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MORPHOLOGICAL ANALYSIS OF JERUSALEM ARTICHOKE (*HELIANTHUS TUBEROSUS* L.) ACCESSIONS OF DIFFERENT ORIGIN FROM VIR COLLECTION

Tamara N. Smekalova#, Natalia V. Lebedeva, and Lyubov Yu. Novikova

N. I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR), 42–44 Bolshaya Morskaya Str., St. Petersburg 190000, RUSSIA

Corresponding author, t.smekalova@vir.nw.ru

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The article is dedicated to morphological analysis of the Jerusalem artichoke genetic resources collected at the N. I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR). The crop has a wide range of various usages, such as: food and feed, and medicinal, melliferous, and ornamental products. In this study, morphological characteristics of vegetative and generative plant organs (stems, leaves, tubers and inflorescences) from the VIR collections in the Maikop Experiment Station of VIR (Russian Caucasus, Republic of Adygea) and in Gatchina District, Leningrad Province, Russia were analysed. The widest range of variability was observed in accessions from Western Europe. Accessions from United States, Japan and Australia were the most unique in their set of traits, which may indicate specific paths of their evolution in these isolated territories. Accessions with unique combinations of studied traits were determined. Some traits characterizing leaf, inflorescence and tuber proved to be valuable for taxonomic and geographic analyses.

Key words: *morphological traits, inflorescence, flowers, stem, leaf, tuber.*

INTRODUCTION

Jerusalem artichoke, sun root or earth apple (*Helianthus tuberosus* L.; synonyms: *Helianthus esculentus* Warsz., *H. serotinus* Tausch, *H. tomentosus* Michx.) is a perennial tuberiferous herbaceous plant of the Asteraceae family. It is native to North America, where its wild populations still occupy vast areas near the Great Lakes. Man exploited this plant as early as 2000 years B.C., and during the first millennium B.C. Jerusalem artichoke was domesticated in India. The plant came to Europe earlier than potato, in the beginning of the 16^{th} century. France was the first to become familiar with this plant, when French sailors brought it with them in 1605 from Lescarbot's expedition; later it came to England (Zelenkov and Romanova, 2019). In France, the *sunroot*, as it was called by American Indians, was called *topinambour*, the name derived from the Tupinambá, a tribe of South America's native Tupi people. It became known in Russia under the same name. From France this crop migrated to the adjacent European countries, and further eastwards. To the Baltic countries, for example, Jerusalem artichoke was imported from Germany (Eiche, 1957; Pasko, 1973; and others). In half a century, the species had dispersed over the continent as a vegetable, fodder or even industrial crop. It can be referred to as a widespread food and feed crop in Europe since the second half of the 19^{th} century. In the 18^{th} century, however, distribution of potato abruptly reduced the consumption of Jerusalem artichoke, but beginning from 1844, thanks to the publications by the French scientist J. B. Boussingault who praised its taste and remedial properties, the plant started to regain its popularity (Zelenkov and Romanova, 2019).

At present, Jerusalem artichoke is cultivated worldwide on 2.5 million ha; it is a popular crop in many countries, especially in France, where the planted area with this crop reached 250 000 ha (almost equal to the area under potato production), and the harvest was 7.5 million tons. In the United States, areas under Jerusalem artichoke cultivation grew from 400 ha in 1981 to 700 000 ha in 1990 with a total harvest of 28 million tons. Canada annually produces 13 million tons of Jerusalem artichoke (Swanton, 1986; Zelenkov and Romanova, 2019). In Germany, Poland, and Hungary Jerusalem artichoke is mostly grown for feed — as a forage and fodder crop for swine. Significant areas are allotted to Jerusalem artichoke production in Scandinavian countries, UK, Japan, China, and in countries of Southwest Asia (Zelenkov and Romanova, 2019). In Austria, the cultivated crop area is 130 000 ha (Lyushinsky, 1983; Smirnov, 1988; Starovoytov, 2002).

More than 300 cultivars and hybrids of Jerusalem artichoke are currently known worldwide (Breton *et al*., 2017). Some of them yield large harvests of tubers, some produce ample herbage (with small tubers), and some are distinguished for their special ornamental qualities, etc.

Several authors presume that Jerusalem artichoke penetrated into Russia from Europe. Some of them insist on the northern route, via Arkhangelsk, while others argue for the southern way, from the Balkans through Romania, because in the south its tuber was called Wallachian turnip. Moving along the southern path, Jerusalem artichoke reached the vicinities of the Russian (Northern) Caucasus, where it became known under the names *bolksh* and *khushkal* (Lekhnovich, 1930). A number of sources have declared that this crop became familiar to Russians as early as in the 17th century when it was brought from China (Beysenbiev, 1956; Eiche, 1957; Pasko, 1973; and others). The evidence of this, according to above authors, is the name by which Jerusalem artichoke is traditionally known in Kazakhstan: *kitay kartoshkasy* (Chinese potato). However, we do not find in the literature any sources with well-argumented proof of the beginning stages of Jerusalem artichoke distribution over Russia's territory.

Active cultivation of Jerusalem artichoke started in Russia in the early 19th century. At the end of the 20th – beginning of the 21st century, it became a widespread crop grown from the northwest European part of Russia to Sakhalin Island (Zhukovsky, 1971; Pasko, 1989; Vinogradova, 2008; Breton *et al*., 2017). Presently, it is cultivated in Russia on a large scale on more than 2000 ha, mostly in Nizhny Novgorod, Tver, Ryazan, Tula, Ulyanovsk, Kostroma, Volgograd, Omsk, Bryansk, Moscow, Saratov and Yaroslavl provinces, Chuvashia, Krasnodar and Stavropol territories. In the 1990s, cultivation of Jerusalem artichoke was launched in Siberia — in Chelyabinsk, Omsk, Kurgan, Novosibirsk and Irkutsk Provinces, Krasnoyarsk Territory, Burtyatia and Yakutia. In 1996, the Irkutsk Province alone accounted for over 100 ha under Jerusalem artichoke production (Kochnev and Kalinicheva, 2002). In recent years, Jerusalem artichoke has been actively grown in Leningrad Province as well (north-western Russia, Zelenkov and Romanova, 2019).

Jerusalem artichoke is used for alimentary, medicinal, industrial, feeding, ornamental and environmental purposes (Baldini *et al*., 2004; Seiler *et al*., 2004; Kiru *et al*., 2010; Puttha *et al*., 2012; Favole *et al*., 2014; and others). The crop has very high plasticity — it can be cultivated under highly variable climate conditions and in diverse types of soil. The latest and most promising usage of Jerusalem artichoke is as a source of biofuel, roughage, and as a sugar substitute for those who suffer from insulin-dependent diabetes (Duke, 1983; Rawate *et al*., 1985; Castellini *et al*., 1989; Curt *et al*., 2006; Yaroshevicz *et al*., 2007; Kays and Nottingham, 2008; Izdebsky, 2009; Breton *et al*., 2017; and others).

To promote rational multipurpose use of Jerusalem artichoke, it is necessary to conduct investigations of the crop in different aspects, including morphological, biochemical and physiological characteristics. For the development of new cultivars phenotypic as well genotypic characterisation of source material is crucial. In this aspect especially important is detailed description of genetic resources kept in different gene bank collections.

The Jerusalem artichoke diversity is conserved worldwide in several research centres in France, Canada, USA, and Russia. Recently, the Chinese collection of Jerusalem artichoke (Chinese Agricultural Academy, Inner Mongolia) has undergone rapid development and replenishment, and its holdings are widely used by plant breeders. In the past decades a number of countries (Australia, Austria, Brazil, Canada, France, Germany, Hungary, Ireland, Italy, Netherlands, Norway, Republic of Korea, Spain, UK, USA and Balkan countries) have launched large-scale research projects on Jerusalem artichoke targeting at various areas of its utilisation (Kochnev and Kalinicheva, 2002).

Presently, the collection of Jerusalem artichoke of the Vavilov Institute of Plant Genetic Resources (VIR) is the world's largest according to the number of samples and geographical origin (Diederichsen, 2010; Series *et al*., 2010; Wangsomnuk *et al*., 2011; Breton *et al*., 2017; and others). The part of collection maintained by VIR's branch at the Maikop Experiment Station (MES-VIR) (Russian Caucasus, Republic of Adygea, near of Maikop town; Fig. 1) consists of more than 250 accessions (excluding hybrids; with hybrids more than 300) from 24 countries, collected during the last 80 years. The VIR collection was founded in the 1930s by N. I. Vavilov. The first curator of the Jerusalem artichoke collection in VIR was N. A. Shchibrya, who also contributed very much to its replenishment, study and utilisation (Semenov *et al*., 2018).

N. I. Vavilov initiated the large-scale introduction of Jerusalem artichoke cultivars to the Soviet Union and promoted breeding work with this crop. By his initiative, the first All-Union Conference on Jerusalem artichoke was held in 1933 in Moscow. A decision of the USSR government supported wider cultivation of Jerusalem artichoke by collective farms. Initially, high yield of the crop was confirmed. However, the attempt to dig tubers out in autumn and to store them in the same manner as potatoes resulted in major losses during storage, because even slight damage led to quick deterioration of the tubers. Later, spring harvest of tubers have started to prevail, while those harvested in autumn were immediately sent for processing.

The first stage of characterisation of any genetic resources is detailed phenotypic description of the available material. However, the analysis of morphological, ecogeographic and biological traits of Jerusalem artichoke, survey of the diversity of its varieties, and identification of taxonomically significant traits for intraspecific classification purposes are rather fragmentary. Most of those studies were conducted several decades ago (Zhukovsky, 1971; Pasko, 1973; 1974; 1989; Kays and Kultur, 2005; and others). The latest research (Kays and Kultur, 2005; Kays and Nottingham, 2008; Puttha *et al*., 2013; Breton *et al*., 2017; Zelenkov, 2017; and others) showed that Jerusalem artichoke phenotypic diversity is rich, while attempts to analyse in detail the species morphological traits and build up its updated intraspecific system have been sporadic. We conducted detailed investigation of inflorescences and flowers traits (Smekalova *et al*., 2018). The literature lacks analysis of the complex set of the Jerusalem artichoke morphological traits. Therefore, there is a great need to describe morphological characteristics of vegetative and generative organs of the species. From a practical point of view the intraspecific diversity of tuber characteristics of *H. tuberosus* has priority (Pasko, 1989; Kays and Kultur, 2005; Kays and Nottingham, 2008; Puttha *et al*., 2013).

The objective of this study was a complex assessment of morphological traits in *H. tuberosus* as the first and important step of work with the collection held by VIR. This would promote its wide exploration for different goals: for use in breeding programmes (pre-genotyping), to identify traits that can be used in intraspecific taxonomy, and to clarify the paths of historical distribution of the species.

MATERIALS AND METHODS

The collection of Jerusalem artichoke maintained by the Vavilov Institute of Plant Genetic Resources (VIR) at its Maikop branch (MES-VIR) served as material for the research. The study was conducted during 2016–2017 in two different geographic localities: in Russian Caucasus, Republic of Adygea (MES-VIR) and in north-western Russia (experimental field of the "Private Enterprise farm N. Yu. Anushkevich", the vicinity of Menkovo Settlement, Gatchina District, Leningrad Province) (Fig. 1).

Fig.1. Locations of investigation.

Tubers for analysis were dug up in spring (in April — in Maikop, in May — in Menkovo), during the planned time for replacing of the collection. Planting of tubers was carried out by the standard method: total of ten tubers taken from ten plants (one tuber from each plant) were planted in a row; the distance between the rows was 50 cm; row spacing was 1 metre. Inflorescences were analysed during their mass flowering (late August – early September). Measurements were taken and calculations were made for three to five plants of each accession; mean data for two years were included in the analysis.

In addition, records for 1973–1975 in the MES-VIR were used for some accessions (field registers of the Jerusalem artichoke collection completed by N. M. Pasko).

The study employed the geomorphological method (analysis of variability of morphological traits of accessions in the context of their geographic origin). One-way ANOVA was used for comparing groups according to their origin. The effect of the cultivation conditions on the accessions in the environments of Maikop and Menkovo was studied using the Student's t-test for dependent samples, and the distribution of qualitative characteristics using the χ^2 test. Correlation analysis was applied to study linkages between traits, and principal component analysis method to analyse polymorphism of traits. Software StatsoftStatistica 13.0 was used for calculations, $p = 0.05$ was defined as significance level.

Leaf characters were analysed for samples of 99 varieties (Table 1, Fig. 2). Eleven traits were studied: plant height; lamina length with petiole; lamina length; lamina width; leaf index (ratio of leaf length to lamina length); lamina shape index (ratio of lamina length to lamina width); leaf shape; leaf base shape; lamina pubescence; leaf edge shape type; and leaf tip shape.

Inflorescence characters were studied for 58 accessions (Table 1, Fig. 3). Eleven characters were measured and calculated: number of inflorescences per plant; inflorescence diameter; anthodium diameter (inflorescence disc without marginal pseudoligulate florets; only receptacles with tubular florets were measured); number, length and limb width of pseudoligulate florets; and number and length of tubular florets; number, length and width of involucre leaflets.

Tuber characters were studied for 75 accessions in Maikop and 102 accessions in Menkovo (Table 1, Fig. 4). Twenty-three tuber characters were analysed: length; width; circumference; number of buds (eyes); number of scale-like rings; tuber shape (pyriform, oval, clavate, rounded, elongated); tuber colour (brown, dark brown, light brown; presence of anthocyanin marked in a separate column); bud skin colour (brown, brown with anthocyanin, light, light with anthocyanin); tuber surface type; tuber pith colour; presence of daughter tubers; dents on tubers; and knobs on tubers.

RESULTS

Plant height, morphological characters of the leaf. Correlation analysis showed that there were clearly correlated pa-

Table 1

NUMBER OF STUDIED JERUSALEM ARTICHOKE ACCESSIONS ACCORDING TO THEIR GEOGRAPHIC ORIGIN (MAIKOP AND MENKOVO)

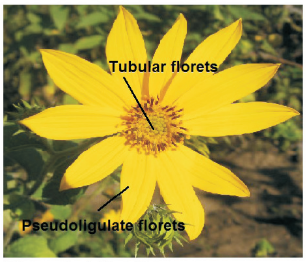
Group No.	Origin (region, country, code of region)		Morphological traits of organs, number of accessions				
			Leaves (Maikop)	Inflores-cences (Maikop)	Tubers		
					Maikop	Menkovo	Maikop & Menkovo
1	Europe (E)	Bulgaria	3	2	1	1	0
		Hungary	2	1	1	1	1
		Germany	3	5	4	4	2
		Latvia	2	1	1	3	1
		Norway	1	0	1	0	0
		Poland	1	2	0	1	0
		France	18	5	10	19	5
		Czechoslovakia (before 1990)	2	0	1	1	1
		Estonia	1	2	0	1	0
2	Ukraine, Belarus BM, Moldova (U)	Ukraine	18	11	20	18	13
		Belarus	1	1	0	0	0
		Moldova	2	3	3	3	2
3	Russia, European part (R)		11	6	9	34	8
4	Russia, Russian Caucasus (C)		11	5	7	2	3
5	Russia, West Siberia (W)		2	1	2	2	1
6	Transcaucasia (T)	Georgia	2	1	2	1	1
		Armenia	2	0	2	0	0
		Azerbaijan	1	0	0	1	0
7	Central Asia (A)	Iran	1	0	0	0	0
		Kyrgyzstan	2	1	1	1	0
		China	1	0	1	0	1
		Tajikistan	3	2	2	2	0
		Turkmenistan	2	2	1	2	2
		Uzbekistan	1	0	1	0	0
8	Japan (J)		3	3	2	3	2
9	USA (S)		3	3	2	1	1
10	Australia (Au)		0	1	1	1	1
	Total:		99	58	75	102	45

Lanceolate, K-56, ‘Sakhalinskiy’, Japan | Oblong-ovoid, K-178 ‘Latvijas Baltais’, Latvia | Ovoid, K-194, ‘Progress’, France

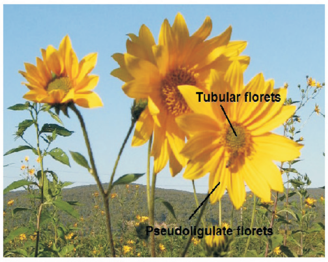
Fig. 2. Leaf shape (Maikop, 2017, K-VIR catalogue number).

rameters. Leaf length with petiole correlated with lamina length (r = 0.98) and lamina width (r = 0.80); lamina length with lamina width (r = 0.79); and leaf index with petiole length (r = 0.81). Lamina index was mainly associated with lamina width (r = –0.77) and conjugated with the lanceolate leaf shape (r = 0.73). Lanceolate leaf shape was associated with the cuneate leaf base (r = 0.80), while oblong-ovate leaf shape, with the subcircular-cuneate base (r = 0.74). The most constant, conservative characters were: leaf shape, leaf base, leaf index, and leaf edge.

Comparing groups of origin. *ANOVA* showed that there were no significant differences between the origin-based groups in plant height. Accessions from Japan had the largest average leaf size (18.2 ± 1.2 cm), lamina size (14.5 ± 1.1 cm), and petiole length (3.7 ± 0.1 cm). In leaf length and lamina length, they significantly differed from the group of accessions from Transcaucasia (12.9 ± 1 and 10.3 ± 0.8 cm, respectively) and Central Asia (13.5 ± 0.7 and 10.7 ± 0.5 cm), and in petiole length, from the Transcaucasian group of accessions (2.5 ± 0.2 cm). Lamina width in Japanese accessions was 5.1 ± 0.2 cm, while in the contrasting group from Central Asia it was 3.7 ± 0.2 cm. Accessions from the USA were noticeable for their leaf index; they had the highest mean value (1.318 ± 0.037) signifi-

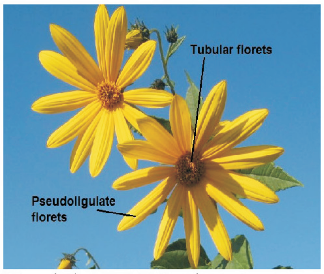


'Vengersky', K-6, Hungary



'Progress',K-194, France

'Progress', K-194, France, involucre leaflets



'Tuapsinsky', K-249, Russia


'D-31', K-206, France, common view to inflorescence brush

Fig. 3. Details of inflorescence of Jerusalem artichoke different varieties (Maikop, 2018; K - VIR catalogue number).

Pyriform, 'Kievskiy uluchshenniy', K-55, Ukraine

Oval, 'Shankhaiskiy', K-153, China

Clavate, 'C-141', K-180, Russia

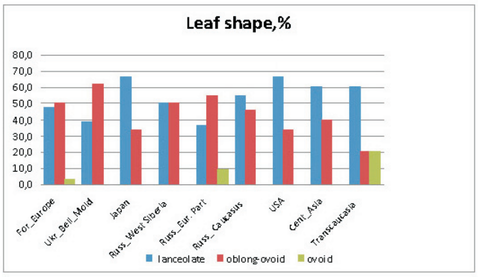
Rounded, 'Priekulsky', K-173, Latvia

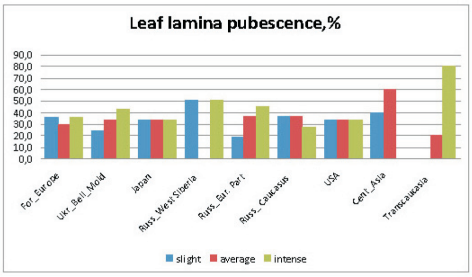
Elongated – 'Progress', K-194, France

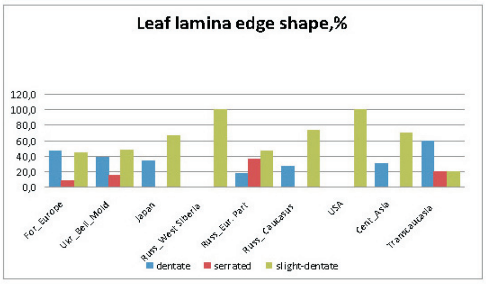
Fig. 4. Variants of the form of tubers (Menkovo, 2017; K - VIR catalogue number).

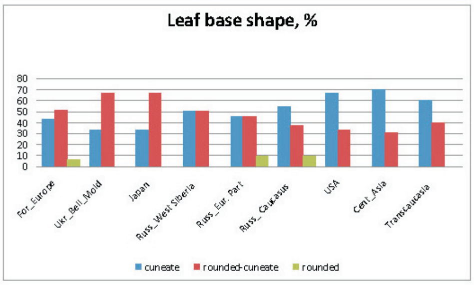
cantly exceeding all other groups, except the accessions from Japan (1.260 ± 0.012). There were no significant differences between groups in the lamina index.

Figure 5 shows qualitative leaf characters of the studied accessions. Ovate leaf shape was observed among the accessions from the Caucasus (one accession out of 5, 20.0%), Europe (one accession, 2.9%), and European part of Russia (one accession, 9.1%). A subcircular shape of the leaf base was found only in the accessions from West and Central Europe (two accessions, 6%), European part (EP) of Russia (one accession, 9.1%), and Russian Caucasus (one accession, 9.1%). The highest percentage of accessions with strong pubescence was recorded for the group from Transcaucasia (80.0%). Serrate leaf edges were found in accessions from Western Europe (three accessions, 8.8%),









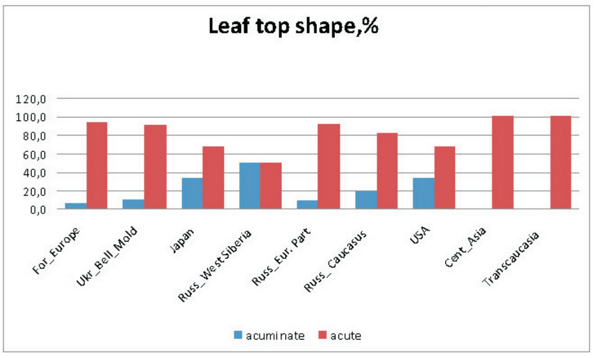


Fig. 5. Qualitative leaf characteristics of Jerusalem artichoke accessions according to their geographic origin (Maikop).

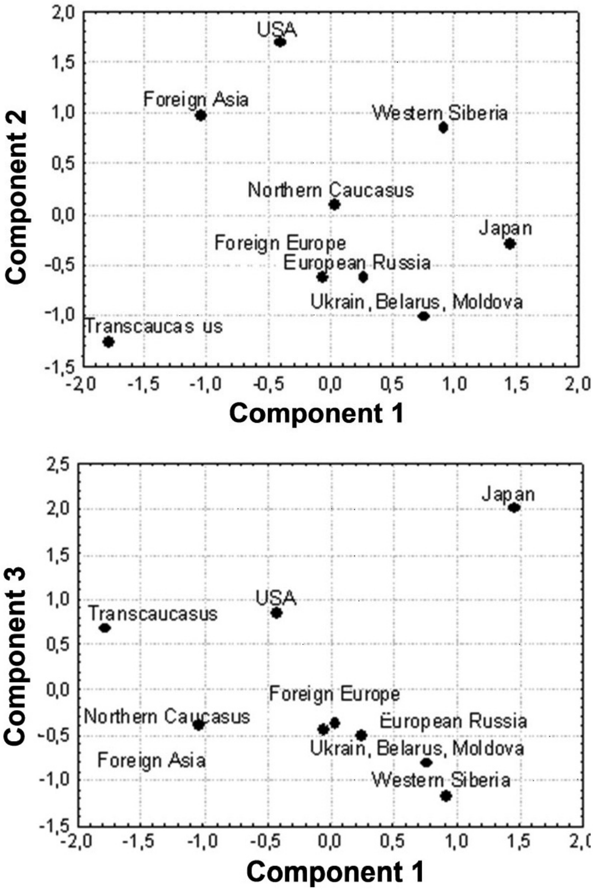


Fig. 6. Distribution of the origin-specific groups of Jerusalem artichoke accessions over the spaces of (a) Component 1 and Component 2, and (b) Component 1 and Component 3, according to morphological leaf characters and plant height.

Ukraine and Moldova (three accessions, 14.3%), European part of Russia (four accessions, 36.4%), and Transcaucasia (one accession, 20.0%). Accessions from Transcaucasia showed the highest percentage of leaves with a dentate margin (three accessions, 60.0%). Thus, the ovate leaf shape, subcircular leaf base, and serrate edge were not observed in accessions from Central Asia, Japan and the United States.

<u>Principal components analysis of the groups of different geographic origin</u>. For calculations, rarely occurring and covariable traits were removed. Analysis of the studied geographic groups was performed for mean values of plant height and morphological leaf traits. The first component explain 35.1% of the variance; it was associated with leaf size: length and width of the lamina, and with leaf base shape. The second component explained 26.7% of the variance and was associated with leaf edge type. The third component explained 13.3% of the variance and was associated with leaf shape. In the ordination space of components 1–2 and 1–3 (Fig. 6) accessions from Japan, USA and Transcaucasia were the most conspicuous.

Inflorescences. Probably one of the most significant results of previous detailed study of inflorescence traits (Smekalova *et al*., 2018) was identification of a number of accessions ('Sakhalinsky Krasny', 'Frantsuzsky Neizvestny', 'Tolbukhin', 'Bely Urozhainy' and 'Vengersky') that di-

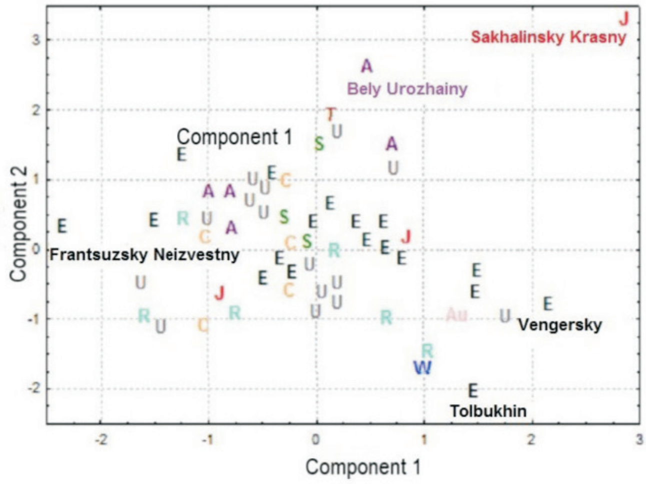


Fig. 7. Distribution of Jerusalem artichoke accessions of different origin over the space of the first two components according to their inflorescence characters (symbols are shown in Table 1).

verged in two-component ordination space from a cluster of the other accessions (Fig. 7). 'Sakhalinsky Krasny' (origin: Japan) was the most unique in its inflorescence characteristics (maximum number of pseudoligulate florets per inflorescence (16.3) with width 1.5 cm; maximum number of involucre leaflets (31.7) with maximum length 2.0 cm) was. Maximum number (100 to 120) of inflorescences and nearly the narrowest (0.3 cm) leaflets of the involucre were observed in 'Vengersky' (origin Hungary). The cultivar 'Tolbukhin' (Bulgaria) had rather broad involucre leaflets (0.4 cm), and 'Bely Urozhainy' (Tajikistan) had rather narrow leaflets (0.2 cm). Cv. 'Frantsuzsky Neizvestny' (France) possessed the shortest (0.9 cm) and narrowest (0.18 cm) involucre leaflets, and the narrowest (0.8 cm) pseudoligulate florets.

Tubers. In our investigation comparison of the groups of different geographic origin by means of ANOVA, correlation and principal component analyses failed to identify significant differences in tuber traits between accessions grown in both localities. Accessions from the USA had the largest mean tuber sizes (Table 2): length (6.3 ± 0.4), width (4.0 ± 0.1), and circumference (12.8 ± 1.5). Significant differences in mean tuber size were found in accessions from Australia (length: 6.1, width: 3.9), circumference: 12.5 cm), Japan (length: 6.1 ± 1.5, width: 3.8 ± 0.4), circumference: 10.3 ± 1.7), and the EP of Russia (length: 6.0 ± 0.4, width: 3.4 ± 0.2), circumference: 10.7 ± 0.4). The number of buds was higher in accessions from Australia (14.7), the U.S. (12.8 ± 1.5), and EP of Russia (12.8 ± 1.1). Accessions from the EP of Russia (7.8 ± 0.4); Australia (7.7); Transcaucasia (7.3 ± 1.4); U.S. (7.2 ± 0.2) and Japan (7.2 ± 0.8) had the largest number of scale-like rings. The smallest mean tuber sizes were in accessions from Russian West Siberia (length: 5.0 ± 0.7, width: 3.1 ± 0.3, circumference: 10.7 ± 0.6); Russian Caucasus (length: 5.5 ± 0.2, width: 3.4 ± 0.3, circumference: 11 ± 0.8); Transcaucasia (length: 5.6 ± 0.6, width: 3.4 ± 0.4, circumference: 10.5 ± 0.9), and Central Asia (length: 5.6 ± 0.5, width: 3.4 ± 0.3, circumference: 10.6 ± 0.8

Table 2

QUANTITATIVE TUBERS TRAITS OF JERUSALEM ARTICHOKE ACCESSIONS ACCORDING TO THEIR GEOGRAPHIC ORIGIN (MEAN ± STD. ERROR, MAIKOP)

Country group	Number of accessions	Length, cm	Width, cm	Circumference, cm	Number of buds	Number of scale-shaped rings
Central Asia (A)	6	5.6 ± 0.5	3.4 ± 0.3	10.6 ± 0.8	10.3 ± 0.6	6.5 ± 0.4
Australia (Au)	1	6.1	3.9	12.5	14.7	7.7
Caucasus (C)	7	5.5 ± 0.2	3.4 ± 0.3	11.0 ± 0.8	12.0 ± 1.4	6.8 ± 0.5
West and Central Europe (E)	19	5.7 ± 0.3	3.2 ± 0.1	10.2 ± 0.3	11.0 ± 0.7	6.6 ± 0.4
Japan (J)	2	6.1 ± 1.5	3.8 ± 0.4	11.1 ± 0.2	10.3 ± 1.7	7.2 ± 0.8
Russia, European part (R)	9	6.0 ± 0.4	3.4 ± 0.2	10.7 ± 0.4	12.8 ± 1.1	7.8 ± 0.4
Transcaucasia (T)	4	5.6 ± 0.6	3.4 ± 0.4	10.5 ± 0.9	11.3 ± 1.3	7.3 ± 1.4
Ukraine, Belarus, Moldova (U)	23	5.8 ± 0.2	3.4 ± 0.1	10.8 ± 0.3	12.3 ± 0.7	7.0 ± 0.3
USA (S)	2	6.3 ± 0.4	4.0 ± 0.1	12.7 ± 0.2	12.8 ± 1.5	7.2 ± 0.2
Russia, West Siberia (W)	2	5.0 ± 0.7	3.1 ± 0.3	10.7 ± 0.6	12.3 ± 0.7	5.7 ± 0.3
Together	75	5.8 ± 0.1	3.4 ± 0.1	10.7 ± 0.2	11.8 ± 0.4	6.9 ± 0.2

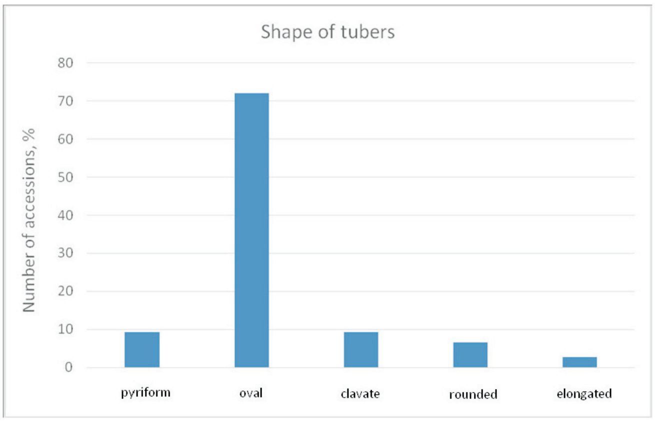


Fig. 8. Tuber shapes of Jerusalem artichoke accessions (Maikop).

Tuber shape appeared to be the most significant among qualitative tuber characters in distinguishing accessions. The majority of the studies accessions (72.0%) had an oval tuber shape (Fig. 8).

Correlation analysis of the accessions grown in Maikop showed significant correlation between: tuber width and circumference (r = 0.92); tuber length and width (r = 0.60); tuber length and number of scale-like rings (r = 0.54); tuber length and circumference (r = 0.49); number of buds and number of scale-like rings (r = 0.46); and tuber circumference and number of buds (r = 0.33). Thus, larger tubers had greater numbers of scale-like rings and buds.

Principal component analysis of the accessions grown in Maikop (Table 3) showed that five components explained

Table 3

PRINCIPAL COMPONENT ANALYSIS OF MORPHOLOGICAL CHARACTERS OF JERUSALEM ARTICHOKE TUBERS FOR ACCESSIONS FROM ALL STUDIED GEOGRAPHIC GROUPS (MAIKOP)

Character	Component 1	Component 2	Component 3	Component 4	Component 5
Length, cm	–0.68	0.39	–0.07	–0.03	–0.22
Width, cm	**–0,90**	0.20	–0.05	0.09	0.10
Circumference, cm	**–0.81**	0.28	–0.06	0.13	0.14
Number of buds	–0.21	**0.73**	0.12	–0.04	–0.10
Number of scale-shaped rings	–0.25	0.69	–0.21	–0.31	–0.25
Oval tuber shape	0.37	0.29	0.43	–0.29	0.04
Rounded tuber shape	–0.29	–0.4	–0.58	0.27	0.29
Tuber colour with anthocyanin	0.04	0.11	**–0.69**	–0.45	0.34
Light brown tuber colour	–0.01	0.16	–0.01	**0.82**	–0.31
Scabrous tuber surface	–0.52	–0.24	0.36	0.16	0.43
Presence of daughter tubers	–0.15	0.28	0.50	–0.03	**0.56**
Presence of knobs on tubers	–0.57	–0.62	0.16	–0.31	–0.29
Absence of knobs on tubers	0.62	0.56	–0.19	0.31	0.27
Proportion	0.25	0.18	0.12	0.11	0.08

The highest loads for each factor are boldfaced.

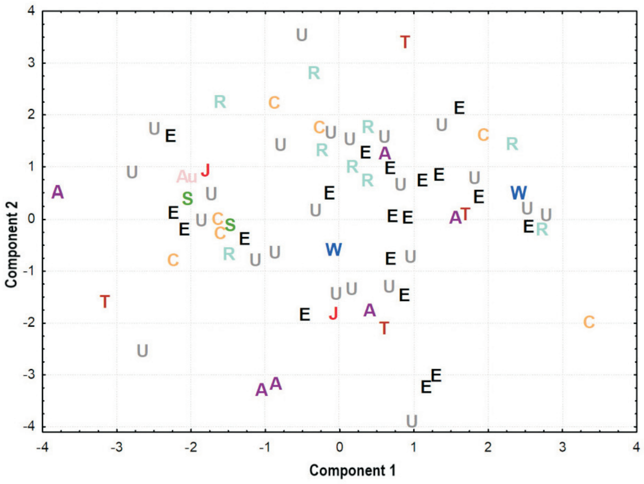


Fig. 9. Principal component analysis of morphological traits of Jerusalem artichoke tubers for accessions of all studied geographic groups (geographic groups codes are given in the Table 1).

70% of variance in the studied accessions. The first component, which explain 24.8% of the variance of the sampled material, was explained by tuber size. It is associated with tuber width and circumference. The second factor, explaining 18.4% of variance, was related to the number of buds. The third factor, explaining 12.1% of variance, was associated with presence of anthocyanin in tuber skin colour. The studied accessions differed less in colour (percentage of tubers with light brown skin). The fourth component, explaining 10.7% of the total variance was associated with light brown skin. The fifth factor, explaining 8.3% of variance, was associated with the presence of 'daughter tubers'.

Grouping of the accessions according to their tuber characteristics in the space of the ordination of first two components (Fig. 9) showed that the sampled batch was relatively uniform, without outlier samples.

Comparison of accessions grown in contrasting ecogeographic environments (Maikop and Menkovo) showed that 45 manifested a number of coinciding characters sensitive to growing conditions, and a number of constant characters non-reactive to growing conditions (Fig. 10). Significant differences depending on growing conditions were found for tuber size: longer in Menkovo (6.3 cm compared with 5.7 cm in Maikop), but less wide (3.1 cm compared with 3.5 cm in Maikop). Tuber circumference was almost the same (10.5 cm in Menkovo, and 10.9 cm in Maikop). The chi-squared test ($\chi^2 = 7.37$) showed that the proportions of tubers with different colour did not differ between geographic locations (p = 0.12). The accessions in Menkovo had darker tuber skin colour (20.0% of dark brown accessions against 0% in Maikop; 31.1% of brown accessions against 2.2% in Maikop), and light brown tubers were fewer (48.9% against 97.8% in Maikop) (Fig. 6). There were considerably fewer accessions with light-coloured bud skin in Menkovo (44.4%) than in Maikop (100%), but accessions with brown bud skin colour were much more numerous (55.6% against 0% in Maikop), and the level of

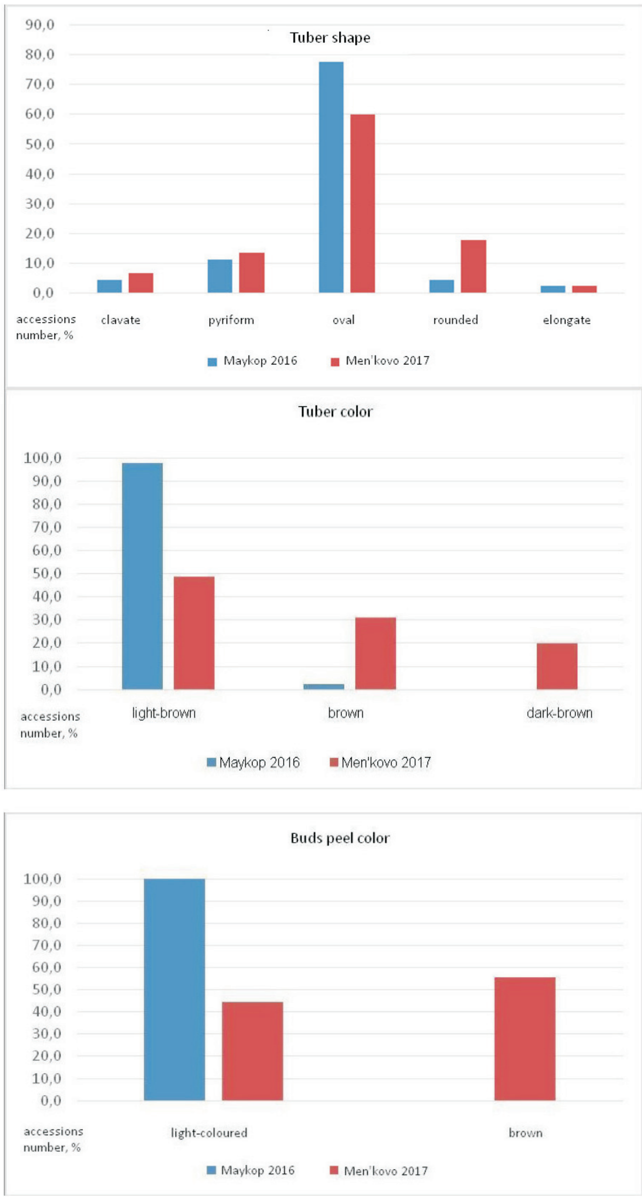


Fig. 10. Qualitative characteristics of Jerusalem artichoke accessions (Maikop and Menkovo).

anthocyanin in bud skin was higher (24.4% against 2.2% in Maikop).

The percentage of accessions with the "knobs on tubers" trait was significantly lower in Menkovo (2.2%) than in Maikop (51.1%), which was probably due to the soil types.

Evaluation performed in contrasting eco-geographic environments showed that tuber traits like tuber circumference and shape were not influenced by soil and climate conditions, and thus can be considered to be constant conservative characteristics.

Significant variance was demonstrated for tuber size, which can be explained by greater amount of positive temperatures during the growing season: tuber shape and size of a given clone depends both on the latitude of its cultivation site and the mean daily temperature during the growing season in the period from planting to harvesting (Breton *et al*., 2017; Puangbut *et al*., 2017; and others). Significant variance was observed in tuber skin colour as well. The last trait is associated with the amount of the colouring pigment — anthocyanin — and with the intensity of its expression, both of which may change with environmental conditions (Noda *et al*., 1994; and others).

DISCUSSION

An aggregate of parameters characterising the leaf, inflorescence (Maikop) and tuber (Maikop and Menkovo) was used in the phenotypic analysis of genetic resources from VIR's collection of Jerusalem artichoke. Polymorphism of the studied characters was analysed in the context of the accessions' geographic origin.

The analysis of leaf characters showed significant differences between accessions from areas considerably remote from each other. Accessions recorded as unique were those from Japan and the USA, and regarding specific characters, also those from Transcaucasia and Central Asia. Western European accessions were similar in the studied characters to those from the European part of Russia, Ukraine, Belarus, and Moldova. This may imply that their migration route into Russia ran from Western Europe (western path) across these countries. The accessions from Transcaucasia and Russian Caucasus differed from others in characters and further research is required to identify their origin and distribution patterns, using more plant materials collected not only in the Caucasus, but also in the adjacent regions (southern Russia, Southwest Asia, etc.). The routes of the crop migration from the east through West Siberia also need to be further studied using a broader range of plant material.

As a result of analysis of the structure of the studied morphological traits, a number of interconnected traits were identified: leaf index with petiole length, leaf lamina length with lamina width, conjugated with the lanceolate leaf shape, total inflorescence diameter with pseudoligulate floret length, total inflorescence diameter with pseudoligulate floret width, width of pseudoligulate florets with their length, number of pseudoligulate florets in the inflorescence with the number of involucre leaflets on the inflorescence, tuber width with its circumference, tuber length with its width, tuber length with the number of scale-like rings, and tuber length with its circumference. These relationships should be taken into account when using the traits to build up an intraspecific system of the species.

Evaluation of the polymorphism in leaf and inflorescence morphological characters of the studied Jerusalem artichoke accessions from VIR collection showed that the following traits had maximum variance between the origin-based groups: leaf size, leaf base shape, leaf edge type, leaf shape, number of inflorescences per plant, number of pseudoligulate florets per inflorescence, total inflorescence diameter, and pseudoligulate floret length and width. These descriptors may be used in geographic analysis of Jerusalem artichoke accessions.

Maximum variance in the set of traits was characteristic of the European group. The most unique in inflorescence characters were the accessions 'Sakhalinsky Krasny' (origin: Japan). Cvs. 'Frantsuzsky Neizvestny', 'Tolbukhin', 'Bely Urozhayny' and 'Vengersky' also possessed a set of unique traits.

A number of studied traits appeared to be constant for individual accessions or to several of them; the tubular floret length was the most constant within the scope of the species. In the studied Jerusalem artichoke collection at Maikop, the most differentiating characters were leaf traits: size (lamina length, petiole length, lamina width), leaf index, leaf shape and leaf edge type; and inflorescence characters: total inflorescence size, number of pseudoligulate florets per inflorescence, pseudoligulate floret length and width. The most constant characters were inflorescence traits: number of inflorescences per plant, and number of pseudoligulate florets per inflorescence (Smekalova *et al*., 2018). These traits are well expressed, contrasting, conservative and usable as diagnostic and taxonomically significant tools in identification of accessions, development of the system of the species, its taxonomic and geographic analyses.

CONCLUSIONS

One of the assumed ways by which Jerusalem artichoke might have penetrated the territory of Europe (southern European route: from France, through Germany, Poland, Ukraine, then — through Belarus and Moldova, to Russia, and then, possibly, to the Russian Caucasus) was confirmed.

Accessions from the USA, Japan and Australia appeared to be the most unique according to the studied set of their characters, which most likely reflects specific ways of their evolution in isolated territories.

Specific traits of the leaf (the most constant, conservative), like shape of leaf, base of leave, leaf index, and the edge of the leaf), and trait of the inflorescence (the number of flowers per inflorescence, number of bracts, length and width of pseudoligulate flowers and bracts) and tuber (shape of tuber and length of the circumference of the tuber) are valuable for taxonomic and geographic analyses of the species.

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BUMBUĻU TOPINAMBŪRA (*HELIANTHUS TUBEROSUS* L.) DAŽĀDAS IZCELSMES VIR KOLEKCIJAS PARAUGU MORFOLOĢISKĀ ANALĪZE

Veikta bumbuļu topinambūra (*Helianthus tuberosus* L.) Viskrievijas Augu ģenētisko resursu institūta (VIR) kolekcijā esošo paraugu dažādu veģetatīvo un ģeneratīvo orgānu mainības analīze divos kontrastainos ekoloģiskos apstākļos. Izdalītas pazīmes, kuras ir būtiskas no taksonomiskā viedokļa, kā arī izvirzīta hipotēze par šī auga izplatīšanās ceļiem Eiropā.