

Alpine tundra in the Hrubý Jeseník Mts., the Sudeten, and its tentative development in the 20th century

Pokus o rekonstrukci vývoje vegetace alpinských holí Hrubého Jeseníku ve 20. století

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Changes in vegetation above the alpine tree line have been evaluated by two approaches: (1) comparison of the species hierarchy in individual plant communities over the past 80 years, (2) comparison of the importance values of main vascular species in plant communities over the same period. Both methods confirm successional changes caused by the cessation of grazing about 50 years ago.

Introduction

Extensive summit area of the Hrubý Jeseník Mts., a range belonging to the Sudeten, is covered by a fairly monotonous alpine tundra. Topmost ridges are dominated by *Deschampsia flexuosa* and *Festuca airoides* (= *F. supina*) grasslands, *Calamagrostis villosa* and *Vaccinium myrtillus* are prevailing on large flanks; ill-drained sites are occupied by stands of *Deschampsia cespitosa*, and scree habitats are inhabited by *Athyrium distentifolium* and other tall herbs. Merely small patches of the alpine belt are occupied by species-rich herbaceous communities whose occurrence resulted from an abnormal regime of abiotic factors, such as snow drifts, avalanches and seepage of water (Bednář 1956, Jeník 1961). Within the Sudeten and neighbouring European mountains, the monotonous vegetational pattern of the Hrubý Jeseník is rather exceptional. The missing krummholz belt of *Pinus mugo* and the markedly small number of vascular species appear as a significant biogeographical feature of this mountain range (Jeník 1973).

In order to explain the present pattern and long-term vegetation dynamics we need either to collect documents of direct topical observations, or to find out indirect evidence of the past events. At the landscape dimension, the following sources of direct evidence can be exploited: (1) old photographs and similar illustration derived from "remote sensing", (2) old maps of vegetation, (3) records on permanent sample plots established in an earlier period, (4) old phytosociological relevés (if adequately localized).

Among the indirect methods, the following procedures can illuminate the past vegetation pattern: (5) comparison with well-known development of vegetation in another areas controlled by similar abiotic factors, (6) analysis of soil samples in comparable plant stands, (7) analysis of available micro- and macrofossils, (8) evidence of written documents in archives, and oral evidence of reliable witnesses, (9) analyses and experiments with dominant and retreating plant species with regard to their life history, competitive status, growth strategy, etc. (for details see Wilmanns et Bogenrieder 1987).

In the present paper we intend to verify the feasibility of a procedure reconstructing recent development of the vegetation from floristic lists and relevés recorded in the period between 1910 and 1985. Earlier evidence of vegetation was not available, and, due to peculiarities of the parent rocks and soils, any analogy with other Hercynian summit regions was doubtful. Old manuscripts and maps in the archives, enable to distinguish merely between forest and non-forest vegetation, and a few more recent documents do not reach beyond the date of botanical publications.

Description of the study area

Our examination in the Hrubý Jeseník's alpine belt refers to its southern section extending between Petrovy Kameny mount (reaching 1440m altitude) at the northern end, and Pec mount (1311m) at the southern promontory. In a study by Alblová (1970) the timberline of this area has been situated between 1250 and 1300m altitude.

Chloritic and sericitic gneisses of the Desná Series represent the main rocks outcropping on Petrovy Kameny, by a remarkable tor. To the south, the ridge consists of graphitic phyllites and of a dyke of quartzites just along the western margin between Pec and Břidličná mounts, and, locally found on Máj and Vysoká Hole (Fišera 1982, Opletal et Hank 1984). According to Pelíšek (1972) podzolic soils prevail on the summit plateaux, but local transitions to alpine brownearths, rankers and cryogenic soils occur, too (Prosová 1963). Large block-fields cover the western slope of Břidličná mount, and small hollows and cirques occur on the eastern side (Malá Kotlina, Velká Kotlina and Mezikotlí). These cirques have been sculptured by glaciers during the glacial periods, and even currently they represent the most active area of the Hrubý Jeseník's topography, particularly due to deposition of large snow drifts, nivation around the late-snow patches, multiple effects of snow avalanches, and related erosion by melt water (Jeník, Bureš et Burešová 1985 - hereafter quoted as JBB 1985).

The summit area of the Hrubý Jeseník has a cold upland climate differentiated by its prominent topography and exposure to the prevailing western winds: while the western windward slopes and plateaux show a certain deficit in snow cover, the eastern leeward slopes receive large quantities of drifted snow, which is the major factor in the vegetation pattern (Piňosová 1986).

Methods

Floristic lists compiled at the beginning of this century by Laus (1910), and phytosociological relevés from the period 1954 to 1955 by Bednář (1956), from 1973 to 1975 by JBB (1985), and from 1985 to 1986 by Piňosová (1987) served as a basic source of information. These publications vary in estimation of cover/abundance of present species. While the paper of Laus (1910) gives a simple species list for each plant community (called

formation or facies), the other articles offer more records presented in the form of phytosociological relevés or synoptic tables.

Because the total number of relevés and their number per a plant community greatly differ at individual authors and, more importantly, so did the sample plot size, the available data could not be compared by common phytosociological methods, e. g. by cluster analysis, ordination and table analysis. We have thus used the hierarchy of important species instead of the complete species lists for description of a stand. In this case, the effect of subordinate species on the similarity coefficients was negligible, and they could be deleted. According to many authors (e. g., de Vita 1982, Ghent 1963, Karnečka 1976, MacArthur 1955, Whittaker 1965) the species hierarchy can be used as a valuable and invariant feature of a community.

We have applied two ways of delimitation of vegetation units: (1) In a broad sense, only two units have been distinguished - one of them representing the vegetation of flat or slightly inclined summit plateaux, the other one representing the vegetation of steep flanks above timberline. (2) In a narrow sense, we have compared plant communities described by individual authors, on the basis of their floristic composition, and with regard to dominant and subdominant species.

In order to compare various phytosociological sources, we used the following importance values for individual plant populations:

a) Laus (1910) ascertained the importance of species according to the Drude scale (Drude 1890); in order to simplify these records we used the following transformation: socialis - 3, gregarius - 2, copiosus - 1. Rare species (sparsus and solitaris) were omitted.

b) Other authors described the alpine tundra of the Hrubý Jeseník by means of phytosociological relevés. The importance value IV of the species i was calculated as follows: $IV_i = (MVA_i \times NR_i) / NR$, where MVA_i is the mode value of abundance/dominance of the species i , NR_i is the number of relevés involving the species i and NR is total number of relevés. The abundance/dominance values were transformed from the Braun-Blanquet scale in the following way:

B-B scale	r	+	1	2	3	4	5
transformation	1	2	3	4	5	6	7

Correlation in the species hierarchy between records and different periods was estimated by the Spearman's correlation coefficient. In this procedure, the species characterized by importance values (IV) lower than one were ignored.

Alterations of the importance value in individual dominant species recorded by different authors were evaluated by Kruskal-Wallis test.

Apparently, a comparison of the importance value in the Drude scale and the abundance/dominance of the Braun-Blanquet scale applied in the phytosociological matrices is possible only in the case of marked differences of pertinent values. To avoid errors caused by exact computations with roughly estimated importance values, the structure of the data was simplified as follows:

importance value (IV)	$IV > 4$	$4 > IV > 2$	$2 > IV > 1$	$IV < 1$
transformations	3	2	1	0

Delimitation of the territory (1), and procedures of the description (2) markedly varied in the papers published by different authors, in spite of their similar goals.

(1) Laus (1910) described a much broader area than that named in the title of his paper ("der grosse Kessel"); actually, he took into account a larger part of the Hrubý Jeseník, possibly the whole area between Petrovy Kameny and Brdličná. Bednář (1956) examined the territory between Praděd and Pecný (op.c., p. 3). For JBB (1985) the area of the study was the Velká Kotlina cirque, including the adjoining alpine tundra on the Vysoká Hole summit (nearly 10 km²). The study area of Piňosová (1987) was the southern crest of Hrubý Jeseník between Pec and Petrovy Kameny (op.c., p. 14). We can conclude that the territory covered by the aforementioned authors varied a great deal, but in all cases (1) the summit area of Vysoká Hole was included, and (2) both the summit vegetation and vegetation of the neighbouring flanks above the timberline were studied.

(2) With regard to the descriptive procedure, Laus (1910) distinguished merely plant formations, i.e., physiognomically defined units. One of them, called "die Ostsudetische Bergheide-Formation", represented the overall alpine tundra (op.c., p. 114-122); this formation was further divided into 8 facies, according to the life forms of dominant vascular species, and according to the habitat. For Bednář (1956) the basic classification unit was the society, a unit subordinated to association, and units of higher rank according

the Zürich-Montpellier system. The latter system was used also by JBB (1985). Piňosová (1987) described plant communities comparable with the societies; the treatise contained mainly records with *Nardus stricta*, however, phytosociological relevés of other vegetation types recorded in the same period are contained in Table 1 of this work. Šmarda (1950) describing various plant communities by a single phytosociological record could not be exploited in this work; his relevés expressed floristically most attractive spots of the actual variability, and thus could not serve as a reliable indication of the common species composition. Nevertheless, Šmarda's vegetation units were included in the following description and Table 5, in order to enable a comparison of all available information.

Species nomenclature follows Neuhäuslová et Kolbek (1982).

Description of alpine tundra on the southern crest of the Hrubý Jeseník

The feasibility of a comparison of vegetation according to the published work of individual authors strongly depends on accuracy of mutual identification of the respective units. For this reason we paid attention to original descriptions and interpretations. We excluded small-sized plant communities concentrated in glacial cirques whose florogenesis and plant succession proceeded in a unique way (see JBB 1985). Also, stands developed on tracks (Piňosová 1987) were excluded. Table 1 contains species composition of the relevant vegetation units. The present-day distribution and habitat of each of the plant communities given in the introductory paragraph is based on Piňosová (1987).

1. Fern tundra

Large stands dominated by *Athyrium distentifolium* are situated along the timberline on the both northern and north-eastern slopes of Petrovy Kameny, in the valley-head between the western flanks of Břidličná and Jelení Hřbet, and also in the Velká Kotlina cirque.

Laus recognized *Athyrium distentifolium* as a prominently dominant species creating stands in the ravines.

Šmarda identified the *Athyrium distentifolium* facies, described by Laus, with the submontane and montane tall-herb communities (p. 106), however, on p. 152 he merged his "tundra" dominated by *A. distentifolium* and *Vaccinium myrtillus* with spruce forest communities distributed in the forest/tundra ecotone.

Bednář described stands of a fern tundra in the lower belt of summit balds, particularly in the area of Petrovy Kameny mount.

JBB described species-poor communities with ferns in the Velká Kotlina cirque.

2. Short-grass community

Small-sized stands of this unit are distinguished by their species richness. They occur on soils enriched by seeping water in the cirques of Velká Kotlina, Malá Kotlina and Mezikotlí, locally also in the lee of the Jelení Hřbet and Petrovy Kameny mounts.

Laus found stands of this type markedly covering smaller plots than other facies. They occurred above the rock faces and, on the so called "Kotlové Louky", on the bottom of the Velká Kotlina; typical stands were recorded near Jelení Studánka, near Tři Studny on Máj, in the Malá Kotlina cirque and on Petrovy Kameny.

Šmarda identified this facies of Laus with submontane and montane grasslands, in contrast to communities of the alpine tundra. His description contains the expression of "diversified mixture of flower-rich species and grasses".

In the work of JBB stands of the *Thesio alpini-Nardetum* (p. 24), occurring on the bottom of the Velká Kotlina cirque correspond with the short-grass facies of Laus.

3. Tall-grass community

Stands with dominant *Calamagrostis villosa* create large patches on flanks of the main crest, and, locally, they occur also in sheltered depressions of the summit plateaux (e.g., Břidličná mount).

Laus described this prominent vegetation type by words "this facies is closely related with the short-grass grasslands and creates conspicuous stands" (op.c., p. 119).

Bednář found stands of this type covering slopes in the transition zone to the summit plateaux (Vysoká Hole, Kamzičník, Máj), locally creating continuous zone above the *Vaccinium myrtillus* shrub (viz No. 4).

JBB considered stands of this type as the common vegetation cover developed due to the absence of the krummholz; they described numerous transitions to the following vegetation type.

4. *Vaccinium myrtillus* shrub

Stands dominated by bilberry cover extensive areas in localities bearing the largest accumulation of snow, viz. in the valley-heads Velká Kotlina, Mezikotlí and Malá Kotlina; small islands also occur amidst the stands of the previous type with *Calamagrostis villosa*; stands of *V. myrtillus* grow also on block-fields and scree, particularly along the timberline.

Laus described a facies marked by the dominance of *Vaccinium myrtillus*, creating a belt above the timberline.

By Šmarda, this ericoid shrublet is considered as an autochthonous type in the area of natural forest.

Bednář holds these stands for wide-spread communities of the summit tundra; they were extensively developed on slopes, irrespectively of their orientation; their lower margin coincided with the timberline.

JBB analyzed stands concentrated in the zone of the maximum accumulation of snow above the Velká Kotlina cirque, and in varied habitats of the summits; they created frequent transitions to the preceding type.

5. *Nardus grassland*

Stands with dominant matgrass are situated in sites with a deep drifts of snow in winter, namely on the north-eastern slopes of a saddle between Jelení hřbet and Máj mounts, and on the summit of Máj; small-sized patches occurred in shallow depressions situated in the lee of the main crest.

Laus mentioned the closed-canopy community of the matgrass, leaving little space for other species; *Nardus*-tundra created transitions to the facies with lichens and mosses (see No. 10); Laus found large areas with prevailing *Nardus stricta* (see also Schindler 1926).

Šmarda took stands of this type for a secondary vegetation induced by pasture and by trampling caused by domestic animals, presumably by cattle and sheep.

Bednář described his "*Nardus stricta-Festuca supina*" society growing on the topmost crest: it was a transitional community leading to the origin of a matgrass tundra; the "*Nardus stricta-Potentilla erecta*" society was a final stage in the regressive succession after deforestation at the timberline; expansion of *Nardus* stands, possibly, was influenced by domestic animals; the *Nardus*-tundra of the Hrubý Jeseník was less extensive but flower-rich than similar vegetation in the Giant Mts.

6. *Deschampsia flexuosa* grassland

A widely spread type of vegetation on the upland summits are grasslands dominated by wavy-hair grass. Their floristic composition resembles that of the foregoing type, but differs mainly by the absence of *Nardus stricta*. For this reason both units were included by Jeník (1961: 307) within a single association called *Carici fyllac-Nardetum*.

Bednář found a similar community on shallow soils of the summit plateaux.

JBB analyzed a vegetation type with predominant *Deschampsia flexuosa*, creating close stands on the summit plateaux of Vysoká Hole.

7. Open-canopy grassland

On the summit of Vysoká Hole and Petrovy Kameny there are large stands of open-canopy grasslands created by *Festuca airoides* and *Carex rigida*, accompanied by extensive layer of mosses.

From the same localities, Laus described a "facies with lichens and mosses", containing sporadical forbs (see No. 10).

Bednář found stands of this type occurring on the topmost crests of Praděd, Petrovy Kameny, Vysoká Hole, and, locally, even on Kamzičnick and Břidličná.

JBB described stands of this type growing on the wind-swept elevations of the alpine tundra.

8. Open-canopy dwarf shrub

Stands with three ericoid species of *Vaccinium vitis-idaea*, *Vaccinium myrtillus* and *Calluna vulgaris*, accompanied by *Cetraria islandica*, occur on the windswept edges of crests lacking snow in winter; they prefer stone-rich soils on quartzite substratum.

Šmarda recorded this type of community in very dry habitats, a feature primarily marked by the presence of *Calluna vulgaris*.

Bednář described this plant community in stone-rich areas of the summit plateaux exposed to wind erosion.

9. Stands of dwarf shrub on wet scree

This type of ericoid stands with *Vaccinium myrtillus*, *Calluna vulgaris* and *Empetrum hermaphroditum* occurs on the wet scree of western slope of Břidličná, on the north-western slope of Vysoká Hole, and on the northern slope of Petrovy Kameny mount.

Laus mentioned this relatively wet vegetation as a type often growing in the vicinity of springs, outside stagnating water, locally on elevations; with graminoids substituted by ericoid shrubs these stands do not contain a marked dominant species.

Bednář encountered these stands mainly on south-facing slopes, creating transitions to the bilberry tundra.

10. Facies with lichens and mosses

This vegetation type was described merely by Laus, from localities covered presently by "open-canopy grasslands" (see No. 7). Stands of this type are distributed on stony soils. Although rather frequent, they create only small patches consisting of lichens of the genera *Cladonia* and *Cetraria*.

11. Facies with *Juncus trifidus*

According to Laus a facies with three-leaved rush occurs only locally, viz. on Petrovy Kameny and Keprník. Similar stands were described by Šmarda from the summit rocks of Vozka and Keprník (outside the territory described in this paper).

According to their occurrence and floristic composition, the above defined communities create two groups. The first group contains vegetation types of the summit plateaux (5, 6, 7, 8, 10, and partly 11). The second group consists of widely occurring vegetation types of the flanks on the crest (1, 2, 3, 4). Stands of dwarf scrub on wet scree (9) create an exception - due to their rare occurrence on the slopes, but their floristic affinity with stands on the summit plateaux.

With regard to the summit plateaux, Laus (1910) declared the mat-grass tundra as the most wide-spread facies. Floristically similar stands were recorded by Šmarda (1950), too. Contrary to the preceding authors, Bednář (1956) described on the summit plateaux not only *Nardus*-tundra, but also stands with *Deschampsia flexuosa* lacking any *Nardus stricta*. In the study area of JBB (1980) stands of mat-grass tundra were missing. Piňosová (1987) summarized the closed-canopy grasslands of the summit plateaux within a single

unit, irrespectively to the presence of *Nardus stricta*; the same author emphasized that *Nardus stricta* was a dominant plant over relatively small patches only.

With regard to the flanks, Laus (1910) described tall-grass communities and bilberry scrub as the most extensive stands in the upper zone; similar appreciation was pronounced by Šmarda (1950), Bednář (1956), JBB (1980) and Piňosová (1987).

Human impact in the Hrubý Jeseník's summit area

Since the 17th century the area of Hrubý Jeseník range was intensively managed (Hošek 1972, 1973). Grazing of domestic animals, hay making and wood cutting were the first human activities in this territory.

In the 18th century, wood cutting in the Hrubý Jeseník expanded and reached the timberline (Hošek 1972). At the beginning of the 19th century, silviculture with artificial regeneration was introduced, and at the end of the same century afforestation of the alpine tundra and efforts to elevate the timberline have been started. Until recently, plantations on treeless summits continued, and extensive krummholz stands of the allochthonous *Pinus mugo* were established in this range. In the period between 1883 and the twenties of our century, a continuous belt of the krummholz derived from an alpine provenance of *Pinus mugo* has been planted on the southern slopes of the Praděd Mt., in the summit area between Pec and Vysoká Hole, and in the Malá Kotlina and Velká Kotlina cirques - altogether 165 ha (Hošek 1972, Leneček 1930). In spite of the arguments advanced against this activity (Jeník 1972, Ovčáčík 1979) plantation of krummholz in the Hrubý Jeseník's alpine tundra have not ceased.

At the beginning of the 18th century, a treeless region of the main range was leased for pasture of cattle (Kneifel 1805). Herds of cattle were kept in the seasonal stable called "Volárna" situated in the Mezikotlí cirque; this centrum of pasture was closed already in the forties of the last century (Hošek 1972). The first sheep-fold was established in the 18th century on the slopes of Malá Hole, within the former Bruntál Estate, however, this area was shortly left and a new sheep-fold was established in 1820 at the track from Karlova Studánka to Vidly, a place later called Stará Ovčárna. Later on, this place became less suitable and a new sheep-fold was established on the site of the present-day Ovčárna, a chalet transformed in 1889 into a hostel (Filip 1988). With some exceptions extensive grazing ceased according to Schindler (1926) in the middle of the 19th century. On the eastern slopes of the crest, in the territory of the Bruntál and Janovice Estate, flocks of 250 to 350 sheep were herded until 1870, a year when pasture in the forest was prohibited (Hošek 1972). On the western slopes belonging to the Loučná Estate, pasture in the forest was prohibited about ten years later. In 1829 the Švýcárna, a stable for young cattle was built on Malý Děd, but due to small yields the same place was transformed into a tourist hostel and seasonal housing facilities in 1860 (Filip 1988).

In the twenties of the 20th century, pasture was performed again (Mácha 1926: 180). Foundation of Desná-Praděd Pasture Co-operation in 1923 was a last attempt to exploit the alpine tundra of the main range of Hrubý Jeseník for pasture. The rangeland of this co-operation covered the south-east slopes of Praděd and north-east slopes of Petrovy Kameny, and the stable was situated in the area of the present-day Kurzovní Chata chalet. About a hundred of head of cattle was raised here during the summer, but during the World

Table 1 - Floristic composition of plant communities in the summit of Hrubý Jeseník Mts. described by Laus 1910 (L), Bednář 1956 (B), Jeník, Bureš et Burešová 1985 (J), and Pinosová 1987 (P). The importance values of individual species are based on Drude's scale (used by Laus 1910); for communities represented by 5 or more relevés, constancy is given; for rare species in one relevé only, r is used instead of 1; when less than 5 relevés are available, the species are marked by the number of pertinent relevés; rare non specific species are omitted (Drude scale: A - socialis, B - gregarius, C - copiosus, D - sparsus, E - solitarius; constancy: 1 - 0 to 20%, 2 - 21 to 40%, 3 - 41 to 60%, 4 - 61 to 80%, 5 - 81 to 100%).

Community No.	1	2	3	4	5	6	7	8	9	10	11
No. of data set	0 0 0 0 1 2 3 4	0 0 0 5 6 7	0 0 1 1 8 9 0 1	1 1 1 1 2 3 4 5	1 1 1 6 7 8	1 2 2 9 0 1	2 2 2 2 3 4	2 2 5 6	2 2 7 8	2 2 9 0	3 0
Number of relevés	0 0 0 0 1 5 4 4 L B J P	0 2 0 1 5 6 L J P	0 1 2 3 1 1 8 8 L B J P	0 2 3 0 1 5 0 9 L B J P	0 1 3 1 6 2 L B P	0 0 0 6 6 9 B J P	1 1 0 0 4 7 B J P	2 2 0 3 B P	0 2 1 0 L B	0 0 1 1 L L	0 1 L
Adenostyles alliariae	D 5 2 3	. . . 3	. . . 1								
Athyrium distentifolium	A 5 4 4		. . 1 1	. 1 . 2							
Oxalis acetosella	. 5 2 4		. . . 1	. . . 2							
Thesium alpinum	C . . .	C 4 5							D . . .		
Briza media		A 2 3									
Phleum alpinum	C . . .	A 5 4			C . . .				C . . .		
Festuca rubra		A 3 5	. . 1 .	. 1 1 .							
Hypericum maculatum		B 2 5	. . . 1	. 1 . .	. 1 . .						
Crepis conyzifolia		B 5 3	. . 1 .	. . 1 .					C . . .		
Rhinanthus alpinus		C 4 4		. 1 . .	. 1 . .				D . . .		
Viola sudetica		C 5 5	D . 1 1	. 1 1 .	D 2 1 .	. 2 . .					
Geranium sylvaticum	E . . .	C 3 5	. . . 1	. 1 . .							
Ranunculus nemorosus		C 4 4	. . 1 .	D . . .							
Achillea sudetica		C 4 4	. . 1 .								
Dianthus superbus		D 4 5		. 1 . .							
Hypochoeris uniflora		D 3 4	. . 1 .	D 1 1 .	E . . .		. 1 . .			. 1 . .	
Potentilla aurea		B 4 5	D 1 . .	. 2 . .	D 2 . .	1 1 . .	. 1 . .			. 1 . .	
Galium boreale		B 1 1									
Leontodon hispidus	C . . .	C 3 .			. 1 . .						
Euphrasia picta		C 2 2									
Crepis mollis	D . . .	C 4 .		D . . .							
Phyteuma orbiculare		C 1 1									
Scabiosa lucida		D 2 2									
Coeloglossum viride		D 1 .									
Ajuga reptans		. 3 5	. . 1 .								
Poa chaixii	D . . .	. 4 5	. . 1 .	. 1 1 .							
Agrostis capillaris		. 3 4	. . 1 .		. 1 . .						
Cardamine pratensis		. 1 3									
Carex pallescens		. 2 2									

2) Includes also *A. odoratum*

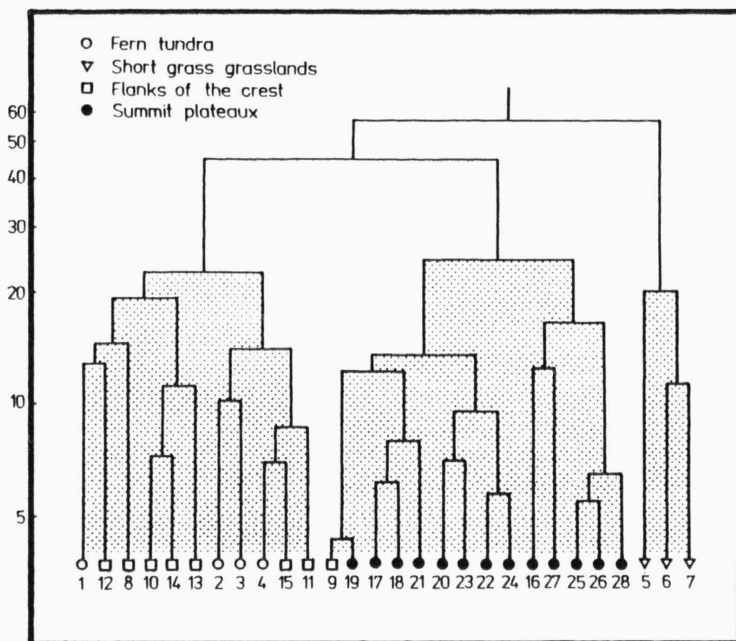


Fig. 1 - Cluster analysis of plant communities of the alpine tundra in the Hrubý Jeseník range (complete linkage, coefficient of similarity after Bray et Curtis 1952); for numbers see the survey of plant communities in Table 1; the dotted clusters represent vegetation types easily identifiable in the elaborated materials (Laus 1910, Bednář 1956, Jeník, Bureš et Burešová 1980 and Piňosová 1987).

War II the numbers reached 350 to 400 head and the rangelands expanded over the entire range (Chloupek 1968). The last season of pasture in this area was in 1943; after the world war pasture of domestic animals on Hrubý Jeseník's summits was never resumed.

In the 20th century, increasing numbers of red deer and chamois became a possible factor affecting the development of vegetation. At the beginning, red deer was raised only in an extensive enclosure (Hošek 1972) but later on in the rutting season, large herds of this influential herbivore kept ascending and grazing the Hrubý Jeseník's summits. An alpine race of the chamois was introduced in the twenties. Starting with a few head released in acclimatization enclosures (Janásek 1983) breeding of the chamois reached about 700 head (Mlčoušek 1987).

Results

In Table 1 an overview of the alpine tundra communities in the southern district of the Hrubý Jeseník is given.

Table 1, Fig. 1 and, partly, Fig. 2 show that in the treatises by Laus (1910), Bednář (1956), JBB (1985) and Piňosová (1987) three or four types of stands based on species

composition can reliably be distinguished: a) stands with dominant *Athyrium distentifolium* - not identifiable in Fig. 1 (No. 1 in Table 1), b) short-grass grasslands (No. 2), c) stands with *Calamagrostis villosa* and *Vaccinium myrtillus* growing on the flanks (Nos. 3 and 4), and d) short grasslands of the summit area with *Nardus stricta*, *Deschampsia flexuosa*, *Festuca airoides* and *Carex rigida* (Nos. 5 to 8). Homologization of vegetation types described by individual authors can be seen in Table 2. A synthesis shown in Table 1 suggests that detailed classification of the four basic units (No. 1, 2, 3-4, 5-9) is based mainly on the dominance of a few species possessing wide phytosociological amplitude. While on the slopes the stands dominated by *Calamagrostis villosa* and *Vaccinium myrtillus* are described in all of the four papers published between 1910 and 1987, on the topmost areas none of the dominant species has been named in all the above-mentioned papers!

A comparison between (a) communities of the topmost tundra and (b) communities of the flanks showed that the hierarchy of species recorded in 1987 did not depend on the hierarchy recorded during the preceding periods between 1910 and 1985, except for one case (Table 3). This conclusion seems to be affected by the fair reaching heterogeneity of the records under comparison.

Similar analysis was performed for all communities described by individual authors. Proportion of significant positive correlation coefficients within individual communities (9.4 %) was higher than that of type I errors expected on a random basis (2.5 %) - see Table 4. Within a community, heterogeneities are not so frequent, especially if the smaller subsample consists of nearly half of relevés - Fig. 3. It means that communities are described by individual authors as homogeneous units but the differences between stands labeled by the same name by different authors (in different periods !) are striking. Nevertheless, the structure of the data in Table 1 is far from random. Correlations between species hierarchy of communities described by JBB (1985) and Piňosová (1987) is significant in three cases (out of six) and those between Laus (1910) and Bednář (1956) are nonsignificant (at $P = 0.05$). Thus, the recent changes in vegetation of Hrubý Jeseník Mts. are not as apparent as those immediately after grazing cessation.

Our next step in the analysis examined sixteen most important species. We have tested a hypothesis that their importance values were the same in the years 1910 to 1987. In 11 species this hypothesis could not be rejected (Table 5); in two species a growing importance was ascertained (*Deschampsia flexuosa*, *Rubus idaeus*), in three taxa a decline was noticeable (*Hieracium* sp. div., *Phleum alpinum*, *Luzula luzuloides*).

Discussion

The above given statistical analysis of floristic and phytosociological data from the summits of the Hrubý Jeseník Mts. suggests that during the past seventy years profound changes took place in the representation of important species of plant communities; moreover, replacement of entire communities could be recorded. Long-term observation in several ranges of Central Europe indicate that, particularly in nutrient poor habitats, the succession is slow, and only little affected by short term climatic changes (Braun-Blanquet 1964, Ellenberg 1988, Malinovskij 1980, Jeník 1961, Osbornová et al. 1990). In order to understand the factors forcing alteration of flora and vegetation of the Hrubý Jeseník summit area, we have to search for factors that changed the habitats in the course of the

Table 2 - List of the alpine plant communities treated in this study (first column), and their relation to the units described by other authors in the Hrubý Jeseník range. Data in the brackets mark the relevant table or page of the works quoted in the headline

Authors Unit	Laus 1910 Facies	Šmarda 1950 Association	Bednář 1956 Sociation	JBB 1980 Association	Piňosová 1987 Community
1 Fern tundra	Athyrium alpestre (p. 117)	Fern tundra (p. 152)	Athyrietum alpestre (p. 114)	Athyrietum alpest- ris (Tab. 1)	unpublished relevés
2 Short-grass community	Ostsudetische (Gesénke) Matte (p. 120)	---	---	Thesio alpini- Nardetum strictae (Tab. 1)	Nardus stricta- Thesium alpinum (Tab. 10)
3 Tall-grass community	Calamagrostis -Deschampsia (p. 119)	Deschampsia flexuosa -Calamagrostis villosa (p. 108)	Deschampsia flexuosa -Calamagrostis villosa (p. 66)	Sileno vulgaris- Calamagrostidetum villosae (Tab. 1)	Molinia caerulea -Nardus stricta (Tab. 4 and unpub- lished relevés)
4 Vaccinium shrub	Vaccinium myrtillus (p. 119)	Calamagrostis villosa -Vaccinium myrtillus (p. 108) Vaccinium myrtillus -Festuca supina (p. 110)	Vaccinium myrtillus -Nardus stricta (p. 71) Vaccinium myrtillus -Calamagrostis villosa (p. 76)	Festuco supinae- Vaccinietum myr- tilli (Tab. 1)	Polytrichum formo- sum-Homogyne alpina (Tab. 9, relevés 1 to 5 and unpubl. relevés)
5 Nardus grassland	Nardus (p. 117)	Nardus stricta -Festuca supina (p. 109)	Nardus stricta -Festuca supina (p. 51) Nardus stricta -Potentilla erecta (p. 56)	---	Carex *rigida- Deschampsia fle- xuosa (Tab. 1) Deschampsia fle- xuosa-Festuca airoides (Tab. 3, relevés 1 to 13, 19, 21 25) Nardus stricta- Potentilla erecta (Tab. 6)

6	Deschampsia flexuosa grassland	---	---	Deschampsia flexuosa -Festuca supina (p. 67)	Cetrario-Festucetum Avenelletosum (Tab. 1)	Deschampsia flexuosa-Festuca airoides (Tab. 3, relevés 14 to 18, 20, 22 to 24)
7	Open-canopy grassland	---	---	Festuca supina -Carex bigelowii (p. 61)	Cetrario-Festucetum typicum and Cetrario-Festucetum Callunetosum (Tab. 1)	Carex *rigida-Calluna vulgaris (Tab. 2)
8	Open-canopy dwarf shrub	---	Calluna vulgaris -Cetraria islandica (p. 108)	Vaccinium myrtillus -vitis-idaea-Cetraria islandica (p. 80) Calluna vulgaris-Cetraria islandica (p. 92)	---	Vaccinium vitis-idaea-Cetraria islandica (Tab. 5)
9	Stands of dwarf shrub on wet scree	Calluna (p. 119)	---	Vaccinium myrtillus -vitis-idaea-Calluna vulgaris (p. 85) Vaccinieto-Empetretum muscosum (p. 89)		
10	Facies with lichens and mosses	Flechten- und Moos- Fazies der Heide (p. 116)	---	---	---	---
11	Facies with Juncus trifidus	Juncus trifidus (p. 118)	Juncus trifidus -Empetrum hermaphroditum (p. 106) Juncus trifidus -Carex rigida (107)	---	---	---

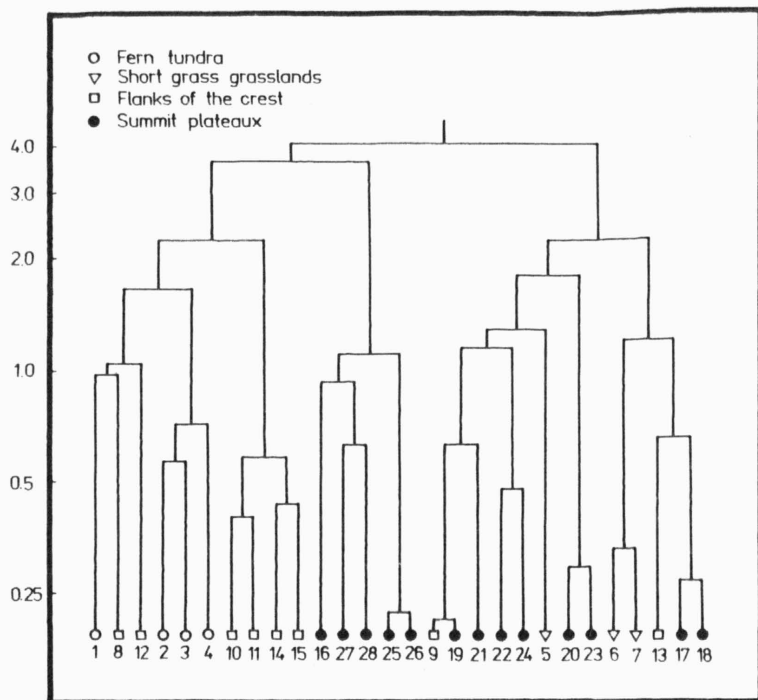


Fig. 2 - Cluster analysis of plant communities of the summit area of the Hrubý Jeseník range (complete linkage, coefficient of similarity: Spearman's rank correlation coefficient); for details see Fig 1.

20th century. This factors undoubtedly refer to direct and indirect human impacts.

At planetary dimension the effects of progressive acidification by acid rains are essential. At the local scale, plantation of *Pinus mugo* krummholz, pasture, activities of tourists, grass cutting and grazing of chamois must be taken into account. Direct evidence of the effects of these factors on vegetation in the Hrubý Jeseník is missing, and we have to rely on indirect data. Our analysis is easier because of the fact that overwhelming majority of changes of vegetation took place in the period between the publication of Laus (1910) and Bednář (1956). Remarkably monotonous stands with dominant *Deschampsia flexuosa* and *Festuca airoides* were first described by Bednář; even the paper by Šmarda (1950) did not describe similar stands. On the contrary, stands of ericoid heath (*Calluna vulgaris*, *Empetrum hermaphroditum* and *Vaccinium vitis-idaea*) retreated, possibly, at the same time to a few small-sized patches (Bednář 1956). Very likely, other qualitative changes of

Table 3 - Dependence of the species hierarchy in the top area and on flanks of the Hrubý Jeseník range evaluated by Spearman's correlation coefficient. Floristic composition of the plant communities was described by Laus 1910 (L), Bednář 1956 (B), Jeník, Bureš et Burešová 1985 (J) and Piňosová 1987 (P); * - $P < 0.05$.

Top area		L	B	J
	B	0.032		
	J	-0.162	0.315	
	P	0.150	0.899*	0.498
Flanks		L	B	J
	B	0.164		
	J	0.199	0.348	
	P	0.334	0.330	0.407

Table 4 - Percentage of the significant Spearman's correlation coefficients based on comparison of plant communities described by individual authors from the Hrubý Jeseník Mts. between 1910 and 1987.

	positive r	negative r
within a community and an author (Fig. 3)	86.3* - 95.3*	0.0
within an author	5.8	15.1*
within a community	9.4*	0.0
others	0.7	5.1*

* - $P < 0.05$, χ^2 -test, H_0 : number of significant coefficients is equal or lower than the number of type I errors expected on a random basis (2.5%).

vegetation did not occur.

For this reason subsequent environmental alteration induced by the air pollution could not affect the ascertained differences in the flora and vegetation. No long-term measurements of pH in precipitations and soils are available; there are no data about deposition and chemical composition of toxic compounds. The data from Rejvíc and Karlova Studánka (Lednický et Kondělka 1979) are of little use for the summit area.

According to Deylová (1966) in Norway spruce age classes of needles on the lateral branches at 1330 to 1350 m altitude on Praděd numbered between six to 14 (modal value was 9). At 950 metres altitude, the modus was 8, and at 1400 m the same value equalled 9. Presently, after about 20 years, needles of many individual trees reach a maximum age of 2 to 3 years, and at the timberline dead trees are very frequent (Klimeš et Klimešová 1987, unpublished). The status of Norway spruce indicated by Deylová corresponded with normal and healthy conditions (Schmid-Vogt 1986) but the present-day condition of this species in the Hrubý Jeseník approached a catastrophic stage. Similar changes in vitality of *Pinus mugo* were recorded as late as in the early eighties (Mikeš 1989).

Only exceptionally the impact of real pollution on alpine plants has been examined (e.g. Trotter 1986). The data published so far suggest a varying tolerance, and decreased

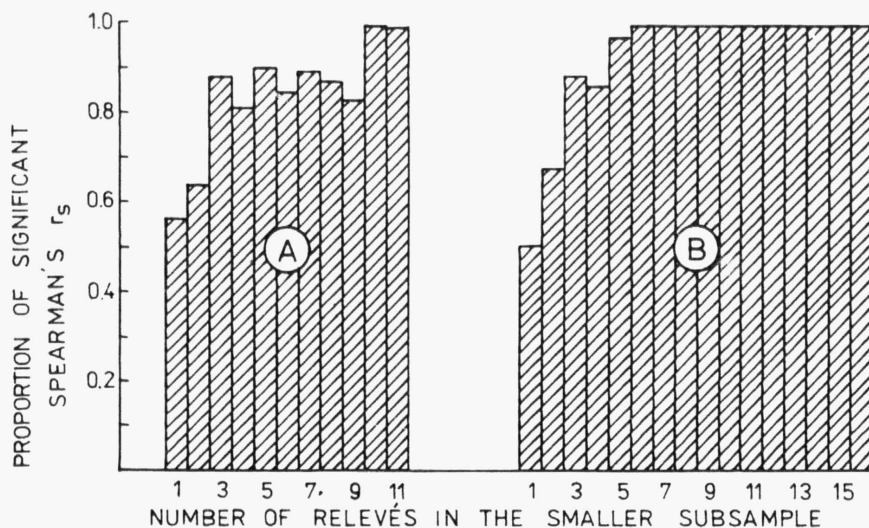


Fig. 3 - The relation between proportion of the significant Spearman's correlation coefficients (r_s) and size inequality of two subsamples. The results are based on two plant communities described by Piňosová (1987): (A) Open-canopy dwarf shrub (No. 8) where seven dominant species were recorded in the individual relevés, and (B) *Nardus grassland* (community No. 5) which represents a homogenous set of data with six dominant species. The phytosociological table was randomly divided into two subsamples and similarity of species hierarchy between them was estimated by the Spearman's r_s . Each value is based on 150 simulations except for the size of 1 where 32 and 23 simulations were performed, respectively.

reproductive capacity of plants affected by large doses of SO_2 (reviewed by Lauenroth et al. 1984, Preston 1984, Lechowicz 1987). Less probably, the air pollutants could result in the decline or disappearance of a larger number of species. In view of relatively better saturation of the sorption complex and good buffer capacity of soils in the Hrubý Jeseník (if compared with that of Giant Mts., see Stejskal 1971) significant changes of the soil chemistry several decades ago were very improbable (but see Veselý 1987).

Plantation of the *Pinus mugo* krummholz took place primarily on the eastern slopes of the southern Hrubý Jeseník's crest. Direct relationships of these plantations to the widely distributed monotonous short grasslands could not be expected. The same refers to local impact of the recreation and tourism.

The impact of chamois on the vegetation in the Hrubý Jeseník has been discussed at several occasions. According to Blahout (1976), Havlas (1964) and Janásek (1973) a rapid increase in the number of head of chamois in the Hrubý Jeseník took place only after 1950, and later again at the end of seventies. The analyses of fodder consumed by chamois (Blahout 1976, Dunant 1977, Hadač 1961, Kožená 1986, Obrtel, Holířová et al. Kožená 1984, Urban 1989) showed that this herbivore preferred both the regressing vascular species, and the species progressively dispersed in the plant communities of the Hrubý Jeseník Mts.

So far available data do not show that during the last 10 to 15 years some vascular species evidently retreated from the upper-most grasslands of the range under the influence

Table 5 - Significance of the changes in the importance values of some plant species in the summit area of the Hrubý Jeseník range, evaluated by Kruskal-Wallis test; NOC - number of communities with increasing, constant or decreasing species importance values, CIV - changes in importance values of individual species in the top area and on flanks (+ increase, - decrease, 0 without change, . not evaluated; the values in brackets indicate less pronounced trend; note that NOC and CIV values and signs are not based on testing).

		NOC			CIV	
		increase	constant	decrease	top area	flanks
<i>Deschampsia cespitosa</i>	*	7	2	0	+	+
<i>Calamagrostis villosa</i>	n.s.	5	3	1	(+)	0
<i>Nardus stricta</i>	n.s.	2	4	1	(-)	(-)
<i>Polygonum bistorta</i>	n.s.	3	5	0	(+)	(+)
<i>Rumex alpestris</i>	n.s.	0	4	0	.	(+)
<i>Rubus idaeus</i>	*	2	1	0	.	+
<i>Polytrichum</i> sp. div.	n.s.	1	2	1	0	0
<i>Vaccinium vitis idaea</i>	n.s.	0	3	1	0	(-)
<i>Hieracium</i> sp. div.	*	0	2	3	-	-
<i>Calamagrostis arundinacea</i>	n.s.	0	1	2	0	0
<i>Cetraria islandica</i>	n.s.	0	4	1	.	0
<i>Vaccinium myrtillus</i>	n.s.	2	5	1	(-)	(-)
<i>Deschampsia cespitosa</i>	n.s.	1	2	1	0	0
<i>Phleum alpinum</i>	*	0	2	1	.	(-)
<i>Anthoxanthum alpinum</i> ¹⁾	n.s.	3	1	4	0	(+)
<i>Luzula luzuloides</i>	*	0	3	1	0	0

1) Includes also *A. odoratum*

* - $P < 0.05$, n.s. - non significant

of chamois. However the rocky and dissected relief and flora of the Velká and Malá Kotlina cirques represents an attractive biotope for this allochthonous ungulate, and may result in decline of rare plant populations primarily not adapted to grazing and browsing (see Fig. 4). Local changes of flora and vegetation caused by the trampling, manuring, grazing and browsing by chamois are unavoidable.

Grass cutting and its impact on vegetation of the Hrubý Jeseník is little known (Hošek 1972, 1973); last evidence of this human activity is from the 19th century, but local hay making could take place even later.

Grazing of sheep and cattle is recorded by documents from the period between 17th century and the World War II. After this period domesticated animals did not graze or browse the alpine tundra in Hrubý Jeseník. The informations on pasture, however, are very incomplete and reliable reports are missing even from the verge of the centuries. In spite of all of these difficulties, pasture, connected, possibly, with grass cutting and termination of these activities, appear as the dominant factors that might have produced the changes of vegetation observable in the current century.

Impact of interrupted pasture on vegetation has been studied by numerous scholars in various regions of Europe and overseas. Exchange of species composition and quantitative representation of plants have been proved in a number of experiments and observations. Contradictory trends in the alteration of species diversity are obviously in relation to the



Fig. 4 - *Plantago atrata* subsp. *sudetica*, a local endemic taxon of rock slopes in the Velká Kotlina cirque, is heavily damaged by grazing chamois.

intensity of pasture, its frequency, given herbivorous species, structure of vegetation, and relevant environmental factors (e.g., Bakker 1987, Cernusca et Nachuzrišvili 1983, Gibson et Kirkpatrick 1989, Hegg 1984, Milchunas, Sala et Lauenroth 1988).

The pasture affects vegetation in several ways: Firstly, it removes the biomass and causes a profound disturbance in the aboveground organs. Other ecological effects derive from the trampling of the sod by hoofs, restriction of generative reproduction in plants, selective consumption of certain organs or species, and assistance in dispersal of seeds - in the exo- and endozoochory. No quantitative data are available with regard to the efficiency of these factors in the Hrubý Jeseník.

With certain restrictions, however, we can use the data ascertained in other mountains (e. g., Pignatti-Wikus 1987). Long-term pasture maintains the canopy of the herbaceous stands open, in spite of that the ready establishment of tiny herbs is prevented due to grazing, trampling and, eventually, competition of perennial graminoids that can vegetatively regenerate and tolerate trampling (*Nardus stricta*, *Deschampsia cespitosa*). This effect is valid only under the impact of an intensive pasture (Grubb 1987) and brings

about decreasing diversity of the plant community and induces over-representation of a few species (e.g. Bowns et Bagley 1986, Jeník 1961, Svoboda 1939). In the case of moderate grazing, changes in vegetation resemble those after interruption of pasture: new species can establish in open-canopy grassland and species diversity of the plant community is higher; it proceeds in agreement with theory of medium disturbance (Connell 1978). In any case, in areas of relatively favourable climatic factors and in fertile soils, after about 4 to 10 years following the termination of pasture, relatively stabilized and close-canopy single-dominant grassland is being developed, and eventually further immigration and ecesis of new species is hardly possible. *Deschampsia flexuosa* and the *Calamagrostis* species belong to competitive grasses easily monopolizing the available space (Jeník 1983, Šmarda et al. 1963). Invasive species supported by the pasture, such as *Vaccinium myrtillus* and *Nardus stricta* (Jeník 1983) successively decline after the termination of this factor and suffer by higher competition ability of the taller graminoid species.

Among the plant genera markedly declining in the alpine tundra the genus *Hieracium* represented, e. g. by the *H. alpinum* aggregate deserves attention. According to literature (Slobodjan 1987, Žiljačev 1984) *Hieracium alpinum* is a favourite pasture of large herbivorous mammals. Prominent decline was observed also in *Phleum alpinum*, a grass similarly palatable for the herbivores (e. g., Dunant 1977, Maloch 1931). In the case of the Hrubý Jeseník, however, conspicuous changes in vegetation took place immediately after the termination of grazing and in the period of a low density of the chamois. The direct effect of herbivory on changes of the density of the above-mentioned species can thus be omitted.

A significant phenomenon in the alpine tundra of the Hrubý Jeseník is the increasing representation of *Rubus idaeus*, mainly on scree in concave relief of the flanks. A marked expansion of this species can be traced only in the eighties, while no increase has been noticed in earlier papers (similar trend is reported from the Krkonoše Mts. - F. Krahulec in litt.). Two hypotheses can be suggested to explain the data: (1) *Rubus idaeus* belongs amongst the species whose expansion is related to the global antropogenic changes, possibly to the increasing deposition of nitrogen-rich compounds, and, (2) successional changes in vegetation of flanks (viz. replacement of short grasses by tall high-productive species) results in increasing accumulation of litter and, latter, in a mild microclimate enabling establishment of *Rubus* seedlings according to the facilitation model of succession by Connell et Slatyer (1977).

It should be noted that these results could be partly modified if other transformation of abundance/dominance values was used. Replacement of some of the above-mentioned species could be expected in this case. Nevertheless, the method is enough robust to eliminate reasonable bias in the data.

Thus, any systematic error in the Laus' data cannot cause complete rejection of any change in the role of important species in the alpine area of the Hrubý Jeseník Mts.

On the background of this analysis we can outline the dynamics of vegetation of Hrubý Jeseník range in the course of the 20th century. To the end of the 19th century, the importance of pasture declined, and residents of the mountain chalets successively turned to various services for tourism (Filip 1988). The variety of vegetation types was relatively large, reflecting not only the climatic and edaphic diversity of the habitats, but also the va-

riable intensity of pasture (Schindler 1926) which concentrated mainly in the surroundings of Petrovy Kameny (Hošek 1988 in litt.). On the verge of the centuries or a few decades earlier, less dramatic changes of vegetation could have occurred, particularly in areas where the pasture was temporarily interrupted; however, Laus (1910) and Schindler (1926) recorded a status with man-induced stands dominated by *Nardus stricta*, containing a few species of open-canopy structure and, necessarily, liable to vanish after the termination of pasture.

With regard to the development until 1923, a year when the Desná-Praděd Pasture Co-operation was founded, neither direct nor indirect evidence is available, so far. In the period between 1923 and 1943, pasture in the Hrubý Jeseník did not continuously affected the entire summit area between Petrovy Kameny and Pec. We can however assume that during the period of maximum concentration of cattle this area was grazed over the whole territory above the timberline (Chloupek 1968).

Ten to fifteen years after the termination of pasture certain vegetation types vanished, and in a number of plant communities the hierarchy of dominance has markedly been changed, too. A number of species was eliminated, mainly by increasing competition of rhizomatous grasses, and also by occasional inability to regenerate generatively within the closed-canopy grassland (see Grubb 1977).

In the last 30 years changes of the vegetation cover on the Hrubý Jeseník's alpine tundra were only small; possibly, none of the existing plant communities vanished and no new vegetation unit have arisen. The same is valid for the species of high dominance, with the exception of *Rubus idaeus*, the only vascular species that significantly expands. The fairly crude procedure of our analysis, however, does not enable to detect changes in the representation of accessory and rare plants.

Conclusions

Vegetation above the alpine tree line in the Hrubý Jeseník range is rather monotonous and species poor. Two main dominants prevail: *Deschampsia flexuosa* on the flat summit plateaux, and *Calamagrostis villosa* on steep flanks. Species-rich plant communities can be found in the corries only. It follows from literature that in the period between the end of the last century and the World War II other dominant species were present than today. On the basis of comparison of vegetation analyses carried out at the beginning of the 20th century (Laus 1910), in the period 1954 to 1955 (Bednář 1956), 1973 to 1975 (JBB 1980) and 1985 to 1986 (Piňosová 1987) we can conclude that:

1) Changes in plant communities can be evaluated by the ranks of important species based their cover degree. The homogeneity of plant communities represented by a set of relevés, is high but the similarity of the community labeled by the same name by different authors at different time is low.

2) Two species, *Deschampsia flexuosa* and *Rubus idaeus* increased significantly in their cover values during the last 80 years; on the contrary, *Phleum alpinum*, *Luzula luzuloides* and several *Hieracium* species declined. Increased cover value in other species, e.g. *Calamagrostis villosa*, *Polygonum bistorta* and *Rumex alpestris* and decline of *Nardus stricta*, *Vaccinium vitis-idaea* and *Vaccinium myrtillus*, have not been confirmed by our testing, nevertheless they seem to be highly probable.

3) Cessation of the grazing of the domestic cattle is the most probable cause of the above described simplification and equalization of vegetation. These changes were apparent in the years immediately following the interruption of grazing; after eight decades, present-day successional changes are negligible.

Souhrn

Vegetace nad lesní hranicí v Hrubém Jeseníku je poměrně jednotvárná a druhově chudá. Ve vrcholových polohách představuje výraznou dominantu *Deschampsia flexuosa*, na svazích *Calamagrostis villosa*. Pestřejší rostlinná společenstva se vyskytují pouze v karoidech. Z literárních údajů však plyne, že se v době od konce minulého století do 2. světové války v alpském stupni více uplatňovaly i jiné dominantní druhy a druhová diverzita společenstev byla větší. Ze srovnání prací popisujících vegetaci holí Jeseníků na začátku našeho století (Laus 1910), v letech 1954-1955 (Bednář 1956), 1973-1975 (Jeník, Bureš a Burešová 1980) a 1985-1986 (Piňosová 1987), plyne:

1) Rostlinná společenstva popsáná z hřebene Hrubého Jeseníku lze dobře rozlišit pomocí pořadí druhů s největší pokryvností. Takto hodnocená společenstva popsáná jednotlivými autory jsou velmi homogenními jednotkami, avšak podobnost snímkových souborů téhož společenstva zaznamenaného různými autory je velmi nízká. Celkem sedm společenstev bylo zaznamenáno třemi nebo čtyřmi autory, avšak žádné z nich nelze charakterizovat stálým pořadím druhů s největší pokryvností.

2) Dva druhy, *Deschampsia flexuosa* a *Rubus idaeus*, se prokazatelně stále více uplatňují na hřebenech Jeseníků; *Phleum alpinum*, *Luzula luzuloides* a *Hieracium* sp. div. naopak ustupují. Významné, ale neprůkazné je dále šíření druhů *Calamagrostis villosa*, *Polygonum bistorta* a *Rumex alpestris*, zatímco *Nardus stricta*, *Vaccinium vitis-idaea* a *Vaccinium myrtillus* pravděpodobně ustupují.

3) Nejpravděpodobnější příčinou popsáných změn je sukcese po skončení pastvy; v současné době jsou probíhající změny jen malé ve srovnání s obdobím těsně po skončení pastvy na konci 40. let.

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