

Population structure of *Carex dioica* L. (Cyperaceae) in Ukraine under different growth conditions

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Abstract. The population structure of *Carex dioica* – a rare boggy species in Ukraine – has been studied for the first time. As a result, five types of spatial arrangement of *C. dioica* individuals, depending on their reproduction and living conditions, were established: scattered-diffuse, densely-diffuse, group, spotted and mosaic. Intensive vegetative propagation (often in the absence of seed reproduction) of individuals contributes to the group and spotted spatial structure of population. For low intensity of seed and vegetative reproduction, the arrangement of generative individuals turned out to be scattered-diffuse. Effective generative reproduction of a population was accompanied by a densely-diffuse distribution of individuals, and a combined type of reproduction (effective generative and vegetative) under favourable growth conditions contributes to its mosaic spatial structure.

Regardless of the growth conditions, all *C. dioica* populations were characterised by a left-hand age spectrum which was the result of an effective vegetative renovation of individuals and a stress-tolerant type of strategy of this species.

Under optimal growth conditions, the *C. dioica* populations were characterised by the prevalence of females compared to male ones (2:1), and under stress – a radical change in their sex ratio was observed towards a complete dominance of one of the genders. It was found that 50% of the studied *C. dioica* populations appeared to be thriving. Regardless of the vitality type of the population, the female individuals of this species, compared to male ones, realised their growth potential much better and, therefore, made a greater contribution to population vitality.

Key words: dioecious sedge, coenopopulation, spatial arrangement, age spectrum, vitality, sex ratio

1. Introduction

A successful solution of one of the most urgent problems concerning nature conservation area, namely preserving rare plant species, calls for comprehensive studies conducted at the population level, since a population is not just a part of the ecosystem but it is also considered as the “unit of use and protection” (Holubets 2000). Negative changes in a species population, both structural and functional, can indicate trends of species extinction. Research in this area is also particularly important for rare and endangered species considered as markers of ecosystem transformation, and as a basis for the effective nature conservation management (Tsaryk & Tsaryk 2008). The most important parameters requiring detailed analysis as the informative criteria for evaluating state of populations are spatial, age and sex structure, population area, density and number of individuals and others (Harvey

1985; Borsukevych *et al.* 2012; Kyyak 2013). For the analysis of those parameters, special attention was paid during the population study of *Carex dioica* L. which is a rare species in Ukraine.

Despite *C. dioica* nature conservation status, in particular, its inclusion in a number of national and regional Red Data Books (Ukraine, Russia, Finland, Poland, the Czech Republic and Slovakia), as well as Red lists (Romania, Austria, Germany, the Netherlands and Switzerland), this species has been poorly studied in Ukraine and abroad. The fact is, that most publications are devoted to the study of species morphology, biology, some coenotic aspects and more often they briefly deal with its systematic position while conducting critical reviews of the *Carex* L. genus and the Cyperaceae Juss. family as a whole (Andrienko & Priadko 1980; Bernard 1990; Egorova 1999; Starr *et al.* 2008; Starr & Ford 2009; Jiménez-Mejías *et al.* 2016). At the same time, there is almost lack of data concerning population

structure of this species. Supposedly, the reason for that is complexity of its studies: small size of plants, hardly noticeable in grass cover, formation of long-rooted clones as well as distribution in bogs etc. However, international experience shows that comprehensive population studies are of great value today; they have become the basis for developing IUCN categorization (IUCN Red List Categories and Criteria 2012), which uses a number of quantitative criteria for assessing population dynamics and, thus, the degree of threat to species existence. They are also the basis for the development of methodical principles of monitoring rare plant species (Perzanowska 2010). Moreover, detailed information on the state of populations of rare species under threat of extinction is crucial not only for of its adequate nature protection assessment but for substantiation of appropriate protection measures.

So, the aim of our study was to conduct original comprehensive studies of *C. dioica* populations in Ukraine, namely to establish its spatial, age, sex structure and the vitality state under different growth conditions in order to provide large audience of researchers with information on the subject that will be of use to compare (e.g. with population structure of this species in neighbouring regions and Europe), to apply it in nature protection management of this rare species and to ensure its wide-range conservation.

2. Material and methods

Carex dioica is a perennial dioecious long-rooted plant species within the *Carex* L. genus, subgenus *Psyllophora* (Degl.) Peterm. (Cyperaceae). It is a boggy species occurring on plains and in the mountains, reaching the subalpine zone. It is widespread in the Arctic and Europe (Chater 1980; Hulten & Fries 1986; Malyshev 1990; Cherepanov 1995; Egorova 1999; Kochur *et al.* 2008; Koopman 2015). According to the conducted analysis, *C. dioica* is widespread in Ukraine, including the territory of Polissia, Podillia, forest-steppe zone, Prycarpathia and the Carpathians. However, most of the localities of this sedge disappeared during the last 50 years, and are known only from literature (Sosnovska *et al.* 2013). Currently, this species has been reported from 13 administrative regions in Ukraine, but at regional level, it is protected only in Vinnytsia, Lviv, Poltava and Zhytomyr region (Andrienko & Peregrym 2012). Since 2009, *C. dioica* has been included in the third edition of the Red Data Book of Ukraine (Didukh 2009) with a status of vulnerable. As was mentioned above, at national level, it is protected in Poland (Western Carpathians), Russia (Briansk region), the Baltic region, Finland, the Czech Republic and Slovakia (Ingelög *et al.* 1993; Rytteri *et al.* 1997; Čeřovský *et al.* 1999; Yevstignieiev *et al.* 2004; Kochur *et al.* 2008).

The basis for conservation of the species in Romania, Austria, Germany, the Netherlands and Switzerland are the Red Lists of these countries (Landolt 1991; Oltean *et al.* 1994; Korneck *et al.* 1998; Niklfeld & Schrattehendrer 1999; Meijden *et al.* 2000). A significant number of localities are in need of protection at European level, belonging to the Natura 2000 habitats, in particular, 91D0 *Bog woodland (priority habitat type), 7140 Transition mires and quaking bogs, 7230 Alkaline fens (Kagalo & Prots 2012; Borsukevych & Sosnovska 2013).

To study the population structure of this species, we used fixed and route research methods according to its distribution in Ukraine (Korchagin *et al.* 1972; Harper 1977; Mirkin & Rozenberg 1978; Falińska 1997; Gibson 2002). The objects of our study were particular coenopopulations, namely populations within coenosis (hereafter populations) – a group of individuals of the species, occupying a territory within the same syntaxon, formed under the influence of similar environmental conditions (Smirnova *et al.* 1976).

Syntaxonomic analysis of plant communities with *C. dioica* was conducted according to Braun-Blanquet classification represented in current publications (Valachovič 2001; Chytrý 2011).

Overall, eight populations were chosen as a model distributed in different physiographic regions of Ukraine, namely:

- D1 – in the vicinity of the village Pulemets, Shatsk district, Volyn region, a bog on the north-east of Lake Pulemets (N51°32'45.91", E23°44'34.68");
- D2 – south of the village Zatyshia, south-east of Lake Luky, Shatsk district, Volyn region (N51°32'39.36", E23°51'48.02");
- D3 – in the vicinity of the village Melnyky, the bog "Unychi", Shatsk district, Volyn region (N51°33'29.35", E23°56'24.91");
- D4 – a bog approximately 1.6 km south of the village Melnyky, south-east of Lake Karasynets, Shatsk district, Volyn region (N51°31'43.26", E23°56'33.88");
- D5 – in the vicinity of the Zamostia village, the bog "Bolittse", Manevychi district, Volyn region (N51°27'13.85", E25°30'32.54");
- D6 – in the vicinity of the village Ozirtsy, Volodymyrets district, Rivne region, the bog "Kosa" (N51°31'22.60", E25°41'39.65");
- D7 – a bog in the vicinity of the village Hlivchany, Sokal district, Lviv region (N50°17'14.58", E23°58'00.19");
- D8 – a bog on the slope of Stih Mt. (Svydovets massif, the Ukrainian Carpathians), Rakhiv district, Transcarpathian region (N48°14'35.62", E24°13'47.81").

Comprehensive population studies were conducted during 2011–2015 on permanent research plots. For this

purpose, we made transects with total areas of at least 10 m² each, divided into squares of 0.5 × 0.5 m. For detailed studies, namely counting vegetative shoots, seedlings, etc. within the transect, we used smaller research plots with areas of 25 × 25 cm each (Korchagin 1964; Rabotnov 1964; Harper 1977).

Taking into consideration the nature conservation status of the species, we tried to use no harmful methods; aiming to minimise removal of plant individuals from nature, most measurements were performed directly in the field, with the exception of detailed morphometric analysis of individuals, e.g. counting flowers in spikes etc. (Zlobin *et al.* 2013).

The spatial distribution of individuals was defined by mapping on permanent transects with an average abundance of species on scale 1:10 (Kyyak 2013). The density of each population was determined by counting the number of individual shoots per 1 m² (Rabotnov 1964).

The peculiarity of the age structure of the populations is determined, primarily, by specific features of reproduction and ontogenesis of the plant object, which makes it necessary to select a proper methodological approach. Given the clone type of population, organisation of long-rooted species when determining the age structure of all *C. dioica* populations, we counted the “ramets”, namely the individual generative and vegetative shoots. The shoots were divided into 4 age groups: young (“before generative”), generative and old ones which included “post-generative” and the shoots with incomplete development cycle, namely those which were dying, which failed to meet the traditional notions of the age structure. However, identification of morphologically integrated individuals both of seed and vegetative origin is an extremely complex task that requires the use of harmful methods, unacceptable in the study of populations of rare and endangered species. In this regard, it was more reasonable to define the ratio of different age shoots in the population, since it made it possible to estimate the value of regeneration and growing processes depending on various environmental conditions, as well as to identify certain dynamic trends and to predict the future prospects of the population with a minimum negative impact (Smirnova *et al.* 1976). During detailed research conducted on small plots (area of 25 × 25 cm), we were able to differentiate seedlings, so they were included in the analysis as well.

To assess the efficiency of a population reproduction, we used the renewal index (R) (the ratio of the number of young and generative shoots) and the substitution index (S) (the ratio of the number of young and generative + post-generative shoots (Zhukova 1987; Tsaryk *et al.* 2004).

The sex structure of populations was determined by counting the ratio of generative shoots of female and

male individuals and the number of flowers in their spikes (Dmytrakh 2013).

To assess the vitality of populations, we used the morphological approach of Zlobin (2009), establishing three vitality levels (classes) of individuals: *a* class (high vitality) – individuals with the highest values of morphometric parameters, *b* class (medium vitality) – which average values of morphometric parameters and *c* class (low vitality) – individuals with the lowest values of morphometric parameters. Selection of parameters – vitality indicators – was conducted statistically. In general, 14 morphological parameters were measured, 8 of them were common for male and female plants: the stem height, the stem width, the leaf length, the leaf width, number of leaves, the length of spike, the width of spike and the number of flowers in spikes. For the females, 6 additional parameters were involved: the length and width of perigynium, the length and width of beak of the perigynium, the length and width of fruit. During the analysis, systematically stable features were excluded, while those which had the highest variability coefficient (Cv) to the gradient of environmental conditions and correlated the least, were selected. Measurements were conducted within the random sample of 25 female and 25 male plants in each population. Ranking of individuals in terms of establishing the limits of vitality classes was conducted within the total sample of individuals of all studied populations. Based on the distribution of individuals of each vitality class in the population, the Quality index (Q) was calculated using the formula:

$$Q = 0.5 \times (a + b)$$

hereinafter: *a* and *b* – the proportion of individuals with high and medium vitality, *c* – those with low vitality. Comparing the index Q with a proportion of individuals with low vitality in a population (class C), we measured the vitality status of the population: *c* > Q – thriving populations, *c* < Q – depressed, *c* = Q – equilibrium (Zlobin 2009).

We also used another method to assess the vitality of populations proposed for rare species – vitality index of populations (IVC) (Ishbirdin *et al.* 2005). The index is calculated using the formula:

$$IVC = \frac{1}{N} \sum_{i=1}^N \frac{x_i}{X_i}$$

where X_1 – the average *i*-th feature in the population; X_i – the average *i*-th feature for all populations and N – number of features.

The data were processed by traditional statistical methods (Lapach *et al.* 2001), using the software package Statistica for Windows v. 12.0.

3. Results

3.1. The spatial structure, population size and density

A significant number of *C. dioica* localities in Ukraine is concentrated in the bogs and wetlands of West Polissia. One of the biggest coenopopulations (D4) was found in a mesotrophic *Carex-Sphagnum* bog near lake Karasynets (Volyn region) in the *Menyantho trifoliatae-Sphagnetum teretis* Warén 1926 association of the *Sphagno warnstorffii-Tomentypnion nitentis* Dahl 1956 alliance and *Scheuchzerio palustris-Caricetea nigrae* Tüxen 1937 class. The optimal ecological and coenotical conditions for the species were observed in this locality (sufficient level of lighting and watering). In particular, the population density was quite high, accounting for 128.0 generative shoots m⁻² and 730.2 young shoots m⁻² (Table 1).

The highest density of the species was observed in so-called “windows” with a free space from *Carex*

lasiocarpa Ehrh., *C. appropinquata* Schum. and other competitive species. On plots with intensive growth of the shrub layer, the density was considerably lower, comprising 5-20 generative shoots. The sex structure was dominated by females, forming lengthy compact groups compared to male ones (Tables 1-2).

The indexes of renewal (547%) and substitution (226%) of the population indicated that the reproduction and aging processes were balanced (Table 1). A significant number of young individuals were formed by seed propagation, as the number of seedlings was the highest in this population (Table 1). Intensive generative and vegetative reproduction promoted spatial overlapping of male and female clones of *C. dioica*, diffusive disposition of single generative shoots and the formation of separate exclaves located at a distance of 0.3-10 m apart, representing a mosaic type of population spatial structure.

A similar spatial structure of *C. dioica* individuals was observed in a coenopopulation in the oligo-

Table 1. Characteristics of *Carex dioica* populations

1	2	3	4	5	6	7	8	9	10
D1	900	241.3 ±7.6	2.0 ±0.1	239.3 ±7.5	1061.8 ±50.1	464.8 ±16.9	–	440	150
D2	10000	55.6 ±2.6	14.4 ±0.7	41.2 ±1.5	147.8 ±6.4	105.6 ±5.0	2.0 ±0.1	266	92
D3	30000	77.6 ±3.0	43.6 ±1.9	34.0 ±1.3	335.2 ±15.4	205.7 ±7.0	20.5 ±0.9	432	118
D4	10000	128.0 ±5.7	32.4 ±1.0	95.6 ±2.5	730.2 ±32.0	194.5 ±9.3	35.2 ±0.8	547	226
D5	7500	95.6 ±3.5	19.6 ±0.8	74.8 ±3.5	812.2 ±35.0	222.9 ±10.1	3.6 ±0.1	849	255
D6	12000	55.2 ±2.4	31.6 ±1.4	23.6 ±1.1	249.3 ±11.4	136.0 ±6.0	8.4 ±0.4	452	130
D7	2500	45.0 ±1.3	13.5 ±0.6	31.5 ±1.0	644.1 ±28.1	186.8 ±9.0	–	1431	278
D8	1400	97.2 ±2.7	97.2 ±2.7	0	368.8 ±16.2	214.3 ±9.0	0	379	118

Explanations: 1 – Number of population (description see Material and methods), 2 – Population area [m²], 3 – Density of generative shoots m⁻², M±m, 4 – Density of male individuals' shoots m⁻², M±m, 5 – Density of female individuals' shoots m⁻², M±m, 6 – Density of young (pre-generative) shoots m⁻², M±m, 7 – Density of post-generative shoots m⁻², M±m, 8 – Density of seedlings m⁻², M±m, 9 – Renewal index (R), % 10 – Substitution index (S), %

Table 2. Characteristics of sex structure of *Carex dioica* populations

1	2		3		4
	♂	♀	♂	♀	
D1	2.0±0.1	239.3±7.5	–	18.9±0.8	–
D2	14.4±0.7	41.2±1.5	42.6±1.6	26.7±1.0	1:1.8
D3	43.6±1.9	34.0±1.3	29.0±1.1	16.8±0.8	2.3:1
D4	32.4±1.0	95.6±2.5	24.9±1.0	16.9±0.6	1:2
D5	19.6±0.8	74.8±3.5	25.6±0.9	21.3±1.0	1:2.3
D6	31.6±1.4	23.6±1.1	17.1±0.7	17.4±0.7	1.3:1
D7	13.5±0.6	31.5±1.0	30.6±1.0	22.3±1.1	1:1.7
D8	97.2±2.7	0	32.0±1.0	0	–

Explanations: 1 – Number of population (description see Material and methods), 2 – Density of generative shoots m⁻², M±m, 3 – Number of flowers per shoot, 4 – Sex ratio, ♂:♀

mesotrophic bog “Bolittse” (D5), Volyn region in the *Sphagno recurvi-Caricetum lasiocarpae* Zólyomi 1931 association of the *Sphagno-Caricion canescentis* Pas-sarge (1964) 1978 (*Scheuchzerio palustris-Caricetea nigrae*) alliance. The generative reproduction intensity here was slightly lower, as evidenced by the number of seedlings identified in the population and, obviously, due to the low participation of male individuals (Table 1). The indices of renewal and substitution – 849% and 255%, respectively, indicated the effective vegetative reproduction of the population. As for its spatial structure, the individual clusters were of a small area and density located at a distance of 0.5-4.0 m apart on somewhat higher plots of the bog with a well-developed *Sphagnum* cover. Spatial overlapping of heterosexual clones of *C. dioica* was mainly caused by vegetative propagation of individuals and the intensive growth of rhizomes in the moss hillocks. On these hillocks, compact groups of male individuals were formed, surrounded by females, much larger in size.

An entirely different type of spatial structure was found in a *C. dioica* coenopopulation in a meso-oligotrophic bog of lake Luky (D2) in the *Sphagno recurvi-Caricetum rostratae* Steffen 1931 association (*Sphagno-Caricion canescentis*, *Scheuchzerio palustris-Caricetea nigrae*). Compared to both described above, this population was characterised by twice lower density of young and generative shoots, obviously due to slightly different ecological and coenotic conditions and anthropogenic load (Table 1). In particular, because of trees and shrubs distributed on most of the bog area, shading was high, forming unfavourable conditions for a typical heliophyte species. Another negative factor was trampling, associated with harvesting of berries of *Oxycoccus palustris* Pers. Such conditions caused low efficiency of both generative and vegetative propagation in the population and promoted formation of its compact-diffuse spatial structure. The individuals of both sexes were characterised by much longer rhizomes, which provided an effective “search” of nutritional resources and formation of separate, extended clusters of generative shoots. Some individuals reached a high density in the central population area, where the shrub layer was sparse, and less – at the periphery. The distance among clusters was small, ranging from 0.2 m to 3.0 m, between which there were up to 3-10 single generative shoots. So, the compact-diffuse spatial structure was typical for a population with low capacity for renewal, which was determined both by anthropogenic influence and ecological conditions (low lighting degree etc.).

Generative reproduction in the population contributed to its densely-diffuse spatial structure which was found in two studied coenopopulations: in the meso-eutrophic bog “Unychi” (D3), Volyn region in the *Drepano-clado revolventis-Caricetum lasiocarpae* (Koch 1926)

Rybniček 1984 association of the *Caricion lasiocarpae* Vanden Berghen alliance in Lebrun *et al.* 1949 and mesotrophic bog “Koza” (D6), Rivne region in the *Menyantho trifoliatae-Sphagnetum teretis* (*Sphagno warnstorffii-Tomentypnion nitentis*, *Scheuchzerio palustris-Caricetea nigrae*) association. These were characterised by a similar ratio of generative and “before generative” young individual shoots and a significant predominance of males in sex structure (Table 2). Perhaps this may have increased the efficiency of pollination and the formation of seedlings. It should also be noted that for the population in the “Koza” bog, a somewhat intense vegetative renewal was observed. This was likely due to the well-developed moss cover and periodic mowing of the bog area. Under the current conditions, the densely-diffuse spatial structure was prevailing in both populations, namely: clusters of generative shoots (especially males) were small in size and number, separated from each other by the distances of 5-15 m; mainly single generative shoots were dominant.

In conditions not fully complying with ecological and coenotic optimum of the species, the generative reproduction was inferior in its effectiveness to the vegetative one. The intensity of the latter contributed to a clonal population organisation and its group spatial structure. This type of location of individuals was found in two coenopopulations in quite different ecological conditions. One of them was in the mesotrophic bog in the vicinity of Hlivchany village (D7), Lviv region in the *Menyantho trifoliatae-Sphagnetum teretis* association. Both low density of generative shoots (45.0 ± 1.3) in the population and a weak ability of individuals to seed reproduction was compensated by effective vegetative renewal, which was indicated by the appropriate indices: renewal index – 1431%; substitution index – 278% (Table 1). Localisation of young individuals directly near the “parent” plants contributed to the formation of clearly separate male and female clones. The main threat to this population was the development of intensive overgrowing processes with trees and shrubs in the bog causing increase of species diversity and, consequently, an increased competition for nutritional resources among plants. The *C. dioica* plants were trying to avoid the threat to be displaced from the community, concentrating on the most favourable for their existence plots. These were so-called *Sphagnum* “pillows”, where the relatively sparse groups numbering 4-9 male and 9-17 female generative shoots were formed. Thus, the group population spatial structure was mainly observed under unfavourable growth conditions causing poor seed propagation and prevalence of vegetative renewal in the population.

The group spatial arrangement of *C. dioica* individuals was also observed in the coenopopulation in the

mesotrophic slope bog of Stih Mt. (the Carpathians, Svydovets) in the *Caricetum nigrae* Braun 1915 association of the *Caricion canescenti-nigrae* Nordhagen 1937 alliance (*Scheuchzerio palustris-Caricetea nigrae*), the most southern isolated locality of the species (D8) in Ukraine. Under the influence of intensive grazing, recreation, etc., this population was divided into separate isolated loci with the area of 25-30 m², mostly represented by male individuals. Given this, its renewal was provided by vegetative propagation. The population density was quite high and reached 97.2 generative shoots m⁻² (Table 1). Some clusters had the area of 0.25 m² comprising 50 generative shoots. The firm ground, a little moss cover led to the presence of extremely short rhizomes in *C. dioica* individuals promoting formation of a specific life form – the so-called “false sod”, not typical for the long-rooted species, and the group spatial structure, respectively. Obviously, it helped to provide a more efficient use of nutrient resources by the plants and colonisation of the limited area.

The spotted type of spatial structure of the species was observed only in one of the studied coenopopulations

(D1) in a dried meso-eutrophic bog near Lake Pulemets (Volyn region) in the *Drepanoclado revolventis-Caricetum lasiocarpae* association (*Caricion lasiocarpae*, *Scheuchzerio palustris-Caricetea nigrae*). This coenopopulation was subjected to intense anthropogenic load and was characterised by an almost complete dominance of females (Table 2). This deviation from the normal sex ratio (1:1) prevented seed renovation of individuals. As a result, massive mobile vegetative female clones located on the moss “pillows” and in the areas with sparse grass cover were formed. Clearly separated *C. dioica* exclaves looked like great spots, reaching areas of 1.5-2.0 m² and a density of 250 generative shoots.

3.2. Age structure

We noticed that, regardless of the growth conditions, all *C. dioica* populations were characterised by a left-hand age spectrum, but with a different ratio of young (before generative), reproductive and old (post-generative etc.) shoots (Fig. 1A-D). A significant number of young shoots (j, im, v) in each of the studied populations, compared to the generative ones, was the

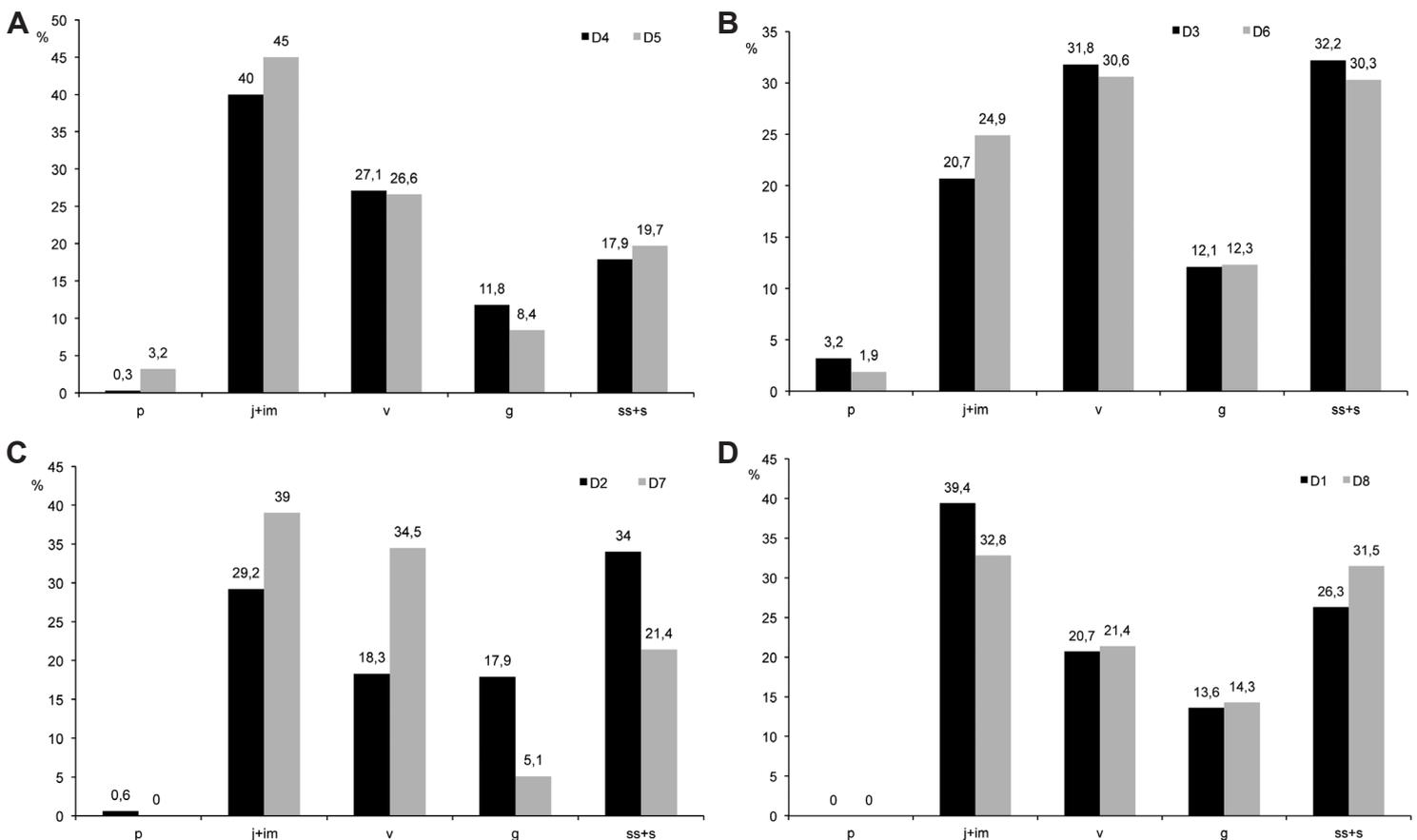


Fig. 1. Distribution of the different age shoots (%) in *Carex dioica* populations under various growth conditions. A – conservation regime (moderately wet mesotrophic and oligo-mesotrophic *Carex-Sphagnum* bogs); B – conservation regime + trampling (mesotrophic and meso-eutrophic extremely watered *Carex-Hypnum* and *Carex-Sphagnum* bogs); C – conservation regime + slight trampling (mesotrophic and meso-oligotrophic bogs subjected to overgrowing); D – anthropogenic load (pasture, trampling, destruction of the habitats)

Explanations: p – seedlings, j+im – juvenile and immature shoots, v – virginile shoots, g – generative shoots, ss+s – post-generative shoots (senile and subsenile)

result of effective vegetative renovation of individuals, as the number of detected seedlings, which, in most cases, did not exceed 4%, was too small to essentially affect the character of the age spectrum, and in some populations seedlings were completely absent.

In conditions close to the ecological and coenotic optimum of *C. dioica*, which we consider to be moderately flooded mesotrophic and oligo-mesotrophic bogs (*Carex-Sphagnum* etc), the biggest part of young shoots occurred in the age range, representing 40.0-45.0% in D4 and D5 populations, while the number of old shoots did not exceed 20% (Fig. 1A). However, in populations subjected to negative impact of trampling and overgrown by communities with shrubs (D3, D6), its part was two times lower: j + im – 20.7-24.9% (Fig. 1B). Despite the presence of seed renovation in D3 and D6 populations, still there was a tendency for the increase in the number of old shoots in their composition, because of the substrate “sodding” and premature dying of damaged vegetative shoots. The number of seedlings in the above mentioned populations naturally varied from 0.3 to 3.2% with an increase in the proportion of generative shoots from 8.4% to 12.3% (Fig. 1A-B).

The prevalence of vegetative reproduction in the D7 population was represented by a small proportion of generative shoots (5.1%), almost complete absence of seedlings and substantial displacement of the age spectrum towards young group of shoots: j + im – 39.0%, v – 34.5% (Fig. 1C). Obviously, the determining factor hindering the seed reproduction within a population was biotope conditions – a bog subjected to overgrowth. Nevertheless, the population was effectively reproduced, as evidenced by the relatively low (21,4%) percentage of post-generative shoots.

A somewhat different shoot ratio was observed in the population south-east of Lake Luky (D2), which was also located in a community with significant development of trees and a shrub layer. The greatest number of generative shoots in this population (17.9%) was not accompanied by an effective seed reproduction, because the proportion of seedlings recorded was one of the smallest. However, due to vegetative reproduction, the ratio between young shoots and post-generative ones remained balanced (Fig. 1C).

There were no essential differences either in the age range of D1 and D8 populations, which were subjected to a great anthropogenic impact (Fig. 1D). A specific feature of these populations was a trend to maintain a balance between the processes of reproduction and dying, which was obviously the result of regular vegetative renewal guaranteeing their stable existence in an anthropogenically transformed area. A significant part of the post-generative shoots was quite normal in these populations because of the influence of constant trampling, grazing etc. As seen in Fig. 1D, the aging

processes were more intense in the D8 population, which was represented almost exclusively by male individuals, while females of the D1 population had a slightly larger reproduction potential, as indicated by a significant number of young shoots in its structure (60.1%).

3.3. Sex structure

The sex structure of *C. dioica* populations turned out to be quite labile depending on the growth conditions. Based on the research, we established four possible combinations of sex ratio of *C. dioica* individuals. The most common appeared the proportion in which the females prevailed (about 2:1). This ratio was recorded for the D2, D4, D5 and D7 populations (Table 2) and was considered as the most typical for dioecious species under more or less favourable growth conditions. In particular, characteristic features of the investigated bogs were an optimal hydrological regime, i.e. moderate watering, 90-100% moss cover and necessary trophic resources (excepting the development of overgrowing processes in D2, D7 coenopopulations). Predominance of females in their composition was also obvious in view of the clonal structure of the studied populations. As shown by previous studies, females have a much more vegetative mobility than males, therefore, they usually form numerous clones providing their high density.

Still, the actual sex ratio should be determined not only by means of counting the number of male and female shoots but also taking into account the number of flowers in their spikes. By estimation of male individual shoots of almost all studied populations, they appeared to have more flowers in their spikes, ranging from 17.1-42.6 flowers per shoot. The observed pattern suggested a compensation for a small number of males in studied populations and relative levelling of the sex ratio, which was mostly 1♂: 2♀ (Table 2).

However, species populations subjected to anthropogenic load (trampling, grazing) and not the best eco-coenotic conditions (changing hydrological regime, etc.) were characterised by a considerable change in the sex ratio towards predominance of male individuals (Fig. 2). Thus, a substantial increase in the proportion of males was observed in the D3 and D6 populations whose habitats were characterised by significant soil “sodding” and overgrowth of the communities. Presumably, under these conditions, the growth of the rhizomes of female plants was somewhat depressed resulting in their low mobility and density. Instead, the males were supported by an effective strength through specialisation to the bushing and forming compact clumps, ensuring their dominance in the sex ratio (Fig. 2).

The extreme adaptation of heterosexual *C. dioica* individuals to the existence in the anthropogenic disturbed area was represented by almost complete superiority of females in the D1 population in West

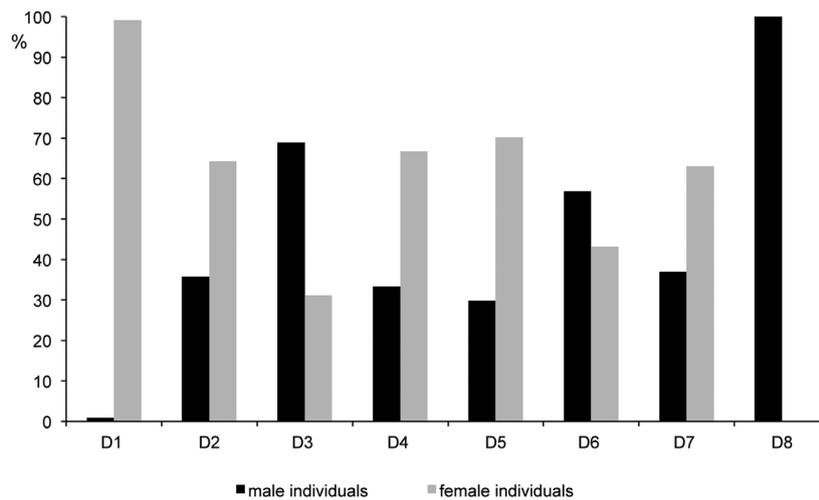


Fig. 2. Sex structure of *Carex dioica* populations in Ukraine

Explanations: D1-D8 – the number of population

Polissia (vicinity of the village Pulemets) and the formation of isolated population – D8 in the Carpathians, represented by male individuals (Table 2). A radically opposite sex ratio fixed for these populations was evidence of incomplete identity of ecological optima and tolerance of heterosexual individuals under stress conditions.

The habitat of the D8 population was the upper limit of the *C. dioica* distribution in the highlands, where the growth conditions were much more extreme than on the plains. Our previous results showed that under stressful conditions, male individuals were more ecologically flexible by a number of parameters, including the observed greater morphological variability and degree of morphological integration (integrity), which led to their high adaptive capacity and provided an effective renewal of the mountain population and their further colonisation of the upper horizons. At the same time, the energy costs needed for reproduction were rather small compared to females, due to their specific participation in the seed and vegetative reproduction and relatively lower mobility. Therefore, minimum nutritional resources of the studied habitat

were insufficient for effective functioning of the female plants, while the formation of dense, compact clumps of males provided them with a more efficient use of the limited resources and colonisation of the available area. The above mentioned heterogeneity and plasticity of males in this case was manifested in the formation of hybrid spikes that had 1-2 sacs (2 such spikes were found in the population). This phenomenon was just a specific adaptation, aimed at preserving the mobilisation provision and seed reproduction in a population for which even isolated cases of successful episodic sex reproduction may be enough.

However, females of *C. dioica* were larger in size with well developed generative and vegetative structures, so they appeared to be more competitive in the early stages of plant succession in the dried meso-eutrophic bog in the vicinity of the village Pulemets (D1). Their significant advantage was the ability to form long rhizomes in the moss “pillows”. Given the small area of the optimal colonisation area, females provided their maximum occupancy due to their great vegetative mobility. Under these conditions, male plants were not able to compete with them in terms of

Table 3. Morphometric features of male individuals of *Carex dioica* populations

	1	2	3	4	5	6	7	8	9
M	22.08	0.49	9.21	0.49	4.49	12.53	1.79	28.88	
m	0.67	0.02	0.42	0.01	0.11	0.35	0.05	1.01	
Min	11.50	0.30	2.80	0.30	3.00	6.10	0.80	10.00	
Max	35.40	0.80	24.00	0.70	5.00	24.00	4.00	62.00	
CV, %	23.49	18.06	57.33	18.18	15.71	33.74	19.82	40.88	

Explanations: 1 – Statistical parameters, 2 – Stem length [cm], 3 – Stem width [mm], 4 – Leaf length [cm], 5 – Leaf width [mm], 6 – Number of leaves, 7 – Spike length [mm], 8 – Spike width [mm], 9 – Number of flowers in spikes

Table 4. Morphometric features of female individuals of *Carex dioica* populations

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
M	25.91	0.58	9.91	0.57	4.68	9.59	5.77	20.07	3.07	1.48	0.97	0.32	1.56	1.09
m	0.61	0.02	0.19	0.02	0.16	0.33	0.17	0.78	0.05	0.02	0.03	0.01	0.02	0.02
Min	14.70	0.30	2.90	0.30	3.00	5.30	2.50	7.00	2.30	0.70	0.60	0.30	1.20	0.70
Max	39.00	0.90	24.90	0.10	5.00	15.20	8.00	40.00	3.70	2.00	1.40	0.90	1.90	1.50
CV, %	19.87	19.29	44.41	17.31	18.49	19.18	19.55	29.49	7.05	12.19	14.32	15.37	7.92	11.18

Explanations: 1 – Statistical parameters, 2 – Stem length [cm], 3 – Stem width [mm], 4 – Leaf length [cm], 5 – Leaf width [mm], 6 – Number of leaves, 7 – Spike length [mm], 8 – Spike width [mm], 9 – Number of flowers in spikes, 10 – Peryginium length [mm], 11 – Peryginium width [mm], 12 – Length of the beak of peryginium [mm], 13 – Width of the beak of peryginium [mm], 14 – Fruit length [mm], 15 – Fruit width [mm]

vegetative renewal, and rather with other bog species, and, therefore, they were displaced from the population.

3.4. Vitality structure

To assess the vitality of *C. dioica* populations, the most variable and less correlated morphological parameters were chosen, namely stem height, leaf length and number of flowers in the spikes (Tables 3, 4).

A vitality analysis was conducted on the basis of sex differentiation of individuals, so the ranking according to the vitality classes and the calculation of the indices was performed within separate samples of male and female individuals. The assessment of the vitality index for the heterosexual plants showed their complete mutual compliance, i.e. the highest values of IVC and Q within the sample of females correspond to maximum values of indices within the sample of the males in each of the studied populations (Table 5). This gave evidence that population of dioecious species reacted to any changes of environment as a complete integrated system.

The IVC index values within the sample of females ranged from 0.77 to 1.36 and, in almost all cases, they exceeded those of males (0.65-1.26) or were less

identical (Table 5). Moreover, the percentage of females of high and medium vitality classes was usually greater than the number of males of these classes. This distribution of values was associated with the advantage of females in the size of most of their morphological parameters, and only by the number of flowers in spikes they were inferior to male ones. The observed pattern suggested that females made a greater contribution to the vitality of the studied populations.

The assessment of the Q index within the samples of male and female individuals showed that 3 populations, such as D2, D4 and D7, were considered to be thriving. These also had the highest values of the IVC index. Population D5, in terms of the Q index for a sample of males, was equilibrium, while as to the corresponding measure for females – it appeared to be thriving. A depressed vitality type was observed in the D3 and D6 populations characterised by prevalence of male plants as well as in the D1 and D8 populations, consisting almost totally of female or male individuals, respectively. A low vitality status of these populations was theoretically expected, because the deviation from the typical sex ratio was already evidence of stress or even critical conditions of their existence. The main

Table 5. Vitality structure of *Carex dioica* populations

1	2 [%]						IVC		Q		3	
	High (class a)		Medium (class b)		Low (class c)		♂	♀	♂	♀	♂	♀
	♂	♀	♂	♀	♂	♀						
D1	-	14.7	-	17.3	-	68.0	-	0.86	-	16.0	-	D
D2	45.3	70.7	40.0	20.0	14.7	9.3	1.26	1.36	42.7	45.4	T	T
D3	13.3	2.7	14.7	26.7	72.0	70.6	0.83	0.85	14.0	14.7	D	D
D4	29.3	38.7	38.7	36.0	32.0	25.3	0.98	1.03	34.0	37.3	T	T
D5	37.3	34.7	29.3	33.3	33.3	32.0	0.96	1.00	33.3	34.0	E	T
D6	6.7	10.7	5.3	16.0	88.0	73.3	0.65	0.77	6.0	13.4	D	D
D7	65.3	65.3	18.7	20.0	16.0	14.7	1.23	1.23	42.0	42.7	T	T
D8	18.7	-	12.0	-	69.3	-	0.82	-	15.3	-	D	-

Explanations: 1 – Number of population (description see Material and methods); 2 – Proportion of individuals in populations in vitality classes; 3 – Vitality type of population, D – depressed, E – equilibril, T – thriving

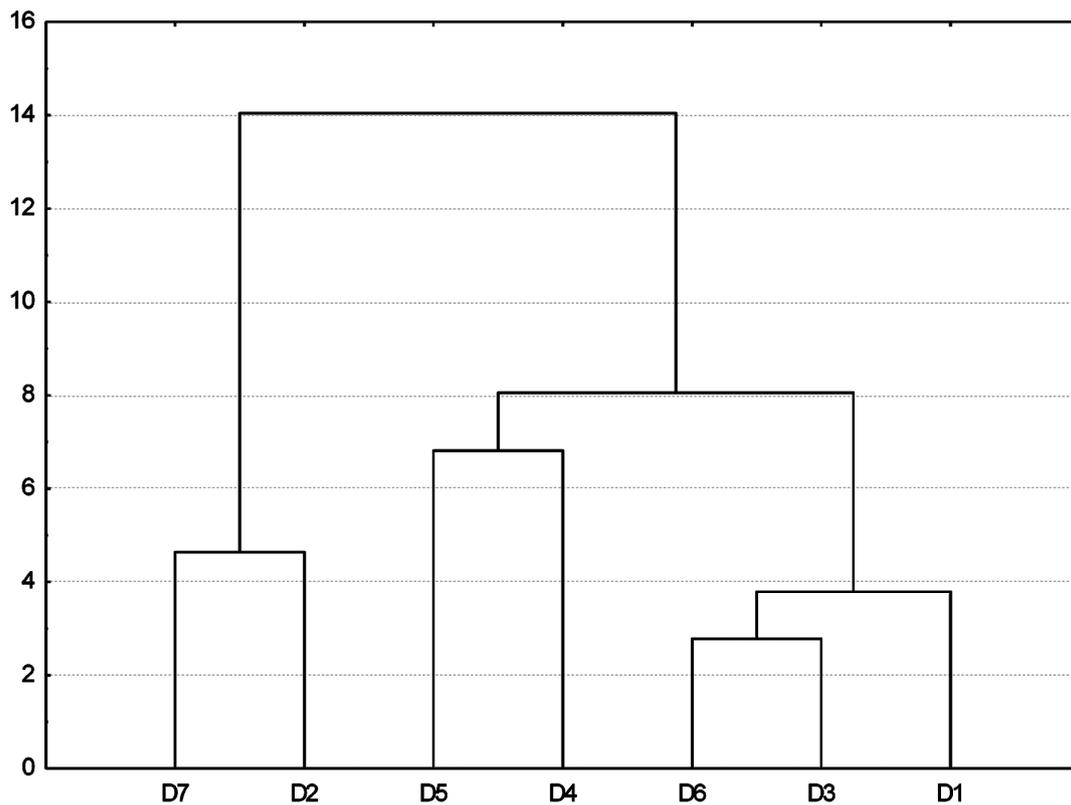


Fig. 3. Diagram of studied populations of *Carex dioica* based on cluster analysis (Euclidean distances) of morphometric features of male individuals

Explanations: D1-D7 – the number of population

factors providing a high number of individuals of low vitality class in these populations were either natural (D3 and D6) or anthropogenic (D1 and D8).

Conducting the cluster analysis of the whole set of morphometric parameters of individuals allowed us to group the most similar populations of *C. dioica* as to their structure and sex differentiation (Figs. 3-4). Given the differences in the average values of the parameters of males and females as well as their number (14 and 8 respectively), we analyzed the separate samples of heterosexual individuals (males – Dm and females – Df) of all studied populations. Subsequently, it allowed us to compare the results concerning the influence of growth conditions on individuals of each gender. Since two studied populations were characterized by almost complete dominance of females (D1 population) or males (D8 population), the analysis of each statistical sample involved 7 populations. Thus, the statistical sample of female individuals (Df) represented the populations: D1, D2, D3, D4, D5, D6, D7, and the sample of males (Dm): D2, D3, D4, D5, D6, D7, D8, respectively.

The populations in each statistical sample were grouped in clusters according to similar features of growth conditions (including geographic distribution and links with particular *syntaxa*), which affected the heterosexual individuals in a different way.

Interestingly, some coenopopulations, belonging to the same association type (D4, D6, D7) appeared in separate clusters, meaning that population structure of *C. dioica* (in particular sex) was affected by a complex of various environmental factors, including both natural and anthropogenic ones.

As shown in Figs. 3 and 4, a separate cluster was formed by D4 and D5 populations which corresponded to most optimal growth conditions both for male and female individuals, including coenotic, ecological factors and the low anthropogenic load. These populations were the most similar for spatial and ontogenetic structure as well as for sex ratio of individuals and their vitality.

A separate cluster within male and female samples was represented by D3 and D6 populations (Figs. 3-4). Mesotrophic bogs with excessive level of humidity, slightly developed sphagnum cover, together with significant soil sodding and human pressure (trampling) defined a set of conditions under which the populations consisting of low vitality individuals with changed sex ratio, dominated by males, were formed.

The populations D1 and D8 formed a separate branch within both samples, which was explained by their existence under stress and even critical conditions causing its significant structural changes, namely incomplete sex

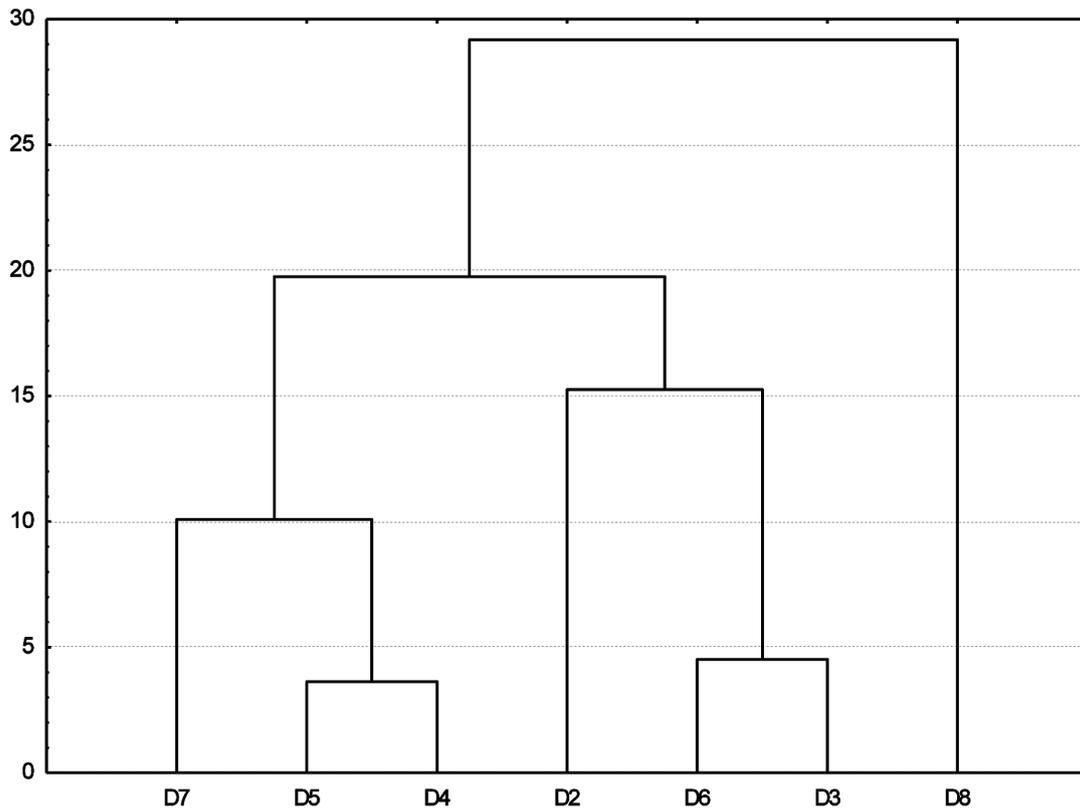


Fig. 4. Diagram of studied populations of *Carex dioica* based on cluster analysis (Euclidean distances) of morphometric features of female individuals

Explanations: D1-D8 – the number of population

(absence of male and female plants, respectively) and ontogenetic structure (lack of seedlings), low morphometric parameters of individuals etc.

Based on the analysis, we found significant differences in the values of the Euclidean distance between the same populations grouped within samples of males and females. In particular, this applied to populations D2 and D7, which occupied cardinally different positions on both tree diagrams (Figs. 3-4). We presume that morphological differences of heterosexual individuals of these populations may provide evidence of varying degrees of their tolerance to the effect of specific environmental factors of their habitats and their ecological needs, namely lighting degree, trophic sources, humidity etc., but this aspect certainly requires further detailed study.

4. Discussion

Thus, the most important quantitative indicators of plant population structure were the density and number of individuals. These options were quite dynamic and depended on a number of exogenous and endogenous factors; their counting enabled to assess the impact of a population on the ecosystem and its functional activity. Spatial distribution of individuals was equally

important since this depended on the characteristics of the population reproduction and the complex of habitat conditions, in particular habitat heterogeneity, specifics of ecosystems, competitive relationships between species and degree of anthropogenic load etc. (Malinovsky *et al.* 1998; Zlobin 2009).

According to the research results, the most numerous populations of *C. dioica* in Ukraine were found in West Polissia under optimal ecological and coenotic conditions (D4, D5), occupying areas of tens to thousands of m² (Sosnovska *et al.* 2013). The maximum density – 241.3 generative shoots m⁻² was observed in the D1 population and was caused by a limited area of colonisation (900 m²). Under the influence of anthropogenic pressure and overgrown of bog communities with trees and shrubs, it hardly reached 45.0-77.6 generative shoots m⁻². In general, the positive dynamics of most of the *C. dioica* population self-renewal ($R = 266-1431\%$, $S = 92-278\%$) by means of vegetative (D1, D7, D8) and a combined reproduction of different intensity (generative and vegetative) (D2, D3, D4, D5, D6) was noted, particularly given the presence of seedlings in their structure (2.0-35.2 seedlings m⁻²).

We found five types of spatial arrangement of individuals depending on their reproduction and living conditions, namely: scattered-diffuse, densely-diffuse,

group, spotted and mosaic. With the prevalence of vegetative propagation in a population with low efficiency of the generative one or with a complete absence of the latter, group and spotted spatial structure were observed. This type of distribution was also typical in the case of a limited colonising space promoting maximum concentration of individuals in the most favourable and suitable habitats loci. For low intensity of seed and vegetative reproduction, the arrangement of generative individuals turned out to be compact-diffuse. An effective generative reproduction of a population was accompanied by a densely-diffuse distribution of individuals, and a combined type of reproduction (effective vegetative and seed renewal) under favourable growth conditions contributed to its mosaic spatial structure (Izmestieva & Danylyk 2013).

The structure of the age spectrum depended on the environmental conditions and the duration of the existence of populations in certain communities; therefore, its analysis allowed studying the way how the populations adapted to specific conditions. Thus, the age range indicated a certain stage of the population development; based on this, it was possible to determine its prospects and sustainability in a coenosis.

It was established that, regardless of the growth conditions, all *C. dioica* populations were characterised by a left-hand age spectrum. A significant number of young shoots in each of the studied populations was the result of effective vegetative renovation of individuals, as the number of detected seedlings in most cases did not exceed 4%. A significant predominance of young shoots may also have been manifestation of a stress-tolerant type of strategy of this species (Tsaryk *et al.* 2001).

The investigation of the population self-renewal unavoidably raises the issue concerning its sex structure. Depending on the characteristics of the genetic structure of populations and the selective influence of anthropogenic and natural factors, the sex ratio can vary widely, affecting the structural and functional organisation of populations both of monoecious and dioecious species. Heterosexual populations require specially detailed study in this regard. Identification of the ways of their functioning and causes of changes in their sex ratio are important for the understanding of dynamic processes in populations, their durability and stability.

In general, we can emphasize a multi-level regulation of sex structure in populations of dioecious species. The high lability of the sex structure of *C. dioica* populations is mainly determined by incomplete identity of ecological optima and tolerance of heterosexual individuals under stress conditions and a specific survival strategy (Dmytrakh 2003, 2008, 2009 and others). Thus, under favourable conditions, female individuals usually prevail in populations. Under conditions limiting the vegetative mobility of

females in *C. dioica* populations (“sodding” of soil etc.), an increase of males in the sex proportion was observed. Under stress conditions, a selective effect of both natural and anthropogenic factors on heterosexual individuals was accompanied by a radical change in the sex ratio towards complete dominance of one of the genders. High competitiveness of females combined with a special adaptive survival strategy promoted their stable positions in the community and provided effective colonisation of the area (Izmestieva & Danylyk 2012). However, the ecological and morphological plasticity of males, together with minimum energy requirements, determined their ability to occupy biotopes with less favourable growth conditions unfit for effective functioning of female individuals, particularly on the limit of species range in the Carpathians (Danylyk *et al.* 2014). We cannot affirm the complete absence of seed reproduction in almost homosexual populations since we found *C. dioica* male individuals with bisexual spikes, a phenomenon already mentioned in literature (Alekseiev & Abramova 1980; Egorova 1999). Therefore, its prospects will depend on the stabilisation of the sex structure under the influence of growth conditions to ensure genetic diversity of the population and successful reproduction in subsequent generations.

Vitality differentiation of individuals, namely their size structure, is one of the indicators of the population state, reflecting various growth conditions for the implementation of productive processes, resource efficiency and stability under stress (Harper 1977; Hutchings 1997; Zhilyaev 2005; Begon *et al.* 2008). According to our analysis, 50% of the studied populations thrived. Regardless of the vitality type of the population, female individuals of this species, compared to the male ones, realised their growth potential much better and, therefore, made a greater contribution to population vitality. The determining factors affecting the vitality of *C. dioica* were either natural (environmental factors, competitive relationship within community etc.) or anthropogenic.

However, it should be noted that ranking of populations by vitality indices does not quite allow evaluating their viability, which is an integral feature of the main population features: renewal (cycling), expansion (settlement), keeping an area and saving evolutionary perspectives (Zhilyaev 2005; Tsaryk *et al.* 2009). In particular, this applies to some studied populations – D2 and D7. The vitality indices of these populations were the highest, but in terms of reproductive capacity, the number of individuals they yielded was lower than in populations D4 and D5. A considerable difference in values of morphological parameters of both male and female plants in these populations may have been caused by their habitus differentiation depending on growth conditions. The

D2 and D7 populations were found in communities with a significant development of trees and shrub layer, so the formation of large-sized specimens may have been an adaptation to living in low-light conditions, while in open light bog sites the plants were usually comparatively smaller. Additionally, the size structure of individuals may depend on a lot on population density, correlating with the available area for colonisation, distribution of nutrient resources as well as competitive

relations in a coenosis (White & Harper 1970; Weiner *et al.* 2001 and others). Therefore, the interpretation of the results regarding the vitality status of populations requires consideration of the impact of individual factors of natural and anthropogenic origin and their complex actions as well as biology of the species.

Acknowledgments. We would like to thank Jacob Koopman and Helena Więclaw for assistance and counselling in preparing this article.

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