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RESEARCH ARTICLE

The enigmatic diploid *Chenopodium ucrainicum* (*Chenopodiaceae* / *Amaranthaceae* s. l.): geographical, ecological, and phytosociological patterns as clues to its origin

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Abstract. *Chenopodium ucrainicum* Mosyakin & Mandák (*Chenopodiaceae*/*Amaranthaceae* s. l.), a newly described diploid species currently known only from Ukraine, is a distinctive yet still enigmatic element of the Ukrainian flora. This study provides a detailed account of its presently known geographical distribution, ecological preferences, and phytosociological features, plus some further information of its morphology, based on field surveys conducted during 2021–2024 across central and western regions of Ukraine. Our fieldwork targeted synanthropic habitats, including roadsides, ruderal zones, forest edges, and undercanopy areas within anthropogenic forests and urban parks. The known range of *C. ucrainicum* is fragmented, with major population clusters in the Dnipro Upland, Male Polissia, and the Podillian Upland. The distribution pattern indicates its primary occurrence in synanthropic environments with moderate moisture levels, and its presence in disturbed habitats suggests its likely status as an alien species in Ukraine. Observations also noted its high projective coverage in plant communities associated with *Acer negundo* and *Robinia pseudoacacia*, where *C. ucrainicum*, if present, frequently plays a dominant role among species of the herbaceous layer. A new association, *Chenopodio ucrainicae-Aceretum negundi* ass. nov., is proposed, highlighting the diagnostic value of *C. ucrainicum* in ruderal and other anthropogenic plant communities. Ecologically, *C. ucrainicum* is classified as a mesophyte with a long vegetation period, making it well-suited to warmer climates with extended growing seasons. Its phenological pattern and tolerance to low temperatures point to its supposed origin in and spread from regions with similar climatic conditions. Although the species exhibits high adaptability within its current range, which corresponds to the recent warming climatic trends in Ukraine, its absence in historical records in herbaria supports the hypothesis that *C. ucrainicum* is a relatively recent immigrant in Ukraine. Its native range may lie in temperate or subtropical regions of southern or southeastern Asia, where other genetically diverse *Chenopodium* species are present. Continued research, including molecular phylogenetic and phylogeographic studies, will be essential for confirming its actual geographic origin and the evolutionary role within the *Chenopodium album* allopolyploid complex. This study contributes valuable insights into the distribution patterns and ecological characteristics of *C. ucrainicum*, highlighting its probable status as an expanding neophyte in the flora of Ukraine, influenced by climate change and anthropogenic factors.

Keywords: biodiversity, *Chenopodium album* complex, climate change, flora, range expansion, taxonomy, Ukraine

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Introduction

Recent molecular phylogenetic studies (Fuentes-Bazan et al., 2012; Walsh et al., 2015, etc.) resulted in a considerable re-circumscription of the Linnaean genus *Chenopodium* L. sensu lato (*Chenopodiaceae* sensu stricto / *Amaranthaceae* sensu lato). Several genera segregated from *Chenopodium* s. l. are now recognized, such as *Dysphania* R. Br. (incl. *Cycloloma* Moq., etc.; see Mosyakin, Clemants, 2002, 2008; Uotila et al., 2021; Mosyakin, 2021, etc.), *Teloxys* Moq., *Oxybasis* Kar. & Kir. (see Mosyakin, de Lange, 2018; Uotila, 2022, and references therein), *Blitum* L., *Chenopodiastrum* S. Fuentes, Uotila & Borsch (see Uotila, 2017, 2020), and *Lipandra* Moq. At the same time, some previously recognized genera, such as *Rhagodia* R. Br. and *Einadia* Raf., are now submerged in *Chenopodium* s. str. based on phylogenetic evidence (Fuentes-Bazan et al., 2012; Mosyakin, Iamonico, 2017, etc.).

The newly re-circumscripted *Chenopodium* s. str. is probably the most phylogenetically and taxonomically complicated group among the genera recognized after the recent splitting of *Chenopodium* s. l. The evolutionary pathways involving widespread hybridization and allopolyploidy (see Mandák et al., 2012, 2018; Walsh et al., 2015; Krak et al., 2016; Young et al., 2023; Maughan et al., 2024, etc.) contributed to an extremely complicated pattern of phylogenetic relationships, which are difficult to reflect in a reliable taxonomic scheme. Diploid species are of special importance in that phylogenetic pattern because they contain genomes that contributed to the formation of allopolyploid taxa, mainly tetraploids and hexaploids, including the tetraploid pseudocereal crop species *C. quinoa* Willd. (see Young et al., 2023; Maughan et al., 2024, and references therein) and one of the most noxious weeds of the world, hexaploid *Chenopodium album* L. and its closest relatives (see Beaugé, 1974; Mandák et al., 2012, 2018; Krak et al., 2016, etc.).

Chenopodium ucrainicum Mosyakin & Mandák is a recently described diploid species known so far only from the territory of Ukraine (Mosyakin, Mandák, 2020a; Mosyakin, Mosyakin, 2021; Orlov et al., 2022; Shynder, Shevchyk, 2022; Habibi et al., 2023). Until recently, information about its geographic range and features of habitats remained little known. This provided an impetus for the present study of the general distribution and ecological and phytosociological (coenotic) peculiarities of *C. ucrainicum*, which continues to remain a rather mysterious element in the flora of Ukraine and of Europe in general.

The aim of the present work was to gather and summarize the available information on the current geographic range of *C. ucrainicum* and to reveal ecological and coenotic features of its habitats, as well as to evaluate available evidence on its probable origin.

Study history

Chenopodium ucrainicum was described as a species new for science in 2020 based on the results of a complex multi-year study of closely related taxa of the *Chenopodium album* aggregate in the floras of Europe and North America (Mosyakin, 1996b, 2012; Clemants, Mosyakin, 2003; Mosyakin, Mandák, 2020a). However, the first samples of *C. ucrainicum* were collected by Sergei Mosyakin much earlier, in 1989, in Hrebinky (alternatively transliterated as Grebinky), Bila Tserkva District (formerly Vasylkiv District), Kyiv Region. The plants were discovered in shady places in a small park and adjacent ruderal habitats near the Kyiv–Odesa highway, not far from a grain elevator. It was evident already in the early 1990s that this *Chenopodium* plant represented a species morphologically different from all other species of the genus known in Ukraine. The proximity of an elevator and a major highway indicated the possible introduction of an alien plant. Consequently, the main task seemed to be to match the newly found plants with some species already known from other area(s) of the Globe. Suggestions were made on possible identifications of these plants as *C. missouriense* Aellen or *C. borbasii* Murr (see Mosyakin, 1996b, 2012); however, they have not been confirmed and it is now evident that the Ukrainian plants do not belong to these two mentioned taxa. In the following years, repeated collections of *C. ucrainicum* were made in the same locality or nearby (Mosyakin, Mandák, 2020a; Mosyakin, Mosyakin, 2021).

Later, in 2003, the plants of *C. ucrainicum* were collected by Liubov Gubar in the northwestern part of Ukraine in Ostroh (sometimes alternatively transliterated as Ostrog), Rivne Region. In recent years, one of us (S. Mosyakin) discovered this species in additional localities in Kyiv City: in Nyvky Park in the western part of the city and along Zagorska (formerly Baggovutivska) Street

in the Tatarka historical neighborhood in the northwestern part of Kyiv. The location from Tatarka became the *locus classicus* of the newly described species, *C. ucrainicum*, and the specimen in the KW herbarium (mounted on four sheets: KW001003108, KW001003109, KW001003110, and KW001003111) was designated as the holotype (Mosyakin, Mandák, 2020a).

At the time of the first description of *C. ucrainicum* it has been already known that this species is diploid and that it is not conspecific with any other species of *Chenopodium* known in Ukraine or adjacent countries (Mosyakin, Mandák, 2020a). Recent karyological and molecular studies of *C. ucrainicum* confirmed that this species has the 'BB' genome and is well differentiated from other closely related species, in particular, BB-diploids *C. suecicum* Murr and *C. ficifolium* Sm. (Habibi et al., 2023). Species with the 'BB' genome played an important role in the evolution of several allopolyploid taxa, in particular, the widespread hexaploid weed *C. album* s. str. and its close hexaploid and tetraploid relatives (see Walsh et al., 2015; Krak et al., 2016; Mandák et al., 2018). Morphologically, the closest species remains *C. suecicum* (but some leaves of *C. ucrainicum* are more similar to leaves of some forms of *C. ficifolium*), which is, however, very well genetically differentiated and rather well morphologically distinguished from our species.

In 2020, Sergei Mosyakin and Andrii Mosyakin discovered an additional locality of *C. ucrainicum* in Salyvonky, Bila Tserkva District (formerly Vasylkiv District), Kyiv Region, quite close to the first known localities in the same district (Mosyakin, Mosyakin, 2021). In 2021 and 2022, numerous new localities of *C. ucrainicum* were discovered in Cherkasy, Kyiv, Rivne, Vinnytsia, and Zhytomyr Regions (Orlov et al., 2022; Shynder, Shevchyk, 2022). It has become clear that *C. ucrainicum* is rather widespread in the central part of Ukraine, at least much more widespread than it was supposed earlier based on the initially known localities. It is also now obvious that the geographical distribution of this species is not continuous. On the other hand, a number of preliminary suggestions about several other possible occurrences of this species in Ukraine and Central and Western Europe (Mosyakin, Mandák, 2020a) have not yet been confirmed.

Until now, the alien *versus* native status of *C. ucrainicum* in the flora of Ukraine remains unclear. The pattern of distribution of the species in Ukraine and its synantropic habitats there may indicate that *C. ucrainicum* is actually alien in Europe, but in that case its primary range is still unknown. The peculiar late-season development and the leaf shape somewhat similar to that of some Asian morphotypes of *C. ficifolium* may suggest some links of *C. ucrainicum* with plants occurring in East and Southeast Asia (Mosyakin, Mandák, 2020a, 2020b). The lack of sufficient information about the new species contributed to a special study of its range and habitat characteristics and became the impetus and basis for this publication.

Materials and Methods

Field surveys were conducted in 2021–2024 in the territory of the plain part of Ukraine, in Cherkasy, Khmelnytsky, Kyiv, Rivne, Vinnytsia, and Zhytomyr administrative regions (Oblasts), and Kyiv City, specifically with radial route expedition studies carried out around the two centers of occurrence of *C. ucrainicum* known in 2021 (southern outskirts of Kyiv City, Kyiv Region, and Ostroh, Rivne Region). Special attention was paid to plants that corresponded to the description of *C. ucrainicum* (Mosyakin, Mandák, 2020a) or were morphologically similar to it, and to collecting them for their further more precise identification. The list of verified localities is provided in Supplement S1. Samples of plants of *C. ucrainicum* from different localities are deposited in the National Herbarium of Ukraine of the M.G. Kholodny Institute of Botany of the National Academy of Sciences of Ukraine (KW; herbarium acronyms follow *Index Herbariorum*: Thiers, 2009–onward) and the herbarium of the M.M. Gryshko National Botanical Garden of the National Academy of Sciences of Ukraine (KWHA). Photographs of plants from most habitats are presented at the *iNaturalist* online resource (https://www.inaturalist.org/observations?taxon_id=1318362), and a large part of this information is duplicated at the GBIF (*Global Biodiversity Information Facility*) resource (https://www.gbif.org/uk/species/11197744).

The phytosociological studies have been performed according to the Braun-Blanquet approach (Braun-Blanquet, 1964; van der Maarel, 1979, etc.). Thirty-four phytosociological relevés were made in various habitats (Didukh et al., 2011), such as antropogenic forests, forest edges, ruderal places, etc. (Supplement S2); they were stored in the phytosociological database format of the *Turboveg* software

package (Hennekens, Schaminée, 2001). Most of these relevés (about 60%) were made on the standard 3–5 m² plots, for the forest vegetation — 100 m². The taxonomy and nomenclature of vascular plant species in phytosociological relevés were harmonised according to the *Plants Of the World Online* (POWO, 2024–onward), with a few taxonomic updates. The diagnostic value of the species was assessed using the Phi coefficient based on the fidelity concept (Chytrý et al., 2002). Soil samples were taken at the end of the growing season from eight biotopes where optimal conditions for the growth and development of *C. ucrainicum* plants were observed (Supplement S3). They were prepared according to the method of H. Rinkis and V. Nollendorf (Rinkis, Nollendorf, 1982). Methods of agrophysical and agrochemical analysis of soil samples were used for the extraction of macro- and microelements (Zaimenko, 2021), and their further content was determined on an ICAP 6300 DUO induced plasma spectrometer (Thermo Fisher Scientific Inc., USA). The acidity of soil samples was measured using a pH-meter H1 2211 (Hanna Instruments, Italy).

Results

Notes on morphology

A detailed morphological description of *Chenopodium ucrainicum* is provided by Mosyakin and Mandák (2020a). Here we provide some additional notes on its morphology based on field observations and herbarium specimens that have become available after the publication of the protologue.

Chenopodium ucrainicum plants are quite polymorphic, depending on the conditions of the place of growth and the phase of vegetative and generative development. Because of that, in some cases, difficulties may arise with identification of this taxon *in situ*, in particular when distinguishing it from *C. album*, *C. opulifolium* Schrad. ex W.D.J. Koch & Ziz, and/or *C. suecicum*. Anyway, *C. ucrainicum* is a genetically isolated species that has well-defined morphological features. It is usually a rather slender and fragile plant that can sometimes grow up to 2 m tall (under most favorable conditions); however, usually the plants are much smaller, up to 1 m tall. Fully developed plants are usually glabrous or nearly so, almost devoid of the mealy indumentum formed by vesicular trichomes, but the remnants of that mealy indumentum are usually present on young shoots, lower sides of leaves, and generative organs. The leaves are thin and mostly light green above, and sometimes whitish- or bluish-green below. The middle cauline leaves are mainly more or less distinctly three-lobed, often with a generally rectangular outline (the lateral edges of the central lobe are usually parallel); the length to width ratio is usually 1.2–2:1, rarely 1:1, but in the latter case the plants always have also more elongated leaves. The edge of the leaf blade is from entire or subentire to peculiarly erose and notched, the teeth are normally rounded or obtuse, rarely acute or slightly acuminate. On well-developed cauline leaves, the teeth are obtuse, often double, with rounded notches between the lobes and teeth that frequently extend beyond 180–200°, creating an arc larger than a semicircle (Fig. 1); as far as we know, this feature is not characteristic of other *Chenopodium* species of the East European flora. It should be noted that although the teeth on the leaves have variable apices (rounded, obtuse, or subacute or even subacuminate), the empty spaces (notches) between individual teeth on the leaf blade are almost exclusively rounded in shape. Cauline leaves above the middle of the stem (and, in less developed plants, sometimes also in the lower part) have reduced lateral lobes and often entire or subentire margins; the general shape of such leaves varies from rectangular to elongate-ovate, with acute apices or sometimes with a slightly mucronate apex, having a short and weak mucro up to 1 mm long. The upper cauline leaves, which develop during the flowering period, are elongate-ovate to lanceolate, mostly entire or subentire at margins, mainly rounded or obtuse at the apex, rarely obtuse-triangular, but often with a small mucro. Inflorescences are normally thin, moniliform. At the end of the flowering period, their axes are usually greatly elongated and partially drooping, due to which the plants acquire a sprawling habit.

Young plants of *C. ucrainicum* are often characterized by the golden-pink or pinkish-red (anthocyanin) shade of the mealy indumentum on growing young leaves (Fig. 2). However, similar coloration patterns are also found occasionally in other species of the genus (e.g., *C. betaceum* Andrz., *C. giganteum* D. Don).

Phenology

Under the conditions of Kyiv City, first seedlings of *Chenopodium ucrainicum* usually appear from the beginning of April. Flowering occurs at the end of

August–September, and the vegetation period lasts until late autumn (in 2020–2021 and 2024 until the middle or end of November, with some plants still with green leaves at the beginning of December), although in some populations the vegetation period ends already at the end of October, especially under dry weather conditions. According to available records, the complete vegetation period of this plant species is about 190–230 days. In general, the phenological phases of flowering and fruiting of *C. ucrainicum* occur 1–2 months later as compared to other species of the *Chenopodium album* aggregate present in the Ukrainian flora. It also helps to identify these plants *in situ*, sometimes even from the distance. Also, such a sharply different duration of vegetation confirms the significant biological isolation of *C. ucrainicum* from other closely related diploid species of the genus, such as *C. ficifolium* or *C. suecicum*, which usually flower and bear fruits earlier, mainly in July–early September (Mosyakin, Mandák, 2020a).

A rather high tolerance of *C. ucrainicum* to low temperatures should also be noted. According to the observations of Sergei Mosyakin for several years in Kyiv (Mosyakin, Mandák, 2020a, and unpublished data), this plant species fully completes its vegetation and fruiting in the late autumn period after the onset of night frosts. Moderately low temperatures (several degrees below 0 °C on the ground), which are currently sometimes observed in the study area in late October and November, normally do not lead to freezing of leaves of these plants.

Distribution

According to the results of our inventory of information on the distribution pattern of *Chenopodium ucrainicum* (Supplement S1), more than 200 locations are now known in approximately 95 separate geographical places (localities) in seven administrative regions (*oblasts*) of Ukraine (Fig. 3).

Most of the newly found locations of *C. ucrainicum* were discovered in 2021 and 2022 during field surveys. Most of the localities of *C. ucrainicum* known at the beginning of the study were located in Kyiv City and its southern suburbs, so it was from here that a number of radial field excursions were carried out in different directions. The search for *C. ucrainicum* was successful only in the southern direction from Kyiv City, where many new localities were discovered in the southern part of Kyiv Region and adjacent territories.

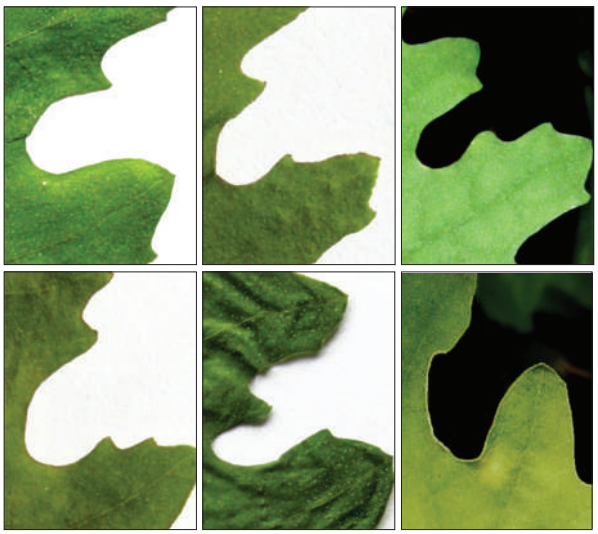

Fig. 1. Typical notches between the lobes and teeth of fully developed lower and middle cauline leaves of *Chenopodium ucrainicum*

Fig. 2. Color features of young plants of *Chenopodium ucrainicum*. Stayky village, Obukhiv District, Kyiv Region, 27 May 2023 (photo by O. Shynder). Close-up: Nyvky Park, Kyiv City, 30 May 2023 (photo by S. Mosyakin)

All known localities of *C. ucrainicum* outline the formed (secondary or primary?) geographic range of this species, which, as we know at present, consists of three fragments in the central and western parts of Ukraine (Fig. 3). Most of localities (about 82%) from Kyiv City, Cherkasy and Kyiv regions, and the adjacent territories of Vinnytsia and Zhytomyr regions, are concentrated in the central part of the Dnipro (Dnieper) Upland area. According to the physical and geographical zoning (physiographic regionalization) of Ukraine (Marynych et

Fig. 3. The known range of *Chenopodium ucrainicum*; for actual updates, see *iNaturalist* (https://www.inaturalist.org/observations?taxon_id=1318362) and GBIF (https://www.gbif.org/uk/species/11197744)

al., 2003), this territory is located within the natural physiographic region of the Right Bank Forest-Steppe (where the first two words refer to the right bank of the Dnipro River, i.e., the areas west of the Dnipro), and only a few localities in Kyiv City are situated at the southern border of the Polissia (the Forest Zone) natural physiographic region. This "Dnipro" fragment of the known range of *C. ucrainicum* is the main one in terms of its area and number of localities. Here this species was collected for the first time in 1989 in Hrebinky, Bila Tserkva (formerly Vasylkiv) District of Kyiv Region, and here its *locus classicus* is located (Tatarka historical district, the northwestern part of Kyiv City).

The second largest fragment of the range of *C. ucrainicum* covers the localities in the town of Ostroh and surrounding areas in the southern part of Rivne Region. According to the physiographic zoning of Ukraine (Marynych et al., 2003), this territory belongs to the natural physiographic region of Male Polissia (Little or Lesser Polissia). For the first time *C. ucrainicum* plants were collected here in 2003 in the city of Ostroh; initially they were reported under the misapplied name "*C. borbasii*" (auct. non Murr).

The smallest fragment of the known range of *C. ucrainicum* was discovered in 2022 in the southern part of Vinnytsia Region, where several colonies of this species were found in Mohyliv-Podilskyi and its surrounding areas. This natural area is locally known as the Middle Dnister Region [*Середнє Подністров'я* in Ukrainian], stretching along the valley of the Dnister (Dniester, Nistru) River. It is a part of the Podillia Upland. According to physical and geographical zoning (physiographic regionalization), this area belongs to the natural physiographic region of the Right-Bank Forest-Steppe, as well as the "Dnipro" fragment of the known range of *C. ucrainicum*.

Within the outlined area, *C. ucrainicum* is distributed heterogeneously. Thus, in the main ("Dnipro") fragment of the range, most localities are concentrated in or between the cities and towns: Kyiv, Bila Tserkva, Stavyshche, Korsun-Shevchenkivskyi, Kaniv, and Rzhyshchiv. This area is mainly confined to the Kyiv Plateau. The most abundant habitats of *C. ucrainicum* are clustered on the slopes of the high right bank of the Dnipro River from the settlement of Trypillia (Obukhiv District, Kyiv Region) to Pekari village (Cherkasy District, Cherkasy Region), as well as in hilly areas along the Ros River valley from Kaniv (Cherkasy District, Cherkasy Region) and Pekari village to the town of Tarashcha (Bila Tserkva District, Kyiv Region).

Within both these geographic segments, *C. ucrainicum* was found almost everywhere. This species formed continuous geographic populations in this area. This is exactly what is observed in Ostroh and its western surroundings, where *C. ucrainicum* was found in many places. These outlined areas are characterized by similar geographical conditions: the soil cover was formed on a thick layer of clayey substrates of the Quaternary origin (loess loam), the terrain is highly rugged, the presence of ravines and clay and loess outcrops, moderate or high natural afforestation of the territory, and moderate amounts of annual precipitation. There is every reason to assume that the specified areas along the right bank of the Dnipro River and along the valley of the Ros River have become a kind of ecological corridors with optimal conditions for the growth and distribution of *C. ucrainicum*.

In other parts of the studied range, localities of *C. ucrainicum* are not so common or are random at all. Yes, in several places in Kyiv there are centers of occurrence this species, for example, in Nyvky Park, or in its *locus classicus* — the hilly area along Zagorska (formerly Baggovutivska) Street. But in general, this species is rarely found in Kyiv, and so far only its occasional colonies are known in the northern, central and southern parts of the city, and only in the areas west of the Dnipro River. The same applies to Hrebinky, Bila Tserkva District, Kyiv Region, where *C. ucrainicum* was found as

early as 1989, and now its several local colonies are still known there.

In this area, the finds of *C. ucrainicum* are rather accidental. We found only a few localities in the towns of Bila Tserkva and Vasylkiv, and here it gave the impression of a recent migration. Occasional small colonies were found in the western and central parts of Cherkasy Region, Vinnytsia Region (Mohyliv-Podilskyi, Pogrebyshche), and Zhytomyr Region (Ruzhyn).

In the course of this research, we noticed that within the studied area *C. ucrainicum* avoids areas with the sandy soil cover, for example, alluvial strips along rivers or stands of pine forests on the Quaternary sands of fluvioglacial origin near Kyiv City.

Information about locations and territories where *C. ucrainicum* has not yet been found despite special searches is also important. Until now, we have not confirmed the occurrence of this species in the zone of mixed forests in the northern part of Ukraine (with the exception of a few localities in Kyiv City, where the growing conditions are more similar to those of the forest-steppe than to the zone of mixed forests), the Left Bank Forest-Steppe, the Steppe zone, Crimea, and the western part of Ukraine (in particular, the Carpathians). We do not rule out that in some of these geographical areas *C. ucrainicum* can be indeed found, but these will be probably occasional localities, and there is no wide distribution of *C. ucrainicum* in these areas at the present stage of its supposed dispersal. Therefore, there are good reasons to assume that we have outlined most of the present-day range of this species in Ukraine. Information about the findings of *C. ucrainicum* outside the studied area (e.g., preliminary identifications in *iNaturalist*) has not yet been confirmed.

Phytosociological features of habitats

All known habitats of *Chenopodium ucrainicum* are found in synanthropic biotopes: first of all, these are various ruderal areas on roadsides, edges of anthropogenic (artificial or at least considerably disrupted) forests, under the canopy of trees and shrubs in parks or anthropogenic forest plantations dominated by the naturalized aliens *Acer negundo* L. and/or *Robinia pseudoacacia* L., less commonly along forest paths (Fig. 4). Sometimes *C. ucrainicum* was found on erosional clay or loess outcrops devoid of vegetation under the canopy of trees and shrubs. We recorded 139 species of vascular plants in the plant communities with the participation of *C. ucrainicum* (Supplement S2). *Acer negundo*, *Ballota nigra* L., *Chelidonium majus* L., *Dactylis glomerata* L., *Lolium perenne* L., and *Poa angustifolia* L. co-occur with *C. ucrainicum* most often (with significant projective cover values), while *Polygonum aviculare* L. s. l., and *Taraxacum officinale* F.H. Wigg. aggr. co-occur with our species only on ruderal sites. Projective coverage values of *C. ucrainicum* in communities vary from 2% to 90%.

Other species of *Chenopodium* occasionally co-occurring with *C. ucrainicum* are diploid taxa *C. suecicum* (mainly in shady habitats) and *C. ficifolium* (very rarely, registered only as growing nearby), tetraploid *C. betaceum* (*C. strictum* auct., non Roth), and hexaploid *C. album* s. l. and *C. opulifolium*, the last three species growing mainly in open and drier areas.

When classifying geobotanical relevés, we singled out two groups of such descriptions. The first group included phytocenoses formed on trampled places in populated areas, with the minor participation of ruderal short-lived plants (13 relevés). Such groups can be attributed to derived plant communities of the class *Polygono arenastri-Poetea annuae* Rivas-Martínez 1975 corr. Rivas-Martínez et al. 1991. In addition to *C. ucrainicum* with an average projective cover of 20–30%, the basis of these coenoses is formed by *Lolium perenne*, *Polygonum aviculare*, and *Taraxacum officinale* aggr. Annuals (*Chenopodium album*, *Erigeron canadensis* L., *Hordeum murinum* L.) and short-lived perennials (*Ballota nigra*, *Chelidonium majus*, *Poa angustifolia*) also occur often. These are phytocenoses of open ruderalized areas, sometimes partially shaded, growing on fertile soils, with some signs of nitrification. Phytocoenoses that are formed on roadsides, under fences, and in other ruderal areas usually have no significant participation of trees and shrubs. The phenological optimum of this vegetation falls on August–November.

The second group (21 relevés) consists of phytocenoses of anthropogenic forests or tree stands of *Acer negundo* and *Robinia pseudoacacia* with dominance in the herbaceous layer of *Chenopodium ucrainicum* (up to 60%). For these plant communities, we describe here the new association, *Chenopodio ucrainicae-Aceretum negundi* ass. nov., assigned to the union *Balloto nigrae-Robinion pseudoacaciae* Hadač et Sofron 1980 of the class *Robinietea* Jurko ex Hadač et Sofron 1980 (see Pashkevych, 2024).

Fig. 4. *Chenopodium ucrainicum* habitats. A: stony banks of the Ros River, Bohuslav, Obukhiv District, Kyiv Region (photo by O. Shynder, 2021); B: shady park habitat, Stavyshche, Bila Tserkva District, Kyiv Region (photo by O. Shynder, 2021); C: forest road, outskirts of the Novomalyn, Rivne Region (photo by O. Holovko, 2021); D: abandoned flowerbed, Tarashcha, Bila Tserkva District, Kyiv Region (photo by O. Shynder, 2021)

Chenopodio ucrainicae-Aceretum negundi Pashkevych, ass. nov., hoc loco (alliance *Balloto nigrae-Robinion pseudoacaciae* Hadač et Sofron 1980; class *Robinietea* Jurko ex Hadač et Sofron 1980).

Diagnostic species: *Chenopodium ucrainicum*. Constant species: *Acer negundo, Alliaria petiolata* (M. Bieb.) Cavara & Grande, *Anthriscus sylvestris* (L.) Hoffm., *Atriplex patula* L., *Ballota nigra, Chelidonium majus, Dactylis glomerata, Galium aparine* L., *Geum urbanum* L., *Humulus lupulus* L., *Poa angustifolia, Robinia pseudoacacia, Urtica dioica* L.

Dominant species: *Acer negundo*, *Anthriscus sylvestris, Ballota nigra, Chenopodium ucrainicum, Galium aparine.*

Holotype: Supplement S2, Table S2, auct. relevé 34 (table number 34).

Species and abundance (Braun-Blanquet cover scale): *Acer negundo* 40%, *Robinia pseudoacacia* 20%, *Rubus caesius* L. 5%, *Chenopodium ucrainicum* 30%, *Ballota nigra* 15%, *Chelidonium majus* 5%, *Geum urbanum* 2%, *Urtica dioica* 2%, and single plants: *Acer platanoides* L., *Lolium perenne, Polygonum aviculare* s. l., *Salix alba* L., *Stellaria media* (L.) Vill., *Ulmus laevis* Pall.

Acer negundo and *Robinia pseudoacacia* groves or communities of other alien tree species with weedy understorey on loamy-sandy dry soils of Central and Eastern Europe.

The investigated phytocoenoses of the association *Chenopodio ucrainicae-Aceretum negundi* (21 relevés) are mainly anthropogenic tree plantations with density up to 8 points on slopes of slight to moderate (up to 30°) steepness. *Acer negundo*, *Robinia pseudoacacia*, *Ulmus laevis*, *Acer platanoides*, and occasionally *Juglans regia* L., prevail in the floristic composition of the tree layer. In the grass layer there are synanthropic native plants species: *Anthriscus sylvestris, Poa angustifolia, Dactylis glomerata, Humulus lupulus, Ballota nigra, Chelidonium majus*, an average of 20–25 species in the group. Projective coverage of *C. ucrainicum* varies from 2 to 60%.

Edaphic features and moisture regime of habitats

Most habitats of *Chenopodium ucrainicum* occur on sites with sufficiently humid and fertile soils. In the known range of *C. ucrainicum*, the most common soils are chernozems on the underlying loess layer, rarely on almost bare loess. The analysis of soil samples from a number of habitats (Supplement S3) proved that *C. ucrainicum* prefers rich soils with high humus content (5.2–14.5%) and moderately alkaline acidity (pH 7.18–7.58). The content of individual biogenic elements in the studied samples is within the limits of optimal indicators or even exceeds these limits. For example, for agricultural crops that are more demanding, the optimal indicators of the content of biogenic elements are as follows (in mg/l): NH_4 — 10–15, P — 110–130, K — 210–250, Ca — 3200–4000, Mg — 70–90, Fe — 50–80, S — 20–30, Mn — 15–20 (Zaimenko, 2021; Kushnir et al., 2023). In the studied habitats of *C. ucrainicum*, the content of such biogenic elements as NH_4 (20–50), P (54–437), Ca (6664–18992), S (37–50), Mn (15–25) at the end of the growing season exceeded the optimal indicators.

Fig. 5. Almost desiccated plants of *Chenopodium ucrainicum* at the end of the dry summer of 2024. Nyvky Park, Kyiv City, 30 August 2024 (photo by S. Mosyakin)

Therefore, *C. ucrainicum* should be classified as a eutrophic species.

In relation to humidity, *C. ucrainicum* is a mesophyte. In most cases, plants have a good or satisfactory appearance in habitats with sufficient humidity. Obviously, soils formed on a clayey or silty (loessy) parent substrate with a dense granulometric composition due to its better water-holding capacity and better water infiltration into the topsoil ensure greater resistance of the plants in dry periods. Also, *C. ucrainicum* prefers shade and semi-shade, where it develops more vigorously, and often acquires large sizes.

On the contrary, a tendency was noted that *C. ucrainicum* avoids habitats with sandy substrates, which quickly dry out and do not retain moisture after rainfall. Under such conditions, this plant species feels good only when it has sufficient moisture supply, in particular, in shaded places protected from drying out quickly. Presumably, similar soils with a light mechanical composition may be also unsuitable for *C. ucrainicum* due to the low content of biogenic elements. Observations of the habitats of *C. ucrainicum* during the summer months indicate that in years with summer drought these plants are poorly developed and may even completely dry out (Fig. 5); in a moist fall season they can recover rather successfully, at least partially. Therefore, the

sufficient availability of atmospheric and soil moisture is a limiting factor for the spread and dispersal of this species.

In connection with the presence of certain requirements for ecological factors of habitats, it is worth paying attention to the boundaries of the currently known range of *C. ucrainicum*. Its known southern limit of distribution does not reach the boundary of the Forest-Steppe and the Steppe (for delimitation of these physiographic zones, see Mala, 2016). One of the main factors that limit the spread of *C. ucrainicum* to the south is, obviously, a lack of moisture. Areas with extensive sands and sandy soils in the north of Ukraine (fluvioglacial Pleistocene deposits of sands in the Polissia — the northern forest zone) and along large rivers (alluvial sands) are also probably not suitable for the growth of *C. ucrainicum* due to the rapid drying out of the substrate that is common there. Thus, these factors may limit the spread of this species to the north and northeast of the presently discovered range.

Another additional limiting factor for the spread of this species can be the excess content of mineral salts in the soil, which can reduce the drought resistance of the mesophytic plants. Saline soils in the southern and eastern regions of Ukraine are probably unfavorable for this species. This assumption has not yet been supported by experimental or direct observational data, but the combination of unfavorable edaphic and climatic factors in general can explain the absence of any (!) known localities of *C. ucrainicum* east of the Dnipro River, in the physiographic region of the Dnipro Lowland. This contrasts sharply with the high density of localities on the right bank of the Dnipro River, on the Dnipro Upland.

Discussion

Immigration status and origin

At present, the origin, primary range, and immigration status in the currently discovered range (native or alien in the flora of Ukraine) of *Chenopodium ucrainicum* remain largely unresolved. However, the currently available phytogeographical, ecological and cenotic, and biological information about *C. ucrainicum* is sufficient for expressing at least preliminary assumptions and conclusions about it as an element of the Ukrainian flora, which will complement our earlier considerations (see Mosyakin, Mandák, 2020a; Habibi et al., 2023).

The current geographical distribution of *C. ucrainicum* in Ukraine seems to be rather heterogeneous. As already noted, most of localities were found in the central part of Ukraine known as the natural region of the Kyiv Plateau and adjacent areas, forming the "Dnipro" fragment of the range. It is advisable to consider it as probably an older center of distribution and dispersal of the species. Here, *C. ucrainicum* showed the greatest phytocenotic activity in plant comunities and it is often found in many settlements and beyond. In general, there is a massive distribution of the species along roads, but it has a tendency to spread at a certain distance from transportation routes. On the periphery of this "Dnipro" fragment, in particular, in Cherkasy, Vinnytsia, and Zhytomyr regions and the northern districts of Kyiv City, only local colonies of *C. ucrainicum* were found, which are mainly confined to the shady roadsides of highways and main roads, especially in hilly areas. This may indicate its recent dispersal in that area. Similar trends are characteristic of two other fragments of the range of *C. ucrainicum*, "Malopolissian" (Male Polissia, Lesser Polissia) and "Dnister". They are characterized by not so many localities found along roads, probably indicating the progressive expansion of the species. Therefore, the spatial distribution patterns of *C. ucrainicum* in Ukraine indicate that this species seems to be in the stage of expansion, and within the studied area the older (one or more) centers and newly formed fragments can be distinguished.

Thus, now *C. ucrainicum* is almost certainly a progressive species of the flora of Ukraine. In this respect, we should again re-consider the problem of its origin, in addition to our considerations and discussions in our earlier articles (Mosyakin, Mandák, 2020a; Habibi et al., 2023). The assumption that *C. ucrainicum* is a native element of the flora of Ukraine (and Eastern Europe in general) seems to be the least probable one. From a phytogeographical viewpoint, if *C. ucrainicum* is a native species, there are reasons to consider it a North Pontic local endemic. However, narrow endemism is not characteristic for the Forest-Steppe zone in the central part of Ukraine. The flora of this area is relatively young, being formed under the influence of the Forest and Steppe floristic elements (see Mala, 2016), and its present-day composition formed mainly during the post-Pleistocene times, in the Holocene (see Bezusko et al., 2011, and references therein). The absence of geographical barriers on

the plain of Eastern Europe did not contribute to any noticeable speciation here. Those plant taxa that are mainly restricted to the North Pontic area and have a rather limited geographical distribution [for example, *Centaurea borysthenica* Gruner, *Cynanchica graveolens* (M. Bieb. ex Schult. & Schult. f.) P. Caputo & Del Guacchio subsp. *leiograveolens* (Popov & Chrshan.) P. Caputo & Del Guacchio (≡ *Asperula graveolens* M. Bieb. ex Schult. & Schult.f. subsp. *leiograveolens* (Popov & Chrshan.) Pjatunina, *A. leiograveolens* Popov & Chrshan.), *Dianthus membranaceus* Borbás, *D. trifasciculatus* Kit. subsp. *pseudobarbatus* (Schmalh.) Jalas (≡ *D. pseudobarbatus* (Schmalh.) Besser ex Klokov), *Jurinea salicifolia* Gruner, etc.] are characterized mainly by their rather wide penetration into neighboring geographical zones, are coenotically confined to sandy and dry grassland (steppe) biotopes, and usually have closely related vicariant taxa (see Klokov, 1981; Fedoronchuk, 2009).

At least some supposedly North Pontic and Sarmatian endemics of the flora of Eastern Europe were probably formed as a result of hybridization (for example, *Galium* × *pseudoboreale* Klokov that probably emerged from *G. boreale* L. × *G. rubioides* L. s. l.; see POWO, 2024–onward), or are in fact ecotypic varieties, for example, *Veronica spicata* L. var. *pseudoorchidea* Pacz. (≡ *V. pseudoorchidea* (Pacz.) Klokov, incl. *V. paczoskiana* Klokov) (see Klokov, 1976; Mosyakin et al., 2023, and Albach et al., in progress). In contrast to that, *C. ucrainicum* does not have the ecological, coenotic and other features shared with the mentioned endemics (or supposed endemics) of this territory. In addition, in the temperate-continental zone of Eastern Europe, endemism is not widespread among annual plants outside the psamophytic ecological complex (see Klokov, 1981).

Another possibility to consider *C. ucrainicum* a native plant is to assume that only some part of its total but fragmented native range is known today. In this case, its distribution pattern and habitats should be similar to the habitats of some plants with disjunctive ranges that are considered relicts in the forest-steppe zone of Ukraine (for example, *Aconitum variegatum* L., *Corydalis intermedia* (L.) Mérat, *Scrophularia vernalis* L., etc.). However, the exclaves of the ranges of such plants in our flora are just remnants of specific cycles of the development of forest vegetation in previous periods, and their total ranges are rather wide and sufficiently well studied. On the other hand, native representatives of *Chenopodiaceae* in the flora of Ukraine with restricted or at least narrowly outlined ranges, for example, *Chenopodium acerifolium* Andrz. (see Uotila, Lomonosova 2016, Mosyakin, 2017), some species of the genera *Atriplex* L., *Bassia* All., *Corispermum* L., *Oxybasis*, *Polycnemum* L., etc., have florogenetic connections with representatives of the Eurasian arid flora (often called the Irano-Turanian floristic complex), and their expansion in the East European plain was mainly associated with the development of pioneer and sometimes halophytic vegetation of periglacial landscapes in the Late Quaternary (see Bezusko et al., 2006, 2011, and references therein).

Also, we may hypothesize that *C. ucrainicum* until recently remained confined to some "hidden" habitats within a restricted geographical area in Ukraine (for example, in localities of the loess outcrops and ravines along the Dnipro), where it persisted as a relict and went unnoticed by botanists until its recent expansion caused by anthropic factors. However, this hypothesis also has rather low chances to be confirmed by new evidence. First of all, the areas in the central part of Ukraine which are covered by the present-day range of *C. ucrainicum* were rather well studied by many keen collectors of the 19th and 20th centuries (see Habibi et al., 2023: 408, and discussion below) and specimens of *C. ucrainicum* are absent among the studied herbarium collections. Second, no other cases of relict taxa with similar ecological, geographical and phytosociological patterns are known in Ukraine.

Besides, our re-assessment of original specimens (syntypes) of *Chenopodium divaricatum* Andrz. (images of the lectotype and isolectotype available from JSTOR Global Plants at: https://plants.jstor.org/stable/10.5555/al.ap.specimen.kw001002777 and https://plants.jstor.org/stable/10.5555/al.ap.specimen.kw001002778), the third species of *Chenopodium* described by Andrzejowski (in addition to the currently recognized and distinct tetraploid species *C. acerifolium* and *C. betaceum*; see Andrzejowski, 1862: 132), demonstrated that this species name is definitely not applicable to *C. ucrainicum* and *C. ficifolium* (see Mosyakin, 2017: 149); an earlier assumption about its possible application to the species currently widely recognized as *C. suecicum* remains uncertain.

Contrary to the hypotheses considered above, from an ecological and coenotic point of view, *C. ucrainicum* is a synanthropic plant, and even in

the Kyiv Plateau, where this species is most widely represented, it has never been registered as part of natural undisturbed phytocenoses. This supports the initial assumption about the likely alien status of this species in the flora of Ukraine (Mosyakin, Mandák, 2020a). The features of numerous populations of *C. ucrainicum* on the eastern edge of the Kyiv Plateau, along the high right bank of the Dnipro River, in the vicinity of Rzhyshchyv town, Kyiv Region, also indicate the non-native status of the species. Here, the slopes above the Dnipro River are covered with natural broad-leaved forests, dominated mainly by *Carpinus betulus* L. However, in various places there are microrefugia where individual relict forest plants from various previous stages of the Holocene have been preserved [for example, *Cypripedium calceolus* L., *Equisetum telmateia* Ehrh., *Polystichum aculeatum* (L.) Roth, *P. braunii* (Spenn.) Fée, etc.; Kleopov, 1990]. If we assume the aboriginal origin of *C. ucrainicum*, and considering its widespread distribution in this area, its presence in phytocenoses (plant communities) together with forest relict plants should be expected. However, this was not observed at all — this species in the studied area is restricted mainly (or almost exclusively) to roads and ruderal habitats.

It should be also noted that in the Kyiv Plateau, the habitats of *C. ucrainicum* on outcrops of loess loams show some similarity with the natural habitats of the annuals *Artemisia scoparia* Waldst. & Kit. and *Atriplex oblongifolia* Waldst. & Kit., which are facultative elements of plant communities on clay and loess outcrops. However, these two species are mesoxerophytes or xeromesophytes and they grow often in less disturbed biotopes with clayey or loess outcrops, while *C. ucrainicum* is found on such a substrate mainly in shaded synanthropic places, for example on the sides of roads laying across slopes and areas planted with *Robinia pseudoacacia*.

Some biological characteristics of *C. ucrainicum* are also important that contradict its hypothetical aboriginal (native) status and origin in our flora area. First of all, the "primitive" diploid chromosome set of *C. ucrainicum* indicates its likely direct formation in some primary center of diversification of the genus *Chenopodium* s. str. (see Krak et al., 2016; Mandák et al., 2018; Mosyakin, Mandák, 2020a; Habibi et al., 2023). The morphological features of *C. ucrainicum* indicate its certain similarity to plants from other parts of the world, in particular from Southern and/or Southeast Asia (Mosyakin, Mandák, 2020a, 2020b), but this remains only an assumption to this day and requires new observations in the mentioned vast regions of Asia.

Another important biological feature of *C. ucrainicum* is the long duration of its vegetation (extended phenology), which in our flora is usually characteristic of alien species introduced from more southern regions of America and/or Asia, and this also indicates the probable alien status of this species in the flora of Ukraine (see earlier comments in Mosyakin, Mandák, 2020a, and Habibi et al., 2023). According to long-term observations of the 20th century, the average duration of the growing season (a period with an average daily temperature above 5 °C) in the central part of Ukraine lasted 210 days, on average from April 3 to October 29 (Lipinsky et al., 2003; Osadchyi et al., 2010). Thus, the average duration of vegetation of *C. ucrainicum* (about 190–230 days) slightly exceeds the average duration of the growing season in the study region. But for the successful completion of all phases of ontogenesis, the duration of vegetation of an annual plant should be usually several weeks shorter than the natural growing season. That is, the climatic conditions of the central mainland regions of Ukraine during the 20th century were mostly not favorable for the completion of the vegetation duration of *C. ucrainicum* and the realization of its full biological productivity.

In recent decades, the climate of Ukraine has been changing in accordance with the influence of the global warming trend, in particular, the average length of the growing season has significantly increased here (see Didukh, 2022; Didukh et al., 2023, and references therein). For example, the average annual temperature in Kyiv increased by 0.8 °C during the period of 1991–2008, and this trend has accelerated in recent years. In addition, there is a general warming trend of the climate of the plain part of Ukraine, which is accompanied by xerophytization (Osadchyi et al., 2010; Boychenko et al., 2016; Didukh, 2022). In connection with this, during the last 1–2 decades, the weather conditions are increasingly developing, under which *C. ucrainicum* completely undergoes its ontogenesis and realizes its biological potential under the conditions of the studied area. Therefore, its phenological features indicate that *C. ucrainicum* as a biological species is adapted to growing in climatic conditions different from those that have long been characteristic of the temperate zone of Eastern Europe. Of

course, the climatic conditions in the territory of the Forest-Steppe zone of Ukraine were not stable, and even during the Holocene there were several alternating cold and warm periods, that is, there were already periods with a relatively long growing season in this territory in the quite recent past. But the native plants of the flora of the plain of Ukraine are adapted precisely to the average growing season duration and conditions that were mainly observed in the 20th century. Even the most late-flowering plants of the Ukrainian native flora (for example, *Erigeron acris* L. and *Hieracium umbellatum* L.) usually end their vegetation in September. Other species of the genus *Chenopodium* present in the flora of Ukraine also have a much shorter duration of their vegetation, although most of them are alien species here.

As we (Mosyakin and Shynder) have mentioned earier (in Habibi et al., 2023: 408), our special search in collections of several Ukrainian herbaria, first of all the National Herbarium of Ukraine (KW), failed to reveal even a single specimen of *C. ucrainicum* collected in Ukraine or elsewhere before our collections. It is hard to believe that such a distinctive and rather locally abundant species evaded attention of many experienced collectors of the Ukrainian flora for so long during the 19th and 20th centuries, such as W.S.J.G. Besser, A. Andrzejowski, V.M. Czernjaiew (Cherniaiev), A.S. Rogowicz (P.S. Rogovich), I.F. Schmalhausen, M.V. Klokov, S.S. Kharkevich, and many others. We concluded that "that absence of *C. ucrainicum* in earlier herbarium collections can be considered additional indirect evidence of the alien status of the species in Ukraine" (Habibi et al., 2023: 408).

Although most of the considered arguments indicate the alien status of *C. ucrainicum* in Central Ukraine, its native status still cannot be excluded as one of working hypotheses. Further search for new areas of distribution and spread of *C. ucrainicum* and new experimental studies may shed additional light upon the mystery of its origin.

Hypothetical native range

If the assumptions about the alien status of *Chenopodium ucrainicum* in the flora of Ukraine are correct, then the native range of this species is outside Europe, namely, probably in some southern or southeastern region of Asia with a mild moderately humid climate and a growing season longer than in the temperate zone of Europe. One of the centers of genetic diversity of the genus *Chenopodium* is located here, but the taxonomic study of its local representatives remains incomplete (see comments and references in Mosyakin, Mandák, 2020b). The tolerance of *C. ucrainicum* to low temperatures is an important feature, which can to some extent reveal the peculiarities of the hypothetical native range. Obviously, it cannot be equatorial and tropical climatic zones, in which there are no frosts. But it is probably the territory of South or Southeast Asia with temperate continental conditions, possibly some low-mountain regions. This assumption can be confirmed only after the (still hypothetical) discovery of plants identical to (or at least closely related to) *C. ucrainicum* in the specified area.

Characteristics of the expansion of *Chenopodium ucrainicum* in the Ukrainian flora

If we consider *C. ucrainicum* as a presumably alien species in the flora of Ukraine, there are reasons to assume that it was probably introduced to Ukraine in the second half of the 20th century. At that time, economic and military-political ties of the former USSR were established with some countries of South and Southeast Asia. In Hrebinky, its colony existed already in the end of the 1980s, and the presence of an elevator and a sugar beet processing factory in this settlement tentatively indicates that the introduction could be related to grain, for example, rice or corn, or it could be just a coincidence. During this period of great political changes in Eastern Europe, many new alien plants were introduced into Ukraine (see, e.g., Mosyakin, 1991) and the expansion of *C. ucrainicum* fits well into this trend. But at the end of the 20th century the climatic conditions of the plain part of Ukraine probably did not contribute to the spread of this species, and for a certain time *C. ucrainicum* remained at the stage of establishment as a colonophyte in the place (or places) of its initial introduction. This model of development of the secondary range is rather typical for invasive plants (see Mosyakin, 1996a). Closer to our time, during the latest decade, as a result of the significant warming of the climate, *C. ucrainicum* acquired significantly greater opportunities to realize its biological potential, and thus entered the stage of expansion.

Observations indicate that *C. ucrainicum* is quite easily established in new habitats under favorable conditions, for example, in the backyard of the M.G. Kholodny Institute of Botany and on some plots of the M.M. Gryshko National Botanical Garden

(both institutions are located in the central part of Kyiv City). This may also support the conclusion that *C. ucrainicum* is probably a xenophyte and neophyte in the studied area and is currently at the stage of invasive dispersal.

In connection with this, a question arises regarding the place of initial introduction of *C. ucrainicum* in Ukraine. Known materials indicate that the primary place of settlement is the southern part of Kyiv Region, but at least a decade later, this species was also recorded in Ostroh, Rivne Region. In addition, the high density of localities of *C. ucrainicum* along the right bank of the Dnipro River indicates that there could also be primary centers of introduction of this species in this area, for example, near the river ports on the Dnipro River (in Trypillya village and Rzhyshchiv town, Kyiv Region, and/or Kaniv City, Cherkasy Region). There are many optimal habitats nearby, where the species was successfully established. To a certain extent, the current dynamics of the expansion of *C. ucrainicum* is confirmed by the restriction of its habitats to areas with more active traffic. Thus, between Rzhyshchiv and Kaniv, the natural conditions along the right bank of the Dnipro River are quite similar, but the degree of modern anthropogenic load in different areas differs significantly. In the sparsely populated territory of the Trakhtemyriv Regional Landscape Park (at the border between Kyiv and Cherkasy regions), we found only one location of *C. ucrainicum* in Velykyi Bukryn village, which is quite close to the Kyiv–Kaniv highway. On the other hand, in the more remote corners of the Trakhtemyriv Landscape Park, where the natural conditions resemble the outskirts of Rzhyshchiv, but there is no active economic activity, this species have not been detected at all. So, now here, as in other regions, there is a gradual expansion of the range of *C. ucrainicum* from busier highways and populated areas to sparsely populated areas. The main likely way that ensures the transfer of diaspores (seeds) of this species is automobile or agricultural transport.

In the near future, it is expected that *C. ucrainicum* will continue its expansion in the territory of Ukraine within the forest-steppe zone (primarily in the central and western parts of the country) and adjacent territories of the forest zone, where there are optimal habitats and a moderately humid climate. Therefore, it is promising to search for new localities of *C. ucrainicum* in the Volhynian-Podolian Upland, Prykarpattia (Cis-Carpathian area), the Carpathians, as well as in some areas in the Poliska (also Polissia, Polesian) Lowland. Presumably, *C. ucrainicum* will penetrate (or has already penetrated) certain habitats in the Left-Bank Forest-Steppe zone of Ukraine; however, the expansion of this species to the east of the Dnipro River is less likely due to the presumably less suitable local ecological and coenotic conditions in this area (see above). The wide expansion of *C. ucrainicum* in the steppe zone is also unlikely, although within the urban zones of large and medium-sized cities and towns in the southern part of Ukraine this species may well find favorable ecological niches for the formation of colonies, if actually introduced. In the more distant future, there are prospects for the penetration of *C. ucrainicum* into the territory of the northern regions of Romania and Moldova, Poland, and some other Central European countries.

Conclusions

According to the results of the study presented here, it has been established that the newly described diploid species *Chenopodium ucrainicum* has a local distribution range in the central and western regions of Ukraine. That range consists of three fragments in the natural regions — the Dnipro Upland (the main fragment), the Podillia (Podolian) Upland, and Male Polissia. In total, *C. ucrainicum* was found in 95 separate geographical locations, although in some areas of its range, the distribution is almost continuous. According to natural zoning, the discovered range of *C. ucrainicum* is confined to the Forest-Steppe zone and the southern strip of the Mixed-Forest (Polissia) zone.

It has been found that all habitats of *C. ucrainicum* are synanthropic. The ecological and phytosociological analysis demonstrated a significant participation of this species in the formation of the summer-autumn aspect of groups of ruderal trampled vegetation and secondary anthropogenic forests and tree plantations. A new association of forests with Black Locust (*Robinia pseudoacacia*) was described, where the diagnostic species is *C. ucrainicum*: *Chenopodio ucrainicae-Aceretum negundi* ass. nov.; alliance *Balloto nigrae–Robinion pseudoacaciae* Hadač et Sofron 1980; class *Robinietea* Jurko ex Hadač et Sofron 1980.

In relation to environmental factors, *C. ucrainicum* is a rather demanding eutrophic and mesophytic species. Sufficient moisture supply, the content of

nutrients in the substrate and its moderate alkaline reaction are probably quite important limiting factors for the spread of the species in certain regions.

Phytogeographical, ecological-cenotic and biological characteristics of *C. ucrainicum* and some other facts do not confirm its possible aboriginal origin in the studied range. Therefore, there are reasons to assume that this is an alien plant in the flora of Ukraine (and, presumably, in Europe in general), a xenophyte and neophyte. Its geographical distribution pattern does not indicate its possible endemism, but is probably the result of a recent accidental introduction, or several immigration events, which could have happened in the territory of Kyiv Region in the second half of the 20th century, probably with imported grain or other agricultural goods. Our analysis of the spatial structure of the currently known range of *C. ucrainicum* shows that this species is now at the stage of expansion. This is most probably facilitated by the significant warming and extension of the growing season in recent years. Due to that, *C. ucrainicum* is now able to more fully realize its biological potential. The hypothetical region of origin of *C. ucrainicum* may be located in the temperate or partly subtropical zones of southern or southeastern Asia, where some centers of genetic diversity of the genus *Chenopodium* is located.

However, the native status *C. ucrainicum* in the flora of Ukraine has not been reliably excluded. Further search for new localities of this still enigmatic species in Ukraine, in Europe, and in Eurasia in general, in combination with molecular phylogenetic and probably phylogeographic studies, will enable us to solve the enigma of its geographical origin and will clarify the role of this diploid in the complex evolutionary patterns of the polyploid species complex of *Chenopodium album* sensu latissimo.

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ETHICS DECLARATION

The authors declare no conflict of interest.

SUPPLEMENTARY MATERIALS

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Загадковий диплоїд *Chenopodium ucrainicum* (*Chenopodiaceae* / *Amaranthaceae* s. l.): географічні, екологічні та фітосоціологічні особливості як свідчення його походження

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Реферат. *Chenopodium ucrainicum* (*Chenopodiaceae* / *Amaranthaceae* s. l.), нещодавно описаний диплоїдний вид, наразі відомий лише в Україні. Це добре окреслений, але досі загадковий елемент української флори. За результатами хорологічних та еколого-ценотичних досліджень, проведених упродовж 2021–2024 років у центральних та західних областях України, представлено узагальнені відомості про географічне поширення *C. ucrainicum*, екологічну приуроченість його місцезростань і фітосоціологічні особливості. Відомий нині ареал *C. ucrainicum* має фрагментований характер, зі скупченнями локалітетів на Придніпровській височині, у Малому Поліссі та на Подільській височині. Характер розповсюдження вказує на переважне його поширення у синантропних місцезростаннях із помірним зволоженням (придорожні смуги, рудеральні ділянки, узлісся, затінені ділянки в антропогенних лісах та міських парках), а присутність *C. ucrainicum* у вторинних біотопах свідчить про його ймовірний статус як адвентивного (чужорідного) виду в Україні. Було зафіксовано високе проєктивне покриття виду у рудеральних угрупованнях за участю *Acer negundo* та *Robinia pseudoacacia*, де *C. ucrainicum* часто відіграє домінуючу роль у трав'яному ярусі. Описана нова асоціація *Chenopodio ucrainicae-Aceretum negundi* ass. nov., що підкреслює діагностичну цінність виду в рудеральних та антропогенних рослинних угрупованнях. В екологічному відношенні *C. ucrainicum* характеризується як довговегетуючий мезофіт, що відзначає його пристосованість до теплішого клімату з подовженим вегетаційним періодом. Його фенологічний ритм і стійкість до порівняно низьких температур вказують на ймовірне походження із більш південних регіонів зі схожими кліматичними умовами. Незважаючи на високу адаптивність у межах виявленого поточного ареалу, що узгоджується з актуальними тенденціями потепління клімату в Україні, відсутність цього виду в історичних гербарних колекціях підтверджує гіпотезу про те, що *C. ucrainicum* є відносно недавнім іммігрантом. Висловлено припущення, що його природний ареал може знаходитися в помірних або субтропічних регіонах Південної або Південно-Східної Азії, де знаходяться центри генетичної різноманітності роду *Chenopodium*. Подальші молекулярно-філогенетичні та філогеографічні дослідження будуть важливими для підтвердження фактичного географічного походження *C. ucrainicum* та еволюційної ролі в алополіплоїдному комплексі *Chenopodium album* s. l. Отримані результати дали цінну інформацію про сучасне поширення та еколого-ценотичні характеристики *C. ucrainicum* і частково підтвердили його ймовірний статус як неофіта, який розширює свій ареал на території України під впливом кліматичних змін та антропогенного впливу.

Ключові слова: біорізноманіття, комплекс *Chenopodium album*, кліматичні зміни, флора, розширення ареалу, таксономія, Україна