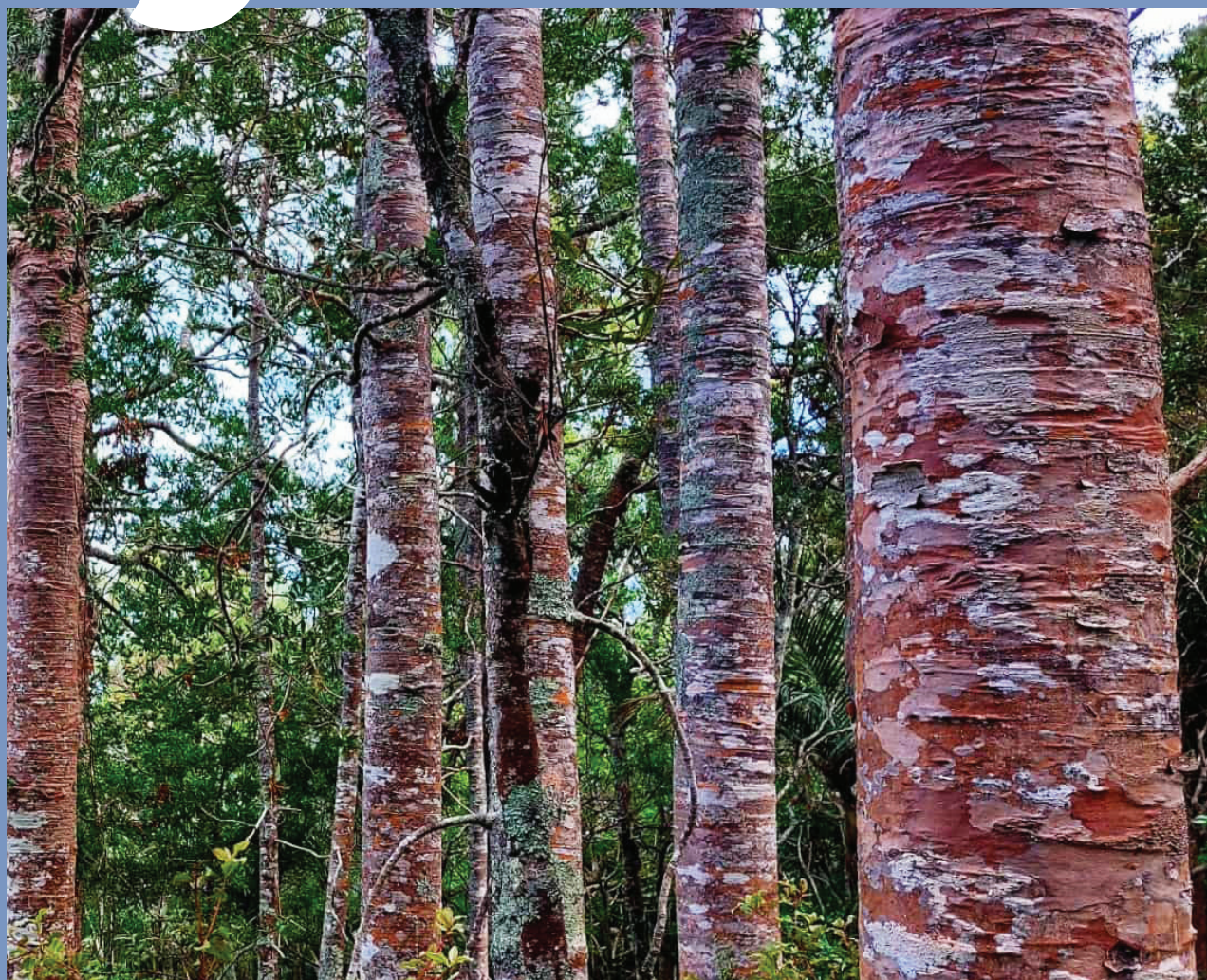
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Front cover: One of the key habitats of *Pyrenula largei* A.J. Marshall, de Lange, Blanchon & Aptroot (*Pyrenulaceae*) — kauri (*Agathis australis*, *Araucariaceae*) / tanekaha (*Phyllocladus trichomanoides*, *Podocarpaceae*) forest, Mataia Queen Elizabeth II Covenant, Mataia Farms, Glorit, Kaipara, Te Ika-a-Māui / North Island, Aotearoa / New Zealand, December 2024 (see the article by Marshall et al. on pages 435–452 in this issue).

Photo by © Peter J. de Lange

На обкладинці: Один із типових біотопів *Pyrenula largei* A.J. Marshall, de Lange, Blanchon & Aptroot (*Pyrenulaceae*) — ліс із *Agathis australis* (*Araucariaceae*) та *Phyllocladus trichomanoides* (*Podocarpaceae*), заповідна територія Матайя королеви Єлизавети II, ферми Матайя, Глоріт, Кайпара, Північний острів, Нова Зеландія, грудень 2024 р. (див. статтю Маршалла та ін. на стор. 435–452 у цьому номері).

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REVIEW ARTICLE

High potential of biosynthesized nanoparticles as an efficient and inexpensive tool for SERS-detection of explosives based on trinitrotoluene

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Abstract. This review is focused on overcoming the consequences of the ruscist invasion in Ukraine and exploring solutions to the problem of contamination by explosives, such as 2,4,6-trinitrotoluene (TNT). Recognizing the need to protect the civilian and military population, it is most important to develop a simple, rapid, and sensitive detection method that first responders can use in the field to identify the TNT threats to the environment or human safety. Surface-enhanced Raman spectroscopy (SERS) is regarded as a novel detection method with high sensitivity, high specificity, and rapid response, which has been successfully applied to the biochemical detection of toxic analytes or environmental pollutants. Green, in particular plant- and fungi-mediated, synthesized metallic nanoparticles are capable of enhancing the SERS signal from various substances, with the ability to register a SERS spectrum from a single target molecule. In general, the method for plant- and fungi-based nanoparticles fabrication is as follows. First, parts of plant or fungal material are selected and crushed to obtain the extract which is processed to remove any impurities. The precursor, typically a metallic solution, is then mixed with the obtained extract, resulting in the production of nanoparticles. Maintaining appropriate pH, temperature, and continuous stirring,which ensures the production of uniformly sized nanoparticles, is crucial to facilitate the reaction effectively. The combination of affordable and sustainable production and high analytical capabilities makes this sort of nanostructure a promising candidate for investigations and decontamination of large territories of Ukraine affected by explosive compounds and products of their decay.

Keywords: green synthesis, localized plasmon resonance, metallic nanoparticles, SERS substrate, trinitrotoluene detection

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The progress of methods for sighting explosives based on Surface-Enhanced Raman Spectroscopy (SERS) is of primary importance from the viewpoint of countering potential threats in the field of national and global security. SERS stands out as a highly promising method for ultra-sensitive chemical analysis of both organic and inorganic substances, bringing it closer to practical utilization (Mazur et al., 2025). According to the Interpol review (Klapec et al., 2023), the analysis and detection of explosives and explosive residues using SERS technology can be adaptable to the current approaches to explosives analysis and will be useful in future real-world applications.

Explosives are widely applied as the explosive charges in artillery pieces and aerial bombs used in military activities, as well as in scientific and technological practice, such as mining and engineering blasting. Incorrect techniques in the manufacturing and use of explosives may be the reason for the pollution of the environment in some areas. Among the various explosives-based nitroaromatic compounds, trinitrotoluene (TNT), cyclotrimethylene-trinitroamine (RDX), and cyclotetramethylene-tetranitramine (HMX) are the most military-used environmental pollutants (Yang et al., 2021).

TNT as the substance successively synthesized by the nitration of toluene was used in weaponry during World War I in 1914–1918 as it is preferred over dynamite since the shock waves produced by TNT can penetrate the steel on armor-plated military transport. During World War II, two new explosives based on toluene were introduced, RDX and PETN (pentaerythrito-tetranitrate). RDX was renamed as Composition-4 or C-4 explosive (Awasthi et al., 2022).

The TNT is the most widespread explosive used by industries, militaries, and terrorists. TNT is widely used in landmines and underwater imploding works, resulting in soil and groundwater contamination. Purification of soil and wastewater from TNT contamination is always difficult and rather expensive (Jamil et al., 2015).

Classified as a Class C carcinogen by the Environmental Protection Agency (USA), TNT exhibits a toxic effect on all tested living organisms: in animals causing hepatitis, cataracts, anemia, skin irritation, and bone marrow hyperplasia; in soil seriously affecting the microbial diversity and vegetation. In plants, most of TNT remains in the root tissues, where growth and development are inhibited, reducing the total biomass (Johnston et al., 2015).

TNT is classified as a worldwide pollutant at concentrations above 2 μg L^{-1} (8.8 nM), contaminating manufacturing waste sites, industrial mines, current and former conflict zones, and military lands (Alizadeh, Yoosefian, 2023). TNT can penetrate human skin and enter the bloodstream, furthermore, as residual TNT in water and soil generally exists at very low concentrations, it must be detected at trace levels to safeguard human health and prevent the environmental pollution (Gao et al., 2022). In order to protect the civilian and military population, it is most important to develop an identification procedure that should be simple, rapid, and sensitive, and which can be applied by first responders in the field for the identification of TNT threats, whether to the environment, or human safety (Jamil et al., 2015).

A variety of techniques are presently approachable for the TNT assay in water and soil samples (To et al., 2020). These methods involve infrared and luminescence spectroscopy (Banas et al., 2023; Li et al., 2023), ion mobility spectrometry (Li et al., 2022), neutron activation analysis (Silarski, Nowakowski, 2022), immunoassays (Devi et al., 2022), electrochemistry (Apak et al., 2023), and molecularly imprinted polymers (Karadurmus et al., 2022). Also currently, TNT can be detected by mass spectrometry (Son, Choi, 2023), electrospray droplet impact/secondary ion mass spectrometry (Hiraoka et al., 2023), gas chromatography (Xu et al., 2023), colorimetry (Junaid et al., 2022), fluorescent polymers (Bener et al., 2022), and sensors based on plasmon resonance (Chegel et al., 2020).

However, most of these methods are expensive, non-portable, and potentially limited by extensive sample preparation. For example, mass spectrometry needs isolation and purification of the analytic probe, usually by chromatography. In addition, the sensitivity, selectivity, reproducibility, operability, and time cost of these techniques are inappropriate for trace detection of TNT. In contrast, Surface-Enhanced Raman Spectroscopy (SERS) is a novel detection method with high sensitivity, high specificity, and rapid response, which has been successfully applied to biochemical detection of toxic analytes or environmental pollutants (Xu et al., 2017, 2022).

As a physical phenomenon, SERS is the vibrational Raman scattering from molecules or inorganic nanostructures placed in the nm-vicinity of

a noble metal nanostructure that strongly concentrates the electric field of the laser light and thus enhances the Raman scattering from the vibrations of molecular bonds in this spatial area. Such a strong local electric field can be created by these types of nanostructured metal because the laser can excite in them strong oscillations of free electron charges, that is called Localized Surface Plasmon Resonance (LSPR). By varying the composition (e.g., Ag, Au, or their alloy), size, and shape of metal nanostructures, the spectral position of LSPR can be tuned over the whole visible and near-infrared range (Demydov et al., 2021), while using semiconductors (Llorente et al., 2017) or some doped oxides allow shifting the LSPR deeper into the IR. Such a spectral tunability of the LSPR, and thus the SERS, allows a resonant detection of certain analytes, employment of the transparency windows of bio-tissues, avoiding fluorescent background, and other benefits. The plasmonic nanostructures capable of the aforementioned enhancement of the Raman signal are generally referred to as "SERS-substrates", even if they are in the form of colloidal nanoparticles (NPs).

Being based on Raman spectroscopy, SERS is thus well known for different toxicant analyses with high specificity — able to provide unique fingerprint-alike data, high sensitivity — possible of single molecules identification, rapid detection, and portability. One of the keys to getting higher sensitivity in a SERS assay is to effectively bring the analyte (target molecule) within the nm-range distance from the surface of the SERS substrate. In particular, it can be achieved by removing the stabilizing molecules around the colloidal NPs (Stefancu et al., 2018) or using additional ions to couple the analyte to the enhancing metal surface electrostatically (Hu et al., 2023).

When the analyte molecule is in direct contact with the metal surface, in addition to the "plasmonic" enhancement described above, the "chemical" enhancement of the Raman signal takes place due to the change in polarization of the studied molecules *via* electronic interaction with a metal (Graham et al., 2017). The latter gives rise to a modification in the electronic structure of molecules, and this modification can manifest itself both in the shift of electron levels and in the emergence of new ones. Because of the resonance Raman scattering between 'new' electron levels, the selective enhancement of separate vibrational bands occurs (Dzhagan et al., 2022a).

The research on the detection and identification of explosives by SERS began through the analysis of TNT in 1995 (Kneipp et al., 1995), and expanded later to many other explosives (Rozo et al., 2007; Gong et al., 2014; Zapata et al., 2016; Chio et al., 2019; Gao et al., 2020). The exciting sensitivity of the SERS method has already been reported — down to 10^{-17} M for TNT and 10^{-13} M for less intensively investigated but also often used explosives (Zapata et al., 2016).

It has been found that even relatively facile routes of obtaining plasmonic NPs by chemical reduction in aqueous solution enable decent levels of TNT detection, ~10^{-10} M. However, this seemed to be efficient in the solution, because of a pronounced dependence of the SERS intensity on pH. Thus the aforementioned low concentration, ~10^{-10} M, was registered only at pH = 13, while at pH = 12 the intensity dropped significantly and no Raman peaks were observed at lower pH (Rozo et al., 2007).

Although facile colloidally synthesized NPs were often applied to TNT detection as mentioned above, most of the works used more sophisticated approaches to reach high sensitivity of detection. Among the reported, there is a novel highly ordered nano-micro hierarchical structure on a flexible polydimethylsiloxane (PDMS) layer as a SERS stamp for ultrasensitive detection, which can generate high SERS signals with silver nanoparticles (Ag-NPs) owing to a multiscale coupling electromagnetic enhancement mechanism (Gao et al., 2020). Note, however, that, compared to the impressive detection limit of 10^{-13} mol/L achieved for a solution dropped on the substrate, the practical application proceeded by wiping the cloth bag resulted in the detection of the TNT residues with an expectedly much lower limit of 10^{-9} mol/L (Gao et al., 2020).

The reproducibility and selectivity of SERS sensors for nitroaromatics can be significantly improved *via* a hierarchical host-guest self-assembly approach mediated by the multifunctional macrocyclic molecule cucurbit[7]uril (CB[7]) (Chio et al., 2019).

Irrespective of a level of complexity/simplicity of the SERS substrate design and fabrication procedure, the free-standing NPs produced by colloidal synthesis can be an essential component in most cases. The reason is that in many real-life situations, sampling needs to be performed from a solid surface and thus requires the SERS-substrate in the form of an elastic polymer or cotton swab (Gong et al., 2014; Liu et al., 2020).

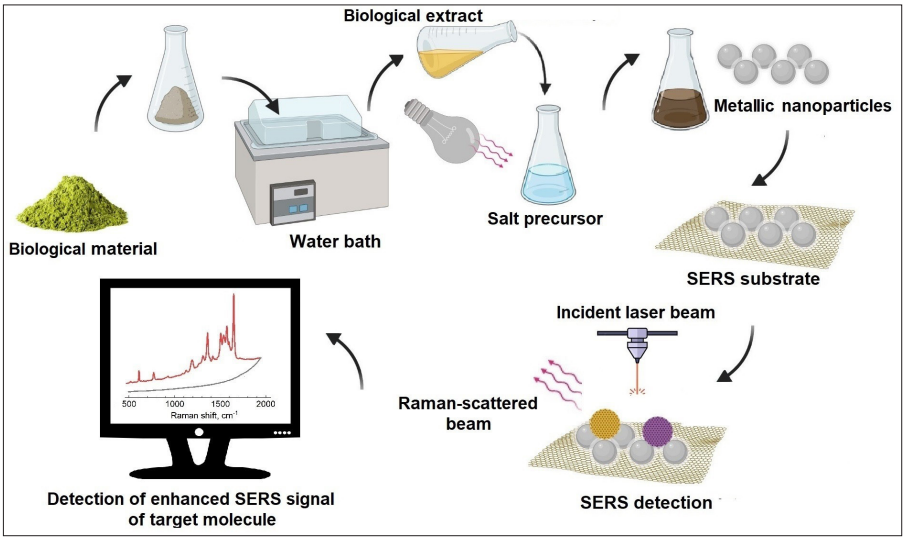


Fig. 1. Schematic illustration of the green synthesis of Ag, ZnO, and Ag/ZnO nanoparticles and its application as SERS substrate

Presently, NPs are characteristically synthesized by physical and chemical methods, which are usually costly and environmentally hazardous. That is why, the eco-safety biosynthesis also known as a green synthesis of NPs has attracted increasing attention in the last decade, in parallel with the increased interest in green chemistry approaches and environmental sustainability (Borovaya et al., 2021; Pandit et al., 2022). Traditional physical and chemical methods used for the synthesis of NPs frequently require scrupulous observance of strict conditions, whereas green synthesis routes involve simple, nontoxic, and eco-friendly protocols at an ambient temperature and pressure (Alharbi et al., 2022).

Modern eco-friendly protocols of NPs fabrication enclose the recent developments in the formulation of plant-mediated and fungal-mediated nanocomposites by using several plant and fungal species and the impact of secondary metabolites on their biocompatible functioning. Phyto (myco)-synthesis produces diverse nanomaterials with biocompatibility, environment-friendliness, and *in vivo* actions, characterized by varying sizes, shapes, and biochemical nature. This process is advantageous to conventional physical and chemical procedures. Diverse plant and fungal species are widely utilized to produce NPs as they form eco-friendly bio-factories capable of converting metal ions into their zerovalent or nanoforms. A variety of secondary metabolites, enzymes, and proteins present in plant sources act as reducing agents in this process (Malik et al., 2025; Meera et al., 2025).

We earlier reported on green synthesis and successful use as an SERS substrate of Ag, ZnO, and Ag/ZnO NPs as summarized in Fig. 1 (Smirnov et al., 2023a).

The based on noble metal NPs with LSPR that can amplify Raman scattering from the analyte are commonly referred to as "SERS substrates". Raman spectroscopy serves as a highly efficient and non-invasive method for the velocity investigation of various materials by investigation of their vibrational spectra. The role of SERS is to enhance weak Raman signals. In contrast to conventional Raman spectroscopy, SERS enables the detection of molecules even in minute concentrations in solutions or when deposited onto nanostructured noble metal films (Langer et al., 2019).

The basis for the synthesis of stable colloidal solutions of NPs were extracts of pericarps of *Capsicum annuum* L. (Dzhagan et al., 2022b), rhizomes and inflorescences of *Lathraea squamaria* L. (Smirnov et al., 2022), and fruiting bodies of *Ganoderma lucidum* (Curtis) P. Karst. (Dzhagan et al., 2023; Smirnov et al., 2023a, 2023b).

Green synthesis techniques are based on the biogenic reduction of metal precursors to produce corresponding NPs (Fig. 2). This route makes use of natural resources, often production waste and bioactive molecules, that can act as reducing, capping, and

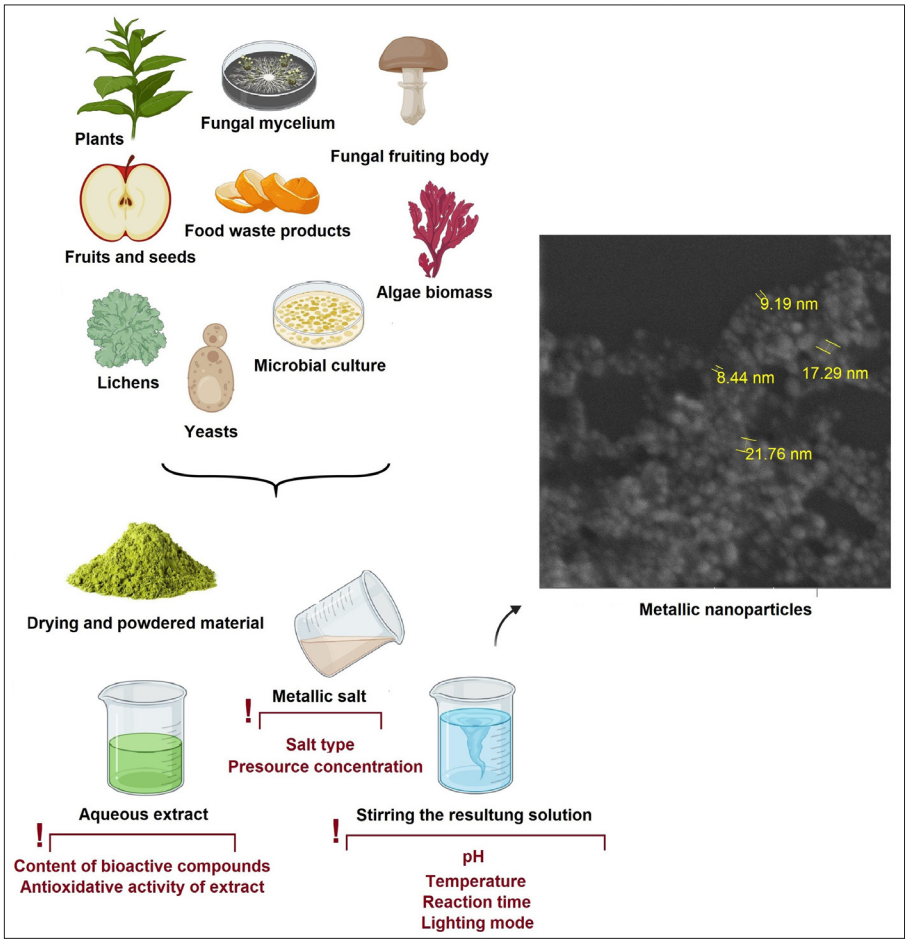


Fig. 2. Schematic diagram of the green synthesis route of metallic nanoparticles

stabilizing components in the facile synthesis of nanoparticles. Green synthesis offers numerous advantages, including the development of processes with minimal environmental impact and improved safety for nanoparticle synthesis. Overall, the synthesis of nanoparticles using green chemistry is a promising approach for sustainable and efficient production (Álvarez-Chimal, Arenas-Alatorre, 2023).

Using plant resources, the green synthesis of nanoparticles is inexpensive, faster, and considered a facile synthesis while canning or even improving the physical and chemical properties of the nanoparticles. With the great potential of this method and the sustainable and efficient production of nanoparticles, different morphology can be synthesized, which makes it a very attractive option not only for the synthesis of nanoparticles but also for the application of this method in the synthesis of other compounds.

They are environment-friendly, less expensive, and free of chemical contaminants for medical and biological applications where the purity of NPs is of main concern. Biogenic reduction is a "Bottom Up" approach similar to chemical reduction where a reducing agent is replaced by an extract of natural products (various parts of plants, fungi, yeasts, microbial cultures) with inherent stabilizing, growth terminating, and capping properties. Furthermore, the nature of biological entities in different concentrations in combination with reducing and capping organic agents influences the size and morphology of green synthesized NPs (Abdelmigid et al., 2022; Habeeb et al., 2022).

The features used for green synthesis, such as temperature, pH, the specification of precursor salts, concentration of the extract, and incubation (reaction) period, have great effects on the formation

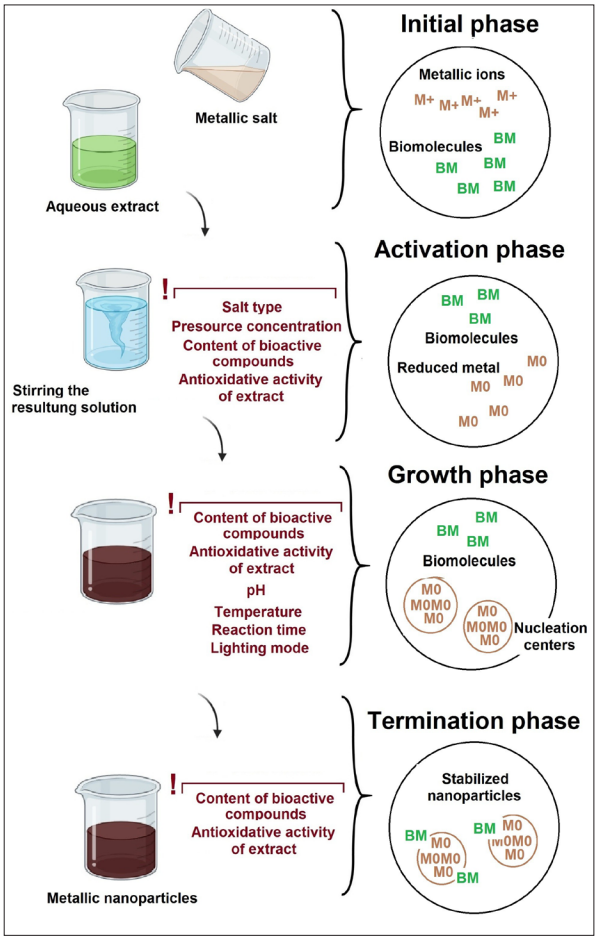


Fig. 3. Schematic diagram of the phases involved in the biosynthesis (green synthesis) of nanoparticles

and characteristics of NPs green synthesis (Fig. 3). Among these parameters, the temperature, pH value, and biological extract play a dominant role in the eco-friendly fabrication of metallic NPs (Fagier et al., 2021; Alharbi et al., 2022).

Temperature is one of the most considerable features that affect the size and shape of green synthesized NPs. Previous investigations have revealed that the dimensions of metallic NPs decrease as the temperature of green synthesis increases, resulting in a change in their shape. Hence, in NPs fabrication, it is well established that high temperatures promote nucleation, whereas low temperatures promote growth processes (Ying et al., 2022).

Numerous research publications do not mention the pH effect in the green synthesis of NPs. Nevertheless, a pH value has a vital role in the synthesis route and characteristics of NPs (Samuel et al., 2022). Phytochemicals and other natural compounds existing in a biological extract are highly linked to the pH changes and consequently to a charge change in the solution, which might change their reducing and capping properties and then NPs nucleation and growth. In conformity with this, pH can affect the morphology and productivity of the green synthesis of NPs (Elsayed et al., 2022).

Previously, we investigated the effects of pH (2.5; 5; 7; 9, and 11) on the green synthesis of AgNPs using the fruiting bodies of *Ganoderma lucidum*. Stable NPs colloids with distinct plasmonic resonance peaked at 408–418 nm are obtained by using photoreduction in a broad pH range (5 to 11). The synthesis efficiency drops only at very acidic conditions, pH = 2.5 (Smirnov et al., 2023).

In total, optimal pH for green synthesis of NPs depends on a substrate and contents of phytochemical molecules as reducing and capping agents to synthesize nanoparticles. However, Mata et al. (2009) indicated clearly that higher pH favored a higher reducing power for the green synthesis of plasmonic NPs. Notably, the high pH values were shown to be required for efficient SERS detection of TNT (Rozo et al., 2007).

The biological extract plays the main role in NPs green synthesis routes due to the presence of reducing agents and other stabilizing and capping agents (Jadoun et al., 2021). As NPs fabrication includes the use of plant extracts, animal proteins, agro-waste, pigments, bacterial cultures, fungal samples, and small viruses, which are difficult to handle with conventional methods, green synthesis of nanoparticles is widely recommended. All these biological objects also include bioactive metabolites such as proteins, polysaccharides, aldehydes, ketones, carboxylic acids, polyphenols, tannins, flavonoids, saponins, terpenoids, amines, and alkaloids, which serve as bio- reducing, stabilizing, and capping agents and are capable of transforming metallic ions into plasmonic NPs, synthesizing required NPs with previously reported beneficial properties (Naveed et al., 2022).

Although the rapid and eco-friendly green synthetic routes using biological extracts have shown their great potential in NPs fabrication, the mechanism by which bioactive metabolites are involved in the synthesis and the mode of plasmonic properties is still not fully understood. In addition, controlling the size range and morphology of green

synthesized NPs, which has many positive effects on its capabilities, remained largely unanswered till today, although chemical methods are already well-known for shape-controlled synthesis (Vanlalveni et al., 2021).

Green (bio-) synthesis, which harnesses the power of biological extracts, has surfaced as a promising alternative. However, green methods face challenges, including prolonged processing times and a reduced ability to control nanoparticle size, morphology, and crystallinity (Secario et al., 2024). Despite these limitations, green-synthesized NPs are increasingly recognized for their potential to mitigate environmental challenges while offering promising avenues in the field of medicine, in the agro-industrial complex, and ecological science. The long-term stability can also be impacted by strict control of temperature, light, and pH levels, which can alter how well they could work in different applications. The wider use and commercialization of green-synthesized AgNPs depend on addressing these issues through more research and development (Dheyab et al., 2025).

In general, the world faces threats that the United Nations has ranked as global problems of humanity into 17 categories with various objectives as solutions for each challenge that are enclosed in the Sustainable Development Goals (SDGs). These responsive solutions involved the prevalence of science and technology as pathways to ensure their implementation. In this regard, sustainability science seeks the research community's contribution to addressing sustainable development challenges. Specifically, green and eco-friendly nanotechnology has been recognized as a key tool for potential applications in disruptive and effective strategies to reach the SDGs (Larrañaga-Tapia et al., 2024).

Nevertheless, statistical data analysis (see Fig. 4) depicted the increasing trend of published research articles in the field of green synthesis of metallic NPs. These data were collected from the National Center for Biotechnology Information (NCBI) using the keywords "Green synthesis of nanoparticles" in the PubMed database. From a meager number of 689 publications in the year of 2015, it has exponentially increased to 2032 publications in 2024.

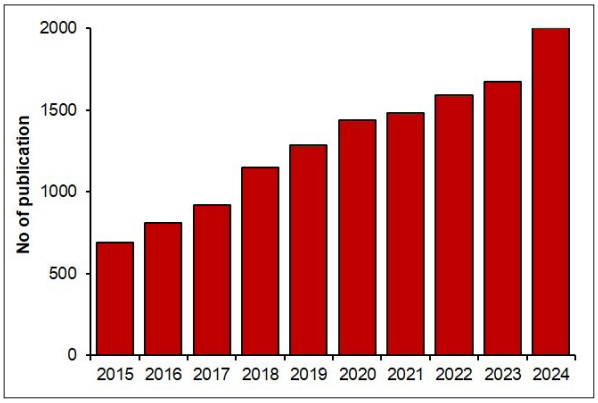


Fig. 4. Publications number per year for green synthesis of NPs since 2015 to 2024 (data collected from the NCBI PubMed database)

Conclusions

The steady growth of interest in the field of green synthesized NPs can be used for development of a TNT and other explosives determination procedure that is simple, rapid, and sensitive, which can be applied for the identification of explosive threats and contaminations for the implementation of the Ukraine's Recovery Plan (https://www.urc-international.com/past-conferences/urc22/urc2022-recovery-plan). In contrast to conventional Raman spectroscopy, SERS enables the detection of molecules even in minute concentrations in solutions or when deposited onto nanostructured noble metal films. This technique can be used to detect contamination in air, soils, and water sources.

At the same time, as the war continues, there are constant massive missile and drone attacks throughout Ukraine, and significant areas remain occupied in the southeast of Ukraine, creating enormous difficulties for research, education, and business. The scientific community in Ukraine has an urgent need to address long-term challenges, to retain its high standards of research and technology and to develop new ideas under the current circumstances (Duszyński et al., 2022; Kondratov et al., 2022).

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ETHICS DECLARATION

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Високий потенціал біосинтезованих наночастинок як ефективного та дешевого засобу для SERS-виявлення вибухових речовин на основі тринітротолуолу

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Реферат. Цей огляд присвячений обговоренню питання подолання наслідків російського вторгнення в Україну та дослідженням щодо вирішення проблеми забруднення вибуховими речовинами, такими як 2,4,6-тринітротолуол (TNT). Для забезпечення захисту цивільного та військового населення надзвичайно важливою є розробка простої, швидкої та чутливої процедури визначення цих речовин, яку можуть використовувати служби першого реагування на місці для виявлення загрози TNT для навколишнього середовища або безпеки людей. Поверхнево-підсилене комбінаційне розсіяння світла (SERS) вважається новим методом детекції з високою чутливістю, високою специфічністю та швидкою реакцією, який успішно застосовувався для біохімічного виявлення токсичних аналітів або забруднювачів навколишнього середовища. При цьому показано, що синтезовані зеленим шляхом металеві наночастинки рослинного та грибного походження здатні посилювати сигнал SERS від різних речовин, з можливістю реєстрації спектру SERS від однієї цільової молекули. Загальний метод синтезу наночастинок на основі рослин та грибів є таким: спочатку обирають рослинний чи грибний матеріал, подрібнюють і отримують екстракт, який обробляють для видалення будь-яких домішок; потім попередник, зазвичай розчин металовмісної солі, змішують із рослинним екстрактом, що призводить до отримання наночастинок. Підтримка відповідного рівня pH, температури та безперервне перемішування, що забезпечує отримання наночастинок рівномірного розміру, має вирішальне значення для ефективного протікання синтезу. Поєднання доступного і сталого виробництва та високих аналітичних можливостей робить таку наноструктуру перспективною для досліджень і дезактивації значних територій України, уражених вибухонебезпечними сполуками та продуктами їхнього розпаду.

Ключові слова: детекція тринітротолуолу, зелений синтез, локалізований плазмонний резонанс, металічні наночастинки, SERS підкладки

FUNGI AND FUNGI-LIKE ORGANISMS
ГРИБИ І ГРИБОПОДІБНІ ОРГАНІЗМИ

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RESEARCH ARTICLE

Which species of *Sawadaea* (*Erysiphaceae*) parasitise *Acer negundo* in Ukraine?

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Abstract. A critical re-examination of powdery mildew collections on boxelder maple (*Acer negundo*, *Sapindaceae*) in Ukraine has demonstrated a shift in fungal pathogens of the genus *Sawadaea* affecting this common tree and introduction of two *Sawadaea* species into the country. The East Asian species *Sawadaea polyfida* was found to have spread on this host plant within the country since the early 21st century, largely displacing the previously dominant *S. bicornis*. Considering recent reports of *S. polyfida* in Western and Southern Europe on other maple species, specimens of powdery mildew collected on *A. negundo* in these regions require further critical study. In October 2025, one more species of East Asian origin, *S. negundinis*, was recorded on *A. negundo* in several locations for the first time in Ukraine. Given the potential for *S. negundinis* to spread rapidly within Europe, this fungus is likely to be expected in, or may have already invaded, other European countries.

Keywords: boxelder maple, distribution, Europe, invasion, powdery mildew

Introduction

Sawadaea Miyabe (*Erysiphaceae*, *Helotiales*, *Ascomycota*) is a relatively small genus of tree-infecting powdery mildew fungi that until recently comprised ten species (Hyde et al., 2024). The majority of them were described as parasites on various species of *Acer* L. (*Sapindaceae*). However, except for maples as principal hosts, some of these fungi are also known to occur on other host genera of *Sapindaceae*, viz. *Aesculus* L., *Alectryon* Gaertn., *Dodonaea* Mill. and *Koelreuteria* Laxm. (Braun, Cook, 2012).

A most recently published comprehensive phylogenetic and taxonomic analysis of powdery mildews on *Acer* spp. from East Asia, Europe and North America revealed three more new species of *Sawadaea* described from Asia (Feng et al., 2025). In that article, a boxelder maple (*Acer negundo* L.) is listed as a host plant for three of the 13 species of *Sawadaea* studied morphologically and genetically. For two species, *S. bicornis* (Wallr.) Homma and *S. negundinis* Homma, numerous collections ex *A. negundo* from different countries were examined, as well as newly obtained sequences and those retrieved from NCBI GenBank database were analysed. *Acer negundo* as a host is also listed for the third species, *S. polyfida* (C.T. Wei) R.Y. Zheng & G.Q. Chen (Feng et al., 2025); however, for the specimen used for DNA extraction (GenBank

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accession number MT174231), this host is apparently mentioned erroneously in the GenBank database and in the article, since Kiss et al. (2020) reported this specimen (BRIP68806) from Australia on *A. palmatum*. *Sawadaea bicornis* is a common and widely distributed species on a wide range of *Acer* spp. in Europe, Asia and North America, introduced in South America and New Zealand. *Sawadaea negundinis* based on the collections confirmed by sequence data, on the contrary, was demonstrated not to be strictly confined to *A. negundo* and known almost exclusively from Asia (Feng et al., 2025), except for a single record from the European part of RF, Rostov Region, which is an area bordering Ukraine.

With respect to the above, a relevant question can be raised: which species of *Sawadaea* occur on *A. negundo* in Ukraine? The present article provides the answer to this question.

Materials and Methods

A collection of all specimens of the leaves of *A. negundo* infected by powdery mildews (Table 1) deposited at the Mycological Herbarium (Fungarium) of the National Herbarium of Ukraine at the M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine (KW-M), was critically studied. The samples prepared in distilled water following standard protocol were examined using light microscopy. Photographs of all microstructures were taken with a Canon A 300 digital camera attached to a Primo Star microscope (Carl Zeiss, Germany). All measurements were made using AxioVision 4.7 software.

Results and Discussion

Prior to this study, only two species of *Sawadaea* have been reported in Ukraine, *S. bicornis* and *S. tulasnei* (Fuckel) Homma. They both are obligate biotrophic fungi infecting various hosts, primarily *Acer* spp., although the former species was also occasionally recorded on *Aesculus hippocastanum* L. (Heluta, Marchenko, 1984; Heluta, 1989; Heluta, Anishchenko, 2021). Morphologically, these species are quite close but distinguishable by different infection appearance on host plant and morphology of chasmothecial appendages. In addition, they have rather distinct host ranges.

Sawadaea bicornis has been reported in Ukraine on a wide range of hosts including *Acer campestre* L., *A. negundo*, *A. platanoides* L., *A. pseudoplatanus* L., *A. saccharinum* L., *A. velutinum* Boiss. and *Aesculus hippocastanum*. Mycelium of this fungus, as well as conidia and chasmothecia, develop on both sides of the leaves (amphigenous), at first as irregular greyish-white patches, later confluent. Chasmothecial appendages are 1–2(3) times dichotomously branched in the upper half of the stalk, with uncinate-circinate apices.

Sawadaea tulasnei was recorded in the country only on *A. platanoides* and *A. tatarica* L. Its mycelium is mostly (on *A. tatarica* almost exclusively) epiphyllous, at first forming distinct white patches, later enlarging to cover the entire leaf surface, so that severely infected leaves appear as if they are covered with a talc-like powder. Chasmothecial appendages are of two types, simple and dichotomously branched, with those unbranched prevailing, all appendages with uncinate apices. However, appendages in *S. tulasnei* are of a peculiar branching pattern, from the middle of the stalk upwards. It is also noteworthy that the two species can simultaneously occur on the same leaves of *A. platanoides*, a host common for both species. Thus, a careful microscopic examination of the infected leaves of this host plant is required for correct identification of the species of *Sawadaea*.

As already noted, following a recent discovery of the record of *S. negundinis* on *Acer negundo* from Rostov Region, RF, confirmed by molecular analysis (Feng et al., 2025), a re-examination of all previously collected specimens of powdery mildews on this host in Ukraine has been made, including not yet identified collections deposited at the Mycological Herbarium of the M.G. Kholodny Institute of Botany, NAS of Ukraine (KW-M). The outcome of the present examination was quite unexpected. Based on morphology of the appendages on chasmothecia, all studied specimens have split into three groups. The first group consisted of the specimens with the appendages dichotomously or trichotomously branched 1–2(–3) times, mainly in the upper half of the stalk (Fig. 1). These specimens are assigned to *S. bicornis*, a common species in Europe, including Ukraine. Majority of them were collected in the second half of the 20th century (Table 1), with the exception of two specimens dated back to the early 2000s (KW-M33244 from Donetsk Region and KW-M71769 from Kyiv City).

The second group of the examined collections proved to be more interesting. It was expected that they would belong to *S. negundinis*. However, chasmothecia in these specimens have numerous

Table 1. **Specimens of the species of *Sawadaea* on *Acer negundo* collected in Ukraine (listed in chronological order)**

Specimen	Locality	Collection date	Collector	Species of *Sawadaea*
KW-M33761	Kyiv, John McCain Str.	10.10.1972	I.O. Dudka	*S. bicornis*
KW-M33766	Kyiv, National Botanical Garden	04.10.1976	Perehon, Potayenko	*S. bicornis*
KW-M33767	Kyiv, National Botanical Garden	12.10.1976	Perehon, Potayenko	*S. bicornis*
KW-M33770	Kyiv Region, Bucha	06.09.1979	V.P. Heluta	*S. bicornis*
KW-M33769	Kyiv, National Botanical Garden	10.09.1979	H.S. Morochkovska	*S. bicornis*
KW-M140	Volyn Region, Lutsk City	30.09.1981	P.D. Marchenko	*S. bicornis*
KW-M33762	Kyiv, Tereshchenkivska Str.	14.09.1987	V.P. Heluta	*S. bicornis*
KW-M33759	Kyiv, Velyka Zhytomyrska Str.	05.10.1987	V.P. Heluta	*S. bicornis*
KW-M33763	Kyiv, Tereshchenkivska Str.	13.10.1987	V.P. Heluta	*S. bicornis*
KW-M33764	Kyiv, Tereshchenkivska Str.	16.10.1987	V.P. Heluta	*S. bicornis*
KW-M31568	Kyiv, T.G. Shevchenko park	17.10.1988	V.P. Heluta	*S. bicornis*
KW-M28199	Kyiv, Feofania	27.09.1990	V.P. Heluta	*S. bicornis*
KW-M28198	Zaporizhzhya Region, Rozivka settl.	26.09.1997	V.P. Heluta	*S. bicornis*
KW-M33625	Kyiv Region, Krasne-Pershe village	02.10.2002	I.O. Dudka	*S. polyfida*
KW-M71775	Kyiv, National Botanical Garden	30.10.2002	S.O. Voityuk	*S. polyfida*
KW-M33244	Donetsk Region, Khomutovskyi Steppe Nature Reserve	20.10.2003	V.P. Heluta	*S. bicornis*
KW-M71772	Donetsk City	30.09.2005	I.V. Bondarenko-Borysova	*S. polyfida*
KW-M71776	Kyiv, National Botanical Garden	04.10.2007	V.P. Heluta, S.O. Voityuk	*S. polyfida*
KW-M71782	Kyiv, Sviatoshyn	12.10.2007	V.P. Heluta	*S. polyfida*
KW-M71773	Donetsk City	21.10.2007	K.G. Savchenko	*S. polyfida*
KW-M71769	Kyiv, Tereshchenkivska Str.	19.10.2009	V.P. Heluta	*S. bicornis*
KW-M71785	Kyiv, Hetman Pavlo Skoropadskyi Str.	12.10.2010	V.P. Heluta	*S. polyfida*
KW-M71783	Kyiv, Kyiv-Volynskyi	19.10.2010	V.P. Heluta	*S. polyfida*
KW-M71777	Kyiv, Acad. Korolyov Avenue	12.10.2011	V.P. Heluta	*S. polyfida*
KW-M71781	Kyiv, Symyrenko Str.	26.10.2011	V.P. Heluta	*S. polyfida*
KW-M71771	Kyiv, Vakhtang Kikabidze Str.	30.10.2011	V.P. Heluta	*S. bicornis* + *S. polyfida*
KW-M71774	Transcarpathian (Zakarpatska) Region, Uzhhorod City	20.09.2012	I. Akata	*S. polyfida*
KW-M71778	Kyiv, Acad. Korolyov Avenue	22.10.2012	V.P. Heluta	*S. polyfida*
KW-M71784	Kyiv, Bohdan Khmelnytskyi Str.	01.11.2012	V.P. Heluta	*S. polyfida*
KW-M71786	Lviv City	14.09.2013	O. Kryva	*S. polyfida*
KW-M71788	Khmelnytskyi Region, Kamianets-Podilskyi District, Sokil village	20.09.2013	V.P. Heluta	*S. polyfida*
KW-M71787	Khmelnytskyi Region, Kamianets-Podilskyi town	22.09.2013	V.P. Heluta	*S. polyfida*
KW-M71770	Kyiv, Acad. Korolyov Avenue	25.10.2015	V.P. Heluta	*S. bicornis* × *S. polyfida*
KW-M71779	Kyiv, Vakhtang Kikabidze Str.	24.10.2019	V.P. Heluta	*S. polyfida*
KW-M71780	Kyiv, Vakhtang Kikabidze Str.	31.10.2022	V.P. Heluta	*S. polyfida*
KW-M71790	Kyiv, Tereshchenkivska Str.	10.10.2025	V.P. Heluta	*S. negundinis*
KW-M71791	Kyiv, Svyatoshyn	15.10.2025	V.P. Hayova	*S. negundinis*
KW-M71794	Kyiv, Vakhtang Kikabidze Str.	21.10.2025	V.P. Heluta	*S. negundinis*
KW-M71795	Kyiv, Yevhen Chykalenko Str.	22.10.2025	V.P. Hayova	*S. negundinis*

appendages (over 100), mostly branched dichotomously, trichotomously to occasionally tetrachotomously from near the middle of the stalk or below, down to the bottom of the stalk, deeply cleft, rarely unbranched (Fig. 2). In *S. negundinis*, appendages are less numerous, usually up to 100 per chasmothecium, branching from almost the middle of the stalk. With regard to the observed characters, according

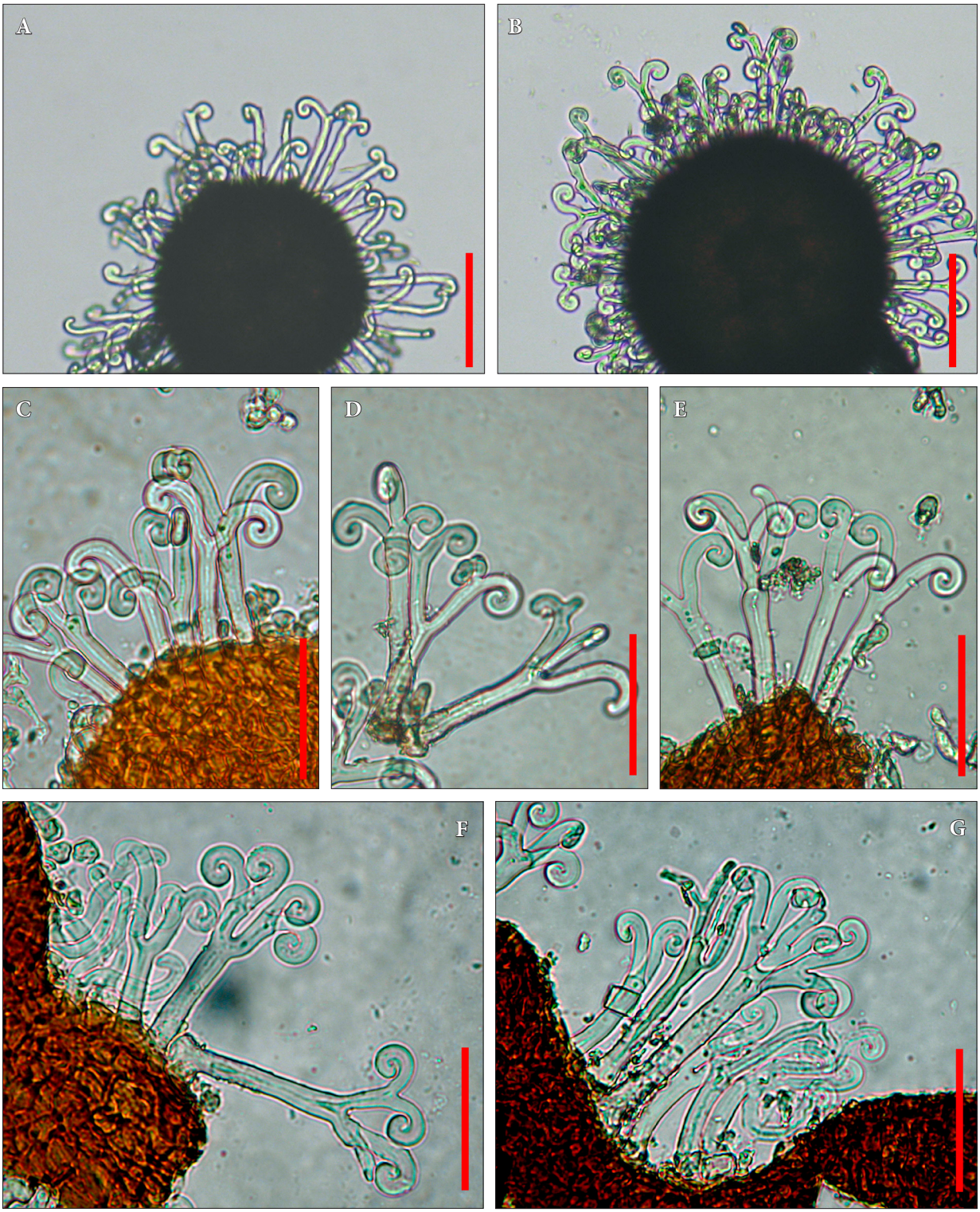


Fig. 1. *Sawadaea bicornis* ex *Acer negundo*: chasmothecia (A, B) and appendages (C–G). A–C: KW-M33763; D: KW-M53578; E–G: KW-M33770. Bars: A, B — 100 µm, C–G — 50 µm

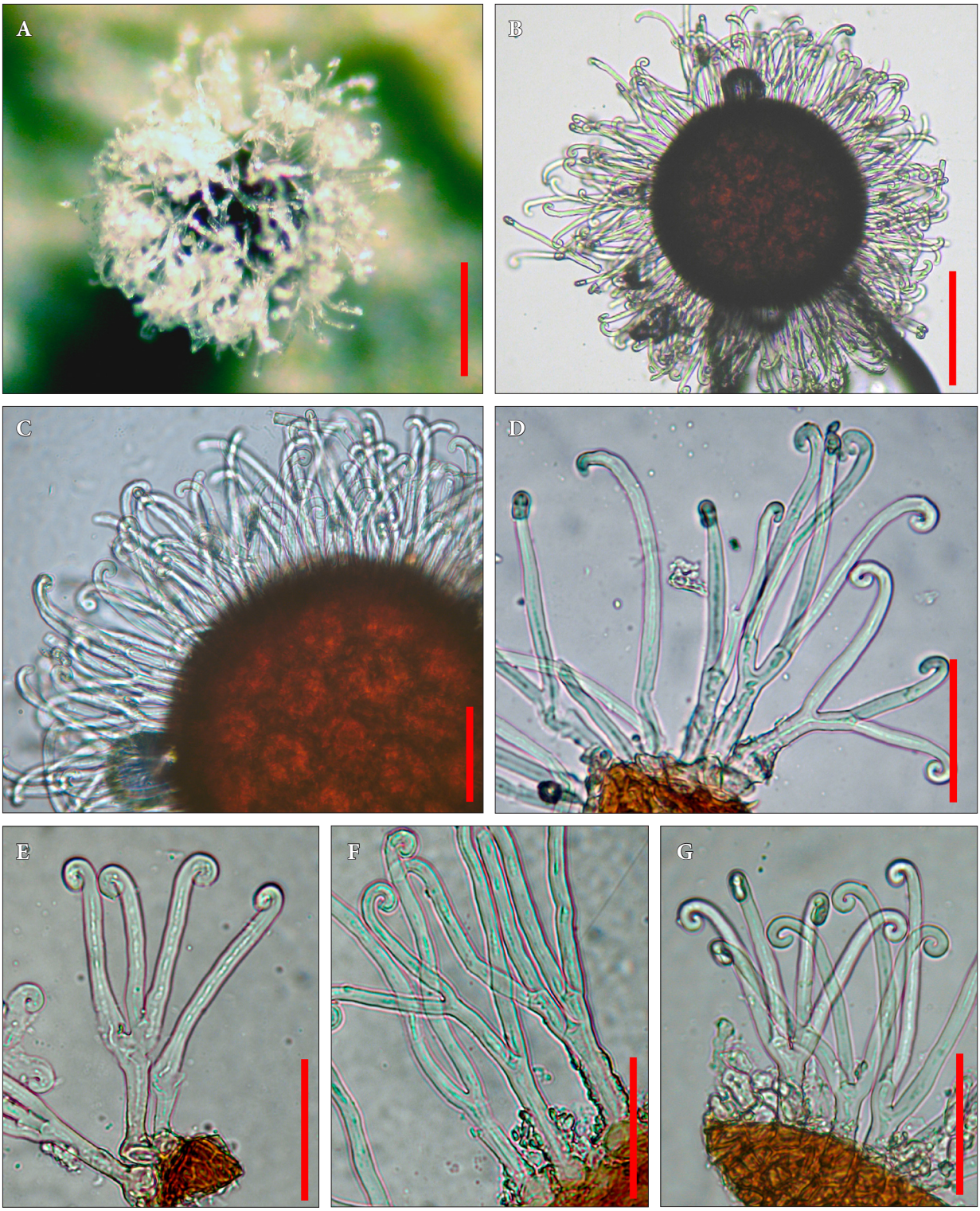


Fig. 2. *Sawadaea polyfida* ex *Acer negundo*: chasmothecia (A, B) and appendages (C–G). A–D: KW-M71786; E: KW-M59233; F: KW-M71772; G: KW-M71787. Bars: A, B — 100 μm, C–G — 50 μm

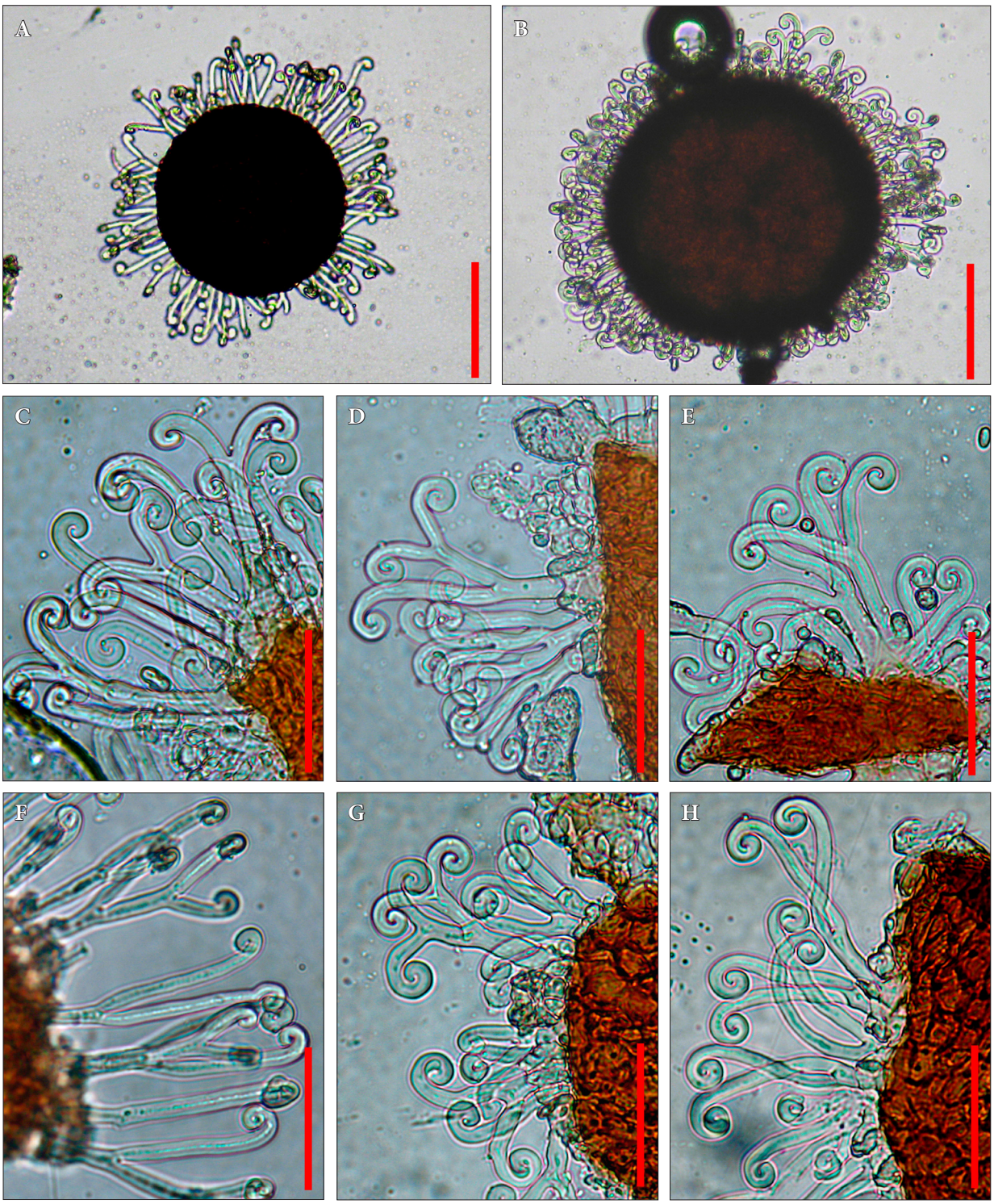


Fig. 3. Chasmothecia (A, B) and appendages (C–F) of a supposed hybrid, *Sawadaea bicornis* × *S. polyfida* ex *Acer negundo* (KW-M71770). Appendages of two different chasmothecia (KW-M71771) morphologically corresponding to *S. bicornis* (G) and *S. polyfida* (H). Bars: A, B — 100 µm, C–G — 50 µm

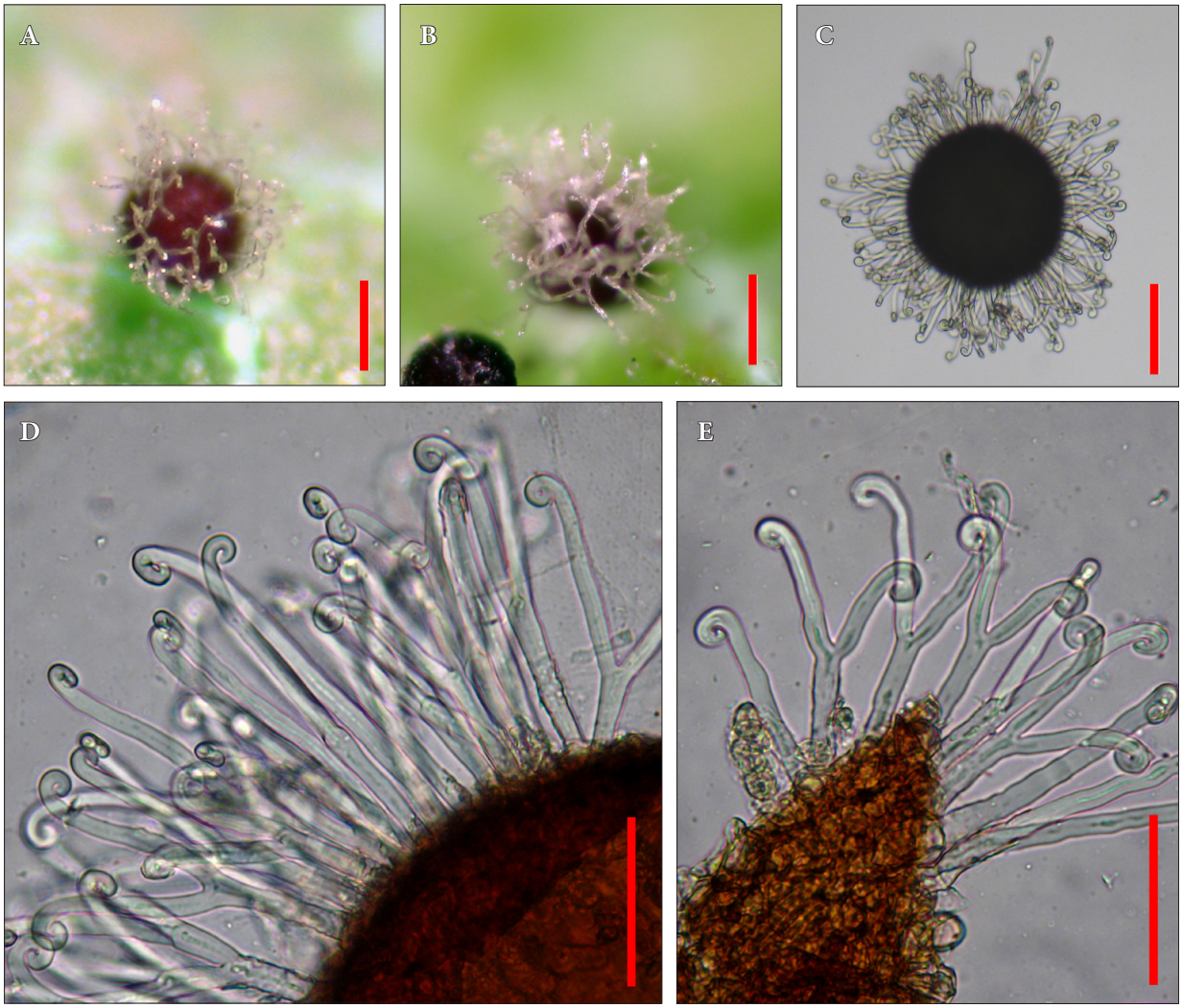


Fig. 4. *Sawadaea negundinis* ex *Acer negundo*: chasmothecia (A–C) and appendages (D, E). A: KW-M71794; B–E: KW-M71795. Bars: A, B — 100 µm, C–G — 50 µm

to the morphology-based key in Braun and Cook (2012), our specimens can be identified as *S. polyfida*. This species, originally described from Eastern Asia, has been recorded in China, Japan and South Korea on various species of *Acer*, predominantly on hosts of *Acer* sect. *Palmata* (Zheng, Chen, 1980; Shin, 2000; Hirose et al., 2005; Lee et al., 2011; Meeboon et al., 2015; Wan et al., 2022; Feng et al., 2025), and introduced to Australia and North America (USA) (Kiss et al., 2020; Feng et al., 2025). Recently, *S. polyfida* was also reported from two countries in Europe, Austria and Switzerland, on the ornamental Japanese maples, *Acer japonicum* Thunb. and *A. palmatum* Thunb. (Beenken et al., 2023; Hofbauer, Braun, 2023), and in Germany, on local maples, *A. campestre* L. and *A. platanoides* L. (Wemheuer et al., 2019).

The morphology of appendages in our samples (Fig. 2) aligns well the descriptions and illustrations of those for *S. polyfida* from Switzerland, an identification confirmed by molecular data (Beenken et al., 2023). The appendage morphology in our specimens is, however, inconsistent with the description of *S. polyfida* on *A. australe* (Momot.) Ohwi & Momot. originating from Japan (Meeboon et al., 2015). The Japanese collection is morphologically distinct, with chasmothecial appendages that branch from the approximate midpoint of the stalk. Furthermore, its nucleotide sequences in the Internal

Transcribed Spacer (ITS) region diverge from other specimens of *S. polyfida* (see Fig. 1 in Feng et al., 2025). This combination of morphological and genetic differences suggests that the Japanese collection may represent a new, yet undescribed species within the *S. polyfida* s. l. species complex.

Thus, our specimens of the second group fully correspond to *S. polyfida* reported on Japanese maples from Western Europe. In Ukraine, however, it has apparently expanded its host range to include *A. negundo*. As indicated in Table 1, the first documented occurrences of *S. polyfida* on this host plant in the country date to the start of the 21st century. It is highly probable that this fungus also occurs on *A. negundo* further west of Ukraine, in Central, South and Western Europe. Consequently, a re-examination of powdery mildew samples collected from this host plant over the past two decades is recommended.

The third group comprises two specimens, KW-M71770 and KW-M71771, which can be assigned neither to *S. bicornis* nor to *S. polyfida*. In the first collection, KW-M71770, some chasmothecia have deeply cleft appendages as in *S. polyfida*, but in lower number (below 100, see Fig. 3A), which does not fit this species. At the same time, there are chasmothecia with very numerous appendages (over 100, see Fig. 3B) typical of *S. bicornis* (Fig. 3B, C). Interestingly, appendages with the intermediate morphological characters can be also observed (Fig. 3D–F). Therefore, this material is apparently of hybrid origin. In the second specimen, KW-M71771, there are two types of chasmothecia: one with those typical of *S. bicornis* (Fig. 3G), other — characteristic of *S. polyfida*, with no intermediate forms (Fig. 3H). In this case, it is evident that both species simultaneously occur on the same leaves. Notably, these two specimens were collected in close proximity within Kyiv City, the first being collected in 2011 and the second in 2015.

Based on the data in Table 1, the first occurrence of *S. polyfida* on *A. negundo* in Ukraine can be documented from at least 2002. Since that time, this species has almost completely replaced *S. bicornis* on this host, so that the latter is now very rarely found. Both species are easily distinguishable by their micromorphological characteristics, although there is no obvious difference in the symptoms; however, *S. polyfida* is likely to cause stronger infection of the host plant than *S. bicornis*.

In mid-October 2025, when this article was undergoing final revision, the authors collected within Kyiv City several additional specimens of leaves of *Acer negundo* infected by powdery mildew (Table 1). Microscopic analysis of the specimens has demonstrated mainly fewer than 100 appendages per chasmothecium (Fig. 4A–C). The appendages were found to be 1(–2) times dichotomously branched, deeply cleft, branching from the middle of the stalk or quite often below, but very rarely above the middle of the stalk (Fig. 4D, E).Therefore, the freshly collected specimens were identified as *Sawadaea negundinis*, the expected in the country species, recently reported near Ukraine's southeastern border. Considering the potential for powdery mildews to spread rapidly, it is presumed that this fungus will soon be recorded in other European countries.

Conclusions

The present critical re-examination of all powdery mildew collections on *Acer negundo* in Ukraine has revealed that since the beginning of the 21st century *Sawadaea bicornis* on this host plant has been largely replaced by *S. polyfida*, a pathogen of maples introduced from East Asia. It is suggested that *S. polyfida* is likely spreading on boxelder maple in Europe beyond Ukraine. Another East Asian species, *S. negundinis*, has been recently recorded in the country on the same host, and its occurrence in several locations is reported in the present study. A comprehensive re-evaluation of the recent herbarium specimens of *Sawadaea* spp. on *Acer negundo* across the continent, followed by molecular confirmation, is therefore essential to understand the current distribution of these pathogens and assess its potential consequences.

ETHICS DECLARATION

The authors declare no conflict of interest.

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Які види роду *Sawadaea* (*Erysiphaceae*) уражують *Acer negundo* в Україні?

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Реферат. Унаслідок критичного перегляду колекції борошнисторосяних грибів доведено, що на початку XXI ст. на території України на американському клені (*Acer negundo*, *Sapindaceae*) поширився східноазійський борошнисторосяний гриб *Sawadaea polyfida*, який майже повністю замістив раніше відомий тут *S. bicornis*. Оскільки *S. polyfida* може траплятися і в Західній та Південній Європі, то зібрані там на *A. negundo* зразки борошнисторосяних грибів потребують додаткового критичного перегляду. У жовтні 2025 р. авторами статті було зібрано на території Києва кілька свіжих зразків листків *Acer negundo*, уражених ще одним грибом східноазійського походження — *Sawadaea negundinis*, якого нещодавно знаходили поблизу південно-східного кордону України. Враховуючи потенційні можливості блискавичного розповсюдження борошнисторосяних грибів, можна припустити, що цей вид найближчим часом також буде зареєстрованим і в інших європейських країнах.

Ключові слова: борошниста роса, Європа, інвазія, клен ясенелистий, поширення

PLANT TAXONOMY, GEOGRAPHY AND FLORISTICS
СИСТЕМАТИКА, ФЛОРИСТИКА, ГЕОГРАФІЯ РОСЛИН

https://doi.org/10.15407/ukrbotj82.05.407
RESEARCH ARTICLE

A new species of *Dysphania* (*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.) from north-central Mexico

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Abstract. *Dysphania siqueirosae* Sandoval-Ortega & Rodríguez-Pérez (*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.) is described as a new species from the states of Aguascalientes and Zacatecas (north-central Mexico). The new species is morphologically similar to *D. dissecta* but it can be distinguished from the latter by the perianth being subglobose to broadly ovate in fruit, utricle not visible between basal parts of the perianth segments, the perianth segments linear-lanceolate, keeled, joined by the scarious, accrescent, and wing-like margins.

Keywords: Aguascalientes, *Dysphanieae*, flora of Mexico

Introduction

With ca. 50 species, *Dysphania* R. Br. is the largest and most widespread genus in the tribe *Dysphanieae* Pax (*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.), with the greatest species diversity currently recorded in Australia and South America (see an overview in Uotila et al., 2021, and references therein).

A total of eight *Dysphania* species were earlier reported for Mexico (Sandoval-Ortega, Zumaya-Mendoza, 2025), of which six are considered native [*Dysphania ambrosioides* (L.) Mosyakin & Clemants, *D. anthelmintica* (L.) Mosyakin & Clemants, *D. atriplicifolia* (Spreng.) G. Kadereit, Sukhor. & Uotila (≡ *Cycloloma atriplicifolium* (Spreng.) Coult.), *D. dissecta* (Moq.) Mosyakin & Clemants, *D. stellata* (S. Watson) Mosyakin & Clemants, and *D. incisa* (Poir.) Sand.-Ort. & Zumaya (see, e.g., Clemants, Mosyakin, 2003; Villaseñor, 2016; Sandoval-Ortega et al., 2017; Mosyakin, 2021; POWO, 2025–onward; Sandoval-Ortega, Zumaya-Mendoza, 2025)] and two alien [*D. carinata* (R. Br.) Mosyakin & Clemants, native to Australia (Sandoval-Ortega et al., 2017) and *D. botrys* (L.) Mosyakin & Clemants, native to Europe and Asia (POWO, 2025–onward)].

In general, the infrageneric taxonomy of *Dysphania* is now rather well understood (see Uotila et al., 2021; Mosyakin, 2021), but several morphologically deviant

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Fig 1. Holotype of *Dysphania siqueirosae* (USON33715)

and geographically restricted taxa, in particular, *D. stellata* (S. Watson) Mosyakin & Clemants and *D. dissecta* (Moq.) Mosyakin & Clemants, and the South American *D. minuata* (Aellen) Mosyakin & Clemants, currently remain unplaced to sections or clades (see Mosyakin, Clemants, 2008; Uotila et al., 2021).



Fig. 2. *Dysphania siqueirosae*. A: general habit; B: close-up of the inflorescence

As part of the study of the flora of the states of Aguascalientes and Zacatecas (Mexico) (see, e.g., Sandoval-Ortega et al., 2019, 2020) and the taxonomic revision of the family *Amaranthaceae* s. l. of Mexico (Sandoval-Ortega, Zumaya-Mendoza, 2023a, 2023b; Zumaya-Mendoza, Sandoval-Ortega, 2025), we consulted herbarium specimens of *Dysphania* deposited in the main Mexican herbaria and noticed that some specimens collected in Aguascalientes did not match any of the species previously described from or reported for the country. Here we describe a new species of *Dysphania* and compare it with its morphologically closest relative.

Materials and Methods

From February 2022 to July 2025, the specimens of the genus *Dysphania* deposited in the herbaria ENCB, HUAA, HZAC, MEXU, UAZ (acronyms follow Thiers, 2025–onward) were examined.

Based on information from the specimens consulted, field surveys were carried out in the states of Aguascalientes and Zacatecas in search of the undescribed *Dysphania*. The material was collected and placed in the herbarium of the University of Sonora, Mexico (USON). Measurements were taken with a stereoscope, and a morphological description of a new taxon of the genus *Dysphania* was drafted.

A distribution map for the new species was prepared using QGIS program (QGIS.org, 2024), and the coordinates, if missing from a specimen, were assigned based on the collection location using Google Earth.

Description of the new species

***Dysphania siqueirosae* Sandoval-Ortega & Rodríguez-Pérez, sp. nov.**

Type: México, Zacatecas, municipio Pánuco, 2 km al NE de Pozo de Gamboa, márgenes del poblado Martín Díaz, 22°57’57”N, 102°32’51.1”W, 2105 m, 26 Jul. 2025, *Sandoval-Ortega 1308* (holotype USON 33715; isotypes HZAC, HUAA, MEXU). — Fig. 1.

Diagnosis:—*Dysphania siqueirosae* is similar to *D. dissecta* but it can be distinguished by the floral morphology: perianth subglobose to broadly ovate in fruit, utricle not visible between basal parts of the perianth segments (*versus* broadly turbinate in fruit, utricle visible between basal parts of the perianth segments), perianth segments linear-lanceolate, keeled, joined by the scarious, accrescent and wing-like margins (*versus* perianth segments spatulate, not contiguous, incurved, margins thin and inconspicuous).

Description:—Herbs, annual, aromatic, 5–20 cm tall, stems erect, pubescent with glandular and multicellular trichomes (Fig. 2). Leaves 20–35(50) × 10–15(25) mm, sparsely pinnatisect, lobes linear, as

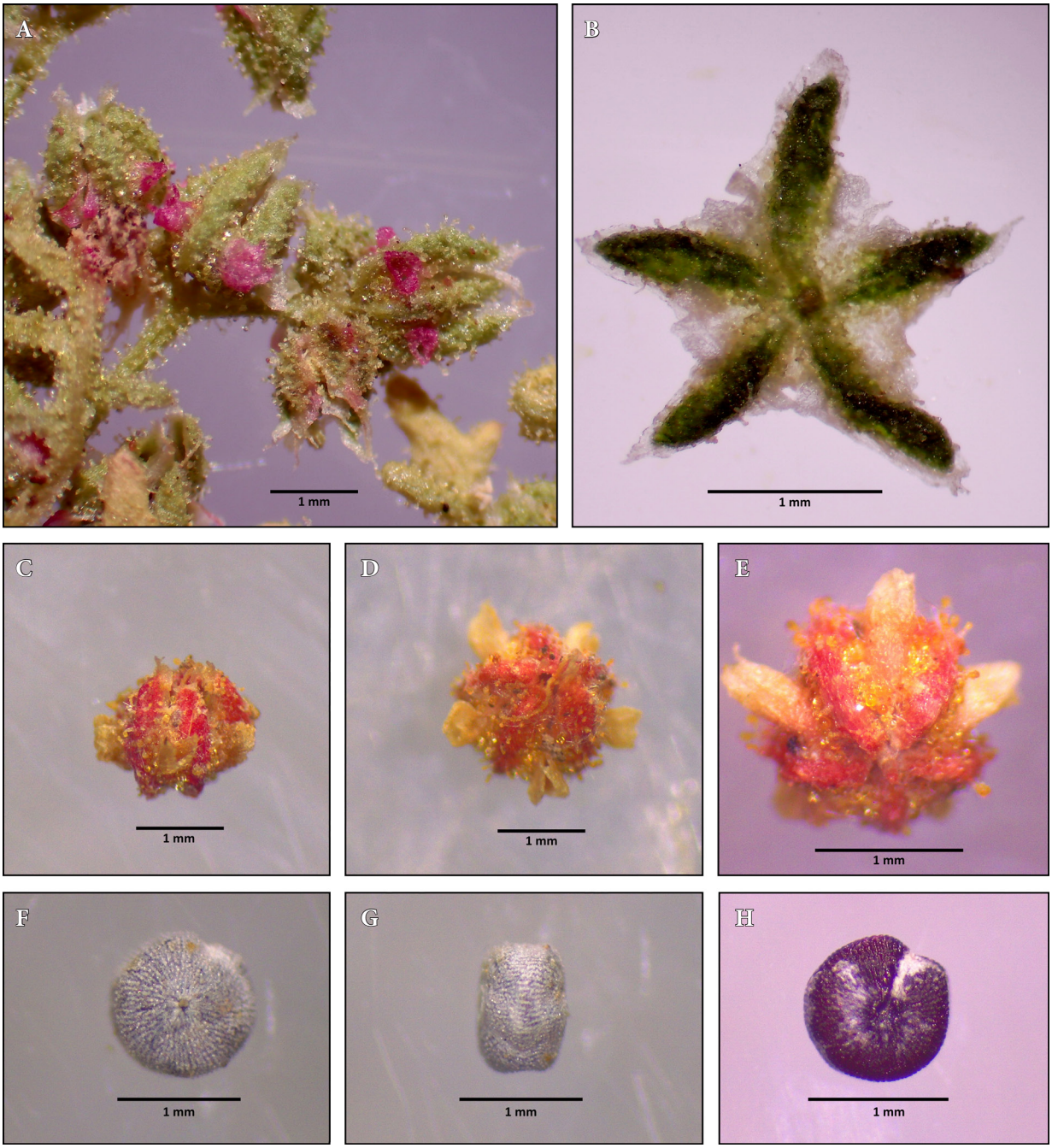


Fig. 3. *Dysphania siqueirosae*. A: inflorescence detail; B: opened perianth seen from below; C: lateral view of a fruiting perianth; D: upper view of a fruiting perianth; E: bottom view of a fruiting perianth; F: upper view of an utricle, with the pericarp attached to the seed; G: lateral view of an utricle, with the pericarp attached to the seed; H: partially naked seed

wide as the rachis or nearly so, with few very short secondary lobes, apex and lobes obtuse, adaxial surface with pubescence similar to the stems, abaxial surface with glandular and multicellular trichomes and sessile yellow glands. Inflorescences axillar and terminal, short paniculate, the branches with pubescence similar to the stems, flowers sessile to subsessile (Fig. 3A). Perianth subglobose to ovate,

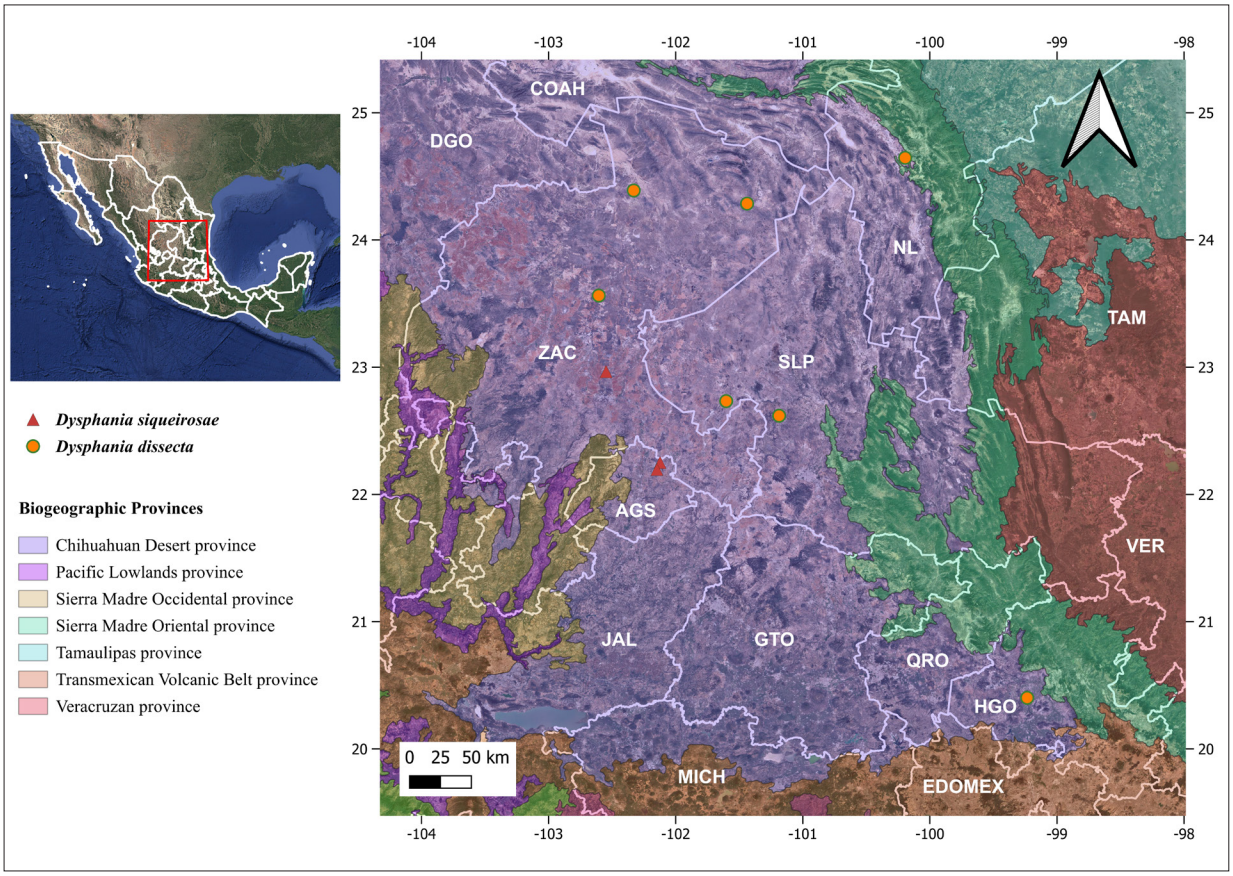


Fig. 4. Distribution of *Dysphania dissecta* and *D. siqueirosae* sp. nov. AGS — Aguascalientes; COAH — Coahuila; DGO — Durango; EDOMEX — Estado de México; GTO — Guanajuato; HGO — Hidalgo; JAL — Jalisco; MICH — Michoacán; NL — Nuevo León; QRO — Querétaro; SLP — San Luis Potosí; TAM — Tamaulipas; VER — Veracruz; ZAC — Zacatecas

segments 5, linear-lanceolate (Fig. 3B), 1.2–1.5 × ca. 0.5 mm, keeled on the midvein, basally joined by the scarious, white to purple, accrescent and wing-like margins that may extend up to 0.5 mm in fruit (Fig. 3C–E), apex acute, pubescent with glandular and multicellular trichomes and sessile yellow glands on the margins. Stamen 1, slightly exserted, ovary subglobose ca. 0.5 mm, stigmas 2, filiform, 1.5–2 mm long. Utricle attached to the seed, white (Fig. 3F, G), not visible between basal parts of the perianth segments. Seed ca. 1 mm in diameter, circular in outline, fairly thick, margins truncate, surface reticulate, black to dark brown (Fig. 3H).

Additional examined material of *Dysphania siqueirosae* (paratypes):—México, Aguascalientes, municipio Asientos, Caliza al S del cerro Palmira, 4 km al W de Asientos, 1 Sep. 1967, *Rzedowski 25089* (ENCB, without catalogue number but labeled as paratype); municipio Tepezalá, cañada arroyo Hondo ± 2 km al W de Puerto La Concepción, 10 Sep. 2000, *Rosales C. 1460* (HUAA 19463), 1 km al W de Puerto La Concepción, 11 Sep. 2000, *De la Cerda 6465* (HUAA 19466). Zacatecas, municipio Pánuco, km 14, carretera Zacatecas-Concepción del Oro, 23 Aug. 2002, *Balleza 13083* (UAZ 6657).

Phenology:—Flowering and fruiting from July to September.

Conservation status:—*Dysphania siqueirosae* is known so far only from three localities from the states of Aguascalientes and Zacatecas in Mexico. However, it is possible that this species has a wider distribution, since it occurs in secondary vegetation, roadsides and margins of crop fields but it is a small plant not so easy to detect, without showy flowers or striking color, which makes it go unnoticed among the neighboring vegetation. More extensive studies on the species are required to determine its conservation status. Therefore, following the guidelines of



Fig. 5. Habitat of *Dysphania siqueirosae*, in the municipality of Pánuco, Zacatecas, Mexico

the IUCN criteria (IUCN, 2025), *D. siqueirosae* is here assessed as Data Deficient (DD).

Etymology:—The new species is named after María Elena Siqueiros Delgado, Mexican botanist who has made great contributions to the study of the flora of Aguascalientes (see, e.g., Siqueiros-Delgado, 1996; Siqueiros-Delgado, González-Adame, 2006; Siqueiros-Delgado et al., 2011, 2016, 2017).

Distribution and habitat:—*Dysphania siqueirosae* grows on plains with gently sloping terrain and calcareous soil in the municipalities of Asientos and Tepezalá, in the NE of the state of Aguascalientes, and in the municipality of Pánuco, in the central part of the state of Zacatecas (Fig. 4). From 1800 to 2200 m a.s.l.

Dysphania siqueirosae is a locally common element of the open or dense xerophilous scrublands (Fig. 5) of the crassicaule, spiny, and microphyllous type in the region. It is also abundant in secondary vegetation derived from these scrublands, in areas near crop fields, roads, and urban zones. The tree layer may be represented by *Neltuma laevigata* (Humb. & Bonpl. ex Willd.) Britton & Rose, *Vachellia schaffneri* (S. Watson) Seigler & Ebinger, and *Yucca* spp. The shrub layer includes *Larrea tridentata* (DC.) Coville, *Vachellia constricta* (Benth.) Seigler & Ebinger, *Aloysia gratissima* (Gillies & Hook.) Tronc., *Brickellia veronicifolia* (Kunth) A. Gray, *Baccharis pteronioides* DC., *Mimosa zygophylla* Benth., *Calliandra eriophylla* Benth., *Dalea bicolor* Humb. & Bonpl. ex Willd., *Buddleja scordioides* Kunth, and *Condalia ericoides* (A. Gray) M.C. Johnst. Succulent species present include *Opuntia leucotricha* DC., *Opuntia robusta* H.L. Wendl. ex Pfeiff., *Cylindropuntia imbricata* (Haw.) F.M. Knuth, *Mammillaria uncinata* Zucc. ex Pfeiff., and *Jatropha dioica* Sessé ex Cerv. The herbaceous layer is composed of *Allionia incarnata* L., *Bouteloua curtipendula* (Michx.) Torr., *Muhlenbergia phleoides* (Kunth) Columbus, *Muhlenbergia rigida* (Kunth)

Table 1. **Morphological comparison between *Dysphania dissecta* and *D. siqueirosae***

Morphological characters	*D. dissecta*	*D. siqueirosae*
Flowers	Subsessile	Sessile to subsessile
Perianth shape	Broadly turbinate	Subglobose to broadly ovate
Shape of perianth segments	Oblanceolate to spatulate, incurved and gibbose near the apex	Linear-lanceolate, keeled, not incurved
Margins of perianth segments	Scarious, thin, inconspicuous	Scarious, prominent and wing-like at base



Fig. 6. Detail of inflorescence of an isolectotype of *Ambrina dissecta* (≡ *Dysphania dissecta*) deposited in Muséum National d'Histoire Naturelle (P00606420)

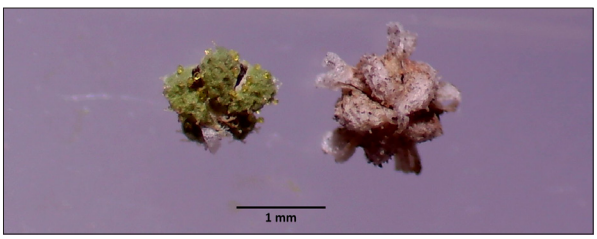


Fig. 7. Comparison of fruiting flowers from above between *Dysphania dissecta* (left) and *D. siqueirosae* (right)

Kunth, *Castilleja mexicana* (Hemsl.) A. Gray, *Oenothera hartwegii* Benth., *Dichondra argentea* Humb. & Bonpl. ex Willd., *Gaillardia comosa* A. Gray, *Zinnia acerosa* (DC.) A. Gray, *Mirabilis glabrifolia* (Ortega) I.M. Johnst., and *Thymophylla setifolia* Lag. In areas affected by disturbance, *Cenchrus ciliaris* L., *Tagetes lunulata* Ortega, *Zinnia peruviana* (L.) L., *Amaranthus palmeri* S. Watson, *Dysphania incisa* (Poir.) Sand.-Ort. & Zumaya, *Heterosperma pinnatum* Cav., *Malva parviflora* L., *Eruca vesicaria* (L.) Cav., and *Dalea foliolosa* (Aiton) Barneby are found.

Notes:—Herbarium specimens of *Dysphania siqueirosae* had been identified as *D. graveolens* (now recognized as *D. incisa*) or *D. dissecta*. However, after consulting the protologue of its basionym *Ambrina dissecta* (Moquin-Tandon, 1840: 38) and detailed images of the perianth of its lectotype and isolectotypes designated by Sandoval-Ortega & Zumaya-Mendoza (2025; Fig. 6), we confirm that the material here referred does not correspond to any previously described species.

Comparison to *Dysphania dissecta.* *Dysphania dissecta* seems to be the closest relative of *D. siqueirosae.* They can be differentiated from the floral morphology (see the diagnosis above, Table 1, and Figs. 3, 6, 7). The seeds of *D. siqueirosae* are also reticulated, a character previously reported only for *D. dissecta* within the genus *Dysphania* (Uotila et al., 2021); the pubescence is also similar, but in the perianth of *D. siqueirosae* is denser and the sessile glands are distributed on the margins of the segments, especially towards the base. They do not differ in habit, size or leaf shape. The habitat and altitudinal range in which they are distributed is also similar, both species are found in xerophilous scrublands and are restricted to the Chihuahuan Desert biogeographic province (*sensu* Morrone et al., 2017). Therefore, they could coexist at least in some places in the states of Aguascalientes, Zacatecas, and probably San Luis Potosí.

Examined material of *Dysphania dissecta* (for comparison):—México, Hidalgo, municipio Ixmiquilpan, Dadhó, 12 km al S de Ixmiquilpan, 10 Sep. 1981, *Hernández Magaña 6432* (MEXU363139). Nuevo León, municipio Galeana, 118 km al Norte de Matehual. S.L.P. sobre la carretera que va hacia Saltillo, Coah., 25 Sep. 1978, *García P. 688* (MEXU766727). San Luis Potosí, municipio Santo Domingo, Salineras de Santa María Salinas, aprox. 25 km al NE de Villa de Cos, Zacatecas, 29 Aug. 1983, *Villaseñor 540a* (MEXU488961); municipio Moctezuma, 35 km al SO de Venado, 10 Sep. 1973, *Banda, García, Rivera S.N.* (MEXU218312). Zacatecas, municipio Concepción del Oro, Campo experimental Noria de Guadalupe, CNIZA, 35 km al S de Concepción de Oro, 12 Jul. 1975, *González Medrano 8021* (MEXU275456); municipio Cañitas de Felipe Pescador, km 45 de

carretera Villa de Cos-Cañitas de Felipe Pescador, 19 Sep. 2002, *Balleza 13490* (UAZ6648); municipio Mazapil, 4 km al sur de Camacho, por la terracería a Opal, 4 Sep. 2003, *Balleza 16530* (UAZ6645).

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ETHICS DECLARATION

The authors declare no conflict of interest.

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Новий вид роду *Dysphania* (*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.) з північно-центральної Мексики

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Реферат. Описано новий вид *Dysphania siqueirosae* Sandoval-Ortega & Rodríguez-Pérez (*Chenopodiaceae* s. str. / *Amaranthaceae* s. l.) зі штатів Агуаскальєнтес і Сакатекас (північно-центральна Мексика). Новий вид є морфологічно подібним до *D. dissecta*, але відрізняється тим, оцвітина при плодах майже куляста до широкояйцеподібної, плід непомітний між базальними частинами листочків оцвітини, листочки оцвітини килюваті, при основі з'єднанні розрослими плівчастими крилоподібними краями.

Ключові слова: *Dysphanieae*, Агуаскальєнтес, флора Мексики

PLANT TAXONOMY, GEOGRAPHY AND FLORISTICS
СИСТЕМАТИКА, ФЛОРИСТИКА, ГЕОГРАФІЯ РОСЛИН

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RESEARCH ARTICLE

Поширення та еколого-ценотичні особливості *Sedum annuum* (*Crassulaceae*) в Україні

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Реферат. У статті узагальнено відомості про поширення аркто-альпійського виду *Sedum annuum* (*Crassulaceae*) в межах України, деякі його еколого-біологічні особливості та описані синантропні місцезростання. В Українських Карпатах *S. annuum* відзначений у 16 локалітетах у межах первинного (природного) ареалу. Зважаючи на порівняно невелику кількість локалітетів виду, він відповідає категорії регіонально рідкісної рослини. Нещодавно декілька місцезнаходжень *S. annuum* вторинного характеру було виявлено на території Житомирській області в басейні р. Уж, у межах Житомирського Полісся. Вторинні місцезростання *S. annuum* приурочені до гранітних відслонень вздовж берегів р. Уж, піщаних узбіч доріг, тріщин бетонних плит тощо, де вид трапляється в угрупованнях трьох синтаксонів: наскельних піонерних фітоценозів класу *Sedo-Scleranthetea* та рудеральних угруповань класів *Digitario sanguinalis-Eragrostietea minoris* і *Sisymbrietea*. Вид трапляється у ксерофітних добре освітлених умовах на субстратах з широким діапазоном кислотності — від кислих до ультраосновних, є невибагливим до трофності ґрунту. Ймовірним шляхом іммігрції виду до складу флори Полісся є колишнє культивування як декоративної рослини. Як адвентивний елемент флори, він має вважатися неофітом, ергазіофігофітом і колонофітом.

Ключові слова: біорізноманіття, Житомирська область, Карпати, натуралізація, популяції, поширення, флора, чужорідний вид

Вступ

На сьогодні флора України загалом є достатньо вивченою, особливо щодо її аборигенної складової. Але дослідження географічних та еколого-ценотичних особливостей окремих її представників, насамперед рідкісних, досі залишається актуальним (Sytnyk et al., 1998; Didukh, 2003; Crain et al., 2015). Вид *Sedum annuum* L. природно поширений в Україні у високогір'ї

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Українських Карпат. Його регіональні хорологічні відомості раніше були висвітлені лише в загальних рисах (Barbarych et al., 1950; Bordzilovskyi, 1953; Chopyk et al., 1977; Fedoronchuk, 2023). Вже давно висловлювалася думка про необхідність спеціального дослідження поширення та умов росту цього виду в Українських Карпатах (Chopyk, 1976), та згодом його було зараховано до категорії рідкісних рослин (Krichfalushiy et al., 1999). Цінність природних місцезростань *S. annuum* полягає в тому, що цей вид вважають гляціальним реліктом на межі його нинішнього природного ареалу (Cherepanyn, 2017).

Нині *S. annuum* офіційно охороняється на регіональному рівні в Закарпатській та Івано-Франківській областях (Ivano-Frankivsk…, 1996; Zakarpattia…, 2015). У зв'язку зі знахідкою вторинних місцезнаходжень *S. annuum* далеко за межами первинного ареалу, а саме в Житомирській області, у статті узагальнено відомості про первинне і вторинне поширення цього виду в Україні та його еколого-біологічні особливості.

Еколого-біологічні особливості. *Sedum annuum* — однорічна або (рідше) малорічна трав'яна рослина із секції *Epeteium* Boiss. роду *Sedum* L. родини *Crassulaceae* J. St.-Hil. (Bordzilovskyi, 1953; Stephenson, 1994; 't Hart, 2003). *Sedum annuum* морфологічно є близьким до *S. alpestre* Vill. та деяких інших видів секції *Epeteium* (Stephenson, 1994). У спробах поділити цю секцію на таксони нижчого рангу дослідники розглядали *S. annuum* у складі різних її рядів: ser. *Alpestria* Berger ('t Hart, 1995, 2003), ser. *Annua* Omelcz. (Omelchuk-Myakushko, 1980, 1981), ser. *Hispanica* Boriss. (Borissova, 1970). Нині *S. annuum* s. l. вважають політипічним видом, який включає типовий підвид *S. annuum* subsp. *annuum* і південноапеннінський ендемічний підвид *S. annuum* subsp. *gussonei* Brullo & Spamp. (Brullo, Spampinato, 2003). У нашій статті мова йтиме саме про *S. annuum* subsp. *annuum*.

Sedum annuum є рослиною, яка добре пристосована до утворення насіння та розмноження за несприятливих для перехресного запилення умов. Зокрема, в її квітці першими розкриваються зовнішні пиляки, вони беруть участь у перехресному запиленні, а внутрішні з'являються пізніше і розташовані на однаковій висоті з приймочками, і тому вони слугують для ефективного самозапилення рослини. В разі, якщо плоди не дозрівають, утворюються окремі розеткоподібні пагони, які беруть участь у вегетативному розмноженні (Hegi, 1975). У такому випадку рослина перетворюється на факультативний короткоживучий багаторічник із монокарпічними генеративними пагонами.

У Карпатах і Балканських горах спорадично трапляється *S. annuum* var. *perdurans* Murb. — багаторічна форма, у рослин якої вегетативні відростки основного пагону вкорінюються (International Crassulaceae Network, 2015). Багаторічні рослини *S. annuum* вказувалися і для Піренеїв (Stephenson, 1994). Крім того, із Греції було описано var. *epirolicum* Bald., а з Альп в Австрії — var. *alpinum* Bech. (Meusel et al., 1965), що вказує на певну поліморфність виду.

Ареал *Sedum annuum*. Цей вид хорологічно є гренландсько-європейсько-субсередземноморським географічним елементом. У роботі (Hultén, Fries, 1986) його охарактеризовано як аркто-монтанний і близький до амфіатлантичного вид. За Л.О. Тасєнкевич (Tasenkevych, 2006) — це аркто-альпійський вид. Первинний ареал *S. annuum* належить до голарктичного типу і складається з трьох основних фрагментів (Jansson, Rechinger, 1970; Gurgenidze, Ter-Khachaturova, 1979; Stephenson, 1994; 't Hart, 2003; Zernov, 2006; https://europlusmed.org):

1) Центральна та Південна Європа: трапляється переважно у гірських районах більшості гірських систем від Піренеїв та інших гір Іспанії до Карпат і Балканського півострова (Австрія, Албанія, Андорра, Болгарія, Греція, Іспанія, Італія, Косово, Німеччина, Північна Македонія, Румунія, Сербія, Словаччина, Словенія, Туреччина (європейська частина), Україна, Франція, Хорватія, Чорногорія, Швейцарія).

2) Гренландія та Північна Європа: острови Гренландія (можливо, адвентивний?) та Ісландія у Північній Атлантиці, Скандинавія та крайній північний захід Східної Європи — узбережжя та острови Фінської затоки (Данія, Ісландія, Норвегія, РФ (європейська частина), Фінляндія, Швеція).

3) Західна Азія: Мала Азія, Кавказ і північний Іран (Азербайджан, Вірменія, Грузія, Іран, РФ (азійська частина), Туреччина (азійська частина).

За межами первинного ареалу *S. annuum* зрідка трапляється як адвентивна рослина в Західній і Центральній Європі (https://www.gbif.org), зокрема в Чехії як випадковий неофіт (Hegi, 1975; Danihelka et al., 2012) та в Німеччині

як локально натуралізований вид (Hegi, 1975). Дещо дискусійний статус має природне походження локалітетів *S. annuum* на крайньому північному заході Східної Європи. Вказівка для Карелії (РФ) є сумнівною (Byalt, 2012), а в "Ленінградській" області він був наведений для двох островів у Фінській затоці і як здичавілий — на її північно-східному узбережжі (Byalt, 2012). Втім, і про локалітет на острові Гогланд ("Ленінградська" область, РФ) висловлено припущення про його вторинність внаслідок втечі з культури (Budantsev, 2006). Останнім часом місцезнаходження *S. annuum* у Ґренландії також зараховують до занесених (Ohba, 2009; https://powo.science.kew.org). Вказівки для материкової частини Північної Америки (https://www.gbif.org), очевидно, стосуються виключно культивованих рослин.

H. Meusel зі співавторами (Meusel et al., 1965) класифікують ареал *S. annuum* як: (m) – am – temp + b – arct • $oz_{1-(5)}$ Eur–Grenl, а діагноз його флористичного елементу як: submed – alpisch – (carp) + norv-grenl.

У межах первинного ареалу *S. annuum* росте на відкритих, переважно кам'янистих ділянках: на скелях, стінах і мурах, дорожніх насипах, щебенистих осипах, річкових відкладах; іноді на рідколіссях, на не надто сухих, багатих гумусом і вапном, ґрунтах. У Центральній і Південній Європі вид трапляється на висотах від (200–) 300 до 2800 м н.р.м., але переважно у субальпійському та альпійському висотних поясах (Meusel et al., 1965; Hegi, 1975; https://www.floraveg.eu/). У Скандинавії він піднімається з рівнини до 1350 м н.р.м. (Meusel et al., 1965), а у Туреччині росте на висотах 1830–2700 м н.р.м. (Chamberlain, 1972).

Ценотична характеристика. *Sedum annuum* є діагностичним видом союзу *Sedo-Scleranthion* Br.-Bl. et Richard 1950 (Korneck, 1975), а в ширшому контексті вважається діагностичним видом класу *Koelerio-Corynephoretea canescentis* Klika in Klika et Novák 1941 (Mucina et al., 2016) та біотопу U32 "Temperate high-mountain siliceous inland cliff" (Hegi, 1975; https://www.floraveg.eu/).

Угруповання з *S. annuum* у карпатській частині його ареалу належать до союзу *Sedo-Scleranthion*, який об'єднує піонерні угруповання кислих малопотужних ґрунтів на відслоненнях силікатних порід в Альпах та Карпатах (Mucina et al., 2016; Preislerová et al., 2022). На жаль, геоботанічні описи згаданих угруповань з території України нам не відомі. Клас *Sedo-Scleranthetea* взагалі поки що є недостатньо дослідженим в Україні (Dubyna et al., 2019). Кілька відомих місцезнаходжень *S. annuum* у межах України є окраїнними локалітетами Мармароського кристалічного масиву, з них наявні більш-менш детальні списки видів, зокрема, з г. Чивчин (Gorbyk, 1969) та г. Кобила (Kobiv et al., 2007). У локалітетах *S. annuum* ґрунти були мікропрофільні, з слабкокислою реакцією. Ймовірно, їх слід розглядати як збіднені варіанти асоціації *Sileno rupestris-Sedetum annuui* Oberd. 1957, яка наводиться, зокрема, для гори Торояги (Роднянські гори) в Румунії (Coldea, 1995, 1996; Sanda et al., 2008). У Словаччині *S. annuum* також зустрічається на скелях та осипищах, зазвичай як піонерна рослина, росте на силікатних породах, бідних на поживні речовини (Bertová, Zahradníková, 1985). В Альпах *S. annuum* трапляється в різноманітних угрупованнях союзу *Sedo-Scleranthion* (Korneck, 1975; Mucina, Kolbek, 1993). За межами Альпійсько-Карпатської системи вид також спостерігався на Балканах у різноманітних піонерних угрупованнях в широкому діапазоні реакції ґрунтів: від хазмофітних угруповань союзу *Edraianthion* Lakušić 1968 на серпентинах (Assenov, Pavlova, 2009; Lakušić, Karadžić, 2010; Dimitrov, Vutov, 2016), які є ультраосновними породами, та розріджених термофільних ценозів на карбонатах союзу *Alysso alyssoidis-Sedion* Oberd. et T. Müller in T. Müller 1961 (http://e-ecodb.bas.bg/rdb/en/vol3/01E1.html) до угруповань ацидофільних ефемерних пасовищ союзу *Romuleion* Oberd. 1954 (Čarni et al., 2014). На широкій екологічній амплітуді виду щодо типів та кислотності субстратів наголошувалося раніше (Niculae, Bârcă, 2006; Lakušić, Karadžić, 2010).

Аналіз місць трапляння *S. annuum* у Румунських Східних Карпатах (Bârcă, 2006) показав, що з 167 виявлених локалітетів вид спостерігався як у природних біотопах — гірських пасмах, де займав скелі та відслонення різноманітних гірських порід (гранітів, вапняків, пісковиків, конгломератів), окремих скель у лісах і луках, так і в антропогенних біотопах (населених пунктах, на узбіччях доріг, парковках) — переважно на окремих скелях та відслоненнях. Крім того, значна кількість локалітетів виду приурочена до штучних біотопів з кальцієвмісними субстратами — бетонних дамб і плит, мостів, старих мурів, дахів, вапнякових кар'єрів тощо.

В Україні вторинні локалітети на Поліссі належать до широкого діапазону угруповань, які утворюються на відкритих відслоненнях гранітів, а також місцезростаннях з несформованими, часто техногенними ґрунтами легкого механічного складу (піщаних або піщано-гравійних) з кислою реакцією, їхню характеристику наведено нижче.

Використання. *Sedum annuum* зрідка використовувався як декоративна рослина, але нині він не належить до популярних культур, зокрема вид відсутній у зведенні європейських декоративних рослин (Groendijk-Wilders, Springate, 2011). Через переважно однорічний цикл відтворення ця рослина рідко зберігається в культурі більше, ніж декілька сезонів поспіль, тому у декоративному садівництві нині розповсюджені стійкіші наскельні види. Успішним є вирощування *S. annuum* лише при забезпеченні особливо сприятливих для нього умов. Можливим є вирощування цього виду в гірських районах, а також за умов культивування його багаторічних форм (Stephenson, 1994). У Східній Європі *S. annuum* зрідка культивують на присадибних ділянках і парках на півночі європейської частини РФ (Budantsev, 2006; Byalt, 2012). В Україні нині *S. annuum* не використовується в озелененні, він відсутній у колекціях роду *Sedum* у ботанічних садах і дендрологічних парках (Sydoruk, 2003; Berezkina, 2007), не згадується серед декоративних рослин взагалі (Popovych et al., 2018). Але в гербарії CHER є один зразок із Косівського р-ну Івано-Франківської обл., на якому представлені ймовірно культивовані рослини, зібрані в 1963 р. біля закинутої садиби.

Вид є джерелом седогептулози (природний моносахарид) і вітаміну С (Hegi, 1975). Вказується, що ця рослина є медоносом (Cherepanyn, 2017).

Матеріали та методи

Вивчення поширення *S. annuum* в Україні було здійснено на основі аналізу гербарних матеріалів: Національного гербарію України Інституту ботаніки ім. М.Г. Холодного НАН України (KW), гербаріїв Національного ботанічного саду імені М.М. Гришка НАН України (KWHA), Інституту екології Карпат НАН України (LWKS), Державного природознавчого музею НАН України (LWS), а також літературних джерел та інших відомостей, зокрема електронних баз даних гербарію Masaryk University, Брно, Чехія (BRNU) (Masaryk…, 2025–onward) та гербарію Adam Mickiewicz University in Poznań, Познань, Польща (POZ) (Adam…, 2025–onward). Дані гербарних етикеток наведені повністю мовою оригіналу. У гербарії ботанічного саду Ужгородського національного університету (UU) зразків *S. annuum* не було виявлено. Акроніми гербаріїв наведено за *Index Herbariorum* (Thiers, 2025–onward).

Геоботанічні описи виконувалися за методикою V. Westhoff та E. van der Maarel (1973). Обробку фітоценотичних матеріалів здійснено за допомогою програми JUICE 7.1 (Tichý, 2002) з використанням модифікованого алгоритму TWINSPAN (Roleček et al., 2009). Класифікацію фітоценозів у місцях зростання *S. annuum* проведено на основі флористичної класифікації рослинності (Braun-Blanquet, 1964; Mucina et al., 2016; Dubyna et al., 2019). Характеристики *S. annuum* як чужорідної рослини у вторинному ареалі наведені за класифікаціями типу іммігрaції (Naegeli, Thellung, 1905) і ступенів натуралізації (Mosyakin, 1996). Назви судинних рослин наведено за ресурсом *Plant of the World Online* (https://powo.science.kew.org), мохів і лишайників — за *Catalogue of Life* (https://www.catalogueoflife.org).

Результати

Природний ареал в Україні

У межах України *S. annuum* був наведений для гірських районів Східних Карпат: Свидовець, Чорногора, Чивчино-Гринявські гори та Мармароські Альпи (Chopyk et al., 1977). У "Визначнику рослин України" (Barbarych, 1950) вид було наведено і для Правобережного Лісостепу України, але, імовірно, помилково. У роботі "Хорология флоры Украины" (Kondratyuk, 1986) поширення *S. annuum* у Карпатах наведено сітковим методом і включає шість комірок (розміром 10,6 × 11,2 км) із локалітетами виду. Нині локалітети *S. annuum* вказуються ще для Чорногори (гори Шпиці та Бребенескул) і Свидовця (гори Близниця та Догяска) (Cherepanyn, 2017), але вони потребують перевірки. За дослідженими матеріалами наводимо найповніший на сьогодні список місцезнаходжень *S. annuum* у межах первинного ареалу в Україні:

Закарпатська область. Рахівський р-н: **1.** Свидовець, 25.07.1975, В.М. Любченко (Каталог KWU54753). **2.** г. Кобила**,** південно-східний схил, 48.036689° N, 24.094747° E, висота 1145 м н.р.м., 09.07.2005, Кіш; г. Кобила, 48.04° N, 24.09° E, на каменях, 30.06.2010, A. Kovalchuk (https://ukrbin.com/index.php?id=96523&action=distribution); г. Кобила, східний край вершини, 29.07.2018, R. Gleb (https://www.inaturalist.org/observations/168635808); західний край вершини, 12.06.2021, R. Gleb (https://www.inaturalist.org/observations/170248686). **3.** Дорога на Піп Іван Мармароський, висота 950–1650 м. н.р.м., 25.07.1967, [В.І.] Чопик, [О.М.] Дубовик (KW s.n.). **4.** Мармароський заповідний масив Карпатського біосферного заповідника (Antosyak et al., 1997). Тячівський р-н: **5.** с. Мала Уголька, скелі Чур., 870 м. н.р.м., 20.06.1973, Тасє[нкевич] (LWS111989). **6.** Distr. Tjačiv, Teresva: pastionis ruderalis ad fluvium Teresva prope pag. Teresva, 25.05.1995, M. Hájek (BRNU587324) (цитовано за Masaryk…, 2025–onward). Ужгородський р-н: **7.** с. Новоселиця, гора Скала, на камнях (Вулканічний хребет), 29.06.1956, В. Чопик (KW s.n.); там само (Chopyk, 1957). **8.** Ужанський [національний] природний парк, хр. Стінка, 11.11.2004, І.М. Лесьо (LWS111357).

Івано-Франківська область. Верховинський р-н: **9.** Carpati Orientalis, Montes Czywczynenses: Budyjowska Wielka — po stronie poln.-wsch., na skalach wybuchowych (cieszynitach) — in rupibus eruptivis (cieszynitis) in latere orient., 15–1550 m, 12.08.1934, E. Czywcz. (KW s.n.); там само (BRNU279335) (цитовано за Masaryk…, 2025–onward); там само (POZ-V0041018) (цитовано за Adam…, 2025–onward); с. Буркут — окол., г. Будичевська, невеликі скелі на пд-сх. схилі (Velychko, 2005); Чивчинські гори (Pawłowski, 1937); г. Чивчин — південний схил, на скелях в субальпійському поясі, 13.06.1958, К. Малиновський (LWS104168); Чивчин. хр., г. Чивчин, пд-сх. схил, вапнякові камні над верх. межею лісу, 1650 м н.р.м., 02.07.1968, анонім (KW s.n.); г. Чивчин, пд-сх. схил, вапняк над верх. межею лісу, h = 1650 м н.р.м., 02.07.1968, анонім (KW s.n.); г. Чивчин, північно-східний схил, скелі, 03.09.1969, В. Чопик, К. Орнст, Г. Варенко, det. 2002, V. Byalt (sub nom. "*S. erythraeum* Griseb.?") (KW s.n.); г. Чивчин, на скелях (Gorbyk, 1969); там же, від лісового до альпійського поясів, 1000–1700 м н.р.м., рідко (Chopyk, 1976); г. Чивчин, 24.07.2003, [І.І.] Чорней, [М.В.] Величко, [В.В.] Буджак, [А.І.] Токарюк (CHER s.n.); г. Чивчин, скелі на верхній межі лісу, 28.05.2004, [І.І.] Чорней, [М.В.] Величко, [А.І.] Токарюк (CHER s.n.); г. Чивчин, вершина, 04.07.2004, [І.І.] Чорней, [М.В.] Величко, [В.В.] Буджак, [А.І.] Токарюк, [І.А.] Коротченко (CHER s.n.). **10.** Між Чивчином і "Peczelui", на скелях (Rehmann, 1868, 1873) [*примітка*: назва "Peczelui", імовірно, стосується якоїсь гори Мармароського масиву в Румунії]. Косівський р-н: **11.** [колишній] Кутский р-н, с. Белая Березка, у горы Писаный Камень, в еловом лесу, 12.07.1954, М. Котов, И. Теличко (sub nom. *S. alpestre* L.), det. 1971, Т. М'якушко (sub nom. *S. annuum*) (KW s.n.). **12.** село Яблуниця, присілок Сеньків [*примітка*: сучасна назва — с. Сеньківське], на подвір'ї закинутої садиби, 25.07.1963, leg. І.В. Артемчук, det. 03.03.1964, [нерозбірливий підпис] (sub nom. *Scleranthus annus* L.), det. 08.06.2003, N. Sytschak (sub nom. *S. annum*) (CHER s.n.) [*примітка*: імовірно, рослини було зібрано на місці культивування].

Чернівецька область. Вижницький р-н: **13.** Шепіт-Камерал, у чагарниках, 26.06.1965, анонім (KW s.n.) [2 гербарні аркуші]. **14.** с. Шепіт, г. Мелиш, 03.07.1966, Крись (KWHA106061, KWHA106062). **15.** окол. с. Селятин Вижницького р-ну, ялиновий ліс, 20.06.1963, Г.М. Сьомко (sub nom. *S. acre*), det. Т. М'якушко (sub nom. *S. annuum*) (CHER s.n.). **16.** Путильський р-н: Путильське лісництво, кв. 39, середина південно-східного схилу, 23.07.1962, З.Н. Горохова (sub nom. *S. acre* L.), det. Т. М'якушко (sub nom. *S. annuum*) (CHER s.n.). **17.** с. Русское, урочище Русское, сєвєро-западний склон, 07.07.1960, І.В. Артемчук (CHER s.n.; LWKS016365).

Отже, за гербарними матеріалами відомо 14 природних локалітетів виду в Українських Карпатах та один, який має культигенне походження (рис. 1). Літературні джерела переважно дублюють ці відомості. Два місцезнаходження з Ужгородського району Закарпатської області наведені для крайнього заходу Українських Карпат і приурочені до невисоких хребтів Попричний Верх (г. Скала) і Стінка. Інші відомі місцезнаходження *S. annuum* зосереджені у південній частині Українських Карпат — на півдні Горган, Свидовці, в Мармароських Альпах, Покутсько-Буковинських Карпатах, Чивчинах. Зважаючи на порівняно невелику кількість локалітетів виду, він відповідає категорії регіонально рідкісної рослини.

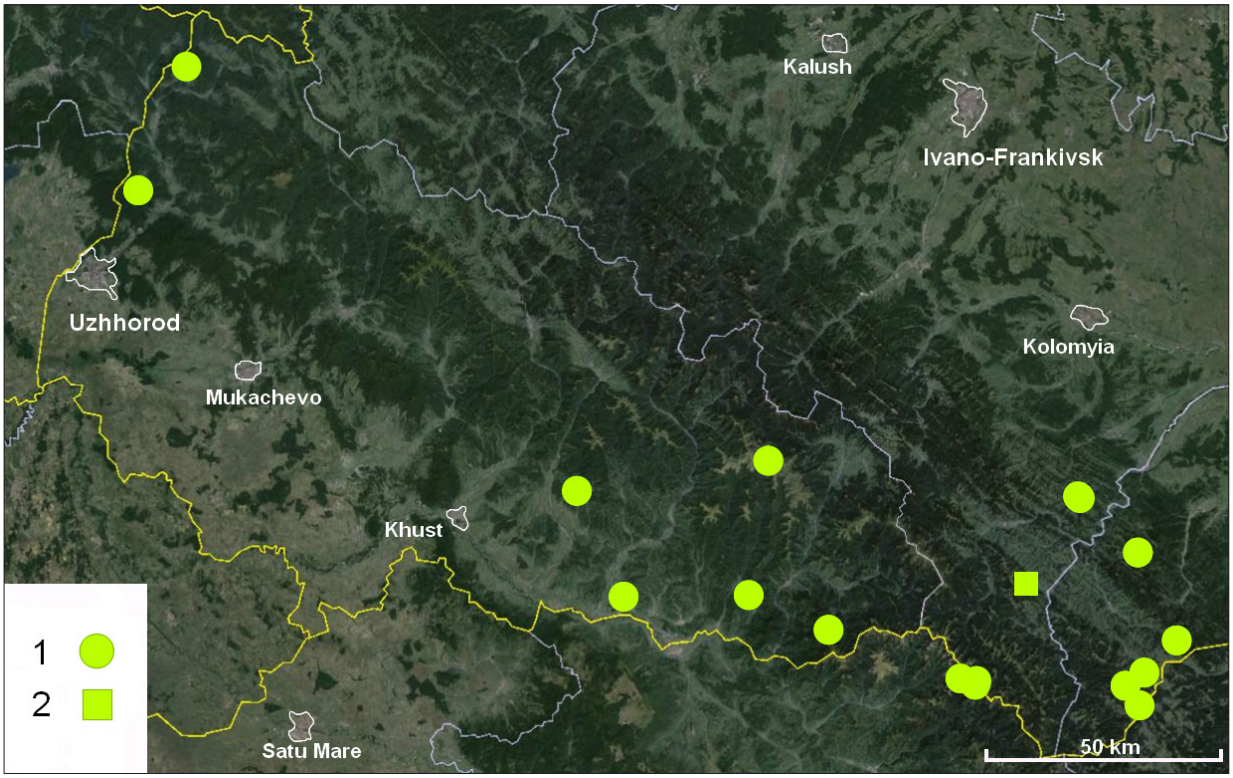


Рис. 1. Поширення *Sedum annuum* в Українських Карпатах: 1 — природні локалітети; 2 — локалітет культигенного походження

Fig. 1. Natural range of *Sedum annuum* in the Ukrainian Carpathians: 1 — native locations; 2 — a synanthropic location

Еколого-ценотичні особливості природних місцезростань

В Україні фітоценотичні умови місцезростань *S. annuum* у високогір'ї Карпат досі вивчені недостатньо. В.П. Горбик (Gorbyk, 1969) навів список рослин у складі високогірної наскельної рослинності на г. Чивчин у Закарпатській області, але не класифікував цей фітоценоз.

Наводимо геоботанічний опис місцезростання *S. annuum* на г. Кобила у Рахівському районі Закарпатськолї області. Ділянка розміром 3 × 1,5 м знаходиться нижче вершини, на південно-східному скелястому схилі крутістю 75–80°. Загальне проєктивне покриття наскельного угруповання — 65%, в т. ч. трав'яного ярусу — 35–40%, мохового — 15%, лишайникового — 20%. Площа незаросших скельних ділянок — 35%. Трав'яний покрив формують: *Asplenium trichomanes* L. (1), *Asplenium ruta-muraria* L. (+), *Campanula carpatica* Jacq. (+), *Dianthus carthusianorum* L. (+), *Euphorbia cyparissias* L. (+), *Festuca* sp. (1), *Galium intermedium* Schult. (+), *Hylotelephium vulgare* (Haw.) Holub (= *H. argutum* (Haw.) Holub) (+), *Poa nemoralis* L. (1), *Polypodium vulgare* L. (+), *Saxifraga paniculata* Mill. (1), *Sedum annuum* (+), *S. hispanicum* L. (+), *Sempervivum marmoreum* Griseb. (2), *Valeriana stolonifera* subsp. *angustifolia* Soó (1), У моховому ярусі переважають *Rhytidium rugosum* (Hedw.) Kindb. (1) та *Pylaisia polyantha* (Hedw.) Schimp. (+).

Незважаючи на те, що на г. Кобила відслонюються рідкісні в Українських Карпатах вапняки, ґрунт у тріщинах скелі в межах дослідженого місцезростання помірно кислий, із pH_{H20} = 5,2. Конгломератна основа не містить значної кількості $CaCO_3$.Однією з причин рідкісності виду в Карпатах вказується його низька конкурентноздатність та приуроченість до динамічних ценозів на початкових та проміжних стадіях сукцесій (Didukh, Chorney, 2016). Нещодавно була висловлена думка про доцільність внесення виду до регіонального Червоного списку Українських Карпат під категорією DD — Data Deficient (Cherepanyn, 2017). Загрозою існування *S. annuum* в Українських Карпатах є зміни



Рис. 2. Рослини *Sedum annuum* із вторинного місцезростання у Древлянському природному заповіднику, Житомирська обл. (фото О. Орлова, 23.06.2018)

Fig. 2. *Sedum annuum* from a secondary habitat in the Drevlyanskyi Nature Reserve, Zhytomyr Region (photo by O. Orlov, June 23, 2018)

оселищ. У межах природних популяцій рослини виду трапляються поодинокими особинами або невеликими групами у невеликих за площею локусах, але його популяційна структура досі залишається недослідженою (Cherepanyn, 2017).

Вторинний ареал в Україні

У публікації В.В. Монтрезора є вказівка, що *S. annuum* (із синонімом *S. saxatile* DC.) був виявлений Й. Собкевичем біля м. Житомир (Житомирська обл.), а професор І.Ф. Шмальгаузен знайшов його в м. Острог (Рівненська обл.) (Montresor, 1898). Згодом автор однієї із цих знахідок — Й.К. Собкевич — у неопублікованому рукописі, який зберігається у фондах Житомирського обласного краєзнавчого музею, написав (орієнтовно у 1901–1905 рр.) про *S. annuum*: "м. Житомир, на скелях, здичавіло". Пізніше *S. annuum* тут не знаходили, і, відповідно, місцезнаходження не цитували. Зокрема, І.Ф Шмальгаузен не навів *S. annuum* у своїй "Флорі" (Schmalhausen, 1895). Ми не бачили зразків виду в гербарії KW та інших гербаріях, тож ці вказівки залишаються непідтвердженими. Насправді достеменно не відомо, які саме рослини І.Ф. Шмальгаузен, Й.К. Собкевич і В.В. Монтрезор наводили під назвою *S. annuum*, оскільки гербарні збори відсутні.

Нещодавно декілька вторинних локалітетів *S. annuum* було виявлено в Житомирській обл. в басейні р. Уж, у межах природного регіону Житомирського Полісся (рис. 2). Вперше цю рослину з нового для Українського Полісся локалітету О.О. Орлов зібрав у 2016 р. в околицях с. Розсохівське колишнього Народицького району (нині — Коростенський), на території Природного заповідника "Древлянський", і вони були помилково визначені як *S. urvillei* DC. У наступні роки нові місця знахідок цього виду були виявлені неподалік. Частина із них — в долині р. Уж у різних місцях на гранітних відслоненнях в околицях с. Розсохівське та на бетонних плитах греблі в с. Поліське значно вище за течією р. Уж Дві локації були приурочені до піщаних узбіч доріг у селах Розсохівське, Малі Кліщі та Шишелівка. Всі ці місцезнаходження, безсумнівно, є вторинними, а їхній перелік наведений нижче.

Житомирська область. Коростенський р-н: **1.** м. Коростень, центр, у міському парку відпочинку, у шпаринах на пласких, добре освітлених верхівках гранітних скель, на правому березі р. Уж, невеликими групами, 10.06.1990,



Рис. 3. Аспект *Sedum annuum* на гранітному відслоненні в долині р. Уж в Древлянському природному заповіднику, Житомирська обл. (фото О. Орлова, 13.05.2024)

Fig. 3. Aspect of *Sedum annuum* on a granite outcrop in the Uzh River valley, Drevlyanskyi Nature Reserve, Zhytomyr Region (photo by O. Orlov, May 13, 2024)



Рис. 4. Аспект *Sedum annuum* у складі синантропного угруповання союзу *Eragrostion* на узбіччі дороги, с. Малі Кліщі, Житомирська обл. (фото О. Орлова, 13.05.2024)

Fig. 4. Aspect of *Sedum annuum* as part of the *Eragrostion* synanthropic communities on the roadside, Mali Klishchi village, Zhytomyr Region (photo by O. Orlov, May 13, 2024)

Орлов (non coll.). **2.** Природний заповідник (ПЗ) "Древлянський", Розсохівське природоохоронне науково-дослідне відділення (ПНДВ), с. Розсохівське, правий берег р. Уж, на відслоненнях гранітів, 09.11.2016, Орлов (sub nom. *S. urvillei* DC.), det. 24.04.2024, Шиндер (sub nom. *S. annuum*) (KW134325); 0.6 км зах. с. Розсохівське, на сонячних відслоненнях гранітів на правому березі р. Уж, 24.05.2018, Орлов (sub nom. *S. urvillei*), det. 24.04.2024, Шиндер (sub nom. *S. annuum*) (KW134381); там само, 13.05.2024, Орлов (https://www.inaturalist.org/observations/225658038) (рис. 3); ПЗ "Древлянський", Розсохівське ПНДВ, 0,6 км від с. Розсохівське, на правому березі р. Уж, на гранітах, 23.06.2018, Орлов (sub nom. *S. urvillei*), det. 24.04.2024, Шиндер (sub nom. *S. annuum*) (KW134378) (https://www.inaturalist.org/observations/223931769) (рис. 2); там само, 12.05.2024, Орлов (KW166234). **3.** с. Поліське, долина р. Уж, у шпаринах бетону на греблі, 25.09.2018, leg. Орлов, det. 04.10.2018, L. Zavialova (sub nom. *S. urvillei*), det. 24.04.2024, Шиндер (sub nom. *S. annuum*) (KW136352). **4.** ПЗ "Древлянський", Базарське ПНДВ, с. Малі Кліщі (нині виселене), на узбіччі дороги, багато, 01.08.2018, leg. Орлов, det. 04.08.2018, Л. Зав'ялова (sub nom. *S. urvillei*), det. 24.04.2024, Шиндер (sub nom. *S. annuum*) (KW134368, KW134479); там само, західні околиці виселеного села Малі Кліщі, на добре освітлених відкритих та напівзатінених, піщаних, слабозадернованих узбіччях дороги, 51.122914° N, 29.150508° E, 28.08.2023, Орлов (KW s.n.); там само, 13.05.2024, Орлов (https://www.inaturalist.org/observations/223931768) (рис. 4). **5.** ПЗ "Древлянський", окол. с. Шишелівка, на піщаному узбіччі дороги, багато, 28.08.2023, Орлов (KW163100).

Отже, загалом виявлено п'ять окремих локалітетів *S. annuum* на Житомирському Поліссі (рис. 5). Вірогідно, *S. annuum* колись вирощувався як декоративна рослина у панському маєтку, який існував наприкінці XIX ст. в крайній західній частині с. Розсохівське Коростенського р-ну, але до нашого часу не зберігся. Однак сліди декоративних рослин, які використовуються в квітниках та рокаріях, в околицях села збереглися й донині на гранітних відслоненнях. Зокрема *Phedimus spurius* (M. Bieb.) 't Hart тут натуралізувався і на пласких, добре освітлених гранітних відслоненнях, сформував колонію на площі близько 150 м^2, поодиноко там само також



Рис. 5. Вторинний ареал *Sedum annuum* у Житомирській області
Fig. 5. Secondary range of *Sedum annuum* in Zhytomyr Region

трапляються особини *P. hybridus* (L.) 't Hart. Імовірно, колишня панська садиба була первинним місцем інтродукції *S. annuum* у долині р. Уж, а згодом цю рослину могли розповсюдити місцеві жителі по прилеглих селах, де вид натуралізувався та нині сформував стійкі колонії.

Особливістю життєвого циклу *S. annuum* на півночі Житомирської області є те, що вид розвивається за типом озимого однорічника. Рослини добре цвітуть (травень — початок червня) і плодоносять (кінець червня — початок липня). Насіння швидко проростає і вже у жовтні–листопаді в місцях трапляння виду формуються молоді кулеподібні імматурні особини, діаметром 1–2 см з щільно розташованим листям коричнево-червоного кольору. Ці особини успішно перезимовують (рис. 6) і вже у травні наступного року формують квітконоси. Це дає підстави зарахувати *S. annuum* в цих умовах до озимих однорічників, хамефітів.

Отже, нині в Україні ареал *S. annuum* складається з двох фрагментів (рис. 7). Природний ареал охоплює високогір'я Українських Карпат у Закарпатській, Івано-Франківській та Чернівецькій областях, а в Житомирській сформувався вторинний синантропний ареал. У цьому фрагменті ареалу *S. annuum* є неофітом, ергазіофігофітом — втікачем із культури, за ступенем натуралізації — колонофітом. Локалітети за старою вказівкою XIX ст. із околиць м. Острог та м. Житомир ми не наводимо через їхній непідтверджений статус і, цілком можливо, помилковість.

Натуралізація *S. annuum* у Житомирській області наразі перебуває на початковій стадії. Ймовірно, етап закріплення в нових еколого-ценотичних умовах уже було пройдено, тож надалі можливе поступове розповсюдження виду вздовж долини р. Уж на прилеглі території. Цьому можуть сприяти особливості життєвого циклу *S. annuum* в умовах Житомирського Полісся. Вид використовує достатню весняну та осінню вологу для розвитку вегетативної частини, а високі температури кінця весни та початку літа — для цвітіння та дозрівання насіння, що збільшує його конкурентоспроможність.

Виникнення вторинного синантропного ареалу як у *S. annuum* характерне для багатьох видів родини *Crassulaceae*. Так, в Україні відомими є факти розповсюдження у вторинних ареалах *S. album* L., *S. hispanicum*, *S. pallidum* M. Bieb., *Sempervivum tectorum* L. (Bordzilovskyi, 1953; Derevinskaya et al., 1998; Davydov, 2021; Shynder, Negrash, 2020; Orlov et al., 2022; Orlov, Shynder, 2024), а також дичавіння і натуралізації чужорідних рослин: *Hylotelephium spectabile* (Boreau) H. Ohba, *Petrosedum rupestre* (L.) P.V. Heath, *P. sediforme* (Jacq.) Grulich, *Phedimus aizoon* (L.) 't Hart, *P. hybridus*, *P. spurius*, *Sedum sarmentosum* Bunge (Fodor, Yantso, 1984; Myakushko et al., 1988; Zavyalova, 2008; Moysiyenko, 2011; Boiko,



Рис. 6. Вегетативні розетки *Sedum annuum* після перезимівлі на гранітних відслоненнях у долині р. Уж, околиці с. Розсохівське, Житомирська обл. (фото М. Весельського, 09.03.2024)

Fig. 6. Vegetative rosettes of *Sedum annuum* after overwintering on granite outcrops in the Uzh River valley, near the village of Rozsokhivske, Zhytomyr Region (Photo by M. Veselsky, March 09, 2024)

Mulienkova, 2014; Boiko, Kolomiychuk, 2015; Vasylyeva et al., 2019; Shynder, Negrash, 2021; Tokaryuk et al., 2022; Kalashnik, Shynder, 2024; Shynder et al., 2024; Andrik et al., 2025).

Еколого-ценотичні особливості у вторинних локалітетах

Було детально обстежено чотири вторинні місцезростання *S. annuum* у Коростенському р-ні Житомирської обл. та описано їхній рослинний покрив, представлений угрупованнями з трьох різних класів (табл. 1).

За результатами фітоценотичного аналізу було встановлено, що місцезростання *S. annuum* із західних околиць с. Розсохівське (описи 1–3) приурочені до угруповання зі складу союзу *Hyperico perforati-Scleranthion perennis* порядку *Sedo-Scleranthetalia* класу *Sedo-Scleranthetea*. Цей союз представляє маловидові піонерні угруповання із помітною роллю мохово-лишайникового ярусу, що формуються на відслоненнях силікатних, зокрема гранітних порід на освітлених або, рідше, затінених схилах різної крутості та експозиції (Dubyna et al., 2019). Ці угруповання в Україні є типовими на відслоненнях Українського кристалічного щита (Kuzemko…, 2018).

Наразі порівняно невеликі розміри виявлених місцезростань *S. annuum* не дають змоги провести класифікацію угруповань із їхньою участю до рівня асоціацій, але за попередньою оцінкою, описані фітоценози зі складу союзу *Hyperico perforati-Scleranthion perennis* представлені імовірно асоціацією *Allio montani-Veronicetum vernae* Oberd. 1957. Ця асоціація включає діагностичні види союзу *Sedo albi-Veronicion dillenii* Korneck 1974 (*Hyperico perforati-Scleranthion perennis* sensu Didukh, 2019), зокрема *Hylotelephium maximum* subsp. *ruprechtii* (Jalas) Dostál, *Hypericum perforatum* L., *Poa compressa* L., *Grimmia pulvinata* (Hedw.) Sm., *Hedwigia ciliata* (Hedw.) Boucher, а також класу *Sedo-Scleranthetea* в цілому, в т. ч. *Allium lusitanicum* Lam., *Arabidopsis arenosa* (L.) Lawalrée, *Draba verna* L., *Hypnum cupressiforme* Hedw., *Niphotrichum canescens* (Hedw.) Bedn.-Ochyra & Ochyra, *Veronica dillenii* Crantz. *Sedum annuum* характеризується проєктивним покриттям 20–35%, утворює невеликі за розміром куртини площею 4–6 м^2, які формуються на відкритих, добре освітлених скелях та відслоненнях гранітів різної експозиції та крутизни — від майже пласких горизонтальних відслонень до гранітних схилів крутизною 15–20° та вузьких "поличок" на майже вертикальних стінках. Проєктивне покриття судинних рослин становить 33–37%, флористична насиченість — 11–18 видів. Для згаданих угруповань характерним є сильний розвиток мохового покриву з проєктивним покриттям від 50 до 95%.

Класифікаційна схема рослинності з участю *Sedum annuum* у Житомирському Поліссі

1. Cl. *Sedo-Scleranthetea* Br.-Bl. 1955
Ord. *Sedo-Scleranthetalia* Br.-Bl. 1955
All. *Sedo albi-Veronicion dillenii* Korneck 1974 (*Hyperico perforati-Scleranthion perennis* Moravec 1967 sensu Didukh, 2019; *Poo compressae-Rumicion acetosellae* Didukh et Kontar 1998) (Didukh, 2019).
2. Cl. *Digitario sanguinalis-Eragrostietea minoris* Mucina, Lososová et Šilc in Mucina et al. 2016
Ord. *Eragrostietalia* J. Tx. ex Poli 1966
All. *Eragrostion* Tx. in Oberd. 1954
3. Cl. *Sisymbrietea* Gutte et Hilbig 1975
Ord. *Sisymbrietalia sophiae* J. Tx. ex Görs 1966
All. *Sisymbrion officinalis* Tx. et al. ex von Rochow 1951

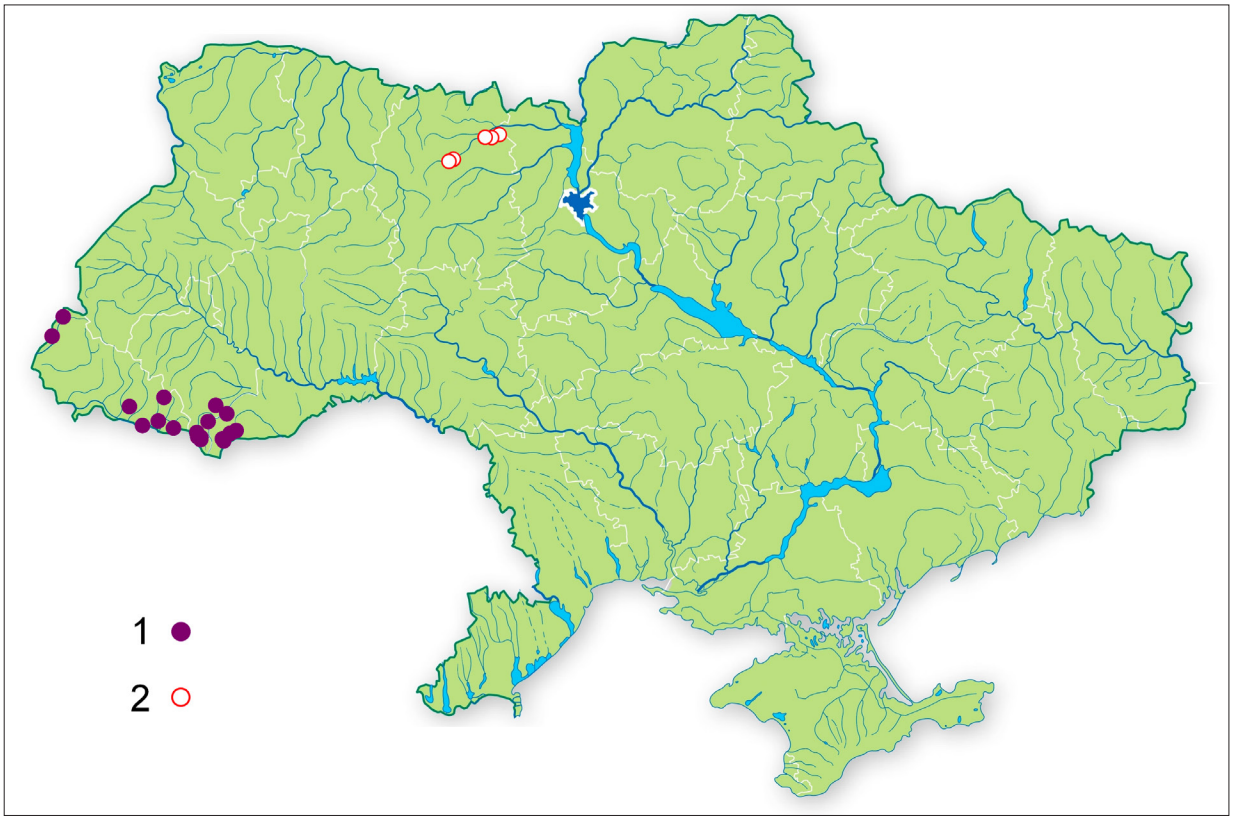


Рис. 7. Загальне поширення *Sedum annuum* в Україні: місцезростання у межах первинного (1) та вторинного (2) ареалів

Fig. 7. General distribution of *Sedum annuum* in Ukraine: 1 — native locations; 2 — secondary locations

Домінують в ньому *Hedwigia ciliata*, *Niphotrichum canescens*, *Hypnum cupressiforme*. Також постійними видами є лишайники з проєктивним покриттям 5–45% — *Aspicilia cinerea* (L.) Körb., *Cladonia mitis* Sandst. та ін.

Участь *S. annuum* у складі петрофітних угруповань союзу *Sedo-Scleranthion* Br.-Bl. et Richard 1950 класу *Sedo-Scleranthetea* було відмічено для Центральної Європи (Ellenberg, 1986). Отже, в Україні локальне проникнення *S. annuum* до складу низовинних наскельних угруповань фітоценотично є подібним до аналогічних умов Центральної Європи.

Оселища в околицях сіл Малі Кліщі та Шишелівка (описи 4 і 5) приурочені до угруповання зі складу союзу *Eragrostion* порядку *Eragrostietalia* класу *Digitario sanguinalis-Eragrostietea minoris*. Цей союз представляє сегетальні і рудеральні угруповання ксерофітних місцезростань, які трапляються по всій території України (Kuzemko…, 2018; Dubyna et al., 2019).

Описані угруповання ймовірно відносяться до асоціації *Digitario sanguinalis-Eragrostietum minoris* Tx. ex von Rochow 1951. Це динамічне рудеральне угруповання, яке характеризується значною участю діагностичних видів класу *Digitario sanguinalis-Eragrostietea minoris* Mucina, Lososová et Šilc in Mucina et al. 2016, зокрема *Bromus tectorum* L. і *Eragrostis minor* Host, які є домінантами й співдомінантами угруповань, та *Portulaca oleracea* L. s. l. За цих умов *S. annuum* має проєктивне покриття 10–30% та утворює смуги шириною 0,4–8,0 м та довжиною 5–6 м, переважно на добре освітлених або затінених меншу частину дня узбіччях доріг з піщаними або гравійно-піщаними кислими техногенними ґрунтами. Проєктивне покриття судинних рослин становить 40–50%, флористична насиченість — 8–10 видів. Значну ценотичну роль

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Таблиця 1. **Фітоценотична характеристика угруповань з участю *Sedum annuum* у Житомирському Поліссі**
Table 1. **Relevés containing *Sedum annuum* in Zhytomyr Polissia**

№ опису	1	2	3	4	5	6
№ синтаксону	1			2		3
Площа опису, м^2	4	4	4	2	2	2
Проєктивне покриття судинних рослин, %	35	33	37	46	38	50
Проєктивне покриття мохів та лишайників, %	70	50	95	0	0	0
Кількість видів судинних рослин	18	16	11	8	8	15
Sedum annuum	2	3	3	3	2	2
Діагностичні види союзу *Sedo albi-Veronicion dillenii* Korneck 1974 (*Hyperico perforati-Scleranthion perennis* sensu Didukh 2019)						
Hylotelephium maximum subsp· *ruprechtii*	+	r	·	·	·	r
Hypericum perforatum	r	r	·	·	·	·
Poa compressa	1	1	+	·	·	·
Grimmia pulvinata	·	1	1	·	·	·
Hedwigia ciliata	2	3	4	·	·	·
Діагностичні види класу *Sedo-Scleranthetea*						
Veronica dillenii	+	1	r	·	r	+
Allium lusitanicum	1	1	+	·	·	·
Draba verna	+	+	·	·	·	·
Arabidopsis arenosa	+	·	·	·	·	·
Sedum acre	+	·	·	·	·	·
Veronica verna	+	·	·	·	·	·
Niphotrichum canescens	2	2	1	·	·	·
Hypnum cupressiforme	3	·	·	·	·	·
Діагностичні види класу *Digitario sanguinalis-Eragrostietea minoris*						
Bromus tectorum	·	·	·	1	1	2
Eragrostis minor	·	·	·	2	2	·
Portulaca oleracea	·	·	·	r	r	·
Діагностичні види класу *Sisymbrietea*						
Bromus hordeaceus	·	·	·	·	·	r
Capsella bursa-pastoris	·	·	·	·	·	r
Інші види						
Psammophiliella muralis	r	r	r	·	r	·
Potentilla argentea	·	r	r	·	·	+
Aspicilia cinerea	1	2	2	·	·	·
Cladonia mitis	·	1	3	·	·	·
Viola tricolor	+	·	·	·	·	r
Poa annua	·	·	·	·	·	1
Viola arvensis	·	·	·	r	r	r
Poa nemoralis	r	·	·	·	·	·
Viscaria vulgaris	·	r	·	·	·	·
Veronica incana	·	r	·	·	·	·
Artemisia scoparia	·	·	·	r	·	·
Erysimum cheiranthoides	·	·	·	r	·	·
Veronica arvensis	·	·	·	r	·	·
Scleranthus annuus	·	·	·	·	r	·
Cerastium semidecandrum	·	·	·	·	·	r
Dactylis glomerata	·	·	·	·	·	r
Elymus repens	·	·	·	·	·	1
Lamium purpureum	·	·	·	·	·	r
Poa pratensis	·	·	·	·	·	1

Опис № 1. Древлянський ПЗ, Розсохівське ПНДВ, зах. окол. с. Розсохівське, освітлені, майже горизонтальні гранітні відслонення на правому березі р. Уж, 13.05.2024, Орлов (KW166234). Координати: 51.130336° N, 29.000547° E.

Опис № 2. Древлянський ПЗ, Розсохівське ПНДВ, зах. окол. с. Розсохівське, освітлені гранітні відслонення на правому березі р. Уж, 13.05.2024, Орлов. Координати: 51.130283° N, 29.00075° E (рис. 3).

Опис № 3. Древлянський ПЗ, Розсохівське ПНДВ, 160 м зах. с. Розсохівське, на відкритих гранітних відслоненнях західної експозиції, крутістю 15–17°, на правому березі р. Уж, 12.05.2023, Орлов. Координати: 51.13015° N, 28.999861° E.

Опис № 4. Древлянський ПЗ, Базарське ПНДВ, західні околиці виселеного с. Малі Кліщі, на добре освітлених відкритих та напівзатінених, піщаних, слабо задернованих узбіччях дороги, 28.08.2023, Орлов (KW163100). Координати: 51.122914° N, 29.150508° E.

Опис № 5. Древлянський ПЗ, Базарське ПНДВ, західні околиці виселеного с. Шишеловка, на добре освітлених відкритих та напівзатінених, піщаних, слабо задернованих узбіччях дороги, 28.08.2023, Орлов (KW163101). Координати: 51.145069° N, 29.222117° E.

Опис № 6. Древлянський ПЗ, с. Розсохівське, піщане освітлене узбіччя дороги, смуга шириною 0,5 м та довжиною 6 м, 13.05.2024, Орлов. Координати: 51.124294° N, 29.002661° E.

відіграють однорічники. Наявна вільна еконіша для вселення інших видів рослин.

Угруповання оселища *S. annuum* в околиці с. Розсохівське, приуроченого до піщаного узбіччя дороги (Опис № 6), класифіковане як союз *Sisymbrion officinalis* класу *Sisymbrietea*. Воно має ознаки асоціації *Linario-Brometum tectorum* Knapp 1961 (syn. *Brometum tectorum* Bojko 1934) і також представляє динамічне рудеральне угруповання з участю діагностичних видів класу *Sisymbrietea*, зокрема *Bromus hordeaceus* L., *Capsella bursa-pastoris* (L.) Medik., а також виду класу *Digitario sanguinalis-Eragrostietea minoris — Bromus tectorum*. Умови зростання *S. annuum* є подібні до таких в асоціації *Digitario sanguinalis-Eragrostietum minoris*, вид має проєктивне покриття 20% і зростає смугами (0,4–0,8 × 5–6 м) переважно на добре освітлених узбіччях доріг з піщаними кислими техногенними ґрунтами. Проєктивне покриття судинних рослин становить 40–50%, флористична насиченість — 12–15 видів. До складу угруповань як домішка входять численні мезотрофні мезофітні види, зокрема *Dactylis glomerata* L., *Elymus repens* (L.) Gould (*Elytrigia repens* (L.) Nevski), *Poa pratensis* L., *P. annua* L. та ін. Наявна вільна еконіша для вселення інших видів рослин.

Отже, у Житомирському Поліссі біотопи, в яких відзначено *S. annuum*, є різноманітними. Вид спостерігався на гранітних скелях та відслоненнях різної експозиції і крутизни (м. Коростень, с. Розсохівське Коростенського р-ну) у біотопі 8230 "Siliceous rock with pioneer vegetation of the *Sedo-Scleranthion* or of the *Sedo albi-Veronicion dillenii*" (Council Directive, 2025), а також на узбіччі доріг з піщаними техногенними ґрунтами (с. Розсохівське, с. Великі Кліщі, с. Шишелівка Коростенського р-ну). В одному локалітеті (с. Поліське Коростенського р-ну) вид траплявся у шпаринах бетонної дамби на р. Уж. Згідно з класифікацією EUNIS, біотопи силікатних та карбонатних скель і відслонень із піонерною рослинністю, багатою на види родини *Crassulaceae*, а також лишайники та мохи, належать до типу R122 "Sparsely vegetated weathered rock and outcrop habitats" (EUNIS, 2021). Такі біотопи охороняються відповідно до Додатку I Оселищної Директиви ЄС як біотопи 6110 "Rupicolous calcareous or basophilic grasslands of *Alysso-Sedion albi*" та 8230 "Siliceous rock with pioneer vegetation of the *Sedo-Scleranthion* or of the *Sedo albi-Veronicion dillenii*" (Council Directive, 2025).

Проникнення *S. annuum* до складу як рудеральних, так і природних піонерних угруповань на території Житомирської області свідчить про успішність початкових етапів натуралізації виду. У теперішній час він є колонофітом, зважаючи на локальність виявлених популяцій виду на гранітних відслоненнях у долині р. Уж.

Висновки

Отже, вперше нами узагальнено гербарні та літературні відомості про поширення *S. annuum* в Україні. Цей вид перебуває на східній межі природного ареалу в Українських Карпатах, а також, як і в деяких інших країнах, сформував ділянку вторинного ареалу. Загалом в Українських Карпатах відомо 16 природних локалітетів *S. annuum*, а в Житомирській області виявлено шість його вторинних локалітетів, із яких два знаходяться на гранітних відслоненнях у долині р. Уж, один — на бетонній греблі на р. Уж, а ще три — у прилеглих населених пунктах на узбіччях доріг.

Вид є новим чужорідним видом для Полісся, як неофіт, ергазіофігофіт. У Поліссі спочатку він був, імовірно, інтродукований як декоративна рослина, а згодом натуралізувався на скельних відслоненнях по р. Уж та у синантропних угрупованнях уздовж доріг. В умовах Житомирського Полісся у *S. annuum* спостерігається життєва форма озимого однорічника, хамефіта.

Встановлено, що вторинні оселища *S. annuum* приурочені до угруповань трьох класів рослинності: наскельних піонерних угруповань союзу *Sedo albi-Veronicion dillenii* класу *Sedo-Scleranthetea* та придорожних рудеральних угруповань союзу *Eragrostion* класу *Digitario sanguinalis-Eragrostietea minoris* та союзу *Sisymbrion officinalis* класу *Sisymbrietea*. Всі місцезростання у Житомирському Поліссі утворилися на несформованих, часто техногенних, ґрунтах легкого механічного складу (піщаних або рухляково-гравійних) з кислою реакцією. За ступенем натуралізації у вторинному ареалі *S. annuum* є колонофітом.

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Distribution, ecological and coenotic features of *Sedum annuum* (*Crassulaceae*) in Ukraine

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Abstract. This article summarizes information on the natural and synanthropic distribution of the arcto-alpine species *Sedum annuum* (*Crassulaceae*) within Ukraine, its ecological and biological characteristics, and descriptions of its synanthropic habitats. In the Ukrainian Carpathians, *S. annuum* has been recorded in 16 localities within its natural range. Given the relatively low number of known occurrences, the species qualifies as regionally rare. Recently, several secondary occurrences of *S. annuum* were discovered in Zhytomyr Region, within the Uzh River basin, in the natural region of Zhytomyr Polissia. The secondary habitats of *S. annuum* are confined to roadsides along asphalted roads, cracks in concrete slabs, and granite outcrops along the Uzh River. The studied secondary habitats of *S. annuum* are associated with plant communities from three syntaxa: pioneer rock communities of the alliance *Sedo albi-Veronicion dillenii* within the class *Sedo-Scleranthetea*, ruderal roadside communities of the alliance *Eragrostion* within the class *Digitario sanguinalis-Eragrostietea minoris*, and the alliance *Sisymbrion officinalis* within the class *Sisymbrietea*. The species grows in xerophytic conditions under full illumination, on substrates with a wide range of soil acidity — from acidic to ultrabasic, is undemanding to soil fertility. As an alien element of the flora, it is classified as a neophyte, ergasiophygophyte, and colonophyte. The probable pathway of *S. annuum*'s introduction into the flora of Polissia is its former cultivation as an ornamental plant.

Keywords: alien species, biodiversity, Carpathians, distribution, flora, naturalization, populations, Zhytomyr Region

FUNGI AND FUNGI-LIKE ORGANISMS
ГРИБИ І ГРИБОПОДІБНІ ОРГАНІЗМИ

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RESEARCH ARTICLE

Four new species of Aotearoa | New Zealand *Pyrenula* (*Pyrenulaceae*) segregated from *P. moniliformis*

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Abstract. The lichen genus *Pyrenula* (*Pyrenulaceae*) in Aotearoa | New Zealand was last comprehensively treated by Galloway (2007), who called for further targeted collecting. Since then, additional material, particularly from northern Te Ika-a-Māui | North Island and Rēkohu | Wharekauri | Chatham Island, has led to revised identifications and an improved understanding of species boundaries within the genus. Among the taxa requiring reassessment is *Pyrenula moniliformis*, an enigmatic species known only from the type. The species was recognised in herbarium specimens held in UNITEC from the Tāmaki Makaurau | Auckland Region of Aotearoa | New Zealand. These collections resulted in its rediscovery. Critical study of specimens and others that had been placed within *P. moniliformis* enabled detailed morphological comparisons, particularly of ascospore septation and size, and revealed that *P. moniliformis sensu lato* encompasses multiple taxa. Here, we present a revised circumscription of *P. moniliformis sensu stricto*, and describe four new species: *P. dalmatioides* A.J. Marshall, Blanchon, Aptroot & de Lange, *P. largei* A.J. Marshall, de Lange, Blanchon & Aptroot, *P. quadratolocularis* A.J. Marshall, de Lange, Blanchon & Aptroot, and *P. solomonii* A.J. Marshall, de Lange, Blanchon & Aptroot. For all five species, we provide morphological descriptions, ecological notes, distribution data, conservation assessments and a revised key to the members of *Pyrenula moniliformis* complex.

Keywords: lichen taxonomy, lichenized mycobiota, *Pyrenula*, *Pyrenula moniliformis*, *Pyrenula dalmatioides* sp. nov., *Pyrenula largei* sp. nov., *Pyrenula quadratolocularis* sp. nov., *Pyrenula solomonii* sp. nov., Aotearoa | New Zealand, Rēkohu | Chatham Islands

Introduction

The *Pyrenula* Ach. (*Pyrenulaceae*) of Aotearoa | New Zealand were last given a full treatment by Galloway (2007) who accepted 12 species. Since then there has been, as Galloway had hoped, further assiduous collecting, especially within northern Aotearoa | New Zealand and the Chatham Islands. This has

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led to publications documenting new records and clarifying names used previously (Marshall et al., 2019; Marshall, de Lange, 2025). Inevitably, as our understanding of *Pyrenula* grows, earlier conclusions need revisiting, and Galloway's 2007 assessment is now well out of date. For example, we had previously reported the presence of specimens of *P. leucostoma* Ach., *P. pyrenuloides* (Mont.) R.C. Harris, and *P. subvariolosa* (C. Knight) Aptroot in New Zealand (Marshall et al., 2019), which we now believe are better accommodated in *P. subumbilicata* (C. Knight) Aptroot and *P. ravenelii* (Tuck.) R.C. Harris. Another enigma has been resolving the status of *Pyrenula moniliformis* (C. Knight) Müll. This is the subject of this paper.

Pyrenula moniliformis (C. Knight) Müll. Arg. (Fig. 1), first described by Charles Knight in 1860 within the genus *Verrucaria* Schrad., has been regarded as a somewhat enigmatic species, as it was only known from the type collection. The species was accepted by Galloway (1985, 2007) and Aptroot (2012) though even its placement within *Pyrenula* was questioned on the basis of its unusual ascospores, which have 8 rather than the usual 4 locules and long-fusiform apices (Galloway, 2007). Without further specimens the species seemed destined to remain in obscurity, assessed as 'Data Deficient' in two Aotearoa | New Zealand Lichenized Mycobiota Threat Assessments (de Lange et al., 2012; de Lange et al., 2018).

Over the last 15 or so years the UNITEC Herbarium (herbarium acronyms follow Thiers 2008– onwards) has acquired a range of *Pyrenula* specimens from northern Te Ika-a-Māui | North Island,



Fig. 1. *Pyrenula moniliformis*. A: *P. moniliformis* on the trunk of māhoe (*Melicytus ramiflorus* subsp. *ramiflorus*) at Jagger's Bush, Tāmaki Makaurau | Auckland, Te Ika-a-Māui | North Island, Aotearoa | New Zealand; B: Close-up of the thallus (scale = 2 mm) with ascomata

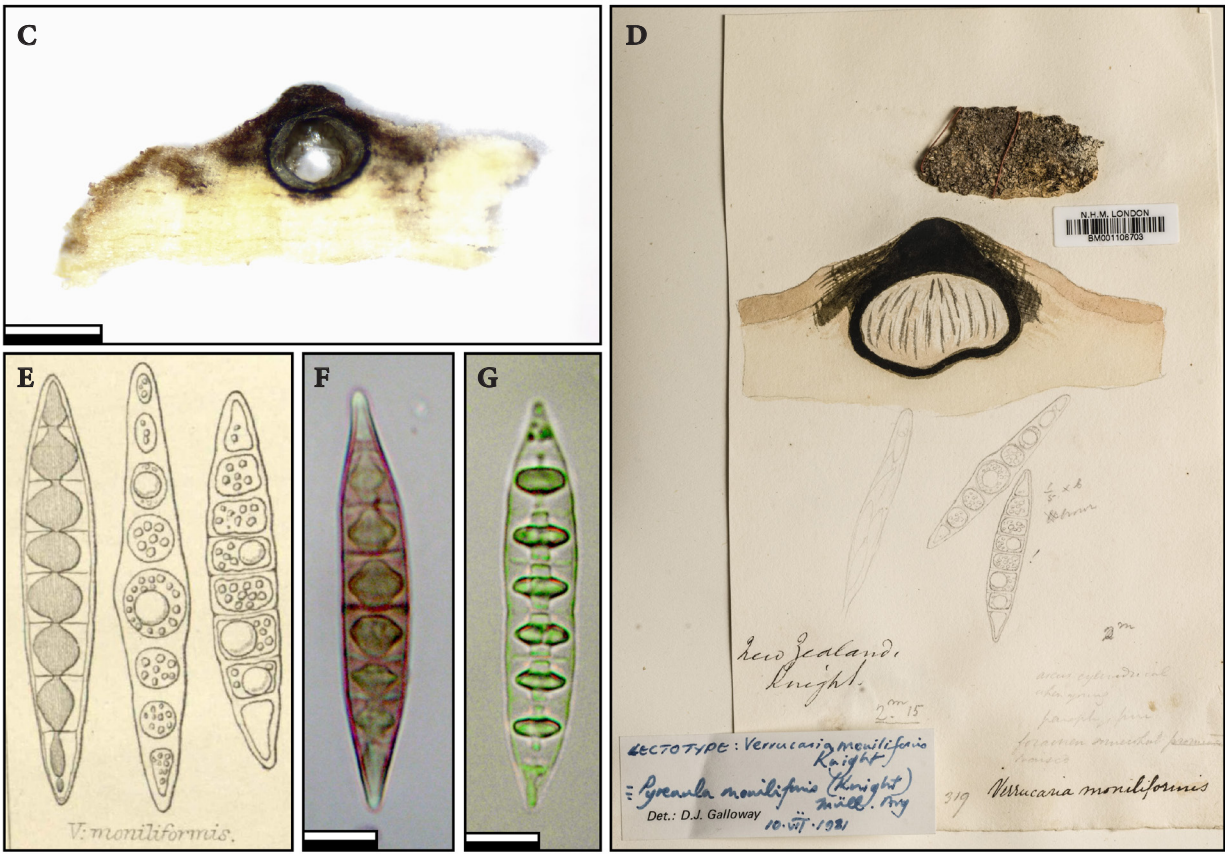


Fig. 1 (Continuation). *Pyrenula moniliformis*. C: Cross-section through ascomatum (scale = 1 mm); D: Charles Knight watercolour of cross-sectioned ascomatum and spores on the holotype (BM); E: Drawings of spores by Knight; F: Mature spore showing brown colouration (scale = 10 µm); G: Immature spore showing distinctive locule shape (scale = 10 µm)

Aotearoa | New Zealand, and Rēkohu | Wharekauri | Chatham Island. These collections matched to an extent the description of *Pyrenula moniliformis* with respect to ascospore characters but are morphologically disparate. The rediscovery of *Pyrenula moniliformis* documented by Marshall, de Lange (2025) in the Auckland Region has however, allowed for a critical reassessment of that species and a revaluation of those UNITEC specimens provisionally placed in that species. This analysis coupled with an investigation of *Pyrenula* collections held in Aotearoa | New Zealand herbaria (AK, CHR, OTA, WELT) confirmed that the variation within *P. moniliformis* s. l. cannot be accommodated within a single entity, so to accommodate this variation we propose a new taxonomy which includes a revised description of *Pyrenula moniliformis* s. str. based on fresh specimens and describe four new species previously assigned by us to *P. moniliformis*: *P. dalmatioides* A.J. Marshall, Blanchon, Aptroot & de Lange, *P. largei* A.J. Marshall, de Lange, Blanchon & Aptroot, *P. quadratolocularis* A.J. Marshall, de Lange, Blanchon & Aptroot, *P. solomonii* A.J. Marshall, de Lange, Blanchon & Aptroot. In addition, the ecology, associations and conservation status of all five species is provided. As these species would currently all key out to *Pyrenula moniliformis* in Galloway (2007) we provide a revised key to that species and those described here.

Materials and Methods

For this study, we examined all *Pyrenula* specimens held in AK, CHR, OTA, UNITEC and WELT. For this analysis we selected specimens corresponding to *Pyrenula moniliformis* s. l. and interloaned these for microscopic analysis at UNITEC. Field work was also conducted at Te Paki (−34.471, 172.764), a range of mānawa | mangrove (*Avicennia marina*

(Forssk.) Vierh. subsp. *australasica* (Walp.) J. Everett (*Acanthaceae* s. l. subfam. *Avicennioideae* Miers, or *Avicenniaceae* Miq. s. str.) swamps from Te Paki south to the Kaipara Harbour (−36.602, 174.349), Mataia Queen Elizabeth II Covenant (−36.493, 174.425), Auckland City, Hunua Range (−37.024, 175.094), and on Rēkohu | Wharekauri | Chatham Island (−43.762, −176.571). Specimens from these locations are cited under the relevant taxon 'representative specimens' listings as well as the distribution maps provided for each taxon in this paper.

At UNITEC specimens were examined with standard microscopic techniques using a Leica S9i and Meiji MT4000H with attached Infinity 1 camera. Microscopic images were taken with material mounted in water and analysed using Infinity Analyze 6.5.5 and Leica Application Suite X 3.8.2.27713. All specimens examined were annotated prior to returning loans.

Taxonomy

Pyrenula moniliformis (C. Knight) Müll. Arg., Bull. Herb. Boissier 2, App. 1: 95 (1894) ≡ *Verrucaria moniliformis* C. Knight, Trans. Linn. Soc. 23: 100 (1860).

Mycobank accession number: 403405

Lectotype: New Zealand. *Sine loco* [probably Auckland], Charles Knight 319 — BM [*fide* Galloway (1985a: 492)].

Notes: The type material (Fig. 1D, E) is assumed to have been collected from Auckland (Galloway, 1985, 2007); on the basis that Charles Knight (1808–1891) was living there when he published a paper on corticolous *Verrucaria* species including "*V. moniliformis*" (Knight, 1860; Galloway, 2013). Charles Knight, an early pioneer of Aotearoa | New Zealand lichenology, collected the more innocuous species from throughout the country. His herbarium contains numerous beautifully presented species, usually with hand-coloured sketches of their internal anatomy, asci and ascospores. However, frustratingly, Knight rarely provided location details on his herbarium specimens, leaving modern users of his herbarium with little choice but to guess locations on the basis of his various places of residence, and publications dated from that time (Galloway, 1985, 2007, 2013; Marshall, de Lange, 2025).

Diagnosis: Distinguished from other species of *Pyrenula* by having apiculate spores which are 5- to 7-septate in the size range 55–68 × 10.0–12.5 µm.

Description (Fig. 1): Corticolous. ***Thallus*** crustose, without pseudocyphellae, cream to pale brown, rugose, often appearing crystalline, usually cracked, corticate, spreading along the substrate in vertical stripes up to 250 mm, 0.4–1.2 mm thick, UV−. ***Prothallus*** not seen. ***Photobiont*** green, trentepohlioid, cells oblong to elongate,12.5–17.5 × 6.25–7.5 µm. ***Ascomata*** solitary, globose, often becoming papilliform at maturity, top half emergent from thallus, black, 1.0–2.3 mm (n = 30) in diameter, ostiole apical to slightly eccentric, often indistinct, 180–220 µm wide, wall carbonised, 65–140 µm thick, K−. ***Hamathecium*** hyaline, not inspersed, IKI−, hamathecium filaments simple or occasionally branched, 0.8–1.2 µm thick. ***Asci*** 8-spored, spores irregularly arranged, cylindrical, 175–225 × 25–35 µm. ***Ascospores*** fusiform, occasionally with apiculate tips, transversely 5–7-septate (mostly 7), cells rounded (resembling a cylinder that is wider at the centre of its axis than the ends) with terminal lumina when present adjacent to the endospore wall, initially hyaline but becoming brown at maturity, 55–68 × 10–12.5 µm (n = 30). ***Pycnidia*** not seen.

Representative Specimens: — AOTEAROA | NEW ZEALAND, TE IKA-A-MĀUI | NORTH ISLAND: Auckland, Titirangi, *A.J. Marshall AJM128*, 12 June 2025, UNITEC14891; Auckland, Meadowbank, Pourewa, *O. Er, C. Reynolds & N. Leddy*, 20 March 2015, UNITEC9328; Auckland, Point Chevalier, Jagger's Bush, *P. de Lange & A.J. Marshall AJM101*, 11 March 2025, UNITEC14865; Auckland, Hunua Ranges, Otau Mountain Road, *A.J. Marshall AJM48AW*, 30 November 2018, UNITEC14006.

Recognition: *Pyrenula moniliformis* differs from other species of *Pyrenula* present in Aotearoa | New Zealand by having 5- to 7-septate ascospores (Fig. 1F, G) that are much larger than those of *P. dalmatioides* A.J. Marshall, Blanchon, de Lange & Aptroot in the range 55–68 × 10.0–12.5 µm rather than 22–30 × 8–10 µm. It differs from *P. largei* by having smaller spores with less septa (70–100 × 10–15 µm for *P. largei* with 10–18 transverse septa), smaller ascomata (up to 3 mm for *P. largei*) and a different thallus appearance (smooth and much darker brown for *P. largei*). From *P. quadratolocularis* it differs by having much more prominent ascomata (Fig. 1B, C), those of *P. quadratolocularis* being flat in appearance, and different spore characters (those of *P. quadratolocularis* are 38–45 × 12–15 µm, curved and with distinctive angular locules). It is closest in spore

morphology to *P. solomonii* although spores are larger (37–52 × 6.0–8.5 µm for *P. solomonii*) with fewer septae (5–7 rather than 7–9). It lacks the characteristic flattened ascomata of *P. solomonii* and the thallus colour is quite different, that of *P. solomonii* appearing pink/orange. Globally, it differs from the Pantropical species *P. sexlocularis* (Nyl.) Müll. Arg. and the Papua New Guinean *P. sexluminata* Aptroot by having spores that are much larger (24–35 µm for these two species), and spores are often 7-septate rather than 5-septate. It also differs by the lack of hymenial IKI reaction (orange for *P. sexlocularis* and blue for *P. sexluminata*). It is distinguished from the Pantropical *P. montagnei* Müll. Arg. by spore size (25–38 × 5–7 µm for *P. montagnei*), thallus colour and the size of the ascomata (0.4–0.6 mm for *P. montagnei*). In the course of collecting specimens in Te Paki ('Broughton's Gully') we encountered an entity whose growth habit and thallus morphology is superficially similar to *Pyrenula moniliformis*. However, collections e.g., *A.J. Marshall 108, P.J. de Lange, C.J. James & E. Kaihe-Wetting*, UNITEC14928, of this were copiously fertile, with 3-septate ascospores, lacked an obvious photobiont, and so is likely a fungus.

Distribution: Endemic to Aotearoa | New Zealand where so far it is known from the Tamaki Makaurau | Auckland, Te Ika-a-Māui | North Island (Fig. 2). However, now that it has been rediscovered (Marshall, de Lange, 2025) it is quite likely to be found outside this region, especially as to date, there have been no targeted surveys for it.

Ecology: So far *Pyrenula moniliformis* appears to be restricted to a single phorophyte, māhoe (*Melicytus ramiflorus* J.R. Forst. & G. Forst subsp. *ramiflorus*) (Marshall, de Lange, 2025), with confirmed specimens collected entirely within the greater Auckland Region (Fig. 6). The lectotype substratum also appears to be mahoe although there are no notes with the specimen to confirm this.

In the locations where it has been collected it is often locally common in shaded situations, and appears to favour early-stage successional forest, in which māhoe is predominant either as canopy or subcanopy. The sole exception to this is a collection from a māhoe tree growing in the subcanopy of a taraire (*Beilschmiedia taraire* (A. Cunn.) Benth. & Hook. f. ex Kirk) / tawa (*Beilschmiedia tawa* A. Cunn.) Benth. & Hook. f. ex Kirk) forest in the Hunua Ranges.

Conservation Status: Marshall, de Lange (2025) expressed a confident view that more locations for *Pyrenula moniliformis* will be found because it is easily recognised in the field (due to its distinctive papilliform ascomata, and apparent restriction to the bark of māhoe), but since then only one new population has been recorded (UNITEC14891). The discovery of an as yet undetermined fungus with very similar macro-morphology, including papilliform fruiting structures (see 'Recognition' above) to *P. moniliformis* suggests that field recognition without follow-up microscopy has the potential to misrepresent the species abundance. Irrespective that the only known phorophyte māhoe is one of the most common indigenous trees of Aotearoa | New Zealand, we feel that the most conservative assessment of 'Data Deficient' *sensu* Rolfe et al. (2022), qualified 'DPR' [Data Poor Recognition], 'DPS' [Data Poor Size] and 'DPT' [Data Poor Trend] applies, because beyond our rediscovery of the species we still have no concept of its abundance, population size and trends. Further, at least for now, the only way to confirm the species presence is to resort to potentially destructive field sampling of specimens that will need to be confirmed by microscopy.

Pyrenula dalmatioides A.J. Marshall, Blanchon, de Lange & Aptroot sp. nov.

Mycobank accession number: 860250

Type: AOTEAROA | NEW ZEALAND, TE IKA-A-MĀUI | NORTH ISLAND. North Island, Northland, Oruaiti River, Mangōnui, 35.0120392°S, 173.5607300°E, 0 m, *A.J. Marshall (AJM102) & H.E. Marshall*, 17 January 2025. On bark of *Avicennia marina* subsp. *australasica* (*holotype* UNITEC14835, *isotype* AK).

Diagnosis: Distinguished from other species of *Pyrenula* by the apiculate spores which are 5- to 7-septate and 22–30 × 8–10 µm.

Description (Fig. 3): Corticolous. ***Thallus*** crustose, without pseudocyphellae, white to cream, minutely roughened (often appearing crystalline), ecorticate, spreading along the substrate up to 200 mm, 65–165 µm thick, UV–. ***Prothallus*** often present between neighbouring thalli although not seen where thallus edge meets the substrate, black, 250–650 µm wide. ***Photobiont*** green, trentepohlioid, cells oblong to elongate, 10.0–17.5 × 7.5 µm. ***Ascomata*** mainly solitary, occasionally clustered in groups of up to 5, subglobose with top half emergent from thallus, black, 0.46–0.75 mm (n = 30) in diameter, slightly less tall than wide, ostiole apical, often indistinct, 65–80 µm wide,

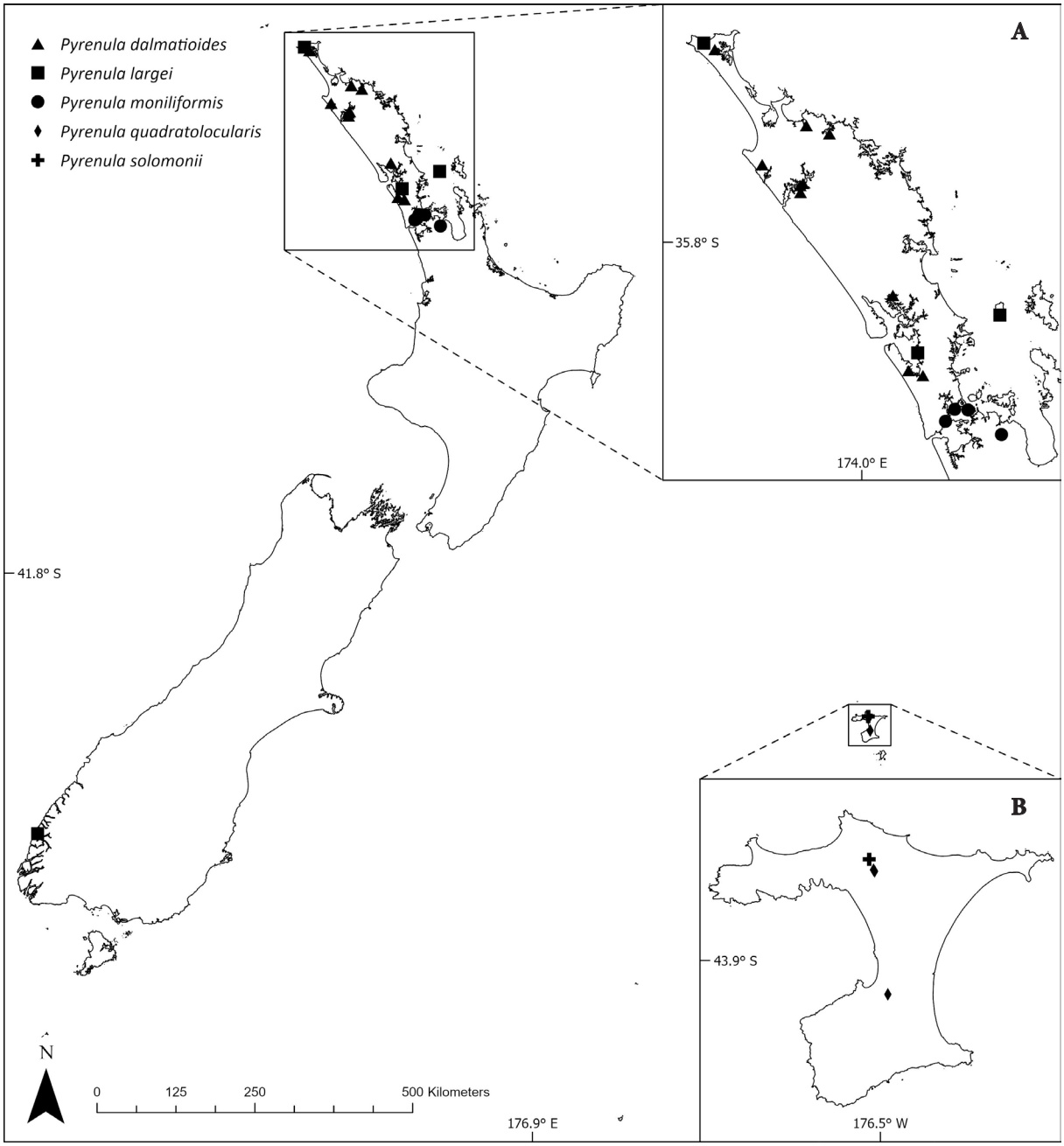


Fig. 2. Map showing the distributions of the taxa discussed. A: locations in Te Hiku-o-te Ika | Far North, Te Tai Tokerau | Northland; B: locations on Rēkohu | Wharekauri | Chatham Island — the largest island in the Chathams group

wall carbonised, 80–120 µm thick, K–. ***Hamathecium*** hyaline, not inspersed, IKI–, hamathecium filaments simple, 1.0–1.5 µm thick. ***Asci*** 8-spored, spores irregularly arranged, cylindrical to clavate, 45–80 × 15–22 µm. ***Ascospores*** fusiform-citriform, often with apiculate tips, transversely 5–7-septate, cells rounded with terminal lumina when present adjacent to the endospore wall, initially hyaline but becoming brown at maturity, 22–30 × 8–10 µm (n = 30). ***Pycnidia*** common, black, punctiform, 200–250 µm. ***Conidia*** filiform, curved, 12–19 × 1.0–1.5 µm (n = 30)

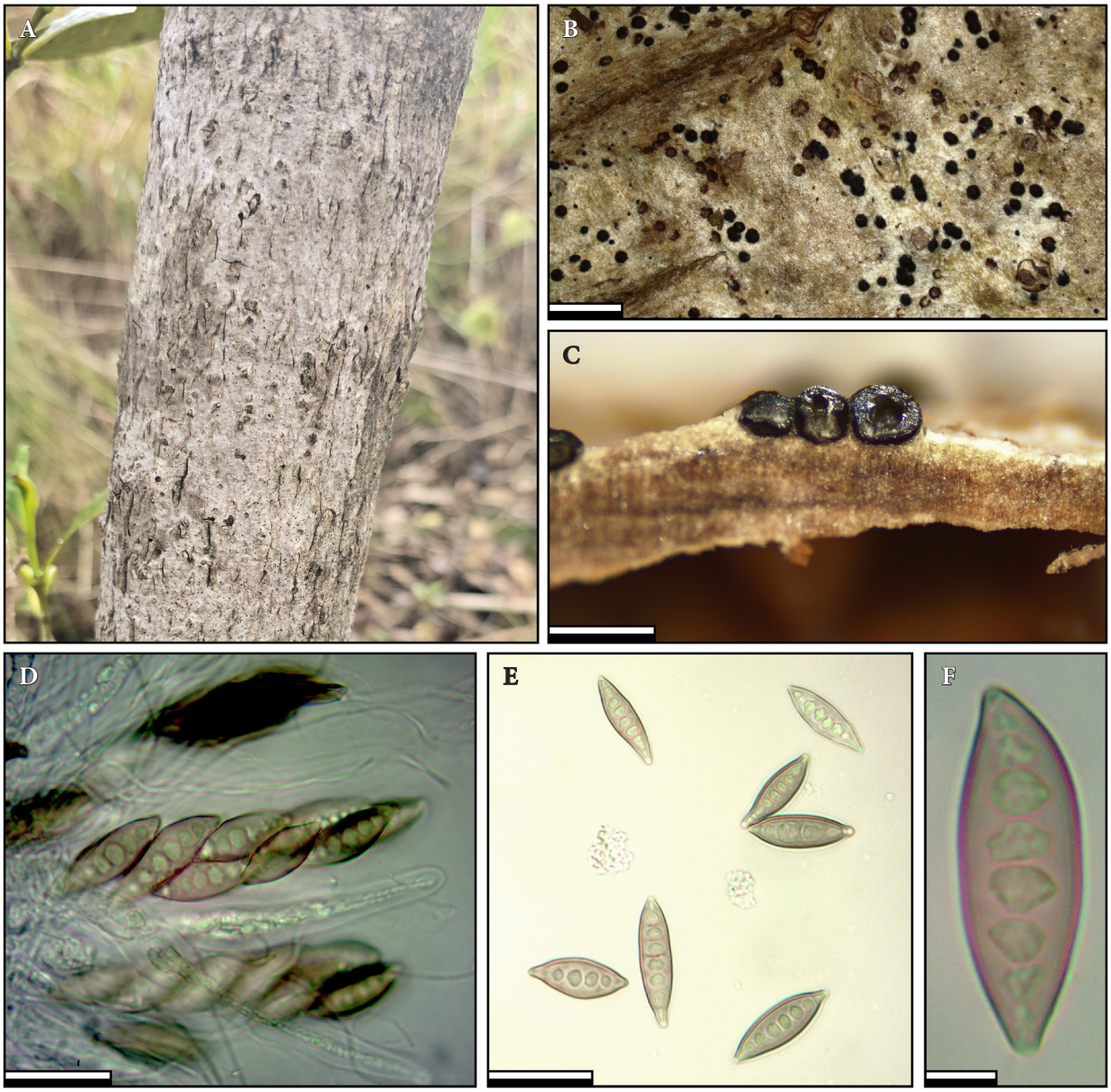


Fig. 3. *Pyrenula dalmatioides.* A: *P. dalmatioides* growing on the trunk of mānawa | mangrove (*Avicennia marina* subsp. *australasica*) at the type locality (Mangōnui, Oruaiti River, Te Tai Tokerau / Northland, Te Ika-ā-Māui / North Island, Aotearoa / New Zealand); B: Close-up of the thallus (scale = 2 mm); C: Cross-section through ascomata (scale = 500 µm); D: Spores in ascus (scale = 20 µm); E: Spores showing variation (scale = 20 µm); F: Spore (scale = 5 µm)

Representative Specimens (of 15 seen): AOTEAROA | NEW ZEALAND, TE IKA-A-MĀUI | NORTH ISLAND, Northland, Kaeo, *P.J. de Lange, C.J. James & A.J. Marshall AJM112*, 17 March 2025, UNITEC14850; Northland, Rawene, *P.J. de Lange, C.J. James & A.J. Marshall AJM123*, 17 March 2025; Auckland; Northland, North Kaipara, Paparoa, *O. Er & C. Reynolds*, 10 February, UNITEC6431.

Recognition: *Pyrenula dalmatioides* differs from all other *Pyrenula* presently recognised in Aotearoa | New Zealand by having 5- to 7-septate ascospores (Fig. 3D–F) in the size range 22–30 × 8–10 µm, a white thallus (Fig. 3A), and by its northern distribution and restriction to coastal mānawa | mangrove habitats. All other novel *Pyrenula* species discussed in this paper have larger ascospores that are



Fig. 4. *Pyrenula largei*. A: *P. largei* growing on the trunk of tanekaha (*Phyllocladus trichomanoides*) at the type locality (Mataia QEII Covenant, Kaipara, Te Ika-a-Māui | North Island, Aotearoa | New Zealand); B: Close-up of the thallus (scale = 3 mm); C: Cross-section through ascomatum (scale = 1 mm); D: Spores in ascus (scale = 20 µm); E: Spores showing variation (scale = 40 µm); F: Spore (scale = 20 µm)

not citriform (see descriptions) and thalli which are not white in appearance. The thallus morphology is similar to that of *P. microcarpa* Müll. Arg., a species with which in the field it is easily confused. However, *P. microcarpa* has 3-septate ascospores rather than 5–7-septate. From a global perspective, *P. dalmatioides* is distinguished from both *P. sexlocularis* and *P. sexluminata* by the lack of hymenial IKI reaction (orange for *P. sexlocularis* and blue for *P. sexluminata*) and the ecorticate thallus (Schumm, Aptroot, 2022). It also differs from both species by having lemon-shaped (citriform) spores with apiculate tips which are less broad (8–10 rather than 10–15 µm). From the South African species *P. wilmsiana* Müll. Arg. it differs by its thallus colouration (not olivaceous), 5–7-septate ascospores rather

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than 5-septate, and which are not uniseriately arranged in the ascus.

Distribution: Presumed endemic to Aotearoa | New Zealand where so far it is known from Te Hiku-o-te-Ika | Far North south to Tāmaki Makaurau | Auckland, Te Ika-a-Māui | North Island (Fig. 2) in mānawa | mangrove swamps.

Ecology: *Pyrenula dalmatioides* is so far known only from two phorophytes; mānawa | mangroves (*Avicennia marina* subsp. *australasica*) and two collections from ngaio (*Myoporum laetum* G. Forst.), both in the immediate vicinity of mānawa forests. It appears to have a distinctly coastal ecology and has not been collected from other vegetation associations. It displays a similar habit to that of the recently described *Lithothelium kiritea* A.J. Marshall, Aptroot, de Lange & Blanchon (Marshall et al., 2024) insofar as it is an early coloniser species and is most common on young adult mānawa | mangrove or isolated trees where it is often the only species present. As the forest ages, other lichen species begin to colonise the bark and *Pyrenula dalmatioides* is displaced.

Conservation Status: *Pyrenula dalmatioides* despite its recognition here as a new species within a notoriously difficult genus to identify, is fortunately so specific in its habitat requirements that it is relatively easy to recognise in the field. The only species with which it could be readily confused, *P. microcarpa*, has so far not been recorded within the same habitat. Although it is not inconceivable that *P. microcarpa* could grow on mānawa, it appears so far that *P. dalmatioides* is the usual white *Pyrenula* on this host. This means that we are more confident of providing a definitive conservation assessment. The species appears to be abundant and secure throughout its range. Its only known habitat, mānawa | mangrove ecosystems are widespread (c. 26,000 ha, Spalding et al., 2010) and ironically increasing their extent as a consequence of ongoing sedimentation of harbours caused by past deforestation of the catchment and from erosion of exposed ground as a consequence of intensive dairy farming and urbanisation (de Lange, de Lange, 1994; de Satgé, 2021). While there has been some loss of mānawa | mangrove ecosystems through deliberate clearance from some harbours (de Satgé, 2021), this has been minimal, and so far has had no obvious impact on the places where *Pyrenula dalmatioides* has been found. Nevertheless, *P. dalmatioides* has not been found in every mānawa | mangrove ecosystem, but our field work has found it in some of the key mānawa | mangrove areas of Te Tai Tokerau | Northland. Accordingly, using the New Zealand Threat Classification System (Rolfe et al., 2022) we assess *Pyrenula dalmatioides* as 'At Risk | Uncommon' (UnCn1 [Naturally small population that is forecast to increase > 10% over the longer of the next 10 years or three generations (maximum 100 years) (UNCn1)], Criterion 'I'[The total area of occupancy is 10 000–100 000 ha (100–1000 km^2)], qualified 'DPR' [Data Poor Recognition], 'DPS' [Data Poor Size] and 'DPT' [Data Poor Trend] because we lack this data making our assessment on our judgement of populations in the field, their security and what is happening to their preferred habitat. Finally, the species should also be marked 'RR' [Range Restricted] due to its apparent phorophyte preference.

Etymology: The species epithet refers to the similarity of the thallus to the patterning on the coat of a Dalmatian dog, a breed of dog originating from historic Dalmatia (now modern-day Croatia) whose coat is white with numerous black spots (see: https://en.wikipedia.org/wiki/Dalmatian_dog). It also honours early Dalmatian settlers who began to emigrate to Aotearoa | New Zealand in waves starting during the 1890s and intensifying during periods of civil unrest and war in the Balkans between 1900 and 1930, and again in the 1990s (see https://teara.govt.nz/en/dalmatians). The initial sites of settlement were in Te Tai Tokerau | Northland of Te Ika-a-Māui | North Island to dig kauri (*Agathis australis* (D. Don) Lindl.) gum from peat bogs that often abut the mānawa | mangrove swamps frequented by *Pyrenula dalmatioides*.

Pyrenula largei A.J. Marshall, de Lange, Blanchon & Aptroot sp. nov.

Mycobank accession number: 860251

Type: AOTEAROA | NEW ZEALAND, TE IKA-A-MĀUI | NORTH ISLAND. North Island, Northland, Auckland, Glorit, Mataia, Mataia QEII Covenant, 36.4932365°S, 174.4248199°E, 30 m, *A.J. Marshall (AJM127) & P.J. de Lange,* 11 December 2024. On bark of *Phyllocladus trichomanoides* (*holotype* UNITEC14864, *isotype* AK).

Diagnosis: Distinguished from other species of *Pyrenula* by the 10–18-transversely septate ascospores (rarely submuriform in overmature spores); these 70–100 × 10–15 µm, and ascomata up to 3 mm in diameter.

Description (Fig. 4): Corticolous. ***Thallus*** crustose, without pseudocyphellae, grey-brown to umber, smooth to minutely rugose, corticate, in semi-circular to irregular bands and patches on the photobiont

substratum; these up to 50 mm in diameter, 125–170 µm thick, UV–. ***Prothallus*** indistinct. Photobiont green, trentepohlioid, cells oblong to elongate, cells 20–28 × 7.5–8 µm. ***Ascomata*** prominent, mainly solitary but occasionally in groups of 2–4, hemispherical, occasionally with a flattened top, black, 1.2–2.9 mm (*n* = 30) in diameter, ostiole white, apical to slightly eccentric, prominent, 150–270 µm wide, wall carbonised, 140–225 µm thick, K–. ***Hamathecium*** hyaline, not inspersed, IKI–, hamathecium filaments simple, 1.0–1.5 µm thick. ***Asci*** 8-spored, spores irregularly arranged, cylindrical to clavate 150–180 × 30–40 µm. ***Ascospores*** fusiform-musiform, often with apiculate tips, with 10–18 transverse septa and occasionally 1 longitudinal septum in central cells, cells rounded to angular, initially hyaline but becoming brown at maturity, 70–100 × 10–15 µm (*n* = 30). ***Pycnidia*** and ***Conidia*** not seen.

Specimens seen: — AOTEAROA | NEW ZEALAND, TE IKA-A-MĀUI | NORTH ISLAND: Te Hiku-o-te-Ika | Northland, Ngāti Kuri, Te Paki, Tahae | Radar Bush, *P.J. de Lange 15833*, 3 April 2024, UNITEC14836; Auckland, Glorit, Mataia, *A. McKenzie & D. Bennett*, 11 May 2018, UNITEC10176; Hauturu-o-Toi | Little Barrier Island, *B.W. Hayward*, August 1981, AK224897. TE WAIPOUNAMU | SOUTH ISLAND: Ka Tū-Waewae-o-Tū | Secretary Island, *[J.] Murray*, February 1959, OTA 67696.

Recognition: *Pyrenula largei* differs from other species of *Pyrenula* present in Aotearoa | New Zealand by having 10- to 18-septate ascospores (Fig. 4D–F) that are the largest in this group, being 70–100 × 10–15 µm. All other novel *Pyrenula* species discussed in this paper have smaller ascospores and fewer septae (see descriptions) and thalli which lack the shiny brown appearance of *P. largei* (Fig. 4B). Ascomata are the largest in the group averaging 2.1 mm in diameter, usually with a prominent pale ostiole (Fig. 3B, C). Without microscopy it could be confused with *Pyrenula ravenelii* with which it often grows and has a similar thallus colour, ascomata size and habitat preference but very different spores — those of *P. ravenelii* being muriform and in the size range 45–70 × 18–28 µm. Keying out at couplet 62 of the world *Pyrenula* key (Schumm, Aptroot, 2022), it differs from *P. cylindrica* Kashiw. by having spores which are larger (70–100 × 10–15 µm rather than 45–60 × 4–6 µm), and from *P. clavatispora* Common & Aptroot by having much larger ascomata (1.2–2.9 mm rather than 0.3–0.5 mm) and a lack of IKI reaction in the hamathecium.

Distribution: Presumed endemic to Aotearoa | New Zealand where so far it is known from Te Paki, Te Hiku-o-te-Ika | Far North, Te-Ika-a-Māui | North Island south to Ka Tū-Waewae-o-Tū | Secretary Island, Murihiku | Southland, Te Waipounamu | South Island (Fig. 2).

Ecology: In the Te Ika-a-Māui | North Island part of its range *Pyrenula largei* is best known from kauri forest associations where it seems to exclusively inhabit the bark of tānekaha (*Phyllocladus trichomanoides* D. Don) (Fig. 4A) a common coniferous associate of kauri. On Hauturu-o-Toi | Little Barrier Island, the species was found in a mixed collection of *Pyrenula* collected from *Myrsine* L. (probably *M. australis* (A. Rich.) Allan) in "kanuka" (*Kunzea robusta* de Lange & Toelken) forest. It is not known what phorophyte it was collected from on Ka Tū-Waewae-o-Tū | Secretary Island, an island well out of the range of tānekaha and kauri but not *Myrsine*. That island has a lowland forest dominated by *Nothofagus* Blume and Podocarp trees, with the montane portion covered in southern rātā (*Metrosideros umbellata* Cav.) and kāmahi (*Pterophylla racemosa* (L. f.) Pillon & H.C. Hopkins) forest associations.

In the northern part of its range, where we have collected *Pyrenula largei*, it can be locally common, though in the field it is easily confused with *P. ravenelii* (see above), with confident determinations requiring microscopy. Irrespective, at Mataia QEII Covenant for example, *Pyrenula largei*, was usually found in association with *Pyrenula ravenelii*, *Ocellularia jacinda-arderniae* A.J. Marshall, Blanchon, Lücking & de Lange, *Thelotrema lepadinum* (Ach.) Ach., *Fissurina* Fée spp., and *Pertusaria* DC. spp. (see: https://inaturalist.nz/observations/254844328). At Mataia it was noted that *Pyrenula largei* occupied a narrow band within regenerating kauri forest; namely sites more influenced by and/or exposed to coastal weather. Above that band *P. ravenelii* dominated. At Te Paki, the species was part of a generic *Pyrenula* sampling from dense kauri forest, noting that all of Te Paki weather is in effect maritime.

Conservation Status: Using the New Zealand Threat Classification System (Rolfe et al., 2022), *Pyrenula largei* best qualifies as 'Data Deficient' qualified 'DPR' [Data Poor Recognition], 'DPS' [Data Poor Size] and 'DPT' [Data Poor Trend] because we have no concept of this species abundance and trends, and without resorting to potentially destructive field sampling for microscopy as field

recognition is, thus far anyway, impossible. Further, our best understanding of this species ecology is based on our field work in kauri forest associations in which it was first recognised by us as potentially distinct. The discovery of herbarium specimens on different phorophytes spanning the range of the two main islands of Aotearoa | New Zealand, increases our uncertainty, especially with respect to potential threats the species may face.

Etymology: *Pyrenula largei* is named in honour of the Aotearoa | New Zealand botanist Dr. Mark Large FLS (31 March 1959 –) (Fig. 5), who specialised in pteridology. Mark started his academic career at Oxford as Royal Society Endeavour Fellow, then continued teaching botany at Massey University of New Zealand | Te Kunenga ki Pūrehuroa in 1993, before moving to what is now Unitec originally as Head of Department, then in a senior role (Associate Professor) and teaching Earth Sciences, Botany and Science Philosophy (2002–2024). During his career Mark supervised and examined a range of dissertations, including M.Sc. and PhD, and was an examiner or supervisor of two of the authors on this article, Andrew Marshall and Dan Blanchon. Mark's contributions to global botanical sciences and indeed the history of science have been remarkable. He is fondly remembered by his past students and graduates for his unique, dry humour and engaging lecturing style that helped encouraged many students to follow a career in botany and taxonomy.

Pyrenula quadratolocularis A.J Marshall, de Lange, Blanchon & Aptroot sp. nov.

Mycobank accession number: 860252

Type: AOTEAROA | NEW ZEALAND, RĒKOHU | WHAREKAURI | CHATHAM ISLAND: Te Whanga, Pana | Blind Jim's, 43.779172°S, 176.557417°W, 15 m, *P. J de Lange (CH4637)*, 30 January 2025. On bark of *Coprosma chathamica* (*holotype* UNITEC14830, *isotype* AK).

Diagnosis: *Pyrenula quadratolocularis* is distinguished from other species of *Pyrenula* by the combination of aggregated ascomata, partially immersed in thallus, and ascospores that are curved, with square locules in the size range 38–45 × 12–15 µm.

Description (Fig. 6): Corticolous. ***Thallus*** crustose, without pseudocyphellae, grey-white (fresh) fading to light brown to tan on storage, smooth to minutely rugose (often appearing crystalline), ecorticate (occasionally corticate), in patches along the substrate up to 40 mm in diameter, 350–650 µm thick, UV–. ***Prothallus*** black, 200–1000 µm wide. ***Photobiont*** green, trentepohlioid, cells oblong to elongate, 20–22 × 9–10 µm. ***Ascomata*** usually confluent but occasionally solitary, flattened, partially immersed in the thallus, black, 1.2–2.1 mm (n = 30) in diameter, ostiole apical, often indistinct, 180–230 µm wide, wall carbonised, appearing cellular in cross-section, 50–150 µm thick, K–. ***Hamathecium*** hyaline, not inspersed, IKI–, hamathecium filaments simple, 1.0–1.5 µm thick. ***Asci*** 8-spored, spores irregularly arranged, cylindrical to clavate 50–100 × 15–20 µm. ***Ascospores*** usually curved, mostly submuriform but occasionally transversely septate, often constricted at septa, especially at maturity, fusiform, 7–9 × 0–3-septate, cells angular, oblong to square, brown, 38–50 × 5.5–8.0 µm (n = 30). ***Pycnidia*** common, black, punctiform, 300–580 µm. ***Conidia*** ellipsoid, 3.5–4.9 × 1.4–2.0 µm (n = 30).



Fig. 5. Adjunct Professor, Dr Mark Large FLS (image: provided by Mark Large)

Specimens seen: — AOTEAROA | NEW ZEALAND, RĒKOHU | WHAREKAURI | CHATHAM ISLAND: Te Whanga, Pana | Blind Jim's, *P.J. de Lange CH4130*, 27 June 2021, UNITEC12907; Te Whanga, Pana | Blind Jim's near Cattle Point, *P.J. de Lange CH4643*, 26 August 2025, UNITEC15024;

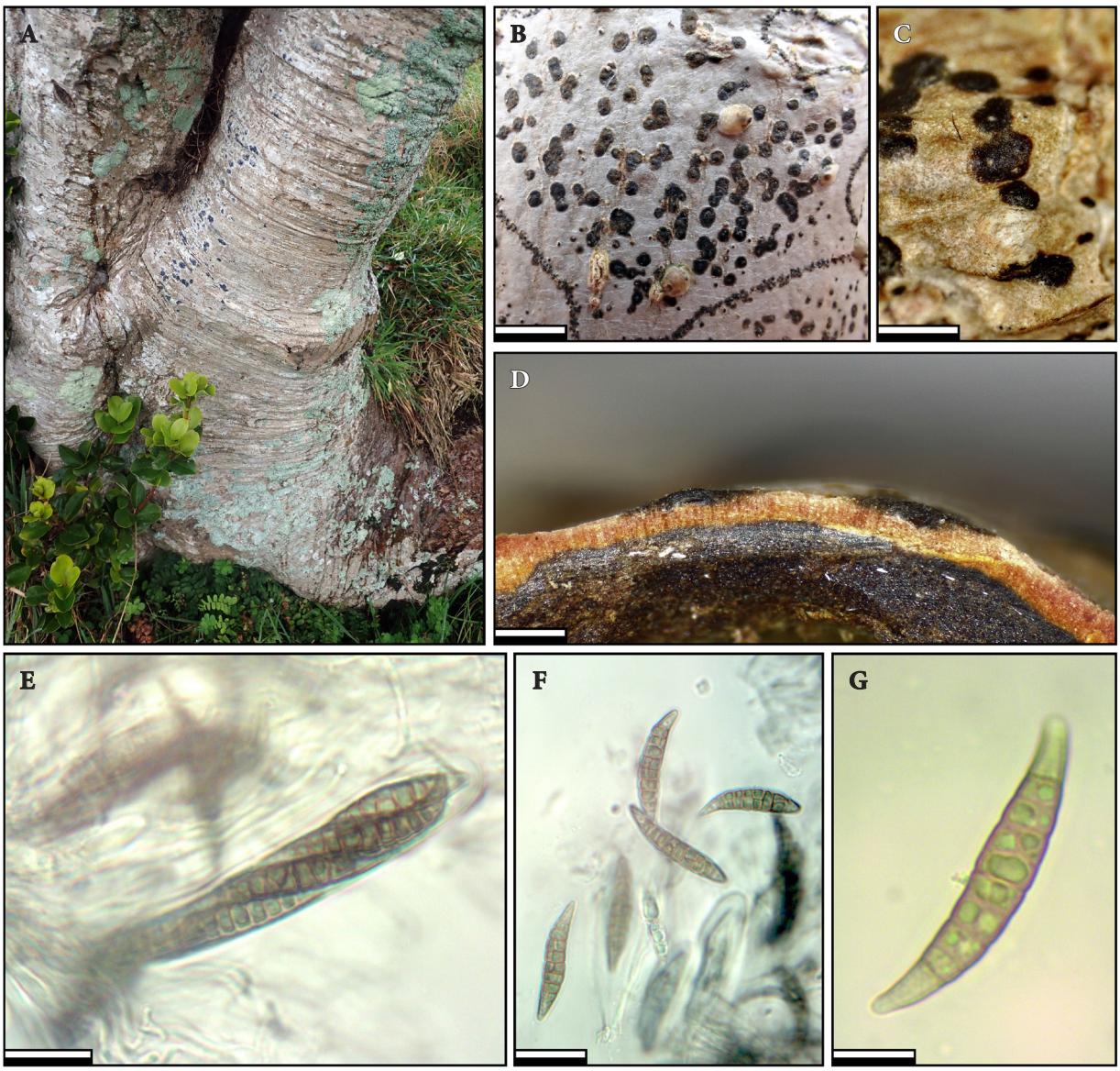


Fig. 6. *Pyrenula quadratolocularis*. A: *P. quadratolocularis* growing on the trunk of karamū hikoa (*Coprosma chathamica*) at the type locality (Pana | Blind Jim's, Te Whanga, Rēkohu | Wharekauri | Chatham Island, Chatham Islands); B: Close-up of the thallus in fresh state (scale = 3 mm); C: Close-up of the thallus after storage (scale = 2 mm); D: Cross–section through ascomata (scale = 500 µm); E: Spores in ascus (scale = 20 µm); F: Spores showing variation (scale = 25 µm); G: Spore (scale = 10 µm)

Lake Huro, Te Awatea, *P.J. de Lange CH4638 & C.J. James*, 3 February 2025, UNITEC14831; Lake Huro, Te Awatea, *P.J. de Lange CH4642 & C.J. James*, 3 February 2025, UNITEC15000.

Recognition: *Pyrenula quadratolocularis*, remarkably for an Aotearoa | New Zealand *Pyrenula*, is easily recognised in the field on account of the (when fresh) grey-white (Fig. 6A) thallus (fading to light brown or tan on storage: see Fig. 6C), delineated by a black prothallus (Fig. 6B), and by the black, confluent, semi-immersed (so appearing 'flat') ascomata (Fig. 6B–D, see also: https://inaturalist.nz/observations/262065399). Spore size is similar to that of *P. solomonii*, but spores are usually curved, submuriform and have distinctive square/rectangular locules (Fig. 6E–G), a character lacking in *P. solomonii* that has

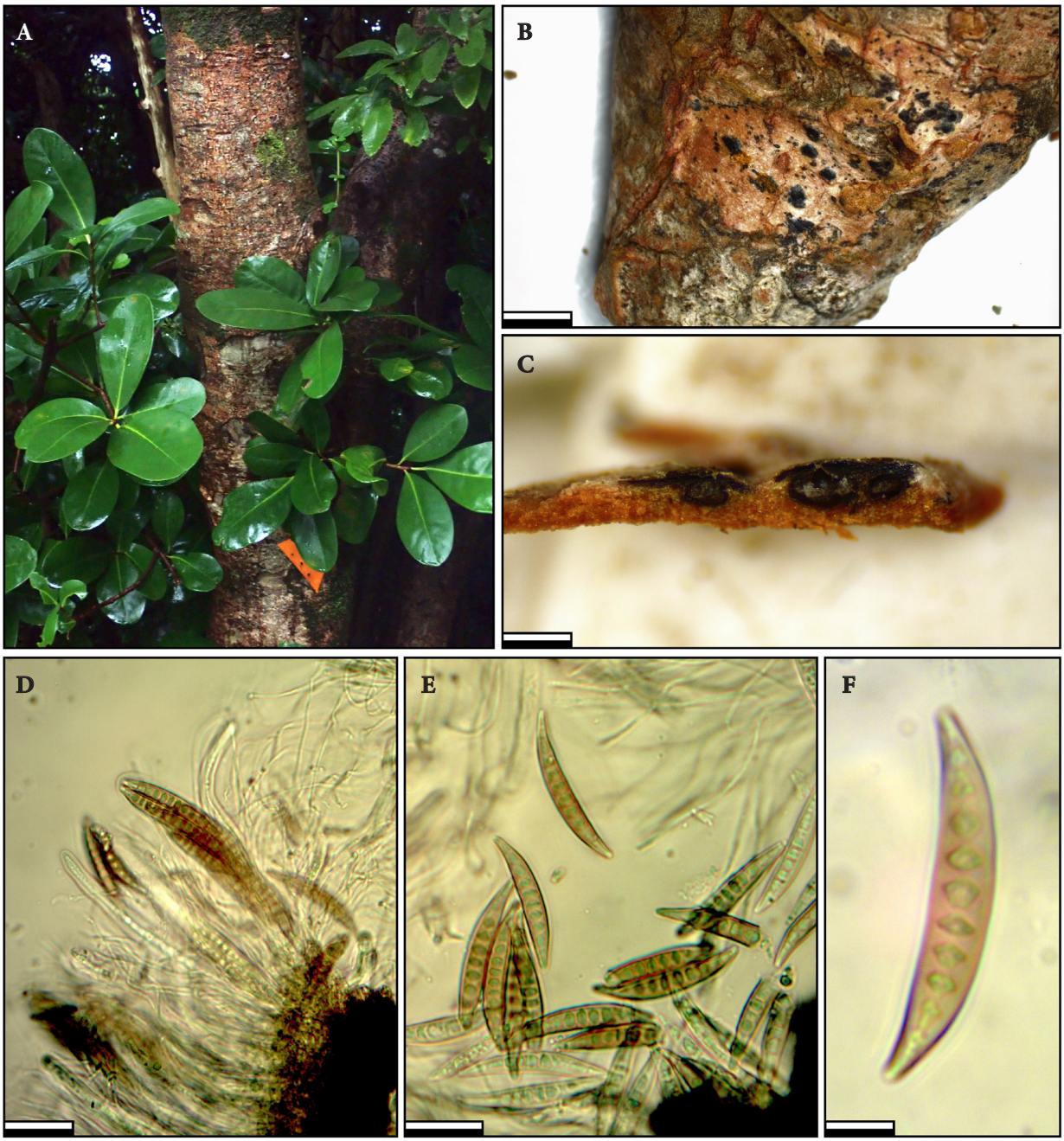


Fig. 7. *Pyrenula solomonii* at the type locality (Nikau Bush Conservation Area, Pana | Blind Jim's, Te Whanga, Rēkohu | Wharekauri | Chatham Island, Chatham Islands). A: *P. solomonii* growing on the trunk of karamū hikoa (*Coprosma chathamica*) tree surrounded by kopi (*Corynocarpus laevigatus*); B: Close-up of the thallus (scale = 2.5 mm); C: Cross-section through ascomata (scale = 1 mm); D: Spores in ascus (scale = 20 µm); E: Spores showing variation (scale = 20 µm); F: Spore (scale = 10 µm)

a locule shape much more like other species of *Pyrenula* (Fig. 7). These spore characteristics are unique for *Pyrenula*, at least for those taxa recognised from Aotearoa | New Zealand. It is described here within *Pyrenula* although further investigation is warranted to explore this (see comments by Galloway, 2007).

From *P. largei* it differs by having smaller ascospores (70–100 × 10–15 µm for *P. largei*) and smaller, much less prominent ascomata (hemispherical rather than flattened for *P. largei*). *Pyrenula dalmatioides* has smaller ascospores (22–30 × 8–10 µm) and those of *P. moniliformis* are larger (55–68 × 10.0–12.5 µm), and both these taxa lack the distinctive locule shape discussed above. *Pyrenula quadratolocularis* differs from the similarly submuriform *P. subumbilicata* by having curved ascospores that are far more pointed at the tips, and lacks the yellow thallus colour and prominent fused ostioles.

Distribution: Presumed endemic to the Chatham Islands, Aotearoa | New Zealand (Fig. 2).

Ecology: In the two locations in which *Pyrenula quadratolocularis* has been found, it is locally common on exposed, often isolated trees or 'stands' of trees; remnants of a formerly contiguous swamp / fen forest and/or shoreline forest that once occupied the frequently flooded margins of Te Whanga and Lake Huro. In these habitats it has been found on two phorophytes, karamū hikoa (*Coprosma chathamica* Cockayne) and tapatapa (*C. propinqua* A. Cunn. var. *martinii* W.R.B. Oliv.). The *Pyrenula* seems to be strongly photophilous, only colonising the most exposed portions of the trunks (Fig. 6A) of these phorophytes and eschewing those shaded portions or areas of denser branching. In these sites, the *Pyrenula* is commonly found associating with another *Pyrenula*, possibly endemic to the islands, *P.* aff. *microcarpa*, *Lecanora kohu* Printzen, Fryday, Blanchon & de Lange, *Physcia adscendens* H. Oliver, *P. poncinsii* Hue and *Ramalina canariensis* J. Steiner.

Conservation Status: *Pyrenula quadratolocularis* has been collected from two sites on Rekohu | Wharekauri | Chatham Island (Pana | Blind Jim's, on the shores of Te Whanga, and from Te Awatea, on the southeastern shoreline of Lake Huro). At both sites it was locally common, on exposed trees of karamū hikoa and tapatapa — remnants from former swamp and shoreline forest. On these phorophytes, especially on the exposed portions of their trunks it can be the dominant lichen. Whilst encouraging these host trees are in reality under extreme stress due to the loss of surrounding forest cover, resulting in their exposure, and some of the trees on which it was found in June 2021 have since toppled in the strong winds typical of the Chatham Islands.

Aside from its ease of field identification, *Pyrenula quadratolocularis* has not yet been surveyed for in all potential habitat. Nevertheless it has been opportunistically looked for in a range of sites around Rēkohu | Wharekauri | Chatham Island, and as yet no further locations have been discovered.

The New Zealand Threat Classification System (Rolfe et al. 2022) requires that assessors try to avoid assessing taxa as 'Data Deficient' if sufficient data exists to place taxa in a more definitive conservation category, such is possible for *Pyrenula quadratolocularis*. In the two locations in where it has been found, as there is no data available on the number of individuals but there is for area of occupancy, and, as was done for *Lecanora kohu* by de Lange (2021), longevity of phorophyte as a proxy for population trend of the lichen.

At Pana | Blind Jim's the *Pyrenula* occupies an area of c. 1 ha, where in June 2021 it was found on 11 karamū hikoa. Of those phorophytes, three were in ill–thrift during an inspection in late January 2025, and one tree had collapsed and was dying.

At Te Awatea, *Pyrenula quadratolocularis* was only seen in the unfenced, cattle-pugged, exposed and seriously degraded fen between the swamp forest of the reserve and farmland. Although locally common on eight karamū hikoa and three tapatapa in an area of c. 1 ha, none of the trees seen were in good condition, many had partially hollowed out, rotted trunks, and others were 'unstable' in the peat due to wind 'rock' and cattle rubbing themselves on the exposed trunks.

Using area as an estimate of population, *Pyrenula quadratolocularis* has a known area of occupancy of c. 2 ha, with both subpopulations (Pana | Blind Jim's and Te Awatea) of roughly equal size. The decline rate of the phorophyte 'hosts' can be estimated from the loss of trees at Pana | Blind Jim's, where four of the original 11 trees had collapsed and were either in ill-thrift or dying — a loss of 36% over four years. This data places the *Pyrenula* in 'Threatened / Nationally Endangered' (NEu3h) ['Small population that is forecast to decline 10–50% over the longer of the next 10 years or three generations (maximum 100 years)'… 'classified as Nationally Endangered when evidence indicates that it will experience a decline of 10–50% over the longer of the next 10 years or three generations (maximum 100 years) and meets one of the following size criteria… 'the total area of occupancy is 1–10 ha (0.01–0.1 km^2) (h)'] (Rolfe et al., 2022: 26). To this assessment the qualifiers 'DPS' [Data Poor Size] and 'DPT' [Data Poor Trend] cannot be added as we have no quantitative data for this conservation

assessment. Other suitable qualifiers suggested here are 'IE' [Island Endemic], 'PF' [Population Fragmentation] because the species is currently believed endemic to the Chatham Islands, and the only known sites are smaller fragments of a formerly contiguous swamp forest / fen system stretching along the shoreline of Te Whanga and Lake Huro.

Etymology: The species epithet *quadratolocularis* refers to the square nature of the spore locules when viewed under the microscope.

Pyrenula solomonii A.J. Marshall, de Lange, Blanchon & Aptroot sp. nov.

Mycobank accession number: 860253

Type: AOTEAROA | NEW ZEALAND, RĒKOHU | WHAREKAURI | CHATHAM ISLAND, Nikau Bush Conservation Area, 43.762203°S, 176.570593°W, 41 m, *P. J de Lange (CH4129)*, 27 June 2021. On bark of *Coprosma chathamica* (*holotype* UNITEC12906, *isotype* AK).

Diagnosis: *Pyrenula solomonii* is distinguished from other species of *Pyrenula* by the pinkish thallus, flattened ascomata largely immersed in the substratum and 7–10 transversely septate ascospores, 37–52 × 6–8.5 µm.

Description (Fig. 7): Corticolous. ***Thallus*** crustose, without pseudocyphellae, pink to pink-grey when fresh, turning beige/orange to pale pink on storage, surface minutely rugose, corticate, in irregular patches up to 30 mm in diameter, 120–280 µm thick, UV–. ***Prothallus*** black, 150–500 µm wide. ***Photobiont*** green, trentepohlioid cells oblong to elongate cells 15.0–17.5 × 7.5 µm. ***Ascomata*** solitary to crowded, flattened, black, 0.5–1.4 mm (n = 30) in diameter, partially immersed in the thallus, ostiole apical, often indistinct, 80–140 µm wide, wall carbonised, 80–300 µm thick, K–. ***Hamathecium*** hyaline, not inspersed, IKI–, hamathecium filaments simple, 0.8–1.3 µm thick. ***Asci*** 8-spored, spores irregularly arranged, cylindrical to clavate, 55–85 × 12–18 µm. ***Ascospores*** fusiform-musiform, 7–9-septate, cells angular with terminal lumina adjacent to the endospore wall, initially hyaline but becoming brown at maturity, 37–52 × 6.0–8.5 µm (n = 30). ***Pycnidia*** common, black, punctiform, 180–340 µm. ***Conidia*** filiform, straight-curved, 12–20 × 0.8–1.4 µm (n = 30).

Paratype: — AOTEAROA | NEW ZEALAND, RĒKOHU | WHAREKAURI | CHATHAM ISLAND: Nikau Bush Conservation Area, *P.J. de Lange CH4105*, 21 September 2019, UNITEC12866.

Recognition: *Pyrenula solomonii* is most similar in its thallus morphology to *P. quadratolocularis*, having somewhat flattened ascomata (Fig. 7C), although it differs in the thallus colour being pinkish rather than grey-white/brown (Fig. 7A, B) and having different spore morphology (see recognition section for *P. quadratolocularis* above). Spore morphology is closest to *P. moniliformis* (Fig. 1F, G), from which it differs by having more septa (7–9 rather than 5–7; Fig. 7D–F) and smaller ascospores (37–52 × 6.0–8.5 µm rather than 55–68 × 10.0–12.5 µm), and *P. largei* from which it differs by having less septa (10–18 for *P. largei*) and smaller spores (70–100 × 10–15 µm for *P. largei*). Differences with internationally recognised taxa are discussed in the recognition sections above.

Distribution: Presumed endemic to the Chatham Islands, Aotearoa | New Zealand.

Ecology: *Pyrenula solomonii* is only known from three collections (the holotype, isotype and an earlier collection) made from the same phorophyte, a solitary karamū hikoa (Fig. 7A) at the type locality Nikau Bush Conservation Area, so little can be said about its ecological preferences and associated species. When it was discovered in September 2019, it was considered common on that tree but it was not seen elsewhere. Since then the adjacent forest canopy of mostly kopi (*Corynocarpus laevigatus* J.R. Forst. & G. Forst.) has thickened around the karamū hikoa, shading it such that it is now in ill-thrift, possibly even terminal decline. At the time of discovery *Pyrenula solomonii* was noted growing with an undetermined species of *Arthonia* Ach.

Conservation Status: Using the New Zealand Threat Classification System (Rolfe et al., 2022), *Pyrenula solomonii* could either be assessed as 'Data Deficient' or 'Threatened | Nationally Critical'. As noted above, the default preference for threat assessments using this classification system is to pick a more definitive category wherever possible (Rolfe et al., 2022: 23) 'Expert panels should use Data Deficient only when there is extreme uncertainty about the abundance and population trend of an organism, i.e. the possible categories it truly occupies cover most or all of the range from Nationally Critical to Not Threatened'. In this case, whilst *Pyrenula solomonii* is certainly cryptic, its pinkish colouration does help distinguish it from other lichens on potential 'host' trees, and there have been dedicated surveys for it in Nikau Bush Conservation Area (between 2020 and 2025) by Peter de Lange, and opportunistic surveys



Fig. 8. Māui Solomon LLB *Canterb.* (image provided by Māui Solomon)

elsewhere on Rēkohu | Wharekauri | Chatham Island so far failing to disclose further specimens. Therefore, we think it appropriate to recommend a conservation assessment of 'Threatened | Nationally Critical' (NCn1a,g) ['Very small population (natural, unnatural or population state unknown) regardless of the trend (NCn1, NCn2, NCu1, NCu2, NCu3, NCu4, NCu5, NCu6, NCx1, NCx2)'…' The total population size is fewer than 250 mature individuals (a), The total area of occupancy is less than 1 ha (0.01 km^2) (g)'] due to the small area of occupancy <1 ha [one tree], an estimated population size of 30 'individuals'(excepting that delineation of an individual in this species is difficult due to the growth habit) in 2019 down to three 'individuals' in 2025 (decline rate of 90% in seven years). To this assessment we suggest adding the qualifiers 'DPR' [Data Poor Recognition], 'IE' [Island Endemic], and 'OL' [One Location].

Etymology: Named in honour of Māui Solomon (6 September 1960 —) (Fig. 8), a resident of Rēkohu, who is a barrister (graduate of the University of Canterbury law school) and indigenous rights activist, mediator and negotiator. Māui was born in Te Muka, Te Waipounamu | South Island. His Moriori hokopapa (descent) is through Tame Horomona Rehe (also known as 'Tommy Solomon') (7 May 1884 — 19 March 1933) his grandfather, often referred to as 'the last full-blooded Moriori', as well Ngāi Tahu and Pakeha [European]. Māui was instrumental in achieving legal recognition for Moriori as a distinct people from Māori, the revival of their language (Ta Re) and culture, the building of Kopinga Marae, and the Moriori Claims Settlement Act 2021. He has been chair of the Moriori Hokotehi Trust Board and is current chair of the Moriori Imi Settlement Trust. Aside from being a passionate and committed advocate for Moriori, Māui is a keen conservationist and together with his hunau [family] has been restoring the korowai [cloak] of indigenous vegetation at Manukau, east of Ouenga | Owenga, on land that was granted by Native Land Court to Moriori (3% of the island) in the 1870s.

Revised key to *Pyrenula moniliformis* and segregates

1. Ascospores under 70 µm long. . . . . 2.

– Thallus brown, corticate, ascospores 70–100 × 10–15 µm . . . . . .*Pyrenula largei*

2. Ascospores greater than 35 µm long . . . . . 3.

– Thallus white-cream, ascospores 22–30 × 8–10 µm . . . . . *Pyrenula dalmatioides*

3. Ascospores transversely septate . . . . . 4.

– Ascospores curved, submuriform with square/rectangular locules, 38–45 × 12–15 µm. . . . . *Pyrenula quadratolocularis*

4. Ascomata flattened, ascospores 7–9-septate, 37–52 × 6.0–8.5 µm . . . . . *Pyrenula solomonii*

– Ascomata erumpent, ascospores 5–7-septate, 55–68 × 10.0–12.5 µm . . . . . *Pyrenula moniliformis*

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ETHICS DECLARATION

The authors declare no conflict of interest.

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Чотири нові види роду *Pyrenula* (*Pyrenulaceae*)
з Аотеароа | Нової Зеландії, виділені з *P. moniliformis*

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Реферат. Лишайники роду *Pyrenula* (*Pyrenulaceae*) в Аотеароа | Новій Зеландії востаннє детально вивчав Галловей (Galloway, 2007), який закликав до подальшого планомірного збору зразків. Зібрані відтоді додаткові матеріали, зокрема з північної частини Північного острова та архіпелагу Чатем, призвели до критичного перегляду раніше ідентифікованих зборів і до кращого розуміння обсягу виду в межах цього роду. Серед таксонів, що потребували перегляду, був загадковий вид *Pyrenula moniliformis*, відомий лише з типового місцезростання. Цей вид віднайшли у колекціях гербарію UNITEC з регіону Окленд у Новій Зеландії. Віднайдення виду і критичне вивчення цих та інших зразків, які включали до складу *P. moniliformis*, дозволили провести детальне морфологічне порівняння, зокрема перегородок і розміру аскоспор, і встановити, що *P. moniliformis sensu lato* насправді містить декілька таксонів. У статті ми подаємо уточнений опис *P. moniliformis sensu stricto*, а також описуємо чотири нові види: *P. dalmatioides* A.J. Marshall, Blanchon, Aptroot & de Lange, *P. largei* A.J. Marshall, de Lange, Blanchon & Aptroot, *P. quadratolocularis* A.J. Marshall, de Lange, Blanchon & Aptroot, і *P. solomonii* A.J. Marshall, de Lange, Blanchon & Aptroot. Для цих п'яти видів наведено морфологічні описи, екологічні особливості, поширення та оцінка природоохоронного статусу, а також ключ для визначення представників комплексу *Pyrenula moniliformis*.

Keywords: Аотеароа | Нова Зеландія, архіпелаг Чатем, ліхенізована мікобіота, таксономія лишайників, *Pyrenula*, *Pyrenula moniliformis*, *Pyrenula dalmatioides* sp. nov., *Pyrenula largei* sp. nov., *Pyrenula quadratolocularis* sp. nov., *Pyrenula solomonii* sp. nov.

FUNGI AND FUNGI-LIKE ORGANISMS
ГРИБИ І ГРИБОПОДІБНІ ОРГАНІЗМИ

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RESEARCH ARTICLE

Molecular detection and symptomatology of *Lasiodiplodia theobromae* (*Ascomycota*) infecting rose apples (*Syzygium samarangense*) in Malaysia

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Abstract. Rose apple (*Syzygium samarangense*, *Myrthaceae*) is considered one of the main tropical fruits native to Southeast Asia. In 2024, rose apples with fruit rot symptoms, characterized by dark, sunken circular lesions on ripening fruits, were observed in two locations in Perak, Malaysia. The identity of the pathogen that was responsible for the diseases was determined using morphological characteristics, DNA sequences, and phylogenetic analyses of internal transcribed spacer (ITS) and elongation translation factor 1-alpha (tef1-α). Morphological patterns of fungal isolates were observed on cultured potato dextrose agar (PDA) plates. The ITS and tef1-α of a fungal isolate were PCR amplified and sequenced, confirming the identity of *Lasiodiplodia theobromae* (GenBank accession nos. PQ584813 and PV155110, respectively). To fulfil Koch's postulates, the fungi were re-isolated and tested for pathogenicity on detached fruits. Symptoms similar to those observed in the market appeared on all inoculated fruits, while control fruits remained symptomless. To our knowledge, this is the first molecular-level report of *L. theobromae* infecting rose apples in Malaysia.

Keywords: fruit anthracnose, *Lasiodiplodia theobromae*, rose apple, *Syzygium samarangense*

Introduction

Rose apple (*Syzygium samarangense* (Blume) Merr. & L.M. Perry, family *Myrtaceae*) is one of the most important tropical fruits that is indigenous to Malaysia and other Southeast Asian countries,

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including Thailand and Indonesia, and cultivated in many other regions, such as Taiwan (Banadka et al., 2022). Rose apples are rich sources of nutrition, with carbohydrates, proteins, minerals, and vitamins (Venkatachalam et al., 2018). The rose apple is also high in vitamin C, polysaccharides, and antioxidant compounds, all of which have important health benefits (Cheng et al., 2022). Additionally, rose apples are used in many value-added products such as candies, jams, juices, and syrups, contributing significantly to their economic value (Banadka et al., 2022). In Malaysia, it is widely cultivated in an area of approximately 3 300 hectares, with an income of more than 9 million US dollars per year (Al-Obaidi et al., 2023). One of the main challenges facing Malaysia's rose apple industry is fungal-related postharvest losses. Due to their high moisture content, thin skin, and high chilling sensitivity, rose apples are susceptible to bacterial and fungal infections (Hasan et al., 2022). Anthracnose disease has significantly affected rose apple fruits, resulting in the loss of around one-third of annual production, leading to significant economic difficulties (Lii et al., 2017).

Previous studies have identified multiple *Lasiodiplodia* Ellis & Everh. (*Botryosphaeriaceae*, *Botryosphaeriales*, *Ascomycota*) species involved in similar infections in other *Myrtaceae* hosts such as guava (*Psidium guajava* L.) (Zee et al., 2021), but limited data exist on their specific impact on *Syzygium samarangense*. Beyond *Myrtaceae*, *Lasiodiplodia* species have been documented infecting a wide range of host plants in Malaysia, including cacao (*Theobroma cacao* L., *Malvaceae*) (Huda-Shakirah et al., 2022) and mango (*Mangifera indica* L., *Anacardiaceae*) (Munirah et al., 2017), highlighting their widespread occurrence and adaptability.

In June 2024, dark, sunken circular lesions on ripening fruits were observed in two locations in the state of Perak, Malaysia (Fig. 1). To date, no detailed etiological investigation has been conducted to characterize the causal pathogen responsible for these symptoms in Malaysian rose apple. The objective of this study was the identification of the causal agent of the postharvest disease in rose apples; this information will be helpful in developing suitable response mechanisms against postharvest fungal infections. This research aims to fill research gaps in the current understanding of fungal infections affecting this economically significant and promising fruit and to provide a foundation for integrated disease management strategies in the region.

Methodology

To identify the causal agent, infected rose apple fruit pieces (5×5×5 mm cubes) were surface sterilized with 1.5% sodium hypochlorite, followed by 70% ethanol, rinsed with sterile distilled water, and plated on potato dextrose agar (PDA). PDA plates were incubated at 25 °C, 50% relative humidity for 12 days. Fungal structures were observed under a microscope using safranin dye to enhance visualization. The stained samples were examined using a Trinocular Microscope Set Model CX33 (Olympus, Japan) to assess morphological characteristics. For molecular identification, internal transcribed spacer (ITS) regions 1 and 2 and elongation translation factor 1-alpha (tef1-α) were amplified by PCR and sequenced (Hami et al., 2021). The total reaction volume of 25 µl contained genomic DNA purified using an in-house optimized protocol, 0.5 pmol of each primer, deoxynucleotides triphosphates (dNTPs, 200 µM each), 0.5 U thermostable DNA polymerase, supplied PCR buffer, and water. The PCR conditions were as follows: one cycle of initial denaturation at 98 °C for 2 minutes; 25 cycles of denaturation at 98 °C for 15 seconds, annealing at 60 °C for 30 seconds, and extension at 72 °C for 30 seconds; and a final extension at 72 °C for 10 minutes (Al-Obaidi, 2017).

PCR products were analyzed using 1.5% agarose gel electrophoresis in 1X TAE buffer. A 100 bp DNA ladder was used as a molecular weight marker (Lane M). A total of two PCR amplicons (Lanes A and B) were loaded, and electrophoresis was performed at 100 V for 40 minutes. The gel was stained with ethidium bromide and visualized under a UV transilluminator using a Bio-Rad Gel Documentation System.

Sequence homology was analyzed using BLAST (http://blast.ncbi.nlm.nih.gov/) to identify the closest reference sequences from the NCBI GenBank database. Phylogenetic analysis of ITS and tef1-α sequences was performed using maximum likelihood in MEGA 11 (Çiftçi et al., 2023). The PCR products were purified by the standard PCR clean-up method. Pathogenicity tests of isolated *L. theobromae* were performed on detached fruits. Healthy fruits were washed thoroughly, surface sterilized with 6% sodium hypochlorite for 10 minutes, and rinsed with sterile distilled water (Karunamoorthy et al., 2023). Rose apple fruits were inoculated with 10 µl conidial suspension (1×10^6 spores/ml) of the pathogens prepared from 2-week-old cultures on PDA, while sterile water was used to inoculate

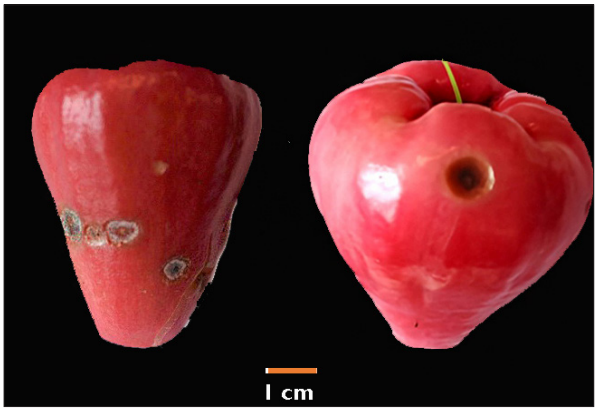


Fig. 1. Early symptoms of rose apple fruit rot caused by *Lasiodiplodia theobromae*

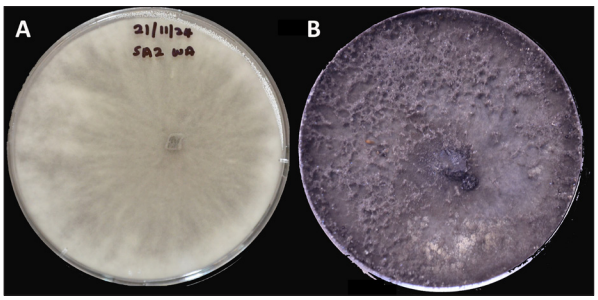


Fig. 2. Morphological characteristics of *Lasiodiplodia theobromae* on potato dextrose agar medium, showing a white to light-cream colony at 6 days (A) and a dark grey to black colony with fluffy aerial mycelium at 14 days (B)

control fruits using the pin-prick method (Chaudhary et al., 2020). Inoculated fruits were placed in plastic containers and incubated at 27 °C for 7 days.

Results

In the cultured plate, a morphological pattern of fungi is shown growing from the pieces of rose apple, initially appearing white and later developing a darker, textured surface (Fig. 2). Fungal conidia were predominantly straight, with lengths ranging from 21–24 µm and widths between 2.2–4.3 µm.

The purified PCR products were subjected to bidirectional sequencing with universal primers M13F (-20) and M13R-pUC (-26) using a BigDye® Terminator v3.1 Cycle Sequencing Kit. The sequence from the plate identified as *L. theobromae* (546 bp) (GenBank accession nos. PQ584813 and PV155110) showed 100% similarity with *L. theobromae* (Fig. 3).

Agarose gel electrophoresis confirmed the successful amplification of the target gene regions, as shown in Fig. 4. The DNA ladder (Lane M) provided size reference bands, with the most relevant markers at 100 bp, 500 bp, and 1000 bp. PCR products in Lanes A and B exhibited strong bands, indicating successful amplification of the target regions. The absence of non-specific bands or primer dimers suggests the high specificity of the primers used (Fig. 4). This result confirms that the ITS and TEF-1α regions were successfully amplified, allowing for further molecular characterization of the *Fusarium* strains through sequencing and phylogenetic analysis.

Phylogenetic clustering revealed a close relationship between our fungal isolates and those from other countries (Fig. 5A, B). The phylogenetic relationships among the *Lasiodiplodia* isolates were analyzed using Maximum Likelihood (ML) based on two genetic regions: the translation elongation factor 1-alpha (tef1-α) gene (Fig. 5A) and the internal transcribed spacer (ITS) regions 1 and 2 (Fig. 5B). In both trees, the isolates consistently clustered within the *L. theobromae* clade, supported by high bootstrap values (ranging from 92% to 100%), strongly confirming their species identity. In the tef1-α tree, representative isolates such as *L. theobromae_PLSB370* and *L. theobromae_CMMP4054* grouped tightly with known *L. theobromae* reference strains, indicating close evolutionary relatedness. Similarly, in the ITS-based tree (Fig. 5B), the isolates *L. theobromae_PLSB370* and *L. theobromae_PDS88* also clustered with authenticated *L. theobromae* sequences, showing congruent topologies with the tef1-α-based tree. The inclusion of other *Lasiodiplodia* species and outgroup taxa, such as *Diplodia seriata* De Not. and *Lasiodiplodia brasiliensis* M.S.B. Netto, M.W. Marques & A.J.L. Phillips, allowed for clear delineation of clade boundaries and rooting of the phylogenetic trees. The consistent placement of isolates in both gene trees provides robust molecular evidence that the studied strains belong to *L. theobromae*. The presence of minor sub-clustering within the *L. theobromae* group may reflect underlying genetic variation, potentially linked to geographical origin or host specificity.

The inoculated rose apple fruits displayed typical white/grey (*L. theobromae*) lesion symptoms after four days, while the control fruits displayed no symptoms (Fig. 6). Koch's postulates were fulfilled when the pathogen was re-isolated from inoculated fruits and confirmed to be identical to the original isolates used in the pathogenicity tests (Al-Obaidi et al., 2023).

Discussion

The identification of *L. theobromae* as the causal agent of postharvest fruit rot in Malaysian rose apples represents a significant advancement in understanding the fungal pathogens affecting this economically important crop. This study provides the first molecular-level confirmation of *L. theobromae* infecting rose apples in Malaysia, complementing previous reports of fungal pathogens such as *Pestalotiopsis samarangensis* in Thailand (Maharachchikumbura et al., 2013) and *Colletotrichum siamense* associated with leaf spot disease in the same region (Khuna et al., 2023). The morphological and molecular characterization of *L. theobromae* isolates, supported by phylogenetic analyses of ITS and tef1-α regions, is consistent with current best practices in fungal taxonomy, as tef1-α has been shown to offer better resolution among species of *Lasiodiplodia*. In our study, BLASTn analysis revealed 100% sequence identity between our isolate (PLS2S20) and reference sequences of *L. theobromae* for both ITS and tef1-α. Furthermore, our phylogenetic trees placed the isolate firmly within a well-supported *L. theobromae* clade, with high bootstrap values confirming its close relationship to authenticated global isolates. Overall, the combined morphological and molecular evidence provides a solid basis for attributing the observed postharvest rot in *Syzygium samarangense* to *L. theobromae*. To the best of our knowledge, this represents the first confirmed report of *L. theobromae* infecting rose apple in Malaysia, filling a significant gap in the regional plant pathology literature and contributing to the broader understanding of this pathogen's host range and geographic distribution.

The pathogenicity tests conducted in this study fulfilled Koch's postulates, confirming *L. theobromae* as the causative agent of the observed symptoms (Úrbez-Torres et al., 2008). The development of dark, sunken lesions on inoculated fruits, coupled with the successful re-isolation of the pathogen, provides robust evidence of its role in postharvest decay. These findings are consistent with previous studies highlighting *L. theobromae* as a significant postharvest pathogen in tropical and subtropical regions, affecting a wide range of fruit crops, including papaya, mango, and citrus (Al-Obaidi et al., 2023; Karunamoorthy et al., 2025). The economic implications of *L. theobromae* infection in rose apples are profound, given the crop's growing contribution to Malaysia's



Fig. 3. Developmental stages of *Lasiodiplodia theobromae* observed under a microscope. A: mycelium; B: mature conidia. Magnification ×100, scale bar 30 μm

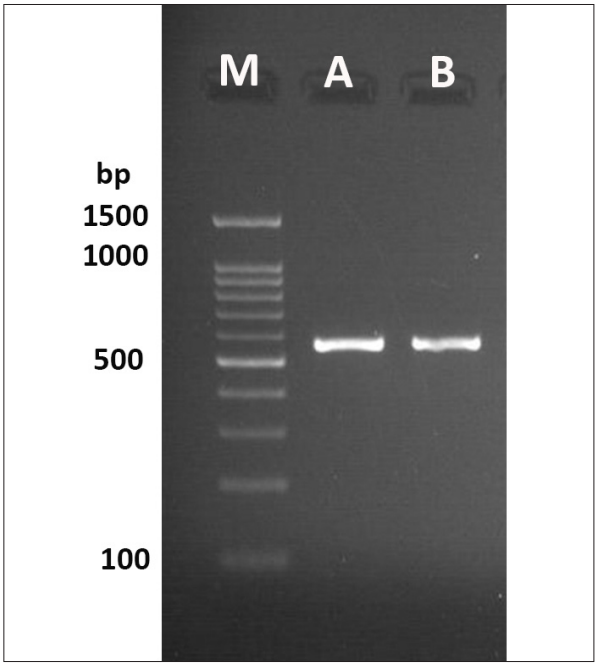


Fig. 4. Agarose gel electrophoresis of PCR-amplified DNA. A: ITS region (546 bp) using universal ITS1 and ITS2 primers; B: tef1-α gene (533 bp)

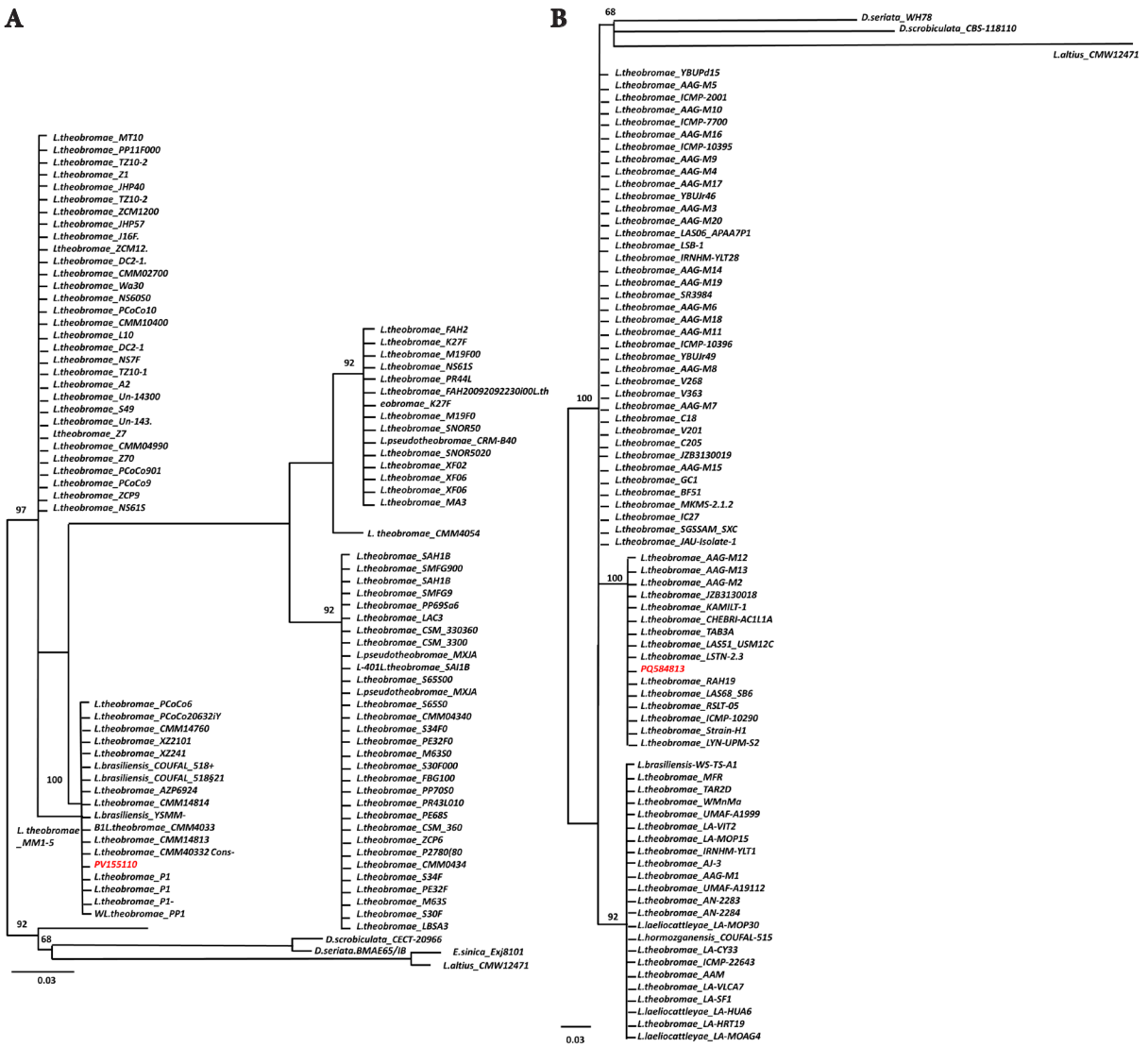


Fig. 5. Phylogenetic tree for *L. theobromae* generated using translation elongation factor 1-alpha (tef1-α) region (A), and internal transcribed spacer (ITS) regions 1 and 2 (B)

agricultural economy. The high moisture content, thin skin, and chilling sensitivity of rose apples make them particularly susceptible to fungal infections, exacerbating postharvest losses during storage and transportation (Zee et al., 2021). Our findings highlight the urgent need for effective management strategies to mitigate the impact of *L. theobromae* on rose apple production. Potential approaches include the development of resistant cultivars through breeding programs, the application of biocontrol agents, and the use of antifungal treatments during postharvest handling. Additionally, enhancing the activity of defence-related enzymes in rose apples could improve their resistance to fungal infections, thereby extending shelf life and reducing losses (McLaughlin et al., 2023). This study also underscores the importance of molecular tools in accurately identifying and characterizing fungal pathogens. The use of ITS and tef1-α sequences for phylogenetic analysis not only confirmed the identity of *L. theobromae* but also revealed its genetic relationship with isolates from other regions (Pornsuriya et al., 2023).

Such insights are crucial for understanding the global distribution and evolution of fungal pathogens, informing the development of targeted control measures. Future research should focus on exploring the environmental and physiological factors influencing *L. theobromae* infection in rose apples. Investigating the role of temperature, humidity, and fruit maturity in disease development could provide valuable insights for optimizing storage conditions and reducing postharvest losses. Furthermore, extending this research to other species could broaden our understanding of *L. theobromae*'s host range and pathogenicity mechanisms. In conclusion, this study provides the first molecular evidence of *L. theobromae* as the causal agent of postharvest fruit rot in Malaysian rose apples. Our findings contribute to the growing body of knowledge on fungal pathogens affecting tropical fruits and highlight the need for integrated management strategies to safeguard rose apple production and enhance its economic value.

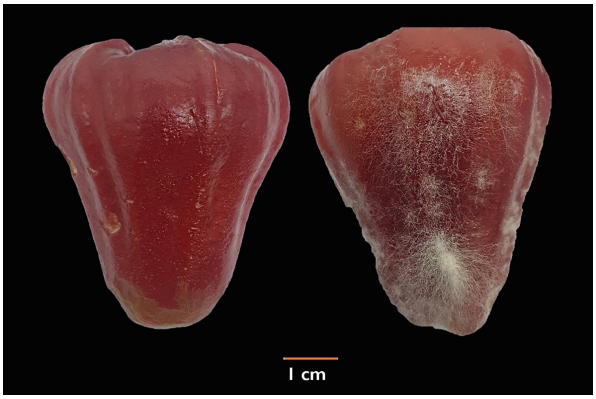


Fig. 6. Pathogenicity test of *L. theobromae* on rose apple fruits: control fruit (left); fruit with signs and symptoms (right)

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ETHICS DECLARATION

Authors have no competing interests to declare.

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Молекулярне визначення і симптоми ураження *Syzygium samarangense* грибом *Lasiodiplodia theobromae* (*Ascomycota*) у Малайзії

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Реферат. Плоди *Syzygium samarangense* вважаються одними з основних тропічних фруктів, що походять із Південно-Східної Азії. У 2024 р. у двох локаціях у штаті Перак, Малайзія на зрілих плодах виявили симптоми плодової гнилі з характерними округлими бурими плямами. Ідентифікацію збудника гнилі проводили з урахуванням морфологічних особливостей і філогенетичного аналізу послідовностей ITS-регіону ДНК із залученням генів tef1-α. Морфолого-культуральні ознаки вивчали при культивуванні гриба у чашках Петрі на картопляно-декстрозному агарі (PDA). Ампліфіковані за допомогою ПЛР та секвеновані послідовності підтвердили належність досліджених культур гриба до *Lasiodiplodia theobromae* (реєстраційні номери у базі даних GenBank PQ584813 і PV155110). Відповідно до постулатів Коха, гриби повторно виділили в культуру та перевірили їхню патогенність на окремих плодах. Подібні до початкових симптоми з'явилися на всіх інокульованих плодах, тоді як контрольні плоди залишалися безсимптомними. Наскільки нам відомо, це перше підтверджене молекулярними методами повідомлення про ураження плодів *S. samarangense* грибом *L. theobromae* в Малайзії.

Ключові слова: *Lasiodiplodia theobromae*, *Syzygium samarangense*, антракноз плодів, “яванське яблуко”

STRUCTURAL BOTANY
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RESEARCH ARTICLE

Morphological features of flowers and fruits of *Valeriana stolonifera* (*Caprifoliaceae*) and their taxonomic significance

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Abstract. Results of macro- and micromorphological studies of flowers and fruits of two subspecies of *Valeriana stolonifera*, subsp. *stolonifera* and subsp. *angustifolia*, are presented. Samples from Ukraine and Poland were studied. The structure of flowers and fruits is described, and their detailed characteristics are identified. Morphological structures were examined using scanning electron microscopy (SEM). New micromorphological features of the fruit surface of the studied taxa have been revealed, including the characters of outer periclinal and anticlinal walls of exocarp cells, trichomes, and stomata. In flowers of both subspecies of *V. stolonifera*, an ovoid protrusion of the connective over the anthers of stamens is present. No significant differences between the studied taxa in their macro- and micromorphological features of fruits and flowers have been found. The obtained results, combined with the known characters of vegetative organs, can be used for more accurate identification of the subspecies of *V. stolonifera* and for resolving taxonomic issues within the group of *V. officinalis* aggr.

Keywords: exocarp, flower, fruit, micromorphology, microstructure, SEM microscope, taxonomy

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Introduction

The genus *Valeriana* L., according to molecular phylogenetic studies and the APG IV system (2016), is placed within the family *Caprifoliaceae* Juss. *sensu lato*, including *Dipsacaceae* Juss., *Morinaceae* Raf., and *Diervillaceae* (Raf.) N. Pyck (Bell et al., 2001; Bell, 2004; Hidalgo et al., 2004; Bell, Donoghue, 2005). According to various authors, the genus includes from 150 to 350 species in the world flora (Dweck, 1997; Takhtajan, 1997, 2009; Bell, Donoghue, 2005) and occurs mainly in Europe, central and northern Asia, North and South America, and North Africa (Grubov, 1958; Katina, 1961; Weberling, 1970; Voroshilov, 1978; Katina, 1987; Gorbunov, 2002; Takhtajan, 2009).

The distribution of *V. stolonifera* covers Western and Central Europe, including many European countries (e.g., Albania, Austria, Baltic countries, Belgium, Bulgaria, Czech Republic, Slovakia, Denmark, France, Germany, Great Britain, Greece, Hungary, Iceland, Ireland, Italy, Norway, Poland, and Ukraine) (Kirschner, Raab-Straube, 2017; POWO, 2025–onward).

The taxonomic status of *V. stolonifera* as a separate species within the genus *Valeriana* remains problematic and is debated among researchers. It is listed as an accepted species in the databases *World Flora Online* (WFO, 2025–onward), *Plants of the World Online* (POWO, 2025–onward), *Catalogue of Life Checklist* (2024), and in a number of floristic publications from the territory of Ukraine and other regions of Europe (Katina, 1961; Mosyakin, Fedoronchuk, 1999; Kirschner, Raab-Straube, 2017, etc.). In the *Flora of the USSR* (Grubov, 1958) most species readily recognized in Ukraine (Katina, 1961), in particular, *V. angustifolia* Tausch ex Host, *V. nitida* Kreyer, *V. rossica* P.A. Smirn., *V. sambucifolia* J.C. Mikan ex Pohl, *V. stolonifera* Czern., *V. wallrothii* Kreyer, and *V. wolgensis* Kazak., have been listed only as synonyms of the species *V. officinalis* L. *sensu latissimo*. Recently, *V. stolonifera* has also been classified within the *V. officinalis* complex (Kirschner, Zeisek, 2017).

To date, the taxonomy of entities within the *V. officinalis* complex has not been definitively clarified (Buttler et al., 2008; Kirschner, Zeisek, 2017). Due to differences in taxonomic treatments, some taxa are recognized as species, subspecies, or varieties, depending on views and species concepts applied by the authors (Bressler et al., 2017; Kirschner, Raab-Straube, 2017), therefore, clarifying the much confusing and complicated nomenclature in the group remains relevant (Kirschner, Zeisek, 2017). The reasons for this taxonomic situation is the fact the *V. officinalis* complex includes many morphologically variable "narrow" species or, alternatively, infraspecific entities, which are variable in many of their characters throughout the vast territory range of the group, covering almost the entire temperate zone of Eurasia. This complex is represented by a polyploid series, ranging from diploids to octoploids, but each karyotype was considered morphologically indistinct (Grubov, 1958). According to a recent taxonomic summary, the *V. officinalis* complex in Central Europe includes *V. officinalis* (2n = 14, diploid), *V. stolonifera* (2n = 28, tetraploid), *V. pratensis* Dierb. (2n = 28, tetraploid), and *V. excelsa* Poir. (2n = 56, octoploid) (Kirschner, Zeisek, 2017; Kirschner, Raab-Straube, 2017).

On the basis of detailed taxonomic and nomenclatural studies of the *V. officinalis* complex, it has been found that the correct and accepted name for tetraploids is *V. stolonifera*, with two currently recognized subspecies, subsp. *stolonifera* and subsp. *angustifolia* Soó (Kirschner, Zeisek, 2017; Kirschner, Raab-Straube, 2017; IPNI, 2025–onward; POWO, 2025–onward). *Valeriana stolonifera* subsp. *stolonifera* has a limited range and is found only in Ukraine, whereas the native range of *V. stolonifera* subsp. *angustifolia* is both in Ukraine and in the rest of Europe where the species occurs.

In Poland *V. stolonifera* subsp. *angustifolia* [reported as *V. angustifolia* Tausch subsp. *angustifolia* in Rostański (1967, 1970), and as *V. angustifolia* Tausch in Mirek et al. (2020)] occurs mainly in the southeastern part of the country. It is predominantly a steppe plant and it belongs to the Pontic elements of the Polish flora (Rostański, 1970). The isolated relict sites are located in Central Poland, Silesia, and Pomerania; in the latter areas, it should be considered within the group of steppe relics (Rostański, 1970).

Previously, based on the comprehensive analysis of herbarium specimens of *Valeriana*, it has been found that species occurring in Poland belong to the section *Valeriana*, and three subsections: *Pinnatisectae*, *Heterophyllae*, and *Officinales* (Janchen, 1958; Rostański, 1970). Within the subsection *Officinales*, *V. officinalis* s. str., *V. sambucifolia* J.C. Mikan ex Pohl, and *V. angustifolia* were placed. The species earlier accepted as *V. angustifolia* has been distinguished on the basis of its morphological and cytological features (2n = 28; Skalińska, 1950). The

recent, detailed taxonomic studies of complicated and inconsistent nomenclature within the group of taxa related to *V. officinalis* s. l. in Central Europe demonstrated that the name *V. angustifolia* Tausch ex Host 1827 is illegitimate, being a later homonym of *V. angustifolia* Mill. 1768, the name which properly applies to the species earlier known as *Centranthus angustifolius* (Mill.) DC. (Kirschner, Zeisek, 2017; Kirschner, Raab-Straube, 2017). Hence, the correct name of the steppe *Valeriana* species occurring in Poland is:

***Valeriana stolonifera* Czern. subsp. *angustifolia* Soó**, Feddes Repert. 83: 208. 1972 ≡ *Valeriana pratensis* Dierb. subsp. *angustifolia* (Soó) Kirschner, Buttler & Hand, Kochia 3: 83. 2008 ≡ *Valeriana angustifolia* Tausch ex Host, Fl. Austriac. 1: 36. 1827, nom. illeg. [non *Valeriana angustifolia* Mill. 1768].

= *Valeriana collina* var. *stolonifera* Wallr., Linnaea 14: 537. 1841.

= *Valeriana wallrothii* Kreyer, Trudy Prikl. Bot. 23: 185. 1930.

Valeriana stolonifera subsp. *stolonifera* is a perennial, widespread subxerophilous species that lives in rather arid conditions in the ground cover of forests, on forest edges, and in meadows. In Ukraine, the subspecies is distributed almost throughout the territory of the country, but it is considered regionally rare in the Dnipropetrovsk, Zaporizhzhia, Mykolaiv, Odesa, and Kharkiv administrative regions (*oblasts*) (Andrienko, Peregrym, 2012). Populations of this species are usually small, and plants are weakly competitive, as compared to other species. They are used as valuable medicinal raw materials (Minarchenko, 2005; Kolomiychuk, 2011; Andrienko, Peregrym, 2012).

Although the species is not currently considered endangered or vulnerable at the national level and is not listed in the *Red Data Book of Ukraine* (2009), it is actually endangered in many regions of Ukraine. *Valeriana stolonifera* subsp. *angustifolia* is rare in the Transcarpathian (Zakarpattia) and Ivano-Frankivsk regions of Ukraine. In Poland, *V. stolonifera* subsp. *angustifolia* (reported as *V. angustifolia*) is listed in the *Polish Red List of Pteridophytes and Flowering Plants* with the status of DD (Data Deficient) (Kaźmierczakowa et al., 2016).

In classifying the patterns of infraspecific variability of *V. stolonifera*, considerable attention is paid to morphological features of vegetative organs, in particular the life form, the rhizome shape (short, cylindrical) and stems (ribbed or not) and their size, details of basal, lower, and stem leaves. *Valeriana stolonifera* subsp. *stolonifera* is characterized by well-developed runners, and leaflets often pointed, whereas subsp. *angustifolia* has no underground runners, or sometimes has short (up to 2 cm maximum) runners, which are easily damaged or overlooked (Katina, 1961; Rostański, 1967).

Considering that the generative organs of *V. stolonifera* (both subspecies) from the territory of Ukraine and *V. stolonifera* subsp. *angustifolia* from Poland are not sufficiently studied morphologically, the detailed study of their flowers and fruits was carried out, and their morphological features were compared. An important addition to previous our research on *V. stolonifera* (Tsarenko et al., 2021) is the inclusion of samples collected from the territory of Poland in order to identify the variability of characters and to reveal differences between both subspecies, which are analyzed in the present study.

The aims of the present study were (1) to analyze and present the macro- and micromorphological characters of fruits and flowers of both subspecies of *V. stolonifera* using SEM microscopy; (2) to identify and assess the taxonomically significant characters of generative organs used for distinguishing *V. stolonifera* subsp. *stolonifera* and subsp. *angustifolia*. The presented results may be useful for further comparative and morphological studies within the *V. officinalis* complex in Europe and, hopefully, will bring researchers closer to solving its taxonomy.

Materials and Methods

We analyzed the characters of flowers and fruits of two subspecies of *V. stolonifera*. The studied samples have been obtained from Ukraine [*V. stolonifera* subsp. *stolonifera* and subsp. *angustifolia* from the National Herbarium of the M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine (KW)] and from Poland [specimens of *V. stolonifera* subsp. *angustifolia* collected in Central Poland (Nizina Południowowielkopolska lowland)].

Examined specimens of flowers

***Valeriana stolonifera* subsp. *stolonifera*: 1.** Khmelnytsky Region, Kamenets-Podilskyi District, near Humentsy village, Mt. Karmalyuka, clearing in an

oak-hornbeam forest, 24.05.1974, leg. [B.V.] Zaveruha, No. 001250 (KW); **2.** Khmelnytsky Region, Vinkovetsky District, Kalyusik village, Kalyusetska Gora, steppe slope, 07.06.2008, leg. [Y.P.] Didukh, [T.V.] Fitsaylo, [I.A.] Korotchenko, [Y.] Vasheny-ak, No. 085520 (KW); **3.** Kyiv Region, Myronivskyi District, between V. [Velykyi] and M. [Malyi] Bukrin, in a ditch, pasture, 17.06.2000, Nsh [N.M. Shiyan]: 000353, leg., det. N. Drapailo [N.M. Shiyan], I. Timchenko (KW s.n.); **4.** Kyiv Region, Pereyaslav-Khmelnitsky District, Studenikivsky forest, 30.05.2001, O. Pryadko, № 009929 (KW); **5.** Ternopil Region, Husyatinsky District, near Vykno village, Mt. Ostra, northwestern slopes of mountains, bushes, 18.06.1974, B. Zaverukha, № 001239 (KW); **6.** Ternopil Region, Kremenets District, near Zholoba village, Mt. Maslyatin, meadow-steppe marginal-grassy glades on boulders, 25.06.1974, leg. [B.V.] Zaverukha, № 001251 (KW). ***Valeriana stolonifera* subsp. *angustifolia*: 7.** Ivano-Frankivsk Region, Tlumachsky District, Oleshiv-Baratyshev, meadow-steppe slopes of the gypsum mountain, 06.1974, leg. [B.V.] Zaverukha, № 001438 (KW); **8.** Transcarpathian Region, Uzhhorod District, Antonivka village, the glade Antonivska Polyana, 09.06.1948, leg. [G.I.] Bilyk, № 007634 (KW); **9.** [*Valeriana officinalis* L. s. l.] Transcarpathian Region, Perechyn District, Vorochevo village, Mt. Sinatoriya, meadow, 03.07.1956, leg. V.I. Chopyk, Notae criticae: *V. angustifolia* Tausch, 14.05.1971, M. Kotov, № 007632 (KW).

Examined specimens of fruits

***Valeriana stolonifera* subsp. *stolonifera*: 1.** Lviv Region, Zolochiv District, Bila Gora, 12.07.1980, M. Fedoronchuk (KW s.n.); **2.** Mykolaiv Region, Domanivskyi District, near Bogdanivka village, floodplain forest, 20.06.2005, O.F. Shcherbakova, L.I. Krytska, V.V. Novosad, S.M. Voronova, № 081710 (KW); **3.** Odesa Region, Rozdilnyanskyi District, near Kuchurhan, in the floodplains of the Dniester, 08.2006, O.Yu. Bondarenko, No. 119251 (KW); **4.** Ternopil Region, Kremenets District, Kremenets, Bozhy Gora, oak-hornbeam forest, 21.06.1986, leg. [A.V.] Shumilova, № 096740–096747 (KW); **5.** Ternopil Region, Kremenets District, Novoselky village, ravine, grassy-shrubby slope, 29.07.1958, M. Klokov, B. Zaverukha (KW s.n.); **6.** Vinnytsia Region, Yampil District, near Mykhailivka village, southern steppe slope, 12.06.2009, leg. [Y.] Vashenyak, № 00102996 (KW). ***Valeriana stolonifera* subsp. *angustifolia*: 7.** Poland, Łódź Voivodeship, Sieradz District, Woźniki forest District, subarea 266h, Dębowiec Forestry, subcontinental thermophilous oak forest *Potentillo albae-Quercetum petraeae*, 19.08.2021, leg., det. K. Kaczmarek; **8.** [*V. angustifolia* Tausch] Odesa Region, Izmail District, near Vylkovo, on the road to Primorske, 01.06.1966, M. Klokov, № 007639 (KW).

Micromorphological features of flowers and fruits were studied using MBS-9 binoculars and examined under a scanning electron microscope (SEM, JSM-6060 LA) at the Centre of Electron Microscopy of the M.G. Kholodny Institute of Botany and under SEM (Phenom Pro X) at the Department of Invertebrate Zoology and Hydrobiology, University of Lodz, Poland. The material was fixed on brass tables and was sputter-coated with a 4 nm layer of gold.

Micromorphological descriptions were performed using the generalized terminology (Fedorov, Artyushenko, 1975, 1979; Barthlott, 1981; Artyushenko, Fedorov, 1986; Karcz, 1996; Plisko, 2000; Zyman et al., 2004). Based on the research results, characters of the inflorescence, bracts, and flower elements of *V. stolonifera* were compiled, which were specified in relation to the data from relevant floristic treatments (Katina, 1961, 1987; Rostański, 1967). Photographs of the general appearance of flowers and fruits and microstructures of the fruit surface were performed at magnifications of ×15 to ×4000. Measurements of inflorescences, bracts and floral elements (length and width of the perianth corolla and pistil ovary, length of stamens, column, and receptacle) and fruits elements were made using the scale line of the MBS-9 binoculars and the AxioVision Rel. 4.8 software.

Results and Discussion

Morphological differentiation of the fruit of *Valeriana stolonifera* subsp. *stolonifera* and subsp. *angustifolia*

Despite many carpological studies of *Valeriana* species, especially those with a controversial taxonomic status (Karcz, 1996; Gorbunov, 2014; Vakulenko et al., 2016; Al-Dabbagh, Saeed, 2020; Tsarenko et al., 2020, 2021), is still quite a challenge to identify the diagnostic features distinguishing taxa. As we have shown in our previous study, the fruits of all species of the genus, in particular *V. stolonifera* group, are quite similar in appearance. They are

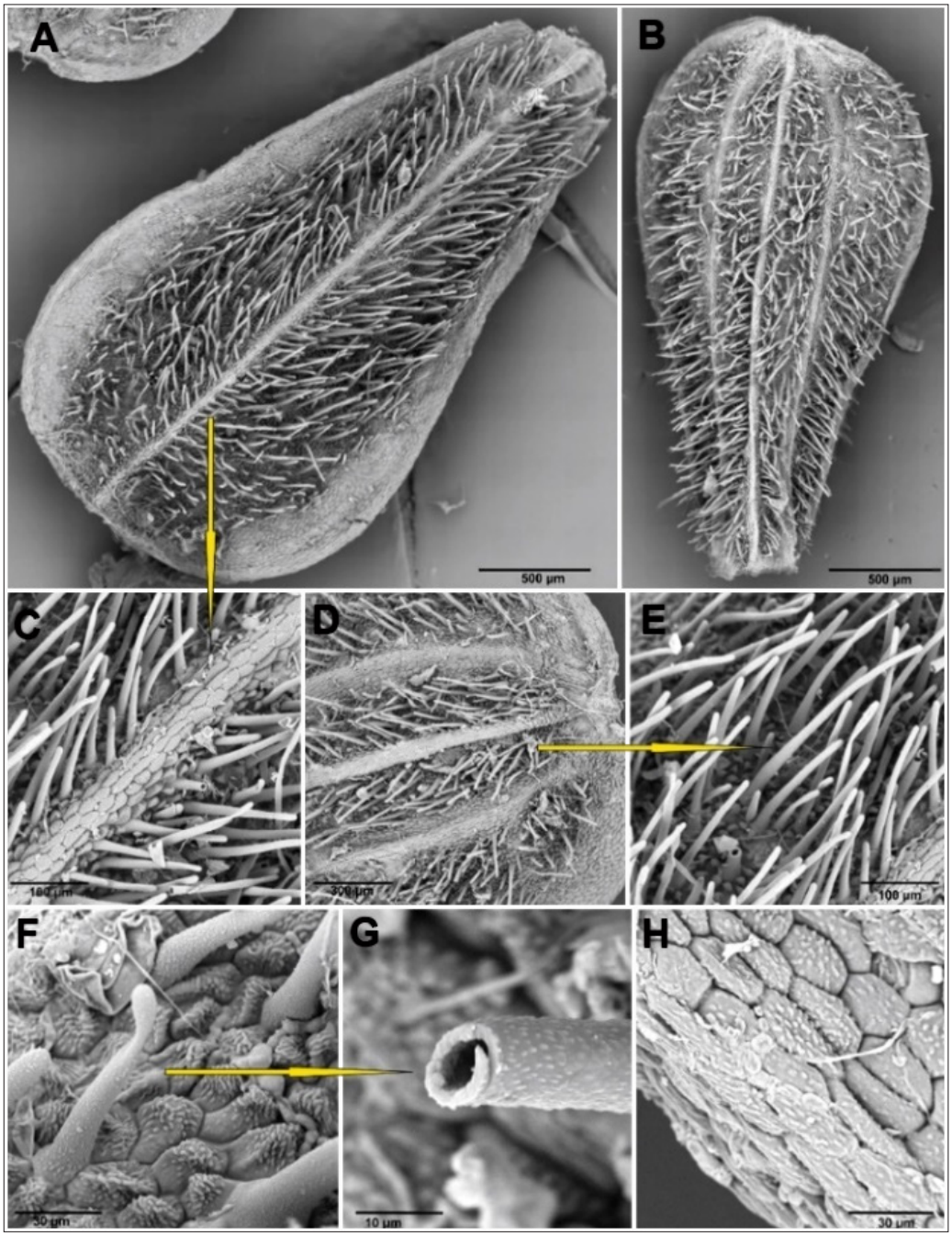


Fig. 1. Fruit of *Valeriana stolonifera* subsp. *angustifolia* (SEM) from Poland. A: adaxial side; B: abaxial side; C: rib; D–F: fragment of the abaxial surface with hairs; G: simple hair; H: verrucose surface of the fruit

somewhat flattened, especially on the adaxial side, mostly oblong-ovate or ovoid. The fruit apex is elongated, the base is rounded and slightly widened, with a slight depression in the middle, and with a basal fruit scar.

The calyx is attached the top of the fruit, which in the process of maturing turns into a white feathery formation similar to a pappus, with long thickened leathery awns covered by numerous white long soft hairs. The awns are united at the base, forming a

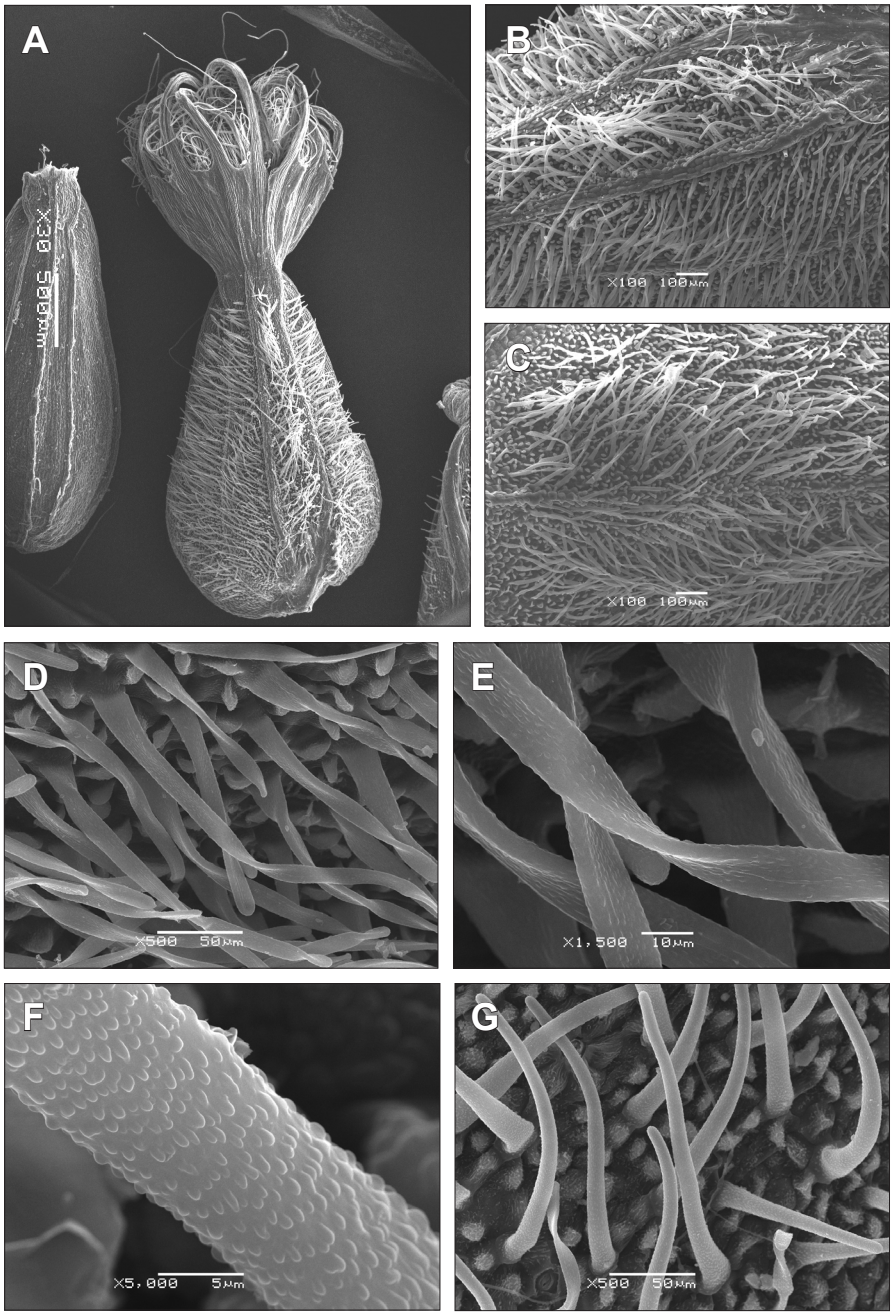


Fig. 2. Fruit of *Valeriana stolonifera* subsp. *angustifolia* (SEM) from Ukraine. A: abaxial side; B: fragment of the abaxial surface with ribs and hairs; C, D: fragment of the adaxial surface with hairs; E: simple hair; F: coarse surface of the hair; G: verrucose microstructure surface

membranous crown. In immature fruits, the awns with hair are wrapped down; they unfold only after ripening. On the adaxial side of the fruit, there is one longitudinal vein in the center; on the abaxial side there are three longitudinal veins (one central and two lateral) with vascular bundles, which look like ribs from the outside (Figs 1A, B; 2A, B; 3A, B).

The fruits of *V. stolonifera* are brown, dull, oblong-ovate, with a rounded base, slightly flattened on the sides, 2.4–3.7 mm long, 1.3–1.6 mm wide,

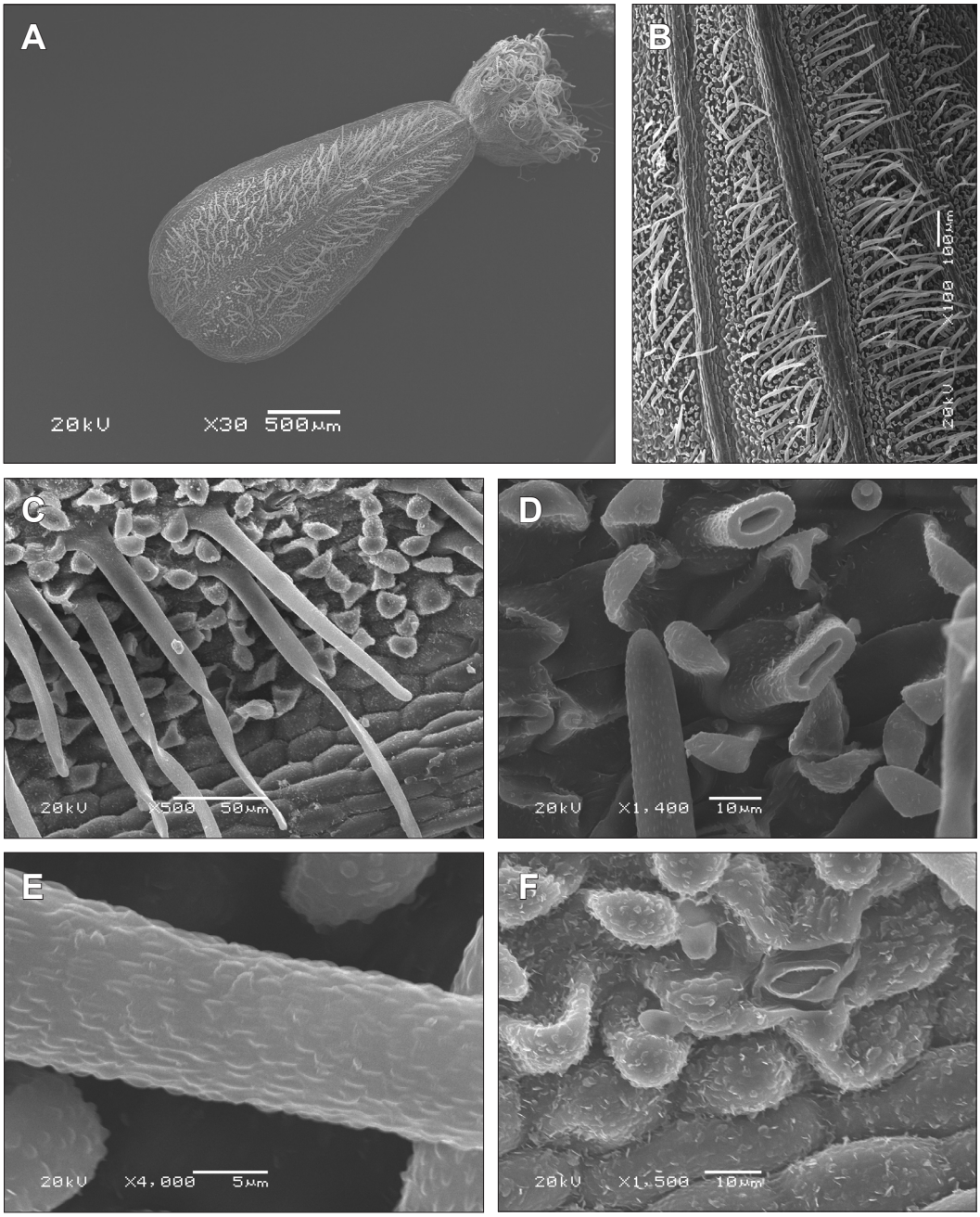


Fig. 3. Fruit of *Valeriana stolonifera* subsp. *stolonifera* (SEM). A: adaxial side; B: fragment of the abaxial fruit surface; C, D: simple hairs; E: coarse surface of the hair; F: verrucose microstructure surface of the fruit with visible stoma

with narrow borders at sides (Figs 1A, B; 2A; 3A). The fruits are pubescent on both sides between the ribs, with simple, short hairs up to 0.2 mm. Ribs are without trichomes (Tsarenko et al., 2021) (Figs 1A–F; 2A–E; 3A–D). The fruits of both subspecies of *V. stolonifera* (subsp. *stolonifera* and subsp. *angustifolia*) are pubescent with tubular and ribbon-like hairs. However, earlier we described for *V. stolonifera* only pubescence with ribbon-like hairs (Tsarenko et al., 2021). The predominance of these

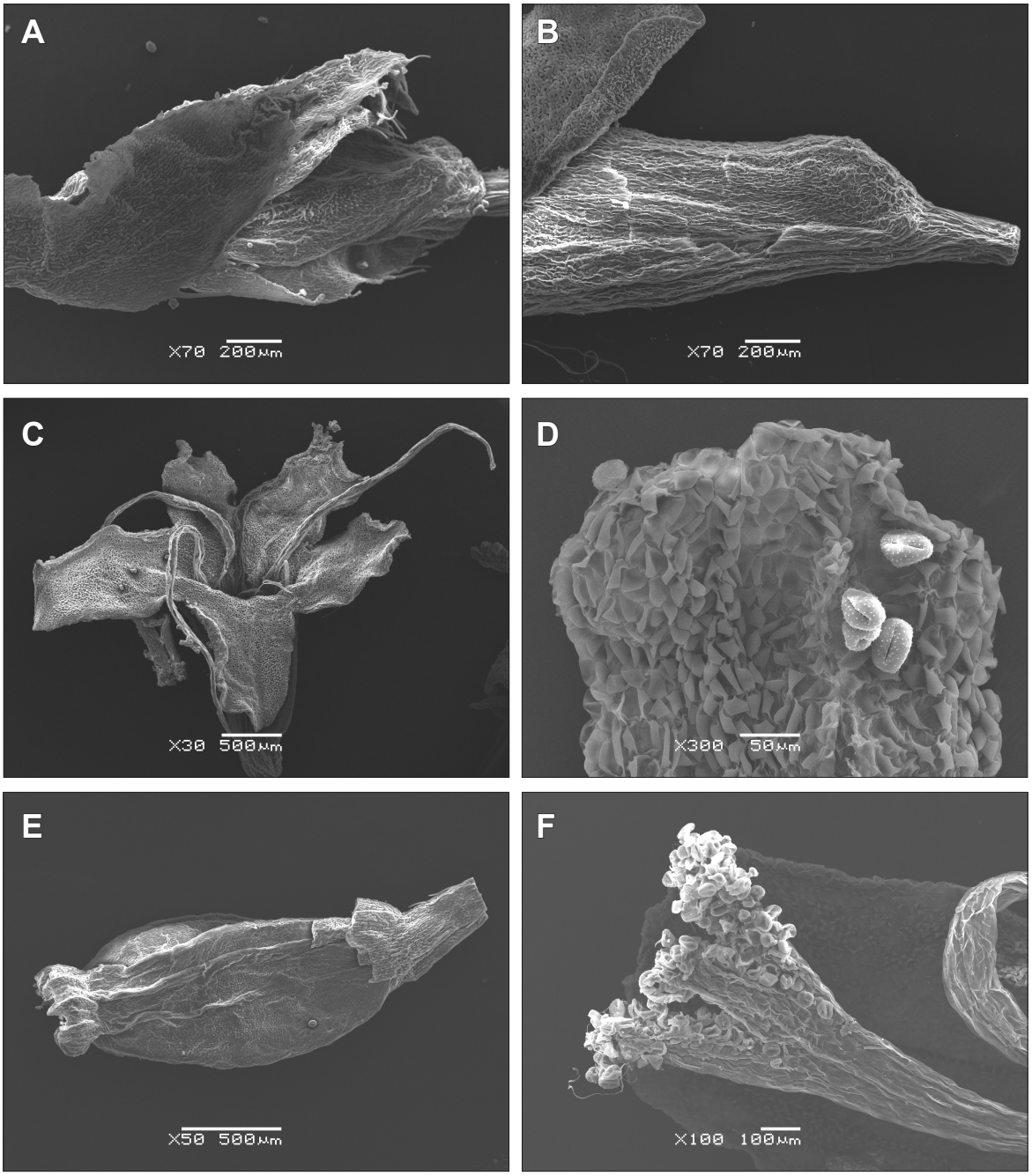


Fig. 4. Flower of *Valeriana stolonifera* subsp. *angustifolia* (SEM) from Ukraine. A: bract and top of the pistil; B: top of the calyx and base of the corolla; C: corolla; D: anther with projection of the connective; E: pistil; F: trifid stigma

or other hairs in pubescence of the fruit depended on the state of maturity and is not a diagnostic character — unripe fruits are mostly covered by ribbon-like hairs (Figs 2D–F; 3C–E). The pubescence on the awns is similar in all studied samples. The awns are covered with long, twisted, mostly ribbon-like hairs.

It should be noted that the use of SEM in our study revealed important features of the fruits surface microstructure. Both subsp. *stolonifera*

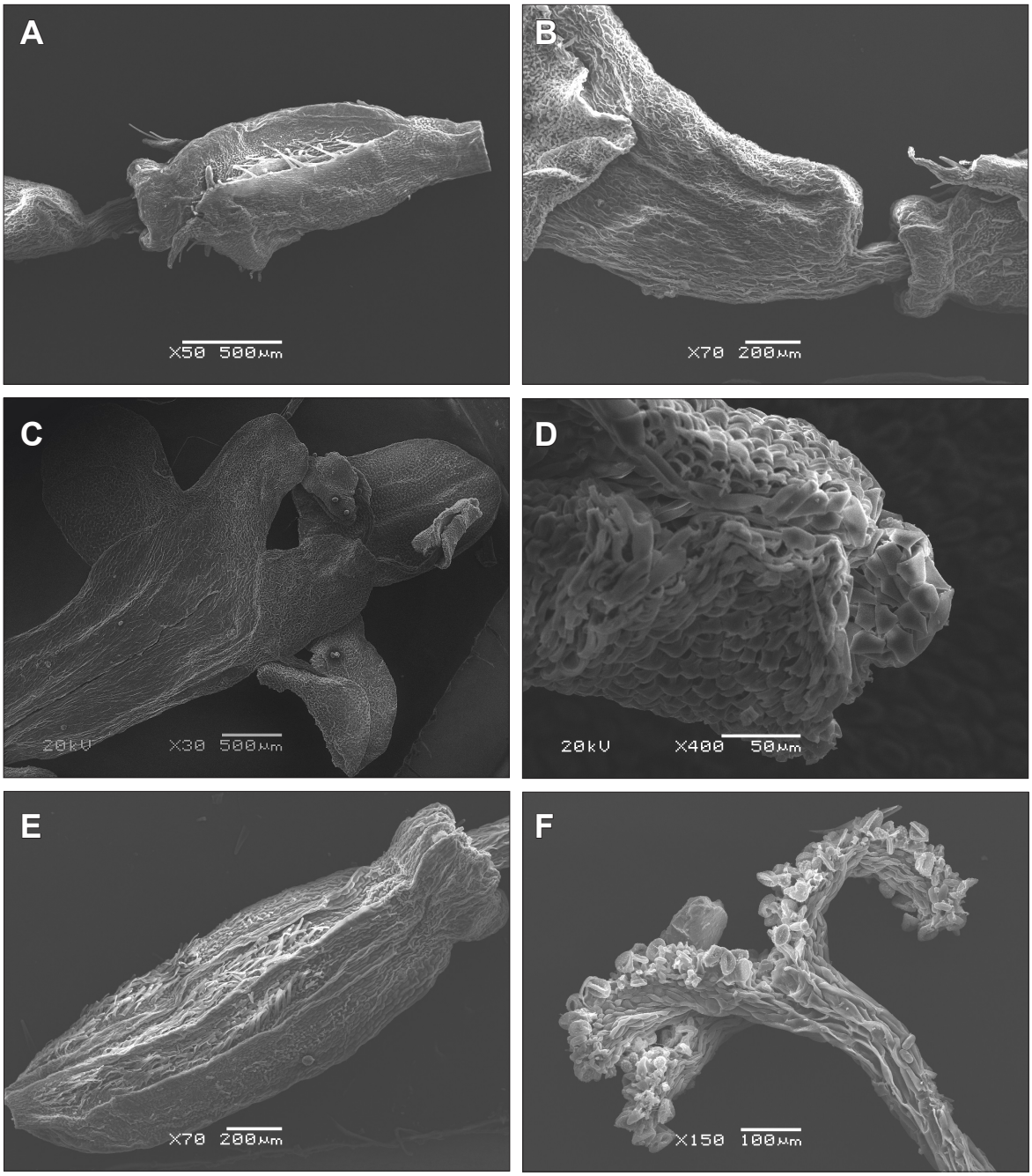


Fig. 5. Flower of *Valeriana stolonifera* subsp. *stolonifera* (SEM) from Ukraine. A: bract and pistil; B: top of the calyx and base of the corolla; C: corolla; D: anther with projection of the connective; E: pistil; F: trifid stigma

and subsp. *angustifolia* are quite similar, having the small tuberculate type of fruits surface. Exocarp cells on the ribs are arranged in rows along the longitudinal axis. They are elongated and have slightly convex outer periclinal walls. The cells of the surface on the interribs areas are without clear orientation, boundaries between the cells of the exocarp are clear. The cells are with slightly convex periclinal walls, angular, rounded, or in some areas elongated, mostly with trichomes, but closer

to the ribs, hairs are absent. The fruit surface of *V. stolonifera* subsp. *stolonifera* is covered with numerous papillae up to 40 μm long and with rounded or linear cuticular formations on the cell surface. In fruit specimens of *V. stolonifera* subsp. *angustifolia*, papillae were very rare or absent. The presence of papillae on the fruit surface may be a result of environmental factors or physiological processes in the plant. Oval stomata were found on the surface of all samples. The stomata are surrounded by two, more often five lateral cells, located radially relative to the stomata. The shape and cuticular sculpture of lateral cells are the same as those of other exocarp cells. On some areas of the surface of the fruit, plates of epicuticular wax were found. As shown by our previous carpological studies of representatives of the genus *Valeriana*, the type of wax formation on the epidermal cell surface cannot be used as an additional diagnostic character (Tsarenko et al., 2021). In conclusion, no significant differences were found in the carpological features between both subspecies. Our study also confirmed that the described micromorphological characteristics of the fruits are stable and do not differ from those described by us (Tsarenko et al., 2021) previously for *V. stolonifera* samples from other parts of Ukraine.

Morphological differentiation of the flower of *Valeriana stolonifera* subsp. *angustifolia* and subsp. *stolonifera*

Inflorescence in both subspecies is corymbose, multiflorous, 5(10)–30 × 5–20 cm, branches of inflorescence arched. Bracts 2–4 × 0.5–0.8 mm, herbaceous, greenish, paired, opposite, elongated, lanceolate (subsp. *angustifolia*) to linear (subsp. *stolonifera*), acute at the apex, slightly fused at the base, with dense pubescence of bristly hairs in the form of spots on the sides, broadly membranous at the edges and with single cilia (Figs 4A; 5A).

The flowers are solely hermaphrodite, 3.5–6.0 mm long in *V. stolonifera* subsp. *stolonifera* and up to 5 mm in *V. stolonifera* subsp. *angustifolia*. We noted that the calyx has 10–12 awns on its apex that wrap inward, and the calyx on the surface has scattered pubescence of simple hairs. The corolla is 2.5–4.5 mm long in both subspecies, white or pale pink in *V. stolonifera* subsp. *stolonifera* and pinkish-lilac in *V. stolonifera* subsp. *angustifolia*, in both subspecies glabrous, funnel-shaped, narrowed at the base. The corolla above its base has a thickening on one side, a characteristic place for the accumulation of nectar (Donoghue et al., 2003). Corolla is tubiform, with five lobes. The lobes are different in shape: two lobes are inverted-ovate, 0.50–0.75 × 0.50 mm, third — oval, 0.75–1.00 × 0.30 mm, making the corolla slightly zygomorphic (Figs 4B, C; 5B, C).

Stamens three, inside the flower, opposite to corolla petal lobes; their filaments are thin, filamentous, exceeding the corolla, up to 5 mm long; anthers ellipsoidal, mobile, about 0.5 mm. We recorded in the stamens of both subspecies of *V. stolonifera* the presence of an ovoid projection of the connective over the anthers, the average length of which is about 0.5 mm (Figs 4D; 5D).

Ovary 1–3 mm long, oblong-ovate, flat, with one rib on the adaxial side and three ribs on the abaxial side, in *V. stolonifera* subsp. *stolonifera* densely pubescent with conspicuous, short bristly hairs on both surfaces except the ribs (Fig. 5E), whereas in *V. stolonifera* subsp. *angustifolia* its pubescence was seen on both sides and on one side of the ovary surface (Fig. 4E); the column is filamentous, exceeding the corolla; the trifid stigma is having three prongs extended from the upper part of the column (Figs 4F; 5F).

Our analysis of flower samples from both subspecies did not reveal significant distinguishing features between them. The differences between these subspecies are only in the color shades of the perianth, in a slight difference in the size of the flowers; we also noted the presence of carpels without pubescence on the abaxial side in some specimens of *V. stolonifera* subsp. *angustifolia.*

Conclusions

The detailed characteristics of the fruits and flowers of *V. stolonifera* subsp. *stolonifera* and *V. stolonifera* subsp. *angustifolia* were compiled based on the results of a comparative morphological study using SEM. No significant differences were found in the macro- and micromorphological features of the plant reproductive organs examined at the subspecies level. Intraspecific differentiation of *V. stolonifera* is likely limited to the vegetative parts of plants.

However, the data obtained made it possible to expand the range of possible morphological characteristics of fruits and flowers. Thus, the revision of carpological samples showed that the pubescence of fruits of both subspecies can be either predominantly of flattened ribbon-like hairs or predominantly tubular, depending on the degree of maturity

of the fruit. It was also found that the papillose formations revealed on the fruit surface are developed to varying degrees, regardless of the subspecies and, possibly, are due to the physiological state of the plant and environmental factors. It is important to consider these fruit features when diagnosing other taxa of the genus *Valeriana*.

For the first time, this study revealed a feature of the flowers of both subspecies of *V. stolonifera* — the presence of an ovoid protrusion of the connective above the anthers of the stamens.

The identified morphological characteristics of generative organs are additional characters that, along with vegetative ones, can be used for more accurate identification of the species, as well as in solving taxonomic issues of the *V. officinalis* complex. To better understand of the taxonomic issues related to the infraspecific differentiation of *V. stolonifera*, molecular studies are needed, which are in our plans for the future.

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ETHICS DECLARATION

The authors declare no conflict of interest.

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Морфологічні особливості квіток і плодів
***Valeriana stolonifera* (*Caprifoliacaea*) та їхнє таксономічне значення**

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Реферат. В роботі представлені результати макро- та мікроморфологічного дослідження квіток і плодів двох підвидів *Valeriana stolonifera*: subsp. *stolonifera* та subsp. *angustifolia*. Вивчено зразки з територій України та Польщі. Описано будову квіток і плодів та визначено їхні детальні характеристики. Морфологічні структури досліджено за допомогою сканувальної електронної мікроскопії. Виявлено нові мікроморфологічні ознаки поверхні плодів представників досліджуваних таксонів, відмічено особливості поверхні — зовнішніх периклінальних і антиклінальних стінок клітин екзокарпію, трихом і продихів. У квітках представників обох підвидів *V. stolonifera* наявний яйцеподібний виступ в'язальця над пиляками тичинок. Суттєвих відмінностей у макро- та мікроморфологічних ознаках плодів і квіток між досліджуваними таксонами не виявлено. Отримані результати в комплексі з відомими ознаками вегетативних органів рослин можуть бути корисними як для точнішої ідентифікації підвидів *V. stolonifera*, так і для вирішення таксономічних питань у групі *V. officinalis* aggr.

Ключові слова: екзокарпій, квітка, мікроморфологія, мікроструктура, плід, СЕМ мікроскоп, таксономія

VEGETATION SCIENCE, ECOLOGY, CONSERVATION
ГЕОБОТАНІКА, ЕКОЛОГІЯ, ОХОРОНА РОСЛИННОГО СВІТУ

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RESEARCH ARTICLE

Structure and dynamics of populations of *Asclepias syriaca* (*Asclepiadaceae*) within the Left-Bank Forest-Steppe of Ukraine

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Abstract. *Asclepias syriaca* (*Asclepiadaceae*) is a clonal plant, a kenophyte native to North America, and it is known for its ability to form colonies. We present here a modern distribution map of *A. syriaca* in Ukraine based on extensive research, including data from numerous herbaria, literature, open biodiversity databases, and our own field observations. Our findings indicate that the highest concentration of this species is found within the Forest-Steppe region. We conducted a comprehensive population study using traditional methods, identifying the above-ground shoot as the main unit of measurement. Our research focused on four population sites in the Left-Bank Forest-Steppe (Poltava Region) and one site in Ukrainian Polissya (Kyiv Region) for comparison. The populations studied are thriving and continuously expanding. Our results indicate that intraspecific competition (self-thinning) plays a significant role in the species' territorial expansion. Under the influence of climate change trends (particularly, warming and a decrease in annual precipitation) observed over the past 14 years, a shift in phenophases has been recorded: shoots of *A. syriaca* emerge approximately three weeks earlier than before. However, other population parameters have not shown significant changes.

Keywords: alien species, *Asclepias syriaca*, common milkweed, invasive species, population structure, population dynamics

Introduction

Phytoinvasions are now recognized as a major destructive factor negatively affecting the environment, particularly the flora (Protopopova et al., 2002, 2003). This issue has become critical because invasions are significant drivers of non-native organisms that inflict irreversible damage on the survival of species and disrupt the normal functioning of ecosystems (Vitousek et al., 1997; Alien species..., 2002; Pejchar, Mooney, 2009; Sesay et al., 2024). The World Conservation Union has identified non-native organisms, particularly invasive plants, as the second most significant threat

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to biodiversity, following only the destruction of habitats. In certain countries, such as the USA and Australia, this issue is considered the most pressing current threat to biodiversity (Canada.ca., 2025–onward; Invasives Canada, 2025–onward). They also present a significant risk to human health (Denóbile et al., 2023). The global economic cost of phytoinvasions amounts to billions of dollars each year, with Europe facing annual losses of 12 billion Euros (Invasive Species Centre, 2025–onward; European Commission, 2025–onward).

Several countries have developed national strategies to prevent and control invasions (Genovesi, Shine, 2004; Ries et al., 2004; Reaser, 2013, etc.). In Europe, the Invasive Alien Species Regulation (Regulation (EU) 1143/2014) has been adopted, which includes measures that must be implemented across the EU regarding invasive alien species. In Ukraine, this issue remains largely unresolved. Currently, A Draft Decree from the Cabinet of Ministers of Ukraine has been developed, entitled "On the Approval of the National Strategy for Managing Invasive Alien Species of the Flora and Fauna in Ukraine for the Period Until 2030". This strategy aims to enhance the country's environmental policy in line with European regulations. Its goals are to prevent the entry and control the introduction of invasive alien species into natural ecosystems, as well as to eliminate or reduce the negative impacts of these species on ecosystems, economic activities, and human health. Such legislative acts address a range of issues, emphasizing, among other aspects, the comprehensive studies of populations. The specific actions for implementing the Strategy in Ukraine include reducing the density and population numbers of invasive alien species. This aims to contain their impact at an acceptable level over a long term, while also ensuring ongoing monitoring of their populations.

The impact of invasive species is often linked to their population size, but data on the size of these populations and the occurrence of high-abundance and expanding populations are frequently insufficient or unavailable (Hansen et al., 2013). Alien species require time to adapt to new environments, and characteristics such as taxonomy, biology, and other ecological factors of alien plants ultimately determine their success in the new habitat (Sakai et al., 2001).

This topic is widely discussed among scientists (Sakai et al., 2001). For example, researchers are studying the age structure and dynamics of *Heracleum mantegazzianum* Sommier & Leviev populations (Pergl et al., 2006, 2007). Some studies focus on seed productivity and germination dynamics, as well as the population structure of *Asclepias syriaca* L. (Sárkány et al., 2008; Pauková et al., 2013; Bacieczko, Borcz, 2015); structures of genomic diversity of *Reynoutria japonica* Houtt in populations (Guerrero et al., 2021; Kawai et al., 2023, etc.), among other examples.

Asclepias syriaca is a species that has been spreading across Ukraine in recent years and successfully occupying new habitats. This species is currently under active studies in Ukraine. The findings from these studies reveal various aspects, including the genetic diversity of the species, its history of cultivation, its past and current distribution, roles within plant communities, characteristics of coenopopulations, methods of utilization, and some data from population studies (Dvirna, 2014, 2015, 2018, 2020, 2021; Dvirna et al., 2023; Didenko et al., 2023; Pashkevich et al., 2023).

Our present research aims are to provide a comprehensive study of the structure and dynamics of populations of *Asclepias syriaca*, as well as the impact of climate on these populations in the Left-Bank Forest-Steppe of Ukraine.

Materials and Methods

Study area

The study is based on original data collected from our field research conducted between 2011 and 2024.

We selected populations of *A. syriaca* from the villages of Lelyukhivka, Sudivka, Kuntseve, and the former village of Pudly in Poltava District, Poltava Region (*Oblast*). This territory is located in the central and central-northeastern parts of Ukraine (Fig. 1). According to botanical and geographical zoning, the studied territory falls within the Left-Bank Forest-Steppe zone (Heluta, 1989). According to the physiographic zoning (Popov, 1968), it belongs to the Forest-Steppe zone. For comparison, a study was conducted in Mykolaivka village of Bucha (Buchanskyi) District, Kyiv Region (*Oblast*) (Fig. 1). It is located in northern Ukraine, in the Kyiv Polissya zone, which is part of Ukrainian Polissya (the northern forest zone).

A mix of highlands and lowlands, with lowlands being more prevalent, characterizes the relief of the Left-Bank Forest-Steppe. The Dnipro Lowland



Fig. 1. Distribution map of the studied *Asclepias syriaca* populations

covers a significant portion of this area, while the eastern foothills of the East European Upland (also sometimes referred to as the Central Russian Upland) rise in the far east. The locality of the village of Mykolaivka belongs to the Polissya Lowland (part of the East European Plain), where flat and slightly undulating relief prevails, with minor differences in elevation.

Soils in the Left-Bank Forest-Steppe exhibit substantial diversity. Chernozems, including both podzolized and typical types, are predominant, while gray forest soils are also common. Additionally, meadow-chernozem and meadow soils are found in the lowlands, while peat soils are present in certain areas (Balaev et al., 2005). The soils include black soil in Kuntseve and Lelyukhivka, while the others consist of sandy and sandy loam types.

The primary soil types in Kyiv Polissya include sod-podzolic (light sandy loam and sandy), sod-weakly podzolic sandy loam, swampy and peat-swampy, and alluvial soils found along river valleys and streams (Balaev et al., 2005). Gray forest soils characterize the research area in Mykolaivka.

The territory of the Left-Bank Forest-Steppe belongs to the temperate climatic zone (Khilchevskyi et al., 2014). Based on data from the Branch State Archive of Hydrometeorological Observation Materials at the Borys Sreznevsky Central Geophysical Observatory, we compiled a database that allowed us to create climate diagrams. These diagrams illustrate the average monthly air temperature, °C (Fig. 2) and the total monthly precipitation (mm) recorded at the weather stations closest to the studied localities. Thus, Lelyukhivka, Pudly, and Sudivka are closest to Kobelyaky; Kuntseve is closest to Poltava; and Mykolaivka is closest to Kyiv.

The climate of the studied region features moderately cold winters and warm summers. At the Poltava weather station (Fig. 2A, D), the average annual temperature from 2011 to 2016 ranged between 7 and 9 °C. Since 2017, a clear warming trend has emerged, with the warmest years being 2020 (about 10.4 °C) and 2023 (approximately 10.9 °C). The maximum temperature reached 24.5 °C in July 2023. Winters in 2015, 2019, and 2020 were unusually warm, with temperatures staying above zero, while winters in 2012, 2014, 2016, and 2017 were colder. Spring is typically warming; from 2019 onward, March averaged above zero, and May was notably warm in 2013 (20.1 °C). From 2016 to 2024, summers have consistently been warm, averaging 22–24 °C, with rising temperatures noted in July and August.

In Kobelyaky (Fig. 2B, E), the lowest average temperature was recorded in 2016 at approximately 7.3 °C, with a rising trend of about 2.5 °C over the past 14 years. Winters after 2018 became milder, with 2016 and 2017 being colder, and 2020 notably

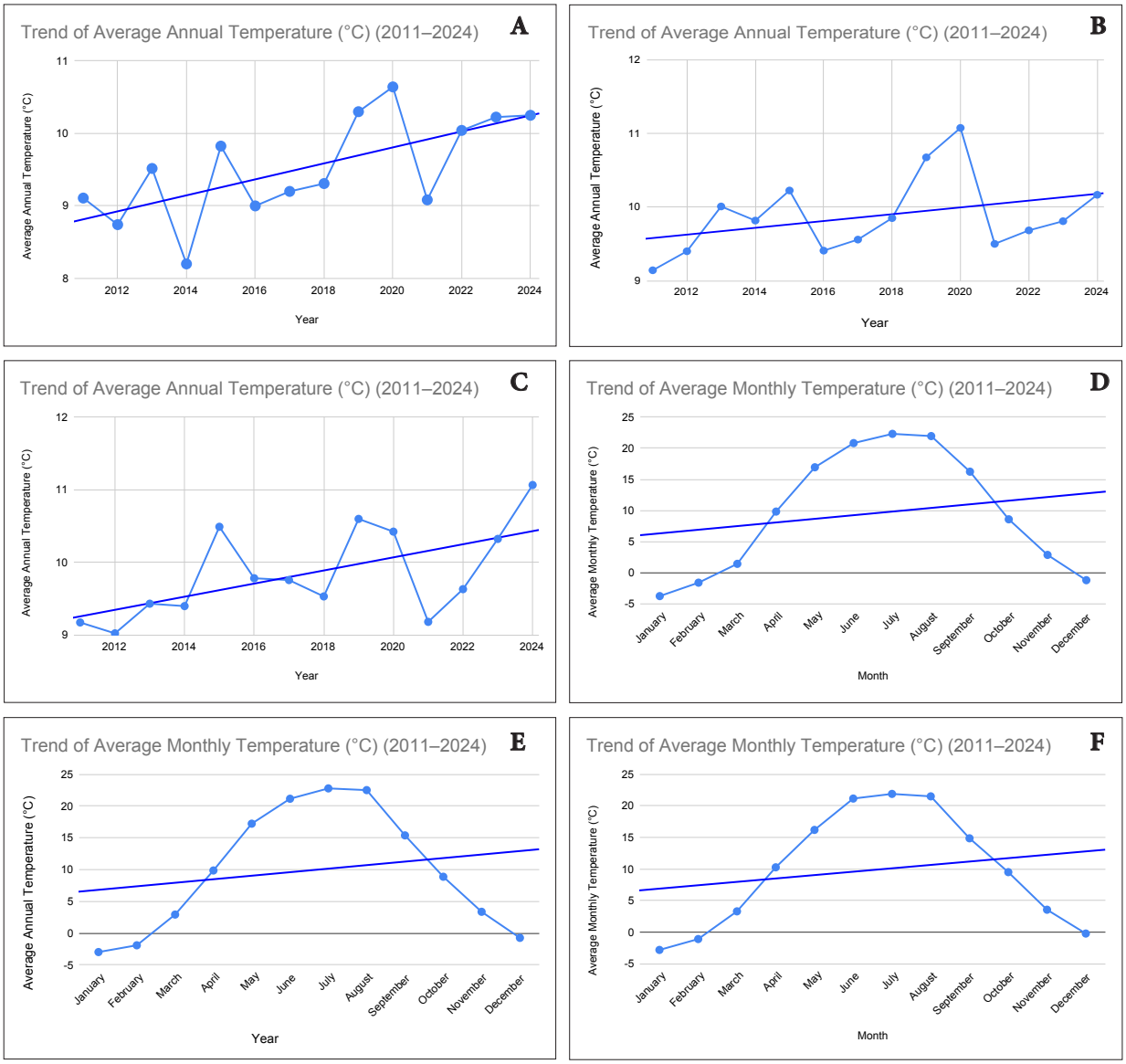


Fig. 2. Graphs of the trend of average annual temperature, and the trend of average monthly temperature (°C), 2011-2024. A, D: at the Poltava weather station; B, E: at the Kobelyaky weather station; C, F: at the Kyiv weather station

warmer. Summer temperatures reached 25.1 °C in July 2023, with trends showing a steady increase, especially since 2017.

At the Kyiv weather station (Fig. 2D, F), 2012 was the coldest year (≈ 9.03 °C), while 2023 was the warmest (≈ 11.04 °C). Since 2018, there has been a noticeable increase in the average temperature. January is the coldest month (around –2.81 °C), and July is the warmest (about 21.89 °C), with notable fluctuations including record lows in February 2012 and peaks in July 2021. The overall trend indicates ongoing climate warming.

Between 2011 and 2024, the climate has demonstrated a distinct warming trend. Winter months are becoming noticeably milder, with fewer frosty periods, while summers are experiencing more frequent heat peaks of 22–24 °C. Spring and autumn also show a gradual increase in temperatures, indicating a shift in climate norms toward overall warming. Consequently, winters are becoming shorter and warmer,

and the annual temperature range is narrowing, with fewer severe frosts and more pronounced high-temperature peaks during summer.

One characteristic of the climate in the Left-Bank Forest-Steppe is its unstable moisture levels (Adamenko, 2014). According to the agro-climatic zoning, the area studied is classified as a weakly humidified zone (Adamenko, 2014). The highest peaks at the Poltava station occurred in June 2014 (134.3 mm), June 2021 (133.3 mm), and May 2016 (126 mm). The lowest values were recorded in September 2015 (4.4 mm), September 2016 (2.2 mm), and August 2018 (1.4 mm). The dynamics are highly variable, with sharp increases alternating with declines. For example, following the 2014 peak, values dropped significantly in 2015. After 2021, a tendency toward reduced fluctuations is observed, with no extreme values exceeding 100. The most "stable" years, showing moderate values, are 2019, 2022, and 2023. Data from the Kobelyaky station demonstrated a pronounced cyclical pattern, with distinct peaks recorded in 2016, 2018, and 2021. However, the subsequent period (2022–2024) indicates a downward trajectory. The variability of the series suggests a lack of stability, as values fluctuate considerably between 28 mm and 73 mm. Data from the Kyiv station exhibited a wave-like dynamic with pronounced peaks in 2013 and 2016, followed by an overall decline in 2024. Thus, the precipitation dynamics at the selected stations exhibit a wave-like pattern, where sharp increases alternate with declines. There is a noticeable trend of decreasing annual precipitation.

Analyzing archival climate data and literature (Adamenko, 2014), we observe that droughts are advancing into regions with sufficient moisture, increasingly covering wider areas. The area of the humid agroclimatic zone (Polissya) and the zone of unstable moisture (Forest-Steppe) is decreasing, while the arid zone (Steppe) is expanding. This shift is occurring alongside a steady increase in air temperatures throughout the year, particularly during the cold months and especially in July and August. Additionally, there is a rise in thermal resources in the region, though some areas are experiencing a slight decrease in annual precipitation.

This territory of Poltava Region is situated on the left bank of the Dnipro River. Numerous rivers drain the studied area, the largest being the basins of the Dnipro, Sula, Psel, and Vorskla rivers (Khilchevskyi et al., 2014).

Data and methods

Based on the original data of our field research, the analysis of herbarium specimens from CHER, CWU, DNU, KHER, KW, KWHA, KWHU, LW, LWKS, LWS, and PWU (Shiyan, 2011), together with data from open-access databases such as GBIF (2025–onward), UkrBin (2025–onward), and iNaturalist (2025–onward), and literature data, a comprehensive database documenting the distribution of the common milkweed has been compiled, and it currently contains over 2.500 localities. A distribution map was compiled using SimpleMappr (https://www.simplemappr.net/), and Google Maps (https://www.google.com/maps).

The populations studied inhabit various types of habitats. In segetal areas, we found *A. syriaca* in Lelyukhivka in a soybean field, and in Pudly and Kuntseve in areas which feature deserted private gardens. In Mykolaivka, we observed it in an abandoned field. In a semi-natural setting, the population in Sudivka is located at the forest edge within a *Pinus sylvestris* L. plantation.

We established randomly selected plots within the population field, each measuring 1 × 1 m. The number of plots varied based on changes in the population field, ranging from one plot (Sudivka, Lelyukhivka, Pudly) to 10 (Kuntseve) and 12 (Mykolaivka) plots.

Population studies were conducted according to the method of Zlobin (1989, 2009; Zlobin et al., 2013). Considering the biological characteristics of the studied species, we use the aboveground shoot as the accounting unit.

Among the ontogenetic periods, we distinguish three. Pre-generative is the period that encompasses the growth of the plants from seedlings to fully mature vegetative plants. The generative period pertains to individuals that are in the flowering and fruiting stages. Post-generative is a period of senescence, when individuals cease growth and reproduction and gradually die out.

During our study of the phenological phases of the species, we recorded the onset of emergence, flowering, fruiting, and seed dispersal, using Holdrege's image and data (Holdrege, 2010) as a reference.

The number of individuals in a population is defined as the total count of population units within it. For small plots, we conducted a complete count of shoots. In larger plots, we estimated the total size of the population area, determined the average



Fig. 3. Geographical distribution of *Asclepias syriaca* in Ukraine

population density by counting shoots in sample plots, and then calculated the average total number of shoots in the entire population. Population density is measured as the number of individuals per unit of area (e.g., 1 × 1 m). When studying the spatial organization of common milkweed populations, we recorded the locations of individuals within the population area, as well as in the sample plots.

The spatial structure, i.e., the nature of the individual's placement within populations, was defined following Kershaw (1964) and Zlobin (1989, 2009). This is the position of plant individuals (ramets / above-ground shoots) in the population area.

Based on the accounting method outlined by Minarchenko (2014), we measured the density of the stock by weighing the freshly harvested raw materials per unit area. The results are expressed in grams per square meter (g/m^2). Additionally, we conducted a second weighing of the dried raw materials.

Results and Discussion

The species is a kenophyte that was introduced to Europe during the late 17th and early 18th centuries (Bagi, 2008). In Ukraine, the wild-growing (escaped) plants were first recorded in Vinnytsia Region at the end of the 19th century: "*Asclepias syriaca* L. Mohileff. Dniester, Podolia gub. ... Montresor, 16 Aug." [sine datum, probably middle of the 1880–1890s]. Montresor" (KW, s.n.).

Common milkweed is native to North America (Woodson, 1954; Bhowmik, Bandeen, 1976; POWO, 2025–onward). The species is commonly found in a variety of habitats in the primary range, including plains, slopes, ridges, valleys, fields, meadows, pastures, ditches, and the banks of ponds and lakes. Additionally, it thrives in swamps, bogs, parks, urban areas, stream banks, hollows, precipices, sand hills, prairies, and forest clearings and edges, as well as in coastal forests (Fishbein, 2023). The species is found in many European countries (Follak et al., 2021). It is considered invasive in Hungary (Bagi, 2008; Zalai et al., 2017; Meinhardt et al., 2024; Tölgyesi et al., 2024), Romania (Sîrbu et al., 2021), Bulgaria (Petrova et al., 2013), Croatia (Boršić et al., 2008, 2018), Bosnia and Herzegovina (Maslo, 2016), Germany (Nehring, Skowronek, 2017), and potentially invasive in Widuchowa, Poland (Bacieczko, Borcz, 2015). The European Union, by Regulation (EU) No 1143/2014, lists the common milkweed as one of the invasive alien species. Since 2017, *A. syriaca* has been included in the Union List, which prohibits the keeping, importing, selling, breeding, and growing of this species within the European Union, as outlined in Article 7 of the Invasive Alien Species regulation (Commission Implementing Regulation (EU) 2017/1263). In the



Fig. 4. Rhizomes of *Asclepias syriaca*. A: gray forest soils; B: black soil

GBIF database (GBIF, 2025–onward), there are available entries for Mexico, Australia, and Kazakhstan. However, the records for Australia and Mexico are considered likely incorrect (Follak et al., 2021).

In recent decades, the species has rapidly spread and become naturalized in Ukraine. The highest density of its localities is found in the central region of Ukraine's Forest-Steppe (Fig. 3). It seems to be completely absent in Crimea, with isolated localities found in the southern, southeastern, and eastern regions of Ukraine. *Asclepias syriaca* is distributed in various types of habitats; ruderal and segetal habitats predominantly occupy roadsides of transport routes, areas near cultivation centers (such as botanical gardens, homesteads, and flowerbeds), and semi-natural areas (including forest edges and meadows).

Asclepias syriaca is a perennial rhizomatous plant with erect herbaceous, mainly unbranched, and annually dying off above-ground shoots up to 1.5–2.0 cm in diameter, 93–220 cm high. The rhizome of this species is plagio-orthotropic, highly branched (Fig. 4), which enables it to adapt to various types of soil.

The rhizomes of the plant from different localities show some variation (Fig. 4). In gray forest soils, the population is relatively young (established in 2012), and the plant rhizomes exhibit fewer branches (Fig. 4A) as compared to those of another population on black soils (Fig. 4B), which has existed for over 20 years. Nevertheless, in both cases, the populations are thriving.

This species is classified as an implicitly polycentric biomorph, as it possesses multiple growth centers that are located so closely together that distinguishing between them is quite challenging. The species under investigation is a typical polycarpic, characterized by a life cycle in which the generative phase lasts significantly longer than both the pre-generative and post-generative periods (Table 1).

Studying phenology reveals plant's biological characteristics, as examining its seasonal development and phenological phases helps identify patterns in its life cycle (Stupak, 2023). In addition, such studies help develop measures to manage invasive species, including common milkweed. Some

Table 1. **The ontogenetic periods for the studied *Asclepias syriaca* populations**

Ontogenetic period	Period in 2011	Period in 2024
Pre-generative	May 11 — June 9	April 20 — May 30
Generative	July 4 (by Holdrege) / June 10 — August 15	June 6 (July 10) — flowering and until September 5 fruiting
Post-generative	From August 28	From September 16

stages of phenological development of *A. syriaca* are depicted in Fig. 5.

The data from 2011 are consistent with the North American findings of Holdrege (2010). We have supplemented his data according to our observations. The time of sprouting depends on the temperature regime; the earlier the air temperature rises, the earlier the sprouts appear. At present, the first shoots (Fig. 5; April 10) typically appear in late April, when the air temperature is between 8 °C and 10 °C (Fig. 2), to early May, when the air temperature is between 12 °C and 20 °C (Fig. 2). Aboveground shoots develop over a month, leading to an increase in the plant's height and the number of leaves. The flowering phase begins in June and July, followed by fruiting from mid-July to September (Table 1, Fig. 5). Seed dispersal continues from September until the first frosts. After this period, the shoots die off and usually persist in a dry state until spring. Over 14 years of observation, we have noted a shift in the timing of phenophases, likely due to climatic factors, specifically warming. Consequently, minor shifts in phenological phases, such as the earlier emergence of seedlings and the somewhat earlier onset of flowering and fruiting, are indicative of warming.

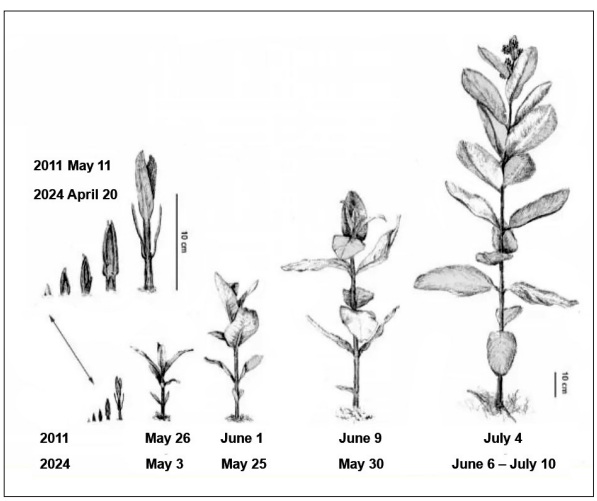


Fig. 5. Some stages of phenological development of *Asclepias syriaca* (based on Holdrege (2010), with dates from the present study)

Asclepias syriaca exhibits two primary growth forms, resulting in either the development of a composite individual or the establishment of a colony. The term "colony" is here synonymous with the term "clone", which is widely accepted. The components of an individual have closely arranged ramets, maintaining a consistent connection with the maternal individual and with each other. The type of clone we are discussing is classified as population-coenotic. In this context, a clone consists of a collection of ramets that share a common origin and occupy a specific area. These ramets do not necessarily exhibit morphological or physiological similarities with one another, but they collectively represent a distinct morphological and coenotic integrity. It is important to note that plants of the same species can produce multiple types of clones simultaneously. We believe this also applies to common milkweed. One possible variant of the clone type is genetic and physiological. However, we have not conducted studies to confirm the genetic similarity of individuals in a clone or the metabolic differences between ramets. Another type is morphostructural, which refers to a collection of ramets situated close to the mother plant and connected through underground or aboveground stem-root formations. One piece of evidence for the morphostructural type is an experiment that involves physically damaging shoots by completely cutting them. This leads to the formation of new shoots next to where the old ones previously grew.

We have examined the spatial structure of populations, which has significant ecological implications. The diversity of spatial organization enables populations to utilize environmental resources and minimize intraspecific competition efficiently. As a result, they can strengthen their positions within their habitats. Additionally, the spatial structure facilitates interactions among individuals within populations, a phenomenon commonly observed during the self-thinning process.

The spatial structure of populations is determined by the arrangement of individuals within a habitat, leading to typical distribution patterns. Our research has identified two types of horizontal

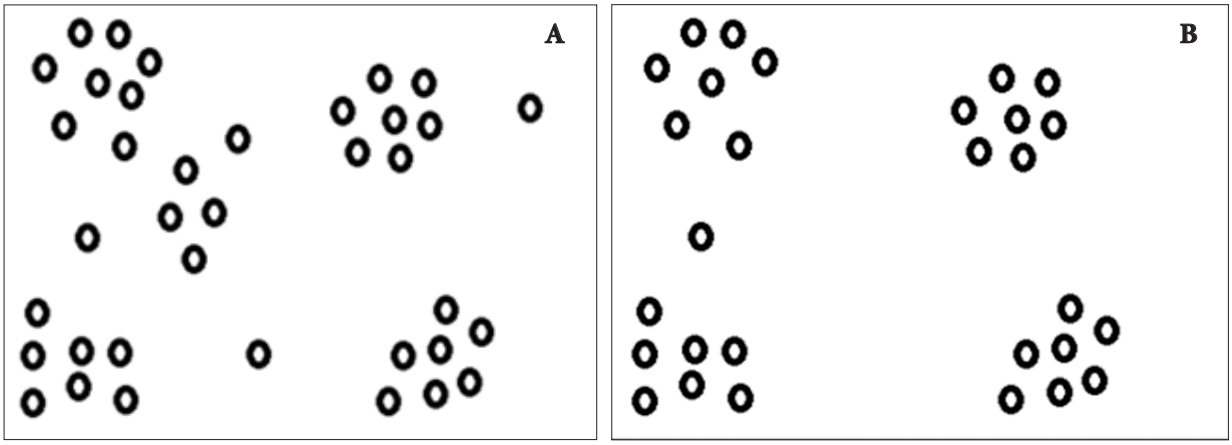


Fig. 6. Type of spatial arrangement of *Asclepias syriaca* individuals in the population field. A: random-contagious; B: contagious

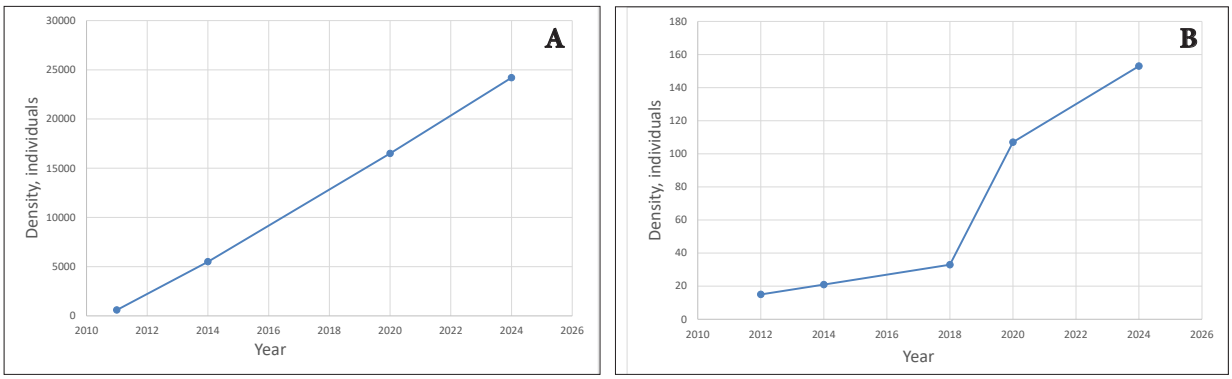


Fig. 7. The number of the *A. syriaca* individuals. A: in Kuntseve village; B: in Sudivka village

structures typical of common milkweed populations: random-contagious and contagious (Fig. 6).

In the random-contagious type of individual placement within a population field, individuals are randomly positioned, resulting in clusters of individuals. Most cases of randomness, or some distance from shoot accumulation centers, result from specific impacts, such as mowing, uprooting, or chemical treatment. The contagious type, or cluster of individuals — or a group, curtain, or mosaic — is influenced by their habitat, the unique characteristics of their ontogeny, and reproduction under specific conditions, as well as various external factors. It is important to highlight that most populations exhibit spatial heterogeneity. The populations of the *A. syriaca* exhibit a specific phytocoenotic pattern.

Population characteristics are commonly evaluated in terms of size and density. Within the 1 × 1 m sampling plot found in the village of Kuntseve (Poltava Region), shoot density ranged from 35 to 55. In 2011, the occupied area of the studied species was 3 × 4 m; by 2014, it had expanded to 10 × 10 m, further increasing to 15 × 20 m in 2020, and to 20 × 22 m in 2024. Consistent with this spatial expansion, the number of *A. syriaca* shoots increased from 600 in 2011 to 5 500 in 2014, 16 500 in 2020, and 24 200 in 2024 (Fig. 7). Overall, the number of shoots in this population increased nearly 40-fold over the 14-year observation period.

In the area near Sudivka village in Poltava Region, the species was first observed at the edge of an artificial plantation of *Pinus sylvestris*. In 2012, there were 15 shoots; by 2018, this number had increased to 33, occupying an area of 2 × 2 m. In 2020, the number of individuals increased to 107 shoots, covering 1.5 × 4.0 m. By 2024, the population had reached 153 shoots, occupying an area of 2 × 8 m (Fig. 7B).

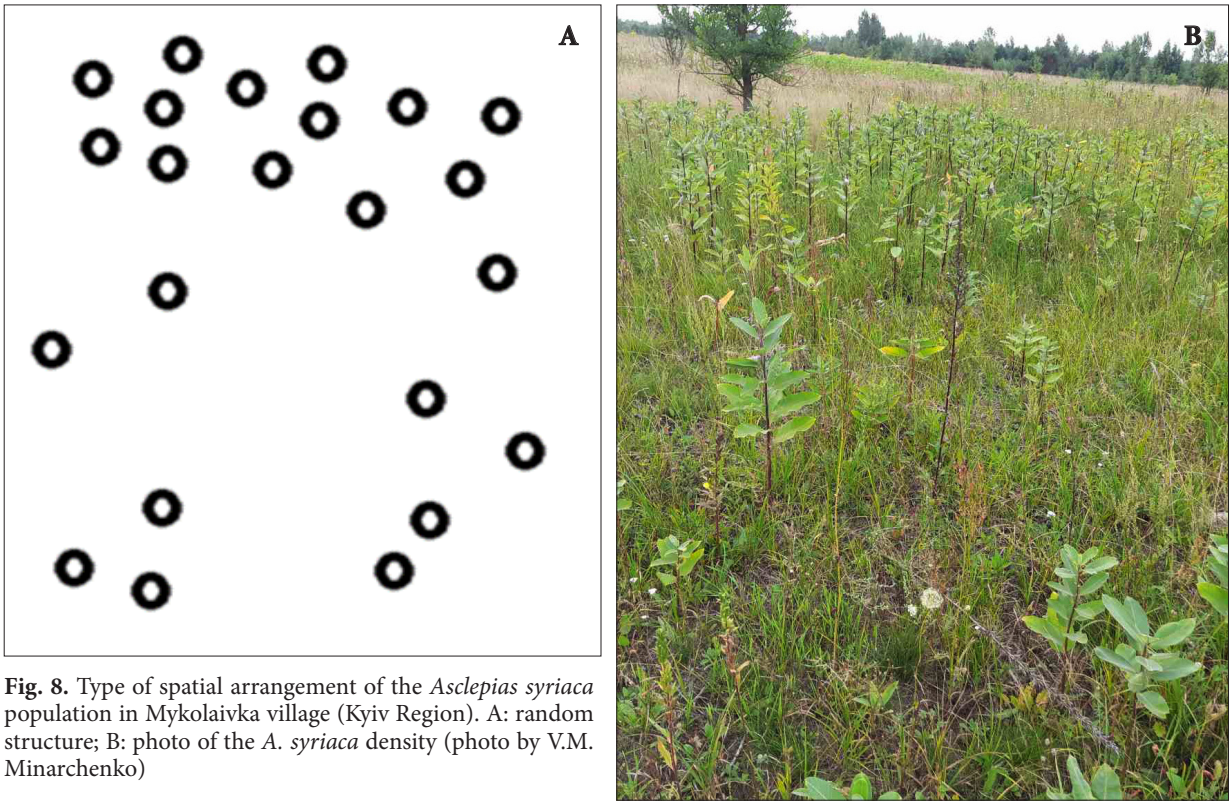


Fig. 8. Type of spatial arrangement of the *Asclepias syriaca* population in Mykolaivka village (Kyiv Region). A: random structure; B: photo of the *A. syriaca* density (photo by V.M. Minarchenko)

We observed a tenfold increase in the common milkweed population. Notably, shoots recorded in 2012 and 2013 did not produce fruits; by 2020, only nine shoots fruited, whereas by 2024, more than half had flowered. This delayed reproductive success is likely attributable to unfavorable microhabitat conditions, as the species occurred entirely beneath the canopy of *Pinus sylvestris* for several years. In 2014, however, 50% of the shoots fruited as most individuals expanded into illuminated areas, with only four remaining under the pine canopy. By 2024, the population was predominantly in well-lit habitats, with just eight shoots persisting in shaded conditions.

In 2023, the *A. syriaca* population was observed in Pudly. This population consisted of 101 shoots, occupying an area of 2.7 × 2.6 m, resulting in an average population density of 25 shoots per square meter. A notable characteristic of the species in this area is the curling of the leaves. By 2024, the population density had increased to 52 shoots per square meter. The total area is approximately 3.5 × 4.0 m with an estimated population size of about 200 shoots. A self-thinning process has been observed within the population. Shoots were also found emerging at a distance of 0.5 m from the main cluster. This year, it is observed that the lower leaves of all shoots have turned yellow and are gradually falling off during the flowering period. Over the year, the number of population individuals has doubled. The causes of the leaves' yellowing and curling remain unidentified.

In 2019, a new locality of common milkweed was recorded among soybean crops in Lelyukhivka. The population consisted of 17 individuals, occupying an area of 0.5 × 0.5 m. Of these individuals, five were flowering and six showed damage characterized by leaf twisting. In 2023, only four shoots were noted. However, systematic spot chemical treatments were applied to this site throughout the entire observation period, and by 2024, the population disappeared.

A somewhat different situation was observed in Mykolaivka village (Kyiv Region). The spatial structures of this common milkweed population are random (Fig. 8).

This population emerged around 2003 and is gradually expanding its area. In the plots, the number of individuals varies from five to 24. The species occupies an area of approximately one hectare,

resulting in a population density of about 240.000 shoots per hectare. Based on our analysis of the data, we conclude that all studied populations of *A. syriaca* are growing and expanding. By the type of vitality, the populations are prosperous.

We also compared our data with similar existing data. We found that the number of shoots is a variant trait influenced by biotype types and both biotic and abiotic factors.

Populations of ruderal habitats in Western Slovakia exhibit a high density, with 45 shoots per square meter recorded. Similarly, an abandoned vineyard in Central Slovakia showed 33 shoots per square meter (Valachovič, 1987; Pauková et al., 2013). These high densities are also observed in populations from Poltava Region. In contrast, a lower density was noted in an abandoned vineyard in Hungary, ranging from 7.4 to 18.1 shoots per square meter in an abandoned field (Csontos et al., 2009). North American studies report even lower figures, with only 1.2 to 8.8 shoots per square meter (Bhowmik, Bandeen, 1976). These lower densities may occur either during the initial establishment of a species in a new area or because of self-thinning processes. Intraspecific competition likely leads to a gradual decrease in population density and range expansion. This phenomenon is a characteristic of *A. syriaca* populations.

Regarding the determination of stock density, we obtained the following results. In 2022, when weighing fresh raw materials (aboveground shoots) in the village of Kuntseve, the weight ranged from 3.5 to 4.0 kg, while the dry weight ranged from 2.8 to 3.0 kg. The number of shoots per square meter was 32–36.

Upon re-examination in 2024, the weight of freshly harvested raw materials ranged from 1.00 kg to 3.08 kg. Correspondingly, the weight of dry raw materials varied from 0.47 kg to 2.79 kg. The number of shoots observed during this period ranged from 20 to 45.

At the experimental site in Mykolaivka village, we recorded the weight of freshly harvested raw materials ranging to 1.530 kg, with dry raw material weights 0.80 kg. In this instance, the number of shoots ranged from 10 to 16.

In both locations, we noted that weight loss was minimal (up to 1 kg). Significant variations in weight can be attributed to the spatial structure of the population field and the density of the rafts. Importantly, climatic conditions do not appear to affect the resource density of *A. syriaca*. The relatively high indicators of stock density suggest promising potential for utilizing this species in industry, such as to produce biofuels or in the pharmaceutical industry.

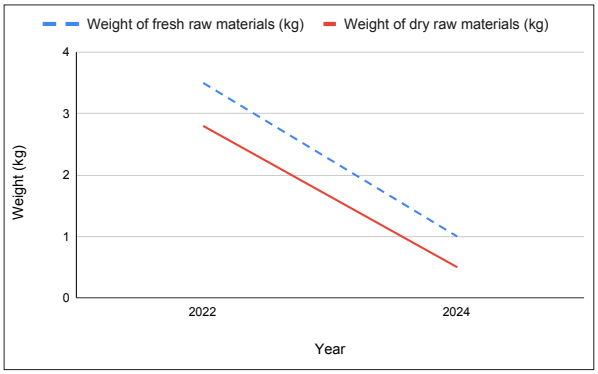


Fig. 9. The stock density of *Asclepias syriaca*

Conclusion

The monitoring studies described above were conducted for the first time in Ukraine. The analysis of selected climate data demonstrates a clear shift in climate over the past 14 years. A trend toward warming and a reduction in annual precipitation is observed. However, it is essential to consider local climatic conditions. For example, in 2018, a flood occurred in Ukraine, and the common milkweed population field was submerged. Therefore, the species can tolerate temporary waterlogging as well as dry periods.

Notably, climatic changes have influenced the phenology of *A. syriaca*, particularly the earlier emergence of seedlings. It was hypothesized that the prolonged lifespan of shoots would lead to increased biomass; however, this expectation was not supported. Despite consistently high shoot density, the stock of raw material did not differ substantially across sites. At the same time, other structural characteristics of the populations appeared unaffected by climate changes and trends.

Populations of the species are thriving and constantly growing due to their complex biology, ecological timing, and behavior. The gradual expansion of this species' range observed over the past decade is likely due not only to the methods of introduction, whether intentional by humans through seeds or unintentional during land cultivation, but also to competition within the species itself. We believe

this is a regular characteristic of the species, observed not only in Ukraine but also throughout Europe and the USA.

Thus, conducting population monitoring studies of invasive species allows for their control and timely eradication, which are effective means of reducing their further spread. We saw this in one of the examples provided above.

ETHICS DECLARATION

The authors declare no conflict of interest.

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Структура та динаміка популяцій *Asclepias syriaca* в межах Лівобережного Лісостепу України

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Реферат. *Asclepias syriaca* — кенофіт північноамериканського походження, клональна рослина, що здатна утворювати колонії. На основі опрацювання значного масиву гербарних, літературних відомостей, відкритих баз даних з біорізноманіття та власних польових даних, нами складено сучасну карту поширення *A. syriaca* в Україні. Виявлено, що найвища концентрація локалітетів виду спостерігається в межах Лісостепу. Комплексне популяційне дослідження проведено із застосуванням класичних методів; обліковою одиницею був визначений надземний пагін. Основну увагу дослідження зосереджено на чотирьох популяційних полях виду у межах Лівобережного Лісостепу (Полтавська обл.) та, для порівняння, на одному в Українському Поліссі (Київська обл.). Досліджувані популяції є процвітаючими і постійно зростають. Дослідження показують, що внутрішньовидова конкуренція (самопроріджування) сприяє розширенню займаної території. Під впливом тенденцій змін клімату (зокрема, потепління та зменшення річної кількості опадів), зафіксованих упродовж останніх 14 років, спостерігається зсув фенофаз — відростання пагонів *A. syriaca* відбувається на три тижні раніше. Водночас інші параметри популяцій істотно не змінюються.

Ключові слова: *Asclepias syriaca*, адвентивний вид, інвазійний вид, структура та динаміка популяції

VEGETATION SCIENCE, ECOLOGY, CONSERVATION
ГЕОБОТАНІКА, ЕКОЛОГІЯ, ОХОРОНА РОСЛИННОГО СВІТУ

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RESEARCH ARTICLE

Initial stages of revegetation at the bottom of the drained Kakhovka Reservoir (Ukraine): synthesis of field surveys and remote sensing

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Abstract. On June 6, 2023, the dam of the Kakhovka Hydroelectric Power Plant was intentionally demolished by Russian troops, who detonated pre-deployed explosives, causing an environmental catastrophe in the Northern Black Sea region. Despite the severe environmental and socioeconomic repercussions, the disaster offered unique opportunities to study vegetation development in the long-flooded but now exposed area. The aim of the present study was to reveal and demonstrate the initial stages of formation of the flora and vegetation in the area of the former Kakhovka Reservoir, combining field research data (flora and vegetation surveys and observations, etc.) and remote sensing techniques (calculation of vegetation indices, supervised machine learning classification, etc.). We visited the area in June and October 2023 and in May 2024; during these visits we georeferenced and outlined various habitat types. These field data were used for geospatial modeling. Our studies found that the number of taxa of vascular plants in the area increased nearly 14 times during the year, thus contradicting initial pessimistic predictions and scenarios of desertification, ruderalization, and large-scale invasions of invasive alien species. We identified main types of newly formed terrestrial habitats, including willow and poplar thickets, marshy habitats, mud-, sand- and shell-covered areas with sparse vegetation. Remote sensing methods, augmented by machine learning techniques, complemented these findings, providing detailed habitat maps for the entire reservoir bed. This study contributes to our understanding of ecological successions and habitat dynamics in post-catastrophic landscapes, informing future management strategies for such areas.

Keywords: dam breach, floodplain, habitats, machine learning, restoration, vegetation

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Introduction

Overexploitation of water resources, including over-regulation of river basins, is a major concern both in terms of water quality and biodiversity loss (Poff et al., 1997). The EU Biodiversity Strategy sets the target to make at least 25,000 km of rivers free-flowing again by 2030, by removing primarily obsolete barriers and restoring floodplains and wetlands (European Commission, 2021).

The drawdown of large and small reservoirs is usually planned and gradual. In the USA, for example, more than 450 dams have been removed during the last century (Graf, 2003; Aube et al., 2007; see also updated information in: American Rivers, 2019–onward). There are positive ecological aspects of reservoir drawdowns, e.g. restoration of natural flow and habitats of wildlife (such as mule deer), no barriers to migratory fish passage, etc. (Poff et al., 1997; Lenhart, 2003; Stanley, Doyle, 2003). Potential risks include the introduction of invasive alien species and slow recovery of natural vegetation (Bednarek, 2001; Stanley, Doyle, 2003; Aube et al., 2007). However, it has been found that invasive species appeared to be much less abundant than initially expected (Prach et al., 2019). Data on the initial stages of succession and the formation of new habitats in drained areas following the release of water as a result of dam failure are reported from the US (Acker et al., 2008; Peterson et al., 2025). Furthermore, various environmental aspects of dams functioning (Johansson, Sellberg, 2006; Schleiss, Boes, 2011) and consequences of deliberate dam removal were also considered (Shafroth et al., 2024, etc.).

However, when the Russians blew up the dam of the Kakhovka Hydroelectric Power Plant on 6 June 2023, similar processes occurred immediately and catastrophically, which triggered a large-scale ecological disaster (Naddaf, 2023; UNEP, 2023; Stone, 2024; Shumilova et al., 2025), directly or indirectly impacting the ecosystems of the Northern Black Sea region in Ukraine and adjacent countries. The socioeconomic connections established in the transformed landscape of the Black Sea lowland over the past 70 years since the reservoir's construction were severed and disrupted. Despite the negative environmental and socioeconomic consequences (Vyshnevskyi et al., 2023), the disaster presented a unique opportunity to observe vegetation development over a vast area that had been flooded for more than six decades. This is what makes the case of Kakhovka so globally remarkable. Unlike the aforementioned examples from the USA, renaturalization in Ukraine was not planned — it is happening naturally, creating a unique "natural testing ground" for science.

Shortly after the water level stabilized, satellite images revealed large drained areas at the Kakhovka Reservoir site. Speculations regarding further scenarios at the reservoir's bed were mostly pessimistic, including the potential release of dried silt contaminated with heavy metals into the air (Naddaf, 2023), and local territorial and ecological expansions of invasive alien plants (UNEP, 2023). The possibility of desertification of this territory is also still being considered (Pichura et al., 2025). These hypotheses could only be tested on-site by examining the actual development of vegetation in the drained areas of the former Kakhovka Reservoir.

However, due to the area's location in the zone of active hostilities (the Right Bank has been liberated by the Ukrainian Armed Forces, while the Left Bank is still occupied by Russian troops), the majority of its territory remains inaccessible to field surveys. In this regard, the role of remote methods for tracking the processes occurring at the bottom of the former reservoir has increased. Multispectral optical images, provided by space missions like Sentinel or Landsat, proved to be valuable data sources for habitat and vegetation mapping (Xie et al., 2008; Fassnacht et al., 2016). Augmented with machine learning techniques for supervised image classification, e.g., Random Forest (RF), Support Vector Machine (SVM), or Classification and Regression Tree (CART), they allow researchers to produce large-scale habitat maps (Gislason et al., 2006; Myroniuk et al., 2020; Kennedy et al., 2021). However, none of these methods can produce accurate habitat maps without reliable and representative on-site training data (Elmes et al., 2020).

There were attempts to assess the overgrowth rate at the former reservoir's bed using satellite imagery data only (Dovhanenko et al., 2024; Shumilova et al., 2025) or combined with on-site observations (Vyshnevskyi, Shevchuk, 2024; Pichura et al., 2025). Due to the lack of solid on-site data, that research mostly operated with general or purely descriptive vegetation categories like "willow" or "dense vegetation", and could not reveal exact plant species composition at the site. On the contrary, a few purely on-site research revealing vegetation structure *in situ* (Didukh et al., 2024; Lisovets et al., 2025) were

Table 1. **Characteristics of the studied localities within the bottom of the former Kakhovka Reservoir**

Location number	Location name	Date	Coordinates of the studied locations, DD.DDDDDD°	
			Latitude	Longitude
1	Mylivska gully	30 June and 19 October 2023	47.085307	33.651769
2	Mylivska gully	30 June and 19 October 2023	47.084841	33.642884
3	Kamianka gully	30 June and 19 October 2023	47.004603	33.581268
4	Khortytsia Island	21 May 2024	47.812642	35.142283
5	Khortytsia Island	21 May 2024	47.811732	35.143677
6	Khortytsia Island	21 May 2024	47.791329	35.145560
7	Malokaterynivka village	22 May 2024	47.653495	35.248407
8	Kanivske village	22 May 2024	47.681092	35.112919

unable to extrapolate the obtained results over the whole reservoir's area. Thus, only a fusion of field, satellite and machine learning methods can solve the issue of monitoring of vegetation and habitats at the drained bottom of the Kakhovka Reservoir.

In this article, we provide an overview and description of the flora and habitats forming at the bottom of the former reservoir based on field data. Combining remote sensing and machine learning methods together with collected field data, we also trace habitat dynamics and provide high-resolution habitat maps for the whole reservoir bed for the first year after the dam breach. Additionally, we discuss the habitat transformation processes currently underway.

Methods

Study area

The former Kakhovka Reservoir was 230 km long, with an average width of 9.4 km and the maximum width of 24 km. Its surface area was 2,155 km². The total coastline length was estimated at 896 km (Heohrafichna…, 1989–1993). The climate of the area is warm and temperate. The mean yearly temperatures recorded vary from 10.7 °C (Zaporizhzhia, the northern part of the reservoir) to 11.6 °C (Nova Kakhovka, at the southern part of the reservoir). The mean precipitation varies from 505 mm in Zaporizhzhia to 449 mm in Nova Kakhovka (Climate-Data.org, 2025–onward). In the northern part of the reservoir, particularly on Khortytsia Island, silicate rocks, including granite, are exposed on the surface (Khodosovtsev et al., 2022), while in the southern part, limestone outcrops are exposed (Khodosovtsev et al., 2025). Also, in the northern part of the reservoir within Zaporizhzhia Region (Oblast), the banks of the former reservoir are covered with sand deposits, and in the southern part, thick shell deposits have formed at the bottom of the former reservoir. These are the remains of dead mollusks, mainly taxa of the genus *Dreissena*, which formed in the waters of the reservoir during its existence (Didukh et al., 2024).

An analysis of literature sources showed that before the creation of the reservoir, there were at least 31 types of habitats corresponding to those listed in the *National Catalogue of Habitats of Ukraine* (2018), including 7 types of tree and shrub, 11 types of meadow and marsh, 2 psammophytic, 3 petrophytic, and 8 aquatic habitat types (Vasyliuk et al., 2024).

Field sampling

The field data were collected during three field visits to the territory of the drained reservoir's bed: 25 days after the destruction of the Kakhovka HPP dam (June 30, 2023), Kamianska Sich National Nature Park, then 4.5 months (October 19, 2023), and 11.5 months after the dam breach (May 25, 2024). Eight locations distributed across the two sites were surveyed: the Kamianska and Mylivska gullies within Kamianska Sich National Nature Park in Kherson Region (Oblast), the southwestern part of the reservoir, and Khortytsia Island, vicinities of Malokaterynivka and Kanivske villages in Zaporizhzhia Region (Oblast), the northern part of the reservoir (Table 1, Fig. 1).

To ensure a comprehensive detection of all vascular plant species, transects were randomly established along and across the bottom of the former bays. Within the surveyed sites, we mapped habitats using GPS and high-resolution satellite images to prepare ground truth data for machine learning habitat mapping.

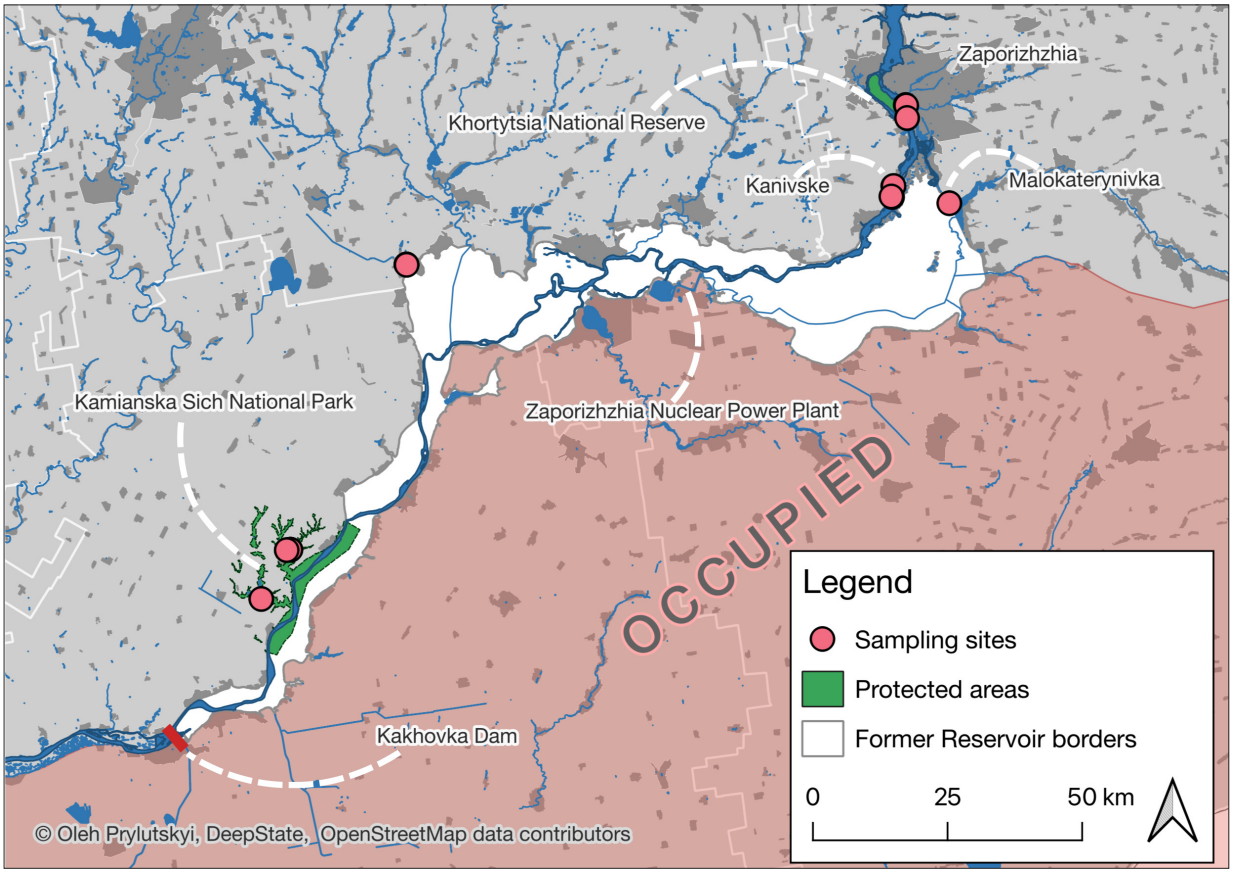


Fig. 1. The map of the surveyed locations

The nomenclature of higher vascular plants mainly follows the *Plants of the World Online* (POWO, 2024–onward). Habitat identification was based on the EUNIS (European Nature Information System) classification (Schaminée et al., 2018; EUNIS…, 2019), as well as the Interpretation Manual of European Union Habitats (2013).

Vegetation indices

To analyse the dynamics of water discharge and vegetation development at the bottom of the reservoir, we used a time series of multispectral data from the Sentinel-2 Level 2A satellite with a spatial resolution of 10 meters (Copernicus, 2023). The criteria for selecting the images for analysis were correspondence to the on-site surveys, as well as the absence of optical obstacles (clouds) that prevent the reflection of the land/water surface. We acquired five images in total: taken a day before the dam was blown up (5 June 2023), closest to the first (20 June 2023), second (7 November 2023) and third (25 May 2024) surveys, as well as intermediate between the first and second survey (19 August 2023). For all images, we calculated two common spectral indices: the Normalized Difference Water Index (NDWI) and the Normalized Difference Vegetation Index (NDVI). NDWI index is defined as the normalized difference between near-infrared and green bands, while NDVI index uses the normalized difference between near-infrared and red bands. Both indices are widely used for mapping water and vegetation, respectively (Gao, 1996; Pettorelli et al., 2005), and they can be used for differentiating moist and vegetated areas (Rogers, Kearney, 2004). We chose this combined approach because NDWI effectively masks water bodies before terrestrial habitat analysis, while NDVI index allows us to distinguish between vegetated and sparsely vegetated surfaces. We calculated both indices using the raster calculator tool in QGIS 3.4.5-Madeira (QGIS.org, 2024).

To determine the threshold value of the NDWI index separating water from other habitat types (set at -0.04), we performed a visual verification. This process involved field photographs and high-resolution satellite imagery to accurately delineate water and land areas along the Dnipro River and its tributaries. The absence of urban surfaces allowed us to clearly separate water surfaces, including shallow water surfaces overgrown with vegetation. To interpret the vegetation index NDVI, we used habitat mapping data based on the results of field surveys, as well as on the identification of photographic materials and their exact location by characteristic terrain features for locations inaccessible to the survey.

We first established distinct training areas for subsequent classification, relying on on-site habitat mapping and ground-truthing photographs that were verified based on precise location and time. By calculating the average spectral reflectance (NDVI) within these verified habitat samples, we were able to identify more generalized habitat classes with clearly discrete NDVI values. As a result, the generalized classes included habitats with closed vegetation (Habitat Group 1), including marshy vegetation (Habitat 1.2) and willow thickets (Habitat 1.1), with an average NDVI value of 0.74 as of 7 November 2023, and habitats with open vegetation (Habitat Group 2), including shell and sandy sediments (Habitat 2.2) with an average NDVI value of 0.08, as well as muddy sediments with sparse vegetation (Habitat 2.1) with an average NDVI value of 0.22 at the date. Also, based on the values of all pixels in the field study and photograph verified areas, we identified the threshold values of the index that can be used to separate Habitat Group 1 from Habitat Group 2 — 0.37, which corresponds to the minimum values of the index for marshy vegetation and effectively matches the maximum values of the index for sparse vegetation on shell, sandy, or muddy sediments. In addition, a group of water bodies and watercourses (Habitat Group 3) was identified.

Geospatial modelling

Using the Google Earth Engine (GEE) cloud computing platform (Gorelick et al., 2017), we applied supervised machine learning classification of satellite multispectral image to make a fine-scale (10 m per pixel) habitat maps of the former Kakhovka Reservoir bed. As input data, we choose harmonized Sentinel-2 Level 2A Surface Reflectance images (Copernicus, 2023) obtained through the GEE Data Catalog (https://developers.google.com/earth-engine/datasets/catalog/COPERNICUS_S2_SR_HARMONIZED), for two dates: 18 October 2023 (second survey) and 25 May 2024 (third survey). Optical bands (B2-B12) were selected, clipped by the contour of the pre-dam burst water surface boundaries, defined based on NDWI at the previous step, cleaned from remaining clouds and cloud shadows, and mosaicked following GEE's Sentinel-2 routine.

As ground truth data, we used spatial polygons of the four terrestrial habitat types, mapped during field sampling (25 for the year of 2023, 31 for 2024). To expand spatial coverage of training data, we also added six polygons with known habitat types from the northern part of the reservoir. To be used for the modeling, such polygons must have met the following criteria: (i) be applicable to accurate georeferencing from input photographic materials and (ii) represent habitat types that corresponded to habitat types delineated during field surveys. The total area of ground truth was 40.3 ha. Ground truth data were randomly split into the 70% training data used further for model fitting, and 30% validation data saved for testing model performance. Since we had only survey data for terrestrial habitat types, we manually added training data for water bodies using natural colors Sentinel-2 images and NDWI values for them, 33 polygons in total. Then, we classified the composite using a Random Forest algorithm (Ho, 1995) with 30 trees, estimating classification performance through the confusion matrix, overall accuracy, and Cohen's Kappa. The number of trees was chosen based on preliminary exploration data, as though the values over 30 did not result in accuracy increase, but caused heavier computational load. The resulting maps did not change with higher parameters.

Data and code availability

All data, including plant survey results, rasters of vegetation and water indices, ground truth polygons for Random Forest training, as well as codes to reproduce satellite image preparation and classification, are publicly available at https://github.com/olehprylutskyi/kakhovka_vegetation_habitats under the MIT license. The high-resolution habitat maps for October 2023 and May 2024 are accessible online at https://ee-olegpril12.projects.earthengine.app/view/kakhovka-habitat-map-oct-2023.

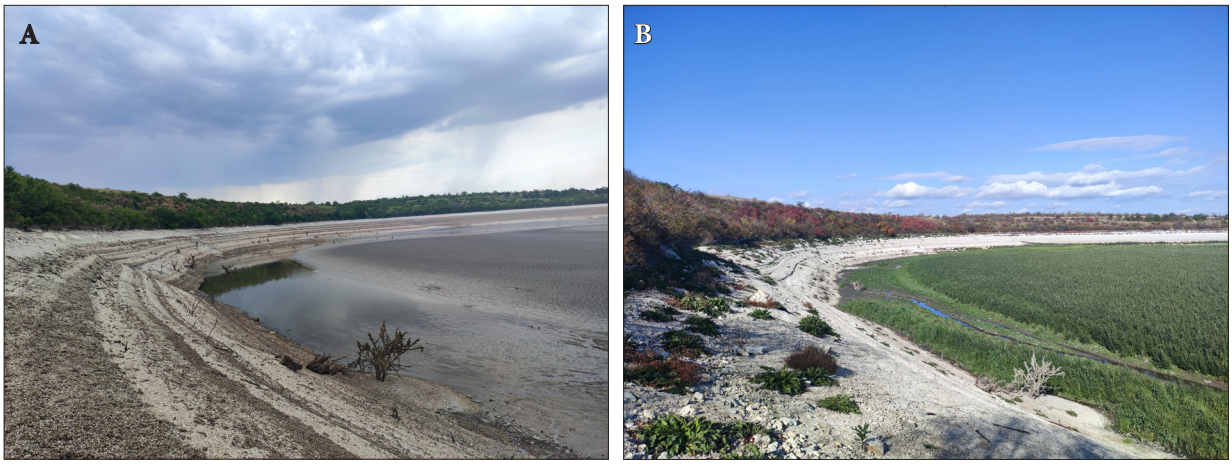


Fig. 2. General view of the bottom of the former Kakhovka Reservoir in the drained Respublikanets Bay in the Kamianka Gully. A: 30 June 2023, with the watercourse (Kamianka River) and shell sediments; B: 19 October 2023, with the willow forest and marshy vegetation along the watercourse. Photo: O. Khodosovtsev

Results

Plant species composition

In June 2023, we detected 10 species of higher vascular plants in the surveyed areas of the former reservoir bottom, while in October 2023 we recorded 68 species (see Supplementary Table S1). The total number of species detected by the end of the third survey reached 147, including 145 taxa of vascular plants and two identified species of bryophytes.

Interpretation of habitats based on survey data

Based on the data from our field surveys, we identified three distinct habitat groups at the bottom of the former reservoir: habitats with closed vegetation (Habitat Group 1), habitats with open vegetation (Habitat Group 2), and ponds and watercourses (Habitat Group 3).

The most prevalent habitat type within the first group was willow and poplar thickets (Habitat 1.1), characterized by the dominance of willow, a hybrid of the native species *Salix alba* L. and the long-naturalized alien species *Salix fragilis* L., known as *Salix* ×*rubens* Schrank. Alternatively, this hybrid is treated as *Salix* ×*fragilis* L. s. str., resulting from supposed crosses between *S. alba* and *S. euxina* I.V. Belyaeva (*S. fragilis* sensu auct.) (Belyaeva, 2009; POWO, 2025–onward); for an overview of the problem, see Marchenko and Kuzovkina (2022) and Stalažs (2024), and references therein. Resolution of these nomenclatural and taxonomic controversies is beyond the scope of the present research; thus, for purely pragmatic reasons, we follow here the traditional nomenclatural convention and use the name *S.* ×*rubens* for this hybrid that dominates the willow thickets in the study area.

In other areas, usually with light sandy soils, *Populus nigra* L. prevails. Among shrubs, *Tamarix ramosissima* Ledeb. is the most widespread taxon. The herb layer is dominated by species characteristic of natural floodplain willow-poplar forests, such as *Carex otrubae* Podp., *Epilobium hirsutum* L., *Lycopus europaeus* L., *Phalaris arundinacea* L., *Mentha aquatica* L., *Lythrum salicaria* L. These habitats also host two species of bryophytes, *Funaria hydrometrica* Hedw. and *Marchantia polymorpha* L.

During our initial visit to the former reservoir, we observed the first stage of formation of this habitat type, with the entire bottom covered in willow seedlings at a very high density — averaging 90 per 1 m^2. Upon our second visit, we witnessed dense willow thickets spanning large areas of the former reservoir bottom (see Fig. 2). Over the 111-day period between our first and second surveys, the average plant height increased from 0.5 cm to 190 cm, with a maximum height of 309 cm. This indicates highly favorable conditions for the formation of this habitat type, with an average daily growth rate of 1.7 cm. In May 2024, the average height of the willows was already about 3 m, with the maximum height of 4.7 m recorded. In the northern part of the former reservoir, we also observed pure poplar thickets formed by young plants of *Populus nigra* L., which are formed mainly on sandy sediments and

in drier conditions as compared to those of willow thickets. The average height of poplar thickets was about 1.5 m, with the maximum measured height of 1.97 m.

Visually, much smaller areas were occupied by another type of habitat with closed vegetation, namely, the marshy habitat (Habitat 1.2). We did not observe such habitats during our first visit in June 2023, only noted a few reed seedlings at that time. However, these habitats were already well-formed by October 2023 along the permanent watercourses. The most common species in these communities are *Phragmites australis* (Cav.) Trin. ex Steud. s.l., *Typha angustifolia* L., *T. latifolia* L., *Oenanthe aquatica* (L.) Poir., and *Rumex hydrolapathum* Huds.

The second group of habitats (Habitat Group 2) consisted of the muddy sediments with sparse vegetation (Habitat 2.1), as well as communities formed on shell and sandy sediments (Habitat 2.2). These substrates are generally composed of alluvial fine- and medium-grained sandy, sandy-loamy, and silty bottom sediments. Polygonal, fissure-divided plates, mostly pentagonal and hexagonal, are clearly visible on the redeposited, well-dried sandy loam-clay deposits. The cracks between these plates were deep due to the thick drying layer, which represented the entire thickness of the bottom silt. In June 2023, the depth and width of the cracks on the still-wet substrates ranged from 3 to 25 cm and 0.5 to 4 cm, respectively. The plates of cracked silt averaged 43 cm wide. After 3.5 months, the average depth and width of the cracks increased by an average of seven times. This structure indicates intensive drying of the dense, viscous substrate and insufficient precipitation during the season of 2023. While the silts, despite their structural features and moisture regime, are intensively overgrown with willow, the vegetation on the shell and sandy deposits was rather sparse and mainly consisted of annuals, e.g., *Lactuca tatarica* (L.) C.A. Mey. or *Portulaca oleracea* L. s.l. In addition, species of plants characteristic of wet grasslands have been observed on muddy deposits. These include, for example, *Alopecurus aequalis* Sobol., *Dactylis glomerata* L., *Geum rivale* L., *Poa palustris* L., *Ranunculus sceleratus* L., etc. We also found terrestrial forms of *Nuphar lutea* (L.) Sm. on muddy deposits. The species composition on shell deposits is interesting. In addition to annuals that are not demanding on soil fertility (e.g., *Amaranthus albus* L., *A. retroflexus* L., *Digitaria sanguinalis* (L.) Scop., *Eragrostis minor* Host), species of plants characteristic of steppe habitats (*Glycyrrhiza echinata* L., *Medicago falcata* L., *Coronilla varia* L., etc.) were found here, whose diaspores were obviously washed away from the surrounding steppe slopes. *Bromus tectorum* L., *Calamagrostis epigejos* (L.) Roth, *Cynodon dactylon* (L.) Pers., *Plantago indica* L., *Trifolium arvense* L. are the most characteristic species for sandy deposits. It should be noted that shell sediments prevailed in the southern part of the reservoir, and sandy sediments in the northern part.

Reservoirs and watercourses (Habitat Group 3) consisted of the riverbeds of the Dnipro River and its tributaries, which were flooded by the reservoir and have re-established their beds following its disappearance. An example is the Kamianka River, whose restored riverbed we observed in June and which, at least visually, remained stable until October 2023, except for the formation of riparian vegetation along its banks. In certain areas of the floodplain, depressions formed temporary reservoirs that dried out rather quickly and were also overgrown with riparian vegetation on their periphery. However, during the year of observation, we did not find any aquatic macrophytes in these reservoirs and watercourses.

Habitat mapping based on remote sensing data

By utilizing an empirically derived threshold value of the Normalized Difference Vegetation Index (NDVI), we identified two composite classes of surface covering the entire territory of the former reservoir bed, corresponding to the terrestrial habitats that we identified during field surveys. These classes included conditionally closed vegetation (Habitat Group 1), comprising willow and poplar thickets and marshy communities, and conditionally open vegetation (Habitat Group 2), encompassing sparse vegetation on muddy, shell, or sandy sediments. We also utilized NDWI water index thresholds to map open water surfaces, constituting Habitat Group 3. Four months after the dam's destruction, the total area of open water surfaces was 256.5 km^2.

By evaluating threshold values of spectral indices from multi-temporal images, we tracked the dynamics of water level decline and the concurrent development of closed vegetation (Fig. 3). The chronological sequence of vegetation and water conditions demonstrated an evident and

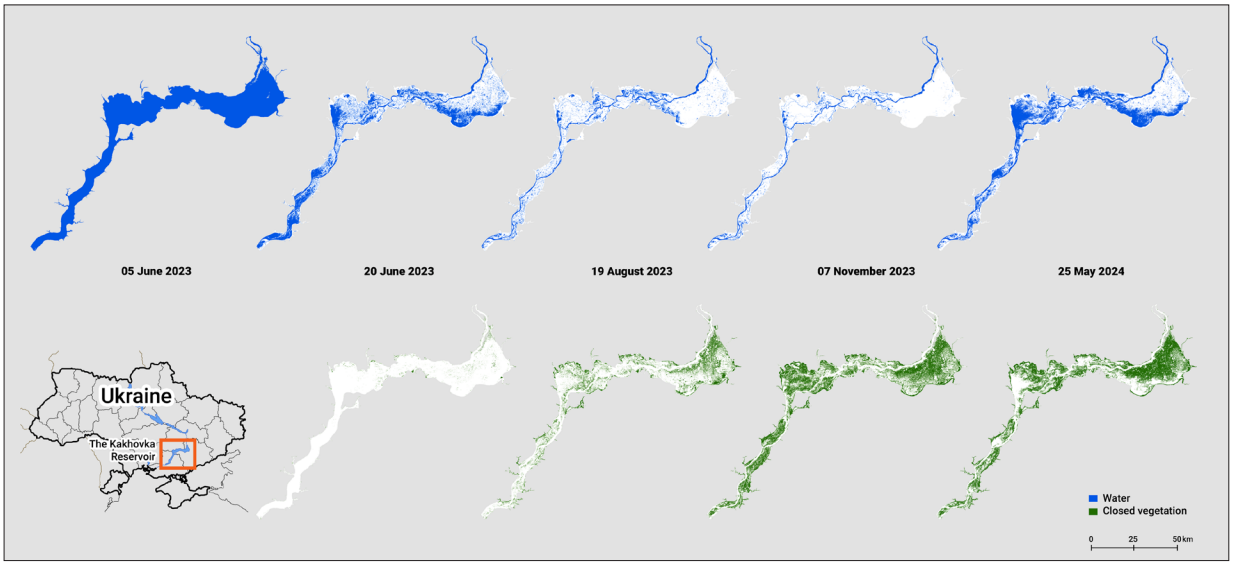


Fig. 3. Water release from the Kakhovka Reservoir bed and vegetation growth on the exposed area (based on NDWI index). In the initial months following the Kakhovka dam breach, the water receded swiftly, gradually revealing old streams and swampy areas that existed before the reservoir was constructed. As the water drained rapidly at first and then more slowly, vast stretches of newly formed land became accessible, creating prime conditions for rapid vegetation colonization (based on NDVI index). In the spring of 2024, the seasonal flood of the Dnipro River has raised the water level again

anticipated restoration process of the natural hydrological state of the river floodplain, accompanied by rapid development of green photosynthetic mass, which correlated with the first group of habitats featuring closed vegetation.

To generate a detailed habitat map for the entire territory of the former reservoir at the moments of the second field surveys (refer to Fig. 4, available for viewing online at https://ee-olegpril12.projects.earthengine.app/view/kakhovka-habitat-map-oct-2023), we leveraged supervised classification of Sentinel-2 multispectral satellite images. The results of the field survey, extended with additional sites from the northern part of the reservoir with known habitat types, served as ground truth for training the Random Forest model. The diagnostic performance of the model was exceptionally high, with an overall accuracy of 0.99 and Cohen's Kappa coefficient of 0.98. The Confusion matrices built on validation datasets (Supplementary Tables S2, S3) indicated only minor confusion between willow thickets and marshy vegetation. The distinction among the other classes was very robust.

The model confirms the findings of the vegetation indices analysis, indicating that as of October 2023, half of the bottom was covered with closed vegetation. Different habitat types are distributed in a mosaic pattern across the territory. Willow and poplar thickets (Habitat 1.1) covered a total area of 614.6 km^2, mostly located in the southern part of the former reservoir, as well as in coastal areas along its entire length. Marshy vegetation (Habitat 1.2) is estimated to cover 332.1 km^2 and tends to occur in near-terrace depressions and bottom hollows. Drying muddy sediments (Habitat 2.1) comprised a total of 70 km^2, with the highest density observed in the central part of the former reservoir, on the right bank of the restored Dnipro riverbed. The largest surface class was shell and sand sediments (totalling 718.5 km^2) (Habitat 2.2), mostly localized on the left bank of the restored Dnipro riverbed in the central and northern, the widest, parts of the former reservoir. The remaining water-covered areas constituted 406.8 km^2.

Seven months later, in May 2024, 48% of the former reservoir (1031.1 km^2) were covered by water due to a seasonal spring flood of the Dnipro River. The area covered by sparse vegetation on shell and sandy sediments decreased near triple (to 247.9 km^2), whereas other terrestrial habitat types remains generally of the same areas (willow and poplar thickets — 611.8 km^2, marshy vegetation — 188.6 km^2, sparse vegetation on muddy sediments — 62.6 km^2). At the same time, by-pixel

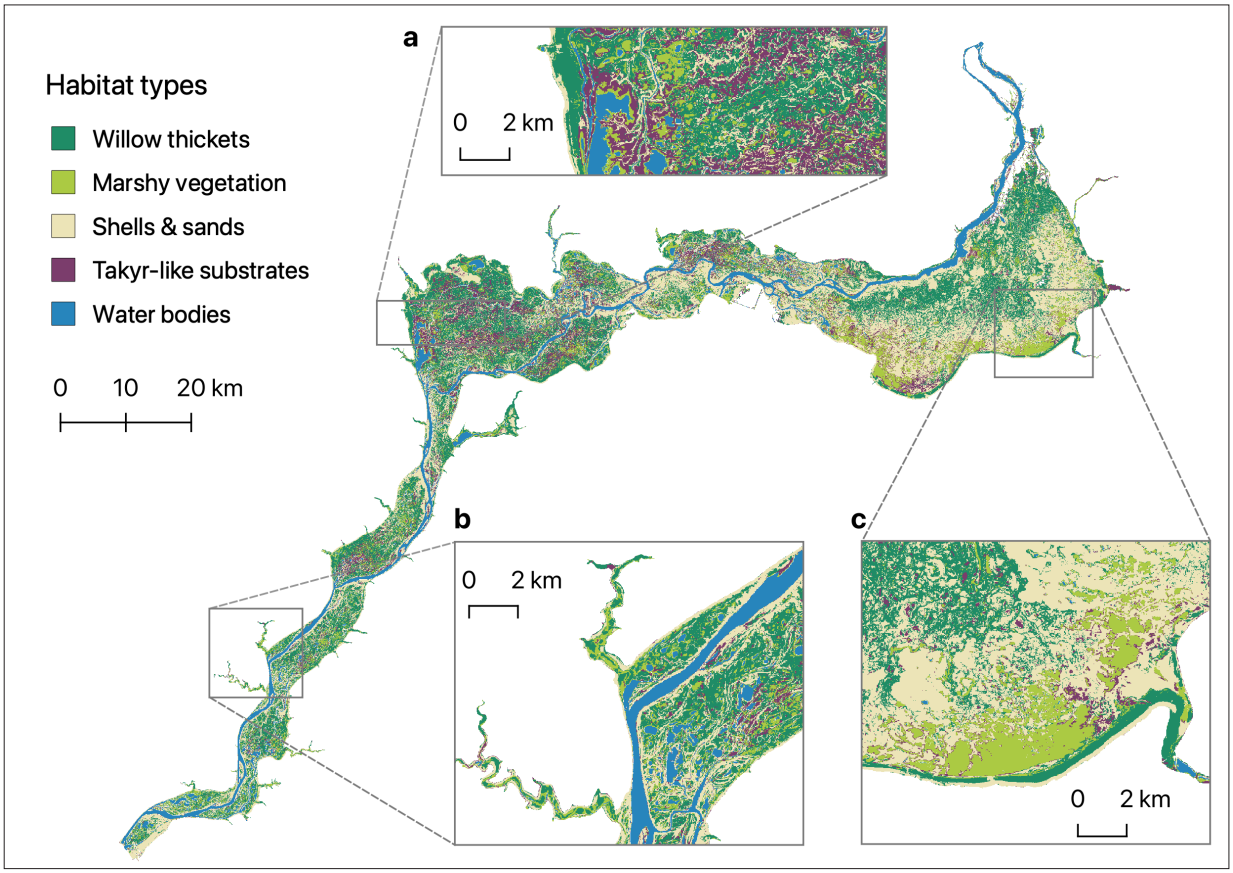


Fig. 4. Distribution of habitat types of the former Kakhovka Reservoir, as of the end of the first vegetation season since the dam breach (October 2023). Pioneer land cover types there seemed to follow the original geomorphology of the Dnipro River valley. In the central part of the former reservoir (a), mostly on the right bank of the Dnipro River, sparse vegetation on muddy sediments prevailed. The southern part (b) with narrower valleys got the most developed vegetation cover, primary willow and poplar thickets. The eastern part (c), which mostly extended across the left bank of the Dnipro River, followed typical floodplain morphology, with willow and poplar thickets on elevated central part of the terrace, followed by sparse vegetation on shell and sand sediments, then marshy vegetation on near-terrace depressions, bordered by willow thickets stretched along the older and higher, not flooded terrace. Spatial prediction based on Random Forest supervised classification of Sentinel-2 satellite imagery, trained by ground truth data collected in October 2023. A scalable high-resolution web maps for October 2023 and May 2024 are available online at https://ee-olegpril12.projects.earthengine.app/view/kakhovka-habitat-map-oct-2023

change detection (Supplementary Fig. S1) showed between-class transmission, supposedly owing to changes in water cover, continuing growing of established willow and poplar trees, and alluvial processes.

Discussion

The environmental catastrophe resulting from the blowing up the dam of the Kakhovka Hydroelectric Power Plant provided us with a unique opportunity to observe the restoration of vegetation at the bottom of the former Kakhovka Reservoir. Our research has revealed that the vegetation cover formation in this area is remarkably rapid. This is facilitated by the presence of a seed bank and the relatively high moisture content of the nutrient-rich substrate. The rapid regeneration of vegetation, which stabilizes the soil structure, makes it unlikely for dried soil contaminated with heavy metals and other potentially hazardous chemicals to disperse, as concerned in some publications (Naddaf, 2023).

The timing of the dam's detonation in early June, coinciding with the ripening of willow seeds,

undoubtedly contributed to the success and competitiveness of this particular plant species in colonizing newly formed substrates and establishing pioneer communities.

We have observed a clear differentiation of habitats in the surveyed areas, with significant areas of willow thickets supporting the hypothesis that it is possible to restore the vegetation cover present in this area before the reservoir was filled, known as the Velykyi Luh (meaning the "Great Meadow"), an area directly related to the history of the Ukrainian Cossacks. We believe that assertions suggesting that these primary habitats will be replaced by something entirely different in the coming years (as mentioned in Stone, 2024) are premature.

Whereas the habitats observed at the bottom of the drained reservoir are currently in the process of formation, they can already be classified according to different European habitat classification systems. Thus, the willow and poplar thickets predominant in the area can be classified as G1.11 Riverine *Salix* woodland in Resolution 4 of the Bern Convention (Revised…, 2019), as well as listed in Annex I of the EU Habitats Directive under 91E0: Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion*, *Alnion incanae*, *Salicion albae*), and 92A0: *Salix alba* and *Populus alba* galleries (Revised…, 2019), and in the *European Red List of Habitats* as G1.1 Temperate and boreal softwood riparian woodland (Janssen et al., 2016). Consequently, this habitat type is protected at the European level. Its significance lies in its ability to structure and purify soils and water by filtering nitrogen and phosphorus compounds, oil products, and adsorbing heavy and toxic metals (Gray, Sotir, 1996; Thompson, 1998; Klang-Westin, Eriksson, 2003; Vervaeke et al., 2003; Mohsin et al., 2021). Similar to the previous habitat type, marshy vegetation is protected at the European level, as it is listed in Resolution 4 of the Bern Convention as C3.2 Water-fringing reedbeds and tall helophytes other than canes, and as type C5.1a Tall-helophyte bed in the *European Red List of Habitats* (Janssen et al., 2016).

The main limitation for mapping habitats at the bottom of the former reservoir is the fact that the majority of the territory remains inaccessible due to the Russian occupation of a significant part of its left (eastern) bank and ongoing hostilities. Most of the territory is reachable for drone attacks, making field surveys dangerous. Under these circumstances, remote methods remain the only reasonable option. Supervised machine learning classifications of Earth Observation data are robust solutions (Rodriguez-Galiano et al., 2012), but they require extensive and representative ground-truth data. In our case, the data point locations were primarily determined by safety concerns. Hence, they better represent the habitats of the southwestern, western, and northern banks of the former reservoir as compared to the eastern part. For this reason, we had to treat the communities formed on shell and sandy sediments (Habitat 2.2) as a single class, since the majority of sandy sediments were allocated close to the left, still occupied bank.

The confusion matrix built upon validation data showed good class separability (Supplementary Tables S2, S3), likely due to the system's simplicity and the low number of classes. Minor intermixture took place only for closed willow and poplar thickets and marshy vegetation (0.007% of misidentifications for 2023, 0.01% for 2024). The main cause of confusion is supposedly the tendency for some sites covered by marshy vegetation to overgrow with willow and poplar thickets over time and drying.

We can expect the formation of a more complex habitat system over time, with diverse transitions among types due to different histories of patch initiation and flooding/overgrowth. That will require revising the habitat type classification and collecting new ground-truth data for future habitat mapping attempts.

The further development of habitats at the bottom of the former reservoir will depend on various factors, primarily weather conditions in winter and spring and the magnitude of spring floods. In the spring–early summer of 2024 we already witnessed the latter, and detected respective changes in the vegetation cover. The main changes included expansion of willow and poplar thickets and shrinking of other habitats, like areas with sparse vegetation on muddy, shell, and sandy substrated, and marshes. Some of these habitats were overgrown with willow and poplar, while others were flooded. Spring floods, alongside with the progressive growth of willow and poplar trees, disproves the idea that this area is destined to be turned into a desert. We intend to continue monitoring the processes of vegetation and habitat formation in the areas we surveyed, as well as in other areas of the former reservoir bottom, as they become available for scientific research. This information is an important

component of the overall situation and will help in establishing the scientific basis for developing scenarios and options for the future destiny of this territory.

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SUPPLEMENTARY MATERIAL

This article includes Supplementary Material (Fig. S1, Tables S1–S3) available as: ukrbotj82-05-488-S1.pdf (325 KB).

ETHICS DECLARATION

The authors declare no competing interests.

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Початкові стадії відновлення рослинності
на дні осушеного Каховського водосховища (Україна):
синтез польових досліджень та дистанційного зондування

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Реферат. 6 червня 2023 року гребля Каховської ГЕС була підірвана російськими військами, що спричинило екологічну катастрофу в Північному Причорномор'ї. Незважаючи на важкі екологічні та соціально-економічні наслідки, катастрофа надала унікальну можливість вивчити розвиток рослинності на території, яка тривалий час була затоплена. Ми відвідали цю територію тричі: через три тижні, 3,5 місяці та 11,5 місяців після катастрофи. Наші дослідження показали, що кількість судинних рослин на цій території збільшилася майже в 14 разів за рік, що суперечить початковим песимістичним прогнозам про опустелювання. Як малорічники, так і багаторічні рослини були представлені майже однаковою кількістю, для більшості з них характерним було поширення вітром. Низька питома вага чужорідних видів спростовує гіпотезу про те, що колишнє водосховище стане джерелом інвазій чужорідних рослин. Ми виділили основні типи новоутворених наземних біотопів, включаючи зарості верб і тополь, прибережні біотопи, мулисті, піщані та вкриті черепашками території з розрідженою рослинністю. Ці дослідження були доповнені даними дистанційного зондування із використанням методів машинного навчання, що дозволило створити детальні карти біотопів для всього дна водосховища. Проведене дослідження сприяє розумінню екологічної сукцесії та динаміки біотопів у пост-катастрофічних ландшафтах, а також формуванню майбутніх стратегій управління такими територіями.

Ключові слова: біотопи, відновлення, заплава, машинне навчання, рослинність, руйнування греблі