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Testing of Ellenberg and Zarzycki indicator values as predictors of soil and light conditions in woodlands

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ABSTRACT: Many authors have successfully applied mean Ellenberg and Zarzycki indicator values to evaluate environmental conditions on the basis of the species composition of plant communities. Using data collected from ancient deciduous woods and recent woods of various ages, we tested whether and to what degree the assessment of soil and light quality using these indicators depends on the age and stability of the communities. We found that the mean Ellenberg and Zarzycki indicator values for light, reaction, nitrogen and fertility provided almost equally good predictions of measured light intensity, soil pH and nutrient availability in ancient woods, where they can be used interchangeably. They were poorer indicators of environmental conditions in recent woods with much less adjusted floristic compositions. This suggests that mean indicator values for such communities should be interpreted with caution. The mean Ellenberg and Zarzycki indicator values for nitrogen and fertility were the best predictors of cation exchange capacity and much weaker indicators of total nitrogen in deciduous woods. In the ancient woods, the mean Ellenberg and Zarzycki indicator values for reaction, nitrogen and fertility, based on the presence/absence of species, correlated better with soil pH and cation exchange capacity than did the mean indicator values based on cover/abundance. Weighted mean indicators for light were better predictors of light intensity than unweighted mean indicators were.

KEY WORDS: ancient and recent woodlands, indicator values, secondary succession, southern Poland

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INTRODUCTION

It has long been known that plants could be indicators of environmental conditions and that the floristic composition of vegetation provides a sensitive, integrated measure of the environment. At present, Ellenberg's system comprising about 3000 taxa is the best known and most extensive set of indicator species (Ellenberg *et al.* 1992). It was developed over several decades beginning in the early 1950s, and the first list of indicator values for the vascular plants of Central Europe was published more than 25 years ago (Ellenberg 1974). More than 15 years ago, Zarzycki (1984) proposed indicator values for more than 2100 taxa occurring in Poland. Similar systems have, for instance, been developed also for Hungary (Zólyomi *et al*. 1967), Switzerland (Landolt 1977) and eastern Germany (Frank & Klotz 1990).

Using indicator species instead of physical and chemical measurements saves time and allows estimation of the values of environmental factors in the past, based only on vegetation data when no environmental measurements are available. It also provides a synthetic measure for temporarily fluctuating factors such as light intensity in woodlands, soil moisture or soil nutrient concentrations.

Many authors have successfully used mean Ellenberg indicator values to evaluate soil, light and climatic conditions in various communities (Roo-Zielińska & Solon 1988; van der Maarel 1993; Diekmann 1994, 1995), to indicate environmental changes resulting from successions of vegetation or past land use (Persson 1980; van der Maarel *et al*. 1985; Dzwonko & Loster 1997; Koerner *et al*. 1997), to assess the degree of acidification and eutrophication in woodlands (Thimonier *et al.* 1992; Thimonier *et al.* 1994; Diekmann & Dupré 1997; Diekmann *et al.* 1999), to investigate desiccation and eutrophication or acidification in grasslands and wetlands (Latour *et al.* 1994; ter Braak & Wiertz 1994), and to determine the response of field layer vegetation to silviculture practices (Hannerz & Hanell 1997). The usefulness of the Zarzycki indicator values has also been demonstrated in analyses of some woodland and grassland communities in Poland (Kwiatkowska & Wyszomirski 1988; Kozłowska 1991).

Various studies indicate that mean Ellenberg indicator values can show high correlations with measured variables. Significant relationships have been found between the mean indicator values for reaction and soil pH (Persson 1980; Ellenberg *et al.* 1992; Seidling & Rohner 1993; Diekmann 1995; Ertsen *et al.* 1998). This indicator can also be strongly correlated with base saturation, calcium content and Al/Ca ratio in soil (Degórski 1982; Seidling & Rohner 1993), as well as with foliar calcium and potassium concentration (Thompson *et al.* 1993; Meerts 1997). Mean indicator values for nitrogen can be significantly correlated with available nitrogen and potassium, phosphorus and C/N ratio in the upper soil level (Ellenberg *et al.* 1992; Latour *et al.* 1994; Diekmann & Falkengren-Grerup 1998). It has also proven to be a good predictor of annual yield in grasslands (Melman *et al.* 1988; Hill & Carey 1997; Ertsen *et al.* 1998) and of nitrogen, potassium and phosphorus concentrations in leaves (Thompson *et al.* 1993; Meerts 1997). The mean indicator values for moisture can be correlated with mean spring groundwater level (Ertsen *et al.* 1998), and the indicator values for light can correlate with relative intensity of light in woodlands (Diekmann 1995).

Problems in using indicator values can arise from various aspects of the biology and ecology of plants, such as intraspecific genetic variability, differences between the ecological and physiological behavior of species, and from the dynamics of communities (Böcker *et al.* 1983; Kowarik & Seidling 1989). Dierschke (1994) compiled and summarized the arguments supporting the use of Ellenberg system values and showing its weaknesses. According to Ellenberg (Ellenberg *et al.* 1992), indicator values apply to the ecological behavior of a distinct plant taxon, that is, to its occurrence in field conditions including competition with many other plants. The accuracy of indicator-value-based predictions of environmental factors may thus depend on the adjustment of community species compositions to local environments.

This study examined the degree to which estimation of light and soil conditions using mean Ellenberg and Zarzycki indicator values depends on the age and stability of woodland communities.

MATERIAL AND METHODS

Study area and data collection

This study used the data collected in three ancient deciduous woods ranging from 0.6 to 11.8 ha in area and four adjacent 70-year-old secondary woods from 1.3 to 3.0 ha in area. All these woods are situated in the Wierzbanówka valley within the Pogórze Wielickie area in the northern part of the Carpathian foothills. In the ancient woods there were two types of communities: *Tilio-Carpinetum*, on proper brown soil, grey-brown soil and leached brown soil, and *Pino-Quercetum* on podzolic soils. The recent woods were growing on the same soils as the adjacent ancient woods. The recent woods either were established naturally or had been planted in places that formerly used as field and pasture for a long time. Both the ancient and recent woods have been managed. In spite of management in the ancient woods the rich woodland flora has been preserved and associations typical of mature woodlands in the submontane zone of the northern Carpathians are present. The data on the field layer vegetation, light and soil conditions were collected from 264 plots 4 m^2 in size, laid out systematically at 20-meter intervals in both the ancient (150 plots) and recent woods (114 plots). Records were made in June and July 1990 and repeated in April and May 1991 for herb species developing in early spring. More details of the study area and vegetation are given by Dzwonko (1993) and Dzwonko and Gawroński (1994).

The study also used data from an overgrowing sandy grassland 0.77 ha in area in the Skołczanka reserve, situated about 8 km southwest of Kraków. These data were collected from 105 plots, each 25 m^2 in area and arranged systematically at 5 m intervals in a grassland (*Festuco-Thymetum* association, 16 plots), in 10-year-old woods with *Pinus sylvestris* (32 plots) and *Robinia pseudacacia* (18 plots) overgrowing grassland, and in two neighbouring planted pine woods 42–50 years old (39 plots). The substrate consisted of a thick layer of loose and slightly clayey sand overlaying limestone rocks. Records were made in June and July 1992 and again in May 1993. More details on the vegetation of this area were published by Dzwonko and Loster (1997).

In all cases, on each plot the percentage cover (at 10% estimation intervals) of vascular plant species in the field layer was estimated, and four subsamples were taken from the topsoil (0–10 cm) and mixed into one composite sample. Air-dried samples were analyzed for pH (in aqueous solution), exchangeable calcium, potassium and magnesium spectrophotometry in 1 N ammonium acetate, and total nitrogen by the Kjeldahl method. Cation exchange capacity (CEC) was calculated as the sum of different cations measured with a flame photometer and a spectrophotometer in 1 N ammonium acetate. Light intensity was measured at four points in each plot in both the ancient and recent woods in the Wierzbanówka valley, using a light meter calibrated in lux, and then the mean values were calculated and expressed as percentages of the light intensity in open space. In order to avoid misleading measures due to short-lived sunflecks, all light measurements were taken under conditions of diffuse light, that is, on overcast days.

Data analysis

The indicator values for light (L), reaction (R), nitrogen (N) and fertility (Tr) were taken from Ellenberg *et al.* (1992) and Zarzycki (1984). Mean characteristic indicator values (cf. Jongman *et al.* 1995) were calculated twice: on the basis of the presence/absence of species (simple mean), and taking into account of cover/abundance values on a 10-degree scale (weighted mean). The species defined in the Ellenberg system as indifferent were omitted from the calculations. As regards the species for which Zarzycki provided the ranges of values, the average values of these ranges were adopted. Only the mean indicator values for plots in which at least three species with known indicator values occurred were included in the analyses. Because of the skewness of their distribution, two variables – light intensity and CEC – were logarithmically transformed prior to statistical analyses.

Canonical correspondence analysis (CCA, CANOCO program, ter Braak 1987; ter Braak & Šmilauer 1998) was used to examine the relations between the species compositions of the three compared wood groups and environmental variables. In CCA, the plot scores along the ordination axes are restricted to a linear combination of measured environmental variables, and the species scores are weighted averages of the plot scores. The weighted averages are the centers of species distributions along the ordination axes. Hence, the ordination axes show the maximum dispersion of the species scores in relation to measured environmental variables. For each wood group the first CCA axis was constrained regarding only one measured variable, and the statistical significance of the relationship between species and an environmental variable was evaluated with the Monte Carlo permutation test. This analysis was repeated for all tested variables. To determine whether there were any relationships between the arrangement of the species on the basis of the measured environmental variables and their Ellenberg indicator values, one-way analysis of variance (ANOVA) and the Tukey test were used to test the differences between the mean values of the scores along the first CCA axes for species with the same indicator values.

Results

In all the woods studied, cation exchange capacity was strongly correlated with calcium, potassium and magnesium. Thus these elements were omitted from further analyses, and CEC was adopted as a general indicator of soil nutrient availability. No evident differences in light intensity, soil pH and CEC were found between ancient and recent woods in the Wierzbanówka valley. The mean values, ranges and distributions of these variables were similar in these woods (Fig. 1). The soils of the ancient woods had only slightly less nitrogen.

In most cases the mean indicator values show evident linear relationships with the corresponding measured environmental variables (Fig. 2). In spite of the very similar light and soil conditions and similar mean numbers of the indicator species on the plots in the Wierzbanówka valley woods, most correlations between the mean Ellenberg and Zarzycki indicator values and the corresponding environmental variables were higher in the ancient woods than in the recent woods (Table 1). The only exceptions were the correlation between the Zarzycki indicator values for fertility and CEC, and the correlation between the Zarzycki indicator for reaction based on cover/abundance and soil pH. In recent woods overgrowing sandy grassland, only the correlations of the Ellenberg and Zarzycki indicator values for nitrogen and fertility with total nitrogen were positive, but they were not significant. Here these indicator values were most strongly correlated with total nitrogen, while in deciduous woods in the Wierzbanówka valley they were the best predictors of cation exchange capacity. In 70-year-old woods the mean indicator values for nitrogen and fertility were not correlated at all with total nitrogen.

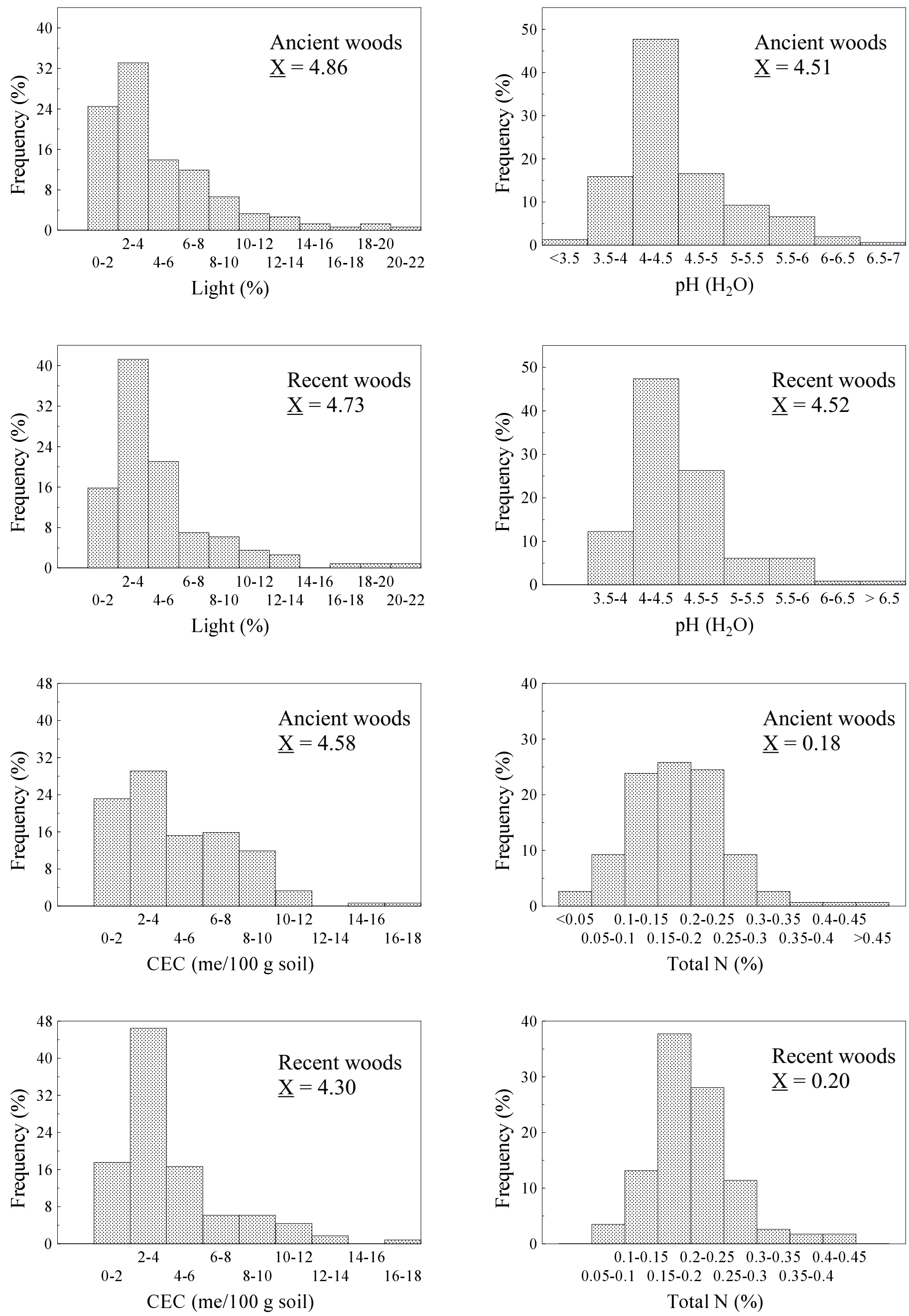

Fig. 1. Histograms of frequency distributions and means (X) of light intensity, soil pH (H_2O), cation exchange capacity (CEC) and total nitrogen (N) in ancient and recent woods in the Wierzbanówka valley. Lower and upper class limits are given in the plots. Measurements were placed in one class if they were greater than the lower class limit and less than or equal to the upper class limit. Means and ranges (in parentheses) of pH, CEC and total N in overgrown sandy grassland are 5.69 (3.70–6.90), 1.80 (0.29–5.86) me/100 g soil, and 0.11 (0.03–0.22), respectively.

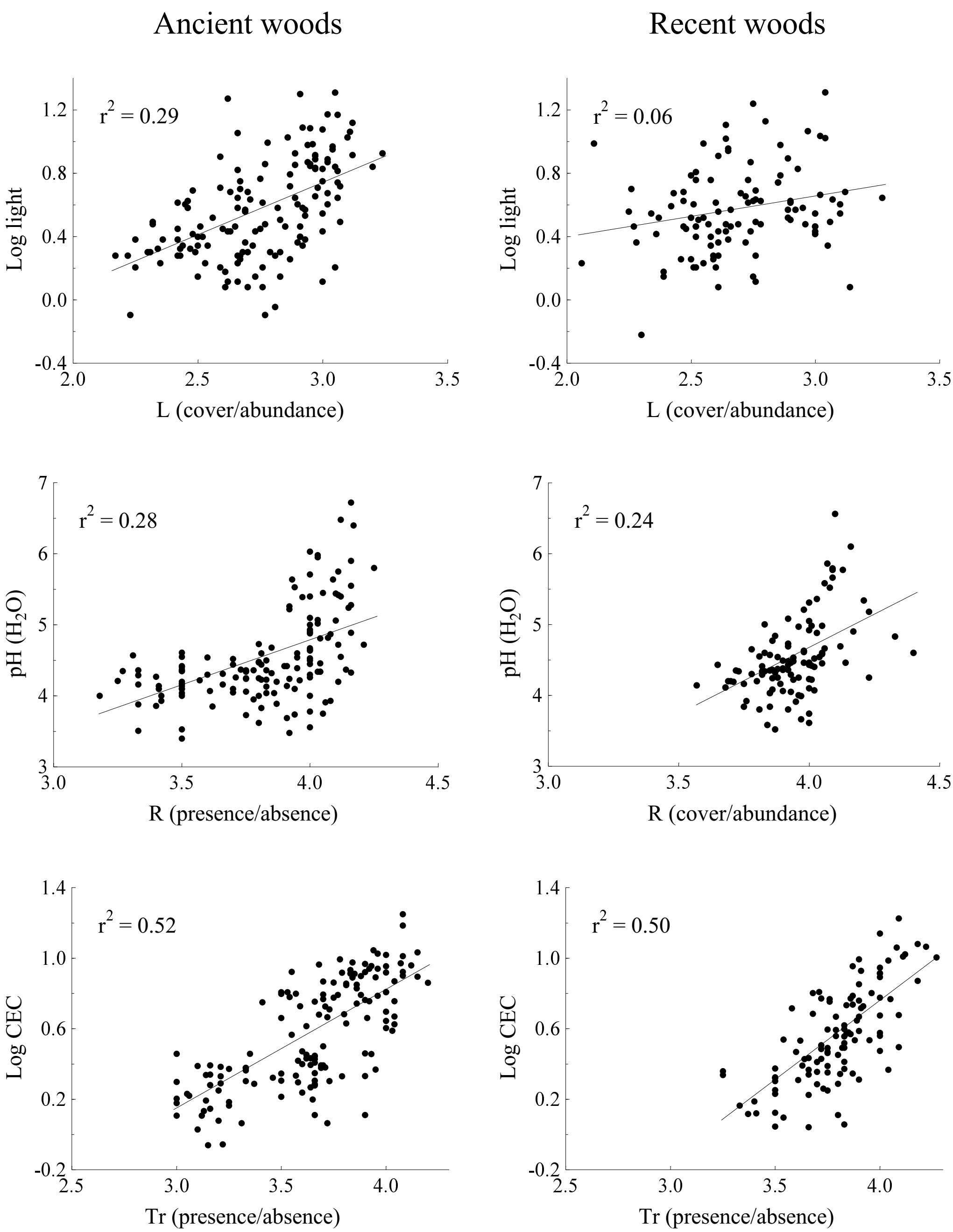

Fig. 2. Light intensity, soil pH and cation exchange capacity (CEC) in relation to mean Zarzycki indicator values for light (L), reaction (R) and fertility (Tr), respectively, in ancient and recent woods in the Wierzbanówka valley. Trend lines fitted by least squares regression.

Table 1. Correlation coefficients (Pearson's *r*) between environmental variables and mean Ellenberg indicator values for light (mL), reaction (mR), nitrogen (mN), and mean Zarzycki indicator values for light (L), reaction (R), and fertility (Tr) in the ancient and recent woods and overgrown grassland. Calculations were made for presence/absence (p/a) and cover/abundance (c/a) values. * significant at 0.05 level after Bonferroni correction.

Variables	mL c/a	mR p/a	mN p/a	L p/a	L c/a	R p/a	R c/p	Tr p/a	Tr c/a
				Ancient woods					
Number of plots	145	130	132	145		146		146	
Mean number of species	8.95	7.56	8.27	9.73		9.68		9.68	
mR p/a	-0.75*								
mN p/a	-0.67*	0.94*							
L p/a	0.58*	-0.47*	-0.46*						
L c/a	0.85*	-0.60*	-0.56*	0.66*					
R p/a	-0.66*	0.92*	0.87*	-0.37*	-0.52*				
R c/a	-0.50*	0.75*	0.72*	-0.22	-0.37*	0.80*			
Tr p/a	-0.66*	0.94*	0.94*	-0.43*	-0.56*	0.93*	0.73*		
Tr c/a	-0.61*	0.71*	0.74*	-0.35*	-0.54*	0.69*	0.46*	0.77*	
Log light	0.59*	-0.42*	-0.36*	0.39*	0.54*	-0.43*	-0.33*	-0.40*	-0.42*
pH (H_2O)	-0.40*	0.56*	0.57*	-0.33*	-0.32*	0.53*	0.46*	0.56*	0.42*
N total	-0.24	0.37*	0.25	-0.09	-0.17	0.33*	0.20	0.32*	0.28*
Log CEC	-0.54*	0.74*	0.72*	-0.51*	-0.49*	0.70*	0.57*	0.72*	0.51*
				Recent woods					
Number of plots	107	92	95	108		108		108	
Mean number of species	9.13	8.16	9.03	9.69		9.70		9.70	
mR p/a	-0.59*								
mN p/a	-0.60*	0.83*							
L p/a	0.53*	-0.17	-0.15						
L c/a	0.85*	-0.53*	-0.50*	0.73*					
R p/a	-0.32	0.47*	0.44*	-0.19	-0.28				
R c/a	-0.39*	0.57*	0.55*	-0.11	-0.33*	0.66*			
Tr p/a	-0.58*	0.79*	0.78*	-0.30	-0.53*	0.71*	0.62*		
Tr c/a	-0.60*	0.78*	0.80*	-0.27	-0.52*	0.55*	0.49*	0.79*	
Log light	0.43*	-0.13	-0.12	0.20	0.24	-0.09	-0.05	-0.08	-0.13
pH (H_2O)	-0.29	0.36*	0.54*	-0.08	-0.24	0.39*	0.49*	0.53*	0.37*
N total	-0.22	0.08	0.05	-0.06	-0.21	0.09	0.13	0.08	0.09
Log CEC	-0.48*	0.51*	0.59*	-0.32	-0.45*	0.49*	0.44*	0.71*	0.53*
				Overgrown grassland					
Number of plots		105	105			105		105	
Mean number of species		10.12	13.02			17.26		17.26	
mN p/a	–	0.65*							
R p/a	–	0.74*	0.48*	–	–				
R c/a	–	0.60*	0.32*	–	–	0.83*			
Tr p/a	–	0.70*	0.96*	–	–	0.48*	0.29		
Tr c/a	–	0.72*	0.89*	–	–	0.46*	0.38*	0.94*	
pH (H_2O)	–	-0.19	-0.63*	–	–	-0.07	0.04	-0.60*	-0.49*
N total	–	0.06	0.29	–	–	0.04	-0.05	0.29	0.26
Log CEC	–	-0.10	-0.04	–	–	-0.14	-0.17	-0.06	-0.06

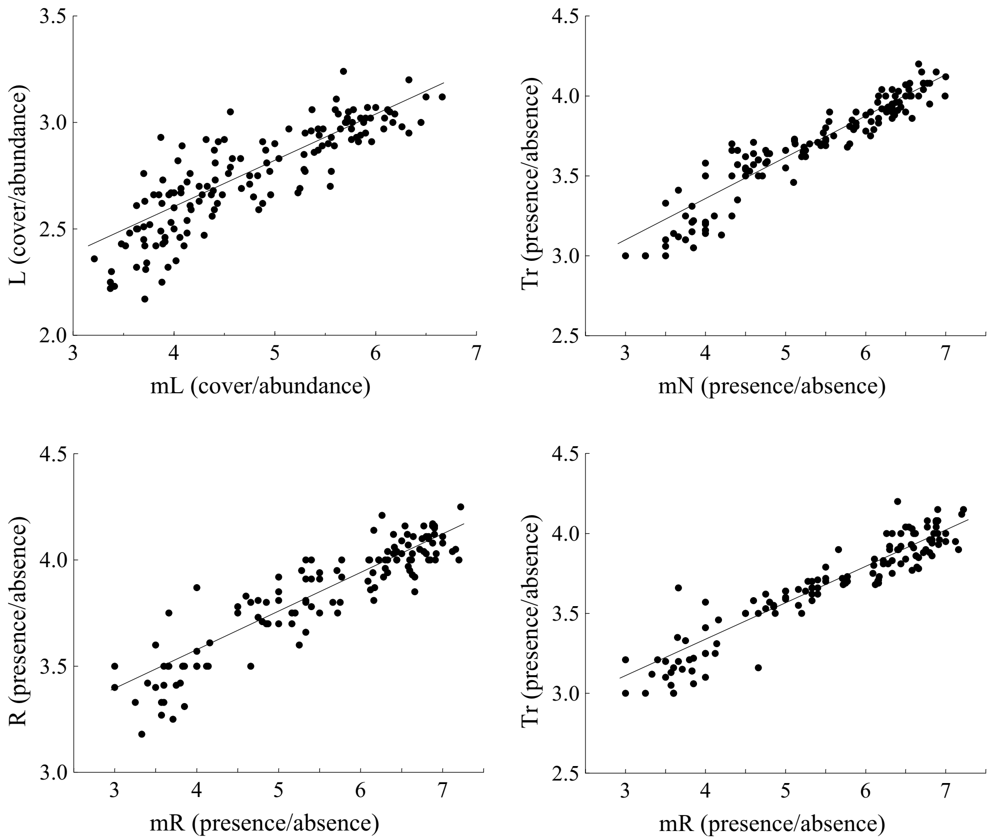

Fig. 3. Relationships between mean Ellenberg indicator values for light (mL), reaction (mR) and nitrogen (mN) and mean Zarzycki indicator values for light (L), reaction (R) and fertility (Tr), respectively, in ancient woods in the Wierzbanówka valley. Trend lines fitted by least squares regression.

The unweighted and weighted means of indicator values were very strongly correlated, but in ancient woods the unweighted mean Ellenberg and Zarzycki indicator values for reaction, nitrogen and fertility had slightly higher correlations with pH and CEC than with the weighted means of these indicator values. It was the same with the corresponding correlations for the Ellenberg indicators in recent woods. For this reason the correlation values for these weighted mean Ellenberg indicators were not included in Table 1. In the case of light intensity, the weighted mean indicators for light turned out to be slightly better predictors than the unweighted mean indicators.

In both the ancient and recent woods the Ellenberg indicator values for light were slightly stronger correlated with the measured light intensity than the Zarzycki indicator values, whereas in the 70-year-old woods the Zarzycki indicators for reaction and fertility had stronger correlations with pH and CEC, respectively. Despite these differences, the mean indicator values from both lists showed linear relationships, and as a rule they

Table 2. Mean scores of the first CCA axes for species as related to Ellenberg indicator values. The first CCA axes were constrained regarding log light, pH (H_2O), total nitrogen and log CEC for indicators for light (L), reaction (R) and nitrogen (N), respectively. Calculations were made for presence/absence (p/a) or cover/abundance (c/a) values. R_S indicates correlation between species and an environmental variable, P_M denotes the probability of relation between species and an environmental variable (Monte Carlo permutation test), and P_F denotes the probability of differences between indicator values (one-way ANOVA). Within a row underlined values are not significantly different at $P > 0.05$, based on the Tukey test.

Ellenberg indicator value	1	2	3	4	5	6	7	8	9	λ_1	R_S	P_M	P_F
Indicator for light (L) and log light													
Ancient woods													
Number of species	1 +	3 +	11	26	15	16	19	–	–				
Mean scores of species (c/a)			-0.25	-0.20	0.25	0.25	0.34	–	–	0.28	0.68	0.001	0.004
Recent woods													
Number of species	1 +	4	10	21	10	14	13 +	1	–				
Mean scores of species (c/a)		0.55	0.05	0.08	0.30	0.15	-0.01		–	0.21	0.68	0.001	0.39 (NS)
Indicator for reaction (R) and pH (H_2O)													
Ancient woods													
Number of species	–	2 +	3	7	5	14	23	9	–				
Mean scores of species (p/a)	–		-0.59	-0.54	-0.32	0.26	0.56	0.95	–	0.28	0.75	0.001	0.001
Recent woods													
Number of species	–	–	1 +	6	6	12	19	6	–				
Mean scores of species (p/a)	–	–		-0.37	0.12	0.45	0.15	0.52	–	0.17	0.77	0.001	0.11 (NS)
Overgrown grassland													
Number of species	1 +	4	13	9	14	13	20	7 +	1				
Mean scores of species (p/a)		0.06	0.24	0.04	0.04	-0.12	-0.17	-0.49		0.42	0.83	0.001	0.47 (NS)
Indicator for nitrogen (N) and total nitrogen													
Ancient woods													
Number of species	–	1 +	11	7	17	15	17	9 +	2				
Mean scores of species (p/a)	–		-0.15	-0.01	0.33	0.24	0.25	0.32		0.14	0.61	0.002	0.51 (NS)
Recent woods													
Number of species	–	1 +	5	3 +	11	17	14	7 +	1				
Mean scores of species (p/a)	–		0.07		0.16	-0.14	0.02	-0.20		0.12	0.69	0.001	0.55 (NS)
Overgrown grassland													
Number of species	5	17	20	12	17	21	12	11	–				
Mean scores of species (p/a)	0.05	-0.23	0.16	-0.09	-0.01	0.18	0.04	0.34	–	0.11	0.54	0.01	0.07 (NS)

Table 2. Continued.

Ellenberg indicator value	1	2	3	4	5	6	7	8	9	λ_1	R_S	P_M	P_F
Indicator for nitrogen (N) and log CEC													
Ancient woods													
Number of species	–	1 +	11	7	17	15	17	9 +	2				
Mean scores of species (p/a)	–		0.67	0.51	-0.10	-0.07	-0.57	-0.51		0.35	0.80	0.001	<0.001
Recent woods													
Number of species	–	1 +	5	3 +	11	17	14	7 +	1				
Mean scores of species (p/a)	–		-0.58		-0.05	0.05	0.34	0.42		0.20	0.80	0.001	0.042
Overgrown grassland													
Number of species	5	17	20	12	17	21	12	11	–				
Mean scores of species (p/a)	-0.06	-0.02	-0.12	-0.04	-0.11	-0.09	-0.08	0.01	–	0.10	0.77	0.012	0.99 (NS)

were very strongly correlated, with the strongest correlations in the case of ancient woodlands (Table 1; Fig. 3).

The CCA results revealed that the species compositions in the studied woods were dependent on light intensity, soil pH, total nitrogen and CEC (Table 2). In most cases these relations were highly significant, but only in the ancient woods was the ordering of species on the basis of light intensity and soil pH significantly related to their Ellenberg indicator values for light and reaction, respectively. The Ellenberg indicator values for nitrogen were significantly related to the ordering of species according to the CEC values in both the ancient and 70-year-old woods, although with a much lower probability in the latter. No relationships were found between the mean scores of species along the first CCA axes constrained regarding total nitrogen and their indicator values for nitrogen. These results suggest that the species compositions of recent woods are more poorly adjusted to light and soil conditions than those of ancient woodlands.

Discussion and conclusions

It is known that over a short span of time the composition of vegetation is determined mostly by the dispersal ability of species and the availability of sites suitable for seed germination and seedling development, whereas over a longer period the species composition depends more on the environmental regime than on the initial conditions. Woodlands take a particularly long time to adjust to local environmental conditions. This study demonstrates that even in 70-year-old secondary woods the Ellenberg indicator values and some of the Zarzycki indicators much less effectively indicate the soil and light conditions than they do in ancient woodlands in a very similar environment.

More detailed studies suggest that the very slow colonization rate of new woods by woodland species may be one of the crucial reasons for the lower correlations between mean indicator values and measured environmental variables (Dzwonko 1993; Dzwonko & Gawroński 1994; Dzwonko & Loster 1997; Dzwonko 2001). Limited dispersal of species can result in a less effective evaluation of environmental factors by the Ellenberg indicator values also in other types of communities. This is suggested by the results of long-term fertilizer application on grasslands in England, presented by Hill and Carey (1997). In that case, these authors believe, limited immigration of species responsive to acidity was the cause of the lower correlation between the mean Ellenberg indicator values for reaction and soil pH.

The unweighted mean Ellenberg and Zarzycki indicator values for reaction, nitrogen and fertility were better predictors of measured variables than the weighted ones. This implies that the presence of species occurring at low abundance is highly informative.

In the woods in the Wierzbanówka valley, the correlations of the Ellenberg indicator values for nitrogen with CEC were much stronger than with total nitrogen. This is consistent with Ellenberg's suggestion (Ellenberg *et al.* 1992) that this indicator may also be interpreted as indicating general nutrient supply.

Our results here imply that the mean Ellenberg and Zarzycki indicator values provided almost equally good predictions of the environmental variables in ancient woodlands, where they can often be used interchangeably. However, when the species for which values are given as ranges were omitted, the correlations of the mean Zarzycki indicator values with the measured variables in both the ancient and 70-year-old woods were lower than the ones given in Table 1. In those cases the correlations between the weighted mean indicator values for light and the light intensity were $r = 0.44$ and $r = 0.29$ for ancient and recent woods, respectively, whereas the correlations between the unweighted mean indicator values for reaction and fertility with soil pH and cation exchange capacity were equal, $r = 0.29$ and $r = 0.70$ in ancient woods and $r = 0.26$ and $r = 0.62$ in recent woods. In the case of these two latter indicators, the correlations for the weighted means were markedly lower than the correlations for the unweighted means. For the mean Zarzycki indicator values calculated in this way, all the correlations with measured variables were lower in the recent woods than in the ancient woods, as in the case of the mean Ellenberg indicator values. Moreover, all correlations for the mean Zarzycki indicators in the ancient woods were slightly lower than the corresponding correlations for the mean Ellenberg indicators.

Mean Ellenberg and Zarzycki indicator values are inferior predictors of ecological variables in young secondary woods, whose floristic composition has not yet adjusted as in ancient woodlands. This suggests that the mean indicator values for such communities should be interpreted with caution and supplemented by measurements of environmental variables.

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References

Böcker R., Kowarik I. & Bornkamm R. 1983. Untersuchungen zur Anwendung der Zeigerwerte nach Ellenberg. – Verh. Gesell. Ökol. **11:** 35–56.

Degórski M. L. 1982. Usefulness of Ellenberg bioindicators in characterizing plant communities and forest habitats on the basis of data from the range "Grabowy" in Kampinos Forest. – Ekol. Pol. **30**(3–4): 453–477.

Diekmann M. 1994. Deciduous forest vegetation in Boreo-nemoral Scandinavia. – Acta Phytogeogr. Suec. **80:** 1–112.

Diekmann M. 1995. Use and improvement of Ellenberg's indicator values in deciduous forests of the Boreo-nemoral zone in Sweden. – Ecography **18:** 178–189.

Diekmann M., Brunet J., Rühling A. & Falkengren-Grerup U. 1999. Effects of nitrogen deposition: results of a temporal-spatial analysis of deciduous forests in South Sweden. – Plant Biol. **1**: 471–481.

Diekmann M. & Dupré C. 1997. Acidification and eutrophication of deciduous forests in northwestern Germany demonstrated by indicator species analysis. – J. Veg. Sci. **8:** 855–864.

Diekmann M. & Falkengren-Grerup U. 1998. A new species index for forest vascular plants: development of functional indices based on mineralization rates of various forms of soil nitrogen. – J. Ecol. **86:** 269–283.

DIERSCHKE H. 1994. Pflanzensoziologie. Grundlagen und Methoden. 683 pp. E. Ulmer, Stuttgart.

DZWONKO Z. 1993. Relations between the floristic composition of isolated young woods and their proximity to ancient woodland. – J. Veg. Sci. **4:** 693–698.

DZWONKO Z. 2001. Assesment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. – J. Appl. Ecol. **38**: 942–951.

DZWONKO Z., & GAWROŃSKI S. 1994. The role of woodland fragments, soil types, and dominant species in secondary succession on the western Carpathians foothills. – Vegetatio **111:** 149–160.

DZWONKO Z. & LOSTER S. 1997. Effects of dominant trees and anthropogenic disturbances on species richness and floristic composition of secondary communities in southern Poland. – J. Appl. Ecol. **34:** 861–870.

ELLENBERG H. 1974. Zeigerwerte der Gefäßpflanzen Mitteleuropas. – Scripta Geobot. **9:** 3–122.

ELLENBERG H., WEBER H. E., DÜLL R., WIRTH V., WERNER W. & PAULIßEN D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. – Scripta Geobot. **18:** 3–258.

ERTSEN A. C. D., ALKEMADE J. R. M. & WASSEN M. J. 1998. Calibrating Ellenberg indicator values for moisture, acidity, nutrient availability and salinity in the Netherlands. – Plant Ecol. **135:** 113–124.

FRANK D. & KLOTZ S. (eds). 1990. Biologisch-ökologische Daten zur Flora der DDR. 2. Aufl. – Wissenschaftl. Beitr. Martin-Luther-Universität Halle-Wittenberg **32**: 1–167.

HANNERZ M. & HANELL B. 1997. Effects on the flora in Norway spruce forests following clearcutting and shelterwood cutting. – Forest Ecol. Manag. **90:** 29–49.

HILL M. O. & CAREY P. D. 1997. Prediction of yield in the Rothamsted Park Grass Experiment by Ellenberg indicator values. – J. Veg. Sci. **8:** 579–586.

JONGMAN R. H. G., TER BRAAK C. J. F. & VAN TONGEREN O. F. R. 1995. Data analysis in community and landscape ecology. 299 pp. Cambridge University Press, Cambridge.

KOERNER W., DUPOUEY J. L., DAMBRINE E. & BENOÎT M. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. – J. Ecol. **85**: 351–358.

KOWARIK I. & SEIDLING W. 1989. Zeigerwertberechnungen nach Ellenberg. Zu Problemen und Einschränkungen einer sinnvollen Methode. – Landschaft & Stadt **21**(4): 132–143

KOZŁOWSKA A. B. 1991. Analiza porównawcza ekologicznych liczb wskaźnikowych (wg Ellenberga i Zarzyckiego) [Comparative analysis of ecological indicative values according to Ellenberg and Zarzycki]. – Wiad. Bot. **35**(1): 11–21 (in Polish with English summary).

KWIATKOWSKA A. J. & WYSZOMIRSKI T. 1988. Decline of *Potentillo albae-Quercetum* phytocoenoses associated with the invasion of *Carpinus betulus*. – Vegetatio **75:** 49–55.

LANDOLT E. 1977. Ökologische Zeigerwerte zur Schweizer Flora. – Veröff. Geobot. Inst. ETH Stiftung Rübel **64:** 1–208.

LATOUR J. B., REILING R. & SLOOFF W. 1994. Ecological standards for eutrophication and desiccation: perspectives for a risk assessment. – Water, Air Soil Pollut. **78:** 265–277.

MEERTS P. 1997. Foliar macronutrient concentrations of forest understorey species in relation to Ellenberg's indices and potential relative growth rate. – Plant and Soil **189:** 257–265.

MELMAN C. P., CLAUSMAN P. H. M. A. & UDO DE HAES H. A. 1988. The testing of three indicator systems for trophic state in grasslands. – Vegetatio **75:** 143–152.

PERSSON S. 1980. Succession in a South-Swedish deciduous wood: a numerical approach. – Vegetatio **43:** 103–122.

ROO-ZIELIŃSKA E. & SOLON J. 1988. Phytosociological typology and bioindicator values of plant communities, as exemplified by meadows in the Nida Valley, Southern Poland. – Doc. Phytosoc. N.S. **11:** 543–554.

SEIDLING W. & ROHNER M.-S. 1993. Zusammenhänge zwischen Reaktions-Zeigerwerten und bodenchemischen Parametern am Beispiel von Waldbodenvegetation. – Phytocenologia **23:** 301–317.

TER BRAAK C. J. F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. – Vegetatio **69**: 69–77.

TER BRAAK C. J. F & ŠMILAUER P. 1998. CANOCO reference manual and user's guide to Canoco for Windows. 351 pp. Centre of Biometry, Wageningen.

TER BRAAK C. J. F. & WIERTZ J. 1994. On the statistical analysis of vegetation change: a wetland affected by water extraction and soil acidification. – J. Veg. Sci. **5:** 361–372.

THIMONIER A., DUPOUEY J. L. & TIMBAL J. 1992. Floristic changes in the herb-layer vegetation of a deciduous forest in the Lorraine Plain under the influence of atmospheric deposition. – Forest Ecol. Manag. **55:** 149–167.

THIMONIER A., DUPOUEY J. L., BOST F. & BECKER M. 1994. Simultaneous eutrophication and acidification of a forest ecosystem in North-East France. – New. Phytol. **126:** 533–539.

THOMPSON K., HODGSON J. G., GRIME J. P., RORISON I. H., BAND S. R. & SPENCER R. E. 1993. Ellenberg numbers revisited. – Phytocoenologia **23:** 277–289.

VAN DER MAAREL E. 1993. Relations between sociological-ecological species groups and Ellenberg indicator values. – Phytocoenologia **23:** 343–362.

VAN DER MAAREL E., BOTT R., VAN DORP D. & RIJNTJES J. 1985. Vegetation succession on the dunes near Oostvoorne, the Netherlands; a comparison of the vegetation in 1959 and 1980. – Vegetatio **58:** 137–187.

ZARZYCKI K. 1984. Ekologiczne liczby wskaźnikowe roślin naczyniowych Polski [Indicator values of vascular plants in Poland]. 45 pp. Instytut Botaniki, Polska Akademia Nauk, Kraków (in Polish).

ZÓLYOMI B., BARÁTH Z., FEKETE G., JAKUCS P., KÁRPÁTI I., KOVÁCS M. & MÁTHE I. 1967. Einreihung von 1400 Arten der ungarischen Flora in ökologische Gruppen nach TWR-Zahlen. – Fragm. Bot. Mus. Hist. Nat. Hung. **4:** 101–142.