

Vegetation analysis along the elevation gradient in the Nízké Tatry Mountains (Central Slovakia)

Analýza vegetace podél gradientu nadmořské výšky v Nízkých Tatrách

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Vegetation along the elevation gradient (Zadná voda valley, the Nízké Tatry Mts., Central Slovakia) was studied using methods of direct and indirect gradient analysis and numerical classification. The results of these numerical techniques were compared mutually as well as with the Zürich-Montpellier classification of the analysed vegetation. The efficiency of the particular ordination methods was then evaluated by comparison of ranking relevés on the first ordination axis with ranking on the elevation gradient.

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Gradient analysis expresses relations between vegetation and environmental factors, its results reflect distribution of individual populations or whole communities within the frame of vegetational continuum on environmental gradients (see WHITTAKER 1975, KRAHULEC et REJMÁNEK 1980 and others). The results of gradient analysis can also call our attention to vegetational discontinuities and it is useful to compare the results of this method with those of numerical and Zürich-Montpellier classifications, respectively.

Vegetation along the elevation gradient can be processed by gradient analysis owing to relatively clear changes on an unambiguously defined gradient (cf. WHITTAKER et NIERING 1965, BEALS 1969, LINDSAY et BRATTON 1979, FOSTER et REINERS 1983 and others). Elevation gradient is a complex gradient comprising particular gradients of many environmental factors changing together in space. Using direct gradient analysis seems to be more convenient in the case of a distinct and evaluated gradient, but indirect gradient analysis can add interesting information especially by comparison of the results with those of other methods. The principal aim of ordination methods used in indirect gradient analysis is to find the direction of community variation (coenocline). In our example, the coenocline obviously corresponds to the elevation gradient. Hence, this clear example may be used for testing the efficiency of different ordination methods. The ranking of relevés by ordination methods should correspond to their position on the elevation gradient.

DESCRIPTION OF THE SITE AND METHODS USED

For analysis, we chose a relatively intact natural vegetation site in Dolina Zadné vody, a valley in the central part of the Nízke Tatry Mts., SW from the touristic base of Jasná (see Fig. 1). The valley is about 4 km in length and has a NE–SW orientation. It begins at Sedlo Polany at 1837 m a.s.l. and ends near Vrbocké pleso, lake at 1100 m a.s.l. Bedrock is formed by middle-grain granite of the Ďumbier massif. Mean annual temperature and precipitation are 0.8° C and 1328 mm respectively, on the crest of the Nízke Tatry Mts. (according to the meteorological station at Chopok).

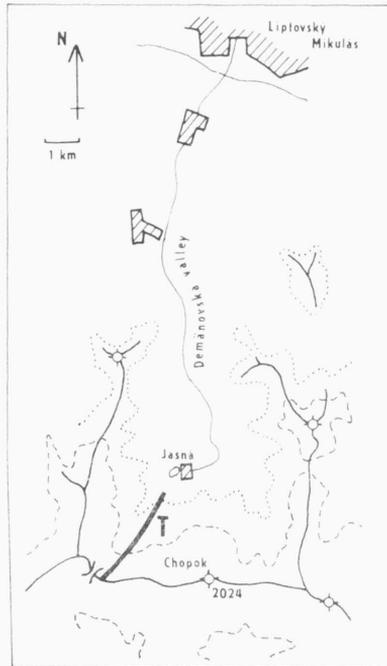


Fig. 1. — Geographical location of the transect in the Nízke Tatry Mountains (Central Slovakia); dotted line corresponds with the isohypse of 1250 m a.s.l., dashed line with the isohypse of 1500 m a.s.l.; T — denotes transect.

Phytosociological relevés were used as the basic data for another evaluation and they were arranged in the sequence along the elevation gradient on the line transect through the slope of the valley. The area of the relevés was 100 m². The relevés were recorded at fixed intervals of 50 m of elevation up a mountain slope. Where the changes of vegetation were abrupt, the intervals were only 25 m elevation (stands No. 5, 6, and 7). Elevation was measured by a pocket elevation-meter Paulinn and compared with a topographical map. Fourteen relevés were recorded using the 7-degree Braun-Blanquet scale. Cover values of phytosociological relevés were converted from the Braun-Blanquet scale to percentage values by Tüxen-Ellenberg transformation (see VAN DER MAAREL 1979) for purposes of direct gradient analysis and for computing the species diversity using Shannon formula:

$$H' = - \sum_i \frac{N_i}{N} \log_2 \frac{N_i}{N}$$

where the N_i is the importance value of the i -th species and $N = \sum_i N_i$.

The following methods of numerical ordination were used:

1. PCA (principal component analysis) based on correlation matrix computed using adapted program PCAR (ORLÓCI 1978). Raw data deck was used.
2. RA (reciprocal averaging, see HILL 1973) computed using adapted program RQT (ORLÓCI 1978). As the first axis was of particular interest, only the basic RA was used. (Otherwise the DCA may be more efficient.) Raw data deck was used.
3. Polar ordination (BRAY et CURTIS 1957) in the modification of ORLÓCI (1974). Standardized Euclidean distance (chord distance, see ORLÓCI 1974) was used as a measure of dissimilarity. There are two distinct parts in polar ordination procedure. The first part provides for determination of the axis and the second one the ranking of relevés on the axis. The first part is done by choosing two relevés as the end-points. It may be done automatically (we adopted the method described by COTTAM, GOFF et WHITTAKER 1973) or by subjective decision, preceding the numerical treatment (usually based on some a priori information; we used the relevés 1 and 14 as end-points).

We have used the Spearman's rank correlation coefficient (SOKAL et ROHLF 1969, p. 538) for the evaluation of correspondence between ranking of relevés on the 1st ordination axis and on the elevation gradient. The rank is of particular interest here. It is not reasonable to suppose that the linear relationship between elevation and environmental factors (temperature, humidity) directly influences the vegetation.

For comparison, the numerical classification of stands was performed with our material, using both non-standardized Euclidean distance and standardized Euclidean distance (chord distance). The Ward's method (MINDISP, see e.g. WISHART 1978), was used as a clustering algorithm.

One of the most important decisions in both numerical classification and ordination is the choice of transformation of original Braun-Blanquet scale to numerical values. We have used the following transformations:

1. Presence-absence transformation: 1 for presence, 0 for absence.
2. Ordinal transformation: the degrees r to 5 are transformed into numbers 1 to 7 respectively.
3. Transformation to cover values (Tüxen — Ellenberg transformation, see e.g. VAN DER MAAREL 1979).

The importance of dominants increases from transformation no. 1 to 3. The treatment using the transformation 1 is purely floristic, whereas that using the transformation 3 is based mainly on dominants. Each of the above mentioned methods has been used with each of these three transformations.

Cluster analysis of species was performed using correlation coefficient as a similarity measure and average linkage as a clustering method. Original data were converted to cover values. Accessory species (listed under Table 1) were not classified. Cluster analysis was computed using our own programs.

RESULTS AND DISCUSSION

Phytosociological relevés with some other characteristics of the stand (elevation, mean height of the vegetation, number of species in relevés, species diversity) are presented in Table 1.

Fig. 2 summarizes the results of the direct gradient analysis. Changes of the stand height (Fig. 2a) and changes of the cover of individual layers along elevation gradient (Fig. 2b—e) are so clear that they do not need any comments. Fig. 2f shows the changes of occurrence of the individual species along the gradient. Interestingly, distributions of *Vaccinium myrtillus* and *Calamagrostis villosa* have antagonistic courses. There are also two pairs of vicariant species in our transect: *Gentiana asclepiadea* and *G. punctata*, *Soldanella hungarica* and *S. carpatica*. At the point of intersection of *Picea abies* with *Pinus mugo* curves the alpine timberline was determined. It seems to be on our transect at 1440 a.s.l. and it is nearly equal to the natural upper forest limit stated by SILLINGER (1933) at 1450 m a.s.l., on the average. The alpine timberline was also determined in nature, according to the definition given by JENÍK et LOKVENC (1962), with the same figure. The upper limit of *Pinus mugo* communities was determined at 1680 m a.s.l.

Tab. 1. — Phytosociological relevés (nomenclature after NEUHÄUSLOVÁ et KOLBEK 1982)

Relevé No.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.
Elevation (m a.s.l.)	1200	1250	1307	1350	1400	1425	1450	1500	1550	1600	1650	1700	1750	1830
Stand height (m)	21	24	16	11	17	15	6.5	6.5	2.5	2	1.2	0.6	0.3	0.1
Species diversity	1.30	2.07	2.02	2.16	2.27	2.35	2.95	1.55	0.96	2.37	2.32	2.70	2.84	2.65
Number of species	12	17	14	15	14	21	23	15	5	20	20	24	21	17
Cover (%) E ₃	75	55	40	38	35	45	20	5
E ₂	2	1	.	.	.	1	60	90	95	70	75	25	2	.
E ₁	40	50	45	60	45	45	80	80	50	85	85	95	95	70
E ₀	40	50	35	45	80	50	80	80	80	40	40	70	50	.
<i>Picea abies</i>	4-5	4	3	3	3	3	2	.	.	.	2	.	.	.
<i>Sorbus aucuparia</i>	r	1	.	r	+	1-2	1-2	1-2
<i>Pinus mugo</i>	+	4	5	5	4	4	2	.	.
<i>Salix silesiaca</i>	2
<i>Juniperus communis</i>	1-2	1	.
<i>Vaccinium myrtillus</i>	1	2	3	1	3	3	3	3	3	+	3	4	2	+
<i>Oxalis acetosella</i>	2	2	+	1	1	.	1	.	.	+
<i>Homogyne alpina</i>	1	1	1	2	1	1	2	1	+	+	1	+	+	1
<i>Soldanella hungarica</i>	+	1	1	1	1
<i>Avenella flexuosa</i> (L.) DREJ.	1	+	2	1	+	1	1	+	+	1	+	.	.	.
<i>Calamagrostis villosa</i>	+	+	+	3-4	2	.	2	1	.	3	1	1	2	.
<i>Gentiana asclepiadea</i>	+	r	+	+	+	+	+	+
<i>Dryopteris dilatata</i>	+	+	+	+	+	+	.	+	.	+
<i>Phegopteris dryopteris</i> (L.) FÉE	+	1	+	+	.	+	+
<i>Prenanthes purpurea</i>	.	r	.	.	.	+
<i>Polygonatum verticillatum</i>	.	+	.	.	.	+	+
<i>Sorbus aucuparia</i> juv.	.	+	+	r
<i>Luzula pilosa</i>	.	r	r
<i>Athyrium distentifolium</i>	.	+	r	+	+	+	2	.	.	2	+	.	.	.
<i>Luzula sylvatica</i>	.	.	+	r	1	+
<i>Rumex arifolius</i> ALL.	.	.	r	+	.	.	1	.	.	+	+	.	.	.
<i>Stellaria nemorum</i>	.	.	.	r	.	.	+
<i>Veratrum lobelianum</i>	r	+	+	+	.	1	+	r	r	.
<i>Ligusticum mutellina</i>	r	+	+	.	.	r	+	+	+	+
<i>Soldanella carpatica</i>	2	1	.	.	.	+	+	+	+
<i>Ranunculus montanus</i>	r	+	+	.

<i>Huperzia selago</i>	r	r	+	.	.	r	r	.	+
<i>Adenostyles alliariae</i>	r	.	.	.	r
<i>Anthoxanthum alpinum</i>	r	.	.	+
<i>Hypericum maculatum</i>	r	.	.	+
<i>Rubus idaeus</i>	r	.	.	+
<i>Geum montanum</i>	r	.	.	+	.	+	+	.
<i>Vaccinium vitis-idaea</i>	+	+	.	+	+ 1	1	+
<i>Pulsatilla alba</i>	+	r	.
<i>Gentiana punctata</i>	+	.	1	+	+	+	.
<i>Solidago virgaurea</i> ssp. <i>minuta</i>	r	.	.	r	.
<i>Luzula luzuloides</i>	+	.	.	1	.
<i>Orechloa disticha</i>	2	2	3	1
<i>Festuca supina</i> SCHUR	+	1	1	1
<i>Campanula alpina</i>	+	1	.	1
<i>Juncus trifidus</i>	1	1	2	+
<i>Luzula alpino-pilosa</i>	+	+	.	.
<i>Hieracium alpinum</i>	r	+	+	.
<i>Carex sempervirens</i>	2	1	2-3
<i>Trisetum fuscum</i>	+	+	.
<i>Potentilla aurea</i>	+	r
<i>Salix herbacea</i>	2
<i>Primula minima</i>	1

In one relevé: *Calamagrostis arundinacea* r (relevé no. 2), *Chrysanthemum alpinum* + (14), *Hypochaeris uniflora* + (12), *Lonicera nigra* r (1), *Iacopodium annotinum* r (8), *Nardus stricta* + (6), *Poa alpina* + (14), *Sempervivum montanum* r (12), *Senecio abrotanifolius* + (14), *Vaccinium gaultherioides* r (8), *Viola biflora* + (7)

The curves characterizing *Picea abies*, *Pinus mugo* and the group of alpine grasses (*Oreochloa disticha*, *Carex sempervirens*, especially) delimitate three types of mountain vegetation: spruce forest, subalpine shrubby communities, and alpine meadows.

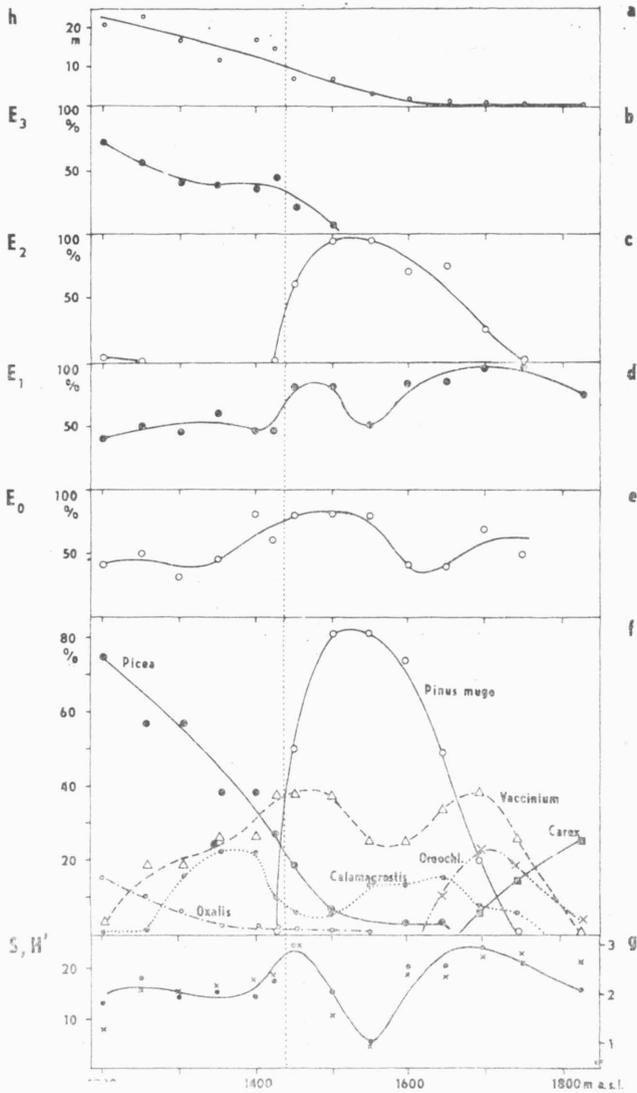


Fig. 2. — Results of the direct gradient analysis of vegetation on the transect: a) stand height; b) cover of the tree layer — E_3 ; c) cover of the shrub layer — E_2 ; d) cover of the herb layer — E_1 ; e) cover of the moss layer — E_0 ; f) changes of the cover values of the main participant species on the transect: *Picea abies* (full circles), *Pinus mugo* (open circles), *Vaccinium myrtillus* (triangles), *Calamagrostis villosa* (full small points), *Oxalis acetosella* (open small circles), *Oreochloa disticha* (crosses) and *Carex sempervirens* (full squares); g) number of species per one relevé S (crosses), species diversity H (full circles and curve). Vertical dotted line marks the alpine timberline.

Tab. 2. — Correspondence between the position of relevés on the elevation gradient and its position on the first ordination axis expressed by the absolute value of Spearman's rank correlation coefficient.

Columns correspond to the particular methods (PO — polar ordination with automatically chosen end-points; PO-Fr — polar ordination with freely chosen end-point relevés 1 and 14; RA — reciprocal averaging; PCA — principal component analysis), rows correspond to the particular transformation of the primary data (PA — presence-absence, Or — ordinal, Co — cover values).

	PO	PO-Fr	RA	PCA
PA	.982	.965	.965	.943
Or	.385	.974	.982	.912
Co	.015	.943	.987	.842

In the contact zones of these basic communities, the highest species richness was found. On the contrary, the lowest number of species was in places with culmination of edicator dominance (*Picea abies*, *Pinus mugo*) — Fig. 2g. Occurrence of maximal species richness on the contacts of different types of vegetation and its minimal at places with a strong dominant confirms the theoretical assumptions of WHITTAKER (1975).

The results of comparison of ranking relevés on the first ordination axis with their position on the elevation gradient are in Table 2. The test of numerical methods based on the analysis of vegetation along the distinct environmental gradient seems to be superior to the analysis of simulated gradients; particular populations differ considerably in the type of their response to environmental gradient in a way that is hardly in keeping with any artificial simulation. In our example, all the monotonous, unimodal and bimodal types of response appeared (see Fig. 2f). In most cases, the first ordination axis corresponds clearly to the elevation gradient. The only exceptions are results of polar ordination. This method failed twice to find the coenocline; relevés chosen as the end-points do not obviously correspond to the extremes of coenocline. However, in case the coenocline is correctly determined, the ordination of relevés is not less successful than by other methods. There are no striking differences between the results based on different transformations (with exception of PO, where the coenocline was recognized using only presence-absence data). This small sensitivity of results to the transformation that was used is probably conditioned in our case by very distinct and well defined changes of vegetation along the elevation gradient. It may be expressed in terms of dominants as well as in terms of floristic composition. The RA seems to be superior to the PCA regardless of the transformation used. However, when considering also a second axis, both the PCA and RA suffer from the "horseshoe" effect — the quadratic dependence of the second axis on the first one (Fig. 3). Use of the DCA (HILL et GAUCH 1980) would probably avoid this drawback. Hence, the interpretation of the second axis is difficult.

Similarly, the methods of cluster analysis (Figs. 4, 5) distinguish the three main community types, i.e. spruce forest, dwarf pine, and alpine meadows, on the bases of all three transformations, regardless of the use of standardization. However, on the floristic basis and on the basis of ordinal trans-

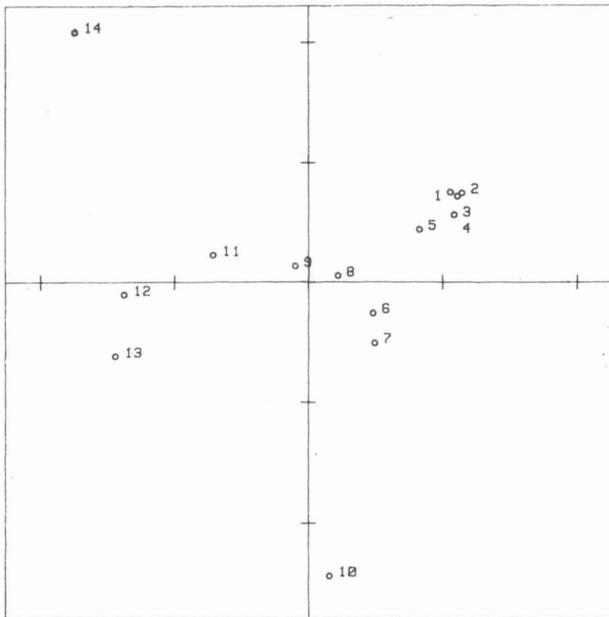
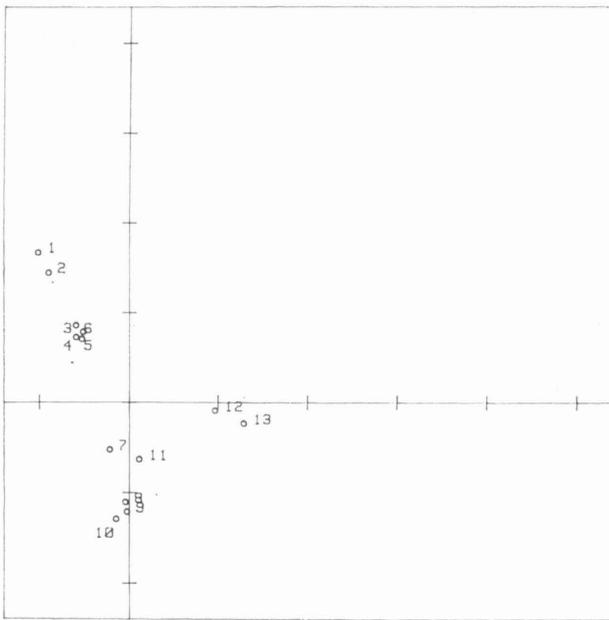


Fig. 3. — The scatter diagram of results of RA ordination (first and second axes). Transformations to cover values (a-above) and to presence-absence data (b-below) are used.

formation, the relevés performing “upper extremes” of the groups are sometimes classified within neighbouring groups. The cluster analysis of species also yielded three distinct groups of species corresponding to their occurrence in the three vegetational types. Inside the three distinct groups of species, corresponding to their coenotic participation, the following are of interest:

(1) a smaller cluster of species occurring in the wet sites in subalpine and low alpine zones: *Gentiana punctata*, *Veratrum lobelianum*, *Salix silesiaca*, and (2) a cluster of typical spruce forest species: *Oxalis acetosella*, *Phego-*

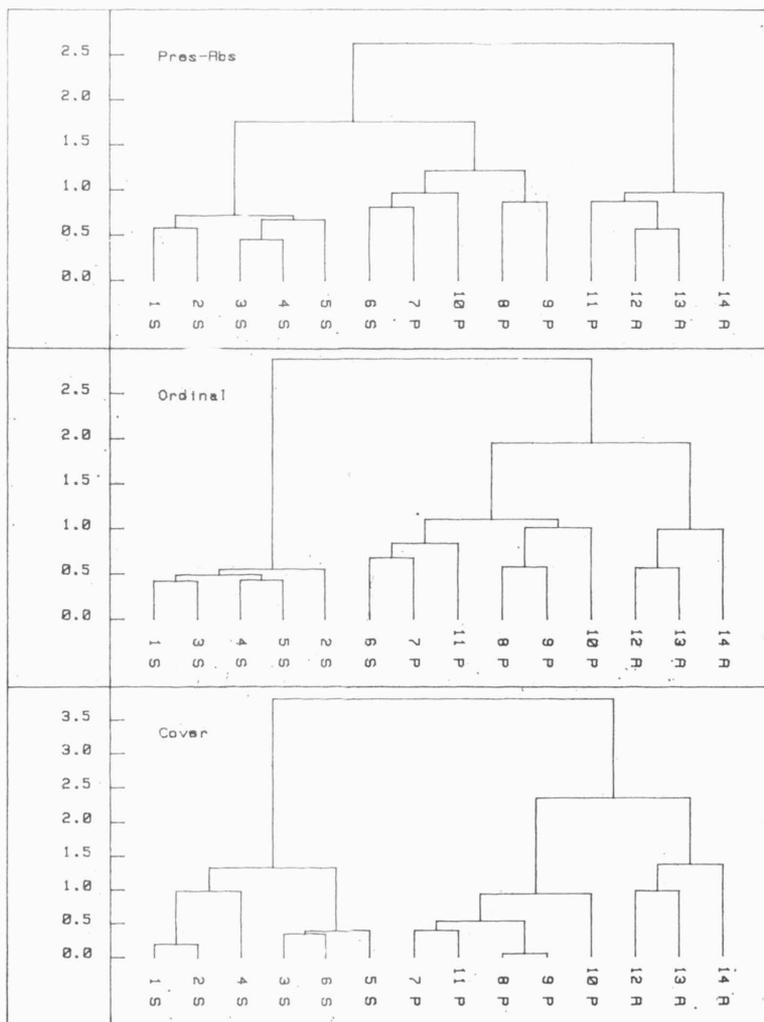


Fig. 4. — Cluster analysis of relevés; following options are used: dissimilarity measure — standardized Euclidean distance, clustering — Ward's method. The transformations of original scale are seen left above.

pteris dryopteris, *Dryopteris dilatata*, *Soldanella hungarica*, *Gentiana asclepiadeae* (Fig. 6). The Zürich-Montpellier classification of the communities studied is in some cases difficult on the level of associations, but on the level of alliances we can clearly distinguish *Vaccinio-Piceion* BR.-BL. in BR.-BL., SISSING et VLEIGER 1939, *Pinion mugii* PAWŁOWSKI 1928 and *Juncion trifidi* PAWŁOWSKI 1928. The spruce forests analysed seem to be a mozaic of as. *Calamagrostio villosae-Piceetum* (TX. 1937) HARTMANN 1953 and as. *Vaccinio myrtilli-Piceetum* (SZAF., PAWL. et KULCZ. 1923) ŚOLTÉS 1976. There is hardly any doubt that subalpine shrubby communities belong

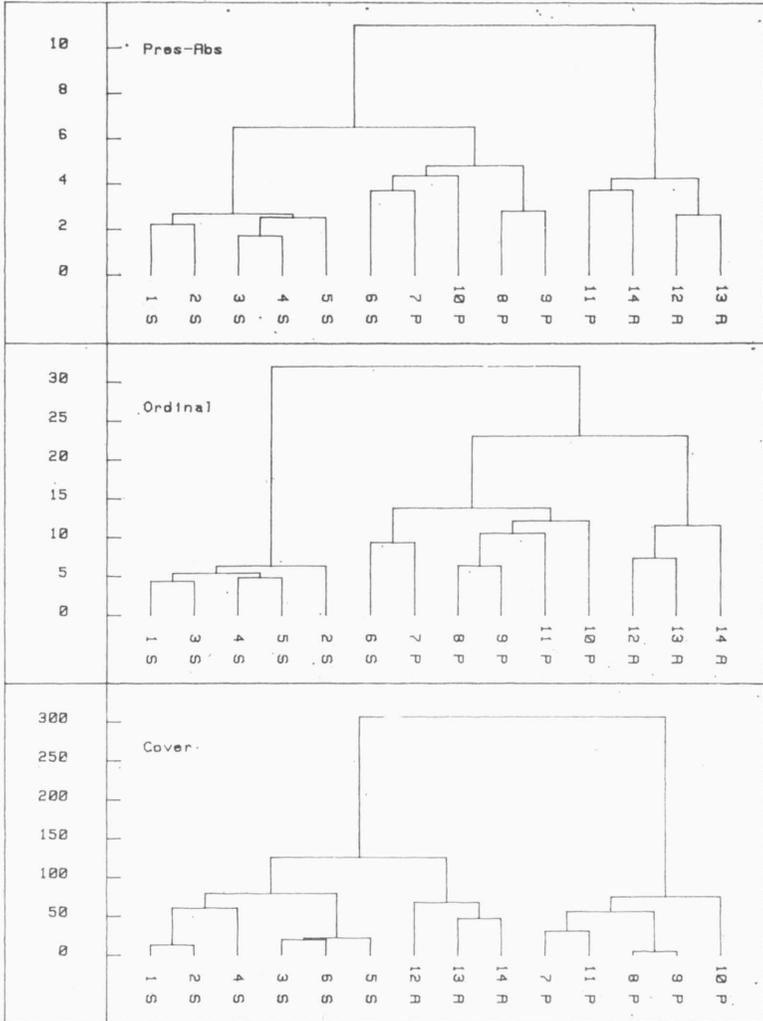


Fig. 5. — Cluster analysis of relevés; following options are used: dissimilarity measure — non-standardized Euclidean distance, clustering — Ward's method. The transformations of original scale are shown left above.

to as. *Myrtillo-Pinetum mughi* (PAWL., SOKOL. et WALLISCH 1928) HADAČ 1956. Alpine meadow stands show tendencies to three associations sensu SILLINGER (1933): *Juncus trifidus-Oreochloa disticha*, *Trifidi-Festucetum supinae*, and *Agrostis rupestris-Carex sempervirens*.

The set of relevés under study is characterized by high beta-diversity (heterogeneity of relevé set) and contains three distinct groups characterized by different dominants. The comparison of efficiency of particular numerical methods is strikingly influenced by those properties of our data set. We have not found any distinct differences either between the particular methods or between the methods based on different transformations of the primary data (the only exception is PO with automatically chosen endpoints). The results of ordinations (e.g. RA, see Fig. 3a and 3b) with data

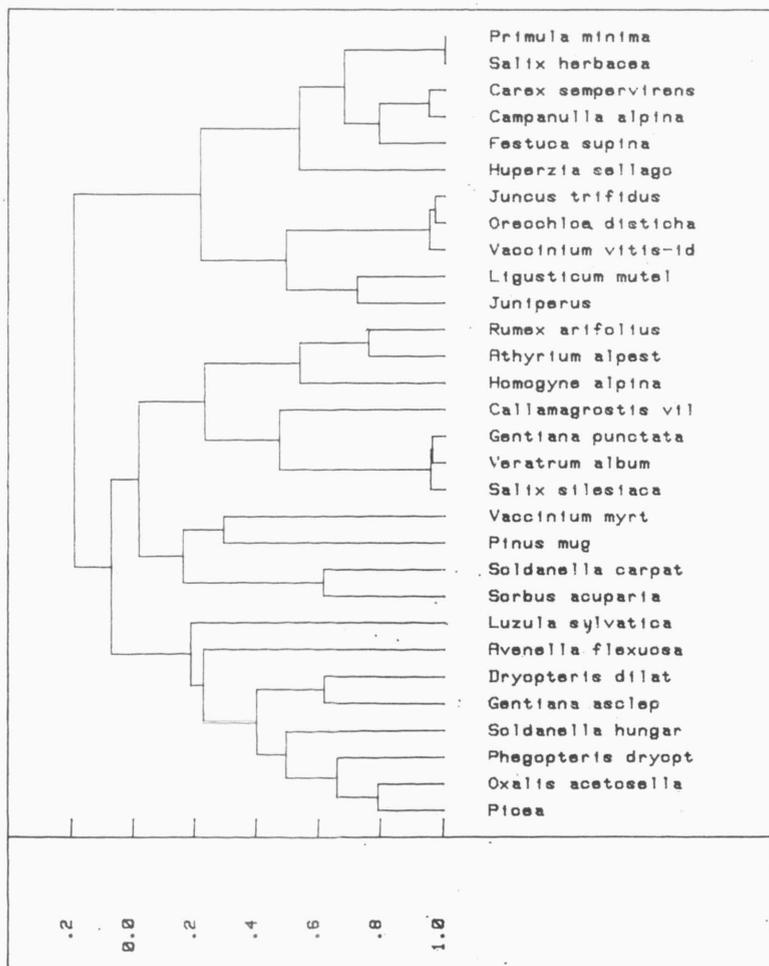


Fig. 6. — Cluster analysis of species on the base of correlation coefficient (numbers on the left side). average-linkage clustering.

after cover transformation show greater discontinuities between the adjoining community types than those based on the presence-absence data. Particularly, differences caused by transformation of the data have been reported many times (e.g. VAN DER MAAREL 1979, LEPŠ et KOVÁŘ 1985, JENSÉN 1978). The presence-absence data sometimes do not yield information enough to recognize particular vegetation types or to find the coenocline, particularly in homogeneous data sets. The efficiency of all ordination methods based on the presence-absence data in our case is undoubtedly conditioned by the heterogeneity of our data set. Similarly, ORLÓCI (1968), GOODALL (1973), and others suggested that species presence is an appropriate variable to use where the set under study is highly heterogeneous. However, the heterogeneity results in the "horseshoe" effect in both the PCA and RA ordinations, as was similarly reported by GAUCH, WHITTAKER et WENTWORTH (1977), HILL et GAUCH (1980) and others. We were not able to find any ecological interpretation of this distortion as had been recommended by VAN DER MAAREL (1980). The superiority of RA to PCA in this case is also in accordance with the previous studies (e.g. GAUCH, WHITTAKER et WENTWORTH 1977).

The complement of traditional and numerical approaches in vegetation science has been reported many times (e.g. VAN DER MAAREL 1975, MORAVEC 1975, DZWONKO 1977, DALE 1982) and follows from our example, too. However, there exist different traditional approaches; similarly, before any numerical treatment we have to choose the methods and their parameters. This may be done appropriately only if we are familiar with the significance and meaning of particular options.

Finally, we wish to stress that the numerical methods used are not antagonistic to the Zürich-Montpellier classification. Their parallel use can give us valuable insights into the problems of vegetation description. An analogous complementary relationship can be seen between the continualistic and discontinualistic views on vegetation which form the background for the use of the mentioned methods (gradient analysis vs. Zürich-Montpellier classification) as well as for the interpretations of their results.

SUMMARY

Vegetation of the Zadná voda valley, the Nízke Tatry Mts., Central Slovakia (Fig. 1), was studied using the methods of direct and indirect gradient analysis and numerical classification. Vegetation data were obtained from phytosociological relevés located on the transect along the elevation gradient (Tab. 1).

With increasing elevation, the mean stand height decreased and the cover of individual vegetation layers changed characteristically. The curves of the occurrence of individual species along the elevation divided the vegetational gradient into three relatively distinct parts corresponding with the three basic types of mountain communities — spruce forests, subalpine shrubby communities and alpine meadows. In the transient zones between these types of vegetation, the highest species richness and diversity were recorded (Tab. 1 and Fig. 2).

The data set was subjected to three ordination methods (PO, PCA, RA). Each ordination was computed after three different transformations of the original Braun-Blanquet scale presence-absence, ordinal, cover values). The efficiency of the particular techniques was evaluated by comparison of relevés ranking on the 1st axis with that on the elevation gradient. RA was found to be more efficient than PCA. PO failed twice to find the coenocline. However, in case the coenocline was correctly determined, the PO was not less efficient than other methods.

The methods of cluster analysis distinguished the three main community types.

The results of numerical treatment were not strikingly dependent on the transformation used with the primary data, unlike the results of other authors. This is probably caused by the heterogeneity (beta-diversity) of our data set. The numerical methods are a very useful tool in

phytosociology; however, they should be used with caution and attention should be paid to the choice of the proper method and its parameters. Results must be interpreted with regard to this choice.

SOUHRN

V článku jsou shrnuty výsledky analýzy vegetace podél komplexního gradientu nadmořské výšky v Dolině Zadné vody, JZ osady Jasná v centrální části Nízkých Tater (obr. 1).

Na transektu mezi 1200 a 1830 m nadmořské výšky byly zapsány fytoecologické snímky (tab. 1), které byly zpracovány metodami přímé a nepřímé gradientové analýzy a numerické klasifikace.

Se vzrůstající nadmořskou výškou klesala výška porostu a charakteristicky se měnila pokrývnost jednotlivých vegetačních pater. Křivky výskytu jednotlivých druhů vymezily na vegetačním gradientu tři výrazné části odpovídající třem základním typům horské vegetace — smrkovým lesem, subalpínským keřovým formacím a alpínským trávníkům, které lze hodnotit fytoecologickým systémem na úrovni svazů jako *Vaccinio-Piceion*, *Pinion mughi* a *Juncion trifidi*. V kontaktních zónách mezi těmito vegetačními typy byla zaznamenána největší druhová pestrost a druhová diverzita (tab. 1, obr. 2).

Soubor snímků byl dále hodnocen třemi různými ordinačními technikami (polární ordinací — PO, analýzou hlavních komponent — PCA, analýzou korespondence neboli reciprokým průměrováním — RA) a metodami shlukové analýzy. Seřazení snímků na první ordinační ose jsme porovnali s polohou snímků na výškovém gradientu pomocí koeficientu pořadové korelace. Hodnota tohoto koeficientu charakterizuje dobře účinnost jednotlivých ordinačních technik (tab. 2). Reciproké průměrování bylo vždy účinnější než analýza hlavních komponent. Polární ordinace nenalezla ve dvou případech správně směr variability souboru (tj. cenoklinu odpovídající výškovému gradientu). Jakmile je však cenoklina správně určena, není tato metoda méně účinná než ostatní. Všechny užití klasifikační techniky odlišily veelku tři hlavní vegetační typy. Výsledky všech numerických metod byly málo závislé na použité transformaci primárních dat. To je způsobeno zřejmě velkou heterogenitou (beta-diverzitou) snímkového materiálu a jasností příkladu. Numerické metody jsou užitečnou pomůckou ve fytoecologii. Nelze je však užívat automaticky; velkou pozornost je třeba věnovat výběru vhodných metod a jejich parametrů.

Lze shrnout, že paralelní užití metod přímé a nepřímé gradientové analýzy a numerické a curyšsko-montpeliérské klasifikace je užitečné a může přinést nové pohledy na konkrétní změny vegetace v prostoru i v čase. Výsledky metod se mohou vzájemně doplňovat, stejně tak jako kontinualistický a diskontinualistický přístup k vegetaci, které jsou ostatně i interpretačním pozadím uvedených metod.

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