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Long-term Changes in the Field Layer of Oak and Oak-hornbeam Forests under the Impact of Deer and Mouflon

KEYWORDS

Grazing, Multivariate analysis, Phytosociological data, Species exchange, Vegetation/animal interactions

ABSTRACT

The resampling of 46 phytosociological plots 39 years later is used to characterize changes in the field layer of oak and oak-hornbeam forests in the South-East of the Czech Republic, where high densities of fallow deer, red deer and mouflon are kept in game preserves. Detrended correspondence analysis is used to demonstrate the general pattern of change. Changes in particular species performance, cover of field and shrub layers, diversity, life form spectrum and performance of zoochores are described. It is suggested that with increasing grazing pressure, native forest species retreat while the performance of species preferring soils rich in nitrogen and species of ruderal habitats increases. Simultaneously, mesic species are gradually replaced by xeric ones. Possible causes of these changes are discussed.

INTRODUCTION

Long-term changes in forest vegetation may be caused by changes in various environmental factors, e.g. slow variations in macroclimate (NEILSON 1987), soil acidification (FALKENGREN-GRERUP and TYLER 1991), fertilization (BECKER et al. 1992), clear-cutting and thinning (NIEPPOLA 1992), etc. Less attention has been paid to the compositional changes in forest field layer affected by game grazing. Nevertheless, the latter presents an important

problem for nature conservation, because the interest of hunters and gamekeepers to keep as high stocking rates as possible often conflict sharply with efforts to conserve natural forest ecosystems in a balanced state especially in reserves.

Studies dealing with herbivore impact on vegetation are mostly concerned with sheep and cattle grazing on non-forest pastures. For example, near the site of the present research, several studies have dealt with the influence of agrimi, mouflon and fallow deer on the steppe and forest vegetation of the limestone klippen range of the Pálava Hills (ŠVANDA 1967, GRULICH 1978, HORÁK 1978, KŘIVÁNKOVÁ 1986, KOCHOVÁ 1990, VARGA 1990, UNAR et al. 1991, KAILER 1993). There are fewer studies on forest grazing in which the main attention is paid to the influence of domesticated herbivores (ADAMS 1975). Game grazing in forests was studied e.g. by VEBLEN and STEWART (1982) and VEBLEN et al. (1989). Generally, these studies mainly evaluate changes in vegetation over a comparatively short period of time.

Assessment of long-term changes in natural forest phytocoenoses caused by large herbivores is a rather rare topic in vegetation science, mainly due to the methodological problems resulting from the general problems of long-term studies. The aims of a long-term study are often different at its inception and when it is evaluated. That is why the obtainable results are often limited by the design of sample plots and sampling methods which are not always the most appropriate for the evaluation (LIKENS 1987).

Typical examples of long-term studies with strongly limited possibilities to contribute to our knowledge of processes in plant communities are the studies based on resampling of permanent plots established using the Zürich-Montpellier approach (PYŠEK and PYŠEK 1991). However, there is a large amount of phytosociological relevé material in Central Europe and a lot of the relevés, when re-established, can provide us with valuable information on the changes of vegetation patterns through time. Recently, several papers have appeared that attempt to analyze succession on the basis of phytosociological data, using both the simple comparison of relevés in a table (HADÁČ 1990, BLAŽKOVÁ 1991) and the more detailed analysis of the species composition (PYŠEK and PYŠEK 1991).

This paper utilizes unpublished relevés recorded by J. Horák during his typological research in the Milovický les forest complex (South Moravia, Czech Republic) in 1953/54 (see HORÁK 1972, 1979, 1980, 1983) and resampled in 1992 to describe changes in the forest field layer after a game preserve was established in 1965-1966.

STUDY AREA

Milovický les forest lies in southernmost Moravia, near the Czech-Austrian border, between the town of Mikulov and the villages of Klentnice, Milovice, Bulhary and Sedlec (ca 48°50' N, 16°40' E). Geomorphologically, the area is hill country made up of flysch claystones and sandstones, locally overlaid by loess deposits. It is dissected by a rectangular net of intermittent water streams (DEMEK et al. 1987). The predominant soil types are luvisols and chernozems. According to the map of climatic regions of the Czech Republic the area is situated in the warm region T4 (QUITT 1975). It is characterized by a very warm and dry summer, very short transient periods of a warm spring and autumn, and a short, mildly warm, dry to very dry winter with a very short period of snow cover (QUITT 1971). There are two climatic stations near the study area, Lednice and Valtice, where the mean annual temperatures for 1901-1950 were 9.0 and 9.1 °C and the mean annual precipitations were 524 and 571 mm, respectively (data from VESECKÝ et al. 1961).

The area is vegetated predominantly by natural forest communities: oak forests of the associations *Potentillo albae-Quercetum* LIBBERT 1933, *Corno-Quercetum* MÁTHÉ et KOVÁCS

1962, and *Pruno mahaleb-Quercetum pubescentis* JAKUCS et FEKETE 1957 and oak-hornbeam forests of the association *Primulo veris-Carpinetum* R. et Z. NEUHÄUSL ex NEUHÄUSLOVÁ-NOVOTNÁ 1964.

In 1965-1966 two game preserves were established on the territory of the Milovický les forest. The larger Bulhary Game Preserve has an area of 1,250 ha and deer are kept there. On March 31st, 1992, according to the official report, 267 head of red deer (*Cervus elaphus*), 169 of fallow deer (*Dama dama*) and 22 of wild boar (*Sus scrofa*) were counted, which means there are about 0.35 head of deer and 0.02 wild boars per hectare. The smaller Klentnice Game Preserve is about 500 ha. Fallow deer and mouflon (*Ovis musimon*) are kept there and their numbers on March 31st, 1992, should have been 431 head of fallow deer and 417 head of mouflon. These numbers represent ca 0.86 head of fallow deer and 0.83 head of mouflon per ha.

METHODS

SAMPLING

The first sampling of forest vegetation in the study area was carried out by J. Horák during his typological research in summer 1953 and the species of vernal aspect were added to the species lists in spring 1954 (before the establishment of the game preserves in the Milovický les forest). Sample plots were subjectively located in order to represent the maximum variability of stands and environmental conditions. Plot size was usually 500 m², only in several cases it was smaller. Data on species cover were estimated using the 7-grade Braun-Blanquet scale (r, +, 1, 2, 3, 4, 5). Tree and shrub seedlings were not distinguished from saplings and smaller shrubs. Total covers of the field layer and woody plants were expressed as percentages.

Each site was indicated on a 1:25,000 map, and data on slope, aspect, and the number of stand according to forest map were given. These indicators together with the information on tree species composition were sufficient to find the stands and perform resampling with a maximum error of ca 50 m. Resampling was carried out in June 1992 by the authors of the paper presented. In each plot we found the vegetation was sampled in the same manner as applied by Horák in 1953/54. From the approximately total 80 plots sampled in 1953/54, only 46 were resampled. The others were either deforested or have not been found with sufficient accuracy, e.g. slope or aspect at the site we found using the map differed remarkably from the values given by Horák; or the stand was dominated by trees younger than ca 50 years and canopy composition was quite different from that given in Horák's samples. From these 46 plots 22 were located in the Bulhary Game Preserve with only deer (Bulhary subset), 15 in the Klentnice Game Preserve with fallow deer and mouflon (Klentnice subset), and 9 outside the game preserves (control subset).

DATA ANALYSIS

Data on species cover in the Braun-Blanquet ordinal scale (r, +, 1, 2, 3, 4, 5) were transformed to cover values using the midpoints of cover interval for the particular degree (i.e. 0.1, 0.5, 3, 15, 37.5, 62.5, 87.5). Vernal species recorded by Horák during spring sampling that could not be recorded during the second sampling in June (*Adoxa moschatellina*, *Anemone ranunculoides*, *Ficaria bulbifera*, *Lathraea squamaria*, *Muscari racemosum*,

Orrhagalum kochii, and *Veronica hederifolia*) were excluded from the data set. Because the total cover of shrub layer was not given in Horák's records, it was calculated as the sum of cover values for particular species.

Temporal compositional change of the vegetation is represented as a vector (community trajectory) connecting two points in species space. Detrended correspondence analysis (DCA, HILL and GAUCH 1980) was applied to the whole data set comprising both 1953/54 and 1992 samples, using the program DECORANA. Mean lengths and slope angles of trajectories were counted from the differences between sample scores on respective axes, using Pythagorean proposition and arc tg function.

Calibration (cf. JONGMAN et al. 1987, TER BRAAK and PRENTICE 1988) was carried out, using Ellenberg's indicator values for nitrogen and moisture (ELLENBERG 1979). Calculating arithmetical means from ordinal data like Ellenberg's values might be a dangerous operation (JONGMAN et al. 1987), so frequency histograms of occurrences for every group of species with the same indicator value were used to characterize particular subsets.

Diversity (H') was calculated according to the Shannon formula (SHANNON and WEAVER 1949). Evenness was expressed as $H'/\ln S$ where S is species richness.

Data on cover of shrub and field layers and species richness and diversity in particular data subsets were tested by Kolmogorov-Smirnov one-sample test for goodness-of-fit (SNEDECOR and COCHRAN 1980) to determine if these data follow normal distribution.

Differences in the above mentioned community parameters were examined between 1953/54 and 1992 for the Bulhary, Klentnice and control subsets, respectively. Percentage cover data that did not follow normal distribution were tested using the Wilcoxon signed rank test and normally distributed data on species richness and diversity were tested using the t-test. The statistical methods used are described by SNEDECOR and COCHRAN (1980).

Data on life forms (RAUNKIAER 1934) and the way of dissemination of species are taken mainly from ROTHMALER et al. (1982).

The plant taxa nomenclature used follows NEUHÄUSLOVÁ and KOLBEK (1982).

RESULTS

ORDINATION

Detrended correspondence analysis revealed the main successional trends in three data subsets (Fig. 1a-d). The first biplot presents the ordination of species in the sample space. The biplots in Fig. 1b-d originate from the same DCA analysis of the whole data set and are presented as three separate biplots showing the pattern of change in three subsets. The arrows represent community trajectories between 1953/54 and 1992, from the same analysis. Eigenvalue of the first axis is 0.693, that of the second 0.599.

In the scatter diagram of species in the sample space (Fig. 1a) two main trends are evident:

(1) The species of disturbed and nitrogen-rich habitats are concentrated in the right part and those of non disturbed and less nitrogen-rich habitats in the left part.

(2) The species preferring xeric habitats are predominant in the upper part while those of mesic habitats in the lower part of the diagram.

Hence, the first axis may be interpreted as a "ruderalization" gradient where the intensity of disturbance and nitrogen supply increase from left to right. Then, the second axis represents a moisture gradient where mesic conditions predominate in the bottom part while xeric ones near the top.

The mean trajectory of the sample plots between 1953/54 and 1992 in the Bulhary subset, i.e. game preserve with deer only (Fig. 1b), is 1.02 ± 0.64 standard deviation units long and the angle is $27.5 \pm 56.5^\circ$. Comparing these values with the two other subsets shows that this subset has an intermediate average length of the trajectories with the highest standard deviation. This means the average compositional change in the Bulhary subset was greater than in the control subset and less than in the Klentnice subset. It is concluded from this relatively high standard deviation of length that this change affected various samples with different intensity. The trajectory angle is intermediate but relatively high with an intermediate standard deviation. This shows that the main trend during the succession was ruderalization and also that the habitat was becoming drier. The intermediate standard deviation suggests that the trend is more pronounced than in the control subset and poorer than in the Klentnice subset.

The average length of the trajectories in the Klentnice subset, i.e. game preserve with fallow deer and mouflon (Fig. 1c), is 2.41 ± 0.56 SDU and the average angle is $35.7 \pm 26.9^\circ$. For both length and angle the average is greater and the standard deviation smaller than in the other subsets. This reveals that the compositional change in the Klentnice subset was the greatest and its intensity was comparatively evenly distributed among the sample plots. The direction of the succession was similar to that of the Bulhary subset but the trend to become dry was stronger. The trend is strongly pronounced as well.

The control subset, i.e. plots outside the preserves (Fig. 1d), is characterized by trajectories of an average length of 0.91 ± 0.61 SDU and average angle of $-11.6 \pm 75.3^\circ$. Both averages are lower than the averages of the two other subsets, the standard deviation of the length is intermediate and that of the angle is the greatest. These results suggest that the compositional change in the control subset was not of such an extent as in the two other subsets. However, the differences in its intensity between particular sample plots are greater than in the Klentnice and less than in the Bulhary subset. Trajectory angles suggest only a slightly pronounced trend towards ruderalization. The trend towards becoming drier is not expressed at all.

PERFORMANCES OF INDIVIDUAL SPECIES

Changes in species performances in three data subsets are summarized in the Appendix. Only species occurring with frequency higher than 25 % in at least one sampling time are included in the table for each subset. The species are ranked according to increasing differences between occurrence frequencies in 1953/54 and 1992.

The highest values in both the decrease of frequency of certain species and the increase of frequency of others were noted in the Klentnice subset, the lowest in the control subset.

In the Bulhary subset the highest decrease of frequency showed indigenous forest species, e.g. *Carex michelii*, *Ajuga genevensis*, *Melittis melissophyllum*, *Calamagrostis arundinacea*, *Iris variegata* etc. On the other hand, the highest increase characterized the species penetrating into the forest as a consequence of disturbance or an increase of nitrogen supply in the soil, e.g. *Urtica dioica*, *Fallopia dumetorum*, *Cardamine impatiens*, *Lapsana communis* etc.

The Klentnice subset shows a similar trend as the Bulhary subset but its expression is stronger. There is a conspicuous number of species that were completely eliminated, e.g. *Convallaria majalis*, *Pulmonaria officinalis*, *Milium effusum*, *Carex michelii*, *Polygonatum multiflorum* etc.

In the control subset the differences were not so clearly pronounced as in the preceding ones and the ruderalization trend was only weakly expressed.

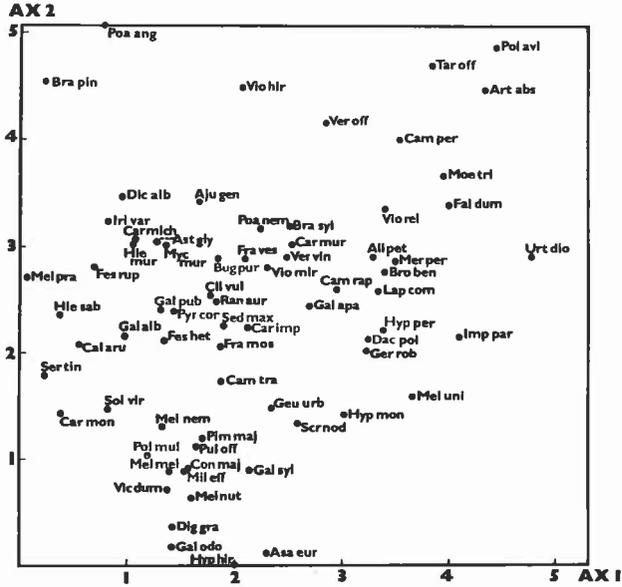


Fig. 1a. DCA ordination biplot: species points in sample space. Only species with at least 25 % occurrence in at least one subset for particular time are depicted. Axes scaled in SD units.

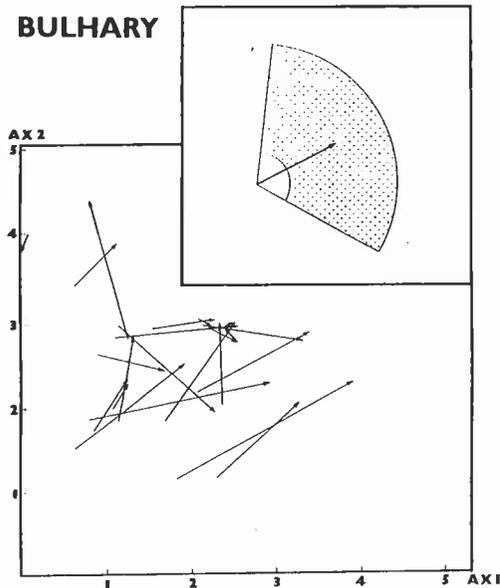


Fig. 1b. DCA ordination biplot: community vectors in species space with resultant vector with standard deviation of length and angle for Bulhary subset. Axes scaled in SD units.

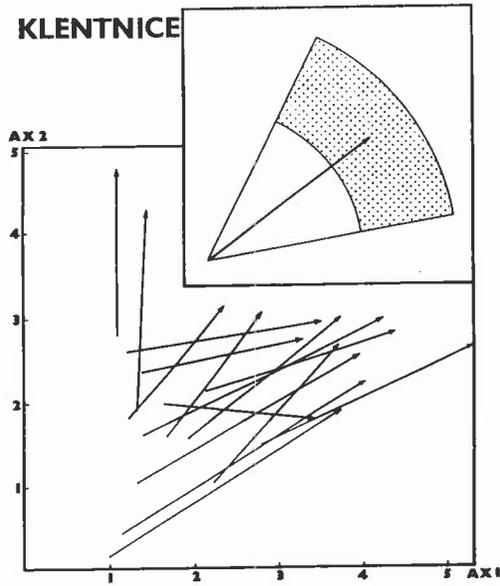


Fig. 1c. DCA ordination biplot: community vectors in species space with resultant vector with standard deviation of length and angle for Klentnice subset. Axes scaled in SD units.

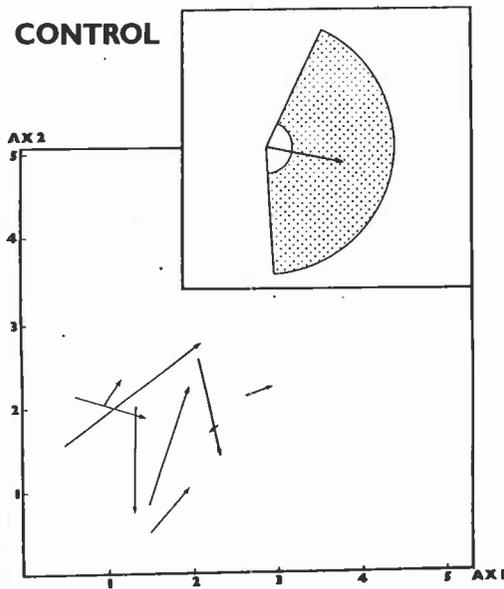


Fig. 1d. DCA ordination biplot: community vectors in species space with resultant vector with standard deviation of length and angle for control subset. Axes scaled in SD units.

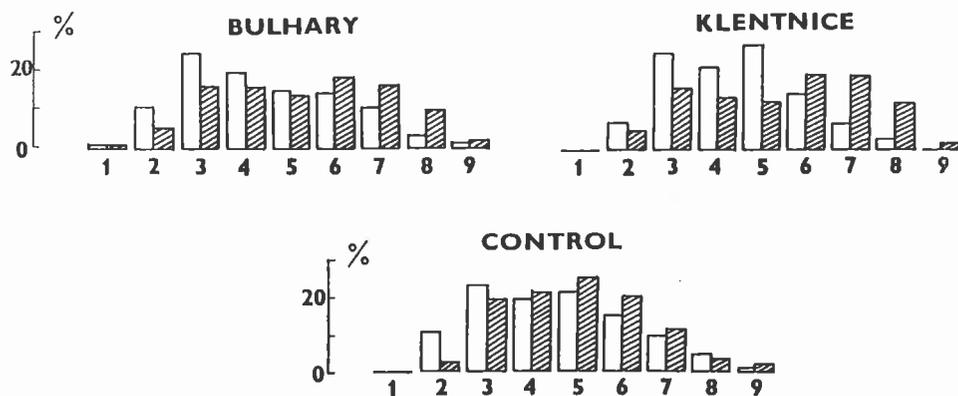


Fig. 2. Calibration for nitrogen. Abscissa figures are Ellenberg's indicator values. Open bars: percentage frequency in 1953/54, hatched bars: in 1992.

NITROGEN AND MOISTURE

Histograms (Fig. 2) show percentage performance of particular Ellenberg's indicator values for nitrogen. A clear trend in the decrease of species with low and average demands for nitrogen (species with values 2-5) and a simultaneous increase of species with higher demands (values 6-9) was found in the Klentnice subset. The same but less conspicuous pattern appeared in the Bulhary subset. The control subset is also characterized by an increase in percentage of nitrogen indicators but it is not so evident (decreases for values 2, 3, and 8, increases for values 4-7 and 9).

Fig. 3 depicts the same distribution for the moisture factor. In the Bulhary and the Klentnice subsets xerophilous species (species with values 2-4) had a greater part in the 1953/54 material than in the 1992 material. The reverse ratio can be seen for values 5-6. The species valued by 7 had the same, very low performance in both 1953/54 and 1992. The histogram for the control subset shows no clear trend because both xerophilous (values 2-4) and slightly hygrophilous (values 6-7) species decreased while the species characterized by 5 increased.

COVER OF FIELD AND SHRUB LAYERS

Results of the tests of the differences in field and shrub layer cover between particular years for particular subsets (Wilcoxon test) are shown in Tab. 1. A striking decrease in field layer cover was found in the Klentnice subset where the differences between 1953/54 and 1992 were significant at $P < 0.01$. On the average the cover had decreased to 33 % of the initial state. The field layer cover also decreased significantly at $P < 0.05$ to 77 % in the control subset between both times. The Bulhary subset showed even a slight increase which is not significant.

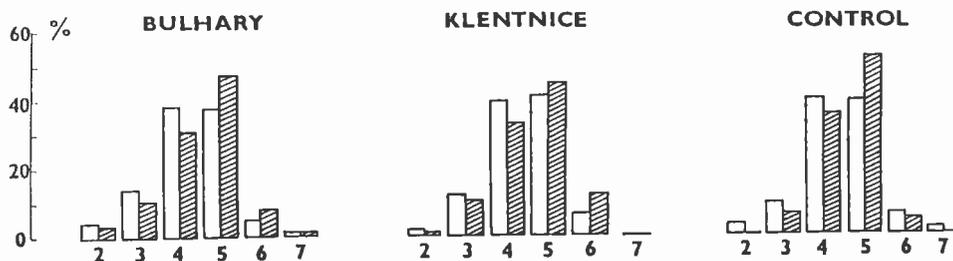


Fig. 3. Calibration for moisture. Abscissa figures are Ellenberg's indicator values. Open bars: percentage frequency in 1953/54, hatched bars: in 1992.

As for the shrub layer, a clear trend of cover decrease was found in both the game preserves (Bulhary and Klentnice subsets). Significant differences at $P < 0.01$ were shown in both subsets between particular years. On the average the cover decreased to 17 % in the Bulhary subset, 7 % in the Klentnice subset and increased to 103 % in the control subset compared with the cover recorded in 1953/54.

DIVERSITY

Differences in species richness, diversity (H') and evenness were tested using the t-test (Tab. 1).

Average species richness decreased in all the subsets between 1953/54 but this difference was significant only in the Klentnice subset ($P < 0.01$). Compared with 1953/54 species richness decreased on the average to 91 % in Bulhary, to 57 % in Klentnice and to 85 % in the control subset.

Significant decrease of H' appeared at $P < 0.01$ in the Klentnice subset and at $P < 0.05$ in the Bulhary subset. H' slightly decreased in the control subset as well but it was not significant. The average diversity decreased to 79 % in the Bulhary subset, to 69 % in the Klentnice subset and to 97 % in the control subset.

Differences in evenness were significant ($P < 0.01$) only in the Bulhary subset. Comparing this significant difference versus the insignificant difference in the Klentnice subset is interesting, with corresponding differences in species richness and diversity; it is suggested that in the Bulhary subset the diversity decreased particularly due to the increased dominance of some species populations while in the Klentnice subset, as a consequence of the decrease in species richness. Evenness in 1992 corresponded in the Bulhary subset to 81 %, in the Klentnice subset to 86 % and in the control subset to 102 % of the 1953/54 values.

Table 1. Differences in covers of particular layers and diversity parameters. Numbers indicate mean \pm standard deviation. Significance: ** - $P < 0.01$, * - $P < 0.05$, NS - not significant.

		1953/54	1992	
Cover E ₁ (%)	Bulhary	73 \pm 24	76 \pm 10	NS
	Klentnice	79 \pm 12	26 \pm 19	**
	Control	79 \pm 10	61 \pm 13	*
Cover E ₂ (%)	Bulhary	25 \pm 23	4 \pm 9	**
	Klentnice	28 \pm 18	2 \pm 3	**
	Control	23 \pm 15	24 \pm 20	NS
No. of species	Bulhary	25.6 \pm 8.5	23.2 \pm 4.7	NS
	Klentnice	30.4 \pm 5.2	17.4 \pm 6.6	**
	Control	25.3 \pm 13.2	21.6 \pm 6.3	NS
Diversity (H')	Bulhary	1.95 \pm 0.52	1.55 \pm 0.39	*
	Klentnice	2.29 \pm 0.32	1.58 \pm 0.47	**
	Control	1.81 \pm 0.66	1.76 \pm 0.50	NS
Evenness	Bulhary	0.61 \pm 0.15	0.49 \pm 0.11	**
	Klentnice	0.67 \pm 0.08	0.58 \pm 0.21	NS
	Control	0.56 \pm 0.13	0.58 \pm 0.14	NS

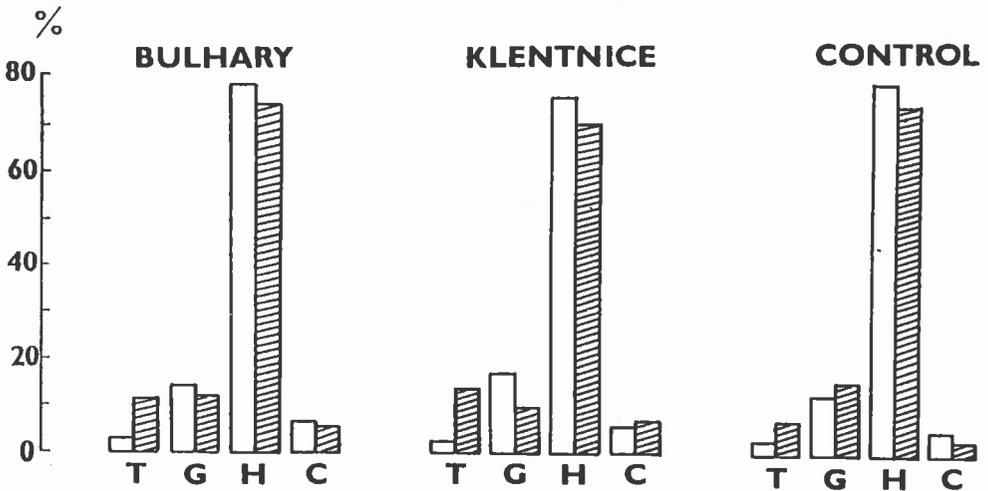


Fig. 4. Percentage frequency of life forms in 1953/54 (open bars) and 1992 (hatched bars). T: therophytes, G: geophytes, H: hemikryptophytes, C: chamaephytes.

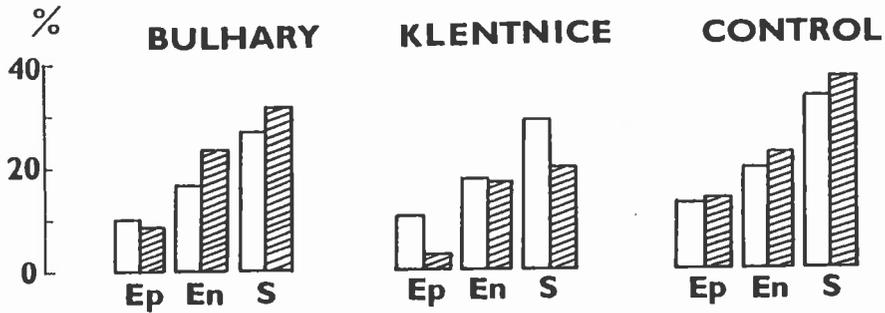


Fig. 5. Percentage frequency of zoochore species in 1953/54 (open bars) and 1992 (hatched bars). Ep: epizoochores, En: endozoochores, S: total zoochores.

LIFE FORMS

Fig. 4 shows the changes in frequencies of particular life forms (RAUNKIAER 1934). In all the subsets the frequency of hemikryptophytes decreased slightly. Therophyte frequency increased in all the subsets, the least in the control and the most in Klentnice. Geophytes increased in the control while in the other subsets they decreased, less in Bulhary and more in Klentnice. The changes in chamaephyte frequencies were small with a slight increase in Klentnice, a moderate decrease in Bulhary, and a slightly higher decrease in the control subset.

ZOOCHORES

Changes in percentage frequencies of zoochore species are shown in histograms in Fig. 5. The proportion of these species increased in the control and Bulhary subsets. In the control subset the proportions of both epi- and endozoochores increased while in the Bulhary subset epizoochores decreased and endozoochores increased. In the Klentnice subset both epi- and endozoochores decreased.

DISCUSSION

LIMITS TO THE INTERPRETATION OF THE RESULTS

Analyses of phytosociological data for other purposes than making vegetation surveys is a rare topic in vegetation science. Such a study faces some particular problems, mainly concerning the reliability of results. The numerical techniques and handling of data may also affect the results. In this context, there are some issues to be pointed out:

(1) Vectors in reduced two- or three- dimensional space are frequently used in ecological ordination literature to demonstrate community changes through time (VAN DER MAAREL 1969, AUSTIN 1977, McCUNE 1992 etc.). Detrended correspondence analysis appears to be an ideal tool for this purpose and its common use makes it possible to compare results of different studies (for some recent examples of the use of DCA in this way see e.g. GROOTJANS et al. 1991 or WHITTAKER 1991). However, there is some evidence that ecological gradients may be recovered in an unacceptable manner, especially by the second and higher DCA axes (e.g. VAN GROENEWOUD 1992). In our case, the interpretation of the second DCA axis as a "moisture gradient" must be approached from this point of view. However, since the calibration for moisture indicated the same trend as DCA, we can conclude a hypothesis that the higher stocking rate implies replacing of the mesic field-layer plants by xeric ones.

(2) Results of an ordination depend on the transformation of the input data. The transformation to cover % values used in the present analysis lays a strong emphasis on dominance (cf. VAN DER MAAREL 1979). To explain variation in plant communities, this is usually not recommended, since it generally gives worse results than intermediate transformations with balanced emphasis on presence and dominance (cf. JENSEN 1978, VAN DER MAAREL 1979, KOVÁŘ and LEPŠ 1986). Transformation to cover percentage values is also found to increase the bias caused by sampling by different researchers (LEPŠ and HADINCOVÁ 1992). In the present study, however, besides the researcher bias, there is still another issue concerning error in re-establishing the sample plots. In some cases the re-established plot may have been located in another place than the original one and it may have not overlapped it at all, though it was located very close to it. From this point of view, the problem is to decide which transformation it is better to use, to obscure the location bias. Intermediate transformations may result in the overweighting of rare species which may have occurred in the original plot but not in the stands neighbouring it, in which the re-established plot may have been located. On the other hand, transformation to cover % values may lead to bad results if there was some variation in dominance in the forest field-layer, e.g. due to gap structure of the canopy etc. HORÁK sampled this vegetation for the purposes of a forest typological mapping, using a method distinguishing forest types intuitively mainly on the basis of certain combination of canopy trees with field-layer dominants. Consequently, he chose plots in "typical" stands, i.e. stands with as homogenous a field layer as possible, remote from the boundaries of forest types distinguished in this manner, that is from marked changes in field-layer dominance (HORÁK - pers. comm.). In the early 1950s, the study site was a comparatively homogenous, more or less even-aged, about 40-60 years old coppiced forest, without gap structure of canopy which could promote the development of a highly patterned field layer (HORÁK - pers. comm.). For this reason, transformation emphasizing dominance is believed to be more reliable in our case than intermediate or presence/absence transformations. It was confirmed by an additional running of the DCA with data subjected to the ordinal transformation of VAN DER MAAREL (1979) which produced results (not indicated in this paper) in which a large proportion of variation accounted for the heterogeneity of the 1953/54 data set with samples often richer in species. Nevertheless, we must approach the DCA results presented here as explaining mainly variation among the dominants, as indicated by the high eigenvalues for the first and second DCA axes. The fact that these results are acceptable follows from a dramatic shift in stands with a high stocking rate which affected not only the performance of rare species but also caused a marked change in dominants.

EFFECTS OF THE DIETARY AND BEHAVIORAL TRAITS OF THE GAME

The design of the present study does not make it possible to differentiate clearly between the impact of deer and mouflon on vegetation. For details we refer to the literary data.

The main diet of fallow deer consists of grasses but forbs, fruits, leaves and sprouts of trees are grazed and browsed as well (CHAPMAN and CHAPMAN 1975, SIEFKE and MEHLITZ 1975, HUSÁK 1986). Mouflon graze especially the field-layer vegetation and browsing on trees is also common, especially in winter when woody plants may make up the main part of the food. Mouflon are not particular about their food. The greater part of the food offered by the biotope is utilized (MOTTL 1960, ULOTH 1976, SABADOŠ and MANICA 1977, HEROLDOVÁ 1988, HOMOLKA 1991). While with deer the plants are predominantly browsed which is combined with grazing (HUSÁK 1986), with mouflon they are grazed which is combined with browsing: each part of the forked upper lip of the mouflon moves independently making it possible to graze the plants very close to the ground (MOTTL 1960, LOCHMAN 1979). Moreover, the pressure of mouflon hooves per unit area is higher than that of fallow deer and consequently trampling by mouflon has a greater impact (GRULICH 1978).

To sum up, the disturbance of vegetation caused by mouflon is greater than that caused by deer. That is why the more intensive changes revealed in the Klentnice subset can not be merely explained as a consequence of the higher stocking rate but also as the effect of the presence of mouflon.

Another important difference between deer and mouflon in the game preserves of the Milovický les forest is deer gathering in certain places in the forests while other places are not visited. On the other hand, mouflon do not appear to have this habit and stay in almost any place in the game preserve (HEROLDOVÁ - pers. comm.).

TEMPORAL PATTERNS OF CHANGE IN FOREST VEGETATION AFFECTED BY GAME

Ordination analysis revealed that the vegetation changes reflect the above mentioned dietary and behavioral traits of the game. Trajectory lengths were the shortest in the control subset, longer in the Bulhary subset with comparatively low numbers of game and the longest in the Klentnice subset with high numbers of game including a large proportion of mouflon. The highest standard deviation of trajectories in the Bulhary subset is probably a consequence of the variable intensity of game influence in various parts of the game preserve: there are considerable changes in some plots while in the others these are lower than the average change in the control subset. The control subset was expected to show only the deviations caused by random errors but it also revealed a systematic trend towards ruderalization. However, this is only natural, because the control plots were by no means "pure controls" strictly devoid of herbivore impact - they experienced "normal" grazing pressure characteristic of forests outside game preserves, which is low compared with that inside. Indeed the random component of error in the control subset was relatively strongly pronounced compared with the systematic trend, and it was shown by the high variance in the trajectory slope angles.

The analysis of changes in particular species performance proved the trends that ordination analysis indicated.

The calibration corroborated with the changes in species composition of the field layer that were mainly caused by an increase of the nitrogen supply in the soil. The soil is supplied by nitrogen in a large amount from animal excrement (sheep droppings contain 0.85 % nitrogen - GRULICH 1978).

Besides the ruderalization of the field layer, the second important trend was the habitat's drying out and consequent increase in the occurrence of xerophilous species, and the decrease of mesophilous species. This trend was confirmed by both ordination and calibration. It was found in both the game preserves but it is lacking in the control subset. These results suggest that the drying up of the habitat is closely related to the influence of game. It is probably caused by several factors. One of the most important ones is soil destruction. The soil becomes highly compacted, and it has a lower initial moisture content in spring and dries out faster in summer (STEINBRENNER 1951). The decrease in air humidity in the forest understorey is probably due to the removal of the shrub layer, although the soil water content in ungrazed areas may be lowered as a consequence of evaporation and the interception of rainfall by the dense cover (STEINBRENNER 1951). Severe impact on shrubs and subcanopy trees is obvious during forest grazing (ADAMS 1975, VEBLEN and STEWART 1982, VEBLEN et al. 1989).

Decreased diversity in the heavily grazed Klentnice Game Preserve was caused by the decrease in species richness due to heavy disturbance. On the contrary, in the Bulhary subset with a lower disturbance intensity the decrease of diversity was especially due to lowered evenness as a consequence of the increased dominance of some species (e.g. heliophyte species *Poa nemoralis* prefers light habitats with eliminated shrub layer).

As for the changes in the life form spectra, the proportion of therophytes and chamaephytes increased while that of geophytes decreased with increased grazing pressure. An increase of therophytes follows from the increased area of patches devoid of field and ground vegetation suitable for the establishment of therophyte populations. The causes of geophyte decrease and chamaephyte increase are harder to explain. A possible explanation for geophytes is their high allocation of underground tissues which may be disadvantageous in nutrient-rich habitats with a high intensity of disturbance. The increased proportion of chamaephytes may be the effect of increased drought which promotes chamaephyte growth versus hemikryptophytes in areas with comparatively warm winters.

Contrary to expectations, zoochore species decreased proportionally with increasing grazing pressure. Hence, changes in species composition of field layer were caused by the above mentioned changes in environmental conditions and not by direct plant dissemination by animals.

Another important feature of game preserves is the absence of natural forest regeneration. The data used did not allow analysis of this phenomenon but it was observed that the abundance of small woody plant seedlings increases. However, game impede their recruitment into larger size-classes. Similar regeneration patterns from forests affected by red deer were described by VEBLEN et al. (1989) from Patagonia.

CONCLUSION

Forest vegetation in the game preserves of the Milovický les forest is strongly affected by dense populations of fallow deer, red deer and mouflon. The main aspects of their impact are as follows:

1. Scrub layer and subcanopy trees are disturbed and sapling recruitment is prevented by browsing. Natural regeneration of the forest is impaired.
2. Increasing nitrogen supply in the soil from animal excrement and heavy grazing and trampling result in extensive ruderalization accompanied by the retreat of naturally occurring species and the invasion of synanthropophytes.

3. Changes in the forest microclimate due to understorey removal, together with presumable soil destruction and lowered water permeability, cause drying out. Mesic species are being replaced by xeric ones, usually of allochthonous origin.
4. Diversity of the field layer decreases. Under moderate grazing pressure this is caused by the increasing dominance of some species while under heavy pressure it is caused by decreasing species richness.

The results obtained indicate that high densities of game may cause damaging effects on understorey vegetation in oak and oak-hornbeam forests. For this reason conservation efforts have to focus on adopting measures to reduce or eliminate such density.

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Appendix

Species exchange survey. A - difference between occurrence frequencies in 1992 and 1953/54; B - occurrence frequency in 1953/54; C - occurrence frequency in 1992; D - percentage number of plots where the species retreated; E - percentage number of plots where the species occurred in 1953/54 and persisted in 1992; F - percentage number of plots where the species emerged (percentages sub D-F are related to the total number of plots where the species occurred in either 1953/54 or 1992); G - difference in median Braun-Blanquet cover grade between 1953/54 and 1992. Only the species occurring with a frequency of 25 % and more in any one of the sampling times in particular subset are included.

BULHARY	A	B	C	D	E	F	G
<i>Carex michelii</i>	-10	13	3	79	14	7	-1
<i>Ajuga genevensis</i>	-9	10	1	91	0	9	0
<i>Melittis melissophyllum</i>	-7	15	8	53	35	12	0
<i>Calamagrostis arundinacea</i>	-6	13	7	46	54	0	1
<i>Iris variegata</i>	-6	6	0	100	0	0	-2
<i>Milium effusum</i>	-6	6	0	100	0	0	-2
<i>Polygonatum multiflorum</i>	-6	8	2	78	11	11	-0.5
<i>Pyrethrum corymbosum</i>	-6	11	5	64	14	22	0
<i>Carex muricata</i> s.l.	-6	14	8	53	29	18	0
<i>Carex montana</i>	-6	14	8	43	57	0	-0.5
<i>Verbascum austriacum</i>	-5	5	0	100	0	0	-1
<i>Fragaria moschata</i>	-5	10	5	58	25	17	-1
<i>Hieracium sabaudum</i>	-5	10	5	58	25	17	0
<i>Campanula trachelium</i>	-4	5	1	83	0	17	0
<i>Ranunculus auricomus</i>	-3	7	4	60	10	30	0
<i>Astragalus glycyphyllos</i>	-3	6	3	57	29	14	-0.5
<i>Veronica vindobonensis</i>	-3	10	7	56	6	38	0
<i>Veronica officinalis</i>	-3	8	5	55	18	27	0
<i>Lathyrus niger</i>	-3	13	8	47	40	13	-1
<i>Pulmonaria officinalis</i>	-3	12	9	40	40	20	-1.5
<i>Convallaria majalis</i>	-3	15	12	37	42	21	-2
<i>Clinopodium vulgare</i>	-2	12	10	33	47	20	0
<i>Lathyrus vernus</i>	-2	14	12	25	63	12	0
<i>Campanula persicifolia</i>	-1	7	6	46	54	0	0
<i>Viola mirabilis</i>	-1	8	7	36	36	28	0
<i>Brachypodium pinnatum</i>	-1	8	7	30	50	20	0.5
<i>Dictamnus albus</i>	-1	11	10	9	91	0	-1.5
<i>Poa nemoralis</i>	0	21	21	5	90	5	2
<i>Brachypodium sylvaticum</i>	0	13	13	7	86	7	0
<i>Buglossoides purpureocaerulea</i>	0	9	9	18	64	18	-1
<i>Campanula rapunculoides</i>	0	7	7	30	40	30	0
<i>Scrophularia nodosa</i>	0	6	6	40	20	40	0
<i>Moehringia trinervia</i>	0	7	7	42	16	42	-1
<i>Melica uniflora</i>	1	5	6	14	57	29	0
<i>Fragaria vesca</i>	1	7	8	38	15	47	0
<i>Mercurialis perennis</i>	2	7	9	10	60	30	1

<i>Hieracium murorum</i>	2	5	7	22	33	45	-1
<i>Bromus benekenii</i>	3	6	9	10	50	40	0
<i>Galium aparine</i>	3	4	7	25	22	56	1
<i>Dactylis polygama</i>	4	17	21	4	73	23	1
<i>Viola hirta</i>	4	3	7	12	25	63	0
<i>Taraxacum officinale</i> s.l.	4	1	5	17	0	83	-1
<i>Festuca heterophylla</i>	5	11	16	16	42	42	0
<i>Alliaria petiolata</i>	5	4	9	18	18	64	0
<i>Viola reichenbachiana</i>	6	3	9	0	33	67	-1
<i>Mycelis muralis</i>	6	0	6	0	0	100	2
<i>Galium sylvaticum</i>	7	8	15	17	27	56	-1
<i>Geum urbanum</i>	7	7	14	13	31	56	0
<i>Geranium robertianum</i>	7	0	7	0	0	100	2
<i>Impatiens parviflora</i>	7	0	7	0	0	100	2
<i>Lapsana communis</i>	8	4	12	14	14	72	1
<i>Cardamine impatiens</i>	8	2	10	0	20	80	0
<i>Fallopia dumetorum</i>	9	4	13	13	13	74	0
<i>Urtica dioica</i>	11	0	11	0	0	100	2

KLENTNICE

	A	B	C	D	E	F	G
<i>Convallaria majalis</i>	-15	15	0	100	0	0	-3
<i>Pulmonaria officinalis</i>	-13	13	0	100	0	0	-2
<i>Melittis melissophyllum</i>	-11	13	2	85	15	0	-1
<i>Milium effusum</i>	-10	10	0	100	0	0	-2
<i>Carex michelii</i>	-10	10	0	100	0	0	-2
<i>Lathyrus vernus</i>	-10	14	4	71	29	0	-1.5
<i>Polygonatum multiflorum</i>	-9	9	0	100	0	0	-2
<i>Galium odoratum</i>	-8	9	1	89	11	0	-1
<i>Solidago virgaurea</i>	-7	7	0	100	0	0	-2
<i>Clinopodium vulgare</i>	-7	9	2	80	10	10	-1
<i>Pyrethrum corymbosum</i>	-7	10	3	70	30	0	-1
<i>Calamagrostis arundinacea</i>	-6	6	0	100	0	0	-3
<i>Fragaria moschata</i>	-6	6	0	100	0	0	-2.5
<i>Asarum europaeum</i>	-6	10	4	60	40	0	-1.5
<i>Vicia dumetorum</i>	-5	5	0	100	0	0	-2
<i>Digitalis grandiflora</i>	-5	5	0	100	0	0	-2
<i>Scrophularia nodosa</i>	-5	6	1	86	0	14	-2
<i>Sedum maximum</i>	-5	6	1	83	17	0	0
<i>Campanula trachelium</i>	-5	6	1	83	17	0	0
<i>Fragaria vesca</i>	-5	7	2	76	12	12	0
<i>Lathyrus niger</i>	-5	11	6	45	55	0	-0.5
<i>Dentaria bulbifera</i>	-4	4	0	100	0	0	-3
<i>Melampyrum nemorosum</i>	-4	4	0	100	0	0	-2
<i>Astragalus glycyphyllos</i>	-4	4	0	100	0	0	-2
<i>Buglossoides purpurocaerulea</i>	-4	4	0	100	0	0	-2
<i>Pimpinella major</i>	-4	4	0	100	0	0	-2
<i>Galium album</i>	-4	4	0	100	0	0	-2
<i>Serratula tinctoria</i>	-4	4	0	100	0	0	-1
<i>Hypericum montanum</i>	-4	5	1	83	0	17	0

<i>Hieracium sabaudum</i>	-4	7	3	62	25	13	-1
<i>Veronica vindobonensis</i>	-4	9	5	58	17	25	0
<i>Festuca heterophylla</i>	-4	10	6	50	33	17	-2
<i>Dactylis polygama</i>	-4	15	11	27	73	0	-1
<i>Galium sylvaticum</i>	-4	15	11	27	73	0	-1
<i>Poa nemoralis</i>	-4	15	11	27	73	0	-1
<i>Hypericum hirsutum</i>	-3	4	1	80	0	20	-1
<i>Bromus benekenii</i>	-3	4	1	75	25	0	-1
<i>Geum urbanum</i>	-3	5	2	67	17	17	-1
<i>Veronica officinalis</i>	-2	9	7	46	23	31	0
<i>Carex muricata</i> s.l.	-1	4	3	50	17	33	0
<i>Melica uniflora</i>	1	9	10	17	58	25	-1
<i>Viola hirta</i>	1	3	4	0	75	25	0
<i>Campanula persicifolia</i>	1	6	7	22	45	33	0.5
<i>Brachypodium sylvaticum</i>	2	4	6	14	43	43	0
<i>Lapsana communis</i>	2	3	5	16	34	50	0
<i>Hypericum perforatum</i>	3	5	8	20	30	50	0
<i>Alliaria petiolata</i>	4	0	4	0	0	100	-1.5
<i>Poa angustifolia</i>	4	0	4	0	0	100	2
<i>Artemisia absinthium</i>	5	0	5	0	0	100	1
<i>Polygonum aviculare</i>	5	0	5	0	0	100	2
<i>Viola reichenbachiana</i>	7	3	10	9	18	73	0
<i>Campanula rapunculoides</i>	7	0	7	0	0	100	2
<i>Taraxacum officinale</i> s.l.	8	0	8	0	0	100	0.5
<i>Fallopia dumetorum</i>	9	1	10	0	10	90	0
<i>Moehringia trinervia</i>	13	2	15	6	6	88	0
<i>Urtica dioica</i>	14	0	14	0	0	100	2

CONTROL

	A	B	C	D	E	F	G
<i>Dictamnus albus</i>	-4	4	0	100	0	0	-2
<i>Melittis melissophyllum</i>	-4	7	3	57	43	0	0
<i>Galeopsis pubescens</i>	-3	3	0	100	0	0	-2
<i>Veronica officinalis</i>	-3	3	0	100	0	0	-2
<i>Sedum maximum</i>	-3	3	0	100	0	0	-1
<i>Melampyrum pratense</i>	-2	3	1	75	0	25	0
<i>Clinopodium vulgare</i>	-2	3	1	67	33	0	-1
<i>Carex muricata</i> s.l.	-2	3	1	67	33	0	0
<i>Carex michelii</i>	-2	4	2	60	20	20	0
<i>Ranunculus auricomus</i>	-2	3	4	50	25	25	0
<i>Carex montana</i>	-2	8	6	25	75	0	-1.5
<i>Astragalus glycyphyllos</i>	-1	3	2	60	0	40	0
<i>Veronica vindobonensis</i>	-1	4	3	40	40	20	0
<i>Lathyrus niger</i>	-1	4	3	25	75	0	0
<i>Convallaria majalis</i>	-1	9	8	20	70	10	-0.5
<i>Dactylis polygama</i>	-1	8	7	13	87	0	1
<i>Pulmonaria officinalis</i>	-1	9	8	11	89	0	0
<i>Hieracium sabaudum</i>	0	4	4	0	100	0	-0.5
<i>Poa nemoralis</i>	0	7	7	12	76	12	2
<i>Fragaria moschata</i>	0	7	7	22	56	22	0
<i>Asarum europaeum</i>	0	3	3	25	50	25	0
<i>Brachypodium sylvaticum</i>	0	3	3	40	20	40	0

<i>Lathyrus vernus</i>	1	7	8	0	88	12	-1
<i>Viola mirabilis</i>	1	4	3	40	40	20	0
<i>Geum urbanum</i>	1	3	4	0	75	25	-1
<i>Festuca heterophylla</i>	1	6	7	12	63	25	0.5
<i>Moehringia trinervia</i>	1	4	5	16	50	34	0.5
<i>Pyrethrum corymbosum</i>	1	3	4	20	40	40	-0.5
<i>Polygonatum multiflorum</i>	1	3	4	33	17	50	1
<i>Galium sylvaticum</i>	2	6	8	0	75	25	-1
<i>Galium odoratum</i>	2	3	5	0	60	40	-2
<i>Milium effusum</i>	2	2	4	20	20	60	0
<i>Scrophularia nodosa</i>	2	1	3	0	33	67	-1
<i>Buglossoides purpureocaerulea</i>	2	1	3	25	0	75	1
<i>Campanula rapunculoides</i>	2	1	3	25	0	75	-1
<i>Hieracium murorum</i>	2	1	3	25	0	75	1
<i>Melica nutans</i>	3	0	3	50	0	50	3
<i>Impatiens parviflora</i>	3	0	3	0	0	100	3
<i>Bromus benekenii</i>	4	1	5	17	0	83	1
<i>Fallopia dumetorum</i>	5	1	6	0	17	83	1