

The role of woodland fragments, soil types, and dominant species in secondary succession on the western Carpathian foothills

Zbigniew Dzwonko & Stefan Gawroński

Institute of Botany, Jagellonian University, Lubicz 46, 31-512 Kraków, Poland

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Abstract

Four seventy-year-old broadleaved recent woods adjacent to three ancient woodland fragments, which all together covered an area of 27.5 ha, were investigated. Two of the recent woods were established naturally and two were planted. The ancient woodlands, including oak-hornbeam and oak-pine woods, were the only near source of diaspores of woodland species. The recent woods differed in area, location, soil richness and light conditions. On the basis of the data from 236 systematically located plots the similarities and differences in ground vegetation between the ancient and recent woods were studied by detrended correspondence analysis (DCA). Even after 70 yr of forest vegetation recovery in the recent woodlands differences were found in the vegetation of the woods examined. The direction of secondary succession was strongly determined by soil conditions. Mature woodlands showed higher beta-diversity. The causes of convergence and divergence in the composition of the communities were analyzed and discussed. The greatest similarity was found between recent and adjacent ancient woods growing on rich brown soils. The greatest divergence was observed in the recent woods growing on poor soils and more open to light, where the very great density of *Carex brizoides* inhibited the rate of succession. The results obtained indicate that with no isolation and only small distances from ancient woods the community composition in recent woods is to a greater degree dependent upon soil conditions, light and the influence of dominants than on the modes of species dispersal. The regeneration of ground vegetation of woodland communities is possible to a high degree, close to ancient woodlands, on rich brown soils.

Nomenclature: Tutin *et al.* (1964–1980), Flora Europaea.

Introduction

Succession towards mature communities proceeds slowly in isolated recent woods developed in places that had been used as fields, meadows and pastures. Such woods are as a rule poorer in woodland species than ancient woodlands occurring under the same climatic and soil conditions.

One of the main causes, emphasized by various authors, is the fact that many woodland species are unable to colonize isolated secondary woods because of insufficient dispersal (Hermy & Stieperaere 1981; Hoehne 1981; Peterken & Game 1984; Whitney & Foster 1988; Dzwonko & Loster 1988, 1989, 1992).

We lack detailed studies on the colonization of

non-isolated recent woods take into account their situation, soil and light conditions, modes of species dispersal and the influence of these factors upon successional convergence and divergence in the composition of communities. Some of the studies suggest that secondary succession proceeds faster in places adjoining ancient woodlands which are the source of diaspores. The lack of isolation allows the tree and many herb species, unable to spread over fairly long distances, as well as some vegetatively propagating herbaceous species to colonize the near places relatively quickly (Rackham 1980; Faliński & Canullo 1985; Hughes & Fahey 1988; Hardt & Forman 1989). Peterken & Game (1984) pointed out that in Lincolnshire recent woods adjacent to ancient woods were significantly richer in woodland species than were isolated recent woods, although the number of species growing in them was significantly smaller than in the ancient woods. Hardt & Forman (1989) showed that the rate of immigration of species was dependent on the shape of the boundary between the woods which were the source of diaspores and the colonizing areas.

Our investigation covered four secondary woods, about 70 years old, adjoining three ancient woodland fragments. They have been situated in the north of the Carpathian foothills and their total area was 27.5 ha. The recent woods were either established naturally or were planted in places that had been used as fields and pastures for a long time. The ancient woodlands were the only near source of diaspores of woodland species. Two types of communities have occurred in the ancient woodlands: oak-hornbeam wood with *Quercus robur* and *Carpinus betulus* (*Tilio-Carpinetum*) on brown soils and oak-pine wood with *Q. robur*, *Pinus sylvestris* and *Fagus sylvatica* (*Pino-Quercetum*) on podzolic soils. The oak-hornbeam and oak-pine woods are mature woodland communities on the above-mentioned soils in this part of southern Poland (Medwecka-Kornaś, Towpasz & Gawroński 1988).

The purpose of our study was to find whether and, if so, to what extent the rate and direction of secondary succession depend on 1) the origin

and location of the recent woods, 2) the soil and light conditions, and 3) modes of species dispersal.

Study area

The study area is situated in the valley of the Wierzbanówka, in the Pogórze Wielickie, close to the northern edge of the Carpathians. It lies about 270 m a.s.l. 25 km south-west of Kraków. This area is built of flysch deposits, composed chiefly of various sandstones and shales. The loess and loess-like formations overlie the flysch substratum. The study area lies within the warmest climatic zone of those distinguished in the Polish Carpathians. Its mean annual temperature is 7.8 °C. The mean and the mean maximum and minimum temperatures for January are, respectively, -3.3°, -0.7°, and -6.2 °C, and for July, respectively, 17.9°, 22.4°, and 13.4 °C. The mean annual precipitation is 748 mm.

A comparison of historical documents and maps showed that nearly the whole Wierzbanówka valley was wooded until the mid-15th century. According to Mieg's map from 1779–1783, the woods under study were still part of a larger ancient woodland in that period. In the twenties and thirties of the 19th century the woodland was very strongly reduced in area (Nowakowski 1987). According to the cadastral map from 1845, there were already three isolated smaller woodlands, varying in area, here. A comparison of the present-day maps, air photographs and forest surveys showed that three ancient woodlands, which have been 0.6, 5.8 and 11.8 ha in area, have not undergone a significant change in area since 1845. In the last 145 years the frequency of various tree species has changed in these woodlands as a result of selective cutting and planting. *Quercus robur* was felled for the most part and *Pinus strobus*, *Q. robur*, *Q. rubra*, *Picea abies*, *Abies alba*, *Fagus sylvatica* and *Pinus sylvestris* were planted. In many places the above-mentioned managements led to a reduction in the canopy cover and a considerable increase in the light available to the ground flora layer. Such changes favoured the

colonization of these places by *Carex brizoides*, which propagates vegetatively very quickly (cf. Faliński 1986). Now this sedge occurs in many ancient and recent woods in the Carpathian foothills, associated mainly with poor podzolic soils and leached brown soils. It often forms very dense and thick layers of tillers, leaves and rhizomes, which hinder the germination of seeds and the establishment of seedlings of many other species (Gawroński unpubl.).

In spite of the management in the ancient woods the rich woodland flora has been preserved and the associations typical of the mature woodlands in the submontane zone of the northern Carpathians have been presented (Medwecka-Kornaś, Towpasz & Gawroński 1988).

After World War I grazing and cultivation were given up in four places adjoining the three ancient woodlands. In two places *Quercus robur* was planted and in one of them also *Populus nigra*; in two other places secondary woods established naturally. In the last case *Betula pendula*, *Carpinus betulus* and *Acer pseudoplatanus* were the main colonizers. In the plantations *Betula pendula* and *Carpinus betulus* were natural colonizers. After World War II *Fagus sylvatica* was planted in one of them. All the recent woods were of similar age, about 70 years. They have grown on different types of soils and varied in area. The places on which the recent woods have developed were used for agriculture for nearly 100 years, which excludes the possibility of the survival of woodland species diaspores in the soil.

Data collection

A network of plots were assigned at 20-metre intervals in four recent woods and in the adjoining ancient woods. The plots were placed all over the recent woods or only in their parts depending on the size and situation of these woods. In the ancient woods the plots were situated in the parts bordering the recent woods (Fig. 1). In quadrats, 4 m² in area, the percentage cover of vascular plant species in the ground flora layer was estimated using 10% intervals. In plots, 50 m² in

area, with the four-square-metre plots in the centre, the presence of species in tree and shrub layers was recorded. Records were made in June and July 1990 and repeated in April and May 1991 for herbaceous species developing in early spring. In sum, records were made on 264 plots.

In order to investigate the relation between modes of species dispersal and their frequency and distribution in the recent woods, all species were divided into seven groups according to van der Pijl (1982): autochores, anemochores, barochores, dyszoochores, endozoochores (only species with fleshy fruits), epizoochores and myrmecochores. The type of dispersal was determined for each species on the basis of direct inspection of propagules and literature. In an analysis of the results also the number of all the species in plots was taken into consideration and so were the numbers of species characteristic of the classes *Quercus-Fagetum* and *Vaccinio-Piceetum*. Moreover, we took into account the number of non-woodland species and that of woodland species, in which the characteristic species of the two classes mentioned and several other species closely associated with the woodland communities in southern Poland were included.

For the general characterization of the environmental conditions mean characteristic Ellenberg indicator values were calculated for the plots: L – light, M – moisture, R – reaction, and N – nitrogen (Ellenberg 1979; cf. Persson 1981; Jongman, ter Braak & van Tongeren 1987).

For estimating the light conditions inside the study woods light intensity was measured in the open area outside the woods and at four points in each four-square-metre plot using a light meter calibrated in lx, then the mean values were computed from the readings and expressed as percentages of light intensity in the open area. In order to avoid misleading measures due to short-lived sunflecks all light measurements were taken under conditions of diffuse light, *i.e.* on overcast days.

During the field work the percent cover of tree layer was subjectively evaluated, and litter depth was measured at four points in each four-square-metre plots, then the mean values were computed.

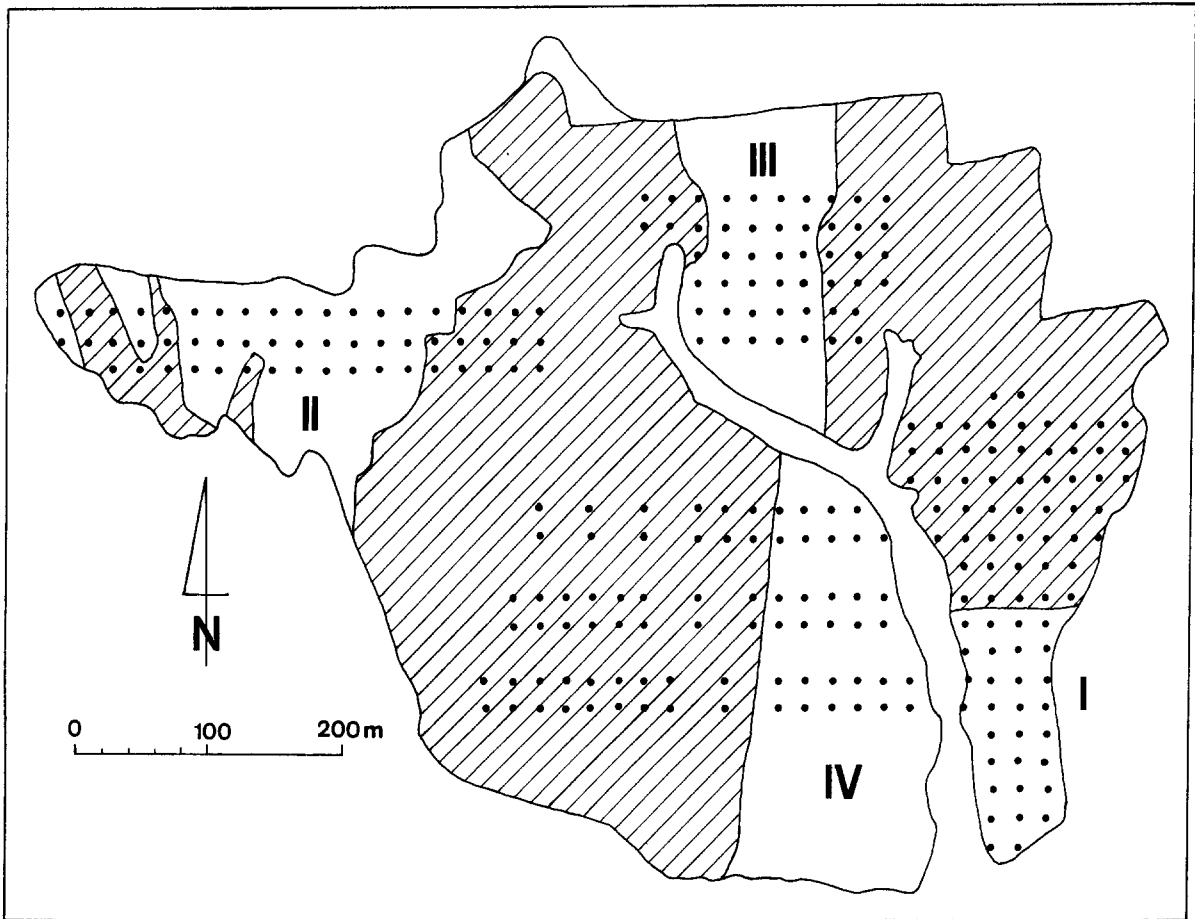


Fig. 1. Location of the ancient (shaded) and recent (I-IV) woods. Dots show the locations of all sample plots.

The type of soil was determined for all plots on the basis of a detailed soil map, scale 1:5000 (Langer 1988). Since the recent woods have been associated with different types of soil, differed in cover of *Carex brizoides* as well as in their location and origin (Fig. 1, Table 1), an analysis of the differentiation of vegetation was carried out sepa-

rately for each wood and for ancient woods neighbouring upon them, in which the following numbers of plots were taken into account:

- I. recent wood established naturally (1.3 ha in area, 30 plots on proper brown soil and grey brown soil), adjacent to the ancient oak-

Table 1. Mean values of some characteristics for recent woods plots. P = wood with *Populus nigra*, Q = wood with *Quercus robur*.

Characteristics	Wood I	Wood II	Wood III/P	Wood III/Q	Wood IV
Number of plots	30	20	14	15	23
Cover of tree layer (%)	69.8	78.3	76.4	62.7	73.0
Light intensity (%)	2.5	5.4	3.0	5.8	7.3
Cover of <i>Carex brizoides</i> (%)	7.5	6.6	5.9	45.4	62.6
Litter depth (cm)	1.5	1.6	1.4	1.5	3.3

hornbeam wood (37 plots on proper brown soil and grey brown soil, 3 plots on ground-water gley soil, and 12 plots on leached brown soil);

- II. disturbed recent wood established naturally (3 ha in area, 20 plots on proper brown soil), between two disturbed ancient oak-hornbeam woods (10 plots on proper brown soil); all these woods were heavily disturbed by cutting many trees during and after World War II.
- III. planted wood (2.3 ha in area) with *Populus nigra* (13 plots on leached brown soil and 1 plot on grey brown soil) and *Quercus robur* (15 plots on leached brown soil), between two ancient oak-hornbeam woods (21 plots on leached brown soil and grey brown soil);
- IV. planted wood with *Quercus robur* and a very abundant cover of *Carex brizoides* (2.7 ha in area, 17 plots on podzolic soil and 6 plots on leached brown soil), bordering upon the oak-pine wood (45 plots on podzolic soil and 6 plots on leached brown soil).

Twenty-eight plots were omitted. They lay on soil types that cover only very small areas in the study woods.

Data analysis

Detrended correspondence analysis (DCA, Hill & Gauch 1980, CANOCO program, ter Braak 1988) was used to analyse the differentiation of the vegetation in the woods. We applied the standard form of this analysis without downweighting of rare species. DCA makes an indirect gradient analysis possible and, owing to non-linear rescaling of the ordination axes in units of mean standard deviation of species turnover, the measurement and comparison of beta-diversity (*sensu* Whittaker 1972) and the floristic or ecological distance between the samples along the ordination axes are possible as well (cf. Økland 1986; Eilertsen *et al.* 1990). The CANODRAW program was applied for the graphical presentation of the results of ordination (Smilauer 1990).

The similarity of vegetation and its differentia-

tion in the ancient woods and in the adjoining recent woods developed on the same or very similar soils were determined by comparing the ranges, means and variances of coordinates of plots along the DCA axes. The ranges of plots are a measure of beta-diversity. By comparing the mean values we were able to find whether there were significant differences in vegetation between the ancient and recent woods, while a comparison of the variances enabled us to appraise the differences in the dispersion of plots and thus to find the pattern of convergence or divergence during secondary succession (cf. Christensen & Peet 1984; Rydin & Borgegård 1988).

Correlations between the variables and DCA axes were calculated using Spearman's rank correlation coefficient (Sokal & Rohlf 1981). Fisher exact test was used to examine the distribution of species in the recent woods.

Results

Comparison of vegetation of ancient and recent woods

An analysis of the results of ordination indicates that the ground vegetation in recent woods differed from that in the ancient woods. The first DCA axes are strongly correlated with the indicator values for reaction and nitrogen in the cases of recent woods I, III and IV, and adjoining ancient woods (Table 2). These axes reflect gradients from plots on richer soils to plots on poorer soils (Figs. 2 and 3) or from poorer to richer soils (Fig. 4). The number of species from the classes *Quercus-Fagetea* and *Vaccinio-Piceetea* are negatively or positively correlated with the values of mentioned axes according to these gradients.

Along the first axis wood I showed convergence with the adjoining ancient wood growing on the same soil and somewhat smaller beta-diversity, while wood III was marked by convergence in the part with *Populus nigra* and divergence in that with *Quercus robur*, and in both cases by considerably smaller beta-diversity. Divergence characterized also wood IV (Table 3). These results in-

Table 2. Rank correlation (values of Spearman's r) between DCA axes 1 and 2 and some characteristics of recent and adjacent ancient woods plots.

Characteristics	Wood I		Wood II		Wood III		Wood IV	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Distance to ancient wood	0.08	-0.61***	0.51**	-0.01	0.32*	-0.75***	0.16	-0.36**
Light intensity	0.19	-0.02	0.49**	-0.09	0.48***	-0.39**	-0.31**	-0.31**
Litter depth	0.32**	0.26*	-0.20	0.51**	0.42**	-0.23	-0.10	-0.08
Ellenberg indicator values:								
Light	0.58***	-0.21	-0.05	-0.25	0.68***	-0.46**	-0.20	-0.55***
Moisture	-0.34**	-0.12	-0.21	-0.77***	-0.28	0.0	-0.48***	-0.52***
Reaction	-0.91***	0.01	-0.16	-0.33	-0.96***	0.57***	0.84***	-0.14
Nitrogen	-0.86***	-0.05	-0.40*	-0.58**	-0.71***	0.32*	0.33**	0.35**
Number of species	-0.23*	-0.12	-0.13	-0.13	-0.41**	0.58***	-0.12	0.69***
Groups of species:								
Woodland species	-0.35**	0.18	-0.27	-0.40*	-0.26	0.58***	-0.09	0.62***
Non-woodland species	0.04	-0.05	0.40*	-0.34	-0.28*	0.27	-0.46***	0.42***
<i>Quercus-Fageteta</i>	-0.55***	-0.02	-0.40*	-0.18	-0.57***	0.56***	0.45***	0.29*
<i>Vaccinio-Piceetea</i>	0.31**	-0.21	-0.31	0.31	0.22	0.42**	-0.44***	0.51***

* $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $P \leq 0.001$.

dicate that soil conditions were most decisive of the direction of secondary succession in woods I and III with *P. nigra*, where the light intensity was weaker (Table 1). The second DCA axes distinctly separate most plots of the all above-

mentioned recent woods from the plots of the ancient woods. These axes are significantly correlated with the distance from the ancient woods. In the case of wood II and the adjoining ancient woods which were associated with only one type

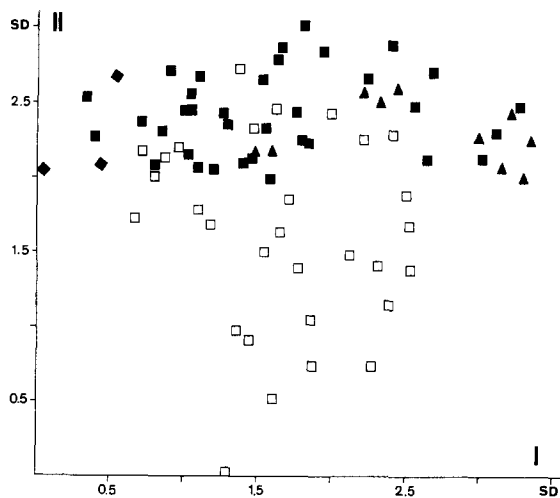


Fig. 2. Ordination of the plots of the wood I (open symbols) and adjacent ancient wood (filled symbols) along the first two DCA axes. Diamonds: proper ground-water gley soil; squares: proper brown soil and grey brown soil; triangles: leached brown soil.

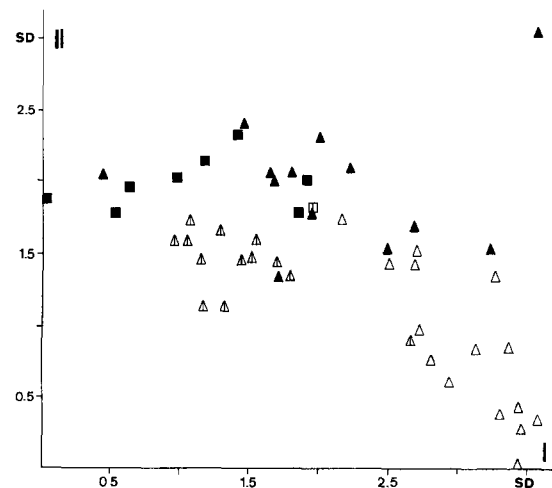


Fig. 3. Ordination of the plots of the wood III (open and lined symbols) and adjacent ancient woods (filled symbols) along the first two DCA axes. Lined symbols: wood III with *Populus nigra*; open triangles: wood III with *Quercus robur*. Soil types as in Fig. 2.

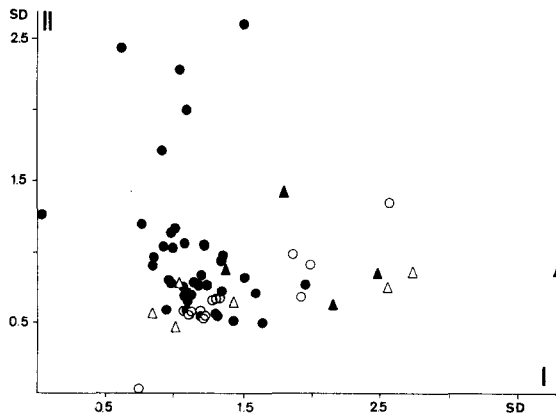


Fig. 4. Ordination of the plots of the wood IV (open symbols) and adjacent ancient wood (filled symbols) along the first two DCA axes. Circles: podzolic soil; triangles: leached brown soil.

of soil, the first DCA axis alone separates these two types of woods (Table 2).

The ranges, means and variances of DCA scores for the naturally established woods along the axes separating these woods from the ancient ones (the second DCA axis for wood I and the first axis for wood II) differ considerably from the corresponding values for the ancient woods, although the differences are significant only for wood I. Distinct divergence occurred in these cases and greater beta-diversity characterized the recent woods.

In the case of wood III there were big differences between its parts dominated by *Populus nigra* and those with *Quercus robur*. The part with

P. nigra much more resembled the ancient wood than does the part with *Q. robur*, in which the tree canopy was less closed and light intensity much stronger (Fig. 3, Tables 1 and 3). The mean values of DCA scores along the second axis differ significantly from the corresponding values for the ancient woods in both cases.

Wood IV showed still greater intensity of light than did wood III with *Q. robur* (Table 1). As regards the second DCA axis, the variability of vegetation was significantly smaller in it than in the ancient wood. This was due to the influence of very densely growing of *Carex brizoides*. In consequence, the ground vegetation in wood IV has been very homogeneous and its flora much poorer than in the adjoining ancient wood.

Distribution of species in recent and ancient woods

In total of 105 species were recorded in all four-square-metre plots. That number included 91 herb and small shrub species, 14 tree species, and 6 shrub species, whereas 150 species were found in the ground flora layer of all the primary and secondary woods. Forty-five species have not been encountered in the plots; they have been rare or very rare in the studied woods.

Tables 4 and 5 show distribution of species occurring in at least three plots in any wood. An analysis of the distribution of these species has revealed that frequency of species in wood II was

Table 3. Variability in vegetation composition in ancient and recent woods plots, as reflected by range, mean and variance of DCA scores (standard deviation units). Compared plots lay on the same soil types. A = ancient wood; R = recent wood; R₁ = recent wood with *Populus nigra*; R₂ = recent wood with *Quercus robur*. Significance of differences in means and variances indicated with: * P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001.

		Wood I		Wood II		Wood III			Wood IV	
		A	R	A	R	A	R ₁	R ₂	A	R
DCA axis 1	Range	2.94	1.86	1.60	3.16	3.56	1.70	1.41	1.94	1.83
	Mean	1.58	1.67	0.97	1.45	1.68	1.44	3.03***	1.12	1.37*
	Variance	0.55	0.33	0.29	0.54	0.79	0.20*	0.18**	0.09	0.20*
DCA axis 2	Range	2.13	2.72	2.21	3.04	1.70	0.82	1.74	2.11	1.35
	Mean	2.38	1.62***	1.37	1.50	1.99	1.43***	0.86***	0.94	0.65**
	Variance	0.14	0.42**	0.43	0.37	0.13	0.06	0.28	0.25	0.07**

Table 4. Frequency of more common species in the tree and shrub layers in ancient and recent woods plots. Compared plots lay on the same soil types. A = ancient wood; R = recent wood; R₁ = recent wood with *Populus nigra*; R₂ = recent wood with *Quercus robur*; An = anemochore; D = dyszoochore; En = endozoochore; a = tree layer (trees > 3 m height); b = shrub layer (trees and shrubs < 3 m height).

Species		Wood I		Wood II		Wood III			Wood IV	
		A	R	A	R	A	R ₁	R ₂	A	R
Number of plots		37	30	10	20	21	13	15	45	17
<i>Betula pendula</i> a	An	21	22	0	0	5	7 ⁺	13 ⁺⁺⁺	2	1
<i>Carpinus betulus</i> a	An	13	6	3	3	16	7	0 ⁻⁻⁻	0	1
<i>Carpinus betulus</i> b	An	1	0	0	1	4	3	4	0	1
<i>Acer pseudoplatanus</i> a	An	0	0	10	13 ⁻⁻	0	0	0	0	0
<i>Pinus sylvestris</i> a	An	8	0 ⁻⁻	0	0	5	0 ⁻	0 ⁻	18	0 ⁻⁻⁻
<i>Picea abies</i> a	An	4	0 ⁻	0	0	1	0	0	17	0 ⁻⁻⁻
<i>Alnus glutinosa</i> a	An	4	2	2	1	1	2	0	0	5 ⁺⁺⁺
<i>Larix decidua</i> a	An	0	0	0	0	0	1	0	9	2
<i>Fraxinus excelsior</i> a	An	0	0	2	3	4	2	0	0	0
<i>Populus tremula</i> a	An	0	1	0	0	0	0	0	9	0 ⁻⁻
<i>Populus nigra</i> a	An	0	1	0	0	1	6 ⁺⁺⁺	0	0	0
<i>Ulmus laevis</i> a	An	0	0	0	6 ⁺	0	0	0	0	0
<i>Quercus robur</i> a	D	21	15	1	8 ⁺	10	8	12 ⁺	40	16
<i>Quercus robur</i> b	D	4	0 ⁻	0	0	0	0	1	2	0
<i>Fagus sylvatica</i> a	D	4	3	1	1	2	0	0	18	8
<i>Fagus sylvatica</i> b	D	0	0	0	0	0	1	0	2	4 ⁺⁺
<i>Corylus avellana</i> b	D	20	16	0	2	3	3	13 ⁺⁺⁺	0	0
<i>Sorbus aucuparia</i> a	En	0	2	0	1	0	0	0	5	1
<i>Sorbus aucuparia</i> b	En	2	7 ⁺⁺	0	2	0	0	2	2	4 ⁺⁺
<i>Sambucus nigra</i> b	En	12	3 ⁻	5	15	3	3	4	1	0
<i>Prunus padus</i> b	En	11	16 ⁺	2	3	1	4 ⁺	4 ⁺	0	0
<i>Frangula alnus</i> b	En	0	1	0	1	0	0	2	22	6
<i>Cornus sanguinea</i> b	En	10	6	0	0	1	3	1	0	0
Number of all species		12	15	10	14	15	13	10	10	8

+/- more/less frequency, 0.1 ≥ P > 0.05; + + / - - 0.05 ≥ P > 0.01; + + + / - - - P ≤ 0.01.

most similar to that in adjacent ancient woods. These woods were however heavily disturbed by tree felling. Wood III with *Quercus robur* and wood IV differed most from the mature woodlands. Wood IV was the poorest; it lacked even such endozoochores abundant in the neighbouring ancient wood as *Vaccinium myrtillus*, *Majanthemum bifolium*, *Rubus idaeus* and *Frangula alnus*. This wood was also marked by the significantly lower frequency of anemochores, e.g. *Pteridium aquilinum* and *Milium effusum* (Table 5). The lack of these easily dispersing species was caused by the mentioned restrictive influence of *Carex brizoides*. In wood III grew fewer endozoochores:

Adoxa moschatellina, *Majanthemum bifolium*, *Hedera helix*, and myrmecochores, e.g. *Anemone nemorosa* and *Pulmonaria obscura*. In part with *Populus nigra* *Aegopodium podagraria* was significantly more frequent, whereas in the part with *Quercus robur* besides *Carex brizoides* more often occurred *Rubus hirtus* and *Equisetum sylvaticum*. Two autochores (*Impatiens noli-tangere* and *Oxalis acetosella*), three myrmecochores (*Lamium galeobdolon*, *Euphorbia amygdaloides* and *Ranunculus ficaria*), two epizoochores (*Stachys sylvatica* and *Urtica dioica*) and only two endozoochores (*Hedera helix* and *Rubus hirtus*) were rarer in wood I. Most of the myrmecochores and anemo-

Table 5. Frequency of more common species in the ground flora layer in ancient and recent woods plots. Compared plots lay on the same soil types. A = ancient wood; R = recent wood; R₁ = recent wood with *Populus nigra*; R₂ = recent wood with *Quercus robur*; An = anemochore; Au = autochore; B = barochore; D = dyszoochore; En = endozoochore; Ep = epizoochore; M = myrmecochore.

Species		Wood I		Wood II		Wood III			Wood IV	
		A	R	A	R	A	R ₁	R ₂	A	R
Number of plots		37	30	10	20	21	13	15	45	17
<i>Milium effusum</i>	An	32	25	8	17	18	11	15	27	5 ⁻
<i>Carex brizoides</i>	An	20	15	0	6 ⁺	10	5	14 ⁺⁺⁺	43	17
<i>Athyrium filix-femina</i>	An	12	4	0	0	6	4	5	1	1
<i>Dryopteris filix-mas</i>	An	7	1 ⁻	2	3	1	0	3	0	0
<i>Dryopteris carthusiana</i>	An	1	4	1	2	1	0	1	4	0
<i>Equisetum sylvaticum</i>	An	2	0	0	1	0	0	10 ⁺⁺⁺	0	1
<i>Populus tremula</i>	An	1	4	0	0	0	0	0	8	1
<i>Pteridium aquilinum</i>	An	0	0	0	0	2	0	0	8	0 ⁻
<i>Carpinus betulus</i>	An	3	1	0	1	3	1	1	0	0
<i>Lysymachia vulgaris</i>	An	0	4 ⁺⁺	0	0	0	0	0	4	0
<i>Acer pseudoplatanus</i>	An	0	0	1	3	0	0	0	0	0
<i>Calamagrostis arundinacea</i>	An	0	0	0	0	0	0	0	3	0
<i>Deschampsia flexuosa</i>	An	0	0	0	0	0	0	0	3	0
<i>Circaea lutetiana</i>	Ep	19	12	6	8	2	3	1	2	0
<i>Urtica dioica</i>	Ep	8	2 ⁻	7	12	10	4	2 ⁻⁻	0	0
<i>Brachypodium sylvaticum</i>	Ep	2	7 ⁺⁺	0	8 ⁺⁺	2	3	3	0	0
<i>Stachys sylvatica</i>	Ep	8	1 ⁻⁻	6	4 ⁻⁻	4	1	0	0	0
<i>Geum urbanum</i>	Ep	1	1	3	3	1	0	0	0	0
<i>Chaerophyllum hirsutum</i>	Ep	1	0	2	3	1	2	0	0	0
<i>Galium aparine</i>	Ep	1	2	0	5	0	0	0	0	0
<i>Chaerophyllum aromaticum</i>	Ep	0	0	1	4	2	0	0	0	0
<i>Sanicula europaea</i>	Ep	3	2	0	0	0	0	0	0	0
<i>Rubus hirtus</i>	En	18	1 ⁻⁻⁻	2	7	8	6	15 ⁺⁺⁺	19	3
<i>Adoxa moschatellina</i>	En	17	18	4	10	9	1 ⁻⁻	0 ⁻⁻⁻	0	0
<i>Rubus idaeus</i>	En	6	8	1	4	5	1	5	17	0 ⁻⁻⁻
<i>Majanthemum bifolium</i>	En	5	8	0	0	5	0 ⁻	1	24	0 ⁻⁻⁻
<i>Euonymus europaeus</i>	En	8	16 ⁺⁺	1	3	3	4	2	0	0
<i>Prunus padus</i>	En	4	24 ⁺⁺⁺	2	2	0	2	2	0	0
<i>Polygonatum multiflorum</i>	En	5	16 ⁺⁺⁺	1	1	4	2	0	1	3 ⁺
<i>Sambucus nigra</i>	En	5	14 ⁺⁺⁺	3	7	2	1	0	0	0
<i>Hedera helix</i>	En	16	0 ⁻⁻⁻	0	0	15	0 ⁻⁻⁻	1 ⁻⁻⁻	0	0
<i>Frangula alnus</i>	En	0	1	0	0	1	0	0	21	3 ⁻
<i>Vaccinium myrtillus</i>	En	0	0	0	0	0	0	0	23	0 ⁻⁻⁻
<i>Ribes uva-crispa</i>	En	1	12 ⁺⁺⁺	0	0	0	0	0	0	0
<i>Cornus sanguinea</i>	En	5	4	0	0	0	2	1	0	0
<i>Paris quadrifolia</i>	En	4	7	0	0	0	0	0	0	0
<i>Sorbus aucuparia</i>	En	0	4 ⁺⁺	0	1	0	0	0	0	0
<i>Prunus avium</i>	En	1	3	0	1	0	0	0	0	0
<i>Quercus robur</i>	D	10	10	2	0	4	2	0	11	11 ⁺⁺⁺
<i>Corylus avellana</i>	D	10	9	0	1	2	2	1	0	1
<i>Lamium strum galeobdolon</i>	M	37	16 ⁻⁻⁻	10	19	21	13	15	0	0
<i>Anemone nemorosa</i>	M	30	18	4	5	21	5 ⁻⁻⁻	6 ⁻⁻⁻	0	6 ⁺⁺⁺
<i>Pulmonaria obscura</i>	M	23	16	5	15	13	10	2 ⁻⁻	0	0
<i>Asarum europaeum</i>	M	25	26	1	9 ⁺	11	4	5	0	0

Table 5. Continued.

Species		Wood I		Wood II		Wood III			Wood IV	
		A	R	A	R	A	R ₁	R ₂	A	R
<i>Ranunculus ficaria</i>	M	16	6 ⁻	8	11	11	1 ⁻⁻⁻	3 ⁻	0	0
<i>Viola reichenbachiana</i>	M	6	5	0	0	2	1	1	0	0
<i>Luzula pilosa</i>	M	0	2	0	0	1	0	0	10	0 ⁻
<i>Melica nutans</i>	M	3	1	0	0	2	0	1	0	0
<i>Moehringia trinervia</i>	M	0	4 ⁺⁺	0	0	0	0	0	0	0
<i>Euphorbia amygdaloides</i>	M	4	0 ⁻	0	0	0	0	0	0	0
<i>Symphytum tuberosum</i>	M	3	0	0	0	1	0	0	0	0
<i>Impatiens noli-tangere</i>	Au	16	1 ⁻⁻⁻	6	13	13	8	8	2	3
<i>Oxalis acetosella</i>	Au	24	8 ⁻⁻⁻	0	0	9	7	8	1	0
<i>Aegopodium podagraria</i>	B	29	10 ⁻⁻⁻	5	5	10	13 ⁺⁺⁺	2 ⁻	0	0
<i>Stellaria holostea</i>	B	10	15 ⁺	0	0	6	5	5	0	1
<i>Galeopsis bifida</i>	B	4	2	4	6	0	0	0	0	0
Number of all species		56	59	33	40	53	33	33	26	13
Number of woodland species		38	33	22	22	36	21	23	19	9

+/- more/less frequency, $0.1 \geq P > 0.05$; + +/- - $0.05 \geq P > 0.01$; + + +/- - - $P \leq 0.01$.

chores were not rarer in wood I and wood III with *P. nigra* than in the adjacent mature woods. Some endozoochores grew more frequently in ground flora layer of the wood I. They were mainly tree and shrub species: *Euonymus europaeus*, *Prunus padus*, *Ribes uva-crispa*, *Sambucus nigra*, and *Sorbus aucuparia* (Table 5). *S. aucuparia* and *P. padus* were more common in the shrub layer too (Table 4).

In all the cases examined the woodland species strongly associated with ancient woods were *Stachys sylvatica* and *Hedera helix* – a species very rarely producing fruits.

Discussion

The mature woodlands examined by us – with the exception of disturbed ones – as a rule showed greater beta-diversity measured along the DCA axes than did the recent woods adjacent to them. Matthews (1979), Pineda *et al.* (1981) and Christensen & Peet (1984) also found the same general relationship for various types of communities, whereas this trend was not recorded by Rydlin &

Borgegard (1988) in the case of succession on the islands in Lake Hjälmaren.

The rate and course of succession may be dependent on many various factors (Pickett, Collins & Armesto 1987; van der Maarel 1988) and successional convergence in the community composition is not a general tendency (cf. Lepš & Rejmánek 1991). The direction of secondary succession in the study woods was strongly determined by soil conditions, but despite a lapse of 70 years the ground vegetation in the recent woods differed from the vegetation of the adjoining ancient woods growing on the same soils. We found that only four mostly vegetatively propagating species (*Aegopodium podagraria*, *Lamium galeobdolon*, *Ranunculus ficaria* and *Rubus hirtus*), two autochores (*Impatiens noli-tangere* and *Oxalis acetosella*), two endozoochores (*Adoxa moschatellina* and *Hedera helix*), one myrmecochore (*Anemone nemorosa*), and one epizoochore (*Stachys sylvatica*) were significantly less frequent in the recent wood I or wood III with *Populus nigra*. We observed the greatest divergence in plantations on poorer soils and more open to light (woods IV and III with *Quercus robur*). The great

density of *Carex brizoides* has hindered the germination of seeds and the establishment and development of other species in these woods (cf. Faliński 1986). The effect of this factor may account for smaller number of all species and woodland species in wood III with *Quercus robur* and in wood IV as well as smaller frequency of endozoochorous species in wood IV, as a rule very effectively dispersed by birds (cf. Debussche, Escarré & Lepart 1982; McDonnell & Stiles 1983; McClanahan & Wolfe 1987; Hoppes 1988). For endozoochore this conclusion is confirmed by their more frequent occurrence in wood I, which had a thinner layer of litter and a much smaller cover of *C. brizoides*. This agrees with Connell & Slatyer's (1977) model of inhibition and was one of the main causes of smaller beta-diversity in the above-mentioned woods.

Christensen & Peet (1984), in their study on secondary succession in the forests of North Carolina piedmont, also found a lack of continuous monotonic shift in the community composition toward that characteristic of mature forests. This they attribute to the thinning of older secondary forests and an increase in the light available to the forest floor, in which they see the cause of divergence in these forests.

In the part of wood III planted with *Populus nigra*, where the tree canopy was fully closed and the light intensity weaker than in the neighbouring wood with *Quercus robur*, the vegetatively propagating species (*Aegopodium podagraria*, *Lamium galeobdolon* and *Milium effusum*) were exclusive dominants in the herb layer. Smaller beta-diversity was here connected with dense shading. Studies carried out by various authors on secondary succession in deciduous woods showed that an increase in shading restricted the development of many species in the herb layer (Malmer, Lindgren & Persson 1978; Persson 1980; Brewer 1980). Denser shading reduces the flowering of woodland species, causing the elongation of vegetative parts. Such a response augments their chance to find less shady places (Mitchell & Woodward 1988).

Our study shows that with no isolation and only small distances from ancient woods the

community composition in recent woods is to a greater degree dependent upon soil resources, light and the influence of dominants than on the modes of species dispersal. The results of our study also indicate that the ground vegetation of woodland communities may regenerate to a high degree in the Carpathian, close to primary woodlands, on rich and moderately moist brown soils (cf. wood I and wood III with *Populus nigra*). However, we do not know any well-documented data which would allow the estimation of the time necessary for such a process.

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