

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

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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 attachment and demography of the species, morphogenesis and ontogenesis 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 ephemeroïd 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 (MARGITAI 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.

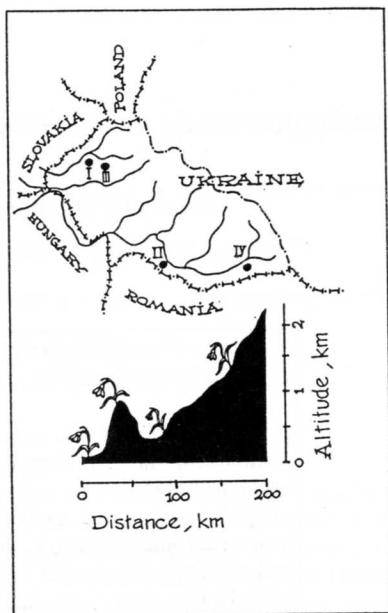


Fig. 2. Sites of the studied *Galanthus nivalis* L. populations in Transcarpathia: I- Vorochevo, II- Shajan, III- Antalovetska Poljana, IV- Menchul - Kvasivskyj.

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

The obtained numerical data were processed by variation statistic methods (PLOKHINSKIJ 1970 and LAKIN 1990). Arithmetical mean (\bar{x}) was calculated by the sums of squares mode. Average standard deviation ($S\bar{x}$), 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 MALYNOVSKIY'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 near its 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 - Tiliatum
 Aceri - Tiliatum 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-petraeae* BR.-BL. et TX. 43
 o *Quercetalia robori-petraeae* TX. 31
 u *Agrostidi - Quercion* SCAM. et PASS. 59
 Ass Quercetum petraeae-cerris
 Orno - Quercetum
 Orno - 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, ephemeroïds like *Scilla kladnii*, *Anemone nemorosa*, *Isopyrum*

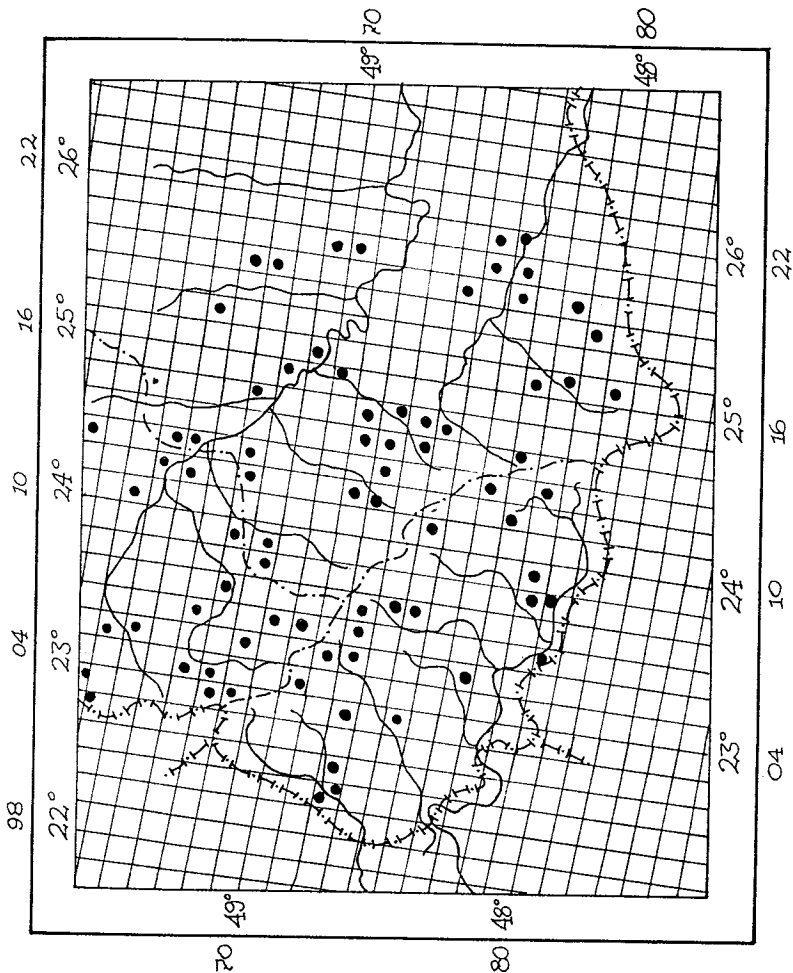


Fig. 3. Distribution of *Galanthus nivalis* L. in the East Carpathians.

thalictroides, *Gagea lutea* form a bright covering. Later on, in the herb layer *Aegopodium podagraria*, *Salvia glutinosa*, *Geranium sanguineum*, *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 ₂ O	pH KCl	Exchange acidity [mg-equiv. per 100 g soil]		% Al to total acidity		Absorbed cations [mg-equiv. per 100 g soil] (according to Hedroicz)			Unsaturated state in		Mobile compounds [mg per 100 g soil] (according to Kirsanov)		
					Total	H ⁺	Al ³⁺	Ca ²⁺	Mg ²⁺	H ⁺	H	H	Fe ₂ O ₃	P ₂ O ₅	K ₂ O	
																%
Mountain forest dark-brown	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.	
	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.	
	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	
	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 soddy-gley	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	
	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	
	25-30	not det.	5.5	4.7	0.66	0.27	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		
						g	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 ephemerals 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 alternifolium*, *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 coalesced 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.

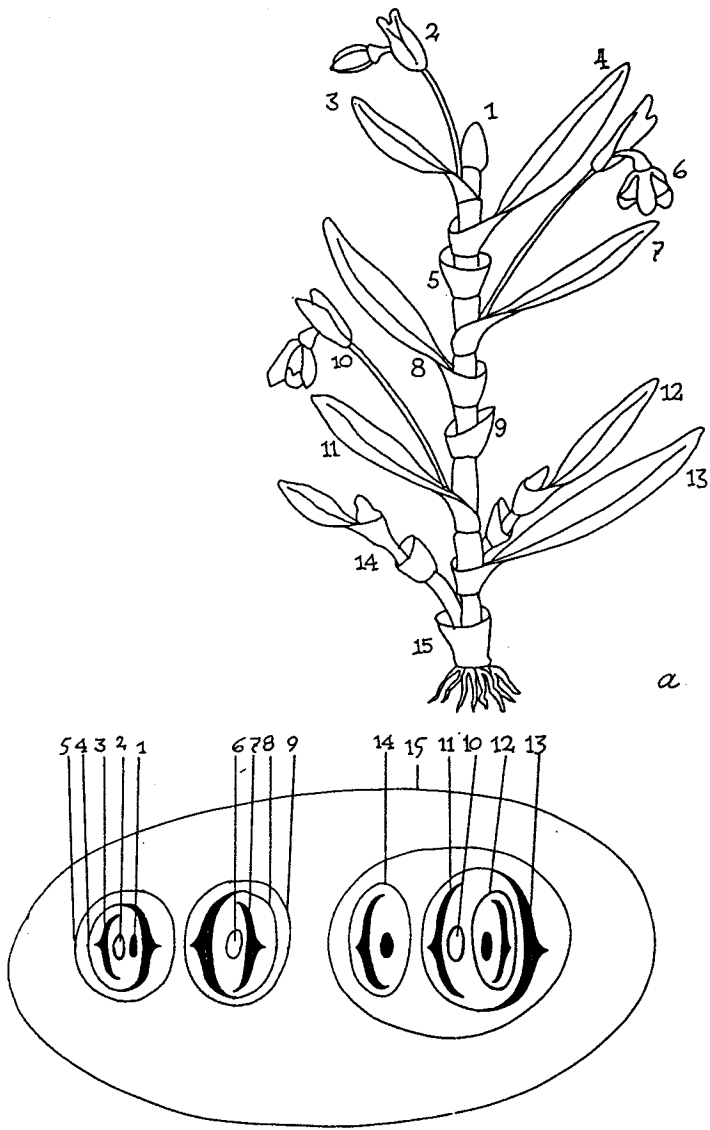
The morphological status of the species is extremely variable. Within the whole area it shows a considerable variability in most of the morphological parameters, and that is why many researchers dealt with the classification of the species and described separate taxonomic units. Thus, SCHUR (1866) splits 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 regularly 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 distinct from the background of the green



a

b

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

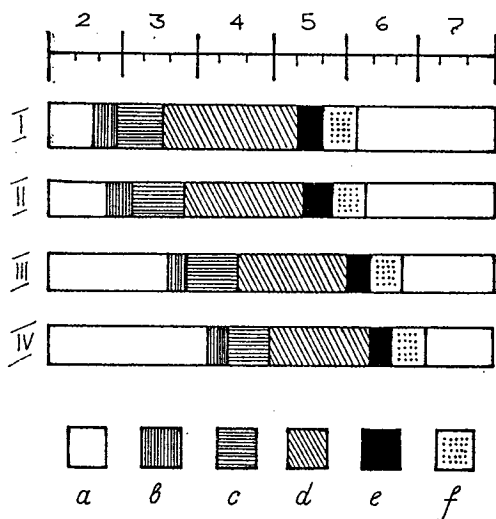


Fig. 5. Phenological spectra of the studied *Galanthus nivalis* L. populations: I-IV - populations as in Fig. 2; a - period of rest, b - beginning of vegetation, c - flowering, d - seed ripening, e - die-out of the above ground part of the plant, f - semination; 2nd-7th month.

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 stage of development. Elaioplasts develop from the chalazal area, which consist mostly of thin-walled cells rich in fats (KOMAR, 1985).

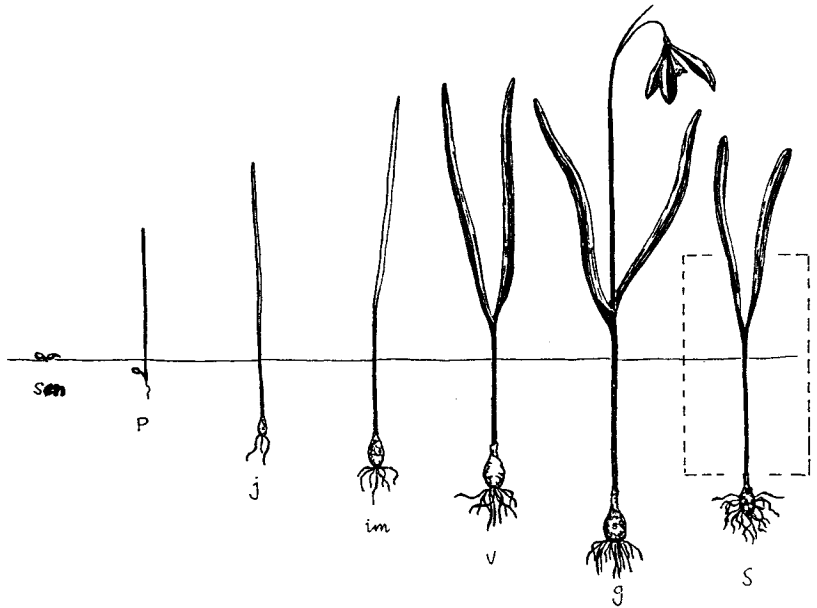


Fig. 6. Ontogenesis of *Galanthus nivalis* L.: sm - seeds, p - shoots, j - juvenile plants, im - immature plants, v - virgin plants, g - generative plants, s - senile plants.

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

