Acta Universitatis Lodziensis
——— 2011 ———
Folia Biologica et Oecologica 7: 27–48
(Acta Univ. Lodz, Folia Biol. Oecol.)

ZBIGNIEW DZWONKO

Institute of Botany, Jagellonian University, Lubicz 46, 31-512 Kraków, Poland, ubdzwonk@cyf-kr.edu.pl

EFFECT OF CHANGES IN LAND USE DURING THE 20TH CENTURY ON WOODLAND AND CALCAREOUS GRASSLAND VEGETATION IN SOUTHERN POLAND

Abstract: In the modern agricultural landscape major threats to plant species diversity are loss and fragmentation of habitats and communities. During the last century natural and semi-natural communities have faced also cessation of tradition management and increased load of nutrients. This paper presents a survey of studies on vegetation dynamics of woodlands in the northern part of the Carpathian foothills and of calcareous grasslands on limestone hills near Kraków. The causes of far-going changes observed in communities of these types and possible management for their conservation are discussed. The nature conservation value of woods can be assessed by means of ancient woodland plant species indicators.

Key words: literature review; nature conservation; permanent plots; species diversity; vegetation change

1. INTRODUCTION

Landscape transformation due to land use changes is one of the main reasons for decline in species diversity in natural and semi-natural habitats in the 20th century. In central Europe changes in land use have occurred since the first Neolithic settlements about 7000-9000 years ago. The first types of land use were grazing of woodlands and alternating arable field-pasture farming (KRUK, MILISAUSKAS 1999; POSCHLOD *et al*. 2005). Since that time the variety of land use types increased until

DOI: 10.2478/v10107-009-0015-0

the 19th century causing a high diversity of habitats and species. The highest plant species diversity occurred probably in the first half of the 19th century. From that period changes in land use have caused a decrease in biodiversity. The novel land use changes have included among other: the intensification of arable field farming due to development of mineral fertilizers, the land consolidation, the drainage of peatlands and wetlands, the abandonment of low-intensity grazing systems, and afforestation with non-indigenous trees (POSCHLOD, BONN 1998; POSCHLOD *et al.* 2005). These changes continued during most decades of the 20th century. Particularly deterioration and fragmentation of habitats have created major extinction threats as they reduce the availability of suitable habitats for many species. Decreasing population sizes lead to an enhanced extinction risk among species with poor dispersal ability, especially when they occur in isolated sites where local extinctions are not counterpoised by colonisations. In a traditional man-made landscape there was the highest diversity of dispersal processes connected with a great diversity of land use practices. In the modern agricultural landscape most of these processes became lost or changed (POSCHLOD, BONN 1998). Many semi-natural grasslands, originating from traditional agriculture and grazing, are nowadays threatened also by habitat degradation due to agricultural or atmospheric inputs or due to secondary succession occurring after land abandonment.

Vegetation changes can be studied in two ways. The first is the space-for-time substitution approach where different phases of a succession are studied in different sites and it is assumed that the changes observed are time-dependent. This approach has been applied most often. It is emphasized that although this approach may be useful for qualitative description and for hypothesis generation, it is unreliable for a deeper understanding of successional changes because site history is also important, and the assumption of similar habitats of different successional phases may not be valid. The second approach is to continuously study vegetation applying some formal monitoring system – above all long-term permanent plot observations. Vegetation changes measured in this way can be related directly to time in combination with other treatments imposed on it. Therefore hypotheses of causes and mechanisms of changes in species composition of communities can be tested in permanent plot experiments. Long-term monitoring, by using permanent plots is the most appropriate method to distinguish between trends and fluctuations in vegetation dynamics, and, in nature preservation, to evaluation whether the applied management is in accordance with the conservation goal (BAKKER *et al*. 1996; BAKKER *et al*. 2002).

Some examples of vegetation changes resulting from different changes in land use in southern Poland between the 1950s and the 1980s were presented and discussed by KORNAŚ (1990). They concerned vegetation in the Gorce Mts. and in the Ojców National Park and were based also on the results of phytosociological studies in which relevés were repeated on marked plots and mapping of the actual vegetation was repeated in the same area. The present paper discusses the causes, rate and direction of changes and possible management for conservation of woodland vegetation in the northern part of the Carpathian foothills, and of calcareous grassland vegetation on limestone hills near Kraków, based on detailed studies including permanent plot observations and experiments.

2. CHANGES IN SPECIES RICHNESS AND COMPOSITION OF WOODLANDS AND THE ASSESSMENT OF THEIR CONSERVATION VALUE

In the present-day agricultural landscapes of southern Poland the ancient deciduous woodlands frequently occupy small, isolated areas, similarly as in other parts of temperate Europe. For example in the northern part of the foothills of the Carpathians only a few woodlands cover large areas, several dozen hectares, while the others are small patches of woods, from several dozen square metres to several hectares, in places unsuitable for agriculture, such as on steep slopes of stream valleys and on hill slopes too steep for cultivation. Most of these woodlands are remnants of primary forests which still covered the greater part of this area during the Middle Ages. Only a few originated later, on land which had previously been in agricultural use. The remnants of ancient forests represent such associations as: *Tilio cordatae-Carpinetum betuli*, *Dentario glandulosae-Fagetum*, *Pino-Quercetum*, and seldom *Carici remotae-Fraxinetum*. As it is difficult to prove that any particular wood is primary it is more useful to discuss ancient woods, which are defined as woods in existence before some date selected on the basis of available historical documents – opposed to those which are more recent. In southern Poland a specified date may be appointed by Mieg's map from 1779-1783. Many authors have pointed out that woodlands which are isolated in an agricultural landscape are habitat islands. The Carpathian foothills were colonized gradually. In some parts intensive colonization began already in the fifteenth century, and most woodland islands currently existing were formed by fragmentation of former large forests earlier than in other parts of this area. The woodlands in the areas colonized earlier and in a much greater extent are often more isolated and also more anthropogenically disturbed because of grazing, trampling, rubbish dumping and the like.

Detailed analyses in the Wierzbanówka valley (Pogórze Wielickie) – a typical fragment of the northern part of the Carpathian foothills, showed that the number of plant species in woodland islands was related to their area, isolation, shape and habitat diversity. Compared with the more recently isolated and less disturbed woodlands, those isolated for longer periods and more anthropogenically disturbed were found to have fewer species, including fewer woodland species, i.e. species characteristic of the classes *Querco-Fagetea* and *Vaccinio-Piceetea*, and some other species closely associated with woodland conditions. On the other hand, significantly more non-woodland species were present here. It was also found that groups of small ancient woods (0.008-2.16 ha) support more woodland species than do single woods equal in area (DZWONKO, LOSTER 1988, 1989). These results indicate that preservation of many small woodland remnants in an agricultural landscape may be of great importance for the maintenance of local species richness and the protection of woodland species. The vegetatively propagating long-lived perennials predominate among the woodland species of temperate deciduous forests. Such species can persist for a very long time in small ancient woods, which may become lasting refuges for many of them if they are not subjected to too strong anthropogenic pressure, including grazing, trampling, and rubbish dumping.

Ancient deciduous woodlands are, as a rule, considerably richer in woodland species than the recent woods and plantations on abandoned fields, meadows and grasslands (PETERKEN, GAME 1984; DZWONKO, LOSTER 1989; WULF 1997; HONNAY *et al*. 1998; HERMY *et al*. 1999). Recent studies have shown that natural regeneration of woodland communities is very slow and it is possible only in sites immediately adjacent to ancient woodlands - the sources of woodland species diaspores (PETERKEN, GAME 1984; DZWONKO 1993; DZWONKO, GAWROŃSKI 1994; MATLACK 1994; BRUNET, VON OHEIMB 1998; BOSSUYT, 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, GRUBB 1997; 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; WARR *et al*. 1994; JANKOWSKA-BŁASZCZUK 1998).

At present natural regeneration of full floristic composition of woodland communities in sites spatially isolated from ancient woodlands is impossible because of poor dispersal ability of many woodland species (WHITNEY, FOSTER 1988; DZWONKO, LOSTER 1989, 1992; MATLACK, 1994; GRASHOF-BOKDAM, GEERTSEMA 1998). Even recent woods adjacent to ancient woodlands are very slowly colonised by woodland species. Migration rates of woodland species to such recent woods varied in general from 0.0 to 1.2 m year^{-1}, and rarely exceed 1.5 m year^{-1} (Table 1). It seems that the secondary woods are generally most quickly colonized by endozoochores and hovering and flying anemochores and most slowly by heavy anemochores, myrmecochores and barochores. The results of detailed studies 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.

Table 1. Frequency of woodland species on the plots in an oak-hornbeam ancient wood (AW, 24 plots) and in an adjacent 52-year old pine wood (RW, 36 plots) in the Skołczanka reserve, and mean migration rates (m year^{-1}) of species in the 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. After DZWONKO (2001).

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

$^{+}$ 0.1 > P > 0.05; * 0.05 > P > 0.01; ** 0.01 > P > 0.001; *** P < 0.001.

Woodland plant species unable to colonise isolated recent woods may be considered as indicators of ancient woodlands, because their presence suggests a long continuous history for the habitat patch, and because they may be indicative of more original woodland conditions. A list of 155 ancient woodland species was generated for Poland on the basis of survey the list of ancient woodland species in north-western and central Europe (HERMY *et al*. 1999), and taking into account ecological characters of vascular plant species associated with deciduous woodlands in Poland (DZWONKO, LOSTER 2001; DZWONKO 2007). This list includes many still common species, e.g. *Anemone nemorosa*, *Asarum europaeum*, *Carex digitata*, *C. sylvatica*, *Convallaria majalis*, *Dryopteris filix-mas*, *Festuca gigantea*, *Lathyrus vernus*, *Luzula pilosa*, *Melica nutans*, *Poa nemoralis*, *Polygonatum multiflorum*, *Stachys sylvatica* and *Viola reichenbachiana*. Ancient woodland species indicators are of high importance for woodland conservation and vegetation studies, because spontaneous restoration of woodland communities in new sites takes centuries. Hence, these plant species indicators may be used for assessing the nature conservation value of woodlands, and to distinguish ancient woodland communities from recent woods. Forest management should aim at favouring ancient woodland species by maintaining traditional deciduous forest management systems.

Eutrophication, just like acidification, has been one of the most often observed processes occurring in woodland ecosystems in many European countries in the last decades of the 20th century (cf. PEARSON, STEWART 1993; BOBBINK *et al.* 1998). An increase in the number or frequency of nitrophilous species in deciduous and mixed woodlands in western, north-western and central Europe has been noted by various authors (FALKENGREN-GRERUP 1986; TYLER 1987; THIMONIER *et al.* 1994; BRUNET *et al*. 1997). Moreover, decline and extinction of acidophilous species were observed in deciduous, coniferous and mixed woods growing on less fertile soils (FANGMEIER *et al*. 1994; VAN TOL *et al*. 1998). MEDWECKA-KORNAŚ and GAWROŃSKI (1990) showed that in the Ojców National Park (established in 1956, about 22 km NNW of Kraków) changes in the structure and composition of the *Pino-Quercetum*, the only acidophilous forest in this area, are so great that most of its stands do not represent this community any more. An evident retreat during 30 years (1958-1988) of such acidophilous woodland species as *Vaccinium myrtillus*, *Luzula luzuloides*, *Majanthemum bifolium*, *Melampyrum pratense*, *Orthilia secunda*, *Veronica officinalis*, *Lycopodium annotinum*, *Polytrichum formosum* and *Pleurozium schreberi* was noted there. Similar changes have been observed also on other sites in southern Poland. In consequence, species richness of many woodlands and local diversity of woodland communities decrease. Considerable increase in air-borne nitrogen and sulphur, observed in the last decades of the 20th century, has been invoked as responsible for eutrophication of woodland communities in most studies.

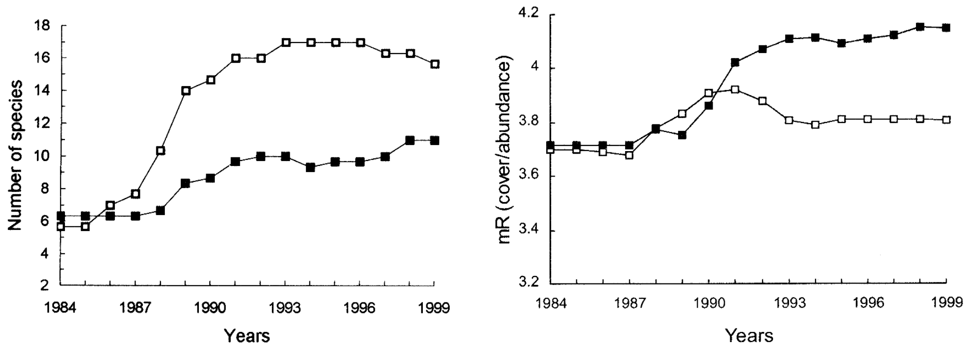

Fig. 1. Mean number of species in the field layer and the mean ELLENBERG indicator values for reaction (mR) in three pairs of the litter removal (☐) and control (■) permanent plots in an oak-pine mixed woodland in the Wierzbanówka valley, during 1984-1999. In the course of 16 years abundance of *Vaccinium myrtillus*, *Majanthemum bifolium* and *Luzula pilosa* considerably decreased in the control plots, while abundance such species as *Carex brizoides*, *Milium effusum* and *Rubus hirtus* increased distinctly. After DZWONKO and GAWROŃSKI (2002).

Extinction of acidophilous species in woodlands and their eutrophication may also arise from other processes. For hundreds of years woods in central Europe have been strongly influenced by human activities. Still in the first half of the 20th century farmers removed litter and grazed domestic animals in many woods (MIKLASZEWSKI 1928; ELLENBERG 1988). Regular litter removal resulted in substantial impoverishment of soils in nitrogen and other nutrients and could lead to considerable reduction of woodland productivity. According to ELLENBERG (1988), as a consequence of material removal, woodland soils in central Europe became less fertile and more acid than they were originally. Yet during the first few decades after World War II litter was removed and animals were grazed in deciduous woods in various parts of Poland (JAKUBOWSKA-GABARA 1993). Cessation of these traditional methods of management coincided with the beginning of air pollution growth. It is possible then that changes in species composition of mixed woods also arose from the accumulation of organic matter and occurrence of thick litter layer. Decomposition of larger quantities of matter enriched soil in nutrients, and thick litter layer could restrict seed germination and development of many species. This opinion is supported by the results of 16-year litter removal experiment in an acidophilous mixed oak-pine woodland in the Wierzbanówka valley (DZWONKO, GAWROŃSKI 2002). It was found that litter removal resulted in substantial impoverishment of soil. Vascular plant species and bryophytes colonized the litter removal plots much more frequently. Within 16 years species richness increased in the field layer of these plots, but abundance of dominant species and character of vegetation remained unchanged, while vegetation of the control plots changed from acidophilous to neutrophilous (Fig. 1).

3. CHANGES IN CALCAREOUS GRASSLAND VEGETATION AND MANAGEMENT FOR ITS CONSERVATION

For several centuries semi-natural calcareous grasslands have been characteristic elements of the agricultural landscapes in the hilly regions of southern Poland. They were composed of species-rich and geographically differentiated communities. Many grassland species reached this area in long time as migratory waves from the southeast and south of Europe. Today, in xerothermic calcareous grasslands of southern Poland occur many Pontic and Pontic-Pannonian plant species, e.g. *Adonis vernalis*, *Campanula sibirica*, *Carex humilis*, *Carlina onopordifolia*, *Chamaecytisus albus*, *Cirsium pannonicum*, *Echium russicum*, *Inula ensifolia*, *Iris aphylla*, *Linum flavum*, *L. hirsutum*, *Scorzonera purpurea*, *Stipa joannis*, *S. pulcherrima* and *Thymus praecox*. Most of these species usually appear in form of rare, isolated populations. Patches of calcareous grasslands represent some associations from the *Festuco-Brometea* class, like: *Inuletum ensifoliae*, *Sisymbrio-Stipetum capillatae*, *Koelerio-Festucetum rupicolae*, *Thalictro-Salvietum pratensis* and *Origano-Brachypodietum*. The first two associations are most common (MEDWECKA-KORNAŚ, KORNAŚ 1966; MICHALIK, ZARZYCKI 1995).

For long time, the grasslands on limestone and chalk hill slopes as well as those on calcareous loess were regularly grazed by domestic animals, most often by sheeps and goats, and their development and maintenance was primarily linked with this type of land use. During the two decades after World War II, the traditional methods of management had been ceased and most of the calcareous grasslands abandoned. Today, remnants of these grasslands, ranging from several dozen square metres to several hectares, are isolated by fields and meadows. The distances between them are from several hundred metres to several kilometres. Only some of abandoned calcareous grasslands have been set aside as nature reserves. The remnants of old grasslands in southern Poland like in other parts of central, western and northern Europe are the only refuges for many grassland and xerothermic species of plants and small animals (MORTIMER *et al*. 1998; DOLEK, GEYER 2002; WAALLISDE VRIES *et al*. 2002). Thus, maintaining grassland communities is of utmost importance to the conservation of local and regional biodiversity.

Unmanaged grasslands have changed as a result of secondary succession. Abandoned grasslands situated in the vicinity of woodlands are often overgrown by shrubs and trees. In many places the effect of this process has been a considerable decrease of the area occupied by grassland communities and its fragmentation into small, often isolated patches (Fig. 2). An increase in tree and shrub cover results in a decrease in the number and cover of grassland species and may lead to their local extinction within decades. In many grasslands after cessation of management practices the cover of tall grasses and forbs with larger leaves as well as of species reproducing vegetatively (e.g. *Arrhenatherum elatius*, *Phleum phleoides*, *Vincetoxicum hirundinaria* and *Galium mollugo*) increases rapidly. They reduce light penetration to lower layers of the grasslands and restrict the development of shorter species. The dominance of tall grasses and non-removal of organic matter lead to the formation of a thick litter layer, which hinder germination and growth of seedlings. A thick litter layer in the dense grassland impedes also seed germination

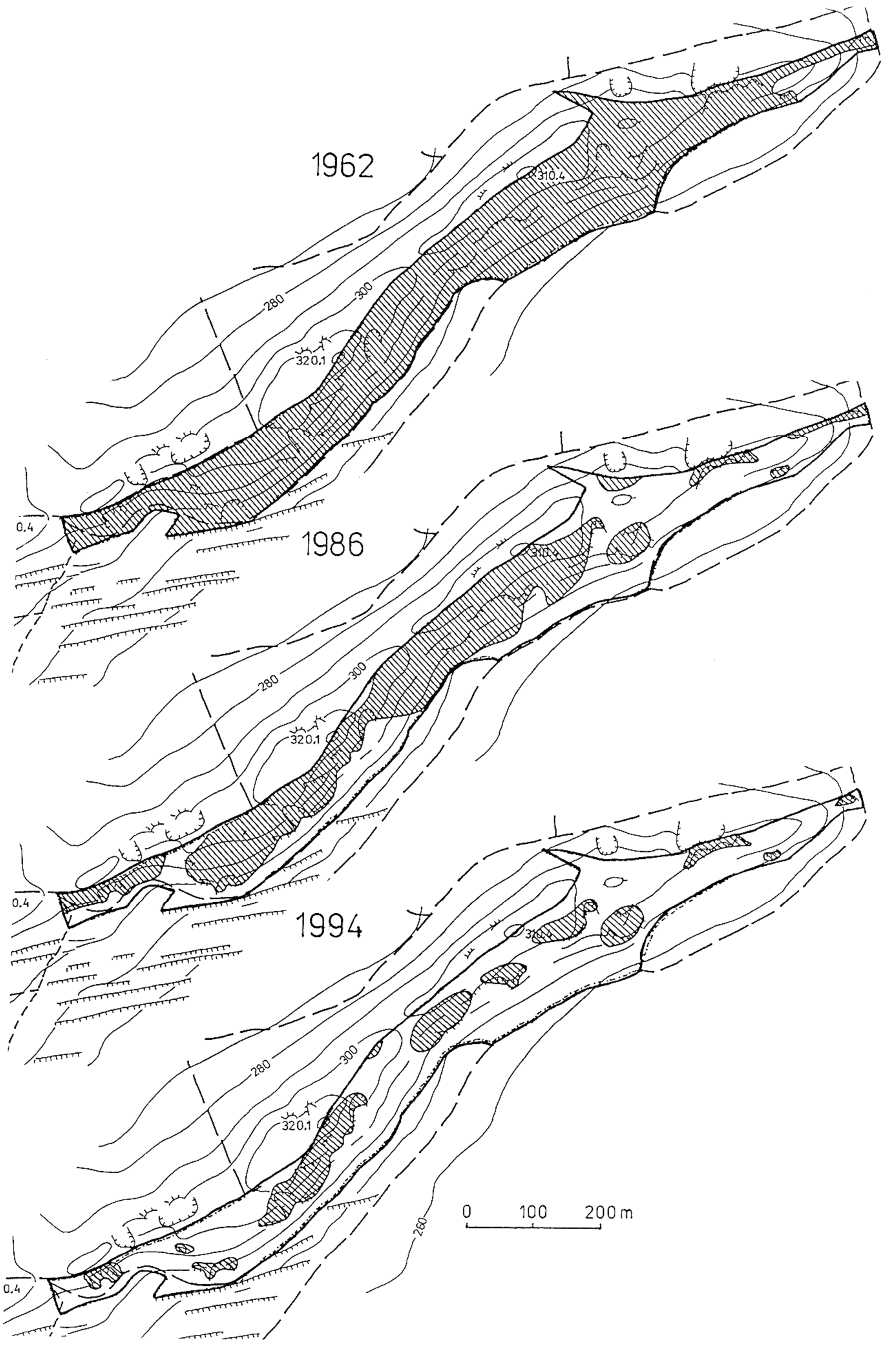

Fig. 2. Changes of area and fragmentation of xerothermic calcareous grassland (shaded) in the Kajasówka reserve near Kraków, during 1962-1994, after cessation of grazing. The reserve (12 ha) was established in 1962. After MICHALIK and ZARZYCKI (1995).

and seedling development of shrubs and trees, thus causing the succession to wood to proceed much slower than in more open grasslands. Such changes, usually with decrease in species diversity, have been observed in abandoned grasslands in different parts of central and western Europe (WILLEMS 1983; WARD, JENINGS 1990; DZWONKO, LOSTER 1998a, 2008; KAHMEN, POSCHLOD 2004).

Various studies revealed that most of the grassland species have poor dispersal ability and cannot, without grazing animals acting as dispersal vectors, re-colonize isolated grasslands nor colonize isolated open sites (GIBSON *et al*. 1987; POSCHLOD, BONN 1998; POSCHLOD *et al*. 1998). The above cited studies showed that herbivores moving between grasslands could disperse enormous numbers of seeds during a year. When grazing is ceased the dispersal of most grassland species is limited to several metres or even to several dozen centimetres (VERKAAR *et al*. 1983; STAMPFLI, ZEITER 1999; KALAMEES, ZOBEL 2002). Species-rich grasslands cannot be restored from soil seed bank because relatively few species of these communities form persistent seed bank in the soil, and seeds of many grassland species have a short life span in soil (DUTOIT, ALARD 1995; BEKKER *et al*. 1997; WILLEMS, BIK 1998; STAMPFLI, ZEITER 1999). Experimental studies suggest that even though the seeds of grassland species do occur in seed rain or soil seed bank, successful restoration of species-rich grasslands may still require additional management such as grazing or mowing in order to facilitate the development of suitable species seedlings (HUTCHINGS, BOOTH 1996). Observation by KARLÍK and POSCHLOD (2009) in southwestern Germany has showed that species composition of ancient calcareous grasslands (i.e. patches continuously used as pasture at least since the first half of the 19th century) differed considerably from that of recent grasslands (no more then 150 years old), and it was possible to identify species indicating the historical status of the grasslands. Regional indicators of ancient grasslands included among others: *Aster amellus*, *Brachypodium pinnatum*, *Carex caryophyllea*, *Carlina vulgaris*, *Hieracium pilosella*, *Linum catharticum*, *Scabiosa columbaria*, and *Vincetoxicum hirundinaria*. Cited authors found that a part of the regional calcareous grassland species pool was restricted to recent grasslands which also contained rare and/or endangered species. Therefore, also these grasslands may have a high conservation value.

Many studies have pointed out that the best way to maintain the species richness and composition of semi-natural grasslands is to re-introduce traditional methods of management i.e. controlled grazing and mowing (Tab. 2; cf. GIBSON *et al*. 1987; GIBSON, BROWN 1991; MOOG *et al*. 2002). In Poland they have been seldom used for both economic and organizational reasons. In many cases periodic cutting of trees and shrubs is the only available and applied conservation management aimed at preservation or regeneration of grassland vegetation.

A 12-year observation in the Skołczanka reserve near Kraków showed that the richness and composition of the restored calcareous grasslands depended significantly on the community composition before tree and shrub cutting (DZWONKO, LOSTER 2007, 2008). This study has suggested that periodical tree cutting enables the maintenance of a temporal-spatial mosaic of scrub-grassland communities and the preservation of local species diversity. But, in practice, cutting trees and shrubs in sites where most grassland species have already vanished, without additional management, such as grazing, mowing, formation of gaps or even sowing seeds is not sufficient to restore grasslands rich in xerothermic species, even though old grassland – a potential source of diaspores is in closed vicinity (Fig. 3). The cited study has showed that developing shrubs and trees can significantly hinder regeneration of xerothermic calcareous grasslands and should be cut more often than in ten years – presumably every five or six years, before their covers increase to about 30%. Long-term monitoring of the vegetation dynamics is crucial in such cases. However, this treatment alone will not stop the changes to communities with the dominance of tall and vegetatively spreading grasses and forbs.

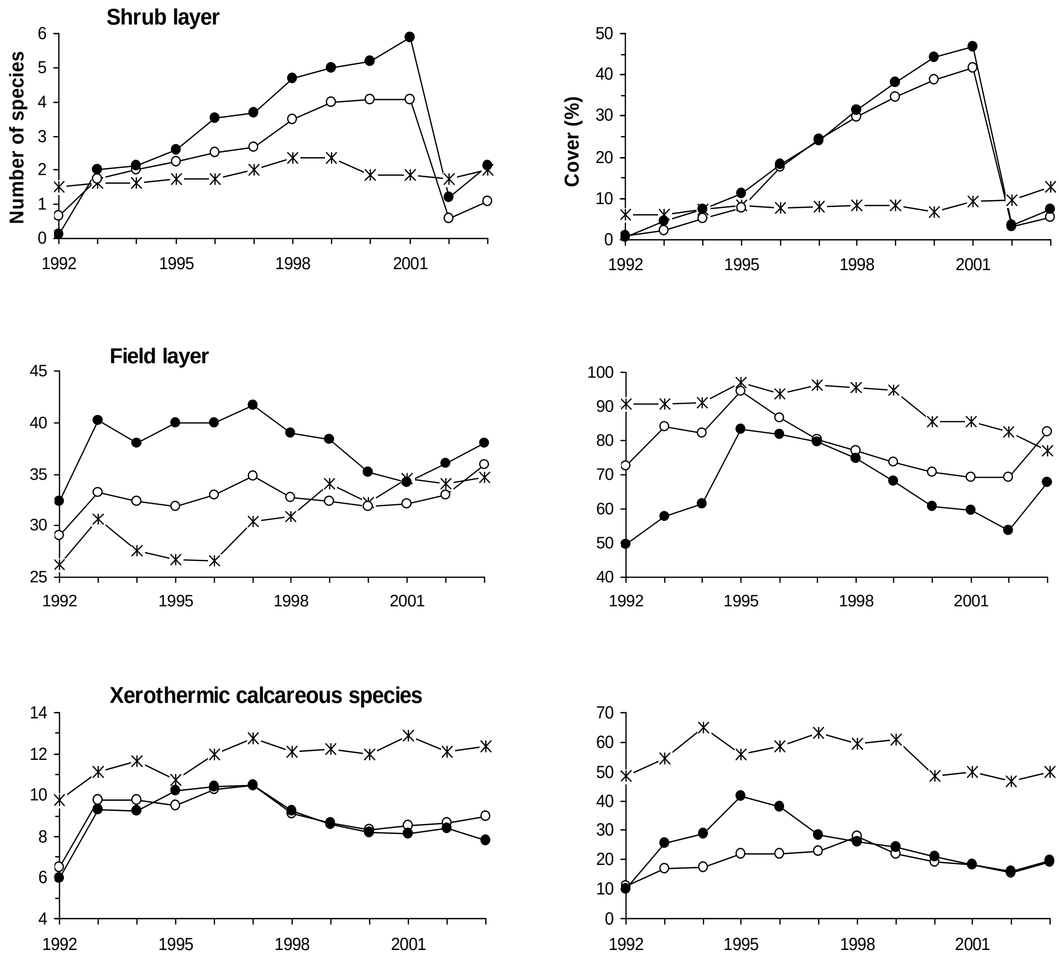

Fig. 3. Mean number and cover of species in shrub and field layers and of xerothermic calcareous species in the permanent plots on the old grassland (∗, 8 plots) and on the grasslands restored in the former open (○, 12 plots) and closed (●, 15 plots) woods, in the Skołczanka reserve close to Kraków, during 1992-2003. The reserve (36 ha) was established in 1957. In 1992 all trees and shrubs overgrew former grasslands were felled. They were cut again in 2002. After DZWONKO and LOSTER (2008).

Table 2. Factors and processes restricting species richness in abandoned calcareous grasslands. After DZWONKO and LOSTER (1998b).

Scale	Factors and processes	Direct causes	Conservation management
Landscape	Isolation	Poor dispersal ability of species	Protection of isolated populations. Sowing and reintroduction of plants.
Community	Transient and short-term persistent soil seed bank of many species.	Poor regeneration ability of many species.	Grazing under control. Mowing. Cutting of trees and shrubs.
	Dominance of tall grasses and forbs.	Reduction of light in lower layers of grassland. Suppression of plants with other growth forms.	
	Thick layer of litter.	Reduction of light near soil. Reduction of seed germination and growth of seedlings and runners.	
	Development of shrubs and trees.	Reduction of light. Suppression of plants with smaller growth forms.	

4. CONCLUSIONS

- Small remnants of ancient woodlands in an agricultural landscape are refuges of numerous woodland species. Therefore, the preservation of such woods carries great weight in the maintenance of local/regional species richness and the protection of woodland species.
- Ancient deciduous woodlands are, as a rule, significantly richer in woodland species than isolated recent woods and plantations because of poor dispersal ability of many woodland species.

- 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.
- The nature conservation value of woodlands can be easily assessed by means of ancient woodland plant species indicators.
- The disappearance of acidophilous species in mixed woodlands of southern Poland may result in a high degree from the cessation of traditional methods of management, above all regular litter removal.
- After abandonment semi-natural calcareous grasslands are overgrown by tall grasses and forbs as well as by shrubs and trees, in consequence, the species-rich communities with many regionally rare and endangered species are vanishing.
- Limited availability of seeds seems the principal reason for the weak regeneration of xerothermic calcareous grasslands.
- Periodical tree and shrub cutting, before their covers increase to about 30%, makes it possible to maintain a temporal-spatial mosaic of species-rich grassland-scrub communities in isolated habitats, and to preserve local species diversity.
- Cutting trees and shrubs in sites where most grassland species have already vanished, without additional managements supporting their dispersal, seedling recruitment and development, is not sufficient to restore calcareous grasslands rich in xerothermic species.

5. REFERENCES

BAKKER, J.P., MARRS, R.H., PAKEMAN, R.J. 2002. Long-term vegetation dynamics: Successional patterns and processes. Introduction. Appl. Veg. Sci. 5: 2–6.

BAKKER, J.P., OLFF, H., WILLEMS, J.H., ZOBEL, M. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? J. Veg. Sci. 7: 147–156.

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.

BEKKER, R.M., VERWEIJ, G.L., SMITH, R.E.N., REINE, R., BAKKER, J.P., SCHNEIDER, S. 1997. Soil seed banks in European grasslands: does land use affect regeneration perspectives? J. Appl. Ecol. 34: 1293–1310.

BOBBINK, R., HORNUNG, M., ROELOFS, J.G.M. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. J. Ecol. 86: 717–738.

BRUNET, J., FALKENGREN-GRERUP, U., RÜHLING, Å., TYLER, G. 1997. Regional differences in floristic change in South Swedish oak forests as related to soil chemistry and land use. J. Veg. Sci. 8: 329–336.

BRUNET, J., VON OHEIMB, G. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. J. Ecol. 86: 429–438.

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.

DOLEK, M., GEYER, A. 2002. Conserving biodiversity on calcareous grasslands in the Franconian Jura by grazing: a comprehensive approach. Biol. Conserv. 104: 351–360.

DUTOIT, T., ALARD, D. 1995. Permanent seed banks in chalk grassland under various management regimes: their role in the restoration of species-rich plant communities. Biodivers. Conserv. 4: 939–950.

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. Migration of vascular plant species to a recent wood adjoining ancien woodland. Acta Soc. Bot. Pol. 70: 71–77.

DZWONKO, Z. 2007. Przewodnik do badań fitosocjologicznych. Wydawnictwo Sorus, Instytut Botaniki UJ, Poznań, Kraków.

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., GAWROŃSKI, S. 2002. Effect of litter removal on species richness and acidification of a mixed oak-pine woodland. Biol. Conserv. 106: 389–398.

DZWONKO, Z., LOSTER, S. 1988. Species richness of small woodlands on the western Carpathian foothills. Vegetatio 76: 15–27.

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. 1992. Species richness and seed dispersal to secondary woods in southern Poland. J. Biogeogr. 19: 195–204.

DZWONKO, Z., LOSTER, S. 1998a. Dynamics of species richness and composition in a limestone grassland restored after tree cutting. J. Veg. Sci. 9: 387–394.

DZWONKO, Z., LOSTER, S. 1998b. Ochrona półnaturalnych muraw nawapiennych we współczesnym krajobrazie: dynamika roślinności po wycięciu drzew. Ochr. Przyr. 55: 3–23.

DZWONKO, Z., LOSTER, S. 2001. Wskaźnikowe gatunki roślin starych lasów i ich znaczenie dla ochrony przyrody i kartografii roślinności. IGiPZ PAN, Prace Geogr. 178: 120–132.

DZWONKO, Z., LOSTER, S. 2007. A functional analysis of vegetation dynamics in abandoned and restored limestone grasslands. J. Veg. Sci. 18: 203–212.

DZWONKO, Z., LOSTER, S. 2008. Changes in plant species composition in abandoned and restored limestone grasslands – the effects of tree and shrub cutting. Acta Soc. Bot. Pol. 77: 67–75.

ELLENBERG, H. 1988. Vegetation ecology of Central Europe. Cambridge University Press, Cambridge.

FALKENGREN-GRERUP, U. 1986. Soil acidification and vegetation changes in deciduous forest in southern Sweden. Oecologia 70: 339–347.

FANGMEIER, A., HADWIGER-FANGMEIER, A., VAN DER EERDEN, L., JÄGER, H-J. 1994. Effects of atmospheric ammonia on vegetation – a review. Env. Pollut. 86: 43–82.

GIBSON, C.W.D., WATT, T.A., BROWN, V.K. 1987. The use of sheep grazing to recreate species-rich grassland from abandoned arable land. Biol. Conserv. 42: 165–183.

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. Biol. Conserv. 91: 9–22.

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.

HUTCHINGS, M.J., BOOTH, K.D. 1996. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land .II. Germination and early survivorship of seedlings under different management regimes. J. Appl. Ecol. 33: 1182–1190.

JAKUBOWSKA-GABARA, J. 1993. Recesja zespołu świetlistej dąbrowy *Potentillo albae-Quercetum* Libb. 1933 w Polsce. Wydawnictwo Uniwersytetu Łódzkiego, Łódź.

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.

KAHMEN, S., POSCHLOD, P. 2004. Plant functional trait responses to grassland succession over 25 years. J. Veg. Sci. 15: 21–32.

KALAMEES, R. ZOBEL, M. 2002. The role of the seed bank in gap regeneration in a calcareous grassland community. Ecology 83: 1017–1025.

KARLÍK, P., POSCHLOD, P. 2009. History or abiotic filter: which is more important in determining the species composition of calcareous grasslands? Preslia 81: 321–340.

KORNAŚ, J. 1990. Jak i dlaczego giną nasze zespoły roślinne. Wiad. Bot. 34: 7–16.

KRUK, J., MILISAUSKAS, S. 1999. Rozkwit i upadek społeczeństw rolniczych neolitu. Instytut Archeologii i Etnologii PAN, Kraków.

MATLACK, G.R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75: 1491–1502.

MEDWECKA–KORNAŚ, A., GAWROŃSKI, S., 1990. The dieback of fir *Abies alba* Mill. and changes in the *Pino-Quercetum* stands in the Ojców National Park (Southern Poland). Vegetatio 87: 175–186.

MEDWECKA–KORNAŚ, A., KORNAŚ, J. 1966. Associations of steppes and dry grasslands. In: W. SZAFER (ed.), The vegetation of Poland. Pergamon Press, PWN, Oxford, Warszawa, pp. 361–377.

MICHALIK, S., ZARZYCKI, K. 1995. Management of xerothermic grasslands in Poland: botanical approach. Colloques Phytosoc. 24: 881–895.

MIKLASZEWSKI, J., 1928. Lasy i leśnictwo w Polsce. Nakładem Związku Zawodowego Leśników w Rzeczypospolitej Polskiej, Warszawa.

MOOG, D., POSCHLOD, P., KAHMEN, S., SCHREIBER, K-F. 2002. Comparison of species composition between different grassland management treatments after 25 years. Appl. Veg. Sci. 5: 99–106.

MORTIMER, S.R., HOLLIER, J.A., BROWN, V.K. 1998. Interactions between plant and insect diversity in the restoration of lowland calcareous grasslands in southern Britain. Appl. Veg. Sci 1: 101–114.

PEARSON, J., STEWART, G.R., 1993. Tansley Review No 56. The deposition of atmospheric ammonia and its effects on plants. New Phytol. 125: 283–305.

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.

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.

POSCHLOD P., BONN S. 1998. Changing dispersal processes in the central European landscape since the last ice age: an explanation for the actual decrease of plant species richness in different habitats? Acta Bot. Neerl. 47: 27–44.

POSCHLOD, P., KIEFER, S., TRÄNKLE, U., FISCHER, S., BONN, S. 1998. Plant species richness in calcareous grasslands as affected by dispersability in space and time. Appl. Veg. Sci. 1: 75–90.

POSCHLOD, P., BAKKER, J.P., KAHMEN, S. 2005. Changing land use and its impact on biodiversity. Basic Appl. Ecol. 6: 93–98.

STAMPFLI, A., ZEITER, M. 1999. Plant species decline due to abandonment of meadows cannot easily be reversed by mowing. A case study from the southern Alps. J. Veg. Sci. 10: 151–164.

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

TYLER, G. 1987. Probable effects of soil acidification and nitrogen deposition on the floristic composition of oak (*Quercus robur* L.) forest. Flora 179: 165–170.

VAN TOL, G., VAN DOBBEN, H.F., SCHMIDT, P., KLAP, J.M. 1998. Biodiversity of Dutch forest ecosystems as affected by recording groundwater levels and atmospheric deposition. Biodiv. and Conserv. 7: 221–228.

VERKAAR, H.J., SCHENKEVELD, A.J., VAN DE KLASHORST, M.P. 1983. The ecology of short-lived forbs in chalk grasslands: dispersal of seeds. New Phytol. 95: 335–344.

WALLISDEVRIES, M.F., POSCHLOD, P., WILLEMS, J.H. 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. Biol. Conserv. 104: 265–273.

WARD, L.K., JENNINGS, R.D. 1990. Succession of disturbed and undisturbed chalk grassland at Aston Rowant National Nature Reserve: dynamics of species changes. J. Appl. Ecol. 27: 897–912.

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.

WILLEMS, J.H. 1983. Species composition and above ground phytomass in chalk grassland with different management. Vegetatio 52: 171–180.

WILLEMS, J.H., BIK, L.P.M. 1998. Restoration of high species density in calcareous grassland: the role of seed rain and soil seed bank. Appl. Veg. Sci. 1: 91–100.

WULF, M. 1997. Plant species as indicators of ancient woodland in northwestern Germany. J. Veg. Sci. 8: 635–642.