Typha Laxmannii (Typhaceae) in Ukraine: Current Distribution, Ecological and Coenotic Pecularities, Invasiveness

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Research Article

Keywords: alien species, chorology, ecology, vegetation, Typha laxmannii, Ukraine.

Posted Date: May 23rd, 2023

DOI: https://doi.org/10.21203/rs.3.rs-2947977/v1

Version of Record: A version of this preprint was published at Biologia on March 19th, 2024. See the published version at https://doi.org/10.1007/s11756-024-01642-4.

Abstract

The results of complex investigations of *Typha laxmannii* Lepech (Typhaceae) in Ukraine are presented. The information on the history and modern distribution of the species, its ecological and phytocoenotic peculiarities are summarized. It is a perennial herbaceous plant, alien species of Asian origin which is characterized by a progressive type of range in the country. For the first time in the flora of Ukraine *T. laxmannii* (under the name *T. stenophylla* Fisch. ex Mey.) was recorded in 1902 in the south of Ukraine (Kherson Oblast) by Paczosky. Maps of distribution of the species was prepared on the basis of Ukrainian Herbaria, literature sources and electronic databases. Distribution took place in the northern, eastern and western directions as a hydrochore and anemochore. Now the species is distributed almost throughout Ukraine, but with a majority of records in the central and western parts of Ukraine. The association *Typhetum laxmannii* formed by this species is common for Ukraine. Depending on the ecological and geographical conditions and floristic composition, 3 following variants in this association were identified: var. *typica*, var. *T. latifola,* and var. *Schoenoplectus lacustris*. Coenoses within this association are distributed almost throughout the whole territory of Ukraine, but the ecological optimum of the species coenotic area is observed in the South of the country, in the Steppe zone, on slightly saline, well-watered substrates. Based on studies conducted in Zhytomyr Oblast in 1995–2021, the expansion rate of *T. laxmannii* was calculated – from the South to the North – in average 16.6±1.09 km·year^{-1}. From the sites of the primary penetration of the species into the region (Forest-Steppe zone), the expansion rate of it toward to the North was significantly lower (7.7–9.0 km·year^{-1}) compared to that in the Forest zone – Ukrainian Polissia (23.4–31.9 km·year^{-1}).

Introduction

Graceful cattail **(***Typha laxmannii* Lepech., Typhaceae) is a perennial herbaceous plant, hemicryptophyte, mesohygrophyte, alien species of Asian origin. It is characterized by a progressive type of range in Eurasia and North America. Like some other alien species in Europe, this species is now increasingly involved in floodplain ecosystems which are characterized by high biodiversity, high dynamics of their ecological conditions, and man-caused load (Schindler et al., 2016). In the Czech Republic, its status is assessed as a naturalized neophyte (Pyšek et al., 2012); in Hungary, it belongs to invasive alien species (Balogh et al., 2005); in Poland, it is an expansive or potentially invasive species (Nobis et al., 2006). In Ukraine and Belarus *T. laxmannii* is considered to be a species that has invasive potential (Dubovik et al., 2020). At the same time, the species was included in the European Red List of vascular plants with the LC category. In Serbia, for example, the species is rated as NT category (Jenačković-Gocić, 2020); and in some regions of Ukraine the plant communities with its participation are assessed as regionally rare (Lukash, Danko, 2019). Its aesthetic features and the possibility of using it as an industrial plant were reported (Lower, 2021).

The primary range of T. laxmannii. A. Kuzmychev (1992) assumed that *Typha laxmannii* has an ancient Mediterranean range. According to other sources (Dubovik, 2013; Krasnova, 2011), *T. laxmannii* is characterized by a wide Eurasian range. In the European part of a primary range the species is confined to the Steppe zone of Ukraine (Krasnova, 2011) and other south-eastern regions of Europe: Albania, Greece, Bulgaria, Romania, South and East of European part of Russia, East of European Russia, North Caucasus (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:836872-1). In the Asian part of its primary range, the species is known mainly in the temperate zone, and less in the subtropical one: Afghanistan, Altay, Azerbaijan, Buryatiya, China North-Central, China South-Central, China Southeast, Inner Mongolia, Iran, Japan, Kazakhstan, Far East (Khabarovsk, Primorye, Amur), Kirgizstan, Korea, Manchuria, Mongolia, Pakistan, Qinghai, Sakhalin, Tadzhikistan, Transcaucasus, Turkey, Turkmenistan, Tuva, Uzbekistan, West Himalaya, West Siberia, East Siberia (Chita, Krasnoyarsk, Irkutsk, Yakutiya), Xinjiang (Fiala, Jankovská, 1968; Sun, Simpson, 1992; Nobis et al., 2006; https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:836872-1).

The secondary range of T. laxmannii. Outside its natural range, the species is known in Europe, North America, Australia and New Zealand. (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:836872-1). Also, it was noticed (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:836872-1) that the species was introduced into

Czechoslovakia, France, Germany, Great Britain, Hungary, Italy, Poland. Its first record in Europe dates from 1889 in Dobrudja (Romania), and later in Greece (Kronfeld, 1889; Halacsy, 1902; Schuler, 2007). The species was recorded for the first time in Ukraine in 1902 (Paczosky, 1902), in Russia – probably since the 1930s. (Krasnova, 2011). In the second half of the XX century, the species was indicated: in former Czechoslovakia (Fiala, Jankovská, 1968; Čvančara, Šourkova, 1973; Dubyna et al., 1993, Pyšek et al., 2012), France (Guinochet, de Vilmorin, 1978), Italy (Pignatti, 1982), Great Britain (Sell P.D. & Murrell, 1996), Belgium (Seebens et al., 2017), the Netherlands (Van der Meijden, 2005), Slovakia (SoC, 1980), Germany (Oberdorfer, 1990), Poland (Zajac et al., 1998; Baryla et al., 2005), Hungary (Balogh et al., 2005), Austria (Melzer, Barta, 1993), Slovenia (Kaligaric, Jogan, 1996), Croatia (Topić, Ozimec, 2001; Šegota et al., 2013), Serbia (Tomović et al., 2020), Albania (Demiri, 1983). In 2000, the species was found in Belarus (Dubovik, 2013); additionally, the author noted that the species is actively spreading toward the North and has already reached the 60ºof the North latitude.

The expansion of the species, in addition to the spontaneous one, is also associated with the cultivation and subsequent distribution from nurseries where plants were mistakenly identified as *T. minima* or *T. angustifolia* (Bernhardt, Wernisch, 2016).

Ways of expansion and life strategy of T. laxmannii. In riparian habitats, the initial settlement of vacant ecological niches by *T. laxmannii* occurs mainly by anemochoria (Shipley et al., 1989; Soons, 2006). The species produces a significant number of one-seed fruits (achenes) with long perianth bristles, that are easily dispersed by wind over long distances (Rasran et al., 2021). It was found that the productivity, viability, and germination of achenes in *T. laxmannii* are higher than in *T. latifolia*; however, the weight of seeds is significantly less (approximately in 2.5 times). Thus, a longer distance of the flight and a higher life span of achenes in *T. laxmannii* are important factors contributed to the spread of the species over long distances (Rasran et al., 2021). After rooting in a favorable econiche, the species firmly holds it due to rapid clonal growth, increased phytomass, and the ability to develop monodominant communities (Bansal et al., 2019). Apical stem buds on the rhizome in *T. laxmannii* are formed at intervals of 5–7 cm, which ensures the formation of dense thickets of the species: 150–200 ramets per m^2 (Plachy, 2017; Rasran et al., 2021). Thus, the generative strategy of *T. laxmannii* consists of a combination of seed propagation providing the long-distance dispersal of the species and vegetative expansion (Grime et al., 1988), which is crucial for holding the occupied econiches and a spread of the species to the adjacent sites. Such mechanism makes the studied species potentially invasive (Nobis et al., 2006).

The species also was noted (Dubyna et al., 1993; Landucci et al., 2013) often growing in ecotopes with variable moisture during the growing season. It has been demonstrated (Kapytonova et al., 2012) that the strategy of the geographical expansion of *T. laxmannii* consists of its invasion in arid and subarid areas with subsequent spread to more northern temperate regions. The species has evolved toward its adaptation to the temporary drying habitats and widening the ecological amplitude, in particular, an increase in the salt concentration in water and substrate.

Like other members of the genus *Typha*, *T. laxmannii* is considered to be anemochore (Shipley et al., 1989; Soons, 2006; Dubovik, 2013; Krasnova, 2011; Rasran et al., 2021). In addition, the seeds of the species are easily transferred by water flows, i. e. they spread by hydrochory (Dubyna and Shelyag-Sosonko, 1989; Krasnova, 2011; Aronson et al., 2017). Zoochory is known as a mechanism for the upstream dispersal of macrophytes in rivers (Figuerola & Green, 2002; Coughlan et al., 2017). Information on the possibility of epi-ornithochory in this species was published (Vasyukov, Novikov, 2017). At the same time, the seed dispersal on the waterfowl feathers and legs to considerable distances was noted to be possible along the Danube River valley as one of the most powerful routes of seasonal bird migration in Europe.

Recreational activity in growing areas of *T. laxmannii* can also contribute to the spread of its diaspores, including seeds and rhizoma pieces. For instance, seeds of this species can easily stick to the boat sides and boat equipment that promotes the transport of diasporas to other water bodies (Johnson et al., 2001; Rothlisberger et al., 2010; Kelly et al., 2013).

Ecological and coenotic features of *T. laxmannii* within the range of its current expansion were described in a number of publications. In the secondary range in Europe, the species grows in unformed plant communities, and also it forms

Typhetum laxmannii association by being dominant (Ubrizsy. 1961; Nedelcu, 1968). Researchers noted that the species is characterized by a wide ecological amplitude (Krasnova, 2011; Felbaba-Klushina, 2009). It grows from fresh (Dubyna, Shelyag-Sosonko, 1989; Topić, Ozimec, 2001) to brackish (Durnikin, 2014; Baryla et al., 2005; Watson and Philip, 1985) and highly saline waters (Pykhalova et al., 2013; Woch and Trzcinska-Tacik, 2014), in coastal biotopes with surface or soil flooding, in shallow waters (with a depth of 10–40 cm) of eutrophic, mostly stagnant or weakly running water bodies (Dubina et al., 1993; Chernaya, 2013; Plachy, 2017; Rasran et al., 2021).

In Ukraine, the following ecotopes of *T. laxmannii* growth were recorded (Dubyna et al., 1993): floodplains (in the lower parts of deltas of the Dnieper and Danube rivers), coastal freshwater areas, in particular reservoirs (the Kremenchuk Reservoir located on the Dnieper River), shallow waters of the Kodyma, Vorskla, Bazavluk, Ingul rivers, coastal areas of the upper reaches of estuaries (Molochny, Berezansky estuaries), brackish lakes (Cahul, Yalpug lakes, etc.), banks of river oxbows (the Siverskyi Donets, the Southern Bug rivers), banks of estuaries and saline lakes (Sivash lake), pond banks (in the Steppe), and various quarries.

Researchers noted that in new regions *T. laxmannii* is confined mainly to secondary, anthropogenically transformed habitats (Baryla et al., 2005; Kapitonova et al., 2012; Woch and Trzcinska-Tacik, 2014 et al.), in particular, to ephemeral reservoirs (Kapitonova et al., 2012); sand quarries in Croatia (Topić and Ozimec, 2001) and Udmurtia (Dyukina and Kapitonova, 2005); clay and dolomite quarries in Poland (Baryla et al., 2005); salt quarries in the Carpathian region of Ukraine [Felbaba-Klushina, 2009; Woch and Trzcinska-Tacik, 2014); coal dumps in Poland (Woch et al., 2013); reclaimed areas after peat extraction in the Ukrainian Polissia (Balashev, 1981). In addition, this species was recorded as growing in roadside ditches and side drains, as well as in other various anthropogenic habitats of settlements (Dyukina and Kapitonova, 2005).

In relation to the soil richness and acidity, *T. laxmannii* also shows a wide amplitude: it grows on poor sandy soils (Dukina and Kapitonova, 2005; Baryla et al., 2005; Topić and Ozimec, 2001); granite grit (Kochjarova et al., 2013), gravel (Dyukina and Kapitonova, 2005), or peat (Balashev, 1981) which have an acidic reaction; clays and dolomites (Baryla et al., 2005) which cause the soil acidity to the range from neutral to alkaline.

The researchers put a special focus on the growth of the studied species within a wide range of watering of biotopes. Thus, in the Volgograd Reservoir on the Volga River, *T. laxmannii* is a component of the vegetation of coastal deep-water sites (Ochetkova, 2013). But the majority of researchers reported that this species grows mainly in shallow coastal waters (Dubina et al., 1993; Plachy, 2017; Krasnova, 2011).

The purpose of the work was to summarize the available data on the current spread of the species in Ukraine; to reconstruct the main stages and ways of *T. laxmannii* introduction in the country; to study the ecological and phytocoenotic confinedness of the species; to find the leading factors of ecological differentiation of plant communities with the participation of the species; to evaluate the expansion rate of the species from south to north of Ukraine on the base of GIS-modeling (on the example of one of the regions where the species is well studied and actively spreading).

Material and methods

The study of *T. laxmannii* is based on critical analysis of herbarium data, literary and DB sources, and the data of field studies carried out by the authors. We analyzed the following herbarium collections: Herbarium of M.G. Kholodny Institute of Botany, NAS of Ukraine (*KW*), Herbarium of M.M. Grysko National Botanical Garden, NAS of Ukraine (*KWHA*), Kryvyi Rih Botanical Garden, NAS of Ukraine (*KRW*), Institute of Ecology of the Carpathians, NAS of Ukraine (*LWKS*), Yu. Fedkovych Chernivtsi National University (*CHER*), Taras Shevchenko National University of Kyiv (*KWU*), I.I. Mechnikov Odesa National University (*MSUD*), Oles' Honchar Dnipro National University (*DSU*), V.N. Karazin Kharkiv National University (*CWU*), Kherson State University (*KHER*), *MW* electronic herbarium. The *T. laxmannii* distribution map, based on the herbarium, DB (i-

Naturalist, UkrBIN, Plantarium) data, and locations identified in the descriptions, was designed in MapInfo Professional Version 7.0 software.

The taxonomic nomenclature for vascular plants follows the Euro + Med Plant Database (Euro + Med 2021). The syntaxonomic nomenclature is unified according to Dubyna et al. (2019) with consideration of the results obtained by Mucina et al., 2016.

Descriptions with the presence of the species were made by the authors according to the standard method. Phytosociological data for the development of syntaxonomy consists of 154 relevés made mainly by the authors, as well as given in literary sources for the territory of Ukraine. Own descriptions (15 relevés.) were made during 2004–2021 mainly on plots of standard size 4x4 m, according to the Braun-Blanquet approach to floristic classification (Westhoff & van der Maarel, 1973; Whittaker, 1978). The data included relevés given in publications (Dubyna, 2006 (36 relevés); Chorna, 2013 (5); Lukash, Danko, 2020 (2); Korzhenevsky, Klyukin, 1990 (5); Voityuk, 2005 (4); Umanets et al., 2001 (2); Woch, Trzcinska-Tacik, 2014 (2); Galchenko, 2006 (2); Shevchik, Solomakha, Voityuk, 1996 (1). The database also included unpublished relevés from manuscripts and dissertations kindly provided to us by A. Kazarinova (11 relevés), D. Vynokurov (18), V. Kolomiychuk (5), V. Konogray (5), L. Borsukevich (11), Chinkina (4), M. Prokopuk (7), O. Kuziarin (6), L. Felbaba-Klushina (9), S. Yemelyanova (3), M. Kozyr (1).

The materials were organized by creating a database of geobotanic relevés in TURBOVEG 2.79 format (Hennekens & Schaminée, 2001). Interpretation of the phytosociological analysis was carried out using the JUICE 7.0.83 software package (Tichý, 2002), in particular Hierarchical Cluster analysis, PC-ORD. The Sörensen coefficient (Sörensen, 1948) was chosen as an index of similarity, and the grouping of relevés was carried out using the beta-flexible method at -0.25. The cutoff level for “pseudospecies” was 0, 5, 15, 25%. Diagnostic species of syntaxons were determined in accordance with the values of *phi* coefficient (Willner et al., 2009), which threshold values were assumed to be 0.25. All description groups were standardized to the same size, and non-significant accuracy values were also extracted based on Fisher’s exact test.

To identify the position of syntaxons in the ecological space, the DCA ordination method (Hill & Gauch, 1980; Ter Braak & Smilauer, 2015) of the R-project program (Venables & Smith, 2008) was used. The calculation of ecological parameters was carried out according to Ya.P. Didukh’s phytoindicative scales (Didukh, 2011) by 12 following factors: soil water regime (Hd), variability of damping (fH), soil aeration (Ae), nitrogen content in the soil (Nt), soil acidity (Rc), salt regime (Sl), carbonate content in the soil (Ca), thermoclimate (Tm), climate humidity (Om), continentality of climate (Kn), cryoclimate (Cr) and light intensity (Lc). A cyclogram of amplitudes of ecofactors was constructed using STATISTICA 10.0 software.

Calculation of *T. laxmannii* expansion rate and the directions of its expansion was carried out for the territory of the Zhytomyr Oblast as one of the best floristically studied regions in Ukraine. All known localities of the studied species within the region were grouped according with the time of their finding. Then, their geographical coordinates were defined using the open Google Earth program, and their localities were plotted on a vector map. On the basis of this database, the dates of *T. laxmannii* expansion within the region were interpolated, and the corresponding isolines were constructed. In this case, the method of IDW (inverse distance weighting) was applied. In this method, the value for each cell is limited by the range of values used for interpolation (Lam, 1983). The IDW method finds the average value based on the weighted distance to reference points, so the average value cannot exceed the maximum input value and cannot be smaller than the minimum value (Watson and Philip, 1985). However, this method cannot be used to extrapolate data outside the range of the given points. After visualization and construction of isolines, further analysis of the results was performed.

Studies of the species phytomass productivity were carried out with specific hydrobotanical methods (Katanskaya, 1981). Phytomass was determined in monodominant phytocoenoses by the method of collection of aboveground phytomass on 1 m^2 experimental plots. The weight method was used to determine the raw weight, air-dry weight, and absolute dry weight (after drying in a thermostat at a temperature of 110ºC for 24 hours). Phytomass stocks of the species were calculated by multiplying the average phytomass per 1 m^2 by the area of phytocoenoses in the studied region and the entire reservoir.

Some statistical calculations were carried out in Excel using stantard methods (Lakin, 1973).

Results

As a result of the study, the primary localities were clarified, the main time stages and directions of distribution were reconstructed; information on *T. laxmannii* current expansion and ecological and phytocoenotic confinedness in Ukraine were summarized.

Distribution of T. laxmannii in Ukraine. For the first time in the flora of Ukraine *T. laxmannii* (under the name *T. stenophylla* Fisch. ex Mey.) was recorded in 1902 in the south of Ukraine (Paczosky, 1902), in the valley of the Dnieper River, in the Kizomys village of the Kherson Oblast, some later than the time of its first registration in Europe. According to data from the *KW* Herbarium, in the 20s–30s of the XX century the species was recorded in the southern and central regions of Ukraine: in 1923 in the Kherson and Donetsk Oblasts, in 1927 in the Zaporizhia Oblast, in 1928 in the Mykolaiv Oblast, and probably in the late 30s of the XX century in the Poltava Oblast, and in 1936 – in the Luhansk Oblast. The next stage (characterized by the expansion of the species' range in the central and southern regions of Ukraine, as well as the formation of its new localities) occurs in the late 60s – early 70s of the XX century. In particular, in 1965 the species was first reported in the Odesa Oblast, in 1966 in the Dnepropetrovsk Oblast, in 1971 in the Kyiv Oblast, and in 1972 in the Cherkasy Oblast and in Crimea. The spread of the species toward the north was facilitated by the construction of reservoirs on the Dnieper River and irrigation systems in the Steppe and Forest-Steppe, drainage of swamps, and the functioning of a significant number of quarries in the Forest-Steppe and Polesie. Since the late 70s of the XX century, the species has still spread in the western, northern, and north-eastern directions, and now, with the exception of the Sumy Oblast, it is known in all regions of the country.

Information on the first findings of the species in administrative regions of Ukraine according to herbarium collections is shown in Table 1. The first finding of the species in Ukraine is given according to the publication of J. Paczsoski (J. Paczsoski, 1902).

Table 1
The first findings of *Typha laxmannii* in administrative regions of Ukraine

Region of Ukraine	**Year of the first record**	**Records**	**Sources**
Kherson	1902	Kherson Oblast, Biloozersky District, village Kizomys	J. Paczsoski (1902)
Poltava	1920 (1930)	Poltava Oblast, Kremenchuk District, station Potoky. On the bank of firth among salines. Yu.D. Kleopov	KW
Donetsk	1923	Donetsk province, near Taganrog city, vicinities of station Uspenskaia, sovkhoz № 6; khutors № 2 and № 3, bottom of Samara beam, near pond. 09.08.1923, E. Lavrenko	KW
Zaporizhzhya	1927	Zaporizhzhya Oblast, Melitopol Okrug, Novotroitsk District, to the west from vil. Novo-Mikhailovka, near khutor № 7, bog near the artesian well (dense thicket of *Typha*). 14.08.1927. F. Levina	KW
Mykolayiv	1928	*As Typha stenophylla* F. et Mey. Mykolayiv Oblast, vicinity of Mykolayiv city. Flood-plaine shore of Pivdennyi Bug River (near kaleyards). Big group. 29.07.1928. P. Opperman	KW
Lugansk	1936	*As Typha stenophylla* F. et Mey. Lugansk Oblast, Stanichno-Lugansk District, vil. Stanitsa Luganska, in depression of saline. 06.09.1936. N. Bilyk	KW
Odesa	1965	Odesa Oblast, Kiliysky District, marine spit Hneush. 10.09.1965. M.V. Klokov	KW
Dnipro	1966	Dnipro Oblast, Dneprodzerzhynskoe reservoir, lower part, left bank. Reservoirs behind the embankment in the area of former vil. Pankovka. 09.08.1966. K. Zerov	KW
Kyiv	1971	Kyiv Oblast, Kyiv city. Near Big Ring Road, behind the Exhibition, on swampy bottom of ditch. 07.08.1971. M.M. Bortnyak	KW
Cherkasy	1972	Cherkasy Oblast, vil. Zhovnin, Kremenchug reservoir, island Zhovnin. Leg. K. Zerov, 16.08.1966; det. A. Krasnova, 02.07.1972	KW
Ivano-Frankivsk	1977	Ivano-Frankivsk Oblast, vic. Kalush city. Industrial ditches. 13.07.1977. V.P. Tkachyk	KW
Kharkiv	1978	Kharkiv Oblast, Chuguev District, vil. Kitsevka. Sandy meadow. 03.09.1978. L.I. Kritskaya	KW
Lviv	1987	Lviv Oblast, Yavoriv District. In riparian communities of ponds-sumps of Yavoriv sulfur combine. 21.07.1987. O. Kahalo	LWKS
Vinnytsia	1987	Vinnytsia Oblast, vicinities of Kalynivka city. In small depression on the meadow. 28.09.1987. V.M. Virchenko	KW
Zhytomyr	1995	Zhytomyr Oblast, Chudniv District, thouthern-west vicinities of village Ivanopil, swamp-saucer on pasture in floodplain of Teteriv river. 11.07.1995, O.O. Orlov	KW
Chernivtsi	1999	Chernivtsi Oblast, Storozhyntsi District, vil. Zavoloka, site «Pidokrug», quarry. 20.07.1999. I.I. Chorney	CHER
Transcarpathia	1999	Transcarpathia Oblast, Volovetsky District, vic. of village Pidpolozzya, valley of Latorytsia river, meliorative chanell near crossing of highway and high voltage line	Kish, Oleksyk, 1999
Khmelnytsky	2001	Khmelnytsky Oblast, Kamianets-Podilsky city, neighborhood Zhovtnevy. Left bank of Smotrych river, on mound of clay. 28.05.2001. N.V. Skibitska	LWKS
Chernihiv	2011	Chernihiv Oblast, Chernihiv city, Liskovytsky sandy quarry, near water. 07.08.2001. L.V. Zavialova	KW

Region of Ukraine	Year of the first record	Records	Sources
Volyn	2006	Volyn Oblast, vic. village Vetly, near lake Rogizne, on meadows. 19.07.2006. Ya.P. Didukh, T.V. Fitsaylo	KW
Ternopil	2006	Ternopil Oblast, Borshchiv District, right bank of Zbruch river, near the bridge in Skala-Podilska city. 17.08.2006. L.M. Borsukevich	KW
Kropyvnytsky	2016	Kropyvnytsky Oblast, south vic. of Svitlovodsk city, right bank of Dnieper river, on the bank where species forms fragments of communities. 02.10.2016. V.P. Kolomiychuk, O.O. Senchylo	KW
Autonomous Republic of Crimea	1972	Autonomous Republic of Crimea, Soviet District, vic. of village Dmitrovka, Sivash lake, in the site of effluent of waters of North-Crimean chanel. 13.07.1972. Leg. N. Loskot; det. A. Krasnova	KW

According to the results of the analysis of data obtained from herbariums, databases, and geobotanic descriptions, 318 localities of *T. laxmannii* were identified in Ukraine. The dynamics of the number of species locations in the country during 1900–2021 is shown on Fig. 1.

The exact age determination of each record allows to approximate the dependence of a number of *T laxmannii* records from a number of years from its first finding in Ukraine (Fig. 2).

Results of the calculation presented in Fig. 2 show that the dependence of a number of *T. laxmannii* records from a number of years from its first finding in Ukraine is approximated by an exponential equation with a high level of determination (R^2 = 0,9932).

We identified 5 periods of *T. laxmannii* expansion on the territory of Ukraine (Fig. 3).

In the 1st and 2nd periods (1900–1950), the species spread rather slowly, only in the southern regions of Ukraine, mainly on sea coasts, estuaries, other reservoirs, and water-related territories. In the 3rd period (1951–1975), its expansion was associated with the construction of reservoirs of the Dnieper cascade; its gradual spread to the north along the Dnieper river is traced from reservoirs in the Steppe zone to the north in the Forest-Steppe zone (Balashev and Parakhonska, 1977). Since the late 60s of the XX century, the species has been recorded in the shallow waters of the Zaporizhzhia (the Dniprovsky) and the Dniprodzerzhinsk (now the Kamianske) reservoirs. Since the end of the 1970s, in the lower part of the Zaporizhzhia reservoir (since the formation of abrasive loess shallow waters), it has gradually formed groupings as part of the helophyte zone among ribbon-like coenoses of *T. angustifolia* (Baranovsky, 2000). Phytocoenoses of *T. laxmanii* were developed at first in shallow waters protected from wave processes (in embayments), and then spread to open shallow waters along the banks of the main water flow (Baranovsky, 2000) and in the downstream floodlands of the left tributaries of the Dnieper river, the Samara river ets. (Baranovski et al., 2021). A massive spread of *T laxmanii* on the first reservoir constructed on the Dnieper river and the involvement of its coenoses in the development of a permanent zone of helophytes occurred during the 80–90s of the XX century. In this period the average phytomass of monodominant sites of *Typhetum laxmannii* association was studied in the Zaporizhzhia reservoir (Ubrizsy, 1961; Nedelcu, 1968). It was equal to: 4653.3 ± 192.38 $g{\cdot}m^{-2}$ in row weight; 1164.9 ± 40.72 $g{\cdot}m^{-2}$ in air-dry weight; 1063.4 ± 47.57 $g{\cdot}m^{-2}$ in absolute dry weight (Baranovsky, 2000). During this period, the species produced significant stocks of phytomass in the mentioned reservoir (Table 3).

Table 3
Stocks of *T. laxmanii* phytomass in the Zaporizhzhia reservoir (1995)

Hydrological type of shallow water (by I. L. Korelyakova, 1977)	**Area, ha**	**Phytomass stocks, t·ha^{-1}**		
		raw	**air-dry**	**absolute dry**
Open	0.7	32.6	8.2	7.4
Sheltered	2.1	139.6	24.5	22.4
Total for the reservoir	2.8	172.2	36.7	29.8

The 4th stage was characterized by the active distribution of *T. laxmannii* from the Dnieper River valley in all directions on the territory of Ukraine, but mainly in the northwest. The 5th (current) stage is characterized by the expansion of this species in the western regions of Ukraine; the number of localities in the east of the country now is much smaller.

Initially, *Typha laxmanii* spreaded through water bodies and in moistened biotopes mainly spontaneously by anemochory. The movement of the species toward the north occurred mainly along the reservoirs of the Dnieper river by hydrochory, since in the lower parts of the delta wind movements of water from the southern to the northern direction sometimes prevail over the southern direction.

The representation of *T. laxmanii* in different ecotopes of Ukraine is shown in Table 4.

Table 4
Distribution of *T. laxmanii* records according to ecotope types in Ukraine

№	Ecotopes	Number of records	Part, %
1	Shores of lakes and ponds, including saline ones	55	17.30
2	Banks of rivers and streams	42	13.21
3	Swamps, including saucer-shaped swamps	41	13.20
4	Estuary banks	20	6.29
5	Reservoir banks	17	5.35
6	Wet sandbars and islands	13	4.09
7	Water bodies in salt mines	13	4.09
8	Downstream floodlands of the Danube, Dnieper, Dniester rivers, etc.	12	3.77
9	Roadside ditches	12	3.77
10	Swampy meadows	12	3.77
11	Reservoirs in clay and kaolin quarries	9	2.83
12	Swampy beam bottoms	8	2.52
13	Marshes at artesian wells	8	2.52
14	Irrigation channels	8	2.52
15	Reservoirs in granite quarries	7	2.20
16	Reservoirs in sand quarries	7	2.20
17	Open slopes with water wedging (granite, limestone, shale, clay, etc.)	7	2.20
18	Wet and swampy synanthropic landscapes	7	2.20
19	Salt marshes	5	1.57
20	Reservoirs in sulfur quarries	5	1.57
21	Reservoirs in limestone and dolomite quarries	3	0.94
22	Drainage channels	3	0.94
23	Rice fields	3	0.94
	Total	318	100.00

The data presented in Table 4 show the prevailing confinedness of *T. laxmannii* in Ukraine to such ecotopes as the banks of lakes and ponds, including saline ones; the banks of rivers and streams; swamps, including saucer-shaped swamps; the banks of estuaries; the banks of reservoirs. The total share of these 5 ecotopes reaches 55.35%. The top five ecotopes include wet sandbars and islands; reservoirs in salt quarries; downstream floodlands of the Danube, Dnieper, Dniester rivers, etc.; roadside ditches; swampy meadows where the total share of *T. laxmannii* locations is equal to 19.49%. In other ecotopes of Ukraine, the species is much rare.

The expansion rate of T. laxmannii in the Zhytomyr Oblast. The Zhytomyr Oblast is a region of Ukraine where the modern flora is studied quite well, and the expansion of *T. laxmannii* was well documented by herbarium collections. For the first time the species was recorded in the Zhytomyr Oblast in 1995; currently, more than 50 of its localities are known here.

Calculation *T. laxmannii* expansion rate in the studied region is of considerable interest, as it allows to determine the the speed of expansion of the species in the region. On the basis of the database created by us, the timing of *T. laxmannii* expansion was interpolated using GIS in the Zhytomyr Oblast (Fig. 4).

We identified and analyzed 3 transects along which the studied species hypothetically spreaded from the South to the North: 1. The A–B transect: Lyubarsky district, vicinities of Hrynivtsi vil., a swamp in the floodplain of the Sluch river (1997) – Yemilchyn district, vicinities of Kochichyne vil. (2005). 2. The C–D transect: Chudnivsky district, south-west vicinities of Ivanopil vil., saucer-shaped swamps on the meadows in the floodplain of the Teteriv River (1995) – Ovrutsky district, Antonovichi vil. (2007). 3. The F–G transects: Berdychiv district, south vicinities of Hryshkivtsi vil. (1999) — Ovrutsky district, south vicinities of Ovruch city, saline marsh meadow (2011).

Below is a detailed analysis of the data obtained from the above-mentioned transects. The A–B transect has a length of 149.6 km, and the duration of *T. laxmannii* expansion along it is 8 years (1997–2005). Thus, the average expansion rate of this species along the such transect was 18.7 km·year^{-1}. Attention needs to be paid to the significantly lower expansion rate of *T. laxmannii* near the site of its introduction in the southern, forest-steppe part of the transect because the species spread in a north-western direction (for 6 years (until 2003), to the northern border of the Forest-Steppe) by 54 km with an average rate of 9 km·year^{-1} from the record of its finding in 1997. This is also clearly evidenced by the significantly higher density of isolines. In the part of the Forest zone of the transect the expansion rate of *T. laxmannii* increased significantly toward the north. So, this species spread along the A–B transect by 95.6 km in three years (2003–2005) with an average rate of 31.9 km·year^{-1}.

The C–D transect has a length of 194.6 km, and the duration of *T. laxmannii* expansion along it is 12 years (1995–2007). Thus, the average expansion rate of this species along this transect was 16.2 km·year^{-1}. As well as for the A–B transect, it was also noted for this transect that the expansion rate of *T. laxmannii* to the north (starting from the probable primary place of the species' introduction in the region) was relatively insignificant because in 7 years the species spread from south to north up to the northern border of the Forest-Steppe by 54 km, with an average rate of 7.7 km·year^{-1}. In the part of the Forest zone of this transect, the expansion rate of *T. laxmannii* significantly increased and reached 23.4 km·year^{-1}.

The F–G transect has a length of 180.0 km, and the duration of *T. laxmannii* expansion along it is 12 years (1999–2011). The average expansion rate of this species along this transect was 15.0 km·year^{-1}. This transect passes through such centers of *T. laxmannii* expansion as Berdychiv town and Zhytomyr city. It is significantly complicated by secondary (radial) transfers of the species diaspores resulting in the occurrence of numerous localities of the species; therefore, it is practically impossible to divide the distribution rate of the studied species in the Forest-Steppe and Forest zones along this transect.

Summarizing the calculations performed on transects, it can be noted that *T. laxmannii* in the research region (the Zhytomyr Oblast) in 1995–2011 was characterized by a significant expansion rate from the South to the North: an average of 16.6 ± 1.09 km·year^{-1}.

Syntaxonomy. In order to find out the phytocoenotic confinedness of *T. laxmannii* in Ukraine, we carried out a cluster analysis of 154 phytosociological relevés with the participation of the species. According to the fidelity index (Phi coefficient), 13 clusters were identified (Fig. 5).

Based on the analysis of the original data, as well as literature information, we present a classification scheme of vegetation with *T. laxmannii* participation.

Bolboschoenetea maritimi **Vicherek et Tx. in Tx. et Hülbusch 1971**

Bolboschoenetalia maritimi Hejný in Holub et al. 1967

Typhion laxmannii Nedelcu 1968

Typhetum laxmannii (Ubrizsy 1961) Nedelcu 1968

Typhetum laxmannii var. *typica*

Typhetum laxmannii var. *Typha latifola*

Typhetum laxmannii var. *Schoenoplectus lacustris*

Scirpion maritimi Dahl et Hadaи 1941

Bolboschoenetum maritimi Eggler 1933

Bolboschoeno-Phragmitetum Borhidi et Balogh 1970

Scirpetum tabernaemontani Soó (1927) 1947

Typho-Schoenoplectetum tabernaemontani Br.-Bl. et

O. de Bolòs 1958

Eleocharitetum uniglumis Almquist 1929
Phragmito-Magnocaricetea **Klika in Klika et Novák 1941**

Oenanthetalia aquaticae Hejný ex Balátová-Tuláčková et al. 1993

Eleocharito palustris-Sagittarion sagittifoliae Passarge 1964

Eleocharitetum palustris Savič 1926

Butomo-Sagittarietum sagittifoliae Losev in Losev et

Golub 1988

Butomo-Alismatetum plantaginis-aquaticae Slavnić 1948

Alismatetum lanceolati Zahlheimer ex Šumberová in Chytrý

2011
Phragmitetalia Koch 1926

Phragmition communis Koch 1926

Phragmitetum australis Savič 1926

Typhetum angustifoliae Pignatti 1953

Typhetum latifoliae Nowicski 1930

Schoenoplectetum triqueteri Zonneveld 1955

Acoretum calami Dagys 1932

Equisetetum fluviatilis Nowicski 1930

Zizanietum Akhtiamov 1987

Sparganietum erecti Roll 1938

Glycerietum maximae Nowicski 1930 corr. Šumberová, Chytrý et Danichelka in Chytrý 2011
Magnocaricetalia Pignatti 1953

Magnocaricion gracilis Géhu 1961

Caricetum acutiformis Eggler 1933
Crypsietea aculeatae **Vicherek 1973**

Crypsietalia aculeatae Vicherek 1973

Heleochloion schoenoidis Br.-Bl. ex Rivas Goday 1956

Polygono salsuginei-Crypsietum aculeatae Korzhenevsky et

Klyukin in Korzhenevsky et al. 1997
Festuco-Puccinellietea **Soó ex Vicherek 1973**

Scorzonero-Juncetalia gerardii Vicherek 1973

Juncion gerardii Wendelberger 1943

Scorzonero parviflorae-Juncetum gerardii (Wenzl 1934)
Puccinellietalia Soó 1947

Puccinellion giganteae Dubyna et Neuhäuslová 2000

Puccinellietum giganteae Solomakha et Shelyag-Sosonko in

Dubyna et Neuhäuslová 2000

Salicornio-Puccinellion Mirkin in Golub et Solomakha 1988

Astero tripolii-Phragmitetum Krisch (1972) 1974

Tripolietum vulgaris Korzhenevsky et Klyukin in

Korzhenevsky, Klyukin et Korzhenevskaya 2000
Oryzetea sativae **Miyawaki 1960**

Cypero difformis-Echinochloetalia oryzoidis O. de Bolòs et Masclans

1955

Oryzo sativae-Echinochloion oryzoidis O. de Bolòs et Masclans

1955

Echinochloo-Oryzetum sativae Soó ex Ubrizsy 1948

Alismato-Monochorietum korsakowii Dziuba 1989
Thus, it was established that *T. laxmannii* in Ukraine participated in 27 plant associations of 5 vegetation classes. Under favorable environmental conditions, the species develops *Typhetum laxmannii* association of *Bolboschoenetea maritimi* class, in which it dominates developing a projective cover of up to 80–90%. With less cover, but with high constancy, the

species occurs in other communities of this class, as well as, quite often, of *Phragmito-Magnocaricetea* class. Significantly less frequently, singly or with coverage up to 5(10) %, *T. laxmannii* participates in coenoses of the following classes: *Crypsietea aculeatae* on areas of mud volcanoes in the Crimea, *Festuco-Puccinellietea* in the Black Sea Biosphere Reserve, and *Oryzetea sativae* in Genichesk district of the Kherson Oblast (Table 1).

The floristic composition of separate communities in *Typhetum laxmannii* association on the territory of Ukraine (depending on the conditions of their development) is somewhat different, which allows us to distinguish several ecological variants. Coenoses of *Typhetum laxmannii* var. *typica* are connected with habitats with the highest concentration of salts in the substrate compared to other variants. They are more common in the Steppe, much less common in the western and northern regions of Ukraine, and are characterized by the participation of species of halophilic flora-complex: *Agrostis stolonifera* L., *Eleocharis uniglumis* (Link) Schult., *Puccinellia distans* (Jacq.) Parl., *P. brachylepis* Klokov, *Bolboschoenus maritimus* (L.) Palla, *Triglochin maritimum* L., *Glaux maritima* L. and others. Communities of *Typhetum laxmannii* var. *Typha latifolia* develope in the conditions of freshwater coastal ecotopes; differential species are *T. latifolia* L., *Persicaria maculosa* S.F. Gray, *Juncus compressus* Jacq., *J. effusus* L., *J. articulatus* L., *Ranunculus flammula* L., *R. repens* L., *Lysimachia nummularia* L., *Eleocharis palustris* (L.) Roem. & Schult., *Rorippa palustris* (L.) Besser, *Epilobium palustre* L., *Leersia oryzoides* (L.) Sw., *Prunella vulgaris* L., *Carex pseudocyperus* L., *Galium palustre* L. They were described mainly from Lviv, Ivano-Frankivsk, Zakarpattia, Chernihiv and Vinnytsia Oblasts of Ukraine. Communities of *Typhetum laxmannii* var. *Schoenoplectus lacustris* variants are typical for the coasts of slightly saline water bodies. They are characterized by the participation of *Eleocharis uniglumis*, *Typha angustifolia, Schoenoplectus lacustris, Bolboschoenus maritimus, Lythrum salicaria, Phragmites australis, Oenanthe aquatica, Lysimachia vulgaris, Sium latifolium*, and others. They were recorded in the different regions of the country, in particular in the Poltava, Cherkasy, Transcarpathian, Vinnytsia, Kharkiv, Lviv, Kiev, Kherson, Kirovohrad, Odesa, and Mykolaiv Oblasts.

Ecological and coenotic features of Typha laxmannii. Phytoindication and ordination analyses of the selected syntaxon groups were performed in order to assess the ecological differentiation of communities with the participation of *T. laxmannii*. Analysis of DCA ordination shows that the leading factors of their ecological differentiation are: the water regime, the content of calcium carbonates in the soil, the aeration of substrates and the climate continentality, the vectors of which are closest to the first and second ordination axes (Fig. 6).

Results of DCA-ordination analysis of communities in *Typhetum laxmannii* association indicate that to the leading factors of their ecological differentiation the also variability of damping and thermal regime can be referred (Fig. 6). In communities of *Typhetum laxmannii* var. *Typha latifolia*, the climate continentality has an important influence on their composition and structure, which confirms their confinedness to Forest-Steppe and Forest zones. The position of plant communities of *typica* variant in the ecological space is mainly determined by the gradients of soil acid and salt regime. The limiting factor for the communities of *Typhetum laxmannii* var. *Schoenoplectus lacustris* is a cryoclimate – climate coldness.

For the purpose of phytoindication analysis of *T. laxmannii* dominant communities, 75 relevés of *Typhetum laxmannii* association were used; ecological indicators of 12 environmental factors were calculated. The results of the analysis indicate that, according to the water regime (Hd), these phytocoenoses were developed mainly in hygrophytic and perhygrophytic conditions, i. e. they are confined to wet ecotopes with sufficient moisture of the root layer of the soil, and which are hemistenotopic by a 4-stage scale (Didukh, 2011) (Fig. 7). According to the indicators of moisture variability (fH), the communities show hemihydrocontrastophobia, i. e. they can exist in conditions of moderately uneven moisture throughout the year. The wideness of the ecological amplitude by this indicator is the highest, which allows attributing them to the hemieurytopic group. By relation to soil acidity (Rc), these coenoses prefer slightly acidic and neutral soils with pH of 6.5–7.1 and belong to hemistenotopic. Indicators of the total salt regime of soil (Sl) ranged from 7 to 11 points on a 19-point scale; therefore, they tend to eutrophic group of edaphotopes and are hemistenotopic. By relation to carbonate (Ca) content in the soil, these plant communities belong to hemicarbonatophobes with stenotopic amplitude and generally avoid carbonate substrates. By relation to the content of available nitrogen (Nt) in the substrate, *Typhetum laxmannii* phytocoenoses belong to heminitrophilic ecological group and can grow on relatively mineral nitrogen-deficient soils (with a nitrogen content of 0.2–0.3%). Coenoses are developed in ecotopes with weak soil aeration (Ae) typical for semi-aquatic biotopes. According to the lighting regime (Lc), the communities are heliophytic and prefer well illuminated open habitats.

Amplitudes of ecological factors based on the results of phytoindication of *Typhetum laxmannii* association are presented in Fig. 8.

Phytoindication analysis of the distribution of communities by climatic factors (cryoclimate, ombroregime, climate continentality, thermoregime) showed that they are developed in subcriophytic, subaride, hemioceanic, subcontinental, submesothermic conditions.

Table 2
Synoptic table of communities with *Typha laxmannii* (by *phi* coefficient)

Number of clasters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Number of releves	5	5	3	5	7	4	5	10	8	9	9	49	20
Halimione verrucifera	76.2	–	–	–	–	–	–	–	–	–	–	–	–
Suaeda acuminata	74.8	–	–	–	–	–	–	–	–	–	–	–	–
Lactuca tatarica	61.7	–	–	–	–	–	–	–	–	–	–	–	–
Puccinellia gigantea	60.2	–	–	–	–	–	–	–	–	–	–	–	–
Tripolium pannonicum	56.5	–	–	–	–	–	–	–	–	–	–	–	–
Scorzonera parviflora	43.3	–	–	–	–	–	–	–	–	–	–	–	–
Tanacetum vulgare	43.3	–	–	–	–	–	–	–	–	–	–	–	–
Atriplex littoralis	43.3	–	–	–	–	–	–	–	–	–	–	–	–
Erigeron canadensis	43.3	–	–	–	–	–	–	–	–	–	–	–	–
Spergularia marina	43.3	–	–	–	–	–	–	–	–	–	–	–	–
Eupatorium cannabinum	43.3	–	–	–	–	–	–	–	–	–	–	–	–
Taraxacum bessarabicum	43.3	–	–	–	–	–	–	–	–	–	–	–	–
Spergularia media	43.3	–	–	–	–	–	–	–	–	–	–	–	–
Halimione pedunculata	43.3	–	–	–	–	–	–	–	–	–	–	–	–
Juncus gerardi	–	77.4	–	–	–	–	–	–	–	–	–	–	–
Calamagrostis canescens	–	76.2	–	–	–	–	–	–	–	–	–	–	–
Lythrum volgense	–	61.7	–	–	–	–	–	–	–	–	–	–	–

Notes: Table 2 is presented in an abbreviated form. Only diagnostically significant indicators of the *phi* coefficient are indicated. Coefficient *phi* multiplied by 100. Numbers of clasters: 1 – *Puccinellietum giganteae* (incl. *Tripolietum vulgaris, Astero tripolii-Phragmitetum*); 2 – *Scorzonero parviflorae-Juncetum gerardii*; 3 – *Echinochloo-Oryzetum sativae* (incl. *Alismato-Monochorietum korsakowii*); 4 – *Scirpetum tabernaemontani* (incl. *Typho-Schoenoplectetum tabernaemontani, Eleocharitetum uniglumis*); 5 – *Phragmitetum australis* (incl. *Caricetum acutiformis*); 6 – *Bolboschoenetum maritimi* (incl. *Bolboschoeno-Phragmitetum*); 7 – *Polygono salsuginei-Crypsietum aculeatae*; 8 – *Sparganietum erecti* (incl. *Equisetetum fluviatilis, Acoretum calami, Typhetum latifoliae*); 9 – *Butomo-Alismatetum plantaginis-aquaticae* (incl. *Butomo-Sagittarietum sagittifoliae*; *Schoenoplectetum triqueteri, Alismatetum lanceolati*); 10 – *Typhetum angustifoliae* (incl. *Glycerietum maximae, Zizanietum*); 11 – *Typhetum laxmannii* var. *Schoenoplectus lacustris*; 12 – *Typhetum laxmannii* var. *typica*; 13 – *Typhetum laxmannii* var. *Typha latifoli*

Number of clasters	1	2	3	4	5	6	7	8	9	10	11	12	13
Centaurium erythraea	–	61.7	–	–	–	–	–	–	–	–	–	–	–
Atriplex calotheca	–	61.7	–	–	–	–	–	–	–	–	–	–	–
Carex vulpina	–	61.7	–	–	–	–	–	–	–	–	–	–	–
Holcus lanatus	–	61.7	–	–	–	–	–	–	–	–	–	–	–
Lotus corniculatus	–	61.7	–	–	–	–	–	–	–	–	–	–	–
Elytrigia repens	–	60.0	–	–	–	–	–	–	–	–	–	–	–
Potentilla reptans	–	51.2	–	–	–	–	–	–	–	–	–	–	–
Carex distans	–	48.7	–	–	–	–	–	–	–	–	–	–	–
Poa angustifolia	–	43.3	–	–	–	–	–	–	–	–	–	–	–
Juncus bulbosus	–	43.3	–	–	–	–	–	–	–	–	–	–	–
Cyperus pannonicus	–	43.3	–	–	–	–	–	–	–	–	–	–	–
Bassia sedoides	–	43.3	–	–	–	–	–	–	–	–	–	–	–
Salicornia perennans	–	42.6	–	–	–	–	–	–	–	–	–	–	–
Oryza sativa	–	–	100.0	–	–	–	–	–	–	–	–	–	–
Echinochloa crus-galli	–	–	88.7	–	–	–	–	–	–	–	–	–	–
Echinochloa oryzoides	–	–	80.5	–	–	–	–	–	–	–	–	–	–
Persicaria lapathifolia	–	–	80.5	–	–	–	–	–	–	–	–	–	–
Monochoria korsakowii	–	–	56.2	–	–	–	–	–	–	–	–	–	–
Cyperus difformis	–	–	56.2	–	–	–	–	–	–	–	–	–	–
Polygonum aviculare	–	–	–	61.7	–	–	–	–	–	–	–	–	–

Notes: Table 2 is presented in an abbreviated form. Only diagnostically significant indicators of the *phi* coefficient are indicated. Coefficient *phi* multiplied by 100. Numbers of clasters: 1 – *Puccinellietum giganteae* (incl. *Tripolietum vulgaris, Astero tripolii-Phragmitetum*); 2 – *Scorzonero parviflorae-Juncetum gerardii*; 3 – *Echinochloo-Oryzetum sativae* (incl. *Alismato-Monochorietum korsakowii*); 4 – *Scirpetum tabernaemontani* (incl. *Typho-Schoenoplectetum tabernaemontani, Eleocharitetum uniglumis*); 5 – *Phragmitetum australis* (incl. *Caricetum acutiformis*); 6 – *Bolboschoenetum maritimi* (incl. *Bolboschoeno-Phragmitetum*); 7 – *Polygono salsuginei-Crypsietum aculeatae*; 8 – *Sparganietum erecti* (incl. *Equisetetum fluviatilis, Acoretum calami, Typhetum latifoliae*); 9 – *Butomo-Alismatetum plantaginis-aquaticae* (incl. *Butomo-Sagittarietum sagittifoliae*; *Schoenoplectetum triqueteri, Alismatetum lanceolati*); 10 – *Typhetum angustifoliae* (incl. *Glycerietum maximae, Zizanietum*); 11 – *Typhetum laxmannii* var. *Schoenoplectus lacustris*; 12 – *Typhetum laxmannii* var. *typica*; 13 – *Typhetum laxmannii* var. *Typha latifoli*

Number of clasters	1	2	3	4	5	6	7	8	9	10	11	12	13
Schedonorus arundinaceus	–	–	–	61.7	–	–	–	–	–	–	–	–	–
Cirsium canum	–	–	–	61.7	–	–	–	–	–	–	–	–	–
Carex divisa	–	–	–	61.7	–	–	–	–	–	–	–	–	–
Verbena officinalis	–	–	–	61.7	–	–	–	–	–	–	–	–	–
Rubus caesius	–	–	–	61.7	–	–	–	–	–	–	–	–	–
Plantago cornutii	–	–	–	51.7	–	–	–	–	–	–	–	–	–
Potamogeton perfoliatus	–	–	–	42.4	–	–	–	–	–	–	–	–	–
Triglochin maritima	–	–	–	42.4	–	–	–	–	–	–	–	–	–
Scirpus lacustris subsp. glaucus	–	–	–	41.2	–	–	–	–	18.1	–	–	–	–
Bidens tripartitus	–	–	–	–	43.6	–	–	–	–	–	–	–	–
Symphytum officinale	–	–	–	–	40.7	–	–	–	–	–	–	–	–
Mentha aquatica	–	–	–	–	40.1	–	–	23.1	–	–	–	–	–
Stachys palustris	–	–	–	–	33.9	–	–	–	–	24.3	–	–	–
Carex acuta	–	–	–	–	31.9	–	–	–	–	–	–	–	–
Calystegia sepium	–	–	–	–	31.5	–	–	–	–	–	–	–	–
Atriplex prostrata	–	–	–	–	–	48.3	–	–	–	–	–	–	–
Bolboschoenus maritimus	–	–	–	–	–	29.7	–	–	22.5	–	–	–	–
Limonium gmelinii	–	–	–	–	–	–	100.0	–	–	–	–	–	–
Polygonum salsugineum	–	–	–	–	–	–	100.0	–	–	–	–	–	–

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Number of clasters	1	2	3	4	5	6	7	8	9	10	11	12	13
Crypsis aculeata	–	–	–	–	–	–	100.0	–	–	–	–	–	–
Rumex stenophyllus	–	–	–	–	–	–	74.8	–	–	–	–	–	–
Salsola tragus	–	–	–	–	–	–	61.7	–	–	–	–	–	–
Beckmannia eruciformis	–	–	–	–	–	–	61.7	–	–	–	–	–	–
Artemisia santonicum	–	–	–	–	–	–	43.3	–	–	–	–	–	–
Elytrigia elongata	–	–	–	–	–	–	43.3	–	–	–	–	–	–
Sparganium erectum	–	–	–	–	–	–	–	52.9	–	–	–	–	–
Carex acutiformis	–	–	–	–	–	–	–	39.8	–	–	–	–	–
Myosotis scorpioides	–	–	–	–	–	–	–	32.0	–	–	–	–	–
Lemna trisulca	–	–	–	–	–	–	–	32.0	–	–	–	–	–
Alisma plantago-aquatica	–	–	–	–	–	–	–	28.0	–	–	–	–	18.3
Persicaria hydropiper	–	–	–	–	–	–	–	–	45.6	–	–	–	20.9
Rorippa amphibia	–	–	–	–	–	–	–	–	44.9	–	–	–	23.6
Bidens frondosus	–	–	–	–	–	–	–	–	36.2	–	–	–	–
Ceratophyllum demersum	–	–	–	–	–	–	–	–	31.2	–	–	–	–
Azolla filiculoides	–	–	–	–	–	–	–	–	31.2	–	–	–	–
Apium graveolens	–	–	–	–	–	–	–	–	26.2	–	–	–	–
Potamogeton berchtoldii	–	–	–	–	–	–	–	–	26.2	–	–	–	–

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Number of clasters	1	2	3	4	5	6	7	8	9	10	11	12	13
Spirodela polyrhiza	–	–	–	–	–	–	–	–	–	50.9	–	–	–
Utricularia vulgaris	–	–	–	–	–	–	–	–	–	45.7	–	–	–
Zizania latifolia	–	–	–	–	–	–	–	–	–	45.7	–	–	–
Typha angustifolia	–	–	–	–	–	–	–	–	–	45.0	–	–	–
Sagittaria sagittifolia	–	–	–	–	–	–	–	24.3	–	40.0	–	–	–
Lemna minor	–	–	–	–	–	–	–	–	–	34.8	–	–	–
Lythrum salicaria	–	–	–	–	–	–	–	–	–	–	39.1	–	–
Schoenoplectus lacustris	–	–	–	–	–	–	–	–	–	–	35.7	–	–
Eleocharis uniglumis	–	–	–	–	–	–	–	–	–	–	29.3	–	–
Persicaria maculosa	–	–	–	–	–	–	–	–	–	–	–	27.5	–
Juncus effusus	–	–	–	–	–	–	–	–	–	–	–	–	53.0
Typha latifolia	–	–	–	–	–	–	–	–	–	–	–	–	49.2
Ranunculus flammula	–	–	–	–	–	–	–	–	–	–	–	–	48.5
Juncus compressus	–	–	–	–	–	–	–	–	–	–	–	–	48.5
Amblystegium riparium	–	–	–	–	–	–	–	–	–	–	–	–	43.3
Ranunculus repens	–	–	–	–	–	–	–	–	–	–	–	–	40.9
Prunella vulgaris	–	–	–	–	–	–	–	–	–	–	–	–	37.4
Eleocharis palustris	–	–	–	–	–	–	–	–	–	–	–	–	32.0
Lysimachia nummularia	–	–	–	–	–	–	–	–	–	–	–	–	31.3
Alnus glutinosa	–	–	–	–	–	–	–	–	–	–	–	–	30.5

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Number of clasters	1	2	3	4	5	6	7	8	9	10	11	12	13
Rorippa palustris	–	–	–	–	–	–	–	–	–	–	–	–	30.5
Carex pseudocyperus	–	–	–	–	–	–	–	–	–	–	–	–	30.5
Equisetum palustre	–	–	–	–	–	–	–	–	–	–	–	–	30.5
Epilobium palustre	–	–	–	–	–	–	–	–	–	–	–	–	30.5
Salix aurita	–	–	–	–	–	–	–	–	–	–	–	–	30.5
Carex hirta	–	–	–	–	–	–	–	–	–	–	–	–	30.5
Juncus articulatus	–	–	–	–	–	–	–	–	–	–	–	–	30.1
Leersia oryzoides	–	–	–	–	–	–	–	–	–	–	–	–	26.7
Galium palustre	–	–	–	–	–	–	–	–	–	–	–	–	25.7
Potentilla anserina	–	–	–	–	–	–	–	–	–	–	–	–	25.3
Puccinellia distans	–	35.8	–	–	–	–	35.8	–	–	–	–	–	–
Juncus maritimus	–	–	–	64.9	–	–	27.5	–	–	–	–	–	–
Crypsis schoenoides	–	–	–	35.0	–	–	56.7	–	–	–	–	–	–
Phragmites australis	–	–	–	28.0	28.0	–	–	–	–	–	15.2	–	–
Acorus calamus	–	–	–	–	36.8	–	–	44.3	–	–	–	–	–
Alisma lanceolatum	–	–	–	–	–	–	37.7	–	29.5	–	–	–	–
Glyceria maxima	–	–	–	–	–	–	–	52.3	–	35.1	–	–	–
Oenanthe aquatica	–	–	–	–	–	–	–	34.3	–	–	32.0	–	–
Hydrocharis morsus-ranae	–	–	–	–	–	–	–	33.7	–	38.2	–	–	–

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Number of clasters	1	2	3	4	5	6	7	8	9	10	11	12	13
Salvinia natans	–	–	–	–	–	–	–	19.8	27.8	32.2	–	–	–
Lysimachia vulgaris	–	–	–	–	–	–	–	–	–	36.8	25.4	–	–
Butomus umbellatus	–	–	–	–	–	–	–	29.3	58.4	34.2	–	–	–
Sium latifolium	–	–	–	–	–	–	–	–	–	24.7	24.7	–	–
Lycopus europaeus	–	–	–	–	–	–	–	21.0	–	–	–	–	–
Carex riparia	–	–	–	–	–	–	–	–	–	–	–	23.8	–
Carex disticha	–	–	–	–	–	–	–	–	–	–	–	23.8	–

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The growth of *T. laxmanii* is of considerable interest in the objects of the nature reserve fund in Ukraine. The species is found on the territory of the Danube and the Black Sea Biosphere Reserves; the Dnieper-Orel, the Kaniv, and the Ukrainian Steppe nature reserves; the Galitsky, the Holosiivskyi, the Skole Beskids, the Pripyat-Stokhid national nature parks (Baranovsky, 2000; Manyuk et al., 2018; Kagalo et al., 2011; Shumskaya, 2019). The species shows a trend to active expansion into native and semi-native biotopes of these nature objects creating a threat to their phytodiversity. The study of such impact in Ukraine is currently at an initial stage, so we believe that monitoring investigations on the distribution and condition of populations of this species in the objects of the nature reserve fund of the country is an important part of long-term monitoring system of their plant world as a whole.

Discussion

In our opinion, the syntaxonomic position of the union *Typhion laxmannii* is now quite controversial. In Prodrome of European vegetation (Mucina et al., 2016) it belongs to the order *Phragmitetalia*. Romanian, Slovak, and Bulgarian phytocoenologists attribute the association *Typhetum laxmannii* to the union *Phragmition communis* Koch 1926 (Ot'ahel'ová et al., 2001; Sanda et al., 2008; Tzonev et al., 2009). Such syntaxonomic decision was also made in the review of the European classification of the vegetation of the class *Phragmito-Magnocaricetea* (Landucci et al., 2020). Obviously, it is based on the confinedness of the plant communities in Central and Southern Europe mainly to freshwater ecotopes. However, in our opinion, since these subhalophytic communities tend to slightly saline substrates (like, in particular, in Ukraine), it would be advisable to assign them to the order *Bolboschoenetalia maritimi* Nejpe in Holub et al. 1967 as the order united brackish swamp reeds of European temperate coasts and the subcontinental inland regions of Europe. These views are held in France (eVeg, http://www.e-veg.net/app/4107) and Russia (Golub and Maltsev, 2013). In Prodrome of the vegetation of Ukraine, which is characterized by a narrow understanding of the volume of syntaxons, the union is subordinated to the order *Bolboschoenetalia maritimi* of the class *Bolboschoenetea maritimi* Tx. et Vicherek in Tx. et Hülbush 1971 (Dubina et al., 2019).

In recent years, the ecological component of phytocoenoses has become increasingly used as an object of study and substantiation for classification (Zhou et al., 2019; Willner et al., 2019) for assessment of the environmental impact on the species richness of phytocoenoses (Yousaf et al., 2016; Slezák et al., 2017), a study of vegetation dynamics (Cao et al., 2019), identification of the main ecological factors of plant communities' differentiation (Özdeniz et al., 2017), ets. Based on the ordination analysis of plant communities with the participation of *T. laxmannii* we have found that the leading factor of their ecological differentiation is the water regime, which is confirmed also by other researches (Ot'ahel'ová et al., 2001; Hrivnák, 2004; Nobis et al., 2006). The results of phytoindication by 12 edaphic and climatic environmental factors allowed us to define the ecological confinedness of the association *Typhetum laxmannii*, its development optimums, and the width of ecological amplitude. It was found that according to the pH of the soil solution its coenoses in Ukraine confine to slightly acidic or neutral soils, in contrast to habitats in Poland where pH values from 7.0 to 8.3 typical for alkaline soils were recorded (Nobis et al., 2006). Obviously, it is related to the predominant confinedness of such communities in Poland to quarries for the extraction of calcium-containing minerals.

According to the data (Rasran et al., 2021), phytocoenoses with dominance of *T. laxmannii* may pose a threat to other wetland plant communities. In general our study have confirmed a significant width of the ecological amplitude of *T. laxmannii* and its confinedness mainly to eutrophic slightly saline ecotopes. Under the increase of anthropogenic influence and eutrophication of water bodies, *T. laxmannii* communities can expand their coenotic area and spread quite quickly, especially in artificial water bodies: sand pits, mineral excavations, especially in quarries, canals, or short-term water reservoirs (Ot'ahel'ová et al., 2001; Nobis et al. 2006), and also in artificial habitats under the influence of winter salting, such as roadside ditches, village ponds and more or less wet waste places in the settlements (Kaplan et al., 2019; Rasran et al., 2001).

The results obtained by syntaxonomy and phytoindication analysis with differentiation of *Typhetum laxmannii* association into 3 variants indicated that the floristic composition of individual communities depends on edaphic conditions and their geographical confinedness, which is in good agreement with results obtained by other phytocoenologists (Nobis et al., 2006).

Conclusion

As a result of the study, the information on the history of settlement and modern distribution of *T. laxmannii* in Ukraine, its ecological, biological peculiarities, ecological and phytocoenotic confinedness was summarized.

It was found that the species initially moved quite slowly from its primary southern localities in Ukraine in the northern direction, mainly along the Dnieper reservoirs as a hydrochore, and later it moved actively in the northern, eastern, and western directions as a hydrochore and anemochore. Now the species is distributed almost throughout Ukraine, but with a majority of records in the central and western parts of Ukraine.

Typha laxmannii in Ukraine is involved in 27 associations of 5 vegetation classes. The association *Typhetum laxmannii* formed by this species is quite common. Depending on the ecological and geographical conditions and floristic composition, 3 following variants in this association were identified: var. *typica*, var. *T. latifola*, and var. *Schoenoplectus lacustris*. Coenoses within this association are distributed almost throughout the entire territory of Ukraine, but the ecological optimum of its coenotic area is situated in the south of the country, in the Steppe zone, on slightly saline, well-watered substrates.

Based on studies conducted in the Zhytomyr Oblast in 1995–2021, the expansion rate of *T. laxmannii* was calculated – from the South to the North – in average 16.6 ± 1.09 km·year^{-1}. From the sites of the primary introduction of the species into the region (Forest-Steppe zone), the expansion rate of it toward the north was significantly lower (7.7–9.0 km·year^{-1}) compared to that in the Forest zone – Ukrainian Polissia (23.4–31.9 km·year^{-1}).

The obtained results demonstrate the role of alien plant species in the processes of general synanthropization of flora and vegetation, as well as the need to consider these data in the development of management plans of water bodies and protected areas which should include methods of restraining expansion and limiting invasions of alien species.

Declarations

Conflict of interest. On behalf of all authors, the corresponding author states that there is no conflict of interest.

Acknowledgments. The authors would like to express their sincere gratitude to Dr. D. Vynokurov, Dr. O. Kazarinova, Dr. L. Borsukevich, Prof. DrSc. L. Felbaba-Klushina, Dr. M. Prokopuk, DrSc. V. Kolomiychuk, Dr. V. Konogray, Dr. T. Chinkina, Dr. S. Yemelyanova, Dr. M. Kozyr and Dr. O. Kuzyarin for the descriptions of vegetation with the participation of *T. laxmannii*, kindly provided by them from the manuscripts of their dissertations.

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Figures

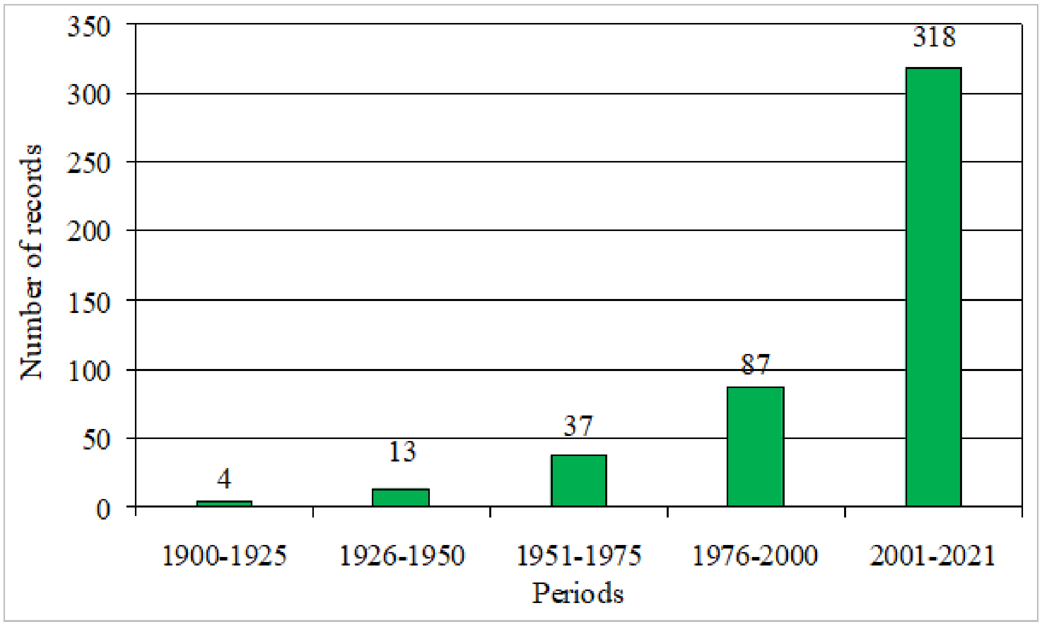


Figure 1

Dynamics of cumulative number of *T. laxmannii* records in Ukraine during 1900–2021

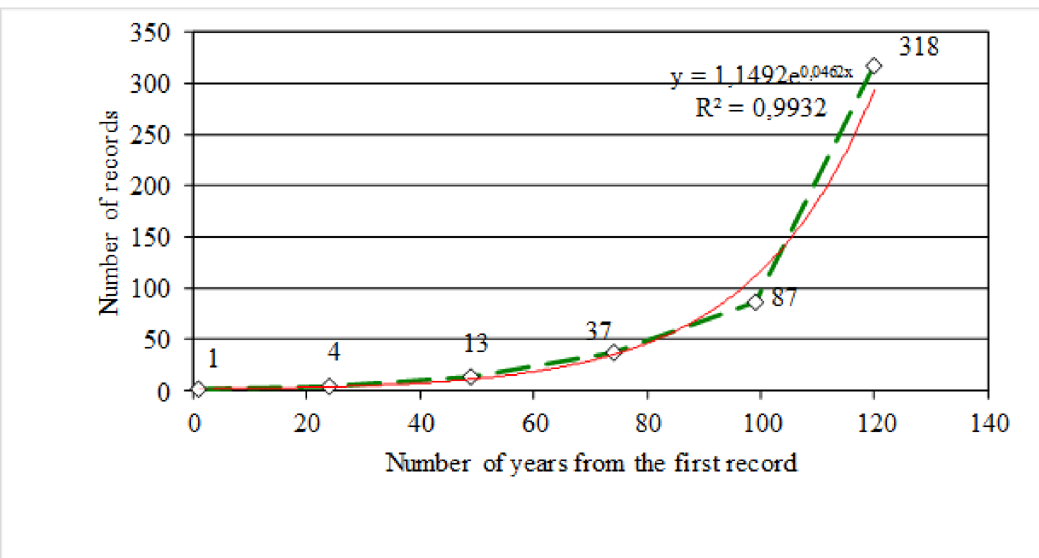
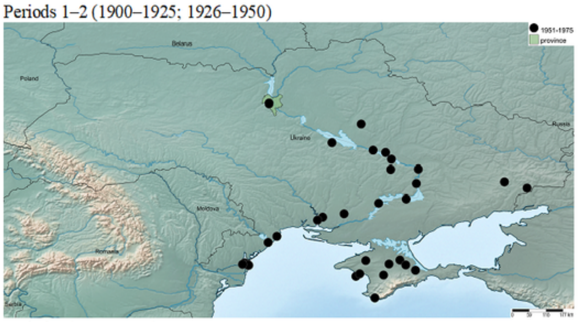


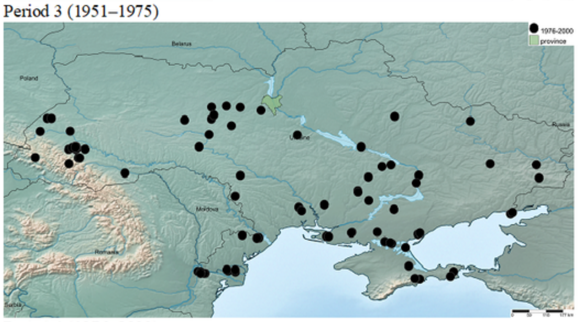
Figure 2

Dependence of cumulative number of *T. laxmannii* records from a number of years from its first finding in Ukraine (red line shows results of approximation)

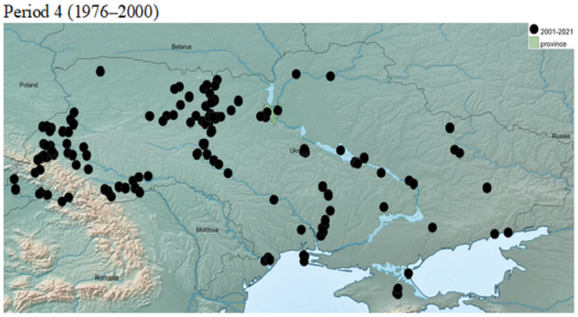
Periods 1–2 (1900–1925; 1926–1950)



Period 3 (1951–1975)



Period 4 (1976–2000)



Period 5 (2001–2021)

Figure 3

Periods of *T. laxmannii* expansion in Ukraine, with cumulative number of its records. Note: in periods 3–5 some part of records was generalized

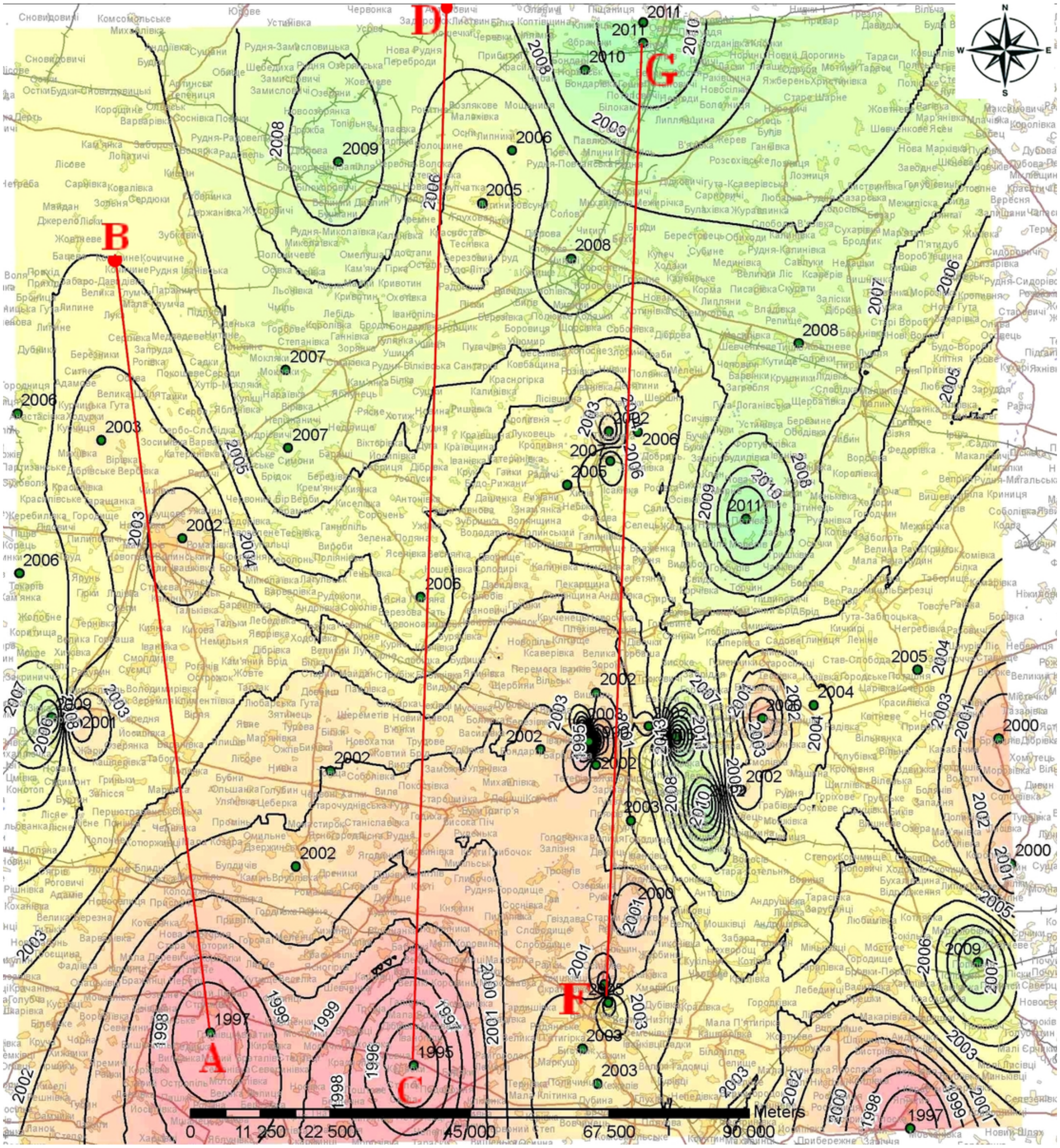


Figure 4

Isolines of the time of *Typha laxmannii* expansion over the territory of the Zhytomyr region. The colors show simulated areas of the species expansion: red: 1990–1998, yellow: 1999–2006, green: 2007–2011.

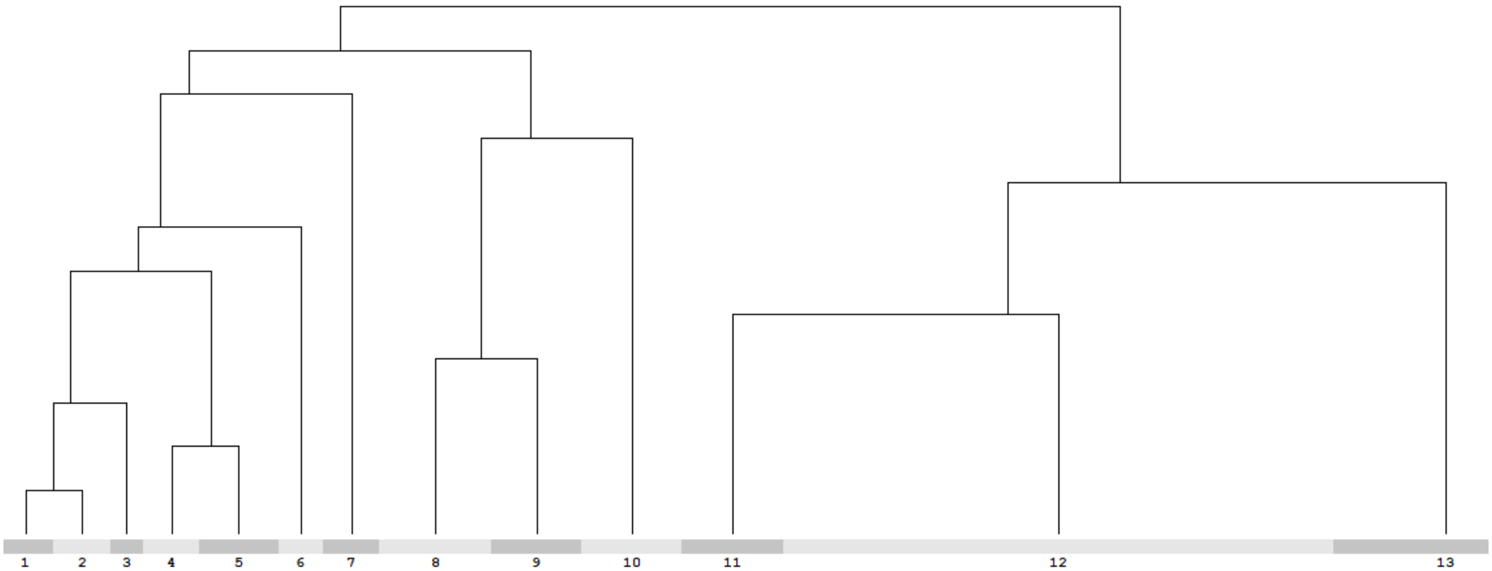


Figure 5

Cluster analysis dendrogram

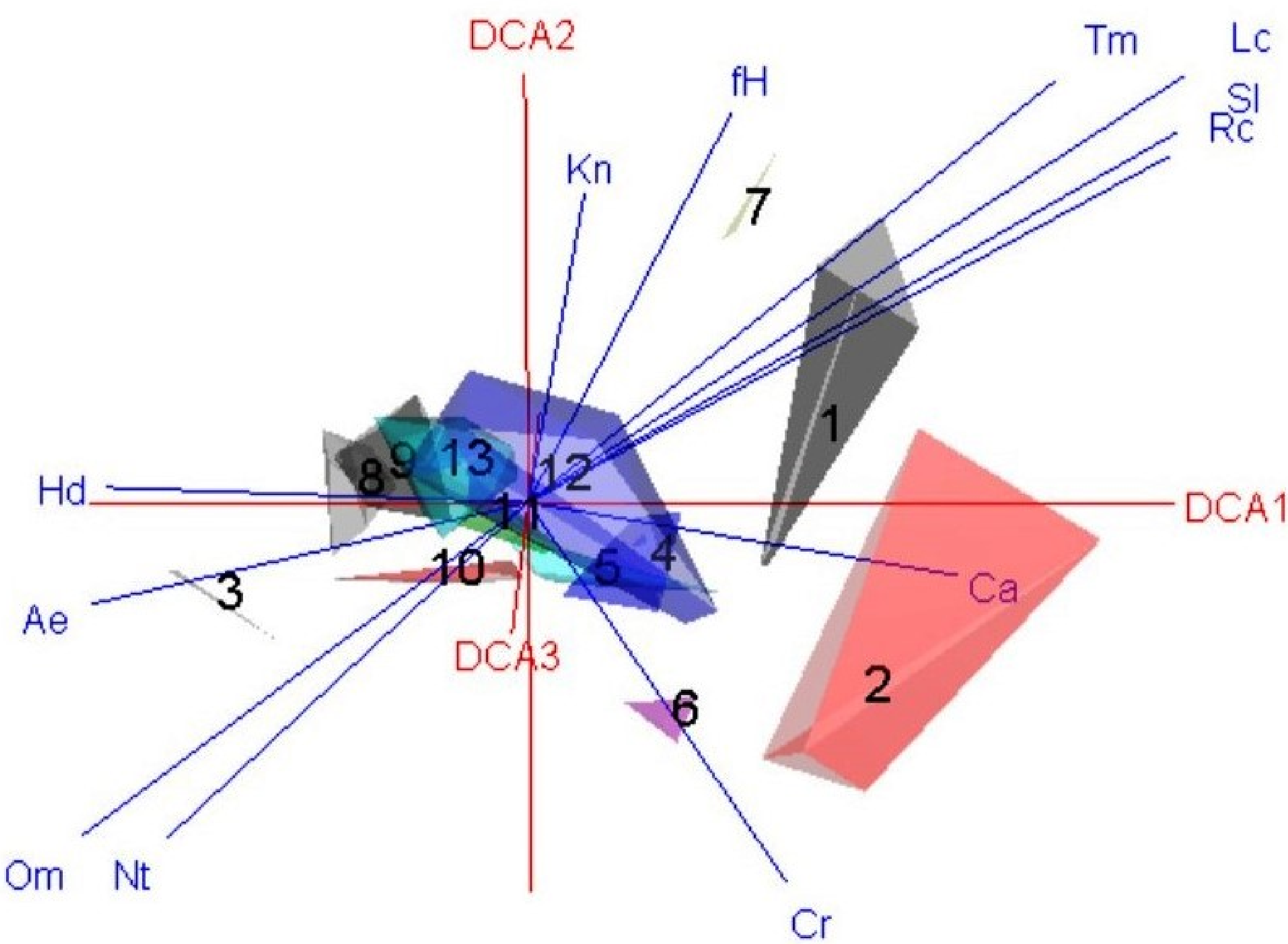


Figure 6

Results of DCA-ordination of clasters involving *Typha laxmannii*

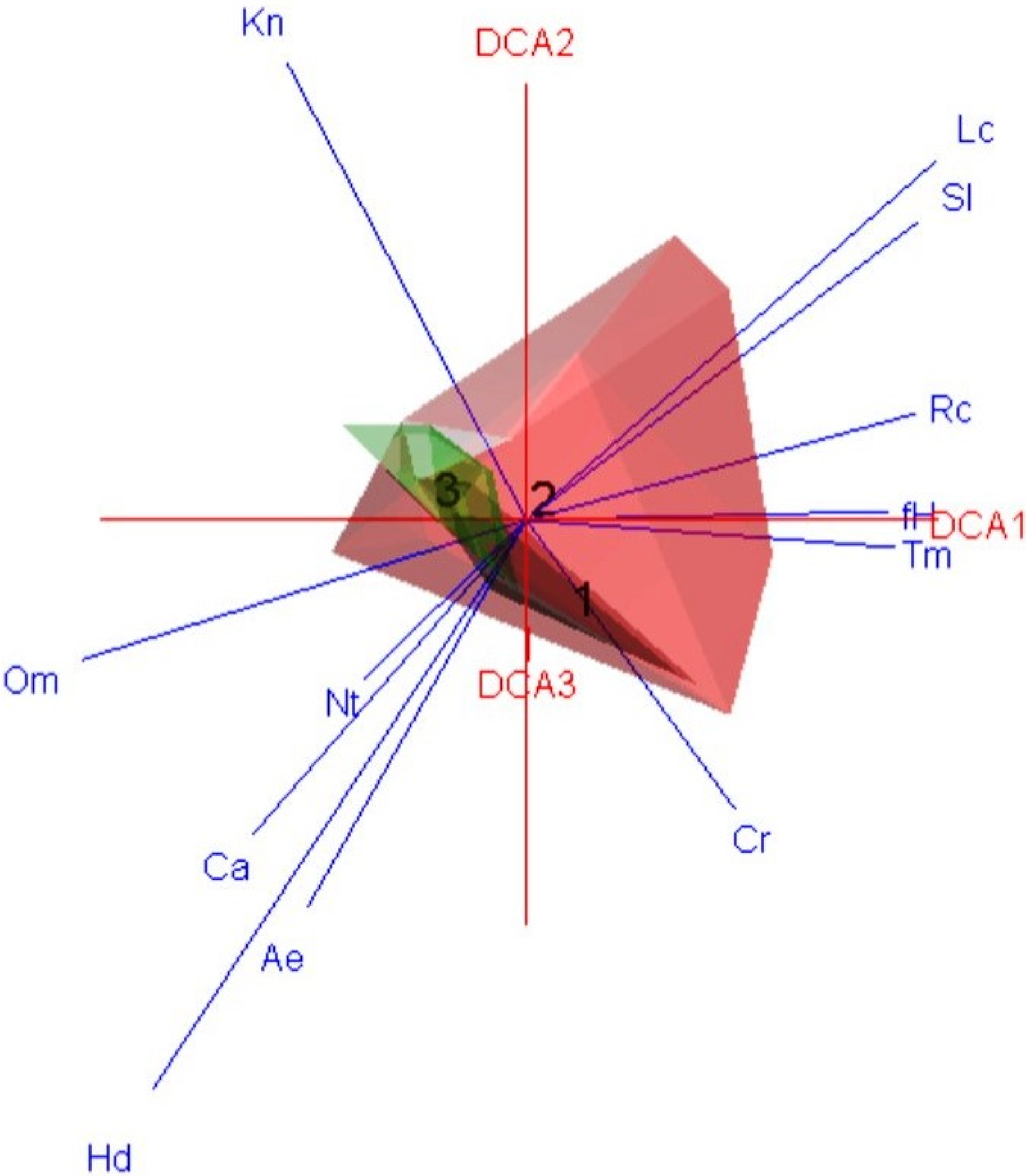


Figure 7

Results of DCA-ordination of *Typhetum laxmannii* association

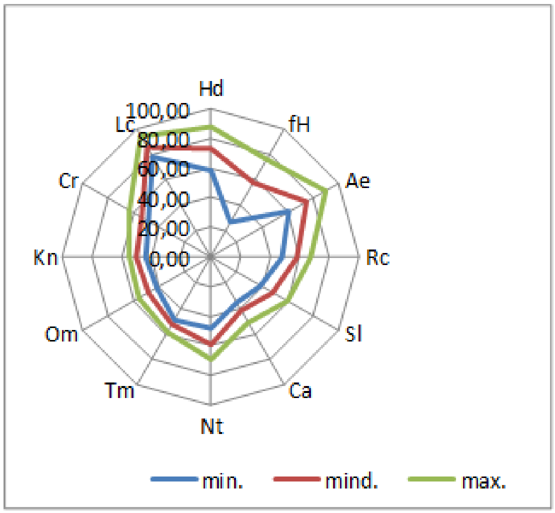


Figure 8

Cyclogram of amplitudes of ecological factors based on the results of phytoindication of *Typhetum laxmannii* association