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Life forms and shoot structure of the invasive species *Geranium sibiricum* l. (Geraniaceae) in two local populations in Ukraine

M.S. Kalista, O.A. Kovalenko

It was found out that the life form of the alien invasive plant species *Geranium sibiricum* is interpreted ambiguously in various literature sources, and in the description of underground organs (shoot and root systems), the statements of different authors are often even contradictory. Eighty individuals of *G. sibiricum* collected in 2019–2021 during field research in two local populations: in Pyriatyn town (Poltava Oblast) and Kyiv City (Kyiv Oblast) were revised by varying the type of growth form and shoot structures using the deep concept of the caudexes diversity and their differences from other structural formations. The basic life form and model of shoot formation of *G. sibiricum*, which is a biennial conode taproot monocarpic with monopodial branching type, were clarified. In the connection with the pronounced polyvariety of the species life form two more types of it were described in *G. sibiricum* individuals: caudex taproot oligocarpic and basiphys fibrousroot oligocarpic with sympodial type of branching. The structure of elementary inflorescences of *G. sibiricum* was analysed, the structure of its above-ground and underground shoot system, as well as the root system, was investigated. It was identified that *G. sibiricum* individuals in Pyriatyn town and Kyiv City populations differ in the length of the flowering shoot, the length of the internodes, and the level of branching, and they have different types of generative shoots according to their location in space. It was found that the diversity of the architectural structure of individuals of this invasive species, associated with different growth conditions, could probably be an adaptation to the specific environmental conditions of their populations and could be valuable for studying the introduction of invasive species and determining the developmental stages at which the management of their populations will be most effective.

Key words*: alien plant, populations, plant structure, life forms, plant morphology, polymorphism*

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Introduction

Plant life and growth forms represent key functional strategies plants in relation to their environment and provide important insights into the ecological constraints acting on the distribution of biodiversity (Taylor et al., 2023). Studies on life forms and a more thorough insight into the plant structure which has enabled a better understanding of the growth strategy of each plant species (Perreta, Vegetti, 2005). This dynamical morphological approach is a comprehensive tool to clarify the various adaptations that occur in species concerning space occupation, competition and resistance to disturbing factors (Fournier, 1982; Barthélémy, Caraglio, 2007; Deellaferrera et al., 2014).

Growth form is considered the complex of genetically constant vegetative and reproductive characters, which vary only within a specific range of phenotypic plasticity. The study of the forms of growth is comparative and is linked to the analysis of the interactions with the habitat. It takes into account the successive stages that lead to the construction of the plant body from germination, and also analyses the different phenological phases through which it goes through during the year, mainly with regard to exomorphology, although it can be complemented with anatomical studies of the different organs. In other

words, it reflects the local and temporal adaptation of the plant to abiotic factors (Meusel, 1952, 1970; Meusel et al., 1977; Montenegro, Ginocchio 1992; Deellaferrera et al., 2014).

The knowledge about life forms is successfully applied in vegetation and floristic studies, to develop programs for the conservation of certain species, in ontogenetic research, and during the analysis of plant populations (Malynovskyi, 1998; Malynovsky, Bilonoha, 2003; Kyyak, 2012; Kalista et al., 2015). The same approach can be used for investigation of invasive species. Whereas both phenotypic plasticity and locally adapted ecotypes may contribute to the success of invasive species in a wide range of habitats (Sakai et al., 2003; Geng et al., 2007; Aniszewski, 2012), the study of the structural features of life forms at different ontogenetic stages could help to determine the strategies of rapid adaptation of invasive species to new habitats, their success and consolidation in habitats. All this information may be valuable for examining the introduction of invasive species and identifying life history stages where management will be most effective (Sakai et al., 2003).

Geranium sibiricum L. is a kenophyte of Asian origin (Protopopova, 1992; Drescher et al., 2012). By the middle of the twentieth century, it was a rare species in Ukraine (Dobrochaieva, 1955). However, in recent decades its localities have been recorded in many biogeographical zones of Ukraine (Kovtun, 2004; Lukash, 2008; Leshchenko, Bengus, 2016) (fig. 1). *G. sibiricum* is naturalized not only in ruderal habitats, but also occupies semi-natural and natural plant communities (Khlystun, 2006; Kovalenko, 2010). Phytocenotic activity of this species on steppe meadows increases under conditions of high anthropogenic pressure (Tishchenko, 2009).

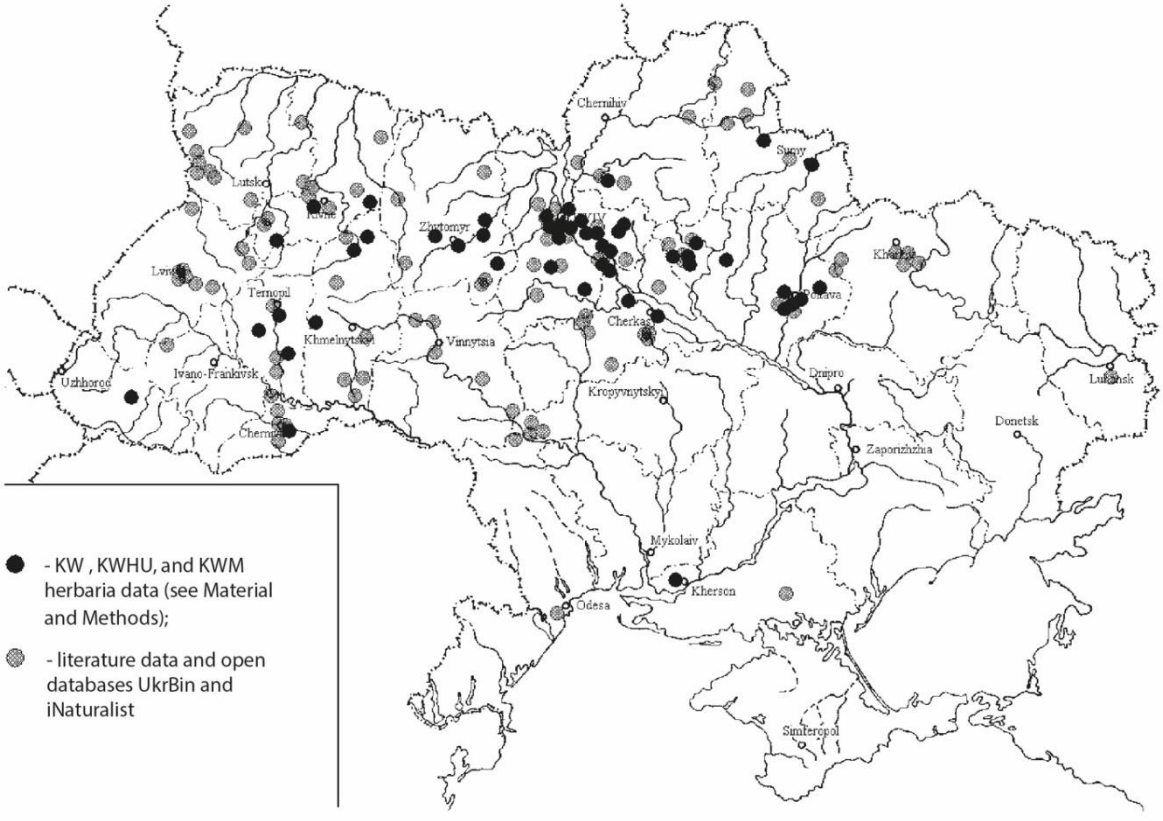

Fig. 1. Distribution map of *Geranium sibiricum* in Ukraine

Biomorphological features and population biology of *G. sibiricum* are poorly studied. Moreover, the life form of this species in the literature sources is interpreted ambiguously, so the statements of different authors sometimes are opposite. And there is no unambiguous definition in the description of its underground organs: as indistinct rhizome or short rhizome with a system of additional roots and even taproot system that is not combined with rhizome at all as with the biennial type of life form monocarpic life cycle. Besides in the literature sources shoot formation model of this plant is given as a semi-rosette

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sympodial or monopodial (Kalista, Kovalenko, 2021a). Therefore, morphological features of *G. sibiricum* life form: shoots (particularly underground) and roots are a poorly or ambiguously studied and there is no common opinion on this, consequently, this study on the structure of *G. sibiricum* growth forms is a valuable and important task for understanding the biology of the species and its adaptive capabilities.

Materials and methods

Fresh plant materials and herbarium specimens of *G. sibiricum* collected in 2019–2021 during field surveys in its local populations. Also, KW (National Herbarium of Ukraine), KWHU (Herbarium of Academic O.V. Fomin Botanical Garden of Taras Shevchenko National University of Kyiv) and KWM (Herbarium of National Museum of Natural History of NAS of Ukraine) herbaria, two open databases UkrBin (https://www.ukrbin.com) and iNaturalist (https://www.inaturalist.org), and literature data used in this paper were revised and applied for species distribution map building. Eighty individuals from each population were analysed for studying their growth form type and structure of shoots according to Harper (1977) approaches.

Population investigations were conducted in two localities within Ukraine: I – roadside in Pyriatyn town (Poltava Oblast) (50.242825, 32.524750) and II – meadows on the territory of Sviatoshyn ponds (pound №14) in Kyiv city (Kyiv Oblast) (50.462757, 30.328101) (fig. 1). Population biology of plants was studied according to Harper (1977) with some changes (Crawley, 1997; Lehmann et al., 1999).

The dynamical morphological approach in this work are based on the study of life forms and plant structure (Meusel, 1952, 1970; Meusel et al., 1977; Montenegro, Ginocchio 1992; Deellaferrera et al., 2014).and a comprehensive analysis based on the ways of their joining in the body of plants (Hallé, Oldeman, 1970; Hallé et al., 1978; Barthélémy, Caraglio, 2007). The organization of the shoot is defined according to the position of its structural and functional differentiation proposed by Troll (1964).

The concept of the variety of caudexes and their difference from other different structural formations, as well as theirs parts – “residues” (consist of the shortened bases of the shoots after the death of their upper, usually elongated, parts and belong to annual, semi-annual, and over annual (oligocyclic) monocarpic shoots) was used according to Nukhimovskiy (1969a; 1969b), who deeply developed this issue and brought into plant morphology some specific terms that absolutely fits the *G. sibiricum* underground organs is reasonably aligned with current investigation (Kalista, Kovalenko, 2021a):

1) “conode” (from the Latin “co” – together, “nodus” – node) is a basal stem part with close nodes in monocarpic plants, which provides stem branching. Monocarpic plants with conode are perennial, biennial and annual. Conode of such plants can have different structural significance: it either whole participates in the stem branching, or only the axillary cones of growth of one or two of its upper nodes form lateral shoots, or does not participate in branching at all;

2)“basiphys” (from the Greek “basis” – base, “physis” – to grow, form) is a perennial stem part, which consists, commonly, of 1–2 (3) minimoresidues, of herbaceous perennials with a sympodial type of branching and a fibrous root system, instead of the caudex.

Results

It was found out that in the floristic publications *G. sibiricum* is characterised as annual or biannual herbaceous taproot monocarpics (Bezdelev, Bezdeleva, 2006), pauciennial (obsolete term for annual and biennial plants with high plasticity of the life cycle and ontogenetic polyvariety) (Bobrov, 1949; Kalista et al., 2015) and perennial (Dobrochaieva, 1955) plant with indistinct rhizome (Webb and Ferguson, 1968) or short rhizome with system of additional roots following Volkova and Osmanova (2012). *G. sibiricum* has one (rarely two or three) strongly branched prostrate or ascending shoot (Dobrochaieva, 1955) or semi-rosette creeping shoot with monopodial (Bezdelev, Bezdeleva, 2006) or sympodial (Tsyrenova, 2007) growth. Therefore, there is no common point of view about life form and growth form of this species. It is typical for many species of *Geranium* L. genus e.g., for *Geranium robertianum* L. that has been referred to as a biennial, but also as an annual, a winter annual, and a monocarpic or polycarpic perennial (Bertin, 2001).

As a result of our field studies of *G. sibiricum* in two local populations, it was found that its individuals collected in populations I and II differ in the length of the flowering shoot, they have different types of generative shoots in space, the length of the internodes and the level of branching (fig. 2). Such differences in plant structure are due to different conditions of their habitat. Thus, developed, tall, prostrate and recumbent generative shoots are characteristic of individuals that grow in conditions of sufficiently high humidity, partial shading by shrubs and with a fairly dense and tall grass are represented completely in

population II. Smaller plants with ascending shoots tend to grow in more open areas with less grass density and predominate in population I.

In the studied places of growth, this plant dominates in the grass cover. The phytocenotic activity of *G. sibiricum* increases with increased anthropogenic load on the flora of stepped meadows. The fruits of *G. sibiricum* open scattering the seeds up to 1–2 m from a mother plant (fig. 3). Due to such autochoria, the seeds are not spread over long distances; they are concentrated around the place of growth of mother plants. In this way a community is formed, which in a few years becomes thicken and slowly increases in size. This phenomenon ensures the dominance of this species in the grass cover in most areas. This is also facilitated by no damage by insects and diseases.

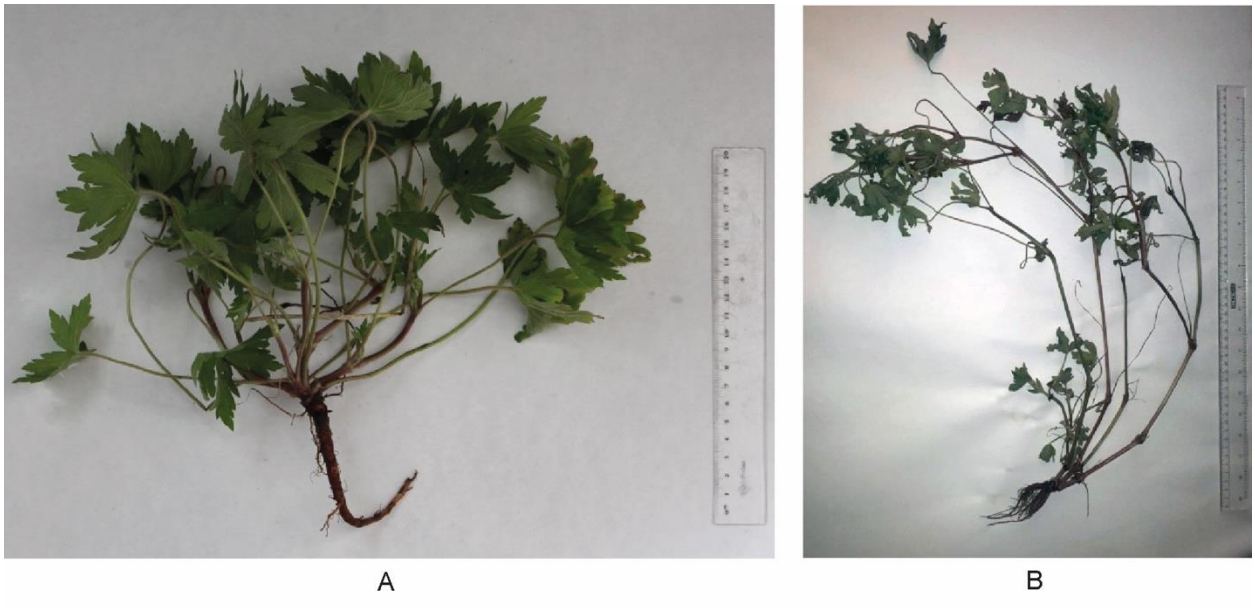

Figure 2. Generative plants of *Geranium sibiricum:* A – in population I, B – in population

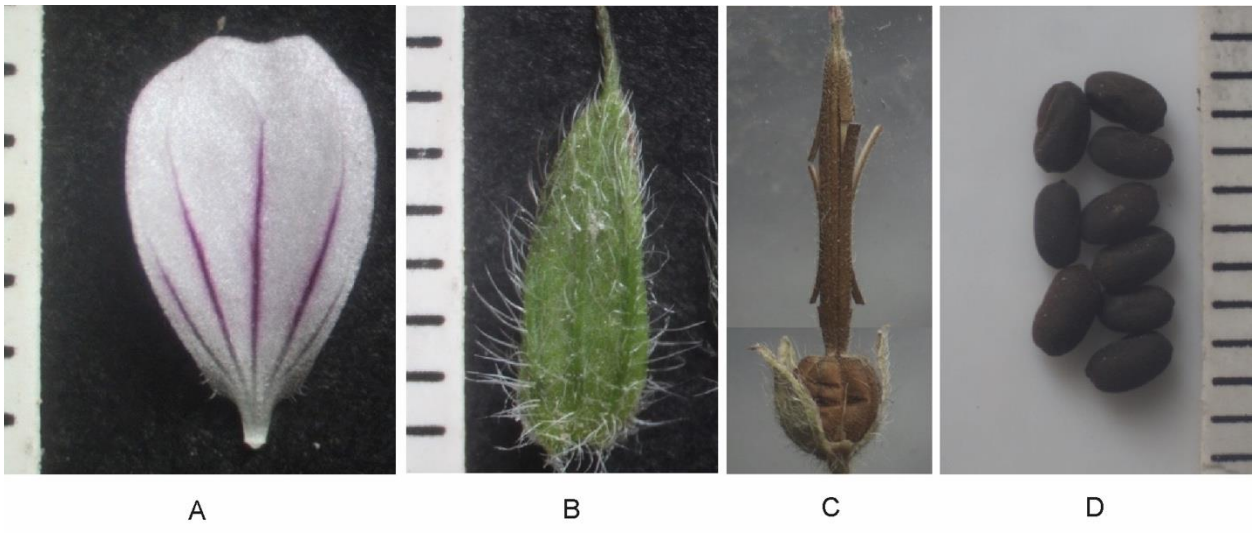

Figure 3. Generative organs of *Geranium sibiricum:* A – petal, B – sepal, C – fruit (fruitcase), D – seeds (division = 1mm)

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Troll (1964) characterized the inflorescences of the family Geraniaceae as cymose, monothelic, closed, in which the main and lateral axes have limited growth and end in a flower on the top. Thus, inflorescence of *G. sibiricum* is a monochasium, and the generative shoots have a sympodial type of branching, because the main axis ends in the cymose inflorescence. Lateral shoots of the first level of branching are formed from axillary buds of opposite leaves in the lower node, also end in apical monochasia and form in the lower node shoots of the next level of branching from axillary buds of opposite leaves (fig. 4).

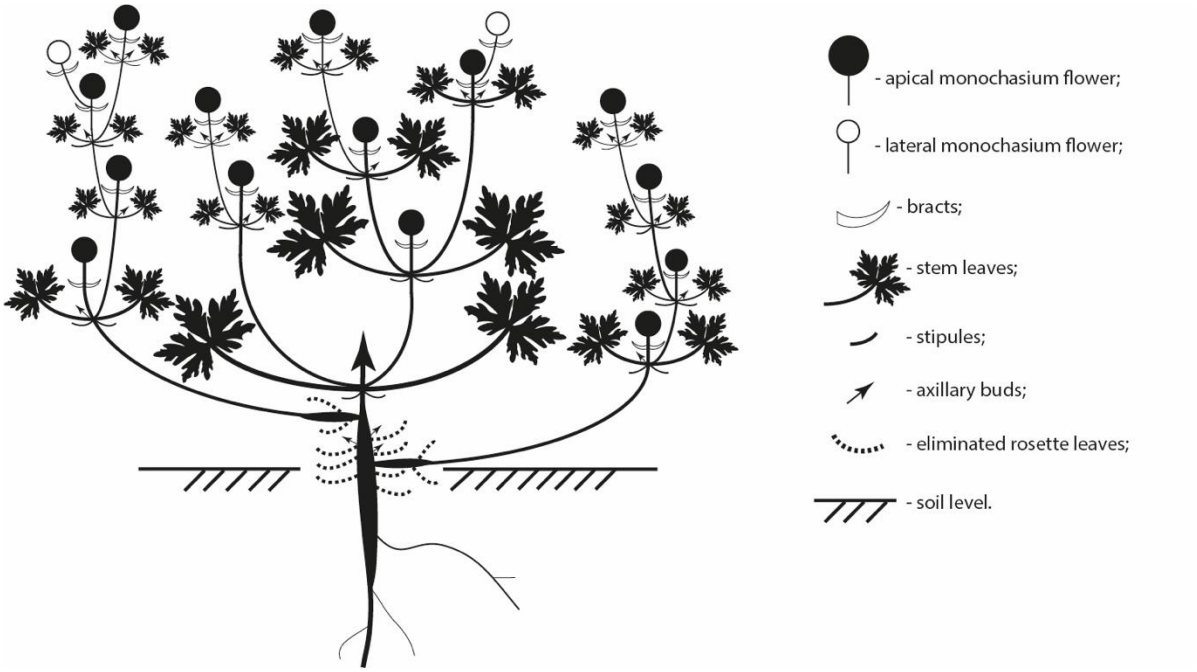

Fig. 4. Morphological structure of *Geranium sibiricum* shoots

Before flowering period, individuals have a main rosette shoot that develops as a polycyclic monocarpic shoot during 1(2) year of growth in seedlings, juvenile, immature and virginal plants. Mainly in the second growing season, the plants begin to bloom and vegetative rosette shoot transforms into monopodial semi-rosette generative shoot. In this shoot renovation, inhibition, and amplification zones are identified for *G. sibiricum* individuals. It was noted that the apex of the main shoot of *G. sibiricum* ends in two (rarely one) flowers on a flowering shoot with peduncles and two opposite underlying leaves with 1–2 (3) lateral shoots (Kalista, Kovalenko, 2021b). Based on our research, the apical bud of main shoot is never developing into an inflorescence or singular flower. Lateral branching of individuals gradually changes to sympodial and after regrowth in the next vegetative period the system of main sympodium is formed (Sugorkina, 1995), thus a subsequent development of *G. sibiricum* shoot system follows the sympodial semi-rosette model of shoot formation.

Probably due to the change in the type of branching during ontogenesis, different types of branching for *G. sibiricum* and even axillary inflorescences are cited in different publications as monopodial (Bezdelev, Bezdeleva, 2006) and sympodial (Tsyrenova, 2007). Although lateral shoots are formed from leaf axils and inflorescences complete axes of all orders of branching of all generative shoots. Since generative plants of *G. sibiricum* are characterized by a sympodial type of branching, we consider it the main in the formation of life forms.

It was also found that in population I generative shoots of individuals are mostly ascending, have 3-5 (7) levels of branching, while in population II generative shoots are ramose and decumbent, order of branching can reach 10–12, and these individuals had up to five times longer internodes and 6-7 times – the total height of plants (up to 1.2–1.6 m), in contrast to plants from population I, in which the shoots are 20-30 cm long. Elemental inflorescences of *G. sibiricum* are mostly monochasia, single-flowered (rarely two-flowered) (fig. 5).

According to our biomorphological studies, we identified that *G. sibiricum* growth forms is characterized by polyvariety and is represented by one main and two additional types. The main one is

mostly biennial conode taproot monocarpic with monopodial branching type. Occasionally, *G. sibiricum* individuals have such types of life forms: 1) caudex taproot oligocarpic with sympodial type of branching (for perennial plants that have connection of the perennial stem with the taproot); 2) basiphys fibrousroot oligocarpic with sympodial type of branching (fig. 6).

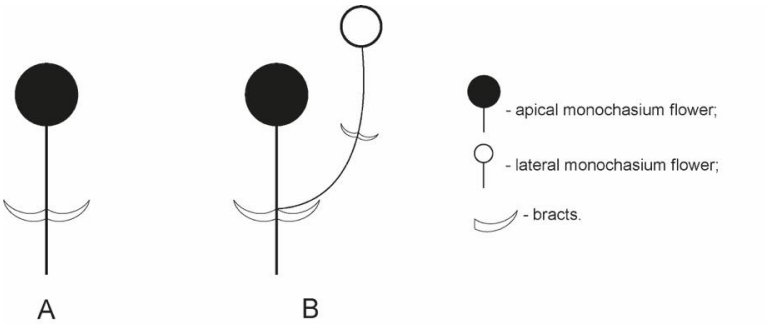

Fig. 5. Principal inflorescence of *Geranium sibiricum:* A – single-flowered monochasium, B – two-flowered monochasium

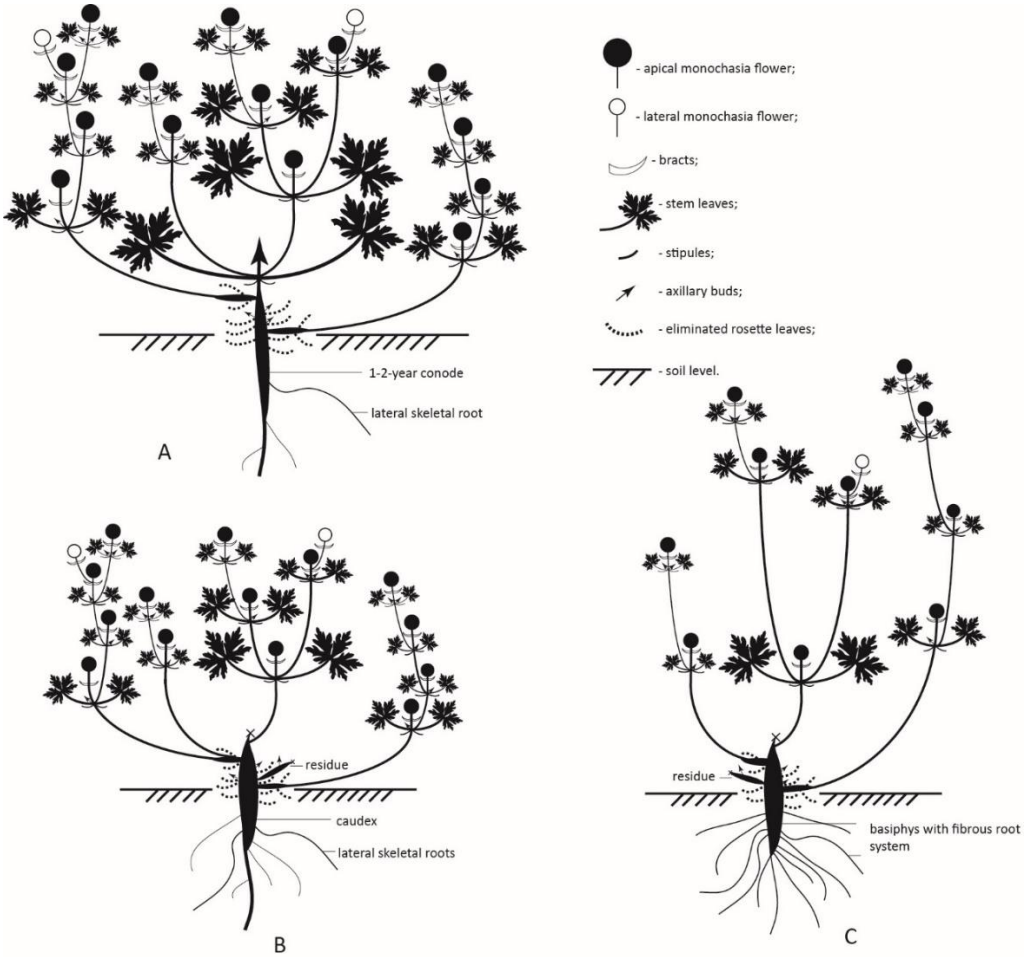

Fig. 6. Shematic growth forms of *Geranium sibiricum:* A – conode taproot monocarpic, B – caudex taproot oligocarpic, C – basiphys fibrousroot oligocarpic

We also have confirmed the data that in the process of ontogenesis the root system of individuals of *G. sibiricum* can be taproot, mixed and fibrous (Volkova and Osmanova, 2012). In plants with conode the

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taproot system (fig. 2A, 6A) persists throughout life. For caudex plants of different levels of vitality after the first year of life with the onset of flowering may retain the taproot or form mixed with a distinct main root. And for basiphys plants, the taproot develops in a mixed with the beginning of flowering and becomes fibrous, while the main root becomes indistinct (but does not die) (Kalista, Kovalenko, 2021a) (fig. 7).

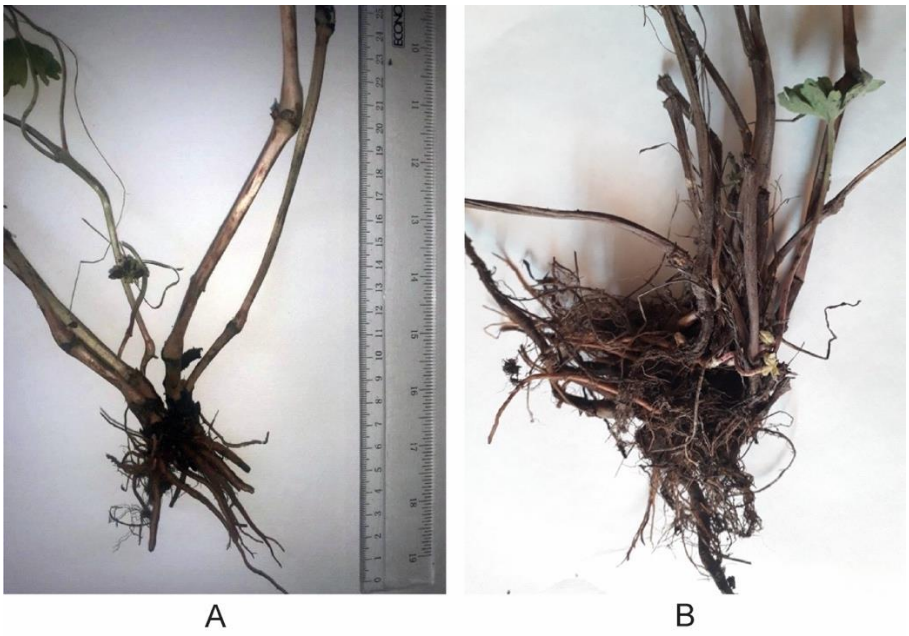

Fig. 7. Types of root systems of *Geranium sibiricum* basiphys plants***:* A – mixed, B – fibrous**

Discussion

Conode is typical of most individuals of population I and small group of individuals of population II. In these plants the main taproot retains, thickens and it is clearly distinguished, root system contains also 1-2 lateral skeletal roots, there are not so many additional roots, they have a much shorter length and diameter than the main and skeletal roots, so we considered it appropriate to use the term “conode” for the main type of *G. sibiricum* life form (fig. 6A).

We have also designated that the life forms of individuals of *G. sibiricum* is polyvariant and it is represented by two more types of life forms:

1) caudex taproot oligocarpic with sympodial type of branching (fig. 6B);

2) basiphys fibrousroot oligocarpic with sympodial type of branching (fig. 6C).

The first type of life form variations – caudex with minimoresidues – is characteristic of individuals of part of both studied populations. Such plants are capable of repeated flowering, forming a caudex with minimoresidues and a taproot or mixed (in individuals with a high level of vitality) root system. Minimoresidues are the main structural elements of the sympodial caudex, which consist of the shortened bases of the shoots after the death of their upper, usually elongated, parts and belong to annual, semi-annual, and over annual (oligocyclic) monocarpic shoots by the features of their external morphology and size. Only plants are considered to be caudex, in which the connection of the perennial stem part with the tap main root is preserved, and the degree of lignification is not of fundamental importance (Nukhimovskiy, 1969a).

Caudex is functionally (both storage nutrients and continue vegetative growth after winter) and morphologically (thickening and shortening of internodes, perenniality) similar to rhizome. That is why, in our opinion, some floristic summaries indicate the presence of an “indistinct rhizome” for *G. sibiricum.* However, unlike rhizomes, caudexes do not die in the basal part and, together with the primary root system of the plant, remain throughout life (Serebryakov and Serebryakova, 1965). Hence, it is necessary to use the term “caudex” to characterize the first type of *G. sibiricum* life form.

Individuals of the second type of life form variation represented by oligocarpic plants with developed, elongated, prostrate and decumbent generative shoots, which grow in conditions of sufficiently high humidity, partial shading by shrubs and the presence of a fairly dense and tall grass cover. They dominate

only in population II, on the other hand, they were not found in the population I at all. And this population I is represented by much smaller plants with ascending shoots that grow in more open areas and have a lower density of grass cover of equal or slightly higher plants then *G. sibiricum*. In such plants at 2-3rd year of life the main root becomes indistinct (but does not die), a large number of powerful additional roots are formed, and a fibrous root system is established. Such herbaceous perennial individuals with a sympodial type of branching and a fibrous root system, instead of the caudex develop basiphys, a perennial stem part, which consists, as a rule, of 1–2 (3) minimoresidues (Nukhimovskiy, 1969b).

Polyvariance of plant development, and, consequently, structural polymorphism are considered as manifestations of the adaptive potential of plants to the ecological and cenotic conditions of specific places of growth. The plant habit that develops under certain environmental conditions, i.e. a certain type of its structural organization is the result of a holistic reaction of the organism, represented by many private responses of its individual parts in their infrastructural organization (Scherbakova, Kalistaya, 2013). Thus, architectural polyvariance of *G. sibiricum* life form indicates shoot system structure of individuals of this species dependance from the growing conditions.

Conclusion

The main type of *G. sibiricum* life form is conode taproot monocarpic with monopodial branching type. There are two additional types of *G. sibiricum* life form: caudex taproot oligocarpic with sympodial type of branching and basiphys fibrousroot oligocarpic with sympodial type of branching. It was found that the diversity of the architectural structure of these invasive species individuals associated with different growth conditions, possibly can be an adaptation to specific environmental conditions of their populations and may be valuable for examining the introduction of invasive species and identifying life history stages where management will be most effective.

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Життєві форми та будова пагонів інвазійного виду *Geranium sibiricum* l. (Geraniaceae) у двох локальних популяціях в Україні

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Було встановлено, що життєва форма чужорідного інвазійного виду рослин *Geranium sibiricum* в різних літературних джерелах трактується неоднозначно, а в описі підземних органів (пагонової та кореневої систем) твердження різних авторів є часто навіть суперечливими. У роботі було проаналізовано вісімдесят особин *G. sibiricum,* зібраних у 2019–2021 рр. під час польових досліджень у двох локальних популяціях: у м. Пирятин (Полтавська область) та м. Києві (Київська область), з метою вивчення типу форми росту та структури пагонів з використанням поглибленої концепції різноманітності каудексів та їх відмінності від інших структурних утворень. Було уточнено основну життєву форму та модель пагоноутворення *G. sibiricum*, яка представлена дворічним конодієвим стрижневокореневим монокарпіком з моноподіальним типом галуження. В зв'язку з вираженою поліваріантністю життєвої форми виду, у особин *G. sibiricum* було описано ще два її типи: каудексовий стрижневокореневий олігокарпік та базифізний мичкуватокореневий олігокарпік з симподіальним типом галуження. Проаналізовано будову елементарних суцвіть *G. sibiricum*, досліджено будову його надземної та підземної пагонової системи, а також кореневої системи. Встановлено, що особини *G. sibiricum* у популяціях м. Пирятина та м. Києва відрізняються довжиною квітконосного пагона, довжиною міжвузлів та рівнем галуження та мають різний тип генеративних пагонів за розміщенням у просторі. Було виявлено, що різноманітність архітектурної структури особин цього інвазійного виду, пов'язана з різними умовами зростання, ймовірно, може бути адаптацією до конкретних умов навколишнього середовища їхніх популяцій і може бути цінною для вивчення інтродукції інвазійних видів та визначення етапів розвитку, на яких менеджмент їхніх популяцій буде найбільш ефективним.

Ключові слова: *чужорідна рослина, популяції, структура рослини, життєві форми, морфологія рослин, поліморфізм*

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