CHANGES IN TYPOLOGICAL AND SPATIAL BOUNDARIES BETWEEN NEIGHBOURING COMMUNITIES OF *POTENTILLO ALBAE-QUERCETUM* AND *TILIO-CARPINETUM*

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ABSTRACT.

The sample area of 2.8 ha, divided into 100 m^2square quadrats, comprised two, distinguishable by traditional methods, oak forest patches and a fragment of a neighbouring mixed oak-hornbeam forest. The classification of quadrats was conducted by association analysis. Their identification and interpretation were performed on the basis of the systematic value and fraction of species of the characteristic oak forest combination in each distinguished quadrat group, as well as the range of distinguished communities. It appeared that due to the hornbeam invasion into the oak forest habitat, species forming the characteristic oak forest combination receded and the community area decreased. The data enabled reconstruction of the phases of oak forest recession. They corresponded to the successive phases of the encroachment of hornbeam undergrowth in the analysed area.

KEY WORDS: community recession, *Carpinus betulus* invasion, systematic value of a group of species.

INTRODUCTION

In the Białowieża Primeval Forest, *Potentillo albae-Quercetum* Libb. 1933 patches occur in the northern limits of its range. They form small-area communities, mostly neighbouring upon *Tilio-Carpinetum* Tracz. 1962 or *Pino-Quercetum* Kozł. 1925 phytocoenoses. They grow on the tops and southern slopes of morraine hills and kames i.e. in relatively warm and fertile, though occasionally dry habitats (Matuszkiewicz 1955).

Numerous observations and studies have shown that for the last thirty or so years the number of oak forest localities have decreased (Faliński 1968, 1986) and the size of their biochores has rapidly diminished (Kwiatkowska 1986). The reasons for this process have not so far been unequivocally explained. In the relevant literature, the lack of oak forest stability has been explained through different hypotheses concerning the genesis of oak forests in the Białowieża Primeval Forest. According to Paczoski (1926, 1927, 1930) and Faliński (1968, 1986) oak forests are natural communities which are relicts of the postglacial climatic optimum. In their opinion, directional changes in species composition indicate degeneration caused by improper human management (Faliński 1968, 1986).

Other researchers consider oak forests to be anthropogenic communities which are permanent only under conditions of cultivating oak in the habitats of mixed oak-hornbeam (further called hornbeam) and mixed pine forests (Karpiński 1949) or cattle grazing and high game density (W.Matuszkiewicz 1952, W. Matuszkiewicz and A. Matuszkiewicz 1956, A. Matuszkiewicz 1955, 1977). These authors hold that deceasing anthropopressure initiates regeneration in the community and itd transformation towards mixed pine or hornbeam forests.

In this author's opinion (Kwiatkowska 1986, Kwiatkowska and Wyszomirski 1988) the reduction in the number and frequency of species in a patch , as well as changes in the species combination and spatial structure of the ground layer are caused by *Carpinus betulus* invasion into oak forest habitats. Encroachment of hornbeam undergrowth must result in considerable deterioration of light conditions in the ground layer. This may be followed by the recession of thermo-and heliophilous oak forest species. The process should cause gradual extinction of the characteristic oak forest species combinations leading, in the long run, to the extinction of a locality.

The regression of *Potentillo albae-Quercetum* forest in the study area involves the following changes occurring in the transition zone between oak and oak-hornbeam forest stands: (1) changes in species compositions within an oak forest gradually invaded by *Carpinus betulus* undergrowth, (2) changes in the range and in the course of boundaries between the patches of the two types of forest communities, (3) increase in the width of a specific transition zone between well preserved fragments of *Potentillo albae-Quercetum* and *Tilio-Carpinetum* forests.

It is impossible to analyse the above processes directly. The course of oak forest regression as a process occurring in space and time can be reconstructed indirectly, and this is the main objective of the study. In this respect, it is necessary to: (1) distinguish locally typical forms of oak and oak-hornbeam forest communities, (2) grade typological differences in each part of the study area.

Kwiatkowska and Wyszomirski (1988, 1990) concluded that in advance of oak forest regression, the total species number decreased, and especially the characteristic combination of *Potentillo albae-Quercetum* species was deleted. Thus different stages of regression can be distinguished and ordered according to their sequence.

Transition zones and boundaries between different communities were most often delineated on the grounds of data collected from separated transects (e.g. Matuszkiewicz 1972, Falińska 1979). Such an approach makes it possible to determine strictly only chosen fragments of boundaries. In this study the arrangement of sample plots was intended to investigate the entire transition zone. Association analysis was used in order to distinguish forest types and to detect spatial boundaries based on objective, statistical criteria of significant interspecies association.

The objectives of this paper are:

(1) to distinguish the community types that correspond to typologically homogeneous quadrat groups and to describe them phytosociologically,

(2) to draw typological and spatial boundaries between neighbouring communities and successive phases,

(3) to reconstruct the old range of the oak forest and successive phases of community recession in the analysed area.

The investigations were conducted in the best-preserved and described phytocoenoses of *Potentillo albae-Quercetum* in the Białowieża Primeval Forest located in the Zwierzyniec forest district (A.Maruszkiewicz 1955, W.Matuszkiewicz and Wydrzycka 1972, Kwiatkowska 1972, 1984, 1986, Faliński 1986, Kwiatkowska and Wyszomirski 1988, 1990).

METHODS

The investigated area (2.8 ha) comprised two patches of an oak forest currently distinguishable by traditional methods and a fragment of a neighbouring hornbeam forest. It was composed of 20 neighbouring transects spreading from oak to oak-hornbeam forest stands sized 140 x 10 m, and divided into 280 square quadrats, each 100 m^2. In July, 1979 all of the species of vascular plants in the ground layer were listed in all of the quadrats.

The classifications of quadrats was done by association analysis (Williams and Lambert 1959, 1960). The maximum value of Chi-square sum was taken as a division criterion, calculated on the grounds of statistically significant (α=0.01) interspecific associations. Division was continued until homogeneous quadrat groups, i.e. those within which no significant associations occurred, were obtained (Williams and Lambert 1960). For quadrat groups containing more than 20 quadrats ($n \geq 20$) a species was ignored in association testing when its frequency was less than 5 or more than n = 5. In the analysed case the first three divisions corresponded to the map level, therefore their distribution was presented. The phytosociological description of quadrat groups which were distinguished in the first three divisions, was done on the grounds of their species composition and each species frequency was expressed in classes. The first frequency class (I) contained the rarest species i.e. those that occurred at most in 20 % of the quadrats in a group, the successive classes (II, III, IV, V) differed from each other by 20 %, respectively.

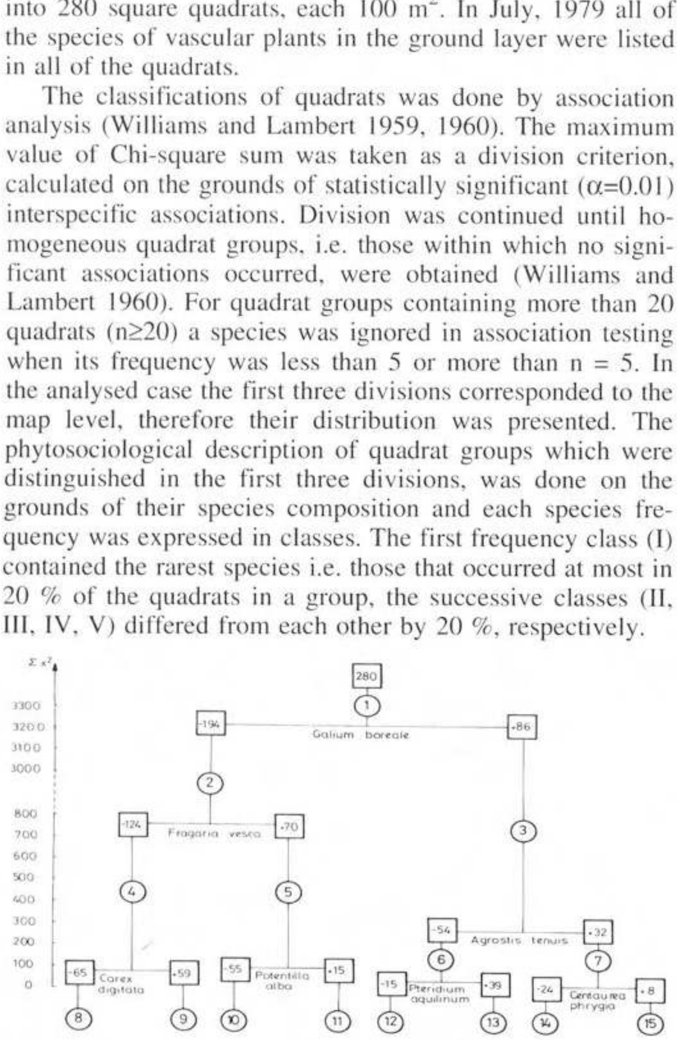

Fig. 1. Diagram of the first three divisions. The number of quadrats where a species was present (+) or absent (-) is given in squares, the number of the obtained quadrat group - in circles.

Interpretation of the quadrat groups was performed on the grounds of the fraction of characteristic-species of various syntaxonomic units taken after Matuszkiewicz (1981). The following species groups were distinguished: (1) wide forest species (character species of the class *Querco-Fagetea* Br.-Bl. et Vlieg. 1937), (2) hornbeam forest species (character-species of the order *Fagetalia* Pawł. 1928), (3) oak forest species (character-species of and differential for the order *Quercetalia pubescentis* Br.-Bl. 1931), (4) pine forest species (character-species of the class Vaccinio-Piceetea Br.-Bl. 1939), (5) species of thermophilous forest margins and xerothermic grasslands (character-species of the classes *Trifolio-Geranietea* Müll. 1962 and *Festuco-Brometea* Br.-Bl. et R.Tx. 1943), (6) meadow species (character-species of the class *Molinio-Arrhenatheretea* R.Tx. 1937). Each species fraction in each quadrat group of the third division was analysed using criteria of systematic value D calculated by Tüxen's and Ellenberg's (1937) method. Spatial variation of the number of species representing those groups was presented cartographically.

RESULTS

Association analysis showed that the third quadrat division was the last to give quadrat groups with a compact range. Quadrat groups with no significant interspecific associations were obtained only in the sixth or seventh division. These homogeneous quadrat groups had a small area, were not compact and were located randomly within the investigated area. Analysis was therefore limited to the first three divisions.

Galium boreale was the species with the highest Chi-square value in the first division. Its presence or absence divided the initial set of 280 quadrats (group 1) into two groups (groups 2 and 3, Fig. 1, Table 1). The floristic composition of group 2 (no *Galium boreale*) corresponded to a wide unit of *Tillo-Carpinetum* distinguished locally by the presence of *Lamiastrum galeobdolon*. The presence of *Galium boreale* was associated with the greater floristic richness of group 3. The character-species of the order *Quercetalia pubescentis* and those differential for it occurred here with a high frequency. These were: *Potentilla alba, Ranunculus polyanthemos, Primula veris,* as well as some thermo- and heliophilous species. The species combination corresponded to that of *Potentillo albae-Quercetum.* Both groups were compact and divided the investigated area into two parts: northen - that of the hornbeam forest, and southern - that of the oak forest (Fig.2).

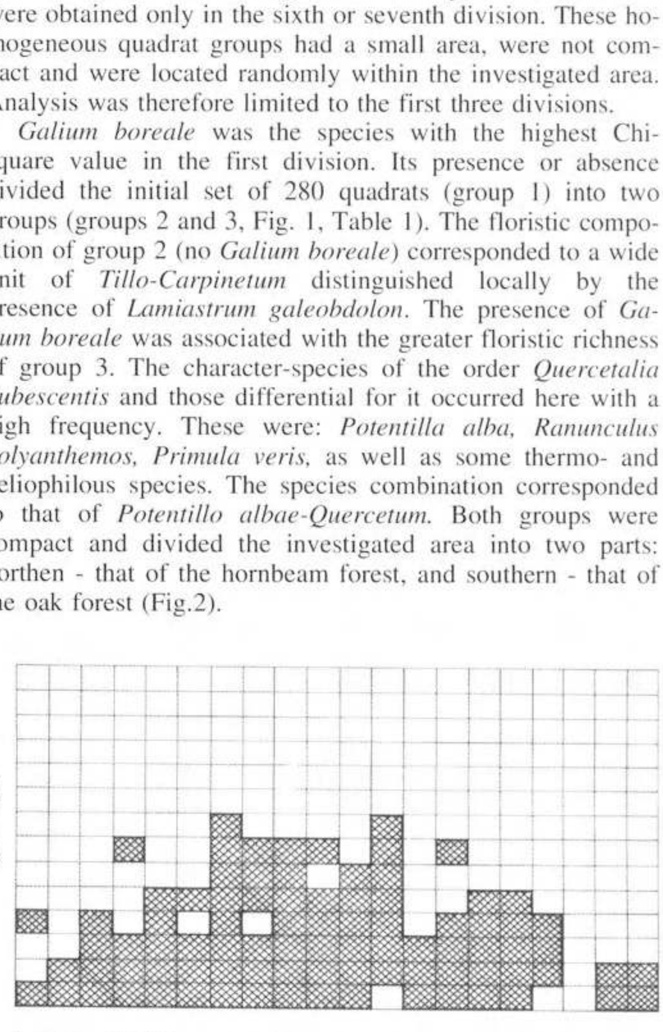

Fig. 2. Distribution of quadrat groups of the first division: 2 and 3 - group number.

TABLE 1. Differential species for quadrat groups of the first division

	Group number Number of quadrate	2 194	3 86
F	*Lamiastrum galeobdolon*	III	I
Q-F	*Carex digitata*	III	I
	Dryopteris carthusiana	I	
M-A	*Galium boreale*		V
	Fragaria vesca	I	V
	Veronica chamaedrys	III	V
T-G	*Clinopodium vulgare*	II	V
M-A	*Serratula tinctoria*	II	V
F	*Melampyrum nemorosum*	II	V
T-G	*Lathyrus niger*	II	IV
F	*Paris quadrifolia*	II	IV
V-P	*Trientalis europaea*	II	IV
Qp	*Potentilla alba*	I	IV
	Pteridium aquilinum	I	IV
V-P	*Vaccinium myrtillus*	I	IV
	Carex montana	I	IV
F-B	*Brachypodium pinnatum*	I	IV
F	*Dactylis polygama*	I	IV
	Hieracium umbellatum	I	III
Qp	*Ranunculus polyanthemos*	I	III
M-A	*Trollius europaeus*	I	III
	Skorzonera humilis	I	III
	Solidago virgauarea	I	III
	Potentilla erecta	I	III
Qp	*Primula veris*	I	III
M-A	*Ranunculus acris*	I	III
	Betonica officinalis	I	III
M-A	*Deschampsia cespitosa*	I	III
Qp	*Pulmonaria angustifolia*		I
Qp	*Vincentoxicum hirundinaria*		I
T-G	*Origanum vulgare*		I
T-G	*Trifolium alpestre*		I
M-A	*Bromus hordeaceus*		I
M-A	*Dactylis glomerata*		I
M-A	*Laserpitium prutenicum*		I
S-S	*Rumex acetosella*		I

Explanations:
Q-F a character-species of the class *Querco-Fagetea*
F a character-species of the order *Fagetalia*
Qp a character- and differential-species of the order *Quercetalia pubescetis*
V-P a character-species of the class *Vaccinio-Piceetea*
S-S a character-species of the class *Sedo-Scleranthetea*
T-G a character species of the class *Trifolio-Geranietea*
F-B a character-species of the class *Festuco-Brometea*
M-A a character-species of the class *Molinio-Arrhenatheretea*
2. *Tilio-Carpinetum* s.l.
3. *Potentillo albae-Quercetum* s.l.

The second stage of association analysis gave four quadrat groups. The hornbeam forest area was divided according to the occurrence of *Fragaria vesca*, that of the oak forest - according to *Agrostis tenuis* (Fig.1). In the majority of the former there was no *fragaria vesca* (group 4). This quadrat group represented a typical hornbeam forest with *Lamiastrum galeobdolon*. It occupied compact north-eastern and north-western fragments of the investigated area (Fig. 3, Table 2).

TABLE 2. Differential species for quadrat groups of the second division

	Group number Number of quadrats	4 124	5 60	6 54	7 32
	Monotropa hypopitys	III	I	I	
Q-F	*Carex digitata*	III	I	I	I
F	*Lamiastrum galeobdolon*	IV	II	I	I
F	*Galium odoratum*	III	II	II	I
	Dryopteris cathrusiana	I	I		
	Fragaria vesca		V	V	V
	Geranium sylvaticum	III	V	V	V
	Veronica chamaedrys	III	IV	V	V
T-G	*Campanula rapunculoides*	II	IV	IV	IV
	Malus sylvestris	II	IV	IV	III
V-P	*Trientalis europaea*	II	III	V	IV
T-G	*Polygonatum odoratum*	II	III	IV	III
Qp	*Lathyrus niger*	I	III	V	IV
F	*Melampyrum nemorosum*	I	III	IV	V
	Pteridium aquilinum	I	III	IV	III
	Torylis japonica	I	III	III	IV
	Thalictrum aquilegiifolium	I	III	III	III
	Galium aparine		I	I	I
	Hieracium lachenalii		I	I	I
Qp	*Hypericum montanum*		I	I	I
	Hypochoeris maculata		I	I	I
Qp	*Digitalis grandiflora*		I	I	II
	Hypericum maculatum		I	I	II
M-A	*Galium boreale*			V	V
M-A	*Serratula tinctoria*	I	III	V	V
V-P	*Vaccinium myrtillus*	I	II	IV	V
Qp	*Potentilla alba*		II	IV	V
F	*Dactylis polygama*	I	II	III	V
	Betonica officinalis	I	II	III	IV
	Scorzonera humilis	I	II	III	III
M-A	*Trolius europaeus*	I	II	III	III
	Carex montana	I	I	IV	IV
F-B	*Brachypodium pinnatum*	I	I	III	IV
	Potentilla erecta		I	III	IV
M-A	*Rannunculus acris*	I	I	III	IV
Qp	*Rannunculus polyanthemos*		I	III	IV
M-A	*Laserpitium prutenicum*			I	I
S-S	*Rumex acetosella*			I	I
	Stelaria media			I	I
M-A	*Bromus hordeaceus*			I	II
	Centaurea phrygia			I	II
M-A	*Dactylis glomerata*			I	II
T-G	*Origanum vulgare*			I	II
T-G	*Trifolium alpestre*			I	II
	Agrostis tenuis	I	I		V
	Hieracium umbellatum		I	III	V
M-A	*Deschampsia cespitosa*	I	I	II	IV
Qp	*Primula veris*		I	II	IV
	Solidago virgaurea	I	I	II	III
M-A	*Vicia cracca*	I	I	II	III
	Lupinus polyphyllus		I	I	IV
	Peucedanum oreoselinum		I	I	IV
T-G	*Astragalus glycophyllos*		I	I	III
T-G	*Trifolium repens*				II

Explanations: Symbols as in Table 1
4. *Tilio-Carpinetum* with *Lamiastrum galeobdolon*
5. *Tilio-Carpinetum* transient form with *Fragaria vesca*
6. *Potentillo albae-Quercetum* poor transient form
7. *Potentillo albae-Quercetum* rich form

The hornbeam forest with *Fragaria vesca* (group 5) showed a high affinity with an oak forest in the presence of such species as *Lathyrus niger*, *Campanula rapunculoides*, *Polygonatum odoratum*, and *Pteridium aquilinum* (Table 2). This particular fragment of a hornbeam forest formed the transient typological and spatial zone between its typical form and the oak forest (Fig. 3).

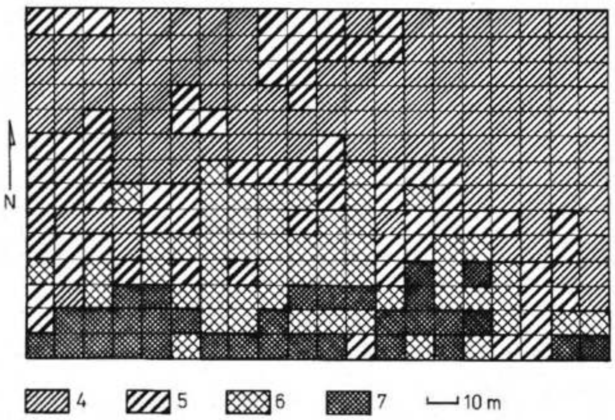

Fig. 3. Distribution of quadrat groups of the second division: 4, 5, 6, 7 - group numbers.

The second division of the oak forest permitted distinction of two forms: the first floristically poorer (group 6), the second floristically richer (group 7) with *Agrostis tenuis* and a higher fraction of non-forest heliophilous species such as *Peucedanum oreoselinum*, *Solidago virgaurea* and *Vicia cracca*. The poorer part of oak forest lay between the hornbeam forest with *Fragaria vesca* and the richer oak forest with *Agrostis tenuis*. Fig. 3 and Table 2 show the regular zonation of transient communities in the contact zone between the hornbeam and oak forests.

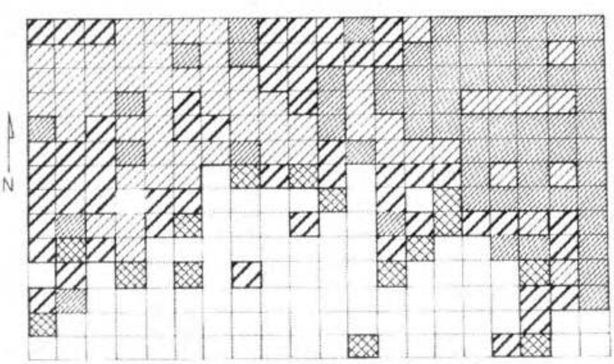

Fig. 4. Distribution of quadrat groups of the third division within the mixed deciduous forest: 8, 9, 10, 11 - group numbers.

The third stage of association analysis gave further divisions of all of the groups distinguished earlier (Figs. 1, 4, 5). Division of the typical hornbeam forest made it possible to distinguish two groups (8 and 9). The small floristic differences between them resulted from inner-community variation. Group 8 in the north-eastern part was characterized by a high occurrence of *Acer platanoides* seedlings, whereas group 9 in the north-western part was distinguished by a high frequency of *Carex digitata* (Fig. 4, Table 3). Both groups differed from all of the others in their considerably higher

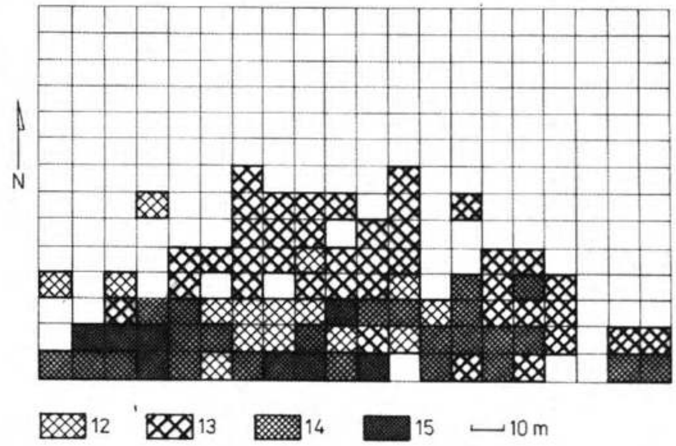

Fig. 5. Distribution of quadrat groups of the third division within the oak forest: 12, 13, 14, 15 - group numbers.

proportion of forest species from the class *Querco-Fagetea* and order *Fagetalia* (Fig. 6). The detailed results obtained in the third division better describe the contact zone between the hornbeam and oak forests in terms of their transient forms. The transient zone, distinguished by the presence of *Fragaria vesca* was divided into the community of transient hornabeam forest (group 10) enriched in helio- and thermophilous species from the classes *Trifolio-Geranietea* and *Festuco-Brometea*, as well as into the oak forest with *Potentilla alba* (group 11), floristically poorer in the margin of its biochore (Fig. 6, Table 3).

The oak forest area was divided into four quadrat groups: 12, 13, 14 and 15 (Figs. 1 and 5). The proportion of wide forest species and those of hornbeam forests gradually decreased within groups, whereas the proportion of species of pine forests, those of meadows, grasslands, and forest margins i.e. forming the characteristic species combination of *Potentillo albae-Quercetum*, increased (Fig. 6).

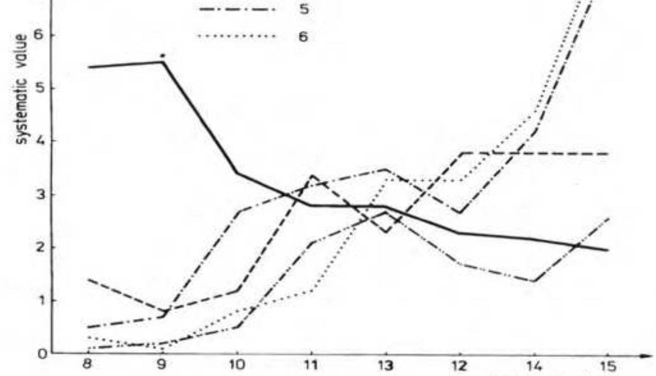

Fig. 6. Systematic values of species groups:
1 - *Querco-Fagetea*, 2 - *Fagetalia*, 3 - *Quercetalia pubescentis*, 4 - *Vaccinio-Piceetea* + *Sedo-Scleranthetea*, 5 - *Trifolio-Geranietea* + *Festuco-Brometea*, 6 - *Molinio-Arrhenatheretea*.

TABLE 3. Floristic composition of quadrat groups of the third division

	Group number	8	9	10	11	13	12	14	15
	Number of quadrats	65	59	55	15	39	15	24	8
	Mean species number per 100 m^2	25	24	34	44	46	41	52	59
	Standard deviation	5	4	6	7	6	7	7	9
Q-F	*Acer platanoides*	V	III	III	II	III	II	II	II
F	*Lamiastrum galeobdolon*	IV	III	II	I	I			
F	*Galium odoratum*	III	IV	II		II	II	I	
	Monotropa hypopitys	II	III	I	I	I	I		
Q-F	*Carex digitata*		V	II	II	I	I	I	
	Dryopteris carthusiana	I	I	I	I	I			
	Betula pubescens	I	I	I	I	I			
Q-F	*Euonymus verrucosa*	I	I	I	I	I			
Q-F	*Corylus avellana*	I	I	I		I			
F	*Ranunculus lanuginosus*	IV	IV	V	III	IV	II	III	II
F	*Daphne mezereum*	IV	IV	V	IV	IV	III	IV	II
	Calamagrostis arundinacea	III	V	V	V	V	V	V	V
	Veronica chamaedrys	III	IV	IV	IV	IV	V	V	V
F	*Lilium martagon*	II	IV	IV	IV	IV	V	IV	IV
Qp	*Melittis melissophyllum*	IV	III	V	V	V	V	V	V
	Geranium sylvaticum	III	III	V	V	V	V	V	V
	Malus sylvestris	II	III	IV	IV	IV	III	IV	V
	Vicia sepium	II	III	IV	IV	IV	IV	IV	IV
T-G	*Campanula rapunculoides*	II	II	IV	V	IV	III	IV	V
T-G	*Clinopodium vulgare*	I	II	IV	V	V	V	V	V
	Fragaria vesca			V	V	V	V	V	V
T-G	*Lathyrus niger*	I	I	III	IV	V	III	IV	IV
F	*Melampyrum nemorosum*	I	I	III	V	IV	V	V	V
M-A	*Serratula tinctoria*	I	I	III	V	V	V	V	V
V-P	*Trientalis europaea*	I	II	III	V	V	IV	IV	IV
	Torilis japonica		I	III	III	III	III	IV	IV
T-G	*Anthericum ramosum*			I	I	I	I	I	I
	Betonica officinalis	I	I	I	IV	III	II		V
Qp	*Potentilla alba*				V	IV	III	V	V
	Hieracium umbellatum				II	IV	II	V	V
M-A	*Ranunculus acris*	I		I	III	II	II	IV	IV
F	*Dactylis polygama*	I	I	I	III	III	III	V	V
	Carex montana		I	I	III	IV	IV	IV	IV
V-P	*Vaccinium myrtillus*	I	I	II	III	IV	IV	V	IV
	Scorzonera humilis	I		I	III	III	II	III	III
	Hypochoeris maculata				I	I	I	I	II
	Hieracium lachenalii				I	I	I	I	I
Qp	*Digitalis grandiflora*				I	I	I	I	I
M-A	*Galium boreale*					V	V	V	V
F-B	*Brachypodium pinnatum*	I	I	I	I	III	III	IV	IV
	Potentilla erecta			I	II	III	IV	IV	IV
T-G	*Trifolium alpestre*					I	I	II	II
	Pteridium aquilinum	I		II	IV	V		III	III
Qp	*Ranunculus polyanthemos*		I	I	II		III	IV	IV
M-A	*Trolius europaeus*	I	I	II	I	I	III	III	IV
M-A	*Bromus hordeaceus*						I	I	II
	Stellaria media						I	I	II
	Athyrium filix-femina	I	I	I		I		IV	
	Agrostis tenuis	I		I	II			V	V
	Solidago virgaurea	I	I	I	II	II	II	IV	IV
	Deschampsia cespitosa	I	I	I	I	II	II	IV	IV
	Peucedanum oreoselinum			I	I	I	II	IV	IV
T-G	*Astragalus glycyphyllos*				I	II	I	III	III
M-A	*Vicia cracca*	I	I	I	I	I	II	III	IV
	Centaurea phrygia					I	I		V
Qp	*Primula veris*				II	II	II	II	V
	Genista tinctoria				I	I	I	II	V
	Hypericum maculatum				I	I	I	II	V
F	*Galium schultesii*			I	I	I	II	II	IV
M-A	*Dactylis glomerata*						II	I	IV
T-G	*Trifolium medium*				I	I	I	II	IV
T-G	*Origanum vulgare*					I	I	I	IV
M-A	*Trifolium repens*							I	IV
V-P	*Pyrola minor*		I	I					IV
Qp	*Vincetoxicum hirundinaria*					I	I	II	III
S-S	*Rumex acetosella*						I	I	III
Qp	*Pulmonaria angustifolia*					I	I	I	III
Q-F	*Hepatica nobilis*	V	V	V	V	V	V	V	V
	Maianthemum bifolium	V	V	V	V	V	V	V	V
	Quercus robur	V	V	V	V	V	V	V	V
Q-F	*Melica nutans*	V	V	V	V	V	V	V	V
F	*Stellaria holostea*	V	V	V	V	V	V	V	V
F	*Carpinus betulus*	V	IV	V	V	V	V	V	V
	Ajuga reptans	IV	V	V	V	IV	V	V	V
	Convallaria majalis	IV	V	V	V	V	V	V	V
F	*Milium effusum*	V	V	V	V	IV	V	IV	IV
	Rubus saxatilis	V	IV	V	V	IV	V	V	IV
	Galeopsis tetrahit	IV	II	IV	IV	III	IV	IV	V
	Oxalis acetosella	IV	III	IV	II	II	III	III	II
F	*Sanicula europaea*	IV	II	III	IV	III	IV	III	III
	Moehringia trinervia	IV	IV	V	IV	III	IV	IV	V
	Urtica dioica	IV	IV	V	V	V	V	V	IV
	Polygonatum odoratum	I	II	III	III	III	IV	IV	V
F	*Festuca gigantea*	II	II	III	III	I	II	II	III
	Thalictrum aquilegiifolium	II	I	II	III	III	III	III	III
Qp	*Campanula persicifolia*	I	I	II	II	III	I	II	II
Q-F	*Campanula trachelium*	I	I	I	I	I	II	I	
F	*Phyteuma spicatum*	I	I	I	II	II	II	III	II
	Platanthera bifolia	I	I	II	I	I	II	I	II
Q-F	*Poa nemoralis*	I	I	I	I	I	II	II	II
Q-F	*Ranunculus auricomus*	I	I	II	II	I	I	II	
F	*Scrophularia nodosa*	I	I	I	I	I	I	I	II
	Sorbus aucuparia	I	I	I	II	I	II	III	III
	Veronica officinalis	I	I	I	II	I	I	II	III
	Taraxacum officinale	I	I	I	I	I		II	II
F	*Tilia cordata*	II	III	III	II	I	II	II	II
T-G	*Vicia sylvatica*	I	I	II	I	I	I	II	
	Aquilegia vulgaris	I		I	II	I	II	II	II
M-A	*Angelica sylvestris*	II	I	II	I	I	I		
F	*Asarum europaeum*	I	I	I	I	II	II	I	
F	*Epilobium montanum*	I	I	I	I	I	II	III	II
V-P	*Picea abies*	I	I	I	I	I	III	I	I
	Lapsana communis	I	I	I	II		I	II	III
	Viburnum opulus	I	I	I	I	I	I		I
	Lupinus polyphyllus			I	I	III	I	III	I
	Populus tremula	I	I	I	I		I	I	I
	Lathyrus laevigatus	I	I	I				I	I
	Ranunculus repens	I	I	I				I	I
M-A	*Succisa pratensis*			I	I	I	I	II	II
	Viola mirabilis	II	II	I	I		II	II	
T-G	*Galium molugo*	I				I	I	II	II
T-G	*Agrimonia procera*				I	I	I	I	II
	Betula pendula	I	I	I		I			I
F-B	*Campanula glomerata*				I			II	I
	Poa angustifolia				I		I	II	II
	Prunella vulgaris					I		II	II
F	*Carex sylvatica*			I				II	I
M-A	*Laserpitium prutenicum*					I	I	II	
	Galium aparine			I	I	I		I	
F	*Neottia nidus-avis*	I		I	I	I	II		
F	*Paris quadrifolia*	I	I	I				I	
	Plantago major				I			I	II

Explanations: Symbols as in Table 1 – 8. *Tilio-Carpinetum* form with *Lamiastrum galeobdolon - Acer platanoides*; 9. *Tilio-Carpinetum* form with *Lamiastrum galeobdolon - Carex digitata*; 10. *Tilio-Carpinetum* transient from with *Fragaria vesca*; 11. *Potentillo albae-Quercetum* poor transient form; 13. **Potentillo albae-Quercetum* the first regression stage, facies nuda; 12. *Potentillo albae-Quercetum* the second regression stage, facies with *Carpinus*; 14. *Potentillo albae-Quercetum* form with *Athyrium filix-femina*; 15. *Potentillo albae-Quercetum* form with *Origanum vulgare*.

*Numbers of quadrat groups according to the rules of division, group order in the table corresponds to their spatial sequence Only those rare species (class I of frequency) which occurred in at least five of the distinguished groups are given in the table.

The oak forest with *Pteridium aquilinum* (group 13) was adjacent to the hornbeam forest and was characterized by the penetration of species from the order *Fagetalia*, such as *Ranunculus lanuginosus*. The ground layer cover was negligible here (*Fracies nuda*, Fig. 5, Table 3).

In group 12 (no *Pteridium aquilinum*) the proportion of hornbeam forest species considerably decreased (Fig. 6). Only the hornbeam undergrowth was fairly abundant (facies with *Carpinus betulus* b/c). Some species differential for oak forests occurrred also, such as *Ranunculus polyanthemos*, *Trollius europaeus*, *Bromus hordaceus*.

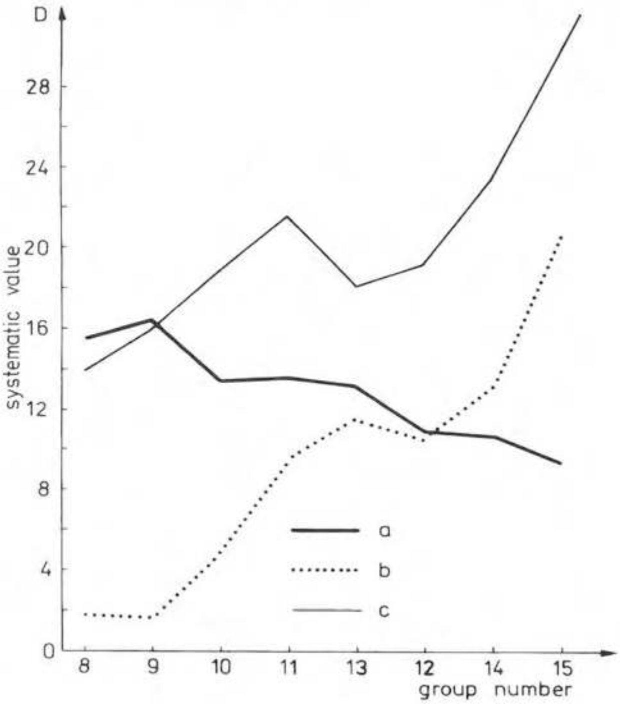

Fig. 7. Systematic values of species groups (a, b, c). Group a consists of character-species of the *Fagetalia and Querco-Fagetea;* group b consists of character-species of the *Quercetalia pubescentis*, *Vaccinio-Piceetea*, *Sedo-Scleranthetea*, *Trifolio-Geranietea*, *Festuco-Brometea*, and *Molinio-Arrhenatheretea*; group c - companion species.

Two groups into which the quadrats of the oak forest with *Agrostis tenuis* were divided, represented a typical *Potentillo albae-Quercetum* association. They were distinguished by the prevalence of species of oak forests over those of hornbeam forests and wide forest species (Fig. 7). The compact range of these groups covered that of physiognomically distinguishable patches of the oak forest. Group 14 (no *Centaurea phrygia*) lacked many meadow and grassland species, but was characterized by a high frequency of *Athyrium filix-femina* (Table 3). Group 15 was distinguished by the presence of many species from the classes *Molinio-Arrhenatheretea* and *Trifolio-Geranietea*, such as *Dactylis glomerata*, *Origanum vulgare*, *Trifolium medium* (Fig. 6, Table 3). *Potentillo albae-Quercetum* with *Athyrium filix-femina* (group 14) and that with *Origanum vulgare* (group 15) are known to be forms of the same association differing in the light conditions of the ground layer.

In general, the differences between the groups distinguished within the oak forest were quantitative and lay in a southwardly increasing proportion of species forming the characteristic species combination of *Potentillo albae-Quercetum*. Typological transition between groups was relatively fluent and occurred through changes in species frequency in a particular part of the investigated area.

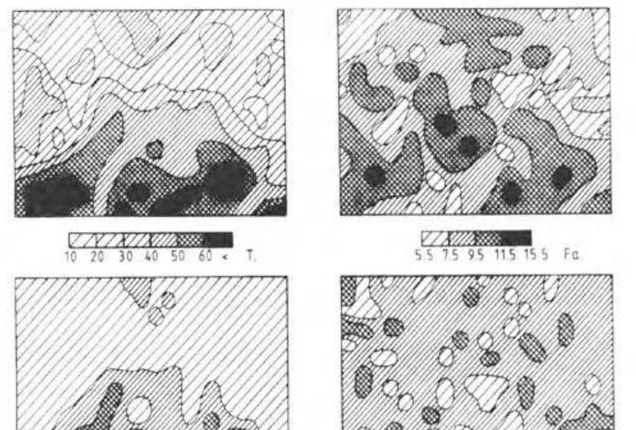

Fig. 8. Spatial variation of the species number. T - total, Character - species of: F. - *Fagetalia*, Q.F. - *Querco-Fagetea*, Q.p - *Quercetalia pubescentis*, V.P. - *Vaccinio-Piceetea*, T.G.+F.B. - *Trifolio Geranietea* + *Festuco-Brometea*, M.A. - *Molinio-Arrhenatheretea*, R - remaining species

The heterogeneity of the study area reflecting the spatial variability of the total number of species, as well as the number of species from the order *Quercetalia pubescentis* and from the classes *Vaccinio-Piceetea*. *Trifolio-Geranietea*, *Festuco-Brometea*, and *Molinio-Arrhenatheretea* corresponded to the results of association analysis (Fig. 8).

Two parts were easily distinguishable within the study area: the northern part where the number of species per 100 m^2 did not exceed 30, and the southern part, richer in plant species. The occurrence of thermophilous and heliophilous species was, almost completely, restricted to the southern part.

Spatial variability of the species was not accidental, but related to recession of *Potentillo albae-Quercetum*. This process was accompanied by a gradual change in the average number of species por 100 m^2: from 40 to 50 in the oldest phase of recession, through 50-60 and up to more than 60 in the still existing patches.

DISCUSSION

Patches of vegetation in the investigated area are differentiated and identified on the basis of the presented results. The distinguished communities can be classified into taxa of various, usually low, syntaxonomic rank. the typological boundary of the first magnitude obtained in the first division of association analysis delineates two associations, *Tilio-Carpinetum* and *Potentillo albae-Quercetum*. In the field it corresponds to the old, spatially non-existent, boundary between patches of the oak and hornbeam forests. From analysis of the systematic value of groups of species forming the characteristic combination of oak forests it is inferred that the proportion of oak forest (especially thermo- and heliophilous) species increases towards the old boundary of the oak forest. The north part of the oak forest neighbouring on the hornbeam forest is characterized by a less diversified floristic composition and low cover of the ground layer (Kwiatkowska 1986). The occurrence of the belt of "no-man's-land" that delineates the old oak forest range is a characteristic phenomenon in the analysed area. Its cover is minimal (ca. 0.5 %). The forest community in the southern, sunniest part of the investigated area is most fully characterized.

Further divisions by association analysis revealed the peculiar nature of the transient zone between the oak and hornbeam forests both in its typological and spatial respect. Literature data show that in the transient zone between two forest communities, the extinction of species of one community is accompanied by an increase in the proportion of species of another community (Traczyk 1960, Matuszkiewicz 1972, Falińska 1978, 1979). In central Poland in the contact zone between the communities of oak and hornbeam forests, a higher number of species than in each of the phytocoenoses has been found (Matuszkiewicz 1972). It is worth noting that an increase in species richness in ecotones is almost an ecological rule, long and frequently discussed (Barick 1950, Falińska 1979). In the contact zone betwenn the studied phytocoenoses, the effect described above does not take place. The extinction of oak forest species is not accompanied by an increase in the number of hornbeam forest species. It might be expected, due to invasion of hornbeam undergrowth into the oak forest, that: (1) heliophilous oak forest species would recess, (2) characteristic combination of oak forest species would disappear in the biochore margins i.e. oak forest patches would become reduced, (3) species of hornbeam forests would follow a hornbeam and the boundary of *Tilio-Carpinetum* would shift into the oak forest area. From the obtained data it may be inferred that only the first two processes are taking place. Species of hornbeam forests are not entering the oak forest habitats, the area occupied by them is not increasing. In the zone where characteristic *Potentillo albae-Quercetum* species combination has recessed, even wide forest species common to both communities do not disperse. Therefore, the oak forest recession is being accompanied by the opposing phenomenon - a considerable decrease in the number of species leading on to the facies nuda.

The distribution and phytosociological characteristics of the distinguished patches, as well as the data on the spatial variation of density and size structure of the hornbeam populations (Falińska 1986, Kwiatkowska and Wyszomirski 1988) enable reconstruction of three successive phases of recession of the oak forest in the analysed area (Fig. 9). The initial biochore of the oak forest was probably the area of

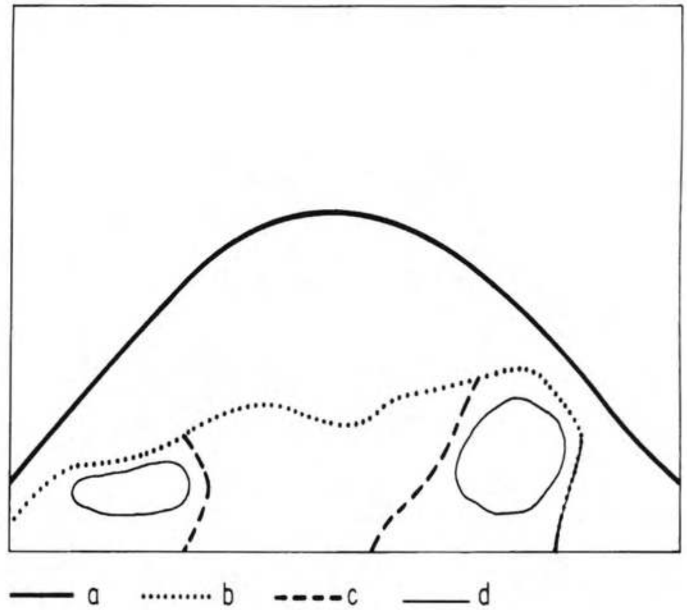

Fig. 9. Successive stages of the oak forest recession.Boundary of the: a - initial biochore, b - biochore in the second stage of recession, c - biochore in the third stage of recession, d - present biochore.

groups: 11, 12, 13, 14, and 15. The boundary between the two analysed communities went along the transient zone - now the area of group 5 (Kwiatkowska 1986). The recession of species of the characteristic oak forest combination most likely started in the northernmost margin of the initial biochore which corresponds to the range of group 13. On the second phase the range of the oak forest was reduced by almost a half. It is delineated by groups 12, 14 and 15. The last phase of recession of the community so far was caused by the encroachment of the hornbeam undergrowth into the shrub layer in the central part of the biochore (group 12). The range of the oak forest, previously compact, was then divided into two separate parts. Currently, the oak forest is limited to two patches in the south-eastern and south-western parts of the investigated area. Both patches are characterized by relatively well-preserved *Potentillo albae-Quercetum* characteristic species combination (group 14 and 15).

From the obtained results it may be inferred that the diminution of the oak forest patches is the result of hornbeam invasion into the oak forest habitat, but the area of the hornbeam forest does not concomitantly increase. At the present stage the community in the old contact zone may be interpreted as a highly impoverished from of *Potentillo albae-Quercetum*.

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ZMIANY TYPOLOGICZNYCH I PRZESTRZENNYCH GRANIC MIĘDZY SĄSIADUJĄCYMI ZBIOROWISKAMI *POTENTILLO ALBAE-QUERCETUM* I *TILIO-CARPINETUM*

STRESZCZENIE

Badania przeprowadzono na powierzchni badawczej Białowieskiej Stacji Geobotanicznej obejmującej fragment grądu (*Tilio-Carpinetum*) oraz dwa wyróżniające się fizjonomicznie płaty świetlistej dąbrowy (*Potentillo albae-Quercetum*).

Zróżnicowanie typologiczne i dynamiczne badanego obszaru dobrze odzwierciedla zmienność przestrzenna liczby wszystkich gatunków roślin naczyniowych oraz gatunków "dąbrowowych" z rzędu *Quercetalia pubescentis* i klas *Vaccinio-Piceetea, Trifolio-Geranietea, Festuco-Brometea* i *Molinio-Arrhenatheretea.* Wyróżnia się część powierzchni, gdzie liczba gatunków na 100 m^2 nie przekracza 30 oraz część bogata gatunkowo. Występowanie termo- i heliofilnych gatunków dąbrowowych jest ograniczone praktycznie wyłącznie do części drugiej. Zmienność przestrzenna liczby tych gatunków jest skorelowana z procesem regresji. W "starej fazie" regresji liczba gatunków na 100 m^2 waha się od 40 do 50, w młodszej fazie od 50 do 60, a w istniejących jeszcze płatach dąbrowy przekracza 60. Uzyskane wyniki pozwoliły na zrekonstruowanie pierwotnego zasięgu dąbrowy i kolejnych faz regresji (Fig.9).

SŁOWA KLUCZOWE: recesja zbiorowiska, inwazja *Carpinus betulus*, wartość systematyczna grupy gatunków