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RESEARCH ARTICLE

AFLP-based genetic diversity and population structure of arctic-alpine relict species *Dryas octopetala* (*Rosaceae*) in Ukraine

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Abstract. Arctic-alpine plant communities host many endemic and relict species. Many such species are sensitive to habitat changes and have been already affected by climate change, which makes their study especially relevant. The current study focuses on the circumpolar arctic-alpine relict diploid subshrub / dwarf shrub *Dryas octopetala* (*Rosaceae*) in Ukraine. Four known and currently available populations were assessed and sampled. Three sets of 50 different AFLP markers each were used to investigate genetic diversity, population structure, and other parameters. STRUCTURE analyses, in conjunction with the phylogenetic network, indicate no significant differences in genetic structure among populations. However, the population on Mt. Brebeneskul shows a very marginal difference in comparison to three other dryad populations in Ukraine. Geographic isolation, differing migration paths, and the potential for interbreeding could explain this outcome. Additional studies using various methods (e.g., SSR, genome-wide SNP analysis, GWAS, WGS) are needed to obtain a clearer picture.

Keywords: AFLP, Carpathians, *Dryas octopetala*, STRUCTURE, PCoA, populations, Ukraine

Introduction

Arctic-alpine plants play a crucial role in the ecosystems of the Arctic and subarctic regions, as well as the mountains of the temperate zone of the Northern Hemisphere. The term "arctic-alpine species" reflects a geographic distribution and encompasses a range of species, from widespread, community-forming species to rare, endemic, and relict ones. Some could be used as model organisms in

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studies on ecosystem responses to climate change, which is especially relevant today. Climate change and high anthropogenic pressure often reduce the distribution areas and alter the population structures of rare arctic-alpine species (Cherepanyn, 2017; Kozlowski, 2024).

Dryas octopetala L. (*Rosaceae*) is a circumpolar (or mainly Eurasian, in the strict sense) arctic-alpine relict diploid dwarf shrub that occurs in the Arctic and Subarctic zones and the mountains of the Northern Hemisphere in the alpine and subalpine zones of Eurasia (replaced by related species in continental North America: see Springer, Parfitt, 2014), mainly on limestone and sandstone rocks with carbonate content, stony slopes with weak soil, and a microphytoclimate present only in the surface horizon (McGraw, Antonovics, 1983; McGraw, 1987). It is an insect-pollinated mesoxerophyte and hemiphanerophyte with seed dispersal by wind (anemochory). In Ukraine, the mountain avens (*Dryas*) are considered rare and are protected at the national level. The species is listed in the *Red Data Book of Ukraine* (Andrienko, Mosyakin, 2009). The *Dryadeta octopetalae* plant community is also protected at the national level and listed in the *Green Data Book of Ukraine* (2009).

Populations of *Dryas octopetala* occur on high mountain meadows and often are dominant in *Achilleo Schurii-Dryadetum* plant communities (*Carici rupestris-Kobresietea ballardii* class) and *Loiseleurio-Vaccinietea* class communities. The species usually occurs together with *Carex sempervirens* Vill., *Campanula alpina* Jacq., *Vaccinium myrtillus* L., *V. vitis-idea* L., *Anemonastrum narcissiflorum* (L.) Holub (= *Anemone narcissiflora* L.), *Bartsia alpina* L., *Homogyne alpina* (L.) Cass., *Sesleria coerulans* Friv., *Salix herbacea* L., etc. It often forms cushion turfs, and the spatial distribution of individuals in populations is uneven (Chopyk, 1976).

Populations of *D. octopetala* have two strategies of propagation, vegetative and generative ones. The first one is crucial for the self-maintenance of populations and leads to the formation of dense clones, genetically identical plants that could even be considered a single individual or super-individual. Genets (vegetative clones) can remain stable and alive for a long time, with some estimates suggesting a lifespan of over 500 years (de Witte et al., 2012). This propagation is typical for many highland and montane species (Tsaryk et al., 2004). Generative propagation is less common, but it is crucial for maintaining genetic diversity and dispersal. It is also reported that *D. octopetala* has high clonal diversity (de Witte et al., 2021)

Historic occurrence of *D. octopetala* in Ukraine, even during the Allerød–Holocene, was much wider than its current distribution, as demonstrated by generalized data of paleopalynofloristic studies (Bezusko et al., 2011, 2025). At present, there are four known localities of *D. octopetala* in the Ukrainian Carpathians, which are located within two mountain ranges: the Svydovets (Blyznytsia and Zhandarmy mountains) and Chornohora (Brebeneskul [Brebenescul in Romanian] and Pip Ivan mountains). These populations occur at high elevations (1645–1988 m a.s.l.) and are associated with alpine and subalpine habitats characterized by rocky substrates and open vegetation.

Previous studies have shown that the population structure and regeneration of *D. octopetala* are influenced by habitat conditions, particularly the availability of open microsites and the degree of competition with the dense grass cover (Cherepanyn, 2018, 2019). In general, exposed and sparsely vegetated areas promote both vegetative and generative reproduction, whereas dense turf-forming species may limit seedling establishment.

In a significant portion of the arctic-alpine and relict species at the southern limit of their distribution ranges in the mountains of temperate latitudes, there is a narrowing or shrinking of the population ranges, changes in the population structure and dynamics due to global warming (Pauli et al., 2007; Erschbamer et al., 2009). The ability to disperse over long distances and to occupy certain ecological niches in mainly unsuitable habitats is crucial for arctic-alpine species for their survival under climate change (Marcysiak, 2010). Due to climate change, species' population structures and vegetation cover change with increasing the elevation above sea level. There is an increase in the occurrence of the shrubs *Pinus mugo* Turra, *Alnus alnobetula* (Ehrh.) K. Koch (= *Alnus viridis* (Chaix.) DC.), and *Juniperus communis* L. var. *saxatilis* Pall. at the border of the subalpine and alpine zones. Additionally, declines in population vitality and shifts in the population structure of some high-altitude species in high mountain meadows have been observed (Kobiv, 2017, 2018; Cherepanyn, 2018, 2019; Kyyak, Shtupun, 2021). Monitoring data within the framework of the GLORIA project (GLobal Observation Research Initiative in Alpine Environments) indicate that the habitat areas of populations of alpine, nival, and subnival species are decreasing (Harald et al., 2007).

It is essential to understand the genetic structure of these species for developing efficient measures for protecting their populations. Such information is crucial when analyzing small populations, where gene drift often occurs, leading to a significant decrease in genetic diversity (Avise, 2008). Additionally, genetic research can provide insights into the mechanisms of gene information exchange, evolutionary and geographical processes within a species, and prospects for the survival of populations (Kreuzer, 2014). Therefore, further molecular genetic research is needed to analyze such issues.

Today, molecular ecological research is particularly popular in Europe in the context of studying rare, endemic, relict, and peripheral-range (marginal) plant species, including *D. octopetala* (De Witte et al., 2012; Varsamis et al., 2021). AFLP data consist of anonymous multilocus dominant marker sets, scored as presence-absence (Vos et al., 1995; Kück et al., 2012). They are commonly used in evolutionary, ecological, and population genetic studies (Mueller, Wolfenbarger, 1999; Meudt, Clarke, 2007). Unfortunately, the studies of the genetic structure of populations in high-altitude species still remain insufficiently represented in Ukraine. This work aims to address the issue of the molecular genetic diversity of small populations of rare plant species in the Ukrainian Carpathians, particularly the high-altitude dwarf shrub *D. octopetala*.

Materials and Methods

Collection of samples. Sampling in *Dryas octopetala* habitats was conducted in 2018 during the growing season, mainly in July and August, across the whole distribution area of *D. octopetala* in Ukraine, namely from 4 populations of the species in the Ukrainian Carpathians (Table 1, Fig. 1). Populations were defined as groups of plants separated within one or different mountain massifs. Populations were sampled evenly along the transects to cover the entire habitat area of the species. To achieve statistically representative sampling, 30 samples were collected per population within one growing season (120 samples from 4 populations). One or two well-developed leaf blades without any visual signs of damage, fungal infestation, or necroses were carefully collected from plants.

Then, the material from each individual was immediately placed in separate bags with silica gel for rapid drying. At the next step, bags with collected samples from each population were grouped and stored in sealed plastic bags with silica gel (Chase, Hills, 1991). The packed material was stored at room temperature (with periodic replacement of the silica gel if necessary).

AFLP-analysis. In 2019, total genomic DNA was extracted from tissue powder using the Qiagen DNeasy Plant Mini Kit (Qiagen, Germany http://www.qiagen.com/) according to the manufacturer's protocol.

For the subsequent molecular genetic analysis of the populations, the analysis based on amplified fragment length polymorphism (AFLP) was performed according to the protocol/procedure developed by Vos et al. (1995) and described in detail in Cieślak et al. (2007, 2015), Meudt and Clarke (2007), Sucher et al. (2012), Paun and Schönswetter (2012). The following markers were selected for AFLP analysis of *D. octopetala*: ATG_CTG_K1, ATC_CAA_K2, ATC_CTG_K3. Fragment analysis was performed with capillary electrophoresis on ABI XL3500 (Applied Biosystems, USA).

Data analysis. AFLP profiles were analyzed using Genographer 2.1 software (Benham, 2001), which read DNA profiles in the 50–500 bp range and coded the presence/absence of profile peaks into a binary matrix of feature absence/presence (0/1).

The obtained binary matrices (Supplementary Material, Matrices S1-S4) were analyzed separately and then combined. Clustering analysis (Neighbour-Joining, with 1000 bootstrap iterations) was performed in PAST 4.16 (Hammer et al., 2001; Hammer, Harper, 2024). Principal coordinate analysis (PCoA) — in GenAlEx 6.51b2 (Peakall, Smouse 2006, 2012). Estimation of genetic structure and inference of basic statistics were performed using AFLP-SURV 1.0. (Vekemans, 2002; Vekemans et al., 2002; https://ebe.ulb.ac.be/ebe/AFLP-SURV.html). Population analysis was performed in STRUCTURE 2.3.4. (Porras-Hurtado et al., 2013; Novembre, 2016; https://web.stanford.edu/group/pritchardlab/structure.html) on the GWGD HPC cluster using the StrAuto 1.0 python utility to automate and parallelize the STRUCTURE analysis (Chhatre, Emerson, 2017; https://vc.popgen.org/software/strauto/) with the following parameters: maxpops = 5, mcmc = 500000, burnin = 100000,

Table 1. **Physical and geographical characteristics of *Dryas octopetala* locations**
(*determined using a GPS navigator "Garmin eTrex 30x")

Population locality	Height above sea level, m	Exposure of the slope	Area of the habitats, m²	Latitude*	Longitude*
Brebeneskul (Chornohora mountain range)	1941	north-west	250	N48°06′17.1″	E024°34′01.7″
Pip Ivan (Chornohora mountain range)	1988	south-west	150	N48°02′54.6″	E024°37′36.6″
Blyznytsia (Svydovets mountain range)	1803	north-east	350	N48°13′09.7″	E024°13′53.3″
Zhandarmy rocks (Svydovets mountain range)	1645	south-east	1250	N48°13′44.0″	E024°13′53.3″

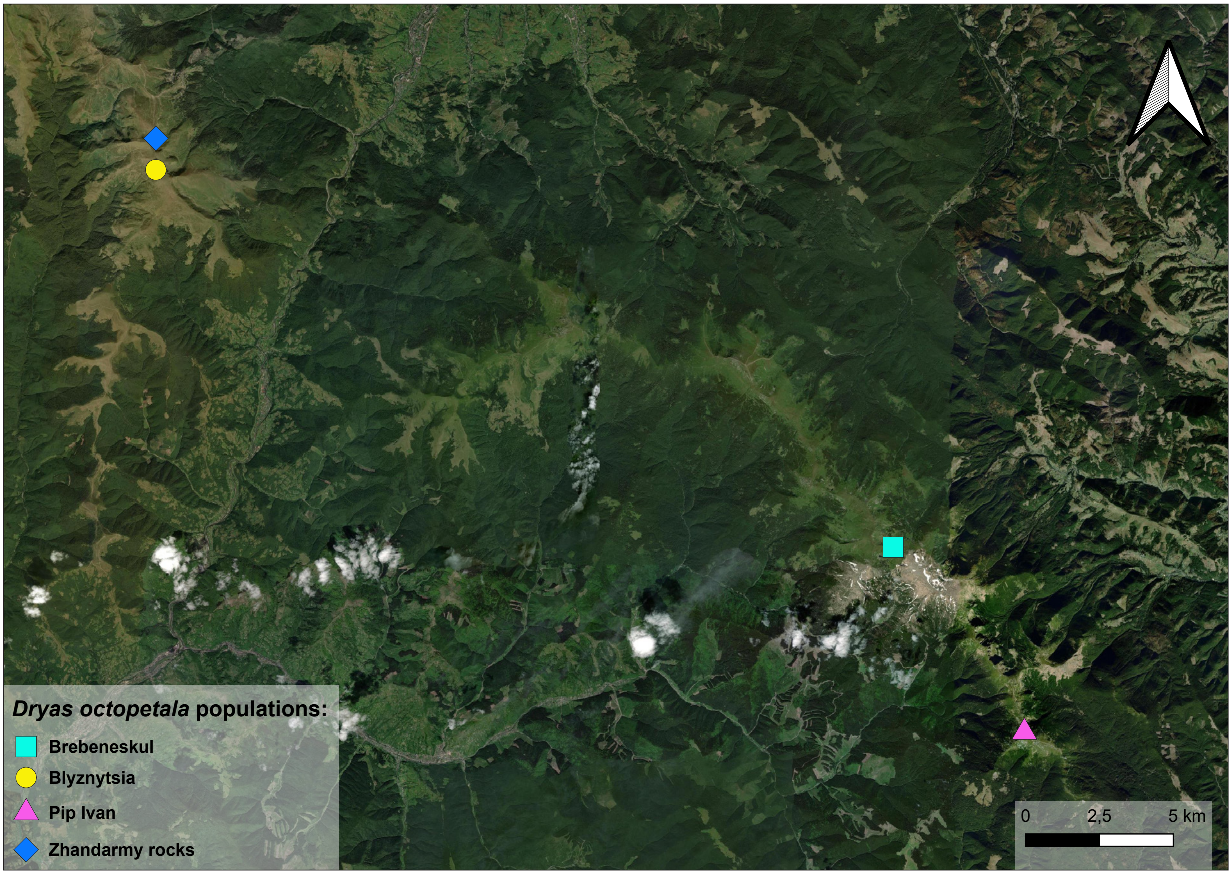

Fig. 1. Locations of the populations of *Dryas octopetala* (created in QGIS 3.44, "Solothurn" based on ESRI Satellite map)

K-runs = 10. STRUCTURE output was analyzed and visualised using the Clustering Markov Packager Across K (CLUMPAK, Kopelman et al., 2015) server (https://tau.evolseq.net/clumpak/). Identification of prospective best K values was performed in StructureSelector (Li, Liu, 2018; https://lmme.ac.cn/StructureSelector/) based on several different approaches: Evanno ΔK method (Evanno et al., 2005), Choose K method (Raj et al., 2014), and Puechmaille method with estimation of four different parameters — medMedK, maxMedK, medMeanK, and maxMeanK (Puechmaille, 2016).

In addition, we converted binary matrices to nexus format and reconstructed the following types of haplotype networks using PopART 1.7 (https://popart.maths.otago.ac.nz/, Leigh, Bryant, 2015): Minimum Spanning Network, Median Joining Network (Bandelt et al., 1999), Integer NJ Net (French et al., 2014; Leigh, Bryant, 2015), and TCS (Clement et al., 2000, 2002). Network types were inferred for each marker set separately and for the combined set.

Results

Cluster analysis. Pairwise genetic distances (Nei's genetic distance after Lynch and Milligan (1994); and Reynolds, Weir, and Cockerham's (1983) genetic distance, respectively, Table 2) were the smallest between *Dryas octopetala* populations on Blyznytsia and Pip Ivan mountains (0.0081 and 0.0326), while the largest were between populations on Pip Ivan

Table 2. **Genetic distances between populations of *Dryas octopetala***
(bold — Nei's genetic distance after Lynch and Milligan (1994); italics — Reynolds, Weir, and Cockerham's genetic distance)

Dryas octopetala populations	Brebeneskul (Chornohora mountain range)	Pip Ivan (Chornohora mountain range)	Blyznytsia (Svydovets mountain range)	Zhandarmy rocks (Svydovets mountain range)
Brebeneskul (Chornohora mountain range)		*0.1077*	*0.0717*	*0.1144*
Pip Ivan (Chornohora mountain range)	**0.0268**		*0.0326*	*0.1352*
Blyznytsia (Svydovets mountain range)	**0.0182**	**0.0081**		*0.1200*
Zhandarmy rocks (Svydovets mountain range)	**0.0259**	**0.0313**	**0.0286**	

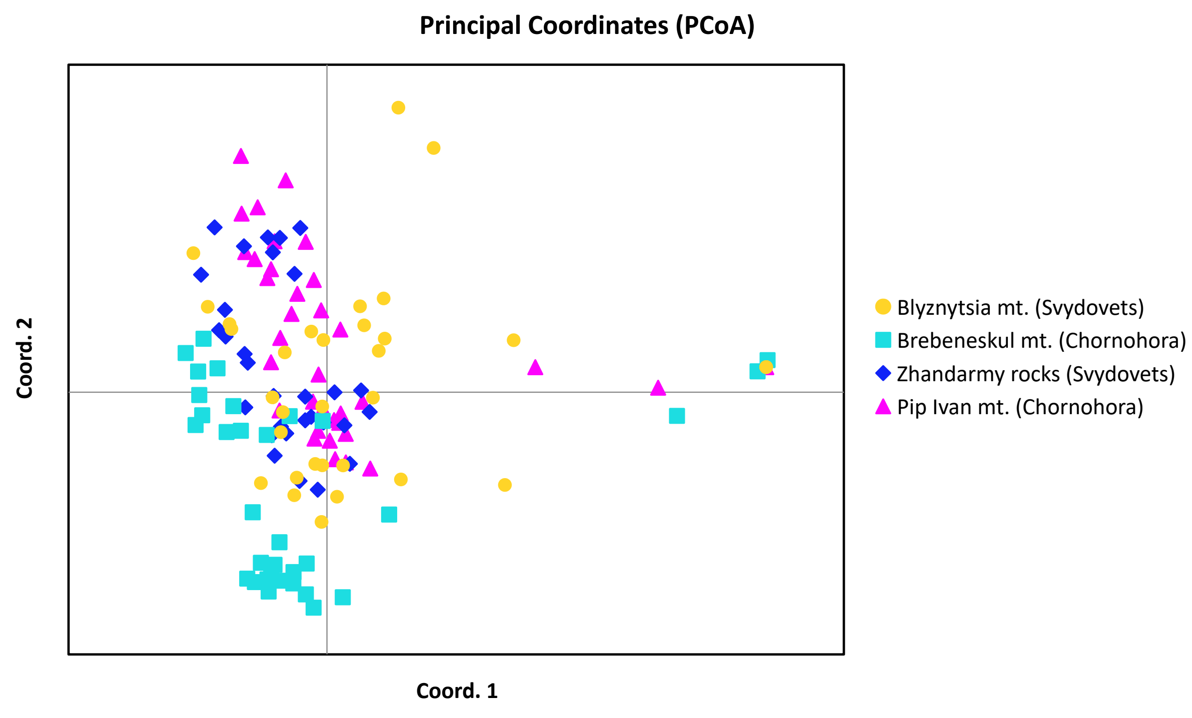

Fig. 2. Principal Coordinate Analysis (PCoA) based on a combined set of markers for all populations of *Dryas octopetala*

and Zhandarmy rocks (0.0313 and 0.1352, respectively).

Pairwise F_{ST} values for all markers show little to moderate differentiation between populations and follow the same pattern as genetic distances, with the lowest differentiation between *D. octopetala* populations on Blyznytsia and Pip Ivan mountains (0.0321), and the highest between populations on Pip Ivan and Zhandarmy rocks (0.1264). F_{ST} values for the rest of the cases in ascending order: between populations on Blyznytsia and Brebeneskul — 0.0692; Pip Ivan and Brebeneskul — 0.1021; Brebeneskul and Zhandarmy rocks — 0.1081; Blyznytsia and Zhandarmy rocks — 0.1131.

Principal Coordinate Analysis (PCoA). PCoA based on a combined set of markers (Fig. 2) shows a distinct grouping of samples by population assignments. However, these clusters are not separated, and there is no geographic pattern (by mountain range) either.

STRUCTURE analysis. Different approaches to optimal K estimation produced different results (Table 3).

STRUCTURE analysis reveals differences between the analyzed populations (Fig. 3). For the best K = 2, the population on the Zhandarmy rocks (3) is entirely monomorphic. At the same time, the other three demonstrate some degree of heterogeneity. We were unable to identify any specific geographic pattern among the individuals assigned to the orange cluster.

In the case of K = 3 (optimal for Puchmaille's medMedK and medMeanK), the population on Zhandarmy rocks revealed two clusters, while the rest revealed three ones. As in the previous case, no specific geographic pattern was identified.

We did not identify any specific structure for K = 4 (optimal for Puchmaille's maxMedK and maxMeanK), which also corresponds to the number of actual populations.

In contrast, in the case of K = 5 (optimal for the Choose K method and optimal for Puchmaille's medMedK and medMeanK), the population on Mt. Brebeneskul (Chornohora mountain range) differs from all others: the majority of samples within it formed a separate cluster, which was almost absent in other populations. The remaining populations were similar, with only minor differences.

STRUCTURE analysis performed for separate populations and three separate sets of markers (50 loci each) presented in Supplementary Material (Figs. S1–S4), and generally agrees with the combined one.

In general, STRUCTURE analysis shows specific patterns of admixture and likely higher admixture rates within populations than between them (which is expected due to geographical isolation).

Haplotype networks. There is no apparent clustering in all the types of haplotype networks (TCS, NJ-Net, Minimum Spanning Network, Median Joining Network). Nevertheless, a specific population grouping pattern exists (Suppl. files S5–S8). At the same time, networks reveal significant differences in the number of reticulations across methods. In particular, NJ-Net (Suppl. file S6) is significantly more reticulated than the other types.

Discussion

The AFLP analysis of four different populations of *Dryas octopetala* in Ukraine revealed genetic differences within and among populations. However, neither a clear genetic structure nor significant genetic differences were detected. The results of PCoA, STRUCTURE analysis and different types of haplotype networks are generally in agreement and demonstrate similar patterns. There were minor differences in the STRUCTURE analysis outcomes depending on the optimal K. At K = 2, the population on the Zhandarmy rocks was monomorphic, whereas the rest were not. We assume the variation is random, as we could not identify any specific geographic pattern in the three populations (Blyznytsia, Pip Ivan, and Brebeneskul). At K = 5, the population on Brebeneskul Mt was distinct from the rest. Besides potential computational issues, such an outcome could be caused by geographic isolation, different migration paths, interbreeding, and/or other factors. To investigate further the possible admixture and other aspects, different markers and approaches are needed (in particular, genomic data could be helpful).

Since *Dryas octopetala* is protected and has a scattered distribution in Ukraine, genetic and genomic data could be useful for organizing specific protection/conservation measures. One key element for the long-term conservation of the species is to save and preserve as much genetic diversity as possible (Centre for Plant Conservation, 2019).

Additional studies, employing more powerful modern methods, such as high throughput whole-genome sequencing followed by different analyses (e.g., genome-wide SNP analyses, plastome & mitochondriome data, designing SSR panels, etc.)

Table 3. **Optimal K estimation uses different methods for each population of *Dryas octopetala*, combining a set of markers**

Dryas octopetala population marker sets	Evanno ΔK method	Choose the K method	Puchmaille method			
			medMedK	maxMedK	medMeanK	maxMeanK
Marker set 1, all populations	2	5	3–5	3–5	3–5	3–5
Marker set 2, all populations	2	4	1–3; 5	1–3; 5	1–3; 5	1–3; 5
Marker set 3, all populations	2	2	1–5	1–5	1–4	1–5
Population 1 (Blyznytsia), all markers	5	5	1–4	1–4	1–3	1–3
Population 2 (Brebeneskul), all markers	2	3	1–4	1–4	1–3	1–3
Population 3 (Zhandarmy rocks), all markers	2	2	1–2	1–2	1–2	1–2
Population 4 (Pip Ivan), all markers	2	4	1–4	1–5	1–4	1–5
Combined, all populations and all markers	2	5	3; 5	4	3; 5	4

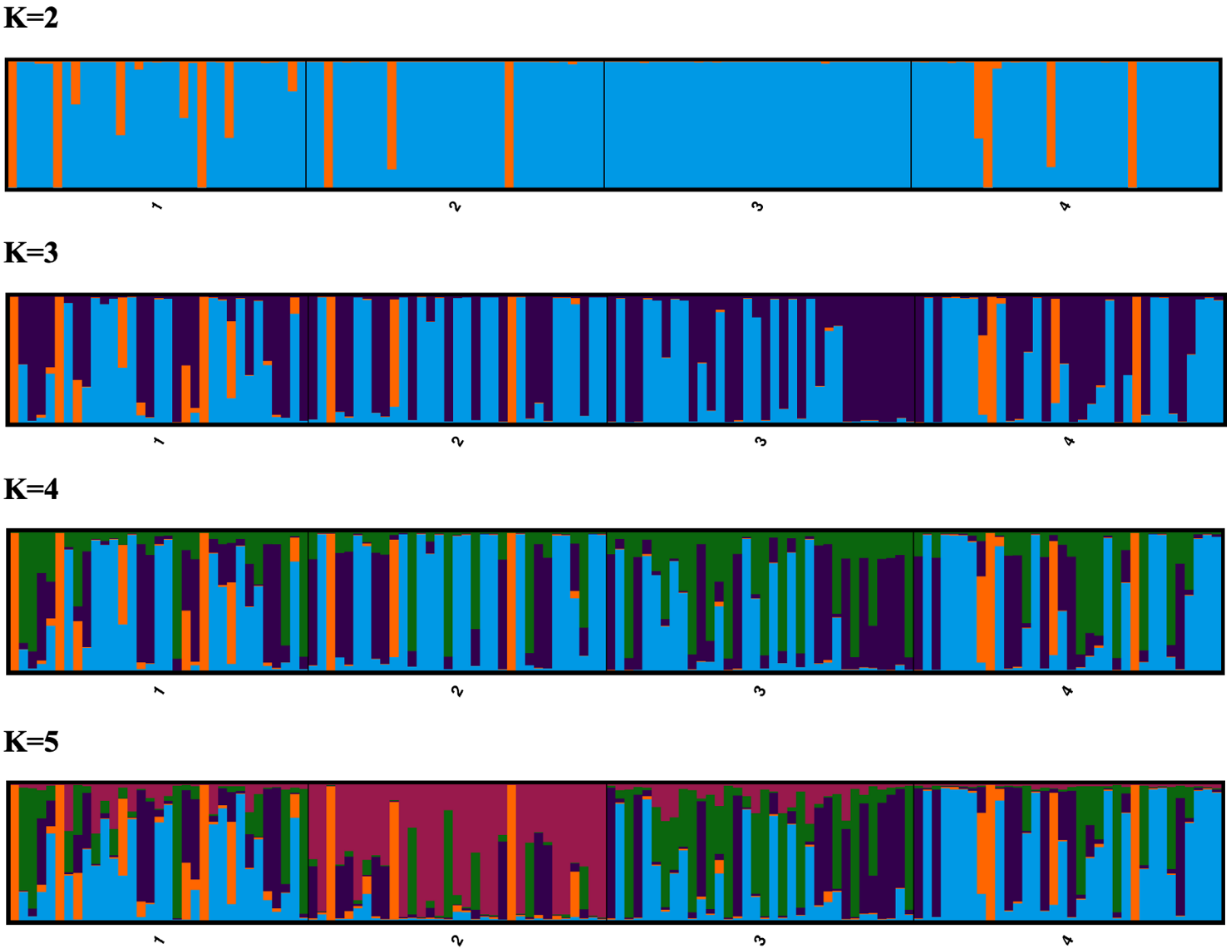

Fig. 3. Genetic structure of populations of *Dryas octopetala* based on STRUCTURE analysis of combined data (150 loci, 4 populations). 1 — Blyznytsia Mt. (Svydovets mountain range); 2 — Brebeneskul Mt. (Chornohora mountain range); 3 — Zhandarmy rocks (Svydovets mountain range); 4 — Pip Ivan Mt. (Chornohora mountain range)

and genome wide association studies (GWAS), are needed to obtain a clearer and more detailed picture. Currently, several genome assemblies are available for *Dryas*, including two for *D. octopetala* (White, Pirro, 2022; DToL), which are based on reference-grade whole-genome sequencing using PacBio long-read sequencing with 83x coverage (DToL; assemblies GCA_963921425.1 and GCA_963921435.1 in the European Nucleotide Archive, ENA). Modern long-read sequencing techniques not only make plant genome assemblies easier (Pucker et al., 2022), but they provide also epigenetic information as a byproduct which could be also useful for population studies (Liu, Zhong, 2024; Liu, Conesa, 2025). The availability of good reference genome assemblies makes it easier and cheaper to organize a separate study on the population genomics of mountain avens from Ukraine. In addition, such a project would be very relevant for several reasons: (1) there are no genomic studies of mountain avens in Ukraine and (2) the populations are relatively small, which makes them especially vulnerable. Although they are located in the Carpathians, there is a constant danger of destruction posed by the ruscist war of aggression against Ukraine.

Conclusions

AFLP analysis of four populations of *Dryas octopetala* in Ukraine reveals significant genetic similarity among them. No clear patterns were revealed within the populations. STRUCTURE analysis reveals specific differences depending on the optimal K value: with K = 2, the population on Zhandarmy rocks is entirely monomorphic, while under optimal K = 5, most samples from the population on Brebeneskul form a separate cluster. These results most probably indicate that disjunctions between the studied populations, with their genetic separation and isolation, occurred comparatively recently, probably already during some phases of the Holocene.

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SUPPLEMENTARY MATERIAL

This article includes following Supplementary Materials: Matrices S1–S4 (K1–K3, combined); Figures S1–S4 (representing STRUCTURE results) and Haplotype networks S5–S8 (for TCS, Nj-Net, Minimum Spanning Network, Minimum Joining Network, respectively) available as: ukrbotj83-03-161-S1-S8.zip. Supplemental data are also available on GitHub by the following link: https://github.com/AndriiTarieiev/Dryas_AFLP

ETHICS DECLARATION

The authors declare no conflict of interest.

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Генетичне різноманіття та структура популяцій аркто-альпійського реліктового виду *Dryas octopetala* (*Rosaceae*) в Україні за даними AFLP-аналізу

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Реферат. Аркто-альпійські рослинні угруповання містять численні ендемічні та реліктові види. Багато з них є чутливими до змін середовища існування і зазнають впливу кліматичних змін, що робить їхнє дослідження особливо актуальним. У цьому дослідженні зосереджено увагу на циркумполярному аркто-альпійському реліктовому диплоїдному чагарничку *Dryas octopetala* в Україні. Було обстежено та відібрано зразки з усіх чотирьох відомих популяцій. Для аналізу генетичного різноманіття, структури популяцій та інших параметрів використано три набори по 50 різних AFLP-маркерів у кожному. Аналізи STRUCTURE у поєднанні з філогенетичною мережею не виявили суттєвих відмінностей у генетичній структурі між популяціями. Водночас популяція на г. Бребенескул демонструє незначні відмінності порівняно з трьома іншими популяціями дріади в Україні. Географічна ізоляція, різні міграційні шляхи та потенційна можливість схрещування можуть пояснювати отримані результати. Для формування більш чіткої картини необхідні додаткові дослідження із застосуванням різних методів (зокрема SSR, повногеномного аналізу SNP, GWAS, WGS).

Ключові слова: *Dryas octopetala*, AFLP, STRUCTURE, PCoA, Карпати, популяції, Україна