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Anna Justyna KWIATKOWSKA

Department of Phytosociology and Plant Ecology, Institute of Botany,
Warsaw University, Al. Ujazdowskie 4, 00–478 Warsaw, Poland

RECONSTRUCTION OF THE OLD RANGE AND THE PRESENT-DAY BOUNDARY OF A POTENTILLO ALBAE-QUERCETUM (LIBB.) 1933 PHYTOCOENOSIS IN THE BIAŁOWIEŻA PRIMAЕVAL FOREST LANDSCAPE

ABSTRACT: An analysis has been carried out of the typological and spatial boundaries between deciduous forest communities of the Potentillo albae-Quercetum and Tilio-Carpinetum types, and the old range has been reconstructed of a selected oak wood in the Białowieża Primaеval Forest. It has been demonstrated that the encroachment of *Carpinus betulus* undergrowth causes thermo- and heliophilous species to retreat, which leads on to the decline of the oak-wood composition of species at the biochore edges and shrinking of the oak-wood area. This process may be the cause of the disappearance of oak-wood sites in north-eastern Poland.

KEY WORDS: Potentillo albae-Quercetum, biochore boundaries, spatial continuum of vegetation, temporal continuum of vegetation.

1. INTRODUCTION

In north-eastern Poland, small-area Potentillo albae-Quercetum communities occupy medium-rich, relatively dry habitats usually on table-like tops and southern slopes of moraine and kame hills. In the Białowieża Primaеval Forest, the total area of oak woods shrinks incessantly (F a l i ń s k i 1968, 1977), but the causes have not so far been established of the decrease in number of sites and biochore area, as well as of the relatively low stability of the oak woods. These phenomena can be explained in different ways, depending on the accepted concept of their origin.

According to P a c z o s k i (1930) and F a l i ń s k i (1968, 1977), Białowieża Forest oak woods are natural climax communities representing relics of a warmer climatic period, whereas directional changes in the dominance structure and species

composition are signs of degradation processes caused by the activity of man. Disregard of the distinctness of the habitats of this community on the part of the forest management is the main cause of the disappearance of oak woods from the Białowieża Primaevial Forest landscape (F a l i ń s k i 1968, 1977).

According to K a r p i ń s k i (1949), M a t u s z k i e w i c z (1955, 1976) and M a t u s z k i e w i c z (1981), the present areas of occurrence of oak woods in north-eastern Poland are outside their natural range, and the development and survival of these communities depend on the type of forest management applied by man. M a t u s z k i e w i c z (1981) clearly states that in the north-eastern part of Poland *Potentillo albae-Quercetum* often represents a secondary, anthropo-zoogenic community, replacing the most fertile mixed oak-pine forests, or thermophilous forms of poorer oak-hornbeam forests, as a result of the favouring of the oak (and in oak-hornbeam habitats – also of the pine), removal of the undergrowth, and extensive, until not long ago, cattle grazing in the woods.

It appears that the same dynamic processes going on in *Potentillo albae-Quercetum* type of phytocoenoses are given contradictory interpretations: on the one hand as a sign of degenerative processes, and on the other – as community regeneration. The difficulty to give an unequivocal interpretation results also from the fact that in the Białowieża Forest landscape oak woods usually border upon oak-hornbeam forests (*Tilio-Carpinetum* Tracz. 1962), less often on mixed oak-pine forests (*Pino-Quercetum* Kozł. 1925 em. Mat. et Polak. 1955), which favours the penetration of species from neighbouring phytocoenoses.

In the relevant literature information can be found about oak wood transformation into mixed oak-pine or oak-hornbeam forests, and about the shrinking of oak-wood biochores (K a r p i ń s k i 1949, M a t u s z k i e w i c z 1955). The data indicate dynamic relationships between these communities. Similar problems appear in the field of typology; for there exist transitional syntaxonomical stages between thermophilous oak-hornbeam forests, rich oak-pine mixed forests and oak woods.

In the case of oak-wood communities all the above-mentioned problems relating to the temporal, spatial and typological continuum are exceptionally significant. It may be expected that near the limit of its range, a community, restricted to a small number of habitats, would be more labile than other communities. For this reason, the problem of typological and spatial boundaries between the communities found in the Białowieża Primaevial Forest landscape becomes particularly important.

The aim of the study presented in this paper was to distinguish the present typological and spatial boundaries between the oak-hornbeam and oak-wood phytocoenoses, and to reconstruct the old spatial boundary between both systems. Hypothetically, hornbeam undergrowth encroachment upon oak-wood biochore margins has been considered to be the main cause of the decrease of the biochore, because this undergrowth reduces the influx of light to the herb layer. A radical change in the microclimatic conditions (primarily the light and thermic conditions) may cause further changes in the dominance structure and species composition.

The study was carried out in 1981 in an area where the occurrence of *Potentillo*

albae-Quercetum communities had been documented in 1955 and 1972 (Matuszkiewicz 1955, Matuszkiewicz and Matuszkiewicz 1956, Kwiatkowska 1972).

2. STUDY OBJECT AND METHODS

2.1. DESCRIPTION OF THE STUDY AREA AND MATERIAL COLLECTING METHOD

The area under study was located in a deciduous forest, mainly consisting of *Quercus robur* L. and *Carpinus betulus* L., with a low contribution of *Tilia cordata* Mill. and *Picea abies* (L.) Karsten. Physiognomically, oak-wood patches are distinguishable due to a considerable proportion of the oak in the stand, a low (about 60%) canopy cover, a comparatively exuberant and tall herb layer, and a closed hornbeam

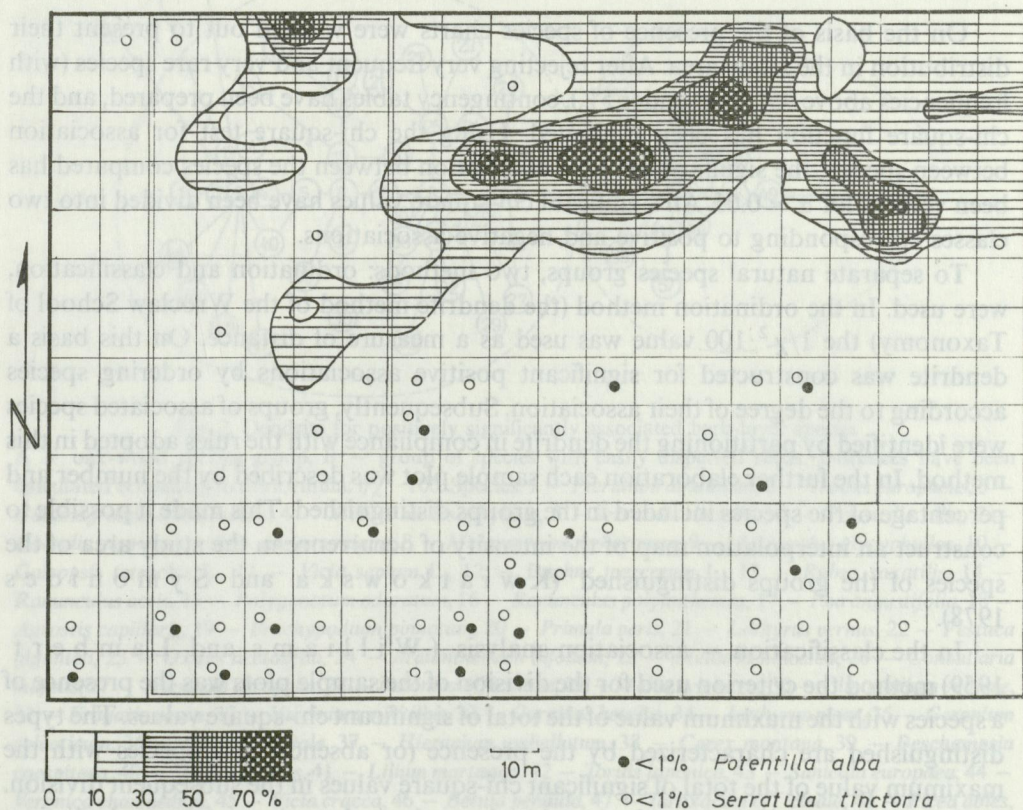


Fig. 1. Spatial variation in the value of *Galeobdolon luteum* cover (in percentages), and the occurrence of *Serratula tinctoria* and *Potentilla alba* in the area under study

Marked with the double line is the experimental plot, from which *Carpinus betulus* was removed

undergrowth belt along the biochore edges. The contribution and height of *C. betulus* trees increases from the oak-wood biochore northwards, to oak-hornbeam phytocoenoses. The herb layer of the oak-hornbeam phytocoenoses is clearly less exuberant and poorer in species than the oak-wood herb layer. The stand is closed, and the shrub layer is well-developed and made up mainly of hornbeam undergrowth.

The study area, of the size of 140×200 m, was divided into a control plot (140×150 m) and an experimental plot (140×50 m). To verify the hypothesis concerning the shrinking of the biochore, in the autumn of 1980 all *C. betulus* trees in the experimental plot were cut down. In that area a network of 280 points, 10 m apart, was laid out and sample plots of the size 2×2 m were set up in them. During the peak of growing season (July and August) all vascular plant species found in each square were recorded, and an estimation was made of their cover, in a 10-grade scale, as well as of the total herb-layer cover (Fig. 1).

2.2. STATISTIC AND CARTOGRAPHIC ELABORATION OF THE DATA

On the basis of the presence of species charts were worked out to present their distribution in the study area. After rejecting very frequent and very rare species (with frequencies above 95% and under 5%), contingency tables have been prepared, and the chi-square function has been evaluated. Using the chi-square test for association between species, the significance of the association between the species compared has been verified for $\alpha = 0.05$. All significant chi-square values have been divided into two classes corresponding to positive and negative associations.

To separate natural species groups, two methods: ordination and classification, were used. In the ordination method (the dendrite method of the Wrocław School of Taxonomy) the $1/\chi^2 \cdot 100$ value was used as a measure of distance. On this basis a dendrite was constructed for significant positive associations by ordering species according to the degree of their association. Subsequently, groups of associated species were identified by partitioning the dendrite in compliance with the rules adopted in this method. In the further elaboration each sample plot was described by the number and percentage of the species included in the groups distinguished. This made it possible to construct an interpolation map of the intensity of occurrence in the study area of the species of the groups distinguished (K w i a t k o w s k a and S y m o n i d e s 1978).

In the classification — association analysis (W i l l i a m s and L a m b e r t 1959) method the criterion used for the division of the sample plots was the presence of a species with the maximum value of the total of significant chi-square values. The types distinguished are characterized by the presence (or absence) of a species with the maximum value of the total of significant chi-square values in the subsequent division. In the association analysis method, and in the ecological species groups made distinct by the dendrite method, the spatial occurrence of the types distinguished was traced on the basis of the cartogram and interpolation maps.

3. RESULTS

An analysis of the inter-species associations, made by using the chi-square test, has demonstrated that in about 90% of cases the presence of a species depends on the presence of another species. Nearly all the species in the study area show a non-random distribution. Positively (groups A and B) and negatively (group C) associated species are spatially mutually exclusive.

Among positively associated species two groups: A and B are distinguishable (Fig. 2). Being very numerous, group A includes 41 species with distinct ecological

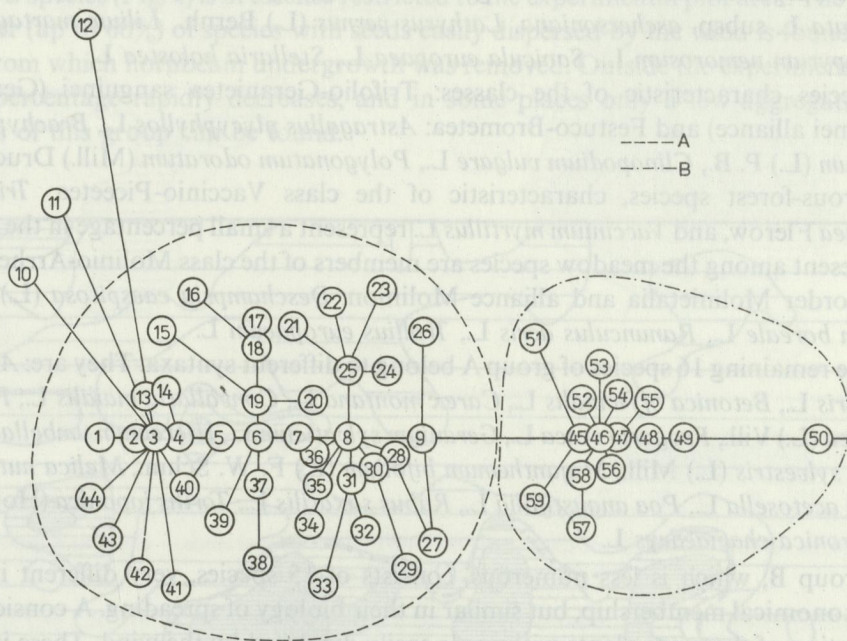


Fig. 2. Dendrite for positively significantly associated herb-layer species

A — oak-wood species group, B — group of species with easily dispersed seeds. Distances have been calculated according to the formula: $1/\chi^2 \cdot 100$. Species: 1 — *Pteridium aquilinum*, 2 — *Trolius europaeus*, 3 — *Calamagrostis arundinacea*, 4 — *Melitis melissophyllum*, 5 — *Serratula tinctoria*, 6 — *Potentilla alba*, 7 — *Dactylis glomerata* subsp. *aschersoniana*, 8 — *Melampyrum nemorosum*, 9 — *Astragalus glycyphyllos*, 10 — *Galeopsis tetrachit* L., 11 — *Vicia sepium* L., 12 — *Daphne mezereum* L., 13 — *Rubus saxatilis*, 14 — *Ranunculus acris*, 15 — *Polygonatum odoratum*, 16 — *Ranunculus polyanthemus*, 17 — *Poa angustifolia*, 18 — *Agrostis capillaris*, 19 — *Brachypodium pinnatum*, 20 — *Primula veris*, 21 — *Lathyrus vernus*, 22 — *Festuca gigantea*, 23 — *Oxalis acetosella*, 24 — *Maianthemum bifolium*, 25 — *Stellaria holostea*, 26 — *Convallaria majalis*, 27 — *Trientalis europaea*, 28 — *Betonica officinalis*, 29 — *Malus sylvestris*, 30 — *Clinopodium vulgare*, 31 — *Fragaria vesca*, 32 — *Vaccinium myrtillus*, 33 — *Carpinus betulus*, 34 — *Lathyrus niger*, 35 — *Geranium sylvaticum*, 36 — *Galium boreale*, 37 — *Hieracium umbellatum*, 38 — *Carex montana*, 39 — *Deschampsia caespitosa*, 40 — *Melica nutans*, 41 — *Lilium martagon*, 42 — *Torilis japonica*, 43 — *Sanicula europaea*, 44 — *Veronica chamaedrys*, 45 — *Vicia cracca*, 46 — *Betula pendula*, 47 — *Taraxacum officinale*, 48 — *Picea abies*, 49 — *Hypericum montanum*, 50 — *Moehringia trinervia*, 51 — *Ajuga reptans*, 52 — *Epilobium montanum*, 53 — *Urtica dioica*, 54 — *Potentilla erecta*, 55 — *Carex digitata*, 56 — *Sonchus asper*, 57 — *Aquilegia vulgaris*, 58 — *Erigeron annuus*, 59 — *Veronica officinalis*

characteristics, and represents a specific combination of oak-wood species. It consists of oak-wood, deciduous-forest, coniferous-forest, thermophilous, and meadow species, characteristic of various syntaxonomical types.

Most numerous are oak-wood species, characteristic (and differentiating) of the order Quercetalia pubescentis and the association Potentilla albae-Quercetum: *Calamagrostis arundinacea* (L.) Roth., *Lathyrus niger* (L.) Bernh., *Melittis melissophyllum* L., *Potentilla alba* L., *Primula veris* L., *Pteridium aquilinum* (L.) Kuhn, *Ranunculus polyanthemos* L., *Serratula tinctoria* L.

Of the deciduous-forest species, characteristic of the order Fagetalia silvaticae and alliance Carpinion betuli the following occurred in group A: *Carpinus betulus*, *Dactylis glomerata* L. subsp. *aschersoniana*, *Lathyrus vernus* (L.) Bernh., *Lilium martagon* L., *Melampyrum nemorosum* L., *Sanicula europaea* L., *Stellaria holostea* L.

Species characteristic of the classes: Trifolio-Geranietea sanguinei (Geranium sanguinei alliance) and Festuco-Brometea: *Astragalus glycyphyllos* L., *Brachypodium pinnatum* (L.) P. B., *Clinopodium vulgare* L., *Polygonatum odoratum* (Mill.) Druce, and coniferous-forest species, characteristic of the class Vaccinio-Piceetea: *Trientalis europaea* Flerow, and *Vaccinium myrtillus* L. represent a small percentage in the group.

Present among the meadow species are members of the class Molinio-Arrhenatheretea, order Molinietales and alliance Molinion: *Deschampsia caespitosa* (L.) P. B., *Galium boreale* L., *Ranunculus acris* L., *Trollius europaeus* L.

The remaining 16 species of group A belong to different syntaxa. They are: *Agrostis capillaris* L., *Betonica officinalis* L., *Carex montana* L., *Convallaria maialis* L., *Festuca gigantea* (L.) Vill., *Fragaria vesca* L., *Geranium sylvaticum* L., *Hieracium umbellatum* L., *Malus sylvestris* (L.) Mill., *Majanthemum bifolium* (L.) F. W. Schm., *Melica nutans* L., *Oxalis acetosella* L., *Poa angustifolia* L., *Rubus saxatilis* L., *Torilis japonica* (Houtt.) D. C., *Veronica chamaedrys* L.

Group B, which is less numerous, consists of 15 species, very different in their syntaxonomical membership, but similar in their biology of spreading. A considerable proportion of them are plants with seeds easily dispersed by the wind. These include: *Ajuga reptans* L., *Aquilegia vulgaris* L., *Betula pendula* Roth., *Carex digitata* L., *Epilobium montanum* L., *Erigeron annuus* (L.) Pers., *Hypericum montanum* L., *Moehringia trinervia* (L.) Clairv., *Potentilla erecta* L., *Picea abies* (L.) Kar., *Sonchus asper* (L.) Hill., *Taraxacum officinale* Web., *Urtica dioica* L., *Veronica officinalis* L., *Vicia cracca* L.

Species of the least numerous group C are negatively associated with group A and B species. They are: *Acer platanoides* L., *Angelica sylvestris* L., *Galeobdolon luteum* Huds. In the Białowieża Primaeval Forest they all occur in oak-hornbeam forests, and in the area under study they are distinctive of the oak-hornbeam forest part of the area analysed.

Maps of distribution of the species of the groups distinguished indicate that the centres of frequent occurrence of species of groups A, B, C are spatially mutually exclusive (Figs. 3–5). Groups: of oak wood – A (Fig. 3), with seeds easily dispersed by the wind – B (Fig. 4) and of oak-hornbeam forest – C (Fig. 5) occupy different parts of

the study area. The frequency of occurrence of group A and C species changes north-southwards. The largest number of group A species is found in the highest-elevated, southern part of the area (Fig. 3). The two areas, standing out on the map, where there occur over 50% of group A species, correspond to physiognomically best-developed oak-wood patches in the study area. Towards the northern, slightly lower part of the area the number of oak-wood species decreases gradually, and an increase in number is seen of oak-hornbeam forest species whose centre of occurrence is in the north-eastern part of the area. The spatial course of the phenomenon is continuous, but there are parts of the area which are characterized exclusively by group A or C. The presence of group B species (Fig. 4) is in essence restricted to the experimental plot area. The largest number (up to 60%) of species with seeds easily dispersed by the wind is found in the area from which hornbeam undergrowth was removed. Outside the experimental plot their percentage rapidly decreases, and in some places only a few aggregations of species of this group can be found.

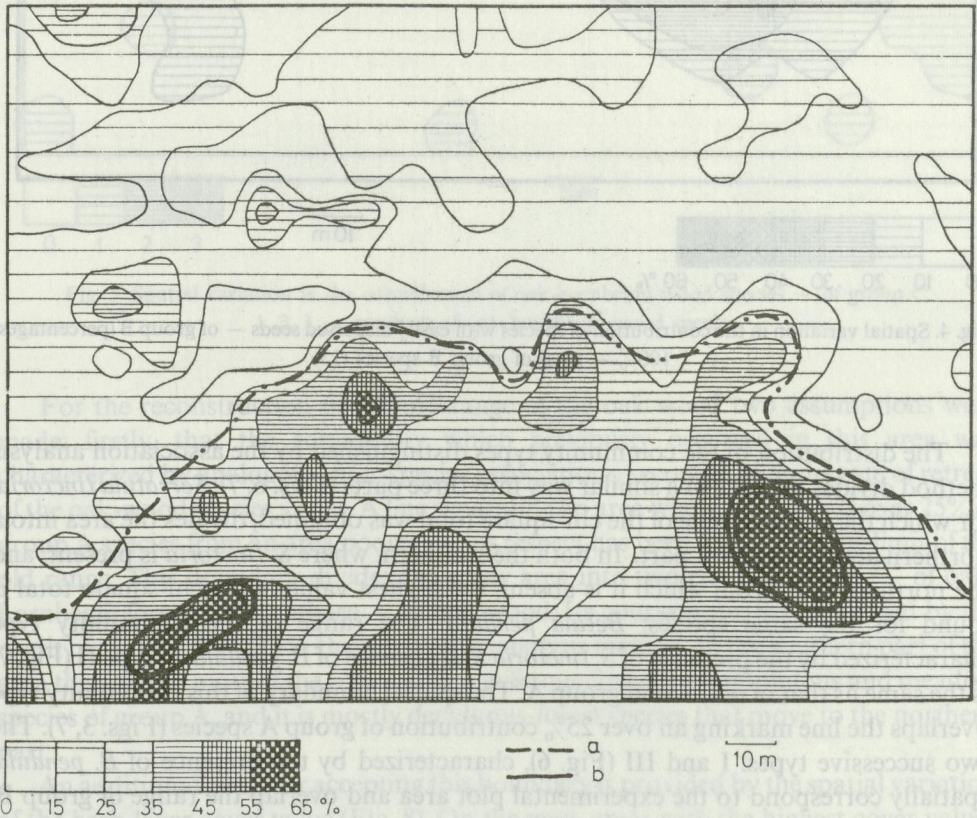


Fig. 3. Spatial variation in the contribution of oak-wood species — of group A (percentages)
 a — reconstructed boundary of the old range of the oak wood, b — present-day boundary of the oak wood.
 100% — total of group A species (41)

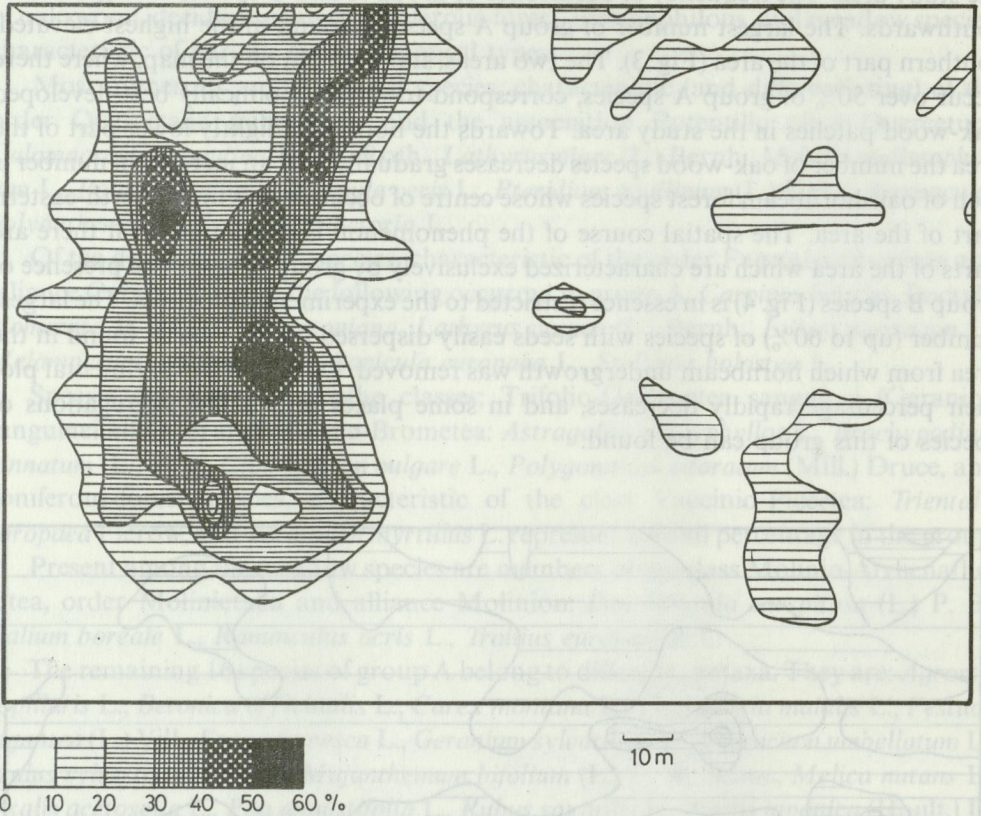


Fig. 4. Spatial variation in the contribution of species with easily dispersed seeds – of group B (percentages) 100% – total of group B species (15)

The distribution of the community types distinguished by the association analysis method divides the area in a similar way into three parts (Figs. 6, 7). *Serratula tinctoria*, for which the highest value of the chi-square total was obtained, divides the area into a northern and a southern part. In both the southern, where *S. tinctoria* is present, and the northern part, from which it is absent, the highest value of the chi-square total is found for the same species: *Betula pendula*. The range of the community type characterized by the presence of *S. tinctoria* and absence of *B. pendula* – type II (Fig. 7) is the same as that of oak-wood group A. The spatial boundary of this community type overlaps the line marking an over 25% contribution of group A species (Figs. 3, 7). The two successive types: I and III (Fig. 6), characterized by the presence of *B. pendula*, spatially correspond to the experimental plot area and overlap the range of group B. Type I corresponds to the oak-wood portion of the experimental plot (*S. tinctoria* is present there), and type II – to the oak-hornbeam forest part (*S. tinctoria* is absent). Type IV, the last one, is negatively characterized by the absence of both *S. tinctoria* and *B. pendula*. Its distribution corresponds to the range of group C.

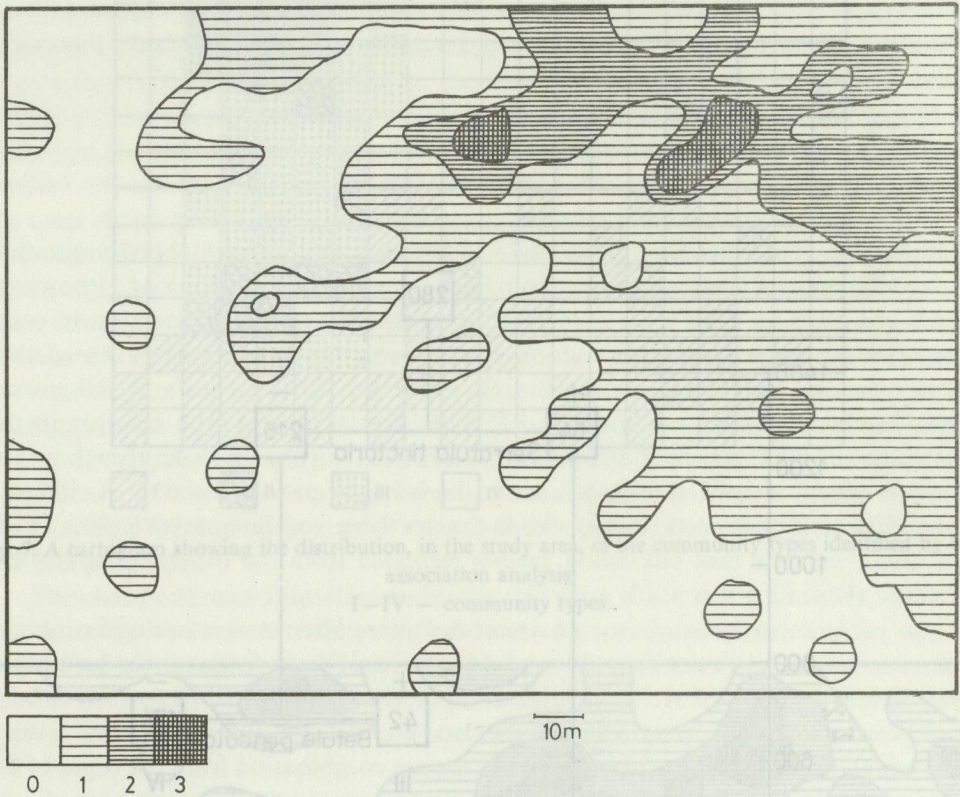
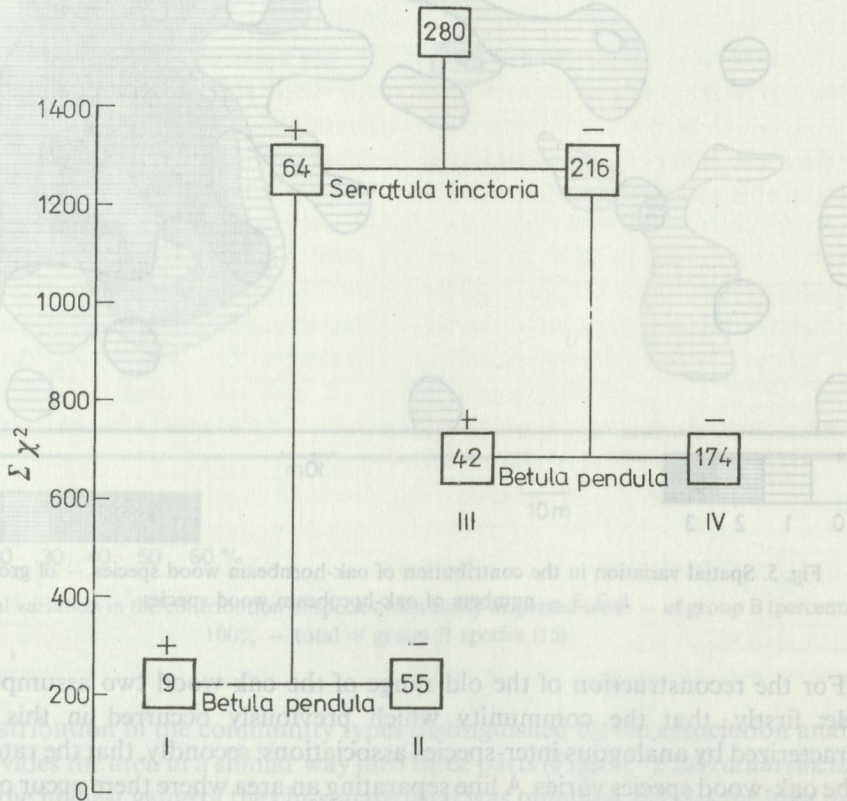


Fig. 5. Spatial variation in the contribution of oak-hornbeam wood species — of group C
1, 2, 3 — numbers of oak-hornbeam wood species

For the reconstruction of the old range of the oak wood two assumptions were made: firstly, that the community which previously occurred in this area was characterized by analogous inter-species associations; secondly, that the rate of retreat of the oak-wood species varies. A line separating an area where there occur over 25% of group A species from an area poorer in this respect has been adopted as the limit of the old range. This boundary divides the study area into two parts: northern — of oak-hornbeam forest, and southern — of oak wood. Its course is further confirmed by the result of the first division in the association analysis method. In the southern part of the area there occur most of the oak-wood, coniferous-forest, thermophilous and meadow species of group A, and it is mostly deciduous-forest species that move to the northern part.

An additional point for accepting this boundary is provided by the spatial variation of the herb-layer cover value (Fig. 8). On the map, areas with the highest cover values are grouped in the southern and north-eastern parts of the study area, and correspond to the centres of occurrence of vegetation of the oak-wood and oak-hornbeam forest types. Slightly lower cover values are also found for the area previously occupied

Fig. 8. Spatial variation in the value of the herb-layer cover (percentages) in the area under study



A diagram presenting maximum values of the chi-square total for the successive divisions of the association analysis

I – IV – community types; in the squares the number of sample plots of a given type is specified; “+” – presence, “-” – absence of a species with the maximum chi-square total for the particular division

area there occur most of the oak-wood, coniferous-forest, thermophilous and meadow species of group A, and it is mostly deciduous-forest species that move to the northern part of the study area. The maximum chi-square total for the particular division is 280. The maximum chi-square total for the particular division is 216. The maximum chi-square total for the particular division is 174. The maximum chi-square total for the particular division is 120. The maximum chi-square total for the particular division is 64. The maximum chi-square total for the particular division is 55. The maximum chi-square total for the particular division is 42. The maximum chi-square total for the particular division is 21. The maximum chi-square total for the particular division is 9.

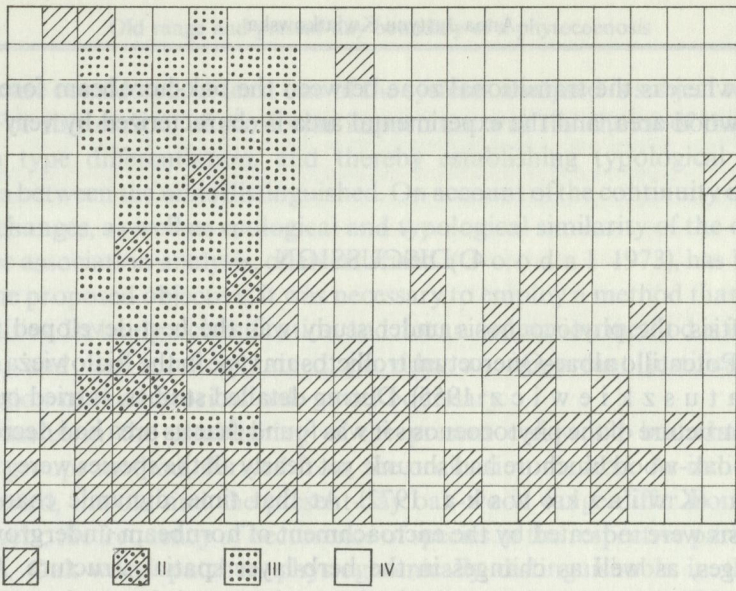
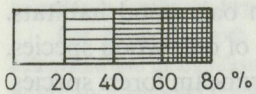
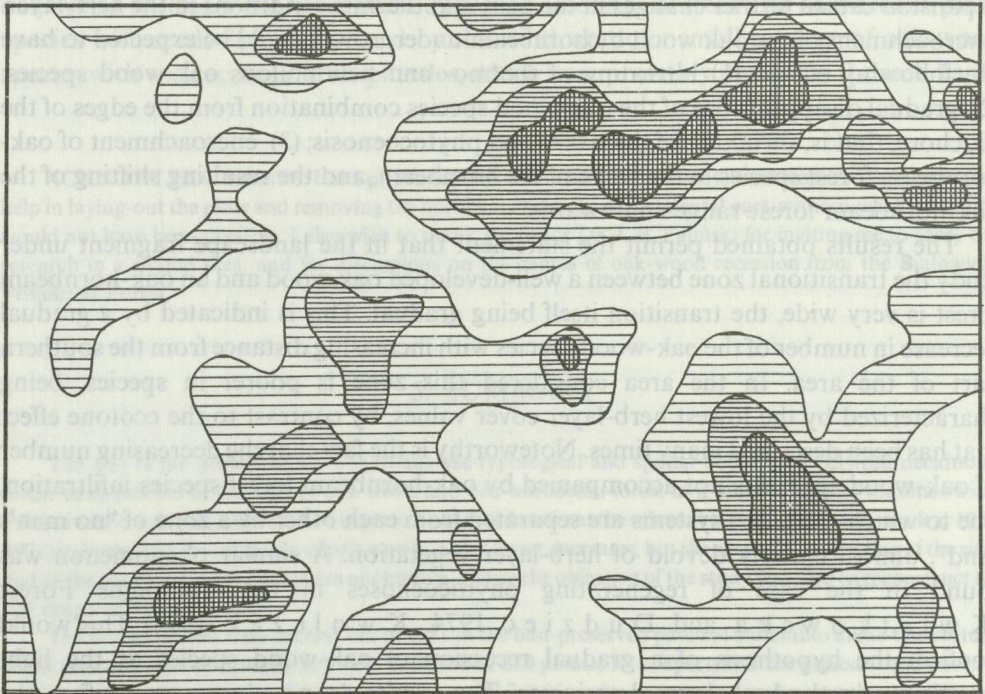


Fig. 7. A cartogram showing the distribution, in the study area, of the community types identified by the association analysis
 I-IV - community types



10 m

Fig. 8. Spatial variation in the value of the herb-layer cover (percentages) in the area under study

oak woods, whereas the transitional zone between the oak-hornbeam forest and the former oak-wood area, and the experimental area is characterized by very low cover values.

4. DISCUSSION

In the fifties, the phytocoenosis under study was the best-developed vegetation patch of the *Potentillo albae-Quercetum trolletosum* type in the Białowieża Primateval Forest (Matuszkiewicz 1955). During detailed studies, carried out 15 years later, of the structure of the phytocoenosis it was found that its area had decreased, that is to say, the oak-wood biochore had shrunk; yet nearly all the species were still present in the patch (Kwiatkowska 1972). At that time, dynamic changes in the phytocoenosis were indicated by the encroachment of hornbeam undergrowth on the biochore edges, as well as changes in the herb-layer spatial structure. A different probability of finding particular species in the northern and the southern parts of the area might indicate that oak-wood species retreated from the northern part of the biochore (Kwiatkowska 1972).

The present studies were started about ten years later. A continuing hornbeam expansion causes further changes in the light and thermic conditions in the herb layer. Encroachment of the oak wood by hornbeam undergrowth could be expected to have the following effects: (1) retreating of thermo- and heliophilous oak-wood species; (2) gradual disappearance of the oak-wood species combination from the edges of the biochore, that is, shrinking of the oak-wood phytocoenosis; (3) encroachment of oak-hornbeam forest species in the wake of the hornbeam, and the resulting shifting of the oak-hornbeam forest range southwards.

The results obtained permit the statement that in the landscape fragment under study the transitional zone between a well-developed oak wood and an oak-hornbeam forest is very wide, the transition itself being gradual. This is indicated by a gradual decrease in number of the oak-wood species with increasing distance from the southern part of the area. In the area considered this zone is poorer in species, being characterized by the lowest herb-layer cover values, by contrast to the ecotone effect that has been described many times. Noteworthy is the fact that the decreasing number of oak-wood species is not accompanied by oak-hornbeam forest species infiltration, due to which these two systems are separated from each other by a zone of "no man's land", almost entirely devoid of herb-layer vegetation. A similar phenomenon was found in the case of regenerating phytocoenoses in the Kampinos Forest (Kwiatkowska and Dudziec 1974, Wolczak 1974). This would confirm the hypothesis of a gradual recession of oak-wood species as the light conditions in the herb layer deteriorate. The results do not, however, confirm the hypothesis assuming oak-hornbeam forest encroachment upon oak-wood habitats. For in the area considered a decrease is found in the percentage of oak-wood species, but this is not followed by an increase in the range of the oak-hornbeam forest species.

In the case considered, at least one of the systems analysed is subject to directional changes. For this reason, of particular importance was the choice of the method for vegetation type differentiation, and thereby establishing typological and spatial boundaries between the units distinguished. On account of the continuity of spatial and temporal changes, as well as ecological and typological similarity of the communities studied, the association analysis, often criticized (Goodall 1973), has been chosen. To meet the proposed objective, it was necessary to employ a method that exaggerates discontinuities. Its being a classification and not an ordination method is in this case of advantage, and the result obtained provides an important justification in the reconstruction of the historical oak-wood boundary.

More useful in the establishing of the present oak-wood boundaries was the ecological groups method, derived from the ordination method. As indicated by the data presented, the old and the present-day oak-wood range differ from each other quantitatively; the frequency of occurrence of species in the respective parts of the area is different. Oak-wood patches, physiognomically distinguishable in the field, are characterized by high proportions of oak-wood species, exceeding 50% of the total number of species.

The change of microclimatic conditions that took place in the first year following the removal of hornbeam undergrowth did not result in a fast expansion of the range of oak-wood species. First of all there appeared seedlings of trees and herbaceous plant species with seeds easily dispersed by the wind, and of a small number of oak-wood species with wide ecological amplitudes, which were probably present in the seed bank.

ACKNOWLEDGMENTS: It is a pleasure to thank the staff of the Białowieża Geobotanical Station for help in laying-out the plots and removing the hornbeam from the experimental part, without which the study would not have been possible. I also wish to thank Professor Dr. J. B. Faliński for inviting me to carry out research in a shared area, and for discussions on the causes of oak-wood recession from the Białowieża Primaeval Forest.

5. SUMMARY

The aim of the present study was to analyse typological and spatial boundaries between deciduous-forest communities of the type of oak wood and oak-hornbeam forest in a selected part of the Białowieża Primaeval Forest. The author's own observations and data from the relevant literature (Faliński 1968, 1977) indicate that the total area of oak woods in this forest decreases, but the causes of the decline of the sites, and of the shrinking of biochores are not known. Hence the objective of the study was also to reconstruct the old range of oak woods.

The investigations were carried out in 1981 in the best-preserved patch of *Potentillo albae-Quercetum*. In an area of 2.8 ha samples (4 m²) were collected at 280 points, 10 m apart, and the presence and cover of species were recorded (Fig. 1). From part of the area (0.7 ha) hornbeam trees and undergrowth were removed in order to verify the hypothesis concerning its role in the shrinking of an oak-wood biochore.

For 93 species with frequencies above 5% and below 95% the association of each with each was calculated and its significance was verified with the chi-square test for association of species. For significantly positively associated species a dendrite was constructed and two species groups were distinguished: of oak

wood — A, and of species with seeds easily dispersed by the wind — B (Fig. 2); negatively associated with either are oak-hornbeam forest species — group C. For each plot the percentages were calculated of the species of these three groups, and interpolation maps were drawn (Figs. 3–5).

The frequency of occurrence of group A and C species changes in the north-south direction. Oak-wood species mainly concentrate in the highest-elevated southern part of the area. Areas with over 50% of group A species on the map correspond to physiognomically best-developed oak-wood patches in the field. Northwards, the number of oak-wood species decreases gradually, and that of oak-hornbeam forest species increases (Figs. 3, 5). The occurrence of group B species is restricted to the experimental plot.

An analogous division of the area into three parts results also from the distribution of the community types identified by the association analysis method (Figs. 6, 7). The main divisional species with the highest chi-square total is *Serratula tinctoria* (Fig. 6). The spatial boundary of this type overlaps the interpolation line marking an over 25% proportion of group A species (Figs. 3, 7) which has been adopted as the limit of the old range of oak woods. This boundary is also confirmed by the spatial variation in the herb-layer cover value (Fig. 8).

In the landscape fragment analysed the transitional zone between a well-developed oak wood and an oak-hornbeam forest is very wide, continuous and characterized by the lowest herb-layer cover values (Fig. 8). A loss of oak-wood species is not accompanied by recruitment of oak-hornbeam forest species, due to which, these two systems are separated by a forest belt almost entirely devoid of herb-layer vegetation.

The study has demonstrated that hornbeam undergrowth encroachment causes thermo- and heliophilous oak-wood species to retreat, and as a result, the oak-wood combination of species gradually disappears from the edges of the biochore and the oak-wood biochore shrinks.

6. POLISH SUMMARY

Przedmiotem pracy jest analiza typologicznych i przestrzennych granic między zbiorowiskami lasu liściastego typu dąbrowy i grądu w wybranym fragmencie Puszczy Białowieskiej. Z obserwacji własnych i danych literaturowych (F a l i Ń s k i 1968, 1977) wynika, że sumaryczny areal dąbrów na tym terenie maleje, przyczyną zaniku stanowisk i „kurczenia się” biochor nie są jednak znane. Stąd też, celem pracy była także rekonstrukcja dawnego zasięgu dąbrowy.

Badania przeprowadzono w 1981 r. w najlepiej zachowanym płacie *Potentillo albae-Quercetum*. Na 2,8 ha powierzchni pobierano próby (4 m²) z 280 punktów, odległych od siebie o 10 m, notując obecność i pokrywanie gatunków (rys. 1). Z części powierzchni (0.7 ha) usunięto drzewa, podrost i nalot graba w celu sprawdzenia hipotezy dotyczącej jego roli w „kurczeniu się” biochory dąbrowy.

Dla 93 gatunków o frekwencji większej niż 5% i mniejszej niż 95% obliczono sprężenie każdego z każdym i zweryfikowano jego istotność testem χ^2 na niezależność cech. Dla istotnie, dodatnio sprzężonych gatunków skonstruowano dendryt i wyróżniono 2 grupy gatunków: „dąbrowową” — A i „lekkonasienną” — B (rys. 2); z obu — ujemnie sprzężone są gatunki „grądowe” — grupa C. Dla każdej powierzchni obliczono udział gatunków tych 3 grup i wykreślono mapy interpolacyjne (rys. 3–5).

Natężenie występowania gatunków grupy A i C zmienia się w kierunku północno-południowym. Gatunki „dąbrowowe” grupują się głównie w najwyższej położonej, południowej części powierzchni. Fragmentom mapy z ponad 50% gatunków grupy A odpowiadają w terenie najlepiej fizjonomicznie wyształcone płaty dąbrowy. W kierunku północnym stopniowo zmniejsza się liczba gatunków „dąbrowowych”, natomiast rośnie udział gatunków „grądowych” (rys. 3, 5). Występowanie gatunków grupy B ograniczone jest do eksperymentalnej części powierzchni.

Analogiczny podział powierzchni na 3 części wynika także z rozmieszczenia typów zbiorowisk wyróżnionych metodą analizy asocjacji (rys. 6, 7). Głównym gatunkiem „podziałowym”, o maksymalnej wartości sumy χ^2 , jest *Serratula tinctoria* (rys. 6). Przestrzenna granica tego typu pokrywa się z przebiegiem linii interpolacyjnej, wyznaczającej ponad 25% udział gatunków z grupy A (rys. 3, 7), którą przyjęto jako granicę dawnego zasięgu dąbrowy. Granicę tę potwierdza także zróżnicowanie przestrzenne wartości pokrywania runa (rys. 8).

W badanym fragmencie krajobrazu strefa przejścia między dobrze wykształconym lasem typu dąbrowy i grądu jest wyjątkowo szeroka, ma charakter ciągły i cechuje się najniższymi wartościami pokrywania runa (rys. 8). Ubywaniu gatunków „dąbrowowych” nie towarzyszy wnikanie „grądowych”, co powoduje, że oba układy są oddzielone od siebie pasem lasu prawie całkowicie pozbawionym runa.

Badania wykazały, że w wyniku wkraczania podrostu grabowego następuje wycofywanie się termofilnych gatunków „dąbrowowych”, a – w efekcie – stopniowy zanik „dąbrowowej” kombinacji gatunków na obrzeżach biochory i „kurczenia się” biochory dąbrowy.

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