Geographia Polonica
2016, Volume 89, Issue 3, pp. 287-309
http://dx.doi.org/10.7163/GPol.0063

INSTITUTE OF GEOGRAPHY AND SPATIAL ORGANIZATION
POLISH ACADEMY OF SCIENCES
www.igipz.pan.pl

www.geographiapolonica.pl

ANCIENT AND RECENT (POST-AGRICULTURAL) FOREST COMMUNITIES AS INDICATORS OF ENVIRONMENTAL CONDITIONS IN NORTH-EASTERN POLAND (MASURIA AND KURPIE REGION)

Ewa Roo-Zielińska • Jan Marek Matuszkiewicz

Institute of Geography and Spatial Organization
Polish Academy of Sciences
Twarda 51/55, 00-818 Warsaw: Poland
e-mails: e.roo@twarda.pan.pl • jan.mat@twarda.pan.pl

Abstract

The paper analyses three forest types belonging to the following associations: (1) fresh pine forest (*Peucedano-Pinetum*), (2) mixed pine forest (*Querco roboris-Pinetum*) and (3) oak-hornbeam forest (*Tilio cordatae-Carpinetum betuli*). They are located in north-eastern Poland. We compared the indicator value of three sets of data: (1) phytosociological relevés representing ancient forests (each type/association), (2) phytosociological relevés representing the youngest recent forests with the shortest regeneration period (each type/association) and (3) the 'abstract pattern' (representing the core of a specific type of plant community with a characteristic combination of species and clearly representing a separate type of ecosystem/association). Three sets of data together with their indicator values/numbers: light intensity (L), soil moisture (F), soil reaction (R), and nitrogen supply (N) according to the Ellenberg scale, constituted the basic material for comparative indicator analysis. The percentage shares of ecological groups of species have been calculated as well as the average indicator values for each of these within a data set. The results obtained show that the 'abstract pattern' can be treated as a good measure for the evaluation of ancient forest habitat conditions; it is clearly visible in the mean L and F indicator values of the *Peucedano-Pinetum* and *Querco-Pinetum* associations, and also in the N of *Peucedano-Pinetum* and R of *Querco-Pinetum*, which are closer to ancient forest than to recent forest. In all cases, we found ecological differences between the ancient and recent forests based on their indicator values. Statistically significant differences of the mean L indicator values between ancient forest and recent forest have been found in three types of forest community.

Key words

characteristic combination of species • Ellenberg ecological indicator values • ancient and recent forests

Introduction

Knowledge of the structure of plant cover, its spatial differentiation, the quantitative and qualitative composition of plant species and their ecological amplitude, enables a determination to be made not just of the current state, but also of processes taking place in those components of the geographical environment which are ecologically significant. This is the subject matter of geobotanical phytoindication (*phyton* – plant, *indico* – to indicate). In this respect the phytosociological and typological system of plant communities (cf. Matuszkiewicz 2001) classifies vegetation primarily on the basis of floristic criteria (mainly species composition) and assigns a plant community to the appropriate hierarchical and typological phytosociological units (Matuszkiewicz 2001). Therefore, plant communities with a known specific structure and species composition together with their indicator values (Ellenberg et al. 1991) can be good indicators of environmental conditions.

The association is a basic unit in the phytosociological typology (classification). It is territorially limited and hierarchically the lowermost type of phytocoenosis. The association with its specific characteristic combination of species[1] differs from other associations in the contribution of at least one characteristic species. It allows syntaxonomic units to be defined with proper sets of characteristic and differential[2] species which are treated as the reference indicators of conditions in the geographical environment and which can be called the 'abstract pattern'. They can be related to the real indicators – which means to real plant communities with a full composition of species as described in phytosociological relevés. It is worth noting that the concept of characteristic plant species results from differences in their range of ecological tolerance. The ecological spectra of plant communities belonging to identified phytosociological units make possible a complete description of conditions in the geographical environment by estimating quantitative indicator values.

The evaluation of environmental conditions using plant species with known ecological and habitat requirements is used to estimate the scale units of ecological indicator values. In statistical terms this is an ordinal scale and these are useful tools for multidirectional and comparative indication analysis. This results in a plant species (usually a vascular plant species) by indicator value matrix containing the estimated responses of the species towards the various ecological indicator values. Ecological indicator values for Central Europe have been presented by Ellenberg et al. (1991) and it is this tool that has been used in the present study (see below). We have described the habitat requirements of the vegetation using the phytosociological relevés plus the indicator values for vascular plant species which were developed by Ellenberg (Ellenberg et al. 1991; Lindacher 1995).

The reader will find detailed information related to geobotanical phytoindication as well as to the ecological scale of indicator values in the books of Roo-Zielińska (2004, 2014) and Roo-Zielińska et al. (2007).

In ecological research much attention is paid to the comparative requirements of different plant communities in relation to natural environmental conditions. It simply uses the indicator values of species or communities for comparative analysis – most often it is the share of the number of species in ecological groups or the average value as a synthetic measure for the real plant community described in the phytosociological relevé (Roo-Zielińska 1993, 1996, 2000, 2004, 2014). It should be noted that the use of indicator species instead of physical and chemical measures saves time, makes it possible to estimate past environmental factors based on vegetation data alone, and gives

---

[1] Characteristic combination of species of different ranks of phytosociological units – it is the set of all characteristic, differential and companion species with the highest degree of stability (Matuszkiewicz 2001).

[2] Differential species occurring in syntaxonomic units and not appearing in comparable syntaxons (Matuszkiewicz 2001).

a synthetic measure of environmental fluctuations in time and space, such as light intensity and soil features such as moisture, acidity, and nitrogen supply, at a local and regional scale (Dzwonko 2001).

Interpretation of the results of indicator values of the vegetation is simple and clear when plant communities belonging to separate phytosociological units with clearly different habitat requirements are the object of comparative analysis. The extreme example could be the comparison of the indicator value of alder forests (*Alnetea glutiinosae* class) occurring on moist, fertile, and neutral soils and pine forests (*Vaccinio-Piceetea* class) occurring on mineral soils on rather dry, poor, and acid soils. It reflects their most frequent spectra of indicator values: F 8-9, R 6-7, N 6-7 for the *Alnetea glutinosae* class and F 4-5, R 2-3, N 2-3 for the *Vaccinio-Piceetea* class (Roo-Zielińska 2014). The situation is quite different if we take a forest community belonging to the same type and phytosociological association, but illustrating different states of recovery associated with the history and long-term evolution of post-agricultural forests (Matuszkiewicz et al. 2013). The authors looked at the problem of forest regeneration in a region of the former German-Polish borderland (East Prussia – Masuria and Kurpie) in a comprehensive study entitled "Long term evolution models of post-agricultural forests".

The study of historical change in vegetation introduced the concept of 'ancient forest' (Peterken 1977; Rackham 1980; Hermy & Stieperaere 1981; Dzwonko & Loster 1988, 1992; Petersen 1994; Wulf 1997; Brunet & von Oheimb 1998; Bossuyt et al. 1999; Orczewska 2003, 2009). This term means a forest that has not had a break in its history via the deforestation process (i.e. was continually under forest) and has not been turned into arable land or pasture. Usually it is taken to mean in the historical period (300-400 years ago), during which uninterrupted forest formation continues. The notion of 'ancient forest', is the opposite of the concept of 'recent forest', i.e. those forest communities occupying habitats on which arable land or other non-forest forms of land use had previously been located. Such forests are clearly different in terms of floristic composition and the structure of the herb layer in relation to 'ancient forests' (Dzwonko & Loster 1992; Dzwonko & Gawroński 1994; Graae & Heskjaer 1997; Honnay et al. 1999; Graae et al. 2003; Petit et al. 2004; Wulf 2004; Góras & Orczewska 2007; Sciama et al. 2009; Orczewska 2010; Matuszkiewicz et al. 2013). Comparing different stages of recovery in recent forests the impact of forest persistence is very important. This means the length of time during which a given piece of land has been afforested and is regenerating. If that period is shorter, then differences in floristic composition are greater due to the limited possibilities for recolonisation by the forest species (Matuszkiewicz et al. 2013).

Matuszkiewicz et al. (2013) demonstrated that recent post-agricultural forests differ from ancient forests in their structure and floristic composition as well as in their indicator value. In the study we took into consideration all recovery states (different ages) of forest belonging to three types and associations: (1) subcontinental fresh pine forest (*Peucedano-Pinetum*), (2) continental mixed pine forest (*Querco roboris-Pinetum*) and (3) subcontinental oak-hornbeam forest (*Tilio cordatae – Carpinetum betuli*). The first two of these belong to the *Vaccinio-Piceetea* class and third to the *Querco-Fagetea* class.

In the present study comparative analysis covered only two categories of forests: the oldest – ancient forest and the youngest – recent forest with the shortest persistence (shortest recovery period) which allows us to capture the maximum differences in the indicator values and relate them to the 'abstract pattern'. In summary, we compared the indicator value of three sets of data: (1) phytosociological relevés representing ancient forests (each type/association), (2) phytosociological relevés representing the youngest short recovery state of recent forests (each type/association) and (3) the characteristic and differential combinations of species as ‘abstract patterns’ defining the three forest associations. The three data sets, together with their indicator values/numbers according to Ellenberg et al. (1991), constitute the basic material presented in the article (Fig. 1).

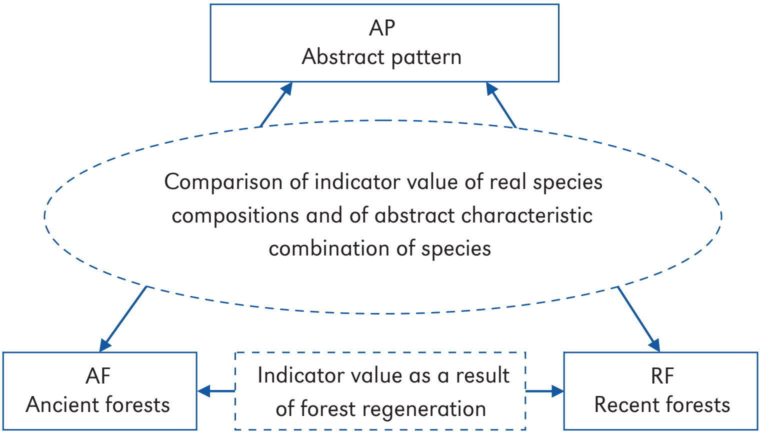


Figure 1. Information value of three data sets/compositions of plant species

We want to answer the following questions: (1) to what extent are the ecological requirements based on a characteristic combination of species (treated as an ‘abstract pattern’) within a similar range as those calculated for real forest communities based on the full list of plant species; (2) what could we expect if the distribution of the percentage share of ecological groups and mean indicator values of the ‘abstract pattern’ are similar to the ancient most stabilised forest and (3) for which ecological variables are there statistically significant light (L), soil moisture (F), soil reaction (R) and nitrogen supply (N) differences between mean indicator values calculated separately for the two data sets (ancient forest and recent forest).

Study area, material and methods

The forest communities analysed as habitat indicators are located in the Kurpie and Masurian regions in northeastern Poland (Fig. 2). The Masurian Plain is to a large extent afforested, and the Kurpie plain was formerly covered by the Green (Kurpie) Forest, but it was heavily cleared and woods mainly persisted on the dunes. Vast valleys are nowadays covered with wet meadows, and agricultural cultivation is limited to sandy plains and loamy mounds. The sandy outwash plain is the habitat of pine forests and mixed oak-pine forests. Typical lime-oak hornbeam forests only developed on the more fertile habitats with moraine forms, and also with marginal and melt-out sands and clay which is found in the north-eastern part of the study area. The study area had either been

Figure 2. Location of the studied forest communities

constantly under forest or had been used for some time in agriculture.

Phytosociological relevés were collected which represented fragments of the forests with an age of not less than 80 years and an aligned structure permitting the identification of plant associations, and these to a large extent reflect the real differentiation of forest vegetation in the study area. Based on historical topographical maps (dating from the middle or end of the XVIII century onwards) and field identification of the plough horizon in the soil, forests were divided into two essential categories – ancient forests (without a plough horizon) and recent forests (with a plough horizon). The selection process was aimed at collecting a possible range of relevés representing three basic types of communities in the region: pine forests (*Peucedano-Pinetum*), mixed oak-pine forests (*Querco-Pinetum*) and lime-oak-hornbeam forests (*Tilio-Carpinetum*). In the studies presented in the article, we only took into consideration phytosociological relevés of two categories of ancient forest and of the recent ones with the shortest persistence – 80-90 (135) years (longer recovery states are omitted) in the three types of community mentioned above (Tab. 1). Phytosociological relevés were collected in accordance with the Braun-Blanquet method (1964). More detailed information about the study area and character of the study forests can be found in Matuszkiewicz et al. (2013).

In Figure 3 the main steps of the comparative indicator analysis used in this paper are summarised.

Two categories, ancient and recent forest communities, have been described by a different number of phytosociological relevés and have been analysed as two data sets (Tab. 1). The third data set ('abstract pattern') is the characteristic combination of species, which means the list of characteristic and differential plant species for each of the three associations (*Peucedano-Pinetum*, *Querco roboris-Pinetum* and *Tilio-Carpinetum*) and these are defined according to the scheme of Matuszkiewicz (2001):

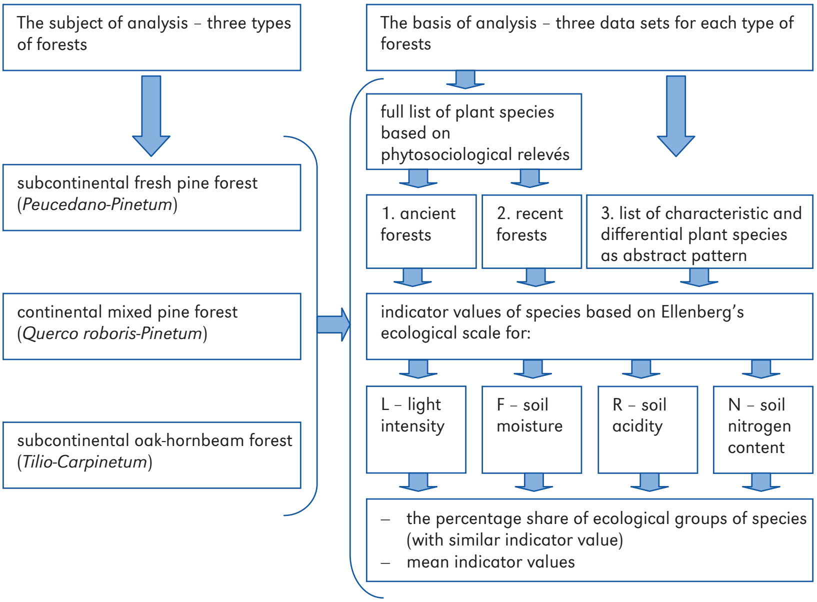


Figure 3. The scheme of comparative analysis of the three data sets in diagnosis of forest communities as indicators of environmental conditions

Table 1. The object of phytoindicative analysis

Symbol	Type of forests	Phytosociological association	Category of forest	Number of relevés
PP1	pine forests	Peucedano-Pinetum	ancient forests	57
PP6	pine forests	Peucedano-Pinetum	recent post-agricultural forests – regeneration period of 80-90 years	8
QP1	mixed oak-pine forests	Querco roboris-Pinetum	ancient forests	33
QP5-6	mixed oak-pine forests	Querco roboris-Pinetum	recent post-agricultural forests – regeneration period of 80-135 years	33
TC1	lime-oak-hornbeam forests	Tilio-Carpinetum	ancient forests	21
TC3-6	lime-oak-hornbeam forests	Tilio-Carpinetum	recent post-agricultural forests – afforested in various periods after 1800 year	10

$$\text{ChSC(Ass.)} = \text{ChAss.} + \text{ChAll.} + \text{ChO.} + \\ + \text{ChCl.} + \text{D} + \text{Comp.}_{\text{IV–V}},$$

where:
ChSC(Ass.) – characteristic species combination of association,
ChAss. – characteristic species of association,
ChAll. – characteristic species of alliance,
ChO. – characteristic species of order,
ChCl. – characteristic species of class,
D – differential species,
Comp.$_{\text{IV–V}}$ – companions of IV and V stability.[3]

That three data sets (ancient forests, recent forests and 'abstract pattern') were used and taken together with the ecological indicator values of the vascular plant species using the nine-degree Ellenberg ordinal scale. These were applied to four environmental factors: light intensity (L), soil moisture (F), soil reaction (R) and soil nitrogen (N) (Ellenberg et al. 1991; Lindacher 1995). Most Ellenberg scales run from 1-9, with moisture from 1-12. The scale value 1 refers to the lowest value of the factor and the scale value 9 to the highest value. No values were assigned to species with unknown ecology, or indifferent to environmental factors (Ellenberg indicator value '0').

The number of vascular herb layer plant species in ancient forest and recent forest communities was different in each phytosociological relevé, and varies in the 'abstract pattern' not only between the three forest associations, but also in relation to the ecological scale, because some of the species had no indicator value (indicator number '0') and were omitted in the calculations (Tab. 2).

The percentage share of ecological groups of a number of vascular plant species was calculated on the nine-degree scale of the Ellenberg ecological indicator values. For a simpler and easier interpretation of the results we combined the scale units as ecological groups of vascular plant species with similar indicator values (Tab. 3) and obtained the results shown in the graphs.

Mean indicator values were calculated for each phytosociological relevé based on the number of species[4] in each Ellenberg scale unit as, for example, for light intensity (L):

$$\text{MLV} = (\text{nsL1} \times \text{L1} + \text{nsL2} \times \text{L2} + \ldots \\ \text{nsL9} \times \text{L9})/\text{tns},$$

---

[3] Companions of IV and V stability have not been analysed, because they do not exist in the "Guide..." of Matuszkiewicz (2001) and they can only be derived from syntaxonomic monographies, in which there is very often a lack of the necessary data.

[4] The cover/abundance of species was not taken into account in the calculations because 'abstract pattern' has no abundance, only a number of species, thus enabling one to compare the three data sets.

where:
MLV – mean L indicator value,
nsL1...nsL9 – number of species (ns) in the interval of the Ellenberg L scale (L1...L9),
tns – total number of species in the phytosociological relevé,
and then these were estimated for the two forest categories (ancient forest and recent forest) and for the 'abstract pattern' for each of the three forest communities/associations.

The mean indicator values and the significance of their differences between the phytosociological relevés corresponding to the three data sets (ancient forest, recent forest and 'abstract pattern') were tested statistically (Kruskal-Wallis test) using the Statistica 7.1 package (*Statistical Yearbook*... 2012). For each of the four ecological factors (L, F, R, N), one figure, broken down into A and B, was prepared for each of the three types of forest.

Results

Pine forest

The pine forest (*Peucedano-Pinetum* association) is composed of Scots pine (*Pinus sylvestris*), with a mossy-dwarf shrub ground layer on poor, sandy podzolic soils with low ground water levels (Fig. 4).

In the three sets of data, a large ecological group was formed by the indicators of moderately light sites (L 6-7). This was largest in the 'abstract pattern' and in the recent forests (ca. 60%). In the ancient forests the percentage share of species tolerating shade (L 2-3) is a little higher than in the recent forests, and in the latter there is a complete lack of species tolerating deep shade (L 1). It is worth noting that the smallest percentage of full light species (L 8-9) (Fig. 5A) is found in the 'abstract pattern'. The mean L indicator values are nearly the same in the ancient forest and in the 'abstract pattern' (L 5.8), while it is slightly higher in the recent forest

Table 2. The number of vascular plant species with indicator value* in phytosociological relevés (minimum and maximum) and in the 'abstract pattern' in analyzed forest associations

Indicator ecological scale	PP (*Peucedano-Pinetum*)			QP (*Querco-Pinetum*)			TC (*Tilio-Carpinetum*)		
	AF	RF	AP	AF	RF	AP	AF	RF	AP
L (light intensity)	4-21	3-13	39	6-31	4-25	34	15-50	19-36	77
F (soil moistre)	1-12	1-7	32	3-22	2-17	25	11-45	11-29	73
R (soil acidity)	4-16	3-11	31	5-24	2-18	24	9-36	13-23	71
N (soil nitrogen)	4-17	3-11	35	7-27	2-21	28	12-47	16-32	74

Explanations: AF – ancient forest, RF – recent forest, AP – 'abstract pattern'
* vascular plant species, indifferent to environmental factors (with indicator value '0') are ommited

Table 3. Ecological groups of vascular plant species as indicators of environmental conditions

L (light intensity of sites)		F (soil moisture)		R (soil reaction/acidity)		N (soil nitrogen)	
1	deep shade	1	extremely dry soils	1	extremely acid soils	1	extremely poor soils
2-3	shade	2-3	dry soils	2-3	acid soils	2-3	poor soils
4-5	half shade	4-5	fresh soils	4-5	moderately acid soils	4-5	moderately rich
6-7	moderate light	6-7	moist soils	6-7	moderately acidic and moderately alkaline soils	6-7	rich soils
8-9	full light	8-9	wet soils	8-9	alkaline soils	8-9	extremely rich soils

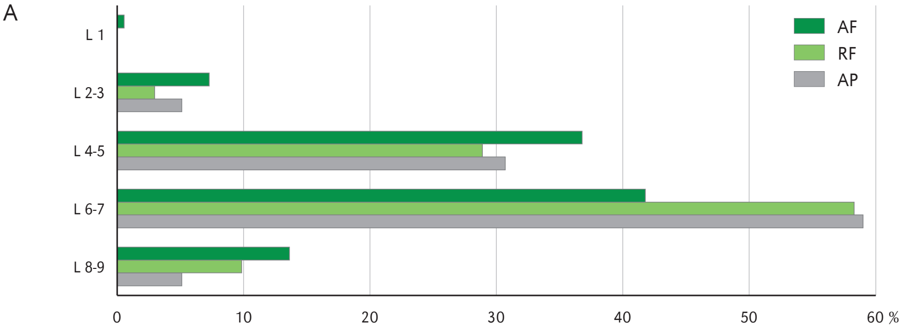
Figure 4. Continental pine forest (*Peucedano-Pinetum*) (Photo J.M. Matuszkiewicz)

(L 6.2) which indicates moderately illuminated sites. The differences in the mean L indicator values between ancient and recent forests are statistically significant, and it is worth underlining that ancient forests are characterised by the widest range of mean L values, and the highest standard deviation while the group of least persistent recent forests is the most uniform, resulting in the smallest range and a narrow standard deviation (Fig. 5B).

In three sets of data a large ecological group is formed by indicators of fresh soils (F 4-5) which is the largest in the ancient forests (ca. 80%). It should be noted that recent forest is characterised by a clearly higher share of species which are indicators of wet soils (F 8-9 – 14.3%) and a lack of those species indicating dry soils (F 2-3). From that point of view recent forests differ from the two other sets (Fig. 6A). The mean F indicator values demonstrated a slight differentiation between the three sets that were analysed (especially a greater number of species that are indicators of wet soils in the recent forests). The difference in the mean F indicator values between ancient forests, recent forests and 'abstract pattern' are statistically insignificant, but it is worth underlining that ancient forests are characterized by a much smaller range of indicator values of F and a narrower standard deviation compared with the recent forest communities (Fig. 6B).

The largest percentage share is formed by species which are indicators of acid soils (R 2-3) which are similar in the three sets of data (ca. 60%). The ancient forest is characterised by a higher share of strongly acidophilic species (R 1 around 16%), compared to the recent forest and 'abstract pattern'. It is worth noting, that there are almost 10% more indicators of moderately acidic and moderately alkaline soils (R 6-7) in the 'abstract pattern' (Fig. 7A). Three mean R values indicate acidic habitats (R 2.7-3.4) and highest' these are more pronounced in the 'abstract pattern'. The differences between ancient forest, recent forest and 'abstract pattern' are statistically insignificant (Fig. 7B).

In three sets of data a large ecological group is formed by species which are indicators of soils poor in nitrogen (N 2-3) and these are most clearly visible in the 'abstract pattern' (80%). Ancient forests are distinguished by the highest percentage of species which are indicators of soils extremely poor in nitrogen (N 1 – ca. 30%). The distribution



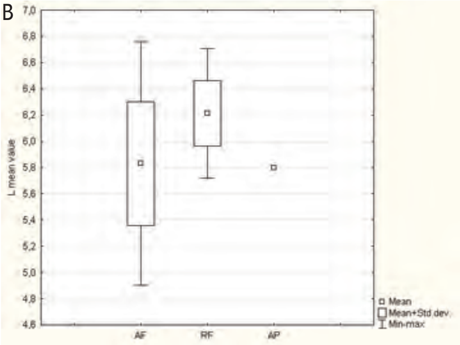
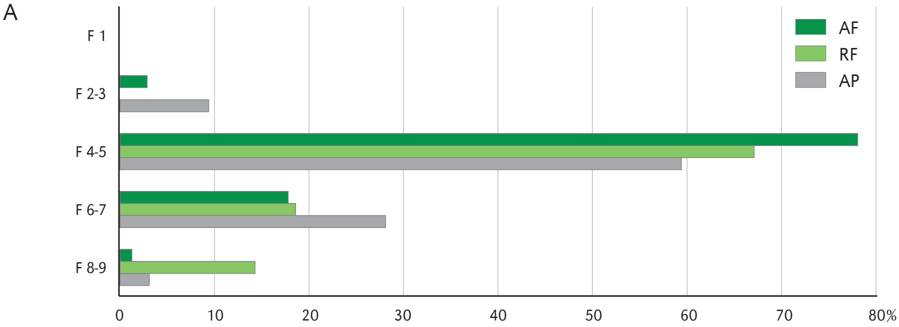


Figure 5. A – The percentage share of species (in total number) in ecological groups as indicators of light intensity (L): ancient forest (AF), recent forest (RF), 'abstract pattern' (AP); B – Mean L indicator values for three data sets: ancient (AF), recent forest (RF) and 'abstract pattern' (AP) in pine forest (*Peucedano-Pinetum* association) – differences between ancient (AF) and recent forests (RF) are statistically significant acc. to Kruskal-Wallis test p ≤ 0.01 [in the following figures captions used abbreviations]



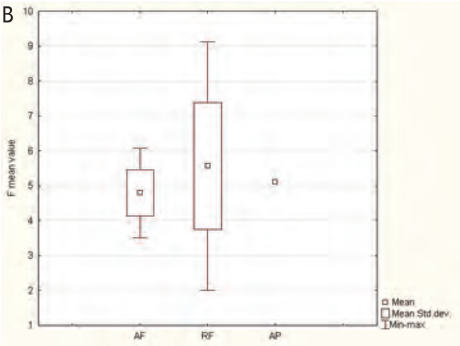
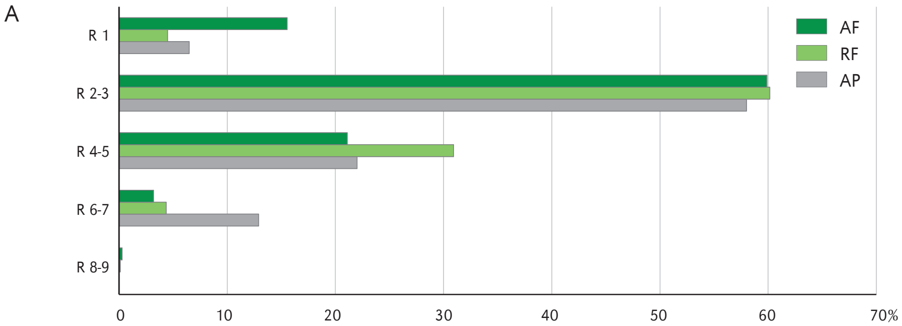


Figure 6. A – The percentage share of species (in total number) in ecological groups as indicators of soil moisture (F): AF, RF and AP; B – Mean F indicator values for three data sets in pine forest (*Peucedano-Pinetum* association) – differences are statistically insignificant acc. to Kruskal-Wallis test p ≤ 0.05



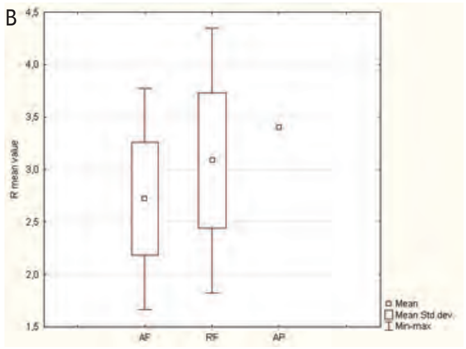
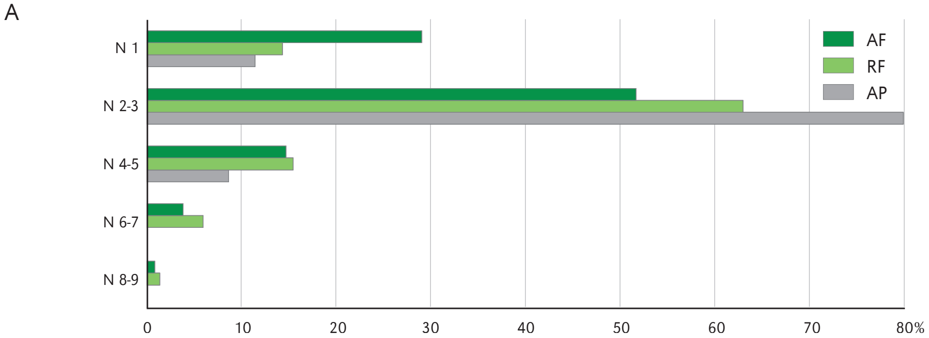


Figure 7. A – The percentage share of species (in total number) in ecological groups as indicators of soil reaction/acidity (R): AF, RF and AP; B – Mean R indicator values for three data sets in pine forest (*Peucedano-Pinetum* association) – differences are statistically insignificant acc. to Kruskal-Wallis test $p \leq 0.05$



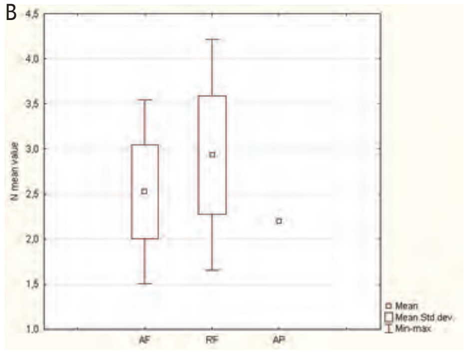


Figure 8. A – The percentage share of species (in total number) in ecological groups as indicators of soil nitrogen (N): AF, RF and AP; B – Mean N indicator values for three data sets in pine forest (*Peucedano-Pinetum* association) – differences are statistically insignificant acc. to Kruskal-Wallis test $p \leq 0.05$

of percentage shares of N-indicators differs in the 'abstract pattern' compared to the ancient forest and recent forest communities due to a complete lack of species that act as indicators of rich (N 6-7) and extremely rich soils (N 8-9) (Fig. 8A). Mean N indicator values point to those habitats poor in nitrogen (N 2.2-2.9). The highest value, attained in the recent forest, defines it as somewhat richer in nitrogen than the remaining communities. The differences between ancient and recent forest communities and the 'abstract pattern' are statistically insignificant (Fig. 8B).

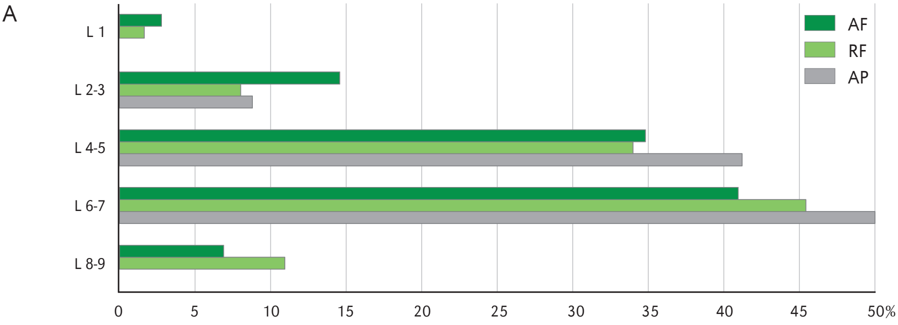
Mixed oak-pine forest

Mixed oak-pine forest (*Querco roboris-Pinetum* association) is formed of Scots pine (*Pinus sylvestris*) and oak (*Quercus robur*) on mesotrophic, slightly podzolic soils (Fig. 9).

In three sets of data the largest percentage share (40-50%) is formed by species which are indicators of moderately light sites (L 6-7), the second most numerous L ecological group is formed by species indicating half shaded sites (L 4-5). The percentage distribution of the ecological groups of species which act as indicators of light intensity is similar in both ancient forests and recent forests, only in ancient forest higher percentages of shade (L 2-3) and deep shade (L 1) tolerant species are noted. In the recent forest there are slightly more species that are indicators of full light sites (L 8-9). The 'abstract pattern' differs from this by its complete lack of ecological groups typical of extreme conditions, i.e. deep shade species (L 1) and full light species (L 8-9) (Fig. 10A). The mean L indicator values show slight differences between the ancient forests and the 'abstract pattern' on one hand (L respectively 5.3 and 5.2) and recent forest on the other (L 5.7). The ancient forests are slightly 'shadier' than the recent ones, and similar to the 'abstract pattern'. The differences between ancient forest and recent forest are statistically significant (Fig. 10B).

The most numerous group is composed of the indicators of fresh soils (F 4-5) in the three data sets (more than 80% in recent forest). It is worth noting that there is a lack of species of extremely dry soils in the three sets of data (F 1). The recent forests are distinguished by a complete lack of indicators of dry soils (F 2-3). The distribution of percentage share of ecological groups of species

Figure 9. Subcontinental mixed oak-pine forest (*Querco roboris-Pinetum*) (Photo J.M. Matuszkiewicz)



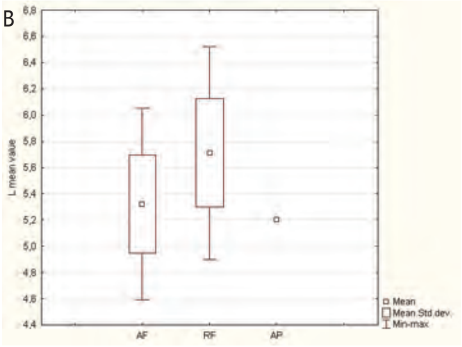
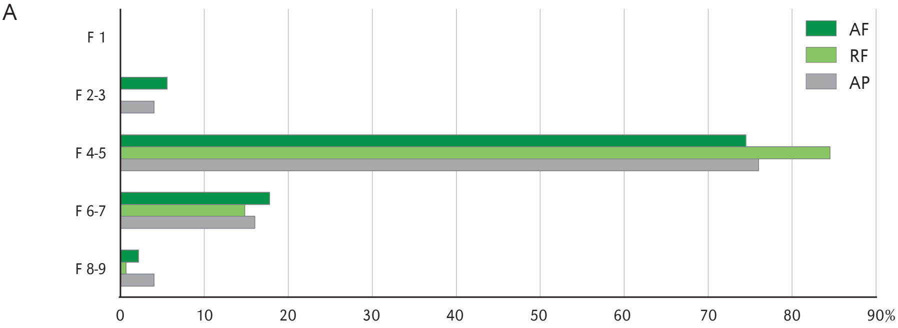


Figure 10. A – The percentage share of species (in total number) in ecological groups as indicators of light intensity (L): AF, RF and AP; B – Average L indicator values for three data sets in mixed oak-pine forest (*Querco roboris-Pinetum* association) – differences between AF and RF are statistically significant acc. to Kruskal-Wallis test $p \leq 0.05$



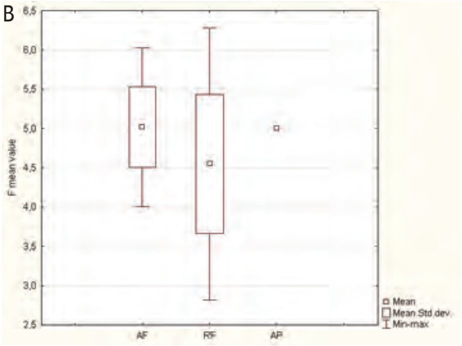
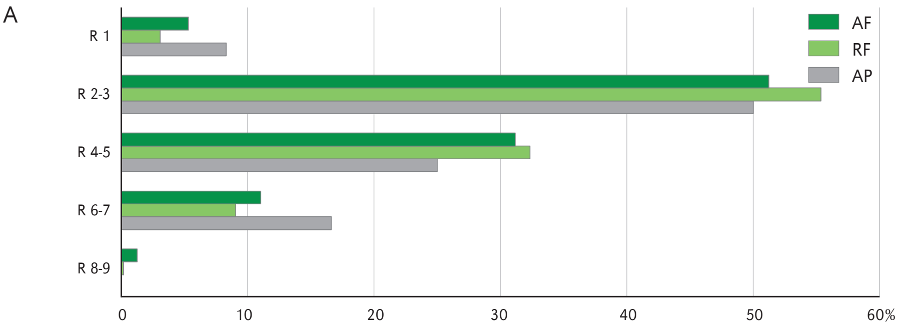


Figure 11. A – The percentage share of species (in total number) in ecological groups as indicators of soil moisture (F): AF, RF and AP; B – mean F indicator values for three data sets in mixed oak-pine forest (*Querco roboris-Pinetum* association) – differences between AF and RF are statistically significant acc. to Kruskal-Wallis test $p \leq 0.05$

are very similar in the 'abstract pattern' and in the ancient forests (Fig. 11A). The mean F indicator values indicate fresh habitats and are identical in ancient forest and in the 'abstract pattern' (F 5). It is worth noting that recent forest, despite the lack of indicators of dry soils (F 2-3), is slightly drier (F 4.7) than the two the other sets, which expresses the statistically significant differences between the mean F values of ancient forest and recent forest communities (Fig. 11B).

In the three sets of data the most numerous group (above 50%) is formed by indicators of acid soils (R 2-3). The percentage shares of ecological groups of species are quite similar in the three sets of data analysed. The 'abstract pattern' differs by a complete lack of indicators of alkaline soil (R 8-9) and a few more species that are indicators of extremely acid soils (R 1) (Fig. 12A). Likewise, the mean R indicator values are similar in all three data sets and highlight the acid habitats (R 3.4-3.6). A slightly higher average R indicator value has been noted in the 'abstract pattern' and in the ancient forest, while a slightly lower one was noted in the recent forest. There were no statistically significant differences between R averages based on the three data sets (Fig. 12B).

The most numerous group (ca. 50-75%) is formed by indicators of soils poor in nitrogen (N 2-3). The share of species that are indicators of extremely poor soils is lowest in the 'abstract pattern' (N 1 – ca. 4%) and there is also a lack of indicators of extremely rich soils (N 8-9) compared to the other two sets (ancient forests and recent forests) in which the distribution of percentages is similar (Fig. 13A). The mean N indicator values imply habitats poor in nitrogen compounds (N 2.8-3.3). The highest average N value was found in the ancient forest but the differences in mean N values between the three sets of data are statistically insignificant (Fig. 13B).



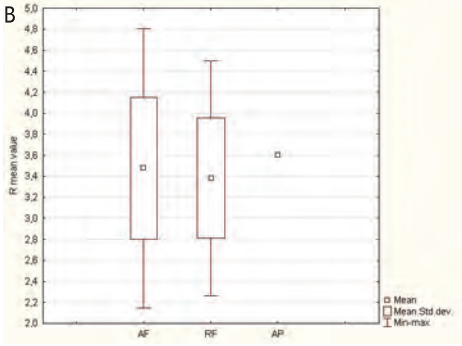


Figure 12. A – The percentage share of species (in total number) in ecological groups as indicators of soil reaction/acidity (R): AF, RF and AP; B – Mean R indicator values for three data sets in mixed oak-pine forest (*Querco roboris-Pinetum* association) – differences are statistically insignificant acc. to Kruskal-Wallis test $p \leq 0.05$

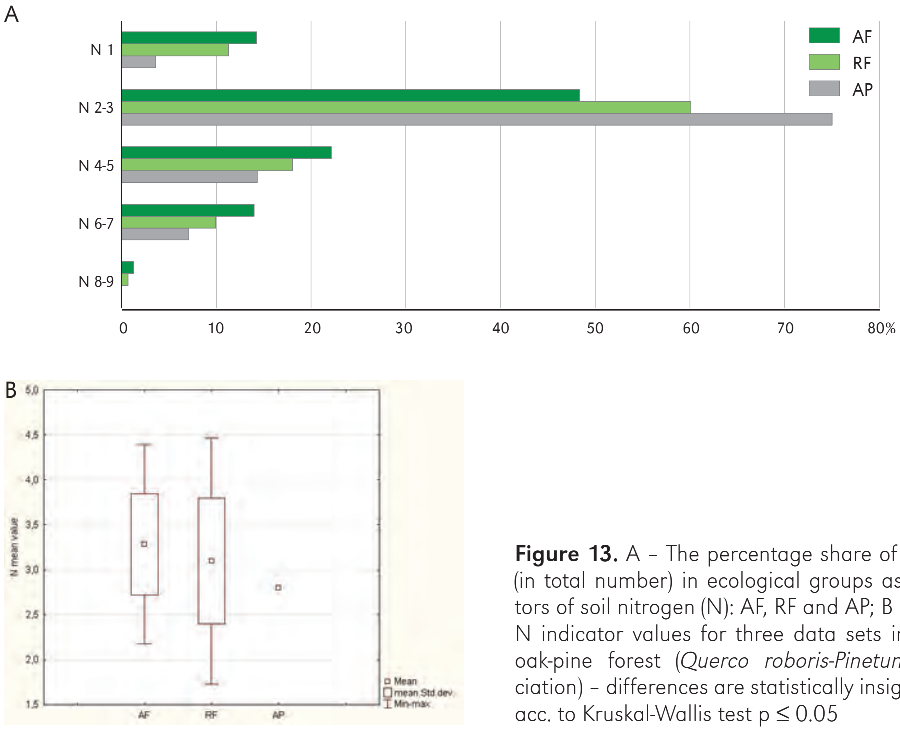


Figure 13. A – The percentage share of species (in total number) in ecological groups as indicators of soil nitrogen (N): AF, RF and AP; B – Mean N indicator values for three data sets in mixed oak-pine forest (*Querco roboris-Pinetum* association) – differences are statistically insignificant acc. to Kruskal-Wallis test $p \leq 0.05$

Oak-hornbeam forest

Oak-hornbeam forest (*Tilio-Carpinetum* association) is mainly formed of oak (*Quercus robur*) and hornbeam (*Carpinus betulus*) with a broad ecological spectrum of habitat conditions especially in terms of soil moisture and soil fertility (Fig. 14)

In three sets of data the most numerous group is formed by indicators of half shaded sites (L 4-5) and there is a similar percentage share in both ancient forests and recent forests (respectively 45% and 49%) and about a 15% higher share of these indicators in the 'abstract pattern'. The recent forests feature a much lower percentage share of shade-tolerant species (L 2-3), and a higher share of indicators of moderately light stands (L 6-7) compared to the ancient forest and 'abstract pattern'. However, the 'abstract pattern' is distinguished by the lowest share of indicators of moderately light sites (L 6-7) and a complete lack of indicators of full light sites (L 8-9) (Fig. 15A). The mean L indicator value is highest (L 5.2) for recent forest which differs from the remaining sites. The value is lowest in the 'abstract pattern' (L 4.2). Statistical significance has been noted with regard to the differences between the mean L values of ancient forest and of recent forest (Fig. 15B).

The most numerous indicators are those of fresh soils (F 4-5) (more than 80% in the recent forest and in the ancient forest). Additionally, there is a lack of species indicating extremely dry (F 1) and wet soils (F 8-9). The percentage shares of the species groups featuring differing requirements with respect to soil moisture are quite similar in the ancient forest and the recent forest. The 'abstract pattern' differs from them by: (1) a lack of dry soil species (F 2-3) and (2) a percentage share of moist soil indicators that is almost twice as large (F 6-7) (Fig. 16A). The mean F indicator values are quite similar and indicate fresh habitats (F 5.1-5.3). It can be noted that the recent forest included

Figure 14. Oak-hornbeam forest (*Tilio-Carpinetum*) – photo J.M. Matuszkiewicz

slightly drier plots, which produce the lowest mean F value. No statistically significant differences were found between the three sets of data (Fig. 16B).

Both ancient forests and recent forests are mainly formed of species which are indicators of moderately acidic and moderately alkaline soils (R 6-7) and by a slightly smaller number of indicators of moderately acidic soils (R 4-5). The recent forest stands differ from ancient forests in their relatively higher share (up to roughly 10%) of acidophilous species (R 2-3), and lower share (around 10%) of indicators of slightly acid or alkaline habitats. The percentage distribution of R ecological groups in the 'abstract pattern' differs from both ancient forest and recent forest by: (1) a lack of acidophilous species, (2) a higher percentage share (ca. 20%) of moderately acid and moderately alkaline soils and (3) a significantly higher share (ca. 25%) of indicators of alkaline soils (R 8-9) (Fig. 17A). The mean R indicator values of the three sets of oak-hornbeam forests reflect the moderately acid and moderately alkaline habitats. A distinctly lower value is observed in the recent forests (R 4.6), and a much higher one (more than two units above) in the 'abstract pattern' (R 6.9). The difference of mean R values between the ancient forest and recent forest is statistically insignificant (Fig. 17B).

It is worth noting that in the case of N, the ecological groups cannot be distinguished by one clearly dominant group. The recent forest is distinguished by the higher percentage share of species that are indicators of soils that are extremely poor (N 1), as well as poor (N 2-3) in nitrogen compared to the ancient forests. The opposite is observed in the 'abstract pattern': there is a complete lack of indicators of extremely poor soils, a low percentage of poor soils and a higher percentage of indicators of rich (N 6-7) and extremely rich (N 8-9) soils compared to recent and ancient forests (Fig. 18A). Mean N values of the three sets of oak-hornbeam forests show habitats moderately rich in nitrogen (N 4.7-5.7) – lowest in the recent forest and highest (about one unit above) in the 'abstract pattern'. Generally ancient forest is characterised by a narrow standard deviation and range of mean N values, while recent forest shows a larger standard deviation and a wider range of N indicator values (Fig. 18B).

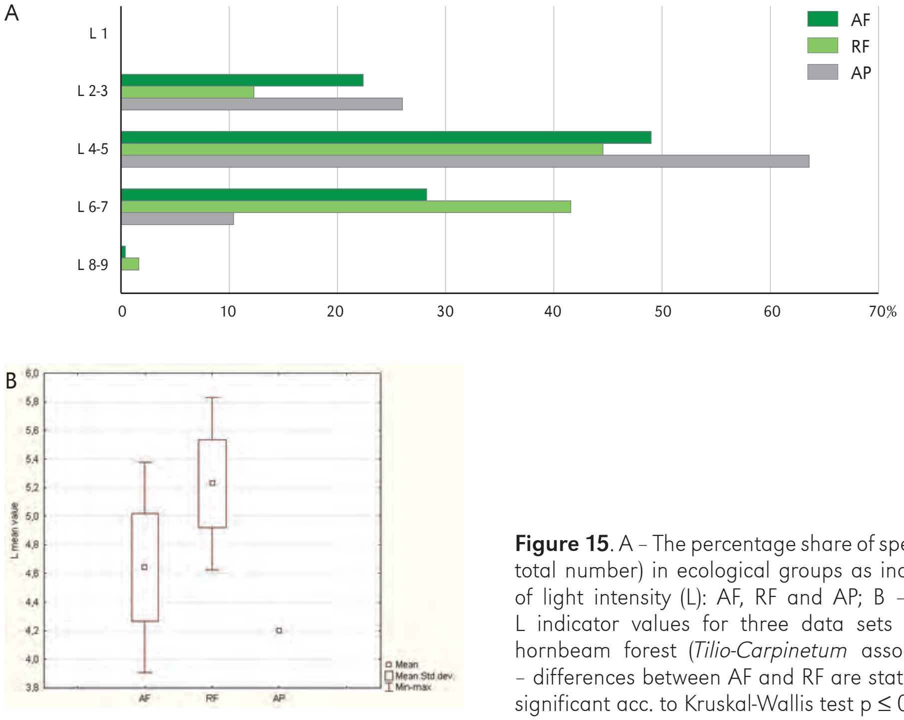


Figure 15. A – The percentage share of species (in total number) in ecological groups as indicators of light intensity (L): AF, RF and AP; B – Mean L indicator values for three data sets in oak-hornbeam forest (*Tilio-Carpinetum* association) – differences between AF and RF are statistically significant acc. to Kruskal-Wallis test p ≤ 0.05

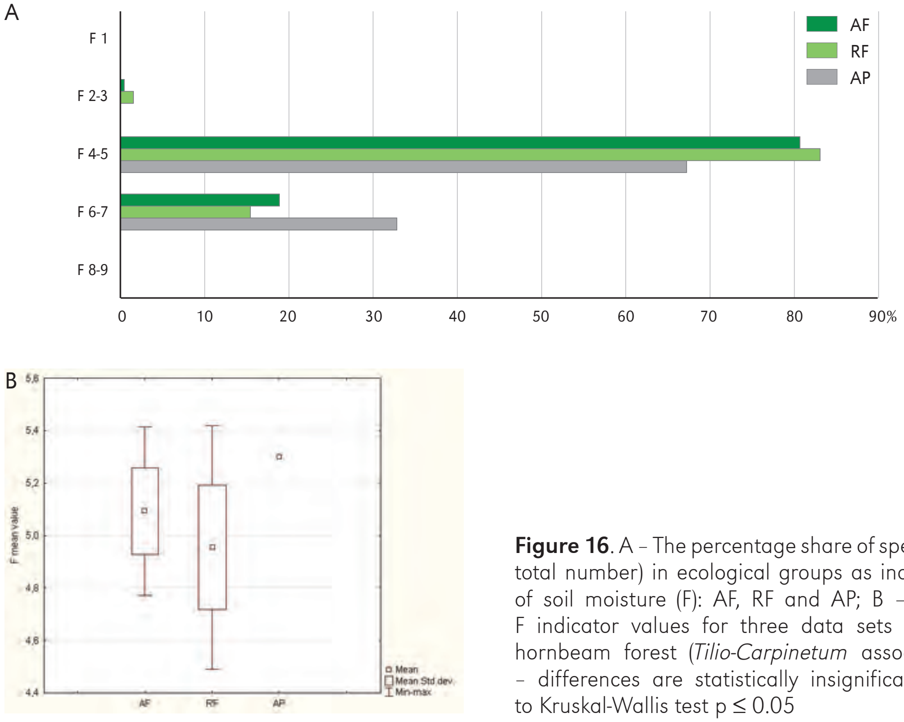
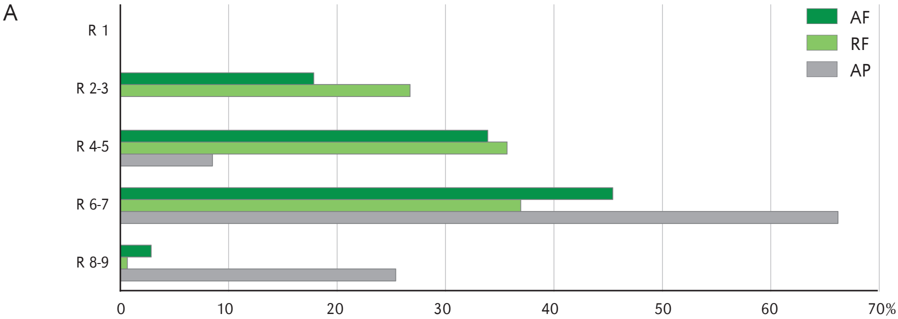


Figure 16. A – The percentage share of species (in total number) in ecological groups as indicators of soil moisture (F): AF, RF and AP; B – Mean F indicator values for three data sets in oak-hornbeam forest (*Tilio-Carpinetum* association) – differences are statistically insignificant acc. to Kruskal-Wallis test p ≤ 0.05



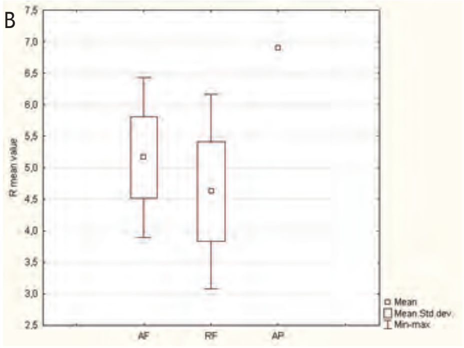
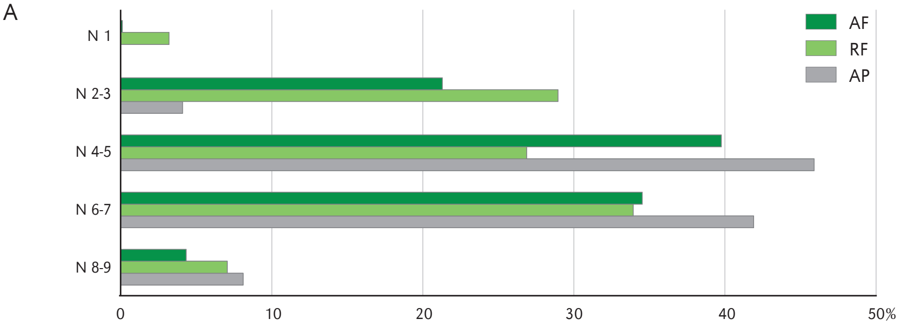


Figure 17. A – The percentage share of species (in total number) in ecological groups as indicators of soil reaction/acidity (R): AF, RF and AP; B – Mean R indicator values for three data sets in oak-hornbeam forest (*Tilio-Carpinetum* association) – differences are statistically insignificant acc. to Kruskal-Wallis test p ≤ 0.05



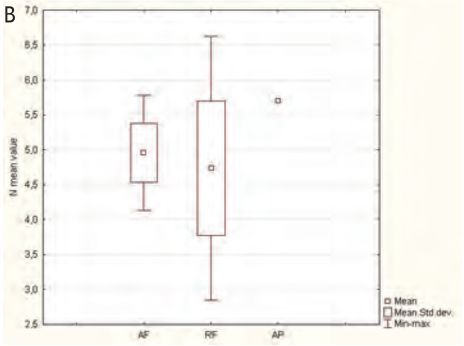


Figure 18. A – The percentage share of species (in total number) in ecological groups as indicators of soil nitrogen (N): AF, RF and AP; B – Mean N indicator values for three data sets in oak-hornbeam forest (*Tilio-Carpinetum* association) – differences are statistically insignificant acc. to Kruskal-Wallis test p ≤ 0.05

Summary of results

In pine forests and mixed pine forests the L ecological group of indicators of moderate light predominate and in oak-hornbeam forests half shaded stands prevail. It is worth noting that in mixed pine and oak-hornbeam forests, the more recent stands are characterised by a slightly higher percentage of species that are indicators of fully illuminated sites. The mean L indicator values of 'abstract pattern' and ancient forest are similar to each other and most visible in pine forest (*Peucedano-Pinetum*). In three types of forest we found a higher mean L indicator value for the recent forest communities. It is worth noting that the differences in mean L indicator values between ancient forest and recent forest are statistically significant for three types of forest community (*Peucedano-Pinetum*, *Querco-Pinetum* and *Tilio-Carpinetum*) (Tab. 4). This results from the fact that they contain many more companion light species typical of open habitats: in oak-hornbeam forests, for example, these are meadow species (*Molinio-Arrhenatheretea* class), for pine forests they are sandy grassland species (*Koelerio glaucae-Corynephoretea canescentis* class).

In all the forests analysed, the F ecological group of indicators of fresh soils is dominant. The distribution of the percentage share of F indicators is very similar in the 'abstract pattern' and in the ancient forest and it mainly concerns mixed pine forest (*Querco roboris-Pinetum*) and pine forest (*Peucedano-Pinetum*). The mean F indicator values are similar in the 'abstract pattern' and in ancient forest, and also most clear in the *Querco roboris-Pinetum* and *Peucedano-Pinetum* associations. It is worth noting that differences between ancient forest and recent forest in mean F indicator values are statistically significant for the *Querco-Pinetum* association (Tab. 4). That result should be expected because ancient forests certainly contain fewer alien species invading from other plant communities/other phytosociological units. In this sense, they are more similar to the 'abstract pattern' than to the recent forests.

In pine and mixed pine forests R indicators of acid and in oak-hornbeam forest slightly acid and slightly alkaline soils dominate. It is worth noting that a higher percentage share of the number of species that are indicators of moderately acid and alkaline soils is observed in the 'abstract pattern' than is observed in the ancient forest and recent forest. This is clearly visible in the *Tilio-Carpinetum* association. That result expresses the mean R indicator values – higher in the 'abstract pattern' compared to the ancient forests and recent forests of the *Tilio-Carpinetum* and *Peucedano-Pinetum* associations – and we found a similarity between the 'abstract pattern' and the ancient forest of the *Querco-Pinetum* association. In the

Table 4. Similarity and differences of the mean indicator values between three data sets in analyzed types of forest communities/associations

Mean indicator values	PP (*Peucedano-Pinetum*)		QP (*Querco-Pinetum*)		TC (*Tilio-Carpinetum*)	
	Similarity	Differences	Similarity	Differences	Similarity	Differences
	AP-AF	AF-RF	AP-AF	AF-RF	AP-AF	AF-RF
L (light intensity)	AP~AF	AF<RF*	AP~AF	**AF<RF**		**AF<RF**
F (soil moisture)	AP~AF	AF<RF	AP~AF	**AF>RF**		AF>RF
R (soil acidity)		AF<RF	AP~AF	AF>RF		AF>RF
N (nitrogen content in the soil)	AP~AF	AF<RF		AF>RF		AF>RF

Explanations: AF – ancient forest, RF – recent forest, AP – 'abstract pattern'

bold – statistically significant difference acc. to the Kruskal-Wallis test $p \leq 0.05$; * – statistically significant difference acc. to the Kruskal-Wallis test $p \leq 0.1$

Tilio-Carpinetum association the mean R indicator value is clearly lower in recent forest (Tab. 4). This may be due to the fact that the 'abstract pattern' applies to typical oak-hornbeam forests – *Tilio-Carpinetum typicum* (with a higher share of species typical of weakly acid and weakly alkaline soils), but we mainly analysed 'slightly more acidic', poor mesotrophic oak-hornbeam forests (*Tilio-Carpinetum calamagrostietosum*). This may also be the result of the process of introducing coniferous trees to deciduous forest habitats and the exchange of the herb layer species typical of oak-hornbeam forests into those typical of coniferous ones. In the recent forest that process could be the reason for the increase in the number of acidophilous species, and a decrease in the indicators of slightly acid and slightly alkaline soils.

In pine and mixed-pine forests N indicators of soils poor in nitrogen content dominate. In oak-hornbeam forest this does not indicate the dominance of any ecological group so that there is definitely a larger differentiation of environmental requirements in oak-hornbeam forests due to their wider ecological spectrum than the more homogeneous habitat conditions of pine and mixed-pine forests. It should be noted that the distributions of the percentage share of N ecological groups in ancient forests and recent forests are similar to each other in the three types of forest. Mean N indicator values show the similarity of ancient forest to the 'abstract pattern' in the *Peucedano-Pinetum* association, while the recent ones clearly have a higher mean N value compared to the 'abstract pattern' and ancient forest (Tab. 4). This may be due to the fact that the dominant plant species in the species composition of ancient forests are so-called 'ancient forest plant species' (Hermy et al. 1999; Dzwonko & Loster 2001)[5]. Very often the characteristic species are the same as the 'ancient forest plant species'. The recent post agricultural pine forests, however, are partially occupied by alien companion species, for example 'refugees' from grassland plant communities, including ruderal and segetal weeds, and partially by plant species from forest communities belonging to other phytosociological units, e.g. species from xerothermic oak forests (*Potentillo albae-Quercetum* association).

Summarizing these results, we can say that, in spite of the different evolution and history of the forests studied (the most natural – ancient forests and the most anthropogenically changed – recent post-agricultural forests) their specific differences between types were preserved, including their ecological characteristics and indicator roles. Pine forests (*Peucedano-Pinetum* association) have in their composition the largest number of species that are indicators of full light sites and the driest, most acid and oligotrophic habitats, whereas oak-hornbeam forests (*Tilio-Carpinetum* association) are the most shaded, slightly moist, less acid and have much more fertile soils than the other two types. Mixed pine forests (*Querco roboris-Pinetum* association) are in between, although in the case of most ecological features they are closer to pine than to oak-hornbeam forests.

Discussion – comparison with other studies

It seems that the results here reported can be considered most comparable with those referring to ancient forest and recent (mainly post-agricultural) forest complexes in Poland. Unfortunately, it should be noted that there is a lack of articles in the literature comparing the indicator results obtained on the basis of a characteristic combination of species named in this article as 'abstract pattern' with complete lists/phytosociological relevés of plant species describing the actual plant communities, especially for the most stable forest complexes.

Dzwonko (2001), when conducting ecological-biological investigations within the

---

[5] Ancient forest plant species are unable to colonise isolated recent forests and may be considered as indicators of ancient forests because their presence suggests a long continuous history for the patch of habitat (Dzwonko & Loster 2001).

Carpathian Foothills, considered the possibility of applying Ellenberg's ecological indicator values, which are widely used for the assessment of light and soil conditions, not only in Central Europe, but also outside it. The purpose of the study referred to was to answer the question of the degree to which the Ellenberg indicator values could be applied to characteristics of the environmental conditions of ancient and recent deciduous forests on the same soil type. It ought to be emphasised that the species with the lowest R and N indicator values were less numerous in the recent forests than in the ancient ones. The recent forest complexes featured higher shares of species with higher R and N indicator values. This partly explains the reason why the indicator species of ancient forests, mostly acidophilous and oligotrophic, hardly colonise the richer habitats of the recent forests. Dzwonko (2001) notes that the average values of the L, R and N indicators were relatively good yardsticks for the assessment of the environmental conditions in the ancient forests with stabilised species composition, while not so good in the case of recent forests with a yet unstable structure, and ought to be verified by direct laboratory measurements of the environmental variables.

Thus, Orczewska (2010) analysed forests of black alder, featuring a high groundwater level, in south-eastern Poland. She demonstrated that the species composition of the herb layer in the recent forests contains a higher number of species indicative of slightly acid or alkaline soils, and there are more species preferring moderately shaded sites and moist soils. On the other hand, in ancient forests there are higher shares of the species indicative of low or moderate nitrogen content than in the recent forests.

It is worth pointing out that our indicator results confirmed the tendencies described by Dzwonko (2001) concerning R and N indicators and by Orczewska (2010) concerning the F indicator for ancient and recent pine forests, but do not show clear differences (not statistically significant) for oak-hornbeam forest. It is noted that light-demanding species appear in recent oak-hornbeam forest, which is consistent with the information from Dzwonko (2001) that shrubs are quite demanding with respect to light, and it is light that influences the increase in the number of light-demanding species in this layer of recent forests.

It should be underlined that studies akin to those conducted in Poland have also been performed in many other European countries, using, in addition, phytoindication analysis, frequently with respect to similar types of forest community. And so results similar to those obtained on the basis of the phytoindication analysis of Polish forests were reported by Wulf (2004) for a study carried out in ancient forests (19th century) and recent forests (20th century) in south-eastern Germany with stands dominated by birch and oak. Here, in addition, the ancient forests hosted a much larger number of species tolerating shade, and also of species indicative of moderately acid soils and avoiding soils rich in nitrogen, as compared to recent forests. Our results confirm the studies of Wulf (2004) and illustrate that ancient oak-hornbeam forests in north-eastern Poland have a similar indicator role and that there is a greater number of species tolerating shade and moderately acid soils in their species composition, and a smaller number of species that act as indicators of soils rich in nitrogen (with an indicator value of N 8-9) as compared to recent oak-hornbeam forests.

In central Belgium, Bossuyt et al. (1999) analysed the migration of vascular plant species in the undergrowth across the ecotones between ancient and recent deciduous forest complexes. Based on the results obtained, these authors showed that species accept the increase in the nitrogen content in the soil (the Ellenberg N indicator value) more easily than ancient forests. Likewise, more species requiring well illuminated sites (L) have been observed in them. These species also encounter difficulties in expanding and occupying new sites, because the ancient forests are characterised by a high degree of cover by the species better adapted to shaded sites (low L value) and low nitrogen content (low N value).

Dumortier et al. (2002) analysed forests belonging to the *Quercion* alliance – also situated in central Belgium. According to these authors habitat quality also constitutes an important factor determining species composition. Thus, for instance, the level of soil reaction (pH) is low in the ancient forests and statistically negatively correlated with forest age.

It is also worth noting the very significant investigations consisting in the compilation of literature-based data originating from various countries. So Hermy et al. (1999), in particular, demonstrated, on the basis of the ecological characteristics of 132 species of ancient deciduous forest plants in Europe taken from 22 literature sources, that these species tolerate the shaded sites better and are indicators of habitats that are moderately moist, moderately acid and moderately rich in nitrogen (that is – they avoid habitats displaying extreme features), when compared to recent forests. Quite similarly, Verheyen et al. (2003), who surveyed literature from eight European countries and four from North America, carried out an analysis of 216 species characteristic of forest which may determine their reaction to changes in land use. Like in the cases of the studies already referred to, the authors demonstrated that forest plant species with heavy seeds, transported by ants (myrmecochores), are more common in ancient forests, while the shares of species with seeds of small dimensions and those transported on the outside of animals (epizoochores) are much more frequent in recent forests. It is worth noting – according to the authors quoted – that many of the species colonising moderately moist (free draining) habitats, do colonise dry habitats more slowly. It appears, therefore, that the production of a large number of easily transported seeds does not guarantee the colonisation of places featuring extreme environmental conditions.

It ought to be emphasised that (despite the not very large number of phytosociological relevés describing the floristic composition of the forest communities) the ecological characteristics, and indicator analysis of forest communities within the Masurian-Kurpie borderland are subject to varied human impacts and are very appropriate to the subject matter of the literature survey commented upon here.

Conclusion – answers to basic questions

1. It should be emphasised that the ‘abstract pattern’ is the core of a specific type of plant community and as a characteristic combination of species clearly represents a separate type of ecosystem without accompanying species which very often have quite different ecological requirements than ‘abstract pattern’ species. The ‘abstract pattern’ is the basic criterion taken into account in the syntaxonomic classification and typology of plant communities, while phytosociological relevés describe the reality of nature, i.e. the actually existing plant communities with their full species composition.
2. The results obtained show that the ‘abstract pattern’, based on a characteristic species combination in the forest associations analysed, can be treated as a good measure for the evaluation of habitat conditions in ancient forests. This is clearly visible in the mean L and F indicator values in the *Peucedano-Pinetum* and *Querco-Pinetum* associations, and additionally in the mean N indicator values in *Peucedano-Pinetum* and mean R indicator values in *Querco-Pinetum*, which are closer to the ancient than to the recent forest, as we would expect.
3. In all cases we found ecological differences between ancient and recent forests based on their indicator values. It is worth noting, that for three types of forest we found statistically significant differences of mean L indicator values between ancient and

recent forest. We could find some differences in standard deviation depending on the environmental factor. For example, the mean F indicator values for pine and N for oak-hornbeam, both more stable and mature ancient forests, characterise narrower standard deviations (mean values are more clustered around the average) than recent forests with a more unstable structure and larger standard deviations.

Editors' note:
Unless otherwise stated, the sources of tables and figures are the authors', on the basis of their own research.

References

Bossuyt B., Hermy M., Deckers J., 1999. *Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium*. Journal of Ecology, vol. 87, no. 4, pp. 628-638.

Braun-Blanquet J., 1964. *Pflanzensoziologie. Grundzüge der Vegetationskunde*. Wien-New York: Springer.

Brunet J., von Oheimb G., 1998. *Migration of vascular plants to secondary woodlands in southern Sweden*. Journal of Ecology, vol. 86, no. 3, pp. 429-438.

Dumortier M., Butaye J., Jacquemyn H., Van Camp N., Lust N., Hermy M., 2002. *Predicting vascular plant species richness of fragmented forests in agricultural landscapes in central Belgium*. Forest Ecology and Management, vol. 158, no. 1-3, pp. 85-102.

Dzwonko Z., 2001. *Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values*. Journal of Applied Ecology, vol. 38, no. 5, pp. 942-951.

Dzwonko Z., Gawroński S., 1994. *The role of woodland fragments, soil types, and dominant species in secondary succession on the western Carpathian foothills*. Vegetatio, vol. 111, no. 2, pp. 149-160.

Dzwonko Z., Loster S., 1988. *Species richness of small woodlands on the western Carpathian foothills*. Vegetatio, vol. 76, no. 1/2, pp. 15-27.

Dzwonko Z., Loster S., 1992. *Species richness and seed dispersal to secondary woods in southern Poland*. Journal of Biogeography, vol. 19, no. 2, pp. 195-204.

Dzwonko Z., Loster S., 2001. *Wskaźnikowe gatunki roślin starych lasów i ich znaczenie dla ochrony przyrody i kartografii roślinności* [in:] E. Roo-Zielińska, J. Solon (eds.), Typologia zbiorowisk i kartografia roślinności w Polsce – rozważania nad stanem współczesnym, Prace Geograficzne, 178, Warszawa: Instytut Geografii i Przestrzennego Zagospodarowania PAN, pp. 119-132.

Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W., Paulissen D., 1991. *Zeigerwerte von Pflanzen in Mitteleuropa*. Scripta Geobotanica, vol. 18, Göttingen: Erich Goltze.

Góras P., Orczewska A., 2007. *Zróżnicowanie runa w lasach sosnowych posadzonych na gruntach porolnych i w starych lasach sosnowych na siedlisku boru mieszanego świeżego*. Przegląd Przyrodniczy, vol. 18, no. 1-2, pp. 227-241.

Graae B.J., Heskjaer V.S., 1997. *A comparison of understorey vegetation between untouched and managed deciduous forest in Denmark*. Forest Ecology and Management, vol. 96, no. 1-2, pp. 111-123.

Graae B.J., Sunde P.B., Fritzbøger B., 2003. *Vegetation and soil differences in ancient opposed to new forests*. Forest Ecology and Management, vol. 177, no. 1-3, pp. 179-190.

Hermy M., Honnay O., Firbank L., Grashof-Bokdam C., Lawesson J.E., 1999. *An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation*. Biological Conservation, vol. 91, no. 1, pp. 9-22.

Hermy M., Stieperaere H., 1981. *An indirect gradient analysis of the ecological relationships between ancient and recent riverine woodlands to the south of Bruges (Flanders, Belgium)*. Vegetatio, vol. 44, no. 1, pp. 43-49.

Honnay O., Hermy M., Coppin P., 1999. *Impact of habitat quality on forest plant species colonization*. Forest Ecology and Management, vol. 115, no. 2-3, pp. 157-170.

Lindacher R. (ed.), 1995. *Phanart, Datenbank der Gefässpflanzen Mitteleuropas. Erklarung der Kennzahlen, Aufbau und Inhalt*. Zürich: Geobotanischen Institute der Eidgenössischen Technischen Hochschule.

Matuszkiewicz J.M., Kowalska A., Kozłowska A., Roo-Zielińska E., Solon J., 2013. *Differences in plant-species composition, richness and community structure in ancient and post-agricultural pine forests in central Poland*. Forest Ecology and Management, vol. 310, pp. 567-576.

Matuszkiewicz J.M., Kowalska A., Solon J., Degórski M., Kozłowska A., Roo-Zielińska E., Zawiska I., Wolski J., 2013. *Long-term evolution models of post-agricultural forests.* Prace Geograficzne, 240, Warszawa: Instytut Geografii i Przestrzennego Zagospodarowania PAN.

Matuszkiewicz W., 2001. *Przewodnik do oznaczania zbiorowisk roślinnych Polski*. Warszawa: Wydawnictwo Naukowe PWN.

Orczewska A., 2003, *Postglacjalna historia lasów południowej Opolszczyzny*. Natura Silesiae Superioris, vol. 7, pp. 79-88.

Orczewska A., 2009. *Migration of herbaceous woodland flora into post-agricultural black alder woods planted on wet and fertile habitats in south western Poland*. Plant Ecology, vol. 204, no. 1, pp. 83-96.

Orczewska A., 2010. *Colonization capacity of herb woodland species in fertile, recent alder woods adjacent to ancient forest sites.* Polish Journal of Ecology, vol. 58, no. 2, pp. 297-310.

Peterken G.F., 1977. *Habitat conservation priorities in British and European woodlands*. Biological Conservation, vol. 11, no. 3, pp. 223-236.

Petersen P.M., 1994. *Flora, vegetation, and soil in broadleaved ancient and planted woodland, and scrub on Røsnæs, Denmark*. Nordic Journal of Botany, vol. 14, no. 6, pp. 693-709.

Petit S., Griffiths L., Smart S.S., Smith G.M., Stuart R.C., Wright S.M., 2004. *Effects of area and isolation of woodland patches on herbaceous plant species richness across Great Britain*. Landscape Ecology, vol. 19, no. 5, pp. 463-471.

Rackham O., 1980. *Ancient woodland: its history, vegetation and uses in England*. London: Edward Arnold.

Roo-Zielińska E., 1993. *The current state and changes in the meadow flora in the Nida valley, southern Poland*. Fragmenta Floristica et Geobotanica, vol. 38, no. 2, pp. 581-592.

Roo-Zielińska E., 1996. *Phytoindicative role of plant communities in a rural landscape (Pińczów case study, south Poland).* Fragmenta Floristica et Geobotanica, vol. 41, no. 1, pp. 379-398.

Roo-Zielińska E., 2000. *Vegetation at different levels of organization as an indicator of environmental conditions* [in:] Proceedings IAVS Symposium. Uppsala: Opulus Press, pp. 178-181.

Roo-Zielińska E., 2004. *Fitoindykacja jako narzędzie oceny środowiska fizycznogeograficznego. Podstawy teoretyczne i analiza porównawcza stosowanych metod.* Prace Geograficzne, 199, Warszawa: Instytut Geografii i Przestrzennego Zagospodarowania PAN.

Roo-Zielińska E., 2014. *Wskaźniki ekologiczne zespołów roślinnych Polski*. Warszawa: Wydawnictwo Akademickie Sedno, Instytut Geografii i Przestrzennego Zagospodarowania PAN.

Roo-Zielińska E., Solon J., Degórski M., 2007. *Ocena stanu i przekształceń środowiska przyrodniczego na podstawie wskaźników geobotanicznych, krajobrazowych i glebowych (podstawy teoretyczne i przykłady zastosowań).* Monografie, 9, Warszawa: Instytut Geografii i Przestrzennego Zagospodarowania PAN.

Sciama D., Augusto L., Dupouey J.-L., Gonzalez M., Dominguez C.M., 2009. *Floristic and ecological differences between recent and ancient forests growing on non-acidic soils.* Forest Ecology and Management, vol. 258, no. 5, pp. 600-608.

Statistical Yearbook of the Republic of Poland 2012. Warsaw: Central Statistical Office.

Verheyen K., Guntenspergen G.R., Biesbrouck B., Hermy M., 2003. *An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale*. Journal of Ecology, vol. 91, no. 5, pp. 731-742.

Wulf M., 1997. *Plant species as indicators of ancient woodland in northwestern Germany.* Journal of Vegetation Science, vol. 8, no. 5, pp. 635-642.

Wulf M., 2004. *Plant species richness of afforestations with different former use and habitat continuity*. Forest Ecology and Management, vol. 195, no. 1-2, pp. 191-204.