detected by different methods of molecular analysis, the obtained results are quite comparable with the data of Choudhury et al. [24], according to which the genetic difference levels for the most popular and widely adapted pea cultivars produced in India are within a range of 0.13–0.30. According to the data of RAPD and AFLP analyses performed by Simioniuc et al. [12], the genetic differences among the genotypes of 21 pea cultivars registered in Germany do not exceed 0.15; this result, however, may be

Pisum sativum samples (1–83) of various cultivars obtained from the VIR collection used in the study

Subspecies, variety		Catalog number	Origin	Use	Flower color	Seed color
P. sat. ssp. *sativum,* *	1	2006	Denmark	Forage	lp	lb
P. sat. ssp. *asiaticum,* *	2	2008	Egypt**	″	″	″
P. sat. ssp. *abyssinicum,* *	3	1937	Austria	″	r	b
	4	2514	Syria**	″	dp	pb
P. sat. ssp. *asiaticum,* *	5	188	Pamir**	″	″	lb
	6	1250	″	″	lp	″
	7	958	Turkestan**	″	dp	pb
	8	1251	Tajikistan	″	lp	lb
	9	1866	India	″	″	″
	10	1022	Germany	″	dp	pb
	11	2182	Iran**	″	″	″
	12	3266	Armenia	″	lp	lb
P. sat. ssp. *transcaucasicum,* *	13	1985	Georgia	″	″	″
	14	3980	″	″	″	pb
	15	2174	Bulgaria	Grain-vegetable	w	ly
P. sat. ssp. *sativum,* *	16	2429	Algeria**	Forage	dp	lb
	17	3429	Egypt**	″	lp	pb
	18	8093	Madagascar	Vegetable	w	yg
	19	6468	Sudan**	Grain	″	yp
	20	7131	Tunisia**	Vegetable	lp	bg
	21	7584	Tunisia**	Grain-forage	″	yp
	22	1836	Africa	Forage	″	lb
	23	3855	Argentina	Grain-forage	w	ly
P. sat. ssp. *sativum,* Ojo Negro	24	5012	Argentina	Grain-vegetable	w	ly
P. sat. ssp. *sativum,* Long drink	25	8261	Brazil	Vegetable	w	ly
P. sat. ssp. *sativum,* *	26	8571	Venezuela	Grain-vegetable	″	yg
	27	693	Canada	Vegetable	″	yp
	28	925	USA	″	″	bg
P. sat. ssp. *sativum,* Mayfair	29	8572	USA	Vegetable	w	bg
P. sat. ssp. *sativum,* *	30	7094	Peru	Forage	lp	lb
	31	6464	Chile	Grain-vegetable	w	ly
	32	1982	Afghanistan**	Forage	lp	lb
	33	2595	Palestine**	Vegetable	w	ly

Table. (Contd.)

Subspecies, variety		Catalog number	Origin	Use	Flower color	Seed color
P. sat. ssp. *sativum*, Bamtam	34	5493	Iraq**	Vegetable	w	yg
P. sat. ssp. *sativum, *	35	7128	Russia, Dagestan	Vegetable	″	ly
	36	3540	Japan	Grain-vegetable	″	bg
	37	3034	″	Vegetable	″	″
	38	8599	Butane	Vegetable	″	″
	39	8456	Burundi	Grain-forage	″	ly
	40	1537	Manchuria	Vegetable	″	bg
	41	4776	Russia	Vegetable	″	yg
	42	6373	Mongolia	Forage	dp	lb
	43	5494	Mongolia	″	lp	″
	44	4788	Mongolia	″	″	″
	45	8702	Vietnam	Vegetable	w	ly
	46	6063	Kazakhstan	″	″	yg
	47	4662	Russia	″	″	ly
	48	6875	Russia	″	″	yp
	49	7700	Bangladesh	Grain-forage	lp	ly
	50	7034	Nepal	″	″	″
P. sat. ssp. *sativum,* Fillbasket	51	8543	United Kingdom, Sri Lanka	Grain-vegetable	w	em
P. sat. ssp. *sativum, *	52	1865	India	Grain-forage	″	ly
	53	1142	France	Forage	dp	lb
	54	4650	Armenia	Vegetable	w	yp
	55	5992	Austria	Forage	lp	pb
	56	8331	Greece**	″	″	lb
	57	2593	Cyprus**	Vegetable	w	ly
	58	2175	Bulgaria	″	″	″
	59	2176	Czech Republic	Forage	lp	lb
	60	8413	Hungary	Vegetable	w	yp
	61	4148	Finland	Forage	dp	lb
	62	7826	Poland	Vegetable	w	bg
	63	6139	Albania	Forage	dp	lb
	64	3970	Belgium	″	lp	″
	65	1027	Germany	″	dp	″
	66	1025	″	″	″	″
	67	8585	″	″	lp	″
	68	3140	Spain**	″	″	″
	69	1930	Italy**	Vegetable	w	ly
	70	1693	United Kingdom	Vegetable	″	bg
	71	1699	″	Grain	″	ly

Table. (Contd.)

Subspecies, variety		Catalog number	Origin	Use	Flower color	Seed color
	72	6883	Uzbekistan	Forage	lp	pb
	73	4170	Latvia	″	dp	lb
	74	3312	Russia	″	lp	″
	75	957	Russia	″	dp	″
	76	1658	Sweden	″	lp	″
	77	3064	Byelorussia	Vegetable	w	ly
	78	3324	Ukraine	Grain-forage	″	″
	79	4108	Ukraine	Grain	w	yp
	80	3358	Russia	″	lp	ly
P. sat. ssp. *sativum,* Troika	81	8522	Russia	Vegetable	w	bg
P. sat. ssp. *sativum,* Vendevil	82	8274	France	Vegetable	w	bg
P. sat. ssp. *sativum,* Panu	83	8638	Finland	Vegetable	w	bg
*P. fulvum****	84	422009		Wild type	ry	

w—white; dp—dirty purple; lp—light purple; r—red; ly—light yellow; yp—yellow–pink; yg—yellow–green; bg—bluish freen; em—emerald; lb—light brown; pb—purple–brown; b—black;ry—red–yellow.

* Local (traditional) cultivar.

** The countries of the centers of *Pisum* origin.

*** Outgroup.

associated with the size and the composition of the selection used by the authors. Similarly, the study of intertransposon polymorphism for the detection of genomic variability in 145 Czech and Slovak cultivars and lines showed that the level of their genetic differences was only 0.11–0.22 [25], which apparently can be explained by the fact that closely related cultivars and local breeding materials were used in the analysis.

In turn, the data of combined RAPD, SSR and ISSR analyses revealed an even broader genome variability for the pea samples than that demonstrated in this study. The genetic difference levels detected in 65 *P. sativum* samples were 0.01–0.66. The result is due to the origin of the material: it contained the cultivars of Western European and North American breeding involving wild gene pool [26].

All modern pea cultivars are based on the material of the *P. sativum* spp. *sativum* subspecies. The narrow genetic basis for these cultivars and for modern breeding material, together with the much greater variety of wild forms and local cultivars, are mentioned in a number of studies [13, 24, 25, 27, 28]. Thus, the study of more than 4500 samples from seven European gene banks has convincingly shown that most of the diversity accounts for the wild material and wild-growing forms (unaffected by breeding) collected in the mountainous areas of the centers of origin for the genus *Pisum* [28].

As noted above, the rather wide diversity that we identified in the selection from the VIR collection may also be associated with the predominance of local cultivars and wild-growing specimens in the selection and with the wide amplitude of their ecological and geographical origin.

According to the results of the cluster analysis (UPGMA) (Fig. 1), all of the studied pea *P. sativum* samples formed a single polymorphic cluster (BI 100%; BI is a bootstrap support index).

Within this cluster, two major subgroups of pea samples could be identified with low bootstrap support values. The most distal and polymorphic group is formed by samples of predominantly East Asian origin from the primary center of the genus biodiversity: Mongolia, Manchuria, Krasnoyarsk region, Afghanistan, Bhutan, Japan, and India.

A main subgroup is formed by pea samples of different origin. Within this subgroup, only certain samples can be combined with significant bootstrap values: samples from Tajikistan and India that belong to the *P. sativum* ssp. *asiaticum* subspecies (BI 85%), as well as samples from the USA and the Peruvian local cultivars (BI 80%). In general, however, no clear clustering of the other samples by their ecological and geographical origin or by belonging to a particular subtype was observed. The samples from Pamir, Syria, and Iran formed a small isolated group. An independent branch was formed by sample 42 from Mongolia. One can also single out a separate group of the main subcluster that comprises samples originating mostly from the European countries located in the latitudinal range of 45°–65° N.

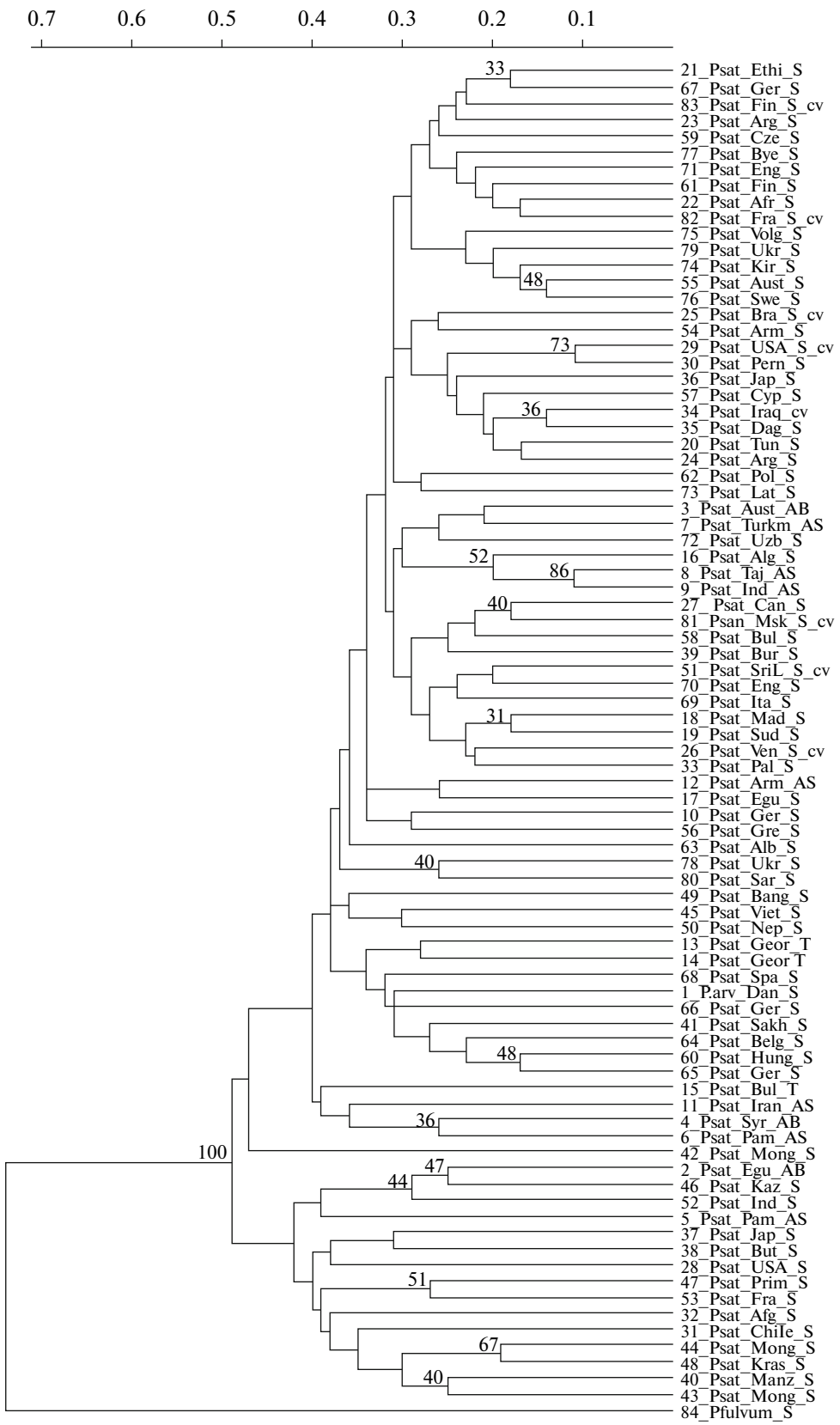

Fig. 1. Dendrogram of genetic differences of *Pisum* samples calculated from AFLP analysis data using the UPGMA method.

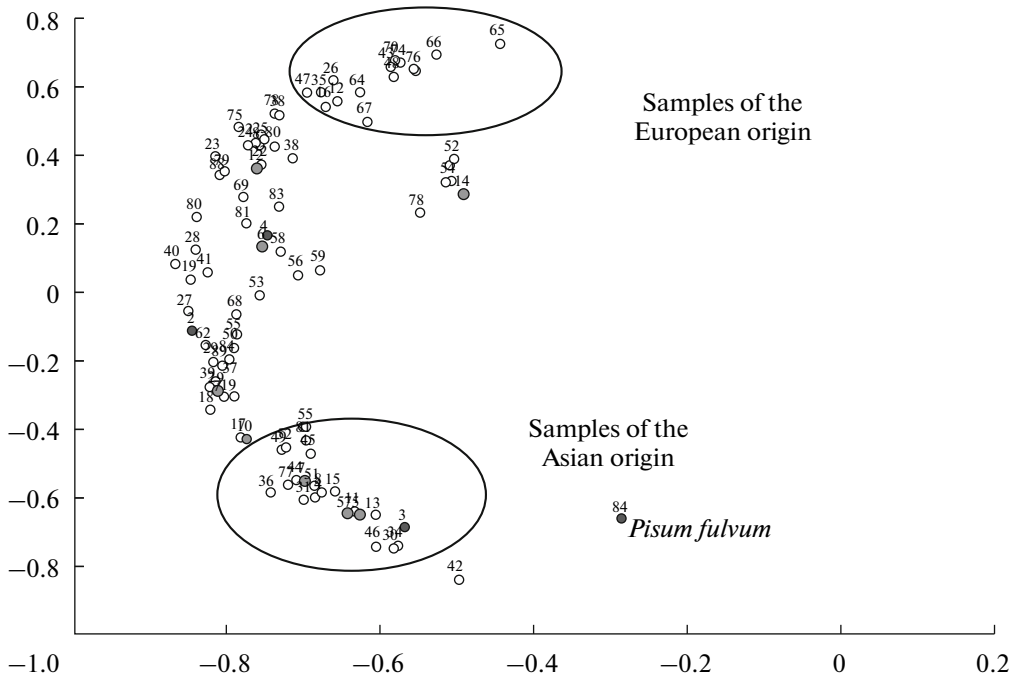

Fig. 2. Differentiation of *Pisum* samples identified according to AFLP analysis data using principal component analysis (PCA). (The chart describes 71.5% polymorphism.)

The group includes a sample from Ethiopia; the pea gene pool in Ethiopia is known for its great plasticity, which allows the plants to grow successfully in territories up to the Arctic Circle [29]. Those samples from Argentina and Africa that belong to this subcluster may originate from mountainous areas characterized by low temperatures; this factor may make the samples similar to plants from northern latitudes.

The genetic similarity of pea samples originating from the northern regions of Russia and the highlands of Central Asia was demonstrated previously in the study of the occurrence frequency of the *His5* allele from the histone gene *H1* [30]. The alleged involvement of histone H1 in the reactions of adaptation to environmental conditions was also noted in the study. We believe that our molecular markers also allow us to identify to a certain extent samples with similar adaptation capabilities.

A multivariate principal component analysis (PCA) was performed in addition to the cluster analysis. On the PCA plot, the analyzed samples formed a continuum with two poles. Samples of predominantly Asian origin were localized on one of these poles, and samples of the European origin were on the other. The majority of analyzed pea samples of different origin occupied an intermediate position between these distant poles (Fig. 2).

Interestingly, classification of the gene pool as European and Asian was also confirmed by molecular analyses of the other plant species. In particular, differentiation of the European and Asian forms was detected in hexaploid wheat using a complex of molecular markers [31]; RAPD analysis revealed the differentiation in chickling vetch [32].

Samples of the *transcaucasicum*, *abyssinicum*, and *asiaticum* subspecies formed no separate groups, either on the PCA plot or on the dendrogram; instead, together with the other *P. sativum* samples, they formed a mixed group. This fact somewhat confirms their status as subspecies.

Analysis of the *P. sativum* population structure confirmed the existence of a single divergent group within the samples, for which there was no clear division into subgroups. By the ecogeographical origin, all of the samples were divided into groups according to the number of subpopulations (from $k = 2$ to $k = 6$). The best a posteriori probability results (LnLike = –6656.8) were obtained for $k = 5$ (Fig. 3).

Analysis of the morphological and biological traits, some of which (flower color and seed color) correlate with the practical use of the cultivars (grain, forage, and vegetable), revealed no correlation with the identified molecular differentiation of the samples. Samples attributable to the *transcaucasicum*, *abyssinicum*, and *asiaticum* taxa displayed no significant similarity to each other within a taxon and formed no separate groups.

Thus, the results of PCA factor analysis, cluster analysis, and population structure analysis do not support the recognition of the *transcaucasicum*, *abyssinicum*, and *asiaticum* samples as the species taxa (they were considered as such by certain authors; particu-

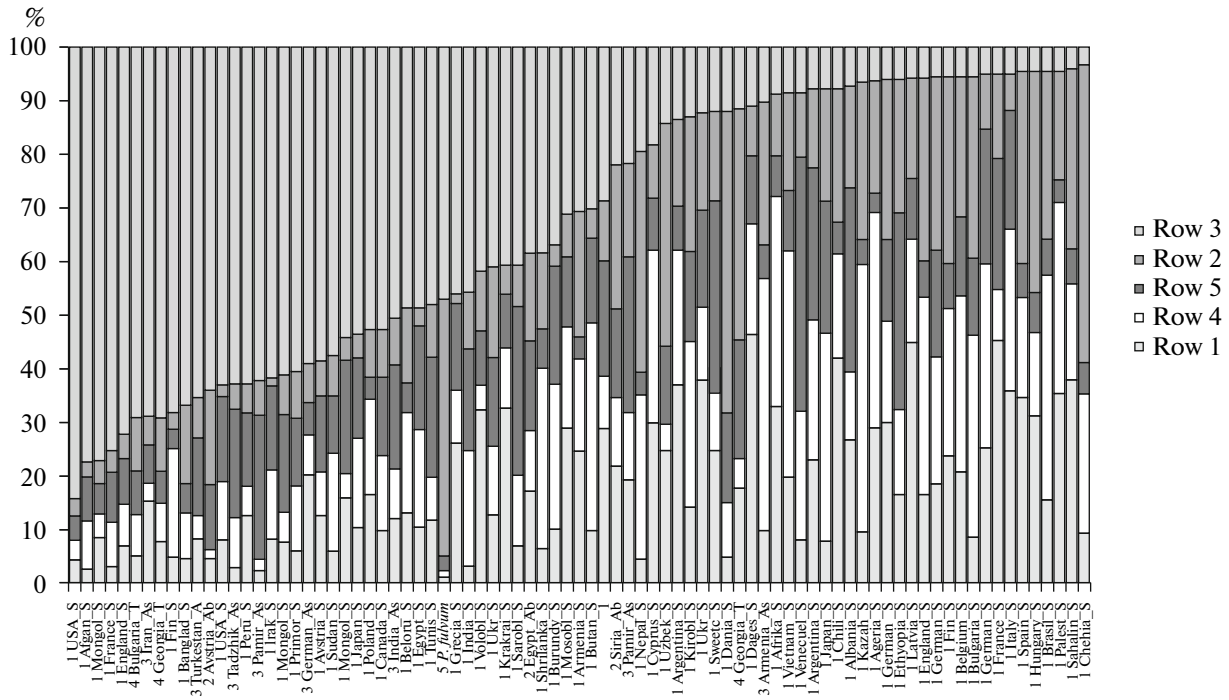

Fig. 3. Possibility of classifying the studied samples of genus *Pisum* as one of the groups according to the analysis using a Structure software at the subpopulation number $k = 5$. Vertical axis—the values of the a posteriori probability, %; horizontal axis—the test samples. Rows 1, 2, 3, 4, 5—sample groups by origin.

larly, *P. abyssinicum* [2, 8, 9]). A clear distinction between *P. sativum* and *P. fulvum* leaves no doubt about their independence as species.

RBIP (retrotransposon based insertion polymorphism) analysis of the pea collection from John Innes Institute (UK) also revealed no clear population structure for *P. sativum*; samples of different ecogeographical origin formed mixed groups [14].

Hence, molecular AFLP-analysis of 84 pea samples from the VIR collection allowed us to obtain specific spectra of the DNA products for each of the samples, to evaluate the genome polymorphism of the selection, and to determine the most similar and the most dissimilar genotypes.

We attribute the existence of the two-poled genotype continuum (one pole is dominated by samples of Asian origin, while the other is dominated by samples from Europe) to the fact that the pea, which had emerged in the culture around 10000 BCE [33], was later widely spread to the east and west from its primary center of origin. As it moved westward (to the European region), cultivation the intense crossing and breeding for useful traits (mostly conditioned by recessive alleles) finally formed the appearances of modern varieties. Pea propagation in East Asia was not accompanied by strong artificial selection; for this reason, many primitive forms were preserved [3]. The lack of molecular or molecular-genetic clustering by geographic origin of the samples can be explained by the fact that the pea is able to adapt to changing environmental factors (photoperiod, the availability of moisture and heat, etc.) and to have a wide cultivation area because of its genomic plasticity. This determines a certain unification of its genetic diversity, which can be detected using AFLP labelling; to some extent, it also reflects the latitudinal gradient of the origin of the studied samples.

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