



A comparison of vegetation patterns in the tree and herb layers of a hardwood forest

T. Tobisch¹ and T. Standovár²

¹ Corresponding author. Department of Silviculture and Yield, Forest Research Institute, Frankel Leó út 42–44, H–1023 Budapest, Hungary. Fax: +36-1-326-1639, E-mail: tobischt@erti.hu

² Department of Plant Taxonomy and Ecology, Eötvös University, Pázmány s. 1/c, H-1117 Budapest, Hungary. Fax: +36-1-381-2188, E-mail: standy@ludens.elte.hu

Keywords: Dendrogram, Distance matrix, Forest layers, Full randomization tests, Mantel-test, Meta-analysis, Monte Carlo simulation, Pattern, Permutation tests.

Abstract: Meta-analysis is used to compare the patterns of the tree and the herb layers in a Central-European deciduous hardwood forest. Vegetation patterns are represented by distance matrices and dendrograms. The significance of the relation between the patterns is evaluated through permutation (Mantel) tests and full randomization (Monte Carlo simulation) tests. The relationship between the two layers is significant but weak. When using ecological indicators as variables for characterising the herb layer, the relation is stronger. Distance matrices and dendrograms describe the vegetation pattern similarly. However, the results of pairwise tests of significance strongly depend on the “level” of comparisons, i.e., whether distance matrices or dendrograms are compared. This follows perhaps from the differences between permutation and full randomization tests.

Nomenclature: Simon (2000) for vascular plants.

Abbreviations: 98 – herb data collected in the summer; 99 – herb data collected in the spring; A – basal area of the tree species; Ch – chord distance; CO – combined data of the herbs; Eu – Euclidean distance; i – frequency data of the ecological indices; N – abundance of the tree species; ns – no standardization; R – relative basal area of the tree species; rs – range standardization. (For example, Euns98 refers to one distance matrix or one dendrogram obtained from species frequency data of the summer herb layer with Euclidean distance and without standardization. Euns98i refers to one distance matrix or one dendrogram obtained in the same way, but from the quadrats by ecological indicators data matrix.)

Introduction

In forests, there is a strong relation between the tree and the herb layers, because the former controls the latter in some direct and indirect ways (Fekete 1974, Peet 1978, Miyata 1983, Gagnon and Bradfield 1986, Skov 1997, Aude and Lawesson 1998, Berger and Puettmann 2000, McKenzie et al. 2000), but coincidence is also conceivable (Del Moral and Watson 1978, Gagnon and Bradfield 1986). However, several authors (Bratton 1975, Glenn-Levin 1977, McCune and Antos 1981, Bradfield and Scagel 1984, Whitney and Foster 1988, Sayers and Lyon 1997, Ewald 2000) found that the pattern of herbs was more or less independent from the pattern of trees. It could be explained, for example, by the following:

- The macroclimate influencing the composition of the tree stand can strongly differ from within-stand climatic factors influencing the composition and the pattern of the herbaceous vegetation;
- Natural and artificial disturbance modifies the two patterns differently;
- The microhabitats in the forests can compensate for the differences between the tree stands.

To examine the relationship between the tree stand and the herb layer (or between any vegetation patterns) three problems must be solved: 1) the pattern of the two layers must be described accurately in a mathematical way; 2) the patterns described must be compared objectively, and 3) the significance of the relation must be

tested. For these three steps, a large body of mathematical tools is available. Methods describing pattern in form of mathematical constructs (OUCs: operational units of comparisons, Podani 1989b, i. e., distance matrices, ordinations, dendrograms) are widely available, they have been compared, for example, by Sokal and Rohlf (1962), Gauch and Whittaker (1972), Campbell (1978), Hajdu (1981), Feoli et al. (1984), Podani (1985, 2000), Kenkel and Orlóci (1986), Batagelj (1995). Comparisons, significance tests and multivariate analyses of results – which can be called meta-analysis (Glass 1976) – are much less known (but see for example: Podani 1989b). Through comparing the patterns of the tree stand and the herb layer, we explore the possibility of using meta-analysis in ecological studies.

We examine three main questions:

- How strong is the relationship between the two layers in a Central European, broad-leaved, managed mixed forest?
- Can we measure the strength of this relationship?

- What are the main differences between the results if the patterns are compared at the distance matrix versus dendrogram level?

Study area

The study area is a 40-year-old stand (around 430 m above sea level) of approximately 6 hectares in the Börzsöny Mountains, northern Hungary. The mean annual precipitation is 550 – 600 mm at the foothills and 800 mm at 800 m above sea level (Danszky 1963). The mean annual temperature at 800 m is 6–6.5 °C, the yearly fluctuation is 19–20 °C (Danszky 1963). The bedrock is andesite (Danszky 1963). According to forestry data the stand is located on ranker soil (Járó 1962). The dominant tree species of this forest are sessile oak (*Quercus petraea*), beech (*Fagus sylvatica*) and lime (*Tilia cordata*). Some patches are characterised by high cover of hornbeam (*Carpinus betulus*) and Turkey oak (*Quercus cerris*). These tree species form more or less pure patches in the forest, but in some parts they are mixed (Fig. 1). The abundance of shrubs is very low. In the southern part of the stand,

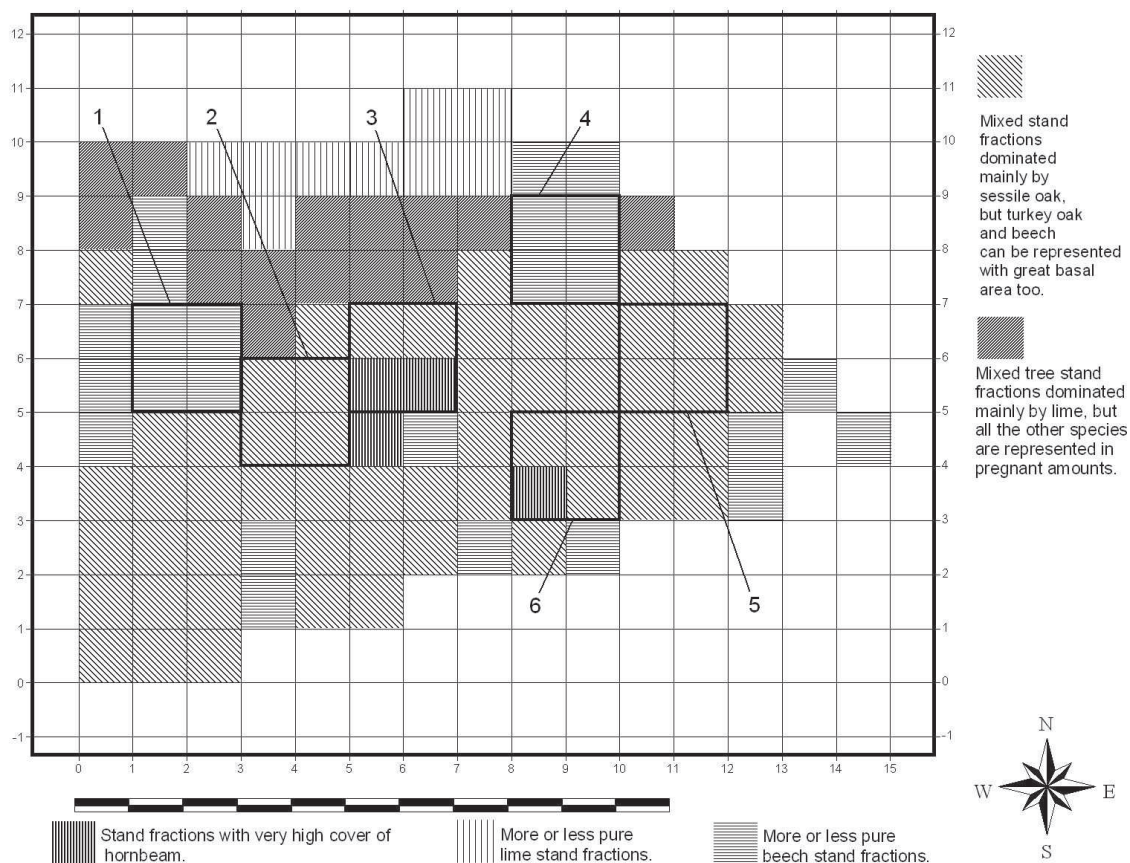


Figure 1. The map of the tree stand. The sampling plots are framed with thick lines and numbered. The different patterns mean different tree species composition.

Melica uniflora and *Carex pilosa* dominate in the herb layer indicating relatively low canopy closure. Under beech and lime patches in the northern part of the forest, the cover of the herbs decreases, but in the spring *Dentaria bulbifera* (on the slopes) and *Ficaria verna* (on less steep places with deeper soil) are abundant in these patches. The south-eastern part of the stand is a little more humid than the other parts (indicated by the great abundance of *Galeobdolon luteum*). Other abundant herbs in the stand are *Galium odoratum*, *Campanula rapunculoides*, *Galium aparine* and *Viola sylvestris*.

Methods

Sampling

The study area was covered with a grid composed of 25 m × 25 m cells (Tobisch 2000, Fig. 1). In these 109 cells, the girth of all trees (greater than 5 cm in perimeter at breast height) was measured. Hierarchical classification of the 25 m × 25 m cells was carried out to find larger patches with similar tree species composition (Tobisch 2000). We used total basal area/species to describe the species composition of each cell, since basal area reflects the importance of a species much better than the number of individuals. Based on the classification results, we managed to select six 50 m × 50 m plots. These plots constitute three pairs, each having similar tree species composition. Processes and changes in the vegetation patterns will be monitored in these plot-pairs in the future.

Each 50 m × 50 m plot consisted of four 25 m × 25 m cells (subplots). In the centre of each subplot, herb layer was sampled twice (in summer 1998, and in spring 1999) in one 5 m × 5 m quadrat. Each quadrat was subdivided into 0.5 m × 0.5 m microquadrats, in which presence/absence data of vascular species were recorded and the number of individuals was estimated for the early spring geophytes.

Data and their analysis

The number of individuals, the basal area and the relative basal area (the basal area of the given species divided by the total basal area of all species) were used as variables for describing the composition of the tree stand. In this way, we obtained three data matrices abbreviated by: N, A and R. The size of these matrices was 24 subplots × 6 species each.

F-type analyses. In this kind of the data processing, species frequencies served as variables for describing the herb layer. Three data sets were used for further analyses: the spring, the summer and the combined data sets referred to as 98 (size: 24 quadrats × 50 species), 99 (size:

24 quadrats × 51 species) and CO (size: 24 quadrats × 61 species).

I-type analyses. For these analyses, we used quadrats by ecological indicator values data matrices (Feoli 1984). In these matrices, each column represents a character state of one of the ecological indices. The value in the i^{th} row and j^{th} column is the total frequency of herb species possessing the j^{th} value of the given index in the i^{th} quadrat. Indicators showing water, light and pH requirements of the species were used as suggested by Borhidi (1995). Similarly to the F-type analyses, we had three data matrices: 98i, 99i and COi, each with the same dimensions: 24 quadrats × 17 ecological indicator character states.

Pairwise comparisons of distance matrices. Resemblance matrices of quadrats were calculated using Euclidean distances with and without standardization by range within variables (abbreviated as Eurs and Euns, respectively) and chord distances (Orlóci 1978, abbreviated as Chns). In this way, two standardization methods (range and chord) were applied to reduce the influence of the dominant species and increase that of the rare species on the results. When the relative basal area of the species served as variables, only Euclidean distance was calculated without standardization. In this way, we had a total of 16 distance matrices. The distance matrices were compared with matrix correlation (Sneath and Sokal 1973). The significance of matrix correlations was tested with the Mantel-test (Mantel 1967), in which the rows and the corresponding columns of one of the matrices being compared were permuted randomly. In 1000 randomizations, the permuted matrices were compared to the intact matrix to yield the distribution of matrix correlation to be used in significance testing.

Pairwise comparisons of dendrograms. Hierarchical classifications were derived from the distance matrices with global optimisation (Podani 1989a). The dendrograms were characterised with a level-free descriptor, cluster membership divergence (Podani and Dickinson 1984) and compared with Euclidean distance. The significance of the similarity was evaluated through Monte Carlo simulation (Steel and Penny 1993), randomizing not only the sequence of the objects but also the structure of the whole dendrogram. That is, not only the sequence of the objects is randomized (which would correspond to a permutation test), but also the whole topology of the dendrograms and the sequence of the hierarchical levels. The number of possible cases is therefore much higher in this case. Another important difference between the permutation and the full randomization tests is that in the former case the distribution must be created for each pairwise comparison, whereas one distribution is enough for den-

dograms having equal number of objects. That's why permutation tests are always much more case-dependent than full randomization tests.

Principal coordinates analysis of distance matrices and dendrograms. To answer the third question more precisely, principal coordinates ordinations (Torgerson 1952, Gower 1966) of distance matrices and dendrograms were created. The complements of matrix correlations were used to express resemblance between distance matrices and Euclidean distances were calculated between descriptor matrices of dendrograms. The ordinations of distance matrices and dendrograms were compared with Procrustes analysis (Green 1952, Gower 1971, Schönemann and Carroll 1970) and the significance of the similarity of the ordinations was evaluated with the randomization technique (Podani 1991). For Procrustes adjustments the first three dimensions of the ordinations being compared were considered.

SYN-TAX 5.02 and SYN-TAX 2000 program packages (Podani 1993, 2001) were used for data processing.

Results

Both F-type and I-type analyses found significant relationships between the tree and herb layers at both levels of comparisons (distance matrix, dendrogram). However, the values of the matrix correlation coefficients are quite low (Tables 1-2). All values are below 0.3 in the case of F-type analyses. Stronger relationship is manifested when the herb species are replaced with indices showing their ecological requirements. It is evident from the higher mean value of the correlation coefficients and from the higher level of significance. It is also clear from the examinations of the dendrograms (see Tables 3-4).

In the ordinations, dendrograms and distance matrices are more or less separated (see Figures 2-5). As these fig-

Table 1. Matrix correlation among distance matrices of tree and herb layers. Herbs data are expressed as species frequencies (F-type analyses). Significance levels are *: $0.01 < p < 0.05$; **: $p \leq 0.01$.

	Euns98	Eurs98	Chns98	Euns99	Eurs99	Chns99	EunsCO	EursCO	ChnsCO
EunsN	0.092	0.042	0.093	0.175	0.132	0.169*	0.120	0.098	0.178*
EursN	0.138	0.236*	0.010	0.222*	0.276**	0.035	0.160	0.246*	0.045
ChnsN	0.064	-0.013	0.152*	0.208*	0.087	0.178*	0.160*	0.053	0.219**
EunsA	0.080	-0.040	0.134	0.200*	0.051	0.265*	0.171	0.030	0.284**
EursA	0.030	-0.032	0.111	0.191	0.092	0.087	0.133	0.065	0.137
ChnsA	0.051	-0.030	0.147*	0.206*	0.080	0.139*	0.159	0.048	0.189**
EunsR	0.055	-0.084	0.155*	0.178	0.011	0.234*	0.145	-0.011	0.261**

Table 2. Matrix correlation among distance matrices of tree and herb layers. Data matrices of the herb layer are quadrats by ecological indicators matrices. In this matrix, each column represents a character state of one of the ecological indices. The value in the i th row and j th column is the total frequency of herb species possessing the j th value of the given index in the i th quadrat (I-type analyses). Indicators showing water, light and pH requirements of the species as suggested by Borhidi (1995) were used. *: $0.01 < p < 0.05$; **: $p \leq 0.01$.

	Euns98i	Eurs98i	Chns98i	Euns99i	Eurs99i	Chns99i	EunsCOi	EursCOi	ChnsCOi
EunsN	0.232*	0.182	0.133	0.324**	0.274*	0.252**	0.277*	0.231*	0.215**
EursN	0.249*	0.288**	0.038	0.294**	0.317**	0.267**	0.234*	0.241*	0.202*
ChnsN	0.219*	0.172*	0.199*	0.362**	0.284**	0.273**	0.331**	0.259**	0.260**
EunsA	0.231*	0.151	0.200*	0.382**	0.264**	0.262**	0.367**	0.273**	0.260**
EursA	0.157	0.120	0.148	0.273**	0.216*	0.214**	0.231*	0.172	0.197*
ChnsA	0.224**	0.174*	0.209*	0.378**	0.285**	0.303**	0.348**	0.269**	0.295**
EunsR	0.209*	0.140	0.239**	0.371**	0.256**	0.283**	0.347**	0.256*	0.287**

Table 3. Euclidean distances among dendrogram descriptor matrices calculated by using F-type analyses of tree and herb data. *: $0.01 < p < 0.05$; **: $p \leq 0.01$.

	Euns98	Eurs98	Chns98	Euns99	Eurs99	Chns99	EunsCO	EursCO	ChnsCO
EunsN	166.31	158.73*	173.82	165.09	172.09	170.02	167.15	165.22	167.45
EursN	185.12	177.39	192.90	186.82	180.66	189.25	183.88	176.89	187.95
ChnsN	163.97	166.58	163.26	160.80	174.52	173.70	165.64	170.93	168.18
EunsA	170.19	167.80	176.48	164.24	171.47	175.10	164.44	165.67	167.96
EursA	167.96	166.13	183.56	175.43	156.49*	176.38	165.65	154.96*	174.67
ChnsA	171.62	160.95	171.85	169.17	164.58	175.58	165.95	164.79	166.83
EunsR	166.05	165.70	171.58	164.08	164.24	169.92	160.52	163.69	162.18

Table 4. Euclidean distances among dendrogram descriptor matrices calculated by using I-type analyses of tree and herb data. *: $0.01 < p < 0.05$; **: $p \leq 0.01$.

	Euns98i	Eurs98i	Chns98i	Euns99i	Eurs99i	Chns99i	EunsCOi	EursCOi	ChnsCOi
EunsN	169.10	153.02*	178.74	162.88	160.08	169.20	162.35	166.79	165.11
EursN	182.96	179.00	188.42	180.26	180.06	185.32	183.86	185.52	185.18
ChnsN	169.16	160.39	178.26	167.72	164.62	164.97	161.38	171.35	165.05
EunsA	165.86	164.95	174.73	165.29	160.45	161.81	151.78*	169.84	162.60
EursA	164.26	162.92	173.05	142.00**	134.39**	163.32	158.93*	153.27*	168.33
ChnsA	169.49	153.91*	178.20	154.21*	152.13*	170.85	162.59	165.11	166.59
EunsR	163.34	161.75	166.73	154.91*	145.99**	154.79*	148.54**	161.59	156.56*

ures show, the pattern of separation is dependent on the variables used (tree versus herb data), i.e., in most cases distance matrices and dendrograms based on tree data are separated from those of herb data along the first ordination axis. However, the applied resemblance functions also affect the results. The effect of data standardization on the separation of OUCs is negligible.

The ordinations of the OUCs are significantly similar in both cases ($SSQ = 0.215$ for the F-type analyses and $SSQ = 0.258$ for the I-type analyses; $p < 0.01$ in both cases). Consequently, the results seem to be unaffected by the level of comparison (i.e., whether distance matrices or dendrograms are compared). However, there are many fewer significant relationships at the level of the dendrograms according to the pairwise comparisons.

Discussion

One possible reason for the weak relationship between the tree stand and the herbaceous vegetation is the

disturbance regime of the forest. Intensive forestry activity and high pressure of ungulates (browsing, trampling) play the main roles in this regime. The obtained dendrograms (not shown) indicate that the pattern of the herb layer is very heterogeneous. Lower heterogeneity was found when species were replaced with their ecological indices. It means perhaps that the steady state equilibrium sensu Cajander (1926), or Borman and Likens (1981) could not have developed yet and may never be reached because of the intensive disturbance. So, the herbaceous vegetation could not have adapted to the local conditions (including the tree stand-structure also greatly influenced by forestry treatments).

Some studies have shown that the recovery of the herbaceous vegetation can be rather fast after management activities of the forest, and – in other cases – the original pattern of the herb layer can be more or less unaffected by these artificial disturbances (see Grigal and Arnemann 1978, Halpern 1989, Halpern and Franklin 1990, Hughes and Fahey 1991, Gilliam et al. 1995, Halpern and Spies

Figure 2. Principal coordinates ordination of distance matrices in F-type analysis before Procrustes adjustments. The first two axes explain a total of 73.65% of the total variance.

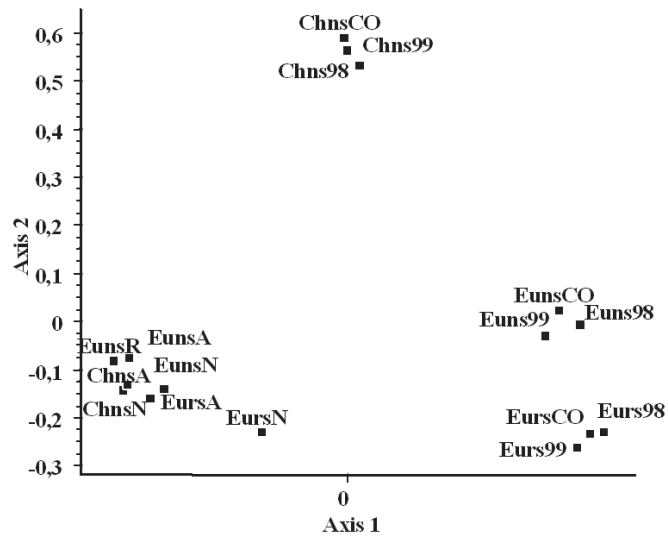


Figure 3. Principal coordinates ordination of distance matrices in I-type analysis before Procrustes adjustments. The first two axes explain a total of 29.81% of the total variance.

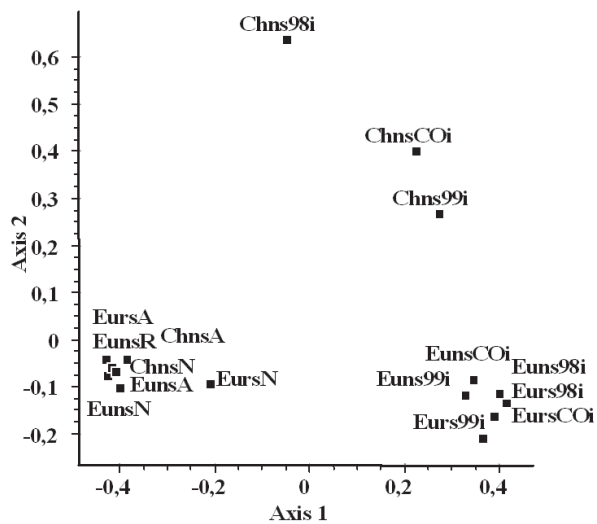
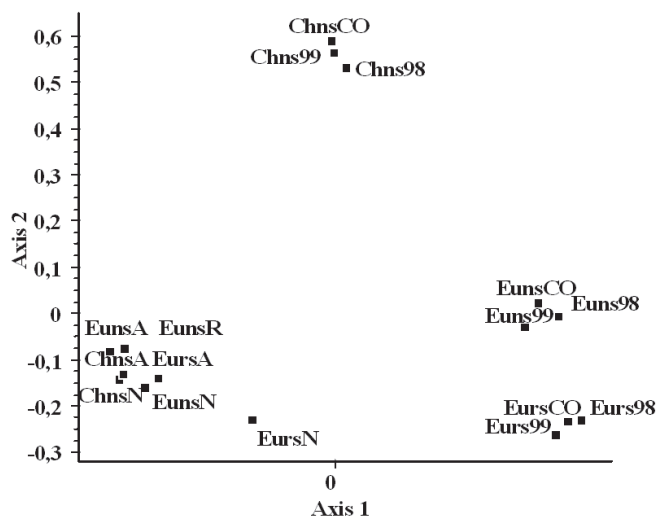


Figure 4. Principal coordinates ordination of dendrograms in F-type analysis before Procrustes adjustments. The first two axes explain a total of 33.41% of the total variance.



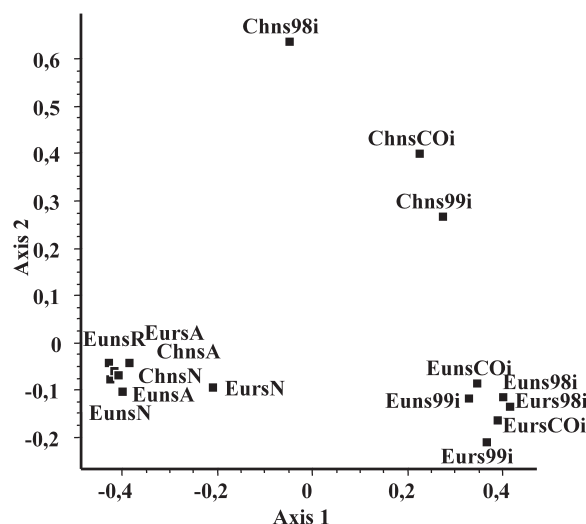


Figure 5. Principal coordinates ordination of dendrograms in I-type analysis before Procrustes adjustments. The first two axes explain a total of 28.93% of the total variance.

1995, Brunet et al. 1996, Gilliam 2002). If this statement is true, other explanations must be found for our stand, and studies cited in the introduction can inform us about the reasons. It is curious, however, that Bradfield and Scagel (1984), Gagnon and Bradfield (1986) as well as Aude and Lawesson (1998) could not explain the major part of the variance of the herb layer with the help of the biotic and abiotic factors measured. This refers to the lack of our knowledge about the complex relations existing in forest communities (see Peet 1978).

The stronger relation between the tree stand and the ecological requirements of the herbs can be explained in two ways:

- Patches with similar tree species composition have an understory indicating similar environmental conditions, but differing in species composition and abundance.
- Fewer (only 17 versus 50, 51 and 61) variables described the ecological requirements rather than species composition of the herb layer. In the latter case, the high number of variables in itself can explain the high heterogeneity of the herb layer, and consequently the weaker relationship.

The pairwise significance tests are strongly affected by the level of the comparisons. The most important difference between the comparisons is the lower number of the significant relations at the level of dendrograms. We examined more thoroughly the significantly similar OUCs and found that there were no contradictions between the results of the two types of significance tests as expected. The OUCs, which are significantly similar at the level of dendrograms seem to be similar at the level of

distance matrices as well. There are some exceptions, but these refer only to the stochastic fluctuations on the given probability level of the significance.

The lower number of significant relations at the dendrogram level may result from two causes:

- The information about the pattern of the objects hidden in the original data or resemblance matrices can be more or less distorted depending on the clustering algorithm (see Introduction).
- It is much more difficult to describe accurately the structure of the dendrograms than that of the distance matrices (see Podani 1989b).

Therefore, at the first sight, distance matrices seem to be more effective if the main objective is to compare the pattern of two sets of objects. Presumably, similar conclusions apply to distance matrices as compared to the level of ordinations (at few dimensions) or non-hierarchical classifications. Although they may be best suited to comparisons, distance matrices give no visible information about the patterns examined.

Based on the results of F- and I-type ordinations one can conclude that OUCs are separated both because of the data (tree versus herb) and the methods ('Eu' versus 'Ch'; 'ns' versus 'rs') used. This is especially valid for the OUCs describing the pattern of the herb layer. The direct cause of separation is the difference in the mathematical representation of patterns used by the different methods. However, another cause of separation is the inner heterogeneity of the herb data, i.e., the objects (5 m × 5 m quadrats) do not have a straightforward group structure (see above). Group structure is much stronger if objects (25 m

× 25 m subplots) are described by tree data. As a result, the mathematical representation of tree layer pattern is less sensitive to the method used.

Ordinations of distance matrices and dendrograms were significantly similar both for F- and I-type analyses. This means that in compliance with the applied methods the distance matrices and the dendrograms represent the vegetation pattern quite similarly. These findings, however, query the above mentioned conclusions that during hierarchical classifications the information hidden in the original data can be highly distorted depending on the algorithm and the applied dendrogram descriptor. It seems probable that in the present case the distortion effects of the applied algorithm and that of the descriptor cluster membership divergence do not explain sufficiently the different results of the significance tests on distance matrices and dendrograms. Thus, presumably the differences between the two kinds of significance tests (permutation versus whole randomization) can contribute to the differences found between the examinations performed at the level of distance matrices and dendrograms.

We find it conceivable that the higher number of significant relations obtained at the level of distance matrices can be attributed to some degree to the lower number of possible cases in the case of Mantel tests compared to the full randomization tests. Because of the much higher number of the possible cases of fully randomized dendrograms, it is more unlikely that two dendrograms are significantly similar at a given probability level.

Another important difference between permutations and full randomization is that the former are not totally independent from the cell values of the distance matrices (or from other parameters of other OUCs). This phenomenon can be called 'case-dependence', as suggested by the surprising results of Mantel tests. It turned out from the pairwise comparisons of the distance matrices that there is no definitely strong relation between the value and the significance level (p) of the of the correlation coefficient (for example, compare the results of the significance tests of the following pairs: ChnsA – ChnsCO, EursA – Euns99, EunsA – Chns99; in the first case: $r=0.189$, $p<0.01$; in the second: $r=0.191$, not significant; in the third: $r=0.265$ and $p<0.05$). This phenomenon indicates the case-dependence of the permutation tests.

It is interesting that not only the cell values but also the size of the analysed distance matrices influence the results of Mantel tests strongly. Tobisch (2000) showed that the distribution of correlation coefficients gained from permutations became more flattened in positive and negative direction as the size of distance matrices de-

creased. For this reason, the number of the significant correlations also decreased.

Acknowledgements. We thank Ipoly Erdő RT, the local forestry enterprise, which made our work possible. We are grateful for the support and help from J. Ruff, the head of the Királyrét District. We thank L. Gálhidy for his contribution in the field works and J. Podani as well as two anonymous reviewers for their useful comments on the manuscript.

References

- Aude, E. and J. E. Lawesson. 1998. Vegetation in Danish beech forests: the importance of soil, microclimate and management factors, evaluated by variation partitioning. *Plant Ecology* 134: 53-65.
- Batagelj, V. 1995. Comparing resemblance measures. *J. Classification* 12: 73-90.
- Berger, A. C. and K. J. Puettmann. 2000. Overstory composition and stand structure influence herbaceous plant diversity in the mixed aspen forest of northern Minnesota. *Am. Midl. Nat.* 143: 111-125.
- Borhidi, A. 1995. Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian Flora. *Acta Bot. Hung.* 39: 97-181.
- Bormann, F. H. and G. E. Likens. 1981. *Pattern and Process in a Forested Ecosystem*. Springer, New York.
- Bradfield, G. E. and A. Scagel. 1984. Correlations among vegetation strata and environment variables in subalpine spruce-fir forests, southeastern British Columbia. *Vegetatio* 55: 105-114.
- Bratton, S. P. 1975. A comparison of the beta diversity functions of the overstory of a deciduous forest. *Bull. Torrey Bot. Club* 102: 55-60.
- Brunet, J., U. Falkengren-Grerup and G. Tyler. 1996. Herb layer vegetation of south Swedish beech and oak forests - effects of management and soil acidity during one decade. *Forest Ecol. Manage.* 88.: 259-272.
- Cajander, A. K. 1926. The theory of forest types. *Acta Forest. Fenn.* 29: 1-108.
- Campbell, B. M. 1978. Similarity coefficients for classifying relevés. *Vegetatio* 37: 101-109.
- Danszky, I. (ed.) 1963. *Magyarország erdőgazdasági tájainak erdőfelújítási, erdőtelepítési irányelvei és eljárásai*. Országos Erdészeti Főigazgatóság, Budapest.
- Del Moral, R. and A. F. Watson. 1978. Gradient structure of forest vegetation in the Central Washington Cascades. *Vegetatio* 38: 29-48.
- Ewald, J. 2000. The influence of coniferous canopies on understorey vegetation and soils in mountain forests of the northern Calcareous Alps. *Appl. Veg. Sci.* 3: 123-134.
- Fekete, G. 1974. Tölgyesek relatív megvilágítása és a gyepszint fajainak eloszlása (in Hungarian). *Studia Bot. Hung.* 9: 87-96.
- Feoli, E. 1984. Some aspects of classification and ordination of vegetation data in perspective. *Stud. Geobot.* 4: 7-21.
- Feoli E., L. Orlóci and M. Scimone. 1984. Comparison of ordinations of some Appennine forest communities based on different characters and methods. *Stud. Geobot.* 4: 137-145.
- Gagnon, D. and G. E. Bradfield. 1986. Relationships among forest strata and environment in Southern Coastal British Columbia. *Can. J. For. Res.* 16: 1264-1271.

- Gauch, H. G. and R. H. Whittaker. 1972. Comparison of ordination techniques. *Ecology* 53: 868-875.
- Gilliam, F. S. 2002. Effects of harvesting on herbaceous layer diversity of a central Appalachian hardwood forest in West Virginia, USA. *Forest Ecol. Manage.* 155: 33-42.
- Gilliam, F. S., N. L. Turrill and M. B. Adams. 1995. Herbaceous-layer and overstory in clear-cut and mature central Appalachian hardwood forests. *Ecol. Applic.* 5: 947-955.
- Glass, G. V. 1976. Primary, secondary and meta-analysis of research. *Educational Researcher* 5: 3-8.
- Glenn-Levin, C. 1977. Species diversity in North American temperate forests. *Vegetatio* 33: 153-162.
- Gower, J. C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* 53: 325-338.
- Gower, J. C. 1971. Statistical methods of comparing different multivariate analyses of the same data. In: F. R. Hodson, D. G. Kendall and P. Tautu (eds.), *Mathematics in the Archaeological and Historical Sciences*. Edinburgh Univ. Press, Edinburgh. pp. 138-149.
- Green, B. F. 1952. The orthogonal approximation of an oblique structure in factor analysis. *Psychometrika* 17: 429-440.
- Grigal, D. F. and H. F. Arnemann. 1978. Quantitative relationships among vegetation and soil classification from northeastern Minnesota. *Can. J. Bot.* 48: 555-566.
- Hajdu, L. J. 1981. Graphical comparison of resemblance measures in phytosociology. *Vegetatio* 48: 47-59.
- Halpern, C. B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. *Ecology* 70: 704-720.
- Halpern, C. B. and J. F. Franklin. 1990. Physiognomic development of *Pseudotsuga* forests in relation to initial structure and disturbance intensity. *J. Veg. Sci.* 1: 475-482.
- Halpern, C. B. and T. A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific northwest. *Ecol. Applic.* 5: 913-934.
- Hughes, J. W. and T. J. Fahey. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. *J. Ecol.* 79: 605-616.
- Járó, Z. 1962. Termőhelyi tényezők ismertetése. In: A. Majer (ed.), *Erdő- és termőhelytípológiai útműtató*. Országos Erdészeti Főigazgatóság, Budapest. pp. 11-69 (in Hungarian).
- Kenkel, N. C. and L. Orlóci. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. *Ecology* 67: 919-928.
- McCune, B. and J. Antos. 1981. Correlations between forest layers in the Swan Valley, Montana. *Ecology* 62: 1196-1204.
- McKenzie, D., C. B. Halpern and C. R. Nelson. 2000. Overstory influences on herb and shrub communities in mature forests of western Washington, USA. *Can. J. For. Res.* 30: 1655-1666.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Res.* 27: 209-220.
- Miyata, I. 1983. Influence of vegetation structure of the tree layer on development of the herb layer in a secondary forest. *Jap. J. Ecol.* 33: 71-78.
- Orlóci, L. 1978. *Multivariate Analysis in Vegetation Research*. 2nd edition Junk, The Hague.
- Peet, R. K. 1978. Forest vegetation of the Colorado front range: patterns of species diversity. *Vegetatio* 37: 65-78.
- Podani, J. 1985. Syntaxonomic congruence in a small - scale vegetation survey. *Abstracta Botanica* 9: 99-128.
- Podani, J. 1989a. A method for generating consensus partitions and its application to community classification. *Coenoses* 4: 1- 10.
- Podani, J. 1989b. Comparison of ordinations and classifications of vegetation data. *Vegetatio* 83: 111-128.
- Podani, J. 1991. On the standardization of Procrustes statistics for the comparison of ordinations. *Abstracta Botanica* 15: 43 - 46.
- Podani, J. 1993. *SYN-TAX-pc, Computer Programs for Multivariate Data Analysis in Ecology and Systematics*. Version 5.0. User's Guide. Scientia Publishing, Budapest.
- Podani, J. 2000. *Introduction to the Exploration of Multivariate Biological Data*. Backhuys, Leiden.
- Podani, J. 2001. SYN-TAX 2000 computer program for data analysis in ecology and systematics for WINDOWS 95, 98 and NT. User's manual. Scientia Publishing, Budapest.
- Podani, J. and T. A. Dickinson. 1984. Comparison of dendrograms: a multivariate approach. *Can. J. Bot.* 62: 2765-2778.
- Sayers, C. L. and J. Lyon. 1997. Gradient analysis in a riparian landscape: contrast among forest layers. *Forest Ecol. Manage.* 96: 13-26.
- Schönemann, P. H. and R. M. Carroll. 1970. Fitting one matrix to another under choice of a central dilation and a rigid motion. *Psychometrika* 35: 245-256.
- Simon, T. 2000. *A magyarországi edényes flóra határozója*. Harasztok-virágos növények. Nemzeti Tankönyvkiadó, Budapest. (in Hungarian).
- Skov, F. 1997. Stand and neighbourhood parameters as determinants of plant species richness in a managed forest. *J. Veg. Sci.* 8: 573-578.
- Sneath, P. H. A. and R. R. Sokal. 1973. *Numerical Taxonomy*. Freeman, San Francisco.
- Sokal, R. R. and F. J. Rohlf. 1962. The comparison of dendrograms by objective methods. *Taxon* 11: 33-40.
- Steel, M. A. and D. Penny. 1993. Distributions of tree comparison metrics - some new results. *Syst. Biol.* 42: 126-141.
- Tobisch, T. 2000. *A faállomány-szerkezet és az aljnövényzet kapcsolatának vizsgálata egy lombhullató gazdasági erdőben*. MSc. Thesis (in Hungarian). Department of Plant Taxonomy and Ecology, L. Eötvös University, Hungary.
- Torgerson, W. S. 1952. Multidimensional scaling: I. Theory and method. *Psychometrika* 17: 401-419.
- Whitney, G. C. and D. R. Foster. 1988. Overstorey composition and age as determinants of the understorey flora of woods of central New England. *J. Ecol.* 76: 867-876.