

PHENOLOGY AND POPULATION STRUCTURE OF FOREST HERBACEOUS SPECIES IN ARTIFICIAL AND NATURAL COMMUNITIES IN THE STEPPE ZONE OF UKRAINE

Iryna Krokhmal, Maksym Netsvetov

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In this paper, we studied features (number, density, age structure, projective cover) of forest spring-flowering mesophyte populations in artificial and natural plant communities. The artificial plant communities formed at the Donetsk Botanical Garden (Ukraine) 40 years ago. We assessed the structure of natural communities in a ravine forest as control. Six species of aboriginal flora and an introduced one dominate by projective cover in artificial plant communities: *Ficaria verna*, *Corydalis solida*, *Anemonoides ranunculoides*, *Corydalis marschalliana*, *Anemonoides blanda* (introduced), *Viola odorata*, *Anemonoides nemorosa*. The age class structure of aboriginal species in artificial community is similar to natural one. An individual growth density is higher in artificial community that implies the possibility of introducing populations of these species in urban greening. We also focused on phenological response to climate predictor variations. All studied species were divided on two groups depending on budding and flowering phenology shifts: 1) seasonal timing depends on the average temperatures of winter and spring months; 2) seasonal timing depends on autumn precipitations of the previous year and the winter and spring precipitations of the current year. Instability of budding and flowering timing caused by variability of winter and spring temperatures. The phenological shift amplitude correlates with stability of the corresponding month's temperature.

Key words: forest species, age structure, projective cover, phenology.

*Iryna Krokhmal, Maksym Netsvetov. Institute for evolutionary ecology of the National Academy of Sciences of Ukraine. 37 Lebedeva str., Kiev, 03143, Ukraine
Donetsk Botanical Garden of the National Academy of Sciences of Ukraine. 8, Sqr. Peremohy, Kostiantynivka, 85110, e-mail: netsvetov76@nas.gov.ua*

INTRODUCTION

Destruction of forest ecosystems in Europe is a result of climate changes and anthropogenic factors threatens the existence of rare and endangered species associated with these habitat conditions. At present, the main task of botanical

gardens is to preserve the biological diversity of the regional and world flora (Heywood 2009). Rich collections of the world flora in the botanical gardens allow testing the suitability of local conditions for potential reserves and introduction centers of plant species. As far as forest herbaceous perennials are concerned,

self-sustainability of a forming population and the degree of its similarity to natural ones are the main criteria for such an assessment. On the other hand, research on man-made populations of forest species has implications for their use in urban greening. This infers determining conditions for (1) long-term existence of populations of forest herbaceous perennials included into artificial plant community (selection of arbor species with different types of crowns to create a variety of lighting conditions, taking into account the species chemical relationship of plants); (2) self-reproduction (managed by humans at first – bringing them into the community, ensuring the presence of zoological agents for seed dispersal).

Donetsk Botanical Garden of the National Academy of the Science of Ukraine (DBG) is located in Donetsk (South East Ukraine, 48°0'32"N, 37°52'46"E) in the steppe zone, on flat terrain, but on the spurs of the Donetsk Ridge, where small ravine forests are found. Collection of DBG includes more than 90 species of forest herbaceous perennials. About 30% of these have formed stable populations. In this article, we studied the condition, i.e. number, density, age structure, projective cover of forest spring-flowering mesophyte populations in artificial and natural plant communities and their seasonal timing dependence from regional climatic predictors.

MATERIAL AND METHODS

We studied the introduced populations of *Helleborus caucasicus* A. Braun, *Ficaria verna* Huds., *Pulmonaria obscura* Dumort., *Hepatica nobilis* Mill., *Gymnospermum odessanum* (DC.) Takht., *Corydalis marshalliana* Pers., *C. solida* (L.) Clairv., *C. paczoskii* N. Busch, *Viola odorata* L., *Anemonoides ranunculoides* (L.) Holub, *A. nemorosa* (L.) Holub, *A. blanda* (Schott & Kotschy) Holub, *Primula veris* Lehm., *Anemona sylvestris* L., which have been growing on the territory of Donetsk Botanical garden for more than for 40 years. These populations were formed by synthetic method, i.e. using samples of different origin (Table 1). We also studied

populations of some species in a ravine forest of the Donetsk Ridge (48°19'24"N, 37°48'35"E).

Tree stand with associations (1)–(5) is composed by *Robinia pseudoacacia* L., *Gleditsia triacanthos* L., *Aesculus hippocastanum* L., *Ulmus campestris* L., *Sambucus nigra* L., *Syringa vulgaris* L. The height of tree stand is 12–15 m. The canopy density is 0.7–0.9. Tree stand with associations (6)–(10) is composed by *Sorbus intermedia* (Ehrh.) Pers., *Betula pendula* Roth., *Biota orientalis* (L.) Endl., *Picea abies* (L.) H. Karst., *P. pungens* Engelm., *Crataegus sanguinea* Pall., *C. monogyna* Jacq., *Fraxinus pensylvanica* Marsh., *F. pubescens* L., *Salix alba* L. The height of tree stand ranges from 7–8 to 12–15 m. The canopy density is 0.8.

Growth conditions of these associations during plants' flowering are following: association (1) – the soil temperature is 16.8°C, the relative lighting at noon is 96%; association (2) – 14.1°C and 56% respectively; association (3) – 12.2°C, 50%; association (4) – 8.5°C, 82%; association (5) – 1.5°C, 65%; association (6) – 16.0°C, 14%; association (7) – 13.2°C, 17%; association (8) – 14°C, 10%; association (9) – no data available.

In the ravine natural forest we studied two associations (11) and (12) of forest mesophytes. Association (11) (oak-forest with lime and ash) is located at the toe near the rivulet. The soil temperature is 11.5°C, the lighting is <10%. The tree stand height is 16–18 m, canopy density is 0.9–1. Association (12) is located in the forest edge under *Crataegus monogyna*, *Rosa* sp., *Fraxinus excelsior* L., *Ulmus campestris* L., *Acer campestre* L., *Prunus stepposa* Kotov. The air temperature is 19.5°C; the soil temperature: in the edge is 13.2°C, in the open space is 16.1°C; the relative lighting is 68%.

Seasonal rhythm and development were studied using standard techniques. The phenology rhythm type was determined according to I.V. Borisova (1972). The number of days was calculated from the calendar beginning of the 7 years of a monitoring (2006–2012). Age structure was described according to A.A. Uranov (1975),

Table 1. Origin of specimens forming the populations in the Donetsk Botanical Garden of NAS of Ukraine

| Species | Year of introduction | Origin |
|---|------------------------------|--|
| <i>Helleborus caucasicus</i> A. Braun | 1969 | Stavropol territory, Ispravnaya village, forest |
| <i>Ficaria verna</i> Huds. | 1973 | Donetsk region, near the town of Yasinovataya, forest |
| <i>Pulmonaria obscura</i> Rehmman | 1980 1982 | Donetsk region, v. Bannoe, forest Donetsk region Slavyanskiy district, Mayatskiy forest |
| <i>Hepatica nobilis</i> Schreb. | 1970 | Moldavia, surroundings of v. Varatik, forest |
| <i>Gymnospermum odessanum</i> (DC.) Takht. | 1978 | Odessa region, Tatarbunarskiy district, v. Lesnoe, forest edges |
| <i>Corydalis marshalliana</i> Pers. | 1968 1977 1979 1982 | Donetsk region, near the town of Yasinovataya town, forest Donetsk region, the town of Yasinovataya, ravine forest in Donetsk region, Telmanovski district, v. Starognatovka, ravine forest Donetsk region, Slavyanskiy district, Mayatskiy forest |
| <i>C. solida</i> Sw. | 1968 1979 1982 | Donetsk region, surroundings of Yasinovataya town, forest Donetsk region, Yasinovataya town, ravine forest in Donetsk region, Telmanovski district, v. Starognatovka, ravine forest Donetsk region, Slavyanskiy district, Mayatskiy forest |
| <i>Viola odorata</i> Thunb. | 1969 | Donetsk region, the town of Yasinovataya, forest margin |
| <i>Anemonoides ranunculoides</i> (L.) Holub | 1968 1982 | Donetsk region, near the town of Yasinovataya, forest Donetsk region Slavyanskiy district, Mayatskiy forest |
| <i>A. nemorosa</i> (L.) Holub | 1976 1977 | Marburg, Germany Oslo, Norway, University Botanical Garden |
| <i>A. blanda</i> (Schott & Kotschy) Holub | 1978 1978 | Antwerp, Belgium, Botanical Garden Mühlhausen, Germany, 1978 |
| <i>Primula veris</i> Lehm. | 1965 1965 1973 | Leningrad, All-Union Research Institute of Plant Breeding of the Academy of Sciences, f. USSR Koknese, Latvia Stavropol, forest edge |

| Species | Year of introduction | Origin |
|------------------------------|----------------------|--|
| <i>Anemona sylvestris</i> L. | 1965 | Novosibirsk |
| | 1965 | Krasnoyarsk Territory |
| | 1965 | Altai |
| | 1965 | Kiev, CRBG |
| | 1967 | Donetsk region, Velikoanadolskiy forest |
| | 1967 | Yalta |
| | 1967 | Estonia, Tallinn |
| | 1967 | Bogatyrskoe forestry, Batumi |
| | 1978 | Donetsk region, Yasinovataya, Vysokiy forest, edge |
| | 1980 | Donetsk region, Amvrosievka, 'Urochishche Pristenskoe' Nature Reserve |
| | 1985 | Lugansk region, Melovoe district, 'Streltsovskaya Step' Nature Reserve |

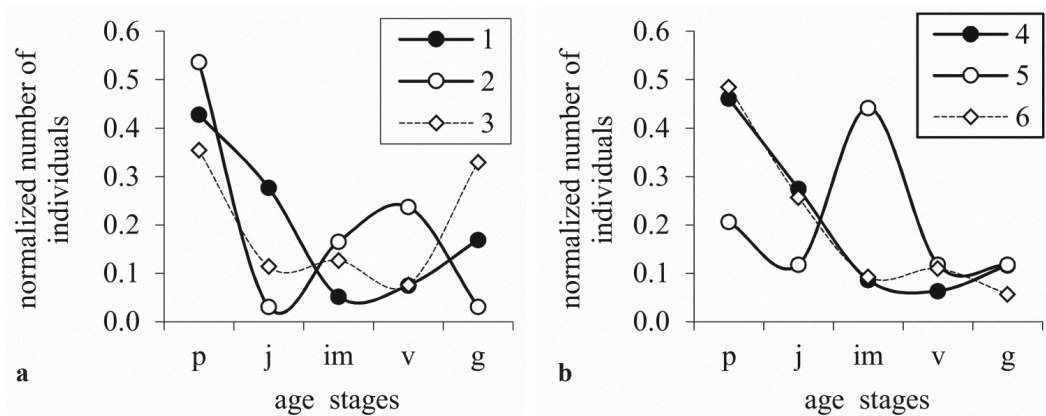


Fig. 1. The age structure of populations in artificial plant community: a – association of *Ficaria verna* (1) + *Anemonoides blanda* (2) + *Corydalis solida* (3), b – “*Ficaria verna* (3)” to “*Ficaria verna* (4)” ; “*Anemonoides blanda* (4)” - “*Anemonoides blanda* (5)” ; “*Corydalis solida* (5)” – “*Corydalis solida* (6)”.

density – to A.P. Shennikov (1965), projective cover – to L.G. Ramensky (1971). Type of normal populations was determined by «delta-omega» criterion. Five trial plots were laid out for each association.

RESULTS

The following herbaceous associations were identified in artificial plant community: *Ficaria verna* + *Anemonoides blanda* + *Corydalis solida* (1); *Corydalis solida* + *Ficaria verna* + *Gymnospermium odessanum* (2); *Anemonoides*

ranunculoides + *Corydalis solida* + *Corydalis marschalliana* (3); *Ficaria verna* + *Anemonoides ranunculoides* + *Anemonoides nemorosa* + *Corydalis solida* (4); *Ficaria verna* + *Corydalis solida* + *Viola odorata* + *Anemonoides blanda* + *Anemonoides ranunculoides* (5); *Glechoma hederaceae* L. + *Pulmonaria obscura* + *Viola odorata* + *Lysimachia nummularia* L. (6); *Pulmonaria obscura* + *Viola odorata* + *Viola alba* + *Primula veris* (7); *Corydalis paczoskii* + *Gymnospermium odessanum* + *Viola wiedemaniai* (8); *Primula veris* + *Corydalis solida* + *Ficaria verna* (9); *Hepatica nobilis* + *Anemonoides blanda* + *Viola odorata* + *Ficaria verna* (10).

Two associations were identified in natural conditions (ravine forest): *Corydalis solida* + *Anemonoides ranunculoides* + *Ficaria verna* + *Corydalis marschalliana* (11); *Ficaria verna* + *Corydalis solida* + *Viola odorata* + *Fragaria vesca* L. (12).

Association (1) is characterized by the following features: 60% is dominated by *Ficaria verna*, 25% – *Anemonoides blanda* and 15 % – *Corydalis solida*. Age range of *Ficaria verna* is left-sided with predominance of plantlets and juveniles (Fig. 1a). Virginal individuals and plantlets dominate among *Anemonoides blanda* plants. Thus generative individuals, though not numerous, provide self-renewal of population of this species. The age range of *Corydalis solida* is bimodal, plantlets and generative individuals prevail.

Association (2) is represented by five species: *Corydalis solida* (50%), *Ficaria verna* (35%), *Gymnospermium odessanum* (5%), *Scilla sibirica* Haw. (5%), and *Vinca minor* L. (5%). Age ranges of *Corydalis solida*, *Ficaria verna* are left-sided, with the peak on plantlets (Fig. 1 b). In *Gymnospermium odessanum* the peak is on immature individuals (~ 20 %).

Projective coverage of the species in association (3) is as follows: *Anemonoides ranunculoides* – 65 %, *Corydalis solida* – 20%, *Corydalis*

marshalliana – 5%, *Scilla sibirica* – 5% and *Viola odorata* – 5%. The age range of *Corydalis solida* is left-sided, peak is on plantlets (Fig. 2a). It should be borne in mind that at the early stages plants of two species of the genus *Corydalis* are not distinguishable. *A. ranunculoides* is characterized by numerous virginal individuals. Number of generative individuals of *A. ranunculoides* is almost the same as *Corydalis solida*, however plantlets are less numerous. *A. ranunculoides* is distributed unevenly and forms dense clumps both in the artificial plant community and in ravines. Density of plants is so high that it prevents colonization, settlement of other species. Individuals of *A. ranunculoides* have high capacity of vegetative propagation due to its rhizomes growth and their patches dying, that lead to the particle formation. New clumps formed due to seed dispersal by ants. Time span from plantlet to generative period is about 10 years in the wild, in artificial community it reduced to 2 years. In the natural conditions, a long life cycle of *A. ranunculoides* is 40–50 years due to the rejuvenation in the process of particulation. All this allows species to form populations in *ex situ* conditions in the course of introduction.

According to projective cover, in association (4) there predominates *Ficaria verna* – 77%. *Anemonoides ranunculoides* and *A. nemorosa* occupy 5 % each, *Corydalis solida* – 3%,

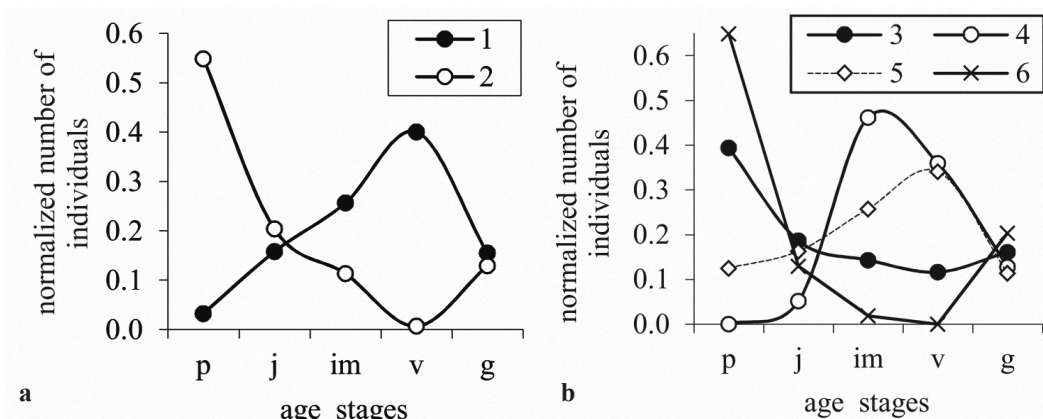


Fig. 2. The age structure of populations in artificial plant community: a - association *Anemonoides ranunculoides* (1) + *Corydalis solida* (2) + *Corydalis marschalliana*, b - association *Ficaria verna* (3) + *Anemonoides ranunculoides* (4) + *Anemonoides nemorosa*, (5) + *Corydalis solida* (6).

Convallaria majalis L. – 10 % (Fig. 2b). The age range of *Ficaria verna* is left-sided with a peak on plantlets. The curve of the age state range of *Corydalis solida* is bimodal with peaks on plantlets and generative individuals. In *Anemonoides ranunculoides* there is a left-sided range with a peak on immature specimens. *Anemonoides nemorosa* is characterized by domination of virginal individuals. The density of *A. nemorosa* in studied artificial plant communities is small. The juveniles of *Anemonoides nemorosa* grow around generative plants of *Ficaria verna*, which

provide for a favorable microclimate (shading, humidity).

Projective cover of species of association (5) is as follows: *Ficaria verna* 65 %, *Corydalis solida* 15 %, *Viola odorata* 15 %, *Anemonoides blanda* 5 %, *A. ranunculoides* – 1%. Plants of early age states in *Anemonoides ranunculoides* are absent, peak is on virginal plants (Fig. 3a). In the site of this association there is a large number of plantlets of *Ficaria verna*, *Corydalis solida*. *Corydalis solida* is characterized by bimodal curve with

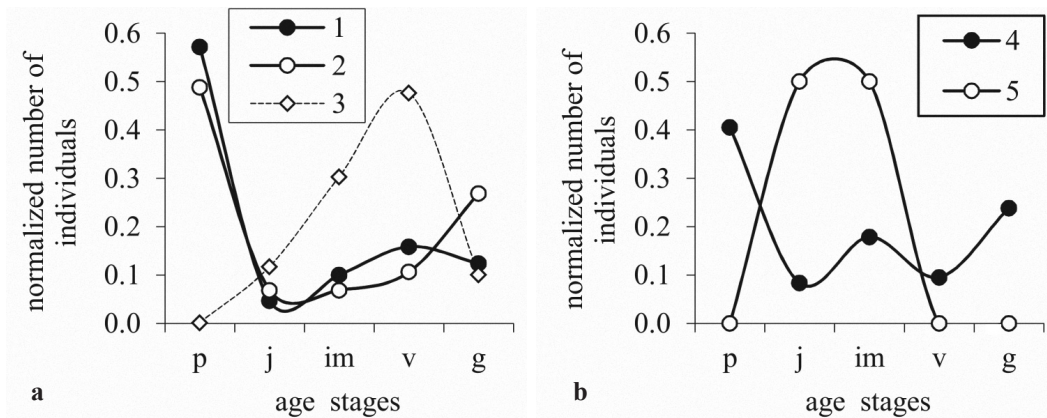


Fig. 3. The age structure of populations in artificial plant community: a – association of *Ficaria verna* (1) + *Corydalis solida* (2) + *Viola odorata* + *Anemonoides blanda* (3) + *Anemonoides ranunculoides*, b – *Corydalis paczoskii* (5)” – “*Corydalis paczoskii* (4)”; “*Gymnospermium odessanum* (6)” – “*Gymnospermium odessanum* (5)”.

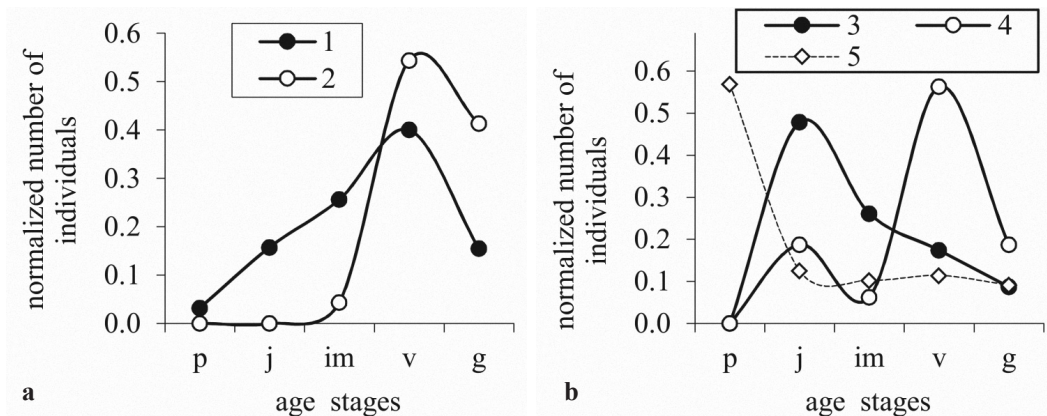


Fig. 4. The age structure of populations in artificial plant community: a – association of *Glechoma hederaceae* L. + *Pulmonaria obscura* (1) + *Viola odorata* + *Lysimachia nummularia* L.; association *Pulmonaria obscura* + *Viola odorata* + *Viola alba* + *Primula veris* (2); b – association of *Hepatica nobilis* (3) + *Anemonoides blanda* (4) + *Viola odorata* + *Ficaria verna* (5).

peaks on plantlets and generative individuals. *Anemonoides blanda* is characterized by a large number of virginal individuals.

In association (8), *Viola wiedemanii* occupies the largest area (projective cover is about 50%). *Corydalis paczoskii* occupies 40% of the total area, *Gymnospermium odessanum* – 10%. Plants of *Viola wiedemanii* are of vegetative origin. The age range of *Corydalis paczoskii* is left-sided with a peak on plantlets, a number of immature and generative plants is large (Fig. 3b). *Gymnospermium odessanum* is characterized by left-sided range with a peak on juvenile and immature specimens. Virginal and generative plants of this species in this association are absent. Relative lighting on this site is lower than on the site of association (2), where the age range of *Gymnospermium odessanum* is more complete. In the artificial plant community *Corydalis paczoskii* grow with *C. solida* and *C. marschalliana* and forms small groups. Apparently, *C. solida* and *C. marschalliana* displace *Corydalis paczoskii* that is likely to happen due to their allelopathic effect. In association (6) projective cover of species is the following: *Glechoma hederaceae* L. (40%), *Pulmonaria obscura* (30%), *Viola odorata* (25%) and *Lysimachia nummularia* L. (5%). Association (7) is characterized by the following projective cover: *Pulmonaria obscura* (50%), *Viola odorata* (40%), *Primula veris* (10%). *Pulmonaria obscura* in these associations is characterized by right-sided age range (Fig. 4a).

Association (9) is represented by *Primula veris* (60%), *Corydalis solida* (10%), *Ficaria verna* (30%). The age range of *Primula veris* is -sided with a peak at virginal specimens (Fig. 4 a).

In association (10) projective cover of species is the following: *Viola odorata* – 30%, *Ficaria verna* – 30%, *Hepatica nobilis* – 25%, *Anemonoides blanda* – 10%. The age range of *Ficaria verna* is left-sided with a peak on plantlets (Fig. 4 b). *Hepatica nobilis* is characterized by left-sided range with a peak at juveniles. *Anemonoides blanda* has a large number of individuals of virginal age state, the same average number of juvenile and generative individuals. Plantlets are absent from population age spectra in *Hepatica nobilis* and *Anemonoides blanda*.

According to projective cover, seven species dominate in artificial plant community: *Ficaria verna* (40%), *Corydalis solida* (19%), *Anemonoides ranunculoides* (13,0%), *Corydalis marschalliana* (9.4%), *Anemonoides blanda* (5.5%), *Viola odorata* (5%), *Anemonoides nemorosa* (4.7%). Projective cover of the rest of 16 species is less than 1%: *Corydalis paczoskii*, *Convallaria majalis* L., *Gymnospermium odessanum*, *Scilla sibirica*, *Gagea lutea* Ker. Gawl., *Allium ursinum* L., *Corydalis cava* (L.) Schweigg. et Koerte, *Primula veris* Mill., *Colchicum autumnale* L., *Fritillaria pallidiflora* Schrenk, *F. meleagris* L., *Tulipa quercetorum* Klokova et Zoz., *Scilla bifolia* L., *Ornithogalum*

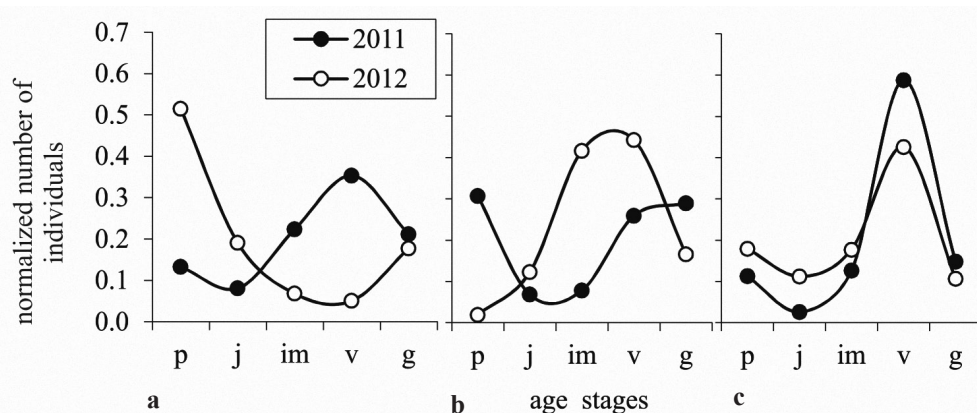


Fig. 5. The age structure of populations of spring ephemeroids in 2011–2012; a – *Corydalis solida*, b – *Anemonoides ranunculoides*, c – *A. blanda*.

boucheanum (Kunth) Aschers, *O. flavescens* Lam., *O. umbellatum* L.

We compared the age structure of introduced populations of three species of spring ephemeroïds in 2011–2012. In 2012, the relative number of plantlets and juveniles increased, the relative number of immature and virginal individuals of *Corydalis solida* decreased. Since the number of generative plants was seeming unchanged, we suggest the elimination of plants of immature and virginal age stage (Fig. 5 a). In 2011 *Anemonoides ranunculoides* plantlets survival rate is high, plants passed to the juvenile age stage (Fig. 5 b). In 2012 there were virtually no plantlets in the population, and the number of generative individuals significantly decreased. The ratio of *Anemonoides blanda* plants of different stages of ontogenesis was practically unchanged in the years of research (Fig. 5 c).

In the natural forest in ravine forest, we studied two associations. Projective cover of the species of association (11), which is located in the toe near the rivulet, is the following: that of *Corydalis solida* – 65 % (this species prevails), that of *Anemonoides ranunculoides* is 25 %, *Ficaria verna* – 5 %, *Corydalis marschalliana* – 5%. *C. solida* and *C. marschalliana* are characterized by right-sided age range with predominance of generative individuals. *Ficaria verna* and *Anemonoides ranunculoides* have left-sided

spectra, the first species has a peak on juveniles, the latter – on virginal. Lack of plants of the initial age states of *Corydalis* species may be accounted for by a rather high density of *Anemonoides ranunculoides* individuals of vegetative origin (Fig. 6 a).

Association (12) of ravine forest is located on the margin under the crown layer of woody plants and is represented by 4 species: *Ficaria verna*, *Corydalis solida*, *Viola odorata* and *Fragaria vesca*, projective cover of which is 60%, 20%, 15% and 5% respectively. Plants of the last two species are of vegetative origin. *Corydalis solida* is characterized by a bimodal curve with a peak is on plantlets and generative individuals. The age range of *Ficaria verna* is aligned, plantlets are less numerous (Fig. 6 b).

In ravine forest in upper third of the slopes under the trees, associations of *Ficaria verna* (projective cover – 70 %), *Corydalis solida* (projective cover – 20 %), *Scilla sibirica* (projective cover – 10%) grow, *Gagea lutea* is found and sometimes abundant. *Viola odorata* occurs in association with *Corydalis solida* and *Ficaria verna*, its number is smaller than that in artificial plant association. *Viola odorata* also grows on the open steppe areas of ravine forest. *Anemonoides ranunculoides* is distributed sporadically at medium altitudes of the slopes and forms clumps with different age state plants. Associations of

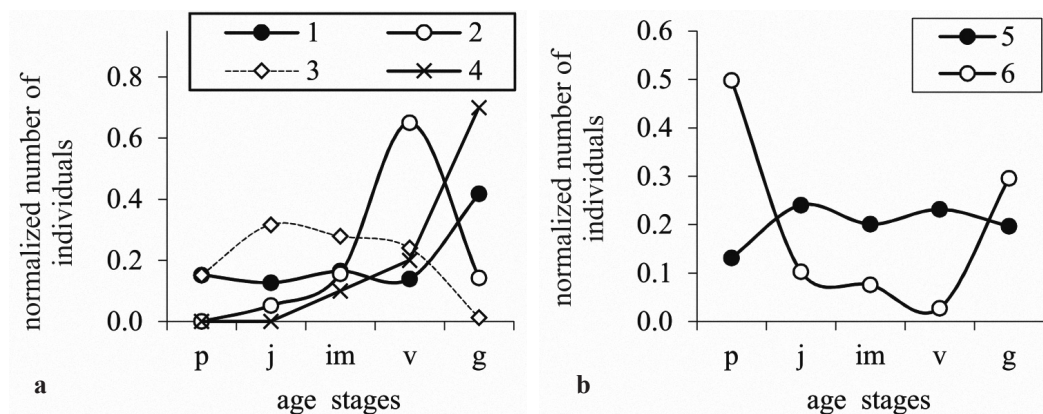


Fig. 6. The age structure of populations in natural plant community: a – association of *Corydalis solida* (1) + *Anemonoides ranunculoides* (2) + *Ficaria verna* (3) + *Corydalis marschalliana* (4); b – Association *Ficaria verna* (5) + *Corydalis solida* (6) + *Viola odorata* + *Fragaria vesca*.

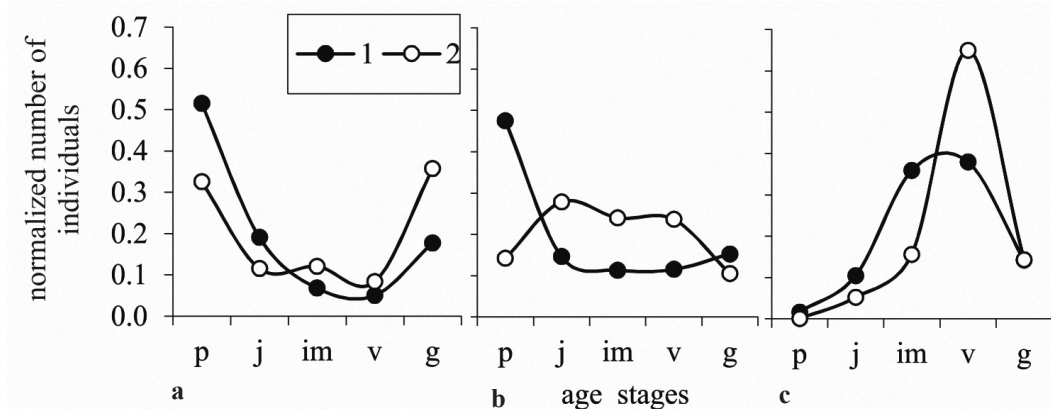


Fig. 7. The age structure of populations of spring ephemeroïds under artificial plant community conditions (1) and natural ravine forest (2): a – *Corydalis solida*, b – *Ficaria verna*, c – *Anemonoides ranunculoides*.

Ficaria verna, *Corydalis solida*, *Scilla sibirica*, *Tulipa quercetorum* are found on the slopes of medium height. A number of *Anemonoides ranunculoides* clumps increases in the lower parts of slopes. *Corydalis marschalliana* is found only in the relief depressions near the rivulet in shaded and wet places. *C. marschalliana* is able to form and maintain a population in the lowland shaded areas in association with *C. solida* in artificial plant community.

There were compared the age spectra of three species of spring ephemeroïds, namely *Corydalis solida*, *Ficaria verna*, *Anemonoides ranunculoides* in the wild and in artificial plant community (Fig. 7 c).

Curves of age states of the species in natural and artificial growing conditions are of the same pattern. *Corydalis solida* is characterized by a large number of plantlets and generative individuals in different conditions. In artificial plant community *Ficaria verna* is characterized by left-sided range with a peak on plantlets. *Anemonoides ranunculoides* in different growing conditions is characterized by a large number of virginal individuals. Density of individuals is higher in introduced populations of these species due to competition reducing: in *Corydalis solida* by 1.8 times, *Ficaria verna* – 2 times, *Anemonoides ranunculoides* – 2.7 times.

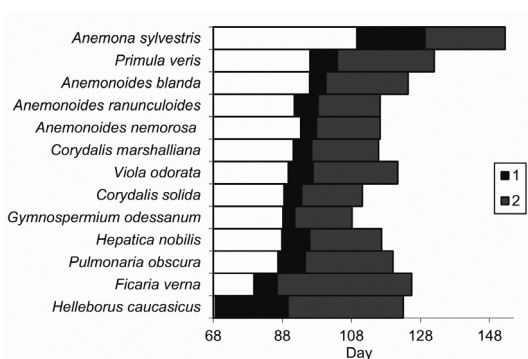


Fig. 8. Dates of onset and duration of budding (1) and flowering (2).

Analysis of type of populations according to “delta-omega” criterion showed that the majority of introduced populations are young. Introduced populations of *Pulmonaria obscura* and *Primula veris* are maturing. *Corydalis marschalliana* populations in ravine forest are maturing.

Despite the spring blooming is a common feature for all studied species they differ by seasonal timing type and life form (Table 2). Budding of *Helleborus caucasicus* occurs in the first decade of March, *Ficaria verna* – the second decade of March. *Pulmonaria obscura*, *Hepatica nobilis*, *Gymnospermium odessanum*, *Corydalis marschalliana*, *C. solida*, *Viola odorata*, *Anemonoides ranunculoides* start budding in the third decade of March, *Anemonoides nemorosa*,

Table 2. Type of seasonal timing and life-form of spring ephemeroids species

| Species | Type of seasonal timing | Life-form |
|----------------------------------|--|--|
| <i>Helleborus caucasicus</i> | wintergreen | rosellate cluster root geophyte |
| <i>Hepatica nobilis</i> | —//— | rosellate cluster root hemicryptophyte |
| <i>Pulmonaria obscura</i> | long-term vegetating spring-summer-autumn-green with a period of winter dormancy period | long rhizome cluster root semirosellate geophyte |
| <i>Anemona sylvestris</i> | —//— | rosellate short rhizome hemicryptophyte |
| <i>Viola odorata</i> | —//— | rosellate rhizomatous geophyte |
| <i>Anemonoides nemorosa</i> | long-term vegetating spring-autumn-green with summer and winter dormancy period | semirosellate short rhizome geophyte |
| <i>Primula veris</i> | —//— | rosellate cluster root hemicryptophyte |
| <i>Ficaria verna</i> | short-term vegetating spring-autumn-green with periods of summer and winter dormancy | tuber root geophyte |
| <i>Corydalis marshalliana</i> | short-term vegetating spring-green ephemeroids with a period of summer, autumn and winter dormancy | rosetteless tuber root geophyte |
| <i>C. solida</i> | —//— | —//— |
| <i>Anemonoides ranunculoides</i> | short-term vegetating spring-green ephemeroid with a period of summer, autumn and winter dormancy | rosetteless rhizomatous geophyte |
| <i>A. blanda</i> | —//— | rosellate stem tuber geophyte |
| <i>Gymnospermum odessanum</i> | spring-green ephemeroid with a period of summer, autumn and winter dormancy | rosetteless stem tuber geophyte |

A. blanda, *Primula veris* – in the first decade of April, *Anemona sylvestris* – in the second decade of April (Fig. 8). Priority of species flowering is the following: *Ficaria verna*, *Helleborus caucasicus*, *Gymnospermum odessanum*, *Corydalis solida*, *Pulmonaria obscura*, *Hepatica nobilis*, *Corydalis marshalliana*, *Viola odorata*, *Anemonoides nemorosa*, *A. ranunculoides*, *A. blanda*, *A. sylvestris*, *Primula veris*. The longest period from budding to flowering was observed in *Helleborus caucasicus* and *Anemona sylvestris* (20–21 days). In *Corydalis solida*,

C. marshalliana, *Anemonoides nemorosa*, *A. blanda*, *Gymnospermum odessanum* this period is 5 days. The duration of this period in other studied species is 7–8 days. The longest duration of flowering was observed in *Ficaria verna* – 39 days, *Helleborus caucasicus* – 33 days, *Primula veris* – 28 days; the shortest at *Gymnospermum odessanum*, *Corydalis solida*, *C. marshalliana*, *Anemonoides nemorosa*, *A. ranunculoides* – 17–18 days. Flowering time-span in other studied species is 21–25 days.

The date of budding and flowering onset correlates with different climate predictors values. January temperature is the main predictor for *Helleborus caucasicus*, and February temperature is the main predictor for *Ficaria verna*. January precipitations and temperature are the predictors for *Hepatica nobilis*. The temperature and precipitation growing result in earlier budding and flowering onset in *H. nobilis*. Phenology of some species correlate with average temperature of periods during few months. January-March temperatures come as the main climatic predictor

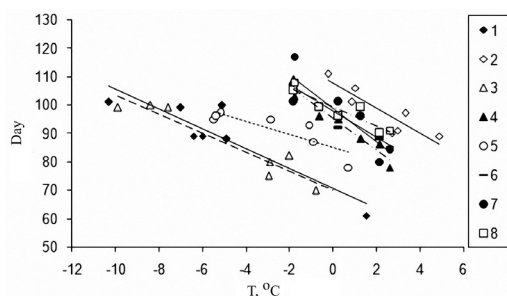


Fig. 9. Influence of monthly average temperatures on date of flowering onset: *Helleborus caucasicus* (1), *Anemonoides nemorosa* (2), *Ficaria verna* (3), *Corydalis solida* (4), *Gymnospermum odesanum* (5), *C. marshalliana* (6), *Viola odorata* (7), *Anemonoides ranunculoides* (8). See explanations in the text.

for *Gymnospermum odesanum*; January-April temperature – for *Corydalis marshalliana*, *C. solida*, *Anemonoides ranunculoides*, *Viola odorata*; February-April – for *Anemonoides nemorosa* (Fig. 9). Temperatures have no effect on the species start budding after 95th day growth.

The precipitations value is also important factor for species phenology. Increased January-April precipitation caused early budding starts of *Primula veris* (Fig. 10). The precipitation in the year preceding growing season also affects flowering of the studied species. Previous year (t-1) September precipitation value influences flowering in *Anemonoides nemorosa*,

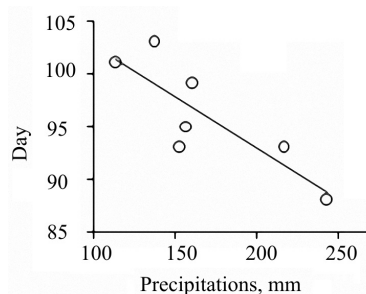


Fig. 10. Influence of January-April total precipitation value on the date of *Primula veris* budding onset.

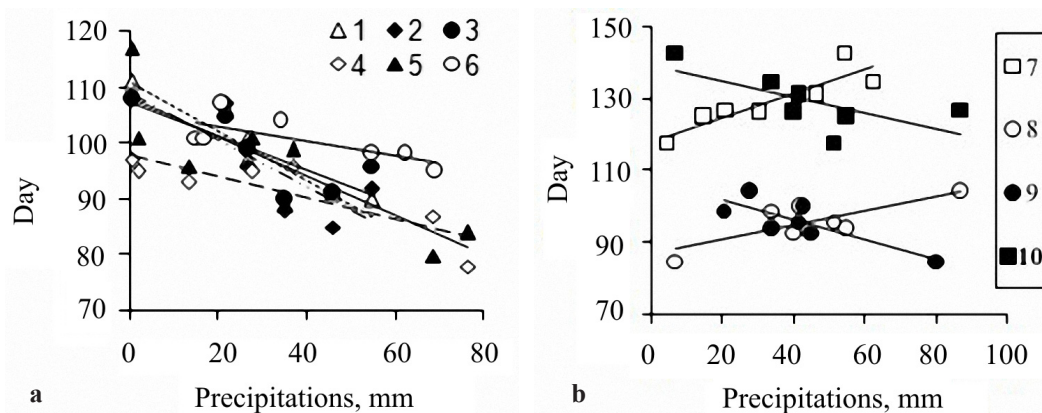


Fig. 11. Dependence of flowering phenophase-starting date onto precipitation in forest herbaceous perennials. a: *Anemonoides nemorosa* (1), *Corydalis marshalliana* (2), *Anemonoides ranunculoides* (3), *Gymnospermum odesanum* (4), *Viola odorata* (5), *Anemonoides blanda* (6). b: *Anemona sylvestris* (7), November precipitation; *Hepatica nobilis* (8), July precipitation; *Hepatica nobilis* (9), January precipitation; *Anemona sylvestris* previous year July precipitation (10)".

A. ranunculoides, *Corydalis marshalliana*. In *Gymnospermum odessanum*, *Viola odorata* flowering date correlate with August (year t-1) precipitation, and *Anemonoides blanda* is under influence of October (year t-1) precipitations (Fig. 11a). Favorable autumn conditions forward normal formation and differentiation of generative buds of these species. Flowering of *Hepatica nobilis* starts earlier if sum of precipitation increases in January and decreases in previous year's July. *Anemona sylvestris* plants flowering date correlates with sum of precipitation in previous year's July and November (Fig. 11b). An amount of November precipitation triggers generative buds developing and repeat flowering of *Anemona sylvestris*.

Growing average temperatures cause flowering prolongations of some species. For example, temperature of January–March is the major predictor for *Helleborus caucasicus* and *Gymnospermum odessanum*; February–March for *Ficaria verna*; March for *Corydalis solida* and *Viola odorata*; September–October of previous year for *Corydalis marshalliana*. The precipitation value effects in different way the flowering period. Increased January–April precipitation value and reduced one in October of the previous year lead to *Corydalis solida* flowering prolongation. *Anemonoides nemorosa* blooms longer due to increased precipitation in February. Flowering in *Primula veris* correlates with precipitation in August–September of the previous year. Flowering duration of *Anemonoides ranunculoides*, *A. blanda*, *Hepatica nobilis* is not preconditioned by average temperatures and total precipitations values.

DISCUSSION

There are several conditions necessary for making up and sustainable existence of populations of forest perennials in artificial coenoses in steppe. The favorable microclimate, ability and conditions for seed or vegetative reproduction are among major factors. For example, the seed dispersal of most studied species relate with

insects. There are many anthills on the territory of DBG. Here, in artificial plant community, *Ficaria verna*, *Anemonoides ranunculoides*, species of the genus *Corydalis* have the largest projective cover. Diversification of *A. ranunculoides* comprises two stages: plants in generative phase produce seed, dispersed by ants, and a new generation forms a new vegetative clump. This results in a sporadic spatial structure of population. The viviparity is typical for species of the genus *Corydalis*. It provides a rapid germination in the current vegetative season before dry season. Among species of the genus *Corydalis* the largest covering is formed by *C. solida*, which have greatest seeds production.

Ephemeroid geophytes constitute a geologically young group of plants, which is confined to two major formations of vegetation: herbaceous (deserts, semi-deserts, steppes, meadows) and woody (deciduous forests) (Scripichinsky 1981). Life form and phenological rhythm type fixed in the ephemeroid species genotype is their adaptation to the specific conditions of existence in the forest community. From a genetic point of view, adaptation is a change in genotype of evolutionary phylums that lead to restriction of further evolution. Forest spring-blooming mesophytes are also evolutionarily static species. Nevertheless, some of these species are capable of adaption to new cenotic conditions. In southwestern Ukraine, destructions of upland and gully forests common from middle ages has forced *Gymnospermum odessanum*, which originate from forest community, to outset on open areas (Litvinenko 2012).

Ephemeroid geophytes are plants with a specific seasonal timing and considered to be the final stage of its specialization in the series: summer-green – winter-green hemiephemeroids (Krylov, Belyanina 1982). According to V.V. Scripichinskiy (1981), the following morphological adaptations contributed to their evolution: perennial underground organs with deposit function and resting buds; recurrent roots dying in summer; development of monocarpic shoot with duration of underground stage inside buds longer than the aboveground stage. This explains the short

observed duration of the period from budding to flowering.

Some authors suppose the stability of the date of flowering (budding) onset to be the criterion for adaptation of species to the new conditions (Bulakh 2005). Taking into account the considerable variation in terms of phenophases in studied species, we used the coefficient of variation as a criterion of stability. Species *Anemonoides blanda*, *Primula veris*, *Hepatica nobilis* are stable, *Gymnospermum odessanum*, *Pulmonaria obscura*, *Corydalis marschalliana*, *Anemonoides ranunculoides*, *A. nemorosa* is of average stability, *Ficaria verna*, *Corydalis solida*, *Viola odorata* are unstable.

Significant deviation of January temperature from the norm causes a shift of budding and blossoming timing both in stable species *Hepatica nobilis*, and unstable one *Helleborus caucasicus*. High temperature in January-April shifts phenology of medium stability or unstable species: *Gymnospermum odessanum*, *Corydalis solida*. It should be noted that *Ficaria verna*, *Corydalis marschalliana*, *C. solida*, *C. paczoskii*, *Viola odorata*, *Pulmonaria obscura*, *Anemonoides ranunculoides*, *A. nemorosa*, *Anemona sylvestris*, are the species of autochthonous flora (Vascular plants of the south-east, ... 2010). Seasonal timing of most of these species is labile, that indicate a high adaptation to growing conditions, except for *Anemona sylvestris*, which comes into

the flowering stage later. Species *Helleborus caucasicus*, *Hepatica nobilis*, *Gymnospermum odessanum*, *Anemonoides blanda*, *Primula veris* are introduced in steppe zone. According to phenological criterion the most adapted introduced species is *Helleborus caucasicus*, which is distinct by labile timing as well as species of local flora. This is partly proven by works by Abraitene J., Marozas V. (2011) and Gherghisan E. (2012). They showed that phenophases of herbaceous forest species vary considerably depending on the fluctuations of climate predictors.

On the other hand the stability of budding and flowering phases correlates with the variability of temperatures of winter and spring months. Smaller amplitude of monthly temperature variations causes stability of phases that occur during these months. For example, species with early flowering are less stable because the monthly temperatures preceding their budding and flowering decrease by variation amplitude from January to June (Fig. 12). Flowering end is determined by a complex of internal and external factors, such as the number of reproduced buds, longevity of an individual flower, order of flowers opening, and thus by the weather conditions not only during the current season, but also during buds setting, i.e. in the previous year.

High temperatures and precipitations in autumn caused repeated flowering, i.e. by repeating

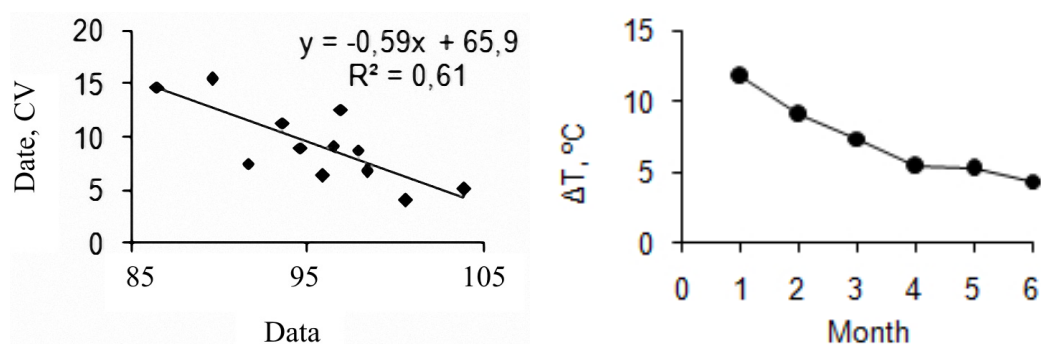


Fig. 12. Dependence of variability of the date (expressed by coefficient of variation) of flowering onset onto its average value (a) and amplitude of variations of monthly average temperatures (b) for 7 years of observations.

conditions that are similar to spring ones and trigger opening of already formed reproductive buds, especially if it followed a dry period. Forming and differentiation of already existing reproductive buds of the second order is delayed. In the autumn, plant expends energy and resources to re-bloom, so it comes later next spring. Flowers in the period of repeat bloom are on a separate generative spear that arose from axillary bud of radical leaf or adventitious bud on the root collar.

Setting of resting bud in early-flowering species occurs in July, differentiation continues until the end of October. Increasing amount of re-flowering species is related to the temperature conditions of the second and third decades of July and the value of precipitation on the first ten days of July (Golovkin 1973). According to B.N. Golovkin (1973) an increase of precipitation in July following June drought accelerates the start of flowering in the next season. The abnormalities in the general course of growth and development caused by lack of moisture may be eliminated by amount of rainfall in the subsequent month. However, this is not a universal rule. Thus, warm and dry July is necessary for the normal developing of *Hepatica nobilis* reproductive buds. Setting of resting bud in early-flowering species occurs in July, differentiation continues until the end of October.

CONCLUSION

One introduced species and six ones of natural flora dominate by projective cover in the artificial plant community: *Ficaria verna*, *Corydalis solida*, *Anemonoides ranunculoides*, *Corydalis marschalliana*, *Anemonoides blanda* (introduced), *Viola odorata*, *Anemonoides nemorosa*.

The populations of three species of local flora, namely *Corydalis solida*, *Ficaria verna*, *Anemonoides ranunculoides* had a similar age structure in natural and artificial plant community, in the last one individuals' density is higher. This

implies the possibility of forming artificial plant communities. included early flowering time forest species. Most populations of introduced species are young, but *Pulmonaria obscura* and *Primula veris* populations are maturing.

All studied species are divided into two groups basing on the character of phenology relation with climatic predictors: 1) budding and flowering timing depends on the average monthly temperatures of winter and spring; 2) it depends on total precipitation value of both previous year autumn and the current year winter and spring. Stability of budding and flowering timing correlates with the variability of winter and spring temperatures. The stability of phenological phases relates with variation of weather conditions of the month, in which they occur. The greater deviation of monthly temperature implies the greater the shift of seasonal timing.

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