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Secondary succession in abandoned "poloniny" meadows, Bukovské vrchy Mts., Eastern Carpathians, Slovakia

DENISA BLAŽKOVÁ & STANISLAV BŘEZINA

Institute of Botany, Academy of Sciences of the Czech Republic, 251 43 Průhonice,
Czech Republic, e-mail: blazkova@ibot.cas.cz, brezina@ibot.cas.cz

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Abstract: Secondary succession in abandoned "poloniny" meadows in the Bukovské vrchy Mts., NE Slovakia, was being observed for 30 years, between years 1969 and 1999. At the beginning of the study most of the meadows were still regularly harvested. There were recognized three phytosociological types of the meadows at this time: *Campanulo abietinae-Nardetum* and *Acetoso-Deschampsietum* at higher altitudes, and *Betonico-Agrostietum* at lower altitudes. After several years, when the utilization stopped, secondary succession went somewhat differently in the stands of the three plant associations. However, some general features of the succession of all three meadow types could be observed. The first successional changes usually became apparent about 1 to 3 years after the meadow abandonment. The first successional stage lasted for up to 7 years. It was characterized by relatively small changes in species composition and by conspicuous changes in quantitative proportions of individual species. Low-growing heliophytes decreased gradually and eventually disappeared, while the phytomass of taller species increased. The next successional stage started between 5 and 8 years and lasted until 15 to 25 years after the end of meadow harvesting. It was characterized by spreading of expansive species, mostly from neighboring stands. The most common expander was *Calamagrostis arundinacea*. At the same time, the number of species decreased: the still surviving low-growing species disappeared, followed by first species of medium stature. Woody plants became established only in few individuals, most of which did not survive for long. The following successional stage usually began between 25 and 35 years after the end of meadow harvesting, in some cases even later. It was characterized by the establishment, gradual increase, and eventual dominance of additional expansive species. At higher elevations (ass. *Campanulo abietinae-Nardetum* and *Acetoso-Deschampsietum*), the most important new expansive species was *Rubus idaeus*; other such species included *Calamagrostis villosa*, and *Carex brizoides*. During the stage with dominant *Rubus idaeus*, successional stands were gradually invaded by herbaceous forest species. The invasion of woody plants and of the forest will take place probably later, in the subsequent stages. At lower elevations (ass. *Betonico-Agrostietum*), forest species appeared earlier, especially in small meadows surrounded by forest.

Keywords: NE Slovakia, National Park Poloniny, succession, abandoned meadows.

Introduction

Mountain meadows cover a considerably smaller area of the Bukovské vrchy mountains than deciduous forests. They contribute, however, significantly to the natural richness of the region. The existence of the meadows - generally known under term “Poloniny” - is criticallly dependedent on regular agricultural activities as haying or grazing. Since 1960’s the utilisation of the meadows has been gradually ceasing. As a result, the meadow vegetation begun to change fundamentally in the course of secondary succession. Restoration of the original meadow composition would be highly valuable, because of their unique species composition. The effort necessary to reach unique species composition of original meadows depends to a great extent on the common vegetation composition and, by analogy, on the successional stage of the site. Long-term studies of secondary succession are thus needed to evaluate the dynamics of original vegetation alteration on various sites.

Present paper describes temporal pattern of particular species abundance changes in the three types of the meadow vegetation between years 1969 and 1999. The changes in total plant richness of the sites are also described. Future successional trends of the vegetation are predicted.

The study area and its history

The study area covers the upper elevations (750-1130 m s.m.) of the Bukovske vrchy Mts., Poloniny mountain region, E Carpathians, NE Slovakia (Fig.1). The main ridge of these mountains separates Slovakia from Poland. The geological substrate consists of flysh rocks from upper Cretaceous and Paleogene, including mainly fine-grained sandstones and claystones. These relatively soft rocks were eroded into more or less uniform relief with gently sloping, smooth, rounded mountain ridges. Most soils belong to brown soils, few to pseudogleys. Climatically, the study area belongs to cold region according to QUITT (1971); the local climate is that of the inner side of the broad bend of the Carpathian mountains. The upper, anthropogenically lowered treeline is formed by deciduous woody species, mainly by beech. The entire study area lies in the Eastern Carpathian gap in the distribution of spruce , which forms mountain forests in most other Carpathian and Alpine mountain areas. VOLOŠČUK et al. (1988) provided detailed environmental conditions in the study area.

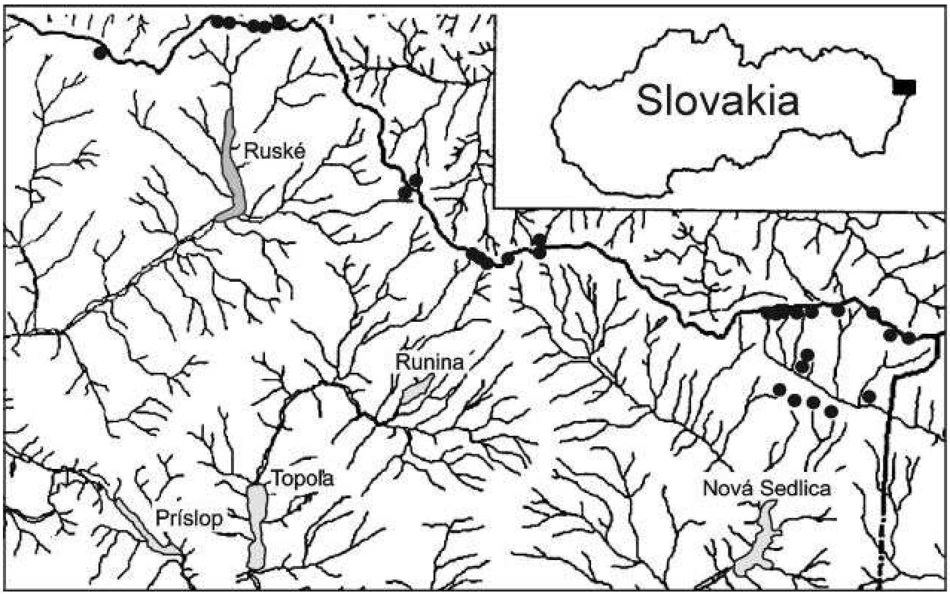

Fig. 1. The study area and plots with repeated relevés in the National Park Poloniny.

Slovak "poloniny" meadows represent the westernmost relatively small part of a widespread mountain meadows and pastures complex spreading along mountain ridges from the Slovakian Eastern Carpathians through the Polish Bieszczady Mts. and the Ukrainian Carpathians all the way to Romania. The Slovak part of the Eastern Carpathians is altitudinally lowest, reaching only 1.221 a.s.l., and apparently it does not rise above the upper climatic treeline. They originated and were maintained primarily as pastures for hundreds of years until. In particular, deforestation of mountain ridges made possible the immigration of many herbaceous species, including a number of Eastern Carpathian floristic elements, representing extensive, already naturally treeless meadows and pastures found at higher altitudes farther east. Past and present, relatively species-rich neighboring deciduous forests also increased the floristic richness of "poloniny" meadows, although typical forest elements are rare. The fact that the "poloniny" meadows are located on formerly deciduous forest soils probably also helped to increase the number of species. In the Ukrainian Carpathians, species-richest "poloniny" meadows and pastures are also found just above the treeline (MALOCH 1932), and lower alpine belt is often relatively species-rich also in other mountains. Species richness is much lower in the naturally treeless "poloniny" meadows and pastures at higher altitudes of Ukrainian, Polish, and Romanian mountains.

The history of the utilization of "poloniny" meadows in the Bukovské vrchy Mts. is complex. The forests on high ridges of the Bukovské vrchy Mts. were cleared already during the Valach colonization during the 14th and 15th centuries. However, the Slovak "poloniny" never reached such extent as these in the Polish and especially the Ukrainian Carpathians. Centuries of utilization of these meadows and pastures led to the development of unique, relatively species-rich mountain plant communities in the Bukovské vrchy Mts. till the World War II. Old residents remember 120 to 150 cattle heads grazing the frontier ridge between Ďurkovec and Kremenec for up to 8 weeks each summer. At that time, the ridge top was covered by an almost continuous strip of pastures, not by alternating narrow forest patches like today. A working "koliba", a temporary shelter used by cattle herders, was located near the summit of Čiertež until the end of the war in 1945. At a lower elevation, sheep grazed a side ridge of Príkrý and there was a "salaš", a hut in which shepherds and sheep could stay overnight. Fierce fighting took place on the summit ridges of the Bukovské vrchy Mts. during the passage of the eastern front during the World War II. Trenches and mounds from that time are still covered by vegetation different from the surrounding meadows.

After the war, "poloniny" meadows were already mostly utilized for haying; grazing was limited to small grassy enclaves in Stužica forest and in the vicinity of settlements. Historical upheavals continued to affect "poloniny" meadows after the World War II. For military reasons, the entire human population of the Polish Bieszczady mountains was relocated from this region during the early postwar years. As a consequence, agricultural activities ceased at the end of 1940's and in the high mountain locations they were renewed not even after the resettlement of this area. In contrast, intensive agricultural activities, including periodic haying of the altitudinally highest meadows, were carried out on the Slovak side until the end of the 1960's. Some Slovak residents even remember secretly haying abandoned meadows on the Polish side and transporting the harvested grass to the Slovak side under the cover of darkness. In this time, the first phytocoenological records of Slovak "poloniny" meadows were published by MÁJOVSKÝ (1956). Also the first relevés included in the present study were recorded between 1969 and 1972, when the most of the meadows were still utilized regularly.

However, modern social and political changes led to progressive departure of young people from mountains to towns in many mountain ranges, including the study area. The aging population gradually abandoned haying of meadows difficult to access, especially of those on ridge tops. Therefore, despite a formerly strong opposition of the local population to the communist government policy, agricultural collectives were established between 1970 and 1972, and significant changes in meadow utilization were instituted subsequently. Meadows on ridge tops, inaccessible for agricultural machinery, were no longer utilized, except for possible infrequent harvesting by individual private farmers. Accessible meadows at lower elevations were partially "cultivated"; they were plowed and, in some places, their overturned sod was seeded with a nonindigenous grass seed mixture. Unfortunately, this even happened to exceptionally species- and orchid-rich meadows on the low, flat Nastase ridge above the village of Starina. Part of these "cultivated" meadows was soon abandoned (e.g., on the ridge of Prikrý) and, as long as the stands were not eutrophized, the original meadow species composition gradually recovered. The data published by HADAČ et al. (1988) and the majority of the first sequentially repeated relevés included in the present paper were collected during this period.

The study area belongs to the National Park Poloniny, established in 1997, and to the tri-national (Poland, Slovakia, Ukraine) East Carpathians Biosphere Reserve, established in 1998. Since the establishment of the preceding Protected Landscape Region Východné Karpaty, the most valuable "poloniny" meadows have been maintained by a management regime. Nature conservation authorities organize regular harvests and the removal of cut phytomass from such meadows. The Institute of Landscape Ecology of the Slovak Academy of Sciences (SAV) has been following both continuing succession in abandoned meadows and the effects of harvests on managed meadows (RUŽIČKOVÁ et al. 1998, 2001). The last data analyzed in the present paper are from 1997 and 1999.

Methods

The data for the present analysis of secondary succession in "poloniny" mountain meadows include phytocoenological relevés recorded in square plots (5 x 5 m) and repeated at irregular intervals (3, 15 to 30 years), determined by the opportunities to revisit the individual sampled localities.

The years when the first sequential relevés were recorded (1969-1972) were the last when most of the meadows on the Slovak side of the mountains were still harvested more or less regularly, and these relevés represent the starting point of successional changes. At that time, only small pastures inside the forest complex of Stužica have already been abandoned for 10 years. The meadows on Kamenná and Ďurkovec were not hayed annually, but their succession was little advanced. In contrast, the meadows on the Polish side were abandoned for 20-23 years already in 1969-1972, when they were first sampled (see Introduction). During the 1980's and 1990's, repeated relevés were recorded in meadows that were no longer utilized for some time.

The initial relevé plots were documented through pacing or estimating distances from forest stands, individual trees, or other permanent points or lines. The corners of relevé plots were not marked permanently, but in 25 m -large, homogeneous stands the precision of relevé location of 1 m does not represent a significant difference in species presence. When species present in the original or subsequent preceding relevés were not found in the original plot but next to it, they were also included in the new relevé. In this way, species present near the original plot but not inside it were not evaluated as absent. During repeated sampling, percentage cover values for individual plant species were estimated in the original plots first and only then the new data were compared to the data collected previously.

Relevés were collected according to the methods of Zürich-Montpellier school of phytocoenology, but the 7 steps of the original scale for combined abundance and percentage cover of individual species were extended to 12 steps. For easy interpretation of the extended scale, the number indicating the steps was the same in both scales and a value slightly higher than the original step was indicated by a symbol +, added in the extended scale. The scale used in the present study is following: r solitary individuals; + species infrequently scattered; ++ species commonly present; cover less than 1%; 1 species cover less than 5%; 1+ species cover about 5%; 2 species cover from 6 to 15%; 2+ species cover from 16 to 25%; 3 species cover from 26 to 35%; 3+ species cover from 36 to 50%; 4 species cover from 51 to 65%; 4+ species cover from 66 to 75%; 5 species cover from 76 to 100%.

Taxonomic interpretation of selected species

The nomenklatory of plant species was united according to the synopsis of the Central European plants (NEUHÄUSLOVÁ & KOLBEK 1982) but a broader species interpretation, taken as aggregat, is often used. This was preferred to the narrow species definitions of the Bukovské vrchy Mts. flora by HADAČ & TERRAY (1991), because the majority of species in the study area have wide vertical distributions and include both lowland and mountain forms. In the broad zone of middle altitudes, the morphological differences between the lowland and mountain forms may disappear or both forms may be present in the same stand, even when they are genetically different (e.g., polyploidy, hybrids). This makes the determination of percentage cover for some narrowly-defined species in the field questionable and decreases the clarity of phytocoenological tables, especially when narrowly-defined species that belong to the same aggregate play the same or similar role in a plant community. On the other hand, some narrowly defined species have highly indicative diacritical or diagnostic value in the phytosociological evaluation of individual syntaxa. To retain this valuable information that some narrowly defined species convey, the problems of some critical taxa is discussed below.

Alchemilla vulgaris agg. included a number of small species, most frequently *A. acutiloba* OPIZ, less frequently *A. crinita* BUSER, *A. pungentiflora* PLOCEK , *A. baltica* JUZ., and others. *A. monticola* OPIZ, *A. gracilis* OPIZ, and *A. xanthochlora* ROTHM. occurred at lower altitudes, mostly outside of the study area.

Anthoxanthum odoratum agg. *A. alpinum* Á. LÖVE et D. LÖVE was predominant on ridges above 900 m s.m., although *A. odoratum* L., determined by both morphological and cytological analysis, was found on the frontier ridge above 1000 m s.m too. Populations usually consisted of both taxa at middle elevations between 700 and 800 m s.m. Only *A. odoratum* s.s. was identified at lower altitudes, where no specimens corresponded to *A. alpinum*. Apparently, this pattern in the distribution of these two taxa is often common. It was also supported by the study by FILIPOVÁ (in verb.) in the Krkonoše mountains.

Centaurea pseudophrygia C. A. MEYER forms a complex in which subordinate units are difficult to differentiate. According to some authors, frontier ridge plants with dark-colored, almost completely overlapping phyllaries belonged to *C. melanocalathia* BORBÁS (HADAČ & TERRAY 1991). Populations with lighter-colored, incompletely overlapped phyllaries also occurred in the study area.

Dactylis glomerata L. This taxon represents mostly *D.g.* subsp. *slovenica* DOMIN common in the vegetation on the frontier ridge. *D.g. glomerata* subsp. *glomerata* grows in a lower part of the study area, still together with *D. g. slovenica.*

Leontodon hispidus L. A glabrous type of *L.h.*subsp. *glabratus* (Koch) Holub was more common at upper altitudes, especially on ridges, and hairy *L. hispidus* s.s. was more common at the lowest altitudes. Both forms often occurred together in the same stands in the broad middle-altitude belt (300-800 m s.m.).

Solidago virgaurea L. Part of the population at the highest altitudes corresponded to subsp. *minuta* (L.) Arcangeli, which is identical with *S.v.* subsp. *alpestris* (Waldst. et Kit. ex Willd) Rchb. The majority of individuals had intermediate characteristics and could not be grouped with any subspecies.

Thymus pulegioides L. This unit groups all the taxa of the genus *Thymus* that occurred in the study area. The majority of individuals on the frontier ridge corresponded to *T. alpestris* Tausch ex Kerner. *T. alterans* Klokov was identified in the studied area by Mártonfi (1996). Typical *T. pulegioides* populations and populations, which are difficult to classify, occurred at middle elevations between 700 and 900 m s.m., but solitary on ridges above 900m s.m. as well.

Statistical methods

There were established 30 monitoring plots in total in the field. 11 of them were located in the *Campanulo-Nardetum* association in an early successional stage. Futher 8, 4 and 7 monitoring plots were established in the *Campanulo-Nardetum* association in a late successional stage, *Acetoso-Deschampsietum* association and *Betonico-Agrostietum* association, respectively. Following statistical analysis were conducted separately for each type of vegetation as there occured large variability in species composition among groups. Only species observed in at least 3 monitoring plots were involved in statistical analysis in order to remove the effect of rare events (i.e. observation of *Chenopodium polyspermum* in one of *Betonico-Agrostietum* plots).

Succesional changes in vegetation composition after grassland abandonment were analysed by redundancy analysis (RDA) using statistical program CANOCO (Ter Braak 1990). RDA is a multivariate linear method and a cannonical form of principal component analysis (Ter Braak 1990) which identifies major gradients in a set of dependent variables. In addition RDA maximizes the correlation of these gradients with another set of a-priori selected independent variables (usually empirically obtained characteristics of environment). RDA assumes linear relationship between the independent and dependent variables.

In this particular case, dependent variables are data about species cover in phytosociological relevés and the only a-priori selected independent variable is succession duration time after grassland abandonment. Linear method was chosed because most species change their cover only in one direction within the duration of observation (i.e. they only increase or decrease within the course of succession time).

The statistical significance of the fit between the floristic composition and length of succession duration was assessed using Monte Carlo permutation test (with 999 permutations). The data were permutated separately for each monitoring plot.

Vegetation of “poloniny” meadows of the Bukovské vrchy Mts.

The vegetation of regularly agriculturally utilized “poloniny” meadows in the Bukovské vrchy Mts. belongs to three principal associations of the Zürich-Montpellier school of phytocoenology, classified in the following way:

- *Nardo-Callunetea* Preising 1949
  - *Nardetalia* Oberd. ex Preising 1949
    - *Nardo-Agrostion* Sillinger 1933
      - *Campanulo abietinae-Nardetum* Hadač et al. 1988
      - *Betonico-Agrostietum* ass. nova
- *Mulgedio-Aconitetea* Hadač et Klika in Klika et Hadač 1944
  - *Calamagrostietalia villosae* Pawl. in Pawl. et al. 1928
    - *Calamagrostion arundinaceae* (Luquet 1926) Jeník 1961
      - *Acetoso carpaticae-Deschampsietum caespitosae* Hadač et al. 1988

Results

The original species composition was observed to be highly significantly ($p < 0.002$) influenced by successional changes in all of the four types of “poloniny” medows (see Tab.1). The exact pattern of successional changes differ, however, according to the particular type of the meadow. Therefore, more detailed information about vegetation changes are presented for each of the meadow type separately.

Campanulo abietinae-Nardetum Hadač, Andresová et KleschT 1988

This association occurs only at highest elevations of the frontier summit ridge in the Bukovské vrchy Mts., between about 900 and 1220 m a.s.l., on brown soils. The authors who described this association collected data between 1984 and 1986, when almost all meadows on the frontier ridge were not agriculturally utilized already for over 10 years. The relatively low number of species in their relevés (17-24 species) and especially the absence of low-growing heliophytes (e.g., *Polygala vulgaris*, *Antennaria dioica*, *Viola canina*, *Lotus corniculatus*) indicate that post-utilization secondary succession was under way and the stands considerably changed when they were sampled. In the years 1954-1958 even Paľczyňski (1962) mentioned the species also in the ass. *Campanulo-Nardetum* (sub. nomine *Nardetum carpaticum orientale*) on the Polish side of the region. Original, still agriculturally utilized plant communities sampled during the present study were usually richer in species (33-55 species), even if differences between individual stands were considerable. The group of relevés sampled between 1969 and 1972 (Tab. 2) represent the high variability of original communities. The last three relevés were harvested only occasionally and have somewhat different species composition than the rest.

The frontier summit ridge supporting this association offers diverse habitats differentiated by geomorphologic landscape formations, exposition, slope inclination, and soil depth, texture, and chemistry. The manner and intensity of previous agricultural utilization of these meadows also varied along the ridge, mostly according to the accessibility of individual meadow patches. These and other environmental variations produced considerable differences in species composition and richness between individual stands. Examples include two stands of this association from the ridge above the Ruské sedlo (Russian Pass), which are situated about 150 m from each other. Relevé 3 ([66/69], Tab. 2), located in a depression below the ridge top on deep, loamy soil, is one of the relevés with highest species richness (70 species) and a relatively low percentage cover of *Nardus stricta*. Relevé 8 ([65/69], Tab. 2), located on a convex ridge top with shallow, rocky, and sandy soil, has only 19 species and it is completely dominated by *Nardus stricta*. However, even the latter relevé belongs to the present association, because its indicator species (*Viola dacica, Cardaminopsis halleri, Rumex alpestris, Poa chaixii)* grow between *Nardus stricta* plants.

Nardus stricta is the most abundant species in most other stands of the association, but it was not always the edificator. Other common grasses include *Agrostis capillaris*, *Festuca rubra,* and *Anthoxanthum odoratum* s.l. (mostly *A. alpinum*), and dicotyledonous forbs *Potentilla erecta*, *Crepis conyzifolia*, *Alchemilla vulgaris,* and *Hypochoeris uniflora*. A number of species with relatively low average percentage cover are frequent, among them: *Gentiana asclepiadea, Rumex alpestris, Poa chaixii, Gymnadenia conopsea, Pyrethrum corymbosum, Achillea stricta,* and *Cardaminopsis halleri.* A number of indicators of this association have Eastern Carpathian distribution; others may have an additional optimum in the study area. Such species differentiate this association from similar Western Carpathian syntaxa (HADAČ 1989). They include, for example, *Viola dacica, Dianthus barbatus, Euphorbia sojakii, Campanula abietina, Aposoeris foetida,* and *Campanula serrata*. Less frequent species from family *Orchidaceae*, such as *Traunsteineria globosa, Listera ovata*, and rare *Coeloglossum viride,* are also among the indicators of this association.

Secondary succession

Preliminary results indicate that under maximum agricultural utilization, almost all “poloniny” meadows on the frontier ridge, including the Polish side, belonged to the ass. *Campanulo abietinae-Nardetum*. Such meadows were sampled only at the beginning of the present study. Already during the first few years (1969-1972), some investigated Slovak meadows on the frontier ridge were utilized only at irregular intervals and somewhat changed by succession. Adjacent meadows on the Polish side were not utilized at all since the end of the 1940’s and most of them were significantly altered when they were first sampled.

Although secondary succession in the stands of the ass. *Campanulo-Nardetum* represents a continuous sequence, the species composition of plots sampled at the beginning of succession and in late successional stages was highly dissimilar. Therefore, all plots were divided into two tables according to the progression of succession at the time of their first sampling. Table 2 includes stands corresponding to the ass. *Campanulo-Nardetum* that at the time of their first sampling were harvested annually or were in the first stage of succession after the harvest stopped. Table 3 includes stands that were at the time of their first sampling already in advanced stages of secondary succession, represented by communities, described by Hadač et al. (1988) as the *Achilleo strictae-Calamagrostietum* followed by the *Homogyno-Vaccinietum myrtilli* Hadač et al. (1988). The relevés placed at the end of both tables are transitional between these two groups. Each table was ordinated separately (see Fig. 2, 3) However, the whole secondary succession of the *Campanulo-Nardetum* presents the only one continuous procedure and it must be evaluated in this way.

Except for the last stage dominated by *Vaccinium myrtillus*, the most conspicuous change after the utilization stops is a gradual disappearance of species. Already during the first few years after the end of harvesting, species richness decreased and the relative significance of species changed gradually before a new expansive and strong competitor species emerged. Among the first species to disappear were low-growing heliophytes *Antennaria dioica, Polygala vulgaris, Euphrasia rostkoviana, Viola canina, Hieracium pilosella*, and *Stellaria graminea* and short-lived species such as *Leucanthemum vulgare*, whose reproduction is impeded by even small amounts of standing dead organic matter. Initially strong populations of low- and medium-growing species, mostly grasses (e.g., *Nardus stricta, Anthoxanthum odoratum* agg., *Agrostis capillaris, Leontodon hispidus* s.l.), decreased in importance, but were still present. At the same time, populations of taller species, which were impeded by regular harvesting (e.g., *Hypericum maculatum, Gentiana asclepiadea, Poa chaixii, Dactylis slovenica, Luzula luzuloides,* in some locations even *Campanula serrata*), gradually increased.These trends also appear in the figure 2. In most cases, only one or few of these species were increasing in the same stand. Which one(s) was determined by the habitat of each stand, the beginning status of the individual species populations, and by the competition conditions. Changes in the species composition and their quantitative relations are still not so dramatic at this successional stadium. The original state could usually be restored by a renewal of periodic harvesting.

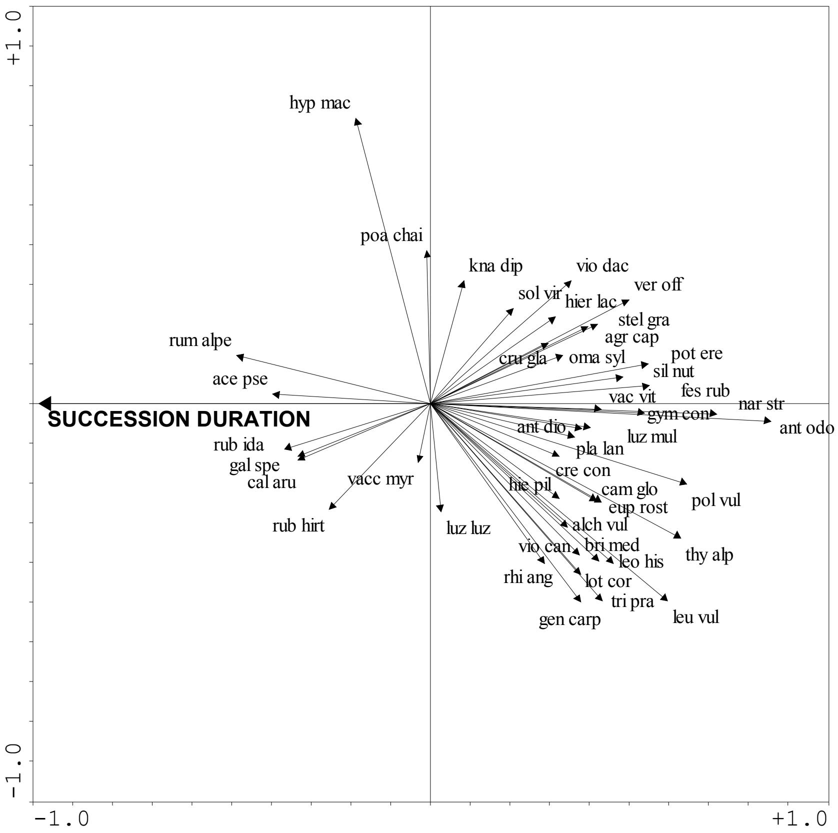

Fig. 2. *Campanulo-Nardetum* association in the early successional stage. RDA biplot between the succession duration time and floristic composition of the stand. The x- axes represents main direction of variation in species abundance that is correlated with succession duration time. The y- axes represents the second main direction of variation in species abundance. The increase in succession time is represented by the pointing direction of arrow marked as succession time. Other arrows represent particular species labelled by short cuts explained below. Coordinates of the arrow ends with respect to the direction of succession time arrow indicate change of species abundance in the time course of succession after abandonment. Long species arrows pointing in the same direction as succession time arrow indicate species abundance increases in the time course of succession, species arrows pointing in the opposite direction means the species abundance decrease in the time course of succession. Long species arrows pointing in any other direction indicate the changes in the species abundance is influenced by unknown variable. Distance between species arrow tips represent general similarity in species abundance pattern in relevés collected. Only species which abundance changes have been to a considerable extent explained by first two axes gradients are presented. More exactly explained: to be visualised species fit with graph presented have to be greater than 15. Short cuts used: *ace pse*-***Acer pseudoplatanus,*** *agr cap*-***Agrostis capillaris,*** *alch vul*-***Alchemilla***

vulgaris, *ant dio*-***Antennaria dioica,*** *bri med*-***Briza media,*** *cal aru*-***Calamagrostis arundinacea,*** *cam glo*-***Campanula glomerata,*** *cre con*-***Crepis conysifolia,*** *cru gla*-***Cruciata glabra,*** *eup rost*-***Euphrasia rostkoviana,*** *fes rub*-***Festuca rubra,*** *gal spe*-***Galeopsis speciosa,*** *gen car*-***Gentianella carpatica,*** *gym noc*-***Gymnadenia conopsea,*** *hie pil*-***Hieracium pilosella,*** *hier lac*-***Hieracium lachenalii,*** *hyp mac*-***Hypericum maculatum,*** *kna dip*-***Knautia dipsacifolia,*** *leo his*-***Leontodon hispidus,*** *leu vul*-***Leucanthemum vulgare,*** *lot cor*-***Lotus corniculatus,*** *luz luz*-***Luzula luzuloides,*** *luz mul*-***Luzula multiflora,*** *oma syl*-***Omalotheca sylvatica,*** *pla lan*-***Plantago lanceolata,*** *poa chai*-***Poa chaixii,*** *pol vul*-***Polygala vulgaris,*** *pot ere*-***Potentilla erecta,*** *rhi ang*-***Rhinanthus angustifolius,*** *rub ida*-***Rubus idaeus,*** *rum alpe*-***Rumex alpestris,*** *sil nut*-***Silene nutans,*** *sol vir*-***Solidago virgaurea,*** *stel gra*-***Stellaria graminea,*** *thy alp*-***Thymus alpestris,*** *tri pra*-***Trifolium pratense,*** *vac vit*-***Vaccinium vitis-idaea,*** *vacc myr*-***Vaccinium myrtillus,*** *ver off*-***Veronica officinalis,*** *vio can*-***Viola canina,*** *vio dac*-***Viola dacica.***

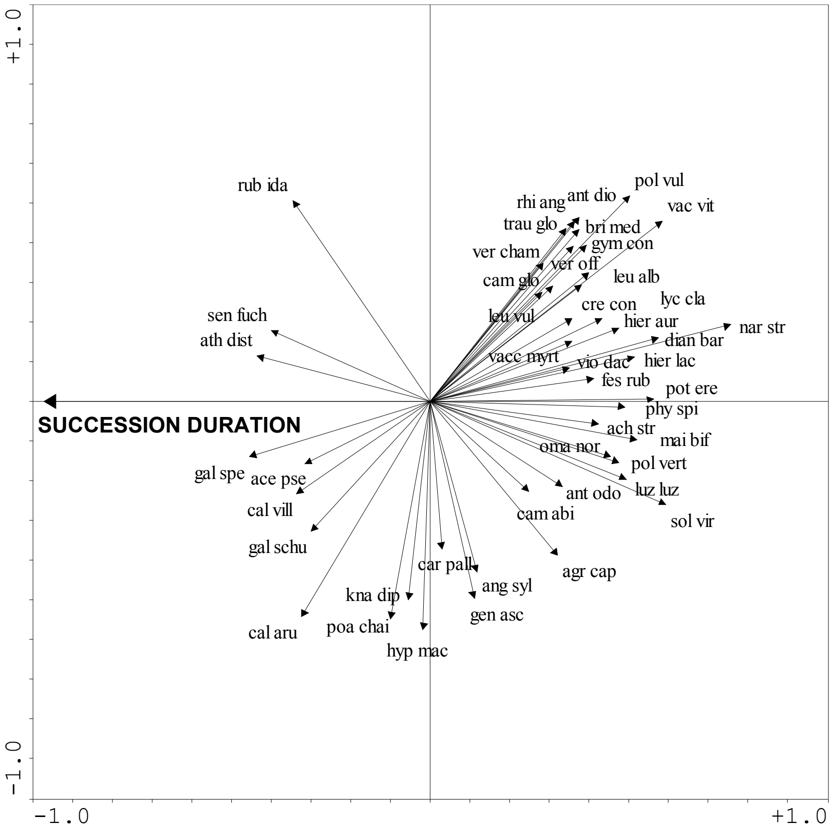

Fig. 3. *Campanulo-Nardetum* association in the late successional stage. RDA biplot between the succession duration time and floristic composition of the stand. For details see explanation under figure 2. Short cuts used: *ace pse*-***Acer pseudoplatanus,*** *agr cap*-***Agrostis capillaris,*** *ach str*-***Achillea stricta,*** *ant dio*-

Antennaria dioica, *ant odo*-***Anthoxanthum odoratum,*** *ath dist*-***Athyrium distentifolium,*** *bri med*-***Briza media,*** *cal aru*-***Calamagrostis arundinacea,*** *cal vill*-***Calamgrostis villosa,*** *cam abi*-***Campanula abietina,*** *cam glo*-***Campanula glomerata,*** *car pall*-***Carex pallescens,*** *cre con*-***Crepis conysifolia,*** *dian bar*-***Dianthus barbatus,*** *fes rub*-***Festuca rubra,*** *gal schu*-***Galium schultesii,*** *gal spe*-***Galeopsis speciosa,*** *gen asc*-***Gentiana asclepiadea,*** *gym con*-***Gymnadenia conopsea,*** *hier aur*-***Hieracium aurantiacum,*** *hier lac*-***Hieracium lachenalii,*** *hyp mac*-***Hypericum maculatum,*** *kna dip*-***Knautia dipsacifolia,*** *leu alb*-***Leucorchis albida,*** *leu vul*-***Leucanthemum vulgare,*** *luz luz*-***Luzula luzuloides,*** *lyc cla*-***Lycopodium clavatum,*** *mai bif*-***Maianthemum bifolium,*** *nar str*-***Nardus stricta,*** *oma nor*-***Omalotheca norvegica,*** *phy spi*-***Phyteuma spicatum,*** *poa chai*-***Poa chaixii,*** *pol vert*-***Polygonatum verticillatum,*** *pol vul*-***Polygala vulgaris,*** *pot ere*-***Potentilla erecta,*** *rhi ang*-***Rhinanthus angustifolius,*** *rub ida*-***Rubus idaeus,*** *sen fuch*-***Snecio fuchsii,*** *sol vir*-***Solidago virgaurea,*** *trau glo*-***Traunsteinera globosa,*** *vac vit*-***Vaccinium vitis-idaea,*** *vacc myrt*-***Vaccinium mytillus,*** *ver cham*-***Veronicachamaedrys,*** *ver off*-***Veronica officinalis,*** *vio dac*-***Viola dacica.***

The first significant change in stands undergoing succession occurred when a strong competitor, expansive species became established. In the investigated stands of the ass. *Campanulo-Nardetum*, this role was most frequently played by *Calamagrostis arundinacea*, but it spreads usually till 10-18 years after the end of harvesting. This species is present in neighboring forests and also appears as solitary scattered individuals in periodically harvested meadows. At the same time, both percentage cover and number of the remaining subordinate species of the original periodically harvested meadows decreased; even some species that increased during the previous stage now decreased. Among decreasing species were not only the remaining low-growing species, but also species of taller stature (*Pyrethrum corymbosum, Rumex acetosa*).

At this successional stage, the effects of gradually accumulating deciduous organic matter, which is not being removed by harvesting, may become more important in determining species relationships and replacement than the competition of adult individuals for light. This organic matter forms a thick, hygrophobic, dense layer of standing dead and litter, which isolates and insulates the surface and impedes plant reproduction. Seeds of some species may not reach the ground, or their seedlings, rhizomes, stolons, and other vegetative reproductive organs cannot grow through it. Accumulated dead organic matter is not such a problem for a small group of species capable of strong initial growth thanks to their well-developed underground storage organs (rhizomes, bulbs). These species infrequently occur in the original still-harvested stands and persist or appear again during succession, also in its late stages. They include *Lilium martagon, Polygonatum verticillatum, Senecio integrifolius, Veratrum album,* and partly also *Astrantia major* and *Ranunculus platanifolius*.

Beginning soon after or even before the end of meadow harvesting, woody plants appear periodically until late successional stages with *Vaccinium myrtillus*, but they never reach permanent presence and sustained growth. Except for common seedlings of *Acer pseudoplatanus*, they do not contribute significantly even to advanced successional stages, recognized as the ass. *Homogyno-Vaccinietum*, during which other previously absent species may slowly, but persistently increase. These species include herbaceous forest pioneers indicating the real advance of forests into abandoned meadows: *Galium schultesii, Trientalis europaea, Athyrium distentifolium, Galeopsis speciosa,* and *Senecio fuchsii*.

The expansion of *Vaccinium myrtillus* occured in two remarkable waves, negatively correlated with the expansion of *Calamagrostis arundinacea*. In the stands in which *Vaccinium myrtillus* appeared before or together with *Calamagrostis arundinacea*, *Vaccinium* mostly died off during the 1980's (stands were sampled in 1985 and 1988) and *Calamagrostis* quickly took its place. Because this die-off of *Vaccinium* occurred in stands of all vegetation at the same time, it was probably related to an environmental disturbance. This disturbance could have been a period of detrimental temperatures or drought, or a one-time or infrequent pollution load input carried by wind from Poland. Acording to SÝKORA (1983), *Vaccinium myrtillus* is even more sensitive towards air pollution than *Picea abies*. During repeated plot sampling in 1997 and 1999, *Vaccinium myrtillus* was fully recovered, highly vigorous and richly fruiting, while *Calamagrostis arundinacea* was partly dying back. Decline of *Vaccinium* populations was positively correlated with decline of populations of species that usually accompany *Vaccinium,* such as *Hypericum maculatum* and *Luzula luzuloides*, and with decrease in species richness. After the recovery of *Vaccinium myrtillus* the species richness increased again.

Successional fluctuations of vascular plant populations were also reflected in the moss layer. In periodically harvested meadows of the ass. *Campanulo-Nardetum*, the moss layer percentage cover is usually 3-25%; it is formed by common meadow species, such as *Brachythecium* and *Plagiomnium* spp., *Rhytidiadelphus squarrosus*, and more oligotrophic *Polytrichum juniperinum* and *Pleurozium schreberi*. During succession, the percentage cover and the number of moss layer species decrease until the complete absence of the moss layer during the stage with dominant *Calamagrostis.* Moss layer species appear again in early stages of the *Homogyno-Vaccinietum*, when *Vaccinium* becomes predominant and mesotrophic meadow species of genera *Brachythecium* and *Plagiomnium* (e.g., *P. affine, P. cuspidatum*) colonize litter and dead bunches of *Calamagrostis*. These mosses again disappear in older stands of the *Homogyno-Vaccinietum*.

An exceptional successional pathway developed in an originally unusually species-rich stand (relevé 3 [66/69], Tab. 2). After 28 years of succession, the stand was predominated by *Dactylis slovenica; Calamagrostis* and *Vaccinium* were still absent, species richness was drastically reduced from 70 taxa to 42, and a number of forest species appeared (e.g., *Helleborus purpurascens, Glechoma hirsuta, Dentaria bulbifera, Asarum europaeum,* even juvenile *Fagus sylvatica)*. This development was probably related to the location of the stand in a relatively moist, concave part of a slope with deep soil, enriched by nutrients leached from the upper parts of the slope and from accumulating litter of deciduous tree leaves blown in from neighboring forest stands (BLAŽKOVÁ 1988). All these factors favor a successional pathway leading directly to forests.

In some stands, succession was affected by additional disturbances. For example, in the locality Čiertež, a distinctive vegetation boundary appeared across an originally homogeneous, successional meadow stand. This boundary delimited two contrasting, previously absent vegetation types: a degraded stand of *Calamagrostis arundinacea,* and a stand completely dominated by *Nardus stricta*. The stand covered by trampling-resistant *Nardus* was used as a rest stop by hikers following an official tourist trail before joining the main ridge. Only the upper stand that was not utilized in this way and was dominated by *Calamagrostis* (relevé 7 [112/72], Tab. 2) was included in the present analysis. A comparison of both stands is in Blažková (1991).

The expansion and eventual dominance of *Calamagrostis arundinacea* and *Vaccinium myrtillus* and their respective communities are only transitory. At the end of the 1990's, about 25 to 30 years after the harvesting ended, some successional stands of the ass. *Campanulo-Nardetum* were expanded by rapidly spreading *Rubus idaeus*. This occurred during the stage with dominant *Calamagrostis*, i.e., much later and less consistently than during succession of the *Acetoso-Deschampsietum*, another association of still-harvested meadows. *Rubus idaeus* contributed to the disappearance of additional species and to many other successional changes (see relevé 3 [115/72], Tab. 3). The stage with *Rubus idaeus* may directly precede forest expansion, indicated by isolated individuals of *Senecio fuchsii* and *Rosa pendulina* in *Rubus idaeus*-dominated stands.

Calamagrostis villosa is another species that may rapidly increase following the stage dominated by *C. arundinacea*. I found the first colonies of *C. villosa* on Malá Rawka in Poland in 1973, and Jeník (1984) studied the first stands where it dominated in the 1980's. By the end of 1990's, or about 50 years after the end of harvesting, *C. villosa* formed continuous large stands on both Velká and Malá Rawka (Blažková 2003). *C. villosa* is already frequent in abandoned meadows also on the Slovak side, especially in the corner border region of Poland, Slovakia, and Ukraine.

Carex brizoides is another important expansive dominant in abandoned "poloniny" meadows. The stands of this sedge on the Slovak side are usually in the vicinity of the large stands it dominates on the Polish side. *C. brizoides,* which prefers deeper soils in depressions, threatens also to overwhelm one of the westernmost localities of *Scorzonera rosea* situated east of Riaba skala. Unfortunately, there are no data on the succession course of *Carex brizoides* in this area. Meadows can be protected against being overwhelmed by this sedge only with difficulty. Some possibility exists in moderate fertilization combined with regularly repeated harvesting. This procedure contributes to the invigorating of meadow, especially grass species and their competition ability against the sedge (Blažková & Hruška 1991).

Acetoso-Deschampsietum Hadač, Andresová et Klescht 1988

This vegetation type is dominated by *Deschampsia cespitosa*. It occurs on broad mountain passes and in slope depressions with fluctuating moist and dry regime. Clayey soil texture and rusty spots in subsoil horizons indicate that pseudogley processes are active. All repeated relevés were recorded on the main frontier ridge, but identical successional pathways are taking place also in abandoned meadows interspersing forests on slopes, where the rate of succession is somewhat higher than on the ridge.

Original, still harvested stands of the *Acetoso-Deschampsietum* are, in comparison with the stands of the other two meadow associations, species-poorest, with a maximum of 24 species per relevé. Constant and often abundant species, usually accompanying dominant *Deschampsia cespitosa,* include *Rumex alpestris, Hypericum maculatum, Dactylis slovenica* and *Lysimachia nemorum*. Among constant, but less abundant species are *Gentiana asclepiadea, Rumex alpinus*, an Eastern Carpathian species *Viola dacica,* and *Campanula abietina*. The species *Geranium palustre*, *Petasites albus*, *Glechoma hirsuta,* and *Carex sylvatica* are less frequent, but are important as indicators. The moss layer is poorly developed or absent.

Secondary succession

During the first 10-14 years after the end of harvesting, successional changes were not significant. Percentage cover of some species increased more conspicuously (e.g., of *Gentiana asclepiadea*, in some stands also of *Rumex alpestris, Dactylis slovenica,* and others), but later it decreased again. Already during this time, usually infrequent, but physiognomically striking species *Petasites albus*, *Chaerophyllum hirsutum*, *Carex sylvatica,* and *Glechoma hirsuta* disappeared, perhaps in response to changes in soil moisture regime after the end of harvesting.

However, the subsequent expansion of *Rubus idaeus* produced dramatic changes, including a rapid disappearance of *Hypericum maculatum* and *Poa chaixii*, species common in the original harvested communities. Other species decreased in importance and gradually disappeared, including both low-growing and taller species (e.g., *Campanula abietina, Viola dacica, Lysimachia nemorum, Achillea stricta,* and *Dactylis slovenica*). These changes are obvious in figure 4.

The dominance of *Deschampsia cespitosa* did not undergo substantial changes during the first 30 years of succession, but in some stands, dieback and die-off of some *D. cespitosa* tussocks and a decrease in their percentage cover occurred during the last years (relevé 2 [116/72], Tab. 4). This cannot be attributed only to competition with expanding *Rubus idaeus*, but mainly to the senescence of the entire tussock population, not yet juvenilized by regular mowing. This is supported by the fact that died-back *Deschampsia cespitosa* tussocks form only solitary, sterile tillers in places, which were no longer colonized by *Rubus idaeus*. Standing dead tussocks have highly sclerenchymatic phytomass and decompose slowly. The newly freed space is colonized by young individuals of *Carex pallescens, Anthoxanthum alpinum, Melandrium rubrum*, and partly by bryophytes. Such stands are enriched in these and similar meadow species at the same time when species typical for forests, such as *Athyrium distentifolium* and *Senecio fuchsii,* begin to appear.

During late successional stages, other species of neighboring forests appear along with the massive expansion of *Rubus idaeus*: *Dryopteris filix-mas*, *Senecio fuchsii, Athyrium distentifolium* and also solitary individuals of *Milium effusum, Oxalis acetosella*, and *Symphytum cordatum* (see Fig. 4). Woody plants do not increase in importance during this stage. Occasionally, seedlings of *Acer pseudoplatanus* occur, but they do not become established and disappear again. Nevertheless, the herbaceous stand composition indicates that after the population of *Rubus idaeus* dies off, succession will probably proceed directly to forest.

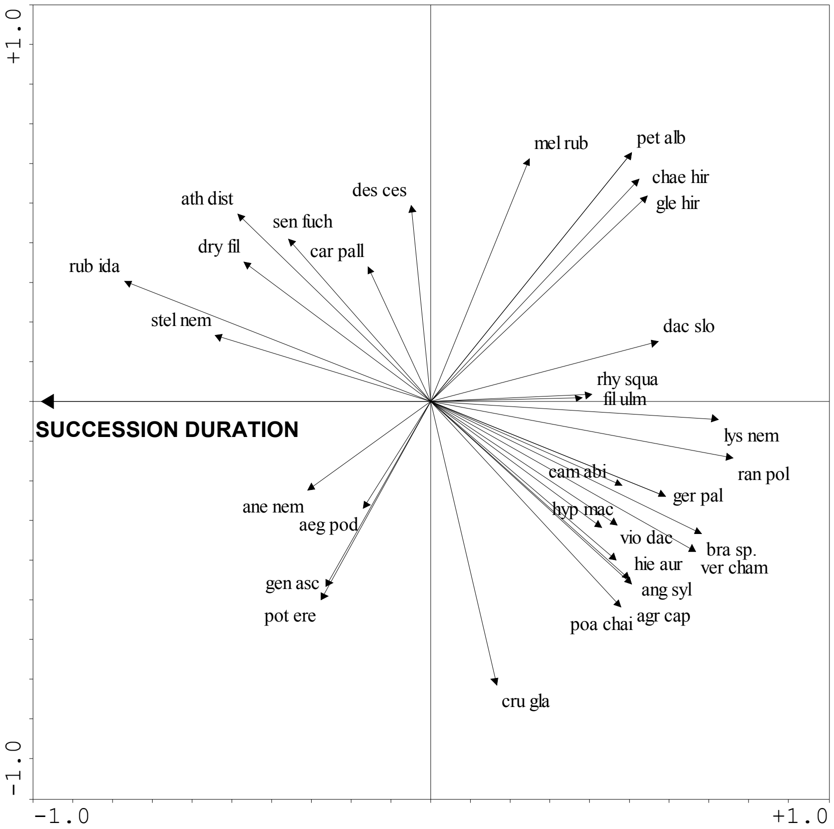

Fig. 4. *Acetoso-Deschampsietum* association. RDA biplot between the succession duration time and floristic composition of the stand. For details see explanation under figure 2. Short cuts used: *aeg pod*-***Aegopodim podagraria,*** *agr cap*-***Agrostis capillaris,*** *ane nem*-***Anemone nemorosa,*** *ang syl*-***Angelica sylvestris,*** *ath dist*-***Athyrium distentifolium,*** *bra sp.*-***Brachythecium sp.,*** *cam abi*-***Campanula abietina,*** *car pall*-***Carex pallescens,*** *cru gla*-***Cruciata glabra,*** *dac slo*-***Dactylis slovenica,*** *des ces*-***Deschampsia cespitosa,*** *dry fil*-***Dryopteris filis-mas,*** *fil ulm*-***Filipendula ulmaria,*** *gen asc*-***Gentiana asclepidea,*** *ger pal*-***Geranium palustre,*** *gle hir*-***Glechoma hirsuta,*** *hie aur*-***Hieracium aurantiacum,*** *hyp mac*-***Hypericum maculatum,*** *lys nem*-***Lysimachia nemorum,*** *mel rub*-***Melandrium rubrum,*** *pet alb*-***Petasites albus,*** *poa chai*-***Poa chaixii,*** *pot ere*-***Potentilla erecta,*** *ran pol*-***Ranunculus polyanthemos,*** *rhy squa*-***Rhytidiadelphus squarrosus,*** *rub ida*-***Rubus idaeus,*** *sen fuch*-***Senecio fuchsii,*** *stel nem*-***Stellaria nemorum,*** *ver cham*-***Veronica chamaedrys,*** *vio dac*-***Viola dacica.***

Betonico-Agrostietum associatio nova (nom. type Tab. 5, relevé 3 [49/69])

This association includes relevés number 9-13, Tab. 1 in (Blažková 1991), where the association was described as provisional and, therefore, invalidly.

Tab. 1. Summary of redundancy analysis (RDA) results. Significance values indicate the proportion of random permutations between species abundances and succession duration time that had the correlation coefficient more extreme than observed in the real data set. Eigenvalues indicate the proportion of data variability which is explained by approppriate axes. In this particular case eigenvalues of the first axis represent the proportion of variability in species abundance pattern explained by succession duration time.

Association	Signifficance value	F - ratio	Eigenvalues of the 1-st axis (succesion duration) %	Eigenvalues of the 2-nd axis %
Campanulo-Nardetum (early succes. stage)	0.001	8.822	12	4.7
Campanulo-Nardetum (late succes. stage)	0.001	8.125	23.3	7.4
Acetoso-Deschampsietum	0.001	7.375	25.7	12.5
Betonico-Agrostietum	0.002	5.417	12.9	9.2

Characteristic and differential species: *Betonica officinalis, Succisa pratensis, Ajuga reptans, Campanula patula, Gentiana asclepiadea, Cardaminopsis halleri, Poa chaixii, Achillea stricta, Crepis conyzifolia, Thuidium delicatulum*.

Dominant or codominant species: *Nardus stricta, Agrostis capillaris, Festuca rubra*.

Prominent constant species: *Leontodon hispidus* s.l., *Thymus pulegioides, Lotus corniculatus, Carlina acaulis, Cruciata glabra, Polygala vulgaris*.

This association occurs in the middle mountain belt of the Bukovské vrchy Mts., at altitudes from about 750 to 950 m s.m. Its stands cover broad, rounded, lower-lying ridges and form meadow patches surrounded by forests on slopes. In its original, still harvested stage, this association is species-rich, usually with more than 50 species per relevé (51-56 species in the herb layer). It occurs on slightly acid brown soils with the sorption-complex more saturated by bivalent cations than the soils of the *Campanulo-Nardetum*, located at higher altitudes.

Secondary succession

Secondary succession in abandoned meadows of the ass. *Betonico-Agrostietum* proceeded more rapidly and produced more conspicuous changes than succession in meadows which occur at higher altitudes (see Fig. 5). This was well documented, because some stands of the *Betonico-Agrostietum* were sampled for the first time before succession started and then resampled for the last time much later. The first records of relevés 40-48 were made during regular meadow harvesting, which in these stands ceased between 1972 and 1973. The last three relevés in the table, located in meadow enclaves in the altitudinally lower part of the natural reserve Stužica, were first recorded 10 years after the utilization of those stands as bull pastures stopped permanently in 1962 (Poliščuk in verb.). The relevés recorded in these stands in 1997 thus represent the state of this association after 35 years of secondary succession.

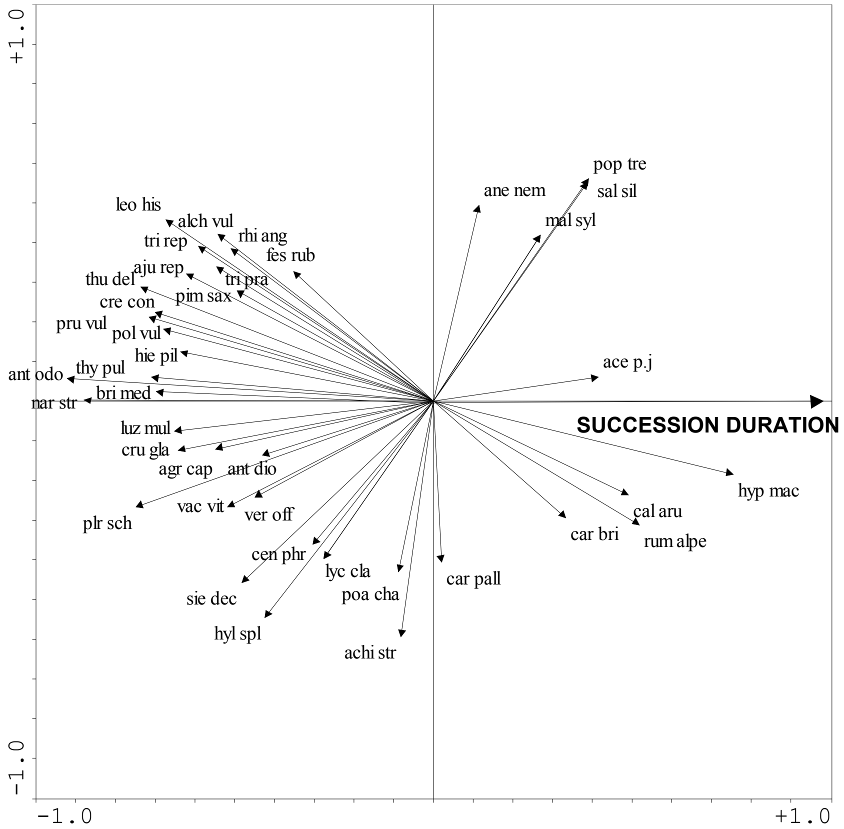

Fig. 5. *Betonico- Agrostietum association.* RDA biplot between the succession duration time and floristic composition of the stand. For details see explanation under figure 2. Short cuts used: *ace p.j*-***Acer pseudoplatanus, juvenilní,*** *agr cap*-***Agrostis capillaris,*** *achi str*-***Achillea stricta,*** *alch vul*-***Alchemilla vulgaris,*** *ane nem*-***Anemone nemorosa,*** *ant dio*-***Antennaria dioica,*** *ant odo*-***Anthoxanthum odoratum,*** *bri med*-***Briza media,*** *cal aru*-***Calamagrostis arundinacea,*** *car bri*-***Carex brizoides,*** *car pall*-***Carex pallescens,*** *cen phr*-***Centaurea phrygia,*** *cre con*-***Crepis conysifolia,*** *cru gla*-***Cruciata glabra,*** *fes rub*-***Festuca rubra,*** *hie pil*-***Hieracium pilosella,*** *hyl spl*-***Hylocomium splendens,*** *hyp mac*-***Hypericum maculatum,*** *leo his*-***Leontodon hispidus,*** *luz mul*-***Luzula multiflora,*** *lyc cla*-***Lycopodium clavatum,*** *mal syl*-***Malus sylvestris,*** *nar str*-***Nardus stricta,*** *pim sax*-***Pimpinella saxifraga,*** *plr sch*-***Pleurosium schreberi,*** *poa cha*-***Poa chaixii,*** *pol vul*-***Polygala vulgaris,*** *pop tre*-***Populus tremuloides,*** *pru vul*-***Prunella vulgaris,*** *rhi ang*-***Rhinanthus angustifolius,*** *rum alpe*-***Rumex alpestris,*** *sal sil*-***Salix silesiaca,*** *sie dec*-***Sieglingia decumbens,*** *thu del*-***Thuidium delicatulum,*** *thy pul*-***Thymus pulegoides,*** *tri pra*-***Trifolium pratense,*** *tri rep*-***Trifolium repens,*** *vac vit*-***Vaccinium vitis-idaea,*** *ver off*-***Veronica officinalis.***

Additional disturbances affected also some successional stands of this association. Stand of the relevé 4 ([123/72], Tab. 5) was plowed in 1989, but the planned planting was not carried out. Although it was relatively species-poor and included scattered weeds indicating soil disturbance, it still corresponded to the ass. *Betonico-Agrostietum* in 1997. During 1995 or 1996, soil surface was mechanically disturbed during the construction of a triangulation point benchmark in another plot, on the summit of Príkrý mountain (relevé 3 [49/69], Tab. 5). This surface disturbance resulted in a sudden increase in species richness, which was markedly decreasing still in 1997 prior to the disturbance in 1988. Because the site was not plowed, agricultural weeds did not appear, except for one plant of *Chenopodium polyspermum*, otherwise unknown in the Bukovské vrchy Mts. (Hadač et al. 1998). Seedlings of species common in the original still-harvested communities, which have disappeared during the preceding succession (e.g., *Polygala vulgaris, Nardus stricta, Veronica officinalis, Plantago lanceolata*), and seedlings of meadow species absent in the initial stand *(Omalotheca sylvatica, Dianthus barbatus*) both colonized the newly bared surfaces and temporarily increased species richness. The surface disturbance did stop a rapid quantitative increase of *Hypericum maculatum*, but limited a spread of *Calamagrostis arundinacea* only to a certain extent.

Despite of some developmental heterogeneity of mentioned stands, successional pathways of this association are well defined. The physiognomy of successional communities mostly reflects an increasing percentage cover of *Hypericum maculatum* and an expansion and eventual dominance of *Calamagrostis arundinacea*. Small amounts of *Hypericum maculatum* were part of regularly harvested meadows, but *C. arundinacea* appeared only after the utilization of meadows ceased: in some stands already after two years, but in other stands after 15 years or even later. Low-growing, strongly heliophilous species were the first to respond to the *Calamagrostis arundinacea* expansions and the first to disappear; they included *Thymus pulegioides, Leontodon hispidus*, *Ajuga reptans, Hieracium pilosella, Prunella vulgaris,* and *Rhinanthus angustifolius*, and among mosses especially *Thuidium delicatulum*. Such heliophytes were recorded only in relevés collected when the sampled meadows were still harvested and *Nardus stricta*, a common dominant of harvested meadows, was still dominant or at least common. Rapid expansion of *C. arundinacea* was positively correlated with a gradual decrease and an eventual disappearance of *Nardus stricta,* which belongs to a larger group of species more resistant to changes and competition, also including *Carlina acaulis, Lotus corniculatus, Betonica officinalis, Briza media, Silene nutans, Veronica chamaedrys, Luzula multiflora, Cruciata glabra,* and many other species. The importance of these species decreased slowly and they disappeared only after about 15-20 years of succession.

Populations of some species, especially of those with medium and tall stature, increased during early successional stages and then decreased during later stages. These changes occurred in populations of *Luzula luzuloides, Hypericum maculatum, Achillea stricta, Knautia dipsacifolia, Crepis conyzifolia*, partly of *Gentiana asclepiadea* and *Rumex acetosa*. Hadač et al. (1988) even described such a successional stage with dominant *Hypericum maculatum* as an independent association *Hyperico-Luzuletum luzuloidis*. These authors designated as the type of this association their relevé in the summit area of Príkrý, where there is also my relevé 3 ([49/69], Tab. 5) sampled periodically from 1969 to 1997 during the present study. Apparently, Hadač et al. (1988) have never seen the original, still-harvested communities of the ass. *Betonico-Agrostietum*. They also did not realize that the following regressive stage, during which the abovementioned species decreased again and *Calamagrostis arundinacea* emerged as a temporary dominant, was a part of the same successional pathway. They recorded these stands in other localities and described the *C. arundinacea* stage, as another independent ass. *Achilleo strictae-Calamagrostietum arundinaceae* (see Fig. 6).

The successional sequence in relatively small abandoned meadows surrounded by forest on Stužica reserve (relevés 100-103) was different from that in open, large abandoned meadows, which constitute the majority of investigated stands. Within the study period, woody plants became established in successional stands of the ass. *Betonico-Agrostietum* only on Stužica, where small meadow patch surface area, close proximity of forest to the entire meadow area, and greater shading all contributed to more rapid progession toward forest (see also Blažková 1988). A number of meadow species common in well-developed stands of the ass. *Betonico-Agrostietum* were missing in the stands on Stužica already when the first relevés were sampled 10 years after the harvesting of these pastures ended. In 1997, or 35 years after the harvesting ended, woody plants and the shrub layer were already developed. The spreading of woody plants, obvious in the ordination (Fig. 5) suggest massive expansion of forest species. Also seedlings of *Malus sylvestris* appeared frequently and those of *Acer pseudoplatanus* only sporadicaly in other successional stands, but woody plants appeared to expand on small, abandoned meadows permanently only on Stužica.

In the original, still-harvested stands of the ass. *Betonico-Agrostietum* the moss layer was relatively common and reached up to 25 percent cover. Among the most important moss species were *Pleurozium schreberi, Thuidium delicatulum, Dicranum scoparium,* and *Polytrichum* sp.div. During succession, bryophytes usually decreased and sometimes disappeared at all. However, in some localities such as Stužica, *Plagiomnium* and *Brachythecium* sp.div. even increased in late successional stadia.

Summary

The successional pathways of the meadow communities in the study area have a number of common characteristics and directions, although locally they may exhibit specific differences, mostly related to somewhat dissimilar local environments, including additional local disturbances.

After the harvest of the original meadows ended, the quantitative proportions of their species changed already during the first successional stage. Species that are sensitive to relatively small changes in their environment may disappear during this time. Among such species are primarily low-growing heliophytes, which are gradually shaded by accumulating litter and standing dead organic matter, which are not being removed, and by taller plants which can now achieve greater stature. In contrast, the absence of removal of aboveground phytomass supports species which tolerate cutting and were present in the original harvested meadows, but which grow, reproduce, and spread more rapidly after the end of harvesting. The physiognomy of this stage is often striking, because these species include herbs with numerous and conspicuous flowers *(*e.g., *Hypericum maculatum, Gentiana asclepiadea, Achillea stricta)*.

However, these species are weaker competitors than cutting-intolerant, expansive, and rapidly growing species, which were absent in the original harvested meadows. These expanders usually become established already during the flower-rich stage, gradually producing large amounts of phytomass, and completely changing the physiognomy of a stand even before they become dominants. They are usually capable of rapid vegetative reproduction and form polycormons and eventually clones, whether in the form of large bunches (*Calamagrostis arundinacea*) or single individuals arising from rhizomes, stolons, or root buds and sprouts *(Carex brizoides, Calamagrostis villosa, Rubus idaeus)*. These three species appear especially in later successional stages and their influence on the rest of the original communities is usually devastating. Not only the remaining low-growing, but also the medium-stature species, which increased during the first successional stage, mostly disappear.

During the 30-year study period, succession in abandoned meadows included more complex changes than the one-way expansions of some species and declines of others that are apparent in most graphs (Figs. 2-5). Some species fluctuated, increasing or declining from time to time, and the ecological roles of other species shifted. For instance, in some stands of the *Campanulo-Nardetum*, *Calamagrostis arundinacea* expanded along with still increasing original meadow species *(Gentiana asclepiadea, Luzula luzuloides, Dactylis slovenica),* although in other stands, the original species were already in decline at the time of its appearance. The development of a specific successional pathway appeared to be related not only to the habitat of the stand in question and to the presence of expansive species *Calamagrostis arundinacea* but also to the presence of other species, *Vaccinium myrtillus* in particular.

The roles of some species may also differ between the successional pathways of the original plant communities discussed here. For example, *Hypericum maculatum* increased in importance until it became dominant in the stands of the association *Betonico-Agrostietum* (a transition to the ass. *Hyperico-Luzuletum luzuloidis* Hadač et al. 1988), although this species always declined in the stands of the ass. *Acetoso-Deschampsietum*. In the stands of the ass. *Campanulo-Nardetum,* the importance of *Hypericum maculatum* fluctuated, usually increasing during the first successional stage and declining during later stages (Figs. 2-5). Apparently, both above- and belowground competition help to determine the progression of successional pathways. Relationships among important successional species are seldom perspicuous, an example is the negative correlation between the spreading of *Calamagrostis arundinacea* and *Vaccinium myrtillus*.

Quantitative successional changes in species proportions may be more significant than qualitative changes, such as appearances of new species. This is true even for early appearances of woody plants common in neighboring forests. Their seedlings may not indicate the beginning of forest expansion even in late meadow successional phase. In stands dominated by strong competitor dominants *Calamagrostis arundinacea, Deschampsia cespitosa*, and *Carex brizoides,* seedlings of woody plants do not survive for long, not even when the dominant herbaceous population becomes largely senescent and necrotic.

Especially on soils that are nutrient-rich or enriched by litter from neighboring deciduous forest trees, an establishment of herbaceous forest species precedes a permanent settlement by woody plants into abandoned meadows (BLAŽKOVÁ 1988). Most likely, the expansion of forest begins during late successional stages with expanding *Rubus idaeus*, when herbaceous forest species appear in the undergrowth. The conditions for relatively rapid succession to forest are more favorable in small meadow enclaves surrounded by forest and in meadows at lower altitudes.

Successional pathways of abandoned “poloniny” meadows are defined well also in the moss layer. The bryophytes markedly decreased during the first five years after the end of harvesting, until they were mostly absent after 15 to 25 years of succession. This is apparent in the ordinations of both the *Betonico-Agrostietum* and the *Acetoso-Deschampsietum* (bryophytes were not included in the analysis of the *Campanulo-Nardetum*). The most sensitive species included *Thuidium delicatulum, Pleurozium schreberi, Polytrichum juniperinum,* and especially *Hylocomium splendens,* which were present only in the first set of relevés recorded at the beginning of the present study. In contrast, species of genera *Brachythecium* (mainly *B. rutabulum*) and *Plagiomnium* (mainly *P. cuspidatum* and *P. affine)* resisted successional changes and persisted until later stages. These two genera appeared again in a newly developed moss layer in stands overgrown by *Vaccinium myrtillus* after 50 years of succession on the Polish side of the mountains. The factors critical for the reappearance of the moss layer include probably availability of light next to the soil surface, and an appropriate quality of humus in surface soil horizons.

The rate of secondary succession differs according to the original vegetation type, the environmental characteristics of individual stands, and the neighboring ecosystems. Successional changes proceeded most rapidly in climatically favorable habitats at lower elevations, especially in small stands of the ass. *Betonico-Agrostietum* surrounded by forest. In the stands of the ass. *Campanulo-Nardetum* on ridges with more severe climatic conditions, successional changes occurred at a slower rate. The slowest succession took place in relatively moist stands of the ass. *Acetoso-Deschampsietum*. There seem to be no species of moist habitats that could outcompete *Deschampsia cespitosa*; its dominance still persisted after 28 years and only quantitative changes in the proportions of subordinate species occurred during that time. Only an expansion of *Rubus idaeus* in late stages, probably facilitated further succession.

Differences in the rate of secondary succession can be large even between stands of the same association. In some stands in which *Vaccinium myrtillus* was absent (relevé 7 [112/72], Tab. 2), only 15 years elapsed between the first penetration of the stand by *Calamagrostis arundinacea* and its complete dominance (i.e., between its percentage cover classes + and 5). In other stands during the same period of time, the percentage cover of *C. arundinacea* increased from 5% to only 30%, especially when its progress was slowed down by a simultaneous expansion of *V. myrtillus*. The expansion of *C. arundinacea* is also faster when it is spreading from the edge of a continuous stand than when it is spreading from scattered individuals.

Successional changes proceed most rapidly in the beginning of the spreading of highly expansive species, either during initial quantitative changes in species percentage cover as one of the originally subordinate species becomes dominant, or during an expansion of new species that was absent previously. After the new dominant becomes established, the stand composition and species proportions stabilize temporarily, or undergo only small fluctuations, until an emergence of a new successful expansive species. These patterns are supported by observations of descelerating succession of abandoned meadows in Belanské Tatry Mts. (HADAČ et al. 1990) and also by observations made by RUŽICKOVÁ et al. (2001) on the "poloniny" meadows. Repeated replacement of successional herbaceous dominants by new species ceases only when the abandoned meadows are colonized by forest-related shrubs and finally recolonized by forest.

Conclusions for "poloniny" meadow conservation and management

The present analysis of secondary succession in the abandoned "poloniny" meadows of the Bukovské vrchy Mts. indicates that the only reliable way how to conserve the infrequent persisting remnants of species-rich, originally regularly harvested meadows is a continuation of regular or at least occasional harvests. The frequency and the timing of harvests should emulate the management regimes applied in the past. The process and likelihood of restoration of stands that have already been degraded depend on their current degree of degradation. In early stages of secondary succession after the cessation of harvests, return to regular harvests and the removal of harvested phytomass are sufficient for the restoration of original species composition. In the beginning of the restoration, markedly degraded stands may have to be harvested more frequently and already accumulated litter and standing dead phytomass may have to be removed to aid recovery.

In Czech mountains, attempts to restore similar anthropogenic abandoned mountain meadows showed that degraded stands already dominated by an expansive species return to their original species composition more readily after fertilized moderately. Meadow species take up available nutrients more rapidly than the majority of expansive species and under a regime of repeated harvests, for which they are better adapted than expansive species, increase their importance until expansive species are strongly limited. This approach successfully suppressed *Carex brizoides* in the Šumava Mts. (BLAŽKOVÁ & HRUŠKA 1999) and *Polygonum bistorta* in Krkonoše Mts. (PECHÁČKOVÁ & KRAHULEC 1995). Abandoned meadows were fertilized using locally procured organic fertilizers (composted grass, animal manure). Another appropriate fertilizer could be wood ash produced by combustion of wood; it is easier to produce, and transport than organic fertilizers. Its effectiveness and the amounts needed would have to be determined experimentally in the meadows in question.

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Appendix 1. Table headings:

relevé number, original relevé number, longitude, latitude, village, locallity, data, altitude, exposition, slope degrees

Tab. 2. *Campanulo-Nardetum*, early successional stage

1. (117/72), 223225, 490545, Nová Sedlica, 0.5km ONO of the top Hrúbky, 15.7.1972, 13.7.1985, 5.7.1997, 1125m, NW 12
2. (118/72), 223155, 490540, Nová Sedlica, 0.3km WSW of the top Hrúbky, 15.7.1972, 13.7.1985, 5.7.1997,18.7.1999, 1120m, WSW 18
3. (66/69), 222045, 490847, Ruské, 1km O of sattle Ruské sedlo, 24.6.1969,1.7.1997, 930m, WSW 10
4. (143/72), 221812, 490827, Ruské 2.2km WSW of the sattle Ruské sedlo, NW downhill the elev. point Šípková, 960m, 19.7.1972, 15.7.1985, 3.7.1997 W 18
5. (61/69), 222125, 490845, Ruské, 1.7km E of the sattle Ruské sedlo, 24.6.1969, 1.7.1997, 930m, S 15
6. (64/69), 222125, 490842, Ruské, 1.6km E of the sattle Ruské sedlo, 24.6.1969, 1.7.1997, 925m, S 20
7. (112/72), 223110, 490528, Nová Sedlica, elevation point Čiertaž, 15.7.1972, 19.8.1988, 5.7.1997, 18.7.1999, 1060m, SE 5
8. (65/69), 222050, 490845, Ruské, 1.1km E of the sattle Ruské sedlo, 24.6.1969, 1.7.1997, 950m, W 12
9. (64/70) 222530, 490555, Runina, Ďurkovec, 0.1km SE of the elev. point 1133.5, 7.7.1970, 16.7.1985, 2.7.1997, 1100m, S 35
10. (114/72), 223320, 490520, Nová Sedlica, Rovná lúka, 15.7.1972, 13.7.1985, 19.8.1988, 15.7.1997, 1120m, SE 3
11. (68/70), 222645, 490612, Runina, 0.6km W of the Riaba skala, 7.7.1970, 14.7.1985, 16.7.1999, 1160m, SSE 20

Tab.3. *Campanulo-Nardetum,* late successional stade

1. (65/70), 222525, 490603, Runina, Ďurkovec (Polish site), 50m NE of the elevation point 1133.5, 7.7.1970, 16.8.1988, 2.7.1997, 1125m, N 8
2. (67/70), 222645, 490617, Runina, 0.6km W of the Riaba skala (Polish site), 7.7.1970, 14.7.1985, 16.7.1999, 1160m, N 18
3. (115/72), 223305, 490525, Nová Sedlica, Stužica, S of the top Kamenná lúka, 15.7.1972, 13.7.1985, 19.8.1988, 5.7.1997, 1195m, S 10
4. (66/70), 222550, 490555, Runina, Ďurkovec, SW downhill the top, 7.7.1970, 14.7.1985, 1188m, WSW 10
5. (61/70), 222415 490652, ancient village Ruské, N of the top Plaša, 7.7.1970, 2.7.1997, 1155m, N 15
6. (62/69), 222105, 490848, ancient village Ruské, 1.7km E of the Ruské sattle, 24.6.1969, 1.7.1997, 950m, N 10
7. (62/70) 222410, 490643, ancient village Ruské, Plaša, W of the top, 7.7.1970, 16.7.1985, 2.7.1997, 1162m SSW 35

8. (63/70), 222512, 490605, Runina, Ďurkovec, 0.25km NW of the elevation point 1133.5, 7.7.1970, 2.7.1997, 1115m, S 25

Tab.4. ***Acetoso-Deschampsietum***

1. (119/72), 223155, 490540, Nová Sedlica, 0.3km WSW of the top Hrúbky,15.7.1972, 13.7.1985, 5.7.1997, 18.7.1999, 1125m, SW 20
2. (116/72), 223225, 490545, Nová Sedlica, E of the top Hrúbky, sattle, 15.7.1972, 12.7.1985, 5.7.1997, 1120m, E 2
3. (113/72), 223355, 490520, Nová Sedlica, 0.3km W of the top Kremenec, 15.7.1972, 13.7.1985, 19.8.1988, 5.7.1997, 18.7.1999, 1140m, E 5
4. (120/72), 223150, 490540, Nová Sedllica, 0.5km W of the top Hrúbky, 15.7.1972, 13.7.1985, 18.7.1999, 1120m, E 2

Tab. 5. ***Betonico-Agrostietum***

1. (48/69), 223125, 490425, Nová Sedlica, 0.2km E of the top Príkrý, 21.6.1969, 4.7.1997, 925m, SSE 25
2. (125/72), 223150, 490425, Nová Sedlica, 0.7km E of the top Príkrý, 16.7.1972, 4.7.1997, 820m, S 20
3. (49/69), 223115, 490425, Nová Sedlica, Príkrý, summit plateau, 21.6.1969, 29.8.1974, 12.7.1985, 17.8.1988, 4.7.1997, 952m, S 2
4. (123/72), 223225, 490413, Nová Sedlica, SW under the top Temmný vršok, 825m, 16.7.1972, 16.8.1988, 4.7.1997, SW 12
5. (100/72), 223245, 490425, Nová Sedlica, Stužica, E of the brook Kamenistý, 13.7.1972, 13.7.1985, 685m, S 10
6. (103/72), 223150, 490448, Nová Sedlica, Stužica, Krtia meadow, lower part, 13.7.1972, 13.7.1985, 4.7.1997, 750m, S 5
7. (102/72), 223150, 490445, Nová Sedlica, Stužica, Krtia meadow, upper part, 13.7.1972, 13.7.1985, 4.7.1997, 750m, S 5

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Tab. 2. Phytosociological relevé of the *Campanulo-Nardetum* association in the early successional stage.

Number of relevé	**1**	1	1	**2**	2	2	2	**3**	3	**4**	4	4	**5**	5	**6**	6	**7**	7	7	7	**8**	8	**9**	9	9	**10**	10	10	10	**11**	11	11
Year (19..)	**72**	85	97	**72**	85	97	99	**69**	97	**72**	85	97	**69**	97	**69**	97	**72**	88	97	99	**69**	97	**70**	85	97	**72**	85	88	97	**70**	85	99
Herb layer (cover in %)	**95**	95	95	**95**	92	93	95	**95**	85	**95**	97	98	**85**	95	**80**	95	**90**	90	80	80	**75**	80	**90**	85	90	**90**	90	90	85	**90**	85	95
Herb layer (no. of sp.)	**45**	40	40	**45**	42	33	32	**70**	42	**55**	46	42	**33**	22	**40**	32	**36**	13	18	16	**19**	24	**61**	44	36	**37**	36	21	15	**46**	38	25
Moss layer (cover in %)	**10**	3	0	**5**	2	2	2	**10**	0	**25**	10	3	**5**	0	**3**	0	**3**	0	0	0	**15**	1	**10**	1	1	**5**	0	0	0	**12**	0	0
Nardus stricta	**3+**	2+	3+	**2+**	2	2	2	**2**	.	**3+**	1	.	**3+**	.	**4**	+	**2+**	+	r	.	**4**	r	**1**	+	.	**3**	+	+	+	**1**	+	.
Polygala vulgaris	**1**	.	.	**1**	+	+	.	**++**	.	**+**	.	.	.	.	**+**	.	**+**	.	.	.	.	.	**1**	.	.	.	.	.	.	**+**	.	.
Veronica officinalis	**1**	.	.	**1**	.	+	+	.	.	**1**	.	.	**+**	.	**+**	+	**1**	.	.	.	.	+	.	.	.	**++**	.	.	.	**+**	.	.
Carex pilulifera	**+**	+	+	**+**	+	+	.	.	.	**+**	.	.	**++**	.	**++**	+	.	.	.	.	**1**	+	.	.	.	.	.	.	.	.	.	.
Viola canina	.	.	.	**+**	.	.	.	**+**	.	**++**	.	.	.	.	.	.	.	.	.	.	.	.	**++**	+	.	.	.	.	.	.	.	.
Omalotheca norvegica	**+**	+	+	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	**+**	.	.
Omalotheca sylvatica	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Antennaria dioica	.	.	.	.	.	.	.	.	.	.	.	.	**2+**	.	**2+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.
Anthoxanthum odoratum agg.	**2+**	2	+	**2+**	2	+	++	**1**	.	**2+**	+	.	**2**	.	**+**	.	**2**	+	r	+	**1**	.	**2+**	+	.	**2**	+	+	.	**1**	+	.
Cruciata glabra	**+**	+	++	**1**	1	1	+	**1**	+	**+**	1	1	**++**	+	**1**	+	**+**	+	.	.	.	.	**1**	2+	1	**+**	+	.	.	**+**	+	+
Veronica chamaedrys	.	+	+	.	.	.	.	**1**	.	**1**	+	++	**+**	+	**++**	.	**+**	.	.	.	.	.	**1**	.	r	.	.	.	.	.	r	.
Leucanthum vulgare agg.	**+**	.	.	**+**	+	.	.	**+**	.	**1**	.	.	**+**	.	**+**	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	.	.	.
Plantago lanceolata	.	.	.	**+**	.	.	.	**1**	.	**++**	+	r	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense	.	.	.	.	.	.	.	**1**	.	**1**	r	.	.	.	**+**	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	.	.	.
Luzula multiflora	**+**	+	+	**+**	+	+	.	**+**	.	**+**	.	.	.	.	**+**	.	**+**	.	.	.	**+**	.	.	.	.	**+**	.	.	.	.	.	.
Trifolium repens	.	.	.	.	.	.	.	**2+**	+	**++**	.	.	.	.	**1**	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	.	.	.
Campanula patula	**+**	.	.	.	.	.	.	**+**	.	**++**	+	+	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*Heracleum *trachycarpum*	.	.	.	.	r	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	**+**	r	.
Alchemilla vulgaris agg.	.	.	.	.	.	.	.	**3**	r	**2+**	+	+	**1**	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Prunella vulgaris	.	.	.	**++**	++	.	.	**1**	.	.	.	+	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	.	.	.
Rhinanthus angustifolius	.	.	.	.	+	.	.	**1**	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Number of relevé	**1**	1	1	**2**	2	2	2	**3**	3	**4**	4	4	**5**	5	**6**	6	**7**	7	7	7	**8**	8	**9**	9	9	**10**	10	10	10	**11**	11	11
Year (19..)	**72**	85	97	**72**	85	97	99	**69**	97	**72**	85	97	**69**	97	**69**	97	**72**	88	97	99	**69**	97	**70**	85	97	**72**	85	88	97	**70**	85	99
Lotus corniculatus	.	.	.	.	.	.	.	**++**	.	**++**	r	.	.	.	**1**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium holosteoides	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca pratensis	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cynosurus cristatus	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crepis succisifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**++**	.	.	.	.	.	.	**++**	.	+
Carum carvi	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum Sect. Ruderalia	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.
Carlina acaulis	.	.	.	.	.	.	.	**++**	.	**2**	+	1	**+**	r	**2**	1	.	.	.	.	.	.	**+**	2	+	.	.	.	.	**+**	.	+
Thymus alpestris	**++**	+	+	**1**	++	++	+	**2**	.	**1**	.	.	**1**	.	**1**	.	**+**	.	.	.	**+**	.	**2+**	+	.	.	.	.	.	.	.	.
Leontodon hispidus agg.	**++**	+	+	**1**	1	.	.	**2+**	.	**1**	+	+	.	.	**+**	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	.	.	.
Euphrasia rostkoviana	**+**	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	**++**	.	.
*Gentianella *carpatica*	.	.	.	.	.	.	.	**+**	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.
Hieracium pilosella	**+**	.	.	**+**	+	.	.	.	.	.	.	.	.	.	**2**	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.
Pimpinella saxifraga	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene nutans	.	.	.	.	.	.	.	**+**	.	.	.	.	**+**	.	**+**	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fragaria vesca	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.
Trifolium montanum	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago media	.	.	.	.	.	.	.	**++**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calamagrostis arundinacea	.	.	+	.	.	.	.	.	.	.	.	.	.	3+	.	3	**+**	5	4	4	.	.	**2**	3+	4	**2+**	3	3	3+	**2+**	4+	5
Vaccinium myrtillus	**+**	+	++	.	.	.	.	.	.	**1**	+	3	**++**	1	**1**	+	.	.	.	.	**2+**	2	**+**	+	.	**++**	2	2	3+	**3**	2	2
Galium schultesii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	++	3	.	.	.	.	**+**	r	.
Rubus hirtus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	.	.	.	.	.	.	.	.	.	.
Calamagrostis epigejos	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.
Helleborus purpurascens	.	.	.	.	.	.	.	**+**	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Number of relevé Year (19..)	**1** **72**	1 85	1 97	**2** **72**	2 85	2 97	2 99	**3** **69**	3 97	**4** **72**	4 85	4 97	**5** **69**	5 97	**6** **69**	6 97	**7** **72**	7 88	7 97	7 99	**8** **69**	8 97	**9** **70**	9 85	9 97	**10** **72**	10 85	10 88	10 97	**11** **70**	11 85	11 99
Malus sylvestris juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	.	**r**	.	r	.	.	.	.
Carex ovalis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.
Galeopsis speciosa	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	++	.	+	.	.	.	.	.	.	.	.	.	.
Rumex acetosella	**r**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Gentiana asclepiadea	**2**	2	2	**1**	2	2+	2+	**+**	2	**+**	2	+	**+**	+	.	+	**2**	3	3	2	.	.	**+**	1	1	**1**	2+	2+	2	**++**	2	2
Polygonatum verticillatum	.	.	.	.	.	.	.	.	.	**1**	+	.	.	+	.	.	**+**	.	+	+	.	.	.	.	.	.	+	+	+	**++**	++	+
Lilium martagon	.	.	.	.	.	.	.	.	.	.	.	.	**+**	r	**+**	+	.	.	.	.	.	.	**++**	.	+	.	.	.	.	.	.	.
Homogyne alpina	**1**	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**++**	+	+	+	**+**	++	+
Maianthemum bifolium	**+**	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Senecio integrifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	+	+	.	.	.	.	.	.	.
Astrantia major	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	+	+	.	.	.	.	**2**	1	++
Rumex acetosa	.	.	.	.	.	.	.	**+**	+	.	.	.	**+**	.	**+**	.	.	.	.	.	**+**	+	.	.	.	.	.	.	.	.	.	.
Veratrum album	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Aegopodium podagraria	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.
Pimpinella major	.	.	.	.	.	.	.	**++**	+	**+**	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vicia sepium	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vicia cracca	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crepis conyzifolia	**2**	2+	1	**2+**	2+	1	+	**1**	.	**2**	1	+	.	.	**1**	1	.	.	.	.	.	.	**2**	2	.	**+**	.	.	.	**3**	1	2
Vaccinium vitis-idaea	.	.	.	.	.	.	.	.	.	.	.	.	**2+**	.	**3**	.	.	.	.	.	.	.	.	.	.	.	+	.	.	**1**	+	.
Aposeris foetida	**+**	+	1	.	.	++	+	**1**	+	**1**	1	+	.	.	.	+	.	.	.	.	.	.	**2+**	1	++	.	.	.	.	**2+**	+	+
Campanula abietina	**+**	+	+	**+**	+	.	.	.	+	.	.	.	.	.	.	.	**+**	.	.	.	.	.	**++**	+	.	**++**	+	+	+	.	.	.
Ranunculus platanifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.
Dianthus barbatus	**1**	+	+	.	+	r	+	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	+	+	**++**	r	.	.	**+**	.	.
Hieracium aurantiacum	**+**	+	1	**+**	+	++	+	**+**	+	**+**	.	.	.	.	.	.	.	.	.	.	.	.	**++**	.	.	**+**	.	.	.	.	.	.
Viola dacica	**+**	+	+	**1**	r	+	+	**+**	.	.	.	.	.	.	.	.	**1**	.	.	.	**+**	.	.	.	+	.	+	.	.	**+**	.	.

Number of relevé	**1**	1	1	**2**	2	2	2	**3**	3	**4**	4	4	**5**	5	**6**	6	**7**	7	7	7	**8**	8	**9**	9	9	**10**	10	10	10	**11**	11	11
Year (19..)	**72**	85	97	**72**	85	97	99	**69**	97	**72**	85	97	**69**	97	**69**	97	**72**	88	97	99	**69**	97	**70**	85	97	**72**	85	88	97	**70**	85	99
Campanula serrata	**1**	2	1	**+**	+	1	++	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**++**	+	+	+	**++**	+	+
Phleum alpinum	**++**	+	+	**+**	+	+	+	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.
Traunsteinera globosa	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Melandrium rubrum	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula sylvatica	.	.	.	**r**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	.	+	.
Luzula luzulina	.	+	+	.	+	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Melampyrum herbichii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Potentilla aurea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.
Lycopodium clavatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	.	.
Chaerophyllum hirsutum	.	.	.	.	.	.	.	**+**	++	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex pallescens	**+**	+	+	**1**	1	+	+	.	.	.	+	.	.	.	.	.	**++**	.	+	+	.	+	.	+	.	**+**	+	+	.	.	.	.
Stellaria graminea	**+**	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.
Ranunculus acris	.	+	.	**+**	+	+	.	**1**	.	**r**	++	+	.	.	.	+	**+**	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Betonica officinalis	.	.	.	.	.	.	.	**+**	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ajuga reptans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa	**+**	+	+	**+**	+	1	1	.	+	**+**	+	+	.	.	.	.	**2**	+	r	.	.	.	**+**	.	.	**1**	2+	2	1	.	.	+
Poa chaixii	**+**	1	1	**+**	+	2	2	**1**	1	**1**	2+	2+	**1**	1	**1**	1	**1**	+	+	.	**+**	+	**1**	2	1	**1**	+	2	++	**++**	+	.
*Dactylis *slovenica*	.	.	.	.	.	.	.	**1**	4	**+**	2	1	.	.	.	.	.	.	.	.	.	.	**1**	+	1	.	.	.	.	.	.	.
Rumex alpestris	.	+	+	**+**	+	2	2	**+**	2	**+**	1	2	.	.	.	+	**1**	1	1	1	**+**	2+	.	.	+	**++**	2	2+	2+	**+**	+	1
Rumex alpinus	.	.	.	**r**	r	.	.	.	+	.	.	.	.	.	.	.	.	.	r	1	.	.	.	.	.	.	.	.	.	.	.	.
Rubus idaeus	.	.	+	.	.	.	+	.	1	.	.	.	.	.	.	.	.	1	+	2	.	.	.	.	.	.	.	.	.	.	.	.
Lysimachia nemorum	.	.	.	.	1	+	1	.	.	**+**	1	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chamerion angustifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.

Number of relevé Year (19..)	**1** **72**	1 85	1 97	**2** **72**	2 85	2 97	2 99	**3** **69**	3 97	**4** **72**	4 85	4 97	**5** **69**	5 97	**6** **69**	6 97	**7** **72**	7 88	7 97	7 99	**8** **69**	8 97	**9** **70**	9 85	9 97	**10** **72**	10 85	10 88	10 97	**11** **70**	11 85	11 99
Gymnadenia conopsea	+	+	.	+	.	.	.	+	.	+	.	+	+	+	+	+	.	.	.	.	.	.	+	+	r	+	+	.	.	+	+	.
Hieracium lachenalii	+	+	+	++	++	.	+	.	.	+	+	+	++	+	++	+	+	.	.	.	.	.	+	++	+	+	+	.	.	+	+	+
Festuca rubra	2	2	2	1	1	1	1	2	.	2	1	1	2	.	1	++	1	.	.	.	1	2	2+	+	.	1	+	+	.	1	.	.
Agrostis capillaris	2+	1	+	3	2+	+	1	2	.	2+	1	1	.	+	.	+	3	.	.	.	+	2	2+	++	+	2+	+	+	.	.	.	.
Briza media	.	.	.	+	+	.	.	1	.	1	+	+	.	.	+	+	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.
Pyrethrum clusii	+	.	+	.	.	.	.	+	.	2	1	1	1	+	+	+	.	.	.	.	.	.	2	2	1	.	.	.	.	2	1	1
Ranunculus polyanthemos	+	+	+	+	+	++	+	1	.	+	+	1	+	.	.	++	+	.	.	.	.	.	1	+	+	.	.	.	.	+	+	.
Campanula glomerata	.	.	.	.	.	.	.	++	+	++	+	.	.	.	++	+	.	.	.	.	.	.	1	+	+	.	.	.	.	+	r	.
Euphorbia sojakii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	++	+	1	.	r	.	.	.	.	.
Angelica sylvestris	.	.	.	.	.	.	.	.	.	.	+	++	.	.	.	.	.	.	.	.	.	.	+	+	++	.	.	+	.	++	++	+
Myosotis nemorosa	.	.	.	.	.	.	.	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Centaurea jacea	.	.	.	+	.	.	.	1	+	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Solidago virgaurea	1	1	1	1	+	+	++	.	.	.	.	+	+	1	.	+	1	1	+	+	+	.	++	+	.	2+	+	1	+	1	1	+
Hypericum maculatum	1	2	1	2	1	2+	3+	+	2+	1	3	2+	1	2+	+	2+	3+	.	+	.	+	2	+	1	1	2+	+	1	+	+	1	1
Achillea stricta	1	1	2	1	1	2	1	1	1	1	2+	1	1	1	+	1	+	.	.	.	+	+	1	2	1	+	+	.	.	++	+	.
Potentilla erecta	2+	2+	2+	3	3	2+	1	1	+	2	2	++	2	+	2+	2	2	+	+	1	2	+	2	1	1	2	1	2	r	2	+	+
Luzula luzuloides	.	.	+	+	+	.	+	1	+	++	2	2+	2+	3	2	3	.	.	r	.	2	2+	++	2+	2+	2+	2	1	++	2	2+	+
Hypochoeris uniflora	2	2	2	1	1	1	.	.	.	.	.	.	++	+	.	.	+	.	.	.	.	.	+	+	+	+	.	.	.	2	1	+
Anemone nemorosa	.	.	+	.	.	+	+	+	+	.	.	+	++	++	.	.	.	.	.	.	+	+	++	r	.	.	r	.	.	+	.	.
Knautia dipsacifolia	+	+	.	.	.	.	.	.	.	+	2+	2	.	.	.	.	+	.	.	.	.	.	2	2+	2+	+	+	.	.	+	+	.
Phyteuma spicatum	.	r	.	.	.	.	.	+	r	+	+	1	+	+	+	+	.	.	.	.	.	.	1	+	+	.	+	.	.	1	+	+
Acer pseudoplatanus juv.	+	+	.	.	.	+	+	.	+	+	r	+	.	+	.	.	.	.	.	+	.	++	.	.	.	r	+	.	.	.	.	+
Centaurea phrygia	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cardaminopsis halleri	.	.	.	.	.	+	.	++	2	1	1	2	+	.	+	+	.	.	.	.	+	.	+	+	++	.	.	.	.	.	+	.
Trifolium medium	.	.	.	.	.	.	.	1	+	.	+	1	.	.	.	1	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.

Number of relevé	**1**	1	1	**2**	2	2	2	**3**	3	**4**	4	4	**5**	5	**6**	6	**7**	7	7	7	**8**	8	**9**	9	9	**10**	10	10	10	**11**	11	11
Year (19..)	**72**	85	97	**72**	85	97	99	**69**	97	**72**	85	97	**69**	97	**69**	97	**72**	88	97	99	**69**	97	**70**	85	97	**72**	85	88	97	**70**	85	99
Chaerophyllum aromaticum	.	.	.	.	.	.	.	**+**	++	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula elatior	.	.	.	.	.	.	.	**2**	2	**++**	+	+	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.
Geranium phaeum	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
Salix caprea agg.	.	.	.	**+**	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Betula pendula juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Filipendula ulmaria	.	.	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	+	.	.	.	.	.	.	.
Lathyrus pratensis	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geranium palustre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	+	+	.	.	.	.	.	.	.
Carex sylvatica	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Listera ovata	.	.	.	.	.	.	.	**+**	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Urtica dioica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Mulgedium alpinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	+	.	.	.	.	.	.	.
Trisetum flavescens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Tragopodon orientalis	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Glechoma hirsuta	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dentaria bulbifera	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juniperus communis juv.	.	.	.	.	.	.	.	.	.	.	.	.	**r**	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Asarum europaeum	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sorbus aucuparia juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	r	.
Fagus sylvestris juv.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Holcus mollis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium prenanthoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	++	1
Coeloglossum viride	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**r**	.	.
Dentaria bulbifera	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa nemoralis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.

Number of relevé	**1**	1	1	**2**	2	2	2	**3**	3	**4**	4	4	**5**	5	**6**	6	**7**	7	7	7	**8**	8	**9**	9	9	**10**	10	10	10	**11**	11	11
Year (19..)	**72**	85	97	**72**	85	97	99	**69**	97	**72**	85	97	**69**	97	**69**	97	**72**	88	97	99	**69**	97	**70**	85	97	**72**	85	88	97	**70**	85	99
Brachythecium sp. div.	**1**	+	.	**1**	+	1	+	**2**	.	**1**	+	1	.	.	.	.	**1**	.	.	.	.	.	**1**	1	+	**1**	.	.	.	**1**	.	.
Rhytiadelphus squarrosus	**+**	.	.	**+**	+	+	+	.	.	**2**	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polytrichum juniperinum	.	.	.	**1**	.	.	.	**1**	.	.	.	.	**1**	.	**1**	.	**1**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cladonia sp. Div	.	.	.	.	.	.	.	.	.	**+**	.	.	**1**	.	**1**	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	**+**	.	.
Plagiomnium sp. div.	.	.	.	.	.	.	.	**1**	.	**1**	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pleurozium schreberi	.	.	.	.	.	.	.	**2**	.	.	.	.	**1**	.	**+**	.	.	.	.	.	**2**	.	.	.	.	.	.	.	.	.	.	.
Polytrichum pallidisetum	**2**	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.
Abietinella abietina	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.
Cirriphyllum piliferum	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.
Bryum capillare agg.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Eurhynchium schleicheri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**2**	.	.
Atrichum undulatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	.	.	.
Fissidens taxifolius	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eurhynchium praelongum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**2**	.	.	.	.	.	.	.	.	.
Tortula mucronifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	.	.	.
Dicranum scoparium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.
Dicranum undulatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	.	.	.	.	.
Hylocomium splendens	.	.	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thuidium delicatulum	.	.	.	.	.	.	.	.	.	**2**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Tab. 3. Phytosociological relevé of the *Campanulo-Nardetum* association in the late successional stage.

Relevé	**1**	1	1	**2**	2	2	**3**	3	3	3	3	**4**	4	**5**	5	**6**	6	**7**	7	7	**8**	8
Year (19..)	**70**	88	97	**70**	85	99	**72**	85	88	97	99	**70**	85	**70**	97	**69**	97	**70**	85	97	**70**	97
Herb layer (cover in %)	**96**	85	85	**98**	75	95	**95**	90	95	85	88	**85**	90	**85**	80	**85**	80	**90**	95	90	**90**	85
Herb layer (number of species)	**17**	11	16	**19**	11	15	**39**	30	26	15	12	**47**	38	**26**	8	**27**	20	**44**	31	29	**48**	26
Moss layer (cover in %)	**0**	0	15	**0**	0	1	**15**	0	0	0	0	**8**	0	**0**	0	**3**	0	**3**	0	0	**15**	0
Nardus stricta	.	.	.	**++**	.	.	**1**	r	.	.	.	.	.	**2**	.	**2**	.	**2+**	r	.	**1**	.
Polygala vulgaris	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	**+**	.	**++**	.	.	**+**	.
Veronica officinalis	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	.	.	**+**	.	.	**+**	.
Carex pilulifera	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.
Omalotheca norvegica	.	.	.	**+**	.	.	**+**	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.
Antennaria dioica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	**+**	.
Anthoxanthum odoratum agg.	.	.	.	.	.	.	**2**	++	.	.	.	**++**	1	.	.	.	.	.	++	.	**2**	.
Cruciata glabra	.	.	.	.	.	.	**+**	.	+	.	.	**+**	++	.	.	.	.	**++**	1	+	**++**	.
Veronica chamaedrys	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	r	.	**++**	.
Leucanthemum vulgare agg.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	**+**	.
Trifolium pratense	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.
*Heracleum *trachycarpum*	.	.	.	.	.	.	**++**	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Prunella vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.
Rhinanthus angustifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**++**	.	.	**+**	.
Crepis succisifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.
Carlina acaulis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**++**	.
Thymus alpestris	.	.	.	.	.	.	**1**	.	r	.	.	**+**	.	.	.	.	.	**1**	.	.	**1**	.
Euphrasia rostkoviana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	.	.	**+**	.
*Gentianella *carpatica*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.
Calamagrostis arundinacea	**3**	4	2	**3**	4	1	**3+**	4+	5	3+	3+	**1**	3	**1**	3+	**+**	2+	**1**	4	3+	**1**	4
Vaccinium myrtillus	**5**	3	5	**5**	3	5	**1**	2	+	++	1	**4**	2+	**4**	4	**3**	1	**4**	4	2	**2+**	1

Relevé Year (19..)	**1** **70**	1 88	1 97	**2** **70**	2 85	2 99	**3** **72**	3 85	3 88	3 97	3 99	**4** **70**	4 85	**5** **70**	5 97	**6** **69**	6 97	**7** **70**	7 85	7 97	**8** **70**	8 97
Senecio fuchsii	.	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.
Galium schultesii	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	+
Trientalis europaea	**+**	++	+	**+**	1	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Athyrium distentifolium	.	.	+	.	.	r	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Calamagrostis villosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	2	.	.
Malus sylvestris juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
Galeopsis speciosa	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.
Gentiana asclepiadea	**+**	++	1	**2**	2	++	**2**	2+	2+	+	++	**2**	+	**1**	1	**2**	2	**++**	1	1	**+**	1
Polygonatum verticillatum	**+**	+	+	**+**	+	+	**++**	+	r	.	.	**+**	+	**+**	.	**+**	+	**+**	.	++	**++**	.
Lilium martagon	**r**	.	r	.	.	.	.	.	.	.	.	**+**	+	.	.	.	.	**+**	.	+	**+**	+
Homogyne alpina	.	.	.	.	++	1	**+**	+	1	.	.	**+**	1	**2**	+	**2**	++	.	.	.	.	.
Maianthemum bifolium	.	.	.	**+**	.	.	.	.	.	.	.	.	.	**+**	.	**+**	.	.	+	.	.	.
Senecio integrifolius	.	.	.	.	.	.	.	.	.	.	.	**1**	r	.	.	.	.	.	.	.	**+**	+
Astrantia major	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	+	**1**	1
Rumex acetosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**++**	.	.	.	.	.	.
Veratrum album	**+**	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.
Aegopodium podagraria	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crepis conyzifolia	.	.	.	.	.	.	**+**	.	.	.	.	**3**	1	**2**	.	**1**	.	**3**	2	+	**3**	1
Vaccinium vitis-idaea	.	.	.	.	.	.	.	.	.	.	.	**2**	r	**2**	.	**2**	.	**2**	+	.	**2+**	.
Aposeris foetida	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	**2**	1	1	**++**	1
Campanula abietina	.	.	.	.	.	.	**+**	+	.	r	.	**+**	.	.	.	.	.	.	r	.	.	.
Ranunculus platanifolius	**1**	.	+	**1**	.	.	**+**	+	.	.	.	**++**	+	.	.	.	.	**+**	.	.	.	.
Dianthus barbatus	.	.	.	.	.	.	**+**	+	+	.	.	**+**	.	**+**	.	.	.	**1**	.	.	**+**	.
Hieracium aurantiacum	.	.	.	.	.	.	**+**	.	r	.	.	**+**	.	.	.	.	.	**+**	+	.	**1**	.
Viola dacica	.	.	.	.	.	.	**+**	.	.	.	.	**++**	.	.	.	.	.	**+**	.	.	**+**	+

Relevé	**1**	1	1	**2**	2	2	**3**	3	3	3	3	**4**	4	**5**	5	**6**	6	**7**	7	7	**8**	8
Year (19..)	**70**	88	97	**70**	85	99	**72**	85	88	97	99	**70**	85	**70**	97	**69**	97	**70**	85	97	**70**	97
Campanula serrata	.	.	.	.	.	.	**++**	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Phleum alpinum	.	.	.	.	.	.	**+**	.	.	.	.	.	+	.	.	.	.	.	.	.	**+**	.
Traunsteinera globosa	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	**++**	.	r	**+**	.
Luzula sylvatica	.	.	.	**+**	+	1	.	.	.	.	.	.	++	**2**	.	.	.	.	.	.	.	.
Luzula luzulina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.
Leucorchis albida	.	.	.	.	.	.	.	.	.	.	.	.	.	**r**	.	.	.	**r**	.	.	.	.
Stellaria holostea	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Melampyrum herbichii	.	.	.	.	.	.	**+**	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
Lycopodium clavatum	.	.	.	.	.	.	.	.	.	.	.	.	.	**2+**	.	.	.	**++**	.	.	.	.
Carex pallescens	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Ranunculus acris	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa	**+**	.	.	**+**	+	.	**2**	2	1	1	++	**+**	+	.	.	.	.	.	.	.	.	.
Poa chaixii	.	.	.	.	.	.	**1**	+	+	.	.	**+**	1	.	.	**+**	2	.	+	+	**+**	1
*Dactylis *slovenica*	.	.	.	.	.	.	**+**	++	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex alpestris	.	.	.	**+**	+	++	**2**	3	3	1	1	**+**	+	.	.	**+**	+	.	.	.	.	.
Rumex alpinus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Rubus idaeus	.	1	+	.	.	+	.	+	1	4	4	.	.	.	.	.	.	.	.	.	.	.
Lysimachia nemorum	.	.	.	.	.	.	**+**	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Gymnadenia conopsea	.	.	.	.	.	.	.	.	.	.	.	**+**	.	**r**	.	.	.	**1**	+	r	**++**	.
Hieracium lachenalii	.	.	.	.	.	.	**+**	.	.	.	.	.	.	**+**	.	**1**	.	**++**	+	.	**+**	+
Festuca rubra	.	.	.	.	.	.	**1**	+	.	.	.	**++**	1	.	.	**2**	1	**1**	+	.	**2**	.
Agrostis capillaris	.	.	.	.	.	.	**2**	+	r	.	.	.	.	.	.	**++**	+	.	.	.	.	.
Briza media	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	r	.	**1**	.
Pyrethrum clusii	.	.	.	.	.	.	.	.	.	.	.	**2**	1	**+**	.	**++**	.	**1**	1	+	**2**	1
Ranunculus polyanthemos	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	.	.	**+**	+	+	**+**	.

Relevé	**1**	1	1	**2**	2	2	**3**	3	3	3	3	**4**	4	**5**	5	**6**	6	**7**	7	7	**8**	8
Year (19..)	**70**	88	97	**70**	85	99	**72**	85	88	97	99	**70**	85	**70**	97	**69**	97	**70**	85	97	**70**	97
Campanula glomerata	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	.	.	**+**	+	.	**++**	.
Euphorbia sojakii	.	.	.	.	.	.	**++**	+	+	.	.	**++**	+	.	.	.	.	.	.	.	.	++
Angelica sylvestris	**+**	.	.	.	.	.	**+**	+	+	.	.	**1**	+	.	.	.	.	.	1	+	**+**	++
Solidago virgaurea	**+**	+	.	**1**	++	+	**2+**	+	1	+	+	**1**	1	**2**	.	**1**	++	**+**	++	+	**1**	++
Hypericum maculatum	.	.	+	**+**	.	.	**3**	3	1	+	+	**+**	2+	**+**	.	**+**	1	**+**	1	1	**+**	2+
Achillea stricta	**+**	.	.	.	.	.	**+**	+	+	.	.	**1**	1	**+**	.	**1**	.	**1**	+	+	**1**	++
Potentilla erecta	**+**	+	+	**+**	.	+	**2+**	1	1	+	+	**2**	1	**1**	+	**2+**	+	**2**	1	+	**2+**	1
Luzula luzuloides	**1**	+	+	**1**	1	+	**2+**	++	+	+	+	**3**	3	**2+**	+	**3**	2+	**2+**	2+	1	**3**	2+
Hypochoeris uniflora	**+**	.	.	.	.	.	.	.	.	.	.	**1**	1	**1**	.	**2+**	+	**2**	2	1	**2**	+
Anemone nemorosa	.	.	.	.	.	.	.	.	.	.	.	**1**	.	**++**	.	**1**	+	**+**	.	+	**++**	.
Knautia dipsacifolia	.	.	.	.	.	.	**+**	+	+	.	.	**+**	+	.	.	.	.	.	.	.	.	1
Phyteuma spicatum	.	.	.	**+**	.	.	.	.	.	.	.	**++**	+	**+**	.	**+**	+	**+**	+	+	**+**	+
Acer pseudoplatanus juv.	.	+	+	.	.	+	**+**	+	+	+	.	.	.	.	.	.	.	.	.	+	**r**	+
Cardaminopsis halleri	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	+	.	.	.
Carex pilosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.
Thalictrum aquilegifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r
Filipendula ulmaria	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	.	.	.	.
Sedum argutum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Salix caprea agg.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juniperus communis juv.	.	.	.	.	.	.	.	.	.	.	.	**r**	.	.	.	.	.	.	.	.	.	.
Orchis mascula	.	.	.	.	.	.	.	.	.	.	.	**r**	.	.	.	.	.	.	.	.	.	.
Sorbus aucuparia juv.	**r**	.	.	**+**	.	+	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.
Rosa pendulina	.	.	.	.	.	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.
Hieracium prenanthoides	.	.	.	**+**	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	.	.	.	.
Rosa pendulina	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
Rosa sp.	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	.	.	.	.

Relevé Year (19..)	**1** **70**	1 88	1 97	**2** **70**	2 85	2 99	**3** **72**	3 85	3 88	3 97	3 99	**4** **70**	4 85	**5** **70**	5 97	**6** **69**	6 97	**7** **70**	7 85	7 97	**8** **70**	8 97
EO																						
Brachythecium sp. div.	**.**	.	.	**.**	.	+	**2**	.	.	.	.	**+**	.	**.**	.	**+**	.	**1**	.	.	**1**	.
Polytrichum juniperinum	**.**	.	1	**.**	.	.	**.**	.	.	.	.	**+**	.	**.**	.	**+**	.	**+**	.	.	**2**	.
Plagiomnium sp.div.	**.**	.	2	**.**	.	.	**.**	.	.	.	.	**.**	.	**.**	.	**.**	.	**+**	.	.	**+**	.
Cladonia sp. div.	**.**	.	.	**.**	.	.	**.**	.	.	.	.	**+**	.	**.**	.	**.**	.	**+**	.	.	**+**	.
Fissidens taxifolius	**.**	.	1	**.**	.	.	**.**	.	.	.	.	**.**	.	**.**	.	**.**	.	**.**	.	.	**1**	.
Plolytrichum schreberi	**.**	.	.	**.**	.	.	**.**	.	.	.	.	**+**	.	**.**	.	**1**	.	**.**	.	.	**.**	.
Lescuraea incurvata	**.**	.	.	**.**	.	.	**.**	.	.	.	.	**.**	.	**.**	.	**.**	.	**+**	.	.	**.**	.
Atrichum undulatum	**.**	.	1	**.**	.	.	**.**	.	.	.	.	**.**	.	**.**	.	**.**	.	**.**	.	.	**.**	.
Rhytidiadelphus triquetrus	**.**	.	.	**.**	.	.	**.**	.	.	.	.	**2**	.	**.**	.	**.**	.	**.**	.	.	**.**	.
Eurhynchium schleicheri	**.**	.	.	**.**	.	+	**.**	.	.	.	.	**.**	.	**.**	.	**.**	.	**.**	.	.	**.**	.
Hylocomium splendens	**.**	.	.	**.**	.	.	**.**	.	.	.	.	**1**	.	**.**	.	**.**	.	**.**	.	.	**.**	.

Tab. 4. Phytosociological relevé of the *Acetoso-Deschampsietum* association.

Relevé	**1**	1	1	1	**2**	2	2	**3**	3	3	3	3	3	**4**	4	4
Year (19..)	**72**	85	97	99	**72**	85	97	**71**	72	85	88	97	99	**72**	85	99
Herb layer (cover in %)	**100**	98	97	98	**100**	95	85	**90**	85	80	95	80	85	**100**	95	80
Herb layer (number of species)	**24**	21	17	15	**11**	10	12	**22**	24	16	14	13	16	**17**	16	12
Moss layer (cover in %)	**5**	0	0	0	**2**	0	0	**10**	2	0	0	0	0	**0**	0	0
Deschampsia cespitosa	**4**	4	3+	3+	**4**	4	3+	**3+**	4	4	5	4+	4+	**4+**	4	4
Rumex alpestris	**2+**	2+	2	1	**2**	2	2+	**2**	2+	3	2+	2	2+	**1**	2+	2+
Rumex alpinus	**+**	+	++	++	.	.	++	**++**	+	+	+	1	1	**1**	2	+
Gentiana asclepiadea	**+**	1	2	2	**1**	2+	+	.	.	.	.	.	.	.	2+	1
Cruciata glabra	.	.	.	+	.	.	.	**++**	++	r	r	.	.	.	++	+
Polygonatum verticillatum	**+**	+	.	.	.	+	.	.	.	+	.	r	r	.	.	.
Aegopodium podagraria	**+**	+	+	+	.	.	.	.	.	.	.	.	.	.	+	+
Hypericum maculatum	**4+**	4	4	3+	**4**	3	+	**2+**	2+	2+	2+	++	++	**2**	3	1
Poa chaixii	**1**	r	+	+	**2**	+	.	**2+**	2	1	1	+	+	.	+	+
Dactylis slovenica	**+**	2+	+	+	**+**	.	.	**+**	++	r	r	.	.	**2+**	1	.
Lysimachia nemorum	**2**	2	+	++	**1**	+	.	**1**	++	+	.	.	.	**++**	.	.
Viola dacica	**+**	.	+	+	.	.	.	**+**	+	.	.	.	.	**+**	+	.
Campanula abietina	**+**	+	+	.	.	.	.	**+**	++	+	+	.	.	.	.	.
Achillea stricta	**+**	.	.	.	.	.	.	**+**	+	.	.	.	.	**+**	1	.
Ranunculus polyanthemos	**+**	.	.	.	.	.	.	**+**	+	.	.	.	.	**+**	+	.
Angelica sylvestris	.	.	.	.	.	.	.	**1**	1	+	+	.	.	.	.	.
Geranium palustre	**+**	.	.	.	.	.	.	**+**	+	.	.	.	.	**+**	1	.
Veronica chamaedrys	**+**	.	.	.	.	.	.	**++**	++	.	.	.	.	.	.	.
Hieracium aurantiacum	.	.	.	.	.	.	.	**+**	+	r	.	.	.	.	.	.
Agrostis capillaris	.	.	.	.	.	.	.	**2**	2	+	.	.	.	.	.	.
Petasites albus	**+**	+	.	.	.	.	.	.	.	.	.	.	.	**1**	.	.
Chaerophyllum hirsutum	**r**	r	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.
Glechoma hirsuta	**+**	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.

Relevé	**1**	1	1	1	**2**	2	2	**3**	3	3	3	3	3	**4**	4	4
Year (19..)	**72**	85	97	99	**72**	85	97	**71**	72	85	88	97	99	**72**	85	99
Carex sylvatica	**+**	.	.	.	.	.	.	.	.	.	.	.	.	**++**	.	.
Veronica officinalis	.	.	.	.	.	.	.	**+**	1	.	.	.	.	.	.	.
Rubus idaeus	**+**	2+	3	4	.	.	3	.	.	2	2+	3	3+	.	.	2
Stellaria nemorum	.	+	+	+	**+**	1	+	.	.	+	+	+	++	.	.	.
Solidago virgaurea	**r**	r	++	.	.	r	.	**1**	2	2	1	1	1	.	.	.
Carex pallescens	.	+	.	.	.	.	.	.	.	+	.	.	+	.	.	.
Athyrium distentifolium	.	.	.	.	.	.	+	.	.	.	.	+	+	.	.	.
Senecio fuchsii	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.
Dryopteris filix-mas	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.
Acer pseudoplatanus juv.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.
Potentilla erecta	.	+	1	++	.	.	.	**+**	.	.	.	.	.	.	+	+
Anemone nemorosa	.	r	+	+	.	.	.	.	+	+	.	+	.	.	.	r
Chamerion angustifolium	.	.	.	.	**+**	+	+	.	.	.	.	.	.	.	.	.
Melandrium rubrum	**+**	.	.	.	.	.	.	.	.	.	.	.	+	**+**	.	.
Galeopsis speciosa	.	.	.	.	**+**	.	+	.	.	.	.	.	.	.	.	.
Omalotheca sylvatica	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Anthoxanthum odoratum	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Alchemilla vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.
Milium effusum	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Carex ovalis	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Polygonatum verticillatum	**+**	+	.	.	.	+	.	.	.	+	.	r	r	.	.	.
Aegopodium podagraria	**+**	+	+	+	.	.	.	.	.	.	.	.	.	.	+	+
Ranunculus platanifolius	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.
Campanula serrata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r
Stellaria graminea	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.

Relevé	**1**	1	1	1	**2**	2	2	**3**	3	3	3	3	3	**4**	4	4
Year (19..)	**72**	85	97	99	**72**	85	97	**71**	72	85	88	97	99	**72**	85	99
Gymnadenia conopsea	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Thalictrum aquilegifolium	.	.	.	.	.	.	.	**r**	.	.	.	.	.	.	.	.
Oxalis acetosella	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Filipendula ulmaria	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
Symphytum cordatum	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phyteuma spicatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Anthriscus sylvestris	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.
Aposoeris foetida	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirsium waldsteinii	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eo																
Brachythecium sp.	**1**	.	.	.	.	.	.	**2**	1	.	.	.	.	.	.	.
Rhytidiadelphus squarrosus	**+**	.	.	.	**1**	.	.	.	.	.	.	.	.	.	.	.
Polytrichum commune	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	.	.
Mnium sp.	.	.	.	.	.	.	.	**1**	.	.	.	.	.	.	.	.
Polytrichum juniperinum	**++**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Tab. 5. Phytosociological relevé of the *Betonico-Agrostietum* association.

Relevé	**1**	1	**2**	2	**3**	3	3	3	3	**4**	4	4	**5**	5	**6**	6	6	**7**	7	7
Year (19..)	**69**	97	**72**	97	**69**	74	85	88	97	**72**	88	97	**72**	85	**72**	85	97	**72**	85	97
Herb layer (cover in %)	**90**	90	**98**	90	**90**	98	98	97	98	**95**	98	95	**85**	85	**85**	90	98	**85**	90	88
Herb layer (number of species)	**51**	23	**53**	28	**54**	51	39	29	42	**56**	42	30	**36**	28	**40**	30	24	**31**	21	11
Moss layer (cover in %)	**25**	0	**5**	0	**15**	5	0	0	3	**15**	3	0	**25**	1	**25**	1	5	**30**	1	2
Shrub layer (cover in %)	**0**	0	**0**	0	**0**	0	0	0	0	**0**	0	0	**0**	0	**0**	0	5	**0**	0	8
Thymus pulegioides	**2**	.	**+**	r	**1**	.	r	r	.	**2**	r	.	**++**	.	**1**	.	.	.	.	.
Leontodon hispidus	**2**	.	**1**	.	**2**	1	.	.	.	**2**	+	.	.	.	.	.	.	.	.	.
Ajuga reptans	**+**	.	**+**	.	**+**	.	.	.	.	**+**	.	.	.	+	**+**	.	.	.	.	.
Prunella vulgaris	**+**	.	.	.	**+**	+	.	.	.	**+**	.	.	.	.	**+**	.	.	.	.	.
Rhinanthus angustifolius	.	.	**1**	.	**+**	+	.	.	.	**1**	.	.	.	.	.	.	.	.	.	.
Sieglingia decumbens	.	.	.	.	.	.	.	.	.	**+**	.	.	**1**	.	**1**	.	.	**+**	.	.
Hieracium pilosella	**+**	.	.	.	**+**	.	.	.	.	**+**	.	.	.	.	**+**	.	.	.	.	.
Antennaria dioica	.	.	.	.	**+**	.	.	.	.	.	.	.	**+**	.	**+**	.	.	.	.	.
Vaccinium vitis-idaea	**++**	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	**++**	.	.
Hieracium aurantiacum	.	.	.	.	**+**	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gentianella carpatica	.	.	**+**	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.
Plantago media	.	.	**++**	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.
Campanula serrata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	r	.	.	.	.
Cerastium holosteoides	.	.	**+**	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.
Festuca pratensis	**+**	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphrasia rostkoviana	.	.	.	.	.	+	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.
Nardus stricta	**3+**	.	**3**	+	**3+**	2+	.	.	+	**3+**	3	.	**4**	+	**3+**	1	.	**2**	+	.
Briza media	**1**	+	**1**	.	**1**	+	+	+	+	**1**	+	.	**+**	.	**1**	+	.	.	.	.
Anthoxanthum odoratum	**1**	.	**1**	.	**1**	1	+	.	.	**2+**	+	.	**1**	.	**2**	+	.	**+**	+	.
Crepis conyzifolia	**1**	.	**1**	.	**1**	2+	2	+	.	**+**	+	.	.	.	**+**	.	.	**+**	.	.
Luzula multiflora	**1**	.	.	.	**1**	+	.	.	.	**+**	+	++	**+**	.	**1**	+	.	**+**	.	.

Relevé	**1**	1	**2**	2	**3**	3	3	3	3	**4**	4	4	**5**	5	**6**	6	6	**7**	7	7
Year (19..)	**69**	97	**72**	97	69	74	85	88	97	**72**	88	97	**72**	85	**72**	85	97	**72**	85	97
Polygala vulgaris	++	.	+	.	2	++	.	.	+	++	+	.	.	.	+	.	.	+	.	.
Veronica officinalis	+	.	.	.	+	.	.	.	+	+	.	+	++	.	+	.	.	+	.	.
Viola canina	2	.	++	.	1	1	.	.	.	+	r	+	.	.	.	.	.	.	.	.
Carex pilulifera	.	.	.	.	++	.	.	.	.	.	.	.	1	.	.	+	.	1	+	.
Carlina acaulis	2	.	2+	+	+	+	+	.	.	2+	1	.	1	.	.	.	.	+	.	.
Silene nutans	+	.	+	+	+	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.
Pimpinella saxifraga	1	.	1	.	.	.	.	.	.	++	+	.	.	.	.	+	.	.	.	.
Fragaria vesca	+	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	2	.	3	1	2+	2+	2	2+	1	2+	2	3	1	1	2+	1	+	1	+	.
Festuca rubra	2+	+	1	++	2+	1	+	+	1	2	1	1	+	+	1	+	+	.	.	+
Centaurea phrygia	+	+	2	+	.	+	r	1	+	2	2	+	+	+	1	++	.	+	.	.
Cruciata glabra	2	+	+	.	2	1	1	1	+	++	+	+	++	+	1	+	.	+	.	.
Veronica chamaedrys	2	1	+	+	2	1	1	1	1	+	+	1	+	.	+	.	.	.	.	.
Betonica officinalis	+	.	2	1	++	+	+	+	+	1	2	+	++	+	.	.	.	.	.	.
Succisa pratensis	.	.	+	+	.	+	.	.	.	.	.	.	1	+	1	++	+	.	.	.
Plantago lanceolata	+	.	1	.	+	+	.	.	+	1	1	1	.	.	+	.	.	.	.	.
Lotus corniculatus	++	.	1	.	++	+	+	.	.	+	+	+	+	.	.	.	.	.	.	.
Leucanthemum vulgare	+	.	+	.	+	+	.	.	.	2	r	+	.	.	+	.	.	.	.	.
Campanula patula	+	.	+	.	+	+	.	.	.	+	r	+	.	.	+	.	.	.	.	.
Trifolium pratense	+	.	+	.	1	1	.	.	+	1	+	.	.	.	.	.	.	.	.	.
Trifolium repens	1	.	.	.	2	+	.	.	.	+	+	.	.	.	.	.	.	.	.	.
Alchemilla vulgaris	+	.	++	.	++	++	.	.	.	++	+	+	.	.	.	.	.	.	.	.
Myosotis nemorosa	.	.	+	.	+	+	r	.	.	+	.	.	.	.	.	.	.	.	.	.
Centaurea jacea	1	.	++	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Melandrium rubrum	+	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.

Relevé	**1**	1	**2**	2	**3**	3	3	3	3	**4**	4	4	**5**	5	**6**	6	6	**7**	7	7
Year (19..)	**69**	97	**72**	97	69	74	85	88	97	**72**	88	97	**72**	85	**72**	85	97	**72**	85	97
Vicia cracca	.	.	+	++	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula elatior	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.
Heracleum sphondylium	.	.	.	.	.	.		.	.	+	+	.	.	.	.	.	.	.	.	.
Gentiana asclepiadea	+	2	.	.	1	2	2+	3	2+	++	+	+	+	2	2	2	2	2+	2+	1
Vaccinium myrtillus	.	.	.	.	+	+	1	2	+	.	.	.	2	+	2+	1	3	3+	2+	2+
Luzula luzuloides	2	2+	.	1	2	2+	3	2	2	2	+	1	+	.	1	1	1	++	+	.
Rumex acetosa	1	+	1	++	+	+	1	+	++	+	1	1	+	+	.	+	.	.	.	.
Solidago virgaurea	.	.	r	.	.	+	+	.	+	.	.	.	1	+	.	.	+	+	+	.
Cardaminopsis halleri	+	.	+	.	+	+	.	.	.	+	2	+	.	.	.	.	.	.	.	.
Carex pilosa	r	.	.	.	.	.	.	.	.	.	.	.	.	+	1	2	1	++	+	.
Phyteuma spicatum	.	+	.	.	1	.	+	.	+	+	.	.	.	.	.	.	++	.	+	.
Anemone nemorosa	++	+	.	.	++	.	.	.	+	.	.	.	.	.	.	.	+	.	+	+
Thalictrum aquilegifolium	+	.	.	.	.	.	r	.	.	+	.	.	.	.	.	.	.	.	.	.
Galium verum	.	++	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa chaixii	1	2	+	1	1	+	++	3	+	+	2	.	.	+	+	+	.	1	+	.
Achillea stricta	1	2	1	2	+	1	3	2+	2	2	2	2+	1	.	2+	1	.	+	.	.
Carex pallescens	.	+	+	+	.	+	+	.	+	.	+	+	1	.	1	1	+	++	+	+
Knautia dipsacifolia	+	1	+	1	+	+	1	+	1	+	.	.	.	.	+	.	.	.	.	.
Hieracium lachenalii	.	.	.	+	.	.	+	+	+	.	.	.	.	.	+	+	.	.	.	.
Stellaria graminea	+	.	+	+	+	+	+	1	+	++	+	1	+	.	+	.	.	.	.	.
Ranunculus acris	1	.	+	.	+	+	+	+	+	+	1	+	.	.	.	.	.	.	.	.
Dactylis slovenica	+	+	+	.	.	.	+	+	+	++	+	.	.	.	.	.	.	.	.	.
Gymnadenia conopsea	.	.	+	+	+	.	r	.	.	.	r	.	.	.	+	+	+	+	.	.
Hypochoeris uniflora	.	.	.	+	2	+	+	r	++	.	.	.	.	.	.	.	.	.	.	.
Trifolium medium	.	.	1	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.

Relevé	**1**	1	**2**	2	**3**	3	3	3	3	**4**	4	4	**5**	5	**6**	6	6	**7**	7	7
Year (19..)	**69**	97	**72**	97	69	74	85	88	97	**72**	88	97	**72**	85	**72**	85	97	**72**	85	97
Potentilla erecta	**1**	2	**1**	2	**2**	2	2+	2	2	**2+**	2	3	**2**	+	**+**	+	+	**+**	+	+
Ranunculus polyanthemos	**1**	+	**++**	++	**1**	1	+	++	+	**++**	1	++	.	.	.	.	.	.	.	.
Pyrethrum corymbosum	.	.	.	.	**+**	+	+	+	+	.	.	.	**+**	+	.	.	.	.	.	.
Digitalis grandiflora	.	.	.	.	.	.	.	.	.	.	.	.	**+**	1	**+**	+	+	**+**	+	.
Polygonatum verticillatum	.	.	.	.	**+**	+	+	+	+	.	.	.	.	+	.	.	.	.	+	.
Cirsium palustre	.	.	.	.	.	.	.	.	.	.	.	.	.	+	**+**	+	+	.	.	.
Populus tremula juv.	.	.	.	.	.	.	.	.	.	.	.	.	**1**	1	.	++	.	**1**	+	.
Salix silesiaca juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	+	+
Genista tinctoria	.	.	.	.	.	.	.	.	.	.	.	.	**+**	+	.	.	.	.	.	.
Ranunculus nemorosus	.	.	**+**	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Luzula sylvatica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.
Carex panicea	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	+	.	.	.	.
Hypericum maculatum	**++**	3	**++**	3	**1**	2	3	4	3	**+**	1	2+	**+**	2+	**1**	2+	2+	**+**	1	1
Calamagrostis arundinacea	.	4	.	4+	.	1	2	2	2+	.	+	.	**3**	3	**2**	4	4	**4+**	5	5
Malus sylvestris juv.	.	r	.	+	.	.	.	.	r	**+**	r	.	.	r	.	.	.	.	.	.
Rumex alpestris	.	1	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Carex brizoides	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.
Deschampsia cespitosa	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.
Acer pseudoplatanus juv.	.	++	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Cynosurus cristatus	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.
Carum carvi	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum officinale	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Traunsteinera globosa	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.
Lycopodium clavatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.

Relevé	**1**	1	**2**	2	**3**	3	3	3	3	**4**	4	4	**5**	5	**6**	6	6	**7**	7	7
Year (19..)	**69**	97	**72**	97	**69**	74	85	88	97	**72**	88	97	**72**	85	**72**	85	97	**72**	85	97
Dactylorhiza sambucina	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calamintha clinopodium	.	.	**r**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linum catharticum	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.
Picea abies juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**r**	.	.
Betula pendula juv.	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.
Omalotheca sylvatica	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Calamagrostis epigeios	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.
Carex ovalis	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Rumex acetosella	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Campanula abietina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dianthus barbatus	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Pteridium aquilinum	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Euphorbia sojakii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Abies alba juv.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Lathyrus pratensis	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Spergula arvensis	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.
Rumex obtusifolius	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Chenopodium polyspermum	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
Verbascum nigrum	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
E2																				
Salix silesiaca	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2
Populus tremula	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Abies alba	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Malus sylvestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Salix aurita	.	.	.	.	.	.		.	.	.	.	.	.	.	.	.	1	.	.	.

Relevé Year (19..)	**1** **69**	1 97	**2** **72**	2 97	**3** 69	3 74	3 85	3 88	3 97	**4** **72**	4 88	4 97	**5** **72**	5 85	**6** **72**	6 85	6 97	**7** **72**	7 85	7 97
Eo																				
Thuidium delicatulum	**2**	.	**1**	.	**1**	.	.	.	.	**2**	.	.	**+**	.	**+**	.	.	.	.	.
Pleurozium schreberi	**2**	.	.	.	**2**	.	.	.	.	**1**	.	.	**2**	.	**2**	+	.	**3**	.	.
Hylocomium splendens	.	.	.	.	.	.	.	.	.	.	.	.	**1**	.	**1**	.	.	**1**	.	.
Cladonia sp.	**+**	.	.	.	.	.	.	.	.	.	.	.	**+**	.	.	.	.	.	.	.
Polytrichum juniperinum	**1**	.	.	.	**1**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polytrichum commune	.	.	.	.	.	.	.	.	.	.	.	.	**+**	.	**+**	.	.	.	.	.
Dicranum scoparium	.	.	**+**	.	**1**	.	.	.	.	**+**	.	.	.	.	.	.	.	.	.	.
Brachythecium albicans	**1**	.	.	.	.	.	.	.	.	**2**	.	.	.	.	.	.	.	.	.	.
Plagiomnium affine	**+**	.	.	.	**+**	1	.	.	.	**1**	+	.	**1**	+	**1**	+	1	**1**	+	+
Brachythecium sp.	.	.	**1**	.	.	1	.	.	.	.	1	.	.	.	.	.	1	.	+	+
Abietinella abietina	.	.	**1**	.	.	+	.	.	1	**+**	.	.	.	.	.	.	.	.	.	.
Rhytidiadelphus squarrosus	.	.	.	.	**+**	+	.	.	.	.	1	.	.	.	**2**	.	.	.	.	.
Cirriphyllum piliferum	.	.	**+**	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Brachythecium rutabulum	.	.	.	.	.	.	.	.	.	**2**	.	.	.	.	.	.	.	.	.	.
Lophocolea bidentata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Bryum cespiticium	.	.	**+**	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Breidleria arcuata	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.

Fig. 6. Initial and successionally derived vegetation units of the "poloniny" meadows.