

## SPECIES RICHNESS AND DIVERSITY RELATED TO ANTHROPOGENIC SOIL DISTURBANCE IN ABANDONED MEADOWS IN THE BIESZCZADY MTS. (EASTERN CARPATHIANS)

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### ABSTRACT

The study was focused on soil factors influencing species richness and diversity after disturbance of the substrate followed by abandonment. Two types of disturbances in the past were considered: the removal of trees and shrubs with the resulting major destruction of soils, and deep ploughing. As a control meadows not covered by any management schemes for 50 years were studied. The topsoil stripping resulted in decrease of potassium, nitrogen and organic carbon contents, while deep ploughing caused less radical effects. Simultaneously, disturbances of the soil delayed the course of succession, and brought increase in species. The most species-rich are ploughed meadows. No differences in terms of species diversity, domination and evenness between the forms of disturbances were identified. However, there were groups of species indicative for soil disturbances. Analysis of the relationships between vegetation differentiation and the properties of soil suggests that available phosphorus may affect species richness and diversity in mountain meadows.

**KEY WORDS:** anthropogenic effects, floristic richness, mountain meadows, soil nutrients, Biosphere Reserve "Eastern Carpathians".

### INTRODUCTION

As a result of a slump in agriculture, the meadows in the Carpathians are undergoing rapid and adverse alterations involving both a decrease in the number of species and the disappearance of specific combination of species. For this reason, the studies in these communities aim mainly at finding the most appropriate method of management (Michalik 1990; Zarzycki 1999; Ružičková et al. 2001). But apart from land use, one of the key factors that shape vegetation is disturbance regime (Armesto and Pickett 1985; McIntyre et al. 1995; Kotanen 1996; Wilby and Brown 2001). According to Denslow (1980) vegetation diversity depends on the evolutionary past of a given area and on the nature of alterations. The community abounds most in those species which are adapted to life on the patches representing the most frequent type of disturbance. Impact on vegetation is particularly strong and long-lasting when the disturbances cause serious changes in the substrate and in the abiotic properties of habitats. Removing the top layer of the soil or even the litter layer only, is of major importance to the species composition of communities (Hobbs and Huenneke 1992; McIntyre 2001). This practice is sometimes recommended in order to increase the number of species in meadows under intensive management (Berendse et al. 1992).

The meadows in the lower mountain zone in the Western Bieszczady Mts. (a western edge of the Eastern Carpathians) are typical anthropogenic semi-natural ecosystems, noted for their floristic and phytocoenotic richness (Denisiuk and Korzeniak 1999; Zemanek and Winnicki 1999). In the second half of the 1980's, some areas in the Bieszczady Mts. were subject to dramatic anthropogenic disturbances of the substrate resulting from the use of explosives to remove trees and shrubs and very deep ploughing. The degradation of soils was so serious that, despite an almost two-decade long process of regenerative succession, the vegetation still bears traces of these already 'historical' alterations.

The aim of this study was to find in what way the anthropogenic disturbances of the soil have affected the vegetation heterogeneity in the mountain meadows; which of the habitat factors were altered most and what is their possible correlation with the basic measures of species diversity. Given that the high levels of nutrients (particularly of N, P and K) do not favour species richness nor species diversity (Carson and Barrett 1988; Carson and Pickett 1990; Grime 1973, 2001; Tilman 1984, 1987, 1988; Wedin and Tilman 1996; Wilson and Tilman 2002), the following hypotheses were formulated: (1) strong, single disturbance of the soil in the past, destruction or disturbance of humus la-

yer, should result in a decrease in nutrient contents compared with undisturbed meadows, and (2) patches with disturbed soil should show a higher diversity of vegetation than undisturbed sites.

For the purpose of this study, the anthropogenic disturbance is any event resulting from human activities which disturbed (or still disturbs) the structure of the ecosystem or of phytocoenosis and modified (or still modifies) the abiotic environment and the availability of nutrients (Pickett and White 1985; Łaska 2001).

## MATERIALS AND METHODS

### Study area

The studies were conducted on meadows in the Wołosatka stream valley in the Bieszczadzki National Park (SE Poland, Biosphere Reserve “Eastern Carpathians”), in a lower part of the beech forest zone (730–880 m a.s.l.) on ca. 650 hectares. The geological substrate is flysch (shales and sandstones of the Przemyślanka Nappe), with eutric cambisols and gleyic cambisols as predominating soils. Dystric cambisols occur only locally on the upper slopes of the valley (Skiba et al. 1998). The climate is of a mountain type with strong continental features. The annual average air temperature in the valley ranges from +4 to +6°C, the estimated annual average precipitation in the Bieszczady Mts. is 1000–1300 mm (Nowosad 1995).

After World War II agricultural management in the valley declined rapidly. Former meadows and pastures underwent spontaneous secondary succession. In 1987 trees and shrubs were cleared from a part of the area in order to establish highly productive permanent grassland operations. Explosives and heavy military equipment were used, which resulted in long-lasting alterations in the environment (Table 1). Since 1991, this part of the valley has not been cultivated in any way.

The vegetation in the study area is a mosaic of non-forest communities at various stages of succession. The most widespread is *Agrostietum capillaris* of Arrhenatherion alliance. It occurs in variants with *Hypericum maculatum*, *Holcus mollis*, *Deschampsia caespitosa* or *Nardus stricta*. Short grassland with *Festuca rubra* and sward with *Nardus stricta* from Nardetalia order are also common. As a result of progressive secondary succession, the area of meadows has decreased gradually overgrown by *Betula pendula*, *Salix* sp., *Juniperus communis* and *Alnus incana* (the nomenclature used follows ‘Flowering plants and pteridophytes of Poland. A checklist (Mirek et al. 2002)).

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### Sample collection

The studies were carried out over three years (1999–2001) on 77 permanent plots within three types of abandoned meadows: (1) Co – without soil disturbances (21 plots), 2) Ex – area where shrubs were removed with the use of explosives (23 plots), 3) Pl – patches which, after removal of trees and shrubs, were ploughed to a depth of 90 cm (33 plots). As these forms of degradation involved almost the entire slopes of the valley up to the tree line, the study plots were laid out along the transects, running through possibly homogenous patches, from the tree line in the direction of the valley bottom, up to a place with a manifest change, e.g. transition of fresh meadows into tall herb communities or mires. The beginning of each transect was marked in the field. Then, along the selected azimuth, in 25-m intervals, 10×10 m study plots were established. Each year, in the period of optimum vegetation development (July), on each plot a relevee was conducted in percentage scales. The cover by species was estimated within 10% intervals, with species with cover below 1% included in a separate category. For lichens and mosses, estimates were limited only to cover for the whole layer without identifying species.

In order to determine the basic properties of the soil, in 1999 from the centre of each plot one sample of the top layer (up to 15 cm) was collected. The soil sample analyses included: pH in water by the potentiometric method, organic C contents by the Tiurin method as modified by Oleksynowa, total N by the Kjeldahl method, contents of available P and K forms by the Egner-Riehm method, and of Mg – by the Schachtschabel method. The rate of organic matter decomposition was evaluated by C: N ratio.

### Data analysis

Using the data from the relevees, the following parameters were determined for each plot:

- 1)  $S$  – number of species in the sample (species richness);
- 2)  $H'$  – Shannon-Wiener index of species diversity (Magurran 1988):

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

where:  $p_i$  – share (here: cover) by  $i$ -th species in the sample;

TABLE 1. Types of human-induced disturbances and their effect on the topography observed in the field.

Type of disturbance		
Co – control (no anthropogenic disturbance)	Pl – deep ploughing	Ex – clearings with topsoil stripping (with explosives)
Alterations to the soil		
no changes	upturned upper horizons of the soil profile – humus horizon under mineral-weathering horizon	destruction of the upper horizons of the soil profile, skeleton on the surface, long-term soil erosion
Microtopography		
slightly undulating	deep parallel furrows	undulating with depressions about 0.5 m deep
Plant cover		
diversified and patchy, mean cover of herbs – 99%, shrubs 5%	luxurious and abundant, mean herbs cover 98%, shrubs – 2%	scanty, lot of gaps of barren soil, mean herbs cover 93%, shrubs 6%

3)  $\lambda$  – Simpson's domination index (Magurran 1988):

$$\lambda = \sum_{i=1}^S (p_i^2)$$

4)  $E$  – evenness index (Magurran 1988):

$$E = H' / H_{\max} \text{ where } H_{\max} = \ln S.$$

The variability in the number of species ( $S$ ) between the types of disturbances defined, was determined by one-way ANOVA. In cases of  $H'$ ,  $\lambda$  and  $E$ , which did not show normal distribution, the Kruskal-Wallis test was used. The same tests were used to compare soil conditions in meadows subjected to various anthropogenic effects. In cases of variables deviating from normal distribution logarithmic transformation (pH in water, the contents organic C, P and K) or square root transformation (total N) was applied. The detailed comparison of the significance of differences in groups was made with a posteriori Scheffé's test. The correlations between abiotic environmental factors and the heterogeneity of vegetation were tested by the Pearson's linear correlation method or Spearman's rank correlation. All statistical calculations were carried out using the STATISTICA software package (StatSoft, Inc. 1997).

## RESULTS

### Diversity measures and species composition in disturbed meadows

Over a period of three years, a total of 218 species of vascular plants were found in all study plots. The meadows

disturbed in various ways did not differ much in terms of the cumulative species richness i.e. species number in the first year plus new species appearing in later years (in Co meadows 180 species occurred, in PI – 189, and in Ex meadows – 172 species). The type of disturbance affected significantly the average number of species per 100 m<sup>2</sup> (ANOVA df=2,207; F=7.08; p=0.001). The most species-rich meadows (after deep ploughing) differed both from undisturbed meadows (p=0.003) and from those where shrubs were cleared (p=0.028), in Scheffé's test. From the viewpoint of species diversity, evenness and domination, there are no differences between the forms of disturbances studied (Table 2).

Meadows subjected to various types of anthropogenic impact differ in their floristic composition. Patches from which shrubs were cleared are distinct for the high abundance of species from Nardo-Callunetea class (Table 3). Synanthropic and ruderal taxa are rare (only 14 species were found) and occur more frequently on the plots after the soil disturbances. The characteristic species of patches with barren soil are: *Corylus avellana*, *Rubus hirtus*, *Dianthus compactus* and *Hypericum perforatum* (Table 4). Also *Betula pendula* and *Alnus incana* saplings occur abundantly. The group of species thriving better on ploughed plots includes: *Listera ovata*, *Tussilago farfara*, *Hieracium umbellatum*, some species of moist meadows and of genus *Alchemilla*. The species characteristic for habitats of disturbed soil are quite numerous (*Rumex acetosella*, *Fragaria vesca*, *Succisa pratensis*, *Hieracium pilosella*, *Hypochoeris radicata*), whereas there are no good indicators discriminating the long-term (i.e. fifty years') abandonment from the shorter (twenty years') one. Frequent occurrence of tree and bush saplings irrespective of the type of disturbance shows

TABLE 2. Species richness  $S$ , species diversity  $H'$ , dominance  $\lambda$  and evenness  $E$  (mean±SD) on plots undisturbed (Co), ploughed (PI) and cleared (Ex) based on data 1999-2001. Different superscript letters indicate significant differences between the diversity characteristics of disturbance types as determined by one-way ANOVA or Kruskal-Wallis test (p<0.05).

Type of disturbance	$S$	$H'$	$\lambda$	$E$
Co	54.04±10.74 <sup>b</sup>	2.80±0.44	0.11±0.09	0.70±0.09
PI	59.62±9.18 <sup>a</sup>	2.86±0.42	0.10±0.06	0.70±0.09
Ex	55.45±8.52 <sup>b</sup>	2.84±0.29	0.10±0.04	0.71±0.05
Statistical significance	F <sub>2,207</sub> = 7.08 p = 0.0011	H <sub>2,210</sub> = 3.92 ns	H <sub>2,210</sub> = 2.10 ns	H <sub>2,210</sub> = 0.62 ns

TABLE 3. Comparison of phytosociological structure of different forms of disturbance. Means are shown with ranges in parentheses. P denotes the probability of difference according to Kruskal-Wallis test. Within the row, values with the same superscript letter are not significantly different at p=0.017 (based on Kruskal-Wallis test, p level after Bonferroni correction).

Characteristics	Co	PI	Ex	P
Number of species/100 m <sup>2</sup>				
Molinio-Arrhenatheretea	21.3 (2-34) <sup>a</sup>	22.7 (10-36) <sup>a</sup>	15.8 (5-31) <sup>b</sup>	<0.0001
Nardo-Callunetea	5.4 (0-10) <sup>a</sup>	6.9 (3-12) <sup>b</sup>	8.4 (5-12) <sup>c</sup>	<0.0001
Betulo-Adenostyletea	2.5 (1-4)	2.1 (0-4)	2.4 (1-4)	ns
Querco-Fagetea	1.3 (0-5) <sup>a</sup>	0.6 (0-3) <sup>b</sup>	1.4 (0-5) <sup>a</sup>	<0.0001
Vaccinio-Piceetea	1.1 (0-3) <sup>a</sup>	0.6 (0-3) <sup>b</sup>	0.9 (0-3) <sup>ab</sup>	0.02
Synanthropic	1.4 (0-4) <sup>a</sup>	2.0 (0-6) <sup>b</sup>	2.4 (0-5) <sup>b</sup>	0.0001
Cover (%) of species				
Molinio-Arrhenatheretea	42.9 (2-99) <sup>ab</sup>	45.2 (9-90) <sup>a</sup>	33.7 (9-86) <sup>b</sup>	0.002
Nardo-Callunetea	17.4 (0-95) <sup>a</sup>	15.5 (1-57) <sup>a</sup>	23.2 (3-62) <sup>b</sup>	0.0001
Betulo-Adenostyletea	12.8 (0-45)	17.1 (0-71)	16.3 (0-45)	ns
Querco-Fagetea	1.2 (0-18) <sup>a</sup>	0.2 (0-4) <sup>b</sup>	2.6 (0-75) <sup>a</sup>	<0.0001
Vaccinio-Piceetea	11.1 (0-87) <sup>a</sup>	0.5 (0-6) <sup>b</sup>	1.0 (0-8) <sup>ab</sup>	0.001
Synanthropic	1.4 (0-15) <sup>a</sup>	1.1 (0-20) <sup>a</sup>	1.8 (0-15) <sup>b</sup>	0.0015

TABLE 4. Distribution (frequency of occurrence/% mean cover) of non-ubiquitous species on the plots. + = cover values <0.5%; \* indicates synanthropic and ruderal species.

	Co	Pl	Ex
<b>Soil disturbance indicators</b>			
<i>Rumex acetosella</i>	-/-	18/+	11/+
<i>Rumex crispus</i>	-/-	11/+	11/+
<i>Succisa pratensis</i>	4/+	51/3	28/1
* <i>Rhinanthus serotinus</i>	2/+	13/+	20/+
<i>Platanthera bifolia</i>	2/+	11/+	11/+
<i>Leontodon autumnalis</i>	4/+	22/+	27/+
<i>Hieracium pilosella</i>	5/+	42/1	48/+
<i>Leontodon hispidus</i>	5/+	24/+	17/+
<i>Hypochoeris radicata</i>	7/+	26/+	53/2
* <i>Gnaphalium sylvaticum</i>	9/+	42/+	73/+
<i>Hieracium laevigatum</i>	9/+	50/+	42/+
<i>Danthonia decumbens</i>	11/+	31/+	52/2
* <i>Fragaria vesca</i>	18/+	46/1	61/1
<b>Barren soil preferers</b>			
<i>Rubus hirtus</i>	5/+	2/+	70/3
<i>Dianthus compactus</i>	9/+	10/+	70/2
<i>Corylus avellana</i> (b)	-/-	-/-	22/+
<i>Hypericum perforatum</i>	4/+	4/+	27/+
<i>Carlina acaulis</i>	4/+	9/+	27/+
* <i>Pastinaca sativa</i>	-/-	-/-	8/+
<i>Euphorbia serrulata</i>	-/-	-/-	8/+
<i>Trifolium aureum</i>	-/-	1/+	6/+
<i>Thesium alpinum</i>	-/-	-/-	5/+
* <i>Centaurium erythraea</i>	-/-	-/-	5/+
<b>Deep ploughing preferers</b>			
<i>Listera ovata</i>	-/-	18/+	-/-
* <i>Tussilago farfara</i>	-/-	14/+	-/-
<i>Hieracium umbellatum</i>	-/-	10/+	-/-
<i>Epilobium palustre</i>	-/-	10/+	-/-
<i>Alchemilla acutiloba</i>	5/+	44/+	19/+
<i>Alchemilla monticola</i>	11/+	44/+	16/+
<i>Alchemilla glabra</i>	2/+	40/1	8/+
<i>Juncus conglomeratus</i>	5/+	29/+	8/+
<i>Galeopsis bifida</i>	7/+	32/1	5/+
<i>Cynosurus cristatus</i>	4/+	19/+	6/+
<i>Taraxacum officinale</i>	9/+	16/+	5/+
<i>Potentilla anserina</i>	-/-	9/+	3/+
* <i>Cirsium arvense</i>	9/+	22/+	-/-
<i>Alchemilla crinita</i>	2/+	18/+	-/-
<b>Trees and shrubs</b>			
<i>Betula pendula</i>	46/1	54/+	83/3
<i>Salix capraea</i>	27/+	61/+	70/+
<i>Juniperus communis</i>	21/1	37/+	38/+
<i>Picea abies</i>	34/+	33/+	27/+
<i>Alnus incana</i>	25/1	19/+	30/2
<i>Salix cinerea</i>	16/+	27/+	20/+
<i>Frangula alnus</i>	29/+	6/+	20/+
<i>Acer pseudoplatanus</i>	20/+	4/+	19/+
<i>Rosa canina</i>	7/+	12/+	20/+
<i>Salix aurita</i>	9/+	13/+	11/+
<i>Sorbus aucuparia</i>	5/+	4/+	20/+
<i>Salix silesiaca</i>	2/+	7/+	9/+
<i>Populus tremula</i>	36/1	33/+	-/-
<i>Larix decidua</i>	9/+	7/+	-/-
<i>Pinus sylvestris</i>	4/+	6/+	-/-
<i>Fagus sylvatica</i>	7/+	-/-	6/+
<i>Viburnum opulus</i>	2/+	-/-	11/+
<i>Crataegus monogyna</i>	4/+	-/-	5/+
<i>Prunus spinosa</i>	9/+	-/-	-/-
<i>Sambucus racemosa</i>	4/+	-/-	-/-

quite rapid progressive changes in the course of secondary succession.

### Effect of ploughing and topsoil stripping on soil properties

The meadows with disturbed substrate are characterised by significantly lower contents of organic C, total N and available K in the soil (Table 5).

A detailed analysis of the significance of differences, by a posteriori Scheffé's test, shows that soils in undisturbed meadows are richer in organic C than soils of ploughed meadows ( $p=0.04$ ) and those with shrubs cleared ( $p=0.009$ ). They also contain more total N and K than the soils of meadows with shrubs cleared ( $p=0.02$  and  $0.002$  respectively).

### Vegetation diversity and selected habitat factors

Irrespective of the degree of modification of the soil, significant but rather weak correlations with species richness appeared only with regard to soil reaction and the contents of available P (Fig. 1). The relationships between particular indices of vegetation diversity and properties of the soil are different for each type of disturbance (Table 6). The effect of P on species richness, diversity and evenness depends on its contents in the soil. Whenever soils are relatively richer in P (Co and Pl meadows), there is a negative correlation between levels of P and  $S$ . On the poorest soils (Ex meadows), where P deficiency may be an essential limiting factor of vegetation growth, correlations of P contents with  $H'$  and  $E$  are positive. The same correlation occurs between K content and evenness. The relationship between the heterogeneity of vegetation and total N content, was shown only in undisturbed meadows of which the soils are relatively rich in this element ( $r_s = -0.569$ ,  $N=21$ ,  $p=0.017$ ; Table 6).

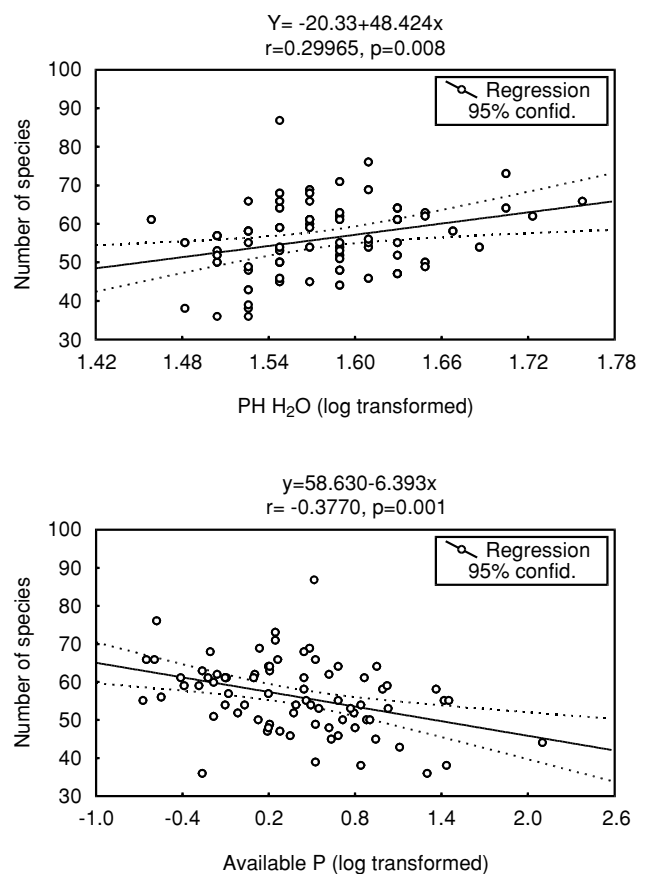


Fig. 1. Result of linear regression of species richness on soil pH and soil concentration of P.



TABLE 5. Soil chemistry (mean±SD) of samples taken in 1999 from topsoil on undisturbed (Co), deep ploughed (Pl) and cleared with explosives (Ex) meadows — results of one-way ANOVA and Kruskal-Wallis test. Means accompanied by the same letter were not significantly different ( $\alpha=0.05$ ).

	Co	Pl	Ex	<i>F</i>	<i>H</i>	<i>df</i>	<i>p</i>
pH (H <sub>2</sub> O)	4.92±0.31	4.88±0.31	4.78±0.25	1.44	-	2, 71	ns
C organic [g/100g]	3.49±0.94 <sup>a</sup>	2.86±0.90 <sup>b</sup>	2.64±0.68 <sup>b</sup>	5.51	-	2, 71	**
total N [g/100g]	0.38±0.09 <sup>a</sup>	0.32±0.08 <sup>ab</sup>	0.30±0.07 <sup>b</sup>	4.44	-	2, 71	*
C:N	9.45±2.38	8.85±1.30	8.62±0.60	-	1.67	2, 74	ns
P <sub>2</sub> O <sub>5</sub> [mg/100g]	1.91±0.91	1.71±1.02	1.34±0.64	2.51	-	2, 70	ns
K <sub>2</sub> O [mg/100g]	10.98±5.73 <sup>a</sup>	7.01±3.23 <sup>b</sup>	6.30±2.39 <sup>b</sup>	7.76	-	2, 71	***
MgO [mg/100g]	1.76±2.12	2.89±4.12	2.35±2.94	-	0.38	2, 73	ns

\*\*\* –  $p<0.001$ ; \*\* –  $p<0.01$ ; \* –  $p<0.05$ ; ns – not significantTABLE 6. Correlation between species richness *S*, Shannon's diversity index *H'*, dominance index  $\lambda$ , evenness index *E* and soil chemistry on undisturbed (Co), deep ploughed (Pl) and cleared (Ex) meadows.

		pH (H <sub>2</sub> O)	C org.	total N	C:N	P <sub>2</sub> O <sub>5</sub>	K <sub>2</sub> O	MgO
<i>S</i>	Co	0.408	-0.064	0.001	-0.103	-0.543*	-0.429	0.129
	Pl	0.177	0.294	0.343	0.089	-0.542*	0.030	0.014
	Ex	0.390	0.119	0.166	0.274	0.167	0.184	-0.036
<i>H'</i>	Co	0.380	-0.328	-0.569*	-0.07	-0.396	0.022	0.449
	Pl	0.340	0.365	0.346	0.251	-0.549*	0.050	0.175
	Ex	0.394	0.308	0.253	0.496	0.516*	0.487	-0.318
$\lambda$	Co	-0.385	0.298	0.473	0.036	0.364	0.182	-0.393
	Pl	-0.274	-0.371	-0.362	-0.256	0.326	-0.293	-0.230
	Ex	-0.418	-0.220	-0.201	-0.330	-0.312	-0.333	0.072
<i>E</i>	Co	0.361	-0.347	-0.645*	-0.055	-0.269	0.223	0.406
	Pl	0.422	0.394	0.312	0.367	-0.507*	0.032	0.280
	Ex	0.290	0.302	0.239	0.459	0.610*	0.548*	-0.331

\* – statistically significant (Spearman rank correlation,  $p=0.017$  after Bonferroni correction)

No relationship was found between the soil reaction, organic matter content, its rate of decomposition (C:N), content of available Mg and any of the variables illustrating the heterogeneity of vegetation.

## DISCUSSION

The results of the study only partly support the two hypotheses. The decrease in nutrient resources related to past destruction of the soil, which was already poor, did not appear to be as manifest as expected. The removing of the topsoil caused intensive erosion and surface runoff and resulted in the long-term reduction of resources, particularly of K, organic C and N. Deep ploughing turned out to be less radical in terms of its effects: meadows subjected to deep ploughing appear similar to the control (undisturbed) plots as far as N contents are concerned.

The presumption that species diversity in meadows on disturbed substrate will be higher than that in patches left without intervention was also only partly confirmed. Almost two decades after the disturbance no significant differences were found in species diversity, evenness and domination. Only in terms of number of species, which is the simplest measure of vegetation diversity, were the meadows subjected to deep ploughing more rich than other meadows. The high species richness of studied meadows (from 21 to 87 species per plot; 57 species/100 m<sup>2</sup> on average) is also related to their abandonment. Certainly, disturbances had interrupted the process of secondary succes-

sion and delayed it. Ploughed and shrub cleared patches are now at the intermediate stage of succession, which is usually characterized by the highest species diversity (Faliński 1998). The similar share of tree saplings in floristic composition of undisturbed and disturbed patches indicates that recolonization after soil degradation proceeded quite rapidly. Dispersion of species was facilitated by lack of isolation, while cessation of any agriculture activities resulted in small share of synanthropic species, usually considered as disturbance indicators.

Some relationships between vegetation differentiation and habitat factors were observed. The positive correlation of species richness and the soil reaction results from the fact that pH strongly affects the availability of P, N and K to plants. A significant, negative correlation occurs between P contents and *H'* and *E* in undisturbed or deeply ploughed meadows. No effects have been found, however between the P content and domination index. Only in meadows with the shrubs cleared, where the soil is particularly low in nutrients, does a high P level support species diversity, as well as most likely being a limiting factor.

A negative correlation between the P level and the number of species was reported in old permanent grasslands (Janssens et al. 1998). Also Gough and Marrs (1990) suggest that in many semi-natural meadow communities, low contents of available P in the soil is the main factor limiting the occurrence of species-rich habitats, whereas the N level is not of major importance. In contrast to nitrogen, which is present in the soil almost entirely in organic form, P occurs also in mineral form and is definitely a less mobi-

le element than N. It should thus be expected that the destruction of topsoil would entail a significant and fairly permanent loss of P. However, the soil in disturbed and undisturbed meadows do not differ in the contents of available P, but on the other hand, the plots within the areas subjected to the same disturbance show a great variability (SD value – Table 5).

Low P contents may limit the rate of N mineralisation and of N fixation by legumes, i.e. limit the supplies from two principal sources (Janssens et al. 1998). In the study plots, the average cover by legumes per 100 m<sup>2</sup> is ca. 8%. Almost 60% of cover by all species of Fabaceae is by *Trifolium medium*, ca. 20% by *Vicia cracca*, with fairly large proportions of *Lathyrus pratensis*, *T. hybridum* and *Vicia sepium*. No relationships between the occurrence of legumes and N contents or mineralisation rate for organic matter were found. The number of occurrences of leguminous species (but not their cover) was indeed dependant on P contents ( $r_s=0.325$ ,  $N=76$ ,  $p=0.004$ ). The interaction between P and N is very likely but proving this is fraught with major difficulties (Janssens et al. 1998).

The correlation between vegetation diversity and one of the basic nutrients i.e. nitrogen, was identified only in undisturbed meadows. Brożek (1993) found that on abandoned lands in the Bieszczady Mts. dense stands of symbiotic nitrogen-fixing *Alnus incana* caused N and organic matter enrichment. However, on the study plots with *Alnus incana* contents of nitrogen did not differ from the mean value for the given form of disturbance or was even lower. Relatively high levels of N in undisturbed plots probably result from an increase of total soil nitrogen during succession. This pattern of successional changes was observed on nutrient-poor soils (Gleeson and Tilman 1990; Dzwonko and Loster 1996).

The results of this study suggest that strong and long-term alteration of soil properties and changes during the course of succession resulting from disturbance in the soil is an important factor favouring species richness. However, the persistence of vegetation pattern of high alpha and beta-diversity is difficult to estimate without long-term studies.

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