Thaiszia - J. Bot., Košice, 4:49-75, 1994

Bioecological study of *Galanthus nivalis* L. in the East Carpathians

Gennadij Budnikov et Vladimir Kricsfalusy

Uzhgorod University, Voloshyna 54, 294000 Uzhgorod, Ukraine

BUDNIKOV G. et KRICSFALUSY V. (1994): Bioecological study of *Galanthus nivalis* L. in the East Carpathians. - Thaiszia - J. Bot., Košice, 4: 49-75. - ISSN 1210-0420.

ABSTRACT: Results of a combined ecological and biological study of *Galanthus nivalis* L. in the East Carpathians are presented. Information on the distribution, ecological-phytocenotic attachement and demography of the species, morphogenesis and onthogenesis are given. Intraspecific morphological, anatomical and karyotypic variation, the most important problems of vegetative and seed reproduction of the species, as well as embryological aspects of the reproductive process are elucidated. Problems of protection and prospects of use are considered.

KEYWORDS: *Galanthus nivalis* L., bioecology, protection, the East Carpathians.

Introduction

Galanthus nivalis L. - snowdrops (Fig.1) is a bulbous ephemeroid geophyte of the family *Amaryllidaceae*. It is a highly decorative early spring species, good honey bearing and perspective medicinal plant, which contains a number of alkaloids, the most valuable of them being galantamin and nivalidin.

G. nivalis was formerly widely distributed in the East Carpathians (MARGITTAI 1923; DOMIN et PODPĚRA 1928) but during the last decades its area has been considerably reduced as a result of destruction of its primary habitats (in particular, lowland - foothill zone) and direct destruction by picking up its flowers and digging its bulbs out. Threatened by complete extinction, this plant has been included in the lists of rare and disappearing species of the Ukrainian flora (CHOPIK 1978) and "Red Data Book of the Ukrainian SSR" (1980) as a species in decline. *G. nivalis* is protected, and it has been included into the national Red Data Books or the lists of the threatened plants of all the neighbouring countries of the Carpathians region - Poland (ZARZYCKI et WOJEWODA 1986), Slovakia (MAGLOCKÝ 1983), Hungary (CZAPODY 1982) and Romania (BOSCAIN et PURDELA 1989).

Taking into consideration the above facts, we carried out bioecological studies of *G. nivalis* in different plant zones of the East Carpathians to estimate the actual degree of danger to its existence, as well as to organize its effective protection and to define prospects of its use (KRICSFALUSY et BUDNIKOV 1992).

Fig. 1. *Galanthus nivalis* L.

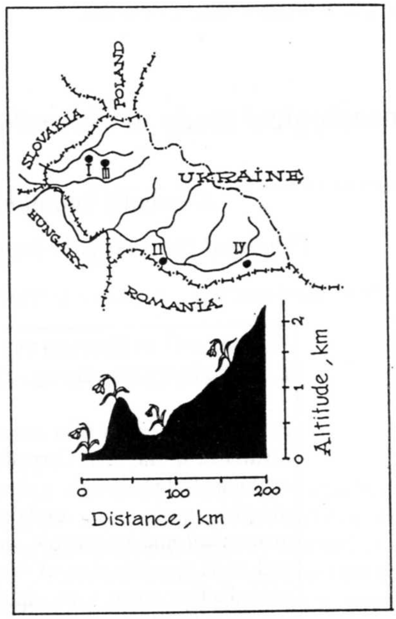

Fig. 2. Sites of the studied *Galanthus nivalis* L. populations in Transcarpathia: I- Vorochevo, II- Shajan, III- Antalovetska Poljana, IV- Menchul - Kvasivskyj.

Materials and methods

Studies carried out in the period of 1988-1992 were used as the material for this paper. Observations and collecting material were carried on at different geographical locations of the East Carpathians (Transcarpathian region)(Fig.2):

Transcarpathian Lowland: I. The environs of Vorochevo village, Perechin district, 130 m

East Carpathians: II. Foothill belt, the environs of Shayan village, Khust district, 260 m

III. Lower mountain belt, Antalovetska Poljana Mountain, Vigorlat-Hutynskyj Range, 810 m.

IV. Upper mountain belt, Menchul-Kvasivskyj Mountain, Chornogora Range, 1320 m.

For comparative analysis we accepted, according to Rabotnov (1950a), a cenopopulation (a part of population) as a convenient working unit. To study biomorphological features and intra- and interpopulational variation of the species, 25 adult individuals were taken from each population following the randomization principle. The following 16 characters were studied:

1. assimilating leaves length (cm)
2. assimilating leaves width (cm)
3. outer perigonium segments length (cm)
4. outer perigonium segments width (cm)
5. inner perigonium segments length (cm)
6. inner perigonium segments width (cm)
7. flower stalk height (cm)
8. pedicel height (cm)
9. spathe length (cm)
10. spot width (cm)
11. anther length (cm)
12. ovary length (cm)
13. ovary width (cm)
14. bulb length (cm)
15. bulb width (cm)
16. bulb weight (g)

The obtained numerical data were processed by variation statistic methods (PLOKHINSKIJ 1970 and LAKIN 1990). Arithmetical mean ($\overline{x}$) was calculated by the sums of squares mode. Average standard deviation ($S\overline{x}$), coefficient of variation (CV, %) and average error have been determined for every arithmetical mean. Reliability of the biometric parameters has been estimated through the Student criterion (t). To determine the measurements accuracy the P exponent (%) has been calculated.

Material for karyological and embryological researches was worked up according to the common cytological methods (PAUSHEVA 1970).

Major life cycle studies, determination of age structure and density of populations in different ecological and phytocenological conditions have been carried out on transects within one plot of a community. Biomorphological characteristics of plants in each age group and subgroup have been estimated using the data of measurement of 12-15 specimens. Age stages have been determined according to RABOTNOV scheme (1950b) completed by SMIRNOVA et al. (1976).

Seed productivity has been determined according to RABOTNOV (1960) and VAJNAGIJ (1973) methods using exponents of potential seed productivity (FSP, i.e. the number of ripe uninjured seeds). Variation and statistic processing of numerical data has been carried out by means of an IBM-PC/AT computer.

Distribution and ecological-phytocenotic requirements

G. nivalis is distributed between the 53rd and 33rd parallels, from the Pyrenees to the Dnieper, from west to east (ARTJUSHENKO 1970). According to MALYNOVSKYJ'S 1980) classification the species belongs to the mountain Middle European group of the European type area. *G. nivalis* is referred to the nemoral element of the flora. In Ukraine, it mainly occurs in the Carpathians. Its habitats are known to be situated in the forest-steppe zone to the west and partially to the east of the Dnieper (PROTOPOPOVA 1987). MELNIK (1987), comparing the present day data with those reported earlier and with the herbarium material from previous years, reports intensive reduction of the species area nearits north-east distribution limit.

In Transcarpathia it occurs in small patches at different altitudes from lowland (100-120 m above sea level) to the upper mountain zone of the East Carpathians (1300-1500 m above sea level). A dot map of the distribution of *G. nivalis* in the East Carpathians has been worked out on the basis of the studies of the herbarium collections belonging to the Uzhgorod (UU), Lviv (LW) and Chernivtsi (CHER) universities as well as to the Lviv Natural History Museum (LWS) and Kholodny Institute of Botany (KW) of the Ukrainian Academy of Sciences (Fig.3).

G. nivalis is a mesohygrophyte, it successfully gets over in temporarily flooded and drying soils. It is distributed on the moist, moderately acidic, humous, sandy, clayey soils, with high level of underground water or superficially moistened soils, the plant being an indicator of humidity and impermeability of the soils.

In the East Carpathians *G. nivalis* grows mainly in deciduous forests, by the streams, on the glades, sometimes in secondary communities. It most often occurs in the moist mature forests, i.e. it is a typical forest species; however, it is missing from very shady localities.

According to the data reported by ROTHMALER (1988), SOÓ (1973) and MORAVEC et al. (1983) the species occurs in the following communities:

- I. c *Carpino - Fagetea* (Br.-Bl. et Vlieg. 37) Jakucs 67
    - o *Fraxinetalia* Scam. et Pass. 59
        - u *Fraxino - Quercion* (Oberd. 53) Pass. 68
            - Ass *Fraxino - Ulmetum* (TX. 52) Oberd. 53
        - u *Tilio - Acerion* Klika 55
            - Ass *Tilio - Fraxinetum*
            - *Stellario - Aceretum*
            - *Mercuriali - Tilietum*
            - *Aceri - Tilietum* Faber 26
        - u *Aceri - Fagion* Ellenb. 63
            - Ass *Corydali - Acereto - Fraxinetum* Willm. 56
    - o *Carpino - Fagetalia* Scam. et Pass. 59
        - u *Asperulo - Fagion* Knapp 42 em. TX. 55
            - Ass *Melitti - Fagetum noricum*
- II. c. *Querco - Fagetea* BR.-BL. et Vlieg. 37 (Ch)
    - o *Fagetalia sylvaticae* Pawl. 28 (Ch)
        - u *Alno - Padion* Knapp 42 (Ch)
        - u *Alno - Ulmion* BR.-BL. et TX. 43 (Ch)
        - u *Fagion* Luquet 26 (Ch)
- III. c *Quercetea robori-petraea* BR.-BL. et TX. 43
    - o *Quercetalia robori-petraeae* TX. 31
        - u *Agrostidi - Quercion* Scam. et Pass. 59
            - Ass *Quercetum petraea-cerris*
            - *Orno - Quercetum*
            - *Òrno - Quercetum*
- IV. c *Quercetea pubescenti-petraeae* (Oberd. 48) Doing 55
    - o *Quercetalia pubescentis* BR.-BL. 31 (Ch)
- V. c *Salicetea purpureae* Moor 58
    - o *Salicetalia purpureae* Moor 58
        - u *Salicion albae* (Soó 36) TX. 55
            - Ass *Salicetum albae* Issl. (24) 26
            - *Salicetum fragilis* Pass. 57
- VI. c *Crataego - Prunetea* TX. 62
    - o *Prunetalia* TX. 52
        - u *Berberidion* BR.-BL. 50
            - Ass *Waldsteinio - Spiracetum mediae*

Optimal distribution of *G. nivalis* is found in the communities for which it is a characteristic species (Ch). According to the data reported by Keller (1984), *G. nivalis* is a good indicator of thermophilic communities of *Carpinion* and *Tilio-Acerion.*

In the Transcarpathian Lowland *G. nivalis* (population I) grows in a secondary community which probably belongs to *Aegopodio-Sambucetum* Doing 61, and is formed by *Corylus avellana, Crataegus oxyacantha, Sambucus nigra.* Tree species *Pyrus communis, Cerasus avium* and *Acer campestre* sometimes occur there as well. In early spring, ephemeroids like *Scilla kladnii, Anemone nemorosa, Isopyrum*

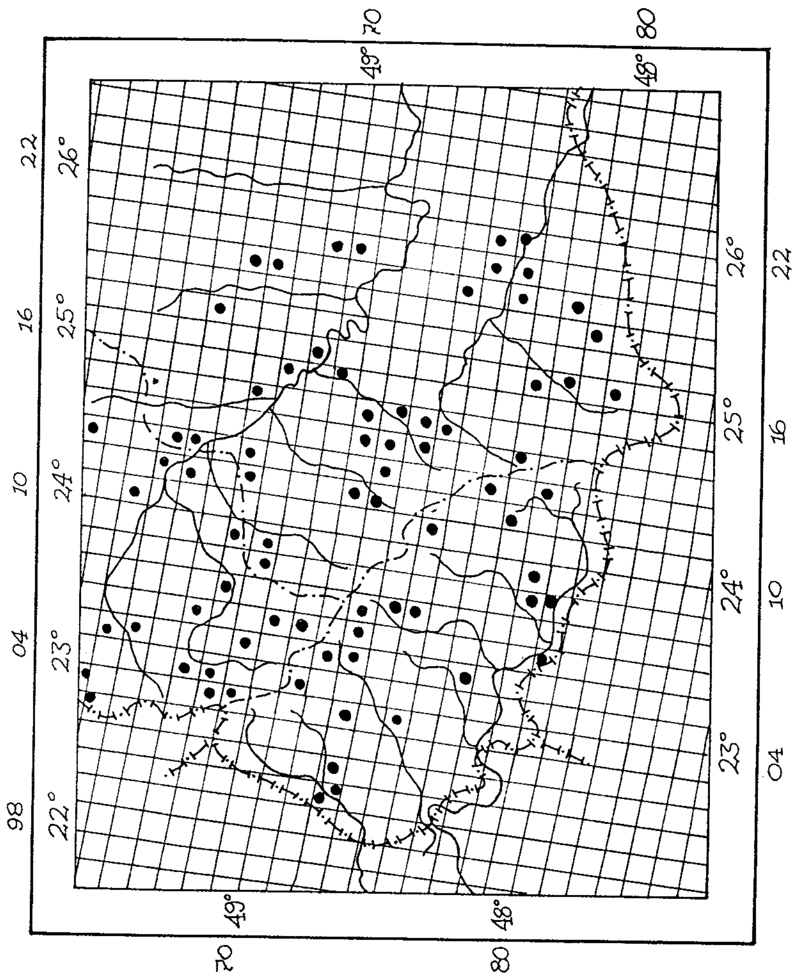

Fig. 3. Distribution of *Galanthus nivalis* L. in the East Carpathians.

thalictroides, Gagea lutea form a bright covering. Later on, in the herb layer *Aegopodium podagraria, Salvia glutinosa, Geranium sanquineum, Asarum europaeum, Impatiens noli-tangere, Galeobdolon luteum* and *Mercurialis perennis* predominate. According to RUDNJEVA (1960) sod-podzolic and silty clay soils are typical for this site (Table 1). This type of soils is formed in depressions. Maternal rocks are alluvial as well as deluvial loams, deposited at a depth of 150-200 cm. In most cases the surface of these soils is constantly waterlogged. This is caused by lateral flows of both surface and underground waters. The soil has acid reaction. The acidity increases from the upper horizons to the lower ones. Exchange acidity in the upper horizon is caused by hydrogen, in the lower one - by aluminium. The soil is relatively rich in humus, the upper horizons contain from 5 to 7% of it. Down the profile the amount of humus decreases markedly.

Tab. 1. Physical and chemical soil composition of habitats of *Galanthus nivalis* L.

Soil type	Depth of horizon [cm]	Humus [%] (acc. to Tyurin)	pH H_2O	pH KCl	Exchange acidity [mg-equiv. per 100 g soil] (according to Sokolov)			% Al to total acidity	Absorbed cations [mg-equiv. per 100 g soil] (according to Hedroicz)			Unsaturated state in H [%]	Mobile compounds [mg per 100 g soil] (according to Kirsanov)		
					Total	H^+	Al^{3+}		Ca^{2+}	Mg^{2+}	H^+		Fe_2O_3	P_2O_5	K_2O
Mountain	1-9	10.3	4.3	3.5	4.5	0.3	4.2	94	5.9	2.9	11.2	56	25	1.7	not det.
forest	15-20	4.7	4.8	3.8	5.7	0.1	5.6	98	0.9	0.6	6.7	82	20	traces	not det.
dark-	35-40	1.6	4.7	3.9	4.8	0.1	4.7	98	0.9	0.9	6.1	77	18	traces	1
brown	70-75	1.2	4.8	3.8	6.4	0.1	6.3	99	0.7	0.9	6.6	80	8	traces	1
	125-130	1.0	4.8	4.2	5.6	0.1	5.5	99	0.8	0.7	5.9	80	8	traces	1
Meadow	0-5	not det.	5.5	4.7	0.29	0.17	0.12	44	3.6	1.3	1.6	25	30.6	traces	9.0
soddy-	10-15	not det.	5.3	4.2	0.56	0.25	0.31	56	3.7	1.3	1.9	28	30.9	traces	8.3
gley	25-30	not det.	5.5	4.7	0.66	0.17	0.49	74	3.5	1.9	1.8	25	20.4	traces	5.9
	40-45	not det.	5.1	4.0	1.39	0.29	1.10	79	2.9	0.9	2.4	38	30.3	traces	7.5
	55-60	not det.	5.1	4.0	1.07	0.24	0.83	77	3.4	2.4	2.1	27	10.4	not det.	not det.
	90-95	not det.	5.3	4.2	0.98	0.29	0.69	70	3.4	5.6	1.9	17	10.2	not det.	not det.
	160-165	not det.	5.0	4.0	1.61	0.29	1.32	82	2.5	1.7	2.1	33	10.2	not det.	not det.

Tab 5. Phytomass of the specimens and populations of *Galanthus nivalis* L. in East Carpathians
(for abbreviation see text p. 59-61)

Pop. no.	Vegetation belt and altitude above sea level [m]	Age group					Phytomass of the population [g/m^2]
		p	j	im	v	g	
I	Transcarpathian Lowland, 130	0,03/0,39	0,07/6,86	0,19/3,42	0,47/33,37	0,86/37,84	81,88
II	Foothill belt, 260	0,04/0,32	0,11/7,48	0,31/3,72	0,59/26,55	1,99/73,63	111,70
III	Lower mountain belt, 810	0,05/0,25	0,14/3,22	0,44/3,08	0,94/22,56	2,56/79,36	108,47
IV	Upper mountain belt, 1320	0,04/0,12	0,08/0,96	0,28/1,12	0,66/11,22	1,15/24,15	37,57

In the foothill belt *G. nivalis* (population II) grows at the lower line of the hornbeam and beech forests in the association of the *Dentario - Fagetum* (ZLATN. 35) HARTM. 53. In the tree layer, besides *Fagus sylvatica*, one can see *Carpinus betulus*, sometimes *Acer pseudoplatanus, A. platanoides, A. campestre, Ulmus scabra*. The undergrowth is formed there by young trees of *Fagus sylvatica*, as well as by the thickets of *Corylus avellana, Sambucus nigra, Euonymus verrucosa, Rubus caesius*. In early spring ephemeroids appear in great numbers: *Dentaria bulbifera, D. glandulosa, Anemone nemorosa, Corydalis solida, Isopyrum thalictroides, Lathraea squamaria*. Later on *Galeobdolon luteum, Urtica dioica, Oxalis acetosella, Mycelis muralis, Carex sylvatica, Mercurialis perennis* can occur there.

In the foothill and mountain belts, the studied populations of *G. nivalis* grow on mountain forest dark brown, slightly podzolod or semi- and sandy-loam soils, which are formed on brownish alluvial-delluvial loams (Table 1). These soils are characterized by a high humus content (7-20%), broad range of the C:N ratio, special organic substance generally formed by iron and aluminium apocrenates and ulmates. It is also typical of them to accumulate the mobile forms of iron the maximum amount of which is attached to the upper humus horizon. The litter consists of partly decayed fallen leaves and beech branches. Further down, at a depth of 15 cm, the soil layer is dark grey with a brown shade, loamy, its structure is cloddy-granular not lasting: the layer is permeated with the roots of shrubs and trees.

In the lower mountain belt *G. nivalis* (population III) grows in the beech forest in *Fraxino - Fagetum* SCAM. 56 association. *Fagus sylvatica* is the basic species, forming the tree layer. In addition, there are also *Fraxinus excelsior, Acer pseudoplatanus*. In the undergrowth there are young trees of *Fraxinus excelsior*, and shrubs of *Rubus caesius, R. idaeus, Daphne mezereum*. In early spring *Leucojum vernum, Scilla kladnii, Helleborus purpurascens, Anemone nemorosa, Dentaria glandulosa* and *D. bulbifera* vegetate in abundance there. Later on, a herb layer is formed by *Aegopodium podagraria, Lunaria rediviva, Mercurialis perennis, Glechoma hirsuta, Galium odoratum, Senecio nemorensis* and *Cicerbita alpina*.

At its altitude limit, *G. nivalis* (population IV) grows at the upper forest line, formed mainly by *Fagus sylvatica*, sometimes by conifers. The species occurs in association with *Luzulo - Fagetum* MEUSEL 37. In the tree layer *Acer platanoides, A. pseudoplatanus* can be found, and the representatives of the shrub vegetation - *Daphne mezereum* and *Lonicera nigra*. Early spring plants occurring there are *Gagea lutea, Crocus heuffelianus, Anemone nemorosa, Primula veris, Chrysosplenium alternifoliumn, Dentaria bulbifera* and *Helleborus purpurascens*. Later on, *Senecio nemorensis, Luzula luzuloides, Veratrum lobelianum, Leucanthemum vulgare, Euphorbia amygdaloides, Poa chaixii, Gentiana asclepiadea, Malachium aquaticum* and *Doronicum austriacum* appear.

Morphology and anatomy

Let us give a brief morphological description of the plant. Bulb is (1.2) 1.5-2.0 cm long, and (0.8) 1.2-1.7 cm diameter. Leaves are dark green, with dove-coloured shade, they emerge from the neck of the bulb; in the flowering plant they are (7.2) 10.0-20.0 (29.6) cm long and 0.4 (0.6)-0.9 (1.4) cm wide. The flower stalk is rounded in the cross section, (7.2) 11.0-17.0 (27.0) cm long, it emerges from the axil of the inner assimilating leaf with the unclosed base; it is a side branch of the monopodial shoot. At the first stage of flowering, the flower stalk is filled with cells and by the end of flowering it is hollow. The spathe is 2.0-5.2 cm long, it consists of two bracts coaleseed together and slightly divided, with two "keels". At the base the bracts form a tube, from which the pedicel comes out. The pedicel can be longer, or shorter than the spathe or of the same length.

Perianth is formed by six separate tepals, placed in two circles. The tepals of the outer circle are purely white, spoonlike in shape, 1.6-3.0 cm long and 0.5-1.5 cm wide; the inner ones are inversely wedged 0.7-1.5 cm long and 0.5-1.0 cm wide, with a green spot at the top. The green spot is not continuous, it consists of some green stripes, their number changes depending on shape and size of the spot. Filaments are short, with narrow triangular anthers, opening at the top. Ovary is inferior, three-celled, oblong, with many ovules in each cell; style is filamentous with a small capitate stigma. Fruit is a polyspermic syncarpous capsule with centragonal placentation, and sutural-dorsal way of opening.

The morphological status of the species is extremely variable. Within the whole area it shows a considerable variability in most of the morphological parameters, and that is why many researchers dealt with the classification of the species and described separate taxonomic units. Thus, SCHUR (1866) splits out a species *montanus* (var. *montanus* (SCHUR)ROUY), but his morphological description does not contain any significant features which would give reasons for doing so.

DOSTÁL (1989) points out that a subspecies is recognized by some authors (BAKER, 1888; et al.). These plants are characterized by larger size of all vegetative and generative parts. Other students gave them different names and grouped them into different taxonomic units (var. *grandior* ROEM. et SCHULT., ssp. *imperati* (BERTOL.) BAKER; var. *imperati* (BERTOL.) RICHT., var *major* RED., etc.).

The most detailed classification of the genus *Galanthus* was brought forward by PRISZTER et ISÉPY (1974). According to these authors there are two subspecies within the species: ssp. *angustifolius* (G. KOSS) ARTJUSH. and ssp. *nivalis* GOTTL.-TANNENH., two variations and 19 forms. Apart from this, 19 forms are recognized on the basis of some teratological changes. The typical subspecies includes 2 var. - *G. nivalis* ssp. *nivalis* var. *nivalis* and *G. nivalis* ssp. *nivalis* var. *major.*

Comparative anatomical studies of the species of the genus *Galanthus* were carried out by ARTJUSHENKO (1970). Her studies show that anatomical structure of the scales of *G. nivalis* has the following features: upper and lower epidermes are made by slightly longitudinally elongated cells. Under the epidermis, there are some layers of parenchymal isodiametric cells, stuffed with starch grains. The scale mass is permeated by the vascular bundles. The intercellular space is filled up with mucous substance.

The leaf epidermis of *G. nivalis* consists of elongated cells slightly narrowed to the ends between them there are stomatal closing apparatuses. Each apparatus consists of 2 closing cells between which there is an orifice. The stomata are placed relularly throughout the blade surface. In the young leaf under the upper and lower epidermes there are assimilation parenchyma cells. There are large parenchymal cells between the assimilation parenchyma layers. The cells are filled up with raphides in young leaves. They do not have green plastids and are distinet from the background of the green

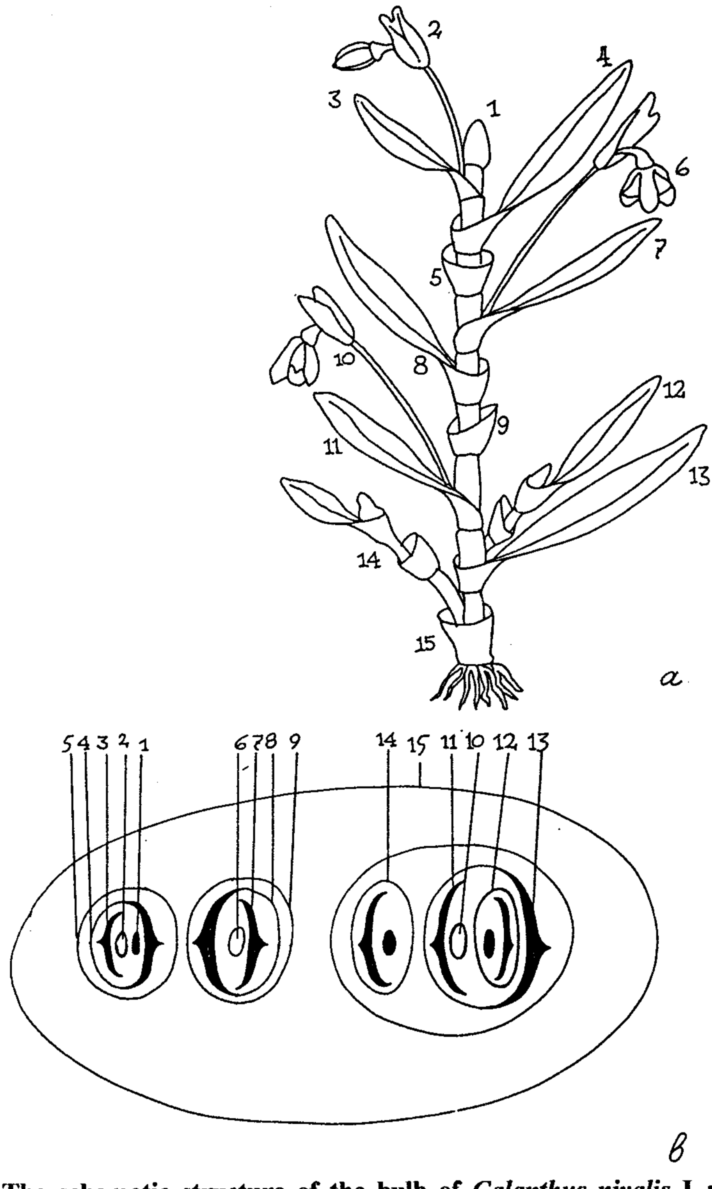

Fig. 4. The schematic structure of the bulb of *Galanthus nivalis* L.: a - vertical section (Braun according to Troll, 1937); b - horizontal section: 1 - growing point; 2, 6, 10 - flowers of shoots of different ages; 3, 4 - assimilating shootleaves of the current year renewal; 5 - basal shoot leaf of the current year renewal; 7, 8 - assimilating shoot leaves of the last year renewal; 9 - basal shoot leaf of the last year renewal; 11, 13 - assimilating leaves of the renewal of the year before last; 12, 14 - lateral vegetative shoots; 15 - basal leaf of the renewal of the year before last.

assimilation tissue. In the process of aging instead of the large parenchymal cells cavities appear. They are full of mucous substance, the nature of which is unknown for the time being. Vascular bundles are placed in the leaf in a single file, regularly througout the leaf blade area. Of all the bundles the best developed is the one of the central vein which protrudes from the lower side of the leaf forming a "keel". Around the bundles there are assimilation cells forming intersections between the assimilating tissue adjoining both upper and lower epidermes. The number of the bundles may vary with the leaf size; on the average it is about 20.

The anatomical structure of the stalk is characterized by the monostratal epidermis with stomata, and parenchymal cells forming large cavities. In the very centre of the stem the cells are obliterated and the central cavity is formed which enlarges with the growth of the pedicle and by the end of the vegetation it occupies the whole central part of the stalk. In the peripheral part of the stalk there are vascular bundles. The mechanical elements in the pedicel are underdeveloped, and when the fruits are ripe the stalk cannot bear their weight and lies on the ground.

The anatomical structure of the spathe is principally the same as that of the leaves, the only difference is that there are no stomata on its upper epidermis. In the place of the coalescence of two bracts forming the spathe, there is an intersection only made of epidermal cells.

In the transversal section of the pedicel, a well marked row of epidermis cells can be seen and parenchymal cells which are inside the pedicel cavity. There are six vascular bundles in the pedicel which consist of several vessels (inside) and sieve tubes (outside). The parenchyma has practically no chloroplasts.

Morphogenesis and seasonal rhythm of development

The morphological structure of the adult plants and seed germination of *G. nivalis* was described in detail for the first time by IRMISCH (1850). His data with some additions were used by VELENOVSKÝ (1907), TROLL (1937), KIRCHNER et al. (1934) and SEREBRJAKOV (1962) in their works, where they described features of vegetative organ structure and ontogeny of *G. nivalis* from seed germination to flowering.

Quite complete information about bulb morphology as well as a brief outline of *G. nivalis* development in cultivation are given in ARTJUSHENKO (1970). According our studies, the bulb of *G. nivalis* is perennial, tunicate, consisting of scales of two types: (a) scales, formed by basal leaves; (b) scales, formed by the bases of the assimilating leaves. Three scales develop yearly, one of which is formed by the basal leaf and two others are formed by the bases of the assimilating leaves. Two scales are concentric, and the third one, formed by the base of the leaf, preceding the flower, is not closed. The scales and leaves are attached to the bottom of the bulb, i.e. to the shortened stem with very closely approximated internodes (Fig. 4).

In the Transcarpathian Lowland vegetation of *G. nivalis* starts in late February. At higher altitudes, the terms of vegetation shift and shorten to some extent. The aboveground part development of the plants is completed in sprouts and leaves yellowing and further dying away. Fruits ripen on the ground and then burst open. The average duration of vegetation is 4 to 4.5 months (Fig. 5).

After the blossom has fallen, the process of differentiation of the next year flower bud shoot, laid down during the previous season, takes place in the bulb. In late June a knob develops by the flower stalk base which then evolves into the renewal bud. Thus, there are two renewal buds in the bulb which are at different stages of development. At the same time, lateral renewal buds which are the organs of the vegetative reproduction start to develop in the axils of the assimilating leaves.

Minor life cycle is completed within 3 years. In the first year rudiments of assimilating leaves are formed in the renewal bud, in the second year reproductive structures are formed, and in the third year the plant comes into flower. The bulb scales in this development cycle retain their vitality for one year more, then die away.

In the courese of morphogenesis of *G. nivalis* the following stages take place: primary shoot (p-v); primary bush (G_1, G_2); bushy particle (G_3).

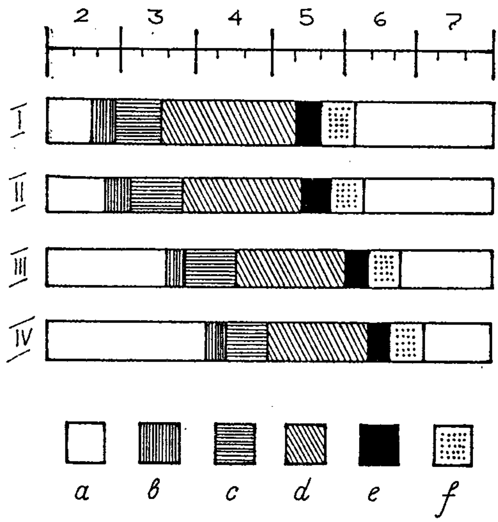

Fig. 5. Phenological spectra of the studied *Galanthus nivalis* L. populations: I-IV - populations as in Fig. 2; a - period of rest, b - beginning of vegetation, c - flowering, d - seed ripening, e - die-out of the above ground part of the plant, f - semination; 2nd-7th month.

Ontogenesis

On the basis of the combination of qualitative and quantitative features, three age stages of *G. nivalis* are distinguished (Fig. 6, Table 2):

I. Latent stage

Sm (seeds)

The seeds are round, yellowish white. The weight of the 1000 seeds ranges from 10.5538 to 12.0667 g. The endosperm is rich, containing much starch in the early srage of development. Elaioplasts develop from the chalazal area, which consist mostly of thin-walled cells rich in fats (KOMAR,1985).

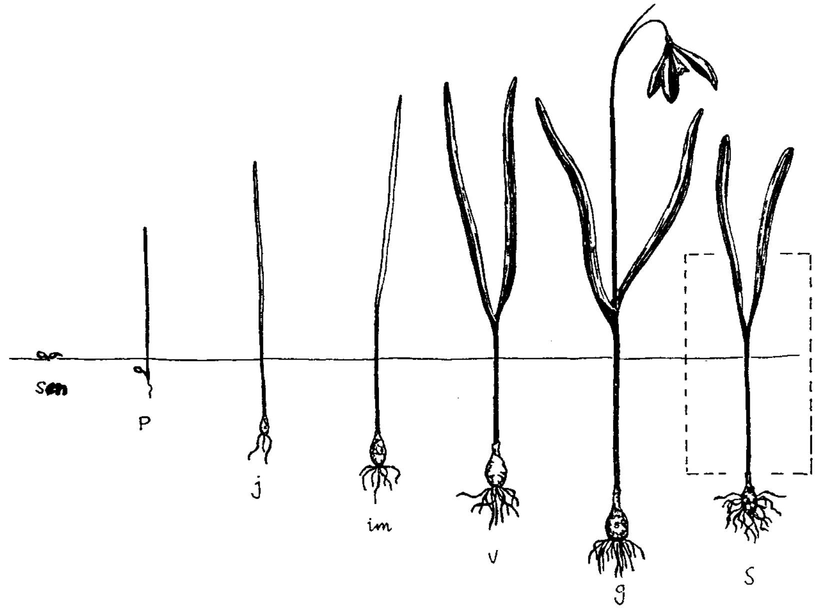

Fig. 6. Ontogenesis of *Galanthus nivalis* L.: sm - seeds, p - shoots, j - juvenile plants, im - immature plants, v - virgin plants, g - generative plants, s - senile plants.

II. Pregenerative stage

P (sprouts)

Fresh seeds, having poured out of the boll in June, germinate on the forest floor after four months, in late September. The seed coat bursts next to the micropyle, then the primary root and the cotyledon sheath appear. During 4 to 5 days they grow intensively down into the soil, then their growth slows down, and in this condition the sprout hibernantes. Some seeds germinate in spring.

J (juvenile plants)

In spring the first green leaf breaks through the cotyledon sheath and comes out of the soil, developing its green blade. The blade is narrow, linear, without a central vein. The primary root comes downward out of the forest floor layer and enters the soil. By that time the endosperm is already exhausted, and the plant begins to secure independent autotrophic nutrition. The closed sheath of the green leaf enlarges, forming the only storing scale of the monopodial bulb. The bulb is covered outside with glumiferous scales, formed by the cotyledon sheath. By late May, the leaf blade dies away, and the stage of summer rest begins.

In the second year 2-3 adventitious roots develop. In spring two leaves appear: one is a basal sheath leaf, the other is a middle assimilating leaf. The sheaths of both leaves enlarge and turn into storing scales.

Im (immature plants)

During the next 2-3 years 2 leaves form yearly, a basal leaf and a middle one The bulb is monopodial and comparatively not large. The number of fleshy scales grows to 3-4, that of dry glumiferous ones - to 2-3.

V (virgin plants)
Annual increment of the virgin specimen is 3 leaves: a basal leaf and two middle leaves. All vegetative organs of the virgin specimens are conspicuously larger, than those of the plants of all the preceding age groups, and they enlarge annually. In the root system 2 types of roots can be found, i.e. feeding roots, which are thin, coiled, growing mainly horizontally, and anchoring, thicker roots, growing downward, having distinct folds in the basal part.

III. Generative stage

G (generative plants)
In specimens of this age group, unlike the previous groups, the upper middle leaf sheath is not closed. From the axile bud of the upper middle leaf a flower stalk appears. Thus, even if the bulbs are going to flower, they retain monopodial growth. A lateral generative shoot bears one bractal membranous leaf and one flower. Detailed morphological descriptions of generative stages of *G. nivalis* specimens were carried out by IRMISCH (1850, 1860), VELENOVSKÝ (1907), TROLL (1937) and SPETA (1984).

Senile specimens occur within the populations very rarely. So this age group is singled out somewhat conventionally.

According to the classification made by SMIRNOVA (1987) on the life cycle duration, *G. nivalis* should be qualified as a plant with long ontogeny and according to its development rate it should be characterized as a plant with slow duration of pregenerative period (5-7 years). Judging by the peculiarities of the major life cycle, *G. nivalis* can be classified as the type of monocentric biomorphs with complete early nonspecialized desintegration (SMIRNOVA et al. 1976).

The studies of *G. nivalis* ontogeny in lower mountain belt have shown that, in general, it coincides with the one described in lowland. Biomorphological features of mountain plants change in the same way as the lowland ones (Table 2), but their qualitative indices are 1.2-1.8 times as large.

G. nivalis ontogenesis in the area of the Ukrainian Woodlands was studied by MELNIK (1987) and ANDRIJENKO et al. (1992). Probably, the authors have no chance to read our earlier works which describe the major life cycle of this plant (BUDNIKOV 1991; KRICSFALUSY et BUDNIKOV 1992). In general the *G. nivalis* ontogeny they have described is in good accordance with our data. However MELNIK (1992) does not recognize the immature age state, which we cannot agree with. Besides, the conventionally senile plants described by the author should be referred to the subgroup of the old generative specimens (G_3) in which recesses in flowering often occur. MELNIK refers these plants as conventionally senile ones on the basis of their transition from the senile state back to the generative one. However, the conventionality of recognizing the senile group consists in the other point - in extremely rare occurrence of the senile specimens and in their facultative growing in most of the cenoses.

Vegetative reproduction

Vegetative reproduction features were described by IRMISCH (1850, 1860), VELENOVSKÝ (1907) and TROLL (1937).

According to our observations in the nature, generative and virgin specimens reproduce vegetatively.

Tab. 2. Biomorphic features variation in *Galanthus nivalis* L. specimens of different age states inhabiting the Transcarpathian Lowland (numerator) and the lower mountain belt of the East Carpathians (denominator)
(for abbreviation, see text p. 59-61).

Age group	Bulb				Roots		Bulb mass to roots number ratio	Bedding depth of the renewal bud [cm]	Assimilating leaves		Leaf area [cm^2]	Flower stalk height [cm]
	Lenght [cm]	Width [cm]	Diameter of the disc[cm]	Mass [g]	Number	Lenght [cm]			lenght [cm]	breadth [cm]		
P	0.2 / 0.3	0.1 / 0.1	0.07 / 0.07	0.01 / 0.02	1.0 / 1.0	1.0±0.1 / 1.5±0.1	0.010 / 0.020	1.5±0.2 / 1.9±0.2	3.8±0.4 / 5.5±0.5	0.1 / 0.1	0.8 / 1.1	
J	0.4 / 0.6	0.2 / 0.3	0.1 / 0.1	0.03 / 0.04	3.3±0.5 / 5.8±1.2	1.2±0.1 / 2.0±0.2	0.009 / 0.007	2.0±0.2 / 3.1±0.3	5.5±0.6 / 6.5±0.8	0.2 / 0.2	2.2 / 3.9	
IM	0.6 / 1.0±0.1	0.5 / 0.7±0.1	0.3 / 0.4	0.06 / 0.1	12.6±1.8 / 17.6±3.0	2.8±0.3 / 3.0±0.3	0.005 / 0.006	4.7±0.4 / 5.3±0.5	8.4±1.1 / 10.0±1.2	0.3 / 0.5±0.1	5.0 / 10.0±0.2	
V	0.9±0.1 / 1.5±0.1	0.8±0.1 / 1.0±0.1	0.5±0.1 / 0.7±0.1	0.2±0.1 / 0.4±0.1	24.8±4.0 / 29.5±4.2	4.2±0.4 / 4.4±0.3	0.008 / 0.013	6.0±0.8 / 6.5±1.0	10.1±1.3 / 14.5±1.9	0.4±0.1 / 0.7±0.1	8.1±0.3 / 20.3±0.4	
G	1.4±0.1 / 1.8±0.1	1.1±0.2 / 1.4±0.1	0.8±0.2 / 1.1±0.2	0.4±0.1 / 0.8±0.3	28.5±4.2 / 31.2±4.4	5.3±0.5 / 5.6±0.8	0.014 / 0.026	6.4±1.1 / 7.5±1.2	11.3±2.6 / 19.0±3.0	0.5±0.1 / 0.9±0.1	11.3±0.5 / 34.2±0.6	11.2±3.2 / 17.5±2.5

Tab. 3. Density of populations and age state of the vegetative offspring of *Galanthus nivalis* L. plants in East Carpathians.
(A: † - the number of specimens per 1 m^2; ‡ - their % to the number of the plants of all age groups. B: # - the number of plants formed vegetatively; § - their percentage to the number of all the adult plants (v+g). For abreviation, see text p. 59-61).

Pop. no.	Veget. belt and alt. above sea level [m]	A. Age group					p+j+im +v+g	v+g	B. Vegetative offspring		
		p	j	im	v	g			Total	v	g
I	Transcarpathian Lowland, 130	13† 5.3‡	98 40.2	18 7.4	71 29.1	44 18.0	244	115	11# 9.6§	7 6.1	4 3.5
II	Foothill belt, 260	8 4.7	68 40.0	12 7.1	45 26.5	37 21.8	170	82	9 11.0	5 6.1	4 4.9
III	Lower mountain belt, 810	5 5.5	23 25.6	7 7.8	24 26.7	31 34.5	90	55	9 16.4	4 7.3	5 9.1
IV	Upper mountain belt, 1320	3 5.3	12 21.1	4 7.0	17 29.8	21 36.8	57	38	7 18.4	2 5.3	5 13.1

Vegetative reproduction begins in the axile bud of the last year lower leaf which starts to grow, forming a latteral vegetative shoot, connected with the maternal bulb during 2.5-3 years. By the end of the second year it forms usually 3 leaves (one basal and two middle). At the end of the third year and the beginning of the fourth year, the daughter bulb finally separates and becomes a quite independent specimen. Maternal plants retain their vitality and go on flowering; lateral vegetative shoots can appear either annually, or in 2 years.

G. nivalis is not a vegetatively mobile plant. In the process of its vegetative reproduction, groups of closely growing specimens appear (usually 2-3 specimens of different age states; rarely - 12-16 sp.), and from their location one can judge more or less precisely of their origin. Age stage of the plants appearing due to the vegetative reproduction is different. On the strength of all their features one part of them can be referred to as virgin plants, the other as generative plants. The plants of vegetative origin in their further development repeat, to a certain extent, ontogeny of the maternal ones, but it happens in a more rapid rate; usually in 1-3 years after separation they in their turn start to reproduce vegetatively.

In the studied *G. nivalis* populations the potential of the vegetative reproduction is different (Table 3); it increases to some extent with the increase of the altitude of the locality above sea level from 9.6 to 18.4% (from the number of all the adult plants).

Embryology

G. nivalis has a 4-celled anther. The anther cell wall consists of the epidermis, endothecium, middle layers and tapetum. In the endothecium fibrous buldges develop. The tapetum cells are double-nucleated. The sporogenous tissue is multicellular, the microsporocytes are arranged in several layers. Meiosis proceeds without any disturbances. Microspore tetrade formation is of the successive type. Pollen grains are two-celled by the moment of pollen discharge. The generative cell is rich in cytoplasm; its division takes place in the pollen tube.

According to the light microscopy studies, carried out by KUPRIJANOVA (1983), and our own data, pollen grains of *G. nivalis* are one-grooved, keeled, oblong; elliptical in shape on the distal side, keeled or bean-shaped on the lateral side; polar axis is 18.0-21.6 μm, major equatorial diameter is (25.2) 28.8-36.6 μm, minor squatorial diameter is 25.2 μm. The groove is long with uneven edges, tucked, more or less fissural, placed in the centre of the distal side or shifted a little to the lateral side; it reaches the ends of the grain, sometimes its ends turn round to the proximal side, in which case the shape of the pollen grains is bean-like. Exine is thin, 1.5 μm on the proximal side, 1.0-1.5 μm on the lateral sides, the relief cannot be seen. The colour of the grains is greenish grey.

Pollen fertility in different populations varies from 95 to 96%.

The ovule has two integuments, it is crassinucellate. The internal integument consists of 2 cell layers and in the area of micropyle it enlarges, and forms 3-4 layers, the external integument has 4-5 layers. The micropyle is narrow, straight, formed by the internal integument. The vasculon bundle ends near the chalaza. Hypostasis consists of large cells with thickened membranes. The ovule tissue in the chalazal part enlarges, forming an arriloid (VORSOBINA et SOLNTSEVA 1990). Archesporium is one-celled (STENAR,1925). A parietal cell separates during its division. In the ovule two megaspores function and form two embryo sacs, one of which dies (VORSOBINA et SOLNTSEVA 1990).

The embryo sac develops according to the Polygonum-type. Together with haploid embryo sacs diploid gametophyte formation has been reported (VORSOBINA et SOLNTSEVA 1990). A mature embryo sac is large, having elongated oval form, often narrowing to wards the chalazal end. The egg apparatus is well differentiated. The egg cell is larger than synergids, having a large nucleus, shifted into the apical part. The synergids are arranged above the egg cell, they have hooked excrescerises, are provided with a fibrous apparatus, have a thick cytoplasm almost lacking vacuoles, and the nucleus located in the middle or apical part of the cell. Polar nuclei usually fuse before fertilization and the central cell nucleus is arranged next to the antipodes. Metabolic activity of the mature embryo sac nuclei is varied; it is highest in the central cell (OSTAPENKO et KHVEDYNCH 1987). Pollen tubes access the embryo sac through the synergid. Male gametes enter the embryo sac as cells (VORSOBINA et SOLNTSEVA 1990). One spermium cell soon fuses with the egg cell. The nucleus of the other cell of the spermium moves to the central cell nucleus located next to the antipodes. The contact of the nuclei lasts about 2 hours. The spermium nucleus gradually enlarges and when it reaches 1/5 of the size of the central cell nucleus nucleole, the nuclei fuse. The fusion of the nuclei lasts from several minutes to 1 hour, depending on the temperature conditions. Double fertilization proceeds according to the premitotic type. Fusion of the egg cell and spermium nuclei proceeds slowly.

Nuclear endosperm development was observed in the lifetime of the ovule (VORSOBINA et SOLNTSEVA 1990). The primary endosperm nucleus is divided earlier than the zygote, in the central zone of the embryo sac: later on the nuclei are grouped in the wall layer of the cytoplasm. When the number of the nuclei reaches several hundred, the process of cell formation starts in the endosperm.

Seed Reproduction

G. nivalis is a cross-pollinating plant but sometimes self-pollination takes place. Ecology of pollination of *G. nivalis* was studied by KNUTH (1899) in outline.

G. nivalis is pollinated by bees. In Transcarpathia it has no specific pollinators. To attract pollinators the flower is supplied with a number of means: a spot in the inner segments of the perianth, strong odour, nectariferous tissue. A green spot signs an entrance for insects, it has stronger odour. Nectariferous tissue on the bottom of the flower tube on the apex of the ovary consists of glandular tissue, covered with thick cuticle. When secreting nectar the cuticle bursts and the nectar pours out through the cracks. According to KNUTH (1899) a little nectar is secreted in furrow on the inner side of green spot of segments of perianth.

Pollinators often come to the flowers not only to get nectar, but for the pollen, which they feed on.

The phase of seeding begins in June. By that time leaves and flower stalks become yellow and are shed, fruits ripen and break open on the fround. The seeds are supplied with elaiosomes: this caruncle is readily eaten by ants, who carry the seeds through the underground tunnels, helping to distribute them. According to the way of semination *G. nivalis* is myrmecochorous.

Considerable difference in conditions of *G. nivalis* growing (from lowland to the upper mountain belt) are reflected by its seed reproduction capacity. Findings of the seed productivity studies give the picture of peculiarities in changing number of seed buds and seeds depending on the conditions of growth.

As can be seen in Table 4, the number of seed buds is more stable than that of seeds. Particularly great variation of the number of seeds was in the plants of mountain populations in comparison with the lowland or foothill populations) where varieties were found that did not form seeds. The accuracy of measurements of seed number is higher than 5%, while that of seed buds number is close to 5% or somewhat higher.

Let us analyze the figures of the seed reproduction elements of the populations studied. According to the data from Table 4 the average values of the potential seed productivity (PSP) for lowland-foothill and mountain populations do not differ significantly and vary within 31.80-39.61 and 26.90-34.30 accordingly. For the 3 years of studies the average index of the PSP of the mountain populations was 88% of that of the lowland-foothill ones. In general, there is the tendency to a slight decrease of the average indices of the PSP in the mountain populations in comparison with the lowland-foothill ones, though in particular years the indices can overlap.

There is a distinct dependence in factual seed productivity (FSP); its average figures decrease with the altitude above sea level. The average index of the FSP in the mountain populations for 3 years of studies was 46% of that in the lowland-foothill ones.

Seed set figures in the lowland-foothill populations vary from 35.76 to 43.93%, in the mountain ones from 19.23 to 23.08%. For three years of studies the average seeding index in the mountain population was 52.20% of that in the lowland-foothill ones. With the increase of the location altitude above sea level the population density and the number of the generative plants in the populations, and therefore the seed yield, decrease. The average index of the seed yield of the population in the lower mountain

Tab. 4. Seed productivity parameters of different populations of *Galanthus nivalis* L. in East Carpathians (for abbreviation see text p. 51)

Vegetation belt and altitude [m]	Year of studies	Potential seed productivity						Factual seed productivity						Seeding percentage [%]	Seed yield [pcs/m^2]
		$\bar{x}$	$S\bar{x}$	CV[%]	t	P[%]	limits	$\bar{x}$	$S\bar{x}$	CV[%]	t	P[%]	limits		
Transcarpathian Lowland, 130	1988	32.00	1.81	28.22	17.83	5.66	15÷51	12.45	0.82	41.85	15.18	6.59	6÷20	38.90	522.90±34.44
	1989	32.40	1.79	27.70	18.10	5.52	13÷51	13.72	0.96	35.27	14.29	6.99	5÷23	42.35	576.24±40.32
	1990	34.30	1.92	26.31	17.86	5.60	14÷53	14.73	0.88	34.70	16.73	5.97	4÷25	42.94	618.66±36.96
Foothill belt, 260	1988	39.61	1.82	22.31	21.76	4.59	22÷58	17.42	1.82	51.73	9.57	10.45	6÷29	43.98	661.96±69.16
	1989	31.80	1.63	25.70	19.50	5.12	12÷51	12.84	0.92	36.02	13.95	7.16	3÷22	40.38	487.92±34.96
	1990	37.80	1.54	26.17	24.54	4.07	16÷58	13.52	1.12	53.64	12.07	8.28	4÷23	35.74	513.76±42.56
Lower mountain belt, 810	1988	32.00	2.00	23.00	16.00	6.25	21÷44	6.41	0.78	62.50	8.22	12.17	0÷12	20.03	217.94±26.52
	1989	34.30	1.78	24.60	19.16	5.19	19÷63	6.98	0.73	52.50	9.56	10.45	4÷9	20.35	237.32±24.82
	1990	30.10	1.24	25.13	24.27	4.12	18÷43	6.32	0.45	51.00	14.04	7.12	4÷10	20.99	214.88±15.30
Upper mountain belt, 1320	1988	26.90	1.35	24.31	19.93	5.02	11÷43	6.21	0.65	54.30	9.55	10.47	3÷10	23.08	105.57±11.05
	1989	28.80	2.00	25.40	14.40	6.94	13÷44	6.58	0.70	53.70	9.40	10.64	0÷10	22.85	111.86±11.90
	1990	30.70	2.12	26.84	16.34	6.91	14÷46	6.34	0.92	51.20	6.89	14.51	4÷9	20.65	107.85±15.64

belt for 3 years of studies was 39.63% of that in the lowland-foothill populations. In the upper mountain belt population the average seed yield index was 48.66% of that in the lower mountain belt and 19.28% of that in the lowland-foothill ones.

On the basis of the seed productivity studies of the *G. nivalis* populations in different belts of the East Carpathians it was found that the populations regularly regenerate through seed reproduction due to which their age structure remains stable. The intensity of the *G. nivalis* seed reproduction varies with different belts which gives us the grounds to divide the studied populations into two groups: lowland-foothill groups with the high generative reproduction capacity, and mountain grops with the satisfactory generative reproduction capacity.

Taking into consideration the findings of our studies, we cannot agree with the statement of MELNIK and PRYNDELAS (1992) that as a result of forest felling and soddiness of the soil surface seed regeneration ceases since the sod prevents the seeds from penetrating into the soil and developing the shoots. According to our data, it is in the meadow cenoses with the greatest soddines where the number of the juvenile specimens attains its maximum.

Field seed viability studies showed that different ecological and cenotic conditions in which the studied populations grow do not substantially influence the seed viability. It varies from 52 to 60% in different populations.

Age structure, density and phytomass of the populations

As a result of age structure studies the character of the age spectra of the populations in lowland and foothills was found to be rather similar (Fig. 7). Juvenile plants predominate there (40.2 and 40.0% of the total number of specimens respectively). Virgin plants are in lower numbers - 29.1 and 26.5%. Generative plants account for only 18.0 and 21.8%. One of the causes of such negligible part of generative specimens in the whole bulk of the populations considered is apparently picking up flowers in masses and digging the plants out (both populations are in the zone of intensive anthropogenic influence).

In the population of the lower mountain belt decreasing number of juvenile specimens can be observed (25.6%) and increasing part of generative (34.5%), while virgin plants amonnt to 26.7%. Still more considerable decrease of the juvenile plants (11.36%) and increase of the generative plants (57.95%) are characteristic of the population of the upper mountain belt. Virgin plants are estimated to represent 21.59% there. Since the group of adult specimens is maximum in the age spectra, these populations can be referred to as mature, normal ones.

Thus, the common feature in the age structure of the studied populations is their complete set of ages and the minimal share of shoots in them (4.7 to 5.5%). Immature plants have also their share, but it is negligible (from 7.0 to 7.8%). In the populations dying out plants (without assimilating leaves) occur; senile specimens have not been found. In single cases in the populations of lowlands and foothills the age spectra are shifted to the left which proves the good seed renewal of the species. These populations can be referred to as young, normal ones.

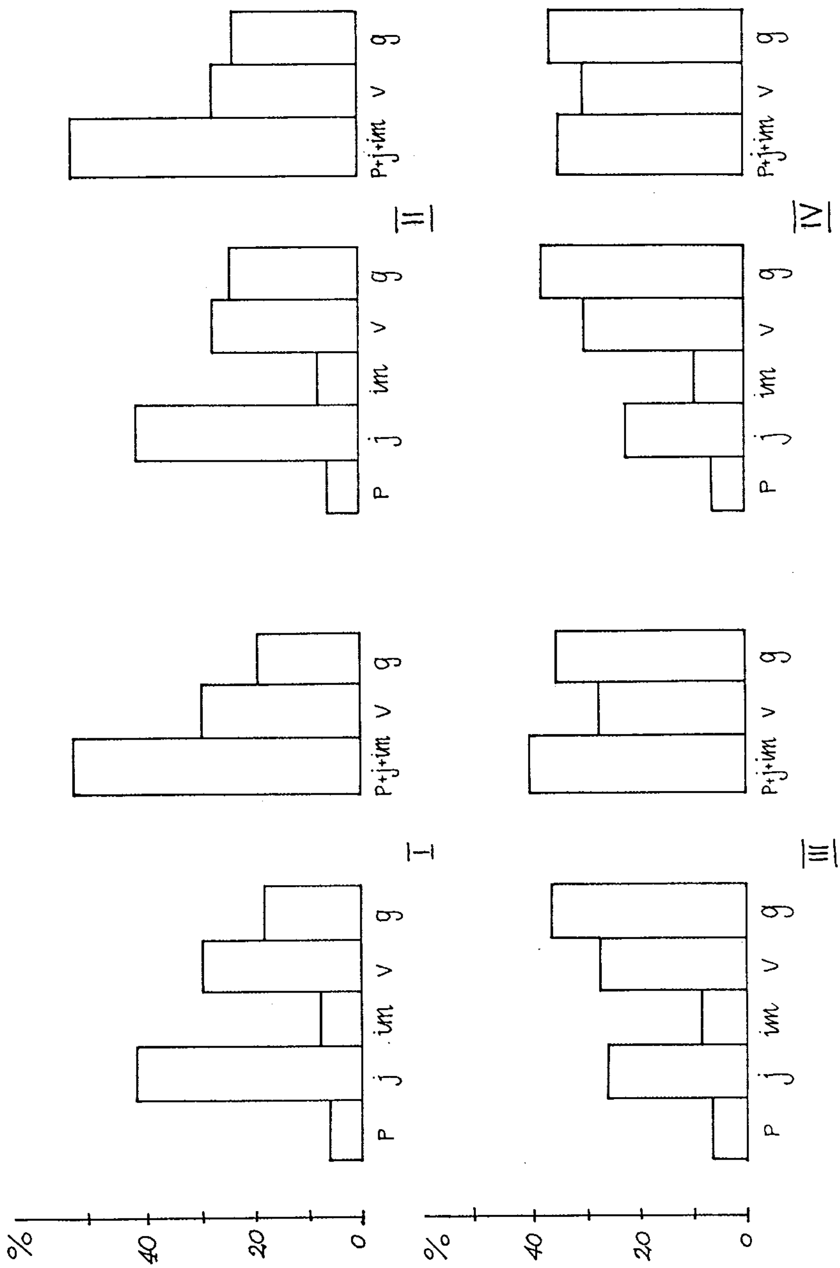

Fig. 7. Age spectra of *Galanthus nivalis* L. populations: I-IV - populations as in Fig. 2; j-g - age groups of plants as in Fig. 6.

To compare the age structure of the studied populations of *G. nivalis* in Transcarpathia and the populations in the eastern part of the area (Khmelnyckyj, Rivne, Kyiv, Chernigiv Regions) we have plotted their age spectra on the basis of the numerical data reported by ANDRIENKO et al. (1992). The species has been found to have a stable age structure within the whole area. Four populations can be referred to the type where young specimens predominate (p+j+im), the number of the virgin plants is somewhat higher than that of the generative ones. In one of the populations generative specimens dominate over virgin ones, while a great proportion of young plants is characteristic of the second type of the age structure. The above authors have found a degrading population of the regressive type with the right hand spectrum, where only generative and senile specimens can be found. It grows under a heavy anthropogenic pressure in a soddy clearing covered with dense tuft plant species.

Population density studies have shown that it decreases with the altitude above sea level (Table 3) reaching maximum values in the lowland.

In all the populations phytomass has been estimated (in fresh state) of the aboveground and underground organs (except for the roots) of specimens of different age groups and the entire populations (Table 5). The greatest number of specimens of all the age states has been found in the lower mountain belt, then it decreases a little in the foothill belt, unevenly falling in the upper mountain belt, and again decreases a little in the lowland. The phytomass reaches its minimum indices in the lowland (81,88 g/m^2) where the density is highest (244 pcs/m^2). In all the populations the maximum development of the specimens has been found in the generative state.

Taking into consideration the values of phytomass, density and age structure of the population, it should be concluded that the ecological and phytocenotic optima of *G. nivalis* coincide and are realized in the conditions of the foothill and lower mountain belts. Although the population density in the lowland reaches the maximum values, at the same time it results in reduced size of specimens.

Morphological variation

Rusults of the *G. nivalis* intraspecific variation studies are presented in Fig. 8. The analysis shows that the most variable features of the population I are the length of the assimilating leaves (CV=22.68%) and the height of the flower stalk (CV=28.63%). The rest of the features, apart from the bulb lenght (CV=8.25%) are characterized by the medium level of variation (CV=10.28-18.57%).

In population II highly variable features other than in population I (CV=20.45 and 23.06%) are the following: widsh of assimilating leaves (CV=20.55%), width of outer sepals, (CV=22.43%), lenght of pedicel (CV=22.38%), lenght of spathe (CV=22.32%) and phytomass of the bulb (CV=26.30%). The rest of the features have a medium level of variation.

In population III only phytomass of the bulb has a high variation level (CV=38.90%). Length of anthers, length and diameter of the bulb are characterized by low variation (CV=6.79, 7.43 and 7.26%). Medium variation indices are observed in the rest of the features.

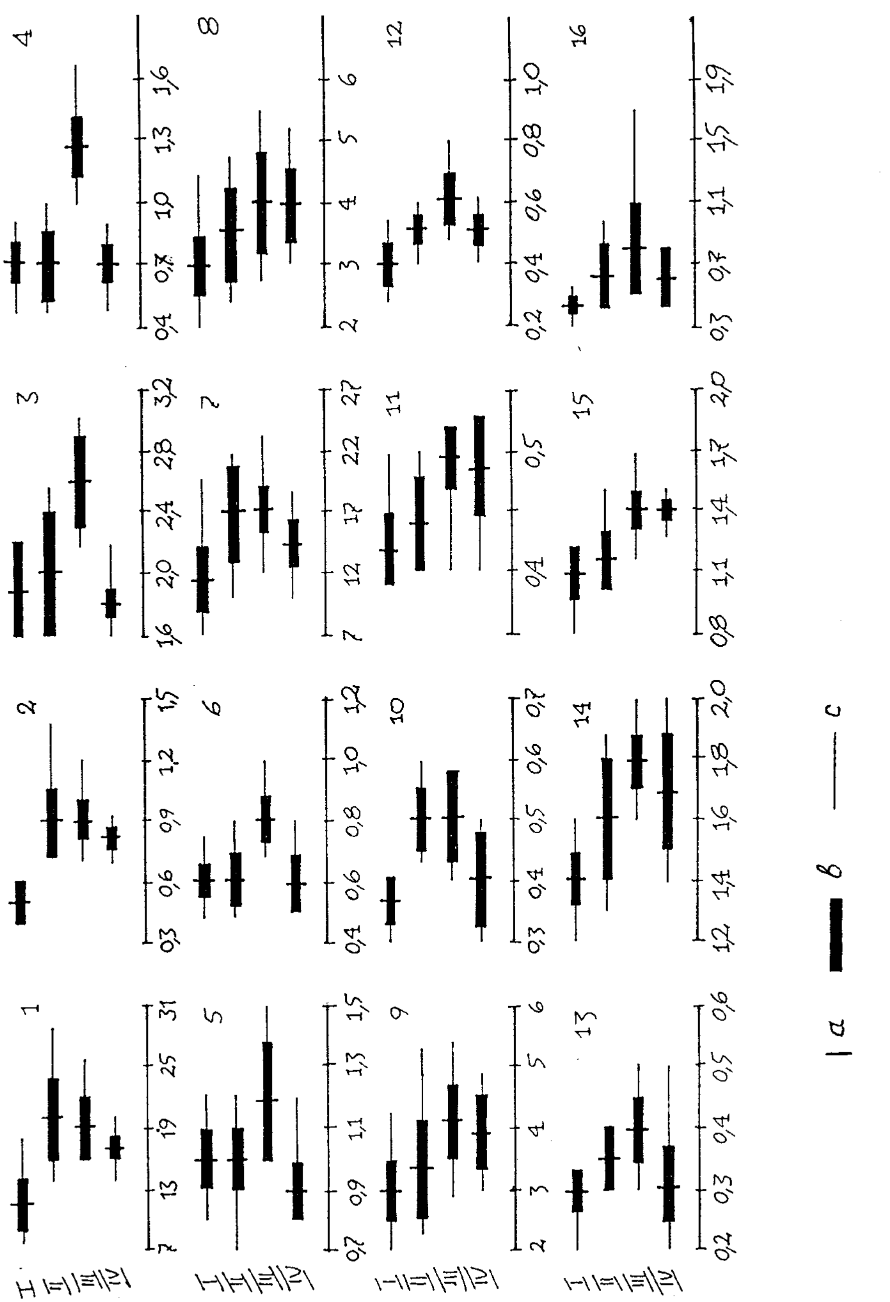

Fig. 8. Intraspecific variation of *Galanthus nivalis* L. morphological features: I-IV - populations as in Fig. 2; 1-16 - features as on p. 50. Presented graphically are: a - average value, b - standard deviation, c - variation range.

In population IV three parameters have a high variation level: width of the spot (CV=23.94%), diameter of ovary, (CV=22.10%) and phytomass of bulb (CV=28.55%). Six features (1,2,3,11,14,15) have low variability, while seven others (4-9.12%) have medium variability.

As can be seen, phytomass of the bulb is the most variable feature. It is explained by the fact that the variation factor of the weight feature is higher than that of the linear ones and by the greater dependence on the ecological and phytocenological conditions of the habitat.

Absence of the transgression of the standard feature deviations in population I and II is observed in three cases (difference 18.75%), in populations I and III - in 13 cases (81.25%), in populations I and IV - in three cases (18.75%) in populations II and III - in two cases (12.50%), in populations II and IV - in one case (6.25%) and in populations III and IV - in three cases (18.75%).

Thus, the populations of *G. nivalis* of different altitude belts do not differ from one another essentially. Morphological parameters reach maximum values in the populations of the lower mountain belt (in the conditions of ecological optimum), while minimum values are reached in lowlands (in condition of phytocenotic optimum).

ARTJUSHENKO et KHARKEVICH (1956) reported a form of *G. nivalis* with larger flowers and other plant parts (bulbs, leaves and flower stalks) on the Antalovetska Poljana Mountain, which was to their opinion identical to *G. nivalis* L. var. *major* Ten. The authors report that this form with large flowers occurs together with the usual one. FODOR (1974) desgribes large-flowered plants of *G. nivalis* as a new taxon - *G. nivalis* L. ssp *carpathicus* FODOR. Later, according to SVESHNIKOVA et FODOR (1983) relegates its taxonomic position and referes to it as *G. nivalis* L. var. *carpathicus* FODOR. According to the rules of Botanical nomenclature the taxa recognized by FODOR should be assigned to the category of synonyms of *G. nivalis* var. *major* described earlier.

The above facts show that the populations of *G. nivalis* in the East Carpathians have a high polymorphism in most of the morphological features. This high variation is characteristic of the species in the entire area. TROTTER (1915) studied the polymorphism of *G. nivalis* in the Alps in detail. Most of the intraspecific units were determined and described by botanists under different names, all of them however can be brought to *G. imperati* BERTOL = *G. nivalis* subsp. *imperati* (BERTOL) BAKER (WEBB 1980).

On the basis of our studies and the analysis of the wide reange of the reported data we came to the conclusion that there are no reasons to recognize any taxa like subspecies in *G. nivalis*. Apparently it was the specimens and populations having reached their maximum development in conditions of ecological optimum which were classified as a new subspecies. Thus, we have found that big specimens occur in all the populations except for the lowland one (population I). Occurrence frequency is highest in the lower mountain belt (population III). Our studies reported earlier (KRICSFALUSY et BUDNIKOV 1992) show that selectively examined big plants of population III distinctly differ in 10 features (out of 16) from the plants of the other populations. However, random registration of specimens showed that population III distinctly differs from the others only in three features. So, there are no reasons to recognize the populations in which big specimens grow as a subspecies. However, they may be considered as a separate variety - *G. nivalis* var. *major*.

Karyotypic variability

G. nivalis karyotype studies including the populations of the East Carpathians were carried out by SVESHNIKOVA et al. (SVESHNIKOVA 1971; SVESHNIKOVA et FODOR 1983; SVESHNIKOVA et KRICSFALUSY1985). It has been stated that the standard karyotype has the following form (Fig. 9): 2n=24=4M+12SM+2ST+6m. In addition, karyotype variants with accessory chromosomes (B-chromosomes, differing in morphology) have been found: 2n=24+1B, 2n=24+5-10B, 2n=24+6B(5+1), as well as aneuploids with one excessive SM chromosome, in the population of the lower mountain belt (Antalovetska Poljana), dicentrics and translocants.

According to the data reported by SVESHNIKOVA et FODOR (1983), the above karyotype variations were found in 28% of the studied plants.

The bioecological studies data are in good accordance with the karyotype variation. Thus, the vegetative reproduction intensity of *G. nivalis* has been stated to be the highest in the lower mountain belt population, which can be explained by the low level of the seed renewal as a result of reduced pollen fertility and seed formation. It is quite probable that these processes are caused by the accumulation of accessory chromosomes as well as the high karyotypic polymorphism. Accumulation processes of these phenomena are fixed at vegetative reproduction. Summing up all the information obtained, we can suppose that in the population intensive microevolutionary processes take place, directed to adaptation of plants to the specific conditions of the site on the slopes of the former volcano with a high radioactive background of the bedding rocks.

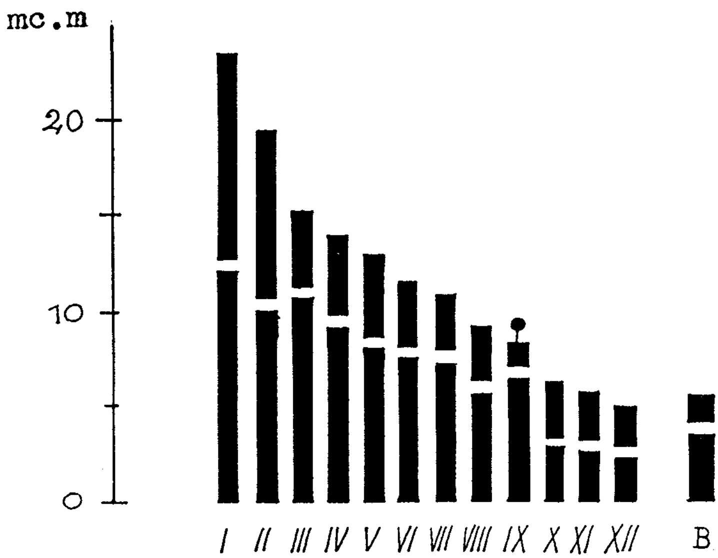

Fig. 9. Karyogram of the *Galanthus nivalis* L. haploid set.

Problems of protection and prospects of use

G. nivalis is at present widely distributed in the mountain areas which are not affected by an anthropogenic impact. But considerable reduction of population size takes place in the regions that adjoin the populated areas or recreation territories. Therefore, in order to preserve the gene pool of *G. nivalis,* it is necessary to provide absolute protection of the sites in the lowland and foothill areas and organize monitoring of conditions of the endangered populations. It is a good idea to collect and preserve *G. nivalis* in cultivation in the Botanical Garden of the Uzhgorod University.

G. nivalis is a good early spring honey bearing plant, a valuable medicinal plant, for it possesses some alkaloids. So, snowdrops are interesting plants for those who deal with medicine and farmacology.

Biochemical composition of *G. nivalis* from West Ukraine was studied in detail by KALASHNIKOV (1970). It is established that 5 alkaloids (likorin, naverdin, galantamin, nivalidin, hippeastrin) are contained in the above-ground part of *G. nivalis* and 5 alkaloids (likorin, naverdin, galantamine, nivalidin, tacetin) - in the underground part. Maximum sum of alkaloids in the above-ground part takes place during the budding phase (about 0,47%) and in underground part - during the fruiting phase (about 0,44%); dirung the mass flowering the sum of alkaloids in the above-ground part and in underground part is almost equal.

Galantamin ($C_{17}H_{21}O_3N$) is a strong poison, it is used in medicine in treating resifual effects after poliomyelitis, myastenia and myopathy, polyneuritis and radiculitis caused by traumatic injuries of the nervous system. Galantamin improves locomotive function and general condition of the patients.

To obtain galantamin the lower mountain belt populations are the most suitable, for the phytomass of the underground organs of the generative plants from these populations reaches the greatest value. The same is true for the foothill populations, where the weight of bulbs is somewhat lower but due to the greater population density their phytomass reaches higher values.

Bulbs of *G. nivalis* also contain mannose-specific lectins (VAN DAMME et al. 1988). These are dimeric proteins composed of subunits of 13 kDa, which are not bound together by disulphide bridges. In the hapten-inhibition assay the lectines exhibited exclusive specificity towards mannose.

Snowdrops have been known in decorative horticulture of the West European countries for a long time. We still fail to use them widely; they are grown mainly in botanical gardens, in private plots, but they are almost missing in city greenbelt settings. Combination of high decorative qualities with early sring blooming makes *G. nivalis* and excellent material for decoration of our gardens and parks.

In the East Carpathians, *G. nivalis* populations attain their maximum decorative effect in the lower mountain belt. Specimens of these sites are most suitable for introduction, material for selection can be taken from there.

Acknowledgements

We would like to express our great thanks to Doc. E. Michaleva for help in translation of the paper to English. We are also grateful to Ing. E. Andrik for her technical assistance in preparing this paper.

References

ANDRIJENKO T.L. MELNIK V.L. et JAKUSHYNA L.A. (1992): Rasprostranenije i structura tsenopopuljatsyj Galanthus nivalis (Amaryllidaceae) na Ukraine. - Botan. zhurn. 77(3): 101-107.

ARTJUSHENKO Z.T. (1970):* Amarillisovyje (Amaryllidaceae Jaume St. - Hillaire) SSSR. - Leningrad.

ARTJUSHENKO Z.T. et KHARKEVICH S.S. (1956): Rannevesennije dekorativnyje rastenija prirodnoj flory sovetskikh Karpat. - Botan. zhurn. 41(11): 1604-1616.

BAKER J. (1888): Handbook of the Amaryllidaceae. - London.

BOSCAIN N. et PURDELA L. (1989): Evaluarea stadiulni actual al protectiei florei Romaniei. - Ocrat. natur. simed. inconj. 33(1): 49-52.

BUDNIKOV G.B. (1991): Ontogenez Galanthus nivalis L. v Zakarpatje. - In: SIKURA I.I. (red.). Ontogenez introdutsyrovannykh rastenij v botanicheskikh sadakh Sovetskogo Sojuza. - Kiev. p. 25.

CZAPODY I. (1982): Védett növényeink. - Budapest.

CHOPIK V.I. (1978): Redkije i ischezajushchije rastenija Ukrainy. - Kiev.

DOMIN K. et PODPĚRA J. (1928): Klíč k úplné květeně Republiky Československé. - Olomouc.

DOSTÁL J. (1989): Nová květena ČSSR, 2. - Praha.

FODOR S.S. (1974): Flora Zakarpattja. - Lviv.

IRMISCH T. (1850): Zur Morphologie der monokotylischen Knollen und Zwiebelgewächse. - Berlin.

IRMISCH T. (1860): Beitrage zur Morphologie der Amaryllideen. - Halle.

KALASHNIKOV I.D. (1970): Issledovanije podsnezhnika belosnezhnogo, proizrastajushchego v zapadnykh oblastjakh USSR, kak istochnika galantamina: Avtoref. dis. kand. farmatsevt. nauk. - Lvov.

KELLER W. (1984): Über die soziologische Bindung von Galanthus nivalis L. im Aarganer Jura. - Rad. Akad. nauka i umjetn. B i H Od. prir. i mat. nauka. 76(23): 115-119.

KIRCHNER O., LOEW E. et SCHRÖTER C. (1934): Lebensgeschichte der Blütenpflanzen Mitteleuropas. - Stuttgart. Bd. 1. Abt. 3. Lief. 17.

KNUTH P. (1899): Handbuch der blütenbiologie. - Leipzig. Bd. II. Teil 2.

KOMAR G.A. (1985): Amaryllidaceae. - In: Sravnitelnaja anatomija semjan: Odnodolnye. - Leningrad. T. 1., p. 83-85.

KRICSFALUSY V.V. et BUDNIKOV G.B. (1992): Biomorfologicheskaja i ekologicheskaja kharakteristika Galanthus nivalis L. v Zakarpatje. - Rast. resursy. 28(1): 13-27.

KUPRIJANOVA L.A. (1983): Galanthus L. - In: KUPRIJANOVA L.A. (red). Spory paporotnikoobraznykh i pyltsa golosemennykh i odnodolnykh rastenij flory evropejskoj chasti SSSR. - Leningrad, p. 81.

LAKIN G.F. (1990): Biometrija. 4-je izd. - Moskva.

MAGLOCKÝ Š. (1983): Zoznam vyhynutých, endemických a ohrozených taxónov vyšších rastlín flóry Slovenska. - Biologia (Bratislava). 38(9): 825-852.

MALYNOVSKYJ K.A. (1980): Roslynnist vysokogirja Karpat. - Kyiv.

MARGITTAI A. (1923): Vznosy k flore Podkarpatskoj Rusi. - Kvartalnik IV sektsii. - Mukachevo. Ch. 1., p. 8-99.

MELNIK V.I. (1987): Sovremennoje sostojanije Galanthus nivalis L. na severo-vostochnoj granitse areala. - Bjul. Gl. botan. sada AN SSSR. 143: 37-39.

MELNIK V.E. et PRYNDELAS Ju.A. (1992): Etapy ontogeneza i vozrastnaja struktura tsenopopuljacij Galanthus nivalis L. na Ukraine. - In: SIKURA I.I. (red). Izuchenije ontogeneza introdutsirovannykh vidov prirodnykh flor v botanicheskikh sadakh. - Kiev. p. 99-100.

MORAVEC J. et al. (1983): Rostlinná spoločenstva České Socialistické Republiky a jejich ohrožení. Severoč. Přír. - Litoměřice.

OSTAPENKO E.K. et KHVEDYNICH O.A. (1987): Citokhimicheskoje issledovanije zarodyshevykh meshkov Galanthus nivalis (Amaryllidaceae). - Botan. zhurn. 72(3): 291-298.
PLOKHINSKIJ N.A. (1970): Biometrija. - Moskva.
PRISZTER SZ. et ISÉPY I. (1974): Chorologische und phanologische Untersuchungen an mediterranen Geophyten. - Ann. Univ. Sci. Budapest. Sect. Biol. 16: 87-101.
PROTOPOPOVA V.V. (1987): Galanthus L. - In: PROKUDIN Ju.N. (red). Opredelitel vysshykh rastenij Ukrainy. - Kiev. p. 402.
RABOTNOV T.A. (1950a): Voprosy izuchenija sostava populatsyj dlya tselej fitotsenologii. - In: GENKEL P.A. (red). Problemy botaniki. - Moskva, Leningrad, 1: 465-483.
RABOTNOV T.A. (1950b): Zhiznennyj tsikl mnogoletnikh travjanistykh rastenij v lugovykh tsenozakh. - Tr. Bot. In-ta AN SSSR. Ser. 3. Geobotanika. 6: 3-208.
ROTHMALER W. (1988): Exkursionsflora für die Gebiete der DDR und der BRD. - 7 Aufl. - Berlin. Bd. 4.
RUDNJEVA E.N. (1960): Pochvennyj pokrov Zakarpatskoj oblasti. - Moskva.
SCHUR F. (1866): Enumeratio plantarum Transsilvaniae. - Vindobonae.
SEREBRJAKOV I.G. (1962): Ekologicheskaja morfologija rastenij. - Moskva.
SMIRNOVA O.V., ZAUGOLNOVA L.B., TOROPOVA N.A. et FALIKOV L.D. (1976): Kriterii vydelenija vozrastnykh sostojanij i osobennosti khoda ontogeneza u rastenij razlichnykh biomorf. - In: URANOV A.A. et SEREBRJAKOVA T.I. (red): Tsenopopuljatsii rastenij (Osnovnyje ponjatija i struktura). - Moskva. p. 14-43.
SMIRNOVA O.V. (1987): Struktura travjanogo pokrova shyrokolistvennykh lesov. - Moskva.
SOÓ R. (1973): A magyar flóra és vegetáció rendszertani-növényföldrajzi kézikönyve V. - Budapest.
SPETA F. (1984): Zwiebeln - versteckte Veilfalt in einfacher Form. - Linzer Biol. Beitr. 16: 3-44.
STENAR H. (1925): Embryologische Studien. I u II: I. Zur Embryologie einiger Columniferen. II. Die Embryologie der Amaryllideen: Diss. - Uppsala.
SVESHNIKOVA L.I. (1971): Sravnitelno-kariologicheskoje issledovanie roda Galanthus L. Sektsija Galanthus. - Botan. zhurn. AN SSSR. 56(1): 118-126.
SVESHNIKOVA L.I. et FODOR S.S. (1983): Vnutrishnyovydovyj kariotypnyj polimorfizm Galanthus nivalis L. - Ukr. botan. zhurn. 40(5): 32-35.
SVESHNIKOVA L.I. et KRICSFALUSY V.V. (1985): Chisla khromosom nekotorykh predstavitelej semejstva Amaryllidaceae i Liliaceae flory USSR i GSSR. - Botan. zhurn. 70(6): 806-814.
TROLL W. (1937): Vergleichende Morphologie der höheren Pflanzen. - Berlin.
TROTTER A. (1915): Galanthus nivalis e G. major Red. Contributo alla studio della variabilita. - Ann. di Bot. 13: 185-236.
VAJNAGIJ I.V. (1973): Metodika statisticheskoj obrabothi materiala po semennoj produktivnosti rastenij na primere Potentilla aurea L. - Rast. resursy. 9(2): 284-296.
VAN DAMME E.J.M., ALLEN A.K. et PEUMANS W.J. (1988): Related mannose-specific lectins from different species of the family Amaryllidaceae. - Physiol. Plant. 73: 52-57.
VELENOVSKÝ I. (1907): Vergleichende Morphologie der Pflanzen. - Prag. Bd. 2.
VORSOBINA L.I. et SOLNTSEVA M.P. (1990): Semejstvo Amaryllidaceae. - In: BATYGINA T.V. et JAKOVLEV M.S. (red). Sravnitelnaja embriologija tsvetkovykh rastenij. Odnodolnyje. - Leningrad. p. 87-96.
WEBB D. (1980): Galanthus. - In: TUTIN T.G. (red). Flora Europaea. - Cambridge. Vol. V., p. 77-78.
ZARZYCKI K. (1986): List of threatened vascular plants in Poland. - In: ZARZYCKI K. et WOJEWODA W. (red). List of threatened plants in Poland. - Warszawa. p. 11-27.

Received: 18 November 1992
Revised: 15 December 1993
Accepted: 27 December 1993