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Genetic diversity of invasive alien species *Lupinus polyphyllus* populations in Lithuania

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Abstract

After appearance in Lithuania at the beginning of the 20th century, large-leaved lupine (*Lupinus polyphyllus* Lindl.) has widely spread throughout the country inhabiting not only forests but also the forest outskirts, roadsides, abandoned uncultivated fields, and its further penetration into natural habitats is observed. The goal of the research was to study the intraspecific diversity of *L. polyphyllus* populations in forests and abandoned fields. Genetic diversity of *L. polyphyllus* populations of forests and abandoned fields was tested using the RAPD method. Genotypes of each population were investigated using six primers. The UPGMA dendrogram revealed that all plants are genetically different, but individuals of each population group together. AMOVA showed significant genetic differentiation of the investigated *L. polyphyllus* populations ($\Phi_{PT} = 0,444, p < 0,001$). Neither UPGMA cluster analysis, nor principal coordinate analysis revealed population grouping regarding the geographic distance between them. On the other hand, UPGMA cluster analysis revealed genetic peculiarities of *L. polyphyllus* populations that probably are associated with adaptation of invasive populations to local conditions. Although *L. polyphyllus* is becoming one of the most aggressive invasive plant species, according to our data, this is just the first study on the genetic diversity of the invasive populations of this species using molecular markers.

Key words: Lupinus polyphyllus, invasive plant species, RAPD, genetic diversity.

Introduction

The landscape of Lithuania rapidly changes under the influence of anthropogenic activity. That leads to the spread of some plant species, changes of plant species composition in natural habitats, thus affecting the extinction of natural habitats. The spread of alien invasive species disrupts the biological diversity, influences the changes in the ecosystem. The spread of invasive species in Lithuania is also determined by climate change stipulated by global factors: temperature changes and environmental pollution. All this could have a negative impact on the Lithuanian natural resources, plant biodiversity and human health. One of the noxious invasive plant species, altering the species composition of plant communities is a large-leaved lupine (Lupinus polyphyllus Lindl.). It is a perennial, diploid (2n = 48) (Góralski et al., 2009), undemanding, cold resistant plant. L. polyphyllus produces plenty of seeds, and it is one of the factors contributing to a wide spread of the plant. The plant is native to North America, but it quickly spread throughout Europe. In Lithuania, this species was for the first time detected in 1931 in the environs of Kaunas (Gudžinskas, 1999).

Recently it has spread in many places: near the roadsides and forest borders, close to the major motorways and in former grazing areas. Its spread in Lithuania was induced by the fact that it was planted in the forests for food of the wild animals and as a precautionary measure against the spread of forest fires (Snarskis, 1968). It is noted that the species aggressively spreads from coniferous forest borders and roadsides into an open, deserted, abandoned fields. This poses a threat to natural plant communities, biodiversity and landscape (Gudžinskas, 1999; NOBA-NIS, 2009–2010). There is evidence that in a new territory the invasive plant populations for some time exist in a kind of latent state, during which due to repeated invasions and hybridization as well as the mutations the level of genetic diversity is restored, which is usually reduced due to genetic processes occurring in the course of invasion (genetic drift, bottleneck, founder effect) (Ellstrand, Schierenbeck, 2000; Prentis et al., 2008). It was interesting to find out the level of genetic diversity of the lupine populations and whether it may be associated with the strategy of adaptation to exist in the new conditions.

In addition, in order to evaluate and identify potential changes in lupine populations, which could have led to increased invasiveness, genetic parameters of forest and field populations were compared and population genetic differentiation level was assessed.

Materials and methods

The study was carried out in 2010–2011 at the Institute of Botany, Nature Research Centre.

Plant material. Ten populations of *Lupinus polypyllus* were sampled in Lithuania (Table 1). A total of 192 plants were analyzed (the sample size per population varied from 12 to 24 plants). The distance between sampled plants in each population was approximately 20–25 meters.

Genomic DNA extraction. Total genomic plant DNA was extracted from young frozen leaves using Genomic DNA purification kit ("Fermentas", Lithuania) according to manufacturer's recommendations. The concentration and the quality of the DNA samples were estimated by a spectrophotometer Helios γ ("Thermo Scientific", USA). DNA samples were diluted to 50 ng μ l⁻¹ and kept at -20°C until use.

RAPD assay. Twenty different RAPD primers were initially screened, but analysis was carried out with 6 of OPB and OPA primers which produced clear and reproducible RAPD profiles. The PCR reaction mixtures had a total volume of 20 µl. The mixture contained 0.5 U of recombinant Taq DNA polymerase ("Fermentas", Lithuania), 0.4 µM primer ("Biomers", Germany), 2 mM of each dNTP ("Fermentas", Lithuania), 1 × appropriate reaction buffer (100 mM Tris-HCl, pH 8.8; 500 mM KCl; 2.5 mM MgCl₂) and 50 ng of template DNA were performed in cycler ("Biometra", Germany) programmed as follows: 1 min at 94°C for initial denaturation, 45 cycles 1 min at 94°C (denaturation), 1 min at 50°C (annealing) and 1 min at 72°C (extension). Reactions final extension step at 72°C for 6 min followed.

RAPD spectra were visualized on 1.5–2% agarose gels stained with ethidium bromide using standard methods. The size of specific RAPD fragments was estimated with DNA size standard (GeneRuler 1kb DNA Ladder, "Fermentas", Lithuania).

Data analysis. RAPD polymorphism data generated from 192 individual plants were scored into binary matrices indicating absence (0) or presence (1) scale of RAPD fragments. Analysis of molecular variance (AMOVA) was carried out on RAPD markers using using *GenAlEx v.6.3* software (Peakall, Smouse, 2006). This data were subjected to analysis TREECON; *PopGene 1.31* software (Van De Peer, De Wachter, 1994; Yeh, Boyle, 1997). Construction of a distance tree (dendrogram) using clustering with the unweighted pair group method with arithmetic mean (UPGMA) was carried out (Nei, 1978).

Results

Intrapopulational genetic diversity of Lupinus polyphyllus. Ten populations of *L. polyphyllus* were investigated. From each lupine population from 12 to 24 individuals of this species were collected. In total 192 plants were analyzed by the RAPD method. According to the type of habitat, the studied lupine populations were divided into forest and abandoned fields' populations (Table 1). Most samples from lupine populations were collected in eastern Lithuania (7), one – in western (Nemirseta), one – in southern (Druskininkai) and one in central part of Lithuania (Vaišvydava) (Table 1).

Table 1. Lupinus polyphyllus populations, their habitats and geographic coordinates

No.	Habitat	District	Geographic coordinates*	Altitude m	Habitat description
1.	Rykantai	Trakai	24°58.71, 54°42.82	161	abandoned field
2.	Pašiekštis	Molėtai	25°48.52, 55°14.65	142	Labanoras regional park, coniferous forest
3.	Antaviliai	Vilnius	25°22.30, 54°48.55	114	coniferous forest
4.	Rūdiškės	Trakai	24°46.38, 54°30.57	160	abandoned field
5.	Vaišniūnai	Ignalina	26°06.76, 55°23.01	149	roadside of forest road
6.	Gražutė	Zarasai	26°11.63, 55°41.08	170	forest, national park
7.	Varniškės	Vilnius	25°20.98, 54°57.73	192	abandoned field
8.	Nemirseta	Palanga	21°03.40, 55°37.45	174	coniferous forest
9.	Ratnyčia	Druskininkai	24°12.00 53°58.00	168	coniferous forest
10.	Vaišvydava	Kaunas	24°05.98, 54°48.47	73	roadside of forest road

* – geographic coordinates: lat N, long E

In a random primer selection by RAPD method 25 oligonucleotide primers were tested. RAPD spectra obtained with OPA 7, OPA 9, OPB 5, OPB 14, OPB 8-2 primers exhibited a large number of monomorphic loci (data not presented). Only 6 primers: OPB 6, OPB 8-3, OPB 17, OPB 18, OPA 13, OPA 18, were chosen for RAPD analysis; RAPD spectra with them were reiterating and informative; a large number of polymorphic

RADP loci were obtained (Table 2). In total 151 loci were scored, 135 of them being polymorphic; average number of loci per primer was 25.17 ± 2.11 , monomorphic loci comprised 3.98%. With these primers RAPD polymorphism was $96.02 \pm 0.31\%$ on average. Most abundant amplification products (30 bands) were obtained with the primer OPB 18. The size of analyzed bands was 180-2000 bp (Table 2).

Primer	Saguanaa	Analyzed bands	Polymorphism	Size of DNA bands	
	Sequence	Analyzeu banus	%	(bp)	
OPB 6	5'-TGC TCT GCC C-3'	25	96	200-2000	
OPB 8-3	5'-TCC GCT CTG G-3'	23	95.7	200-2000	
OPB 17	5'-AGG GAA CGA G-3'	26	96.2	180-1000	
OPB 18	5'-CCA CAG CAG T-3'	30	96.7	180-2000	
OPA 13	5'-CAG CAC CCA C-3'	23	95.7	180-1400	
OPA 18	5'-AGG TGA CCG T-3'	24	95.8	200-1600	
	Total	151			
	Average	25.17 ± 2.11	96.02 ± 0.31		

Table 2. Genomic DNA polymorphism of Lupinus polyphyllus populations following RAPD analysis

Following Nei's (1978), genetic distances between individuals in ten lupine populations were calculated. The average genetic distance (GDxy_{aver}) between the plants was 0.272 ± 0.025 . The minimum genetic distance between the plants was in Rūdiškės populations

(0.187 ± 0.016), the maximum genetic distance between the plants was registered in Nemirseta (GDxy_{aver} = 0.399 ± 0.042) and Vaišvydava (GDxy_{aver} = 0.328 ± 0.017) *L. polyphyllus* populations (Table 3).

Table 3. Genetic distances between individual plants in Lupinus polyphyllus populations

Population	Genetic distance (GDxy)					
	Average	Minimum	Maximum			
	Abandoned field p	opulations				
Rykantai	0.248 ± 0.020	0.100	0.439			
Rūdiškės	0.187 ± 0.016	0.080	0.339			
Varniškės	0.253 ± 0.043	0.081	0.689			
Average	0.229 ± 0.037					
	Forest popula	ations				
Pašiekštis	0.231 ± 0.029	0.097	0.485			
Antaviliai	0.219 ± 0.029	0.109	0.386			
Vaišniūnai	0.267 ± 0.016	0.122	0.494			
Gražutė	0.276 ± 0.014	0.106	0.488			
Vaišvydava	0.328 ± 0.017	0.140	0.493			
Ratnyčia	0.311 ± 0.026	0.176	0.477			
Nemirseta	0.399 ± 0.042	0.108	0.692			
Average	0.290 ± 0.062					
otal: 192 individuals	0.272 ± 0.025	0.112	0.498			

Using the UPGMA method, according to genetic distances between plants, the dendrogram of ten *L. polyphyllus* populations, comprising 192 plants, was drawn. It showed all plants to be genetically different (Fig. 1).

The dendrogram shows that in each population individuals form the groups. The populations also group accordingly: Vaišniūnai and Rūdiškės together with Gražutė form a larger cluster. A similar cluster is formed of Antaviliai and Pašiekštis together with Rykantai. These two clusters form one large group of populations, which is connected with another group that consists of four *L. polyphyllus* populations from geographically distant regions of Lithuania: Nemirseta, Ratnyčia, Vaišvydava and Varniškės.

Interpopulational genetic diversity of Lupinus polyphyllus. Using a computer program *PopGene v.1.32* the data characterizing the genetic diversity of ten surveyed *L. polyphyllus* populations were obtained (Table 4). An average DNA polymorphism of ten *L. polyphyllus* populations was $52.58 \pm 1.48\%$, the lowest being in Rūdiškės (45.68%) and Rykantai (46.36%) populations, the largest – in Gražutė, Pašiekštis (56.95% each) and Ratnyčia (58.94%) populations. The highest Nei's genetic diversity was obtained in Varniškės and Gražutė populations (0.1781 ± 0.2021 and 0.1760 ± 0.1925, respectively), the lowest – in Rūdiškės population (0.1196 ± 0.1672). The average Nei's genetic diversity in all *L. polyphyllus* populations was 0.1552 ± 0.1860. The average value of Shannon's information index in the studied populations was 0.2384 ± 0.265 (Table 4).

AMOVA showed that the genetic diversity among populations was 44%, and among individuals within populations it was higher and amounted to 56%. So, AMOVA revealed significant genetic differentiation of the investigated *L. polyphyllus* populations ($\Phi_{PT} =$ 0.444, *p* < 0.001).

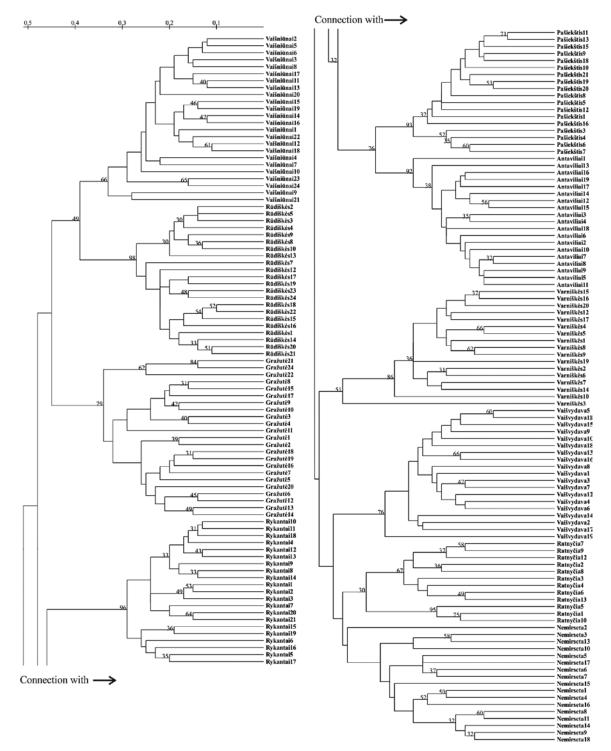


Figure 1. UPGMA dendrogram of the genetic relationships of ten *Lupinus polyphyllus* populations according to Nei's (1978) genetic distances

All genetic distances of the studied *L. polyphyllus* populations were calculated employing 151 polymorphic loci and *PopGene* program; genetic similarity tree of the populations was drawn employing the UPGMA method (Fig. 2).

The average genetic distance between populations was 0.142 ± 0.010 , the largest genetic distance was between Rūdiškės and Rykantai populations (amounting to 0.218), while the smallest genetic distance (0.065) was recorded between Nemirseta and Ratnyčia populations, which are geographically very remote (Table 5). The genetic similarity tree (Fig. 2) shows no clear correlation between geographic and genetic distances of the studied populations. Some geographically close populations group in the same cluster. For example, Pašiekštis (Molėtai distr.) and Antaviliai (Vilnius distr.) as well as Gražutė (Zarasai distr.) and Vaišniūnai (Ignalina distr.) populations, but most geographically remote Nemirseta and Ratnyčia populations also group close.

Population	Р	Ν	n _a	n _e	h	Ι			
Abandoned field populations									
Rykantai	46.36	70	1.464 ± 0.500	1.260 ± 0.361	0.151 ± 0.195	0.227 ± 0.279			
Rūdiškės	45.68	68	1.450 ± 0.499	1.190 ± 0.293	0.120 ± 0.167	0.188 ± 0.246			
Varniškės	51.78	78	1.517 ± 0.501	1.308 ± 0.379	0.178 ± 0.202	0.266 ± 0.288			
Average	47.94 ± 3.34	72 ± 5.29	1.477 ± 0.035	1.253 ± 0.059	0.150 ± 0.030	0.227 ± 0.040			
Forest populations									
Pašiekštis	56.95	86	1.570 ± 0.497	1.266 ± 0.345	0.160 ± 0.187	0.247 ± 0.267			
Antaviliai	49.67	75	1.497 ± 0.502	1.241 ± 0.323	0.148 ± 0.181	0.228 ± 0.264			
Vaišniūnai	52.32	79	1.523 ± 0.501	1.251 ± 0.338	0.152 ± 0.184	0.234 ± 0.265			
Gražutė	45.03	86	1.570 ± 0.497	1.296 ± 0.358	0.176 ± 0.193	0.268 ± 0.275			
Ratnyčia	58.94	89	1.589 ± 0.494	1.273 ± 0.352	0.164 ± 0.187	0.253 ± 0.266			
Nemirseta	54.30	82	1.543 ± 0.500	1.254 ± 0.324	0.157 ± 0.179	0.244 ± 0.260			
Vaišvydava	54.97	83	1.550 ± 0.499	1.246 ± 0.342	0.148 ± 0.184	0.229 ± 0.263			
Average	53.17 ± 4.68	82.857 ± 4.741	1.549 ± 0.031	1.261 ± 0.019	0.158 ± 0.010	0.243 ± 0.01			
Total average	52.58 ± 1.48	79 ± 4.33	1.527 ± 0.500	1.258 ± 0.342	0.155 ± 0.186	0.238 ± 0.26			

Table 4. Genetic variation of Lupinus polyphyllus population based on RAPD data

Note. P – polymorphism (%), N – number of polymorphic loci, n_a – number of polymorphic alleles, n_e – number of effective alleles, h – Nei's genetic diversity, *I* – Shannon's information index.

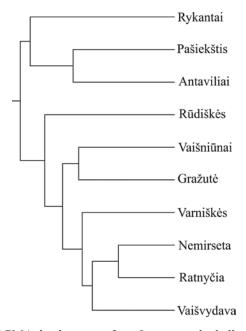


Figure 2. Genetic similarity UPGMA dendrogram of ten Lupinus polyphyllus populations

Table 5. Nei's genetic distance between Lupinus polyphyllus populations based on RAPD data

Population	Rykantai	Pašiekštis	Antaviliai	Rūdiškės	Vaišniūnai	Gražutė	Varniškės	Nemirseta	Ratnyčia
Pašiekštis	0.137								
Antaviliai	0.173	0.110							
Rūdiškės	0.218	0.184	0.163						
Vaišniūnai	0.176	0.131	0.123	0.105					
Gražutė	0.182	0.180	0.158	0.137	0.104				
Varniškės	0.171	0.164	0.189	0.161	0.135	0.117			
Nemirseta	0.159	0.146	0.181	0.133	0.121	0.110	0.095		
Ratnyčia	0.156	0.139	0.191	0.172	0.127	0.108	0.120	0.065	
Vaišvydava	0.174	0.134	0.174	0.133	0.120	0.141	0.109	0.083	0.100

Similar results were obtained after principal coordinate analysis of the studied populations, which shows the location of all studied populations in a coordinate system (Fig. 3).

Three coordinate axes described 63.58% of the total genetic diversity; the first axis described 27.55%, the second -20.41% and the third -15.62% of genetic diversity.

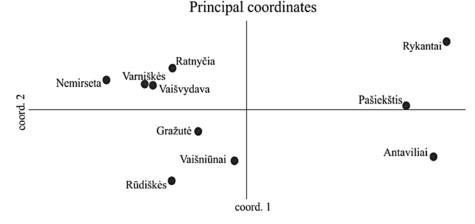


Figure 3. Principal coordinate analysis of genetic similarity of 10 Lupinus polyphyllus populations

Discussion

Although L. polyphyllus is included in the list of 150 most widespread alien plants in Europe (Lambdon et al., 2008), research on genetic diversity of this species populations is just starting. As an invasive species, L. polyphyllus has not been studied at molecular level. This species is far more studied phylogenetically and as a feed crop (Ainouche, Bayer, 1999; Talhinhas et al., 2003; Kurlowitch et al., 2008). In Russia, Poland and Finland, this species is used for selection purposes, in creation of interspecific hybrids with a lower amount of alkaloids for animal feed, which are also characterized by abundant biomass and winter hardiness. Due to their ability to form a symbiosis with nitrogen-fixating bacteria, plants of the Lupinus genus are successfully used to enrich and restore fire-exhausted soils (Lara-Cabrera et al., 2009; Miller et al., 2011). However, the use of lupine for afforestation of fire sites disagrees with a threat to native ecosystems caused by it as an invasive species. To our knowledge, natural settlement of this species in forest fire sites has not been tested. Investigations carried out in pine stands after thinning indicate that the settlement in this niche, at least at the beginning, is not strongly expressed regarding other herbaceous plant species.

This study is the first attempt to investigate the genetic diversity of *L. polyphyllus* in Lithuania. Using 6 oligonucleotide primers 192 plants were tested. Each primer accounted for an average of 24.17 ± 2.11 RAPD bands. The chosen primers were very informative; 151 reliable polymorphic bands were produced with them. This set of primers could be used in further studies on genetic diversity of lupine populations.

The average DNA polymorphism in the studied populations was 52.6%. Nei's genetic diversity in the studied *L. polyphyllus* populations in Lithuania was 0.1552 ± 0.1860 . Since *L. polyphyllus* is a sexually reproducing cross-pollinating species, it is characterized by higher levels of DNA polymorphism in comparison with the self-pollinating and apomictic plants (Nybom, Bartish, 2000); therefore the absence of studies in natural habitats of this species makes it difficult to decide whether the recorded DNA polymorphism level is changed. Similar polymorphism (51.8%) has been determined for *L. elegans* in populations of natural habitats in Mexico (Lara-Cabrera et al., 2009) after testing five populations with 10 primers.

When analyzing the distribution of separate individuals in a dendrogram (Fig. 1), genetic similarity of individuals forming the populations is observed and, therefore, there is almost no intermixing of separate populations. This suggests that lupine populations are perhaps characterized by adaptation to local conditions. Local adaptation and phenotypic plasticity are considered to be the two main ways for alien plants to adapt to new conditions (Sullivan et al., 2009; Riis et al., 2010). Local adaptation leads to survival of the individuals with certain genetic characteristics that ensure the best adaptation to current conditions. Such evolutionary changes may occur over a relatively short period of time. They may depend on neutral or even slightly harmful alleles present in the genome of an invasive species, which under new conditions and the influence of natural selection may have adaptive value (Prentis et al., 2008).

According to AMOVA results, the highest genetic diversity (56%) was observed between individuals in *L. polyphyllus* populations, interpopulational diversity accounted for 44%, while no genetic differentiation between populations from different habitat types was revealed (Table 4). It is noteworthy that the level of DNA polymorphism in populations of both types somewhat differed: in forest populations – 53.17 ± 4.679, in field populations – 47.94 ± 3.343. The average genetic distance between individuals in forest populations was also higher (0.290 ± 0.062) than in field (0.229 ± 0.037) populations. The presented parameters suggest a supposition

that there are no larger genetic differences between forest and field populations of *L. polyphyllus*, or those changes are associated with adaptive loci, which are not always successfully determined using molecular markers (Volis et al., 2001; McRay, Latta, 2002). However, significant genetic differentiation among populations may be caused by genetically heterogeneous seed stock, low gene flow between populations and, possibly, local adaptation. High levels of population genetic differentiation for invasive plant species has been also determined by other authors (Bonnin et al., 2001; Chapman et al., 2004; Ye et al., 2004; Song et al., 2006).

Principal coordinates analysis and UPGMA cluster analysis (Figs 1 and 3) demonstrated that the majority of the studied populations group regardless of the geographical distances between them. Average genetic distance between populations was 0.148 ± 0.021 . The smallest genetic distances were determined between Nemirseta and Ratnyčia (0.065) as well as between Nemirseta and Vaišvydava (0.083) L. polyphyllus populations that are separated by several hundred kilometers. Absence of correlation between genetic and geographic distances of populations has been also noted by other authors (Fahima et al., 1999; Abeysinghe et al., 2000). Since L. polyphyllus was intentionally distributed on the forest edges, it is hardly possible that genetic diversity of populations of such various origins could be influenced by gene flow between them. Apparently the greatest impact on genetic diversity was produced by random processes in the populations and, perhaps, the ensuing local adaptation. Absence of more distinct genetic differences between forest and abandoned field populations suggests that the spread of this species to new habitats may not be associated with pronounced changes in genetic diversity. High DNA polymorphism and population differentiation will require a wider range of possible measures to stop the spread of this invasive species.

Conclusion

Genetic diversity of ten *Lupinus polyphyllus* populations of forests and abandoned fields was assessed using the RAPD method. Analysis of molecular variance AMOVA showed significant genetic differentiation of the investigated *L. polyphyllus* populations ($\Phi_{PT} = 0,444$, p < 0,001). Neither UPGMA cluster analysis, nor principal coordinate analysis revealed population grouping regarding the geographic distance between them. On the other hand, UPGMA cluster analysis revealed genetic peculiarities of *L. polyphyllus* populations that probably are associated with adaptation of invasive populations to local conditions.

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Gausialapio lubino (*Lupinus polyphyllus* Lindl.) invazinės rūšies populiacijų genetinė įvairovė Lietuvoje

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Santrauka

Patekęs į Lietuvą XX a. pradžioje, gausialapis lubinas (*Lupinus polyphyllus* Lindl.) gausiai išplito visoje šalies teritorijoje, apimdamas ne tik miškus, bet ir pamiškes, pakeles, apleistus nedirbamų laukų plotus, ir toliau skverbiasi į natūralias augalų augavietes. Tyrimų tikslas – ištirti miškų ir apleistų laukų lubino populiacijų įvairovę. Lubino populiacijų genetinė įvairovė tirta taikant RAPD metodą. Kiekvienos populiacijos genotipai tirti naudojant 6 pradmenis. UPGMA dendrograma parodė, kad visi tirti augalai yra genetiškai skirtingi. AMOVA parodė didelę *L. polyphyllus* populiacijų genetinę diferenciaciją ($\Phi_{PT} = 0,444, p < 0,001$). Nei UPGMA klasterių, nei principinių koordinačių analizės neatskleidė populiacijų grupavimosi dėsningumų, priklausomai nuo geografinio atstumo tarp jų. Tačiau UPGMA klasterinė analizė parodė *Lupinus polyphyllus* populiacijų ypatumus, galimai susijusius su invazinių populiacijų adaptacija vietos sąlygoms. Nors gausialapis lubinas tampa vienu agresyviausių invazinių rūšių augalų, tačiau tai tik pirmasis šios rūšies populiacijų genetinės įvairovės tyrimas Lietuvoje.

Reikšminiai žodžiai: Lupinus polyphyllus, augalų invazinė rūšis, RAPD, genetinė įvairovė.