MIGRATION OF VASCULAR PLANT SPECIES TO A RECENT WOOD ADJOINING ANCIENT WOODLAND

ZBIGNIEW DZWONKO

Institute of Botany, Jagellonian University
Lubicz 46, 31-512 Kraków, Poland; Fax +48 12 423 09 49
E-mail ubdzwonk@cyf-kr.edu.pl

(Received: June 8, 2000. Accepted: November 30, 2000)

ABSTRACT

Woodland communities can be restored by natural succession in sites adjoining ancient woodlands which can act as seed sources for trees, shrubs and woodland herbs. The influence of dominant tree species and the distance from an adjacent ancient oak-hornbeam woodland upon the floristic composition of species in a recent pine wood planted on dry rendzina soil were studied. It was found that, in spite of a 52-year long succession, the border between woods was sharp and the composition of species in the recent wood were significantly different than in the adjacent ancient woodland. Canonical correspondence analysis (CCA) showed that the distance to the ancient woodland had a significant influence on species distributions in the recent wood. The numbers of species from the *Quercus-Fagetum* class, vegetatively reproducing species and myrmecochores decreased with this distance, whereas the numbers of anemochores increased. The migration rate of many woodland species, calculated on occurrence of the farthest individuals was very slow, varying from 0.0 m year⁻¹ to 0.38 m year⁻¹. The restoration of the field layer vegetation in the studied pine wood was much slower than in recent deciduous woods on rich and moist soils where the migration rate of some species exceeded 1.50 m year⁻¹. Recent woods adjacent to ancient woodlands can be more effectively colonised by woodland species only when they are dominated by broad-leaved trees with quickly decomposing litter, and the spatial continuity of these woods persists for a long period.

KEY WORDS: ancient woodlands, recent woods, woodland restoration, secondary succession, seed dispersal, southern Poland.

INTRODUCTION

In the present-day agricultural landscapes of southern Poland the ancient deciduous woodland frequently occupy small, isolated areas, similarly as in other parts of temperate Europe. They are, as a rule, considerably richer in woodland species than the recent woods and plantations on abandoned fields, meadows and grasslands (Peterken and Game 1984; Dzwonko and Loster 1989; Brunet 1993; Petersen 1994; Wulf 1997; Honnay et al. 1998; Hermy et al. 1999). Recent studies have shown that natural regeneration of woodland communities is very slow and at present it is possible only in sites immediately adjacent to ancient woodlands – the sources of woodland species diaspores (Peterken and Game 1984; Dzwonko 1993; Dzwonko and Gawroński 1994; Matlack 1994; Brunet and von Oheimb 1998a; Bossuyt and Hermy 2000). The soil seed banks cannot be sources of diaspores even in the sites agriculturally used for a short period since a majority of the woodland vascular plant species form only transient or short-term persistent seed banks and their seeds do not survive in the soil longer than few years (Jankowska-Błaszczuk and Grubb 1997; Thompson et al. 1998; Bekker et al. 1998). Even in the soil seed banks in ancient woods many woodland species are scarce or absent;

shade-intolerant species, representing earlier stages of succession predominate there generally (Pirożnikow 1983; Kjellsson 1992; Warr et al. 1994; Rydgren and Hestmark 1997; Jankowska-Błaszczuk 1998; Jankowska-Błaszczuk et al. 1998).

At present natural regeneration of full floristic composition of woodland communities in sites spatially isolated from ancient woodland is impossible because of poor dispersal ability of many woodland species (Peterken and Game 1984; Whitney and Foster 1988; Dzwonko and Loster 1989, 1992; Duffy and Meier 1992; Matlack 1994; Grashof-Bokdam 1997; Grashof-Bokdam and Geertsema 1998). Even recent woods adjacent to ancient woodlands are very slowly colonised by woodland species. Brunet and von Oheimb (1998a, b) showed that migration rates of these species to such recent deciduous woods in southern Sweden varied from 0.0 to 1.25 m year⁻¹, and establishment of a field layer vegetation in secondary woods comparable to that of adjacent ancient woodlands proceeded at a rate of c. 0.3-0.5 m year⁻¹. Similar migration rates of woodland species were recorded by Honnay et al. (1999) and Bossuyt et al. (1999) in secondary woods in Belgium. Studies by Matlack (1994) show similar migration rates of species (0.0-2.5 m year⁻¹) from ancient to recent woods also in eastern North America. It seems that the secondary woods are generally most quickly

colonised by endozoochore and hovering and flying anemochore and most slowly by heavy anemochore, myrmecochore and barochore (Dzwonko and Loster 1992; Dzwonko 1993; Matlack 1994).

It may be assumed that the regeneration rate of the field layer vegetation in secondary woods is very much differentiated, because seed germination and development of seedlings of migrating woodland species can be strongly restricted by a thick layer of a slowly decomposing litter, grass and sedges, dominating in places of a less dense tree canopy, as well as by soil conditions and the activity of seed predators (Sydes and Grime 1981a, b; Dzwonko and Gawroński 1994; Eriksson 1995; Holderegger 1996; Brunet and von Oheimb 1998a, b; Dzwonko 2001). The studies quoted above suggest that the secondary woods on rich soils with quickly decomposing litter of broad-leaved trees are the fastest colonised ones. However, any more detailed investigations of the restoration of field layer vegetation in recent woods of different origin, dominant tree species and soil conditions are not available. The purpose of the present study was to estimate migration rates of woodland species to a secondary pine wood, planted in an abandoned limestone grassland close to an ancient deciduous woodland.

STUDY AREA

The study was carried out in the Skotczanka grassland-woodland reserve situated about 8 km south-west of Kraków. The reserve occupies a hill built of Jurassic limestone. The mean annual air temperature reaches there 8.1°C, the mean January and July temperatures are -3.1° and 18.5°C respectively. The mean annual rainfall is 665 mm. It is assumed that the oak-hornbeam wood (*Tilio-Carpinetum*) and oak-pine wood (*Pino-Quercetum*) are the main mature types of woodland communities occurring originally in this area, on the rendzina soils developed on the limestone substratum and on podzolic soils on the sandy deposit, respectively (Kornaś and Medwecka-Kornaś 1974). At present more than 47% of the reserve area is covered by the remnants of the ancient woodlands. The oak-hornbeam woodland with well preserved field layer vegetation occupies about half of this area. Before establishment of the reserve in 1957, in several sites on the calcareous and sandy soils *Pinus sylvestris* had been planted.

The main study area was a 52-year old secondary pine wood, 1.34 ha in area and an ancient oak-hornbeam woodland adjoining it, both growing on flat ground in the top part of the hill on the same rendzina soil. The secondary wood had been planted in a limestone grassland. A comparison of the cadastral surveys of 1845 and aerial photographs of 1957 shows that this limestone grassland had been managed as pasture for dozens of years. Therefore, one may be certain that no seeds of woodland species had remained in the soil. More details on the differentiation of the reserve vegetation, species richness of communities, and colonization of the secondary woods by woodland species are given by Dzwonko and Loster (1990, 1992, 1997, 1998) and Dzwonko (2001).

METHODS

In the spring 1996, six parallel transects, 50 m long, were set up at intervals of 5 m, perpendicularly to the boundary between the ancient deciduous woodland and the recent pine wood. Each

of the transects consisted of 10 plots, 5 × 5 m in size. Four plots of each transect were laid in the ancient woodland and six plots in the adjacent recent wood. In each plot the percentage cover of vascular plant species (10% estimation intervals) and the percentage cover of tree, shrub and field layers, were estimated. The records of species developing in spring were made in May and the cover of the remaining species and the vegetation layers were estimated in July. In October the litter cover of the dominant tree and shrub species was estimated. The nomenclature of species is that used in Flora Europaea by Tutin et al. (1964-1980).

The number and cover of non-woodland species, species characteristic of the class *Quercio-Fagetea*, and woodland species, i.e. species characteristic of the *Quercio-Fagetea* and *Vaccinio-Piceetea*, including several others closely associated with the woodland communities, were calculated for all plots. The species were divided into four dispersal groups: anemochore (diaspores with pappus or winged diaspores of less than 3 mg in weight or unwinged ones no more than 1.5 mg in weight), endozoochore (diaspores with fleshy fruits), myrmecochore and barochore (cf. van der Pijl 1982). In addition, a group of vegetatively reproducing species, i.e. with runners or rhizomes, was distinguished.

Differences in vegetation characteristics between the ancient and recent woods were analysed by Mann-Whitney U test. The chi-square test or Fisher's exact probability test was used to examine frequency of woodland species in the study woods. As most woodland species had cover lower than 5% in the recent wood, their migration rates were calculated as the ratio of the distance to the boundary with the ancient woodland to the age of the recent wood for the farthest individuals (cf. Matlack 1994; Brunet and von Oheimb 1998a). The calculations were carried out separately for every transect, in which the species occurred. Then the mean value was calculated. For comparison, mean migration rates of some species found in three transects in the 70-year-old secondary deciduous wood on rich proper brown soil and grey brown soil in the Carpathian foothills (Dzwonko 1993; Dzwonko and Gawroński 1994; the wood A and I, respectively) were calculated.

Canonical correspondence analysis (CCA, CANOCO program, ter Braak 1987; ter Braak and Šmilauer 1998) was applied to examine the dependence of the cover of field layer species in the recent wood on the distance from the ancient woodland and shrub cover. The statistical significance of the relations between the species and environmental variables were evaluated using Monte Carlo permutation tests with the split-plot design option. Detrended correspondence analysis in its standard form (DCA, CANOCO program) was used to identify the main directions of the plots variations and to examine relations between the floristic composition and cover of the field layer species and the distance from the border between the woods. The differences between the mean values of the scores along the DCA axis for the plots located at the same distance from the border between the woods were tested by one-way analysis of variance (ANOVA) and the Tukey test.

RESULTS

Community composition

In the recent wood the mean cover of pine litter was much greater than in the ancient woodland (59.3% and 9.4%, respectively) and cover of quickly decomposing litter of broad-leaved

TABLE 1. Mean values of vegetation variables for the ancient and recent woods plots. P denotes the probability of difference (Mann-Whitney U test).

Variables	Cover of species (%)			Number of species		
	Ancient wood	Recent wood	P	Ancient wood	Recent wood	P
Tree layer	86.3	60.7	< 0.001	2.3	1.7	NS
Shrub layer	11.0	48.1	< 0.001	0.8	3.5	< 0.001
Field layer						
All species	52.8	24.6	< 0.001	14.5	13.3	NS
Trees and shrubs	3.1	8.7	< 0.001	3.0	5.2	< 0.001
Woodland species	52.5	19.4	< 0.001	9.7	6.3	< 0.001
Quercus-Fagetea	49.9	15.7	< 0.001	7.9	3.9	< 0.001
Non-woodland species	2.0	2.1	NS	1.9	1.8	NS
All anemochores	2.6	7.8	< 0.001	2.3	4.2	< 0.001
Woodland anemochores	1.2	3.2	< 0.001	1.0	1.9	< 0.001
All endozoochors	19.9	17.1	NS	3.5	4.4	< 0.05
Woodland endozoochors	18.3	13.5	NS	1.8	1.7	NS
Woodland myrmecochores	31.4	1.8	< 0.001	5.6	1.8	< 0.001
All barochores	1.7	0.8	NS	1.0	0.7	NS
Vegetatively propagating species	45.3	14.0	< 0.001	5.4	2.2	< 0.001

woody species (*Acer platanoides*, *Carpinus betulus*, *Tilia cordata*, *Cornus sanguinea*, *Crataegus monogyna*, *Sambucus nigra*, *S. racemosa*) was much lower than in the ancient wood (28.0% and 81.7%, respectively). After 52 years of secondary succession the mean cover of the field layer vegetation in the recent wood was half that in the adjacent ancient woodland, but there was no significant difference in the mean number of all species (Table 1). The recent wood had a significantly lower cover and number of woodland species, species of the *Quercus-Fagetea* class, myrmecochores and the vegetatively reproducing species. On the other hand, trees and shrubs in the shrub and field layers as well as anemochorous species had a greater cover and number here than in the ancient woodland.

Indirect gradient analysis by DCA showed the main directions of the plots variation, based on the cover and presence of all field layer species and woodland species. In all four cases the first DCA axes arranged the plots relative to their position within transects and the plot scores along these axes were strongly correlated with the distance of the plots from the transect origins (Table 2). The results of ANOVA with the Tukey test for the plot scores along the gradients determined by the first DCA axes based on the cover of all species and woodland species lead to the conclusion that the plots from the ancient and recent woods formed two distinctly separated groups, with a clear boundary between them. On the other hand, the analysis of the

ordering of the plots along the first DCA axes according to species presence revealed that the species composition changed gradually within the 10 m zone around the boundary between the woods (Fig. 1, Table 2). There were no significant differences in the floristic composition between the plots located close to the boundary. These results show that the majority of woodland species migrating to the recent wood had only a low cover and occurred only in the closest neighbourhood of the ancient woodland.

Species distributions and migration rates

CCA with the Monte Carlo test showed that the pattern of species cover in the recent wood was significantly related ($P = 0.007$) to distance from the ancient woodland, which accounted for 5.0% of the total variation in the cover of the field layer species. This relation is visualized by a biplot based on CCA with distance to the ancient wood and shrub cover as variables (Fig. 2). The distance to the ancient wood was negatively correlated with the number of *Quercus-Fagetea* species per plot (Spearman correlation coefficient, $r = -0.49$, $P < 0.01$), with the number of vegetatively reproducing woodland species ($r = -0.45$, $P < 0.01$), and with the number and cover of myrmecochores ($r = -0.39$, $P < 0.05$); positive correlations appeared with the number and cover of woodland anemochores ($r = 0.40$, $P < 0.05$, and $r = 0.52$, $P < 0.01$, respectively).

TABLE 2. Mean scores ($n = 6$) of the first DCA axes for the ancient (1-4) and recent (5-10) woods plots as related to distance from the ancient-recent wood border to the plot centres (all Spearman's correlation coefficients r_s are significant at $P < 0.001$). Species occurring in the field layer in at least three plots were taken into consideration. P denotes the probability of difference (one-way ANOVA). Within a row underlined values are not significantly different at $P > 0.05$, based on the Tukey test.

Number of plot	1	2	3	4	5	6	7	8	9	10	P	λ	Gradient length	r_s
Distance (m)	-17.5	-12.5	-7.5	-2.5	2.5	7.5	12.5	17.5	22.5	27.5				
Vegetation data														
All species	<u>0.68</u>	0.51	0.56	<u>1.26</u>	<u>2.50</u>	2.93	2.88	3.11	3.22	<u>3.23</u>	< 0.001	0.75	3.91	0.87
Woodland species	<u>0.77</u>	0.61	0.56	<u>1.18</u>	<u>2.36</u>	2.95	2.77	2.95	3.12	<u>3.11</u>	< 0.001	0.78	3.30	0.85
Floristic data														
All species	<u>0.27</u>	0.29	<u>0.59</u>	<u>1.06</u>	<u>1.48</u>	<u>1.66</u>	2.01	2.02	2.17	<u>2.07</u>	< 0.001	0.37	2.50	0.91
Woodland species	<u>0.34</u>	0.43	<u>0.77</u>	<u>0.98</u>	<u>1.38</u>	<u>1.78</u>	1.92	2.09	2.29	<u>2.30</u>	< 0.001	0.39	2.81	0.92

Fig. 1. Ordination of plots in the recent pine wood (open circles) and adjacent ancient woodland (filled circles) along the first two DCA axes on the basis of presence/absence of all species occurring in at least three plots. 1-10 are numbers of plots within transects.

Fig. 2. Biplot of field layer species and distance to the ancient wood (AW) and shrub cover on the first two CCA axes ($\lambda_1 = 0.22$, $\lambda_2 = 0.08$) for the plots in the recent wood. Species occurring in at least two plots were taken into consideration. The diagram accounts for 9.6% and 100% of variance of species cover data and fitted species data, respectively. Stars = anemochores; circles = endozoochore; diamonds = dyszoochore; squares = myrmecochore; up-triangle = epizoochore; down-triangle = autochore; box = barochore; filled symbols = vegetatively reproducing species. The names of species from the *Quercus-Fagetum* class are in bold. Species abbreviations are based on the three letters of the genus and species.

TABLE 3. Frequency of woodland species occurring in at least two plots in the ancient (AW) or recent (RW) wood, and mean migration rates (m year^{-1}) of species in the recent pine wood based on the farthest individuals. For comparison, mean migration rates of species in recent deciduous woods in the Carpathian foothills (CF), southern Sweden (SS; Brunet & von Oheimb 1998), and central Belgium (CB; Bossuyt et al. 1999; Honnay et al. 1999) are given. An = anemochore, Au = autochore, B = barochore, En = endozoochore, M = myrmecochore, V = vegetative reproduction.

			Frequency		Migration rate			
Species			AW	RW	RW	CF	SS	CB
Species more frequent in the ancient wood								
<i>Convallaria majalis</i>	En	V	22***	10	0.18	–	0.43	0.45
<i>Melica nutans</i>	M	V	22***	9	0.29	–	0.42	–
<i>Lamiastrum galeobdolon</i>	M	V	22***	3	0.27	2.28	0.50	1.15
<i>Viola reichenbachiana</i>	M		21***	13	0.24	1.00	0.67	–
<i>Anemone nemorosa</i>	M	V	20***	6	0.21	2.09	0.85	0.55
<i>Mercurialis perennis</i>	M	V	18***	2	0.05	–	0.73	0.28
<i>Polygonatum multiflorum</i>	En	V	15*	10	0.24	2.09	0.63	0.25
<i>Ajuga reptans</i>	M	V	8***	0	0.00	–	–	–
<i>Aegopodium podagraria</i>	B	V	6**	0	0.00	0.95	–	–
<i>Carex digitata</i>	M		3	0	0.00	–	0.00	–
<i>Lilium martagon</i>	An		3	0	0.00	–	–	–
Species more frequent in the recent wood								
<i>Rubus hirtus</i>	En	V	6	36***	> 0.53	–	0.88	–
<i>Dryopteris carthusiana</i>	An		2	26***	> 0.53	1.57	0.44	–
<i>Hieracium murorum</i>	An		0	6*	–	–	–	–
<i>Vaccinium myrtillus</i>	En	V	0	5	–	–	–	–
Other species								
<i>Geranium robertianum</i>	Au		20	33	> 0.53	–	–	–
<i>Mycelis muralis</i>	An		14	30	> 0.53	–	–	–
<i>Moehringia trinervia</i>	M		13	17	> 0.53	1.29	–	–
<i>Luzula pilosa</i>	M		8	13	0.38	0.72	–	–
<i>Solidago virgaurea</i>	An		2	4	0.34	–	–	–

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

From among 19 woodland species found in the recent pine wood five occurred in the whole area, irrespective of the distance from the ancient woodland and they were much frequent (*Rubus hirtus* and *Dryopteris carthusiana*) or equally frequent (*Geranium robertianum*, *Mycelis muralis*, *Moehringia trinervia*) as in the ancient woodland (Table 3). It seems that these species colonised new places relatively fast. Migration rates of the remaining species were much slower. In Fig. 2 the extreme positions along the opposite direction of the arrow of distance from the ancient wood are occupied by the species more frequent only in the closest neighbourhood of the ancient woodland (*Mercurialis perennis*, *Polygonatum multiflorum*, *Convallaria majalis*, *Viola reichenbachiana*, *Anemone nemorosa*). For 13 species found in at least two plots in the ancient wood the migration rates varied from 0.0 m year^{-1} (*Ajuga reptans*, *Aegopodium podagraria*, *Carex digitata*, *Lilium martagon*) to 0.38 m year^{-1} (*Luzula pilosa*), and were considerably lower than the migration rates of these species in the recent deciduous woods in the Carpathian foothills, southern Sweden and central Belgium, calculated in a similar way. Only two woodland species (*Hieracium murorum*, *Vaccinium myrtillus*) occurred exclusively in the recent wood. They dispersed most probably from other woods – isolated from the recent pine wood.

DISCUSSION

This study has shown that the natural regeneration of woodland community is very slow even in a site adjacent to an ancient woodland. After 52 years of succession, only in places

distant no more than 5 meters from the border between woods the species composition of the field layer in the recent pine wood was similar to that at the edge of the ancient woodland. It was however significantly different from the interior of the ancient wood. Some studies suggest that various species may migrate with different rates, depending to a great extent on the modes of diaspore dispersal, and that the migration rate of the same species may be considerably variable, depending on the local availability of micro-sites suitable for seed germination and seedling development. In the recent pine wood the numbers of myrmecochores and vegetatively reproducing species decreased significantly with distance from the ancient woodland, while the number of anemochores increased. A similar pattern of colonization was revealed also in other secondary woods (Dzwonko 1993; Matlack 1994; Brunet and von Oheimb 1998a). Ants transport seeds for a distance usually no longer than a few meters and very rarely across longer distances (Ulbrich 1939; Beattie and Culver 1981; Gorb and Gorb 1995; Gómez and Espadaler 1998).

Brunet and von Oheimb (1998b) found that *Anemone nemorosa* had colonised recently established deciduous woods in southern Sweden with rates varying from 0.28 to 1.34 m year^{-1} , calculated for the farthest individuals. Moreover, they pointed out that the migration rate of this species, calculated for half maximum cover, increased with tree canopy cover – especially cover of broad-leaved trees with quickly decomposing litter, with soil pH, and decreased with increasing grass cover. In the recent pine wood, on the rather dry calcareous soil with slowly decomposing litter, the majority of analysed woodland species migrated with a several times lower rate than in secondary

deciduous woods on rich soil. These results indicate that the availability of places suitable for seed germination and plant development is as important for successful colonization as seed dispersal. The litter has a negative effect on the recruitment of the majority, if not all species in deciduous woods (Sydes and Grime 1981a, b; Persson et al. 1987; Facelli and Pickett 1991; Myster 1994; Eriksson 1995; Brunet and von Oheimb 1998b; Dzwonko 2001). Eriksson (1995) distinguished two species groups depending on their reaction on the litter and the persistence of their soil seed bank. The first group includes the species capable of germination under at least moderate litter layers that do not develop a persistent seed bank (e.g. *Anemone nemorosa*, *Actaea spicata*, *Hepatica nobilis*, *Convallaria majalis* and *Lathyrus vernus*). Removal of litter affects positively the recruitment of such species in this group as e.g. *Anemone nemorosa* (Eriksson 1995; Holderegger 1996). The second group consists of the species which are not able to be recruited at all if litter is not removed, but which develop a persistent seed bank (e.g. *Poa nemoralis*, *Viola riviniana*, *Rubus idaeus* and *Urtica dioica*).

The decomposition rate of litter depends on several factors (Berg et al. 1996). In general, the litter of deciduous tree species is decomposed twice faster than the litter of evergreen species (Cornelissen 1996). Therefore the sites with deciduous tree litter in the secondary woods are much more suitable for recruitment and development of the majority of woodland species than the sites with pine litter. The pine litter deteriorates the growth conditions of these plants, also by increase of the C/N ratio and by acidification of the top soil (Augusto et al. 1998; Dzwonko 2001). Falkengren-Grerup and Tyler (1993) showed that many woodland species are sensitive to increased soil acidity (cf. also Brunet and von Oheimb 1998b).

The results obtained suggest that in the present-day landscapes, species-rich woodland communities can be maintained first of all in the remnants of ancient woodlands and these woods should be protected in the first place. Recent woods may be more effectively colonised by woodland species only when they are directly adjacent to ancient woodlands, and are dominated by broad-leaved trees with quickly decomposing litter, and if these relationships will be stable for a relatively long period.

ACKNOWLEDGMENTS

I would like to thank S. Gawroński for their assistance with field work. I also thank a reviewer for his helpful comments.

LITERATURE CITED

- AUGUSTO L., BONNAUD P., RANGER J. 1998. Impact of tree species on forest soil acidification. *For. Ecol. Manage.* 105: 67-78.
- BEATTIE A.J., CULVER D.C. 1981. The guild of myrmecochores in the herbaceous flora of West Virginia forests. *Ecology* 62: 107-115.
- BEKKER R.M., SCHAMINÉE J.H.J., BAKKER J.P., THOMPSON K. 1998. Seed bank characteristics of Dutch plant communities. *Acta Bot. Neerl.* 47: 15-26.
- BERG B., EKBOHM G., JOHANSSON M.B., McCLAUGHERTY C., RUTIGLIANO F., VIRZO DE SANTO A. 1996. Maximum decomposition limits of forest litter types: a synthesis. *Can. J. Bot.* 74: 659-672.
- BOSSUYT B., HERMY M. 2000. Restoration of the understorey layer of recent forest bordering ancient forest. *Appl. Veg. Sci.* 3: 43-50.
- BOSSUYT B., HERMY M., DECKERS J. 1999. Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *J. Ecol.* 87: 628-638.
- BRUNET J. 1993. Environmental and historical factors limiting the distribution of rare forest grasses in south Sweden. *For. Ecol. Manage.* 61: 263-275.
- BRUNET J., VON OHEIMB G. 1998a. Migration of vascular plants to secondary woodlands in southern Sweden. *J. Ecol.* 86: 429-438.
- BRUNET J., VON OHEIMB G. 1998b. Colonization of secondary woodlands by *Anemone nemorosa*. *Nord. J. Bot.* 18: 369-377.
- CORNELISSEN J.H.C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *J. Ecol.* 84: 573-582.
- DUFFY D.C., MEIER A.J. 1992. Do Appalachian herbaceous understoreys ever recover from clearcutting? *Conserv. Biol.* 6: 196-201.
- DZWONKO Z. 1993. Relations between the floristic composition of isolated young woods and their proximity to ancient woodland. *J. Veg. Sci.* 4: 693-698.
- DZWONKO Z. 2001. Effect of proximity to ancient deciduous woodland on restoration of the field layer vegetation in a pine plantation. *Ecography* 24 (in press).
- DZWONKO Z., GAWROŃSKI S. 1994. The role of woodland fragments, soil types, and dominant species in secondary succession on the western Carpathian foothills. *Vegetatio* 111: 149-160.
- DZWONKO Z., LOSTER S. 1989. Distribution of vascular plant species in small woodlands on the Western Carpathian foothills. *Oikos* 56: 77-86.
- DZWONKO Z., LOSTER S. 1990. Vegetation differentiation and secondary succession on a limestone hill in southern Poland. *J. Veg. Sci.* 1: 615-622.
- DZWONKO Z., LOSTER S. 1992. Species richness and seed dispersal to secondary woods in southern Poland. *J. Biogeogr.* 19: 195-204.
- DZWONKO Z., LOSTER S. 1997. Effects of dominant trees and anthropogenic disturbances on species richness and floristic composition of secondary communities in southern Poland. *J. Appl. Ecol.* 34: 861-870.
- DZWONKO Z., LOSTER S. 1998. Dynamics of species richness and composition in a limestone grassland restored after tree cutting. *J. Veg. Sci.* 9: 387-394.
- ERIKSSON O. 1995. Seedling recruitment in deciduous forest herbs: the effects of litter, soil chemistry and seed bank. *Flora* 190: 65-70.
- FACELLI J.M., PICKETT S.T.A. 1991. Plant litter: its dynamics and effects on plant community structure. *Bot. Rev.* 57: 1-32.
- FALKENGREN-GRERUP U., TYLER G. 1993. Experimental evidence for the relative sensitivity of deciduous forest plants to high soil acidity. *For. Ecol. Manage.* 60: 311-326.
- GÓMEZ C., ESPADALER X. 1998. Myrmecochorous dispersal distances: a world survey. *J. Biogeogr.* 25: 573-580.
- GORB S.N., GORB E.V. 1995. Removal rates of seeds of five myrmecochorous plants by the ant *Formica polyctena* (Hymenoptera: Formicidae). *Oikos* 73: 367-374.
- GRASHOF-BOKDAM C. 1997. Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. *J. Veg. Sci.* 8: 21-28.
- GRASHOF-BOKDAM C., GEERTSEMA W. 1998. The effect of isolation and history on colonization patterns of plant species in secondary woodland. *J. Biogeogr.* 25: 837-846.
- 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* 91: 9-22.
- HOLDEREGGER R. 1996. Effects of litter removal on the germination of *Anemone nemorosa* L. *Flora* 191: 175-178.
- HONNAY O., DEGROOTE B., HERMY M. 1998. Ancient-forest plant species in Western Belgium: a species list and possible ecological mechanisms. *Belg. J. Bot.* 130: 139-154.
- HONNAY O., HERMY M., COPPIN P. 1999. Impact of habitat quality on forest plant species colonization. *For. Ecol. Manage.* 115: 157-170.
- JANKOWSKA-BŁASZCZUK M. 1998. Variability of the soil seed banks in the natural deciduous forest in the Białowieża National Park. *Acta Soc. Bot. Pol.* 67: 313-324.

- JANKOWSKA-BŁASZCZUK M., GRUBB P.J. 1997. Soil seed banks in primary and secondary deciduous forest in Białowieża, Poland. *Seed Sci. Res.* 7: 281-292.
- JANKOWSKA-BŁASZCZUK M., KWIATKOWSKA A.J., PANUFNIK D., TANNER E. 1998. The size and diversity of the soil seed banks and the light requirements of the species in sunny and shady natural communities of the Białowieża Primeval Forest. *Plant Ecol.* 136: 105-118.
- KJELLSSON G. 1992. Seed bank in Danish deciduous forests: species composition, seed influx and distribution pattern in soil. *Ecography* 15: 86-100.
- KORNAŚ J., MEDWECKA-KORNAŚ A. 1974. The vegetation of Cracow. *Folia Geogr., Ser. Geogr.-Phys.* 8: 153-169.
- MATLACK G.R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75: 1491-1502.
- MYSTER R.W. 1994. Contrasting litter effects on old field tree germination and emergence. *Vegetatio* 114: 169-174.
- PERSSON S., MALMER N., WALLÉN B. 1987. Leaf litter fall and soil acidity during half a century of secondary succession in a temperate deciduous forest. *Vegetatio* 73: 31-45.
- PETERKEN G.F., GAME M. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *J. Ecol.* 72: 155-182.
- PETERSEN P.M. 1994. Flora, vegetation, and soil in broadleaved ancient and planted woodland, and scrub on Røsnæs, Denmark. *Nord. J. Bot.* 14: 693-709.
- PIROŻNIKOW E. 1983. Seed bank in the soil of stabilized ecosystem of a deciduous forest (*Tilio-Carpinetum*) in the Białowieża National Park. *Ekol. pol.* 31: 145-172.
- RYDGREN K., HESTMARK G. 1997. The soil propagule bank in a boreal old-growth spruce forest: changes with depth and relationship to aboveground vegetation. *Can. J. Bot.* 75: 121-128.
- SYDES C., GRIME J.P. 1981a. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. I. Field investigations. *J. Ecol.* 69: 237-248.
- SYDES C., GRIME J.P. 1981b. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. II. An experimental investigation. *J. Ecol.* 69: 249-262.
- TER BRAAK C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69: 69-77.
- TER BRAAK C.J.F., ŠMILAUER P. 1998. CANOCO reference manual and user's guide to Canoco for Windows. Centre for Biometry, Wageningen.
- THOMPSON K., BAKKER J.P., BEKKER R.M., HODGSON J.G. 1998. Ecological correlates of seed persistence in soil in the north-west European flora. *J. Ecol.* 86: 163-169.
- TUTIN T.G., HEYWOOD V.H., BURGESS N.A., MOORE D.M., VALENTINE D.H., WALTERS S.M., WEBB D.A. 1964-1980. *Flora Europaea*. Cambridge Univ. Press, Cambridge.
- ULBRICH E. 1939. Deutsche Myrmekochoren. *Repertorium specierum novarum regni vegetabilis* 117: 1-60.
- VAN DER PIJL L. 1982. Principles of dispersal in higher plants. Springer, Berlin.
- WARR S.J., KENT M., THOMPSON K. 1994. Seed bank composition and variability in five woodlands in south-west England. *J. Biogeogr.* 21: 151-168.
- WHITNEY G.G., FOSTER D.R. 1988. Overstorey composition and age as determinants of the understorey flora of woods of central New England. *J. Ecol.* 76: 867-876.
- WULF M. 1997. Plant species as indicators of ancient woodland in northwestern Germany. *J. Veg. Sci.* 8: 635-642.

MIGRACJA GATUNKÓW ROŚLIN NACZYNIOWYCH ZE STAREGO ZBIOROWISKA LEŚNEGO DO PRZYLEGAJĄCEGO NOWEGO LASU

STRESZCZENIE

We współczesnym krajobrazie pełny skład gatunkowy zbiorowisk lasów liściastych może być odtworzony jedynie w miejscach przylegających do starych lasów, które są źródłem nasion drzew, krzewów i leśnych roślin zielnych. Zbadano wpływ dominujących gatunków drzew i odległości od przylegającego starego lasu grądowego (*Tilio-Carpinetum*) na skład florystyczny runa w lesie sosnowym, posadzonego na siedlisku lasu grądowego, na raczej suchej rędzinowej glebie, w rezerwacie Skołczanka koło Krakowa. Stwierdzono, że pomimo trwającej 52 lata sukcesji granica między lasami była ostra, a skład gatunkowy w nowym lesie był istotnie różny, niż w przylegającym starym grądzie. Kanoniczna analiza korespondencji (CCA) wykazała, że odległość od starego lasu miała istotny wpływ na rozmieszczenie gatunków w nowym lesie. Liczba gatunków z klasy *Quercus-Fagetea*, gatunków rozmnażających się wegetatywnie i gatunków myrmekochorycznych malała ze wzrostem odległości od starego lasu, podczas gdy liczba anemochorów wzrastała. Tempo migracji wielu gatunków leśnych, obliczone dla osobników występujących najdalej, było bardzo wolne, od 0,0 m rok⁻¹ do 0,38 m rok⁻¹. Tempo regeneracji roślinności runa w badanym lesie sosnowym było dużo wolniejsze, niż w porównywanych wtórnych lasach liściastych na żyznych i wilgotnych glebach, gdzie niektóre gatunki migrowały w tempie przekraczającym 1,50 m rok⁻¹. Można zatem sądzić, że nowe lasy sąsiadujące ze starymi lasami mogą być bardziej efektywnie kolonizowane przez gatunki lasów liściastych jedynie wtedy, gdy dominują w nich drzewa tworzące szybko rozkładającą się ściółkę, a przestrzenna ciągłość tych lasów jest zachowana przez długi czas.

SŁOWA KLUCZOWE: południowa Polska, regeneracja lasów, rozsiewanie nasion, stare lasy, wtórna sukcesja, wtórne lasy.