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LONG-TERM EVOLUTION MODELS OF POST-AGRICULTURAL FORESTS

PAN IGiPZ

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MODELE DŁUGOOKRESOWEJ EWOLUCJI FITOCENOZ LEŚNYCH REGENERUJĄCYCH NA TERENACH POROLNYCH

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1. SHORT DESCRIPTION OF THE STUDY

1.1. PROBLEMS ADDRESSED AND OBJECTIVES OF THE STUDY

Turning forests into arable land had been constituting one of the crucial aspects of the man and environment relations during the last couple of millennia in Central Europe. Though, this was not entirely one-way process, and, side by side with deforestation, we deal also with afforestation of the post-agricultural land. This took place at various times – formerly as the effect of changes in the population (wanderings of peoples, wars, pests) or of the authorities change. For more than a century this is, as well, the result of the decreasing, in multiple regions and for many reasons, demand for arable land as the base of the society existence.

The spontaneous or intentional afforestation of the post-agricultural land constitutes the starting point for the forests regeneration. Yet, it is observed that even if the stands attain the mature age, this does not mean that the forest returned to its natural state. The secondary forest differs distinctly as to its floristic composition of the spontaneous species from the analogous forest growing in the places that have never (or – sufficiently long ago) been permanently deforested. These observations and the associated in-depth studies resulted in the introduction of the ancient forest concept (Peterken 1974, 1977, 1996; Rackham 1980), while the issue itself became the subject of numerous studies (Hermy, Stieperaere 1981; Petersem 1994; Dzwonko, Loster 1988, 19891992; De Frenne et al. 2011; Góras, Orczewska 2007; Orczewska 2009a, b, c; 2010a, b, c), and, in particular, of the designation of the lists of ancient forests species in western Europe (Peterken 1974; Honney et al. 1998; Hermy et al. 1999; Wolf 1997), and also in Poland (Dzwonko, Loster 2001). It is very important, as well, to note that the return of the ancient forest is conditioned by the presence of species propagation sources, which, for some of them, means the presence of the ancient forest patches, located not too far. They act as the refuge of the forest species, eliminated from the cultivated land (Dzwonko 1993, 2001a, b; Dzwonko, Gawroński 1994; Matlack 1994; Bossuyt i in. 1999a; Bossuyt, Hermy 2000; Orczewska 2007; 2010; Orczewska, Fernes 2011). In this context the role of the *forest islands* in the farming landscape was noted as the places of the forest flora refuge (Orczewska 1999; Dzwonko, Gawroński 1994; Dzwonko 1993; Dzwonko, Loster 1992; Wójcik 1991; Wójcik, Wasiłowska 1995).

Our study aimed, therefore, at the problem of forests regeneration on the areas that had been at some time in the past deforested and used for farming. This problem being important both from cognitive and practical points of view. It is assumed that the regeneration process in its later phase can be treated as the re-establishment of the potential natural vegetation community, specific in terms of structure and floristic composition, including the exchange of the 'pool of alien species' (corresponding to non-forest habitats) for the 'pool of native species', or the 'ecological pool' (Balyea, Lancaster 1999), or the 'community pool' (Zobel et al. 1998), corresponding to the characteristic species combination of the given phytosociological unit.

One of the areas, within which there are relatively a lot of recent forests, growing on the post-agricultural land, is the territory of the large outwash plain, for centuries divided up by the ethnic-and-political boundary. Our investigations focussed on this territory (see Chapter 2). Owing to the historical cartographic documentation it was possible to analyse afforestation on this territory over the period of the last 200–270 years.

Based on the studies conducted before, as well as on field observations, it can be concluded that the ancient forests differ in the floristic composition, forming the undergrowth, from the recent forests growing on the post-agricultural land. Hence, the **hypothesis was formulated** as follows:

- The regeneration process of the recent forest takes a long time, longer than reaching the stands maturity (the felling age in forestry), with the regeneration degree being dependent upon the period of regeneration (the forest persistence) and upon a number of factors, including the community type and the distance of the patch from the ancient forest stand.

Verification of this hypothesis was the subject of the research project, carried out in the years 2008–2012, funded by the Polish Ministry of Science and Higher Education, at the Institute of Geography and Spatial Organization, Polish Academy of Sciences in Warsaw. More precisely, the project concerned also the historical landscape transformations, considered in the perspective of sustainable use of landscape. This aspect of the study, though, is presented in another work.

The general objective of the study was to develop a model – different, in principle, for each of the forest communities types, which would define the rate and the course of the advanced forest regeneration process concerning the undergrowth on the post-agricultural land, along with the most important factors influencing this process.

The project had also a number of secondary objectives, namely:

- to grasp the differences as to the floristic composition, undergrowth layer structure, and soil specificity between the ancient forests and the recent forests of varying persistence, and to establish the list of the differentiating species;

- to verify in the regional conditions the list of ancient forests species, known from the literature (Hermy et al. 1999; Dzwonko, Loster 2001) as a tool for identification of the recent forests regeneration degree;
- to develop a new indicator of forest maturity, useful for evaluation of recent forest regeneration degree;
- to indicate the factors that have the biggest impact on the recent forests regeneration rate, and, in particular, determination of the role played – side by side with time – by the distance to the ancient forest as the refuge of the typical forest species.

The objectives of the project include also the **pragmatic goals**, linked with the improvement of forest management to conduct ecological forestry.

1.2. THE STUDY PROCEDURE: THE SCHEME AND THE SCOPE OF TASKS

Considering the main purpose of the study, we adopted the following scheme of the study process. This means to lead from the general concept and hypothesis towards the models, based on, real, repeatable investigations of the actual forest associations.

The scheme of the study was as follows:

In order to develop a model, a data set was needed (the phytosociological relevés, describing the mature phytocoenoses), representing three plant associations. Hence, the diversity of the communities and habitats was analysed on the basis of the potential natural vegetation map (the map being elaborated by the study team using the available forest maps and field studies).

So as to determine the connection between the regeneration of each association and the persistence period, the phytosociological relevés were needed describing the mature phytocoenoses of the ancient and recent forests, featuring different regeneration periods. Therefore, contemporary forests were analysed from the point of view of their history. The sites of the relevés were selected to achieve an appropriate quantitative representation of all the persistence categories for a type. (This postulate, though, was not fully realised in some cases.)

Determination of relation between the regeneration of the recent forests and the distance to ancient forests requires a set of the phytosociological relevés, describing the mature phytocoenoses of definite types and categories, located at different distances to the fragments of ancient forests. Hence, ancient forests were identified on the basis of cartographic materials, and then the sites for the relevés in the appropriate recent forests were selected. They were located at various distances to the ancient forests, preferably measured over the straight line and with no essential barriers in the terrain.

(This requirement turned out impossible to fulfil. The relevés were partly substituted by the simplified data.)

The set of the phytosociological relevés was classified into groups according to the type of association and the persistence of the forest stand, so as to obtain sufficiently numerous sets, describing the mature phytocoenoses of the ancient and recent forests of various regeneration stages (1). Floristic characteristic was determined for each of the persistence categories and for each association (species composition, frequency and cover). Relation was determined between persistence and changes in floristic characteristics, treated as the regeneration symptom.

In order to link the phytosociological changes with the habitat, the description and analysis of soil profiles were conducted in specially selected locations, representing all the analysed forest types and the distinguished categories of forest stand persistence.

Metrics were necessary in construction of the model(s). For this purpose basic measures of forest regeneration were developed, encompassing: (a) verification of the ancient forest species list and its adaptation to the local conditions; (b) defining and calculating the synthetic Forest Maturity Index (FMI); (c) checking the possibility of treating the state of individual species populations as the regeneration indicators (in particular – of *Vaccinium myrtillus*).

The last step towards construction of the model was preceded by the identification of the most important relationships between the variables, describing the state of the forest stand, along with persistence and distance to the ancient forest (correlation and regression analysis). Interpretation was performed of the distinguished dependences in terms of the functional relationships.

The main aim was attained through (a) development of models of the recent forest regeneration rate of the particular community types; (b) description of the regeneration process as the process of species pools exchange featuring different dynamics and ecological characteristics, considering the specificity of individual species.

The pragmatic goal was attained through elaboration of the simplified versions of the community regeneration models for the potential needs of forest management practice.

The **scope of the study, in terms of its object,** encompassed:

- forest communities classified into three associations: *Peucedano-Pinetum*, *Querco-Pinetum*, and *Tilio-Carpinetum* (see Matuszkiewicz J.M., 2001),
- floristic composition of the phytocoenoses with respect to vascular plants, as well as overground mosses and lichens, appearing in forest patches,

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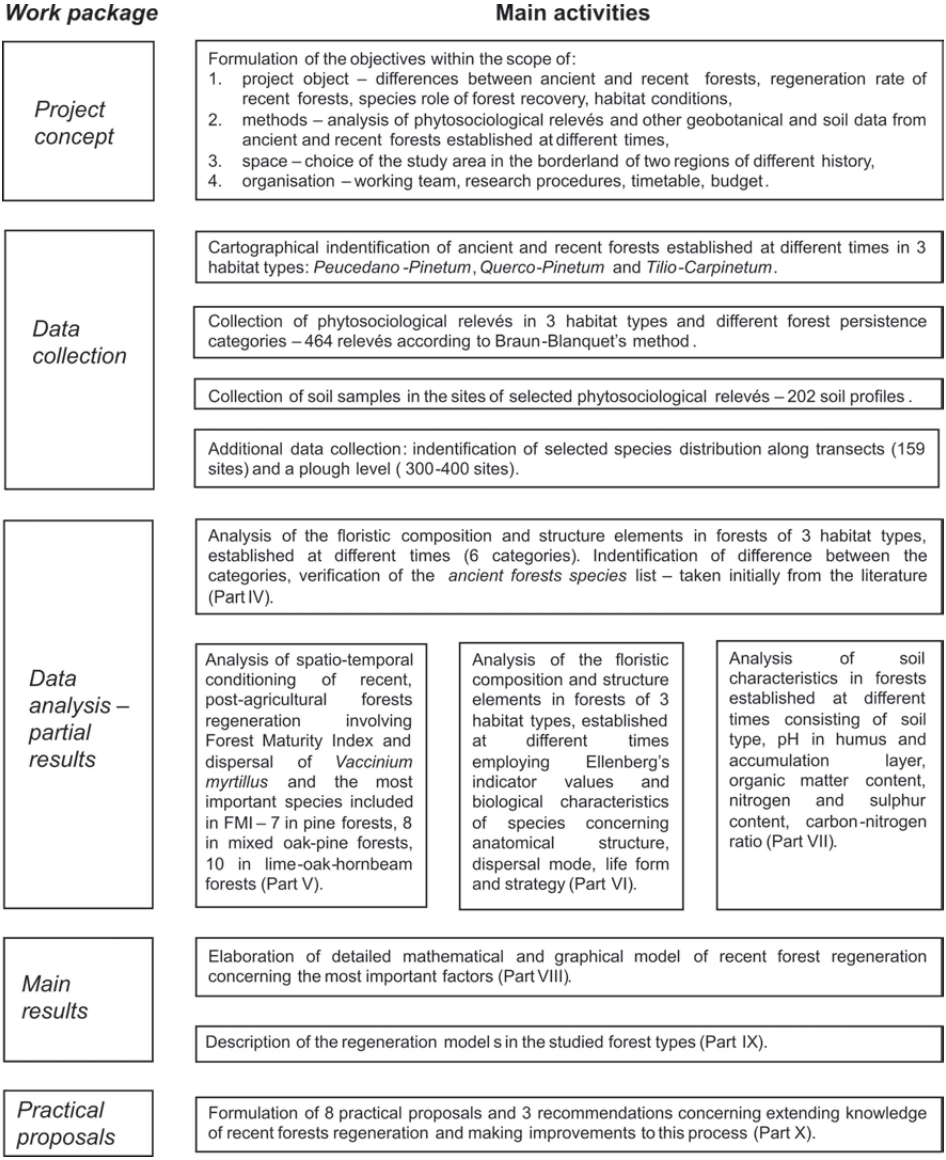
[1] The postulate of the appropriate items number in each groups of the phytosociological relevés was not always fulfilled.

- quantitative shares of species, distinguished in the phytocoenoses,
- characteristics of the forest topsoils.

The **spatial scope of the study** encompassed six state forest management districts: Jedwabno, Szczytno, Spychowo, Wielbark, Parciaki (except for its southern fragment), and Myszyniec, along with small fragments of the district of Korpele (see Chapter 2).

The basic elements of the study characteristics are shown in Figure 1.



Work package	**Main activities**
Project concept	Formulation of the objectives within the scope of: 1. project object – differences between ancient and recent forests, regeneration rate of recent forests, species role of forest recovery, habitat conditions, 2. methods – analysis of phytosociological relevés and other geobotanical and soil data from ancient and recent forests established at different times, 3. space – choice of the study area in the borderland of two regions of different history, 4. organisation – working team, research procedures, timetable, budget.
Data collection	Cartographical indentification of ancient and recent forests established at different times in 3 habitat types: *Peucedano-Pinetum*, *Querco-Pinetum* and *Tilio-Carpinetum*. Collection of phytosociological relevés in 3 habitat types and different forest persistence categories – 464 relevés according to Braun-Blanquet's method. Collection of soil samples in the sites of selected phytosociological relevés – 202 soil profiles. Additional data collection: indentification of selected species distribution along transects (159 sites) and a plough level (300-400 sites).
Data analysis – partial results	Analysis of the floristic composition and structure elements in forests of 3 habitat types, established at different times (6 categories). Indentification of difference between the categories, verification of the *ancient forests species* list – taken initially from the literature (Part IV). Analysis of spatio-temporal conditioning of recent, post-agricultural forests regeneration involving Forest Maturity Index and dispersal of *Vaccinium myrtillus* and the most important species included in FMI – 7 in pine forests, 8 in mixed oak-pine forests, 10 in lime-oak-hornbeam forests (Part V). Analysis of the floristic composition and structure elements in forests of 3 habitat types, established at different times employing Ellenberg's indicator values and biological characteristics of species concerning anatomical structure, dispersal mode, life form and strategy (Part VI). Analysis of soil characteristics in forests established at different times consisting of soil type, pH in humus and accumulation layer, organic matter content, nitrogen and sulphur content, carbon-nitrogen ratio (Part VII).
Main results	Elaboration of detailed mathematical and graphical model of recent forest regeneration concerning the most important factors (Part VIII). Description of the regeneration models in the studied forest types (Part IX).
Practical proposals	Formulation of 8 practical proposals and 3 recommendations concerning extending knowledge of recent forests regeneration and making improvements to this process (Part X).

Fig. 1. Schematic outline of the contents

Ryc. 1. Schematyczny zarys treści pracy

1.3. MATERIALS AND METHODS

The materials used in the study consist of two essential groups:

- materials presenting spatial heterogeneity of the vegetation cover (especially of the forest formations), at present and in the past, consisting mainly of the cartographic materials;
- materials documenting plant and soil characteristics of the particular forest patches, selected as representative for the types and categories, encompassing mainly the phytosociological relevés and the results of soil analyses, related to them.

The most important material for the study is constituted by the set of precisely located 464 phytosociological relevés, collected according to the Braun-Blanquet methodology (Wysocki, Sikorski 2009), presenting the floristic composition and the structure of the plant community, completed, additionally, with a set of simplified descriptions of the plant community patches. In the locations of 202 phytosociological relevés the topsoil horizons were examined.

The set of the phytosociological relevés has the character of a biased sample. Selection of the relevés locations was performed in the field, considering the information collected from the maps, concerning the history of the particular forest patch and the current state of the forest (first of all the stand age). Selection was guided by two basic and two additional criteria.

The basic criteria applied were:

- the maturity and the stable structure of phytocoenosis,
- identified forest history over the given fragment of the terrain.

The additional criteria were:

- typological classification of the community in terms of the potential natural vegetation,
- location of the patch with respect to the present and past forest complexes.

Hence, the fragments of the forests were selected for analysis that had sufficiently mature stands, namely – at least 80–90 years of age, and featuring structure possibly little deformed. Based on the historical maps and the field identification of the plough horizon in the soil forests were divided into two essential categories: ancient forests and recent forests. The latter were subdivided into categories depending upon the regeneration period (forest persistence), that is – the time having elapsed since the given fragment of the post-agricultural land, was afforested. The division into categories and the adoption of the persistence values resulted from the historical maps analysis dating from various periods. An important factor, taken into consideration, was also location of the given recent forest fragment in terms of distance to the ancient forest. The selection process was aimed at collecting possibly rich set of the relevés representing three basic types of communities in the region: pine forests (*Peucedano-Pinetum*), mixed oak-pine forests (*Querco-Pinetum*), and lime-oak-hornbeam forests (*Tilio-Carpinetum*), varied in the persistence categories.

The phytosociological materials, focussing on the species appearance and their quantitative shares, were processed with the use of the following groups of methods:

- the classical analysis of the phytosociological tables, based on the comparison of species frequencies in the subsets and the analysis of differences in the species appearance characteristic of the community groups;
- bioindication methods, making use of the plants biological classifications, including the so-called indicator values after Ellenberg et al. (1991);
- the similarity calculation with regard to the floristic composition of forest categories;
- analysis of species frequency in the relevés subsets, using the statistical software for calculation of the mean, testing significance of differences (Fisher test) and distinguishing on this basis the species groups associated with different regeneration stages;
- analysis of differences between the relevés and the forest categories with regard to the synthetic Forest Maturity Index (FMI), calculated on the basis of appearance of the selected plants species;
- modelling the changes in the selected characteristics of the phytocoenoses in the regeneration process in relation to two independent variables: persistence and distance to ancient forests, using regression analysis in the choice of the best functions, describing the relations.

Investigation of 2–3 soil horizons consisted in:

- diagnosis of the soil and the humus type,
- measurement of soil reaction (pH measured potentiometrically in H_2O),
- measurement of the organic carbon and total nitrogen content (with the TOCN FormacsTM analyser) and calculation of the C:N ratio,
- measurement of the sulphur content (with the Butters-Chenery method).

1.4. THE MOST IMPORTANT RESULTS

The present section lists these results, which we consider to be the most significant, and which are described fully in the consecutive book chapters.

The area studied, homogeneous under many respects, features distinct division in terms of geomorphology (age of glaciation), climate, geobotany, as well as in social and historical terms, into the northern (Masuria) and the southern (Kurpie) parts [See Chapter 2.3–4].

Regarding forest cover, the study area underwent very important changes over the last 200 years. These changes had a different course in the Masurian and Kurpie parts. The visible difference between Masuria and Kurpie does not alter, though, the general tendency of the forest cover increase in relation to the minimum, which took place in the middle of the 19th century (Masuria) or at the beginning of the 20th century (Kurpie) [See Chapter 2.5].

The fact that during the last 100–150 years there has been an increase in the overall forest cover, and also the fact that some of the forest complexes shifted in space over the past 200 years, cause the differences in persistence period of the present forests patches. Thus, among the contemporary forests, the ancient forests and five categories of recent forests were distinguished, characterised by different periods since afforestation, the minimum period being around 70–80 years [See Chapter 3.5].

The recent post-agricultural forests, representing *Peucedano-Pinetum*, *Querco-Pinetum*, and *Tilio-Carpinetum*, display significant differences in the floristic composition and the shares of some species, when compared to the ancient forests. Individual species may display preference for various persistence forests categories. Similarity of the recent forests to the corresponding ancient forests increases with the time period since the afforestation of the post-agricultural land i.e. with persistence [See Chapter 4.2–3].

In the pine forests, as well as in the mixed oak-pine forests, the species characteristic of the communities from the *Vaccinio-Piceetea* class are divided into three groups associated with the ancient or recent forests. Thus, a distinct preference for the ancient forests is observed in the case of *Hylocomium splendens, Trientalis europaea, Vaccinium vitis-idaea*; also in the case of *Vaccinium myrtillus* as far as its cover is concerned (much less so regarding its frequency). A moderate preference for the recent forests is displayed, on the other hand, by *Chimaphila umbellata, Pyrola chlorantha, Orthilia secunda, Diphasiastrum complanatum, Monotropa hypopitys*. The third group is constituted by the plants that do not show clear differences in their frequency between the recent and the ancient forests. These are: *Melampyrum pratense, Pleurozium schreberi, Dicranum polysetum, Dicranum scoparium, Ptilium crista-castrensis, Lycopodium annotinum* [See Chapter 4.2].

In the pine and mixed oak-pine forests the species that display a distinct preference for the recent forests, especially for those with short persistence periods, belong in their vast majority to the species characteristic of the open habitat associations: sandy grasslands (*Koelerio glaucae-Corynephoretea canescentis* class), mat-weed grasslands (*Nardo-Callunetea* class), and meadows (*Molinio-Arrhenatheretea* class) [See Chapter 4.2].

In the lime-oak-hornbeam forests a vast majority of species characteristic of the *Querco-Fagetea* class displays a more or less distinct connection with the ancient forests, appearing in the recent forests more rarely or altogether not at all. There are, however, such species, considered to be characteristic of this class, which are equally frequent in the recent forests as in the ancient ones (*Dryopteris filix-mas*) [See Chapter 4.2].

The frequency of *Festuca ovina* and *Cladonia arbuscula* in the recent pine forests, originating from the first half of the 19th century, is clearly higher than in the ancient forests and in the recent ones of the shorter persistence. On this basis it can be supposed that this is the remnant of the now abandoned, but formerly common practice of pasturing domestic animals in the forests [See Chapter 4.2].

Identification of the post-agricultural forests regeneration degree using the species frequencies gains an extra precision and reliability owing to the additional analysis of species cover in the patches. This, however, requires having a bigger number of relevés and more precise data on the quantitative species characteristics in the patches than those that can be obtained from the transformation of the Braun-Blanquet quantitative scale from the phytosociological relevés [See Chapter 4.3].

Not all of species from the ancient forest species lists after Hermy et al. (1999) and Dzwonko and Loster (2001) got confirmed in the regional verification. This might have resulted from the scarcity of the empirical material (the lime-oak-hornbeam forests), but can also be partly treated as the regional specificity [See Chapter 4.4].

The indicator value of the particular species as ancient forest species should be referred to the definite habitat types. A number of species that satisfy this criterion in one forest type (e.g. in the pine forest or in the oak-pine forest) might not satisfy it in another forest type (e.g. in the lime-oak-hornbeam forest), and even to the contrary – might constitute the indicator of recent forest [See Chapter 4.4].

Verification of the regional ancient forest species list was performed in the pine forests (*Peucedano-Pinetum*), based on ample empirical material, (Hermy et al., 1999). The status of the ancient forest species was confirmed for two species, characteristic of the class *Vaccinio-Piceetea* (*Vaccinium vitis-idaea* and *Trientalis europaea*) and for two commonly appearing companions (*Convallaria majalis* and *Luzula pilosa*), of which the former one is considered as the differential species of the *Peucedano-Pinetum* association, as well as for two relatively rare species: *Athyrium filix-femina* and *Oxalis acetosella*. The group of species, for which the results of analyses have not confirmed the status of ancient forest species in the pine forests includes the species characteristic of the class *Vaccinio-Piceetea* (*Melampyrum pratense*), and the companion *Dryopteris carthusiana*. The situation, concerning *Vaccinium myrtillus* is quite particular. This species does not fulfil (or fulfils very poorly) the criteria of the ancient forest species status in terms of frequency, but in terms of the cover reveals a positive and unambiguous relation [See Chapter 4.4].

In the mixed oak-pine forests (*Querco-Pinetum*) the status of ancient forest species was confirmed for one species, characteristic of the *Vaccinio-Piceetea* class (*Trientalis europaea*), for one species characteristic of the *Querco-Fagetea* class (*Athyrium filix-femina*), and for four species of the general forest character (*Convallaria majalis, Pteridium aquilinum, Luzula pilosa, Maianthemum bifolium*). Three species from the ancient forest species list (*Vaccinium vitis-idaea*, *Oxalis acetosella* and *Carex digitata*) have an unclear status. Then three other species from the list (*Melampyrum pratense, Dryopteris filix-mas* and *Dryopteris carthusiana*) do not display in the mixed oak-pine forests analysed, in terms of frequency, the difference between ancient and recent forest, this meaning that their status was effectively denied. Similarly as in the pine forests, the status of *Vaccinium myrtillus* may depend upon the form of registering its appearance (the frequency or the quantitative share) [See Chapter 4.4].

The species from the ancient forest species list, observed in the lime-oak-hornbeam forests (*Tilio-Carpinetum*) can be classified into five groups:

1. Ten species, whose status has been confirmed, among which one can distinguish such that appear only in the ancient forests and in the recent ones with the longest persistence (the 'Hepatica' group, comprising *Hepatica nobilis, Galium odoratum, Lathyrus vernus*), as well as those that may appear in the recent forests, but appear in the ancient ones significantly more frequently (the 'Anemone' group - *Anemone nemorosa, Convallaria majalis, Galeobdolon luteum, Milium effusum, Polygonatum multiflorum*);
2. The 'Melica' group, comprising 13 species of a doubtful status (perhaps just due to the too small number of relevés): *Actea spicata, Athyrium filix-femina, Carex digitata, Festuca gigantea, Gymnocarpium dryopteris, Lilium martagon, Maianthemum bifolium, Melica nutans, Oxalis acetosella, Paris quadrifolia, Phyteuma spicatum, Ranunculus lanuginosus, Scrophularia nodosa*;
3. The 'Luzula' group, composed of eight species, whose status has been weakly negated, comprising *Dactylis polygama, Dryopteris carthusiana, Dryopteris filix-mas, Luzula pilosa, Melampyrum pratense, Pteridium aquilinum, Trientalis europaea, Vaccinium myrtillus*;
4. *Vaccinium vitis-idaea*, the species, whose status was unambiguously denied (distinctly more frequent in the recent forests, with the significant difference) [See Chapter 4.4].

The floristic distinction between the ancient and the recent forest may be assessed by identification of species set unambiguously linked with the ancient forests, constituting the model pattern of the given forest type. The species percentage from the model list, which appear in a given patch may constitute a measure (Forest Maturity Index) of disturbance degree or, otherwise, of patch regeneration degree [See Chapter 5.1].

The patch regeneration degree of recent forests, as measured with the Forest Maturity Index, shows the correlation with two independent variables: the regeneration period ('persistence') and the distance to a patch of the ancient forest ('distance'). The dependence of FMI upon distance of the particular forests categories has approximately the character of the logarithmic function [see Chapter 5.2–3], although more detailed analyses indicate also some more intricate formal relationships [See Chapter 8].

The regeneration rate of the *Vaccinium myrtillus* population is in the recent post-agricultural pine forests generally slow; thus, even forests with around 230 years of the regeneration period still display a difference in the spread of this species in comparison with the ancient forests. In the mixed oak-pine forests the regeneration of *Vaccinium myrtillus* takes place faster than in the typical pine forests. In the pine and mixed oak-pine forests on the fresh habitats the possibilities of *Vaccinium myrtillus* regeneration in the recent forests get better on the richer and more humid habitats [See Chapter 5.4].

The results indicate unambiguously the dependence of the *Vaccinium myrtillus* cover in the recent forests upon distance between the regenerating patch and the fragments of the ancient forest, in which this species could survive and then from where it could again spread out [See Chapter 5.4].

Numerous species typical of ancient forests return to recent forests the faster the closer the given forest patch is situated to their refuge in the ancient forest. This relation is entirely unambiguous in the case of species reproducing in a vegetative manner, but concerns also the species with various types of seed dispersal [See Chapter 5.5].

The regeneration period of the recent forest and the distance to the species refuge, constituting theoretically independent variables, display in practice a clear relation (recent forests of a longer persistence period are usually more similar to the ancient forests than the recent younger forests), and so exert impact in a cumulative manner on the ancient forests species, returning to the recent forests [See Chapter 5.5].

One can distinguish among the species, composing the FMI sets, two groups of the colonisers: the relatively faster ones, which may appear even after a relatively short regeneration period and even at a significant distance from the refuge, and the very reluctant colonisers, returning very slowly, clearly moving away from the refuge of the given community type. These are the species of the 'short step' [See Chapter 5.5].

One of the best ancient forest indicator species and of the regeneration conditions of recent forest depending upon the forest persistence and distance to the ancient forest is *Convallaria majalis*. This species, even though considered to be endozoochorous, meaning that it could be transported over significant distances away from the refuge, spreads out in practice as if it reproduced mainly in the vegetative manner. Its merit as an indicator results also from the fact that it can play this role for all three types of communities analysed [See Chapter 5.5].

The ancient forests and the recent ones, featuring different persistence periods, differ also as to the average and the distributions of the Ellenberg's indicator values, and in terms of species biological characteristics. Irrespective of community type, the ancient forests, when compared to the recent ones, feature relatively higher shares of the geophytes, autochorous species, and the shade-tolerant species. The recent forests – irrespective of the community type – are characterised by the relatively higher share of the competitive type, *c* species [See Chapter 6].

Soils under the ancient forests (podzolic, rusty with traces of podzolisation, typically rusty, brown and lessive) display the properties, showing that they feature higher biochemical stability than the analogous post-agricultural soils. The post-agricultural soils of the same type differ from the 'natural' soils by their physical and chemical characteristics, depending upon the age and the regeneration period of the forest ecosystems. In the case of the rusty soils under mixed oak-pine forests and the fallow and brown soils with the deciduous forest vegetation it is observed that the longer persistence of the recent post-agricultural forest, the higher quality and biological activity of these soils. On the other hand, the poorest podzolic and rusty soils with traces of podzolisation under the pine forests do not display a clear dependence upon the persistence. This is the consequence of the low buffer capacities of these soils and low resistance to external factors [See Chapter 7].

The results of the partial correlation analysis, aiming at identification of the influence, exerted by the three main factors: persistence, distance and tree stand age, with due account of a number of control variables, on the selected characteristics values of the pine forest (*Peucedano-Pinetum*) phytocoenoses, demonstrate that:

- the FMI index and the cover of *Vaccinium myrtillus*, *Calluna vulgaris* and *Vaccinium vitis-idaea* depend mainly, and strongly, upon persistence and distance;
- the cover of *Convallaria majalis* and *Hylocomium splendens* depends mainly and strongly upon persistence, with a limited modifying influence of distance and tree stand age;
- the number of ancient forest species depends mainly upon persistence and distance, with, however, perceptible modifying impact of tree stand age;
- the cover of *Luzula pilosa*, *Frangula alnus* and *Calamagrostis arundinacea* depends significantly, but weakly, upon persistence, while the slight modifying influence of the tree stand age is stronger than the influence of distance;

- the number of moss and lichen species displays a slight, but statistically significant dependence upon the tree stand age, with no perceptible influence of distance and persistence;
- the total number of species, as well as the numbers of the *Vaccinio-Piceetea* moss species, of shrub species, of herb species, of the *Vaccinio-Piceetea* herb species and of the tree species do not reveal significant correlations with persistence, distance and tree stand age [See Chapter 8.1].

The detailed correlation models between FMI on the one hand and distance and persistence on the other in the recent pine forests (*Peucedano-Pinetum*), mixed oak-pine forests (*Querco-Pinetum*) and the lime-oak-hornbeam forests (*Tilio-Carpinetum*) indicate nonlinear relations between FMI and distance, as well as between FMI and persistence. Joint influence of the two independent variables on the FMI values has a complex character. In all three communities types the decrease rate of the FMI values drops with increasing distance, both in case of stands with longer persistence and those afforested not so long ago [See Chapter 8.2, in particular Figs. 155, 156, 157].

The detailed correlation models of the *Vaccinium myrtillus* cover upon distance and persistence in the recent pine (*Peucedano-Pinetum*) and mixed oak-pine forests (*Querco-Pinetum*) indicate that at not too big distances from the ancient forest (up to roughly 500 m) bilberry appears earlier in the mixed oak-pine forest and attains earlier high cover values, while in the typical pine forest the analogous cover values are attained by about 100 years later. On the other hand, the decrease of *Vaccinium myrtillus* cover with distance is much more pronounced in the case of the mixed oak-pine forests than in the fresh pine forests [See Chapter 8.2, in particular – Figs. 158 and 159].

The detailed models representing dependence of *Convallaria majalis* frequency upon distance and persistence in the recent pine (*Peucedano-Pinetum*) and the mixed oak-pine forests (*Querco-Pinetum*) indicate that at shorter distances to the ancient forest (up to roughly 100 m) the frequencies of the lily-of-the-valley exceeding 10% appear somewhat earlier in the fresh pine forests than in the mixed oak-pine forests, but older sites feature already almost identical frequencies. At the same time, irrespective of the persistence class, in the fresh pine forests the influence of distance stops being significant for the values exceeding 200–300 m, while in the mixed oak-pine forests a regular decrease in *Convallaria majalis* frequency with distance is observed [See Chapter 8.2, and particularly Figs. 160 and 161].

In the framework of the developed scheme of the course of post-agricultural recent forests regeneration, classification was performed of species into the ‘pool of native species’, comprising the groups of species, referred to as fast and lasting re-colonisers, fast but not-lasting colonisers, moderate colonisers, as well as slow colonisers, and the ‘pool of alien species’, comprising such groups as ‘relict’ species, ‘visitor’ species, introduced species, as well as ‘the past witnesses species’ [See Chapter 9, and in particular – Fig. 162].

For purposes of forest management practice a table was elaborated of the probable recent forests disturbance degrees due to incomplete regeneration, depending upon the type of plant community (*Peucedano-Pinetum*, *Querco-Pinetum* and *Tilio-Carpinetum*), as well as persistence and distance. The statements formulated are presented in a non-specialist manner, along with the postulates to forest managing methods providing forest revitalisation. Attention was, in particular, paid to the need of supporting the *Vaccinium myrtillus* regeneration in the recent forests, situated far from the ancient or already regenerated stands [See Chapter 10, and particularly Table 34].

1.5. BASIC CONCLUSIONS

The results collected allow for making a general observation that the most important factor for the spontaneous regeneration of post-agricultural forests is constituted by time, referred to here as persistence.

The results collected allow also for the formulation of the conclusion that in the case of the fresh habitats analysed the fertility of the habitat is to an extent decisive for the regeneration rate of both vegetation and soil. The regularity observed might be described in a simplified manner as 'the poorer the habitat, the slower the regeneration'.

Based on models it can be assumed that on the poorest habitats the regeneration rate is most probably so low that complete regeneration, especially as regards the soli properties, may take many centuries, that is – may exceed the historical time horizon of states and societies.

Main factors, conditioning the regeneration rate of the post-agricultural forests, include distance to the refuge of 'native species'. The respective relation is not represented by a straight line, but is in general terms similar to the logarithmic function. It is also highly probable that one deals in this case not with a 'physical', but with an 'ecological' dependence, incorporating the possibilities and the modes of the propagulae dispersal of individual species, as well as existence of barriers and corridors.

The results confirm the well-known regularity, namely that the regeneration rate of the recent forest depends strongly upon the dominant tree species (usually with human assistance) in the initial phase of regeneration.

The results obtained, demonstrating the correlation of persistence and distance, allow for drawing of conclusion regarding the complexity of regeneration conditions in the post-agricultural forests. These conditions depend, in general terms, upon the landscape structures, including, in particular, the component elements (types of habitats, forms and types of plant community), the spatial structure (e.g. distribution and structure of ancient forest patches), and the historical development of landscape.

Models of regeneration in the pine and mixed oak-pine forests, concerning the important species of *Vaccinium myrtillus* and *Convallaria majalis*, as well as data on other ancient forests species of the may indicate that the role of vegetative reproduction could be dominating in the case of numerous forest species.

The results demonstrate very clearly that the re-establishment of the *Vaccinium myrtillus* population is a very important element in the regeneration of the natural floristic composition and the community structure in the pine forests, and, to lesser degree, also in mixed oak-pine forests.

The conclusion, concerning the complex character of dependence of the *Vaccinium myrtillus* spread upon distance to ancient forest, appears to result from the diversity of the vegetative and generative reproduction, as well as the varied types of its propagulae dispersal. The species in question is highly endozoochorous. It is probable that animals transporting its seeds can be classified into groups, featuring various movement capacities. Possibly, small animals, moving on the ground, are responsible for transport over small distances, while highly mobile animals, such as birds and bigger mammals, are responsible for transport over larger distances.

On the basis of the data comparison from the recent forests growing on post-agricultural land with those from the analysed recent forests, growing on the land that had been temporarily deforested, but not used for agricultural purposes, involving ploughing, it can be admitted that existence of the plough horizon in the soil has an essential significance for the slow return of *Vaccinium myrtillus*. This conclusion is supported by the fact that the cover of *Vaccinium myrtillus* is higher in the recent forests without the plough horizon than on the areas with the plough horizon, given the same persistence (period of regeneration).

In the perspective of forest management practice, it is definitely worth to consider the possibility of supporting the regeneration of the recent post-agricultural forests through introduction of plant species, essential for the regeneration, first of all *Vaccinium myrtillus* in the pine forests.

2. ANCIENT AND RECENT FORESTS IN THE BORDERLAND OF MASURIA AND KURPIE

2.1. THE STUDY AREA – REASONS FOR SELECTION

A large scale outwash area in the north-eastern part of Poland – the only such area in this part of Europe

In the central part of north-eastern Poland, there is situated a large area, very distinct from its surroundings in the composition and the spatial pattern of potential natural vegetation (Matuszkiewicz W. et al. 1995; Matuszkiewicz J.M. 2008a) – Fig. 2. It is a vast outwash area, shaped by the successive glaciation phases. Against the background of the surrounding moraine uplands it features a high share of sandy habitats. This area is also characteristic due to the combination of sandy outwash habitats with peaty valleys of small rivers flowing in parallel from the north to the south, in the direction of Narew river, one of the major tributaries of Vistula river. It can be depicted as a large triangle, with a broad basis in the north and the apex in the southern part. There are two large forest complexes in the northern part of the area, while in the south there is a parallel setting of woods and relatively broader forestless grounds, mainly occupied by meadows.

The unity and the dichotomy of the area – Kurpie and Masuria

The area considered displays, on the one hand, a high degree of unity. This results from the geological structure, domination of the definite basal complex types, types of the potential natural vegetation habitats, and other aspects. The area features a distinct unity in hydrological terms – it belongs in its entirety to the right-hand part of the basin of middle course of Narew river.

On the other hand, though, there are several factors that divide the area into the southern and northern parts. In particular, from the natural point of view there is a significant division between the late-glacial north and the early-glacial south, with and without the lakes, respectively. The line of the maximum reach of the Baltic glaciation crossing the area. The differences between the north and the south are visible in the climate and in vegetation. The natural differences mentioned caused that in physico-geographical and geobotanical regional divisions compiled by different authors, this area is crossed by the boundaries of the very high rank.

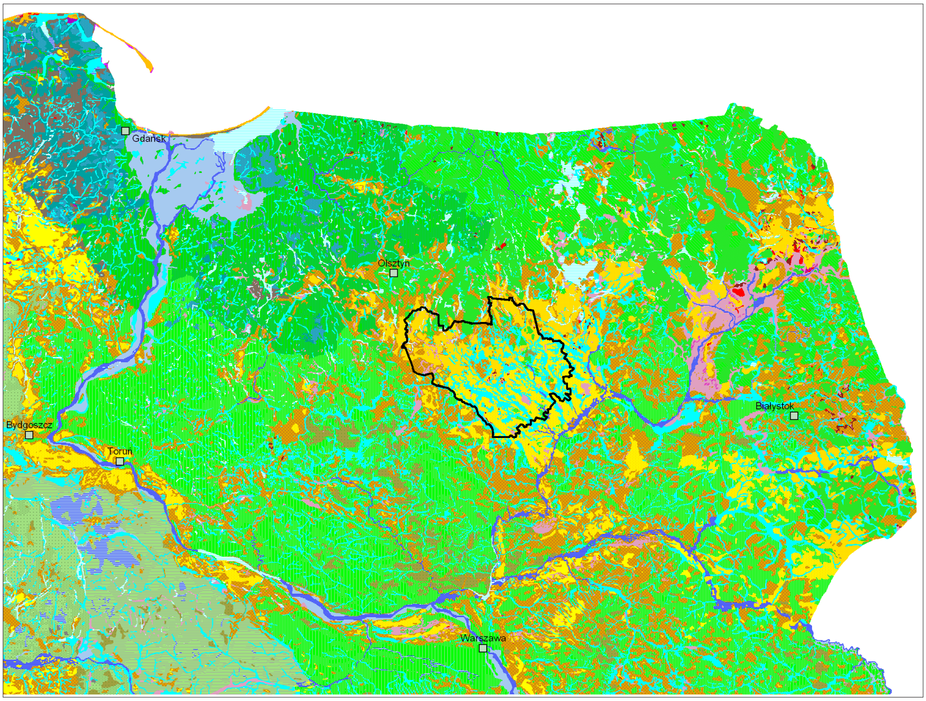


Fig. 2. Location of the study area on the potential, natural vegetation map (Matuszkiewicz J.M. 2008a)

Ryc. 2. Lokalizacja terenu badań na tle przeglądowej mapy potencjalnej roślinności naturalnej (Matuszkiewicz J.M. 2008a)

This natural heterogeneity is overlaid with the surprisingly coincident historical differentiation in the political and social domains. The entire area has been for only 65 years now in one state and is inhabited for the same short period by a relatively homogeneous ethnic-cultural group. Earlier, over at least 1000 years the northern and southern parts functioned separately. The northern part of the study area constituted a fragment of the Prussian territory, understood initially in ethnic terms, and thereafter in political terms, while the southern part is a very specific region of Kurpie, being a fragment of the Polish province of Masovia.

This dichotomous character of the otherwise homogeneous area was very attractive in the research perspective. The actually adopted boundaries of the study area resulted partly from the division of forests into forest districts. The study area was divided into two essential parts:

- Masuria, encompassing the northern part, in its majority of late glacial character, having belonged to Germany before World War II, referred then to as East Prussia (Ostpreussen);
- Kurpie, corresponding to the southern part, of early glacial character, which had belonged to Poland before World War II.

The boundary between the two parts of the study area was adopted according to the secular political border. It had persisted for more than 600 years and has this advantage over the hypothetical natural boundaries of the regions that it is defined in a clear and precise manner.

An area at the periphery of history and progress

The study area, both in its Masurian and Kurpie parts, has had the peripheral character. The settlement processes and the associated transformations in the landscape came here later than on the neighbouring areas. Other kinds of changes also took place here with a delay and in a somewhat weaker form. Owing to this, the area features a number of characteristics of ancient times. This is an advantageous situation for a researcher, especially when looking for past states and the consequences of the processes no longer active.

In particular, the region of Kurpie is the treasure box of various local customs, nonexistent already in other areas. Kurpie preserved, for instance, true living folklore, visible in some elements, such as the settlement system, house construction, folk art. Likewise, the relations between people and nature are in a way conservative there. We can cite two small, but attractive examples of the latter.

Cattle in the forest. One can encounter in some places in the forests of Kurpie cattle (mainly cows), this being the effect of the landscape structure and the ownership structure, owing to which cattle is driven over several kilometres for grazing. Nowadays, of course, the presence of cattle in the forest does not have, any more, the character of regular pasturing, which was still a rule 50 years ago, but it remains a visible element of tradition, kind of a relic of ancient strong anthropogenic pressure, and it might exert a definite impact on forests even today.

Picking of plants in the forests. Whoever wants to see the quintessence of the traditional Kurpie culture, ought to come on the Palm Sunday, a week before Easter Sunday, to Łyse. The parish church of Łyse is then the place of the great competition for the most exuberant Easter Palms, associated with folk picnic. The palms themselves are very tall and beautiful, but a scientist ought to take a closer look at what they are made of. Many of the palms, especially those more traditional ones, are made with the use of forest plants, including the protected club-mosses, *Diphasiastrum complanatum* and *Lycopodium clavatum*. This activity does most probably not play an important role for the existence of these species, quite common in the area, but is a reflection of the very strong pressure, exerted in the past by the village communities on the forests of Kurpie, consisting, in particular, in gathering of brushwood, pine cones, individual plants, as well as raking of needles. The traces of this pressure are still visible. This is a highly interesting possibility of tracking the human pressure in its very primeval form, even if the issue shall remain a side aspect of the present study.

The region of Masuria, more diversified in terms of natural conditions, having featured a very distinct local specificity in social terms before the World War II, has lost this specific character to a large degree, owing to the population movements after the war. On this area of high interest for a naturalist are the very common occurrences of vast afforestation developments on the land previously used for agriculture. The afforestation has been taking place in different periods at least for the last 230 years and encompassed significant area, what has been observed in earlier studies (Matuszkiewicz J.M. et al., 2007). This situation is very advantageous for the analysis of forests regeneration on the past-agricultural land and that is why, in particular, the area considered was selected for the study.

2.2. AN OUTLINE FOR THE SOCIO-POLITICAL HISTORY OF THE STUDY AREA

The socio-political history of the study area, spanning the last millennium, took, for most of this period, a different course in the northern part (Masuria) and in the southern one (Kurpie). This history was both influenced by the local and regional events, as well as, quite often, by the events of the European scale. It is not our aim nor task to provide a detailed description and analysis of these historical events, but for the purpose of our study, at least an abbreviated sketch of the socio-political history seems necessary.

2.2.1. THE HISTORY OF KURPIE

More than 1000 years ago, in the 10th and 11th centuries, the historically identifiable Polish statehood was taking shape under the leadership of the rulers from Piast family, originating from Wielkopolska (‘Greater Poland‘). The first ruler, who became Christian and introduced the nation into the circle of the European culture and history was Mieszko I, and the second, who succeeded to obtain royal crown from the Pope, was Bolesław Chrobry (‘the Brave‘). The state encompassed also the region of Masovia, as a part, featuring a definite ethnic specificity in the set of tribes meant to form later on the Polish nation. The region of Masovia included also the region of Kurpie, though the area was virtually uninhabited and covered with large forests. It was undoubtedly a fringe of the territory of Masovia, but definitely closely associated with it. The cultural and political centres of Masovia were concentrated mainly in the Vistula river valley, initially this was Płock, and thereafter also Warsaw, Czersk and Ciechanów. These were the foci of strengthening of the ducal power, of Christianisation, as well as the socio-economic development.

In the middle of the 12th century, owing to the testament of the seventh Christian ruler of Poland, Bolesław Krzywousty (‘the Twisted-Mouth‘), feudal division of the Polish territory took place, with Masovia becoming practically one of the independent states, ruled by Piasts. Later on, this duchy also underwent divisions. The second ruler after the division in the line of those who reigned in Masovia was the grandson of Bolesław Krzywousty – Konrad I, who must be mentioned in this place, for his role in the history of the lands here considered, especially of Masuria, is extremely important. We should note that a great problem for the potential economic development of Masovia in the 12th and 13th centuries, and especially with respect to its northern part, that is – the areas neighbouring upon the Kurpie was constituted by the plundering attacks of the tribes from the Baltic group (Prusses, Jaćwingi, Lithuanians), inhabiting the areas to the north-east and the north of Masovia. Those peoples, not yet incorporated into the circle of Christian culture and not yet having developed feudal state structures, organised frequent and devastating inroads into the more densely populated areas of Masovia. Three serious aggressions of Prusses took place, for instance, in the years 1219–1222. One of the measures meant to improve the situation in northern Masovia was to bring in the Cistercian monks in 1206. This gave a positive civilisation effect, but did not safeguard against the aggression.

In the 13th–16th centuries the Masovia history was to some extent independent from the history of other Polish territories. Masovia was, namely, not included in the re-integration process of the 14th century, which resulted in the restitution of the unified Polish kingdom (1320) with the capital in Cracow, under the rule of the grandson of Konrad I, king Władysław Łokietek (‘the Ell‘). The independent Masovian duchies persisted until 1526, when the last Masovian Piasts died with no successors and Masovia returned to the kingdom of Poland, ruled from Cracow by the two last elected kings of the Jagiellonian dynasty. Thereafter, since 1596 the capital moved from Cracow to Warsaw and from this place, much closer to the study area, the country, the Commonwealth of Both Nations, i.e. Polish and Lithuanian, was ruled by the successive elected kings. The area of Kurpie, almost uninhabited and still covered with forests, constituted at that time in its majority the royal domain. This meant, in particular, that peasants, living there, and their successors, were not typical villein peasants. Kurpie went through ups and downs of history of Poland along with entire Masovia. In economic terms exceptional losses were borne by the region during the Swedish invasion of 1655–60, after which the economy of Masovia – and of Poland as a whole – has never returned to its previous state and dynamics.

Functioning of the northern Masovia, including Kurpie, in the framework of the Polish statehood terminated at the end of the 18th century with the partition of the Polish-Lithuanian Commonwealth by Russia, Prussia and Austria on the basis of the treaty of October 24th, 1795. Kurpie, together with a large part of Masovia, including Warsaw, became for more than ten years a part of New East Prussia, a newly established part of the Prussian Kingdom with the capital in Berlin. Thereafter a short episode occurred of a half-independent Polish state, called Warsaw Duchy, during the period of Napoleon’s campaigns (1807–1815).

Starting with 1815 Kurpie were a part of the Russian Empire, in the framework of the so-called Polish Kingdom, where the Russian tsar was the king. Initially, Polish Kingdom enjoyed a certain degree of autonomy, which was gradually limited, especially in the years 1832 and 1866, as a consequence of the Polish uprisings. In administrative terms Kurpie belonged to the governorship of Łomża and partly to that of Płock. This situation persisted for a century – until the end of the World War I. Following the end of war Kurpie was incorporated into the sovereign Poland. Except for the episode of the Nazi occupation during the World War II, this situation did not change until now.

The history of Kurpie is in a way linear. It starts with an uninhabited periphery of the Masovian settlement processes, followed by the entry of the population from the south, becoming local residents. This population was in vast majority Polish, Christian, or, more precisely, Roman Catholic. The descendants of this population inhabit, in principle, this area nowadays. They developed a specific folk culture. The area went many times through real hardships – wars, occupations, epidemics, hungers and was extremely poor. Due to this, many of its inhabitants emigrated to North America and to other places. As a consequence of the World War II the Jewish part of the population, exterminated by the Nazis, disappeared. After the war many inhabitants moved to Masuria or to other parts of Poland. Yet, since the time of the first settling there has been no essential ethnic shift on this area. In terms of relations between people and nature – especially as regards deforestation – a definite continuity and lack of clear turning points is also observed.

2.2.2. THE HISTORY OF MASURIA

The history of the territories, referred to here as Masuria, had a different course. One thousand years ago the areas to the north of Masovia were inhabited by the Pruss tribes belonging to the Western Baltic peoples. In the 12th-13th centuries the study area constituted the western fringe of the territory inhabited by the tribe of Sasini, with the majority of the area covered by the virtually uninhabited Galindzka Forest, its name derived from the already previously having disappeared tribe of Galindzi (Długokęcki 2008).

The Pruss society has not developed the state organisms analogous to those that arose in Poland after Christianisation. Prusses lived in tribal communities and would not be lured to adopt Christianity despite the attempts by the Polish rulers and the church hierarchy. This was one of the sources of conflict with the Masovian duchies. On the one hand the expansion of the Polish feudal state and on the other hand the pillaging inroads into the territory of the richer neighbour by the Pruss tribes created a difficult situation. This lasted until the beginning of the 13th century. At this instant we must explain one of the turning points in the history of this region, and, indeed, of Europe.

The Christian Europe of the 12th and 13th centuries was overwhelmed with the vision of crusades. They started in 1096 with the quest for Jerusalem and lasted for two centuries, to end under all aspects in a bad way. According to Norman Davies (2003) *Obsession at the point of regaining the Holy Land lasted for 200 years and ended with a defeat. In the years 1096–1291 seven large crusades were organised and a number of smaller ones*. The zeal for converting by force was, however, so strong, that in various places of Europe crusades were organised on a smaller scale against the faithful of the non-Christian religions. The Pruss tribes did also become the object of small crusades, meant to turn them into Christians (Dygo 2008). This, however, was only the beginning of what was to come.

In 1228 to Masovia, and more precisely to the Land of Chełmno, the representatives of the knightly order having a lengthy name of 'Order of the Hospital of Our Lady of the German House in Jerusalem' came. This order had been active since 1190 in Palestine and has been also trying to acquire strongholds in continental Europe. On April 23rd 1228 Konrad, the prince of Masovia, for whom – and for whose realm – Prusses constituted a serious problem, conferred upon the Order the feudal right to land, motivating this step by the care for salvation of the souls of himself and his parents. This act was the beginning of the power of the Order, and, in fact, a turning point in the history of Europe. The donation from prince Konrad was followed by that from bishop Christian (a missionary bishop for the land of Prusses), done on May 3rd, 1228. In the subsequent years there were also other donations and privileges, which made more precise, but also broader, the rights of the Order in the land of Prusses, issued by the Masovian prince and by the bishop, or by the Pope and the German emperor. It was the task of the Order not only to defend against the Prusses the territory of Masovia and of other Polish lands, but also, as this was put down on January 18th, 1230, by the Pope Gregory XII, to *tear away from the hands of Prusses* their land and to christianise it. A similar objective has been indicated in the so-called 'golden bulla of Rimini', issued by the Emperor Frederic II in 1235 (and antedated to the year 1226), see Dygo (2008).

In theory, within the Land of Chełmno, the Order was to remain the feudal vassal of the Masovian prince, and, conform to the papal bulla of 1234 the state organism, having appeared on the Pruss lands was to be the papal fief. Yet, the actual situation developed otherwise. Norman Davies writes in an abbreviated manner: *The Order (…) pushed relentlessly forward, building successive strongholds and trade outposts – in Toruń (1231), Kwidzyn (1233), Elbląg (1237). In 1295, after the last mutiny of the heathen population, Prussia finally became the Order's state – an independent crusaders' enterprise, established in the very heart of Europe*. The Masurian part of the study area was also included in that state, even though initially as a far periphery.

The Order's state, with the capital in Malbork (Marienburg), and thereafter in Królewiec (Königsberg), persisted within the territory conquered, irrespective of the numerous wars with Poland, until the Order was self-dissolved, and the state secularised, which took place in 1525. The successor was named the 'Duchy in Prussia', and was a vassal of Poland, with the first prince being simply the last of the Grand Masters of the Order, with the seat in Królewiec. He was Albrecht Hohenzollern, who descended from the dynasty of the rulers of Brandenburg (Biskup 2008). Since that instant the history of the former Order's state has been associated with that of Brandenburg, meaning – with Berlin. The territory of the former realm of the Teutonic Knights started to be called Princely Prussia (as distinct from Royal Prussia, which made a part of the Kingdom of Poland), this name later on replaced by East Prussia (Ostpreussen).

The feudal dependence of the Princely Prussia on Poland, which had been anyway quite loose, terminated in 1657 and Friedrich Wilhelm I, called the Great Elector, gained full control over the territory (Salmonowicz 2004). In 1701 the status of the statehood changed and the Kingdom of Prussia was established, with the same ruling dynasty – elector Friedrich III having become king Friedrich I. This dynasty ruled in Prussia, and then in entire Germany until November 28th, 1918. It ended due to the defeat in the World War I, this particular war marking with significant events the study area. Thus, in 1914 the Russian army under general Samsonov and the German one under the field marshal Hindenburg fought there in the great battle called the battle of Tannenberg. World War I was followed by the period of Weimar Republic and then the terrifying period of the Nazi Third Reich. The World War II, started by the Germans, ultimately caused that East Prussia – and Masuria – made the second essential and dramatic turn in its history.

The existence of the German Teutonic Order's state, followed by the German lay state entirely changed the ethnic situation on the territory that we refer to as Masuria, which had been called East Prussia before, and earlier – Princely Prussia, and yet earlier – Order's Prussia. The ancient inhabitants of these areas, the Prusses, quite soon disappeared as a separate ethnic element. In order to replace the Prusses and to increase the population number in these quite sparsely populated areas, successive waves of new population came and were settled during centuries from various parts of Europe, but first of all from the German countries and from Poland. In particular, in the southern parts of East Prussia (that is – on the area of interest to us) the share of the newcomer population from Polish Masovia was dominating. This brought about the development of a definite ethnic group, using a dialect close to the Polish language, the so-called Masurs (since they came from Masovia). At the beginning of the 20th century this group was only partly aware of their national identity and of their association with Poland, so that the plebiscite, organised after the World War I in the southern parts of East Prussia gave in the vast majority of commune the outcome that was disadvantageous for the then reconstructing Poland, re-emerging after the long period of partitions. The inhabitants of those areas preferred a known and stable situation to an uncertain future in the unknown Poland, The situation of the Masur population in Prussia was not particularly bad, it worsened truly only due to the intensive Germanisation conducted by the Nazi authorities. Besides, it should be mentioned that the population of East Prussia, also those of Slavic origin, was in its majority of Lutheran religion (except for the territory of Warmia, i.e. a part of Royal Prussia, which was incorporated into East Prussia only following the partitions of Poland, i.e. at the end of the 18th century). The Lutheran denomination became dominant in Prussia after the period of Reformation and the religious wars that ravaged Prussia in the 17th century.

Thus, if we looked at the study area on the side of East Prussia on the eve of the World War II we would see the towns inhabited almost uniquely by the German population and the countryside, inhabited in its majority by the Masur population, speaking a dialect of Polish language. Thus, for instance, in the village of Małga, in 1912, the sole existing there Evangelical parish was inhabited by 769 persons, of whom 671 (87%) were Masurs. According to the data of 1890 and 1910 in the German counties of Szczytno (Ortelsburg) and Nidzica (Neidenburg) Polish (Masur) population constituted at least 72–79%. The situation might have been quite similar just before the World War II, although this can hardly be demonstrated, since the explicitly falsified statistics as of 1939, presented by the Nazis, show 100% of the German population in both these counties.

The political stability of the territory of Masuria over quite a long time period did not, however, mean that there was a steady relation between the population and the environment. Without entering the details of the socio-economic history it must be noted that these areas went through a series of events which resulted in changes concerning population, and, which is of special interest for us – in the intensity of deforestation. These events were constituted by, on the one hand, the settling of the area by the local and the newcomer populations in the framework of the colonisation processes, and – on the other hand – the events of depopulation due to pests, hungers, and, in a particular manner, wars. Significant population losses occurred on the area, for instance, due to the invasion of the Tatar troops under Polish banner, led by the Lithuanian Hetman Gosiewski in 1656, then during the Napoleon's wars, in the World War I, and, of course, the World War II. Likewise, the economic crises, especially those of the 19th century, impacted on the proportion between the agricultural and forest land. Starting with the virtually uninhabited Galindzka Forest of the time, when the Teutonic Order was establishing their state, the area in question underwent an evolution toward the landscape, in which, at the beginning of the 19th century, the forestless land dominated, with the forests concentrated mainly in the complexes constituting royal property.

The study area in its East Prussian part was being settled mainly from the North (e.g. Szczytno around 1360, Jedwabno around 1380), which was connected, on the one hand, with the appearance of better soils there, formed on the moraine structures, than on the outwash forms in the south, but also, on the other hand, with the fact that the centres of the Teutonic Order's state were to the north and west of the area. Thus, in the parts situated farther south the settlement system commenced later, although even there the villages are noted that appeared already in the 14th century, like the village of Małga, mentioned in the documents dated for 1343, as well as Kucbork (1374), Wielbark (1361) and others. The settlement system developed on a larger scale within this part of the area later on, in the 18th century, like, for instance, the village of Wały, established on the formerly afforested land, with formal date of location on September 19th, 1708. In 1756 this village was inhabited by 23 families, and in 1933 it had 399 inhabitants. It is worth noting that when one analyses the map from the year 1800, one concludes that almost all of the villages existing today were there already 200 years ago, and even there were a bit more of them.

The end of East Prussia as a part of Germany and its division between Poland and the Soviet Union was initially decided in general terms at the conference of the allies in Teheran in November 1943, and then in details in the agreement between the Polish temporary administration, formed by the communists (Polish Committee of the National Liberation), and the Soviet authorities in Moscow on July 27th, 1944. The actual implementation of this plan occurred owing to the offensive of the Red Army, which started in the middle of January 1945. It was an apocalypse for East Prussia, bringing about destruction unprecedented in its scope and intensity, especially in towns, and enormous losses among the civilian population.

As the military operations ended, the southern part of East Prussia was taken over, after some period of time, by the Polish administration, while the German population was forced to leave, conform to the stipulations of the Potsdam Conference. The Masurian population could stay, but an important part of them left, anyway, if not during and just after the war, then later on, especially during the 1970s. When this territory, called henceforth Masuria (in Polish: Mazury), had been taken over by the Polish administration, movements of Polish population took place, coming from different directions, with particularly significant groups of settlers having moved from the region of Vilnius, incorporated into the Soviet Union after the war. There were also numerous spontaneous movements of the population from Masovia, especially from Kurpie. The territory of Masuria accommodated also significant groups of the Ukrainian (Ruthenian) population, forced to move from the south-eastern Poland. These demographic changes, coupled with the complete change of the socio-economic system, brought almost complete shift in ethnic and cultural, as well as economic terms in the study area. One of the consequences consisted in the widespread afforestation of the agricultural plots.

The end of war and the ensuing mass movements of the population did not terminate the great changes within the Masurian part of the study area. Even though the changes that we shall be commenting upon now had only a local reach, but, regarding their intensity and depth of influence on the environment and population, they were more significant than war. We mean the establishment of a large military exercise facility in the 1950s. For this purpose several villages were resettled, whose inhabitants, both native and newcomers, were then just regaining normality after the war. The biggest of these villages was Małga, an important village, known from the documents dating back to 1343, in 1885 inhabited by 700 persons. There was a church in this village already in 1579 (since 1900 as a brick structure). The village went through dramatic moments on January 20th, 1945, but started to come back to life afterwards. The resettlement mentioned entailed abandonment of fields and partly spontaneous afforestation. The military area functioned until the 1980s, constraining the forest economy and having a specific impact on the vegetation cover. More important afforestation took place only during the last two decades. Yet, a part of the open space is in a way artificially (i.e. without an economic reason) maintained to protect habitats of some bird species, in the framework of Natura 2000 programme.

2.2.3. THE BOUNDARY

Thus, the study area has been split between two different state organisms for the majority of the time period here considered. The boundary that divided it belonged among the exceptionally persistent ones in the history of Central Europe (Plit 2006). It is, of course, hard to unambiguously delineate the course of the boundary between Masovia and Prussia before the 13th century, since the respective areas were virtually uninhabited. The boundary fortifications (earth banks) made by Mazovian sovereigns are still observed in the area e.g. in the vicinity of Wały village, Jedwabno forest district (Kowalczyk 2003). Yet, the documents from the years 1335–1343 provide rather precise information on the subject, and the delimitation due to the 'Toruń Peace' of 1466 is quite certain. Since that time the course of the boundary was stable, until the end of World War II (Fig. 3). So, it can be assumed that the boundary lasted for at least 600 years. It lost significance only after World War II. In general terms, the course of this boundary was followed in the consecutive administrative divisions of Poland after the war. Yet, there were some places, where the boundaries of municipalities – and hence also of counties and provinces – did not follow the historical state boundary. On the other hand, the boundaries of the forest districts follow more accurately (even though not everywhere, as well) this historical line. This ancient line is still visible in the field in many locations, in the form of various landscape elements (earth banks, ditches, mounds).

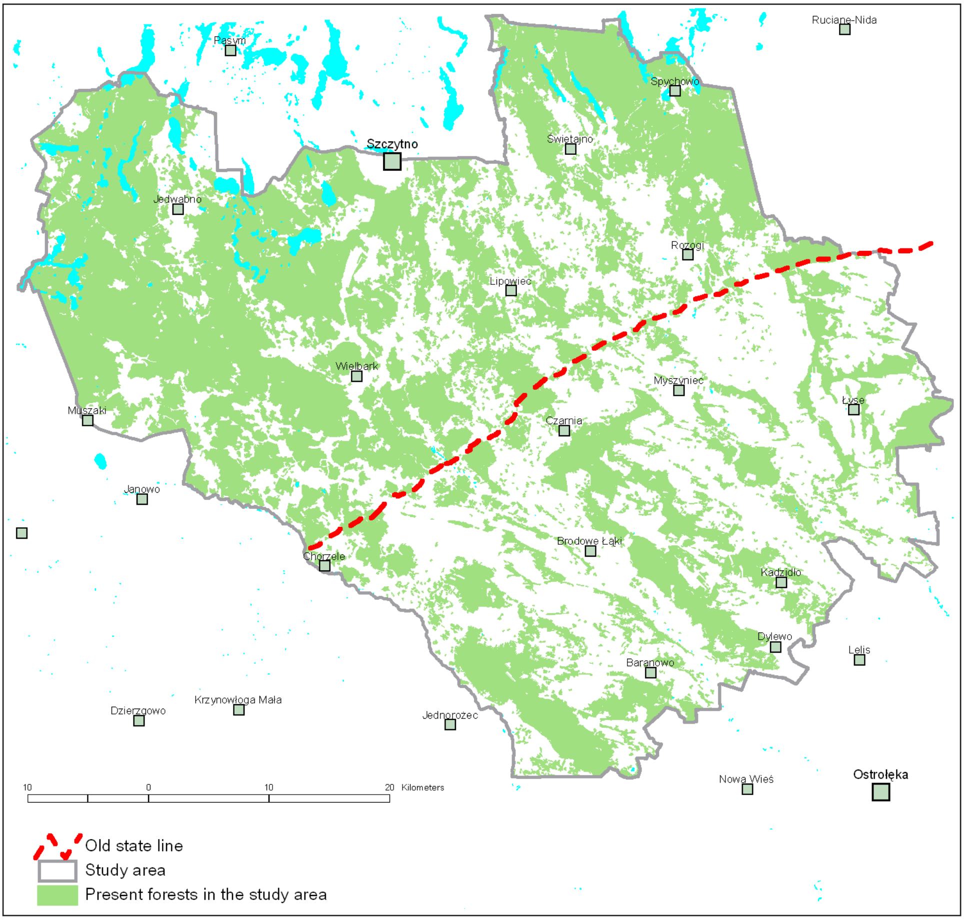


Fig. 3. Historical border between East Prussia and Mazovia in the study area
Ryc. 3. Historyczna granica między Prusami a Mazowszem na badanym terenie

2.2.4. THE HISTORICAL STATE OF THE TERRAIN AT THE MAPS DOCUMENTING FOREST AREAS

The reaches of forests analysed in the study here reported are based on topographic maps from various periods. The oldest ones showing sufficiently precisely the area of East Prussia date from around 1730. This is the period of rule (since 1713) of Friedrich Wilhelm I, called king of soldiers, who founded the military power of Prussia, but also a dozen or so years since the introduction of obligatory schooling in Prussia (since 1717). The subsequent maps, used by us, both for the Masurian and the Kurpie parts, date from the years around 1800. At that time Prussia incorporated northern Masovia – including Kurpie – according to the 3rd partition treaty of October 24th, 1795, between Prussia, Russia and Austria. This third partition treaty formally terminated more than 800 years of Polish statehood. The area newly acquired by Prussia formed a part of the so-called New East Prussia. This was the time of the rule of Friedrich Wilhelm II, the successor to the reformer Friedrich II the Great. It is starting with that instant that we shall be analysing in this study the changes in the forest cover, to a large extent associated with the previous and the subsequent history.

The consecutive time point considered is – nominally – the year 1830. In political terms it was a period of stabilisation after the Vienna Treaty of 1815. The area was split between Prussia of the Hohenzollern and the Polish Kingdom, being a part of the Russian Empire of the Romanovs. Then, in the next time point of 1885 the situation was similar.

In the period of the 1920s the northern part of the area belonged to East Prussia of the Weimar Germany. The southern part belonged to Poland. The subsequent analysed cases of 1950, 1970 and 2000 were placed in the period, when the entire study area has belonged to Poland.

2.3. PHYSICO-GEOGRAPHICAL CHARACTERISTICS OF THE AREA

2.3.1. SPATIAL EXTEND OF THE STUDY

The study area was delimited (see Fig. 3) within a vast outwash area, covered to a large extent by the extensive forest complexes, referring to the research that had been conducted there earlier (Matuszkiewicz et al., 2007). The study area encompasses 2 843,7 km^2 and is located between the geographical coordinates from 53,10^o to 53,67^o of northern latitude and from 20,53^o to 21,69^o of eastern longitude. This area covers entire five state forest districts: Jedwabno, Szczytno, Wielbark, Spychowo and Myszyniec, as well as an important part of the forest district of Parciaki, and some fragments of the district of Korpele.

From the point of view of the physico-geographical regionalisation (Kondracki, 1991) the study area occupies the border zone of two regional units of highest rank in the division of Europe, namely Western and Eastern Europe (Fig. 4). The regional division in the international setting for the investigated fragment of Europe is as follows:

3 – Subarea: Extra-Alpine Central Europe
31 – Province: Central European Plain
318 – Subprovince: Central Polish Plains
    318.6 – Macroregion: Northern Masovian Plain
    318.65 – Mesoregion: Kurpie Plain – where the middle and the southern parts of the study area are situated

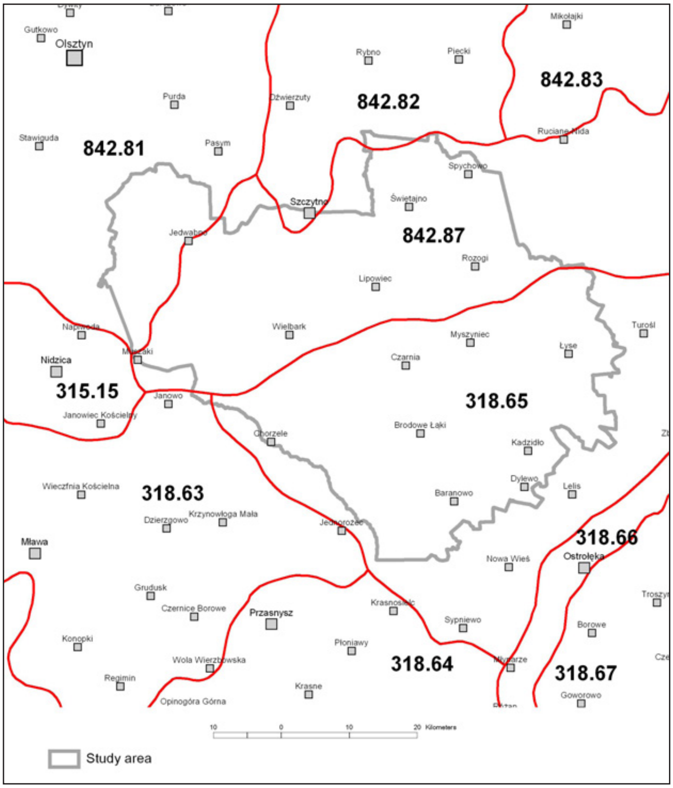


Fig. 4. Location of the study area – regional divisions (Kondracki 1994)

Ryc. 4. Regionalizacja fizycznogeograficzna badanego terenu (Kondracki 1994)

8 – Subarea: Eastern European Plain

84 – Province: Western Russian Plain

842 – Subprovince: Eastern Baltic Lakelands

842.8 – Macroregion: Masurian Lakeland

  842.81 – Mesoregion: Olsztyn Lakeland – where the north-western part of the study area is situated

  842.82 – Mesoregion: Mrągowo Lakeland – where fragments of the study area in its northern part are situated

  842.87 – Mesoregion: Masurian Plain – where an important portion of the study area in its northern part is situated

Regarding the geobotanical regionalisation (Matuszkiewicz J.M., 2001, 2008b) the study area represents the interface of two high ranking regions, i.e. the geobotanical divides (Fig. 5), and within them – the interfaces of two regions and subregions of Kurpie and of Masuria-West. We list below the units of the geo-botanical regionalisation, which pertain to a greater or lesser extent to the study area:

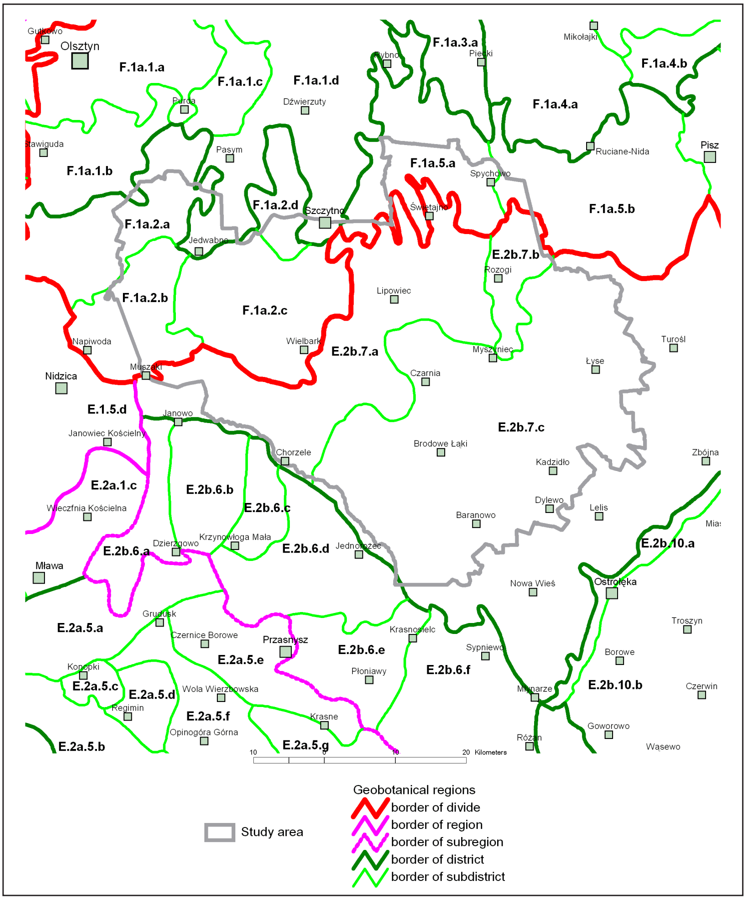


Fig. 5. Location of the study area – geobotanical regions (Matuszkiewicz J.M. 2008b)
Ryc. 5. Regionalizacja geobotaniczna badanego terenu (Matuszkiewicz J.M. 2008b)

E. Masovian and Polesye Divide
E. Masovian Subdivide
  E.2. Northern Masovian-Kurpie Region
    E.2b. Kurpie Subregion
    E.2b.7. Green Kurpie Forest District
      E.2b.7.a. Chorzele-Lipowiec Subdistrict
      E.2b.7.b. Myszyniec Ridge Subdistrict
      E.2b.7.c. Kurpie Plain Subdistrict
F. Mazurian and Belarusian North Divide
  F.1. Masuria Region
  F.1a. Masuria-West Subregion

- F.1a.1. Olsztyn-Szczytno District
  - F.1a.1.d. Pasym-Szczytno Subdistrict (fragments)
- F.1a.2. Napiwodzka Forest District
  - F.1a.2.a. Maróz-Kośno Subdistrict
  - F.1a.2.b. Omulew-Muszaki Subdistrict
  - F.1a.2.c. Piduń-Wielbark Subdistrict
  - F.1a.2.d. Kobylocha Subdistrict
- F.1a.5. Pisz Forest District
  - F.1a.5.a. Babięta Subdistrict
  - F.1a.5.b. Nida Subdistrict.

2.3.2. MORPHOLOGY OF THE STUDY AREA

The study area constitutes a vast and flat outwash plain with numerous dunes, systematically cut across by the valleys of small rivers, tributaries of Narew, of NW–SE orientation. The absolute altitudes, spanning some 130 metres of difference, range from 100 m a.s.l. in the Rozoga valley to 230 m a.s.l. in the north-western part of the study area (Złote Góry – 228,6 m). Moraine islands crop out from beneath the outwash formations, along with the weathered frontal moraines, constituting the marginal forms of the Leszno stage of the Baltic ice period. Existence of the outwash is associated with the Poznań and Pomeranian glaciation stages (Fig. 6).

The area considered, referred to by Galon (1972) as the Kurpie Forest, even though quite uniform in terms of the natural landscape type, is composed of two different genetic forms. In the northern part the outwash material reside over the moraine forms of the last glaciation, while in the melt-out basins having appeared after the outwash material settled, lakes occur. In the southern part, more monotonous, the outwash forms lie on the older Pleistocene sediments, originating in the middle Polish glaciation. Hence the division within the framework of a relatively homogeneous outwash land into two regional units of the rank of mesoregions (Kondracki, 2002) – the northern Masurian Plain, classified as late glacial, and the early glacial Kurpie Plain (Fig. 4).

The southern boundary of the Masurian Plain is vague, indicated by the moraine mounds of Leszno stage in the vicinity of Chorzele and to the east of Wielbark, in Rozogi and Faryny (Kondracki, 1972). To the north of these moraine mounds, within the confines of the outwash, numerous boggy hollows exist, having the character of melt-out pots, and to the East of Szczytno – also lakes (Walpusz, Marksoby, Nożyce, Świętajno, Zyzdrój, Spychowskie, Zdrożno and Kiprwik). Along the ancient course of the outflow of waters from the melting glacier, the rivers Omulew, Szkwa, Rozoga and Pisa flow

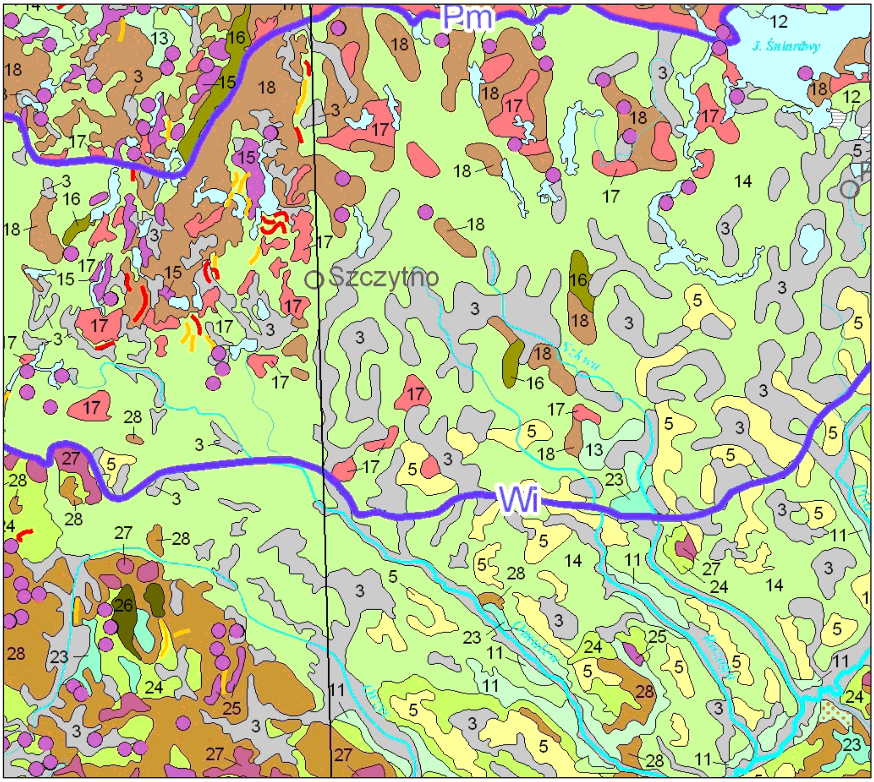


Fig. 6. Geomorphological structure of the study area (*Geological map of Poland* 1:500 000). Wi – last Glacial (Vistulian) Maximum; Pm – The Pomeranian Phase of Vistulian Glaciation limit. Holocene: 3 – Fluvial sands, gravels, mud, peats and organic sits; 5 – Eolian sands, locally in dunes. Pleistocene: 11 – Fluvial sands, gravels and sits; 12 – Lake sands and sits; 13, 23 – Ice-dam clays, sits and sands; 14, 24 – Outwash sands and gravels; 15, 25 – Came sands and sits; 16, 26 – Esker sands, sits and gravels; 17, 27 – End moraine gravels, sands, boulders and tills; 18, 28 – Tills, weathered tills, glacial sands and gravels.

Ryc. 6. Zarys budowy geomorfologicznej badanego terenu (*Mapa geologiczna Polski* 1:500 000). Wi – zasięg zlodowacenia Wisły; Pm – Zasięg fazy pomorskiej zlodowacenia Wisły. Holocen: 3 – Piaski, żwiry, mady rzeczne oraz torfy i namuły; 5 – Piaski eoliczne, lokalnie w wydmach. Plejstocen: 11 – Piaski, żwiry i mułki rzeczne; 12 – Piaski i mułki jeziorne; 13, 23 – Iły, mułki i piaski zastoiskowe; 14, 24 – Piaski i żwiry sandrowe; 15, 25 – Piaski i mułki kemów; 16, 26 – Piaski, mułki i żwiry ozów; 17, 27 – Żwiry, piaski, głazy i gliny moren czołowych; 18, 28 – Gliny zwałowe, ich zwietrzeliny oraz piaski i żwiry lodowcowe.

southwards to Narew. They cross the sandy, monotone Kurpie Plain, within which, on the low watersheds between valleys, dunes appear. There are also places, where from beneath the sands older formations emerge, the moraine forms of the Wkra stage of middle Polish ice period (Różycki 1972).

Over the entire area sandy surface forms dominate (*Szczegółowa mapa geologiczna Polski* 1:50 000). These are mainly the outwash sands and gravels, brought by waters flowing from the front of the melting glacier. In the river valleys sands, gravels and river silts are deposited. A large area, especially in the southern part, is occupied by the wind-blown sands, forming tall dunes in some places. Peat, sometimes of quite important thickness (the peat-bogs of Karaska and Serafin), appears in the numerous melt-out basins. This peat is commonly industrially exploited. Locally, larger surfaces are occupied by the sands, loam and silts of the melt-out and marginal origin. Moraine structures are formed by the boulder clays, as well as sands, gravels, boulders and tills moraines.

2.3.3. CLIMATE

The difference between the Masurian and Kurpie Plains has a counterpart in the climatic conditions (Matuszkiewicz 2001). In order to characterise the climatic conditions one can use the data from two weather stations: the one located at the northern fringe of the study area, in Szczytno, and the second, situated to the south-east of the boundary of the study area, in Ostrołęka (Table 1).

Table 1. Selected climatic data – characteristics of the study area

Name of the station	Szczytno	Ostrołęka
Latitude	53.34	53.05
Longitude	21.02	21.34
Mean annual temperature	6.5	7.1
Annual amplitude	22.0	22.3
Ewert's climate continentality index (Ewert 1972)	49.1	50.2
Number of days with min. < 0	144	128
Number of days with max < 0	54	49
Number of days with min. < -10	33	27
The lowest absolute min.	-31.3	-30.2
Number of days with max > 25	28	36
Number of days from last to first ground frost	125	155
Number of days with mean temperature over 10	149	155
Number of days with mean temperature over 15	88	99
Mean annual precipitation [mm]	610	555
Winter precipitation [mm]	115	109
Spring precipitation [mm]	122	119
Summer precipitation [mm]	234	197
Autumn precipitation [mm]	139	130
Number of days with snow cover	90	83
Ellenberg's index acc. to Ellenberg 1978	28.4	32.6
Pluviothermal index acc. to Matuszkiewicz 2001	37.5	19.6

Source: authors' study according to *Chomicz (1977)*

Regarding thermal conditions it can be stated that the northern part features lower average annual temperature – and especially lower temperature of spring and summer (Fig. 7). All the other indicators, shown in Table 1 confirm the cooler climate in Szczytno than in Ostrołęka:

- the number of days in which temperature falls below zero centigrade is bigger by more than a fortnight,
- the number of days, during which temperature is below zero over the entire day, is bigger by five,
- the number of days, during which temperature falls below –10 centigrade, is bigger by a week,
- the period between the last and the first frost is shorter by as much as a month,
- the growing season is shorter by roughly a week,
- the snow cover lasts for a week longer.

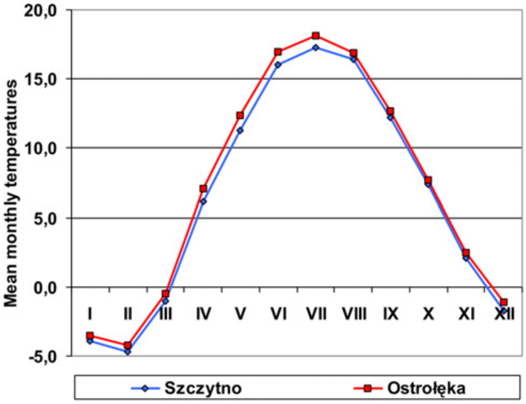


Fig. 7. Thermal conditions in the study area (according to data of Chomicz 1977 from 1951–70)

Ryc. 7. Charakterystyka warunków termicznych terenu badań (na podstawie danych z: Chomicz 1977 za lata 1951–70)

Annual temperature amplitudes and the climate continentality index, following Ewert (1972), suggest a weakly continental character of climate, somewhat more continental than in Ostrołęka, even though the latter is located further east.

Concerning precipitation, it can be noted that it is higher in Masuria than in Kurpie (Fig. 8). This applies to the average annual precipitation, but particularly so – the summer (June-August) precipitation, especially significant for plant growth (Table 1).

It is worth paying attention to two climatic indicators, following Ellenberg and following Matuszkiewicz. The one proposed by Ellenberg (1978), the indicator of beech growth capacity, is based on the data on the mean temperature of July and the annual total precipitation. When its value falls below 30, the conditions should be advantageous for beech, when it exceeds 30, the conditions are disadvantageous. In the case of the two weather stations, the indicator shows the advantageous conditions in Szczytno, and disadvantageous in Ostrołęka.

Now, the pluviometric indicator, proposed by J.M. Matuszkiewicz (2001) is based on the data on monthly averages of precipitation and temperature for the months from May to September – the higher the indicator, the more humid the climate during the growing season. In the case of the two weather stations compared here the indicator shows a much more humid climate in Szczytno. The value of this indicator exceeding 35 in Szczytno marks the conditions convenient for the development of beech forests, while the value well below this threshold in Ostrołęka indicates – conform to the actual situation – the climate too dry for the beech woods.

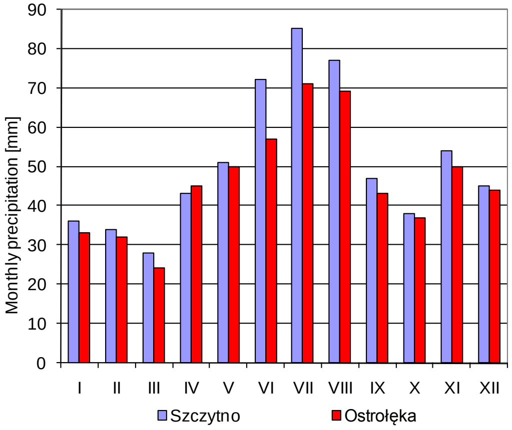


Fig. 8. Precipitation in the study area (according to data of Chomicz 1977 from 1951–70)

Ryc. 8. Charakterystyka opadów atmosferycznych na terenie badań (na podstawie danych z: Chomicz 1977 za lata 1951–70)

2.4. SPATIAL AND TYPOLOGICAL DIFFERENTIATION OF HABITATS AND VEGETATION

2.4.1. GENERAL DIFFERENTIATION OF THE PLANT COVER

Masurian Plain is to a large extent afforested, and the Kurpie Plain was in older times covered by the Green (Kurpie) Forest, but it was strongly felled and woods persisted mainly on the dunes. Vast valleys are covered nowadays with wet meadows, and agricultural cultivation is limited to sandy plains and loamy mounds. On the sandy outwash covers the habitats of pine forests and mixed oak-pine forests developed. They endow the landscapes of the Kurpie Forest with characteristic features and are in the majority covered with forest communities. Pine forests are associated mainly with the wind-blown sands and dunes, mixed oak-pine forests – with the sands brought by waters from the melting glacier. Boreal forest communities, containing spruce, are also encountered within the study area on the same type of habitat.

Pine forests grow within the study area on the dry to wet, or even boggy habitats. The biggest area (roughly 15% of the entire area) is occupied by the continental fresh pine forests (*Peucedano-Pinetum*), in the northern part of the Kurpie Forest – in the subboreal variant (with spruce), while in the southern part – in the Sarmatian variant. Their stands are formed by Scots pine, the undergrowth is mossy-dwarf shrub. The driest parts of dunes are overgrown with the dry pine forest (*Cladonio-Pinetum*), lichens, and, of course, mainly cup-mosses, playing an important role in its undergrowth. The potential habitats of this type of pine forest are much smaller when compared to the actually occupied area, since the anthropogenic degenerate forms of the fresh pine forests are frequently similar to the poor, dry pine forests. Within the study area a bigger patch of the potential dry pine forest, amounting to roughly 0.04% of the entire area, exists in only one place, between Czarnia and Zieleniec Duży. On the wet habitats, moist pine forest with moor grass (*Molinio coeruleae-Pinetum*) grows, smaller patches of this forest type being dispersed across the entire area among the fresh pine forests, altogether accounting for roughly 0.53% of the total area. Stands in this type of forest are composed of pine and two species of birch; the undergrowth has the grassy-dwarf shrub character.

In the local depressions of the terrain, filled with peat, habitats develop proper for the bog pine forests (*Vaccinio uliginosi-Pinetum*), which appear there in two subdivisions – as the typical sub-association and the sub-association with moor-grass (*Molinia caerulea*). These are small area associations, occurring rarely, somewhat more frequently in the northern part of the area, covering altogether about 0.2% of the whole area. The stands are low, thin, formed by the Scots pine and the mossy birch.

The habitats of the mixed oak-pine forests (*Querco roboris-Pinetum*) occupy the area almost twice as big as the fresh pine forests (approximately 29.9%). Nowadays, these habitats accommodate both forest associations, conform to the type, and the pine monocultures, as well as dry sand grasslands (*Sileno otitis-Festucetum, Festuco psammophilae-Kolerietum glaucae*), dry heaths (*Calluno-Genistetum*), and the poor mat-weed grasslands (*Polygalo-Nardetum*). Within the study area it is also not uncommon to have arable lands on the habitats of the mixed oak-pine forest, and in some places in these fields, especially of rye, there are well-preserved segetal communities *Arnoserido-Scleranthetum*. The mixed oak-pine forests of this area are divided among the typical (fresh) subassociation and the moor grass (moist) one.

In the northern part of the area there are locations, featuring specific habitat conditions, where coniferous and mixed forests have subboreal character. These cases are the ones of subboreal spruce forests (*Sphagno girgensohni-Piceetum*), moist mixed oak-spruce forest (*Querco-Piceetum*) and subboreal mixed oak-pine forest (*Serratulo-Pinetum*). The two former associations, with a share of spruce, appear on the moist mineral or peaty soils, primarily in the north-eastern part of the study area, and occupy only about 3% of its acreage. Likewise, within the north-eastern fringe of the study area, but on the dry and mesotrophic habitats, the subboreal mixed oak-pine forest grows (*Serratulo-Pinetum*), whose species composition contains, side by side with the brushwood and moss species typical of the pine forests, also those characteristic of the thermophilous oak forests and the forest edge associations, as well as of the grassland associations.

The more fertile habitats, linked with the moraine forms, and also with the marginal and melt-out sands and silts, belong to the potential lime-oak-hornbeam forests (*Tilio-Carpinetum*), occupying approximately 34% of the study area. Currently, these habitats are mostly (especially as regards the Kurpie Plain) used for arable lands, where the association *Vicietum tetraspermae* appears in the cereals and the lowland hay meadows (*Arrhenatherion*), with the mass appearance of *Holcus mollis*, and only in the north of the study area the proper lime-oak-hornbeam forests are encountered. A vast majority of the potential habitats is covered by the poor lime-oak-hornbeam forests of the reed-grass subassociation (*calamagrostietosum*) and the poor form of the typical lime-oak-hornbeam forest (*typicum*). Small eutrophic habitats of typical lime-oak-hornbeam forest occur rarely in the north-eastern part of the study area. On the fine-grained glacial and fluvial sands and the melt-out silts the habitats of the moist lime-oak-hornbeam forests developed, mainly from the subassociation of *stachyetosum*.

In few places within the north-western part of the study area, on the fresh forest habitats, beech forests are encountered, constituting, perhaps, the marginal sites of the acidophilous beech forests *Luzulo pilosae-Fagetum*; the documented sites of the lowland beech forests, considered until now to be marginal, are situated near to the study area.

Vast river valleys constitute the habitats of alder and ash-alder forests. They occupy almost 19% of the study area. The habitats of the ash-alder forests (*Fraxino-Alnetum*) are linked with the flat valleys of slowly flowing rivers and streams on low peats and alluvial soils. They also appear on the place of the former alder forests as the vast peaty areas are cut across by the drainage system, and the water flow as well as peat mineralisation processes are triggered off. Currently, the majority of the riverine forest habitats in the Kurpie Forest have been deforested and are used as wet mowed meadows and pastures (*Angelico-Cirsietum oleracei, Cirsietum rivularis*) with the fragments of tall herb communities (*Filipendulo-Geranietum*), sedge communities (*Magnocaricion*), as well as rushes (*Phragmition*), and clumps of alders and willows. Remnants of the forests persisted only in the form of narrow belts along rivers and smaller patches within forest complexes.

Wetlands areas, with peat layer, constitute the habitats of alder fen forests, differentiated as to their fertility among the eutrophic currant alder swamps (*Ribeso nigri-Alnetum*) having tuft-mosaic undergrowth structure, the mesotrophic peat moss alder forests (*Sphagno squarrosi-Alnetum*) with alder, mossy birch, and less distinctly expressed tufty undergrowth structure, as well as the subboreal swampy birch forests (communities of *Betula pubescens – Thelypteris palustris*). These habitats, amounting to roughly 3% of the total area, are currently only partly occupied by forest communities, frequently in the degenerate form. The deforested areas are overgrown by the associations of the moss-sedge peat bogs (*Scheuchzerio-Caricetea nigrae*) and the rushes (*Phragmition*). In some depressions without outflow, on poor soils, amidst vast areas of peat lands, the morass associations develop (*Ledo-Sphagnetum magellanici*) with sparse and very low pine stands.

2.4.2. SPATIAL PATTERN OF THE POTENTIAL NATURAL VEGETATION

Spatial heterogeneity of the potential natural vegetation was determined on the basis of the map, elaborated within the study framework. This map was prepared in the digital form on the topographical base on the scale of 1:25 000. Its simplified version is shown in Figure 9. It is easily visible that the most important are the habitats of four forest associations (Table 2): *Tilio-Carpinetum*, *Querco-Pinetum*, *Fraxino-Alnetum* and *Peucedano-Pinetum*. These habitats occupy approximately 95% of the entire area. As we assign the habitats to the corresponding systematic classes of associations (Fig. 10), we can conclude that there is an almost equal division among the habitats from the class of *Querco-Fagetea* (close to 50%) and those from the class of *Vaccinio-Piceetea* (a bit over 46%).

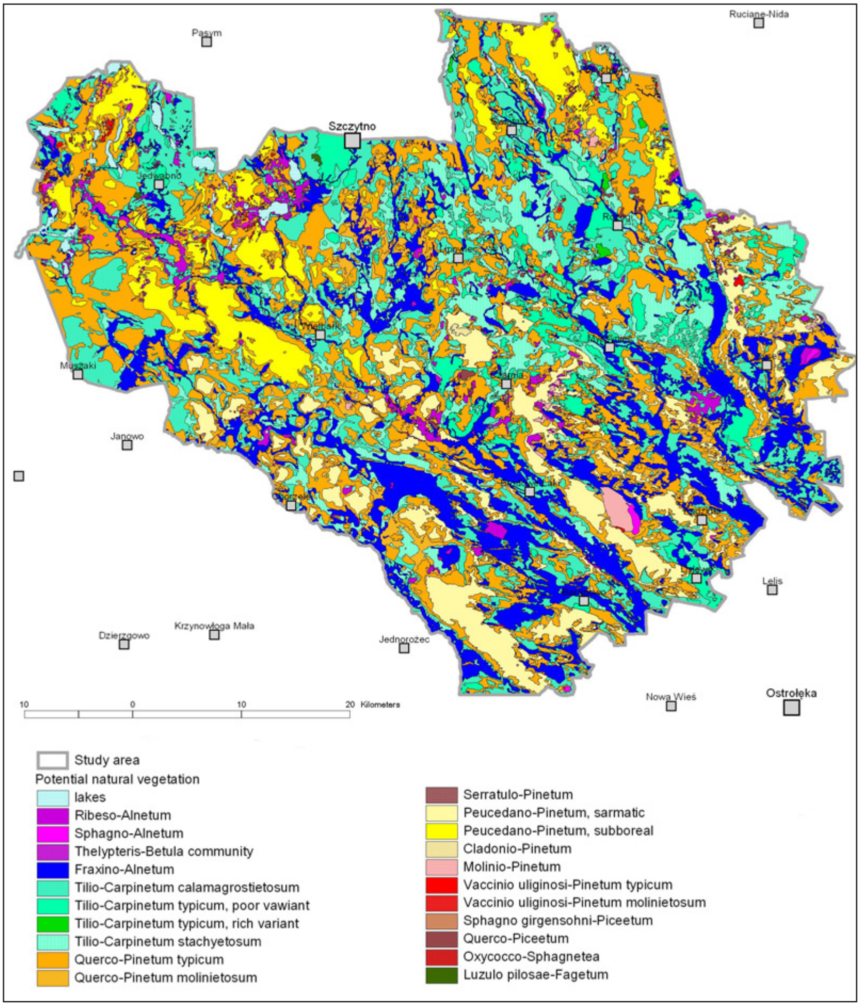


Fig. 9. Detailed map of potential natural vegetation
Ryc. 9. Mapa szczegółowa potencjalnej roślinności naturalnej

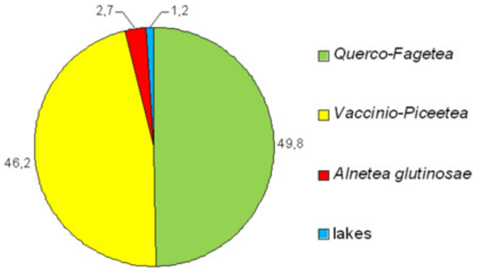


Fig. 10. Potential natural vegetation – spatial share of classes of plant communities
Ryc. 10. Potencjalna roślinność naturalna – udział typów w podziale na klasy zbiorowisk

There is a visible difference in the potential natural vegetation structure between Masuria and Kurpie. Within the Masurian part the inventory of the associations is somewhat richer, since it contains, on the one hand, the associations of the subboreal character (*Querco-Piceetum* and other), and – on the other hand – the associations of Atlantic character (*Luzulo-Fagetum*). The shares of basic habitat types are also somewhat different (Fig. 11). On the area of Kurpie the share of the lime-oak-hornbeam forests (*Tilio-Carpinetum*) and of the mixed oak-pine forests (*Querco-Pinetum*) is relatively lower than in the Masurian part, while the share of riverine ash-alder forest habitats (*Fraxino-Alnetum*) is much higher. The shares of typical pine forests (*Peucedano-Pinetum*) are similar.

Table 2. Share of potential natural vegetation types

Habitat name	Area [sq km]	Habitat share [%]		
		the whole area	Mazury	Kurpie
Lakes	34,1	1,20	2,15	0,02
Ribeso nigri-Alnetum	70,9	2,49	2,98	1,89
Sphagno squarrosi-Alnetum	5,9	0,21	0,19	0,23
Betula pubescens - Thelypteris palustris community	0,4	0,01	0,02	-
Fraxino-Alnetum (=Circaeo-Alnetum)	452,4	15,91	9,92	23,32
Tilio-Carpinetum calamagrostietosum	481,7	16,94	19,97	13,20
Tilio-Carpinetum typicum	168,6	5,93	5,19	6,85
Tilio-Carpinetum stachyetosum	313,5	11,02	11,70	10,19
Tilio-Carpinetum (all)	963,8	33,89	36,85	30,23
Querco roboris-Pinetum typicum	740,7	26,05	28,40	23,13
Querco roboris-Pinetum molinietosum	109,6	3,86	3,76	3,97
Serratulo-Pinetum	0,8	0,03	0,05	-
Peucedano-Pinetum	433,9	15,26	14,68	15,98
Cladonio-Pinetum	1,1	0,04	0,07	-
Molinio-Pinetum	15,2	0,53	0,25	0,89
Vaccinio uliginosi-Pinetum	5,4	0,19	0,28	0,09
Querco-Piceetum	7,6	0,27	0,27	0,27
Sphagnetalia magellanici	0,9	0,03	0,06	-
Luzulo-Fagetum	0,8	0,03	0,05	-
Total	2843,7	100,00	100,00	100,00

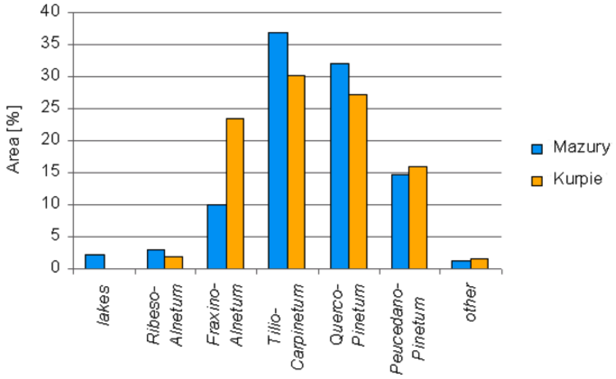


Fig. 11. Potential natural vegetation – spatial share of associations
Ryc. 11. Potencjalna roślinność naturalna – udział typów w podziale na zespoły

The spatial pattern of the potential natural vegetation reflects the diversity of the morphology of the terrain and the nature of the geological surface deposits. In general terms, the study area could be divided with this respect into three parts: two, in a sense, typical ones, and one having a transitory character.

In the southern part of the area, typical of the Kurpie region, there is a distinct setting of the sandy hills chains of the NW-SE orientation, separated by the vast and swampy river valleys. Pine and mixed oak-pine forest habitats are associated with the sandy mounds, while the habitats of the ash-alder floodplain forests are associated with of water flows valleys; the habitats of the lime-oak-hornbeam forests appearing mainly between the mounds and the valleys.

The pattern in the northern part of the study area, typical of Masuria, is also quite distinct. There, the moraine lobes are visible, entering the study area from the north, with domination of the lime-oak-hornbeam forest habitats, and the vast outwash fields in front of and between the moraine lobes, with the habitats of pine and mixed oak-pine forests. Separate fragments of moraine hills, with habitats of lime-oak-hornbeam forests, are located in numerous places among the outwash fields. The habitats of the wet forests (*Fraxino-Alnetum* and *Ribeso-Alnetum*) form not too wide chains and a bigger number of isolated patches, partly on the lakes or on the locations of the already overgrown lakes, mostly in the melt-out basins of the dead ice blocks.

The least legible is the pattern of the potential natural vegetation in what was referred to as the transitory zone. In that zone the relatively narrow valleys of water flows separate the fragments of terrain of diverse origins. In some places these are the outwash formations, in other places – isolated old moraines. Depending upon the bedrock and the relief the potential vegetation changes, from the one with domination of the mixed oak-pine and pine forests to the habitats of lime-oak-hornbeam forests.

The visible differences within the study area could have constituted the basis for delimitation of smaller regional-landscape units, this, though, being outside of the scope of this report. The geobotanical division of the study area (see Fig. 5), provided in the regionalisation according to Matuszkiewicz (1993, 2008b) reflects the split of the area into the northern part (districts F1a.2 and F.1a.5), encompassing the areas of typical late glacial outwashes, and the southern part (district E.2b.7), within which the subdistrict E.2b.7.c represents a typical landscape sequences of dunes and valleys, while the two other districts (E.2b.7.a and E.2b.7.b) have transitional character.

2.5. CHANGES IN THE FOREST COVER OF THE STUDY AREA OVER THE LAST 250 YEARS

2.5.1. CARTOGRAPHIC SOURCES

The extend and spatial distribution of forests substantially changed during the last 250 years. These changes were identified and their typology was proposed on the basis of the detailed analysis of the set of archival and contemporary topographic maps. These cartographic data are listed and characterized in Table 3. Selection of materials had been preceded by an in-depth query in the archival sources. Attempt was undertaken of checking various maps, especially the oldest ones. Ultimately, the oldest and at the same time sufficiently detailed and reliable maps that could be used in the study dated from the end of the 18th and beginning of the 19th century.

The maps collected were processed with the use of the GIS techniques in order to possibly fully transfer the data from the ancient maps into the contemporary map. Resulting were the derivative maps of the forest reaches, dating from different periods, as well as an aggregate map, presenting the sequence of changes of the states ‘forest-non forest’ in the particular locations between the years 1800 and 2000. Some of the archival maps provided direct basis for development of thematic maps, while other ones provided auxiliary information. It should be noted that the oldest maps (from the first half of the 19th century and the earlier ones) were elaborated in the way which makes practically impossible their complete adaptation to the contemporary maps. Even if these maps turn out to be unexpectedly detailed, the setting of angles and distances on them is to such an extent imprecise that concrete points cannot in many cases be properly determined. In particular, any sort of automatic data processing in the GIS systems is very difficult. At the same time, though, we are full of admiration for the cartographers from 200 years ago, who were capable of creating unexpectedly detailed and beautiful in its form image of the Earth surface. As an example a fragment of such a map is presented in Figure 12.

Table 3. Cartographic data used to ascertaine the origin of each wood

Name of the map	Scale	Edition date	Preparation period	Used as:
Prussian map: *XXIX Vergrösserte Sectiones der General-Carte von dem Königreich Preussen...* (called Suchodolec's map)	1:100 000	unpublish	1732–1739	Auxiliary map to define forest range in 1740; Mazury
Prussian map: *Topographisch-Militärische Karte vom vormaligen Neu Ostpreussen…* (called Textor's map)	1:150 000	1806–1808	1795–1800	Basic map to define forest range in 1800; Kurpie
Prussian map: *Karte von den Provinzen Litthauen, Ost- und West-Preussen u. d. Netz-Distrikte* (called Schrötter-Engelhardt's map)	1:50 000	unpublish	1796–1802	Basic map to define forest range in 1800; Mazury
Prussian map: *Karte von Ost-Preussen nebst Preussisch Litthauen und West-Preussen...* (called Schrötter-Engelhardt's map)	1:150 000	1802–1810	1796–1802	Subsidiary map to define forest range in 1800; Mazury
Prussian map: *Topographische Specialkarte des Preussischen Staats und der angrenzenden Länder* (called Reymann's map)	1:200 000	1844–1873	1844–1860	Basic map to define forest range in 1830; the whole area
Prussian topographical map: *Topographische Karte vom Preussischen Staate...*	1:100 000	1869–1872	1860–1872	Basic map to define forest range in 1872; Mazury
Russian map: *Nowa Topograficzeskaja Karta Zapadnoj Rosiji*	1:84 000	1913	1885–1886	Basic map to define forest range in 1885; Kurpie
German maps: *Messtischblätter*	1:25 000	1911–1944	1911–1943	Basic map to define forest range in 1928; almost the whole area
Polish map of Military Institute of Geography	1:100 000	1930–1932	1920–1930	Subsidiary map to define forest range in 1928; a part of Kurpie region
Topographical map of the General Staff in Borowa Góra reference system	1:100 000	1951–1953	1950–1951	Basic map to define forest range in 1950; the whole area
Polish topographical map in „1965" reference system	1:50 000	1977	1970–1973	Basic map to define forest range in 1970; the whole area
VMap Level2 – vector reference map	1:50 000	2000–2004	1980–1993	Basic map to define forest range in 2000; the whole area

Fig. 12. The fragment of Karte von den Provinzen Litthauen, Ost- und West-Preussen u. d. Netz-Distrikte so called Schrötter-Engelhardt map from 1800, at the 1:50.000 scale

Ryc. 12. Fragment mapy: Karte von den Provinzen Litthauen, Ost- und West-Preussen u. d. Netz-Distrikte (tzw. mapa Schröttera-Engelhardta) w skali 1:50.000 z roku 1800

2.5.2. CHANGES IN FOREST COVER SINCE THE YEAR 1800

Owing to the comparison of maps from various periods it became possible to carry out the analysis of afforestation degree in the study area in seven time instants, nominally referred to as the years 1800, 1830, 1885, 1928, 1950, 1970 and 2000. The reach of forests in six of these time points is shown in a simplified manner in Fig. 13. It is noteworthy how significant were the changes in the share of forest cover during only 200 years. These changes concern not only the overall area, but also the locations of forest patches. Moreover, it can be seen that the changes are not unidirectional and have not been proceeding uniformly over the entire study area.

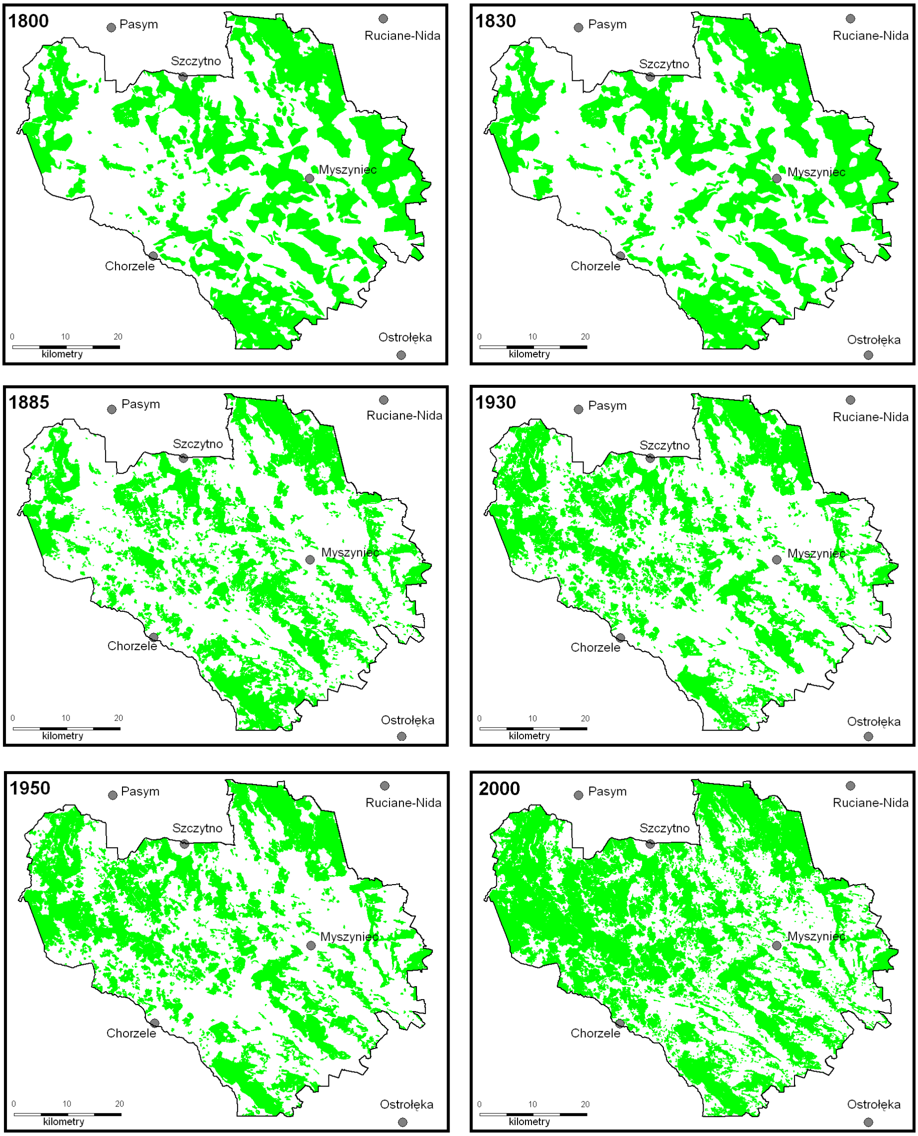


Fig. 13. The range of forests in the study area in 6 time periods from 1800 to 2000
Ryc. 13. Zasięgi lasów na badanym terenie w sześciu terminach od 1800 do 2000 roku

Taking only into account the percentage share of forest cover (Fig. 14), it can be concluded that the study area underwent during 200 years great transformations. These transformations were different on the territory of Masuria and in Kurpie. At the beginning of the 19th century the share of forests in the Masurian part was moderate, around 35% (more or less like nowadays for the entire Poland), and somewhat higher in Kurpie, but still below 50%. This means that already 200 years ago the area was considerably deforested, and the difference between the Masurian and Kurpie parts, although quite distinct, was not great. It can be inferred that the period of deforestation did most probably take place earlier in Masuria than in Kurpie. Later on the differences between the two parts get significantly deeper. In the middle of the 19th century further deforestation proceeded, relatively limited in Masuria, and much more pronounced in Kurpie. Forest share in Kurpie fell below the one in Masuria. Since that time forest share in Masuria has started to grow, rather slowly at the turn of the 20th century and especially fast in the period after the World War II. Nowadays, the share of forest cover there reaches almost 60%.

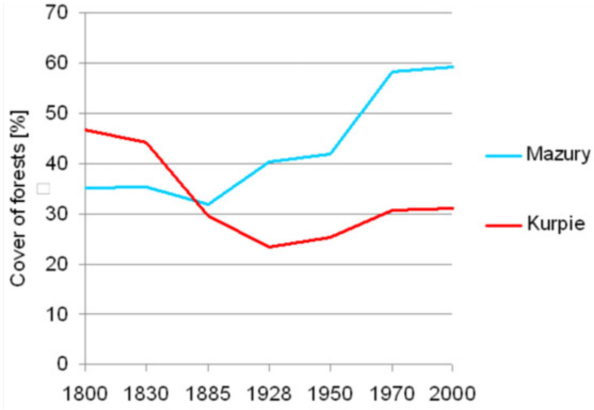


Fig. 14. Changes in the area of forests in Mazury and Kurpie in 19th and 20th century
Ryc. 14. Zmiany lesistości na badanym terenie w XIX i XX wieku

The changes have had a different course in Kurpie. The minimum share of forest occurred there in the 1920s, following a slow increase, after 1970 really only marginal. Nowadays, forest share remains at the level only slightly higher than 30%. Hence, one can say that during the 19th and 20th centuries there has been a very distinct diversification of the forest cover dynamics in two parts of the study area. This different dynamics occurred when two parts belonged to different political-economic organisms. Yet, it continued when both parts belonged already to Poland after 1945.

The distinct difference in the character of the processes, visible between Masuria and Kurpie, does not change the general upward tendency of the forest cover share, compared to the minimum, which took place in the middle of the 19th century in Masuria, or at the beginning of the 20th century in Kurpie.

2.5.3. THE ANCIENT AND THE RECENT FORESTS OF VARIOUS TEMPORAL PERSISTENCE

Comparison of maps from different periods allows for identifying such fragments of forests, which persist on their place at least since the time of the oldest cartographic sources – in our case: since the end of the 18th century. At the same time, there are forest fragments, which appeared later on, and those that existed in the earlier periods, but disappeared. On this basis the sequences of changes for the particular fragments of the area were determined. Given that there are two states (‘forest’ and ‘non forest’) and seven dates, there may be, theoretically, $2^7 = 128$ combinations of sequences. Actually, 123 combinations were observed, of which only some 40 have any spatial significance whatsoever. For obvious reasons we are interested only in the sequences, which end with forest, i.e. altogether 64 sequences. In the material collected only 22 sequences are worth analysing in terms of the respective area (see Table 4). Of these, we can exclude from further investigations twelve sequences, because the stands must be of the minimum age of 70-80 years (and better even more) to be useful for the study, which means that the area should have been under forest at least on the map from 1950.

The fact that during the last 100–150 years there has been a general increase of the forest share, as well as the fact of spatial shift of certain forest complexes over the last 200 years imply a different temporal continuity of the particular fragments of the contemporary forests. The notion of forest persistence is here used to denote the period of time since the given piece of land had been afforested, i.e. the duration of regeneration of the forest community after deforestation. This idea of forest persistence is different from the stand age, which might be even quite short in the case of a permanent forest, because, for instance, the previous stand was felled and the new one planted not so long ago. Yet, also in this aspect, when speaking of the forest communities, we should consider sufficiently old stands to deal with the phytocoenosis to some extent developed.

Table 4. Sequence of „forest-not forest" changes in the present-day woods area

Sequence	Description	Forest marked on the map in:							Area and share of the sequence					
									Mazury			Kurpie		
		1800	1830	1885	1928	1950	1970	2000	km2	% of the area	% of forests area	km2	% of the area	% of forests area
FFFFFFF	always forest	F	F	F	F	F	F	F	342,6	21,8	36,9	184,2	14,5	47,3
NFFFFFF	afforested in 1830		F	F	F	F	F	F	7,5	0,5	0,8	3,5	0,3	0,9
NNFFFFF	afforested in 1885			F	F	F	F	F	91,3	5,8	9,8	52,6	4,1	13,5
FNFFFFF	afforested in 1885	F		F	F	F	F	F	1,0	0,1	0,1	0,7	0,1	0,2
NNNFFFF	afforested in 1928				F	F	F	F	130,3	8,3	14,0	8,2	0,6	2,1
FFNFFFF	afforested in 1928	F	F		F	F	F	F	25,2	1,6	2,7	11,9	0,9	3,1
NNNNFFF	afforested in 1950					F	F	F	26,7	1,7	2,9	4,3	0,3	1,1
FFNNFFF	afforested in 1950	F	F			F	F	F	5,2	0,3	0,6	7,7	0,6	2,0
FFFNFFF	afforested in 1950	F	F	F		F	F	F	2,1	0,1	0,2	13,7	1,1	3,5
NNFNFFF	afforested in 1950			F		F	F	F	3,1	0,2	0,3	4,3	0,3	1,1
FNNNNFF	permanently afforested after 1950	F					F	F	3,7	0,2	0,4	0,7	0,1	0,2
FFNNNFF	permanently afforested after 1950	F	F				F	F	34,2	2,2	3,7	20,7	1,6	5,3
FFNNNNF	permanently afforested after 1950	F	F					F	6,4	0,4	0,7	5,4	0,4	1,4
FFFNNNF	permanently afforested after 1950	F	F	F				F	1,2	0,1	0,1	1,5	0,1	0,4
FFFNNFF	permanently afforested after 1950	F	F	F			F	F	8,2	0,5	0,9	9,0	0,7	2,3
FFFFNFF	permanently afforested after 1950	F	F	F	F		F	F	1,3	0,1	0,1	4,3	0,3	1,1
FFFFFNF	permanently afforested after 1950	F	F	F	F	F		F	0,7	0,0	0,1	1,1	0,1	0,3
NNFFNFF	permanently afforested after 1950			F	F		F	F	3,2	0,2	0,3	2,7	0,2	0,7
NNFNNFF	permanently afforested after 1950			F			F	F	10,7	0,7	1,2	9,3	0,7	2,4
NNNFNFF	permanently afforested after 1950				F		F	F	5,9	0,4	0,6	0,9	0,1	0,2
NNNNNFF	permanently afforested after 1950						F	F	184,9	11,7	19,9	32,7	2,6	8,4
NNNNNNF	permanently afforested after 1950							F	32,8	2,1	3,5	9,6	0,8	2,5
Total									928,0	59,0	100,0	389,0	30,5	100,0

The sequences presented in Table 4 allow for the distinction of six categories of forest persistence, that is – with forest existing at all dates considered, with forests existing since 1830, since 1885, since 1928, and since 1950, and finally – forests of the age too short to be the object of our study. These categories have very different area shares in the contemporary forests (Fig. 15). The largest proportion of the contemporary forests is taken by those that have been persistently present since the maps of 1800. Forests planted after 1950, which are not interesting for the present study, are also widely present nowadays. The areas taken by the forests having appeared in the meantime are much smaller. A particularly small share is taken by forests, which were planted between the years 1800 and 1830. On the other hand, the shares of forests having appeared in the second half of the 19th century and in the first half of the 20th century are significant.

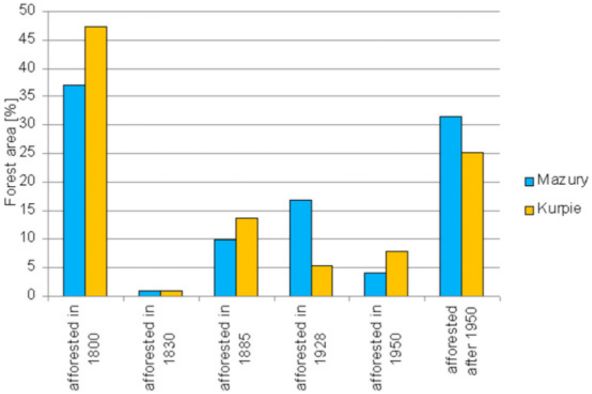


Fig. 15. The share of different persistence categories in present forests
Ryc. 15. Udział we współczesnych lasach terenów o rozmaitej sekwencji stanów „las – nie las"

The categories of forests with more or less precisely determined persistence – i.e. those having appeared between the dates of maps elaboration, do not require here a deeper consideration. The ones, though, with a permanent reach since the very first relatively precise maps of the study area are worth looking at. Can those forests be identified with the notion of ancient forests (Peterken 1977; Rackham 1980). Definitely not!

The notion of ancient forest applies to such a fragment of the contemporary forest, which does not feature the traces of deforestation in the past – in particular, does not display the traces of agricultural land-use. An ancient forest may be the one that was in its past many times felled or even burned down, but not the one, growing on the place where for some period of time (even if quite short) there had been an arable land. This is caused by the fact that ploughing and plant cultivation transform the soil in an essential manner. The traces of this transformation being more or less persistent (Honney et al.

1999; Verheyen et al. 1999; Dupouey et al. 2002; Flinn et al. 2005; Dambrine et al. 2007; Flinn, Marks 2007). That is why in our case we looked for the ancient forests among those having persisted since 1800, but not every forest of this kind shall be automatically considered ancient.

Thus, we shall classify as ancient forests those having persisted since 1800, which:

- do not bear the traces of agricultural use in the form of the plough horizon in the soil, which can be stated by visual inspection (or analyses) of the top layers in the soil profile;
- did not go through an episode of deforestation before 1800, which can sometimes be observed on the earlier maps, if such ones exist;
- had not been extremely deformed in the past, which may sometimes by concluded on the basis of ancient maps and the pattern of the habitat;
- have existed all the time in sufficiently large complexes to assume that the set of species, characteristic of the natural forests, could be preserved.

Taking into account different sequences of changes we can distinguish seven categories of the contemporary forests:

- Ancient forests, i.e. such fragments of forests, of which we can presume, on the basis of maps analysis, soil data and other information, that they have been persisting in a given place for a sufficiently long time.
- Recent forests of the age not shorter than 210 years, i.e. the fragments having been incessantly afforested since 1800 conform to topographical maps, but which display the traces of the plough horizon in the soil, or deforestation is documented by the maps dating from before the year 1800.
- Recent forests of the age of roughly 180–210 years, i.e. those that in the year 1800 had not been forests, but have persisted incessantly since 1830.
- Recent forests of the age of roughly 130–180 years, i.e. those that had had a period of deforestation, but have permanently constituted forests since 1876 (Masuria) or 1885 (Kurpie).
- Recent forests of the age of around 100–130 years, i.e. the ones that after a period of deforestation have been permanently forests since the 1920s.
- Recent forests of the age of some 70–90 years, i.e. the ones have been permanently existed since the 1950s.
- Recent forests of a short age (less than 70 years), which are not taken into account in this study.

The reaches of the forest categories distinguished over the study area are shown in a simplified manner in Fig. 16. The basis of the respective map was constituted by the map of sequences of the states 'forest – non forest'. It enabled direct distinction of the categories 3 through 7, and was the basis for determination of categories 1 and 2.

At this place an explanation is due on the way, in which the reach of ancient forests, i.e. the category 1, was determined. The fundamental material was in this case constituted by the map of the sequences ’forest – non forest‘, derived from the set of six maps of the ’forest reach in a definite time interval‘, and on the basis of this map the reach of forests unchanged since the year 1800 could be determined. Then, for a part of the area a map of 1740 was analysed, so as to exclude from the earlier determined reach of ’the unchanged state of the forest since 1800‘ these fragments that had been deforested conform to the earlier map. Further, it had to be accounted for that not every fragment of forest, which is shown as forest on all maps considered might fulfil the conditions for the ancient forest, as it would have to be assumed that the species proper for the ancient forests exist in it for the entire period of time. Hence, forests with preserved plough horizon, very small forest patches, and forest currently highly deformed could not be treated as ancient forests. Thus, the patches of ancient forests were identified not only on the basis of historical maps analysis, but also on the basis of the in-field reconnaissance. The traces of the plough horizon were sought at numerous sites, also outside of the locations, where phytosociological relevés were made. Further, traces of the ancient divides of forests and fields were sought (e.g. in the form of border walls). All these aspects were taken into consideration when the probable reach of the ancient forests was determined. The forest reach of category 2 were obtained by the juxtaposition of the initial reach of the forests persisting since 1800 with the actual reach of the ancient forests. The reach of the ancient forests in the Masurian part accounts for 34.2% of the contemporary forests, while in the Kurpie part – for 45.8%. Category 2 of the recent forests, featuring the oldest age, occupies in Masuria 2.7%, and in Kurpie – 1.6% of the contemporary forests. The shares of these forest categories in the both regions are shown in Fig.17. It is worth noting that despite the significant changes in the forest reach during the last 200-300 years the share of ancient forests is important both as a proportion of the currently existing forests and in the area of the regions as a whole. The recent forests of the categories 2 through 6 – occupy an important area in Masuria (roughly 20% of the terrain), and much less so in Kurpie (approximately 9% of the area).

3. BASIC ASSUMPTIONS FOR THE GEOBOTANICAL, ECOLOGICAL AND SOIL STUDIES IN ANCIENT AND RECENT FORESTS

3.1. THE ISSUE OF ANCIENT AND RECENT FORESTS

In the studies of vegetation, underway for several decades in Europe, the research on historical changes in vegetation plays a key role. After the current diversity of the plant communities had been sufficiently well recognised, the question arose as to how the plant communities and landscapes looked in more or less distant historical periods. In the zone of temperate deciduous forests, like, for instance, in Central Europe, one of the most important processes in the man-made transformation of vegetation was deforestation and turning the forest areas into arable land. This, however, is not the only process observed in the landscape. Side by side with deforestation, there have been going on for a long time already the processes of the forest return onto the agricultural land, taking place either spontaneously through secondary succession, or – which is much more frequent in Central Europe – through explicit afforestation. It is essential for the study of landscape transformations and for the practice of environmental protection or forest management to be able to identify which of the forest fragments observed nowadays grow on the sites having a history of agricultural use, and which have been persisting for a very long time, maintaining the character of the forest associations, irrespective of the current stand age. In order to refer to these forests that have preserved habitat continuity and a relatively natural character, the term of ʾancient forests‘ has been adopted. This term is applied to the remnants of natural forests and to recent forests that have persisted in the landscape for a long time, at least since roughly 200 years ago (Peterken 1977; Rackham 1980). The selected threshold date depends mostly upon the time period, for which historical data are available, documenting the existence of forests on a given area. In Europe such materials go back to the 17th century (England – Peterken 1977), and to the 18th and 19th centuries (other regions, including Poland – Stieperaere 1981; Dzwonko, Loster 1988, 1992; Petersen 1994; Wulf 1997; Brunet, von Oheimb 1998; Bossuyt et al. 1999a; Orczewska 2003, 2009). For the regions of Masuria and Kurpie the source of information on the age of forests might be constituted by the maps of Suchodolec from the years 1732–1739, as well as those by Schrötter from 1796–1802 and Textor from 1795–1800.

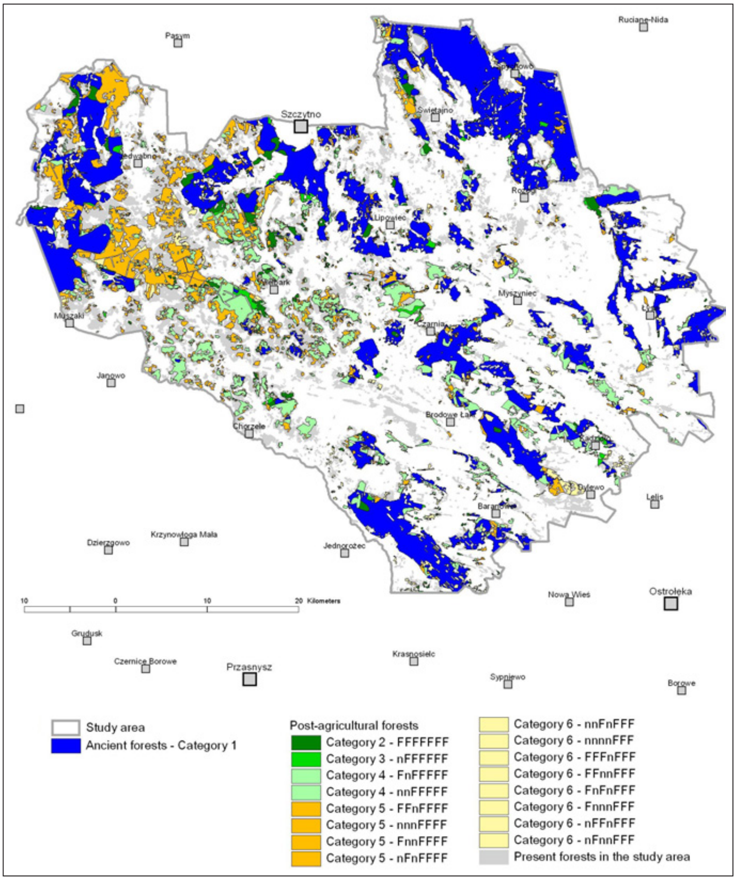


Fig. 16. Map of the distinguished forest categories
Ryc. 16. Mapa wyróżnionych kategorii lasów

The notion of ancient forests ought to be opposed to that of recent forests, i.e. the forest communities, occupying habitats, on which arable lands or other non-forest forms of land use had been located before. The more or less permanent deforestation of an area, especially when associated with land cultivation and ploughing, introduces drastic changes into the environment. First of all the consequence consists of the elimination of the forest phytoceonosis and appearance of the community having the character of agrocoenosis on its place. This means, in practice, a complete exchange of the floristic composition, since the majority of the forest vascular plant species form a short-lived seed bank and their seeds do not survive in the soil longer than one year (Jankowska-Błaszczuk, Grubb 1997; Bekker et al. 1998; Thompson et al. 1998; Bossuyt, Hermy 2001). In case forest is planted on such a site or there is forest re-entry through natural secondary succession, the species composition and the structure of the new community shapes slowly, with particular species colonising the area in different time rate and over different paths. Some of them are introduced by people, including,

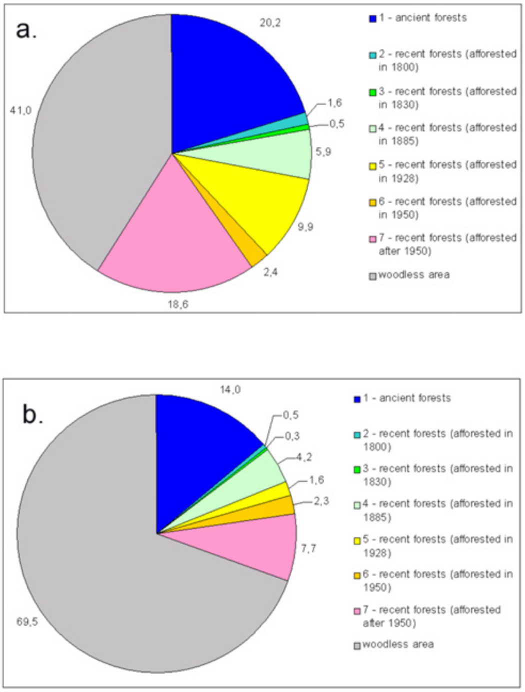


Fig. 17. Spatial share of forest categories in (a) Mazury and (b) Kurpie

Ryc. 17. Kategorie lasów na Mazurach (a) i na Kurpiach (b)

especially the dominant and the admixture stand species, while other ones appear spontaneously. After the stand reaches an appropriate age, the first generation of recent forest community forms. It changes thereafter in the successive stand generations, through replacement performed by humans or due to spontaneous processes. The direction of these changes may differ, depending upon the degree of consistence of species introduced with the natural stand type, proper for a given habitat. In case the introduced stand species is fully consistent with natural habitat (e.g. introduction of Scots pine onto the pine forest habitats) and provided the habitat conditions have not undergone an essential change, the chance appears to have the community regenerate towards the one of similar type to that preceding deforestation. This direction of change is theoretically possible, but does not necessarily have to actually take place, and, moreover, the process can be very long and the reconstruction of the original community does not have to be complete. Spontaneous colonisation of isolated recent forests is very slow and may take hundreds of years (Peterken 1977, 1996; Faliński 1986; Brunet, von Oheimb 1998). Re-colonisation of the herb layer in recent forests, situated in the vicinity of the ancient forests is much quicker, since the latter are the source of forest species propagulae (Dzwonko 1993; Dzwonko, Gawroński 1994; Matlack 1994; Bossuyt et al. 1999a; Bossuyt, Hermy 2000; Dzwonko 2001; Orczewska 2010; Orczewska, Fernes 2011). In this context it ought to be assumed that the earlier regeneration stages would display lower similarity to the type, represented by the ancient forest on the given habitat, than the older stages, having passed through more than one generation of a tree stand. Based on the observations and the results of studies carried out (Peterken, Game 1984; Whitney, Foster 1988; Dzwonko, Gawroński 1994; Wulf 1997: Honney et al. 1998; Bossuyt et al. 1999a; Graae 2000; Dzwonko 2001; Endels et al. 2004; Orczewska 2009d; Verheyen et al. 2006), it ought to be assumed that individual species, proper for ancient forests might return at different time since afforestation of the post-agricultural land, while, simultaneously, species linked with the early stages of forest regeneration shall be disappearing unevenly, this fact resulting from their different biology and the changing phytocoenotic and soil conditions (Honney et al. 1998; Hermy et al. 1999; Dzwonko 2001; Graae et al. 2003; Verheyen et al. 2003; Keersmaeker et al. 2004; Orczewska, Fernes 2006; Sciama et al. 2009).

The recent forests, especially when located on the former agricultural lands, display lower or higher difference in terms of floristic composition in relation to the communities without agricultural use in their history. We know this both from observation and from the geobotanical studies, performed in some regions of Poland and Europe (Dzwonko, Loster,1992; Dzwonko, Gawroński 1994; Graae, Heskjær 1997; Honney et al. 1999; Graae et al. 2003; Petit et al. 2004; Wolf 2004; Góras, Orczewska 2007; Sciama et al. 2009; Orczewska 2010). The purpose of the research here reported was to indicate the differences in the floristic composition between the recent forests established at different times and the ancient forests, in a concrete region, with consideration of various forest association types, defined by the potential natural vegetation. The analysis concerned first of all the shares of species characteristic of various syntaxonomic units. On the one hand, these units, to which the ancient forests belonged (*Vaccinio-Piceetea* and *Querco-Fagetea* classes), and on the other hand – units of the associations linked with the early phases of forest regeneration (grasslands or synantropic communities). Analysis was also performed of the differences in the floristic composition in terms of phytoindication (considering the so-called indicator values), as well as biology of particular species, their life forms, ways of reproduction, and of the spread of propagulae.

3.2. THE LIST OF SPECIES WITH PREFERENCE FOR THE ANCIENT FORESTS

Herb layer of the ancient forests is formed by species, featuring a number of ecological characteristics that limit their appearance on other habitats. These characteristics include, in particular, shade tolerance, low dispersal capacity, and limited mobility outside of the forest environment, lack of persistent seed bank and the ability of competing with the expansive species of non-forest habitats (Peterken, Game 1984; Dzwonko, Loster 1992; 2001; Jankowska Błaszczuk, Grubb 1997; Hermy et al. 1999; Bossuyt et al. 1999a;

Orczewska 2007). The list of the ancient forests indicator species for Central and Western Europe was proposed by Hermy et al. (1999). Then, for Polish conditions it was complemented by Dzwonko and Loster (2001). Its usefulness was confirmed in numerous studies (Wulf 1997, 2003; Honney et al. 1999; Sienkiewicz, Kloss 2001; Dumortier et al. 2002; Orczewska 2004, 2007; Petit et al. 2004; Szwed et al. 2009; De Frenne et al. 2011; Orczewska, Ferens,2011). Yet, under a more detailed analysis, certain doubts may arise.

The very first doubt is connected with the odd compatibility. The list of ancient forest species, mentioned above, encompassing the species of herbaceous plants (it does not contain trees nor mosses), is almost identical with the lists of species characteristic of various forest syntaxonomic units. This leads to the question whether a not too simple hypothesis was put forward, namely that the characteristic species ought to be (by definition, in a way) also the ancient forests indicator species. The general compatibility between the lists is quite obvious, but the very high degree of the accordance provokes discussion whether this corresponds to the reality.

The second doubt results from the direct observations. If we encounter, many times over, a species of ancient forests in places, of which we precisely know that only 50 years ago an arable land was, the need arises of checking whether the respective list is reliable, or what is its scope of reliability.

For these reasons an attempt was undertaken of verifying the list of ancient forest species, based on numerous geobotanical materials from a particular region. The pertinence of such studies was demonstrated both by the authors of the two lists mentioned and by other researchers dealing with the same issues (e.g. Peterken 1974; Wulf 1997; Honney et al. 1998). Verification of the list constituted the methodological objective of the study reported in the region of Masuria-Kurpie. The verified list shall be used to assess the degree of the recent forests regeneration at particular sites, considering thetype of habitat, the time of regeneration and the distance to the ancient forest, being the refuge of the forest flora in the period of agricultural use.

3.3. RELATIONSHIPS BETWEEN THE GEOBOTANICAL AND SOIL STUDIES

Forest regeneration processes on the former agricultural land, as characterised by the changes in floristic composition and in the structure of phytoceonoses, ought to be considered in parallel with the analysis of soil evolution. Land cultivation brings about significant transformations in soil environment, consisting mainly in changes of water balance, soil reaction and biochemical components (Puchalski, Prusinkiewicz 1975; Degórski 1990), which leads to an essential change in soil conditions, including soil parameters important for plant life (Hermy, Stieperaere 1981; Koerner et al. 1997; Bossuyt et al. 1999b; Honnay et al. 1999, Verheyen et al. 1999; Brunet et al. 2000; Falkengren-Grerup et al. 2006).

Afforestation of formerly agricultural land initiates soil transformation processes, first of all due to elimination of ploughing and other argotechnical measures, as well as the development of forest phytocoenosis, exerting also an impact on the soil processes. Forest tree layer has a very special impact on the soil properties. It influences groundwater conditions, accumulation of forest litter and humus layer with specific fraction composition as well as carbon-nitrogen ratio (Bossuyt et al. 1999; Bossuyt, Hermy 2000; Verheyen, Hermy 2001; Wulf, Heinken 2008). The process of soil change is by its very nature lengthy, while some effects of agricultural use are persistently marked (at least on the scale of hundreds years) in profile morphology and changed chemical soil characteristics (Honney et al. 1999; Verheyen et al. 1999; Dupouey et al. 2002; Flinn et al. 2005; Dambrine et al. 2007; Flinn, Marks 2007). In the perspective of roughly 200-300 years, encompassed by the analysis of changes, taking place on the former agricultural land, in a clear majority of cases the so-called plough horizon (Ap) is observed. Identification of this horizon in the soil allows for an unambiguous statement that a given area was in agricultural use in the past, and so – for a well-founded classification of the given forest as recent. Lack of such a horizon in the soil under a forest community is an indication that the given area had not been cultivated over the last several hundred years, but does not suffice for stating that we deal with an ancient forest in the previously quoted sense. It might namely be so that the area had been deforested, and that for a longer period of time, but ploughing was not performed there, instead, it could have been used, for instance, as a pasture.

In the framework of the study reported here the analysis was carried out of the soil characteristics in recent forests with different conditions and period of regeneration, compared to the ancient forests of corresponding types. This comparison concerned the following soil features and parameters: plough horizon thickness, soil reaction, organic carbon content, total nitrogen and sulphur content, the C:N ratio. The direction and rate of soil changes were determined, witnessing to the forest soils regeneration.

Data on the floristic composition and on soil characteristics, collected at the same sites allowed for the analysis of joint habitat characteristics based on the so-called ecological indicator values and on the direct soil indicators. This enabled more precise ecological characteristic of the communities, described through the phytoindicators in the places, where soil analyses have not been carried out.

3.4. *VACCINIUM MYRTILLUS* – A SPECIES PARTICULARLY IMPORTANT FOR POST-AGRICULTURAL FOREST REGENERATION

Bilberry *Vaccinium myrtillus* is one of the most important components of the herb layer in pine and mixed oak-pine forests. It dominates among other dwarf shrub plants and herbs, contributing significantly to the biomass production and to the matter cycle of substances rich in elements important for functioning of forest ecosystems. The flow of the matter varies, depending upon the environment richness. Along with the decreasing trophism of habitats, the share of dwarf shrub overground parts in the biomass and of elements transfer to the litter increases (Moszyńska 1983). Bilberry presence prevents soil erosion (Gądziński 1967), it is advantageous for the formation and accumulation of humus layer (Grochowski 1976), for the renewal of tree species (Jäderlund et al. 1996), and for the development of other undergrowth species (Parlane et al. 2006). Bilberry increases also the natural resistance of stands, providing refuge for insects that attack forest pest species (Karczewski 1962), and is the main source of nutrition for many animal species (Atlegrim 1989; Kirby 2001; Schaumann, Heineken 2002; Fernandes-Calvo, Obeso 2004).

Vaccinium myrtillus is found on fresh and humid soils, oligo- and mesotrophic, acid and moderately acid ones. The plant is very sensitive to high concentrations of nitrogen in the soil, although on more fertile habitats this factor has a lower impact on its appearance (Ingestad 1973; Mäkipää 1999; Ihalainen et al. 2002). Adaptation to life on poor habitats consists in the symbiosis of bilberry with fungi in the form of mycorrhiza (Madej 1968) and the capacity of transferring organic and mineral compounds from older to younger tissues, and vice versa (Harper 1977).

An important factor, influencing the appearance of bilberry in the forests, is constituted by the light conditions (Mäkipää 1999; Parlane et al. 2006). This dwarf shrub decidedly prefers half-shade or moderate light (Szmeja 1993), and so develops most abundantly in tree stands of the age between, roughly 40 and 80 years, under moderate canopy cover, while in older stands bilberry patches regress, appearing sporadically, in small clusters (Nieppola 1992; Storch 1993; Głowacki 1999; Ihalainen et al. 2002; Kalinowski 2004; Nielsen et al. 2007).

The shrub reproduces primarily in a vegetative manner through the underground, brittle rhizomes (Tolvanen, Laine 1997; Tomanek 1997). The process is enhanced by moderate pasturing. Herbivores grazing results in gaps in the plant cover, quickly settled by new bilberry shrubs (Kirby 2001; Olofsson et al. 2005). Moreover, bilberry exhibits a capacity to recover after the ungulate herbivore damage, especially when current-year branches are removed because apical dominance is broken and this activates bud development and compensatory responses (Tolvanen et al. 1992).

The generative reproduction has a smaller significance for bilberry (Ericsson 1989). With this respect it is a typical endozoochorous species, as seeds are, in particular, transported by the animals feeding on berries. During fruits digestion, the shells of seeds are disintegrated, so that after excretion they are more penetrable for water and oxygen, this being essential during sprouting (Clergeau 1992). The attractiveness of the bilberry fruit is high for numerous animal species. Its consumers belong to different groups in terms of their behavior. Small mammals of limited mobility transport the propagulae over the distances of tens meters. Medium sized mammals, like, for instance, pine marten, bring the seeds for the distance of approximately half kilometer – even though they move over much greater distances, but for physiological reasons the transport of seeds is limited in space (Schaumann, Heineken 2002). Then, birds and bigger mammals contribute in an essential manner to the transport of fruits and seeds over bigger distances, thereby participating in the colonization of the newly emerging, often entirely isolated, forest patches (Atlegrim 2005; Schaumann, Heineken 2002).

The development of fruits and seeds might be hampered by the herbivorous insects (Atlegrim 1989). Destruction brought about by these invertebrates is limited owing to the presence of ants. It was observed that in the neighborhood of anthills (within the radius of roughly 2 meters) the share of twigs with untouched berries significantly increases (Atlegrim 2005).

The role played by the bilberry in the pine forest ecosystems makes this species particularly important for the regeneration of post-agricultural forest communities. Ensuring adequate conditions for development of bilberry may essentially accelerate this process. Based on the results of the research performed in Scotland by S. Parlane et al. (2006) care should first of all be taken of the appropriate light conditions. This could be achieved by avoiding complete clearing and applying only partial thinning, in order to enable the upper self-seeding over the entire regenerating area, with the young generation growing under the upper shelter of the stand. Optimum light conditions can be attained through manipulation of the stand cover for the given trees height. Moreover, within forest management, control ought to be secured over the number of herbivorous animals. In general, they do not constitute a threat to the *Vaccinium* species, but their excessive pressure may significantly limit the bilberry appearance.

3.5. THE SCHEME OF DATA COLLECTION

The basic material for the present part of the work is constituted by the collection of 464 phytosociological relevés taken conform to the Braun-Blanquet methodology (1964) in the sufficiently ’mature‘ forest communities (stands of at least 80-90 years old) within the study area (Fig. 18). Spatial location of the relevés was meant to ensure obtaining a possibly high number of such relevés in the recent forests established at different times, as well as in the ancient forests, corresponding to the former in habitat terms, and possibly close to their location. The preliminary list of 1500 possible locations of relevés was based on the cartographic study of sequences 'forest – non-forest' on the particular fragments of the area, along with the data from the forest maps (the stand age and the forest habitat type), as well as potential natural vegetation. The selected sites in the contemporary forests were characterised by:

- sequence of 'forest – non-forest' states, that is – whether for a given location the cartographic materials demonstrate a reliable continuous existence of forest, or appearance of forest at a definite time instant and persistence until today;
- forest type, derived from the habitat type, provided by the forest map and the map of potential natural vegetation;
- sufficiently mature phytocoenosis, as judged on the basis of the tree stand age;
- sufficient representation of the forest types and persistence categories;
- not too distant and habitat-wise homogeneous location of recent and ancient forest sites.

Selected sites were visited and in places, where this was possible, given the community state (existence of the tree stand and an appropriate forest structure, lack of significant disruptions to the soil cover, lack of local deformations, garbage, etc.), the phytosociological relevés were made, and the presence or absence of plough horizon was examined. Notwithstanding the cartographic data, on particular sites the potential natural vegetation type was identified and other features of the community were determined, including, especially, spatial distribution and cover of selected species. For 200 relevés soil samples were also taken. Particular relevés points were introduced onto the contemporary digital map, and then their locations were analysed (on historical maps) in terms of forest appearance in five time instants, roughly corresponding to the years 1800, 1830, 1885, 1928, 1950 (for the Masurian area it was also possible to consider the state as of around 1740).

The collected phytosociological relevés were classified, owing to identification of the potential natural vegetation, into three basic forest types, all of them exploited for economic purposes and common on the area considered: pine forests of *Peucedano-Pinetum* association, mixed oak-pine forests of *Querco-Pinetum* association, and lime-oak-hornbeam forests of the *Tilio-Carpinetum* association. Rare community types have not been analysed.

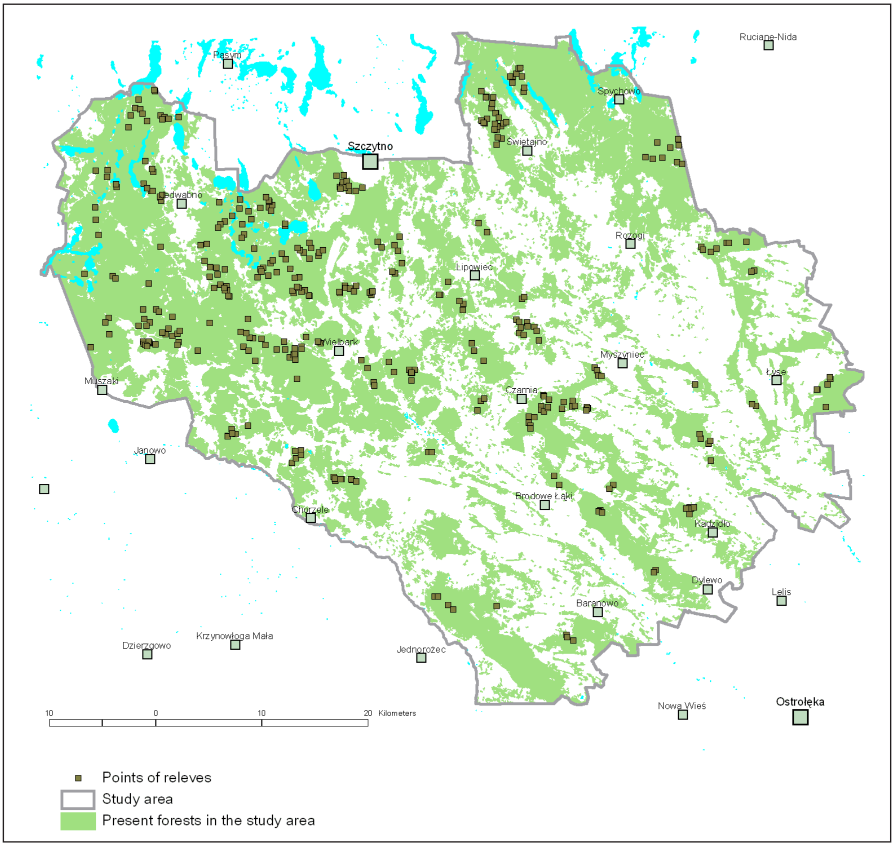


Fig. 18. Location of the phytosociological relevés
Ryc. 18. Lokalizacja zdjęć fitosocjologicznych

Two criteria of classification have been applied to the relevés set of each type:

- according to the existence or non-existence of a plough horizon in the soil – identifi in the field;
- according to the forest persistence, it was adopted that marking of the forest on a map corresponds to a forest with the stands at least 20 years old – established on the basis of cartographic materials.

The above bi-criteria classification allowed for the indication of ancient forests, i.e. forests communities appearing in places, where no plough horizon has been observed in the soil, while the available maps show that since at least 1800 the respective areas have been covered by forests, and a few categories of recent forests (Table 5). In practice, the categories of recent not post-agricultural forests were represented by very few locations and so were neglected in the analysis. Regarding recent post-agricultural forests, it turned out possible to divide them into five categories mentioned only in the case of the most common association on pine forest habitat, while in the cases of mixed oak-pine forests and lime-oak-hornbeam forests it was necessary to combine the categories, because of lack of relevés representing them, or because their number was too low to calculate respective frequencies.

Table 5. Forest categories

Forest origin ascertained with the help of map from:	Plough horizon in the soil:	
	observed	not observed
1800	Recent, post-agricultural forest of the regeneration period exceeding 230 years (category – 2)	Ancient forest (category – 1)
1830	Recent, post-agricultural forest of the regeneration period of roughly 200 years (category – 3)	Recent, not post-agricultural forest of the regeneration period of roughly 200 years
1885	Recent, post-agricultural forest of the regeneration period of roughly 135–180 years (category – 4)	Recent, not post-agricultural forest of the regeneration period of roughly 135–180 years
1928	Recent, post-agricultural forest of the regeneration period of roughly 90–135 years (category – 5)	Recent, not post-agricultural forest of the regeneration period of roughly 90–135 years
1950	Recent, post-agricultural forest of the regeneration period of roughly 80–90 years (category – 6)	Recent, not post-agricultural forest of the regeneration period of roughly 80–90 years

The basic set of relevés was complemented with 29 relevés taken before on the area considered (Matuszkiewicz J. M. et al., 2007). Besides, to study a structure of recent forests, located in the neighbourhood of ancient forests, 140 notes were made in the transects, including the spread of several important species. 127 notes collected in the earlier studies (Matuszkiewicz J.M. et al., 2007) were also included in this set. There are altogether 600 points in the database with their locations on the digital map and their geobotanical characteristics.

4. FLORISTIC-ECOLOGICAL DIVERSITY WITHIN AND BETWEEN ANCIENT AND RECENT FORESTS

In this part of the work analysis of the floristic composition is provided in terms of species frequency in the distinguished categories of ancient and recent forests.

The material for the present part of the work consists of 339 phytosociological relevés, selected from the set previously mentioned. The selected relevés represent the pine forests of *Peucedano-Pinetum* association (202 items), the mixed oak-pine forests of *Querco-Pinetum* association (93 items) and the lime-oak-hornbeam forests of *Tilio-Carpinetum* association (44 items).

The species frequency observed in the communities considered are shown in 6, 9 and 12.

4.1. DIFFERENCES IN THE SPECIES FREQUENCY OF THE STUDIED FOREST COMMUNITIES

4.1.1. FLORISTIC COMPOSITION OF PINE FORESTS

The communities of *Peucedano-Pinetum* habitats were represented by 202 phytosociological relevés. Six categories of forests were distinguished among them:

- PP1 – ancient forests – 58 relevés;
- PP2 – recent post-agricultural forests with the regeneration period exceeding 230 years – 14 relevés;
- PP3 – recent post-agricultural forests with the regeneration period of around 200 years – 42 relevés;
- PP4 – recent post-agricultural forests with the regeneration period of roughly 135-180 years – 69 relevés;
- PP5 – recent post-agricultural forests with the regeneration period of roughly 90-135 years – 10 relevés;
- PP6 – recent post-agricultural forests with the regeneration period of roughly 80-90 years – 6 relevés.

The total number of phytosociological relevés from the recent forests, accounted for in the analysis (categories PP2-6) amounted to 141. They were compared to 58 relevés from the ancient forests (category PP1). The analysis did not include the recent forests, in which the plough horizon had not been observed. The frequencies of plant species in pine forests are shown in Table 6. Test of frequency difference between forest categories is according to a Fisher's exact test (Fisher, Van Belle 1996). The significance of the results is presented in table 7 (insignificance may sometimes result from the low number of relevés classified in a given category). The results of statistical significance test were accounted for in Table 6 and in further considerations. Actually, Table 6, side by side with the species frequency in the pine forests categories, contains also frequencies in all recent forests, frequency differences between the ancient forests and the recent forests, as well as total frequency of species in all pine forests analysed (the table as published does not account for rare companions).

Table 6. Diversity of plant composition in pine forests (*Peucedano-Pinetum*)

Pine forests categories	PP1	PP2	PP3	PP4	PP5	PP6			
	Ancient forests	Recent, post-agricultural forest regenerated in the last-230-year period	Recent, post-agricultural forest regenerated in the last-200-year period	Recent, post-agricultural forest regenerated in the last-135-180-year period	Recent, post-agricultural forest regenerated in the last-90-135-year period	Recent, post-agricultural forest regenerated in the last-80-90-year period	All recent forests (PP2-6)	Difference between ancient and recent forests (PP1-PP2-6)	All pine forests
No. of relevés	57	12	16	44	65	8	145		202
Forest stand age acc. to forest map	113.3	107.2	97.6	100.9	103.8	87.4	101.6		105.3
Share of habitat types acc. to forest map	BŚW-82%, BMŚW-18%	BŚW-86%, BMŚW-7%, BW-7%	BŚW-88%, BMŚW-12%	BS-3%, BŚW-97%, BMŚW-1%	BŚW-100%	BŚW-100%			
Tree cover [%]	62.1	59.6	57.8	57.7	59.6	60.6	58.9	**3.2**	59.9
Shrub cover [%]	14.9	14.4	12.9	14.3	14.9	12.8	14.3	**0.6**	14.3
Herb cover [%]	65.4	46.7	40.1	32.0	31.8	18.4	33.3	**32.1**	42.3
Moss cover [%]	92.2	94.6	93.1	92.7	95.9	98.8	94.7	**-2.5**	93.5
Frequency [%] **Tree species**									
Betula pendula-a1	5.3	8.3	25.0	11.4	9.2	12.5	11.7	**-6.5**	10.0
Betula pendula-a2	12.3	25.0	25.0	34.1	20.0	25.0	25.5	**-13.2**	21.8
Betula pendula-a3	31.6	50.0	43.8	52.3	69.2	50.0	58.6	**-27.0**	49.8
Betula pendula-b	47.4	33.3	62.5	56.8	72.3	62.5	62.8	**-15.4**	58.8
Betula pendula-c	21.1	50.0	25.0	29.5	26.2	62.5	31.0	**-10.0**	27.5
Padus serotina-a3	0.0	0.0	0.0	2.3	1.5	0.0	1.4	**-1.4**	0.9

Padus serotina-b		1.8	8.3	6.3	20.5	4.6	25.0	11.0	**-9.3**	8.5
Padus serotina-c		5.3	16.7	25.0	29.5	16.9	25.0	22.1	**-16.8**	16.6
Picea abies-a1		7.0	8.3	12.5	4.5	9.2	0.0	7.6	**-0.6**	7.6
Picea abies-a2		47.4	41.7	37.5	20.5	44.6	37.5	35.9	**11.5**	38.9
Picea abies-a3		49.1	41.7	37.5	34.1	41.5	50.0	39.3	**9.8**	42.2
Picea abies-b		66.7	75.0	56.3	45.5	69.2	62.5	60.7	**6.0**	62.6
Picea abies-c		14.0	16.7	0.0	4.5	9.2	25.0	8.3	**5.8**	10.0
Pinus sylvestris-a1		100.0	100.0	100.0	100.0	100.0	100.0	100.0	**0.0**	100.0
Pinus sylvestris-a2		8.8	16.7	31.3	22.7	15.4	25.0	20.0	**-11.2**	16.1
Pinus sylvestris-a3		17.5	33.3	43.8	63.6	43.1	37.5	48.3	**-30.7**	38.9
Pinus sylvestris-b		57.9	41.7	68.8	61.4	53.8	75.0	57.9	**0.0**	58.3
Pinus sylvestris-c		47.4	75.0	75.0	56.8	55.4	75.0	60.7	**-13.3**	55.9
Quercus robur-a2		0.0	0.0	12.5	2.3	0.0	0.0	2.1	**-2.1**	1.4
Quercus robur-a3		28.1	8.3	12.5	15.9	7.7	0.0	10.3	**17.7**	15.6
Quercus robur-b		59.6	8.3	18.8	34.1	15.4	12.5	20.7	**39.0**	33.6
Quercus robur-c		49.1	75.0	81.3	50.0	55.4	75.0	59.3	**-10.2**	55.9
Quercus rubra-a3		0.0	0.0	0.0	0.0	1.5	0.0	0.7	**-0.7**	0.5
Quercus rubra-b		1.8	0.0	0.0	2.3	1.5	0.0	1.4	**0.4**	1.4
Quercus rubra-c		0.0	0.0	0.0	9.1	9.2	25.0	8.3	**-8.3**	5.7
Sorbus aucuparia-a3		1.8	0.0	0.0	0.0	0.0	0.0	0.0	**1.8**	0.5
Sorbus aucuparia-b		19.3	0.0	0.0	2.3	6.2	12.5	4.1	**15.2**	8.5
Sorbus aucuparia-c		29.8	66.7	50.0	40.9	26.2	25.0	36.6	**-6.7**	33.2
Herb and moss species										
Species characteristic of the class and alliance with preference for ancient forests										
Vaccinium vitis-idaea	*	100.0	91.7	93.8	72.7	67.7	50.0	73.1	**26.9**	80.6
Hylocomium splendens		91.2	91.7	56.3	43.2	72.3	62.5	62.8	**28.5**	70.6
Trientalis europaea	*	33.3	16.7	0.0	4.5	9.2	0.0	6.9	**26.4**	14.7
Vaccinium uliginosum		14.0	0.0	0.0	0.0	0.0	0.0	0.0	**14.0**	4.3
Total frequency of of the group		**238.6**	**200.0**	**150.0**	**120.5**	**149.2**	**112.5**	**142.8**	**95.8**	**170.1**
Species characteristic of the class and alliance with preference for some recent forests										
Chimaphila umbelata		5.3	0.0	6.3	13.6	47.7	12.5	26.9	**-21.6**	19.9
Pyrola chlorantha		0.0	0.0	6.3	6.8	18.5	0.0	11.0	**-11.0**	7.6
Total frequency of of the group		**5.3**	**0.0**	**12.5**	**20.5**	**66.2**	**12.5**	**37.9**	**-32.7**	**32.2**
Other species characteristic of the class *Vaccinio-Piceetea*										
Pleurozium schreberi		100.0	100.0	100.0	100.0	100.0	100.0	100.0	**0.0**	100.0
Vaccinium myrtillus	*	100.0	100.0	93.8	95.5	100.0	87.5	97.2	**2.8**	98.1
Dicranum polysetum		98.2	100.0	100.0	100.0	95.4	100.0	97.9	**0.3**	98.1
Melampyrum pratense	*	96.5	100.0	93.8	75.0	93.8	87.5	88.3	**8.2**	89.6
Dicranum scoparium		38.6	33.3	25.0	40.9	16.9	37.5	27.6	**11.0**	30.8
Ptilium crista-castrensis		28.1	50.0	6.3	9.1	38.5	50.0	27.6	**0.5**	27.5
Lycopodium annotinum		10.5	16.7	6.3	11.4	15.4	25.0	13.8	**-3.3**	12.3
Monotropa hypopitys		1.8	16.7	6.3	6.8	16.9	0.0	11.7	**-10.0**	8.5
Diphasiastrum complanatum		5.3	0.0	0.0	11.4	7.7	0.0	6.9	**-1.6**	6.2
Orthilia secunda		3.5	0.0	6.3	6.8	6.2	0.0	5.5	**-2.0**	4.7

Total frequency of of the group		**482.5**	**516.7**	**437.5**	**456.8**	**490.8**	**487.5**	**476.6**	**5.9**	**475.8**
Differential species of association *Peucedano-Pinetum*										
Convallaria majalis	*	43.9	41.7	0.0	2.3	3.1	0.0	5.5	**38.3**	16.1
Scorzonera humilis		29.8	0.0	0.0	13.6	1.5	0.0	4.8	**25.0**	11.4
Solidago virgaurea		10.5	0.0	6.3	18.2	9.2	0.0	10.3	**0.2**	10.0
Peucedanum oreoselinum		15.8	8.3	6.3	9.1	6.2	0.0	6.9	**8.9**	9.5
Polygonatum odoratum		1.8	0.0	0.0	2.3	1.5	0.0	1.4	**0.4**	1.9
Rubus saxatilis		3.5	0.0	0.0	0.0	1.5	0.0	0.7	**2.8**	1.4
Total frequency of of the group		**105.3**	**50.0**	**12.5**	**45.5**	**23.1**	**0.0**	**29.7**	**75.6**	**50.2**
Companions with preference for ancient forests										
Calluna vulgaris		98.2	83.3	75.0	68.2	36.9	25.0	53.8	**44.5**	65.9
Frangula alnus		49.1	41.7	37.5	40.9	23.1	12.5	31.0	**18.1**	36.0
Luzula pilosa	*	42.1	33.3	18.8	9.1	23.1	12.5	18.6	**23.5**	25.1
Calamagrostis arundinacea		38.6	25.0	12.5	13.6	18.5	12.5	16.6	**22.0**	21.8
Pohlia nutans		17.5	0.0	0.0	0.0	0.0	0.0	0.0	**17.5**	5.7
Molinia caerulea		19.3	8.3	6.3	2.3	1.5	0.0	2.8	**16.5**	8.5
Athyrium filix-femina	*	15.8	8.3	0.0	0.0	1.5	0.0	1.4	**14.4**	6.2
Oxalis acetosella	*	7.0	0.0	0.0	0.0	1.5	0.0	0.7	**6.3**	2.5
Total frequency of of the group		**280.7**	**200.0**	**150.0**	**134.1**	**104.6**	**62.5**	**124.1**	**156.6**	**169.2**
Companions with preference for recent forests										
Festuca ovina		19.3	25.0	62.5	61.4	32.3	12.5	42.8	**-23.5**	35.1
Cladonia arbuscula		24.6	41.7	50.0	65.9	38.5	37.5	48.3	**-23.7**	42.2
Dryopteris carthusiana	*	24.6	41.7	18.8	40.9	41.5	50.0	39.3	**-14.7**	34.1
Anthoxanthum odoratum		1.8	8.3	18.8	22.7	40.0	25.0	29.0	**-27.2**	20.4
Rumex acetosella		3.5	25.0	31.3	43.2	40.0	37.5	38.6	**-35.1**	28.0
Polytrichum juniperinum		3.5	25.0	18.8	18.2	53.8	37.5	35.9	**-32.4**	26.5
Lycopodium clavatum		5.3	8.3	18.8	13.6	36.9	25.0	24.8	**-19.6**	18.5
Deschampsia flexuosa		77.2	83.3	75.0	84.1	95.4	87.5	88.3	**-11.1**	83.9
Agrostis capillaris		8.8	0.0	6.3	6.8	10.8	50.0	10.3	**-1.6**	9.5
Hieracium lachenalii		3.5	0.0	0.0	6.8	12.3	25.0	9.0	**-5.5**	7.1
Total frequency of of the group		**171.9**	**258.3**	**300.0**	**363.6**	**401.5**	**387.5**	**366.2**	**-194.3**	**305.2**
Other frequent species										
Juniperus communis		78.9	83.3	81.3	81.8	76.9	37.5	77.2	**1.7**	76.8
Polytrichastrum formosum		43.9	41.7	18.8	31.8	30.8	75.0	33.1	**10.8**	35.5
Cladonia furcata		22.8	33.3	37.5	31.8	16.9	37.5	26.2	**-3.4**	25.1
Leucobrium glaucum		22.8	16.7	37.5	18.2	16.9	37.5	20.7	**2.1**	21.8
Cladonia rangiferina		22.8	0.0	25.0	22.7	20.0	25.0	20.0	**2.8**	20.9
Cetraria islandica		5.3	0.0	12.5	18.2	3.1	0.0	8.3	**-3.0**	8.5
Hieracium pilosella		1.8	0.0	6.3	11.4	6.2	0.0	6.9	**-5.1**	6.2
Calamagrostis epigejos		7.0	25.0	0.0	2.3	6.2	0.0	5.5	**1.5**	5.7
Total frequency of species with preference for ancient forests		**624.6**	**450.0**	**312.5**	**300.0**	**276.9**	**175.0**	**296.6**	**328.0**	**389.6**
Total frequency of species with preference for recent forests		**177.2**	**258.3**	**312.5**	**384.1**	**467.7**	**400.0**	**404.1**	**-226.9**	**337.4**

* – *ancient forest species* acc. to Hermy et al. (1999) and Dzwonko and Loster (2001)

The analysis of the results indicates floristic-structural differences between the distinguished forest categories:

Cover of the herb layer is distinctly higher in the ancient than in the recent forests, especially those featuring a shorter regeneration period (Fig. 19).

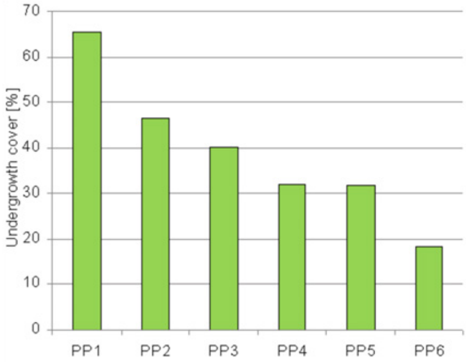


Fig. 19. Cover of the herb layer in the forest categories of *Peucedano-Pinetum* communities

Ryc. 19. Zróżnicowanie pokrycia warstwy runa w kategoriach borów (*Peucedano-Pinetum*)

The share of alien species, introduced into tree stands – *Padus serotina* and *Quercus rubra* – is higher in recent forests. However, these species have practically not entered yet the tree layer.

Among the species characteristic of *Vaccinio-Piceetea* class, three display a significant frequency domination (see Fig. 20a) in ancient forests over recent ones (*Vaccinium vitis-idaea*, *Hylocomium splendens*, *Trientalis europaea*). Both these species of vascular plants are considered by Dzwonko and Loster (2001) to be ancient forest species. Besides, this group would contain also *Vaccinium uliginosum*, the species rare in the fresh pine forests, appearing uniquely in the ancient forests.

Among the species characteristic of *Vaccinio-Piceetea* class there are also the ones featuring higher frequency in the recent than in the ancient forests. This group would contain, in particular, three species from the *Pyrolaceae* family (*Chimaphila umbellata*, *Pyrola chlorantha*, *Orthilia secunda*), of which the first two display a statistically significant difference. This group is most numerous in the recent forests of category PP5, which were planted on post-agricultural land at the end of the 19th century or at the turn of the 20th century (Fig. 20b). Both in the forests planted in the 20th century, and in those with a longer history of regeneration (having appeared at the end of the 18th century and at the beginning of the 19th century) their shares are lower. Interestingly, the share of these species (considered to be characteristic of *Vaccinio-Piceetea* class) is even lower in the ancient forests (category PP1).

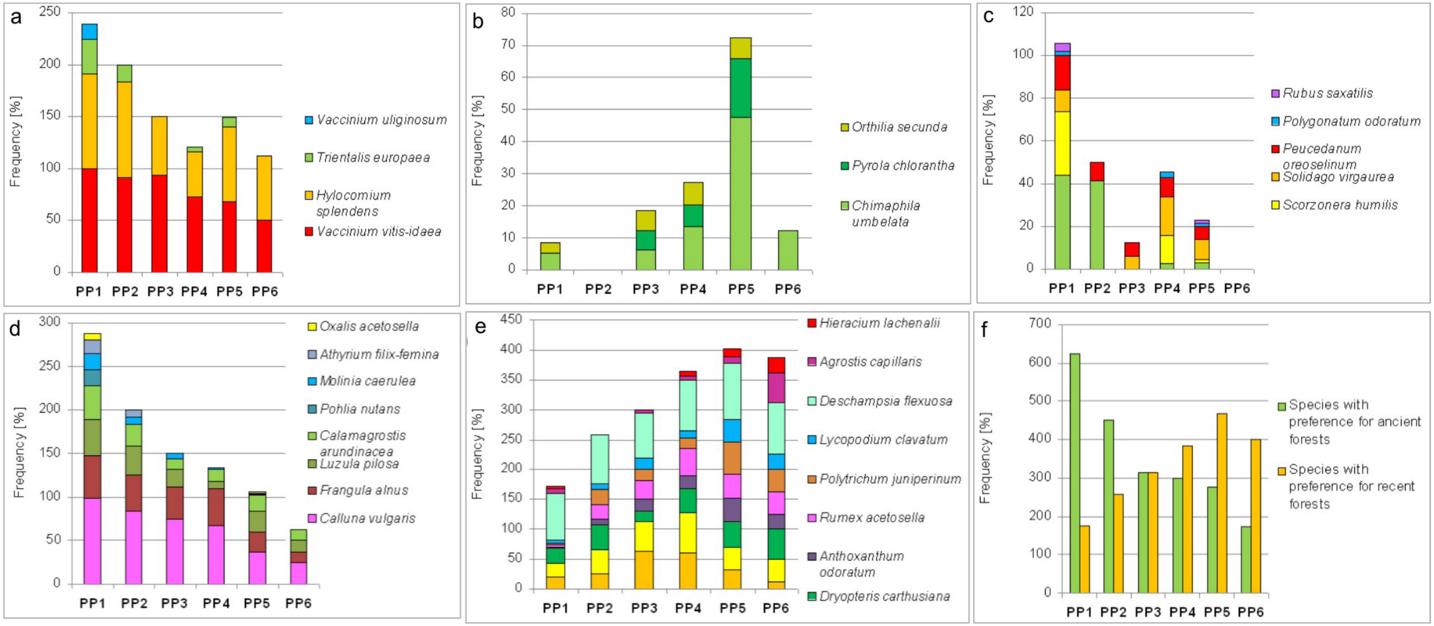


Fig. 20. Frequency of selected species group in the forest categories of *Peucedano-Pinetum* communities: species characteristic of *Vaccinio-Piceetea* class with preference for ancient forests (a), with preference for recent forests (b), differential species of the association (c), companions with preference for ancient forests (d), companions with preference for recent forests (e), total frequency of differential species (f)

Ryc. 20. Frekwencje wybranych grup gatunków w kategoriach borów (*Peucedano-Pinetum*): gatunki charakterystyczne klasy *Vaccinio-Piceetea* preferujące "stare lasy" (a), preferujące lasy wtórne (b), gatunki wyróżniające zespołu (c), gatunki towarzyszące preferujące "stare lasy" (d), towarzyszące preferujące lasy wtórne (e), łączna frekwencja różnicujących gatunków (f).

Of species characteristic of *Vaccinio-Piceetea* class the most numerous group is constituted by those that do not display distinct differences in frequency between the ancient forests and the recent ones. This group includes two species considered as ancient forest species (according to Hermy et al., 1999), i.e. *Vaccinium myrtillus* and *Melampyrum pratense,* which does not find confirmation here. Concerning the frequency of the most important species for the pine forests structure, that is – *Vaccinium myrtillus* – the difference between the ancient forests and the recent ones is very small. This, however, concerns only the presence of this species in the patches, the situation is different when we consider the quantitative shares in particular communities.

The differential species of *Peucedano-Pinetum* association are unexpectedly poorly represented (Fig. 20c). In the ancient forests the frequency of 30–50% is attained uniquely by *Convallaria majalis* and *Scorzonera humilis*; roughly 10–20% of frequency is attained by *Peucedanum oreoselinum* and *Solidago virgaurea*. In the recent forests the species of this group are distinctly less frequently encountered (two first of them displaying a significant statistical difference). They are virtually absent in the recent forests with a short period of regeneration. In the recent forests with the longest period of regeneration, that is – the ones that already in 1800 had been forests, the shares of two species from the group considered, *Convallaria majalis* and *Solidago virgaurea*, are similar as in the ancient forests. Under a more detailed analysis – not presented here – it is seen that the species of the group considered are relatively more frequently encountered in the forests of Kurpie than in those of Masuria.

The group of the so-called companions, featuring significantly lower frequency in the recent forests (at least the younger ones), compared to ancient forests, is composed of eight species (Fig. 20d): *Calluna vulgaris*, *Luzula pilosa*, *Calamagrostis arundinacea*, *Pohlia nutans*, *Frangula alnus*, *Molinia caerulea*, *Athyrium filix-femina*, *Oxalis acetosella*. The distribution of the first of these species is particularly regular (the shorter the regeneration period, the less of it), which is insofar interesting as this is not so much a forest species (like the majority of the remaining ones) as a species of open heather lands, which constitute often a stage in the succession, leading to pine forest. This group contains three species considered to be the ancient forest species (Hermy et al. 1999) – *Luzula pilosa*, *Oxalis acetosella* and *Athyrium filix-femina*.

The group of the companions, which feature higher frequency in the recent than in the ancient forests (see Fig. 20e) is formed primarily by the species of open habitats – associated with the dry sandy grasslands (the class of *Koelerio glaucae-Corynephoretea canescentis*): *Festuca ovina, Rumex acetosella, Anthoxanthum odoratum, Agrostis capillaris*, and the mat-grass grasslands (*Nardo-Callunetea* class) – *Lycopodium clavatum*. The expansive grass species *Deschampsia flexuosa* also belongs among the species more often appearing in the recent than in the ancient forests. Similar situation was

Table 7. Significance of the frequency difference between the forest categories according to a Fisher's exact test in pine forests (*Peucedano-Pinetum*)

Species	*Scorzonera humilis*	*Pohlia nutans*	*Molinia caerulea*	*Athyrium filix-femina*	*Vaccinium uliginosum*	*Calluna vulgaris*	*Hylocomium splendens*	*Frangula alnus b/c*	*Vaccinium vitis-idaea*	*Calamagrostis arundinacea*	*Convallaria majalis*	*Luzula pilosa*	*Trientalis europaea*	*Oxalis acetosella*	*Peucedanum oreoselinum*	*Festuca ovina*	*Chimaphila umbellata*	*Pyrola chlorantha*	*Cladonia arbuscula*	*Rumex acetosella*	*Deschampsia flexuosa*	*Dryopteris carthusiana*	*Lycopodium clavatum*	*Polytrichum juniperinum*	*Anthoxanthum odoratum*	*Agrostis capillaris*	*Hieracium lachenalii*
f% PP1	30	18	19	16	14	98	91	49	100	39	44	42	33	7	16	19	5	0	25	4	77	25	5	4	2	9	4
f% PP2	0	0	8	8	0	83	92	42	92	25	42	33	17	0	8	25	0	0	42	25	83	42	8	25	8	0	0
f% PP3	0	0	6	0	0	75	56	38	94	13	0	19	0	0	6	63	6	6	50	31	75	19	19	19	19	6	0
f% PP4	14	0	2	0	0	68	43	41	73	14	2	9	5	0	9	61	14	7	66	43	84	41	14	18	23	7	7
f% PP5	2	0	2	2	0	37	72	23	68	18	3	23	9	2	6	32	48	18	38	40	95	42	37	54	40	11	12
f% PP6	0	0	0	0	0	25	63	13	50	13	0	13	0	0	0	13	13	0	38	38	88	50	25	38	25	50	25
f% PP2-6	5	0	3	1	0	54	63	31	73	17	6	19	7	1	7	43	27	11	48	39	88	39	25	36	29	10	9
f% PP3-6	5	0	2	1	0	51	60	30	71	16	2	17	6	1	7	44	29	12	49	40	89	39	26	37	31	11	10
f% PP4-6	6	0	2	1	0	48	61	29	68	16	3	17	7	1	7	42	32	13	49	41	91	42	27	39	32	12	11
f% PP5-6	1	0	1	1	0	36	71	22	66	18	3	22	8	1	5	30	44	16	38	40	95	42	36	52	38	15	14
Significance of the frequency difference - Fisher's exact test																											
PP1:PP2-6	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,02	0,00	0,00	0,00	0,00	0,00	0,02	0,06	0,00	0,00	0,01	0,00	0,00	0,08	0,05	0,00	0,00	0,00	1,00	0,24
PP1:PP3-6	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,01	0,00	0,00	0,00	0,00	0,00	0,03	0,06	0,00	0,00	0,00	0,00	0,00	0,05	0,07	0,00	0,00	0,00	0,80	0,24
PP1:PP4-6	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,01	0,00	0,00	0,00	0,00	0,00	0,04	0,10	0,00	0,00	0,00	0,00	0,00	0,02	0,03	0,00	0,00	0,00	0,61	0,15
PP1:PP5-6	0,00	0,00	0,00	0,00	0,00	0,00	0,01	0,00	0,00	0,01	0,00	0,02	0,00	0,17	0,08	0,22	0,00	0,00	0,13	0,00	0,01	0,04	0,00	0,00	0,00	0,42	0,07
PP1:PP2	0,03	0,19	0,68	0,68	0,33	0,08	1,00	0,76	0,17	0,51	1,00	0,75	0,32	1,00	0,68	0,70	1,00	1,00	0,29	0,03	1,00	0,29	0,54	0,03	0,32	0,58	1,00
PP1:PP3	0,02	0,10	0,28	0,19	0,19	0,01	0,00	0,57	0,22	0,07	0,00	0,14	0,01	0,57	0,44	0,00	1,00	0,22	0,07	0,00	1,00	0,75	0,11	0,07	0,03	1,00	1,00
PP1:PP4	0,06	0,00	0,01	0,00	0,01	0,00	0,00	0,43	0,00	0,01	0,00	0,00	0,00	0,13	0,38	0,00	0,17	0,08	0,00	0,00	0,46	0,09	0,17	0,02	0,00	1,00	0,65
PP1:PP5	0,00	0,00	0,00	0,01	0,00	0,00	0,01	0,00	0,00	0,02	0,00	0,03	0,00	0,18	0,14	0,15	0,00	0,00	0,12	0,00	0,01	0,06	0,00	0,00	0,00	0,77	0,10
PP1:PP6	0,10	0,34	0,33	0,59	0,58	0,00	0,05	0,07	0,00	0,24	0,02	0,14	0,09	1,00	0,59	1,00	0,42	1,00	0,42	0,01	0,68	0,20	0,11	0,01	0,04	0,01	0,07
PP2:PP3	1,00	1,00	1,00	0,43	1,00	0,67	0,09	1,00	1,00	0,62	0,01	0,42	0,17	1,00	1,00	0,07	1,00	1,00	0,72	1,00	0,67	0,23	0,61	1,00	0,61	1,00	1,00
PP2:PP4	0,32	1,00	0,39	0,21	1,00	0,48	0,00	1,00	0,26	0,39	0,00	0,06	0,20	1,00	1,00	0,05	0,32	1,00	0,18	0,33	1,00	1,00	1,00	0,69	0,42	1,00	1,00
PP2:PP5	1,00	1,00	0,29	0,29	1,00	0,00	0,27	0,28	0,16	0,69	0,00	0,48	0,60	1,00	0,58	0,74	0,00	0,19	1,00	0,52	0,17	1,00	0,09	0,11	0,05	0,59	0,34
PP2:PP6	1,00	1,00	1,00	1,00	1,00	0,02	0,26	0,32	0,11	0,62	0,05	0,60	0,49	1,00	1,00	0,62	0,40	1,00	1,00	0,64	1,00	1,00	0,54	0,64	0,54	0,01	0,15
PP3:PP4	0,18	1,00	0,47	1,00	1,00	0,75	0,40	1,00	0,15	1,00	1,00	0,37	1,00	1,00	1,00	1,00	0,66	1,00	0,37	0,55	0,46	0,14	0,69	1,00	1,00	1,00	0,56
PP3:PP5	1,00	1,00	0,36	1,00	1,00	0,01	0,24	0,34	0,06	0,73	1,00	1,00	0,59	1,00	1,00	0,04	0,00	0,45	0,41	0,58	0,03	0,15	0,24	0,01	0,15	1,00	0,35
PP3:PP6	1,00	1,00	1,00	1,00	1,00	0,03	1,00	0,35	0,03	1,00	1,00	1,00	1,00	1,00	1,00	0,03	1,00	1,00	0,68	1,00	0,63	0,17	1,00	0,36	1,00	0,03	0,10
PP4:PP5	0,02	1,00	1,00	1,00	1,00	0,00	0,00	0,06	0,67	0,60	1,00	0,07	0,47	1,00	0,71	0,00	0,00	0,10	0,01	0,84	0,09	1,00	0,01	0,00	0,07	0,74	0,52
PP4:PP6	0,57	1,00	1,00	1,00	1,00	0,04	0,45	0,23	0,23	1,00	1,00	1,00	1,00	1,00	1,00	0,02	1,00	1,00	0,23	1,00	1,00	0,71	0,59	0,34	1,00	0,01	0,16
PP5:PP6	1,00	1,00	1,00	1,00	1,00	0,70	0,68	0,68	0,43	1,00	1,00	0,68	1,00	1,00	1,00	0,42	0,07	0,34	1,00	1,00	0,38	0,72	0,70	0,47	0,70	0,02	0,30

Table 8. Species with preference for different pine forests categories

Species	Distinguished pine forest categories
Scorzonera humilis *Pohlia nutans*	Species with preference for ancient forests (PP1).
Vaccinium uliginosum *Oxalis acetosella*	Species with preference for ancient forests (PP1), but rare.
Peucedanum oreoselinum	Species with likely preference for ancient forests (PP1).
Convallaria majalis *Hylocomium splendens*	Species with preference for ancient forests (PP1) and the oldest recent forests (PP2).
Athyrium filix-femina *Calamagrostis arundinacea* *Luzula pilosa* *Trientalis europaea*	Species with preference for ancient forests (PP1) and partly for the oldest recent forests (PP2).
Molinia caerulea *Frangula alnus b/c* *Vaccinium vitis-idaea*	Species with preference for ancient forests (PP1) and partly for the recent forests (PP2 and PP3).
Calluna vulgaris	Species with preference for ancient forests (PP1), well graded regeneration stages, distinctly rarer in younger recent forests (PP5 and PP6).
Festuca ovina	Species with preference for recent forests (PP3 and PP4).
Chimaphila umbellata *Pyrola chlorantha*	Species with preference for recent forests (PP5).
Cladonia arbuscula	Species with preference for recent forests, max value in PP4 category.
Rumex acetosella	Species with preference for recent forests (PP2-PP6), max value in PP4 category.
Deschampsia flexuosa	Species with preference for recent forests, especially younger.
Dryopteris carthusiana	Species with slight preference for recent forests, especially younger.
Lycopodium clavatum *Anthoxanthum odoratum* *Polytrichum juniperinum*	Species with preference for recent forests, especially categories PP3-PP6, max value in PP5 category.
Agrostis capillaris	Species with preference for the youngest recent forests (PP6).
Hieracium lachenalii	Species with likely preference for the youngest recent forests (PP6).

observed by Góras and Orczewska (2007). This results from environmental conditions promoting this perennial grass in recent forests (Emmer, 1995). The group considered encompasses, as well, the species, which are characterised by increasing frequency along with the shortening of forest regeneration period (*Agrostis capillaris*), and also such that are most frequent in the forests with longer, but not the longest period of regeneration (*Festuca ovina*, *Cladonia arbuscula*). Attention ought to be paid to the fact that this group includes also *Dryopteris carthusiana* a species from the list of ancient forest species, conform to Hermy et al. (1999). It has very small wind-dispersed propagulae, which probably explains their ability to colonize isolated stands (Brunet 2007).

Joint consideration of the frequencies of these species, which display preference for the ancient forests with those that are more frequent in the recent forests allows to find some definite frequency regularities (see Fig. 20f). The proportion between the total frequency of the first species group and that of the second ranges from more than 3.5 for the ancient forests to 0.4 for the forests with the shortest regeneration period. Proportions close to 1.1 are observed for the forests of the category PP3, whose regeneration started in the first half of the 19th century, i.e. the recent post-agricultural forests, which had not been afforested yet in 1800, but were in 1830. Such forests display, when compared to ancient forests, roughly half of species frequency associated with the ancient forests and, in comparison with the youngest forests roughly 80% of species typical of the recent forests.

A detailed analysis of Table 7 with the Fisher's test results makes possible the classification of species with different frequency in pine forests categories (Tab. 8).

4.1.2. FLORISTIC COMPOSITION OF MIXED OAK-PINE FORESTS

The communities connected with the mixed oak-pine forest of *Querco-Pinetum* habitat are represented by 94 phytosociological relevés.

Four forest categories have been distinguished among them:

QP1 – Ancient forests – 33 relevés,

QP2 – Recent post-agricultural forests with the regeneration period of more than 230 years – 10 relevés,

QP3-4 – Recent post-agricultural forests with the regeneration period between roughly 135-200 years – 18 relevés,

QP5-6 – Recent post-agricultural forests with the regeneration period of around 80-135 years – 33 relevés.

Table 9 contains frequency values of the plant species in mixed oak-pine forests, while Table 10 shows the significance of differences in the species frequency between particular categories of forests, determined with the Fisher's test. Table 9 contains, side by side with the species frequencies in the abovementioned categories of mixed oak-pine forests, also the mean frequencies for all recent forests (QP2-6), and for all communities investigated.

Table 9. Diversity of plant composition in mixed oak-pine forests (*Querco roboris-Pinetum*)

Mixed oak-pine forests categories	QP1	QP2	QP3-4	QP5-6	QP2-6 together	QP1 - QP2-6	QP1 - QP5-6	QP1-6 together
	Ancient forests	Recent, post-agricultural forest afforested before 1800	Recent, post-agricultural forest afforested between 1800 and 1885	Recent, post-agricultural forest afforested after 1885 (or 1928)	All recent forests (QP2-6)	Difference between ancient and recent forests	Difference between ancient and younger recent forests	All mixed oak-pine forests
No. of relevés	30	13	18	33	64			94
Forest stand age acc. to forest map	107.9	115.7	107.9	100.1	105.4	2.5	7.8	106.2
Tree cover [%]	67.0	61.5	65.6	61.8	62.8	4.2	5.2	64.1
Shrub cover [%]	13.3	20.8	18.1	17.2	18.2	-4.8	-3.8	16.6
Herb cover [%]	69.3	71.5	59.4	59.8	62.1	7.2	9.5	64.4
Moss cover [%]	75.8	81.5	76.7	86.5	82.7	-6.9	-10.7	80.5
Frequency [%] **Tree species**								
Betula pendula-a1	20.0	0.0	16.7	15.2	12.5	7.5	4.8	14.9
Betula pendula-a2	40.0	30.8	33.3	57.6	45.3	-5.3	-17.6	43.6
Betula pendula-a3	46.7	69.2	27.8	63.6	54.7	-8.0	-17.0	52.1
Betula pendula-b	43.3	69.2	50.0	60.6	59.4	-16.0	-17.3	54.3
Betula pendula-c	20.0	30.8	11.1	30.3	25.0	-5.0	-10.3	23.4
Fagus sylvatica-a3	10.0	7.7	0.0	3.0	3.1	6.9	7.0	5.3
Fagus sylvatica-b	26.7	7.7	5.6	9.1	7.8	18.9	17.6	13.8
Fagus sylvatica-c	3.3	0.0	0.0	0.0	0.0	3.3	3.3	1.1
Padus serotina-a3	6.7	15.4	5.6	12.1	10.9	-4.3	-5.5	9.6
Padus serotina-b	13.3	7.7	22.2	18.2	17.2	-3.9	-4.8	16.0
Padus serotina-c	13.3	0.0	11.1	33.3	20.3	-7.0	-20.0	18.1
Picea abies-a1	20.0	30.8	16.7	15.2	18.8	1.3	4.8	19.1
Picea abies-a2	83.3	76.9	50.0	60.6	60.9	22.4	22.7	68.1
Picea abies-a3	46.7	76.9	22.2	60.6	53.1	-6.5	-13.9	51.1
Picea abies-b	66.7	69.2	55.6	57.6	59.4	7.3	9.1	61.7
Picea abies-c	30.0	15.4	16.7	30.3	23.4	6.6	-0.3	25.5
Pinus sylvestris-a1	100.0	100.0	100.0	100.0	100.0	0.0	0.0	100.0

Pinus sylvestris-a2		0.0	0.0	16.7	21.2	15.6	-15.6	-21.2	10.6
Pinus sylvestris-a3		3.3	15.4	11.1	12.1	12.5	-9.2	-8.8	9.6
Pinus sylvestris-b		10.0	30.8	33.3	24.2	28.1	-18.1	-14.2	22.3
Pinus sylvestris-c		23.3	46.2	27.8	54.5	45.3	-22.0	-31.2	38.3
Quercus robur-a1		6.7	0.0	16.7	6.1	7.8	-1.1	0.6	7.4
Quercus robur-a2		23.3	0.0	44.4	9.1	17.2	6.1	14.2	19.1
Quercus robur-a3		53.3	53.8	61.1	45.5	51.6	1.8	7.9	52.1
Quercus robur-b		56.7	76.9	77.8	78.8	78.1	-21.5	-22.1	71.3
Quercus robur-c		60.0	61.5	66.7	84.8	75.0	-15.0	-24.8	70.2
Sorbus aucuparia-a2		0.0	0.0	0.0	6.1	3.1	-3.1	-6.1	2.1
Sorbus aucuparia-a3		3.3	0.0	5.6	6.1	4.7	-1.4	-2.7	4.3
Sorbus aucuparia-b		53.3	53.8	50.0	33.3	42.2	11.1	20.0	45.7
Sorbus aucuparia-c		33.3	30.8	44.4	60.6	50.0	-16.7	-27.3	44.7
Herb and moss species									
Species with preference for ancient forests									
Convallaria majalis	*	76.7	30.8	27.8	12.1	20.3	56.4	64.5	38.3
Pteridium aquilinum	*	46.7	30.8	33.3	3.0	17.2	29.5	43.6	26.6
Luzula pilosa	*	90.0	76.9	50.0	57.6	59.4	30.6	32.4	69.1
Maianthemum bifolium	*	53.3	23.1	33.3	15.2	21.9	31.5	38.2	31.9
Trientalis europaea (ch.)	*	83.3	69.2	38.9	57.6	54.7	28.6	25.8	63.8
Polygonatum odoratum		33.3	7.7	11.1	0.0	4.7	28.6	33.3	13.8
Athyrium filix-femina	*	33.3	30.8	16.7	6.1	14.1	19.3	27.3	20.2
Sciuro-hypnum oedipodium		23.3	7.7	0.0	3.0	3.1	20.2	20.3	9.6
Polytrichastrum formosum		70.0	38.5	50.0	42.4	43.8	26.3	27.6	52.1
Molinia caerulea		26.7	7.7	16.7	3.0	7.8	18.9	23.6	13.8
Scorzonera humilis		20.0	7.7	5.6	0.0	3.1	16.9	20.0	8.5
Peucedanum oreoselinum		26.7	15.4	22.2	0.0	9.4	17.3	26.7	14.9
Total frequency of the group		**583.3**	**346.2**	**305.6**	**200.0**	**259.4**	**324.0**	**383.3**	**362.8**
Species with preference for some recent forests									
Anthoxanthum odoratum		10.0	15.4	16.7	60.6	39.1	-29.1	-50.6	29.8
Lycopodium clavatum		0.0	30.8	11.1	33.3	26.6	-26.6	-33.3	18.1
Chimaphila umbellata (ch.)		3.3	23.1	11.1	39.4	28.1	-24.8	-36.1	20.2
Cytisus scoparius		3.3	7.7	11.1	36.4	23.4	-20.1	-33.0	17.0
Rumex acetosella		13.3	7.7	22.2	45.5	31.3	-17.9	-32.1	25.5
Holcus mollis		0.0	0.0	5.6	21.2	12.5	-12.5	-21.2	8.5
Total frequency of the group		**30.0**	**84.6**	**77.8**	**236.4**	**160.9**	**-130.9**	**-206.4**	**119.1**
Species with preference for younger recent forests									
Ptilium crista-castrensis		40.0	38.5	11.1	72.7	48.4	-8.4	-32.7	45.7
Veronica officinalis		6.7	7.7	5.6	30.3	18.8	-12.1	-23.6	14.9
Galium mollugo		10.0	7.7	11.1	33.3	21.9	-11.9	-23.3	18.1
Polytrichum juniperinum		13.3	0.0	5.6	33.3	18.8	-5.4	-20.0	17.0
Total frequency of the group		70.0	53.8	33.3	169.7	107.8	-37.8	-99.7	95.7
Species characteristic of the class Vaccinio-Piceetea present in all pine forest categories									
Vaccinium myrtillus	*	100.0	100.0	100.0	100.0	100.0	0.0	0.0	100.0
Pleurozium schreberi		100.0	100.0	100.0	97.0	98.4	1.6	3.0	98.9
Hylocomium splendens		90.0	84.6	100.0	90.9	92.2	-2.2	-0.9	91.5
Melampyrum pratense	*	83.3	100.0	88.9	90.9	92.2	-8.9	-7.6	89.4
Vaccinium vitis-idaea	*	86.7	100.0	61.1	69.7	73.4	13.2	17.0	77.7
Dicranum polysetum		83.3	69.2	83.3	69.7	73.4	9.9	13.6	76.6

Lycopodium annotinum		26.7	23.1	33.3	33.3	31.3	-4.6	-6.7	29.8
Dicranum scoparium		26.7	23.1	38.9	15.2	23.4	3.2	11.5	24.5
Orthilia secunda		16.7	0.0	5.6	27.3	15.6	1.0	-10.6	16.0
Diphasiastrum complanatum		3.3	15.4	11.1	3.0	7.8	-4.5	0.3	6.4
Pyrola chlorantha		0.0	0.0	0.0	12.1	6.3	-6.3	-12.1	4.3
Pyrola rotundifolia		0.0	0.0	0.0	12.1	6.3	-6.3	-12.1	4.3
Ledum palustre		6.7	0.0	5.6	0.0	1.6	5.1	6.7	3.2
Total frequency of the group		**623.3**	**615.4**	**627.8**	**621.2**	**621.9**	**1.5**	**2.1**	**622.3**
Species characteristic of the class *Querco-Fagetea*									
Carex digitata	*	16.7	7.7	11.1	3.0	6.3	10.4	13.6	9.6
Dryopteris filix-mas	*	13.3	0.0	5.6	12.1	7.8	5.5	1.2	9.6
Viola reichenbachiana	*	6.7	23.1	0.0	0.0	4.7	2.0	6.7	5.3
Total frequency of the group		36.7	30.8	16.7	15.2	18.8	17.9	21.5	24.5
Other frequent species (f > 10%)									
Deschampsia flexuosa		83.3	76.9	83.3	87.9	84.4	-1.0	-4.5	84.0
Dryopteris carthusiana	*	70.0	46.2	66.7	69.7	64.1	5.9	0.3	66.0
Frangula alnus bc		70.0	53.8	83.3	45.5	57.8	12.2	24.5	61.7
Calamagrostis arundinacea		73.3	61.5	44.4	54.5	53.1	20.2	18.8	59.6
Juniperus communis bc		50.0	69.2	66.7	57.6	62.5	-12.5	-7.6	58.5
Calluna vulgaris		50.0	69.2	33.3	30.3	39.1	10.9	19.7	42.6
Oxalis acetosella	*	53.3	38.5	33.3	30.3	32.8	20.5	23.0	39.4
Rubus idaeus		40.0	38.5	38.9	33.3	35.9	4.1	6.7	37.2
Festuca ovina		26.7	23.1	22.2	18.2	20.3	6.4	8.5	22.3
Fragaria vesca		26.7	15.4	5.6	30.3	20.3	6.4	-3.6	22.3
Rubus saxatilis		26.7	38.5	11.1	15.2	18.8	7.9	11.5	21.3
Agrostis capillaris		23.3	15.4	5.6	18.2	14.1	9.3	5.2	17.0
Plagiomnium affine		23.3	7.7	22.2	12.1	14.1	9.3	11.2	17.0
Hieracium lachenalii		10.0	7.7	5.6	24.2	15.6	-5.6	-14.2	13.8
Moehringia trinervia		13.3	0.0	11.1	18.2	12.5	0.8	-4.8	12.8
Solidago virgaurea		20.0	23.1	11.1	3.0	9.4	10.6	17.0	12.8
Mycelis muralis		20.0	7.7	11.1	6.1	7.8	12.2	13.9	11.7
Chamaenerion angustifolium		16.7	7.7	11.1	6.1	7.8	8.9	10.6	10.6
Danthonia decumbens		10.0	7.7	22.2	6.1	10.9	-0.9	3.9	10.6
Rubus nessensis		10.0	15.4	16.7	6.1	10.9	-0.9	3.9	10.6
Cladonia arbuscula		0.0	15.4	16.7	9.1	12.5	-12.5	-9.1	8.5
Pohlia nutans		10.0	23.1	0.0	6.1	7.8	2.2	3.9	8.5
Viola riviniana		16.7	7.7	5.6	3.0	4.7	12.0	13.6	8.5
Hieracium pilosella		6.7	0.0	11.1	9.1	7.8	-1.1	-2.4	7.4
Plagiothecium curvifolium		6.7	0.0	11.1	9.1	7.8	-1.1	-2.4	7.4
Poa augustifolia		10.0	0.0	11.1	6.1	6.3	3.8	3.9	7.4
Knautia arvensis		0.0	7.7	0.0	15.2	9.4	-9.4	-15.2	6.4
Cladonia rangiferina		3.3	0.0	16.7	3.0	6.3	-2.9	0.3	5.3
Hypochoeris radicata		3.3	7.7	11.1	3.0	6.3	-2.9	0.3	5.3
Leucobrium glaucum		0.0	0.0	5.6	0.0	1.6	-1.6	0.0	1.1
Polytrichum commune		3.3	15.4	5.6	3.0	6.3	-2.9	0.3	5.3
Cladonia furcata		0.0	0.0	11.1	6.1	6.3	-6.3	-6.1	4.3
Cladonia glauca		3.3	0.0	16.7	0.0	4.7	-1.4	3.3	4.3

* - *ancient forest species* acc. to Hermy et al. (1999) and Dzwonko and Loster (2001)

Table 10. Significance of frequency difference between the forest categories according to a Fisher's exact test in mixed oak-pine forests (*Querco-Pinetum*)

	Convallaria majalis	*Luzula pilosa*	*Sciuro-hypnum oedipodium*	*Trientalis europaea (ch.)*	*Pteridium aquilinum*	*Maianthemum bifolium*	*Polygonatum odoratum*	*Athyrium filix-femina*	*Molinia caerulea*	*Scorzonera humilis*	*Polytrichastrum formosum*	*Peucedanum oreoselinum*	*Vaccinium vitis-idaea (ch.)*	*Calamagrostis arundinacea*	*Oxalis acetosella*	*Calluna vulgaris*	*Frangula alnus bc*	*Anthoxanthum odoratum*	*Lycopodium clavatum*	*Chimaphila umbellata(ch.)*	*Cytisus scoparius*	*Rumex acetosella*	*Holcus mollis*	*Galium molugo*	*Veronica officinalis*	*Ptilium crista-castrensis (ch.)*	*Polytrichum juniperinum*
f% QP1	70	91	24	82	48	52	30	36	27	21	67	24	88	73	52	52	70	9	3	6	3	12	0	9	6	39	12
f% QP2	40	70	0	70	20	20	10	20	0	0	40	20	100	60	40	70	50	20	30	20	10	10	0	10	10	40	0
f% QP3-4	28	50	0	39	33	33	11	17	17	6	50	22	61	44	33	33	83	17	11	11	11	22	6	11	6	11	6
f% QP5-6	12	58	3	58	3	15	0	6	3	0	42	0	70	55	30	30	45	61	33	39	36	45	21	33	30	73	33
f% QP2-6	22	58	2	55	15	22	5	12	7	2	45	10	73	53	33	38	58	42	27	28	25	33	13	23	20	50	20
Significance of the frequency difference - Fisher's exact test																											
QP1 : QP2	0.14	0.13	0.17	0.41	0.15	0.14	0.41	0.46	0.09	0.17	0.16	1.00	0.56	0.46	0.72	0.47	0.28	0.57	0.03	0.23	0.42	1.00	1.00	1.00	0.56	1.00	0.56
QP1 : QP3-4	0.01	0.00	0.04	0.00	0.38	0.25	0.17	0.20	0.50	0.23	0.37	1.00	0.04	0.07	0.25	0.25	0.34	0.65	0.28	0.61	0.28	0.43	0.35	1.00	1.00	0.05	0.64
QP1 : QP5-6	0.00	0.00	0.03	0.06	0.00	0.00	0.00	0.01	0.01	0.01	0.08	0.00	0.13	0.20	0.13	0.13	0.08	0.00	0.00	0.00	0.00	0.01	0.01	0.03	0.02	0.01	0.08
QP1 : QP2-6	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.01	0.00	0.05	0.08	0.12	0.08	0.08	0.27	0.37	0.00	0.00	0.01	0.01	0.05	0.05	0.10	0.13	0.39	0.40
QP2 : QP3-4	0.68	0.43	1.00	0.24	0.67	0.67	1.00	1.00	0.53	1.00	0.71	1.00	0.03	0.69	1.00	0.11	0.09	1.00	0.32	0.60	1.00	0.63	1.00	1.00	1.00	0.15	1.00
QP2 : QP5-6	0.07	0.71	1.00	0.71	0.13	0.66	0.23	0.23	1.00	1.00	1.00	0.05	0.08	1.00	0.70	0.03	1.00	0.03	1.00	0.45	0.24	0.06	0.17	0.24	0.66	0.07	0.04
QP3-4 : QP5-6	0.25	0.77	1.00	0.25	0.01	0.16	0.12	0.33	0.12	0.35	0.77	0.01	0.55	0.57	1.00	1.00	0.02	0.00	0.10	0.05	0.10	0.14	0.23	0.10	0.07	0.00	0.04

The analysis of the results indicates the floristic-structural differences between the distinguished forest categories:

The cover of herb layer in the recent forests is slightly lower than in the ancient forests, while it is opposite with the moss layer, which is higher in the recent forests (Fig. 21).

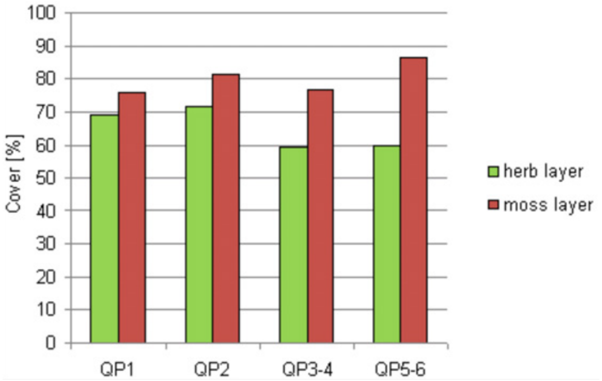


Fig. 21. Cover of the herb and moss layer in the forest categories of *Querco-Pinetum* communities

Ryc. 21. Zróżnicowanie pokrycia warstwy runa i mszaków w kategoriach borów mieszanych (*Querco-Pinetum*)

The frequency of tree species bears the effect of additional planting of black cherry and beech

In all of the communities investigated Scots pine is the main species in the tree stand. The group of species, which are significantly more frequent in the ancient forests than in the recent ones (i.e. those, for which the Fisher's test showed the statistical significance of difference in frequency between the category QP1 and the joint categories QP2-6) encompasses 12 species, of which 10 are vascular plants species and two are mosses (Fig. 22a). Among the vascular plants there are typical of mixed oak-pine forests moderately photophilous perennial plants (*Convallaria majalis, Polygonatum odoratum, Scorzonera humilis, Peucedanum oreoselinum, Pteridium aquilinum),* the generally forest-related species of mesotrophic habitats *(Luzula pilosa, Maianthemum bifolium*), as well as the species characteristic of *Vaccinio-Piceetea class – Trientalis europaea* and of *Querco-Fagetea* class – *Athyrium filix-femina.* Mosses in this group are represented by *Polytrichastrum formosum* and *Sciuro-hypnum oedipodium*. There are six species in this group, which are considered to be ancient forest species (*Convallaria majalis, Luzula pilosa, Maianthemum bifolium, Pteridium aquilinum, Trientalis europaea* and *Athyrium filix-femina).* It should be noted that the group of species, generally distinguishing ancient forests, is not homogeneous in terms of appearance in the recent forests. Some species display the frequency in the recent forests that is systematically lower for shorter periods since afforestation. This kind of frequency pattern is characteristic, for instance, of *Convallaria majalis* and *Athyrium filix-femina*. There are species that appear in the ancient forests with a limited frequency, while almost not at all in the recent ones (*Scorzonera humilis, Sciuro-hypnum oedipodium*), and such ones that display an especially pronounced difference between the ancient forests and the recent ones with the shortest period of regeneration *(Pteridium aquilinum, Peucedanum oreoselinum, Polygonatum odoratum*). It can also be remarked that none of species from this group alone can be treated as an unambiguous indicator of ancient forests for the mixed oak-pine forests, because either it is too rare in the ancient stands, or it appears (even though with a lower frequency) in the recent forests. On the other hand, the group, as a whole, quite clearly distinguishes ancient forests from the recent ones. In the latter – total frequency of the species from the group considered attains at most (for the forests with a relatively long regeneration period) slightly more than half of the respective value, recorded for the ancient forests, and in the case of the recent forests with a short period of regeneration (the first generation of tree stands on post-agricultural land) attains only a bit more than 1/3 of this value.

The group of species, which display higher constancy in the recent forest communities than in the ancient forests (Fig. 22b) is composed of ten species, of which an important part is linked with the associations of open areas (*Anthoxanthum odoratum and Rumex acetosella),* with the associations of dry sandy grasslands *(*order *Corynephoretalia canescentis): Lycopodium clavatum* and *Veronica officinalis* - species that are frequent in pine forests and in mixed oak-pine forests, but considered to be characteristic of the mat-grass grasslands and heather associations (*Nardo-Callunetea* class): *Cytisus scoparius* – belonging to the differential species in the syntaxa classified among the heather lands (*Nardo-Callunetea* class) and the shrub (*Rhamno-Prunetea* class*), Galium mollugo* – the species characteristic of the meadows (*Molinio-Arrhenatheretea* class). It is interesting to note that this group contains also species treated as characteristic of *Vaccinio-Piceetea* class – *Chimaphila umbellata* and *Ptilium crista-castrensis*. The species of the group considered have a significantly higher frequency in the recent forests than in the ancient forests, and, moreover, display in general terms (as a whole group) a relation with the recent forest persistence – their highest numbers are observed in the forests with short regeneration period. This concerns, in particular, two species: *Rumex acetosella* and *Anthoxanthum odoratum*.

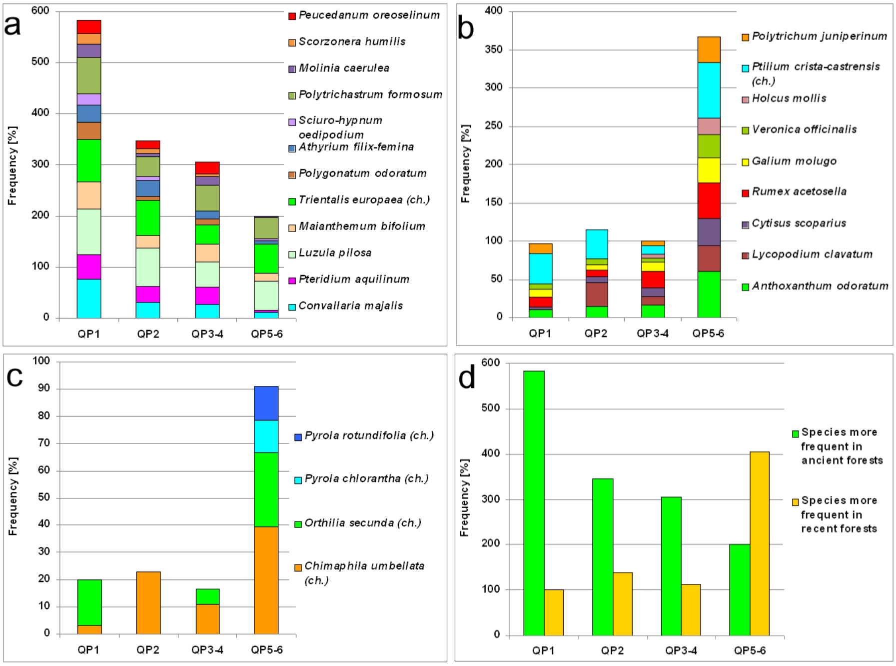


Fig. 22. Frequency of selected species group in the forest categories of *Querco-Pinetum* communities: (a) species with preference for ancient forests, (b) species with preference for recent forests, (c) species of *Pyrolaceae* family with preference for recent forests, (d) total frequency of differential species

Ryc. 22. Frekwencje gatunków wybranych grup w kategoriach borów mieszanych (*Querco-Pinetum*): (a) gatunki wykazujące preferencje dla "starych lasów", (b) gatunki wykazujące preferencje dla lasów wtórnych, (c) gatunki z rodziny gruszyczkowatych, (d) łączna frekwencja gatunków różnicujących

The numerous group of species, which do not feature a clearly higher frequency either in the ancient forests or in the recent ones (at least according to the material collected and the applied method of comparison) encompassed in the majority the species characteristic of the pine forests (*Vaccinio-Piceetea* class), besides the ones mentioned before.

Among the species characteristic of *Vaccinio-Piceetea* class one should pay attention to the species from the family of *Pyrolaceae* (*Chimaphila umbellata, Orthilia secunda, Pyrola chlorantha, Pyrola rotundifolia*), these species being most frequent in the forests on post-agricultural land (categories QP5-6), which occupy the locations that yet in 1885 were arable lands, i.e. the ones that have some 80-135 years of regeneration behind them (Fig. 22c).

The species important for the structure of mixed oak-pine forests, *Vaccinium myrtillus,* does not display – in terms of frequency – distinct preference for any of the categories of mixed oak-pine forests investigated – it appears on all patches, although in diverse numbers (as analysed in the further part of the work). Similarly, three important moss species – *Pleurozium schreberi, Hylocomium splendens* and *Dicranium polysetum,* as well as herb species *Melampyrum pratense* and *Deschampsia flexuosa,* do not feature pronounced differences in their frequencies.

The shares of species characteristic of *Querco-Fagetea* class are quite low in the investigated mixed oak-pine forests. One can indicate among them *Athyrium filix-femina,* as a species weakly linked to the ancient forests, while the other ones do not display such a connection.

It can be generally noted that the unambiguous differences in frequency of species between the ancient and the recent forests can be observed for groups rather than for individual species. As said, none of the individual species could be referred to as an indicator in the sense that it appears with a high frequency in a definite forest category and does not appear in some other ones.

Table 11. Species with preference for different mixed oak-pine forests categories

Species	Distinguished mixed oak-pine forest categories
Sciuro-hypnum oedipodium *Scorzonera humilis*	Species with preference for ancient forests, but rare, almost absent in recent forests.
Convallaria majalis	Species with preference for ancient forests, well graded regeneration stages, rarer in younger forests.
Athyrium filix-femina	
Luzula pilosa *Trientalis europaea (ch.)* *Pteridium aquilinum* *Maianthemum bifolium* *Polygonatum odoratum* *Molinia caerulea* *Polytrichastrum formosum*	Species with preference for ancient forests, slightly or not at all graded regeneration stages.
Peucedanum oreoselinum	Species with preference for ancient forests (QP1) and the oldest recent forests (QP2, QP3-4) in comparison to younger recent forests (QP5-6).
Calamagrostis arundinacea *Oxalis acetosella*	Species with likely preference for ancient forests.
Calluna vulgaris	Species with likely preference for ancient forests and the oldest recent forests.
Lycopodium clavatum	Species with preference for recent forests.
Chimaphila umbellata (ch.) *Cytisus scoparius* *Rumex acetosella* *Galium molugo* *Veronica officinalis*	Species with preference for recent forests, especially younger (QP5-6).
Anthoxanthum odoratum *Holcus mollis* *Ptilium crista-castrensis (ch.)* *Polytrichum juniperinum*	Species with preference for the youngest recent forests (QP5-6).

It can also be observed that the consequences of agricultural land-use are visible for a long time in the mixed oak-pine forests, with their regeneration taking place very slowly (Fig. 22d). Even the sites, where already at the end of the 18th century forests grew, but the plough horizon exists there (category QP2), clearly differ as to their floristic composition from the forests at these sites, which had never been permanently deforested (QP1). In the case of the mixed oak-pine forest the regeneration process consists primarily in the return of species typical of ancient forests and to a lesser degree in the recession of species proper for recent forests, whose presence is distinctly marked only in the forests with relatively short period of regeneration.

A detailed analysis of table 10, containing the results of the Fisher's test, allows for the classification of species with different frequencies in the mixed oak-pine forests categories presented in table 11.

4.1.3. FLORISTIC COMPOSITION OF LIME-OAK-HORNBEAM FORESTS

The communities on the lime-oak-hornbeam forest (*Tilio-Carpinetum*) habitats are represented by 44 phytosociological relevés. The lesser number of relevés, compared to the previous types results from the fact of relatively more scarce, especially in the southern part of the study area, appearance of forests on this habitat type. It should be noted that the communities of lime-oak-hornbeam forests display distinct, much stronger than pine forests and mixed oak-pine forests, habitat-related diversity. Among the analysed patches of lime-oak-hornbeam forests one can distinguish poor mesotrophic forests – *Tilio-Carpinetum calamagrostetiosum* and the typical ones – *Tilio-Carpinetum typicum*. In the basic analysis of differences between the ancient forests and the recent ones the aspect of habitat difference was neglected and three forest categories have been distinguished:

TC1 – Ancient forests – 21 relevés,

TC2 – Recent post-agricultural forests (i.e. with a visible plough horizon), afforested before the year 1800 – 13 relevés,

TC3-6 – Recent post-agricultural forests, afforested in various periods after the year 1800 – 10 relevés.

Table 12. Diversity of plant composition in lime-oak-hornbeam forests (*Tilio-Carpinetum*)

Lime-oak-hornbeam forests categories		TC1	TC2	TC3-6	TC2-6	TC1 - TC2-6	TC1 - TC3-6	TC1-6
		Ancient forests	Recent, post-agricultural forest afforested before 1800	Recent, post-agricultural forest afforested after 1800	All recent forests	Difference between ancient and recent forests	Difference between ancient and younger recent forests	All lime-oak-hornbeam forests
No. of relevés		21	13	10	23			44
Forest stand age acc. to forest map		116.8	121.2	112.9	117.6	-0.8	3.9	117.2
Tree cover [%]		84.8	81.5	74.0	78.3	6.5	10.8	81.4
Shrub cover [%]		11.6	18.7	23.5	20.8	-9.2	-11.9	16.4
Herb cover [%]		51.9	58.1	55.0	56.7	-4.8	-3.1	54.4
Moss cover [%]		7.0	11.2	18.4	14.3	-7.3	-11.4	10.8
Frequency [%] **Tree species**								
Acer platanoides-a1		9.5	7.7	0.0	4.3	5.2	9.5	6.8
Acer platanoides-a2		9.5	30.8	20.0	26.1	-16.6	-10.5	18.2
Acer platanoides-a3		0.0	15.4	0.0	8.7	-8.7	0.0	4.5
Acer platanoides-b		14.3	7.7	10.0	8.7	5.6	4.3	11.4
Acer platanoides-c		23.8	38.5	30.0	34.8	-11.0	-6.2	29.5
Acer pseudoplatanus-a3		4.8	0.0	0.0	0.0	4.8	4.8	2.3
Acer pseudoplatanus-b		0.0	7.7	0.0	4.3	-4.3	0.0	2.3
Acer pseudoplatanus-c		14.3	38.5	10.0	26.1	-11.8	4.3	20.5
Betula pendula-a1		23.8	7.7	0.0	4.3	19.5	23.8	13.6
Betula pendula-a2		9.5	7.7	50.0	26.1	-16.6	-40.5	18.2
Betula pendula-a3		9.5	0.0	0.0	0.0	9.5	9.5	4.5
Betula pendula-c		0.0	0.0	10.0	4.3	-4.3	-10.0	2.3
Carpinus betulus-a2		85.7	53.8	30.0	43.5	42.2	55.7	63.6
Carpinus betulus-a3		61.9	61.5	20.0	43.5	18.4	41.9	52.3
Carpinus betulus-b		85.7	46.2	60.0	52.2	33.5	25.7	68.2
Carpinus betulus-c		57.1	23.1	50.0	34.8	22.4	7.1	45.5
Corylus avelana-a2		4.8	0.0	0.0	0.0	4.8	4.8	2.3
Corylus avelana-a3		9.5	7.7	30.0	17.4	-7.9	-20.5	13.6
Fagus sylvatica-a1		23.8	15.4	0.0	8.7	15.1	23.8	15.9
Fagus sylvatica-a2		28.6	15.4	10.0	13.0	15.5	18.6	20.5
Fagus sylvatica-a3		14.3	23.1	0.0	13.0	1.2	14.3	13.6
Fagus sylvatica-b		19.0	46.2	30.0	39.1	-20.1	-11.0	29.5
Fagus sylvatica-c		14.3	23.1	10.0	17.4	-3.1	4.3	15.9

Fraxinus excelsior-a1		0.0	23.1	0.0	13.0	-13.0	0.0	6.8
Fraxinus excelsior-a2		4.8	0.0	0.0	0.0	4.8	4.8	2.3
Fraxinus excelsior-a3		0.0	7.7	0.0	4.3	-4.3	0.0	2.3
Fraxinus excelsior-b		4.8	23.1	0.0	13.0	-8.3	4.8	9.1
Fraxinus excelsior-c		4.8	7.7	0.0	4.3	0.4	4.8	4.5
Padus avium-b		0.0	7.7	10.0	8.7	-8.7	-10.0	4.5
Padus serotina-a3		4.8	15.4	10.0	13.0	-8.3	-5.2	9.1
Padus serotina-b		4.8	30.8	20.0	26.1	-21.3	-15.2	15.9
Padus serotina-c		0.0	7.7	20.0	13.0	-13.0	-20.0	6.8
Picea abies-a1		33.3	23.1	10.0	17.4	15.9	23.3	25.0
Picea abies-a2		38.1	53.8	60.0	56.5	-18.4	-21.9	47.7
Picea abies-a3		23.8	30.8	10.0	21.7	2.1	13.8	22.7
Picea abies-b		9.5	23.1	30.0	26.1	-16.6	-20.5	18.2
Picea abies-c		23.8	23.1	50.0	34.8	-11.0	-26.2	29.5
Pinus sylvestris-a1		90.5	84.6	100.0	91.3	-0.8	-9.5	90.9
Pinus sylvestris-a2		0.0	15.4	10.0	13.0	-13.0	-10.0	6.8
Pinus sylvestris-c		4.8	15.4	20.0	17.4	-12.6	-15.2	11.4
Populus tremula-a1		9.5	7.7	0.0	4.3	5.2	9.5	6.8
Populus tremula-b		4.8	0.0	0.0	0.0	4.8	4.8	2.3
Populus tremula-c		23.8	15.4	0.0	8.7	15.1	23.8	15.9
Quercus robur-a1		71.4	53.8	30.0	43.5	28.0	41.4	56.8
Quercus robur-a2		23.8	30.8	60.0	43.5	-19.7	-36.2	34.1
Quercus robur-a3		4.8	38.5	20.0	30.4	-25.7	-15.2	18.2
Quercus robur-b		9.5	15.4	30.0	21.7	-12.2	-20.5	15.9
Quercus robur-c		23.8	15.4	0.0	8.7	15.1	23.8	15.9
Quercus rubra-a1		4.8	0.0	0.0	0.0	4.8	4.8	2.3
Quercus rubra-b		4.8	0.0	10.0	4.3	0.4	-5.2	4.5
Quercus rubra-c		14.3	0.0	20.0	8.7	5.6	-5.7	11.4
Sorbus aucuparia-a3		4.8	15.4	0.0	8.7	-3.9	4.8	6.8
Sorbus aucuparia-b		28.6	38.5	40.0	39.1	-10.6	-11.4	34.1
Sorbus aucuparia-c		57.1	53.8	60.0	56.5	0.6	-2.9	56.8
Tilia cordata-a1		0.0	7.7	10.0	8.7	-8.7	-10.0	4.5
Tilia cordata-a2		14.3	0.0	20.0	8.7	5.6	-5.7	11.4
Tilia cordata-a3		0.0	15.4	20.0	17.4	-17.4	-20.0	9.1
Tilia cordata-b		9.5	23.1	30.0	26.1	-16.6	-20.5	18.2
Tilia cordata-c		4.8	15.4	10.0	13.0	-8.3	-5.2	9.1
Herb and moss species								
Species with preference for ancient forests								
Hypnum cupressiforme		52.4	30.8	0.0	17.4	35.0	52.4	34.1
Hepatica nobilis (ch. Q-F)	*	52.4	61.5	0.0	34.8	17.6	52.4	43.2
Ajuga reptans		61.9	76.9	10.0	47.8	14.1	51.9	54.5
Milium effusum (ch. Q-F)	*	71.4	76.9	20.0	52.2	19.3	51.4	61.4
Anemone nemorosa (ch. Q-F)	*	100.0	69.2	50.0	60.9	39.1	50.0	79.5
Atrichum undulatum (ch. Q-F)		42.9	46.2	0.0	26.1	16.8	42.9	34.1

Convallaria majalis	*	81.0	53.8	40.0	47.8	33.1	41.0	63.6
Galeobdolon luteum (ch. Q-F)	*	57.1	76.9	20.0	52.2	5.0	37.1	54.5
Stellaria holostea (ch. Q-F)	*	85.7	84.6	50.0	69.6	16.1	35.7	77.3
Lathyrus vernus (ch. Q-F)	*	33.3	38.5	0.0	21.7	11.6	33.3	27.3
Viola reichenbachiana (ch. Q-F)	*	71.4	92.3	40.0	69.6	1.9	31.4	70.5
Galium odoratum (ch. Q-F)	*	28.6	53.8	0.0	30.4	-1.9	28.6	29.5
Polygonatum multiflorum (ch. Q-F)	*	42.9	69.2	20.0	47.8	-5.0	22.9	45.5
Total frequency of of the group		**781.0**	**830.8**	**250.0**	**578.3**	**202.7**	**531.0**	675.0
Species with preference for recent forests								
Frangula alnus-b/c		4.8	23.1	60.0	39.1	-34.4	-55.2	22.7
Fragaria vesca		23.8	53.8	60.0	56.5	-32.7	-36.2	40.9
Pleurozium schreberi (ch. V-P)		14.3	23.1	70.0	43.5	-29.2	-55.7	29.5
Vaccinium vitis-idaea (ch. V-P)	*	0.0	15.4	40.0	26.1	-26.1	-40.0	13.6
Geranium robertianum		4.8	15.4	50.0	30.4	-25.7	-45.2	18.2
Galium molugo		9.5	15.4	50.0	30.4	-20.9	-40.5	20.5
Hylocomium splendens (ch. V-P)		4.8	15.4	30.0	21.7	-17.0	-25.2	13.6
Deschampsia flexuosa		14.3	0.0	70.0	30.4	-16.1	-55.7	22.7
Veronica officinalis		14.3	15.4	50.0	30.4	-16.1	-35.7	22.7
Rubus idaeus		47.6	38.5	90.0	60.9	-13.3	-42.4	54.5
Juniperus communis-b/c		0.0	0.0	30.0	13.0	-13.0	-30.0	6.8
Total frequency of of the group		**138.1**	**215.4**	**600.0**	**382.6**	**-244.5**	**-461.9**	265.9
Other frequent species f>15% listed acc. to difference score between ancient and recent forests								
Polytrichastrum formosum		47.6	7.7	40.0	21.7	25.9	7.6	34.1
Calamagrostis arundinacea		85.7	53.8	70.0	60.9	24.8	15.7	72.7
Scrophularia nodosa (ch. Q-F)	*	33.3	15.4	10.0	13.0	20.3	23.3	22.7
Dicranella heteromalla		23.8	7.7	10.0	8.7	15.1	13.8	15.9
Galium schultesii (ch. Q-F)		19.0	7.7	0.0	4.3	14.7	19.0	11.4
Trientalis europaea (ch. V-P)	*	47.6	15.4	60.0	34.8	12.8	-12.4	40.9
Moehringia trinervia		42.9	7.7	60.0	30.4	12.4	-17.1	36.4
Maianthemum bifolium	*	90.5	92.3	60.0	78.3	12.2	30.5	84.1
Herzogiella seligeri		28.6	15.4	20.0	17.4	11.2	8.6	22.7
Festuca gigantea (ch. Q-F)	*	19.0	7.7	10.0	8.7	10.4	9.0	13.6
Gymnocarpium dryopteris	*	19.0	0.0	20.0	8.7	10.4	-1.0	13.6
Ranunculus lanuginosus (ch. Q-F)	*	19.0	15.4	0.0	8.7	10.4	19.0	13.6
Melica nutans (ch. Q-F)	*	47.6	46.2	30.0	39.1	8.5	17.6	43.2
Carex digitata (ch. Q-F)	*	85.7	92.3	60.0	78.3	7.5	25.7	81.8
Galeopsis tetrahit		28.6	0.0	50.0	21.7	6.8	-21.4	25.0
Impatiens noli-tangere (ch. Q-F)		14.3	0.0	20.0	8.7	5.6	-5.7	11.4
Lophocolea heterophylla		14.3	15.4	0.0	8.7	5.6	14.3	11.4
Oxalis acetosella	*	100.0	100.0	90.0	95.7	4.3	10.0	97.7
Aegopodium podagraria		47.6	61.5	20.0	43.5	4.1	27.6	45.5
Corylus avelana-bc (ch. Q-F)		47.6	30.8	60.0	43.5	4.1	-12.4	45.5
Pteridium aquilinum	*	38.1	30.8	40.0	34.8	3.3	-1.9	36.4
Hieracium lachenalii		23.8	7.7	40.0	21.7	2.1	-16.2	22.7

Dryopteris dilatata		19.0	30.8	0.0	17.4	1.7	19.0	18.2
Brachythecium rutabulum		14.3	23.1	0.0	13.0	1.2	14.3	13.6
Epilobium montanum (ch. Q-F)	*	9.5	0.0	20.0	8.7	0.8	-10.5	9.1
Vaccinium myrtillus (ch. V-P)	*	57.1	46.2	70.0	56.5	0.6	-12.9	56.8
Luzula pilosa	*	47.6	46.2	50.0	47.8	-0.2	-2.4	47.7
Athyrium filix-femina (ch. Q-F)	*	23.8	38.5	10.0	26.1	-2.3	13.8	25.0
Dryopteris carthusiana	*	66.7	61.5	80.0	69.6	-2.9	-13.3	68.2
Polygonatum odoratum		9.5	7.7	20.0	13.0	-3.5	-10.5	11.4
Brachythecium oedipodium		4.8	0.0	20.0	8.7	-3.9	-15.2	6.8
Carex sylvatica (ch. Q-F)	*	4.8	15.4	0.0	8.7	-3.9	4.8	6.8
Ranunculus repens		4.8	0.0	20.0	8.7	-3.9	-15.2	6.8
Dryopteris filix-mas (ch. Q-F)	*	47.6	61.5	40.0	52.2	-4.6	7.6	50.0
Plagiomnium affine (ch. Q-F)		38.1	38.5	50.0	43.5	-5.4	-11.9	40.9
Geum urbanum		23.8	30.8	30.0	30.4	-6.6	-6.2	27.3
Euonymus verrucosa-b/c		14.3	7.7	40.0	21.7	-7.5	-25.7	18.2
Melampyrum pratense (ch. V-P)	*	14.3	15.4	30.0	21.7	-7.5	-15.7	18.2
Eurhynchium angustirete (ch. Q-F)		9.5	30.8	0.0	17.4	-7.9	9.5	13.6
Stachys sylvatica (ch. Q-F)	*	9.5	30.8	0.0	17.4	-7.9	9.5	13.6
Dicranum polysetum (ch. V-P)		4.8	7.7	20.0	13.0	-8.3	-15.2	9.1
Stellaria graminea		4.8	7.7	20.0	13.0	-8.3	-15.2	9.1
Adoxa moschatellina (ch. Q-F)	*	0.0	0.0	20.0	8.7	-8.7	-20.0	4.5
Anthriscus sylvestris		0.0	0.0	20.0	8.7	-8.7	-20.0	4.5
Festuca ovina		0.0	0.0	20.0	8.7	-8.7	-20.0	4.5
Lycopodium annotinum (ch. V-P)		0.0	0.0	20.0	8.7	-8.7	-20.0	4.5
Polygonum convolvulus		0.0	0.0	20.0	8.7	-8.7	-20.0	4.5
Solidago virgaurea		0.0	0.0	20.0	8.7	-8.7	-20.0	4.5
Paris quadrifolia (ch. Q-F)	*	19.0	46.2	10.0	30.4	-11.4	9.0	25.0
Veronica chamaedrys		9.5	23.1	20.0	21.7	-12.2	-10.5	15.9
Urtica dioica		42.9	53.8	60.0	56.5	-13.7	-17.1	50.0
Mycelis muralis		66.7	84.6	80.0	82.6	-15.9	-13.3	75.0
Rubus saxatilis		42.9	76.9	40.0	60.9	-18.0	2.9	52.3
Impatiens parviflora		33.3	61.5	40.0	52.2	-18.8	-6.7	43.2
Dactylis polygama (ch. Q-F)	*	9.5	46.2	10.0	30.4	-20.9	-0.5	20.5

There were selected species with f>15%
* - *ancient forest species* acc. to Hermy et al. (1999) and Dzwonko and Loster (2001)
ch. *Q-F* - Species characteristic of the class *Querco-Fagetea;* ch. *V-P* – Species characteristic of the class *Vaccinio-Piceetea*

Table 12 contains the frequencies of particular species in the lime-oak-hornbeam forests. Test of frequency difference between forest categories is according to a Fisher's exact test. The significance of the results is presented in table 13.

Table 13. Significance of the frequency difference between the forest categories according to a Fisher's exact test in lime-oak-pine forests (*Tilio-Carpinetum*)

	Anemone nemorosa	*Carpinus betulus-a2*	*Hypnum cupressiforme*	*Convallaria majalis*	*Calamagrostis arundinacea*	*Hepatica nobilis*	*Ajuga reptans*	*Milium effusum*	*Atrichum undulatum*	*Carpinus betulus-a3*	*Galeobdolon luteum*	*Lathyrus vernus*	*Maianthemum bifolium*	*Stellaria holostea*	*Viola reichenbachiana*	*Galium odoratum*	*Polygonatum multiflorum*	*Dactylis polygama (ch. Q-F)*	*Fragaria vesca*	*Pleurozium schreberi*	*Juniperus communis b/c*	*Deschampsia flexuosa*	*Rubus idaeus*	*Frangula alnus b/c*	*Vaccinium vitis-idaea*	*Geranium robertianum*	*Galium mollugo*	*Hylocomium splendens*	*Veronica officinalis*
f% TC1	100	86	52	81	86	52	62	71	43	62	57	33	90	86	71	29	43	10	24	14	0	14	48	5	0	5	10	5	14
f% TC2	69	54	31	54	54	62	77	77	46	62	77	38	92	85	92	54	69	46	54	23	0	0	38	23	15	15	15	15	15
f% TC3-6	50	30	0	40	70	0	10	20	0	20	20	0	60	50	40	0	20	10	60	70	30	70	90	60	40	50	50	30	50
f% TC2-6	61	43	17	48	61	35	48	52	26	43	52	22	78	70	70	30	48	30	57	43	13	30	61	39	26	30	30	22	30
Significance of the frequency difference - Fisher's exact test																													
TC1 : TC2	0.02	0.06	0.30	0.13	0.06	0.73	0.47	1.00	1.00	1.00	0.29	1.00	1.00	1.00	0.21	0.17	0.17	0.03	0.14	0.65	1.00	0.27	0.73	0.27	0.14	0.54	0.63	0.54	1.00
TC1 : TC3-6	0.00	0.00	0.00	0.04	0.36	0.00	0.01	0.02	0.03	0.05	0.07	0.07	0.07	0.07	0.13	0.14	0.26	1.00	0.11	0.00	0.03	0.00	0.05	0.00	0.01	0.01	0.02	0.09	0.07
TC1 : TC2-6	0.00	0.01	0.03	0.03	0.09	0.36	0.38	0.23	0.34	0.25	0.77	0.50	0.42	0.29	1.00	1.00	0.77	0.14	0.04	0.05	0.23	0.29	0.55	0.01	0.02	0.05	0.14	0.19	0.29
TC2 : TC3-6	0.42	0.40	0.10	0.68	0.67	0.00	0.00	0.01	0.02	0.09	0.01	0.05	0.13	0.17	0.02	0.01	0.04	0.09	1.00	0.04	0.07	0.00	0.03	0.10	0.34	0.17	0.17	0.62	0.17

Data provided in the tables shows the floristic-structural differences between the distinguished forest classes

The cover of the moss layer in the recent forests is clearly higher than in the ancient forests.

Acer platanoides appears in the upper tree layer rarely only in the ancient or in the recent forests of long regeneration period, while in the lower stand layers it appears also in the recent forests in general. This species is not planted, and so its quite slow colonisation into the recent forests is visible.

Betula pendula in the upper stand layer appears not too frequently only in the ancient forests or in the recent ones of long regeneration period, while in the lower tree layers it appears quite frequently in all recent forests.

Carpinus betulus in the tree layer displays significantly higher frequency in the ancient forests than in the recent ones; in the lower layers its shares are similar, which demonstrates that this species enters the recent post-agricultural pine forests communities at some time after the Scots pine stand had been planted. It can be also noted that hornbeam in the tree layers appears only in the forests featuring a longer history of regeneration, that is – in the second generation of the stands on post-agricultural land.

Spruce in the upper tree layer is encountered in the ancient forests and those with long regeneration period; it is recorded in the recent forests solely in the lower tree layers.

Scots pine, a commonly appearing species in all the analysed lime-oak-hornbeam forests, appears with constancy of 100% only in the recent forests.

Oak in the upper tree layer is encountered more frequently in the ancient forests and the ones regenerating for a long time than in the recent ones; in the latter it is often a component of the lower tree layers, which is the evidence for the oak entry into these stands as the introduced Scots pines get mature.

The group of species, appearing in the ancient forests with a significantly higher frequency than in the recent forests (at least those with a shorter regeneration period) (Fig. 23a) is composed in a vast majority of species considered to be characteristic of *Querco-Fagetea* class (*Anemone nemorosa, Atrichum undulatum, Galeobdolon luteum, Galium odoratum, Hepatica nobilis, Lathyrus vernus, Milium effusum, Polygonatum multiflorum, Stellaria holostea* and *Viola reichenbachiana)*, and, besides, the generally forest-related ones, *Ajuga reptans, Convallaria majalis,* along with the moss *Hypnum cupressiforme.* These species appear not only in the ancient forests (category TC1), but also in the recent forests with the long period of regeneration (TC2), or even those recent ones with a shorter regeneration period (TC3-6), with a significantly lower frequency, though. There is no species that would appear solely in the ancient forests with a sufficiently high frequency to be able to state the significance of respective difference. Hence, one can look in this group for the ’re-colonising‘ species of both the first and the second waves. All the species of this group, except for non-classified mosses and *Aiuga reptans,* are the ancient forest species according to Hermy et al. (1999).

In the group of species displaying a significantly higher frequency in the recent forests or the recent forests of shorter regeneration period (Fig. 23b) one can indicate species characteristic of the pine forests (*Vaccinium vitis-idaea, Pleurozium schreberi, Hylocomium splendens)*, which, side by side with *Fragaria vesca, Juniperus communis* and *Veronica officinalis,* frequent in the mixed oak-pine forests, entail a closer similarity of the recent forests on habitats of lime-oak-hornbeam forests to mixed oak-pine forests. Besides the above mentioned species, higher frequencies are observed in the recent lime-oak-hornbeam forests of the expansive native species *Deschampsia flexuosa* and the species of forests with disturbed tree stands – *Rubus idaeus,* the meadow species – *Galium mollugo,* as well as *Geranium robertianum.* These species indicate, on the one hand, a disturbance in the community structure, and on the other hand – a consequence of the Scots pine introduction.

Among the species that have not demonstrated a sufficiently documented preference for the ancient nor the recent forests one can mention, in particular: species characteristic of *Querco-Fagetea* class (*Athyrium filix-femina, Melica nutans, Carex digitata, Carex sylvatica, Dryopteris filix-mas, Festuca gigantea, Paris quadrifolia, Galium schulthesi, Dactylis polygamma, Impatiens noli-tangere, Corylus avellana,* and other ones), as well as the species characteristic of *Vaccinio-Piceetea c*lass, featuring broader ecological amplitude (*Vaccinium myrtillus, Trientalis europaea, Melampyrum pratense).*

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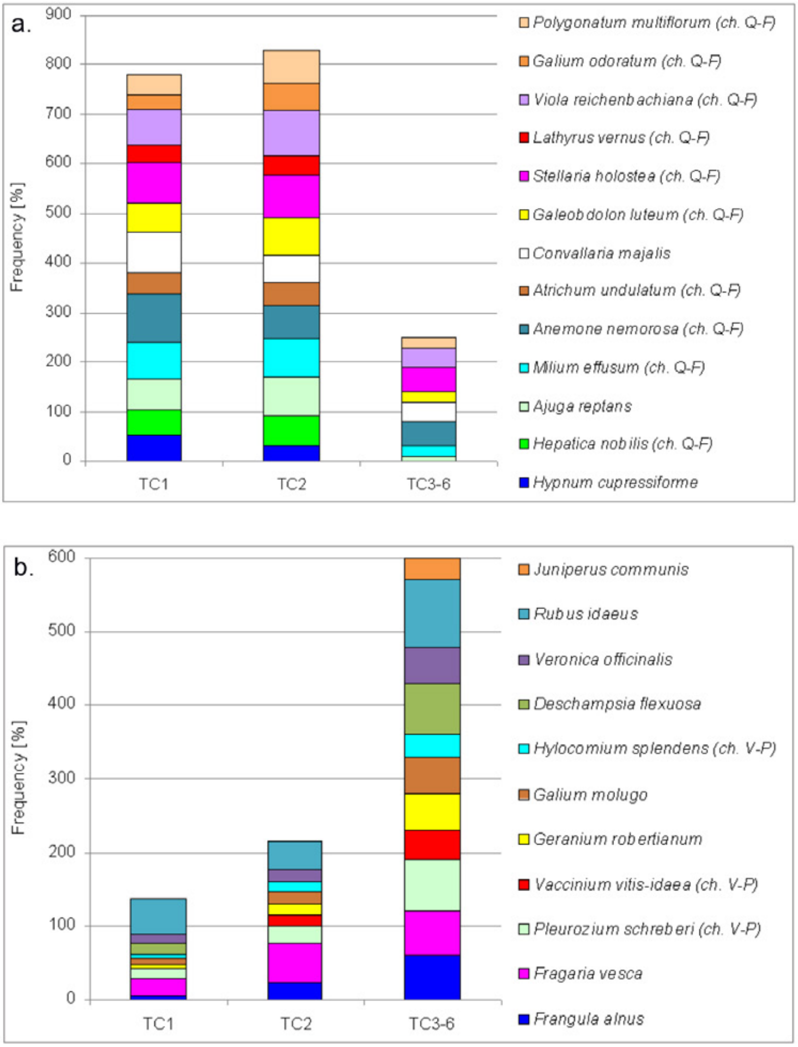


Fig. 23. Frequency of selected species group in the forest categories in *Tilio-Carpinetum* communities: (a) species with preference for ancient forests, (b) species with preference for recent forests

Ryc. 23. Frekwencje gatunków wybranych grup w kategoriach lasów dębowo-grabowych (*Tilio-Carpinetum*): (a) gatunki wykazujące preferencje dla "starych lasów", (b) gatunki wykazujące preferencje dla lasów wtórnych.

Table 14. Species with preference for different lime-oak-hornbeam forests categories

Species	Distinguished lime-oak-hornbeam forest categories
Anemone nemorosa (ch. Q-F) *Carpinus betulus-a2 (ch. Q-F)* *Convallaria majalis*	Species with preference for ancient forests (TC1).
Calamagrostis arundinacea	Species with likely preference for ancient forests (TC1).
Hepatica nobilis (ch. Q-F) *Ajuga reptans* *Milium effusum (ch. Q-F)* *Atrichum undulatum (ch. Q-F)* *Carpinus betulus-a3 (ch. Q-F)* *Galeobdolon luteum (ch. Q-F)*	Species with preference for ancient forests (TC1) and the oldest recent forests (TC2).
Lathyrus vernus (ch. Q-F) *Maianthemum bifolium* *Stellaria holostea (ch. Q-F)* *Viola reichenbachiana (ch. Q-F)* *Galium odoratum (ch. Q-F)* *Polygonatum multiflorum (ch. Q-F)*	Species with likely preference for ancient forests (TC1) and the oldest recent forests (TC2).
Dactylis polygama (ch. Q-F)	Species with likely preference for the oldest recent forests (TC2).
Fragaria vesca *Pleurozium schreberi (ch. V-P)*	Species with preference for recent forests (TC2-6).
Juniperus communis bc *Deschampsia flexuosa* *Rubus idaeus* *Frangula alnus b/c* *Vaccinium vitis-idaea (ch. V-P)* *Geranium robertianum* *Galium molugo*	Species with preference for younger recent forests (TC3-6).
Hylocomium splendens (ch. V-P) *Veronica officinalis*	Species with likely preference for younger recent forests (TC3-6).
Polytrichastrum formosum *Galeopsis tetrahit*	Species of unclear status.
Actea spicata (ch. Q-F) *Athyrium filix-femina (ch. Q-F)* *Euonymus verrucosa bc* *Lilium martagon (ch. Q-F)* *Melica nutans (ch. Q-F)* *Paris quadrifolia (ch. Q-F)* *Phyteuma spicatum (ch. Q-F)* *Ranunculus lanuginosus (ch. Q-F)* *Scrophularia nodosa (ch. Q-F)* *Stachys sylvatica (ch. Q-F)* *Stellaria graminea* *Carex digitata (ch. Q-F)* *Aegopodium podagraria*	Species of insignificant difference (selected).

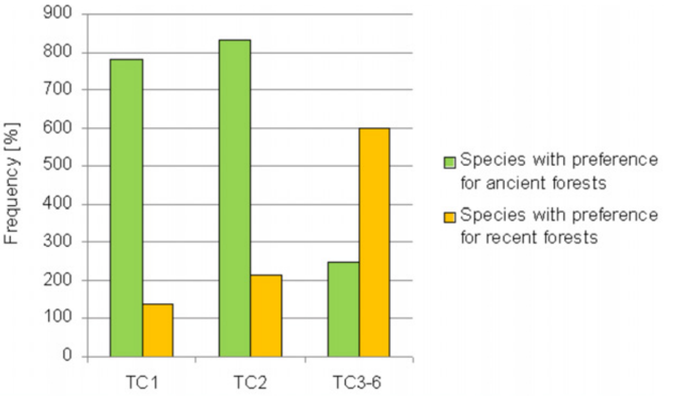


Fig. 24. Total frequency of differential species in the forest categories of *Tilio-Carpinetum* communities

Ryc. 24. Frekwencje łączne gatunków różnicujących w kategoriach lasów dębowo-grabowych (*Tilio-Carpinetum*)

Comparison of the joint frequencies of species dominating in the ancient forests or in the recent ones (Fig. 24) makes it possible to note that the recent forests with the regeneration period longer than 200 years do not differ from the ancient forests in terms of their floristic composition. There is, on the other hand, a clear difference with respect to the recent forests with shorter regeneration periods.

The analysis of Table 13, containing the results from the Fisher's test, allows for the classification of species according to the frequency difference among the lime-oak-hornbeam forests categories presented in Tab. 14.

4.1.4. FLORISTIC SIMILARITY BETWEEN RECENT FOREST REGENERATION PHASES AND ANCIENT FOREST COMMUNITIES

Similarity coefficients of the floristic composition were calculated, defined by the species frequencies, between the particular communities categories in different forest types, using the Jaccard coefficient (Jaccard 1908). It was calculated for the entire floristic composition (including tree species in different forest layers), as well as for the floristic composition without trees (partly introduced by man).

Pine forests

In the case of pine forests categories (see Table 15) the similarity of the entire floristic composition ranges between 67.5 and 84.4%, with the average equal 77.3%. The similarity, calculated for the floristic composition without the tree species, range between 63.8% and 84.8%, the average being 75.3%. The similarity matrix (both for the complete floristic composition and that without trees) points out to the ordering of the persistence classes according to an unambiguous sequence: (PP1 – PP2) – (PP3 – PP4 – PP5) – PP6, in which the highest similarity is observed between PP3 and PP4, as well as PP1 and PP2, while the lowest one – between PP5 and PP6.

Table 15. Similarity of floristic composition in pine forests

P = 2c/(a + b) * 100%		all species					
		PP1	PP2	PP3	PP4	PP5	PP6
without tree species	PP1	x	79.9	74.3	74.4	74.7	67.5
	PP2	81.7	x	80.9	76.6	79.4	76.5
	PP3	73.9	78.8	x	84.4	79.6	76.9
	PP4	73.0	75.9	84.8	x	80.9	75.2
	PP5	71.2	77.1	77.4	79.1	x	78.3
	PP6	63.8	72.4	72.6	72.2	75.9	x

P - Jaccard's similarity coefficient
c - number of species common to both relevés
a - number of species in relevé 1.
b - number of species in relevé 2.

Mixed oak-pine forests

In the case of mixed oak-pine forests (see Table 16) the similarity between the forest categories for the entire floristic composition ranges between 72.5% and 77.2%, the average being 74.7%. The similarity of communities analysed for the floristic composition without trees range between 69.2% and 76.4%, with the average equal 72.5%.

Table 16. Similarity of floristic composition in mixed oak-pine forests

P = 2c/(a + b) * 100%		all species			
		QP1	QP2	QP3-4	QP5-6
without tree species	QP1	x	75.6	77.2	72.5
	QP2	74.5	x	73.8	75
	QP-4	76.4	72.7	x	74.3
	QP5-6	69.2	71.1	71.5	x

P - Jaccard's similarity coefficient
c - number of species common to both relevés
a - number of species in relevé 1.
b - number of species in relevé 2.

Lime-oak-hornbeam forests

For the lime-oak-hornbeam forests (see Table 17) the similarity between the categories in terms of the entire floristic composition range from 59.2% to 74.1%, with the average of 65.0%. The similarities of the analysed objects for the floristic composition without th tree species range from 55.4% to 75.7%, and the average is 64.1%.

Table 17. Similarity of floristic composition in lime-oak-hornbeam forests

P = 2c/(a + b) 100%		all species		
		TC1	TC2	TC3-6
without tree species	TC1	x	74.1	61.6
	TC2	75.7	x	59.2
	TC3-6	61.3	55.4	x

P - Jaccard's similarity coefficient
c - number of species common to both relevés
a - number of species in relevé 1
b - number of species in relevé 2

Comparison of the similarity coefficients between the ancient and the recent forests with different periods of regeneration brings the results that are quite alike for all three types of communities considered. The following interrelations can be observed:

- the similarity of the recent forests to the corresponding ancient ones is bigger for the longer time periods since post-agricultural land had been afforested, which might indicate homogeneity of the regeneration process, for which time is the main independent variable;
- the similarity of complete floristic composition, including trees in all layers, in which they appear, is generally slightly higher than the similarity of floristic composition without trees, which means that changes having the character of deformations concern first of all the non-tree species, and so it is easier to find among them elements for diagnosing the regeneration degree of recent forests; an explanation for this interrelations may consist in the human influence on the forests, which entails an evening out impact on the tree species composition due to forest management;
- the similarity of the recent forests with different periods of regeneration and the ancient forests displays a surprisingly close range of values for three forest types considered: the oldest recent forests, with the regeneration period of 230 years and more, feature similarity to the ancient forests of about 74–84%, the youngest ones, regenerating for some 150-100 years – the similarity of roughly 55–70%; it can be noticed in this context that the differences between types are quite systematic – the relatively highest similarity is observed in the pine forest categories, somewhat lower in the mixed oak-pine forests, and the lowest – in the lime-oak-hornbeam forests.

4.2. THE DIFFERENCES IN THE COVER OF SELECTED SPECIES BETWEEN RECENT AND ANCIENT FORESTS

Analysis was carried out of the differences among the recent forests categories and the ancient ones in the cover of species important for the communities, i.e. those attaining higher cover levels in the selected types of communities. In the case of the lime-oak-hornbeam forests, which feature a significant habitat difference (classification into the subassociations: *Tilio-Carpinetum typicum* and *T.-C. calamagrostietosum*), division according to this criterion was accounted for in the analysis of cover differences.

4.2.1. *VACCINIUM MYRTILLUS* AND *VACCINIUM VITIS-IDAEA* IN PINE FORESTS AND IN MIXED OAK-PINE FORESTS

In the structure of herb layer in pine and mixed oak-pine forests an important role is played by two small dwarf shrub species - *Vaccinium myrtillus* and *Vaccinium vitis-idaea*. These species are characteristic of *Vaccinio-Piceetea* class (Matuszkiewicz J.M. 2001; Matuszkiewicz W. 2001). They are quite common, and, regarding forests displaying natural features – practically always present, with important cover value in many cases. In particular, in typical pine forests they are often the main species composing herb layer. This is why it is worth to take a look at their role in the analysed phytocoenoses concerning the differences between the ancient forests and the recent ones with different periods of regeneration.

Both of these two species may also appear in lime-oak-hornbeam forests. Thus, *Vaccinium myrtillus* is a constant component – also in natural conditions – of poor lime-oak-hornbeam forests (*Tilio-Carpinetum calamagrostietosum*). Both these species appear, as well, in these forests as the consequence of introduction of coniferous species into stand, especially pine. Yet, since their cover in lime-oak-hornbeam forests is usually – but for the exceptional cases – not high, they will not be considered with respect to such forests here.

Frequency analysis of both *Vaccinium* species in the pine (Fig. 25a) and in the mixed oak-pine forests (Fig. 25b) allows for indication of the following regularities:

Vaccinium myrtillus features 100% frequency in the ancient forests, both the pine forests and the mixed oak-pine ones, and also 100% frequency in the patches of recent forests on the habitats of mixed oak-pine forest, while it is somewhat less frequent in the patches of recent pine forests, especially those with a relatively short period of regeneration; yet, as indicated already before, these differences are not statistically significant; hence, in terms of frequency this species does not differentiate (or differentiates to an insignificant degree) the recent forests with respect to the ancient forests.

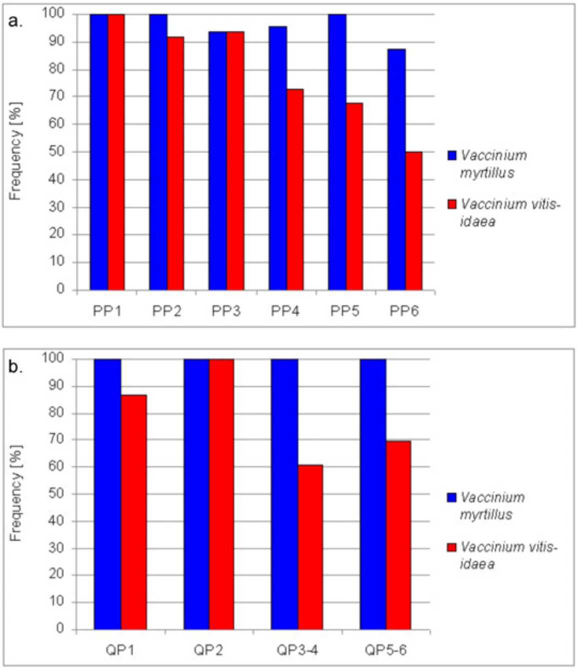


Fig. 25. Frequency of *Vaccinium myrtillus* and *V. vitis-idaea* in the forest categories of *Peucedano-Pinetum* communities (a) and of *Querco-Pinetum* communities (b)
Ryc. 25. Frekwencje dwu gatunków borówki (*Vaccinium myrtillus* i *V. vitis-idaea*) w kategoriach borów (*Peucedano-Pinetum*) (a) i borów mieszanych (*Querco-Pinetum*) (b).

Vaccinium vitis-idaea features 100% frequency in the ancient forests on the habitats of pine forests and slightly lower one on the habitats of mixed oak-pine forests, while in the recent forests, both on the habitats of pine forests and mixed oak-pine forests, the frequency of this species is generally lower; thus, in terms of its frequency, this species differentiates well the pine forests (the significance of differences having been proved) and less the mixed oak-pine forests.

The analysis of *Vaccinium myrtillus* cover in the relevés sets of pine forests categories (Fig. 26a) makes it possible to note that the ancient forests differ clearly from the recent forests with respect to the distribution of cover degrees on the Braun-Blanquet scale; in the ancient forests most often we deal with degree ’3‘, quite often also with ’4‘, less often with ’2‘, and no lower degrees are noted; on the other hand – in the recent forests a tendency is observed of decreasing shares of the lower degree values and increasing – of the higher ones, as we pass from the forests with shorter regeneration periods to those with longer periods since afforestation; it can be assumed that the cover degrees below ’2‘ indicate recent character of the forest.

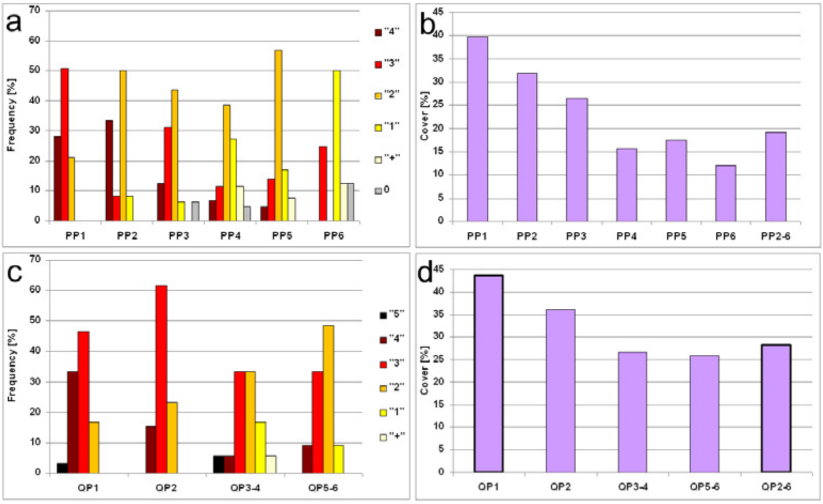


Fig. 26. Cover of *Vaccinium myrtillus* according to the Braun-Blanquet scale (a) and mean cover of *Vaccinium myrtillus* (b) in the forest categories in *Peucedano-Pinetum* communities; cover of *Vaccinium myrtillus* according to the Braun-Blanquet scale (c) and mean cover of *Vaccinium myrtillus* (d) in the forest categories in *Querco-Pinetum* communities

Ryc. 26. Pokrywanie borówki czernicy (*Vaccinium myrtillus*). Stopnie ilościowości wg skali Braun-Blanqueta (a), i średnie pokrywanie (b) w kategoriach borów (*Peucedano-Pinetum*); stopnie ilościowości wg skali Braun-Blanqueta (c), i średnie pokrywanie (d) w kategoriach borów mieszanych (*Querco roboris-Pinetum*)

The average cover of *Vaccinium myrtillus* in the pine forests (Fig. 26b) shows that while in the ancient forests on pine forest habitats the mean attains 40%, in the recent forests it is systematically lower for the shorter periods since afforestation, in those with the shortest regeneration periods reaching only a dozen or so per cent; the ratio of the mean cover between the extreme categories is roughly equal 3:1; the comparison of the ancient forests and the recent ones together shows the difference between some 40 and some 20% of the cover, that is – the ratio of about 2:1.

In the mixed oak-pine forests the distribution of *Vaccinium myrtillus* cover in the forests categories (Fig. 26c) is not so consistent as in the pine forests, but in this case, as well, the differences in the distributions of frequencies of cover degrees are quite distinct; in the ancient forests the distribution is approximately symmetric, with the maximum between the degrees '3' and '4' (jointly more than ¾ of the patches), and not too frequent patches with cover value '2', as well as quite rare ones with '5'; no patches were observed with cover lower than '2'; on the other hand – in the recent forests with the shortest regeneration periods the distribution is asymmetric with the maximum of frequency of the cover degree '2' and much less frequent appearance of patches with the value ’3‘ and ’4‘ (jointly about 40%); the consequence is the difference of the mean cover of this species in the categories of mixed oak-pine forests (Fig. 26d) between the ancient forests (43%) and the recent ones (28% for treated jointly). It can be noted that compared to the pine forests, in the mixed oak-pine forests the difference between the ancient forests and the recent ones, treated jointly, or those with the relatively shorter period of regeneration, is smaller; this shows that regeneration of *Vaccinium myrtillus* takes place in the mixed oak-pine forests generally faster than in the typical pine forests.

The distribution of the cover degrees of *Vaccinium vitis-idaea* in the pine forests categories (Fig. 27a) indicates that the recent forests differ first of all by the relatively much more frequent lack of this species, while when appearance of species in the patches is analysed, it can attain similar cover values as in the ancient forests. In the ancient forests the distribution of frequencies of cover degrees is roughly symmetric, with a clear dominance (almost 2/3 of the patches) of the degree ’2‘ and quite similar shares of the patches with higher (‘3‘) and lower (‘1‘) values; on the other hand in the least regenerated recent forests this distribution is clearly asymmetric; definitely the most frequent fraction is constituted by the patches without this species, while cases of abundant appearance are not observed.

The estimate of the mean cover of *Vaccinium vitis-idaea* in the pine forests categories (Fig. 27b), shows a significant difference between the ancient and the recent forests; the proportion of the mean *Vaccinium vitis-idaea* cover between the extreme categories is 4.5:1, and even if we treat the recent forests jointly, this proportion remains quite significant (2.2:1).

The distribution of *Vaccinium vitis-idaea* cover in the mixed oak-pine forests categories (Fig. 27c) makes it possible to note that, on the one hand, higher frequency of the degree ’2‘ in the ancient forests and in the recent forests with long periods of regeneration is observed, and on the other hand – much more often encountered patches without this species in the recent forests of short regeneration periods; consequently, the mean (Fig. 27d) *Vaccinium vitis-idaea* cover in the mixed oak-pine forests displays a regular increase during the process of forest regeneration; it seems, in this context, that in the case of mixed oak-pine forests the oldest phases of recent forests regeneration do not show already a difference with respect to the ancient forests, which may signify a faster regeneration of *Vaccinium vitis-idaea* in the mixed oak-pine forests than in the typical pine forests.

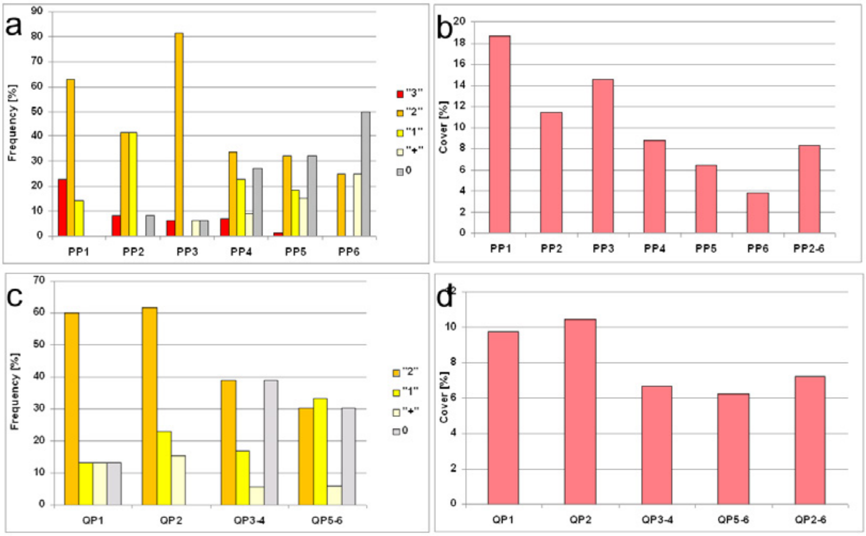


Fig. 27. Cover of *Vaccinium vitis-idaea* according to the Braun-Blanquet scale (a) and mean cover of *Vaccinium vitis-idaea* (b) in the forest categories of *Peucedano-Pinetum* communities; cover of *Vaccinium vitis-idaea* according to the Braun-Blanquet scale (c) and mean cover of *Vaccinium vitis-idaea* (d) in the forest categories of *Querco-Pinetum* communities

Ryc. 27. Pokrywanie borówki brusznicy (*Vaccinium vitis-idaea*). Stopnie ilościowości wg skali Braun-Blanqueta (a), i średnie pokrywanie (b) w kategoriach borów (*Peucedano-Pinetum*); stopnie ilościowości wg skali Braun-Blanqueta (c), i średnie pokrywanie (d) w kategoriach borów mieszanych (*Querco roboris-Pinetum*)

Summing up the results of analysis of two *Vaccinium* species shares in the pine and mixed oak-pine forests, we can state that:

- both species show a connection with the ancient forests, this relation being for *Vaccinium vitis-idaea* visible both in terms of frequency and mean cover, while in the case of *Vaccinium myrtillus* the relation of frequency is weak or not visible, the relation of spatial share (cover) of this species in the patches being very distinct;
- both species feature a slow re-colonisation of the recent forests, with the colonisation process on the poor mesotrophic habitats of mixed oak-pine forests taking place faster than on the strongly oligotrophic habitats of fresh pine forests.

4.2.2. OTHER HERBACEOUS SPECIES OF THE PINE FORESTS

In the case of pine forests analysis was performed regarding three species, which display in some patches higher cover degrees on the Braun-Blanquet scale, that is:

Deschampsia flexuosa – an expansive grass species, increasingly frequently entering forest communities, yet 50 years ago much rarer in this region (Matuszkiewicz J. M. et al. 2007);

Melampyrum pratense – a species considered to be characteristic of pine forest associations, and also considered to be ʾancient forest speciesʿ according to Hermy et al. (1999),

Calluna vulgaris – a species frequent in pine forests, which featured a relation to ancient forests in terms of frequency.

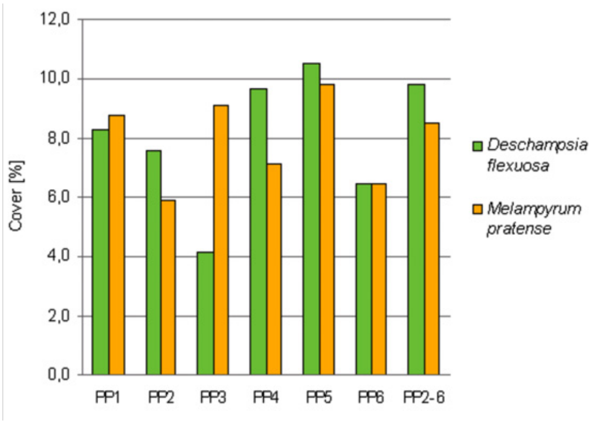


Fig. 28. Mean cover of *Deschampsia flexuosa* and *Melampyrum pratense* in the forest categories of *Peucedano-Pinetum* communities
Ryc. 28. Średnie pokrywanie *Deschampsia flexuosa* i *Melampyrum pratense* w kategoriach borów (*Peucedano-Pinetum*)

The results of cover analysis of the first two species are shown in Fig. 28. It can be concluded from them that both species analysed do not show, in terms of mean cover, a distinct relation to the specific pine forests categories. This is particularly true for *Melampyrum pratense* although it is included in the list of ancient forests species proposed by Hermy et al. (1999). *Deschampsia flexuosa* displays perhaps even higher cover values in the recent forests.

In the case of *Calluna vulgaris* the cover analysis in the patches representing the distinguished pine forest categories (Fig. 29a) shows, first of all, that what was already known from the frequency analysis, i.e. dependence of the frequency upon the degree of forest regeneration. This results in the difference of the mean *Calluna* cover (Fig. 29b) between the ancient forests and the recent ones, especially those with a short period of regeneration.

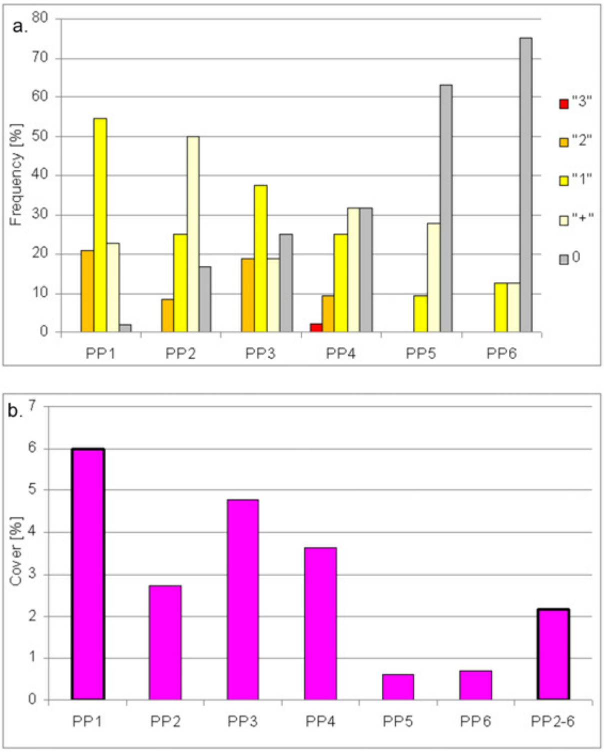


Fig. 29. Cover of *Calluna vulgaris* according to the Braun-Blanquet scale (a) and mean cover (b) in the forest categories of *Peucedano-Pinetum* communities
Ryc. 29. Pokrywanie wrzosu (*Calluna vulgaris*) w kategoriach borów (*Peucedano-Pinetum*): stopnie ilościowości wg skali Braun-Blanqueta (a) i średnie pokrywanie (b)

4.2.3. THE MOST IMPORTANT MOSS SPECIES IN THE PINE FORESTS

The most frequent moss species in pine forests communities are: *Pleurozium schreberi, Dicranum polysetum* and *Hylocomium splendens*, all of them considered as species characteristic of *Vaccinio-Piceetea* class. In the pine forests analysed *Pleurozium schreberi* was observed in all the patches, *Dicranum polysetum* in almost all of them, while *Hylocomium splendens* displayed preference for the ancient forests (Fig. 30a).

The cover of *Pleurozium schreberi* is weakly differentiated within the pine forests categories (Fig. 30b); the only pronouced difference is a more frequent attainment of the highest cover degrees in the younger recent forests. Likewise, *Dicranum polysetum*, generally featuring lower cover degrees, attains the highest respective values in the recent forests (Fig. 30c).

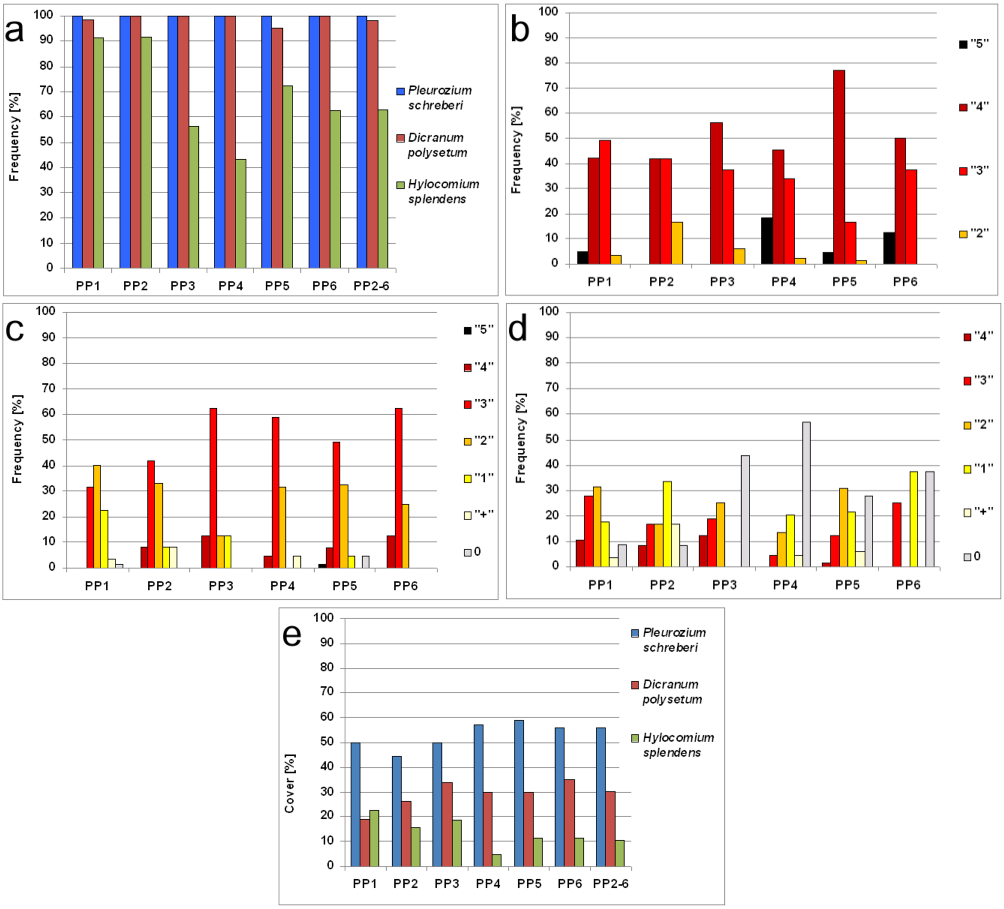


Fig. 30. Frequency of *Pleurozium schreberi*, *Dicranum polysetum*, *Hylocomium splendens* (a), cover of *Pleurozium schreberi* (b), *Dicranum polysetum* (c), *Hylocomium splendens* (d) and mean cover of *Pleurozium schreberi*, *Dicranum polysetum*, *Hylocomium splendens* (e) in the forest categories of *Peucedano-Pinetum* communities
Ryc. 30. Frekwencja mchów: *Pleurozium schreberi*, *Dicranum polysetum*, *Hylocomium splendens* (a), stopnie pokrywania w skali Braun-Blanqueta *Pleurozium schreberi* (b), *Dicranum polysetum* (c), *Hylocomium splendens* (d); średnie pokrywanie tych gatunków (e) w kategoriach borów (*Peucedano-Pinetum*)

On the other hand, *Hylocomium splendens* shows a certain connection with the ancient forests and the recent ones with the longer regeneration periods (Fig. 30d). Both the frequencies and the shares of the highest cover degrees point out towards such a dependence, although it does not have an unambiguous character.

An attempt of estimation of the mean cover of three moss species in the pine forest categories (Fig. 30e) enables noting that both of the most common ones, *Pleurozium schreberi* and *Dicranum polysetum*, show a slightly higher cover in the recent forests than in the ancient forests. This is insofar understandable as an opposite regularity is displayed by the most important herbaceous species of the undergrowth, i.e. *Vaccinium myrtillus* and *Vaccinium vitis-idaea*. Whereas, *Hylocomium splendens* has insignificantly higher mean cover in the ancient forests.

4.2.4. THE MOST IMPORTANT MOSS SPECIES IN THE MIXED OAK-PINE FORESTS

For the mixed oak-pine forests analysis was performed of the shares of four moss species. Their frequencies are given in Fig. 31a, while mean cover in the patches in Fig. 31b. The highest uniformity in terms of frequency is observed for *Pleurozium schreberi*, which appears in almost all patches of the mixed oak-pine forests considered (it was absent in just one patch of the recent forest, which may be simply an incidental case). Generally, the mean cover of this species is quite distinctly higher in the recent forests than in the ancient ones. This is, most probably, the effect of the more common appearance of the undergrowth species – like, especially, of *Vaccinium myrtillus* – in the ancient forests.

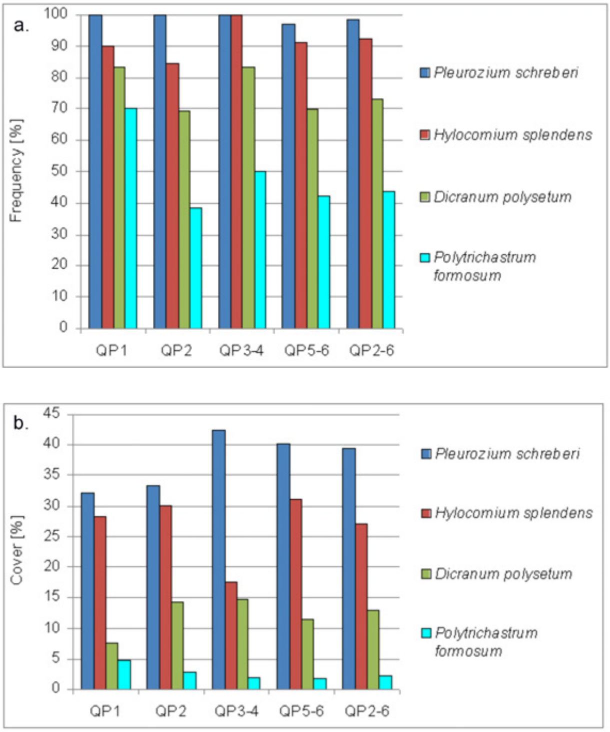


Fig. 31. Frequency (a) and mean cover (b) of *Pleurozium schreberi*, *Dicranum polysetum*, *Hylocomium splendens* and *Polytrichastrum formosum* in the forest categories of *Querco-Pinetum* communities

Ryc. 31. Frekwencja (a) i średnie pokrycie (b) czterech gatunków mchów: *Pleurozium schreberi*, *Dicranum polysetum*, *Hylocomium splendens* i *Polytrichastrum formosum* w kategoriach borów mieszanych (*Querco-Pinetum*)

The very frequent two species – *Hylocomium splendens* and *Dicranum polysetum* show in terms of frequency and mean cover quite limited differences between the mixed oak-pine forests categories, most regularly and most abundantly appearing in the recent forests with relatively long regeneration periods.

The last moss species, which attained frequency exceeding 50% in all the mixed oak-pine forests, is *Polytrichastrum formosum*. It displays a relatively higher frequency and mean cover in the ancient forests, but the differences are not very pronounced and may be incidental.

4.2.5. SELECTED HERBACEOUS SPECIES OF THE MIXED OAK-PINE FORESTS

The cover analysis in the mixed oak-pine forests categories was carried out for the following frequent or abundantly appearing herbaceous plants species: *Melampyrum pratense, Luzula pilosa, Pteridium aquilinum, Calamagrostis arundinacea* and *Deschampsia flexuosa*. Among these plants the first three are considered to be ancient forest species according to Hermy et al. (1999). The frequencies of the selected species in the oak-mixed pine forests are shown in Fig. 32. The figure implies that *Melampyrum pratense* and *Deschampsia flexuosa* do not display a distinct difference between the categories in terms of frequency or perhaps just slightly higher values in the recent forests, while the three remaining ones feature higher frequency in the ancient forests, as noted already before.

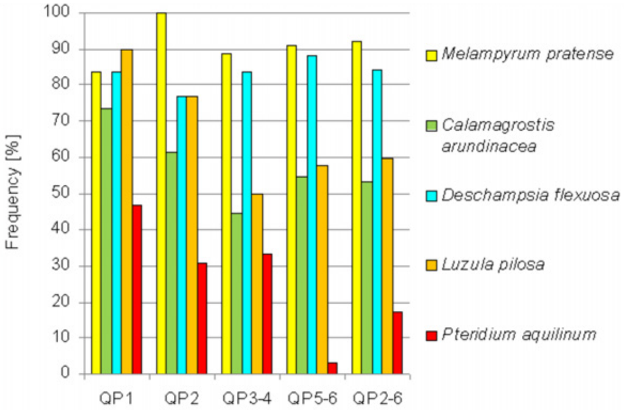


Fig. 32. Frequency of selected herb layer species in the forest categories of *Querco-Pinetum* communities

Ryc. 32. Frekwencja wybranych gatunków ziół w kategoriach borów mieszanych (*Querco-Pinetum*)

The analysis of cover values distribution regarding *Melampyrum pratense* in the categories of mixed oak-pine forests (Fig. 33a) shows that in the ancient forests one encounters relatively more frequently the patches without this species, and simultaneously – in the recent forests relatively higher abundance is observed. Hence, regarding the mixed oak-pine forests this species cannot be considered to be ancient forest species neither in terms of frequency nor in terms of cover, contrary to the assertion of Hermy et al. (1999).

In the case of *Calamagrostis arundinacea* (Fig. 33b) the distribution of cover values across the patches shows, on the one hand, a clearly more frequent appearance of species in the ancient forests than in the recent forests, but, on the other hand, only in the recent forests this species attains high cover degrees. In the ancient forests this species appears frequently, but not too abundantly, while in the recent forests it appears more rarely, but sometimes in large patches (the so-called facial appearance).

Deschampsia flexuosa is characterised in the mixed oak-pine forests by limited differences as to the frequency, while in terms of cover values (Fig. 33c) it features decidedly more frequent high degrees in the younger recent forests than in the remaining categories of mixed oak-pine forests, and in particular – than in the ancient forests. So, in these communities high share of this species (exceeding 25% of the occupied area) takes place in less than 10% of the patches, compared to 20-30% of such occurrences in the recent forests with shorter periods of regeneration. If we adopt 10% of cover (abundance degrees from ’2‘ upwards) as the threshold, then the ratio of patches number with a significant share of this species in the ancient forests and in the recent forests is approximately 1:2 (24% and 56%), and in the case of the younger recent forests even close to 1:3 (24% and 71%).

Luzula pilosa, which features clearly higher frequency in the ancient forests than in the recent ones, is also characterised by the higher (although generally low) cover in the former ones (Fig. 33d). Therefore, it was entirely proper to include this species to ancient forest species by Hermy et al. (1999).

Pteridium aquilinum is a species featuring frequency of 50% in the ancient forests and only roughly 10-20% in the recent forests. Thus, in the statistical sense it is a good indicator of ancient forests, conform to the list provided by Hermy et al. (1999). At the same time, there are observed the patches of recent forests with a high or even very high share of this species (Fig. 33e). Hence, diagnosis of individual patches as representing ancient forest uniquely on the basis of high share of this plant would not be reliable.

Upon the analysis of five selected undergrowth species within the patches of mixed oak-pine forests categories (Fig. 33f), constituting usually, side by side with two species: bilberry and cowberry, the basis of undergrowth structure, one can state that in the ancient forests mean cover of these species shows not too pronounced differences. *Deschampsia flexuosa*, *Pteridium aquilinum*

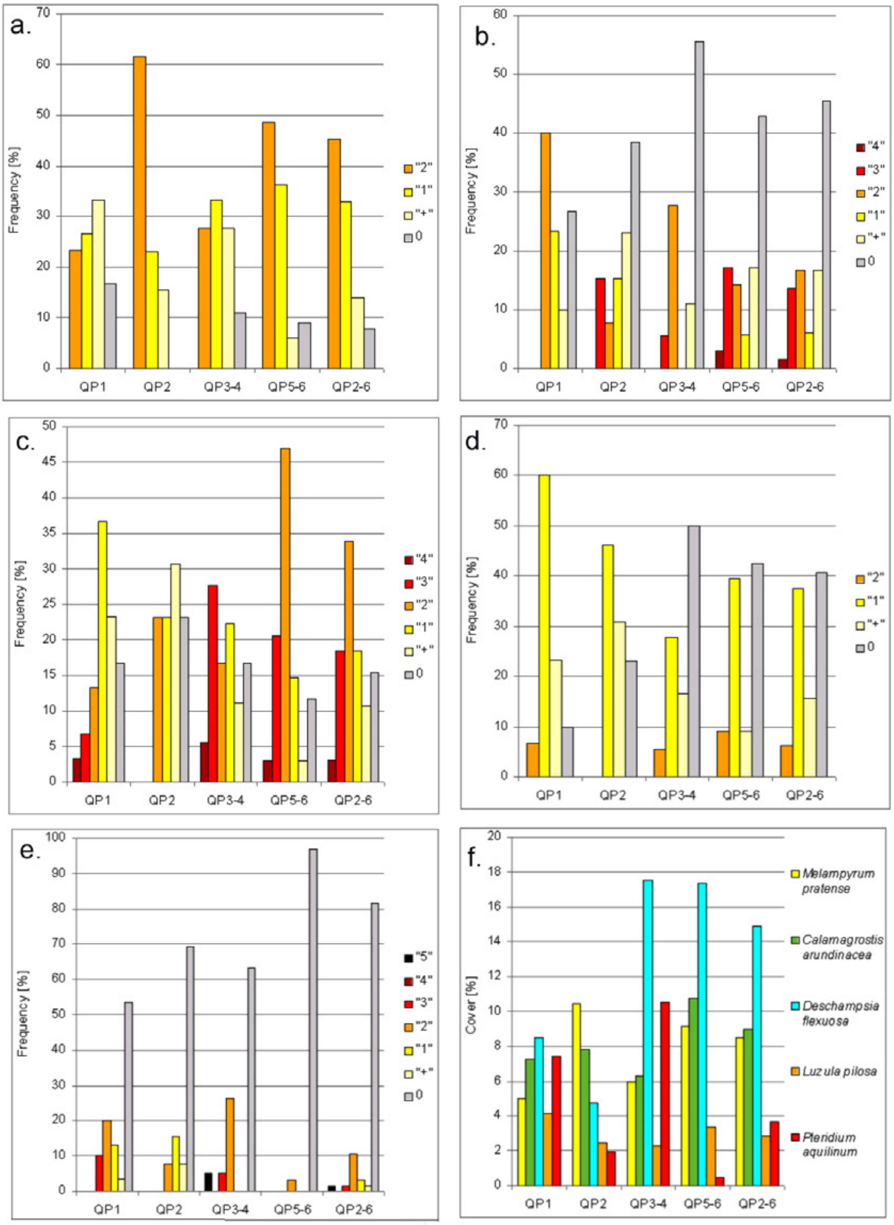


Fig. 33. Cover of *Melampyrum pratense* (a), *Calamagrostis arundinacea* (b), *Deschampsia flexuosa* (c), *Luzula pilosa* (d), *Pteridium aquilinum* (e) according to the Braun-Blanquet scale and mean cover of selected herb layer species (f) in the forest categories of *Querco-Pinetum* communities

Ryc. 33. Stopnie pokrywania w skali Braun-Blanqueta gatunków: *Melampyrum pratense* (a), *Calamagrostis arundinacea* (b), *Deschampsia flexuosa* (c), *Luzula pilosa* (d), *Pteridium aquilinum* (e) oraz średnie pokrywanie tych gatunków (f) w kategoriach borów mieszanych (*Querco-Pinetum*) and *Calamagrostis arundinacea* feature mean cover of about 7-8%, while *Melampyrum pratense* and *Luzula pilosa* – roughly 4-5%. Situation is different in the recent forests, especially those with shorter regeneration periods. Here, we deal with a diversification within this group of species. *Pteridium aquilinum* features diverse cover values, *Luzula pilosa* – considered to be an ancient forest species features low values of mean cover, lower than in the ancient forests. *Melampyrum pratense* and *Calamagrostis arundinacea* show mean cover that is slightly higher, while *Deschampsia flexuosa* features in the recent forests of a short regeneration period much higher mean cover. This is insofar interesting as *Deschampsia* is clearly expanding in the pine and mixed oak-pine forests of the region considered. As shown by the comparative studies, carried out within the forest district of Wielbark and in the reserve of 'Czarnia', based on the phytosociological materials from 40-50 years ago and the contemporary ones (Matuszkiewicz J.M. et al. 2007), the frequency of this species significantly increased during this time period. The results obtained in the study show that this expansion is taking place in particular in the younger – in terms of persistence – recent post-agricultural forests.

4.2.6. SELECTED HERBACEOUS SPECIES OF THE LIME-OAK-HORNBEAM FORESTS

The analysis of quantitative shares in the lime-oak-hornbeam forests has been performed for nine species of herbaceous plants, including four species characteristic of *Querco-Fagetea* class, which are also considered to be ancient forest species (*Anemone nemorosa, Galeobdolon luteum, Galium odoratum, Stellaria holostea*), three generally forest species (*Maianthemum bifolium, Oxalis acetosella, Calamagrostis arundinacea*), of which first two are considered to be the ancient forest species, a species characteristic of the class *Vaccinio-Piceetea*, also considered to be an ancient forest species (*Vaccinium myrtillus*), and one species of an expansive neophyte (*Impatiens parviflora*). For each of these species the frequencies and the mean cover are presented further on for four categories of the lime-oak-hornbeam forest, classified according to two criteria: participation in the subassociation and division into the ancient and recent forests (the latter not distinguished for the regeneration period in view of the limited quantity of material gathered). Symbols used are as below (Table 18).

Table 18. Categories of the lime-oak-hornbeam forests

Categories	*Tilio-Carpinetum calamagrostietosum*	*Tilio-Carpinetum typicum*
Ancient forests	TC1 cal	TC1 typ
Recent forests	TC2-6 cal	TC2-6 typ

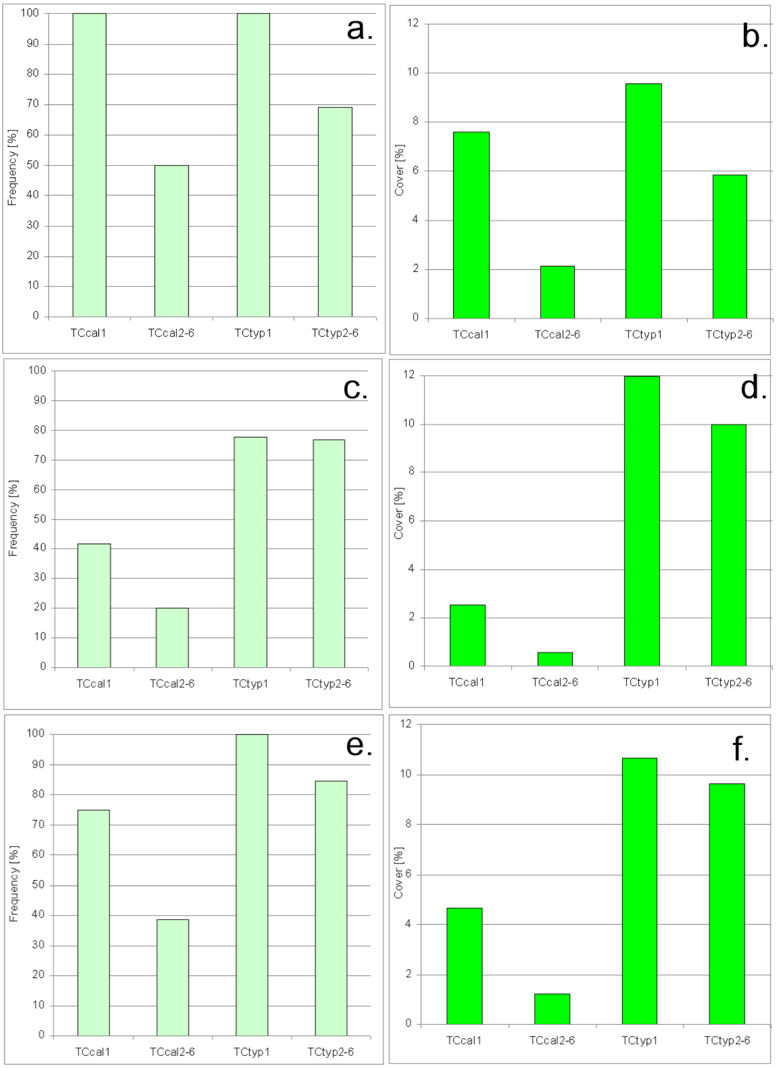


Fig. 34. Frequency (a) and mean cover (b) of *Anemone nemorosa* in the forest categories of *Tilio-Carpinetum* communities; frequency (c) and mean cover (d) of *Geleobdolon luteum* in the forest categories of *Tilio-Carpinetum* communities; frequency (e) and mean cover (f) of *Stellaria holostea* in the forest categories of *Tilio-Carpinetum* communities
Ryc. 34. Frekwencja i średnie pokrywanie wybranych gatunków w kategoriach grądów (*Tilio-Carpinetum*): *Anemone nemorosa* (a, b), *Geleobdolon luteum* (c, d), *Stellaria holostea* (e, f)

Anemone nemorosa (an ancient forest species), one of quite widespread species, characteristic of *Querco-Fagetea* class, was observed in all patches of the ancient forests. Its frequency values are significantly lower (Fig. 34a), just like those of the mean cover (Fig. 34b) in the recent forests, as compared to the ancient forests. This is well visible both in *Tilio-Carpinetum typicum* and in *T.-C. calamagrostietosum*. Under a more detailed analysis of the data from the recent forests it is noted (even though the number of relevés does not allow for any categorical statements) that the younger phases of regeneration present particularly distinctly lower cover. It might be supposed that in the recent forests with the regeneration period of 220-230 years the population structure of this species is closer to that existing in the ancient forests than to that taking place in the recent forests of the regeneration period shorter than 200 years, although it is still not the same as in the ancient forests. Such propositions enable designation of this species as a good indicator of regeneration, provided that its contribution to phytocoenoses is analysed with statistical tools. This species may, most probably, be classified among the first wave of the re-colonising species, under condition that its role in phytocoenoses increases slowly with the period of regeneration. Further, it should be noted with respect to this species that the relevés were made in the summer season, that is – after the maximum spring appearance. Descriptions of the spring aspect might have given a different result, especially in terms of mean cover. That is why it seems that the analysis of frequency must suffice for the diagnostic studies.

Galeobdolon luteum (an ancient forest species), being the species characteristic of the order *Fagetalia sylvaticae*, displays a clearly higher frequency in the typical subassociation than in *calamagrostietosum* (Fig. 34c), with its cover especially higher (Fig. 34d). When the recent forests are treated jointly, the differences between them and the ancient forests are not very pronounced. Under a closer scrutiny one notices that the role of this species in the ancient forests and in the recent forests with longer regeneration periods is similar, while this role is distinctly lower (in terms of frequency, but especially concerning cover) in the recent forests with shorter regeneration periods. This species might probably be classified among the first wave of the re-colonising species which relatively fast gain in the lime-oak-hornbeam forest a role similar to the one they play in the ancient forests.

Stellaria holostea (an ancient forest species), species characteristic of the alliance *Carpinion betuli* from the class *Querco-Fagetea*, shows slightly higher frequency (Fig. 34e) and distinctly higher values of the cover (Fig. 34f) in the typical lime-oak-hornbeam forests than in those of the *calamagrostietosum* subassociation. Generally, this species displays a relation to the ancient forests, but its value as a diagnostic species in concrete cases may be doubtful, since in the recent forests (even those regenerating for a relatively short period of time), with lower frequency, sometimes appears with quite significant cover. It might probably be considered among the first wave of the re-colonising species, those that in some cases quickly (especially in typical lime-oak-hornbeam forests) gain a role similar to that played in the ancient forests.

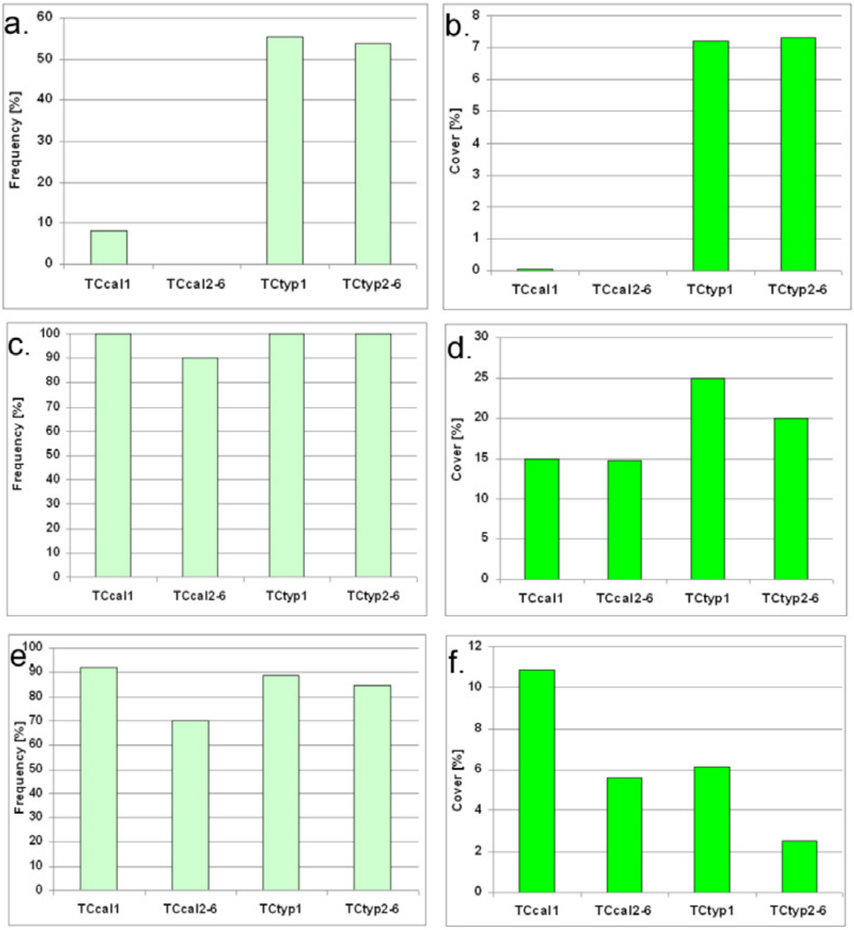


Fig. 35. Frequency (a) and mean cover (b) of *Galium odoratum* in the forest categories of *Tilio-Carpinetum* communities; frequency (c) and mean cover (d) of *Oxalis acetosella* in the forest categories of *Tilio-Carpinetum* communities; frequency (e) and mean cover (f) of *Maianthemum bifolium* in the forest categories of *Tilio-Carpinetum* communities

Ryc. 35. Frekwencja i średnie pokrywanie wybranych gatunków w kategoriach grądów (*Tilio-Carpinetum*): *Galium odoratum* (a, b), *Oxalis acetosella* (c, d), *Maianthemum bifolium* (e, f).

Galium odoratum (an ancient forest species), characteristic species of the order *Fagetalia sylvaticae*, was noted uniquely in the subassociation *Tilio-Carpinetum typicum*, both in the ancient forests, and in the recent ones with a long period of regeneration (Figs. 35a, 35b). When recent forests are treated jointly, the differences with respect to the ancient forests are not significant. In a more detailed analysis one notices less frequent appearance of the species in the younger regeneration stages of recent forests. Hence, with respect to typical lime-oak-hornbeam forests this is a diagnostic species, separating the older phases of regeneration (as well as ancient forests) from the younger phases. This species can be classified among the re-colonisers of the first wave in typical lime-oak-hornbeam forests, which relatively quickly gain a position similar to the one they take in the ancient forests.

Oxalis acetosella (an ancient forest species) demonstrated practically equal, high frequency (Fig. 35c), as well as relatively even (also high when compared to other species) values of mean cover in the ancient forests and in the recent ones (Fig. 35d), irrespective of the regeneration period and irrespective of the subassociation. This means that the species does not fulfil the criteria of a diagnostic species with respect to the lime-oak-hornbeam forests considered.

Maianthemum bifolium (an ancient forest species) showed in the ancient forests similar or only slightly higher frequency values than in the recent forests (Fig. 35e). So, with this respect the plant can hardly be considered to be a good diagnostic species. On the other hand, the differences of the mean cover in the lime-oak-hornbeam forest categories studied are quite interesting (Fig. 35f). Two remarks can be made here: a distinctly lower cover of this species in *Tilio-Carpinetum calamagrostietosum* than in *T.-C. typicum*, and systematically lower values of cover in the recent forests than in the ancient ones. Yet, this criterion can hardly be applied as a diagnostic feature, for under a closer frequency analysis of the cover degrees, one cannot indicate the value that could be assume to play the role of diagnostic threshold.

Calamagrostis arundinacea demonstrates, understandably, significantly higher frequency (Fig. 36a), and especially cover (Fig. 36b) in the subassociation *Tilio-Carpinetum calamagrostietosum* than in the subassociation *T.-C. typicum*. In both subassociations the difference between the ancient and the recent forests is visible in terms of frequency and cover. Yet, taking into account low number of relevés, no far-reaching conclusions can be drawn upon this basis. The analysis performed suggests that this species be rather not advised for diagnosis in concrete cases.

Vaccinium myrtillus (an ancient forest species) is a characteristic species of the class *Vaccinio-Piceetea*, appearing very often in the subassociation *Tilio-Carpinetum calamagrostietosum* and much less often in *T.-C. typicum* (Fig. 36c). It is held that the species is a differential species of the former subassociation. The quantitative share of this species in the patches of the poorer form of lime-oak-hornbeam forest is much higher in recent forests than in the ancient forests (Fig. 36d). This is, most probably, the effect of introduction of Scots pine into recent tree stands in a larger extent than into ancient forests. In all investigated patches of the recent forests of this subassociation pine is the main species of tree stands (according to the forest management documentation), while in the ancient forests such cases constitute roughly ¾. So, *Vaccinium myrtillus*, generally considered to be an ancient forest species, conform to Hermy et al. (1999) and appearing often in the ancient forests studied, cannot be treated as such for the case of lime-oak-hornbeam forests,

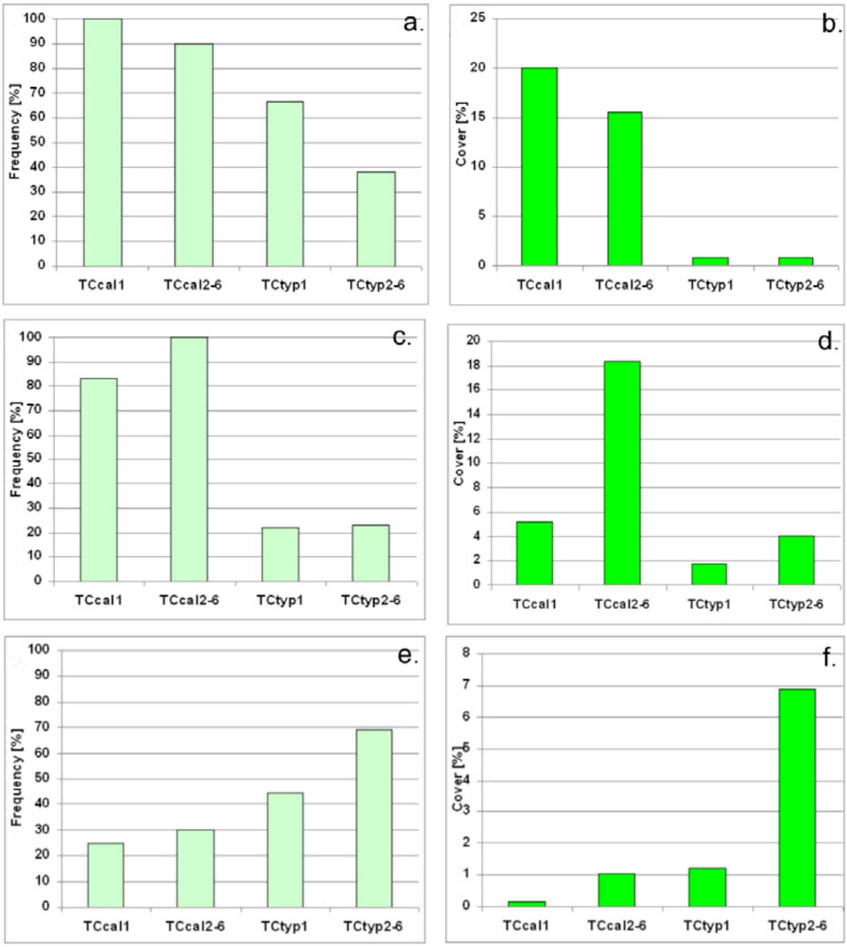


Fig. 36. Frequency (a) and mean cover (b) of *Calamagrostis arundinacea* in the forest categories of *Tilio-Carpinetum* communities; frequency (c) and mean cover (d) of *Vaccinium myrtillus* in the forest categories of *Tilio-Carpinetum* communities; frequency (e) and mean cover (f) of *Impatiens parviflora* in the forest categories of *Tilio-Carpinetum* communities

Ryc. 36. Frekwencja i średnie pokrywanie wybranych gatunków w kategoriach grądów (*Tilio-Carpinetum*): *Calamagrostis arundinacea* (a, b), *Vaccinium myrtillus* (c, d), *Impatiens parviflora* (e, f).

since it appears in the recent forests on lime-oak-hornbeam forest habitats more frequently and more abundantly. It is probable, although the materials we dispose of constitute insufficient evidence for proving this, that *Vaccinium myrtillus* on post-agricultural land, on the poor lime-oak-hornbeam forest habitats with planted Scots pine stands, appears not at once, but after a definite period since afforestation. Afterwards, it gradually increases its cover, and then – when the regeneration of species typical of deciduous forest has already taken place – gradually decreases its cover. Finally, it remains a constant species, but with rather low cover values in the patches. With respect to typical lime-oak-hornbeam forests it can be supposed that *Vaccinium myrtillus* is a species linked with the introduction of pine (pinetisation) to these communities.

Impatiens parviflora is an alien invading species, entering numerous communities, especially of meso- and eutrophic forests. In the analysed lime-oak-hornbeam forests this species displayed quite high frequency (Fig. 36e), relatively higher in more eutrophic typical lime-oak-hornbeam forests than in the poor ones, and also relatively higher in recent than in ancient forests. It is particularly visible how this species intensively enters the typical recent forests of this type (Fig. 36f). A more detailed analysis shows that in the typical recent lime-oak-hornbeam forests with rather short regeneration periods *Impatiens parviflora* attained the cover degree of ’2‘ or even more on the Braun-Blanquet scale. Low number of relevés, though, implies care in drawing respective conclusions, although it is tempting to state that the recent forests are more susceptible to invasion.

4.3. THE LIST OF INDICATOR SPECIES OF ANCIENT FORESTS – A REGIONAL VERIFICATION

Taking as the starting point the list of ancient forest species, according to Hermy et al. (1999), along with the complements, proposed by Dzwonko and Loster (2001), the analysis was carried out of the floristic composition in the forest categories of three habitat types considered (see Tables 6, 9 and 12) regarding the appearance of species from these lists. On this basis a verified regional list of ancient forest species was developed (Table 19).

Table 19. Verification of the ancient forests species list in local conditions. *Ancient forest species* acc. to Hermy et al. (1999) and Dzwonko and Loster (2001)

Habitat type	Pine forests				Mixed oak-pine forests				Lime-oak-hornbeam forests			
Species from the list of *ancient forests species*	Frequency [%] in ancient forests	*Difference in frequency between ancient (PP1) and recent forests (PP2-6)*	*Difference in frequency between ancient (PP1) and younger recent forests (PP5-6)*	Diagnosis of species status	Frequency [%] in ancient forests	*Difference in frequency between ancient (QP1) and recent forests (Q2-6)*	*Difference in frequency between ancient (QP1) and younger recent forests (QP5-6)*	Diagnosis of species status	Frequency [%] in ancient forests	*Difference in frequency between ancient (TC1) and recent forests (TC2-6)*	*Difference in frequency between ancient (TC1) and younger recent forests (TC5-6)*	Diagnosis of species status
Actea spicata									14.3	*9.9*	*14.3*	B
Adoxa moschatellina									0.0	*-8.7*	*-20.0*	n
Anemone nemorosa					3.3	*1.8*	*3.3*	n	100.0	*39.1*	*50.0*	A
Athyrium filix-femina	15.8	*14.4*	*14.4*	A	33.3	*19.3*	*27.3*	A	23.8	*-2.3*	*13.8*	B
Brachypodium sylvaticum									4.8	*4.8*	*4.8*	n
Carex digitata					16.7	*10.4*	*13.6*	B	85.7	*7.5*	*25.7*	B
Carex pilosa					3.3	*1.8*	*3.3*	n				
Carex sylvatica					3.3	*1.8*	*3.3*	n	4.8	*-3.9*	*4.8*	n
Circaea alpina									0.0	*-4.3*	*-10.0*	n
Convallaria majalis	43.9	*38.3*	*41.1*	A	76.7	*56.4*	*64.5*	A	81.0	*33.1*	*41.0*	A
Dactylis polygama									9.5	*-20.9*	*-0.5*	C
Daphne mezereum									9.5	*0.8*	*-0.5*	n
Dryopteris carthusiana	24.6	*-14.7*	*-17.9*	C	70.0	*5.9*	*0.3*	C	66.7	*-2.9*	*-13.3*	C
Dryopteris filix-mas	3.5	*2.1*	*0.8*	n	13.3	*5.5*	*1.2*	C	47.6	*-4.6*	*7.6*	C
Epilobium montanum									9.5	*0.8*	*-10.5*	n
Equisetum hyemale	0.0	*-0.7*	*-1.4*	n								
Equisetum sylvaticum					0.0	*-4.7*	*-6.1*	n	9.5	*9.5*	*9.5*	n
Festuca gigantea									19.0	*10.4*	*9.0*	B
Galeobdolon luteum									57.1	*5.0*	*37.1*	A?
Galium odoratum									28.6	*-1.9*	*28.6*	A?
Gymnocarpium dryopteris									19.0	*10.4*	*-1.0*	B
Hepatica nobilis									52.4	*17.6*	*52.4*	A
Lathyrus vernus									33.3	*11.6*	*33.3*	A
Lilium martagon									14.3	*9.9*	*14.3*	B
Luzula pilosa	42.1	*23.5*	*20.2*	A	90.0	*30.6*	*32.4*	A	47.6	*-0.2*	*-2.4*	C
Lysimachia nemorum									0.0	*-4.3*	*0.0*	n

Maianthemum bifolium	5.3	3.9	5.3	n	53.3	31.5	38.2	A	90.5	12.2	30.5	B
Melampyrum pratense	96.5	8.2	3.3	C	83.3	-8.9	-7.6	C	14.3	-7.5	-15.7	C
Melica nutans					3.3	3.3	3.3	n	47.6	8.5	17.6	B
Mercurialis perennis									4.8	4.8	4.8	n
Milium effusum					3.3	1.8	3.3	n	71.4	19.3	51.4	A
Oxalis acetosella	7.0	6.3	5.6	A	53.3	20.5	23.0	B	100.0	4.3	10.0	B
Paris quadrifolia									19.0	-11.4	9.0	B
Phyteuma spicatum									14.3	9.9	14.3	B
Poa nemoralis									0.0	-4.3	0.0	n
Polygonatum multiflorum					3.3	1.8	3.3	n	42.9	-5.0	22.9	A?
Pteridium aquilinum	3.5	3.5	3.5	n	46.7	29.5	43.6	A	38.1	3.3	-1.9	C
Pulmonaria obscura									4.8	0.4	4.8	n
Ranunculus lanuginosus					3.3	3.3	3.3	n	19.0	10.4	19.0	B
Sanicula europaea									4.8	0.4	4.8	n
Scrophularia nodosa									33.3	20.3	23.3	B
Stachys sylvatica									9.5	-7.9	9.5	n
Stellaria holostea					3.3	0.2	3.3	n	85.7	16.1	35.7	A?
Stellaria nemorum					3.3	3.3	3.3	n				
Trientalis europaea	33.3	26.4	25.1	A	83.3	28.6	25.8	A	47.6	12.8	-12.4	C
Vaccinium myrtillus	100.0	2.8	1.4	C	100.0	0.0	0.0	C	57.1	0.6	-12.9	C
Vaccinium vitis-idaea	100.0	26.9	34.2	A	86.7	13.2	17.0	B	0.0	-26.1	-40.0	D
Viola mirabilis					3.3	1.8	3.3	n				
Viola reichenbachiana					6.7	2.0	6.7	n	71.4	1.9	31.4	A?

Diagnosis of species status as *ancient forests species*

A - confirmed - higher frequency in ancient forests, the difference is significant

B - doubtful - higher frequency in ancient forests, the difference is not significant

C - poorly questioned - frequency in ancient forests is similar or smaller then in recent forests, the difference is not significant

D - clearly questioned - frequency in ancient forests is visibly smaller then in recent forests, the difference is significant

n - unspecified - rare species

4.3.1. THE ANCIENT FOREST SPECIES IN THE PINE FORESTS

Based on the frequency analysis of ancient forest species in the pine forests (data from Table 6) the following conclusions can be drawn:

- the ancient forest species, even though not too numerous (Fig. 37a), constitute a significant part of herbaceous plants composition in the undergrowth (Fig. 37b);
- the shares of ancient forest species in the floristic composition of recent forests are lower than in the ancient forests, although it actually concerns only a part of species from the group; it can be seen that this concerns the species, for which the status of ancient forest species in the pine forests communities has been confirmed;

- the group of species, which appear in the ancient forest with a significantly higher frequency than in the recent forests, treated as a whole, which confirms their status of ancient forest species, encompasses two species characteristic of the class *Vaccinio-Piceetea* (*Vaccinium vitis-idaea* and *Trientalis europaea*) and two often appearing companions (*Convallaria majalis* and *Luzula pilosa*), of which the former is considered to be the differential one of the association *Peucedano-Pinetum*, and, finally, two relatively rare species: *Athyrium filix-femina* and *Oxalis acetosella*;
- the group of species, which do not confirm the status of ancient forest species in the pine forests, since they appear in the recent forests with a similar, or even higher frequency compared to the ancient forests, includes two species characteristic of the class *Vaccinio-Piceetea* (*Vaccinium myrtillus* and *Melampyrum pratense*) and a companion *Dryopteris carthusiana*;
- regarding *Vaccinium myrtillus* it should be additionally accounted for that the above statement refers only to the frequency of this species, while in consideration of the cover it is possible to demonstrate significant differences between the ancient and the recent forests; according to the results it can be assumed that the cover degree lower than ʼ2ʻ on the Braun-Blanquet scale indicates unambiguously the recent character of the forest (which does not imply that a higher value corresponds unambiguously to the ancient forest);
- appearance of several species from the list of ancient forest species was noted in the pine forest, but their rare appearance did not allow for the establishment of their status with this respect (*Dryopteris filix-mas, Equisetum hyemale, Maianthemum bifolium, Pteridium aquilinum*);
- of the distinguished two groups of ancient forest species, the first group in terms of frequency differentiates the studied communities according to the forest persistence, while the second one does not display such a differentiation.

4.3.2. THE ANCIENT FOREST SPECIES IN THE MIXED OAK-PINE FORESTS

On the basis of frequency analysis of species from the group studied in the mixed oak-pine forests (Tables 9 and 19), it can be stated that:

- joint frequency of ancient forest species is in the ancient stands clearly higher than in the recent ones; among the recent forests one can notice the dependence of their frequency increase upon the time period since the post-agricultural land had been afforested (Fig. 37c);
- there is no species on the ancient forest species list that would be closely associated with the actual ancient forests and would not appear in the recent forests;

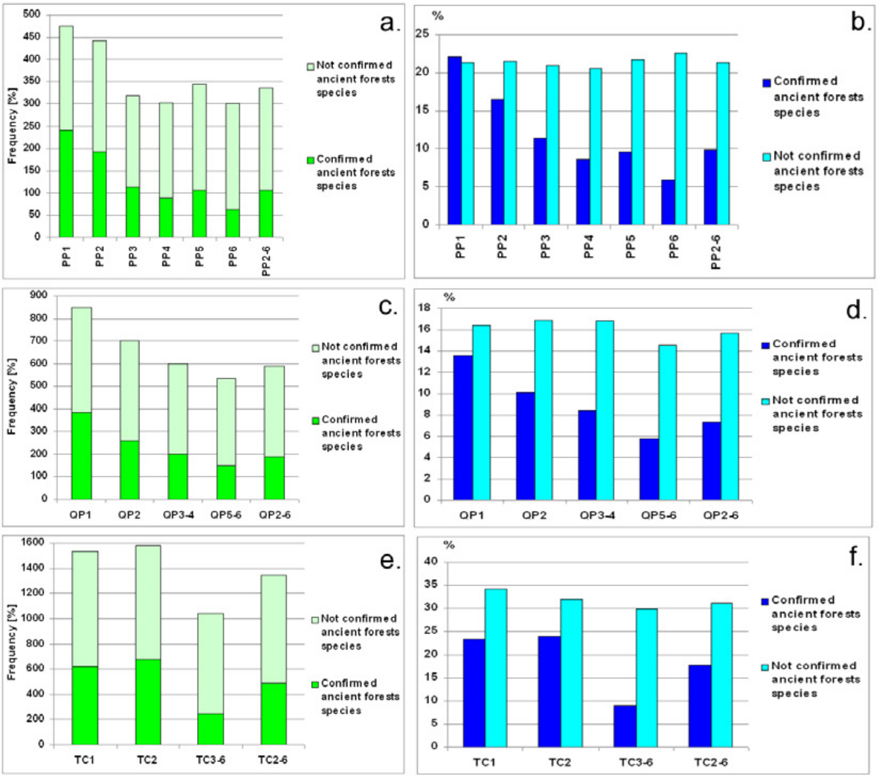


Fig. 37. Total frequency (a) and the share (b) of ancient forest species in the forest categories of *Peucedano-Pinetum* communities; total frequency (c) and the share (d) of ancient forest species in the forest categories of *Querco-Pinetum* communities; total frequency (e) and the share (f) of ancient forest species in the forest categories of *Tilio-Carpinetum* communities
Ryc. 37. Łączna frekwencja i udział w całkowitym składzie florystycznym gatunków z listy "gatunków starych lasów" potwierdzonych i nie potwierdzonych w niniejszych badaniach w trzech typach zbiorowisk: borów (a, b), borów mieszanych (c, d) i grądów (e, f)

- among the species displaying significantly higher frequency in the ancient forests, compared to the recent forests, that is – the ones, whose status has been confirmed, there is one species characteristic of the class *Vaccinio-Piceetea* (*Trientalis europea*), one species characteristic of the class *Querco-Fagetea* (*Athyrium filix-femina*) and four generally forest-related species (*Convallaria majalis, Pteridium aquilinum, Luzula pilosa, Maianthemum bifolium*); this group of species displays a tendency towards an increase in frequency with higher persistence of the recent forest (Fig. 37c);

- three species from the list of ancient forest species (*Vaccinium vitis-idaea*, *Oxalis acetosella* and *Carex digitata*) demonstrate higher frequency in the ancient forests than in the recent ones, but the differences are statistically insignificant, and so their status seems questionable, but it is plausible that it could be confirmed for a broader empirical material;
- four species from the list of ancient forest species (*Vaccinum myrtillus, Melampyrum pratense, Dryopteris filix-mas* and *Dryopteris carthusiana*) do not display the differences in terms of frequency between the ancient and the recent forests, this meaning that their status of ancient forest species has been negated;
- in the case of *Vaccinium myrtillus* a positive dependence is observed of the mean cover upon the forest category; further, it is also observed that the very low cover degrees (below ’2‘ on the Braun-Blanquet scale) indicate unambiguously the recent character of forest and a relatively short period of forest regeneration on post-agricultural land, but the reverse regularity has not been observed, i.e. the high cover values potentially indicating clearly the ancient forests;
- in mixed oak-pine forests communities there have been also observed of 12 species from the ancient forest species list (Table 19), whose frequency was to such an extent small that no conclusions concerning their status could be drawn;
- when comparing the shares in floristic composition of species belonging to two groups mentioned – those with confirmed status and those with non-confirmed or negated status (Fig. 37d) one concludes that the first of these groups differentiates the communities investigated, while the second one does not, similarly as the group of species appearing sporadically; in this context it can be noted that the recent forests, even those with a long regeneration history (not less than 220-230 years) differ significantly from the ancient forests; this difference is in the mixed oak-pine forests similar to that in the typical pine forests (compare Figs. 37b and 37d).

4.3.3. THE ANCIENT FOREST SPECIES IN THE LIME-OAK-HORNBEAM FORESTS

Analysis of ancient forest species in the lime-oak-hornbeam forests is more difficult than in two previously mentioned types of communities because of a much smaller number of phytosociological relevés and a distinct division of this type into two subtypes. That is why the results ought to be treated with greater care. On the basis of frequency analysis of species from the group considered (Tables 12 and 19) verification of their status could be undertaken.

The species from the ancient forest species list, encountered in the lime-oak-hornbeam forests can be classified into five groups:

- ten species with the confirmed status (more frequent in the ancient than in the recent forest, the difference being statistically significant), among which one can distinguish such ones that appear only in the ancient forests and in the recent ones with the longest period of regeneration (the ’*Hepatica* group‘, containing: *Hepatica nobilis, Galium odoratum, Lathyrus vernus*) and those that can appear in the recent forests, but appear in the ancient ones significantly more frequently (the ’*Anemone* group‘: *Anemone nemorosa, Convallaria majalis, Galeobdolon luteum, Milium effusum, Polygonatum multiflorum, Stellaria holostea, Viola reichenbachiana*); in this group all species, except for *Convallaria majalis*, are characteristic of the class *Querco-Fagetea*;
- the ’*Melica* group‘ – thirteen species of a doubtful status (more frequent in the ancient than in the recent forests, with statistically insignificant difference), containing: *Actea spicata, Athyrium filix-femina, Carex digitata, Festuca gigantea, Gymnocarpium dryopteris, Lilium martagon, Maianthemum bifolium, Melica nutans, Oxalis acetosella, Paris quadrifolia, Phyteuma spicatum, Ranunculus lanuginosus, Scrophularia nodosa*; among them, 11 are species characteristic of the class *Querco-Fagetea*;
- the ’*Luzula* group‘ – eight species with a weakly negated status (having similar frequencies in the ancient and recent forests, or being more frequent in the recent ones, but with the difference statistically insignificant); this group includes: *Dactylis polygama, Dryopteris carthusiana, Dryopteris filix-mas, Luzula pilosa, Melampyrum pratense, Pteridium aquilinum, Trientalis europaea, Vaccinium myrtillus*; among these species two are characteristic of the class *Querco-Fagetea*, three – of the class *Vaccinio-Piceetea*, and three are generally forest-related species;
- the ’*Vaccinium vitis-idaea* group‘ – just one species, whose status was definitively negated (distinctly more frequent in the recent forests with statistically significant difference); this species is characteristic of the class *Vaccinio-Piceetea*;
- 13 rare species, whose status cannot be verified on the basis of the material collected (*Adoxa moschatellina, Brachypodium sylvaticum, Carex sylvatica, Circaea alpina, Daphne mezereum, Epilobium montanum, Equisetum sylvaticum, Lysimachia nemorum, Mercurialis perennis, Poa nemoralis, Pulmonaria obscura, Sanicula europaea, Stachys sylvatica*).

The frequency of ancient forest species is in the lime-oak-hornbeam forests generally high (Fig. 37e) and they constitute a significant part of floristic composition of respective communities (Fig. 37f), which signifies that an important part of their floristic composition was included in this category. Moreover, the recent forests, i.e. the ones with the traces of the plough horizon in their soils, but the very old ones (as they were forests already on the maps from 1800) do not differ from the ancient forests, while the recent forests with less than 200 years of regeneration are characterised by a distinctly lower share of species from this group.

When analysing the appearance of groups from the list of ancient forest species in the lime-oak-hornbeam forest communities (Fig. 38) one can notice that the recent forests with a long period of regeneration (i.e. those that were forests already in the year 1800) do not differ in the frequency of undergrowth species from the ancient forests. This means that the period of about 220-230 years is sufficient for the regeneration of floristic composition of lime-oak-hornbeam forest, despite a moderate pinetisation, to which the commercially managed forests are subject to a lesser or bigger extent. This distinguishes the lime-oak-hornbeam forest associations from the pine and mixed oak-pine forests, which demonstrated deformations in terms of floristic composition in the recent forests with even the longest period of regeneration; at the same time, it should be noted that the reconstruction of floristic composition in the lime-oak-hornbeam forests does not yet signify the recovery of natural phytocoenoses structure, as implied by the previously commented data concerning the cover of species important for the undergrowth structure of lime-oak-hornbeam forests.

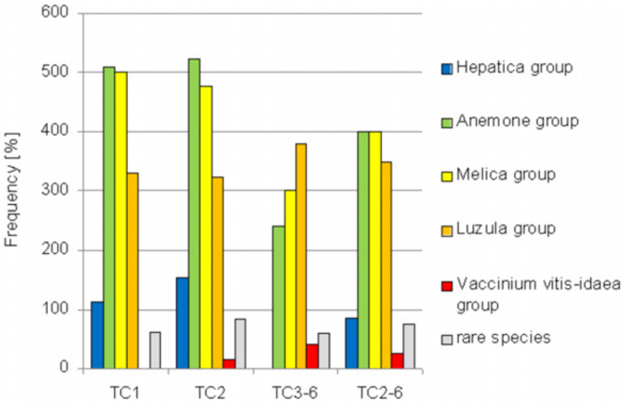


Fig. 38. Total frequency of selected ancient forest species in the forest categories of *Tilio-Carpinetum* communities (see in the text)
Ryc. 38. Frekwencje łączne wydzielonych (patrz w tekście) grup „gatunków starych lasów” z list Hermy i in. (1999) oraz Dzwonko i Loster (2001) w kategoriach grądów (*Tilio-Carpinetum*)

4.3.4. DIAGNOSIS OF SPECIES FROM THE ANCIENT FOREST SPECIES LIST

The analysis of appearance of individual species from the ancient forest species list, carried out in the distinguished categories of ancient and recent forests made it possible to verify the list mentioned in local conditions, as presented in Table 19. By grouping the species according to habitats we can present the verification of the list (except for rare species, whose status could not be effectively verified) as follows (Table 20).

Table 20. Status of ancient forest species

Type	Confirmed species	Questionable species	Negated species
Pine forests	*Athyrium filix-femina, Convallaria majalis, Luzula pilosa, Oxalis acetosella, Trientalis europaea, Vaccinium vitis-idae*		*Dryopteris carthusiana, Melampyrum pretense, Vaccinium myrtillus*
Mixed oak-pine forests	*Athyrium filix-femina, Convallaria majalis, Luzula pilosa, Maianthemum bifolium, Pteridium aquilinum, Trientalis europaea*	*Carex digitata, Oxalis acetosella, Vaccinium vitis-idaea*	*Dryopteris carthusiana, Dryopteris filix-mas, Melampyrum pratense, Vaccinium myrtillus*
Lime-oak-hornbeam forests	*Anemone nemorosa, Convallaria majalis, Galeobdolon luteum, Galium odoratum, Hepatica nobilis, Lathyrus vernus, Milium effusum, Polygonatum multiflorum, Stellaria holostea, Viola reichenbachiana*	*Actea spicata, Athyrium filix-femina, Carex digitata, Festuca gigantea, Gymnocarpium dryopteris, Lilium martagon, Maianthemum bifolium, Melica nutans, Oxalis acetosella, Paris quadrifolia, Phyteuma spicatum, Ranunculus lanuginosus, Scrophularia nodosa*	*Dactylis polygama, Dryopteris carthusiana, Dryopteris filix-mas, Luzula pilosa, Melampyrum pratense, Pteridium aquilinum, Trientalis europaea, Vaccinium myrtillus, Vaccinium vitis-idaea*

In addition, when analysing Table 19 one can observe that:

- the presence of species from the list is highly differentiated among the associations; they are present to the highest extent in the lime-oak-hornbeam forests, less in mixed oak-pine forests, and the least in the pine forests;
- it is very clearly seen that the status analysis of species as ancient forest species requires large sets of phytosociological relevés; it is, namely, characteristic that in the case of pine forests (202 phytosociological relevés) no species of questionable status were registered – the status was either confirmed or negated; in the case of the mixed oak-pine forests (94 relevés) there are already three species of questionable status, and in the case of lime-oak-hornbeam forests (44 relevés) – as many as 13;

- the sole species that had its status confirmed for all three types of associations studied is *Convallaria majalis*; *Athyrium filix-femina* was close to this, as was perhaps also *Oxalis acetosella*;
- the species, whose status was negated in all the types of associations considered are: *Dryopteris carthusiana, Melampyrum pratense* and *Vaccinium myrtillus* (the latter one only in terms of frequency); moreover, the status of *Dryopteris filix-mas* was negated in mixed oak-pine forests and in the lime-oak-hornbeam forests (it is almost absent in the pine forests);
- the list of species with confirmed status in the lime-oak-hornbeam forests is ample, and a vast majority of species do not at all or only rarely appear in the mixed oak-pine forests, and even less in the pine forests;
- the species, whose status was confirmed in pine and mixed oak-pine forests, while being negated in the lime-oak-hornbeam forests are: *Luzula pilosa* and *Trientalis europaea*, while *Vaccinium vitis-idaea* is close to that situation (status confirmed in pine forests, not too certain in the mixed oak-pine forests, and decidedly negated in the lime-oak-hornbeam forests);
- the species with the status confirmed in the mixed oak-pine forests, while being negated or undefined in the remaining types, are: *Maianthemum bifolium* and *Pteridium aquilinum*.

4.3.5. GENERAL CONCLUSIONS CONCERNING ANCIENT FOREST SPECIES

Not all species from the list of ancient forest species according to Hermy et al. (1999) and Dzwonko and Loster (2001) have been confirmed in the regional verification. This may partly be due to the scarcity of empirical materials (the lime-oak-hornbeam forests), but partly can also be treated as a symptom of regional specificity.

The indicator value of particular species as ancient forest species should be considered with respect to particular habitat types. A number of species, which fulfil the criterion in one forest type (like, e.g. in the pine forests or in the oak-pine forests) may not fulfil it in another forest type (e.g. in the lime-oak-hornbeam forests), or even to the contrary – may in fact constitute an indicator of recent forest.

The regeneration processes of natural forest communities on post-agricultural land, diagnosed through the shares of ancient forest species, are in general terms slow, featuring differentiated speed, depending upon the habitat type. Among three types of forest associations considered the lime-oak-hornbeam forests appear to be regenerating the quickest. In their case the regeneration period of approximately 200 years seems to be sufficient for the reconstruction of specific floristic composition (although not necessarily the structure). The average number of ancient forest species with the confirmed status amounts in the ancient forests (TC1) to 6.2, while in the recent ones with a long regeneration period (TC2) even 6.8. Regeneration of the pine forests, and especially of the mixed oak-pine forests is distinctly slower. In their case the forests having regenerated for 230-250 years do still feature a clearly different composition in comparison with the ancient forests. In the pine forests PP2 there are on the average 1.9 ancient forest species per relevé with confirmed status, compared to 2.4 in PP1, which amounts to 79%, and in the mixed oak-pine forests – 2.4 in QP2 compared to 3.8 in QP1, i.e. merely 63%.

5. DIAGNOSIS OF THE REGENERATION PROCESSES IN THE RECENT FORESTS BASED ON THE ANALYSIS OF APPEARANCE OF ANCIENT FOREST SPECIES

5.1. FLORISTIC PATTERNS OF ANCIENT FORESTS AS A BASIS FOR THE ASSESSMENT OF RECENT FORESTS REGENERATION DEGREE

Based on the previously performed analysis of species appearance and distribution in the distinguished categories of three forest community types the ancient forests patterns have been elaborated (Table 21). These patterns refer to the data contained in Tables 6, 7, 9, 10, 12, 13 and 19, as well as the data of *Vaccinium myrtillus* cover as the species of special significance for the majority of the plant communities studied. It has been adopted that the characteristics positively indicating the ancient forest are considered and scored. Thus, the ancient forest pattern of a definite type constitutes a certain 'score'. Then, for the particular phytosociological relevés analysis was performed to show the degree, to which the pattern is realised in a given case (the representation or forest maturity index). This served as basis for making a respective survey of the phytosociological relevés, considering the distance to the ancient forest, determined with the historical cartographic materials, i.e. the forest having persisted in a given location since the earliest cartographic records.

Aggregate results from the comparison of phytosociological relevés with respective ancient forests pattern, with regard to particular types and their categories are shown in Figs. 39 through 43. The quantities analysed are the percentages of pattern realisation of a given community in the particular location (relevé). It is understandable that since some of species, adopted for the patterns do not feature 100% of frequency even in the ancient forests, one cannot expect 100% of pattern representation in particular relevés, including those representing ancient forests. Attention ought to be paid to the fact that the scoring system was prepared for each type of association separately, so that comparison of scores between types can be done only with this condition kept to. On the other hand, relations between categories for the same type of association can be analysed directly.

Table 21. Patterns of ancient forests floristic composition

Type of plant community	Attributes and scoring	Maximal scoring
Peucedano-Pinetum	Species occurence: *Athyrium filix-femina, Calamagrostis arundinacea, Calluna vulgaris, Convallaria majalis, Frangula alnus, Hylocomium splendens, Luzula pilosa, Molinia caerulea, Oxalis acetosella, Peucedanum oreoselinum, Pohlia nutans, Scorzonera humilis, Trientalis europaea, Vaccinium uliginosum, Vaccinium vitis-idaea* – 1 point each.	15 + 2 = 17
	Vaccinium myrtillus cover: cover degree „4” – 2 points, „3” – 1 point, ≥ „2” – 0 points.	
Querco-Pinetum	Species occurence: *Athyrium filix-femina, Convallaria majalis, Luzula pilosa, Maianthemum bifolium, Molinia caerulea, Peucedanum oreoselinum, Polygonatum odoratum, Polytrichastrum formosum, Pteridium aquilinum, Sciuro-hypnum oedipodium, Scorzonera humilis, Trientalis europaea* – 1 point each.	12 + 3 = 15
	Vaccinium myrtillus cover: cover degree „5” – 3 points, „4” – 2 points, „3” – 1 point, ≥ „2” – 0 points.	
Tilio-Carpinetum calamagrostietosum	Species occurence: *Hepatica nobilis, Lathyrus vernus* – 2 points each.	2x2 + 15 = 19
	Species occurence: *Ajuga reptans, Anemone nemorosa, Atrichum undulatum, Calamagrostis arundinacea, Carpinus betulus* (t2 layer), *Convallaria majalis, Galeobdolon luteum, Hypnum cupressiforme, Lilium martagon, Milium effusum, Phyteuma spicatum, Polygonatum multiflorum, Scrophularia nodosa, Stellaria holostea, Viola reichenbachiana* – 1 point each.	
Tilio-Carpinetum typicum	Species occurence: *Galium odoratum, Hepatica nobilis, Lathyrus vernus, Ranunculus lanuginosus* – 2 points each.	4x2 + 15 = 23
	Species occurence: *Ajuga reptans, Anemone nemorosa, Atrichum undulatum, Calamagrostis arundinacea, Carpinus betulus* (t2 layer), *Convallaria majalis, Galeobdolon luteum, Hypnum cupressiforme, Lilium martagon, Milium effusum, Phyteuma spicatum, Polygonatum multiflorum, Scrophularia nodosa, Stellaria holostea, Viola reichenbachiana* – 1 point each.	

It should be kept in mind that the floristic composition and the undergrowth structure of particular patches of the associations are influenced not only by the regeneration period (i.e. time having elapsed since afforestation), which was taken into account in the classification of forest stands categories, but also by other factors. These factors include, undoubtedly, the direct present and past impacts on the patches (forest management, animals, fires, etc.), causing that there are few or perhaps even there are no ’ideal patches’.

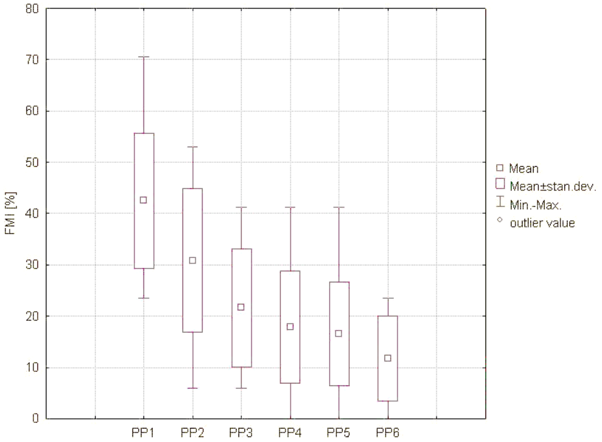


Fig. 39. Values of Forest Maturity Index (FMI) in the forest categories of *Peucedano-Pinetum* communities
Ryc. 39. Wartości wskaźnika dojrzałości lasu (FMI) w kategoriach borów (*Peucedano-Pinetum*)

In each case figures show, on the one hand, overlapping the ranges of Forest Maturity Index (FMI) values, and, at the same time – a systematic distribution of the mean values for the categories of community types. The image is particularly pronounced for the data concerning pine forests (Fig. 39). In the ancient forests the values of FMI attain 70%, but there are also cases with less than 25% of representation, the average being slightly over 40%. In the recent forests the values are lower as the forest regeneration period gets shorter. In the case of recent forests with the shortest regeneration period (some 80-90 years since afforestation) the average value of the index is only a bit over 10%.

The relevés of pine forests have been analysed also in terms of the FMI with division into two areas: Masurian (forest districts of Jedwabno, Wielbark, Szczytno, Spychowo) and Kurpie (districts of Parciaki and Myszyniec) (Fig. 40). (Note: for the area of Kurpie data were not available from the recent forests with short regeneration periods on pine forest habitats). It is visible that for the ancient forests and the recent forests with long regeneration period those from Kurpie (k) feature lower values of the index than those from Masuria (m). This might indicate a relatively stronger pressure on forests in the region of Kurpie than in Masuria, especially during the 19th century.

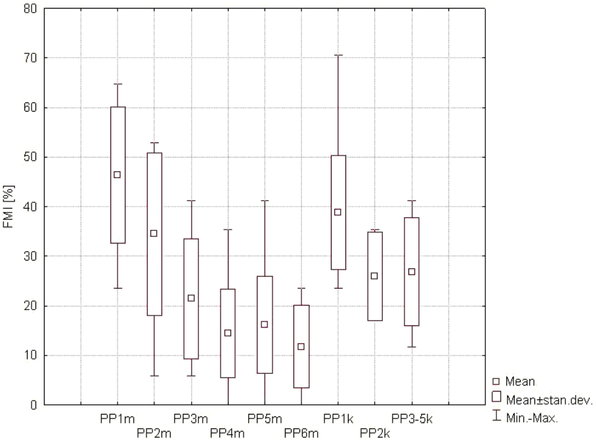


Fig. 40. Values of Forest Maturity Index (FMI) in the forest categories of *Peucedano-Pinetum* communities - in Mazury (m) and Kurpie (k)
Ryc. 40. Wartości wskaźnika dojrzałości lasu (FMI) w kategoriach borów (*Peucedano-Pinetum*) na Mazurach (m) i Kurpiach (k)

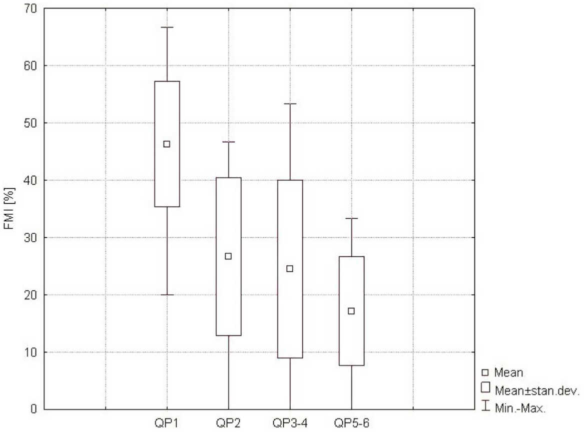


Fig. 41. Values of Forest Maturity Index (FMI) in the forest categories of *Querco-Pinetum* communities
Ryc. 41. Wartości wskaźnika dojrzałości lasu (FMI) w kategoriach borów mieszanych (*Querco-Pinetum*)

Regarding mixed oak-pine forests (Fig. 41) the differentiation of the FMI is relatively smaller than in the pine forests, but equally consistent. Just like in pine forests one notices that the largest dispersion of the index values is observed for the category of recent forests with the ʼaverageʻ regeneration period. It is highly probable that in these categories various historical events are most markedly imprinted. For the mixed oak-pine forests – similarly as for the pine forests – a limited differentiation can be observed between the area of Masuria and the one of Kurpie (the latter being less cognised in terms of mixed oak-pine forests), see Fig. 42. In the area of Kurpie ancient forests on the habitats of mixed oak-pine forests feature lower values of the FMI than in Masuria. This may be the effect of a poorer habitat or of a stronger pressure, causing deformations.

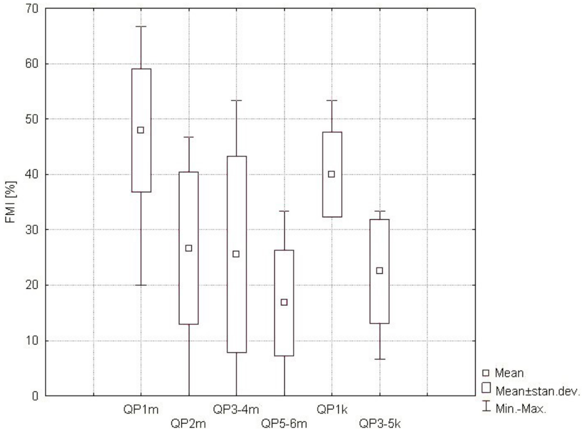


Fig. 42. Values of Forest Maturity Index (FMI) in the forest categories of *Querco-Pinetum* communities - in Mazury (m) and Kurpie (k)

Ryc. 42. Wartości wskaźnika dojrzałości lasu (FMI) w kategoriach borów mieszanych (*Querco-Pinetum*) na Mazurach (m) i Kurpiach (k)

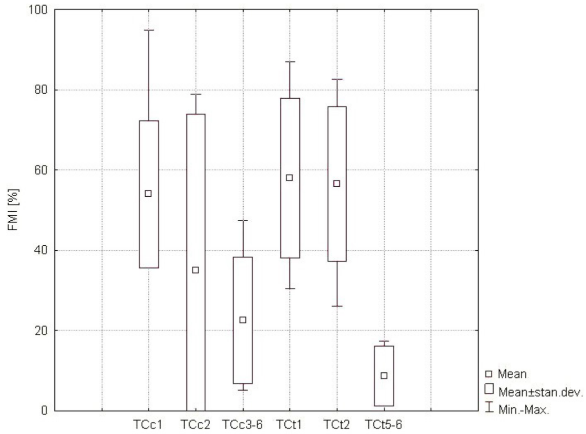


Fig. 43. Values of Forest Maturity Index (FMI) in the forest categories of *Tilio-Carpinetum* communities

Ryc. 43. Wartości wskaźnika dojrzałości lasu (FMI) w kategoriach grądów (*Tilio-Carpinetum*)

The analysis of the FMI for *Tilio-Carpinetum calamagrostietosum* and *Tilio-Carpinetum typicum* (Fig. 43), carried out only in the area of Masuria, shows – despite quite scarce data – tendencies similar to those commented upon for pine and mixed oak-pine forests. It seems that the recent forests with long regeneration period are more regenerated in the case of *Tilio-Carpinetum typicum* than in the case of *Tilio-Carpinetum calamagrostietosum*, but one should remember that the sets of species, on which the indicator is based for these two subtypes are partly different.

When comparing the results shown in Figs. 39 through 43 (the previously indicated condition concerning such a comparison being valid) one can notice that proportions between the index values for the ancient forest and the one for the recent forest of category 2 (i.e. regenerating on the post-agricultural land for 220-230 years) within the same type are surprisingly similar. In the pine forests of Masuria and Kurpie, and in *Tilio-Carpinetum calamagrostietosum* its value is at about ¾. The difference is bigger for the mixed oak-pine forests (average proportion of roughly 2/3), while it is definitely smaller for typical lime-oak-hornbeam forests.

The analyses of the developed FMI, carried out on the aggregate data for the communities types and categories were first of all meant to give the answer whether the index proposed is useful for the analysis of individual forest patch (phytosociological relevé) with consideration of various conditions, having exerted impact on particular locations.

5.2. INTERRELATIONS BETWEEN THREE FOREST CHARACTERISTICS: FOREST PERSISTENCE, DISTANCE TO ANCIENT FOREST AND FOREST MATURITY INDEX

5.2.1. METHODOLOGICAL ISSUES

Three following variables can be ascribed to each forest stand characterized by the phytosociological relevé:

- forest persistence, that is – the time period, deduced from the analysis of topographical maps and other materials, for which a forest community has existed at a given location,
- distance to the ancient forest, that is – the length of a straight line between the location of phytosociological relevé and the closest forest patch of a given type, which has been persistently a forest at least since the year 1800,
- forest maturity index, i.e. the measure, presented before, of the degree to which a given patch represents an ideal set of species, discerning natural forests from recent ones.

Forest persistence

Forest persistence is accounted for in almost all previous analyses, primarily in the form of classification into the forest categories. When delimiting the categories the analysis was referred to the content of topographical maps for the five time periods (not considering the current map). These time periods nominally correspond to the years 1800, 1830, 1872-85, 1928 and 1950 (see Table 3). It was assumed that if on an older map forest had not been recorded in a given place, but it was registered on a later map and then persisted without a break until now, then it actually appeared in the time span between the elaboration of these two maps. In theory this seems to be simple and the respective studies concerning the sequence of states ’forest – no forest‘ have been carried out for the area considered and reported separately. Yet, determining the forest persistence appearing at a given location based on such procedure is by no means easy.

The very first difficulty consists in the reliability and accuracy of maps that differ significantly under both aspects. As it is known, a map is a two-dimensional model of the three-dimensional surface of Earth, presented in definite projection, based on data collected in the field. Without entering into deeper cartographic considerations we should state that among the maps collected only those dating from the second half of the 19th century and from the 20th century were executed according to the projections that allow for the sufficiently precise comparison with the contemporary maps. Comparisons were performed, for higher precision, using the GIS techniques (changing the scale and the projection) – Wolski (2012). Maps from the beginning of the 19th century and the older ones cannot in practice be transformed in such a way as to allow for their strict comparison with the contemporary maps. For this reason in some cases it was hard to determine whether at a given location, where a phytosociological relevé was made, there was forest 200 years ago or not. Besides, the degree of detail, with which the actual state was presented on a map, depended upon the scale of a map, as well as the method of its elaboration and publication. The scale of a map influences detail level, while the technique of rendition, the possibility of reading out of the map content. The historical maps used were elaborated on the scales ranging from 25 000 to 200 000 and so the detail levels and the precision of forests delimitation definitely varied. In addition, the mapping technique makes it in some cases difficult to discern what was and what was not a forest. Some maps signatures are ambiguous, and it is then hard to clearly distinguish between forest proper and bushes or single trees. Moreover, on older maps the delimitations could happen to have no uniquely defined boundaries. All this causes that there have been frequent doubts as to whether at a given point there was forest 170 or 200 years ago, or this point was just situated near to a forest. Therefore, the respective site classification was not adopted uniquely on the basis of maps, but was confronted with the data on the plough horizon in the soil, which in some situations was the decisive argument.

The second difficulty was related to the year, for which a given map presented the state of environment. It is practically impossible to establish dating of environment state, presented on the maps, in terms of the dichotomy 'forest – no forest', since the year of publication does not correspond to the date when the field inventory was made. Furthermore, it was also frequent to use earlier maps in producing a given map, with a various updating degree. These are the reasons for doubts, concerning the time period corresponding to the rendition on the map. Definitely, it is an earlier period than the year of map publication, but it cannot be established to what extent earlier. Moreover, for a definite map series, the publication year can differ for particular sheets. Another difficulty is constituted by the fact that only few maps were made at the same time for the entire study area. These were the reasons why the nominal dates were adopted, used as reference in the cartographic analysis (see Table 3).

Another difficulty was: how to calculate when afforestation took place? It was assumed on the basis of historical topographical maps. For instance, if on a map, for which we adopted the year 1885 as the date of rendition, there is forest, and on an earlier map, dated 1830, i.e. 55 years earlier, there was no forest, then we must assume that forest appeared between those two dates. Moreover, it was in 1885 sufficiently mature to be qualified as a forest, and not as bushes or overgrown fallow land, or yet otherwise. Identification of a forest on a later map – when there had been no forest on an earlier one – implies that it could enter the area (by self-seeding or planting) in the years 1820-1830 at the earliest (would then not be treated as forest when the map of 1830 was executed), and roughly in the years 1875-80 at the latest (and so could be qualified as a young forest in mapping the later). This, indeed, is a broad range of uncertainty – in the case of Scots pine this is more than a half of the cutting age, and in the case of trees like birch or aspen (frequent on post-agricultural land) this is even their full cutting age. Therefore, it was assumed that the forest registered on a later map had appeared some 5-10 years after the date of earlier map. The problem with forest persistence is even more serious for the communities, which occupy inevitable post-agricultural sites (plough horizon is visible in the soil), but are marked as forests already on the maps from 1800 and later on. This means that afforestation of arable land took place even earlier, at least by some 20 years. Although we dispose for a part of the area of a map presenting the situation as of 1732-39, but it is a map of little precision and encompasses only the 'Prussian' part of the study area, so that no detailed analyses could be conducted. Taking all this into account, 6 persistence categories of recent forests were adopted (relative to the nominally taken year 2010): category 2 – 230 years, category 3 – 200 years, category 4 – 170 years, category 5 – 120 years, category 6 – 90 years. For the sites of ancient forests (category 1), where no plough horizon was identified and forests are registered on even the oldest maps it was assumed that the forest persistence would be 350 years.

DISTANCE TO ANCIENT FOREST

The second variable, used to characterise the studied stands of recent forests, is constituted by the distance to ancient forest, which existed, when the secondary succession on the post-agricultural land started and continued. Measurements were performed automatically along a straight line on the juxtaposed digital maps: point map of phytosociological relevés location and polygon maps showing the distribution of ancient forests on habitats of pine and mixed oak-pine forests and on habitats of lime-oak-hornbeam forests respectively (Fig. 44). The use of two maps of ancient forests was based on the assumption that the source of propagulae for the recent forest of a definite type may be constituted by the ancient forest of the same or similar, but not of a distinctly different type. Thus, the possibility that a patch of a pine forest was supplied by a mixed oak-pine forest – and vice versa – was supposed to be high, while for the case of relation between pine forest and lime-oak-hornbeam forest – was taken as close to zero.

Naturally, by definition, the distance from an ancient forest to an ancient forest equals zero.

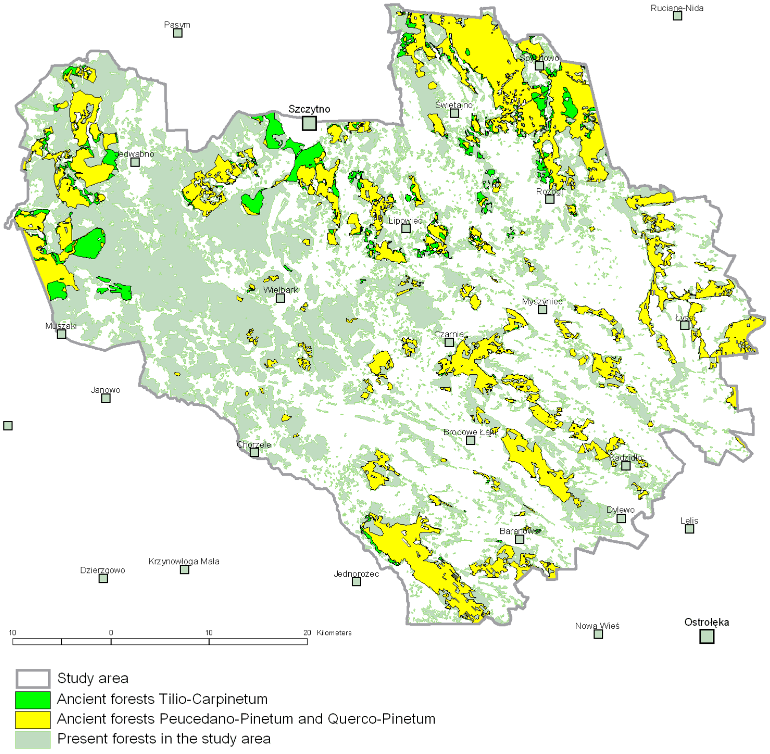


Fig. 44. Spatial distribution of ancient forests on pine and mixed oak-pine and on lime-oak-hornbeam habitats
Ryc. 44. Zasięgi „starych lasów”: w typie borów i borów mieszanych oraz grądów

5.2.2. CORRELATION ANALYSIS

The analysis accounted for the complete set of phytosociological relevés, encompassing ancient forests (categories PP1, QP1, TC1), recent post-agricultural forests (categories PP, QP and TC 2-6), and recent forests, at some time in the past deforested, but not used as arable land, which were omitted in a part of analyses, presented in this volume. The set of relevés with the characteristics consisting of the three above mentioned variables was classified a priori into three types: pine forests, mixed oak-pine forests and lime-oak-hornbeam forests. Then, each of the subsets was analysed with the use of Statistica 7.1 software.

Firstly, the results of analysis based on non-parametric tests meant to determine the relation between the variables were considered. Three test were applied: Spearman's rank correlation (Spearman 1904), Kendall's tau correlation (Kendall 1955), gamma correlation (Goodman, Kruskall 1954), whose results were consistent. The results of analysis performed with the first of these tests are shown in Table 22.

Table 22. Spearman's rank correlation

Comparison of parameter pairs	Community type		
	Pine forests	Mixed oak-pine forests	Lime-oak-hornbeam forests
Forest persistence – distance from ancient forest	-0.78	-0.81	-0.88
FMI – forest persistence	0.63	0.71	0.53
FMI – distance from ancient forest	-0.74	-0.74	-0.42

all correlations are significant $p < .05$

On the basis of the results presented the following conclusions can be drawn:

- regarding all community types the results imply the existence of significant correlations between all variables analysed;
- in all cases the highest values of correlation coefficient correspond to the pair distance to ancient forest – forest persistence, this correlation being negative. Such correlation might be explained either by the method of data collection – the respective distribution not being random – or by the actual regularity, resulting from the fact that afforestation took place initially in the vicinity of old forest complexes, to then spread out to areas farther away from the forests later on. This kind of regularity is being quite commonly observed, and so it is plausible as the explanation of the observed correlation. This hypothesis is confirmed by the spatial analyses of areas featuring different sequence of states ’forest – no forest‘, provided in another work by the present authors;

- the values of correlation coefficients for the pairs FMI – forest persistence and FMI – distance to ancient forest are similar in absolute terms, but have opposing signs – the former is positive, while the latter is negative. In the pine forests relations of FMI with distance to ancient forest seem to be stronger, while in lime-oak-hornbeam forests – relations with forest persistence appear to be stronger, and in mixed oak-pine forests they seem to be very similar in strength.

Relation between forest persistence and distance to ancient forest

The analysis of relation forest persistence – distance to ancient forest (Figs. 45, 46, 47, 48) confirms the earlier observed regularity that recent forests of longer persistence are located in close neighbourhood of the ancient forests. This distance increases for the recent forests of shorter regeneration period. The dependence described is unequivocally visible irrespective of the way, in which data are presented (Figs. 45 to 47 compared to Fig. 48), and irrespective of community type (Fig. 48). All relations betwen persistence and distance are rather of logarithmic character (higher values of R2) than linear one. All regression lines presented on Fig. 48 and other in this chapter show only the simplest models from chosen families of curves. The in-depth regression analysis with the search of optimal functions and respective equations is presented in the chapter 8.

This demonstrates that expansion of afforested areas at the end of the 18th century and at the beginning of the 19th century took place largely from the already existing ancient forests. It was only at the end of the 19th century and in the 20th century that afforestations at significant distance from the ancient forests occurred. It can be supposed that this resulted from various reasons of afforestation. Most probably, initially, spontaneous succession processes dominated, and in such cases the rate of forest development is higher for the areas situated closer to the already existing mature forest. Only much later forests developed owing to planting of trees. The conjunction of two variables here analysed influences in a natural manner the distribution of the third one, that is forest maturity index.

Relation between forest persistence and forest maturity index (FMI)

The relationship between FMI and forest persistence (Figs. 49, 50, 51) is not unambiguous everywhere – even though not all classes of forest persistence differ between themselves in a significant manner. The pattern of data is most regular in the case of pine forests, where the two oldest classes and the youngest class differ significantly from the other ones. In the case of mixed oak-pine forests we deal with partition into the oldest, two younger and three youngest classes. For lime-oak-hornbeam forests high similarity of the two oldest classes is observed. These observations confirm the data presented earlier for the forest categories (see Section 5.1).

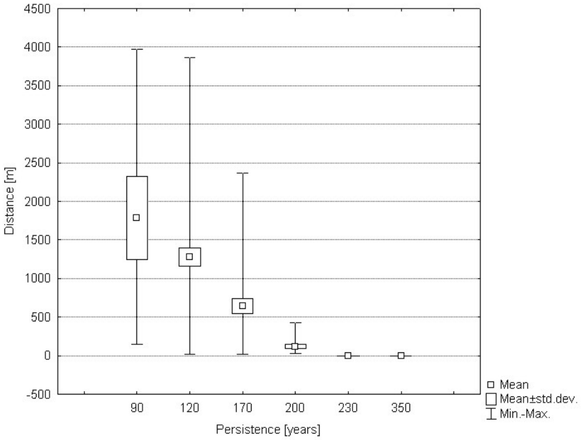


Fig. 45. Relationship between forest persistence and distance from ancient forest in recent forests of *Peucedano-Pinetum* type
Ryc. 45. Związek stażu lasu i odległości od "starego lasu" we wtórnych lasach typu boru (*Peucedano-Pinetum*)

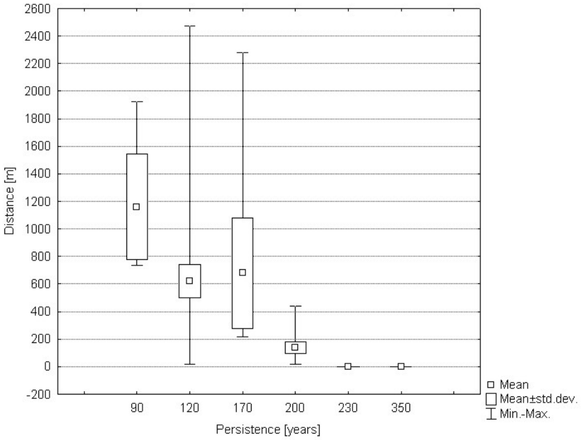


Fig. 46. Relationship between forest persistence and distance from ancient forest in recent forests of *Querco-Pinetum* type
Ryc. 46. Związek stażu lasu i odległości od "starego lasu" we wtórnych lasach typu boru mieszanego (*Querco-Pinetum*)

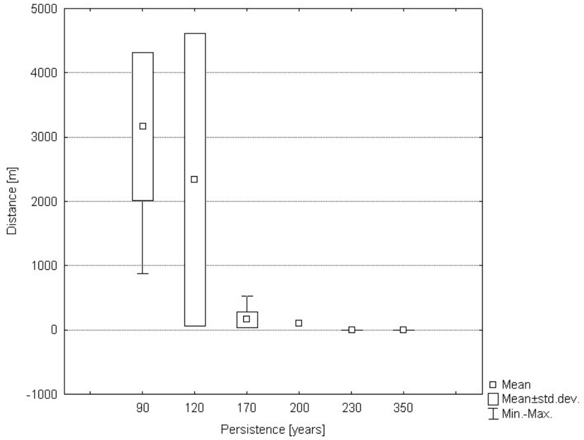


Fig. 47. Relationship between forest persistence and distance from ancient forest in recent forests of *Tilio-Carpinetum* type
Ryc. 47. Związek stażu lasu i odległości od "starego lasu" we wtórnych lasach typu grądu (*Tilio-Carpinetum*)

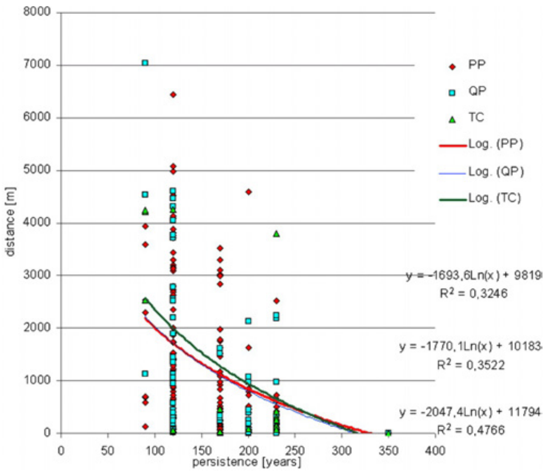


Fig. 48. Chosen regression models of relationship between forest persistence and distance from ancient forest in three types of recent forests
Ryc. 48. Poszukiwanie związku funkcjonalnego stażu lasu i odległości od starego lasu we wtórnych lasach z podziałem na trzy typy podstawowe

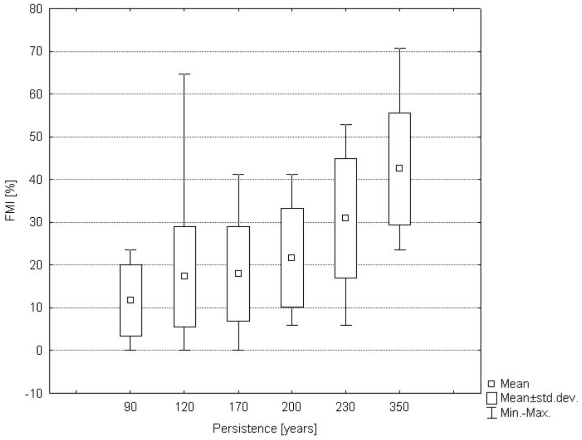
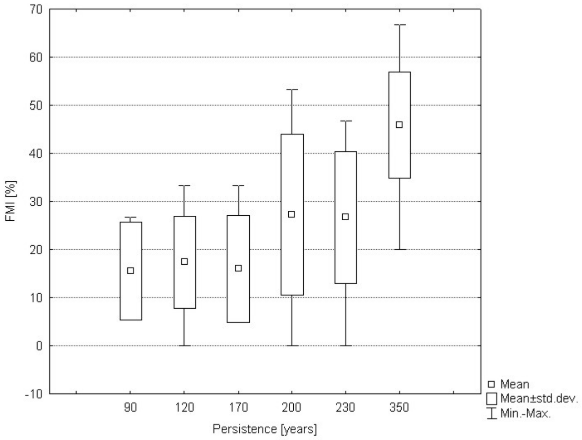


Fig. 49. Relationship between forest persistence and Forest Maturity Index in recent forests of *Peucedano-Pinetum* type

Ryc. 49. Związek stażu lasu i wskaźnika dojrzałości lasu (FMI) we wtórnych lasach typu boru (*Peucedano-Pinetum*)

Fig. 50. Relationship between forest persistence and Forest Maturity Index in recent forests of *Querco-Pinetum* type

Ryc. 50. Związek stażu lasu i wskaźnika dojrzałości lasu (FMI) we wtórnych lasach typu boru mieszanego (*Querco-Pinetum*)



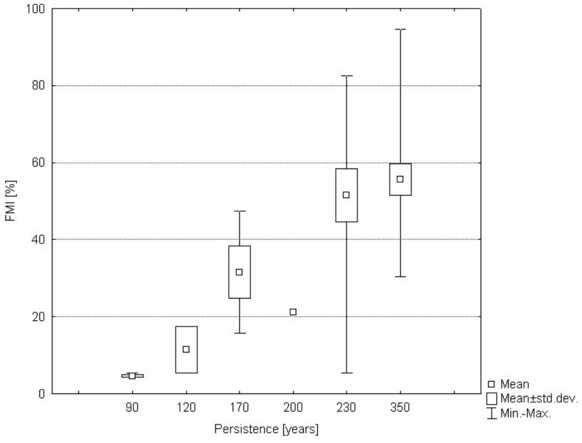


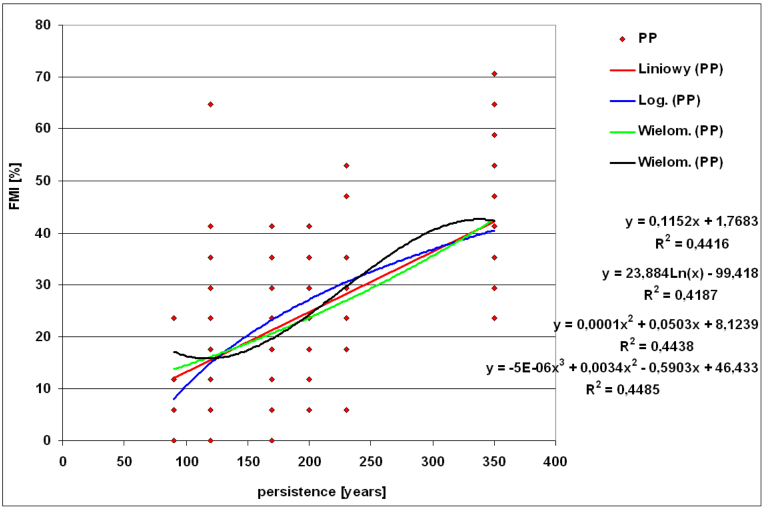
Fig. 51. Relationship between forest persistence and Forest Maturity Index in recent forests of *Tilio-Carpinetum* type

Ryc. 51. Związek stażu lasu i wskaźnika dojrzałości lasu (FMI) we wtórnych lasach typu grądu (*Tilio-Carpinetum*)

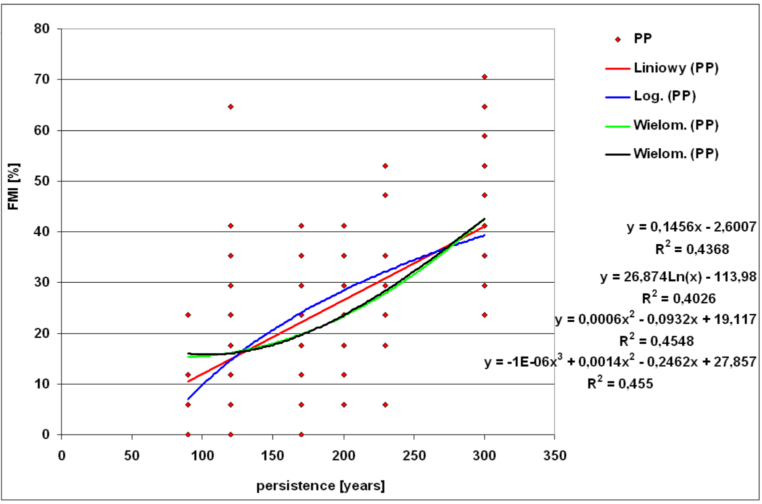
Figures 52, 53, 54 show the most popular functions, describing the dependence of forest maturity index upon forest persistence, for three forest types. In the case of pine forests (Fig. 52) the linear function describes the data better than the logarithmic function and only slightly worse than both of the polynomials. It should, however, be considered that the results are strongly influenced by the arbitrarily assumed persistence for the ancient forests (350 years). When we adopt longer or shorter persistence (Fig. 52a and 52b), we obtain different results. Yet, in any case it can be assumed that the linear function describes the relation considered for pine forests quite well. The results are very similar for the case of mixed oak-pine forests (Fig. 53). Adoption of the linear dependence for the time span that is considered for the recent forests is in this case also a sufficient solution. The linear function as describing the best relation between forest persistence and FMI signifies that the regeneration period in post-agricultural pine and mixed oak-pine forests is very long. It is too long to estimate it.

Now, for lime-oak-hornbeam forests (Fig. 54), the linear function describes the relation in question clearly worse than the polynomial functions, and even than the logarithmic function. This results from the fact that the recent forests, whose persistence was assumed (partly arbitrarily) to be 230 years, display only slightly lower values of FMI than the ancient forests, for which the persistence assumed is 350 years. It can be observed that when these two values are changed, the functions changes considerably. Yet, it must be noted that the ʾconvex' functions describe this relation better than the linear one. This means that regeneration of lime-oak-hornbeam forest is relatively more effective than in the case of pine and mixed oak-pine forests. After about 230-250 years since afforestation the forest maturity index assumes already values that do not differ from those of the ancient forests. This does not mean that such forest is identical with ancient forest and no differences can be indicated, but at least in terms of the basic floristic composition these differences are evened out.

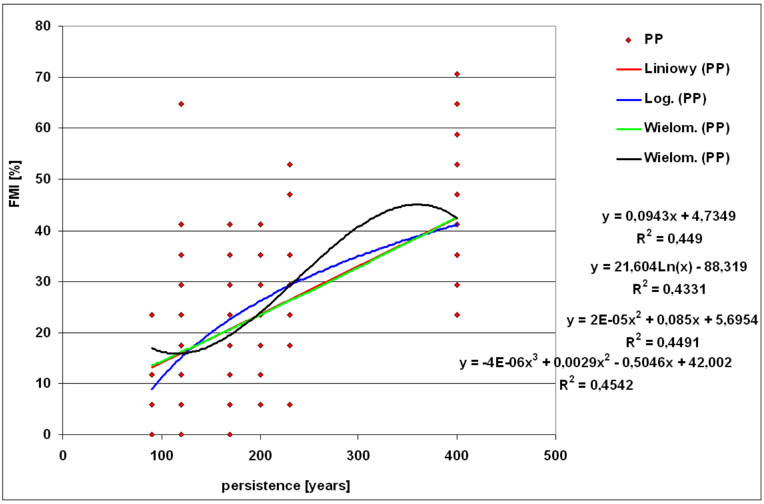
a.


FMI [%]
0
10
20
30
40
50
60
70
80
0
50
100
150
200
250
300
350
400
persistence [years]
PP
Liniowy (PP)
Log. (PP)
Wielom. (PP)
Wielom. (PP)
y = 0,1152x + 1,7683
R² = 0,4416
y = 23,884Ln(x) - 99,418
R² = 0,4187
y = 0,0001x² + 0,0503x + 8,1239
R² = 0,4438
y = -5E-06x³ + 0,0034x² - 0,5903x + 46,433
R² = 0,4485

b.


FMI [%]
0
10
20
30
40
50
60
70
80
0
50
100
150
200
250
300
350
persistence [years]
PP
Liniowy (PP)
Log. (PP)
Wielom. (PP)
Wielom. (PP)
y = 0,1456x - 2,6007
R² = 0,4368
y = 26,874Ln(x) - 113,98
R² = 0,4026
y = 0,0006x² - 0,0932x + 19,117
R² = 0,4548
y = -1E-06x³ + 0,0014x² - 0,2462x + 27,857
R² = 0,455

c.


FMI [%]
0
10
20
30
40
50
60
70
80
0
100
200
300
400
500
persistence [years]
PP
Liniowy (PP)
Log. (PP)
Wielom. (PP)
Wielom. (PP)
y = 0,0943x + 4,7349
R² = 0,449
y = 21,604Ln(x) - 88,319
R² = 0,4331
y = 2E-05x² + 0,085x + 5,6954
R² = 0,4491
y = -4E-06x³ + 0,0029x² - 0,5046x + 42,002
R² = 0,4542

Relation between distance to ancient forest and forest maturity index

The set of phytosociological relevés, divided up into three types was subject to analysis of the relation between distance to ancient forest and forest maturity index, showing the degree, to which a given patch corresponds to the ideal ancient forest set of species of a given type (Fig. 55). In these analyses the relevés of ancient forests were neglected, for the value of distance to ancient forest is zero there (it could potentially also be negative!). Hence, analysis concerned only recent forests. Attention ought to be paid to the fact that forest maturity index is to a certain degree specific for forest type and so direct comparison of results is not always sensible, and that this particular analysis does not account for the differences in recent forests persistence.

The results, shown in Figure 55, allow for making the following observations:

- in the case of pine and mixed oak-pine forests the logarithmic function describes better the relation in question than the linear one; this applies particularly to the pine forests, for which the number of relevés is the biggest, and for which the distribution of distance variable is relatively most regular; it can be noted that in this case the expectation of logarithmic character of dependence was confirmed. In the case of lime-oak-hornbeam forests the results indicate that the linear function is better than the logarithmic one. However, one should take into account a relatively small number of relevés made in the recent lime-oak-hornbeam forests, and, in addition, they were located in a vast majority not too far from the ancient forests. Therefore, the result is little reliable.

Fig. 52. Chosen regression models of relationship between forest persistence and Forest Maturity Index in recent forests of *Peucedano-Pinetum*: a – with ancient forests persistence of 350 years, b – with ancient forests persistence of 300 years, c – with ancient forests persistence of 400 years
Ryc. 52. Związek funkcjonalnego stażu lasu i wskaźnika dojrzałości lasu (FMI) we wtórnych lasach typu boru (*Peucedano-Pinetum*). a – staż „starego lasu" – 350 lat; b - staż „starego lasu" – 300 lat; c – staż „starego lasu" – 400 lat

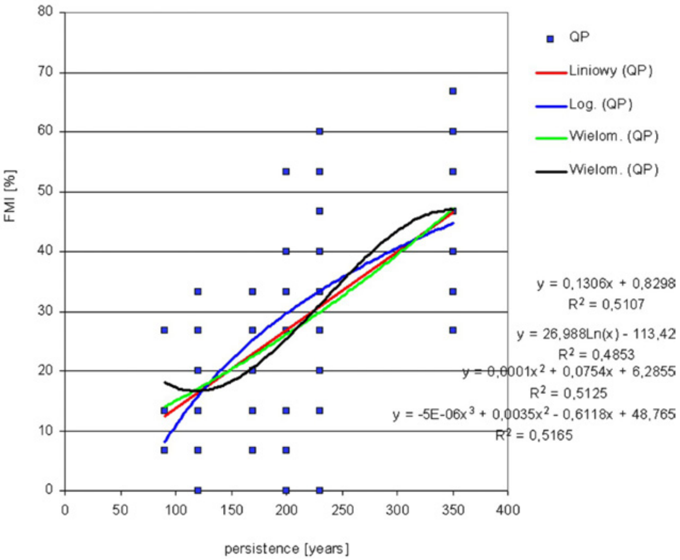


Fig. 53. Chosen regression models of relationship between forest persistence and Forest Maturity Index in recent forests of *Querco-Pinetum* type
Ryc. 53. Związek funkcjonalnego stażu lasu i wskaźnika dojrzałości lasu (FMI) we wtórnych lasach typu boru mieszanego (*Querco-Pinetum*).

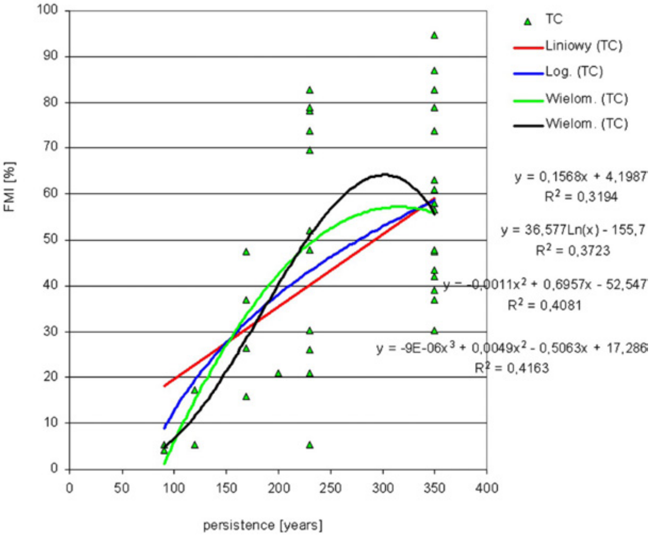


Fig. 54. Chosen regression models of relationship between forest persistence and Forest Maturity Index in recent forests of *Tilio-Carpinetum* type
Ryc. 54. Związek funkcjonalnego stażu lasu i wskaźnika dojrzałości lasu (FMI) we wtórnych lasach typu grądu (*Tilio-Carpinetum*)

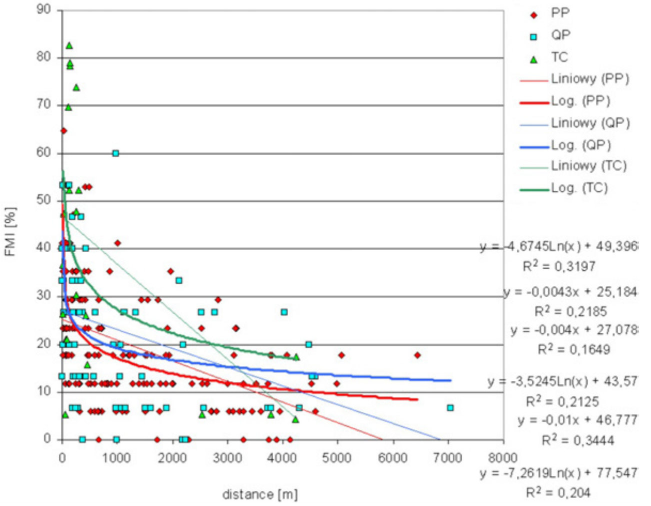


Fig. 55. Chosen regression models of relationship between distance from ancient forest and Forest Maturity Index in three types of recent forests
Ryc. 55. Związek funkcjonalnego odległości od starego lasu i wskaźnika dojrzałości lasu (FMI) we wtórnych lasach trzech typów

5.3. RELATION BETWEEN FOREST MATURITY AND DISTANCE TO ANCIENT FOREST IN THE REGENERATING RECENT FORESTS

Numerous studies, conducted in Europe, provide the evidence that the possibility of species return proper of ancient forests to recent ones is influenced not only by the time, but also by the distance from the species propagulae source (Dzwonko 1993; Dzwonko 2001a, b; Dzwonko, Gawroński 1994; Matlack 1994; Bossuyt et al. 1999; Bossuyt, Hermy 2000; Dzwonko 2001; Orczewska 2007; Orczewska 2010; Orczewska, Fernes 2011). As shown before, the forest maturity index clearly depends on forest category. This is the evidence for relation between FMI and forest persistence. The diversity of plant reproduction methods is very significant. There are distinguished several ways of propagulae spread: autochorous, endozoochorous, epizoochorous, myrmecochorous, anemochorous. It is undoubtful that species with various dispersal types show different relations between colonization rate and distance from recent forest to the propagulae source. In the case of autochorous species, the distance of seeds spread is smaller, than in the case of myrmecochorous species, i.e. the ones, whose seeds are spread by ants. Another way, in the case of endozoochorous species, whose seeds are transported over large distances by the mobile animals (like birds or ungulate mammals), and also of anemochorous species, their seeds being transported over different distances by wind. In this context one should also consider the fact that in the majority of cases plant species feature mixed ways of seed dispersal, and the influence of various factors on the mobility of propagulae and on the seeding effects is altogether hard to assess. However, being aware of the conditions complexity, a connection can be assumed between the number of species typical of ancient forests, observed within a patch of recent forest, and the distance to the closest fragment of persistent ancient forest was noticed.

Pine forests

The analysis results of the relation forest maturity index – distance to the refuge in recent pine forests, are shown with respect to five categories in Figs. 56a through 56e, and, jointly, in Figure 57.

Figure 56a shows that the recent forests growing on post-agricultural land, which had appeared yet before the year 1800 (category PP2) were in a vast majority situated in the neighbourhood of ancient forests. Only two cases of distance exceeding 500 metres were registered. Owing partly to the limited relevés number the results are hard to interpret, and the derived functions, linear and nonlinear, are highly uncertain.

Figure 56b indicates that the recent pine forests, which are marked as forests on the maps beginning with the year 1830 (and had not been marked as forests on the map of 1800), were mainly found at relatively small distances from the ancient forests. This image is similar to that for the category PP2, although the respective distances are bigger than for the former category. This is most probably due to the fact that at the turn of the 19th century afforestation (possibly primarily spontaneous) took place in the neighbourhood of already existing forests. In a way, forests extended their reach, starting from the existing one. Of the proposed two trend lines, describing the results, better fit is secured by the logarithmic curve.

Concerning the recent pine forests, documented on the maps starting with the year 1876 (German map for the territory of Masuria) and 1885 (Russian map for the area of Kurpie) – category PP4 – the distance range is decidedly bigger. Apart from numerous forests, which appeared next to the ancient forests or at the distance of up to around 1 kilometre, there are such ones that are situated at the distance of more than three kilometres from the ancient forests (Fig. 56c). It can be assumed for this category that along with the spontaneous afforestation there were conscious and purposeful planting undertakings. Like in the preceding case, a logarithmic curve represents better the results than a straight line.

The broader scope of observed distances between the recent forests and the refuges of ancient forests is even more clearly visible for the forests that appear first on the maps from the 1920s and 1930s (category PP5 – Fig. 56d). Forests having appeared at that time had locations ranging from the direct neighbourhood of the refuge up to almost seven kilometres away. Beyond any doubt, these were to a large extent purposeful forest planting undertakings. In this case, as well, a logarithmic curve represents better the data than a linear model.

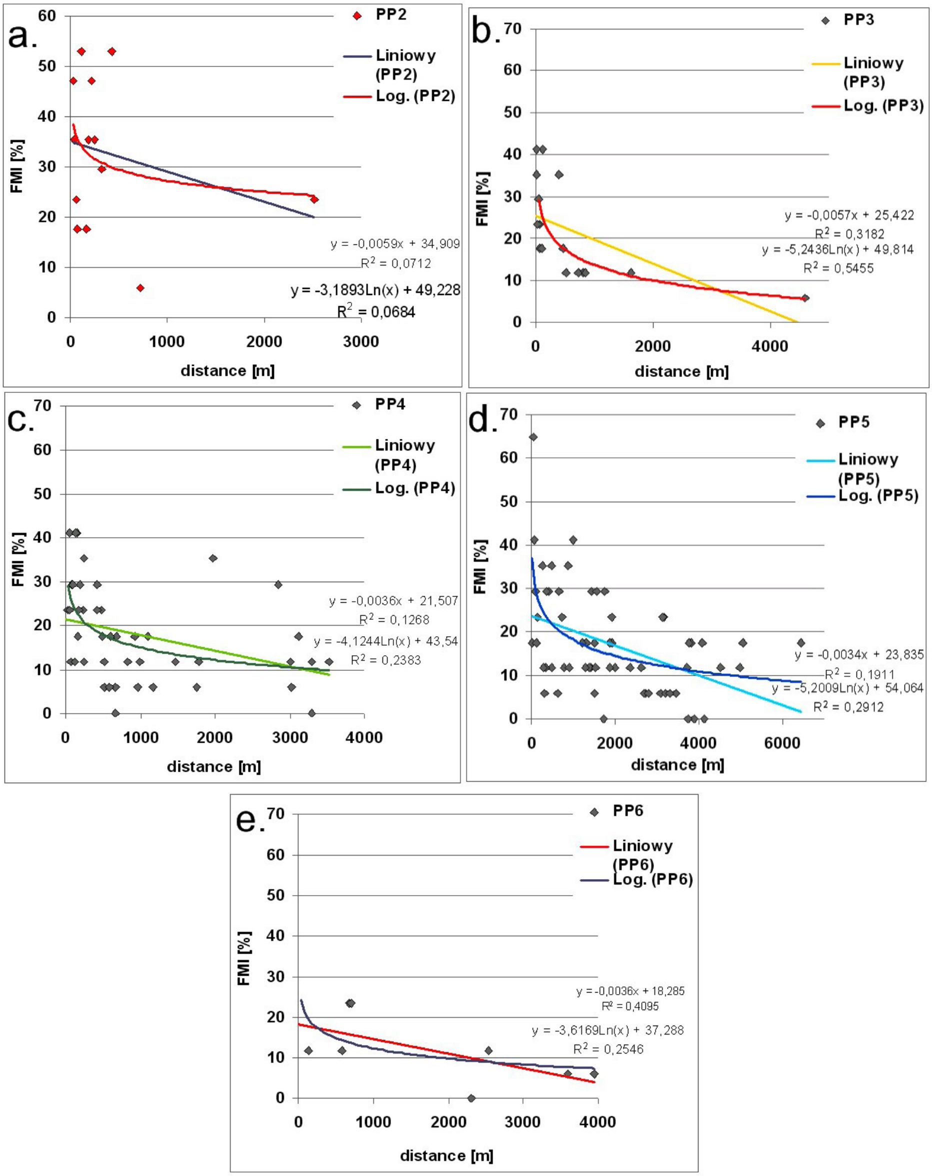


Fig. 56. Chosen regression models of relationship between distance from ancient forest and Forest Maturity Index in recent forests of *Peucedano-Pinetum* type with persistence of about 230 years (category PP2) – a, 200 years (category PP3) – b, 170 years (category PP4) – c, 120 years (category PP5) – d, 90 years (category PP6) – e.

Ryc. 56. Związek funkcjonalnego wskaźnika dojrzałości lasu (FMI) od odległości od “starego lasu” we wtórnych lasach typu boru (*Peucedano-Pinetum*) o stażu: a - ok. 230 lat (kategoria PP2), b - ok. 200 lat (kategoria PP3), c - ok. 170 lat (kategoria PP4), d - ok. 120 lat (kategoria PP5), e - ok. 90 lat (kategoria PP6).

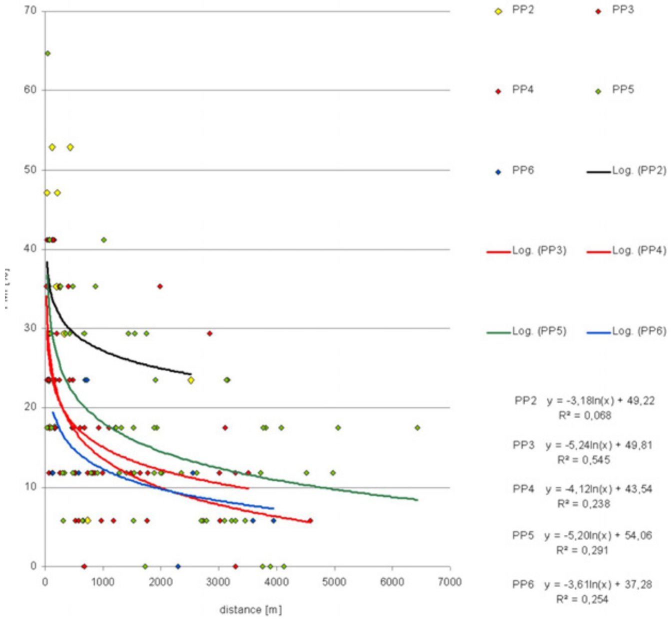


Fig. 57. Regression lines of logarithmic type showing relationship between distance from ancient forest and Forest Maturity Index in recent forests of *Peucedano-Pinetum* type with different persistence (categories PP2-6)
Ryc. 57. Związek funkcjonalny o charakterze logarytmicznym wskaźnika dojrzałości lasu (FMI) od odległości od “starego lasu” we wtórnych lasach typu boru (*Peucedano-Pinetum*) o różnym stażu (kategorie: PP2-6)

The cases of recent pine forests that were registered for the first time as late as on the map of 1950 (category PP6) are only few (Fig. 56e) and feature a broad distance range to the ancient forest – from tens of metres to four kilometres. For this category, a linear model represents better the data than a logarithmic one. This, however, might result from the small test sample number and the wide dispersion of distance values.

The results here presented allow for the conclusion that the relation between FMI of recent pine forests and distance to ancient forests has the character of a logarithmic function. Data of five recent pine forests categories, collected in Fig. 57, make it possible to note that the curves of a part of the older recent forests (categories PP3-PP4) differ quite distinctly from the curves of the younger recent forests (categories PP5-PP6). The curves, corresponding to the categories PP5 and PP6 (forests having appeared at the end of the 19th century and in the first half of the 20th century) are compatible, meaning that the values of FMI in the category of younger forests (PP6) are somewhat lower than in the forests a bit older (PP5), while the general dependence course is similar. This principle seems also to hold for the category PP2, that is – the recent forests having appeared already in the 18th

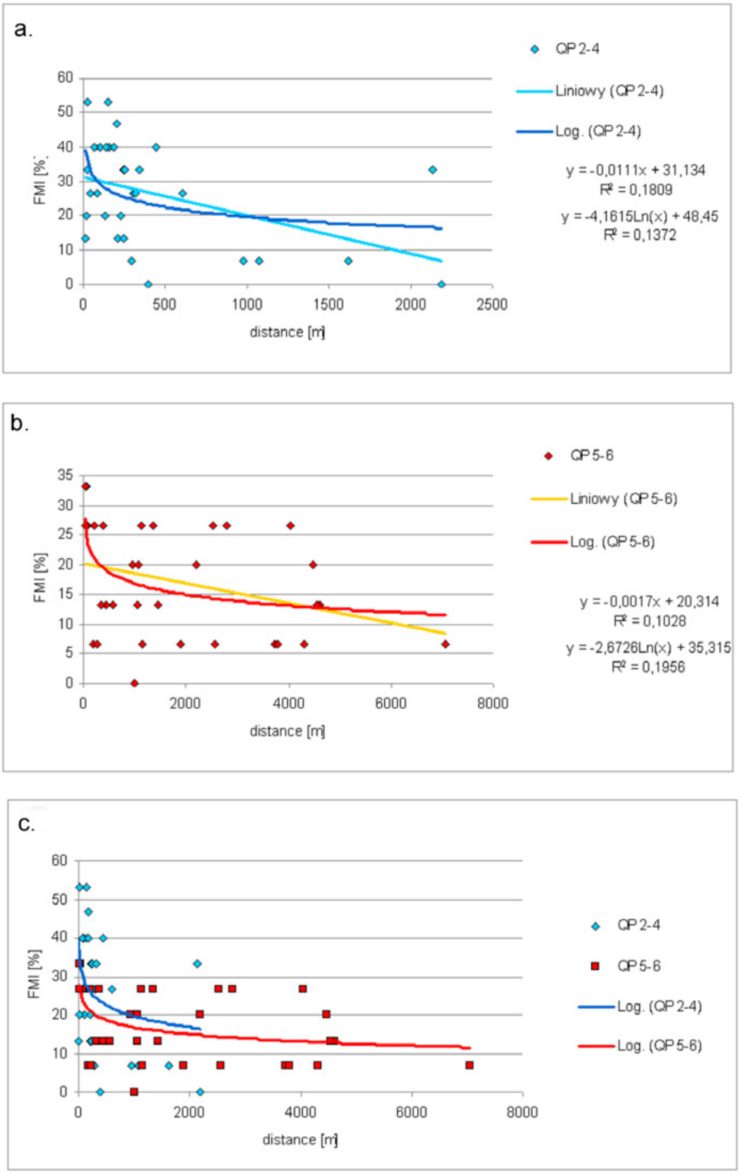


Fig. 58. Chosen regression models of relationship between distance from ancient forest and Forest Maturity Index in recent forests of *Querco-Pinetum* type with persistence of about 230-170 years (category QP2-4) – a, 120-90 years (category QP5-6) – b, with different persistence (categories QP2-4, QP5-6) – c

Ryc. 58. Związek funkcjonalny (liniowy, logarytmiczny) wskaźnika dojrzałości lasu (FMI) od odległości od starego lasu we wtórnych lasach typu boru mieszanego (*Querco-Pinetum*) o stażu: a - ok. 230-170 lat (kategorie QP2-4), b - ok. 120-90 lat (kategorie QP5-6), oraz porównanie zależności logarytmicznych (c) pomiędzy kategoriami century. On the other hand, it is more difficult to explain the curves course and their mutual relations with the category of recent forests originating from the first half of the 19th century. The course of these curves may indicate that the regeneration conditions were relatively less advantageous for this forests category than for those having appeared later.

Mixed oak-pine forests

The results of analysis of relations between the FMI and distance to the ancient forest in the mixed oak-pine forests (Fig. 58) confirm in general terms the principle of their logarithmic character, although with low observation numbers they might be unreliable. Likewise, the pattern is also confirmed here that the higher values are observed in older recent forests then in younger.

Lime-oak-hornbeam forests

The dependence of FMI upon distance to ancient forest in the lime-oak-hornbeam forests, (Fig. 59) confirms also the general character of relation. Yet, in view of the low relevés number and the fact that the vast majority of relevés are situated close to the ancient forests (up to 400 m of distance and there are only four situated at much bigger distances, and no one at medium distances), it is not possible to determine this relation with sufficient precision. For these forests the analysis accounting for various persistence periods can also hardly be conducted. Therefore, one can only state the general relationship, as noted already before (see Table 22 and Fig. 55).

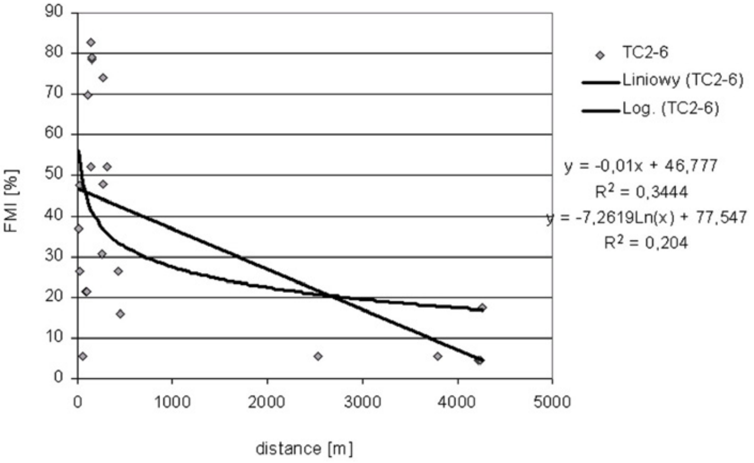


Fig. 59. Chosen regression models of relationship between distance from ancient forest and Forest Maturity Index in recent forests of *Tilio-Carpinetum* type
Ryc. 59. Związek funkcjonalny wskaźnika dojrzałości lasu (FMI) od odległości od starego lasu we wtórnych lasach typu grądu (*Tilio-Carpinetum*)

5.4. *VACCINIUM MYRTILLUS* IN THE REGENERATING FORESTS ON POST-AGRICULTURAL LAND

5.4.1. DATA AND METHODS OF EVALUATION

Bilberry (*Vaccinium myrtillus*) is a species having particular significance for the development of pine forests undergrowth structure. It can even be assumed that the role of this species in this community type is greater than of any other species of herb layer. Bilberry has also a significant contribution to the formation of surface moulder, which means that it also influences the soil processes. In mixed oak-pine forests the role of this species is somewhat smaller, but it still belongs among the main undergrowth components (see Section 4.3.1). In our opinion, namely, it is impossible to establish the regeneration model of pine forest or mixed oak-pine forest without taking into account this species of specific features (see Section 3.4). In the phytocoenoses of pine and mixed oak-pine ancient forests *Vaccinium myrtillus* appears in every patch (see Tables 6 and 9), and its share in the undergrowth is high or very high. In ancient forests only in the locations where, for some reasons, there occurred destruction or limitation of the bilberry population (locations of the former forest fires, the undergrowth destruction because of felling, very intensive growth of younger spruce trees, or other ones), the cover is lower than roughly 40–50%. In typical cases the species occupies the great majority of the patch. On the other hand, in the recent pine and mixed oak-pine forests, even though the frequency is high (in the majority of categories exceeding 90%), the cover is distinctly lower. This is noticeable in the data provided in Figs. 26a through 26d.

On the basis of the results reffered in chapters 3 and 4 we may assume that:

- the various share of bilberry in the recent post-agricultural forests depends, in particular, upon the persistence of regenerating forest. In the older recent forests the bilberry cover ought to resemble that observed in the ancient forests.
- the regeneration rate of *Vaccinium myrtillus* in the post-agricultural forests is correlated with the distance to the pine or mixed oak-pine ancient forests where this species could persist incessantly (see Sections 5.2 and 5.3).

In this part analyses are focused on evaluation of bilberry cover regeneration rate. They are based on the analyses of differences in *Vaccinium myrtillus* cover in recent post-agricultural pine and mixed oak-pine forests differing in persistence. Lime-oak-hornbeam forests are excluded from analysis, because *Vaccinium myrtillus* appears only in their poorer forms, or in the disturbed plots, and that much less abundantly, while not appearing in the typical forms at all.

Opposite to previous analyses, in which the *Vaccinium myrtillus* cover was expressed with the quantitative scale of Braun-Blanquet, for this study the cover was calculated as a percentage of the area occupied by the whole species population. The difference between two type of estimation is unquestionable. In many cases the *Vaccinium myrtillus* population could occupy the entire area, but its low density caused that the cover degree was below 5.

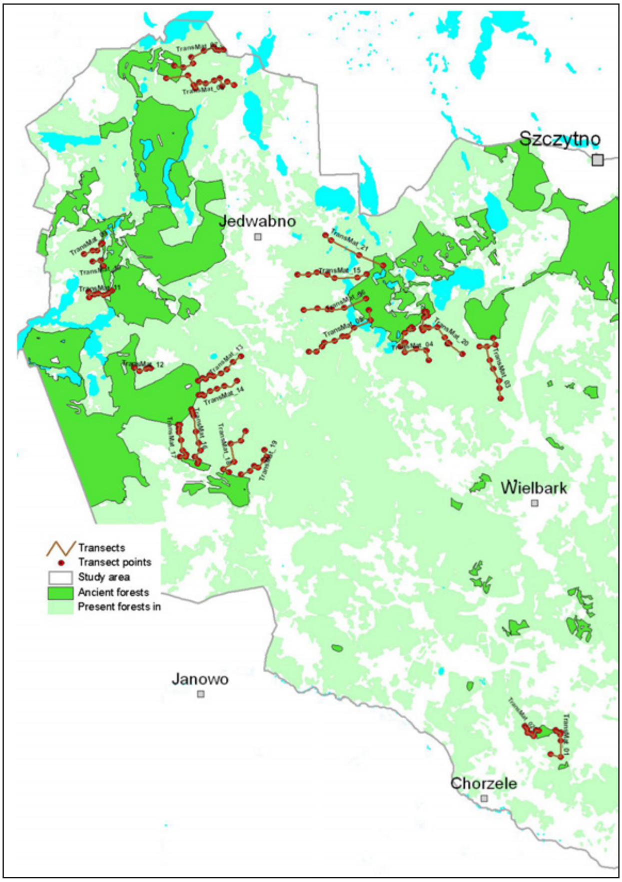


Fig. 60. Transects location to study the influence of distance from ancient forest on *Vaccinium myrtillus* cover in recent forests
Ryc. 60. Lokalizacja transektów do szczegółowych badań wpływu odległości od "starego lasu" na pokrycie *Vaccinium myrtillus* w lasach wtórnych

The analysis is based on two data sets. The first set includes phytosociological relevés from the pine and mixed oak-pine forests (Tables 6 and 9). The second set constitutes description of 21 transects, i.e. linear arrangements of study points, distributed in such a way to preserve possibly homogeneous geomorphic and habitat conditions, as well as the same or similar persistence degree, while their distances to the ancient forest should vary. It was usually so that the first point of transect represented ancient forest, while the subsequent ones – various categories of recent forests, increasingly distant from the ancient forest. Because of the above methodological limitations, the studied transects are mainly located in the north-western part of the area, primarily in the Masurian part (Fig. 60).

The analysis was conducted twice. Firstly only transects were analysed, secondly, all data (relevés and transect points) were joined together as a set of independent point data. In both approaches each observation was characterised by:

- forest category, corresponding to its persistence (according to the adopted time intervals),
- distance of the point considered to be ancient forest (value in metres, determined on the basis of the past states sequence),
- percentage reach of the bilberry population (based on the field estimates),
- the clustering scheme of the *Vaccinium* population in the community (in the form of a verbal description – nominal variable).

5.4.2. *VACCINIUM MYRTILLUS* COVER OVER 21 TRANSECTS

The transects analysed are either one-sided (with ancient forest at one end), or double-sided – with ancient forest at both ends. For calculations, the position of points had no significance, for they were ordered according to the distance from the ancient forest, irrespective of the fragment considered. The ancient forest reference of *Vaccinium myrtillus* could be constituted also by the poor mesotrophic lime-oak-hornbeam forest (*Tilio-Carpinetum calamagrostietosum*), with bilberry as a constant composition element.

Analysed transects differ in a number of points – from three to thirteen, and the maximum distances from the ancient forest range between 435 m and 3 135 m. On all transects there is visible a clear decrease in the *Vaccinium myrtillus* cover with the increasing distance to ancient forest. The above interdependences could be described by the linear function. These regression lines are statistically significant in all cases (Fig. 61; Table 23). It is worth to underline that the biggest value of the parameter ʼaʻ of all regression lines is almost 11 times higher as the smallest one (Fig. 62), what indicate groups of transects, with the different course of *Vaccinium myrtillus* cover changes.

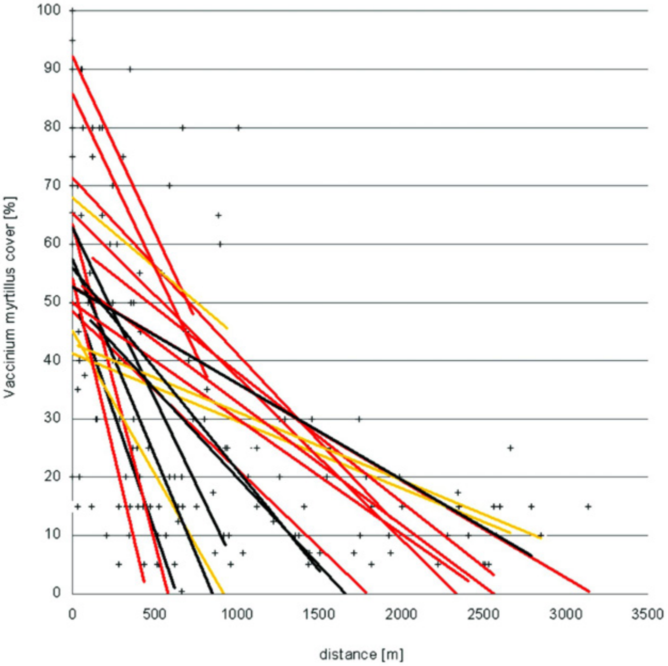


Fig. 61. Relationship between *Vaccinium myrtillus* cover and distance from ancient forest for 21 transects according to linear model
Ryc. 61. Linie funkcji liniowej trendu zależności pokrywania *Vaccinium myrtillus* od odległości od "starego lasu" dla punktów zebranych w ramach 21 transektów

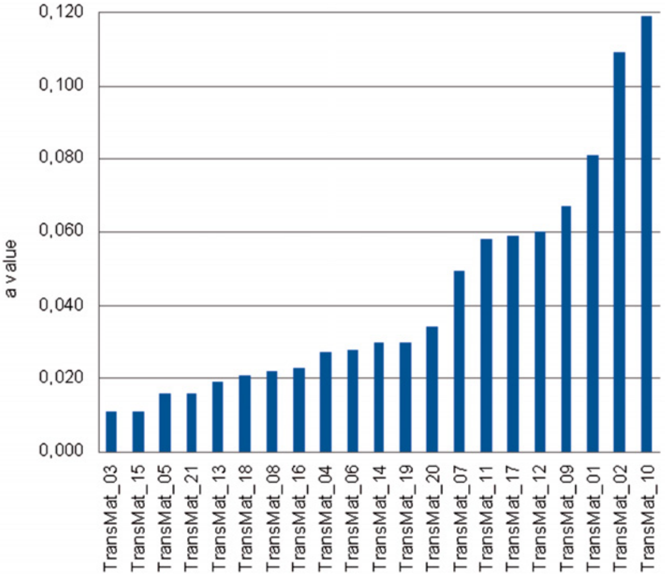


Fig. 62. The range of "a" constant from equations describing linear functions presented on Fig. 61
Ryc. 62. Wartości stałej „a" w funkcjach prostoliniowych dla 21 transektów zamieszczonych na ryc. 61.

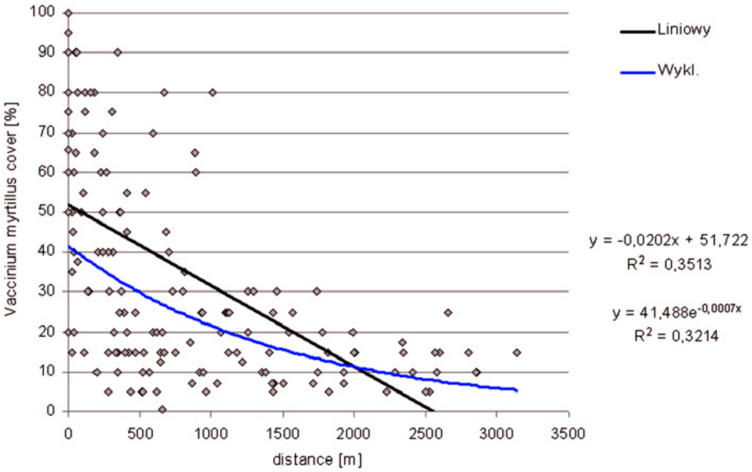


Fig. 63. Chosen regression models of relationship between *Vaccinium myrtillus* cover and distance from ancient forest
Ryc. 63. Analiza zależności pokrywania *Vaccinium myrtillus* od odległości od "starego lasu" w punktach transektów potraktowanych jako zbiór punktów niezależnych

Taking all the transects points as a set of independent data (Fig. 63) makes it possible to note that the linear correlation, describing the dependence of bilberry cover rate upon the distance to ancient forest is lower that the mean of correlation coefficients calculated separately for transects. This result indicates that transects are differentiated from the point of view of other variables influencing *Vaccinium myrtillus* cover, mainly the persistence of recent forests.

Table 23. Linear trend functions of *Vaccinium myrtillus* cover in 21 special transects

Transect number	No. of points in the transect	Maximal distance from ancient forest [m]	Linear function of trend	R2 value	*
TransMat_01	6	745	$y = -0{,}081x + 51{,}42$	$R^2 = 0{,}816$	1
TransMat_02	8	662	$y = -0{,}109x + 63{,}48$	$R^2 = 0{,}485$	2
TransMat_03	9	2660	$y = -0{,}011x + 41{,}12$	$R^2 = 0{,}293$	3
TransMat_04	10	1780	$y = -0{,}027x + 48{,}41$	$R^2 = 0{,}485$	2
TransMat_05	10	3135	$y = -0{,}016x + 52{,}78$	$R^2 = 0{,}510$	2
TransMat_06	6	2529	$y = -0{,}028x + 65{,}29$	$R^2 = 0{,}577$	2
TransMat_07	9	949	$y = -0{,}049x + 45{,}17$	$R^2 = 0{,}318$	3
TransMat_08	11	2561	$y = -0{,}022x + 60{,}19$	$R^2 = 0{,}414$	2
TransMat_09	5	960	$y = -0{,}067x + 57{,}44$	$R^2 = 0{,}713$	1
TransMat_10	3	435	$y = -0{,}119x + 54{,}18$	$R^2 = 0{,}522$	2
TransMat_11	7	930	$y = -0{,}058x + 62{,}73$	$R^2 = 0{,}808$	1
TransMat_12	5	730	$y = -0{,}060x + 92{,}14$	$R^2 = 0{,}561$	2
TransMat_13	9	2409	$y = -0{,}019x + 50{,}02$	$R^2 = 0{,}438$	2
TransMat_14	7	1928	$y = -0{,}030x + 71{,}41$	$R^2 = 0{,}684$	2
TransMat_15	7	2850	$y = -0{,}011x + 42{,}96$	$R^2 = 0{,}300$	3
TransMat_16	8	940	$y = -0{,}023x + 68{,}01$	$R^2 = 0{,}263$	3
TransMat_17	9	819	$y = -0{,}059x + 85{,}82$	$R^2 = 0{,}636$	2
TransMat_18	6	2580	$y = -0{,}021x + 54{,}04$	$R^2 = 0{,}480$	2
TransMat_19	7	1711	$y = -0{,}030x + 50{,}14$	$R^2 = 0{,}746$	1
TransMat_20	13	1506	$y = -0{,}034x + 55{,}97$	$R^2 = 0{,}735$	1
TransMat_21	4	2792	$y = -0{,}016x + 52{,}61$	$R^2 = 0{,}852$	1

* - classes of function significance

5.4.3. VARIABILITY OF BILBERRY COVER BASED ON THE POINT DATA SET

Data collected from the phytosociological relevés and the additional points from the transects constituted the basis of the analysis of relation between *Vaccinium myrtillus* cover and forest persistence as well as distance to ancient forest. Analysis was performed on the sets of independent points (i.e. spatial relations between points were not considered), separately for pine forests and for mixed oak-pine forests. Data of 422 points were available altogether, of which 270 points in the pine forests – 57 in ancient forests and 213 in recent post-agricultural forests, and 152 points in the mixed oak-pine forests – 40 in ancient forests and 112 in recent ones.

The following characteristics and relations were examined:

- Average values of *Vaccinium myrtillus* cover in distinguished classes, obtained through joint consideration of forest persistence and distance to the ancient forest (Tables 24 and 25);

- Frequency in the set of a definite category in the framework of the classification, mentioned above;
- Changeability of the average *Vaccinium myrtillus* cover in the classes distinguished;
- Relation between *Vaccinium myrtillus* cover and distance to ancient forest in the recent forests of different persistence, based on regression analysis (in order to enable application of various functions the observed values of cover and distance variables, which were equal 0, were changed to 0.0001.)

Table 24. *Vaccinium myrtillus* cover in pine forests depending on forest category and distance from ancient forest

Distance from AF [m]	PP1		PP2-3		PP4		PP5-6		all PP	
	No	Cover [%]	No	Cover [%]	No	Cover [%]	No	Cover [%]	No	Cover [%]
<0	57	55.2	0	-	0	-	0	-	57	55.2
0-200	0	-	19	45.8	14	31.8	7	36.1	40	39.2
200-400	0	-	8	44.4	8	17.6	10	28.0	26	29.8
400-800	0	-	7	20.4	12	13.3	18	30.1	37	22.8
800-1600	0	-	2	17.5	13	9.8	32	22.3	47	18.6
1600-3200	0	-	2	10.0	8	15.1	34	13.4	44	13.5
3200-6400	0	-	1	0.0	3	9.0	15	8.8	19	8.4
total	57	55.2	39	36.5	58	17.6	116	20.5	270	29.5

Pine forests

Data, collected in Table 24, show the difference between ancient and recent forests in the bilberry cover, and then – the differences in recent forests depending upon persistence and distance to ancient forest. When interpreting these data, one should pay attention to the uneven distribution of the empirical material collected, meaning that the classes, resulting from the joint consideration of forest persistence categories and the intervals of distance values, are represented by the essentially varying numbers of points (Fig. 64). Points, representing older recent forests are in a vast majority situated close to the ancient forest, and conversely – points, representing younger recent forest are situated in a large proportion far from the ancient forest. It results, as it was indicated already before, from the fact that forests expanded over the post-agricultural land largely systematically from the ancient complexes. This strong connection between persistence and distance to ancient forest constitutes a difficulty for the study of relation between the *Vaccinium myrtillus* spread and these factors. Yet, Fig. 65 shows a decrease in the bilberry cover along the increasing distance from the ancient forest for each forest persistence category.

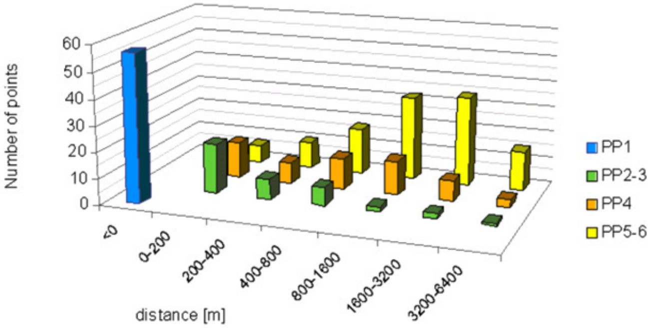


Fig. 64. Number of points with data of *Vaccinium myrtillus* cover in *Peucedano-Pinetum* forests in relation to forest category and distance from ancient forest
Ryc. 64. Liczby punktów z danymi o pokryciu *Vaccinium myrtillus* w borach sosnowych (*Peucedano-Pinetum*) z uwzględnieniem stażu (kategorii) i odległości od starego lasu

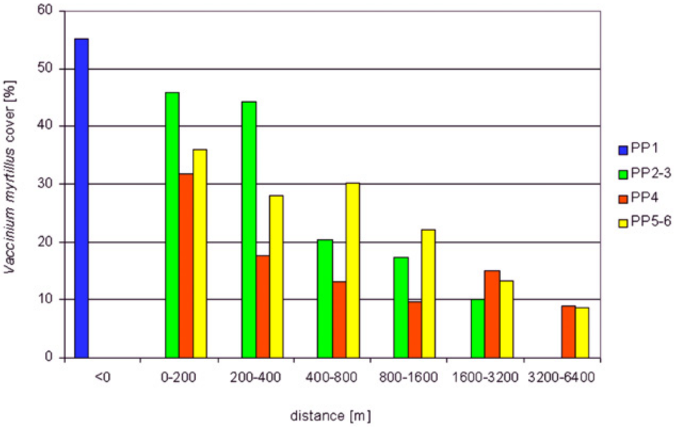


Fig. 65. Mean values of *Vaccinium myrtillus* cover in *Peucedano-Pinetum* forests in relation to forest category and distance from ancient forest
Ryc. 65. Wartości średniego pokrycia *Vaccinium myrtillus* w borach (*Peucedano-Pinetum*) z uwzględnieniem zróżnicowania na kategorie stażu i odległość od starego lasu

Mixed oak-pine forests

In view of the smaller number of study sites, for mixed oak-pine forests the data has been aggregated regarding the persistence of recent forests (Table 25). Here, as well, one can easily see that there are ample representations of the oldest recent forests close to the ancient forest and of the youngest recent forests far from the ancient stands (Fig. 67). The difference between the ancient forests and the recent ones is relatively smaller, but still, the general tendency of decrease in the *Vaccinium myrtillus* cover along the increasing distance to ancient forest is visible (Fig. 68).

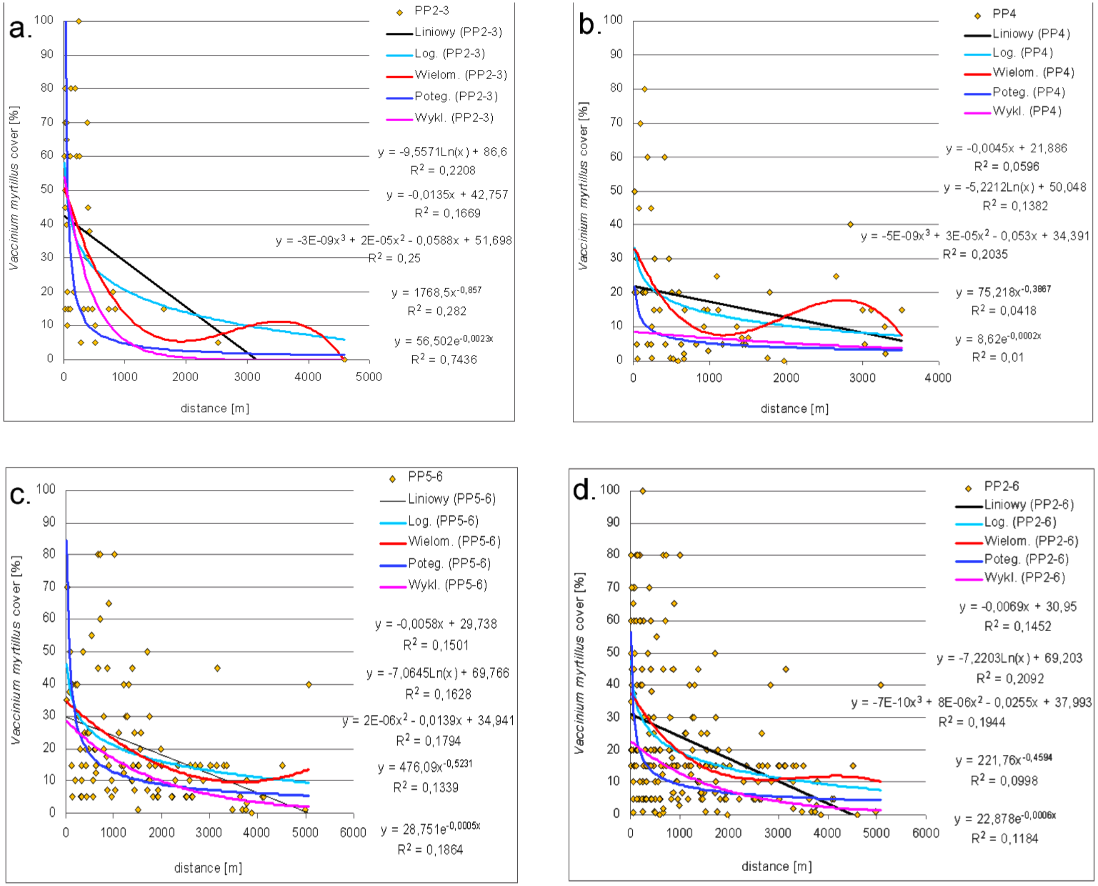


Fig. 66. Chosen regression models of relationship between *Vaccinium myrtillus* cover and distance from ancient forest in recent forests of *Peucedano-Pinetum* type with persistence of: 200–230 years (category PP2–3) – a, 170 years (category PP4) – b, 90–120 years (category PP5–6) – c, in all recent forests of *Peucedano-Pinetum* type (categories PP2–6) – d

Ryc. 66. Związek funkcjonalny pokrycia *Vaccinium myrtillus* od odległości od "starego lasu" we wtórnych lasach typu boru (*Peucedano-Pinetum*) o stażu: a – ok. 200–230 lat (kategorie PP2–3), b – ok. 170 lat (kategoria PP4), c - ok. 90–120 lat (kategorie PP5–6), d – bez względu na staż regeneracji (kategorie PP2–6)

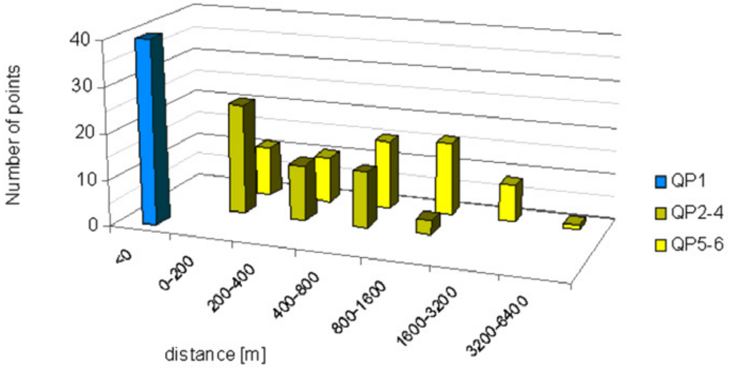


Fig. 67. Number of points with data of *Vaccinium myrtillus* cover in *Querco-Pinetum* forests in relation to forest category and distance from ancient forest
Ryc. 67. Liczby punktów z danymi o pokryciu *Vaccinium myrtillus* w borach mieszanych (*Querco-Pinetum*) z uwzględnieniem stażu (kategorii) i odległości od "starego lasu"

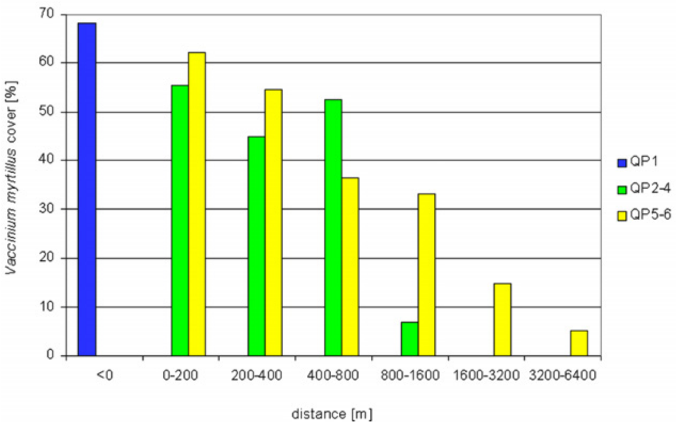
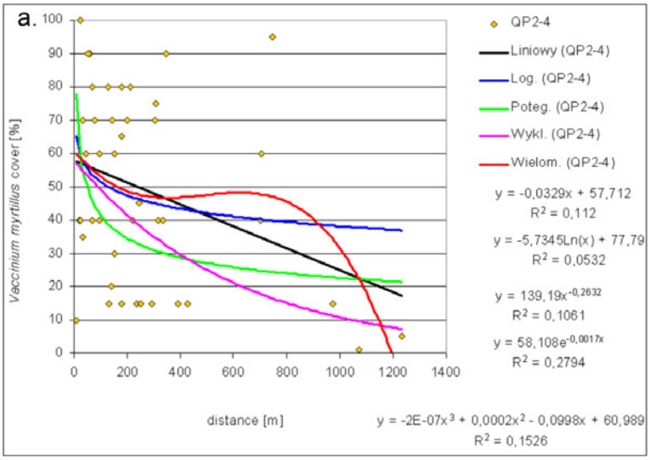
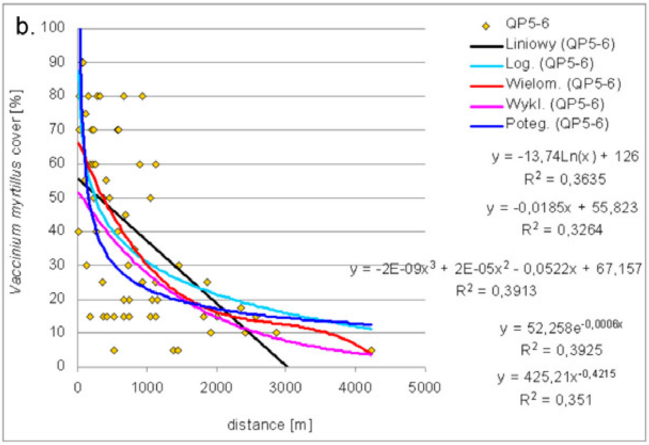


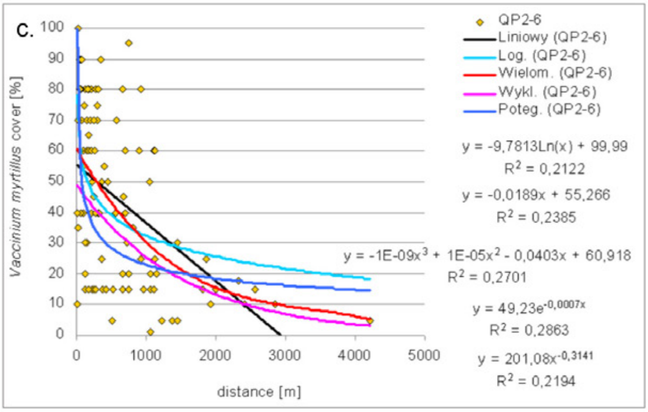
Fig. 68. Mean values of *Vaccinium myrtillus* cover in *Querco-Pinetum* forests in relation to forest category and distance from ancient forest
Ryc. 68. Wartości średniego pokrycia *Vaccinium myrtillus* w borach mieszanych (*Querco-Pinetum*) z uwzględnieniem zróżnicowania na kategorie stażu i odległość od "starego lasu".

→

Fig. 69. Chosen regression models of relationship between *Vaccinium myrtillus* cover and distance from ancient forest in recent forests of *Querco-Pinetum* type with persistence of 170-230 years (categories QP2-4) – a, 90-120 years (categories QP5-6) – b, in all recent forests of *Querco-Pinetum* type (categories QP2-6) – c
Ryc. 69. Związek funkcjonalny pokrycia *Vaccinium myrtillus* od odległości od "starego lasu" we wtórnych lasach typu boru mieszanego (*Querco-Pinetum*) o stażu: a - ok. 170-230 lat (kategorie QP2-4), b - ok. 90-120 lat (kategorie QP5-6), c - bez uwzględniania stażu (kategorie QP2-6).


a.
Vaccinium myrtillus cover [%]
100
90
80
70
60
50
40
30
20
10
0
0
200
400
600
800
1000
1200
1400
distance [m]
QP2-4
Liniowy (QP2-4)
Log. (QP2-4)
Poteg. (QP2-4)
Wykl. (QP2-4)
Wielom. (QP2-4)
y = -0,0329x + 57,712
R² = 0,112
y = -5,7345Ln(x) + 77,79
R² = 0,0532
y = 139,19x^-0,2632
R² = 0,1061
y = 58,108e^-0,0017x
R² = 0,2794
y = -2E-07x³ + 0,0002x² - 0,0998x + 60,989
R² = 0,1526


b.
Vaccinium myrtillus cover [%]
100
90
80
70
60
50
40
30
20
10
0
0
1000
2000
3000
4000
5000
distance [m]
QP5-6
Liniowy (QP5-6)
Log. (QP5-6)
Wielom. (QP5-6)
Wykl. (QP5-6)
Poteg. (QP5-6)
y = -13,74Ln(x) + 126
R² = 0,3635
y = -0,0185x + 55,823
R² = 0,3264
y = -2E-09x³ + 2E-05x² - 0,0522x + 67,157
R² = 0,3913
y = 52,258e^-0,0006x
R² = 0,3925
y = 425,21x^-0,4215
R² = 0,351


c.
Vaccinium myrtillus cover [%]
100
90
80
70
60
50
40
30
20
10
0
0
1000
2000
3000
4000
5000
distance [m]
QP2-6
Liniowy (QP2-6)
Log. (QP2-6)
Wielom. (QP2-6)
Wykl. (QP2-6)
Poteg. (QP2-6)
y = -9,7813Ln(x) + 99,99
R² = 0,2122
y = -0,0189x + 55,266
R² = 0,2385
y = -1E-09x³ + 1E-05x² - 0,0403x + 60,918
R² = 0,2701
y = 49,23e^-0,0007x
R² = 0,2863
y = 201,08x^-0,3141
R² = 0,2194

Similarly to results obtained for pine forests, in the case of mixed oak-pine forests the analyses of interrelation between *Vaccinium myrtillus* cover and distance to the ancient forest according to two categories of recent forests (Figs. 69a, and 69b), and for all recent forests together (Fig. 69c) show generally very weak correlations between data and respective functions. Among all functions applied for analysed categories of persistence, the best fit gives exponential one. It is also worth to underline that for younger persistence class and all recent forests taken together correlation coefficients are higher in the case of mixed oak-pine forest in comparison to pine forests.

Table 25. *Vaccinium myrtillus* cover in mixed oak-pine forests depending on forest category and distance from ancient forest

Distance from AF [m]	QP1		QP2-4		QP5-6		all QP	
	No	Cover [%]	No	Cover [%]	No	Cover [%]	No	Cover [%]
<0	40	68.1	0	-	0	-	40	68.1
0-200	0	-	24	55.4	11	62.3	35	57.6
200-400	0	-	12	45.0	10	54.5	22	49.6
400-800	0	-	12	52.5	15	36.3	27	39.7
800-1600	0	-	3	7.0	16	33.1	19	29.0
1600-3200	0	-		-	8	14.7	8	14.7
3200-6400	0	-		-	1	5.0	1	5.0
total	40	68.1	51	48.9	61	40.0	152	50.4

5.4.4. RELATION OF THE *VACCINIUM MYRTILLUS* COVER WITH THE FMI

The value of Forest Maturity Index (FMI) is influenced by *Vaccinium myrtillus* cover, as abudance of this species, higher than ’2‘ on the Braun-Blanquet scale, is one of the building blocks of FMI. In this context, two problems are worth further consideration:

1. relation of the FMI with the *Vaccinium myrtillus* cover,
2. relation of the modified FMI (FMI2 - the index not taking into account the abundance of *Vaccinium myrtillus*) with the cover of this species.

The relation of the FMI with the bilberry cover in pine forests is shown in Fig. 70a. One can see a very clear relationship, well modelled by the polynomial of second degree, and the linear function. When the polynomial function is used, the curve attains the maximum for the cover of 100%, and becomes almost horizontal (i.e. the increase in the FMI is then already very slow) for the cover values of about 80%. When the modified FMI is considered (Fig. 70b) the relation is of the same character, but with lower correlation coefficients. This result demonstrates a very high significance of *Vaccinium myrtillus* in the regeneration of typical floristic composition of *Peucedano-Pinetum* association. On the other hand it shows also, that when the undergrowth is dominated by bilberry there may be no space for some other species.

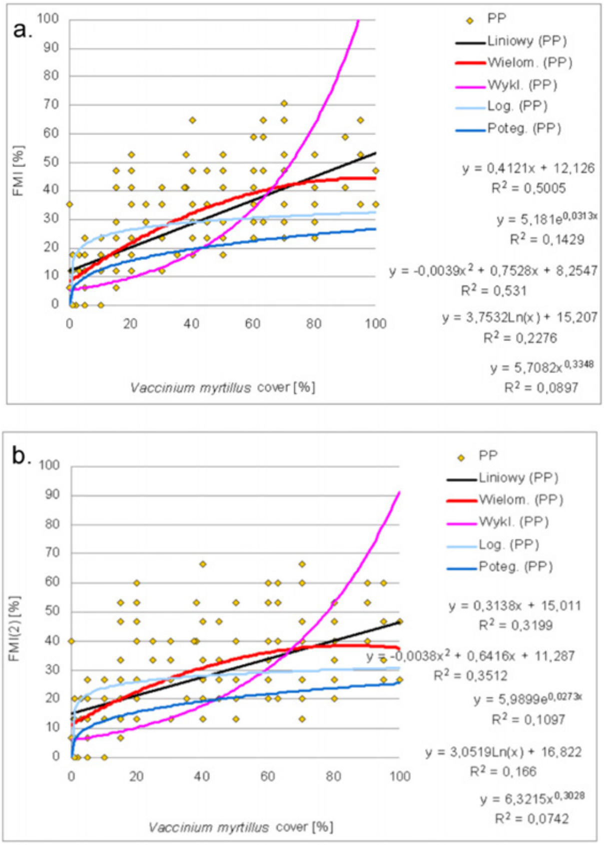


Fig. 70. Chosen regression models of relationship between *Vaccinium myrtillus* cover and Forest Maturity Index in recent forests of *Peucedano-Pinetum* type: a – *Vaccinium myrtillus* cover is included in FMI, b – *Vaccinium myrtillus* cover is excluded from FMI

Ryc. 70. Związek funkcjonalny pokrycia *Vaccinium myrtillus* i wskaźnika dojrzałości lasu (FMI) w lasach typu boru (*Peucedano-Pinetum*): a – *Vaccinium myrtillus* wchodzi do FMI, b – *Vaccinium myrtillus* jest wyłączone z FMI

In the case of mixed oak-pine forests the relation of the FMI with the *Vaccinium myrtillus* cover is weak (Fig. 71a), but of the same character as in case of pine forests. When the modified FMI is considered all models examined are not statistically significant (Fig. 71b). This result indicates a limited role of *Vaccinium myrtillus* during the regeneration of post-agricultural mixed oak-pine forest.

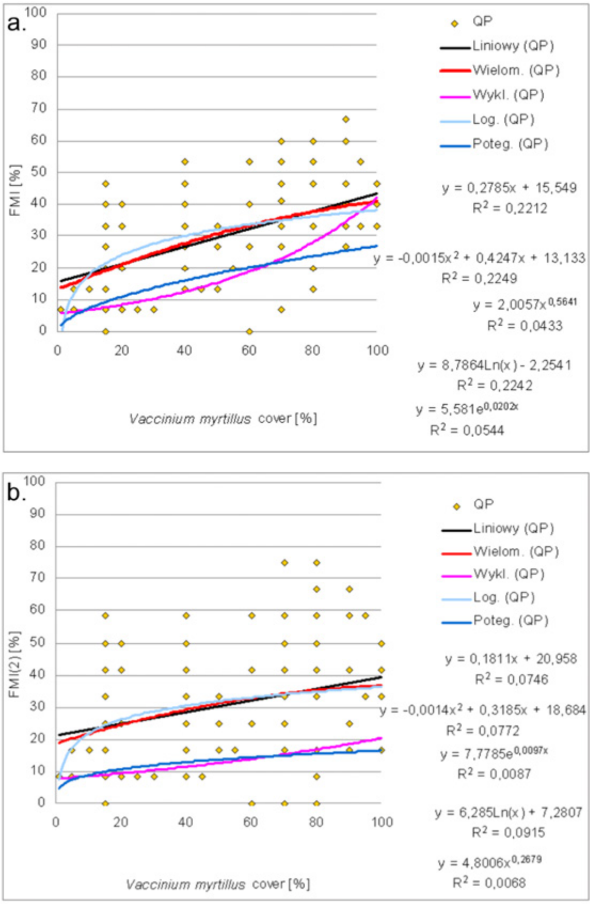


Fig. 71. Chosen regression models of relationship between *Vaccinium myrtillus* cover and Forest Maturity Index in recent forests of *Querco-Pinetum* type: a – *Vaccinium myrtillus* cover is included in FMI, b – *Vaccinium myrtillus* cover is excluded from FMI

Ryc. 71. Związek funkcjonalny pokrycia *Vaccinium myrtillus* i wskaźnika dojrzałości lasu (FMI) w lasach typu boru mieszanego (*Querco-Pinetum*): a – *Vaccinium myrtillus* wchodzi do FMI, b – *Vaccinium myrtillus* jest wyłączone z FMI

5.4.5. GENERAL REMARKS ON THE SPREAD OF *VACCINIUM MYRTILLUS* IN THE POST-AGRICULTURAL PINE AND MIXED OAK-PINE FORESTS

- The regeneration of the bilberry population in the recent post-agricultural pine forests is generally slow; even forests of approximately 230 years of persistence show lower spread of this species in comparison with the ancient forests.

- In the mixed oak-pine forests the regeneration of bilberry is faster than in the typical pine forests.
- The results show the relationship of the *Vaccinium myrtillus* cover in the recent forest upon the distance between the regenerating patch and the fragments of the ancient forests, in which the species could persist, and thereafter could spread again from there.
- The relation of the bilberry spread with the distance to the ancient forest appears to have a complex character, probably resulting from the various ways of *Vaccinium myrtillus* propagulae dispersal. This species is very strongly endozoochorous. Most probably, the transmitting factors are divided into groups distinctly differing as to the capacity of movement. Thus, possibly, transport over small distances is due to small animals, moving on the ground, while transport over larger distances is performed by the truly mobile animals, such as birds and bigger mammals (Atlegrim 2005; Schaumann, Heinken 2002).
- It is highly probable that changes in the soil due to ploughing cause the slow return of bilberry (Ingestad 1973; Mäkipää 1999; Ihalainen et al. 2002). Such a conclusion can be deduced from the comparison of data from the investigated recent forests on post-agricultural land with a few cases of the recent forests without the plough horizon in the soil. The fragments of recent forests, which have not been cultivated when there had been no forest there (16 such cases were identified and described, eight in pine forests and eight in mixed oak-pine forests) display higher *Vaccinium myrtillus* cover compared to the post-agricultural forests of the same persistence. This applies equally to pine and mixed oak-pine forests.
- When analysing the *Vaccinium myrtillus* cover in the particular categories distinguished both in terms of persistence and of distance to the ancient forest, one ought to pay attention not only to the average values, but, first of all, to the cases of relatively high values. One should namely be aware that even in optimum conditions in terms of persistence and distance, there might have been circumstances, due to which *Vaccinium myrtillus* attained lower cover. These might be both mechanical destructions and consequences of fire, but also the biocoenotic causes, including, in particular, the shading of the surface by the growing trees and shrubs (Nieppola 1992; Storch 1993; Głowacki 1999; Ihalainen et al. 2002; Kalinowski 2004; Nielsen et al. 2007). Hence, lower values of the *Vaccinium myrtillus* cover in certain situations do not have a bigger significance for the studied relations (while pushing down the average), the high values being, instead, worth special attention. They, namely, define the upper limit of regeneration possibilities. In addition, there may be cases, in which the values stand-off from the other ones may simply correspond to erroneous assumptions as to persistence or distance.

- The results suggest that in typical pine and mixed oak-pine forests the possibility of *Vaccillum myrtillus* regeneration in the recent forests is higher on richer and more humid places, sometimes expressed as micro-habitat differentiation.
- Spatial spread of *Vaccinium myrtillus* is a very important process in the regeneration of natural floristic composition and the structure of pine forests. This concerns also, but to a lesser degree, the mixed oak-pine forests (Gądziński 1967; Grochowski 1976; Jäderlund et al. 1996; Parlane et al. 2006).

5.5. RECOVERY OF ANCIENT FORESTS SPECIES

Based on the frequency of species in ancient and recent forests the groups of species were identified, with preference for ancient forests (see Chapter 4). These species groups served to formulate (see Section 5.1) the synthetic indicator, referred to as the Forest Maturity Index (FMI). The FMI allows for the assessment of regeneration degree of a recent post-agricultural forest patch. In Sections 5.2 and 5.3 the relationship was considered of the FMI value upon the distance to ancient forest, while in Section 5.4 the analysis was presented of relation between the *Vaccinium myrtillus* spread and this variable in the pine and mixed oak-pine forests. In this section the problem whether the recovery of other species, composing the FMI depends on the distance to ancient forest will be considered.

5.5.1. RECOVERY OF SPECIES FROM THE FMI COMPOSITION IN THE PINE FORESTS

The FMI indicator in the pine forests (*Peucedano-Pinetum*) accounts for the presence of *Vaccinium myrtillus* in a given patch with medium or high cover (the very presence not being accounted for), along with the potential share of 15 other species (see Table 21). Not all of these species can be analysed in the recent forests, since some of them appear there rarely. Thus, of the list of 15 species seven were selected – the ones appearing in the recent forests sufficiently frequently to study them in terms of the distance to ancient forest. These species are: *Calamagrostis arundinacea, Calluna vulgaris, Convallaria majalis, Frangula alnus, Hylocomium splendens, Luzula pilosa, Vaccinium vitis-idaea*. The analysis is based on the set of 202 phytosociological relevés, of which 146 represent the recent forests, and 56 – the ancient forests, for comparison. The relevés from the recent post-agricultural forests were classified into three categories in terms of the persistence and into four categories in terms of the distance to ancient forest. This produced 12 categories – the additional, 13th category being constituted by the ancient forest. Alas, the numbers of relevés in the particular categories (see Fig. 72) are highly uneven, this being the consequence of the very different reach of various persistence forests and their specific spatial structure. There are only few older recent forests and they are mostly situated close to the ancient forests, while there are relatively many younger recent forests and they are primarily located far from the ancient forests.

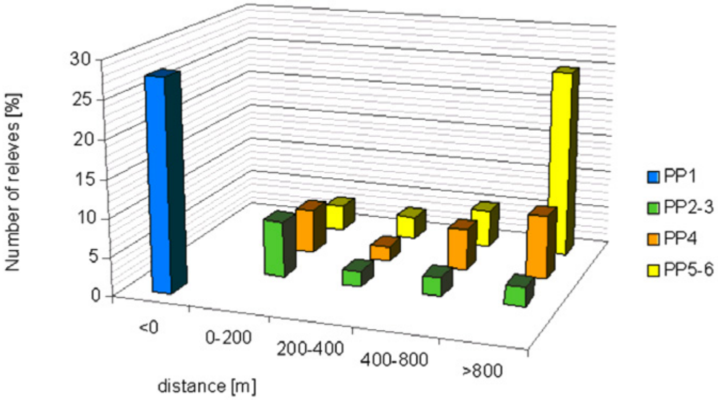


Fig. 72. Distribution of 202 phytosociological relevés of *Peucedano-Pinetum* forests in relation to forest category and distance from ancient forest

Ryc. 72. Podział 202 zdjęć fitosocjologicznych wykonanych w borach sosnowych (*Peucedano-Pinetum*) z uwzględnieniem stażu (kategorii) i odległości od "starego lasu"

For each of seven selected species the frequency (in %) was calculated in the patches belonging to 13 categories and presented in figures. On the basis of these figures one can observe that:

Convallaria majalis displays (Fig. 73a) clear dependence upon forest persistence and, at the same time, upon distance to ancient forest. In older recent forests it is most frequent in the patches situated the closest to the ancient forest, while it has not been registered in patches located more than 800 m away from the ancient forest. It appears much less frequently in the younger recent forests and that only in the patches situated in the direct neighbourhood of the ancient forest. This result may indicate the dominating role of vegetative reproduction in the case of this species. Lilies of the valley may also be sown by endozoochory, but one would expect then a farther spread away from the refuge. Hence, the results imply an unexpectedly slow colonization and 'short step' of species, at least within the pine forest habitat. For the sake of the toxicity of *Convallaria* fruits (and other parts as well) only some animals may contribute to this kind of dispersal. Rodents consume its seeds (Ehrlén, Eriksson 1993) but eat just a small proportion of the pulp and facilitate only short-distance dispersal. This is insofar important from the phytosociological point of view as this species is considered among those differential of *Peucedano-Pinetum* association. Its slow colonization rate in the post-agricultural forests means slow reconstruction of the characteristic species combination.

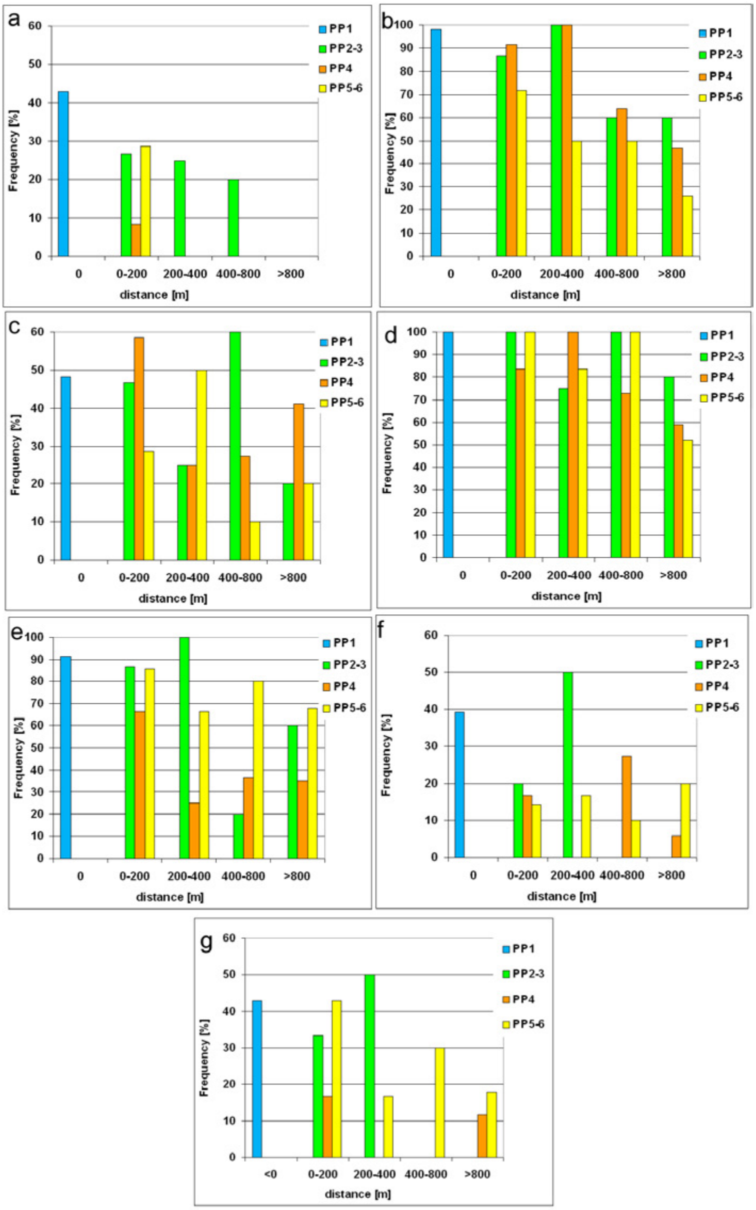


Fig. 73. Frequency of *Convallaria majalis* (a), *Calluna vulgaris* (b), *Frangula alnus* (c), *Vaccinium vitis-idaea* (d), *Hylocomium splendens* (e), *Calamagrostis arundinacea* (f), *Luzula pilosa* (g) in *Peucedano-Pinetum* forests in relation to forest category and distance from ancient forest

Ryc. 73. Frekwencja *Convallaria majalis* (a), *Calluna vulgaris* (b), *Frangula alnus* (c), *Vaccinium vitis-idaea* (d), *Hylocomium splendens* (e), *Calamagrostis arundinacea* (f), *Luzula pilosa* (g) w borach sosnowych (*Peucedano-Pinetum*) z uwzględnieniem stażu (kategorii) i odległości od "starego lasu".

In the case of species: *Calluna vulgaris* (Fig. 73b), *Frangula alnus* (Fig. 73c), *Vaccinium vitis-idaea* (Fig. 73d) and *Hylocomium splendens* (Fig. 73e) the relation between the frequency in the recent forests and the distance to ancient forest is visible, but the relationships are not so clear any more. Relatively the simplest is the relation for the anemochorous species of *Calluna vulgaris*, somewhat more ambiguous are the results for the endozoochorous species of *Frangula alnus* and *Vaccinium vitis-idaea*. For cowberry, Mäkipää (1999) demonstrated that its frequency (abundance) in boreal forests is mainly determined by environmental factors like moisture availability and light conditions and it demands less fertile sites than *V. myrtillus*. In the research of Wulf and Heinken (2008) *Frangula alnus* was classified as a species with preference for recent forests without migration limits as its propagulae are easily carried by birds (Dzwonko, Loster 1990). In the research in pine forests of Góras and Orczewska (2007) *Calluna vulgaris* was observed only in ancient forests.

For *Calamagrostis arundinacea* (Fig. 73f) and *Luzula pilosa* (Fig. 73g) the results do not show the relationship between the frequency and the distance to ancient forest, and that despite the visible lower frequency in recent forests. Butaye et al. (2001) not found any correlation between the distance from the refuge and the frequency of *Luzula pilosa* in recent forests. It was totally absent there. The relatively large difference in soil conditions between source and target patches may explain why this species is not able to colonize recent forest patches, even when situated next to occupied source patches.

5.5.2. RECOVERY OF SPECIES FROM THE FMI COMPOSITION IN THE MIXED OAK-PINE FORESTS

The values of FMI in the mixed oak-pine forests (*Querco-Pinetum*) were (see Table 21) based on the occurrence of twelve species and higher values of *Vaccinium myrtillus* cover. Eight of these species were selected for the study of relations between their frequency in recent mixed oak-pine forests and distance to ancient forests fragments, namely *Athyrium filix-femina, Convallaria majalis, Luzula pilosa, Maianthemum bifolium, Peucedanum oreoselinum, Polytrichastrum formosum, Pteridium aquilinum, Trientalis europaea*. The data constituted 98 relevés, of which 66 made in the recent forests and 32 in the ancient forests (Fig. 74). In view of lower relevés number, the division into categories was less detailed than in the case of pine forests. Thus, two categories of persistence and three categories of distance to the ancient forests were distinguished. For the so defined six categories of the recent forests and one category of ancient forest the frequency values of species listed were calculated, as presented in the figures. With full awareness of the relatively low number of relevés, some observations may, however, be forwarded:

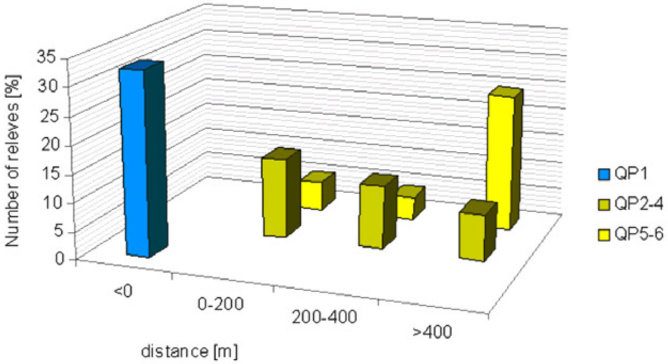


Fig. 74. Distribution of 98 phytosociological relevés of *Querco-Pinetum* forests in relation to forest category and distance from ancient forest

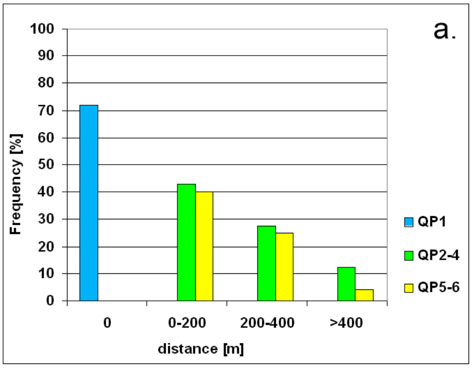
Ryc. 74. Podział 98 zdjęć fitosocjologicznych wykonanych w borach mieszanych (*Querco-Pinetum*) z uwzględnieniem stażu (kategorii) i odległości od "starego lasu"

- The results for *Convallaria majalis* (Fig. 75a) are clearly unambiguous and understandable. This species, similarly as in the pine forests (see Fig. 73a) displays a negative relation with distance to ancient forest, both in the older and younger recent forests. Lilly of the valley has better living conditions in mixed oak-pine forests, and therefore its higher frequency is registered in both ancient and recent forests. It also appears in the mixed oak-pine forests on the earlier stages of regeneration, but always close to the refuge in the ancient forest.
- Somewhat less unambiguous, but still clear relation with distance to ancient forest was observed, as well, for *Polytrichastrum formosum* (Fig. 75b) and *Maianthemum bifolium* (Fig. 75c), and, under certain conditions, for *Athyrium filix-femina* (Fig. 75d). In the research of Brunet (2007) as well as Wulf and Heinken (2008) *Maianthemum bifolium* was classified as a species with preference for ancient forests while *Athyrium filix-femina* as a species without any clear preference.

→

Fig. 75. Frequency of *Convallaria majalis* (a), *Polytrichastrum formosum* (b), *Maianthemum bifolium* (c), *Athyrium filix-femina* (d), *Pteridium aquilinum* (e), *Trientalis europaea* (f), *Luzula pilosa* (g), *Peucedanum oreoselinum* (h) in *Querco-Pinetum* forests in relation to forest category and distance from ancient forest

Ryc. 75. Frekwencja *Convallaria majalis* (a), *Polytrichastrum formosum* (b), *Maianthemum bifolium* (c), *Athyrium filix-femina* (d), *Pteridium aquilinum* (e), *Trientalis europaea* (f), *Luzula pilosa* (g), *Peucedanum oreoselinum* (h) w borach mieszanych (*Querco-Pinetum*) z uwzględnieniem stażu (kategorii) i odległości od "starego lasu"


a.
Frequency [%]
100
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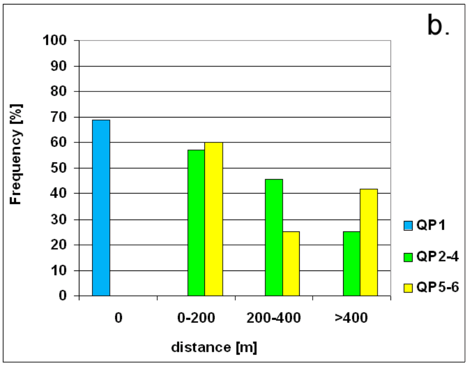
distance [m]
QP1
QP2-4
QP5-6


b.
Frequency [%]
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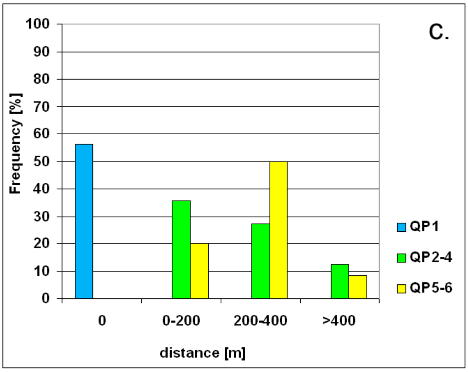
QP1
QP2-4
QP5-6


c.
Frequency [%]
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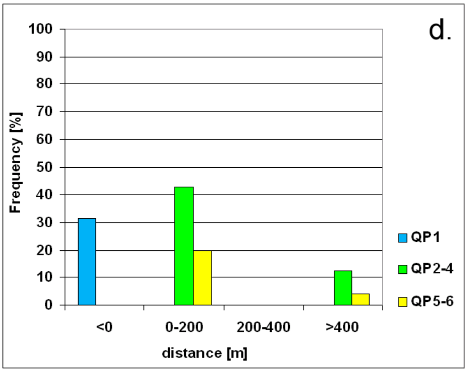
QP1
QP2-4
QP5-6


d.
Frequency [%]
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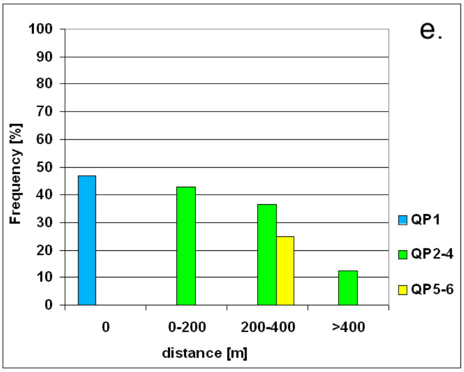
QP5-6


e.
Frequency [%]
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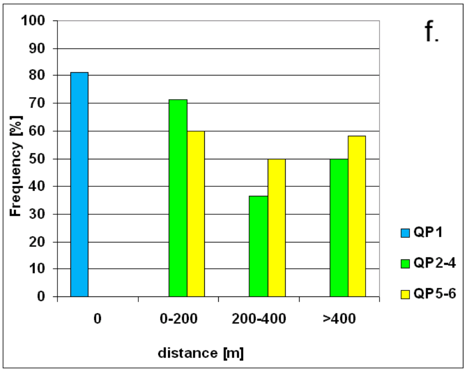
distance [m]
QP1
QP2-4
QP5-6


f.
Frequency [%]
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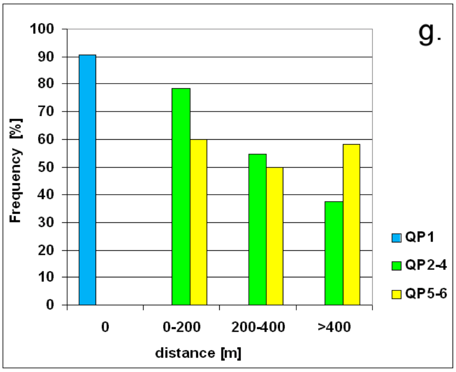
g.
Frequency [%]
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QP2-4
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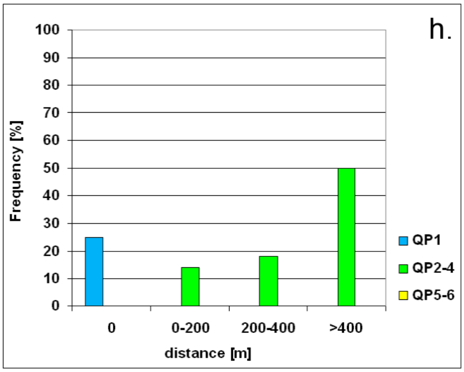
h.
Frequency [%]
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0
0-200
200-400
>400
distance [m]
QP1
QP2-4
QP5-6

- *Pteridium aquilinum* displays well pronounced relation with the distance to refuge in the older recent forests (Fig. 75e). Although its propagulae are easily carried by the wind (Dzwonko, Loster 1990; Hermy, Verheyen 2007), the species appears rarely in the younger recent forests, as if randomly. It produces large amounts of small spores in warm summers, but requires open ground for germination, which is often not available in recent forests (Hermy et al. 1999).
- *Trientalis europaea* (Fig. 75f) and *Luzula pilosa* (Fig. 75g) display quite clear correlation with distance to refuge in the case of older recent forests, while the dependence is weaker for forests having regenerated for a shorter time period. Yet, low number of samples does rather not allow for drawing of too far reaching conclusions. For comparison, in the research of Góras and Orczewska (2007) *Luzula pilosa* was observed only in the ancient forests or migrated into recent pine forests very slowly (Orczewska and Fernes 2011), while *Trientalis europaea was* classified as a species without any clear preference.
- Surprising results have been obtained for the perennial plant *Peucedanum oreoselinum* (Fig. 75h). This species appears in the ancient forests and only in the older recent forests and seems to prefer locations farther away from the ancient forest. Would this be linked with the former kind of use, which occurred in the ancient forests and in the older recent forests, and has not taken place in the younger forests?

5.5.3. RECOVERY OF SPECIES FROM THE FMI COMPOSITION IN THE LIME-OAK-HORNBEAM FORESTS

The values of the FMI in the lime-oak-hornbeam forests (*Tilio-Carpinetum*) were based on the occurrence of 19 species (see Table 21). Those more frequent in recent forests (*Ajuga reptans*, *Anemone nemorosa*, *Calamagrostis arundinacea*, *Convallaria majalis*, *Galeobdolon luteum*, *Milium effusum*, *Polygonatum multiflorum*, *Stellaria holostea*, *Viola reichenbachiana* and *Carpinus betulus* in the tree layer and in undergrowth) were analysed in relation to forest persistence and distance to ancient forest. Very limited number of relevés (just 23 in all recent forests) did not allow for the analysis similar in the form to that applied for pine and mixed oak-pine forests. For an introductory assessment the figures display the presence or absence of the particular species in the phytosociological relevés, ordered according to forest persistence (in nominal terms) and distance to ancient forest. It should be noted that the lime-oak-hornbeam forests are classified into two sub-associations: *Tilio-Carpinetum typicum* and *Tilio-Carpinetum calamagrostietosum*, and this fact should, as well, be somehow accounted for in any analysis (Fig. 76a). Additionally, the lime-oak-hornbeam forests are often represented by smallish patches situated in quite particular topographical circumstances (like, e.g., on slopes), which makes unambiguous identification of the past situations concerning forest presence, on the basis of historical maps, quite difficult.

After analysis of the figures presented the following conclusions might be drawn:

- There is a group of species, which comprises *Convallaria majalis* (Fig. 76b) – an autochorous and endozoochorous species, *Polygnatum multiflorum* (Fig. 76c) – an anemochorous and endozoochorous species, and *Aiuga reptans* (Fig. 76d) – an autochorous species, clearly concentrating in the older recent forests. If they appear in those of lower persistence, they are situated close to the respective refuges. This fact can be explained by the significant role of vegetative reproduction in case of all these species. Though *Convallaria majalis* and *Polygnatum multiflorum* belong to ornithochorous species the modest size of their fruits may reduce their availability to dispersal vectors (Bossuyt et al. 1999a). The similar results for these three species were observed by Z. Dzwonko (2001a) in southern Poland. In his research *Ajuga reptans* occurred in the ancient forests exclusively, but it was not the case in the studies carried out by Orczewska (2007, 2010a) or Bossuyt and Hermy (2000). The remarkably high colonization rate of *Polygnatum multiflorum* was observed by Grashof-Bokdam and Geertsema (1998).
- The subsequent group of species, formed by *Milium effusum* (Fig. 76e), *Galeobdolon luteum* (Fig. 76f), *Stellaria holostea* (Fig. 77a), *Viola reichenbachiana* (Fig. 77b) and *Anemone nemorosa* (Fig. 77c) display, as well, a preference for the older recent forests, located closer to the respective refuges, but they can also appear in younger recent forests and forests located farther away from the refuges. This group features also good capacity of vegetative reproduction, the two latter species being characterised by myrmecochory. Species with this kind of dispersal mode revealed also significantly slower migration in other studies (Hermy, Stieperaere 1981; Dzwonko, Loster 1988; Matlack 1994; Brunet, von Oheimb 1998; Dzwonko 2001; Verheyen, Hermy 2001; Verheyen et al. 2003b; Baeten et al. 2009; Orczewska 2010a). However, in the research of Orczewska concerning alder woods some of these species did not show colonisation limits i.e. *Anemone nemorosa, Milium effusum, Stellaria holostea.* Faliński and Canullo (1985) noticed high colonization rate of *Anemone nemorosa* (600 m in 20 years) on post-argicultural land in Bialowieża Forest.

Relation between appearance of *Calamagrostis arundinacea* and distance to refuge can hardly be demonstrated (Fig. 77d). Two elements, though, ought to be taken into account. First, this species propagates its seeds through anemochory and epizoochory, and so larger dispersal distance is fully possible. Second, this species is not closely attached to the lime-oak-hornbeam forests – it appears also in pine forests, and, especially, in mixed oak-pine forests. Hence, its refuges may be constituted also by other kinds of communities.

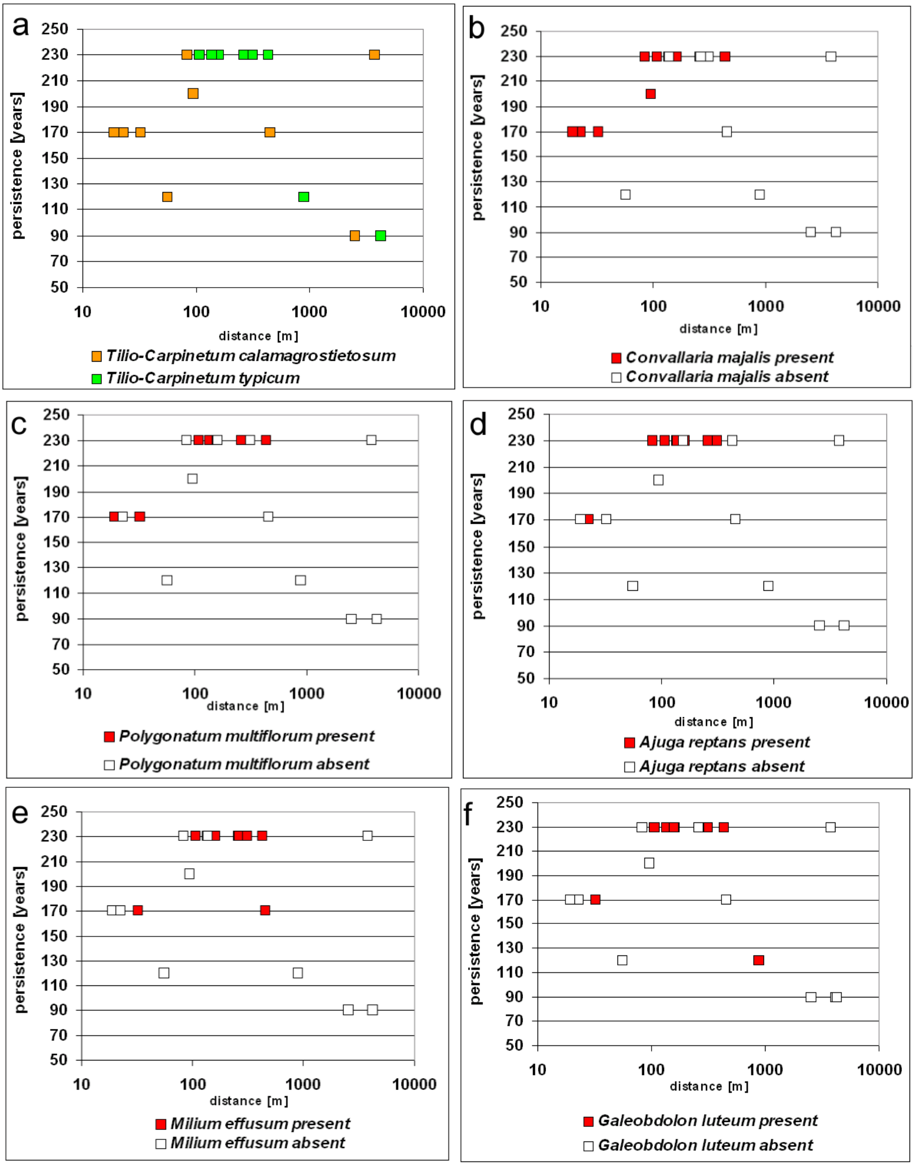


Fig. 76. Distribution of phytosociological relevés of *Tilio-Carpinetum* forests (a) and presence of *Convallaria majalis* (b), *Polygonatum multiflorum* (c), *Ajuga reptans* (d), *Milium effusum* (e), *Galeobdolon luteum* (f) in relation to persistence and distance from ancient forest

Ryc. 76. Analiza przynależności zdjęć do podzespołów (a) oraz występowanie *Convallaria maialis* (b), *Polygonatum multiflorum* (c), *Ajuga reptans* (d), *Milium effusum* (e), *Galeobdolon luteum* (f) we wtórnych lasach grądowych (*Tilio-Carpinetum*) w zależności od stażu i odległości od "starego lasu".

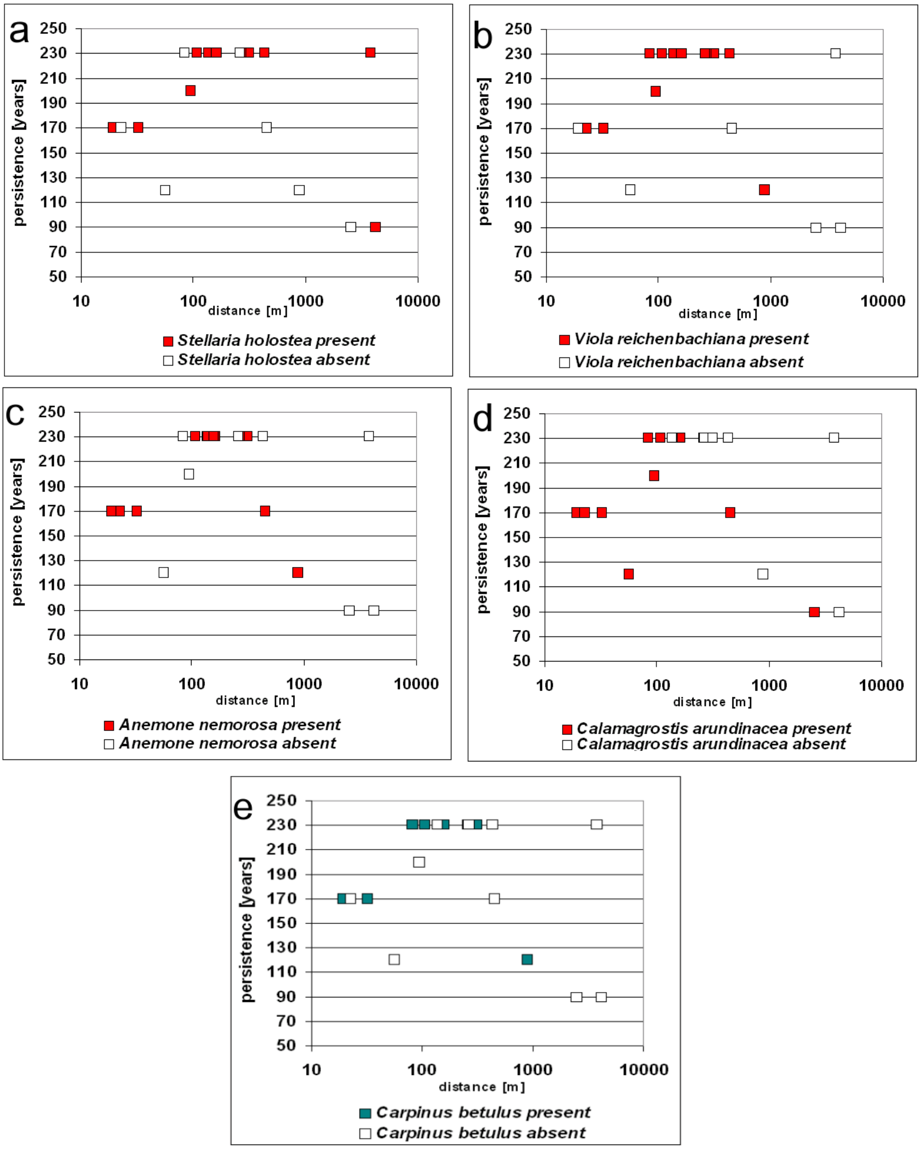


Fig. 77. Presence of *Stellaria holostea* (a), *Viola reichenbachiana* (b), *Anemone nemorosa* (c), *Calamagrostis arundinacea* (d), *Carpinus betulus* (as a tree) (e) in *Tilio-Carpinetum* forests in relation to persistence and distance from ancient forest

Ryc. 77. Występowanie *Stellaria holostea* (a), *Viola reichenbachiana* (b), *Anemone nemorosa* (c), *Calamagrostis arundinacea* (d), *Carpinus betulus* (jako drzewo) (e) we wtórnych lasach grądowych (*Tilio-Carpinetum*) w zależności od stażu i odległości od "starego lasu"

A tree species that is fundamental for the lime-oak-hornbeam forests, *Carpinus betulus*, is thought to display a connection with distance to the respective refuges (Fig. 77e). This species was not promoted in forests by planting. It can therefore be assumed that the spread of hornbeam is spontaneous. Despite the fact that it is an anemochorous species, its expansion in the recent forests is limited. It may be caused by its habitat requirements – *Carpinus* avoids acid soils (Tomanek 1997) that might occur in the sites with pine litter.

5.5.4. GENERAL REMARKS ON SPATIAL DISTRIBUTION AND RECOVERY OF SPECIES COMPOSING THE FMI IN RECENT FORESTS

There are a number of species typical of ancient forests that return to the recent forests quicker, when a given forest patch is located closer to the respective refuge. This is quite straightforward for the species reproducing mainly in vegetative manner, but occurs, as well, for the species, which reproduce in various generative manners.

The recent forest persistence and the distance to the refuge – even though theoretically two independent variables – affect actually in a similar way the ancient forests species returning to the recent forests. Detailed analysis would most probably indicate the species, for which recovery rate depends mainly on the forest persistence, and those, for which the distance to the refuge is more important, but, in general terms, these two factors produce a conjoint effect.

Generally, all species composing the FMI are typical of ancient forests (so included in the characteristic species combination) with more or less slow colonization rate in recent forests. They can therefore be called moderate re-colonizers. One can distinguish two groups of species, composing the FMI:

- moderate colonisers – the species, which may appear already within a relatively short regeneration time period, and also at bigger distances to the refuge;
- slow colonisers – the species, which return to the recent forests slowly, very clearly moving from the refuge towards a given type of community; these are the species of a ’short step’.

The above classification into the fast and moderate colonisers is shown in Table 26. We should emphasise here, though, that the classification shown has a relative character – it splits with respect to the rate of return of species from the FMI list corresponding to a given type. Comparing the regeneration rates of the forest types as a whole is a different matter.

Table 26. Species groups in the Forest Maturity Index sets distinguished according to colonization rate

Community type	Moderate colonizers	Slow colonizers
Pine forest (*Peucedano-Pinetum*)	Frequent species: *Calamagrostis arundinacea, Calluna vulgaris, Frangula alnus, Hylocomium splendens, Luzula pilosa, Vaccinium vitis-idaea*. Rare species: *Molinia caerulea, Peucedanum oreoselinum(?), Pohlia nutans(?)*.	Frequent species: *Convallaria majalis*; *Vaccinium myrtillus* within typical migration range. Rare species: *Athyrium filix-femina, Oxalis acetosella, Scorzonera humilis(?), Trientalis europaea(?), Vaccinium uliginosum*.
Mixed oak-pine forest (*Querco-Pinetum*)	Frequent species: *Luzula pilosa, Maianthemum bifolium, Polytrichum formosum, Trientalis europaea*. Rare species: *Molinia caerulea*(?).	Frequent species: *Convallaria majalis, Athyrium filix-femina (?), Pteridium aquilinum (?), Peucedanum oreoselinum (?)*; *Vaccinium myrtillus* within typical migration range (it is not so slow as in pine forests). Rare species: *Polygonatum odoratum, Sciuro-hypnum oedipodium, Scorzonera humilis*.
Lime-oak-hornbeam forest (*Tilio-Carpinetum*)	Frequent species: *Calamagrostis arundinacea*.	Frequent species: *Convallaria majalis, Ajuga reptans, Polygonatum multiflorum, Milium effusum, Geleobdolon luteum, Stellaria holostea, Anemone* nemorosa, *Viola reichenbachiana*; *Carpinus betulus* (tree species with long period before reproduction start). Rare species: *Galium odoratum, Hepatica nobilis, Lathyrus vernus, Ranunculus lanuginosus, Atrichum undulatum, Hypnum cupressiforme, Lilium martagon, Phyteuma spicatum, Scrophularia nodosa*.

6. ECOLOGICAL CHARACTERISTIC OF THE HERB LAYER IN ANCIENT AND RECENT FORESTS

6.1. ECOLOGICAL INDICATOR VALUES AS STUDY TOOLS

Every plant species has a specific set of properties and features, which shape its ecological requirements and allow for the occupation of a definite environment. These are, in particular, the properties of external and internal structure, the life form, the biology of reproduction, the way of dispersal, as well as life strategy type. Such adaptations to the environment cause that plant species have definite spectra of appearance in the physico-geographical environment. This is the fundamental assumption behind geobotanical phytoindication (from Greek – *phyto* – plant, and Latin – *indico* – to point out), and especially of the ecological scales of plant indicator values (Ellenberg et al. 1991; Zarzycki et al. 2002, Roo-Zielińska, Solon 1991; Roo-Zielińska 2004; Roo-Zielińska et al. 2007). The majority of the contemporary phytoindication studies is constituted by the so-called ’lists of ecological indicator values of plant species’. These are the lists of species along with the values, expressing the reaction (ecological amplitude) of species to definite habitat factors, or with the symbols, defining the feature of species - the adaptation to the environment (like its life form or anatomic structure). Among those, the scale of Ellenberg indicator values (see Ellenberg et al. 1991) is the most popular. This scale was adopted in the present study for the requirements assessment of the forest communities with respect to selected elements of the natural environment.

Table 27. List of diagnostic features and indicator values of ecolgical scales applied for characteristic of forest communities

Symbol	Classification and scales	Original references
	Diagnostic features	
AB	anatomical structure type	Ellenberg (1979)
LF	life form	Raunkier (1934), Zarzycki (2002)
VT	dispersal mode	Frank, Klotz (1990)
STR	life strategy type	Grime (1979); Frank, Klotz (1990), Falińska (1997)
	Indicator values	
L	intensity of light	Ellenberg et al. (1991)
F	soil moisture	Ellenberg et al. (1991)
R	soil acidity	Ellenberg et al. (1991)
N	nitrogen content in the soil	Ellenberg et al. (1991)

In our study altogether eight features were analysed, classified in two groups (Table 27). The first group concerns morphological-anatomic adaptations:

- anatomic structure type (AB),
- life form (LF),
- seed dispersal mode (VT),
- life strategy type (STR).

The second group is linked with habitat requirements, the so-called ecological amplitude, that is – the spectrum of appearance of plant species in definite conditions of the physico-geographical environment. In the present study the nine-degree Ellenberg scale was applied with regard to four environmental factors:

- light intensity (L),
- soil moisture (F),
- soil reaction (R),
- supply in nitrogen (N).

The phytosociological relevés, grouped within the forest types and categories (see the division presented in Chapter 4) constituted the basic starting material for determination of the scope of ecological requirements of the forest communities analysed.

For each morphological-anatomic adaptations and all indices of ecological requirements, separately for each phytosociological relevé, percentage share of species number representing a given feature class have been calculated. On this basis mean values for all patches, persistence categories and forest types (pine forests, mixed oak-pine forests and lime-oak-hornbeam forests) were calculated.

6.2. CLASSIFICATION OF SPECIES ON THE BASIS OF THEIR ADAPTIVE FEATURES AND ECOLOGICAL AMPLITUDE

Anatomic structure type [AB]

Depending upon the soil moisture in a given place, only such plants can live there, whose water economy and the corresponding ecological constitution ’fit‘ the local conditions – that is: the ones that have an appropriate set of adaptive features. On this basis, Ellenberg (1979) classified plant species into six groups with regard to water as habitat factor (Table 28).

Table 28. Plant classifications based on anatomic-morphological, physiological and environmental diagnostic features

Symbol	Name	Characteristic
Anatomical structure types [AB]		
1	hydromorfic species	aquatic plants
2	helomorfic species	marsh plants
3	hygromorphic species	plants growing on moist soils
4	mesomorfic species	plants growing on fresh soils
5	scleromorphic species	plants growing on dry soils
6	succulents	plants with developed water tissue
Life forms [LF]		
M	megaphanerophytes	trees normally growing more than 5 m tall
N	nanophanerophytes	shrubs or small trees, 0,5-5 m tall
Ch	woody chamaephytes	dwarf shrubs with buds >25 cm above the ground
C	herbaceous chamephytes	herbs with buds < 25 cm above the ground
H	hemicryptophyte	buds near the ground
G	geophytes	buds within the soil, often with storage organs
T	therophytes	short-lived, annual
Hy	hydrophytes	aquatic plants with normally submerged buds
li	lianas	rooting in the soil but leaning on other plants
ep	epiphytes	plants not rooting in the soil
Basic dispersal modes [VT]		
a	myrmecochores	seed are dispersed by ants
e	epizoochores	seeds are dispersed by attachment to the surface of animals
v	endozoochores	seeds are dispersed by the agency of animals, typically and especially after passage of non-digestable fruits or seeds through the gut.
s	autochores	plant distributed by its own mobility, some action of the parent plant is the chief force for dissemination, e.g., the mechanical projection of seeds in jewelweed
w	anemochores	seeds or fruits are dispersed by wind
Life strategy types [STR]		
c	competitors	plant species that thrive in areas of low intensity stress and disturbance and excel in biological competition; mainly trees and shrubs
s	stress tolerators	plant species that live in areas of high intensity stress and low intensity disturbance; often found in stressful environments (deep shade, nutrient deficient soils, and extreme pH levels)
r	ruderal species	plant species that prosper in situations of high intensity disturbance and low intensity stress; fast-growing and rapidly complete their life cycles, and generally produce large amounts of seeds. Plants that have adapted this strategy are often found colonizing recently disturbed land, and are often annuals.
cr	mixed type	plant species living in areas of low intensity stress and competition is limited by disturbance
sr	mixed type	plant species living in low disturbed areas
cs	mixed type	plant species living in relatvely not disturbed areas with moderate intensity stress
csr	mixed type	plant species living in areas with limited competition level influenced by moderate stress and disturbances

Life form [LF]

Life forms are the morphological types of plants, constituting their adaptation to the environment. Most often the ecological classification of plants by Raunkiaer (1934) is referred to, applied, in particular, by K. Zarzycki (2002). The fundamental criterion of this classification is location of the renewal buds with respect to the soil surface, enabling them to survive adverse climatic conditions (e.g. frost or drought). Based on the species shares of various life forms the biological spectrum of plant community is determined. These spectra define the adaptation degrees of plants to the existing climatic conditions and may be useful in the comparative analysis of plant communities, depending upon the diverse environmental conditions (Table 28).

Seed dispersal mode [VT]

Depending upon the basic factors: the maternal plant forces, propagulae weight and the use of ballistic mechanisms participating in the spread of them. In our study five of them, occurring most frequently in the analysed forest communities were taken into account (Table 28).

Life strategy types [STR]

The term of life strategy refers to the genetically conditioned characteristics of individuals, enabling the species to persist in a definite environment. These are: size, type of growth, rate of ontogenetic development, fertility, longevity and the fundamental living processes – persistence, growth, development and reproduction (Grime 1977; Falińska 1997). The shares of species representing various kinds of strategies in a given plant community provides information on the chances of further existence in conditions of definite natural and man-made influences (Table 28).

Light [L]

The scale of light intensity (L) indicates the range of relative light intensity of the places, where a given species lives (Table 29).

Moisture [F]

The scale of moisture (F), expresses the ecological reaction of species with respect to substratum moisture in the growing season. Although moisture, as an ecological factor, is subject to very significant fluctuations, yet, numerous studies of the mutual relations between plant communities and the groundwater level allow for determining the total demand of plants, and hence for adoption of a reliable graduation of demand of the particular species regarding substratum moisture (Table 29).

Table 29. Ecological indicator values (according to Ellenberg et al. 1991)

Indicator value	Light intensity [L]	Soil moisture [F]	Soil acidity [R]	Soil nitrogen content [N]
1	deep shade (plant species growing only in very shady places)	extremely dry soils	extremely acidic soils (plant species never occuring on neutral and alkaline soils)	extremely poor soils
2	between 1 and 3	between 1and 3	between 1 and 3	between 1 and 3
3	shade (plant species occuring chiefly in shady places)	dry soils (plant species occuring more often on dry than on fresh soils; never on moist soils)	acidic soils (plant species occuring very rarely on alkaline soils)	poor soils, (plant species can occur on moderately rich in nitrogen content soils, and very rarely on rich soils)
4	between 3 and 5	between 3 and 5	between 3 and 5	between 3 and 5
5	half-shade (plant species growing often in half-shade)	fresh soils (plant species never occuring on wet and extremely dry soils)	moderately acidic soils (plant species occuring very rarely on exteremely acidic, neutral and alkaline soils)	moderately rich (plant species occuring very rarely on poor and rich in nitrogn content soils)
6	between 5 and 7	between 5 and 7	between 5 and 7	between 5 and 7
7	moderate light (plant species occuring chiefly in full light)	moist soils (plant species never occuring on wet soils)	moderately acidic and moderately alkaline soils (plant species never occuring on extremely acidic soils)	rich soils (plant species sometimes occuring on moderately rich soils, but only occasionally on low nitrogen content soils)
8	light (plant species occuring chiefly in full light)	between 7 and 9	between 7 and 9	extremely rich soils (plant species are indicators of high nitrogen content in the soils)
9	full light (plant species growing only in full light)	wet, heavy soils	alkaline soils (plant species as indicators of rich calcium soils)	extremely fertile soils (plant species as indicators of nitrogen fertlization)

Soil reaction [R]

The scale of soil reaction (R) expresses the ecological requirements of species in relation the soil acidity (pH), see Table 29.

Nitrogen [N]

The nitrogen scale (N) expresses the ecological reaction of species in relation the soil nitrogen content see Table 29.

6.3. ECOLOGICAL CHARACTERISTIC OF FOREST COMMUNITIES TYPES AND THEIR CATEGORIES

6.3.1. ECOLOGICAL CHARACTERISTICS OF THE PINE FORESTS (*PEUCEDANO-PINETUM*)

Anatomic structure type [AB]

Analysis of phytosociological relevés, encompassing all pine forests (Fig. 78) shows a strong domination of mesomorphs (roughly 67%), with scleromorphs constituting also quite a significant group (around 32%). The helomorphs and hygromorphs add up to just a fraction of one percent. This, however, is understandable, since the association of *Peucedano-Pinetum* encompasses fresh and moderately dry pine forests.

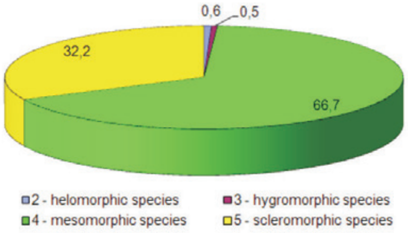


Fig. 78. The percentage share of plant species number (in total number) with given anatomical structure type (AB) in pine forests

Ryc. 78. Udział gatunków o różnej budowie anatomicznej (AB) w borach sosnowych

As we consider the differences between the pine forests categories, the shares of mesomorphs range from about 61% in the category PP3 up to some 77% in the category PP6. At the same time, in the latter category the share of scleromorphs is the lowest (at roughly 23%), and complete absence of hygromorphs and helomorphs was observed, while their marginal share (at about 2%) was noted first of all in the first category (PP1) – Fig. 79.

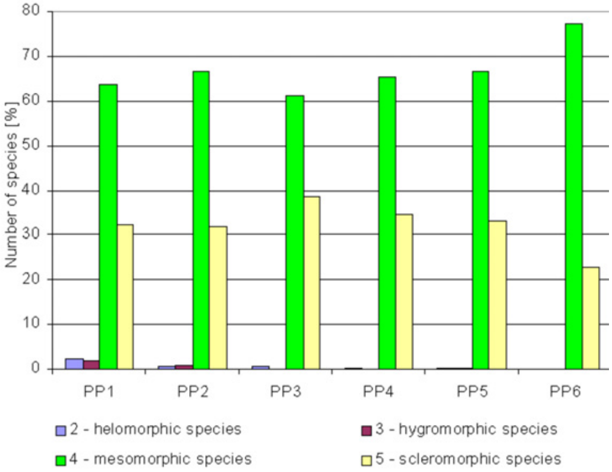


Fig. 79. The percentage share of plant species number (in total number) with given anatomical structure type (AB) in the categories of pine forests
Ryc. 79. Udział gatunków o różnej budowie anatomicznej (AB) w kategoriach borów sosnowych

Life form [LF]

The average values of the percentage shares of species number in the pine forests as a whole indicate the domination of three life forms: hemicryptophytes (around 27%), tree-like chamephytes – 25%, as well as the seedlings of megaphanerophytes – approximately 22%. Quite a significant group is also constituted by therophytes – at around 12%. The remaining life forms amount to a small share – these are geophytes, nanophanerophytes (shrubs and low trees), and also herbaceous chamephytes (Fig. 80).

Among the life forms, there are three: (1) tree-form chamephytes (dwarf shrub and half-shrubs), (2) geophytes and (3) herbaceous chamephytes that most distinctly differentiate the pine forests categories (Fig. 81).

The regularity is observed of the decreasing share of tree-form chamephytes, that is – first of all dwarf shrub – as we pass from the ancient forests to the recent stands with longer and shorter regeneration periods on post-agricultural sites. Thus, the share is the highest in the first category, PP1 (around 32%), and the lowest in the last category, PP6, amounting to only around 15%. This regularity is understandable, since the share of dwarf shrub in the pine forest is due primarily to the contribution of *Vaccinium myrtillus, Vaccinium vitis-idaea, Calluna vulgaris,* and somewhat less frequently *Chimaphila umbellata, Orthilia secunda, Vaccinium uliginosum*. These species are all more or less associated with the ancient forests (see Chapters 4 and 5), colonizing recent forests at various rate. They appear in the ancient forests in the complete set, and less frequently so in the recent forests – usually less frequently in the younger recent forests.

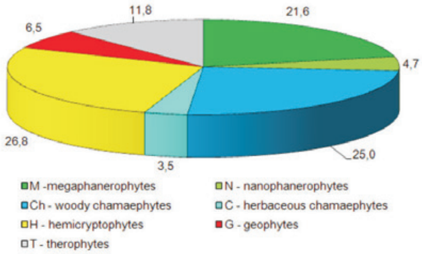


Fig. 80. The percentage share of plant species number (in total number) with given life form (LF) in pine forests
Ryc. 80. Udział gatunków o różnej formie życiowej (LF) w borach sosnowych

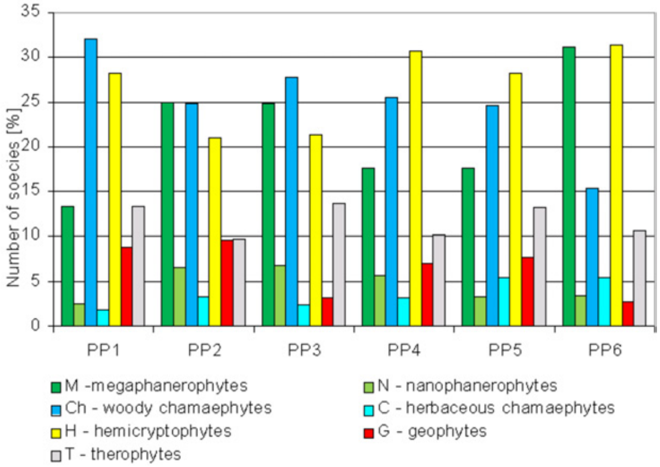


Fig. 81. The percentage share of plant species number (in total number) with given life form (LF) in the categories of pine forests
Ryc. 81. Udział gatunków o różnej formie życiowej (LF) w kategoriach borów sosnowych

A similar distribution is observed for geophytes, accounting for a limited share in the pine forests. This share is the highest (roughly 9-10%) in the first two categories, i.e. in the ancient forests and in the recent forests with a very long period since the post-agricultural land had been afforested, while being the lowest in the youngest category of recent forests (not quite 3% for PP6). The group of geophytes is formed in the pine forests by species featuring not too high frequencies, such as *Convallaria majalis, Maianthemum bifolium, Polygonatum odoratum, Pteridium aquilinum, Trientalis europaea, Oxalis acetosella*. The majority of these species is also associated with the ancient forests.

Herbaceous chamephytes display a different distribution. They constitute a small percentage in the fresh pine forests, but are the most numerous in the two last categories (above 5%), while being the least numerous in the category of ancient forests (less than 2% in PP1). This group of species is represented in the pine forests by not too frequently appearing *Diphasiastrum complanatum, Lycopodium annotinum, Lycopodium clavatum, Thymus serpyllum, Equisetum hyemale, Veronica officinalis*. None of these species is considered to be an ancient forest species (see Chapter 5). At the same time, though, it is worth noting that the first two are the species characteristic of the broadly conceived pine forests (*Vaccinio-Piceetea* class) or even for the proper pine forests (*Dicrano-Pinion* alliance).

Seed dispersal mode (VT)

In the pine forests as a whole there is domination of anemochores (roughly 53%). There is also a significant share of endozoochores (around 25%). Quite important groups are myrmecochores (around 12%) and autochores (roughly 10%) – Fig. 82.

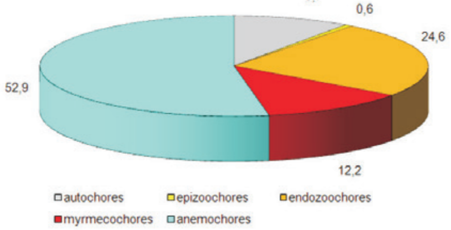


Fig. 82. The percentage share of plant species number (in total number) with given dispersal mode (VT) in pine forests
Ryc. 82. Udział gatunków o różnym typie rozsiewania w borach sosnowych

The percentage shares of species featuring three types of seed dispersal: myrmecochores, endozoochores and anemochores differentiate most effectively the categories of fresh pine forests and display quite regular downward or upward tendency along the categories (Fig. 83).

The species distributed by ants (myrmecochores) are relatively most numerous in the first three categories (PP1-PP3), with the shares ranging from roughly 13% to 14%. Their share is the lowest in the last category, PP6 (around 11%). This group is considered to comprise in the pine forests two very common species: *Melampyrum pratense* and *Luzula pilosa* and three much rarer ones: *Danthonia decumbens, Knautia arvensis, Luzula multiflora*. The two first are considered in some works to be ancient forest species (Hermy et al. 1999). In the framework of our study there has been demonstrated the association of *Luzula pilosa* with the ancient forests, and lack of such a relationship for *Melampyrum pratense*. Consequently, we deal with a partial connection between this group of species and the ancient forests.

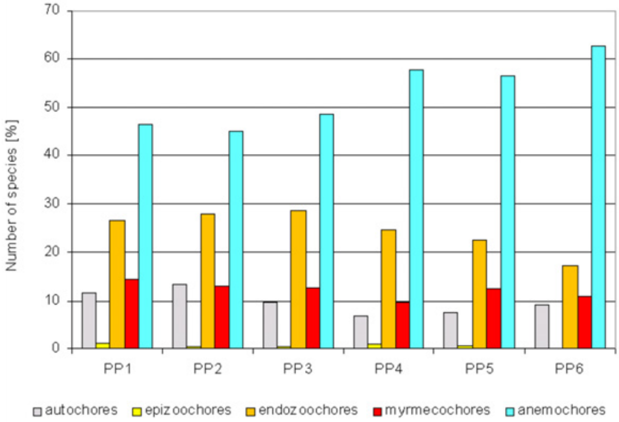


Fig. 83. The percentage share of plant species number(in total number) with given dispersal mode (VT) in the categories of pine forests
Ryc. 83. Udział gatunków o różnym typie rozsiewania w kategoriach borów sosnowych

The share of endozoochores is generally higher in the ancient forests and in the recent forest with long regeneration periods than in the recent forests of shorter persistence. In the first three categories the share ranges between around 27% to 29%, while in two categories of the recent forests, PP5, and especially so in PP6, it takes, respectively, the values of approximately 23% and 27%. Endozoochores of the pine forests comprise: two very common species, being also clearly linked with the ancient forests, namely *Vaccinium myrtillus* and *Vaccinium vitis-idaea*, then much less frequent in the pine forests, but typical of them - *Arctostaphylos uva-ursi, Rubus saxatilis, Vaccinium uliginosum*, and quite frequent in both ancient and recent pine forests *Sorbus aucuparia*, often planted in the forests – especially the recent ones – *Padus serotina*, as well as a number of species, which are more associated with the degenerate forms of pine forests, i.e. *Malus sylvestris, Pyrus communis, Rubus caesius, Rubus idaeus, Rubus nessensis, Sambucus racemosa, Fragaria vesca*. Thus, it can be seen that the group of endozoochores comprises both species that are linked with natural pine forests and with disturbed ones, occupying the sites on post-agricultural land.

The shares of anemochores are distinctly higher in the recent forests of shorter regeneration period than in the ancient forests and the recent ones having regenerated for a long-time period. In the three last categories of fresh pine forests (PP4-6), and particularly in the last category, the share of species dispersed by the wind is the highest (from approximately 57% to 63%), while it does not attain 50% in the first three categories. The list of anemochores appearing in the pine forests is long. It contains both species common for pine forests and the much less frequent ones. This group includes, in particular:

Calluna vulgaris, *Calamagrostis arundinacea*, typical of the ancient forests, *Pinus sylvestris, Betula pendula, Deschampsia flexuosa*, common both in the ancient and in the recent forests, as well as numerous grass species, displaying higher frequency in the recent forests, such as, for instance, *Festuca ovina, Agrostis capillaris, Anthoxanthum odoratum*, and *Rumex acetosella*, clearly more frequent in the recent forests. When considering the list of anemochorous species, one can notice that a part of them can also be distributed as endozoochores, this applying especially to grasses, whose seeds are eaten by herbivores, and then excreted in a completely different location.

Life strategy type [STR]

Two types of life strategy dominate – the mixed type *cs* (around 49%) and the competitive type *c* (32%). Quite a significant group is also constituted by species featuring the mixed type *csr* (roughly 16%). A relatively small group (only 3%) is constituted by the type *s*. (see Table 28, Fig. 84).

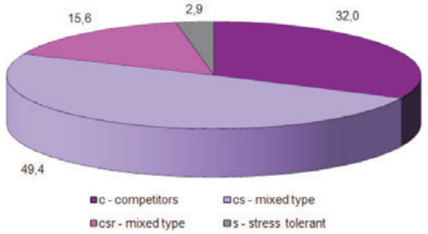


Fig. 84. The percentage share of plant species number (in total number) with given life strategy type (STR) in pine forests
Ryc. 84. Udział gatunków o różnym typie strategii życia borów sosnowych

Two types of plant life strategies, *c* and *cs*, most distinctly differentiate the categories of fresh pine forests (Fig. 85). The *cs* type is most numerous in the ancient forests (PP1: around 61%), and also in the recent forests with very long regeneration periods (PP2), while their share is the lowest in the category of recent forests with a very short period since afforestation of post-agricultural land, PP6 (roughly 40%). Among the species appearing in the pine forests, a lot belong to the *cs* type, some of them having essential importance for the pine forest phytocoenoses. In this group, species typical of the ancient forests include both the very commonly appearing *Vaccinium myrtillus, Vaccinium vitis-idaea, Calluna vulgaris*, and the rarer *Convallaria majalis, Peucedanum oreoselinum, Athyrium filix-femina, Molinia caerulea, Ledum palustre, Vaccinium uliginosum*. At the same time, this type of life strategy is characterised also by some species displaying higher frequency in the recent forests, such as the common ones – like *Deschampsia flexuosa, Dryopteris carthusiana, Lycopodium annotinum, Lycopodium clavatum*, or somewhat less frequent *Hieracium lachenalii, Dryopteris filix-mas, Stellaria graminea*.

A reverse distribution characterises species, representing the competitive type *c*. Their share is the highest in the category of the youngest recent forests (PP6: 41%), while being the lowest in the ancient forest category (PP1). Only few of these species are typical of ancient forests (*Calamagrostis arundinacea, Pteridium aquilinum, Solidago virgaurea*). Some are generally common in the pine forests, both in the ancient ones and in the recent (like the trees: *Pinus sylvestris, Picea abies, Betula pendula, Sorbus aucuparia*). Besides, this strategy type is represented by a large group of species to an extent incidental in the pine forests, appearing relatively rarely there, most often in the deformed stands (*Acer pseudoplatanus, Alnus incana, Calamagrostis epigejos, Carpinus betulus, Chamaenerion angustifolium, Cytisus scoparius, Dactylis glomerata, Deschampsia caespitosa, Fagus sylvatica, Galium mologo, Holcus lanatus, Hypericum perforatum, Knautia arvensis, Malus sylvestris, Padus serotina, Populus tremula, Pyrus communis, Quercus robur, Rubus caesius, Rubus idaeus, Rubus nessensis, Veronica officinalis*).

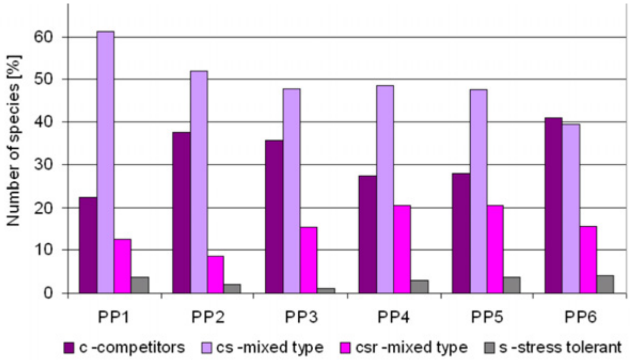


Fig. 85. The percentage share of plant species number (in total number) with given life strategy type (STR) in the categories of pine forests
Ryc. 85. Udział gatunków o różnym typie strategii życia w kategoriach borów sosnowych

Requirements to light intensity [L]

In the fresh pine forests, the indicators of moderate light (L 6-7: roughly 49%) and moderate shade (L 4-5: roughly 33%) have the highest share. A significant percentage is also constituted by the species of full light (L 8-9: around 14%). The shade-tolerant species (L 2-3) account for around 5%, while the smallest share, just a fraction of one per cent, falls upon the species of deep shade (L 1) – Fig. 86.

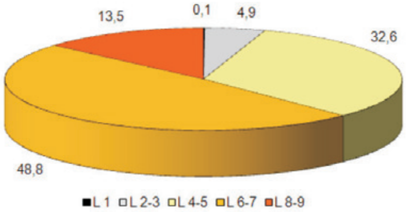


Fig. 86. The percentage share of plant species number (in total number) as indicators of light intensity (L) in pine forests

Ryc. 86. Udział liczby gatunków o różnych wymaganiach względem naświetlenia (L) borów sosnowych

The light intensity indicators differentiate poorly the pine forests categories (Fig. 87). Yet, it can be noticed that the share of species tolerating shade (L 2-3) is definitely the highest (roughly 7%) in the ancient forest category. The list of species, appearing in the pine forests with the value L equals 2-3 is composed of *Luzula pilosa, Athyrium filix-femina, Maianthemum bifolium, Monotropa hypopitys, Lycopodium annotinum, Dryopteris filix-mas, Epipactis helleborine, Fagus sylvatica*. The three first of these species (the first one being quite common) are the ancient forest species, while the remaining ones, appearing not too frequently, or rarely, do not display such an association.

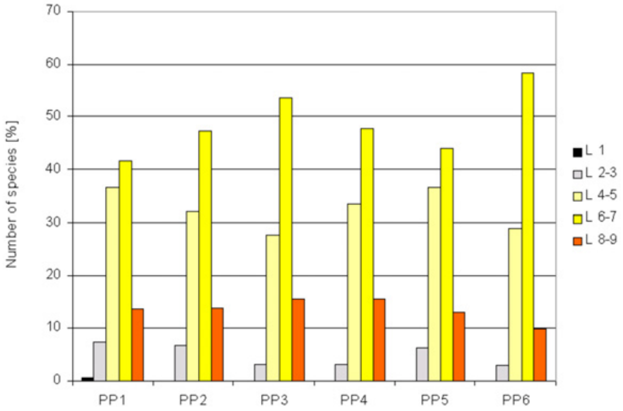


Fig. 87. The percentage share of plant species number (in total number) as indicators of light intensity (L) in the categories of pine forests

Ryc. 87. Udział gatunków o różnych wymaganiach względem naświetlenia (L) w kategoriach borów sosnowych

On the other hand, in the recent forests featuring the shortest regeneration period, the highest is the share of species indicative of moderately light sites (L 6-7). The list of these species, registered in the pine forests, comprises 48 items. This list includes both very common species, like *Pinus sylvestris,* *Deschampsia flexuosa, Betula pendula*, *Sorbus aucuparia*, and – in a vast majority – the rarely appearing ones. The group considered contains some species, featuring preference for the ancient forests (e.g. *Calamagrostis arundinacea, Scorzonera humilis, Peucedanum oreoselinum*), and much more of those that do not display such a relation (e.g. *Pinus sylvestris, Quercus robur, Betula pendula*, *Sorbus aucuparia*), or even display an association with the recent forests (e.g. *Deschampsia flexuosa, Festuca ovina, Padus serotina, Rubus idaeus, Agrostis capillaris*). The latter species dominate in the recent forests.

Mean values of L indicator are the lowest in the case of PP1 and PP2 categories (5.8 and 5.9 respectively) and the highest for PP6 category (6.2), but differences are not statistically significant. It is worth to underline that the ancient forests (category PP1) are characterised by the widest range of values, and the highest standard deviation of the mean, while the group of the least persistent forests (PP6) is most uniform what results in the smallest range and standard deviation – Fig. 88.

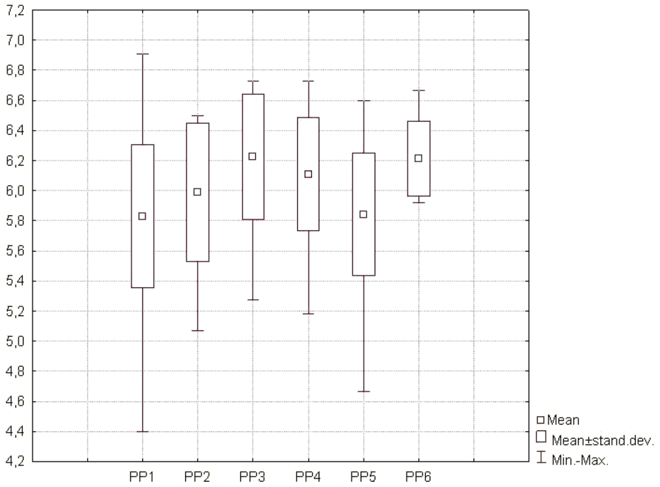


Fig. 88. Changeability of L-mean value in the categories of pine forests
Ryc. 88. Zmienność średnich wartości L w kategoriach borów sosnowych

Requirements to soil moisture [F]

In the fresh pine forests there is a clear dominance of species being indicative for fresh soils (with limited moisture) – F 4-5 (81%). The share of species indicative for moist soils (F 6-7) is at around 11%. Percentage shares of species with extreme requirements, i.e. dry and wet soils, are the lowest – some 2% and 5%, respectively (Fig. 89).

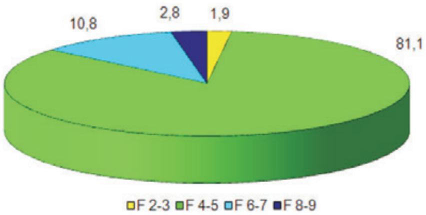


Fig. 89. The percentage share of plant species number (in total number) as indicators of the soil moisture (F) in pine forests
Ryc. 89. Udział gatunków o różnych wymaganiach względem wilgotności gleb (F) w borach sosnowych

In the particular categories of fresh pine forests the shares of species indicative of fresh soils (F 4-5) range from 54.6% in category PP6 to around 91% in category PP3. It should be noted that the last category, PP6, features a clearly higher share of species proper for moist soils (F 8-9: around 14.3%) than the other categories, and also – the complete lack of species indicative of dry soils (F 2-3) – Fig. 90.

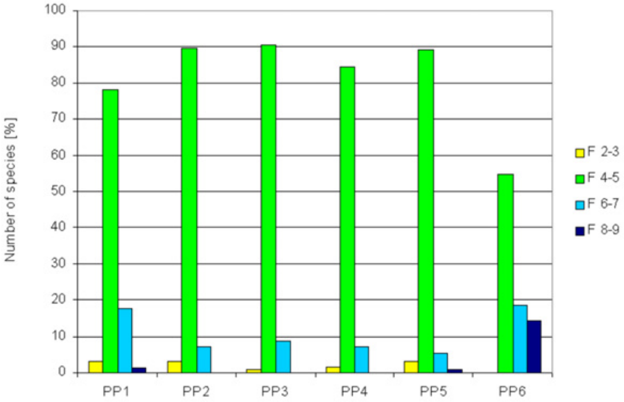


Fig. 90. The percentage share of plant species number (in total number) as indicators of the soil moisture (F) in the categories of pine forests
Ryc. 90. Udział gatunków o różnych wymaganiach względem wilgotności gleb (F) w kategoriach borów sosnowych

Mean values of F indicator imply fresh habitats for PP1 - PP5 categories, and more moist (F 5.6) in PP6 category, albeit differences are not statistically significant - Fig. 91.

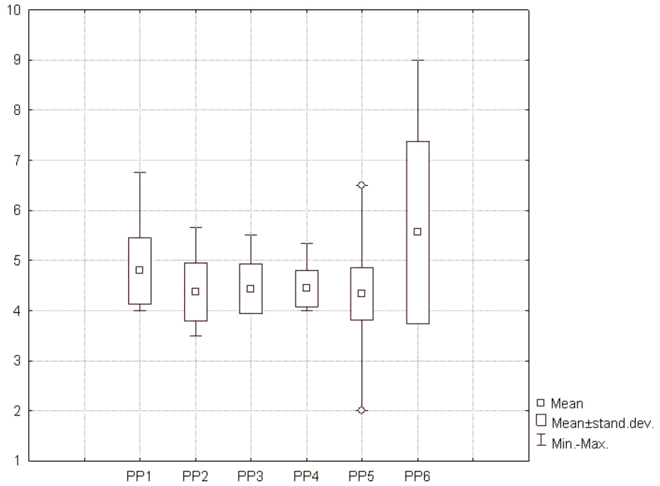


Fig. 91. Changeability of F-mean value in the categories of pine forests
Ryc. 91. Zmienność średnich wartości F w kategoriach borów sosnowych

Requirements to soil reaction [R]

In the fresh pine forests the share of species indicative of acid soils is clearly dominating (R 2-3: around 64%). The second quite numerous group (approximately 23%) is constituted by species that are indicative of moderately acid soils (R 4-5). There is also a significant share of species growing on strongly acid soils (R1; around 10%). The groups of species indicative of weakly alkaline (R 6-7) and alkaline (R 8-9) soils account for a marginal percentage of the composition (around 3% and 0.6%, respectively) – Fig. 92.

In the particular categories of fresh pine forests the share of species indicative of acid soils (R 2-3) is relatively even and ranges from approximately 60% (in category PP1) to around 69% (in category PP3). The share of species indicative of moderately acid soils (R 4-5) is the highest (at around 31%) in the last category, PP6. Besides, there is distinct downward trend in the shares of species indicative of strongly acid soils (R 1). The ancient forest category (PP1) is characterised by the highest share of strongly acidophilous species (around 16%), compared to other categories, and especially against the two categories of recent forests with the shortest regeneration periods, where this share is only at around 5%. (Fig. 93). The list of species characterised by R1 value in the pine forests is composed of the common *Calluna vulgaris* and much rarer *Vaccinium uliginosum* and *Diphasiastrum complanatum*. The first two are treated as the ancient forests indicators (see Chapter 4), while all of them belong to the characteristic species combination of *Peucedano-Pinetum* association.

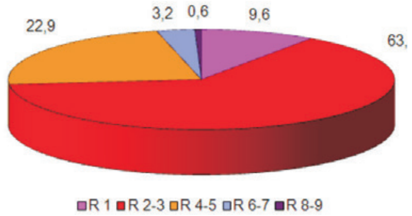


Fig. 92. The percentage share of plant species number (in total number) as indicators of the soil reaction (R) in pine forests

Ryc. 92. Udział gatunków o różnych wymaganiach względem kwasowości gleb (R) borów sosnowych

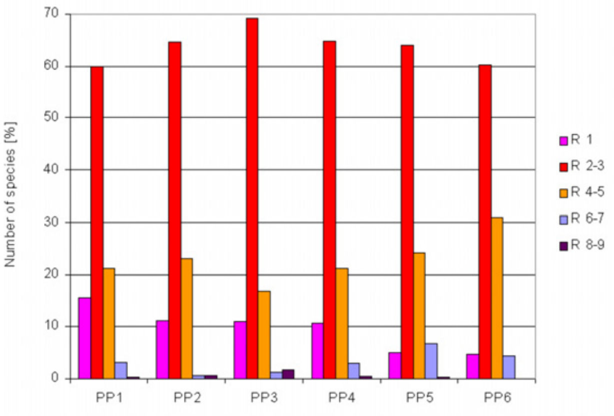


Fig. 93. The percentage share of plant species number (in total number) as indicators of the soil reaction (R) in the categories of pine forests

Ryc. 93. Udział gatunków o różnych wymaganiach względem kwasowości gleb (R) w kategoriach borów sosnowych

Mean values R for all six categories of pine forests indicate acid habitats (R 2.7-3.1). The highest values are taken by the indicator in two categories with the shortest regeneration period (PP5 and PP6), respectively R 3.0 and R 3.1, while being quite even in the four first categories PP1-PP4 (R 2.7) – Fig. 94.

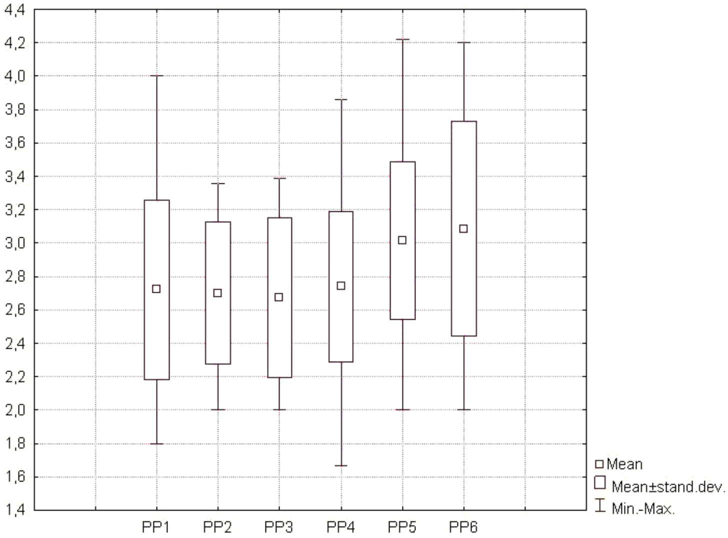


Fig. 94. Changeability of R-mean value in the categories of pine forests
Ryc. 94. Zmienność średnich wartości R w kategoriach borów sosnowych

Requirements to nitrogen content [N]

Plant composition of the pine forests is clearly dominated by species indicative of soils poor in nitrogen compounds (N 2-3) – roughly 60%. The second quite numerous group (around 25%) comprises indicators of extremely poor soils (N 1). On the other hand, there is also a significant share of species indicative of soils moderately rich in nitrogen (N 4-5: around 11%). The groups of species, corresponding to soils rich in nitrogen (N 6-7), and especially those very rich, account for a small percentage of the whole (respectively – around 3% and 0.5%) – Fig. 95.

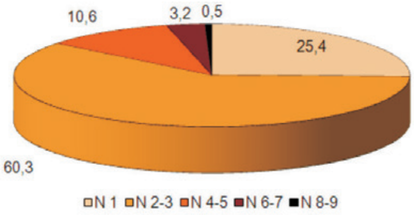


Fig. 95. The percentage share of plant species number (in total number) as an indicators of soil nitrogen content (N) in pine forests
Ryc. 95. Udział gatunków o różnych wymaganiach względem zawartości azotu w glebie (N) w borach sosnowych

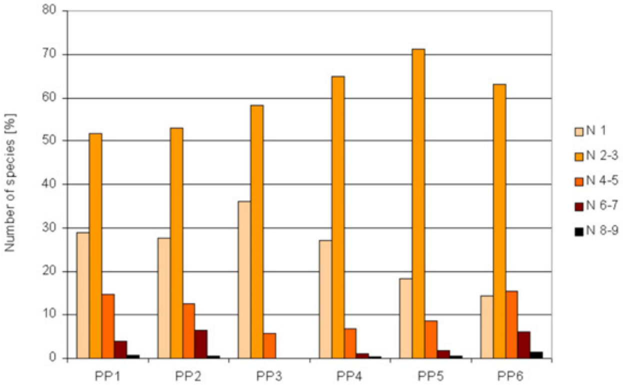


Fig. 96. The percentage share of plant species number (in total number) as indicators of soil nitrogen content (N) in the categories of pine forests

Ryc. 96. Udział gatunków o różnych wymaganiach względem zawartości azotu w glebie (N) w kategoriach borów sosnowych

In particular categories of the pine forests the shares of species indicative of soils poor in nitrogen (N 2-3) range from roughly 58% to 51%. It should be emphasised that the share is somewhat lower in the first three categories (PP1, PP2 and PP3) and the lowest in the first category, i.e. in the ancient forests, while it is somewhat higher in the three consecutive categories (PP4, PP5 and PP6), being the highest in category PP5. The percentage share of species being indicators of soils extremely poor in nitrogen (N 1) ranges in the analysed categories of pine forests from around 14% to around 36%, and it is distinctly lower in the two last categories (PP5, PP6), taking actually the lowest value in the last one (Fig. 96). The list of species featuring N1 value in the communities analysed comprises the common *Calluna vulgaris* and *Vaccinium vitis-idaea*, both of them typical of the ancient forests, a less frequent – appearing mainly in the recent forests having regenerated for a long period (PP3 and PP4) – grass species *Festuca ovina*, as well as much rarer *Molinia caerulea* and *Thymus serpyllum*.

The mean values of the indicator (N) in all six forest categories point to the habitats poor in nitrogen compounds (N 2.1-2.9). The relatively highest value, attained in the last category, PP6, defines it as somewhat richer in nitrogen than the remaining ones (Fig. 97).

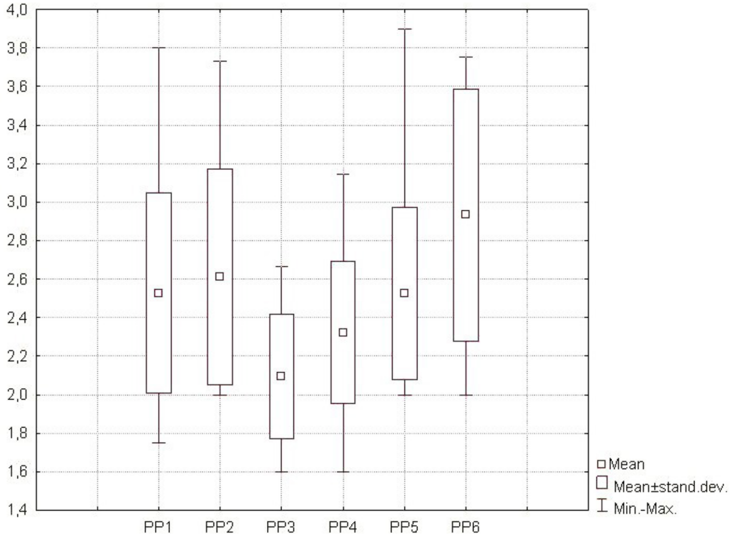


Fig. 97. Changeability of N-mean value in the categories of pine forests
Ryc. 97. Zmienność średnich wartości N w kategoriach borów sosnowych

6.3.2. ECOLOGICAL CHARACTERISTICS OF THE MIXED OAK-PINE FORESTS (*QUERCO-PINETUM*)

Anatomic structure type [AB]

In the species composition of the mixed oak-pine forests clearly dominate mesomorphs (around 69%), with scleromorphs (around 24%) as a subdominating group. The share of hygromorphs is low (roughly 6%), and the lowest is that of helomorphs (roughly 1%) –Fig. 98.

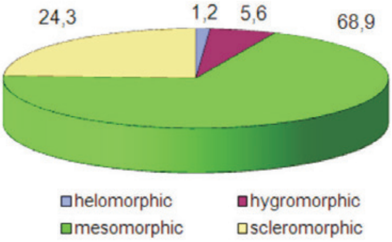


Fig. 98. The percentage share of plant species number (in total number) with given anatomical structure type (AB) in mixed oak-pine forests
Ryc. 98. Udział gatunków o różnej budowie anatomicznej (AB) w borach mieszanych

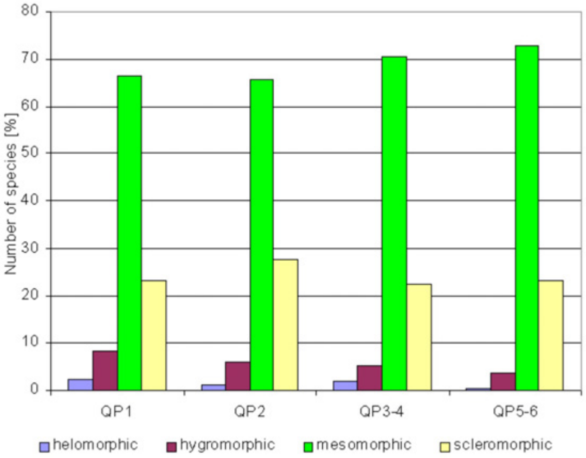


Fig. 99. The percentage share of plant species number (in total number) with given anatomical structure type (AB) in the categories of mixed oak-pine forests
Ryc. 99. Udział gatunków o różnej budowie anatomicznej (AB) w kategoriach borów mieszanych

The share of hygromorphs and mesomorphs best differentiate the mixed oak-pine forests categories (Fig. 99). The share of hygromorphs is generally not too high in the mixed oak-pine forests, but is decidedly the highest (roughly 8%) in the ancient forest category, QP1, compared to other categories, especially to the last one (around 4%). Hygromorphs are represented by species appearing quite frequently in the mixed oak-pine forests, *Athyrium filix-femina* and *Oxalis acetosella*, of which the first one definitely is, and the second one might be associated with the ancient forests (besides the less frequently appearing *Impatiens parviflora, Ranunculus lanuginosus, Stellaria media*).

The share of mesomorphs is high, and increases with the shortening of regeneration period and so is the lowest in the ancient forest category (QP1: around 66%) and the highest in the category of the youngest recent forests (QP5-6: approximately 73%). This group contains many species, those that are associated with the ancient forests, neutral with this respect, and those associated with the recent forests, both frequently and rarely appearing. The share of this group in the particular categories of mixed oak-pine forests depends not so much on the number of species actually appearing and representing this group as on the number of species from other groups.

Life form type [LF]

Among different types of life forms in mixed oak-pine forests there is the domination of hemicryptophytes (around 37%). The tree-like chamephytes (mainly dwarf shrubs) account for roughly 19%, geophytes for around 14%, while the seedlings of megaphanerophytes account for around 15%. The share of therophytes amounts to 7.0% only. The remaining life forms are nanophanerophytes and herbaceous chamephytes, which do not attain the share of 5% (Fig. 100).

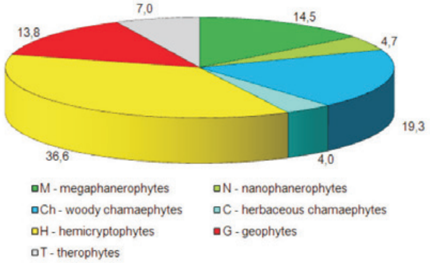


Fig. 100. The percentage share of plant species number (in total number) with given life form (LF) in mixed oak-pine forests
Ryc. 100. Udział gatunków o różnej formie życiowej (LF) w borach mieszanych

Among the life forms there are four: herbaceous chamephytes, geophytes, megaphanerophytes (tree seedlings), nanophanerophytes (shrubs seedlings), that differentiate most distinctly the categories of mixed oak-pine forests (Fig. 101). The shares of herbaceous chamephytes, which constitute quite limited percentage in the mixed oak-pine forests, demonstrates that they are relatively most numerous in two last categories, QP3-4 and QP5-6 (between roughly 4% and 6%), and least numerous in category QP2 (around 2%). The group of herbaceous chamephytes includes in the mixed oak-pine forests both the species displaying preference for the recent forests (*Lycopodium clavatum, Veronica officinalis*), and the ones that do not display any association with forest persistence (*Diphasiastrum complanatum, Lycopodium annotinum, Stellaria holostea, Veronica chamaedrys*).

The share of geophytes is the highest in the category of ancient forests (QP1: approximately 19%), while it is the lowest in the younger recent forests (QP 5-6: around 11%). The list of geophytes in the mixed oak-pine forests contains species that are frequent and clearly linked with the ancient forests, *Convallaria majalis, Maianthemum bifolium, Trientalis europaea, Pteridium aquilinum, Polygonatum odoratum*, as well as the much less frequent, but also with preference for ancient forests (for the lime-oak-hornbeam forests), *Anemone nemorosa, Polygonatum multiflorum, Galium schultesii, Equisetum sylvaticum*.

The share of trees seedlings (megaphanerophytes) in the herb layer of mixed oak-pine forests differs also distinctly between the categories and is the lowest in the ancient forest category (QP1: roughly 9%), and the highest in the youngest recent forests (QP 5-6: around 18%).

The shares of the nanophanerophytes in the herb layer of mixed oak-pine forests is small, with the lowest shares registered in the two first categories (between around 3% and 4%), compared to between roughly 6% and 7% in the two last ones. The species, which represent this group (*Cytisus scoparius, Ribes spicatum, Rubus caesius, Rubus fruticosus, Rubus idaeus, Rubus nessensis, Salix cinerea, Sambucus nigra, Rosa canina, Padus serotina*) display definitely a preference for the more disturbed communities, that is – such as the recent forests considered.

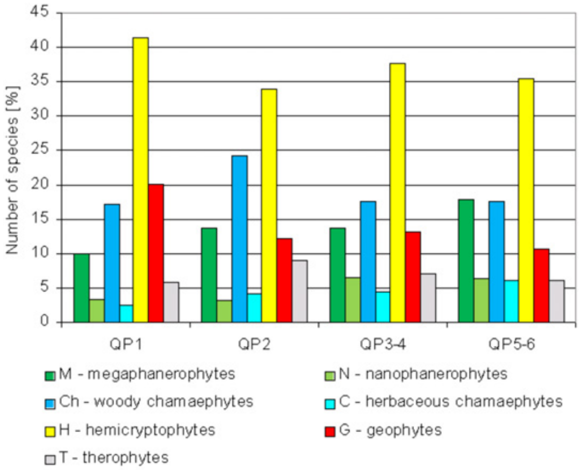


Fig. 101. The percentage share of plant species number (in total number) with given life form (LF) in the categories of mixed oak-pine forests
Ryc. 101. Udział gatunków o różnej formie życiowej (LF) w kategoriach borów mieszanych

Seed dispersal mode [VT]

In the mixed oak-pine forests as a whole there is a clear domination of anemochores (roughly 47%). There is also a significant share of endozoochores (around 22%). Autochores and myrmecochores are also numerous (roughly 16% and 13% respectively) - Fig. 102.

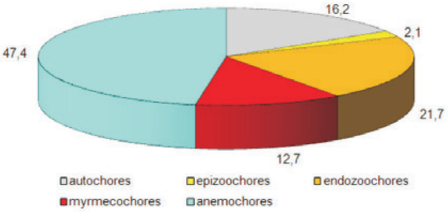


Fig. 102. The percentage share of plant species number (in total number) with given dispersal mode (VT) in mixed oak-pine forests
Ryc. 102. Udział gatunków o różnym typie rozsiewania w borach mieszanych

The shares of autochores and anemochores differentiate categories of the mixed oak-pine forests in the best way (Fig. 103). The ancient forests and the recent forests having regenerated for a longer period (QP1 and QP2) are characterised by the share of autochores higher by about 5% than in the two remaining recent forests categories. This is the consequence of the fact that among herbaceous autochores *Oxalis acetosella* and *Trientalis europaea* feature quite high frequency. Both these species are more or less distinctly associated with the ancient forests.

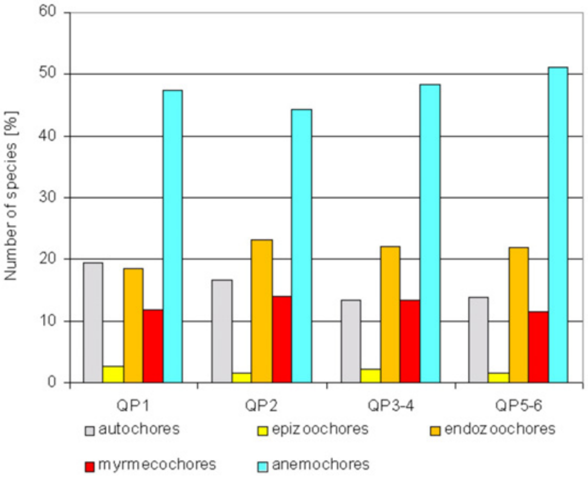


Fig. 103. The percentage share of plant species number (in total number) with given dispersal mode (VT) in the categories of mixed oak-pine forests
Ryc. 103. Udział gatunków o różnym typie rozsiewania w kategoriach borów mieszanych

On the other hand, the share of anemochores is somewhat higher in the recent forests of a shorter regeneration period (QP 5-6: 51%). This group encompasses numerous species, both the ones that display a positive or negative association with the ancient forests, and those that are neutral with this respect. A relatively higher share of anemochores in the younger successional communities, altogether with the higher share of autochores in the mature communities, seem to confirm the general ecological rules.

Life strategy type [STR]

Among the herb layer species in the mixed oak-pine forests, two types of life strategies are most frequent: the mixed type *cs* (approximately 41%) and the competitive type *c* (approximately 30%). Quite a large group is also constituted by species featuring the mixed type *csr* (roughly 21%). A truly small group (roughly 7%) is formed by the type *s*. The most numerous type *cs* is proper for species adapted to relatively undisturbed conditions and to moderately intensive stress, while type *c* is reserved for trees, shrubs and dwarf shrubs (featuring high competitive force), (see Table 28, Fig. 104).

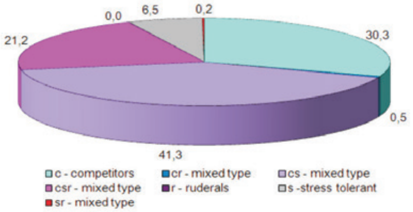


Fig. 104. The percentage share of plant species number (in total number) with given life strategy type (STR) in mixed oak-pine forests
Ryc. 104. Udział gatunków o różnym typie strategii życia w borach mieszanych

Among the types of plant life strategies there are two, *c* and *cs*, which most distinctly differentiate the categories of mixed oak-pine forests (Fig. 105). The *cs* type is most feebly represented in the category of recent forests having regenerated for a shorter time period QP 5-6: around 34%), while its shares are somewhat higher in the remaining categories (around 43-44%). This type is represented in the mixed oak-pine forests by numerous and partly important species, whose majority demonstrates a weaker or stronger association with the ancient forests (*Vaccinium vitis-idaea, Convallaria majalis, Peucedanum oreoselinum, Athyrium filix-femina, Calluna vulgaris*), but which also may not display any difference of appearance between the ancient and recent forests (*Vaccinium myrtillus, Deschampsia flexuosa, Dryopteris carthusiana, Lycopodium annotinum, Dryopteris filix-mas, Danthonia decumbens*). There are very few species in this group that demonstrate an association with the recent forests (*Hieracium lachenalii, Lycopodium clavatum*).

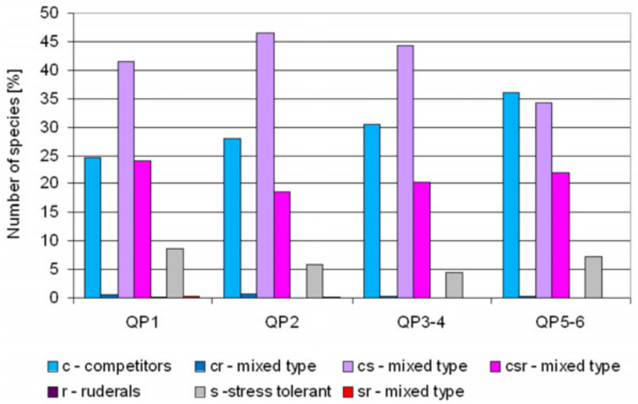


Fig. 105. The percentage share of plant species number (in total number) with given life strategy type (STR) in the categories of mixed oak-pine forests

Ryc. 105. Udział gatunków o różnym typie strategii życia w kategoriach borów mieszanych

A reverse distribution characterises species representing the competitive type. Their share is the highest in the category of younger recent forests (QP 5-6: around 36%), while it is the lowest in the ancient forest category (QP1: around 24%). Among quite a lot of species, belonging to type *c*, and appearing in the herb layer of mixed oak-pine forests, there are many trees, shrubs seedlings (23 species), and grasses (6 species). A vast majority of these species do not demonstrate any association with the ancient forests. Only *Pteridium aquilinum* and *Calamagrostis arundinacea* display such an association to a certain degree.

Requirements to light intensity [L]

In the mixed oak-pine forests the highest share is taken by species indicative of moderate light (L 6-7: around 43%) and of moderate shade (L 4-5: approximately 34%). The shares of shade-tolerant (L 2-3) and of full-light species (L 8-9) are 10% each. The shade-tolerant species account for 5%, while the least numerous, accounting for ca. 2%, are the species requiring locations in deep shade (L 1) – Fig. 106.

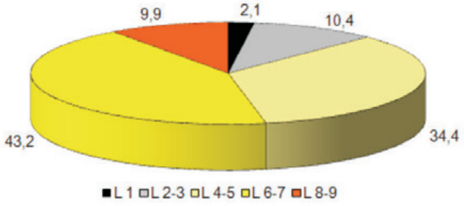


Fig. 106. The percentage share of plant species number (in total number) as indicators of light intensity (L) in mixed oak-pine forests

Ryc. 106. Udział liczby gatunków o różnych wymaganiach względem naświetlenia (L) w borach mieszanych

The share of species indicative of moderate light (L 6-7) is somewhat higher (by some 4-5%) in the categories of recent forests (QP3-4 and QP5-6), featuring shorter periods of regeneration, compared to the categories of ancient forests and these recent ones that feature long periods of regeneration (QP1 and QP2). The share of full–light species (L 8-9) is somewhat lower (roughly 8%) in the category of ancient forest (QP1), while in the remaining ones it is quite even (at around 11%). The share of species indicative of shaded sites (L 2-3) is generally quite limited in the mixed oak-pine forests (around 10%), and it is the highest in the category of ancient forests (QP1), at around 15% (Fig. 107).

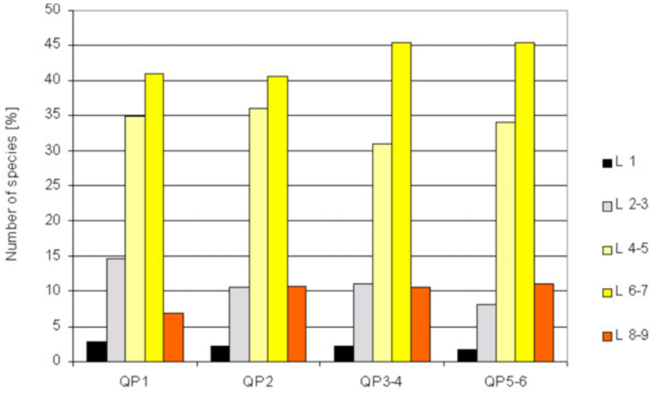


Fig. 107. The percentage share of plant species number (in total number) as indicators of light intensity (L) in the categories of mixed oak-pine forests
Ryc. 107. Udział gatunków o różnych wymaganiach względem naświetlenia (L) w kategoriach borów mieszanych

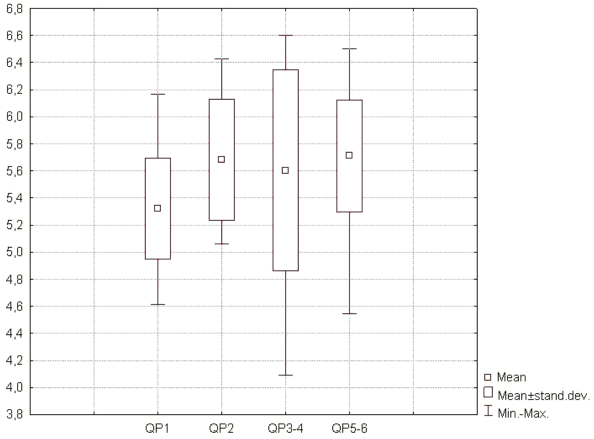


Fig. 108. Changeability of L-mean value in the categories of mixed pine forests
Ryc. 108. Zmienność średnich wartości L w kategoriach borów mieszanych

Mean values of the L indicator in the mixed forests show differences between the category of ancient forests (QP1 - L 5.3), and the last category of recent woods (QP5-6 – L 5.7). Thus, according to this indicator, the ancient forests are slightly shadier than the recent ones, but differences are not statistically significant (Fig. 108).

Requirements to soil moisture [F]

The mixed oak-pine forests are clearly dominated by species indicative of fresh soils (i.e. those of moderate moisture), F 4-5 (roughly 81%). The share of species indicative of moist soils (F 6-7) is around 13%, while the shares of species of extreme requirements (dry and wet soils) constitute the smallest percentages – around 3% and around 1%, respectively (Fig. 109).

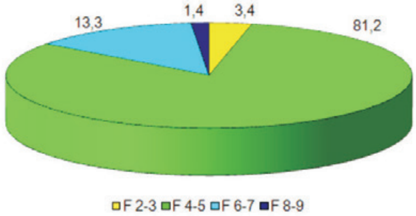


Fig. 109. The percentage share of plant species number (in total number) as indicators of the soil moisture (F) in mixed oak-pine forests

Ryc. 109. Udział gatunków o różnych wymaganiach względem wilgotności gleb (F) w borach mieszanych

In the particular categories of mixed oak-pine forests the share of species indicative of moderately moist soils (F 4-5) ranges from approximately 74% (in the QP1 category) to roughly 90% (in the QP2 category). It is worth noting that the category of ancient forests (QP1) features higher share of species of wet soils (F 8-9: approximately 19%), while in the last category of recent forests (QP5-6) there are no species of dry soils (F 2-3) at all (Fig. 110).

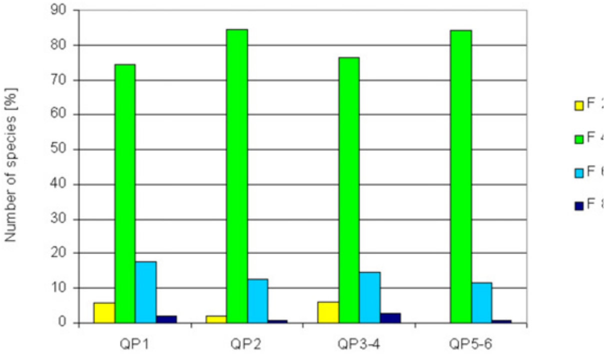


Fig. 110. The percentage share of plant species number (in total number) as indicators of the soil moisture (F) in the categories of mixed oak-pine forests

Ryc. 110. Udział gatunków o różnych wymaganiach względem wilgotności gleb (F) w kategoriach borów mieszanych

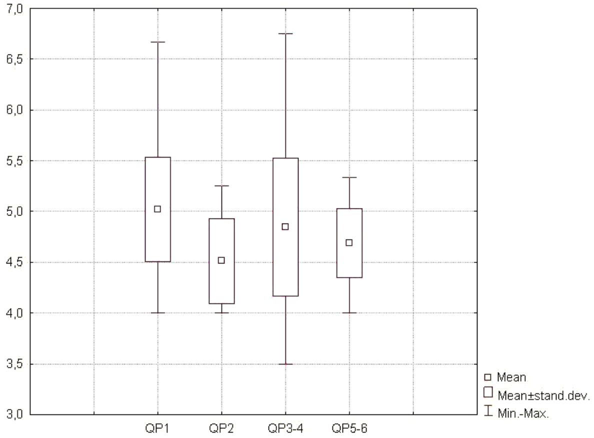


Fig. 111. Changeability of F-mean value in the categories of mixed oak-pine forests
Ryc. 111. Zmienność średnich wartości F w kategoriach borów mieszanych

Mean F values indicate the fresh habitats (F 4.6-5.0) with no statistical differences between the categories of mixed oak-pine forests albeit the value of F is the lowest for the category QP2, the driest one (F at around 4.5), while it is the highest for the first one, QP1, which is the ’most moist’ between analysed categories (F 5.0),- Fig. 111.

Requirements to soil reaction [R]

In the mixed oak-pine forests the share of species indicative of acid soils, R 2-3, is dominating (around 55%). The species indicative of moderately acid soils (R 4-5) constitute the second quite numerous group (around 29%). The share of species corresponding to slightly alkaline soils (R 6-7) is relatively important, as well (roughly 10%). The share of the indicators of strongly acid soils amounts to around 6% (Fig. 112).

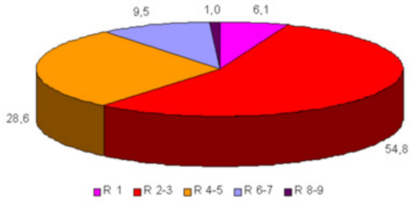


Fig. 112. The percentage share of plant species number (in total number) as indicators of the soil reaction (R) in mixed oak-pine forests
Ryc. 112. Udział gatunków o różnych wymaganiach względem kwasowości gleb (R) w borach mieszanych

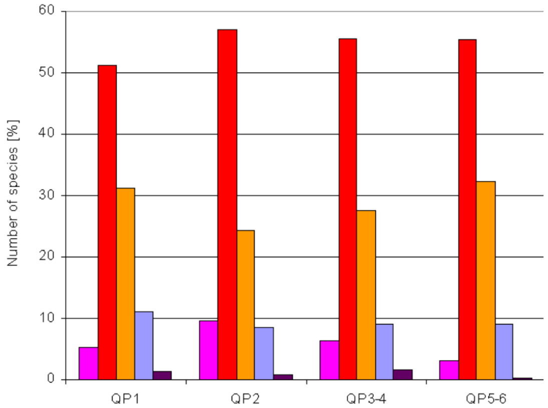


Fig. 113. The percentage share of plant species number (in total number) as indicators of the soil reaction (R) in the categories of mixed oak-pine forests
Ryc. 113. Udział gatunków o różnych wymaganiach względem kwasowości gleb (R) w kategoriach borów mieszanych

In the particular categories of mixed oak-pine forests the shares of species indicative of acid soils (R 2-3) is quite even and ranges from 52% (in the category QP1) to approximately 56% (in the category QP2). The share of the indicators of moderately acid soils is somewhat higher in the last category, QP5-6 (around 32%), than in the other categories. The groups of species featuring extreme habitat requirements, namely the indicators of strongly acid (R1) and strongly basic (R 8-9) soils are the least frequent in the last category (QP 5-6), at respectively 3.1% and 0.2% (Fig. 113).

The total average values of the R indicator in all four categories point to acid habitats (R 3.1-3.5). Slightly higher average R value has been observed in the ancient forest (QP1), while a bit lower – for the category QP2 (Fig. 114).

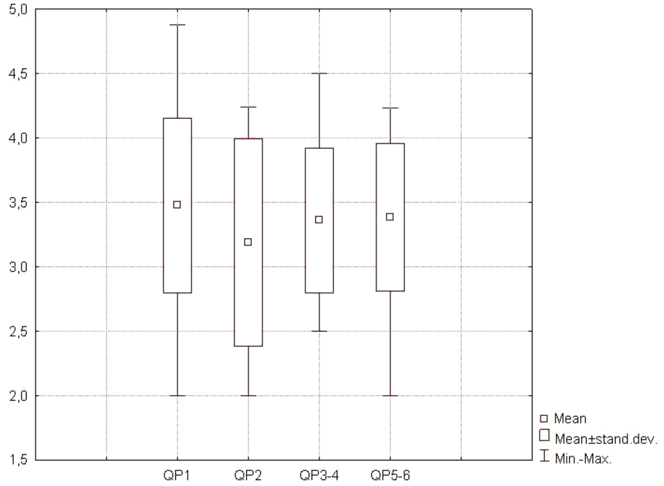


Fig. 114. Changeability of R-mean value in the categories of mixed oak-pine forests
Ryc. 114. Zmienność średnich wartości R w kategoriach borów mieszanych

Requirements to nitrogen content in soil [N]

The share of species indicative of soils poor in nitrogen compounds (N 2-3) dominates in the mixed oak-pine forests (share of roughly 55%). The second group (approximately 19%) is constituted by species indicative of soils moderately rich in nitrogen (N 4-5). There are also significant shares of species indicative of the habitats extremely poor in nitrogen (N 1: around 15%) and of those rich in nitrogen (N 6-7: around 11%). The group of species corresponding to soils with high nitrogen content (N 8-9) accounts for only approximately 1% (Fig. 115).

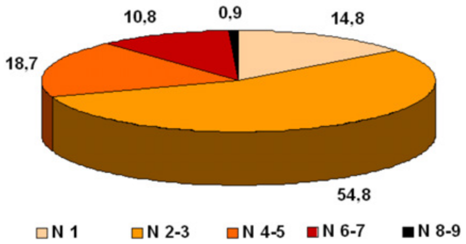


Fig. 115. The percentage share of plant species number (in total number) as indicators of soil nitrogen content (N) in mixed oak-pine forests

Ryc. 115. Udział gatunków o różnych wymaganiach względem zawartości azotu w glebie (N) w borach mieszanych

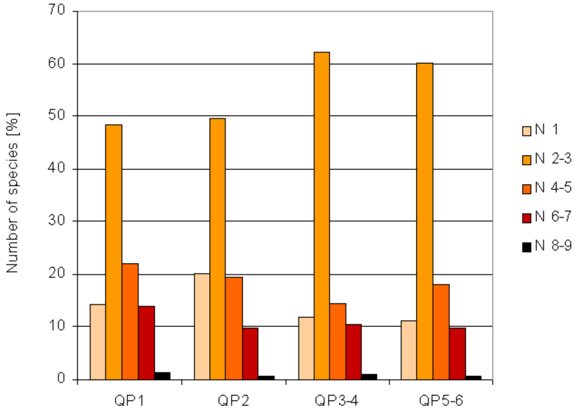


Fig. 116. The percentage share of plant species number (in total number) as indicators of soil nitrogen content (N) in the categories of mixed oak-pine forests

Ryc. 116. Udział gatunków o różnych wymaganiach względem zawartości azotu w glebie (N) w kategoriach borów mieszanych

The share of species being the indicators of soils poor in nitrogen compounds (N 2-3) is significantly lower (by some 10-12%) in the first two categories (QP1 and QP2) in comparison with the third and fourth ones (QP3-4 and QP 5-6). The percentage shares of species indicative of soils moderately rich in nitrogen (N 4-5) are somewhat higher in the first two categories (exceeding 20%) than in the two remaining ones (QP 3-4 and QP 5-6), where their values are around 14% and 18%, respectively. Compared to other categories, the one of ancient forests (QP1) features the highest share of species indicating habitats rich in nitrogen (N 6-7: around 14%) - Fig. 116.

Mean values of the N indicator of four categories of mixed oak-pine forests imply habitats poor in nitrogen compounds (N 2.9-3.3). The highest average value of N characterises the ancient forest category (QP1). But differences between categories are not significant (Fig. 117).

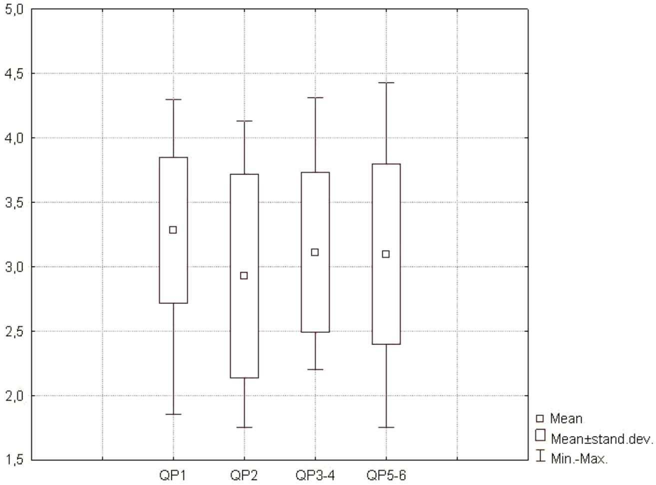


Fig. 117. Changeability of N-value in the categories of mixed oak-pine forests
Ryc. 117. Zmienność średnich wartości R w kategoriach borów mieszanych

6.3.3. ECOLOGICAL CHARACTERISTICS OF THE LIME-OAK-HORNBEAM FORESTS (*TILIO-CARPINETUM*)

Anatomic structure type [AB]

The herb layer of lime-oak-hornbeam forests is dominated by mesomorphs (around 62%), followed by hygromorphs (roughly 25%), and scleromorphs (roughly 13%). The share of helomorphs is only marginal (approximately 0.7%) (Fig. 118).

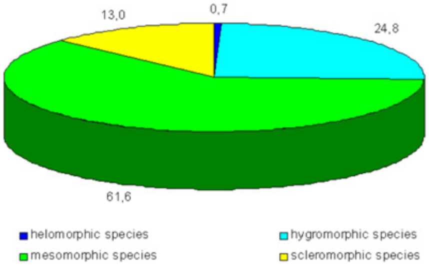


Fig. 118. The percentage share of plant species number (in total number) with given anatomical structure type (AB) in lime-oak-hornbeam forests
Ryc. 118. Udział gatunków o różnej budowie anatomicznej (AB) w grądach

The shares of hygromorphs and scleromorphs differentiate well the categories of lime-oak-hornbeam forests. The share of hygromorphs is lower by some 5% in the third category, TC3-6, when compared to two other ones. On the other hand, in the first category the share of scleromorphs is slightly lower (at most by 1%) than in the remaining categories (Fig. 119).

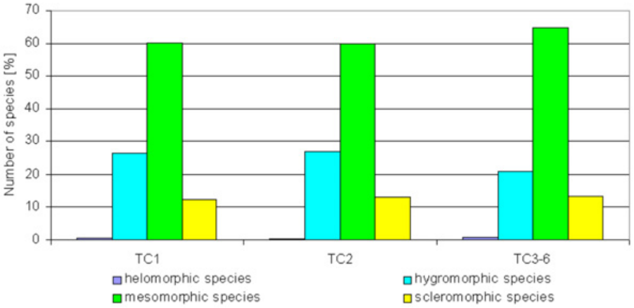


Fig. 119. The percentage share of plant species number (in total number) with given anatomical structure type (AB) in the categories of lime-oak-hornbeam forests
Ryc. 119. Udział gatunków o różnej budowie anatomicznej (AB) w kategoriach grądów

Life form [LF]

The herb layer of lime-oak-hornbeam forests is dominated by hemicryptophytes (around 45%). Geophytes constitute, as well, a significant group (around 25%). The share of trees seedlings (megaphanerophytes) amounts to approximately 12%. The remaining groups of species account for a small percentage, and this applies, in particular, to the tree-like chamephytes (around 3%) – Fig. 120.

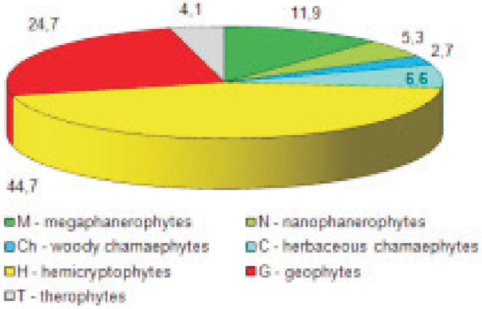


Fig. 120. The percentage share of plant species numbers (in total number) with given life form (LF) in lime-oak-hornbeam forests
Ryc. 120. Udział gatunków o różnej formie życiowej (LF) w grądach

There are three life forms that distinctly differentiate the categories of lime-oak-hornbeam forests These are: geophytes, nanophanerophytes and therophytes - (Fig. 121).

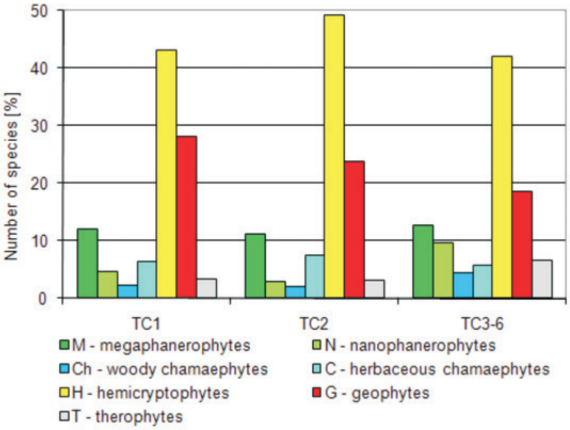


Fig. 121. The percentage share of plant species number (in total number) with given life form (LF) in the categories of lime-oak-hornbeam forests
Ryc. 121. Udział gatunków o różnej formie życiowej (LF) w kategoriach grądów

Particularly pronounced and unambiguous are differences of the geophytes share. This share is the highest in the category of ancient forests (TC1: around 28%), while it is the lowest in the young recent forests (TC 3-6: around 19%). The list of geophytes registered in the lime-oak-hornbeam forests considered is quite long. It contains a couple of species, which appear with high frequency, at least in some categories. These frequent ones encompass: *Anemone nemorosa, Convallaria majalis, Maianthemum bifolium, Polygonatum multiflorum, Pteridium aquilinum, Trientalis europaea*. Those less frequent are: *Adoxa moschatellina, Epipactis helleborine, Equisetum sylvaticum, Galium* *schultesii, Gymnocarpium dryopteris, Lathyrus vernus, Lilium martagon, Paris quadrifolia, Platanthera bifolia, Polygonatum odoratum*. A vast majority of the geophytes display preference for the ancient forests, though, *Pteridium aquilinum* and *Trientalis europaea* are good indicators of ancient forests, but for the mixed oak-pine and fresh pine forests, while in the lime-oak-hornbeam forests, quite differently, they are often the indicators of disturbance (especially of the Scots pine introduction into the stands) and are more frequently encountered in the recent forests.

The two other plant life forms have the distribution along the categories opposite to that of geophytes. The shares of nanophanerophytes and of therophytes are, generally, in the lime-oak-hornbeam forests not too high. Their highest share in the category of younger recent forests (TC 3-6) is well pronounced. This does not result from the lower share of geophytes, but from the actually more frequent appearance of species from these two groups in the younger recent forests.

Seed dispersal mode [VT]

Anemochores dominate in the lime-oak-hornbeam forests (around 43%). There is also a significant share of autochores (around 27%). The shares of myrmecochores, and endozoochores are similar – around 12% each. The least numerous group (around 7%) is constituted by epizoochores Fig. 122.

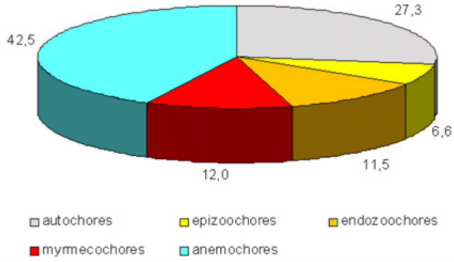


Fig. 122. The percentage share of plant species number (in total number) with given dispersal mode (VT) in lime-oak-hornbeam forests
Ryc. 122. Udział gatunków o różnym typie rozsiewania w grądach

Among the seed dispersal types only one sufficiently distinctly differentiates the categories of lime-oak-hornbeam forests, namely the epizoochores (Fig. 123). The share of epizoochores is almost two times higher in the younger category of recent forest (TC 3-6) than in the ancient forest category (TC1). The group of epizoochorous species, registered in the lime-oak-hornbeam forests, encompasses 13 species, of which the more frequently appearing, and associated with the ancient forests, are: *Galium odoratum, Galium schultesii*, those associated more with the recent forests are: *Galium mologo, Galeopsis tetrahit, Geranium robertianum*, while *Geum urbanum* does not display any relation to ancient nor to recent forests.

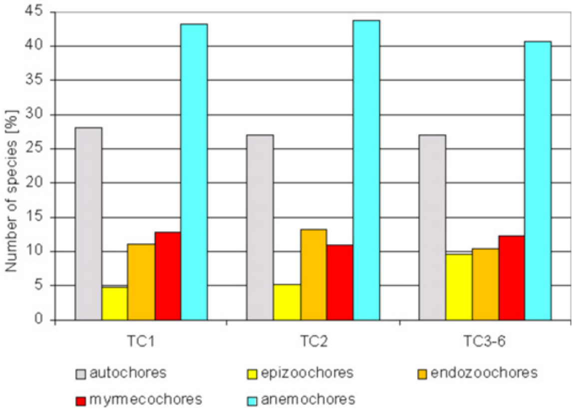


Fig. 123. The percentage share of plant species number (in total number) with given dispersal mode (VT) in the categories of lime-oak-hornbeam forests
Ryc. 123. Udział gatunków o różnym typie rozsiewania w kategoriach grądów

Life strategy type (STR]

Among the vascular plants species, forming the herb layer of lime-oak-hornbeam forests, the mixed type *csr* dominates (around 41%). The competitive type *c* accounts for 29% of share. The species of mixed type *cs* constitute also quite a numerous group (around 20%). A smaller group (roughly 6%) is constituted by the type *s*. The shares of the life strategy types *cr* and *sr* are definitely insignificant in the lime-oak-hornbeam forests – around 2% each (Fig. 124).

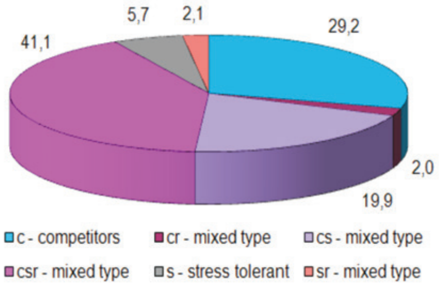


Fig. 124. The percentage share of plant species number (in total number) with given life strategy type (STR) in lime-oak-hornbeam forests
Ryc. 124. Udział gatunków o różnym typie strategii życia w grądach

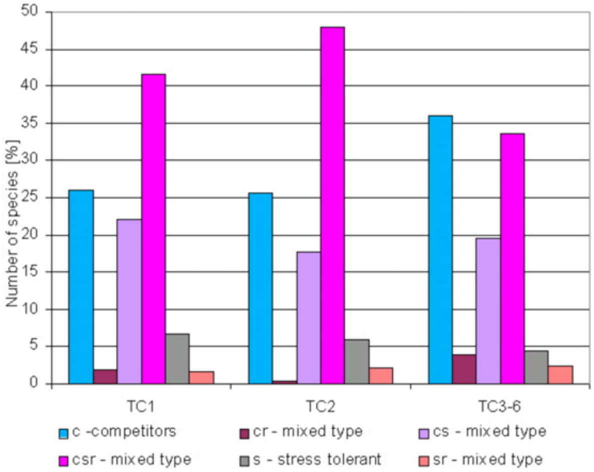


Fig. 125. The percentage share of plant species numbers (in total number) with given life strategy type (STR) in lime-oak-hornbeam forests

Ryc. 125. Udział gatunków o różnym typie strategii życia w kategoriach grądów

Two types of plants life strategies, *c* and *csr*, differentiate to some extent the categories of lime-oak-hornbeam forest, distinguishing younger recent forests (TC3-6) from the ancient forests and the older recent forests (TC1 and TC2). The mixed *csr* type is represented in the lowest values in the category of recent forests with a shorter regeneration period, while the competitive type *c* is relatively most numerous in this category (Fig. 125).

Requirements to light intensity [L]

The species indicative of moderate shade (L 4-5) take the highest share in the lime-oak-hornbeam forests (around 47%), followed by those indicative of moderate light intensity (L 6-7 around 32%). The communities considered display also a significant share (roughly 20%), of the shaded sites indicators (L 2-3) while the group of species, whose optimum sites ought to have full light (L 8-9) takes a truly marginal share (roughly 1%) – Fig. 126.

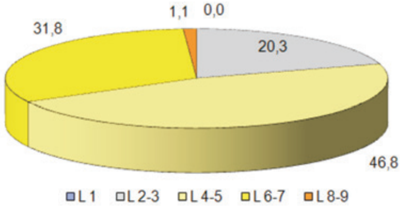


Fig. 126. The percentage share of plant species number (in total number) as indicators of the light intensity (L) in lime-oak-hornbeam forests

Ryc. 126. Udział liczby gatunków o różnych wymaganiach względem naświetlenia (L) w grądach

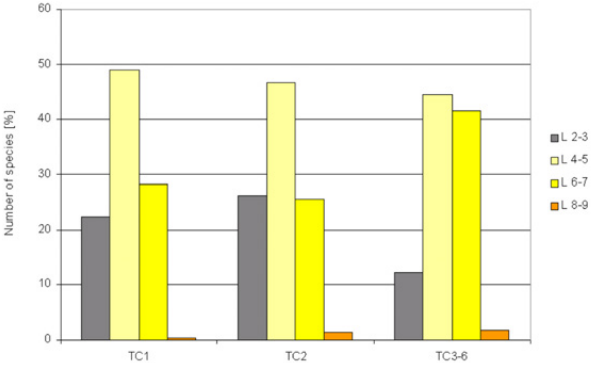


Fig. 127. The percentage share of plant species number (in total number) as indicators of the light intensity (L) in the categories of lime-oak-hornbeam forests

Ryc. 127. Udział gatunków o różnych wymaganiach względem naświetlenia (L) w kategoriach grądów

The younger recent forests (TC 3-6) category features much lower share of shade-tolerant species (L 2-3), and a much higher share of species indicative of moderately sites of light intensity (L 6-7) (Fig. 127).This indicates the fact that there is much more light at the bottom of forest in this category. An explanation thereof can be found in Table 12, which provides the average values of the tree layer cover in the particular categories. They are as follows: TC1: 84.8%, TC2: 81.5%, TC3-6: 74.0%. Besides, the same category is characterised by a relatively higher share of the Scots pine, introduced into the stands. Compared to the deciduous trees (hornbeam, oak), Scots pine provides less intensive shade than the deciduous trees.

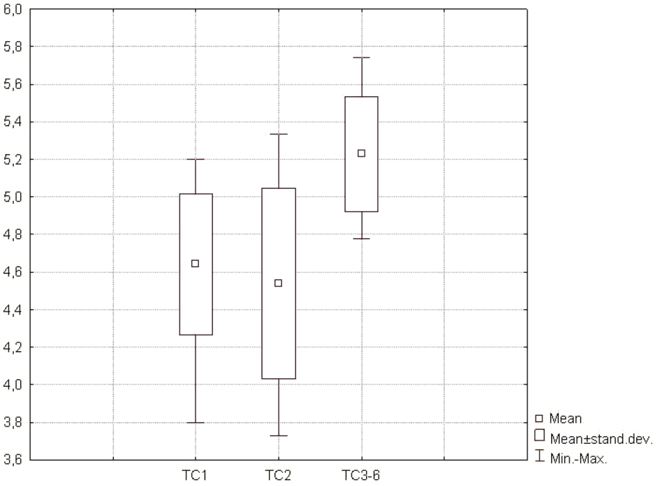


Fig. 128. Changeability of L-mean value in the categories of lime-oak-hornbeam forests

Ryc. 128. Zmienność średnich wartości L w kategoriach grądów

Mean L value of the third category of lime-oak-hornbeam forests (TC3-6) differs from the remaining ones (TC1 and TC2). It amounts to 5.2 with rather small data scatter and, what is worthy to note, with significantly higher minimum and maximum than in TC1 and TC2 categories (Fig. 128).

Requirements to soil moisture [F]

Species indicative of fresh soils (F 4-5) clearly dominate (around 80%) in the herb layer of lime-oak-hornbeam forests. The share of the moist soils indicators (F 6-7) equals around 19%, while species indicative of dry soils accounted merely for 1%. Indicators of wet soils (F 8-9) were not observed in the species composition of lime-oak-hornbeam forests analysed (Fig. 129).

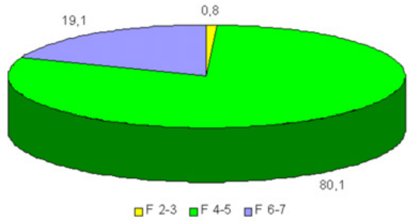


Fig. 129. The percentage share of plant species number (in total number) as indicators of the soil moisture (F) in lime-oak-hornbeam forests
Ryc. 129. Udział gatunków o różnych wymaganiach względem wilgotności gleb (F) w grądach

The shares of species groups featuring diverse requirements with respect to the soil moisture are quite similar in the distinguished categories of lime-oak-hornbeam forests (Fig. 130).

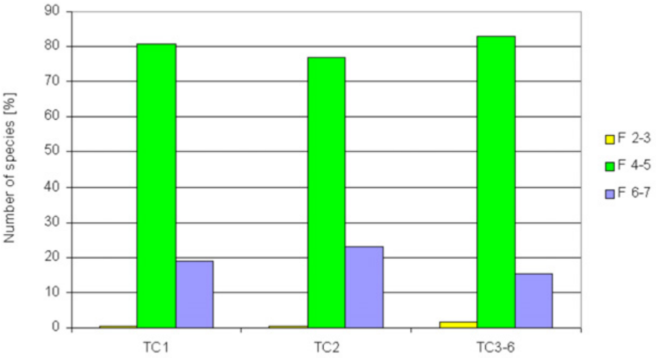


Fig. 130. The percentage share of plant species number (in total number) as indicators of the soil moisture (F) in the categories of lime-oak-hornbeam forests
Ryc. 130. Udział gatunków o różnych wymaganiach względem wilgotności gleb (F) w kategoriach grądów

Even though mean F values are quite even and indicating in the three categories of the lime-oak-hornbeam forests the fresh habitats (F 5.0-5.1), it can be noted that the third category (TC 3-6) includes also relatively drier plots, what is expressed by minimal F values and a shift in standard deviation (Fig, 131.)

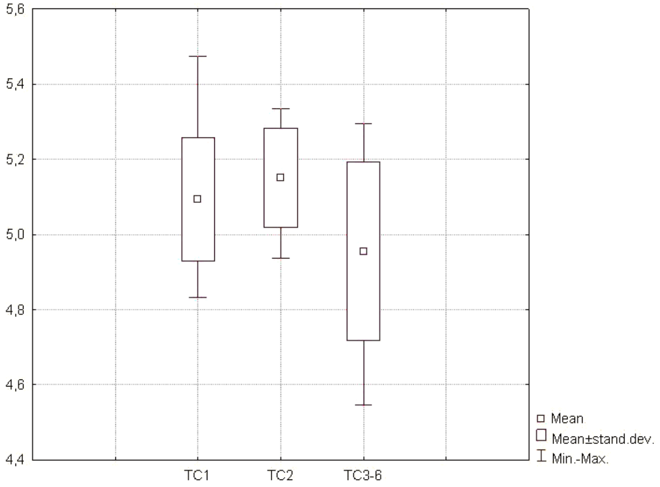


Fig. 131. Changeability of F-mean value in the categories of lime-oak-hornbeam forests
Ryc. 131. Zmienność średnich wartości F w kategoriach grądów

Requirements to soil reaction [R]

Indicators of slightly acid or alkaline soils (R 6-7) dominate in the lime-oak-hornbeam forests (around 46%). A somewhat smaller group (roughly 33%) is made up of moderately acid soils indicators (R 4-5). Then, the species indicative of acid soils (R 2-3) take the share of around 20%. The indicators of alkaline soils (R 8-9) account only for 3%, while no indicators of strongly acid soils were registered in the forests analysed (Fig. 132).

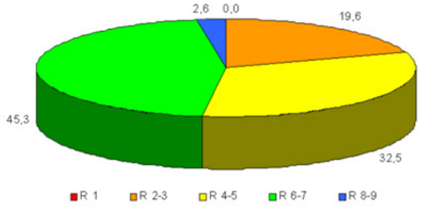


Fig. 132. The percentage share of plant species (in total number) as indicators of the soil reaction (R) in lime-oak-hornbeam forests
Ryc. 132. Udział gatunków o różnych wymaganiach względem kwasowości gleb (R) w grądach

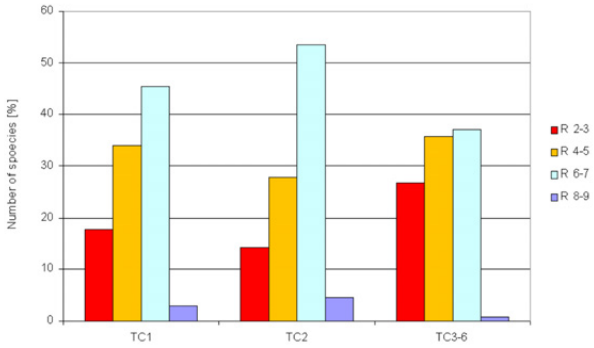


Fig. 133. The percentage share of plant species (in total number) as indicators of the soil reaction (R) in the categories of lime-oak-hornbeam forests

Ryc. 133. Udział gatunków o różnych wymaganiach względem kwasowości gleb (R) w kategoriach grądów

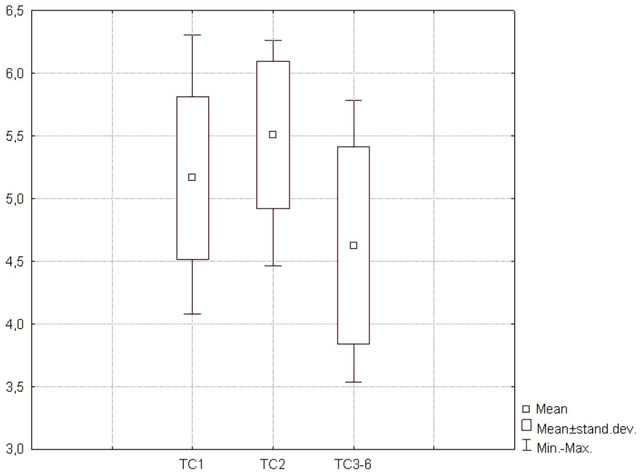


Fig. 134. Changeability of R-mean value in the categories of lime-oak-hornbeam forests

Ryc. 134. Zmienność średnich wartości R w kategoriach grądów

The category of younger recent forests (TC 3-6) stands again apart from the other ones, with its relatively higher share (up to roughly 13%) of acidophilous species (R 2-3), and much lower (at most around 17%) of the indicators of slightly acid or alkaline habitats (R 6-7) - (Fig. 133). This is, without any doubt, the effect of pine planting on habitats of the lime-oak-hornbeam forests. Acidification of the soil upper horizons took place, and, consequently, the floristic composition contains much more – when compared to the ancient forest – acidophilous species, which are proper for mixed oak-pine forests, namely such as *Vaccinium myrtillus, Vaccinium vitis-idaea, Deschampsia flexuosa* and so on.

Mean R values of the three lime-oak-hornbeam forests categories (Fig. 134) show the moderately and slightly acid habitats (R 4.6-5.5). A distinctly lower value of this indicator is observed in the category of younger recent forests (TC 3-6) albeit the difference is not significant.

Requirements to nitrogen content in soil [N]

Two species groups dominate in the lime-oak-hornbeam forests (roughly 35% each), namely the indicators of the soils moderately rich in nitrogen compounds (N 4-5) and those rich in nitrogen (N 6-7). There is also a significant share of oligotrophes indicative of habitats poor in nitrogen (N 2-3: roughly 22%). The shares of species indicative of soils very poor in nitrogen (N1) and very rich (N 8-9) are small, respectively around 3% and 7% (Fig. 135).

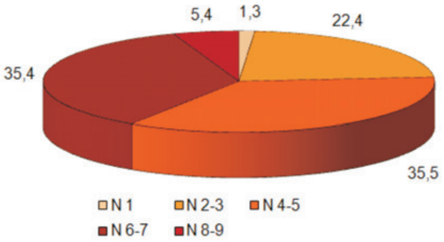


Fig. 135. The percentage share of plant species (in total number) as indicators of soil nitrogen content (N) in lime-oak-hornbeam forests

Ryc. 135. Udział gatunków o różnych wymaganiach względem zawartości azotu w glebie (N) w grądach

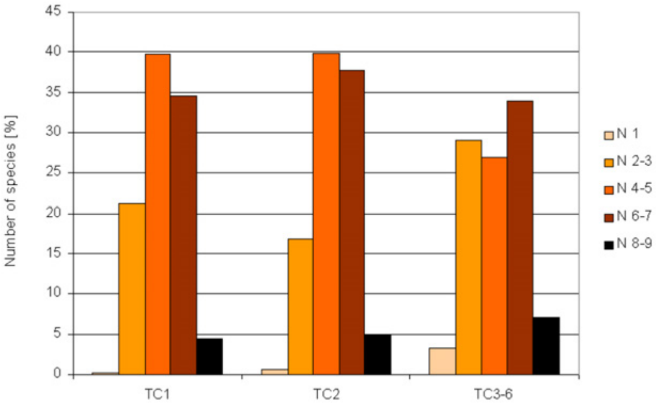


Fig. 136. The percentage share of plant species (in total number) as indicators of soil nitrogen content (N) in the categories of lime-oak-hornbeam forests

Ryc. 136. Udział procentowy grup gatunków pod względem zawartości azotu w glebach różnicujących kategorie grądów

The third category, TC3-6, distinguishes itself by the higher share of species indicative of soils extremely poor (N1), as well as poor (N 2-3) in nitrogen compounds (Fig. 136). This is the effect – similarly as in the case of soil acidity – of appearance of acidophilous and oligotrophic species that accompany pine planted on post-agricultural lands.

Mean N values of the three categories of oak-and-hornbeam forests show habitats moderately rich in nitrogen (N 4.7-5.0). Generally categories TC1 and TC2 are characterised by almost the same mean values, standard deviation and the range, while TC3 shows lower mean but bigger standard deviation and the wider range of values - Fig. 137.

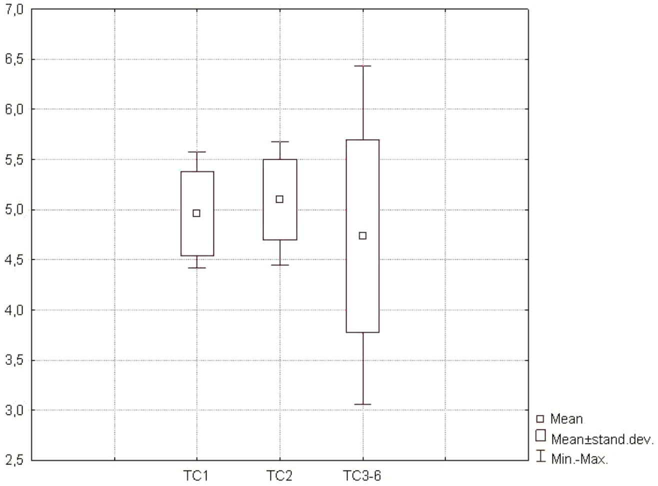


Fig. 137. Changeability of N-mean value in the categories of lime-oak-hornbeam forests

Ryc. 137. Zmienność średnich wartości N w kategoriach grądów

6.4. ECOLOGICAL DIFFERENCES BETWEEN THREE FOREST TYPE

Anatomic structure type [AB]

The hygromorphs and the scleromorphs are the types of plant anatomic structure, which differentiate the most forests types. The share of hygromorphs is slight in the pine forests, amounting to only 0.5%, while it is higher in the mixed oak-pine forests (around 6%), and clearly the highest in the lime-oak-hornbeam forests (25%). An opposite tendency is observed for the scleromorphs, whose shares are definitely the highest in the pine forests (approximately 32%), somewhat lower in the mixed oak-pine forests (around 24%), and the lowest in the lime-oak-hornbeam forests (Fig. 138).

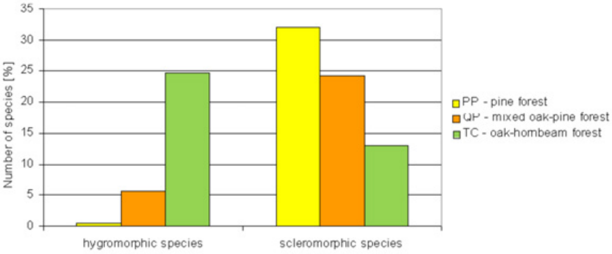


Fig. 138. Share of species with given anatomical structure type (AB) in three types of forest communities

Ryc. 138. Udział procentowy gatunków o określonej budowie anatomicznej w trzech typach zbiorowisk leśnych

Life form [LF]

Two life forms differentiate most distinctly the forest types considered, namely the tree-form chamephytes and the geophytes. The share of dwarf shrubs is the highest in the pine forests (25%), somewhat lower in the mixed oak-pine forests, and very low indeed in the lime-oak-hornbeam forests (around 3%). The opposite situation is in the case of geophytes – their number being relatively the lowest in the pine forests, a bit higher in the mixed oak-pine forests, and the highest in the lime-oak-hornbeam forests (Fig. 139).

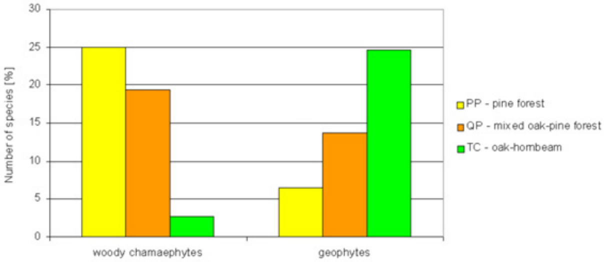


Fig. 139. Share of species with given life form (LF) in three types of forest communities

Ryc. 139. Udział procentowy gatunków o określonej formie życiowej w trzech typach zbiorowisk leśnych

Seed dispersal mode [VT]

Three types of seed dispersal mechanism: autochores, endozoochores, and anemochores differentiate the forests analysed (Fig. 140). The autochores play the smallest role in the pine forests (at around 10%), there is a bit more of them in the mixed oak-pine forests (approximately 16%), their share being decidedly the highest in the lime-oak-hornbeam forests (around 27%). The shares of endozoochores and anemochores assume an opposite profile. The endozoochores are most numerous in the pine forests (at roughly 25%), only a bit less numerous in the mixed oak-pine forests (around 22%), and clearly least numerous in the lime-oak-hornbeam forests (around 12%). In all three types of forests the species dispersed by the wind dominate, their share being the highest in the pine forests (approximately 53%), a bit less in the mixed oak-pine forests and in lime-oak-hornbeam forests, roughly 47% and 43%, respectively.

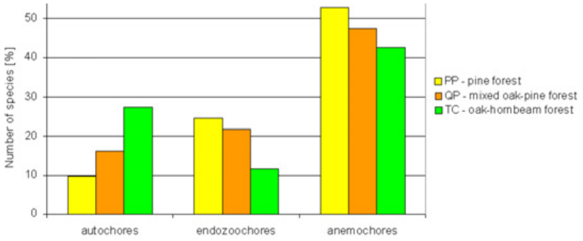


Fig. 140. Share of species with given dispersal mode (VT) in three types of forest communities

Ryc. 140. Udział procentowy gatunków o określonym typie rozsiewania w trzech typach zbiorowisk leśnych

Life strategy type [STR]

Two types of plant life strategies, namely *cs* and *csr*, differentiate most distinctly the forest types analysed. The *cs* type is represented in the highest values in the fresh pine forests, with only a bit smaller representation in the mixed oak-pine forests (around 41%), while the share in the lime-oak-hornbeam forests is decidedly the lowest (approximately 20%). An opposite distribution is observed for the *csr* strategy. The *csr* - strategists are the least numerous in the pine forests (roughly 16%), their share is a bit higher in the mixed oak-pine forests, and definitely it is the highest in the lime-oak-hornbeam forests (at around 41%)- Fig. 141.

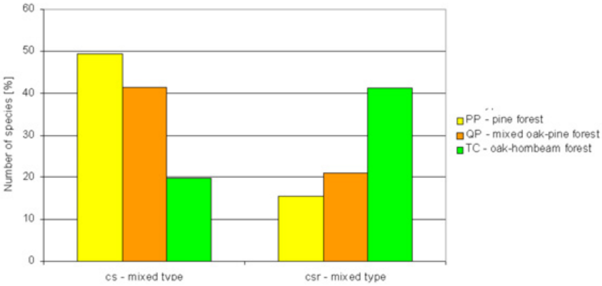


Fig. 141. Share of species with given life strategy type (STR) in three types of forest communities

Ryc. 141. Udział procentowy gatunków o określonym typie strategii życia roślin w trzech typach zbiorowisk leśnych

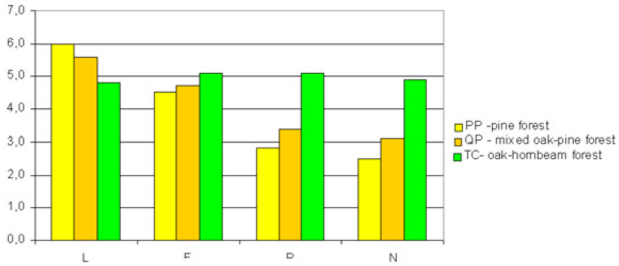


Fig. 142. Mean ecological indicator values in three types of forest communities
Ryc. 142. Wartości średnie liczb ekologicznych w analizowanych zbiorowiskach leśnych

Mean L value is the highest in the fresh pine forests (L6.0), somewhat lower in the mixed oak-pine forests (L 5.6), and the lowest in the lime-oak-hornbeam forests (L 4.8) - (Fig. 142). This implies a higher share of species requiring more light in the fresh pine forests, contrary to the lime-oak-hornbeam forests, where the share of species requiring moderate shade is higher. This is, obviously, the effect of specific characteristics of these forest communities, and especially of the respective tree layers, composed in the latter case mainly of leaved trees, and so the herb layer is formed there by species requiring relatively shady sites.

Mean F value is relatively even across the forest communities considered (F 4.5-5.1) - (Fig. 142), and it indicates that in all forests analysed the vascular plants species dominate having optimum of appearance on fresh soils. The F value is actually the highest in the lime-oak-hornbeam forests, and the lowest in the pine forests, the mixed oak-pine forests occupying the middle position, although the mean F value is only slightly higher there than that in the fresh pine forests.

Mean R values differ especially between the fresh pine forests and the lime-oak-hornbeam forests. In the fresh pine forests species displaying preference for acid soils (R 2.8) dominate, while in the lime-oak-hornbeam forests – those preferring moderately acid soils (R 5.1). Mean R value of the mixed oak-pine forests is closer to that of the fresh pine forests (0.6 of difference) than to that of the lime-oak-hornbeam forests (1.7 of difference).

There is also a distinct difference in the mean N value between the forest types. The richest in nitrogen compounds are the lime-oak-hornbeam forests (N 4.9), while most oligotrophic (the apparently poorest in nitrogen) are the fresh pine forests (N 2.5). The latter is the effect of clear domination in the herb layer of species preferring soils poor in nitrogen content, contrary to the lime-oak-hornbeam forests, where the species indicative of habitats rich in nitrogen dominate. Similarly to the previously considered features, the mean N value in the mixed oak-pine forests is closer to that of the fresh pine forests (0.8 of difference) than to that of the lime-oak-hornbeam forests (1.8 of difference) - (Fig. 142).

Summing up the results here reported, it can be stated that despite the differences in forests history (from the most natural to those most strongly disturbed by human), their specific characteristics, corresponding to types, have been preserved, in particular – regarding the ecological characteristics. And so, the fresh pine forests are most lit, their habitats are the driest, most acid and oligotrophic (the poorest in nitrogen compounds), while the lime-oak-hornbeam forests are most shady, their habitats somewhat more moist than the other ones, but, at the same time, distinctly less acid and decidedly more fertile. The mixed oak-pine forests occupy an intermediate position, although in terms of the majority of features they are more similar, as to their requirements, to the fresh pine forests than to the lime-oak-hornbeam forests.

6.5. COMPARISON OF ECOLOGICAL CHARACTERISTICS BETWEEN ANCIENT AND RECENT FORESTS ON THE BASIS OF THEIR SPECIES COMPOSITIONS – SUMMARY

Synthetic and simple comparison of diagnostic features (morphological-anatomic features and indicator values) between ancient and recent forests in three types of forest communities illustrate Figure 143.

Pine forests

The ancient and the recent pine forests differ in the shares of herb layer plants, featuring definite spectra of: (1) life form (LF), (2) type of seed dispersal (VT), and (3) plants life strategy (STR). Their shares differ also in case of: (1) light (L), (2) soil reaction (R), and (3) nitrogen compound content in the soil (N) indicators.

Regarding life forms, a relatively higher share is observed in the ancient forests than in the recent ones of the tree-form chamephytes and of geophytes, as to the seed dispersal mode – of myrmecochores, autochores and endozoochores, and as to the types of plants life strategies – of the *cs* type, i.e. of the plants adapted to the environments, in which the stress impact is limited. Further, a higher share than in the recent forests is observed of shade-tolerant species (L 2-3), and of indicators of strongly acid soils (R1) and of extremely oligotrophic ones (N1).

On the other hand, in the recent forests higher shares are observed of herbaceous chamephytes, of anemochores, and of species of competitive type *c*. In addition, the average values of L, R and N are also higher than in the ancient forests, which demonstrates higher alkalinity and higher fertility of soils in the recent forests than in the ancient pine forests.

Mixed oak-pine forests

The ancient mixed oak-pine forests are characterised by relatively higher shares, compared to the recent forests, of: hygromorphs, geophytes, autochores, species with the *cs* life strategy, species of deep shade (L1) and shade (L 2-3).

The average values of F, R and N indicators are higher in the ancient mixed oak-pine forests, indicating higher shares of: hydrophilous species (F 6-7), indicators of moderately acid and moderately alkaline habitats (R 6-7), and habitats rich in nitrogen compounds (N 6-7).

The recent forests, on the other hand, differ from the ancient forests by the higher share of: herbaceous chamephytes, megaphanerophytes and nanophanerophytes, anemochores, species with *c* life strategy, and photophilous species (L 6-7).

Lime-oak-hornbeam forests

The ancient forests are characterised by the higher shares, compared to the recent forests, of: hygromorphs, geophytes, autochores, *csr* – strategists and species preferring shaded habitats (L 2-3).

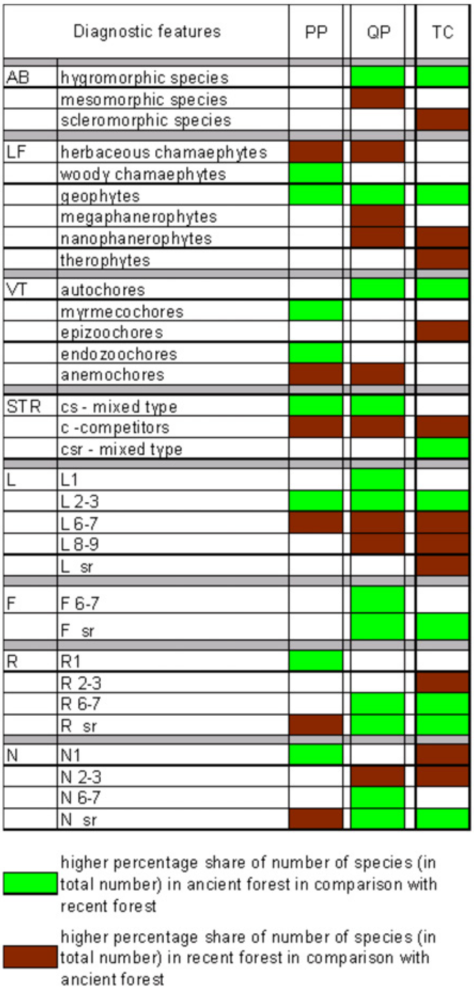
The ancient forests are also characterised by the somewhat higher – than in the recent forests – shares of species preferring the habitats that are: moist (hence a somewhat higher average F value), moderately acid and moderately alkaline, R 6-7 (and so the average R value is higher), rich in nitrogen compounds, N 6-7 (as reflected by the higher average N value).

The recent lime-oak-hornbeam forests feature, on the other hand, higher shares of: scleromorphs, nanophanerophytes, therophytes, *c* – strategists, photophilous (L 6-7 and L 8-9) species, which results in the higher average L value, acidophilous (R 2-3) species, indicators of extremely poor (N1) and poor (N 2-3) habitats.

All types

As we consider all types of forests together (pine, mixed oak-pine and lime-oak-hornbeam forests), we can state that irrespective of the community type, the ancient forests, when compared to the recent ones, are characterised by the relatively higher shares of: geophytes, autochorous species, shade-tolerating species.

The recent forests, irrespective also of the association type, are characterised by the relatively higher than in the ancient forests species share of the competitive type *c*.



Diagnostic features		PP	QP	TC
AB	hygromorphic species		🟩	🟩
	mesomorphic species		🟫	
	scleromorphic species			🟫
LF	herbaceous chamaephytes	🟫	🟫	
	woody chamaephytes	🟩		
	geophytes	🟩	🟩	🟩
	megaphanerophytes		🟫	
	nanophanerophytes		🟫	🟫
	therophytes			🟫
VT	autochores		🟩	🟩
	myrmecochores	🟩		
	epizoochores			🟫
	endozoochores	🟩		
	anemochores	🟫	🟫	
STR	cs - mixed type	🟩	🟩	
	c -competitors	🟫	🟫	🟫
	csr - mixed type			🟩
L	L1		🟩	
	L 2-3	🟩	🟩	🟩
	L 6-7	🟫	🟫	🟫
	L 8-9		🟫	🟫
	L sr			🟫
F	F 6-7		🟩	
	F sr		🟩	🟩
R	R1	🟩		
	R 2-3			🟫
	R 6-7		🟩	🟩
	R sr	🟫	🟩	🟩
N	N1	🟩		🟫
	N 2-3		🟫	🟫
	N 6-7		🟩	
	N sr	🟫	🟩	🟩

🟩 higher percentage share of number of species (in total number) in ancient forest in comparison with recent forest

🟫 higher percentage share of number of species (in total number) in recent forest in comparison with ancient forest

Fig. 143. Summary comparison of ancient and recent plots in three types of forest communities based on diagnostic features and ecological indicator values

Ryc. 143. Syntetyczne porównanie lasów starych i wtórnych badanych typów – na podstawie analizy fitoindykacyjnej ich składów gatunkowych.

6.6. COMPARISON TO OTHER STUDIES

The results, which have been reported in this chapter, are in accordance with those known from the literature, even though the majority of studies concern the floristic composition of ancient and recent deciduous forests. There is less information on pine and mixed oak-pine forests. It seems that the results here reported can be considered most comparable to those referring to Polish ancient and recent (post-agricultural in their majority) forest complexes.

Thus, A. Orczewska (2010) analysed in south-eastern Poland forests with black alder, featuring high groundwater level. She demonstrated that the species composition of herb layer in the ancient forests contains a higher number of geophytes, while in the recent forests – of therophytes. In the ancient forests the *s*-strategists dominate, along with myrmecochores and autochores. In the recent forests the *sr*- and *cr*-strategists dominate, together with anemochores, epizoochores and endozoochores. The recent forests host a higher number of species indicative of slightly acid or alkaline soils, and there are more species preferring moderately shaded sites and moist soils. On the other hand, in the ancient forests there are higher shares of species indicative of low or moderate nitrogen content than in the recent forests.

The very same author (Orczewska 2007) analysed the communities of lime-oak-hornbeam forest, alluvial deciduous forest, alder carr, as well as planted pine woods on the fallowed fields adjacent to the ancient pine forest communities on the habitat of fresh pine or mixed oak-pine forests, within the area of Oleśnica Plain. She demonstrated that in the ancient forests the spectrum of life forms contains a significant share of herbaceous or lignified (depending upon the forest type) chamephytes and of geophytes, while therophytes are less numerous, and in the recent forests growing on post-agricultural land the proportions are reversed. The absence of geophytes and chamephytes in the post-agricultural forests can be explained, according to the author quoted, by the narrow ecological amplitude of these species, their lack of resistance to competition, as well as mechanical cultivation operations. The high share of therophytes in the forests of recent origin is due to the disturbances, to which this species group is resistant. The spectrum of life strategies in the ancient forests contains a high share of *s*-strategists, plants resistant to stress in the sense that they withstand limitations to photosynthesis (shortages of light, water, nutrients). Domination of the strategists of types *r* and *c* (capable of competing), *cr* or *sr*, along with a marginal share or lack of plants resistant to stress, is, on the other hand, a typical feature of post-agricultural forests. There is a significant share of myrmecochores and autochores, characteristic of the ancient forests. Then, in the post-agricultural forests the species dominate that are dispersed by the wind (anemochores), by the animals (epizoochores or endozoochores), and those, whose spread is facilitated by farming operations.

Studies within Oleśnica Plain in the province of Opole were also carried out by Góras and Orczewska (2007) in the ancient and recent forests on similar habitats, taking into account, as well, their proximity, in order to exclude the influence of spatial isolation. All the floristic relevés were made in the pine forests on the mixed oak-pine forest habitat, in the 40-years old recent pine woods and in the ancient more than 100 years old pine forests. The analysis of the results allowed for the observation that the floristic composition of ancient forests contains by about half less of hemicryptophytes than that of the post-agricultural forests, while containing roughly 30% more phanerophytes (trees and shrubs) than in the recent forests. On the other hand, the average values showed that the values of chamephytes and cryptophytes were higher in the ancient forests, and of the remaining forms – phanerophytes and hemicryptophytes – in the recent forests. The post-agricultural forests contained more species tolerating disturbances of different intensity: types *r*, *cr*, *sr* and *csr*. These forests contained also close to two times more epizoochores, and many more endozoochores and anemochores than the ancient forests. At the same time, the share of myrmecochores in the ancient forests was almost twice as high as in the forests of recent origin.

Similarly, Dzwonko (1993), having carried out ecological analysis of the deciduous and the mixed oak-pine forests in Wierzbanówka in the northern part of the Carpathian Foothills (Wielickie Foothills), found close relation between the seed dispersal types of species and their capacity of colonising the recent forests. The lightweight anemochores and the endozoochores turned out to be the best colonisers, while the heavyweight anemochores and the myrmecochores could hardly colonise the new sites. Studies much like this were also performed in the Landscape Park of Bolimów in central Poland by Jakubowska-Gabara and Mitka (2007). They considered three types of habitats: pine plantings, recent and ancient deciduous forests *Tilio-Carpinetum*. It can be deduced from the analysis, carried out by them, that the lightweight anemochores, typical of the recent forests, appear only sporadically in the ancient forests, while the *s*-strategists, mainly grass species, dominate in the ancient forests.

Z. Dzwonko (2001) conducted, as well, investigations in the Skołczanka Reserve in the unmanaged recent pine forests with the neighbouring ancient lime-oak-hornbeam forests (*Tilio-Carpinetum*) on dry rendzina soil. The author writes that the distance of recent forest complexes to the ancient forests has a significant influence on their species composition and ecological features. Thus, the share of myrmecochores decreases with the increase of distance from the ancient forests, while the number of trees and shrubs, and of anemochores, increases. Likewise, the number of photophilous species also increases. Dzwonko (2001) writes that the litter of deciduous forests decays two times faster than that of coniferous forests. This means that the sites with the leaved litter of recent forests can be colonised faster by the majority of ancient forests species than in the case of coniferous forests. Shrubs are quite demanding with respect to light, and it is light that influences the increase in species number in this layer of the recent forests. Summing up, the recent forests communities rich in species may be maintained in the fragments of ancient forests only when they directly neighbour and are dominated by deciduous tree species with quickly decomposing litter, and when these conditions are over long-term period.

The same author (Dzwonko, 2001), when conducting ecological-biological investigations within the Carpathian Foothills, considered the possibility of applying the ecological Ellenberg indicator values, which is used widely for the assessment of light and soil conditions, not only in Central Europe, but also outside of it. The purpose of the study referred to was to answer the question of the degree, to which the Ellenberg indicator values could be applied in characteristics of environmental conditions of the ancient and recent deciduous (neighbouring) forests on the same soil type. It ought to be emphasised that the species with the lowest indicator R and N values were less numerous in the recent forests than in the ancient ones. The recent forest complexes featured higher shares of species with higher indicator R and N values. This explains partly, why the ancient forests indicator species, mostly acidophilous and oligotrophic, hardly colonise the richer habitats of recent forests. Z. Dzwonko (2001) notes that the average values of the L, R and N indicators were relatively good yardsticks for the assessment of environmental conditions in the ancient forests with stabilised species composition, while not so good in the case of recent forests with yet unstable structure, and ought to be verified by direct laboratory measurements of the environmental variables.

It should be underlined that studies akin to those conducted in Poland have been also performed in many other European countries, using, as well, phytoindication analysis, frequently with respect to similar forest communities types.

And so, results similar to those obtained on the basis of the phytoindication analysis of Polish forests, were reported by M. Wulf (2004) for the study carried out in south-eastern Germany in ancient forests (19th century) and recent forests (20th century), with domination of birch and oak in the stands. Here, as well, the ancient forests hosted much higher number of species tolerating shade, and also of species indicative of moderately acid soils and avoiding soils rich in nitrogen compounds, as compared to recent forests. The same author (Wulf 1997), demonstrated on the basis of studies carried out in deciduous forests from the order *Fagetalia sylvaticae* (*Fagion*, *Carpinion*, *Alno-Ulmion* alliances), also situated in south-eastern Germany, that investigations of historical ecology help in explaining the floristic composition of contemporary forests, featuring usually different degrees of anthropogenic transformation. The author referred to notes that lack of the ancient forest species in the recent complexes is mostly caused by the lack of possibility of long-distance dispersal (most of these species are the myrmecochores and autochores, their seeds being transported over short distances), and by the isolation of ancient forests in the landscape. This conclusion is confirmed by the results of studies, reported by Dzwonko and Gawroński (1994), who demonstrate that the ancient forest species usually relatively quickly colonise the recent forests located in direct vicinity of the ancient forests. Wulf (1997) observes also that based on the Ellenberg N indicator value some species of recent forests display higher requirements with respect to nitrogen, or are better adapted to higher content of this element in comparison with the ancient forest species.

In north-western Belgium deciduous and recent forests belonging to *Alno-Padion* and *Quercion* alliances were analysed (Verheyen et al. 2003a). Authors of the respective work noted low number and low cover of geophytes in recent forests, this being explained by the production of a small number of hardly dispersed seeds, which lowers their chances for an early colonisation of new sites.

Also in Belgium, but in its central part, B. Bossuyt et al. (1999) analysed migrations of the undergrowth vascular plant species across the ecotones between the ancient and recent deciduous forest complexes. Based on the results obtained these authors showed that myrmecochores, hardly capable of swift colonisation of new places, are the dominat species in the ancient forests, contrary to endozoochores and anemochores, whose higher shares were observed in the recent forests. Their species bear more easily the increase of nitrogen content in the soil (the Ellenberg N indicator value), compared to the ancient forests. Likewise, more species have been observed in them that require well lit plots (L). These species encounter difficulties in expansion and occupation of new sites also because the ancient forests are characterised by high cover degree by species better adapted to the shaded sites (low L value) and low nitrogen content (low N value).

M. Dumortieri et al. (2002) analysed forests belonging to *Quercion* alliance – also situated in central Belgium – and demonstrated that autochores and myrmecochores dominate in ancient forests, and are absent in the recent forests, in which, in turn, the shares of endozoochores and anemochores are higher. According to these authors an important factor, determining species composition, is also constituted by the habitat quality. Thus, for instance, the level of soil reaction (pH) is low in the ancient forests and statistically negatively correlated with the forest age.

In a similar vein, the migration rate of 49 species across the ecotones between the ancient and recent (post-agricultural) forests was measured in southern Sweden (Brunet, von Oheimb 1998). The authors referred to show, just like those mentioned before, that the species distributed by ants have a lower rate of migration than the epi- and endo-zoochorous species.

Likewise, B. J. Graae et al. (2003) showed for the forest complexes in Denmark with domination of birch and planted spruce that many of the ancient forest species very slowly colonise the recent forests habitats. Even when the recent forests, having persisted for 100-200 years neighbour upon the ancient forests, the effect of past land use has left an imprint on the vegetation, including species composition. On the basis of the results obtained the authors concluded that the soil variables on the recent plots were not linked with the past land use. These studies showed that even if a number of recent forest complexes are planted within the confines of a large ancient forests complex, the species migrate to the new stands and colonise the new places very slowly. The authors quoted suggest, therefore, that it is not the soil type that is responsible for the phenomenon. The main conclusion from these studies is, therefore, that dispersal over far distances is not characteristic of the ancient forest species and this fact – rather than soil conditions – constitutes the limiting factor.

It is also worth noting the very significant investigations, consisting in the compilation of the literature-based data originating from various countries. So, in particular, M. Hermy et al. (1999) demonstrated, on the basis of ecological characteristics of 132 species of ancient deciduous forest plants in Europe, taken from 22 literature sources, that these species tolerate better shaded sites, are the indicators of moderately moist, moderately acid and moderately rich in nitrogen habitats (that is – avoid habitats displaying extreme features), when compared to recent forests. According to Hermy et al. (1999) the composition of ancient forests is dominated by geophytes and hemicryptophytes, *s*-strategists, as well as species featuring low seed production, meaning that they encounter difficulties in colonising new places. The recent forests, on the other hand, are dominated by the *c*-strategists.

Quite similarly, K. Verheyen et al. (2003b), who surveyed literature from eight European countries and four from the North America, carried out the analysis of 216 forest plant species characteristics, that may determine their reaction to changes in land use. Like in the cases of the studies already referred to, the authors demonstrated that the forest plant species with heavy seeds, transported by ants (myrmecochores), are more common in the ancient forests, while the shares of species with seeds of small dimensions and those transported on the outside of animals (epizoochores) are much more frequent in the recent forests. It is worth noting – according to the authors quoted – that many of species colonising moderately moist (fresh) habitats, do colonise dry habitats slower. It appears, therefore, that production of a large number of easily transported seeds does not guarantee colonisation of places featuring extreme environmental conditions.

Further, P. de Frenne et al. (2011), having compiled 18 independent sources, originating from 18 European countries, meaning, actually, the continental scale, obtained the results showing that over a long time horizon (more than 370 years) the species having limited capacity of spreading shall disappear from the forest communities planted on post-agricultural habitats, and may altogether disappear in Europe.

It ought to be emphasised that the ecological characteristics, presented in this chapter, involving application of the phytoindication analysis of forest communities on different soil habitats and subject to diversified human impact within the Masurian-Kurpie borderland fits perfectly well the subject matter of the literature survey here commented upon. The results obtained by us showed, as well, that first of all the species shares featuring definite adaptation properties, namely: type of life form, type of seed dispersal, and type of life strategy, are the determinants of two groups – the ancient and the recent forests. These properties, therefore, ought to be an important tool for comparing ecological characteristics of ancient and recent forests. It is, on the other hand, hard to unambiguously establish the indicator value of plant species forming the compositions of ancient and recent forests, since this depends upon the type of phytocoenosis and its habitat conditions. This was also confirmed by the results of B. J. Graae et al. (2003). According to them, the species of ancient forests are more effectively constrained by the dispersal mode than by their microhabitats. Conclusions from our studies are in agreement with the results obtained by many of the authors quoted, and they show that the Ellenberg indicator L value unequivocally distinguishes ancient and recent forests, irrespective of the type and the habitat conditions, in which they occur.

Given that in ancient forests vascular plants species featuring low capacity of spatial spreading (being mainly myrmecochores and autochores) dominate in the herb layer, they might be considered the ancient forest indicator species, since their appearance outside of such areas is quite limited (see e.g. Orczewska 2007). The ancient forest species conform to their ecology and low capacity of colonising new locations, ought also to be treated as an important indicator of biodiversity (Hermy et al. 1999).

7. THE ANCIENT AND THE RECENT FORESTS – ANALYSIS OF SOILS DIVERSITY

7.1. PREREQUISITES FOR THE SOIL STUDY

Investigations of the soil cover, carried out in the study plots, determined on the basis of phytosociological criteria, encompassed soils not bearing the traces of farming activities, as well as those having been used for agriculture in the historical past. Altogether 200 soil profiles were made, which served to assess the morphology of soil profile and to diagnose soil and humus types. Samples were also collected from each genetic horizon of the soil, meant for the indication of pH value (potentiometric measurement in H_2O), and of organic carbon, total nitrogen and sulphur content (using VarioMax CNS Elementar analyser). The quantity of organic carbon was determined as TOC = TC-TIC (TOC – total organic carbon, TC – total carbon, TIC – total inorganic carbon). The CNS measurements quality was verified with the use of reference materials: Sulphadiazin, CP1 and SQC001S. On the basis of the results obtained the ratio C:N was calculated.

The soils analysed belong to four orders, conform to the Soils Systematic of Poland (2011), that is: brown-earths (type: brown-dystrophic), rusty-earths (type: rusty soils, sub-type: typical and rusty with traces of podzolic), lessive-earths (type: fallow soils), and podzolic-earths (type: podzolic).

7.2. THE SOILS THICKNESS

Podzolic soils

Podzolic soils, appearing over the entire study area, both within the Masurian and Kurpie parts, are associated with the pine forests, constituting consecutive forest generations. They do not display any traces of farming activities. They are characterised by the following sequence of distinctly developed genetic horizons: O – Aees – Ees – Bh – Bfe – C, or O – A – Ees – Bh – Bfe – C, with different thickness, depending, in particular, upon the time factor, as the determinant of soil-forming process, and the habitat fertility. The biggest thicknesses of soils appear, therefore, in the optimum habitat conditions for the development of podzolic soils, on which ancient pine forest grows. The thickness of organic horizon (O) ranges from 5 to 15 cm, of humus horizon (A) – from 8 to 18 cm, and of eluvial horizon (E) – from 12 to 21 cm. The illuvial horizons Bh and Bfe attain together the thickness between

18 and 47 cm. Podzolic soils are characterised by the mor-humus type, with the organic layer split into three subhorizons: litter (Ol), rotting (Of), and epi-humus (Oh). The humus of these soils is represented by two sub-types: drosomor, appearing in the majority of the profiles investigated, and hygromor, characteristic of more humid sites.

Rusty soils with podzolic traces

The highest share among the soils investigated is taken by the rusty soils with traces of podzolisation, featuring the profile structure O – AE – Bsv – Bv – C, and the post-agricultural, featuring the profile O – Ap – AE – Bsv – Bv – C. Podzolisation in these soils is a process overlaying the rustification processes and it is more distinct in the soils having been longer influenced by the coniferous monocultures or the pine forest communities. In their vast majority, these soils have been subject to agricultural use in the past. Yet, most probably in view of their low fertility, farming operations have been given up at various time points. Hence, depending upon the period since cultivation has been abandoned and natural soil processes were initiated, the soils investigated feature diverse thicknesses of genetic horizons. The humus-eluvial horizon (AE) is best developed in the soils not transformed by human intervention, its thickness ranging from 6 to 12 cm. In the remaining soils, given the superposition of ploughing features in the profiles, together with the plough horizon (Ap) it attains the depth of approximately 17–18 cm. Yet, the thickness of humus-eluvial horizon (ApE), found over the Ap horizon, is very clearly dependent upon the duration of this process in the soil. In the soils, under older recent pine forests, that is – at least of 230–170 years persistence (categories PP2, PP3, PP4), the thickness of ApE horizon amounts to approximately 4.1 cm, while on the areas featuring a shorter presence of the recent forests this thickness drops to 2.9 cm on the areas with the forest persisting for some 120 years, and yet to 2.0 cm in the soils with forests of 90 years persistence. The humus type, characterising the rusty soils with traces of podzolisation, is mor/moder, while the thickness of organic horizon equals on the average 7 cm.

Typical rusty soils

Rusty soils of the study area are associated mainly with the habitats of mixed oak-pine forests, only sporadically with pine forests or lime-oak-hornbeam forests. In the soils not having undergone anthropogenic transformation the sequence of horizons looks like: O – A – Bv – C, while in the soils after past agricultural cultivation: O – Ap – Bv – C. Similarly as in the rusty soils with traces of podzolisation, also in the typical rusty soils the thickness of plough horizon (Ap) is much alike in all persistence categories of recent mixed oak-pine forest, amounting to 18–19 cm. Humus in the rusty soils is of moder type, and thickness of the organic horizon equals 5–6 cm.

Fallow and brown soils

Fallow soils: O – A – Et – Bt – C, and brown dystrophic soils: O – A – Bw – C are covered by the lime-oak-hornbeam forests, and in some parts of the study area – by the mixed oak-pine forests. For the majority of profiles investigated, the tree stands growing on these soils are old, and forests exist there for more than 230 years. In the post-agricultural soils, plough horizon is visible in the profiles, its thickness being at around 20 cm. These soils are characterised by the moder/mull type of humus, and the organic layer attains the thickness ranging from 0.5 to 3 cm.

7.3. SOIL REACTION (PH)

Soil reaction is one of the diagnostic features of the soils investigated. The soils analysed do not diverge in terms of the pH values range from their analogues in other regions of Central European Plains, covered by the vegetation of pine forests, mixed oak-pine forests, or lime-oak-hornbeam forests. The pH value is the lowest in the soils, which do not bear the traces of farming activities, i.e. these soils feature the highest acidity. In the humus horizon (A) of brown and fallow soils, constituting the habitats of lime-oak-hornbeam forests, it amounts on the average to 4.6 (H^+0.00025 mole/dm^3), in the podzolic soils and the rusty ones with traces of podzolisation, overgrown with pine forest this value is 4.5 (H^+0.00031 mole/dm^3), while in rusty soils covered by mixed oak-pine forest – 4.4 (H^+0.00041 mole/dm^3). Fig. 144 shows the concentrations of hydrogen ions in the soils of ancient forests.

Lower acidity of soils, and hence also lower concentration of hydrogen ions (Fig. 145) is observed in the soils that have been subject to agricultural use. The biggest differences between the soils without the footprints of human activity and those with distinct plough horizon are observed in the rusty soils with traces of podzolisation, covered by the pine forests (PP). One registers in these soils a general tendency towards the decrease in pH value of the plough horizon along with the forest persistence and their contemporary state. The shorter the forest persistence, the less acid the soil and the lower concentration of hydrogen ions (Fig. 145). It can be supposed that such a situation is the consequence of agrotechnical measures, carried out during soil cultivation , including introduction of natural fertilisers, containing, in particular, chemical compounds of calcium.

In the soils, covered by pine forests for around 120 years (PP 5-6), the value of pH in Ap horizon is at around 5.5 (H^+0.000005 mole/dm^3), while in the soils afforested 170-200 years ago, this value is at 5.1 (H^+0.000079 mole/dm^3), see Fig. 145. Lower pH values than those commented above, and therefore also higher concentrations of hydrogen ions have been observed in the Ap horizons of soils overgrown by pine forests for at least 230 years (PP2).

Lower pH in these soils may result from the state of geochemical equilibrium and the stable buffering properties attained by these soils.

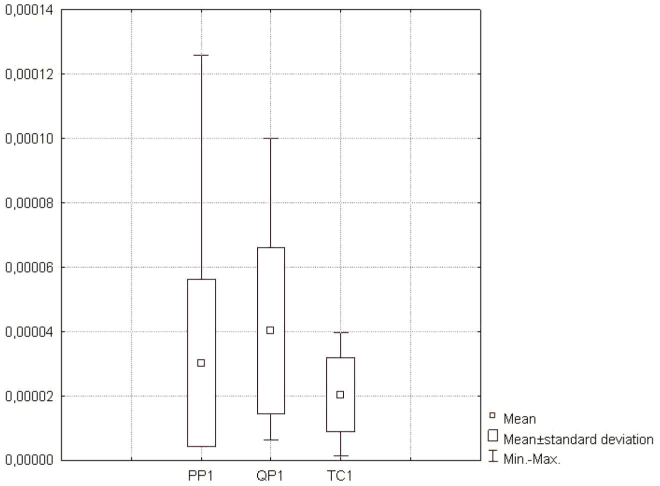


Fig. 144. The hydrogen ion concentration (mol/dm3) in humus horizon (A) in ancient forests of three community types. (PP1 – pine forests, QP1 – mixed oak-pine forests, TC1 – lime-oak-hornbeam forests).

Ryc. 144. Stężenie jonów wodorowych (mol/dm3) w poziomie próchnicznym (A) gleb w „starych lasach" trzech typów. (PP1 – bory, QP1 – bory mieszane, TC1 – grądy)

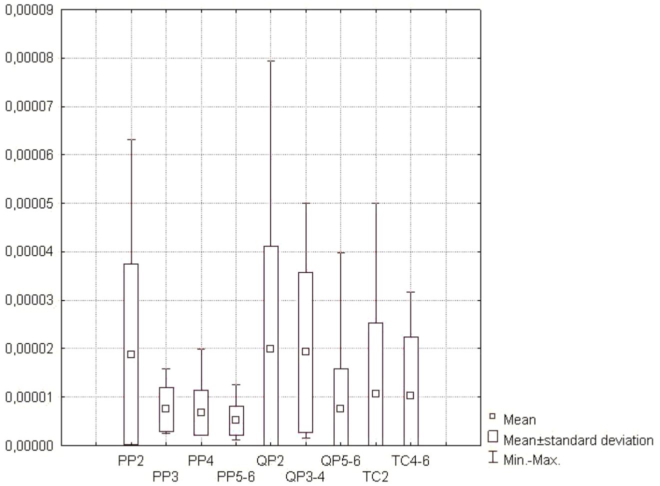


Fig. 145. The hydrogen ion concentration (mol/dm3) in humus horizon (Ap) in post-agricultural soils.

Ryc. 145. Stężenie jonów wodorowych (mol/dm3) w poziomie próchnicznym (Ap) w glebach porolnych

7.4. ORGANIC MATTER

The profile-wise distribution of organic carbon (CTO) in the soils investigated is a clear reflection of typological differences between soil types, quantitative and qualitative characteristics of nutrient content, granulation, as well as water-and-air properties.

Organic matter is accumulated in the soils analysed mainly in the sub-horizons of organic horizon and in the humus layers. The quantity of organic carbon (CTO) in the sub-horizons of organic layer decreases with the increase in the organic material humification degree , from the litter sub-horizon (Ol) to the epi-humus sub-horizon (Oh). In the mineral part of soil profiles (solum) the content of organic matter decreases with depth, except for the diagnostic horizon spodic in podzolic soils. A significant increase in the carbon content is particularly observed – in relation to the neighbouring genetic horizons – in the sub-horizon of enrichment (Bh) with illuvial accumulation of organic matter.

In the humus horizons, the highest carbon content is observed in the brown and fallow soils, being the habitats of lime-oak-hornbeam forests. It exceeds there 3%. In the pine forests with podzolic and rusty soils bearing traces of podzolisation, and in mixed oak-pine forests mainly with rusty soils without traces of human farming activities, organic carbon content is lower, between 1.9 and 2.2% (Fig. 146).

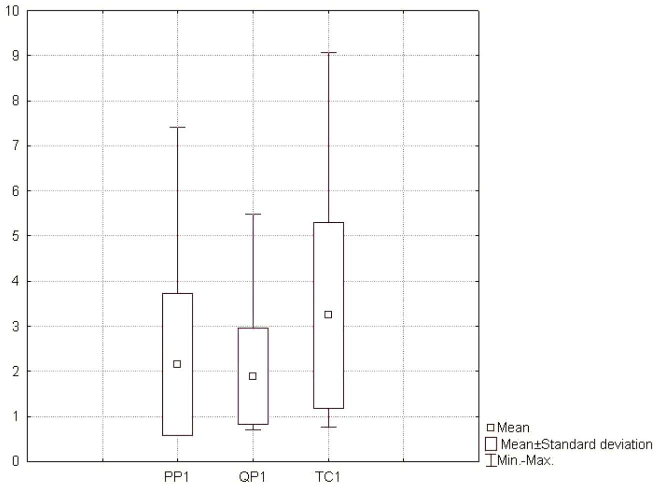


Fig. 146. The content of organic carbon in humus horizon (A) in ancient forests of three community types. (PP1 – pine forests, QP1 – oak-mixed pine forests, TC1 – lime-oak-hornbeam forests).

Ryc. 146. Zawartość węgla organicznego w poziomie próchnicznym (A) gleb w „starych lasach” trzech typów. (PP1 – bory, QP1 – bory mieszane, TC1 – grądy)

Lower contents of organic carbon are observed in the plough horizon (Ap). The reserves of organic carbon in these soils result, on the one hand, from the habitat conditions and the agrotechnical measures during cultivation, and on the other hand – from the degree of removal of this element as the component of agricultural products biomass. The lowest content is observed in the rusty soils with traces of podzolisation, which had been under agricultural use more than 230 and 120 years ago. This might indicate the most intensive degradation of these soils, lack or very primitive application of fertilisers, as well as a significant disturbance of the ecosystem biochemical equilibrium. In the plough horizon of soils considered the CTO content amounts to, respectively, 1.02 and 0.97%. In the recent forests belonging to remaining persistence categories, i.e. 200, 170 and 90 years, the CTO content values in the plough horizons of podzolic soils and rusty soils with traces of podzolisation are quite similar and range between 1.12 and 1.16% (Fig. 147).

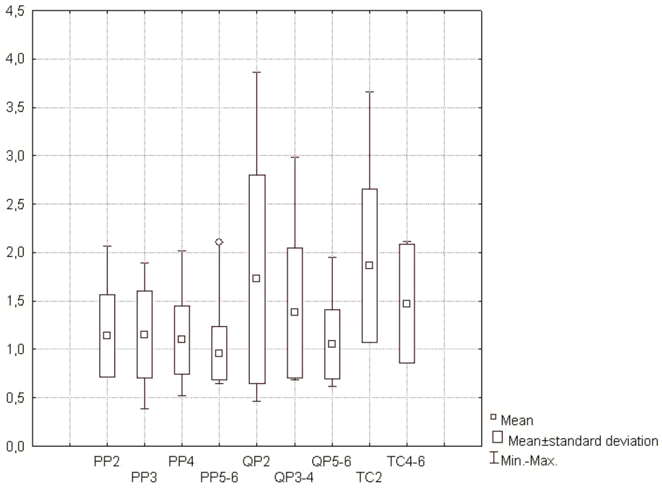


Fig. 147. The content of organic carbon in humus horizon (Ap) in post-agricultural soils.
Ryc. 147. Zawartość węgla organicznego w poziomie próchnicznym (Ap) gleb porolnych

Organic carbon content has different characteristics in the rusty soils of mixed oak-pine forests and in the brown and fallow soils of lime-oak-hornbeam forests. In these soils the reserves of organic carbon decrease with the shortening period of recent forests persistence, that is – the shorter the forest grows on post-agricultural land, the lower the content of organic carbon in the soil. In the plough horizon of rusty soils the decrease is observed from 1.76% in the soils having been for more than 230 years under the influence of recent mixed oak-pine forests, down to 1.04% in the forests not older than 90 years. Similarly, in the brown and fallow soils under lime-oak-hornbeam forests the content decreases from 1.87% in forests with more than 230 years of persistence to 1.44% in the younger ones (Fig. 147). The observed relationship between the CTO content in the soils and the forest persistence demonstrates the preservation of biochemical equilibrium in the ecosystems and the regeneration capacity .

Altogether, the data collected allow for the establishment of the following regularities:

- the plough horizon on the more fertile habitats, i.e. those of mixed oak--pine forests, and especially of lime-oak-hornbeam forests, displays progressing regeneration of the soils, conform to the increasing persistence of recent forest;
- the plough horizon within the poor habitats of pine forests displays an insignificant degree of soil regeneration along with the persistence of recent forest, so that its permanent existence in the ecosystem can be assumed, at least over the time horizon of several centuries.

7.5. NITROGEN

Nitrogen, side by side with carbon, belongs among the most important biogenic elements, decisive for the activity of biochemical processes in soils. Its content in the soils analysed does not differ from that found in the analogous types of soils by other authors (Białousz 1978; Bednarek1991; Räisänen 1996; Degórski 2007).

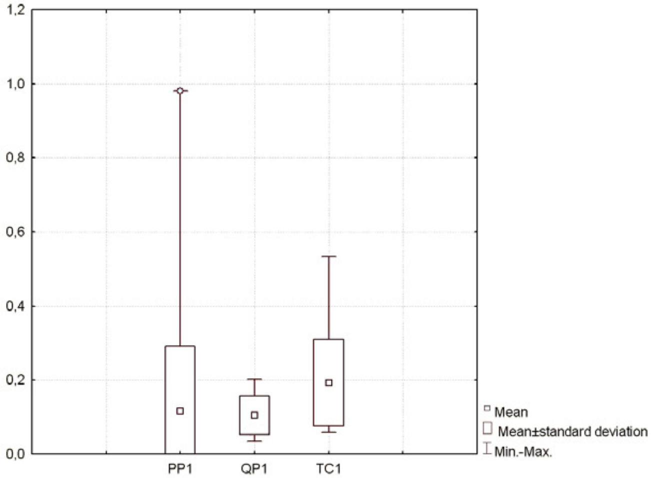


Fig. 148. The content of nitrogen in humus horizon (A) in ancient forests of three community types. (PP1 – pine forests, QP1 – oak-mixed pine forests, TC1 – lime-oak-hornbeam forests).

Ryc. 148. Zawartość azotu ogółem w poziomie próchnicznym (A) gleb w „starych lasach" trzech typów. (PP1 – bory, QP1 – bory mieszane, TC1 – grądy)

The average content of total nitrogen (NT) in the humus horizons of soils not bearing the footprints of farming activity amounted to roughly 0.11-0.12% in the podzolic and rusty soils, as well as in rusty soils with podzolisation traces, and to roughly 0.18-0.19% in the brown and fallow soils (Fig. 148).

The analogous soil types, covered by the recent post-agricultural forests, are characterised by somewhat lower nitrogen content. The result obtained unambiguously demonstrates the significant influence of the way of forest use on the development of nitrogen reserves in the soils. In the rusty post-agricultural soils with traces of podzolisation the NT content in the plough horizon amounts to 0.04-0.05%. The highest NT values were observed in the profiles of rusty soils with traces of podzolisation, which were afforested around 200 years ago. Nitrogen content in the younger forests decreases, to then slightly increase again in the youngest forest areas, with the stands 90 years old (Fig. 148). The latter increase, though, is statistically insignificant. It can, therefore, be admitted that in the post-agricultural rusty podzolised soils on the habitats of recent pine forests, nitrogen content is quite evenly distributed, and is distinctly lower than under the ancient forests on the same habitats. This might be interpreted as lack of significant regeneration of post-agricultural soils under the recent pine forests.

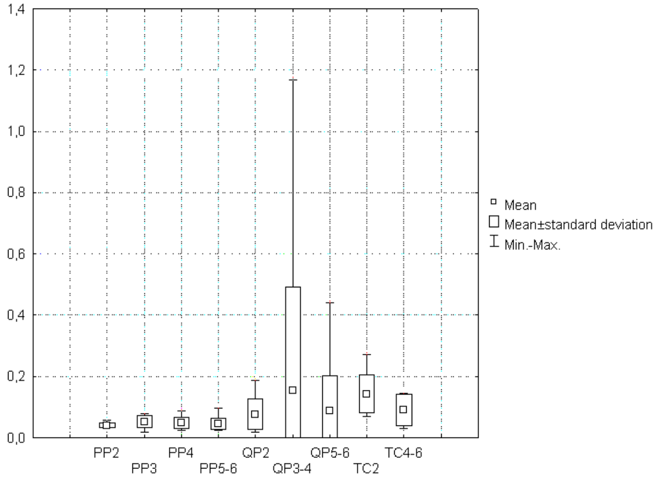


Fig. 149. The content of nitrogen in humus horizon (Ap) in post-agricultural soils.
Ryc. 149. Zawartość azotu ogółem w poziomie próchnicznym (Ap) gleb porolnych

A decrease in the soil nitrogen content is also observed in the case of rusty soils, associated with the mixed oak-pine forests, as well as the lime-oak-hornbeam forests, growing on brown and fallow soils of younger than 230 years forests (Fig. 149). The differences are pronounced and statistically significant. In the rusty soils, covered by the mixed oak-pine forests, the differences in the plough horizon attain close to 100% of the total nitrogen content, while in brown and fallow soils they exceed 60% (Fig. 149).

In view of the fact that nitrogen is present in the soil both in organic and in mineral forms, with the organic compounds decidedly dominating – potentially up to 99% of total nitrogen content – strict relation exists in the soils analysed between organic carbon and total nitrogen contents. In the soils under the recent forests, in which the content of organic matter increased, there was also an increase in nitrogen content. The sum of organic carbon and total nitrogen contents ranges from 1.0 to 1.2% in the plough horizons of rusty soils with traces of podzolisation, from 1.1 to 1.8% in the rusty soils under mixed oak-pine forests, and from close to 1.8 to more than 2.0% in the fallow and brown soils overgrown by the lime-oak-hornbeam forests. In the case of mixed oak-pine forests and lime-oak-hornbeam forests soils the content of two elements decreases with the shortening period of forest persistence. In the case of pine forests this dependence is not so unambiguous, since in the forests with the shortest persistence period on post-agricultural land, an increase in content of two nutrients considered is observed (Fig. 150).

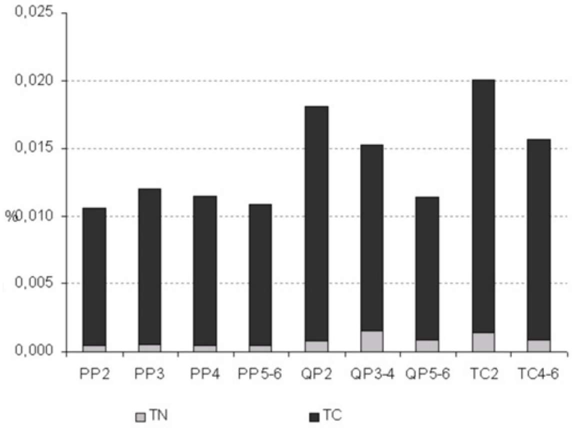


Fig. 150. The content of organic carbon (TC) and nitrogen (TN) in humus horizon (Ap) in post-agricultural soils.
Ryc. 150. Zawartość organicznego węgla (TC) i azotu (TN) w poziomie próchnicznym (Ap) w glebach porolnych

This result might also be interpreted as the indication of a clear regeneration of the post-agricultural soils on the habitats of mixed oak-pine forests and lime-oak-hornbeam forests, while there is no (or only a very limited) regeneration of soils under recent pine forests.

7.6. C:N RATIO

Mutual relations of organic carbon and nitrogen content belong among the basic yardsticks of the soil biological activity, and hence of the entire ecosystem efficiency. Thus, for instance, the nitrogen availability, released in the course of plant rests disintegration, for the plants, depends upon the C:N ratio in the decomposing organic substance. When this ratio is too high (exceeding 32:1), then mineralisation of organic substance becomes slower, and microorganisms absorb the nitrogen possible to be assimilated by the plants. On the other hand, for the lower values of C:N ratio, mineralisation of nitrogen follows, and this element is not used by plants (Thompson, Troeh 1978).

In the analysed soils not bearing traces of agricultural use the C:N ratio ranges in the humus layer from, on the average, 21.5 in the podzolic soils and rusty soils with traces of podzolisation to around 19.5 in the fallow soils (Fig. 151). This result confirms the ordering of habitats in terms of advantageous conditions for plants, starting from the most oligotrophic pine forests, through moderately oligotrophic mixed oak-pine forests, up to meso- and eutrophic lime-oak-hornbeam forests.

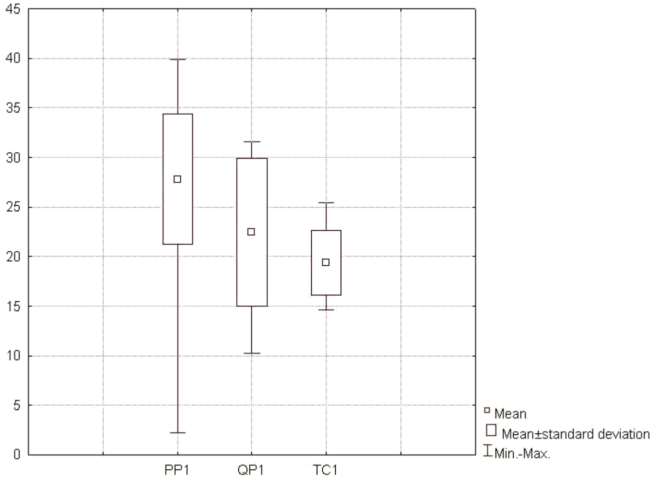


Fig. 151. The C:N ratio in humus horizon (A) in ancient forests of three community types. (PP1 – pine forests, QP1 – mixed oak-pine forests, TC1 – lime-oak-hornbeam forests).

Ryc. 151. Stosunek C:N w poziomie próchnicznym (A) gleb w „starych lasach" trzech typów. (PP1 – bory, QP1 – bory mieszane, TC1 – grądy)

Much higher values of the C:N ratio were observed in the post-agricultural soils. In the plough horizon of rusty soils with traces of podzolisation this value ranges from around 24 to 29. The results obtained indicate that a slow mineralisation of organic substance takes place in these soils. The best bio-ecological properties among the pedons analysed are displayed by rusty soils under the mixed oak-pine forests and by fallow as well as brown soils covered by the lime-oak-hornbeam forests (Fig. 152). The lowest C:N ratios were registered in the soils with the longest forest persistence, that is – the ones that feature nowadays only marginal anthropogenic deformations. This is, in particular, conducive to the development of soil micro- and macro-fauna (Jefremow, Degórski 1998). The C:N ratios in the plough horizon of these soils range from 10.5 to 18 (Fig. 152).

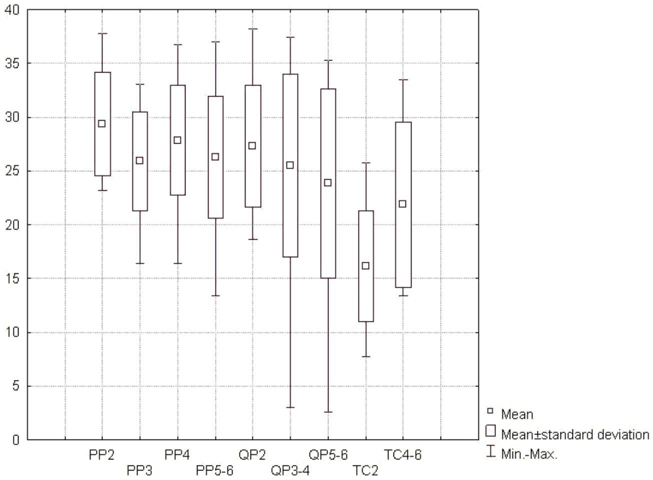


Fig. 152. The C:N ratio in humus horizon (Ap) in post-agricultural soils.
Ryc. 152. Stosunek węgla do azotu (C:N) w poziomie próchnicznym (Ap) w glebach porolnych

7.7. SULPHUR

Sulphur content in the soil, side by side with the content of heavy metals, belongs among the indicators of soil quality and degree of anthropogenic pollution. Total sulphur content in the soils mineral horizons in Poland does not exceed 0.1%. In the humus layers of podzolic forest soils it amounts to approximately 0.01%, and of brown soils – to 0.02% (Puchalski, Prusinkiewicz 1975). In the analysed podzolic soils of pine forests, sulphur content in the humus layer amounted on the average to roughly 0.017%, and in the rusty soils with traces of podzolisation to 0.013%, while in the brown and fallow soils – to 0.023% (Fig. 153).

Higher values of sulphur content were registered in the post-agricultural soils. Thus, in the plough horizon of rusty soils with traces of podzolisation, in the youngest recent forest, the content equals approximately 0.037% (Fig. 154). This may probably be linked to the agricultural measures, especially the use of natural fertilisers. Indeed, along with atmospheric sulphur, some quantities of this element are also introduced into the soil with natural fertilisers. Thus, for instance, stable manure contains from 0.9 to 1.2 kg of sulphur per Mg, while liquid manure from pig or cattle raising – between 0.4 and 0.5 kg of sulphur per Mg. This sulphur appears in the form of various compounds. It is estimated that, on the average, 20% of total sulphur appears in the form of sulphides, 40% is constituted by the organic structures of sulphur and carbon, and the remaining 40% is contained in organic and inorganic sulphates (Haneklaus et al. 2000; Pedersen et al. 1998). In the soils, to which fertilisers have been intensively applied, the effects may be visible until today.

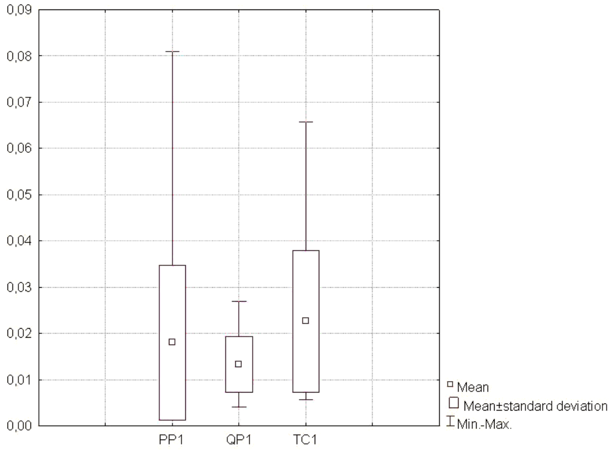


Fig. 153. The content of sulphur in humus horizon (A) in ancient forests of three community types. (PP1 – pine forests, QP1 – mixed oak-pine forests, TC1 – lime-oak-hornbeam forests).

Ryc. 153. Zawartość siarki ogółem w poziomie próchnicznym (A) gleb w „starych lasach" trzech typów. (PP1 – bory, QP1 – bory mieszane, TC1 – grądy)

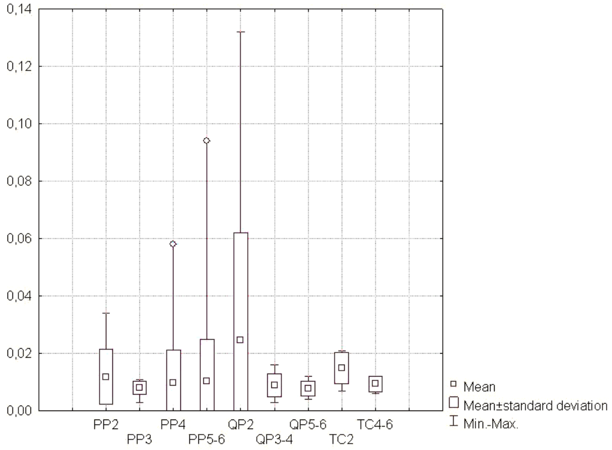


Fig. 154. The content of sulphur in humus horizon (Ap) in post-agricultural soils.

Ryc. 154. Zawartość siarki w poziomie próchnicznym (Ap) w glebach porolnych

7.8. THE INFLUENCE OF TIME FACTOR AND HUMAN PRESSURE ON THE PROPERTIES OF SOILS STUDIED

The soil analyses conducted in the context of development of their basic properties depending upon the way land has been used, including also the forest persistence, demonstrated a number of regularities:

- the closest to the biochemical equilibrium are the soils not bearing the footprints of agrotechnical measures; thus, the podzolic soils and the rusty soils with traces of podzolisation, poor in nutrients, as well as the rusty soils with the mixed oak-pine forests, or the brown and fallow soils, on which lime-oak-hornbeam forests grow, all of them feature better chemical properties than the analogous post-agricultural soil types;
- the same type of soil, having been in the past the arable land, features different physical and chemical properties depending upon the persistence of post-agricultural forest ecosystems; in the case of rusty soils with mixed oak-pine forests and the brown and fallow soils with lime-oak-hornbeam forest vegetation the regularity is observed such that the longer the recent forest exists on the post-agricultural land, the higher the quality and the biological activity of these soils;
- in the case of the least fertile soils, that is – the podzolic and the rusty ones with traces of podzolisation – the dependence between the persistence of post-agricultural forest and the soils properties is not as unambiguous as in the case of rusty, fallow and brown soils; this results, first of all, from the low buffering capacities of these soils and their low resistance to external conditions, which may, even for limited scopes of change, transform the biochemical conditions of the pedons; these soils are, therefore, little resistant to external factors, which may ’wash away‘ the general trends of change, resulting from the development of soil forming processes over time.

8. MODELLING CHANGES OF SELECTED FOREST PROPERTIES IN THE COURSE OF POST-AGRICULTURAL FOREST REGENERATION

8.1. PARTIAL CORRELATION ANALYSIS OF THE PINE FORESTS (*PEUCEDANO-PINETUM*)

The detailed analyses, presented in Chapter 5, suggest the existence of relationships between, on the one hand, the period of forest persistence ('persistence') and the distance of analysed forest patch from the ancient forest ('distance'), and, on the other hand, the species composition and some structural features of the phytocoenosis. A deeper analysis of these correlations may constitute the basis for modelling of changes in the properties of forest communities during the regeneration process. Such analysis ought to account also for other controlling variables and connections between them.

Table 30 presents the results of partial correlation analysis, concerning the influence of three factors – persistence, distance and tree stand age, on the values of selected phytocoenoses variables of the pine forests (*Peucedano-Pinetum*). Based on the data from this table one can distinguish several groups of characteristics, depending in different ways upon the driving variables:

- the first group encompasses the following variables: FMI total, FMI2 (*Vaccinium myrtillus* excluded), cover of *Vaccinium myrtillus*, *Calluna vulgaris*, *Vaccinium vitis-idaea*; these variables are mainly – and strongly – dependent upon persistence and distance;
- the second group comprises the cover of *Convallaria majalis* and *Hylocomium splendens*; the cover of these species depends mainly and strongly upon persistence, with a slight modifying influence of distance and tree stand age;
- the third group consists of the number of ancient forests species (according to Hermy et al. and those verified for the area analysed); this number depends mainly upon persistence and distance, but with a perceptible modifying influence of tree stand age;
- the fourth group contains the following variables: cover of *Luzula pilosa*, *Frangula alnus* and *Calamagrostis arundinacea* depending significantly, but weakly, upon persistence, while a slight modifying influence of tree stand age is stronger than the influence of distance;
- the fifth group comprises only one variable: the number of moss and lichen species; a slight, but statistically significant dependence upon the tree stand age is observed, with lack of perceptible influence of distance and persistence.

The remaining variables analysed (total number of species, number of *Vaccinio-Piceetea* moss species, number of shrub species, number of herb species, number of *Vaccinio-Piceetea* herb species, number of tree species) do not display significant correlation with persistence, distance or tree stand age.

When analysing the data from Table 30 one ought to pay attention also to the strong negative correlation between distance and persistence. This relation reflects, beyond any doubt, the non-random spatial distribution of the study plots. It should be emphasised, though, that this does not result from the tendentious/subjective selection of the study plots, but reflects the spatial distribution pattern of forests featuring different persistence. This issue is a subject of a separate, detailed cartographic analysis.

Emphasis should be also placed on only a slight correlation of the selected characteristics with the tree stand age. The analysed plots of fresh pine forests (*Peucedano-Pinetum*), are 62-190 years old. This resulted primarily from the well-known regularity, according to which the number of species and their ecological character undergo relatively fast changes in the younger tree stands classes (up to approximately 60 years), and then slow down or even stabilise.

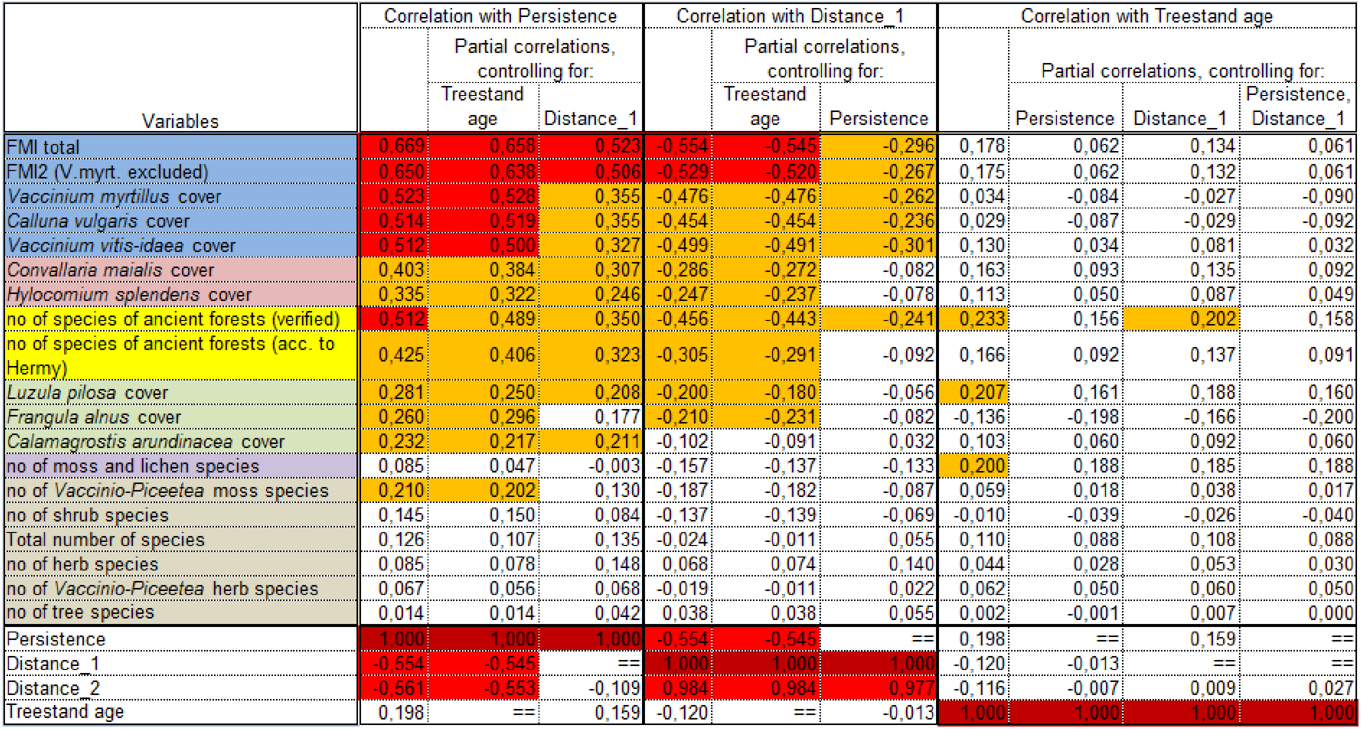
8.2. MODELS OF THE INFLUENCE OF PERSISTENCE AND DISTANCE ON FOREST MATURITY INDEX, COVER OF *VACCINIUM MYRTILLUS* AND FREQUENCY OF *CONVALLARIA MAJALIS*

The detailed considerations, referred to, concerned the relations within the pine forests (*Peucedano-Pinetum*). Yet, the analyses reported in Chapter 5 imply the similar relationships also in the case of other forest types. Based on the partial correlation values, two characteristics were selected for further studies (FMI and the cover of *Vaccinium myrtillus*), these two depending the strongest upon persistence and distance. Additionally, variability of *Convallaria majalis* frequency was analysed, given that the presence and abundance of this species depends mainly upon the forest site persistence.

8.2.1. THE FOREST MATURITY INDEX IN THREE COMMUNITIES TYPES

The relations between FMI and distance, and between FMI and persistence, were analysed for pine forests, mixed oak-pine forests and lime-oak-hornbeam forests (see Table 31, Figs. 155, 156, 157). It turns out that for these three plant communities the dependence between the value of FMI (expressed as ln(FMI+1)) and distance is best described by the Harris model, with the correlation coefficient between data and model ranging from 0.61 to 0.75. It is worth emphasising that the lime-oak-hornbeam forests are characterised by the most even decrease in the FMI value along distance, while in the mixed oak-pine forests there is a characteristic, very strong drop of this value at a small distance from the ancient forest already.

Table 30. Main partial correlations between chosen variables describing the state of pine forest (Peucedano-Pinetum) ecosystems



Variables	Correlation with Persistence			Correlation with Distance_1			Correlation with Treestand age			
		Partial correlations, controlling for:			Partial correlations, controlling for:			Partial correlations, controlling for:		
		Treestand age	Distance_1		Treestand age	Persistence		Persistence	Distance_1	Persistence, Distance_1
FMI total	0,669	0,658	0,523	-0,554	-0,545	-0,296	0,178	0,062	0,134	0,061
FMI2 (V.myrt. excluded)	0,650	0,638	0,506	-0,529	-0,520	-0,267	0,175	0,062	0,132	0,061
Vaccinium myrtillus cover	0,523	0,528	0,355	-0,476	-0,476	-0,262	0,034	-0,084	-0,027	-0,090
Calluna vulgaris cover	0,514	0,519	0,355	-0,454	-0,454	-0,236	0,029	-0,087	-0,029	-0,092
Vaccinium vitis-idaea cover	0,512	0,500	0,327	-0,499	-0,491	-0,301	0,130	0,034	0,081	0,032
Convallaria maialis cover	0,403	0,384	0,307	-0,286	-0,272	-0,082	0,163	0,093	0,135	0,092
Hylocomium splendens cover	0,335	0,322	0,246	-0,247	-0,237	-0,078	0,113	0,050	0,087	0,049
no of species of ancient forests (verified)	0,512	0,489	0,350	-0,456	-0,443	-0,241	0,233	0,156	0,202	0,158
no of species of ancient forests (acc. to Hermy)	0,425	0,406	0,323	-0,305	-0,291	-0,092	0,166	0,092	0,137	0,091
Luzula pilosa cover	0,281	0,250	0,208	-0,200	-0,180	-0,056	0,207	0,161	0,188	0,160
Frangula alnus cover	0,260	0,296	0,177	-0,210	-0,231	-0,082	-0,136	-0,198	-0,166	-0,200
Calamagrostis arundinacea cover	0,232	0,217	0,211	-0,102	-0,091	0,032	0,103	0,060	0,092	0,060
no of moss and lichen species	0,085	0,047	-0,003	-0,157	-0,137	-0,133	0,200	0,188	0,185	0,188
no of *Vaccinio-Piceetea* moss species	0,210	0,202	0,130	-0,187	-0,182	-0,087	0,059	0,018	0,038	0,017
no of shrub species	0,145	0,150	0,084	-0,137	-0,139	-0,069	-0,010	-0,039	-0,026	-0,040
Total number of species	0,126	0,107	0,135	-0,024	-0,011	0,055	0,110	0,088	0,108	0,088
no of herb species	0,085	0,078	0,148	0,068	0,074	0,140	0,044	0,028	0,053	0,030
no of *Vaccinio-Piceetea* herb species	0,067	0,056	0,068	-0,019	-0,011	0,022	0,062	0,050	0,060	0,050
no of tree species	0,014	0,014	0,042	0,038	0,038	0,055	0,002	-0,001	0,007	0,000
Persistence	1,000	1,000	1,000	-0,554	-0,545	==	0,198	==	0,159	==
Distance_1	-0,554	-0,545	==	1,000	1,000	1,000	-0,120	-0,013	==	==
Distance_2	-0,561	-0,553	-0,109	0,984	0,984	0,977	-0,116	-0,007	0,009	0,027
Treestand age	0,198	==	0,159	-0,120	==	-0,013	1,000	1,000	1,000	1,000

- 🟦 First group consists of: FMI total, FMI2 (Vaccinium myrtillus excluded), cover of Vaccinium myrtillus, Calluna vulgaris, Vaccinium vitis-idaea. They mainly and graetly depend on persistence and distance.
- 🟥 Second group consists of: cover of Convallaria maialis and Hylocomium splendens. Their cover mainly and greatly depends on persistence, with slight modifying influence of distance and treestand age.
- 🟨 Third group consists of ancient forests species (acc. to Hermy and verified in the research). Their number mainly depends on persistence and distance, with significant influence of treestand age.
- 🟩 Fourth group consists of: cover of Luzula pilosa, Frangula alnus and Calamagrostis arundinacea. Their cover significantly but poorly depends on persistence, while slight modifying influence of treestand age is stronger than influence of distance.
- 🟪 Fifth group consists of only one variable - number of moss and lichen species. There is slight but statistically significant correlation with treestand age, while distance and persistence do not have any influence.
- 🟫 Remaining variables (total number of species, number of Vaccinio-Piceetea moss species, number of shrub species, number of herb species, number of Vaccinio-Piceetea herb species, number of tree species) do not show any significant correlations with persistence, distance and treestand age.

Table 31. Main characteristics of regression curves presented on figures 1-7. Values rounded to 4 digits.

Forest type	Dependent variable	Independent variable	Model name	Model formula	Parameters				Standard Error	Correlation coefficient
					a	b	c	d		
Pine forest (*Peucedano-Pinetum*)	ln(FMI+1)	Distance+1	Harris Model	y=1/(a+bx^c)	0.2630	0.0054	0.441		0.6371	0.6673
	ln(FMI+1)	Persistence	Exponential Association	y=a(1-exp(-bx)	3.8422	0.0087			0.7077	0.5429
	FMI modelled	FMI data	Linear Fit	y=a+bx	8.3253	0.5988			9.242	0.7256
	V. myrtillus cover	Distance+1	Harris Model	y=1/(a+bx^c)	0.0180	0.0004	0.6371		21.2032	0.5903
	V. myrtillus cover	Persistence	Modified Geometric Fit	y=a*x^(b/x)	123.6798	-49.6874			22.4164	0.5189
	V. myrtillus cover modelled	*V. myrtillus* cover observed	Linear Fit	y=a+bx	19.7947	0.3454			13.6804	0.5521
	C. majalis probability	Distatnce	Exponential Association	y=a(b-exp(-cx))	-0.3494	0.0007	0.004		0.1624	0.5749
	(*C. majalis* probability)+1	Persistence	MMF Model	y=(a*b+c*x^d)/(b+x^d)	1.0025	439870850	1.6601	3.5551	0.1744	0.5834
	C. majalis probability modelled	*C. majalis* frequency observed	Linear Fit	y=a+bx	0.0506	0.51			0.1157	0.6502
Mixed forest (*Querco roboris-Pinetum*)	ln(FMI+1)	Distance+1	Harris Model	y=1/(a+bx^c)	0.2469	0.0141	0.3177		0.7179	0.6172
	ln(FMI+1)	Persistence	Exponential Association	y=a(1-exp(-bx)	3.8388	0.0092			0.7981	0.4767
	FMI modelled	FMI data	Linear Fit	y=a+bx	5.6357	0.8761			13.9103	0.7362
	V. myrtillus cover	Distance	Modified Power Model	y=a*b^x	65.9257	0.9993			23.2433	0.5658
	V. myrtillus cover	Persistence	Exponential Association	y=a(1-exp(-bx)	75.7675	0.0062			24.8457	0.5561
	V. myrtillus cover modelled	*V. myrtillus* cover observed	Linear Fit	y=a+bx	33.8688	0.3417			15.5911	0.5256
	C. majalis probability	Distatnce	Harris Model	y=1/(a+bx^c)	1.4808	0.0007	1.3579		0.1906	0.7928
	C. majalis probability	Persistence	Power Fit	y=ax^b	0.0000	1.697			0.1825	0.8129
	C. majalis probability modelled	*C. majalis* frequency observed	Linear Fit	y=a+bx	0.0012	0.7303			0.1555	0.8252
Oak-hornbeam forest (*Tilio-Carpinetum*)	ln(FMI+1)	Distance+1	Harris Model	y=1/(a+bx^c)	0.2556	0.00006	1.0193		0.5358	0.7521
	ln(FMI+1)	Persistence	Exponential Association	y=a(1-exp(-bx)	4.3517	0.0077			0.5148	0.7676
	FMI modelled	FMI data	Linear Fit	y=a+bx	8.2724	0.6796			12.7491	0.847

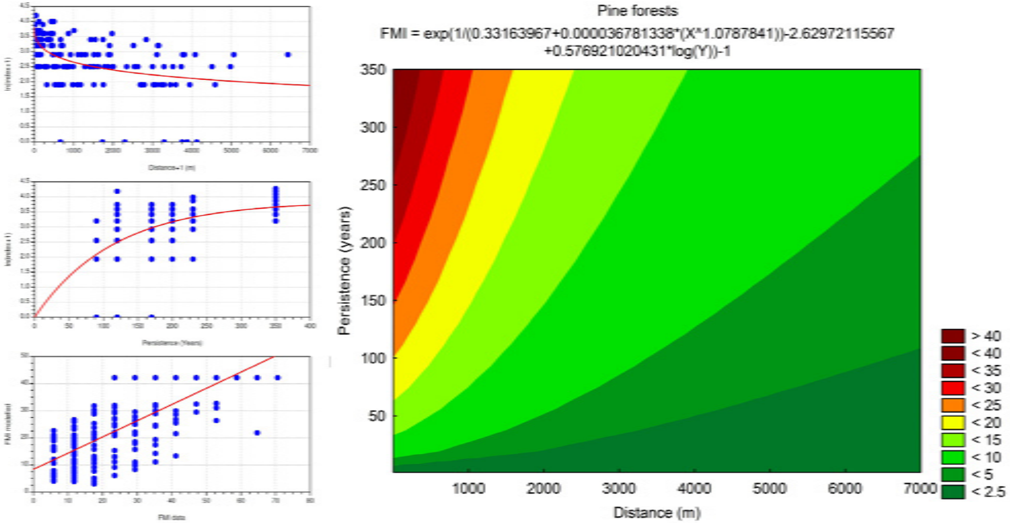


Fig. 155. Relationship between FMI and persistence and distance in pine forests (*Peucedano-Pinetum*). Left side from top to bottom - (a) regression curve for relation between the distance to the nearest ancient forest (expressed as Distance+1) and FMI expressed as ln(FMI+1); (b) regression curve for relation between persistence and FMI expressed as ln(FMI+1); (c) linear regression curve between observed FMI values and modeled values according to the model presented on the right side. Right side - two dimensional model of the relationship between FMI and persistence and distance. Parameters of regression curves are presented in Table 31.

Ryc. 155. Zależności między wskaźnikiem dojrzałości lasu (FMI), trwałością lasu i odległością od starego lasu w borach sosnowych (*Peucedano-Pinetum*). Lewa strona, z góry na dół - (a) krzywa regresji dla zależności pomiędzy odległością od starego lasu (oznaczoną jako Distance+1) i wskaźnikiem dojrzałości lasu oznaczonym jako ln(FMI+1); (b) krzywa regresji dla zależności pomiędzy trwałością lasu i FMI wskaźnikiem dojrzałości lasu oznaczonym jako ln(FMI+1); (c) liniowa krzywa regresji dla obserwowanych wartości wskaźnika FMI i wartości modelowych wg modelu przedstawionego z prawej strony. Prawa strona – dwuwymiarowy model zależności między wskaźnikiem dojrzałości lasu (FMI), trwałością lasu i odległością od starego lasu. Parametry krzywych regresji zamieszczone są w Tabeli 31.

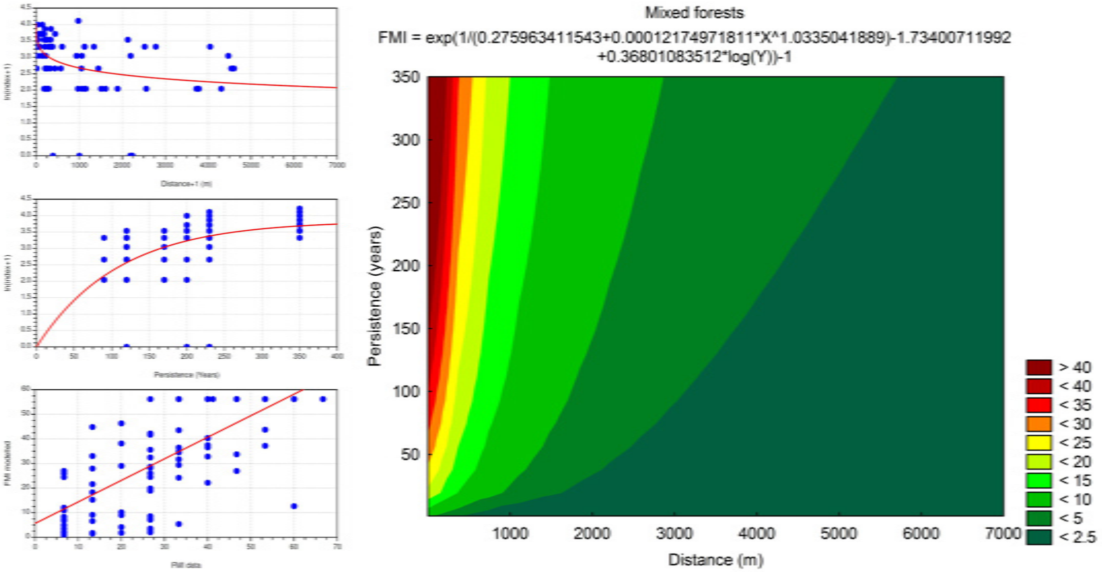


Fig. 156. Relationship between FMI and persistence and distance in mixed pine forests (*Querco roboris-Pinetum*). Left side from top to bottom - (a) regression curve for relation between the distance to the nearest ancient forest (expressed as Distance+1) and FMI expressed as ln(FMI+1); (b) regression curve for relation between persistence and FMI expressed as ln(FMI+1); (c) linear regression curve between observed FMI values and modeled values according to the model presented on the right side. Right side - two dimensional model of the relationship between FMI and persistence and distance. Parameters of regression curves are presented in Table 31.

Ryc. 156. Zależności między wskaźnikiem dojrzałości lasu (FMI), trwałością lasu i odległością od starego lasu w borach mieszanych (*Querco roboris-Pinetum*). Lewa strona, z góry na dół - (a) krzywa regresji dla zależności pomiędzy odległością od starego lasu (oznaczoną jako Distance+1) i wskaźnikiem dojrzałości lasu oznaczonym jako ln(FMI+1); (b) krzywa regresji dla zależności pomiędzy trwałością lasu i FMI wskaźnikiem dojrzałości lasu oznaczonym jako ln(FMI+1); (c) liniowa krzywa regresji dla obserwowanych wartości wskaźnika FMI i wartości modelowych wg modelu przedstawionego z prawej strony. Prawa strona – dwuwymiarowy model zależności między wskaźnikiem dojrzałości lasu (FMI), trwałością lasu i odległością od starego lasu. Parametry krzywych regresji zamieszczone są w Tabeli 31.

The dependence between FMI (again expressed as ln(FMI+1)) and forest persistence is best described with the exponential model for all of the plant communities analysed. In the pine and mixed oak-pine forests the correlation between data and model was equal, respectively, 0.54 and 0.48 (clearly lower than the relation between FMI and distance), while in the lime-oak-hornbeam forests it was equal 0.77, comparable to the correlation between FMI and distance.

The presented models of joint dependence of FMI upon persistence and distance describe quite well the variability of actual data, as confirmed by the correlation coefficients values between data and models, amounting in the cases of pine and mixed oak-pine forests to approximately 0.73, and to ca. 0.85 in the lime-oak-hornbeam forests.

Nonlinear dependences between FMI and distance and between FMI and persistence cause that the combined effect of two variables upon the values of FMI has quite a complex character. When analysing the model one can state that in all three communities types the rate of decrease in the FMI value diminishes with distance and this fact is visible both for the sites featuring longer persistence and for those afforested recently. In the forests with persistence of around 300 years the most pronounced changes along distance take place in the case of mixed oak-pine forests, where the value of FMI drops from more than 40% to 30% already at the distance of approximately 500 m from the ancient forest, and then yet to 20% at the distance of roughly 800 m. In the remaining types the decrease to 30% takes place at the distance of more than 800 m, and to 20% - at the distance of more than 1 km in the lime-oak-hornbeam forests and at approximately 2 km in the fresh pine forests. A similar pattern, in principle, is observed for the surfaces having persisted for roughly 60 years, even though the differences between communities are smaller. In the mixed oak-pine forests the drop of the FMI value from approximately 25% to 10% occurs at the distance of around 600 m, and then to 5% - at the distance of around 1 300 m, while in the fresh pine forests and the lime-oak-hornbeam forests the decrease of FMI from 15% to 10% takes places at the distance of some 400-500 m, and to 5% - at the distance of approximately 1 200 m (in lime-oak-hornbeam forests) or around 2 km (in fresh pine forests).

Analysis of the model leads to the conclusion that it is almost entirely impossible to re-establish the natural species composition (as reflected through the high value of FMI) in the natural manner on the areas far from ancient forests, even after a long period of time since afforestation. If we accept that a well developed patch ought to have the value of FMI not lower than 25%, then in the case of mixed oak-pine forests the threshold distance value is 500 m (and persistence of at least 150 years), in the lime-oak-hornbeam forests – distance not bigger than 700 m (and persistence of at least 150 years as well), while for the fresh pine forests – the threshold distance depends to a much higher degree upon persistence and amounts to approximately 500 m for forests with persistence of ca 200 years and to approximately 1 000 m in the sites with persistence of about 300 years.

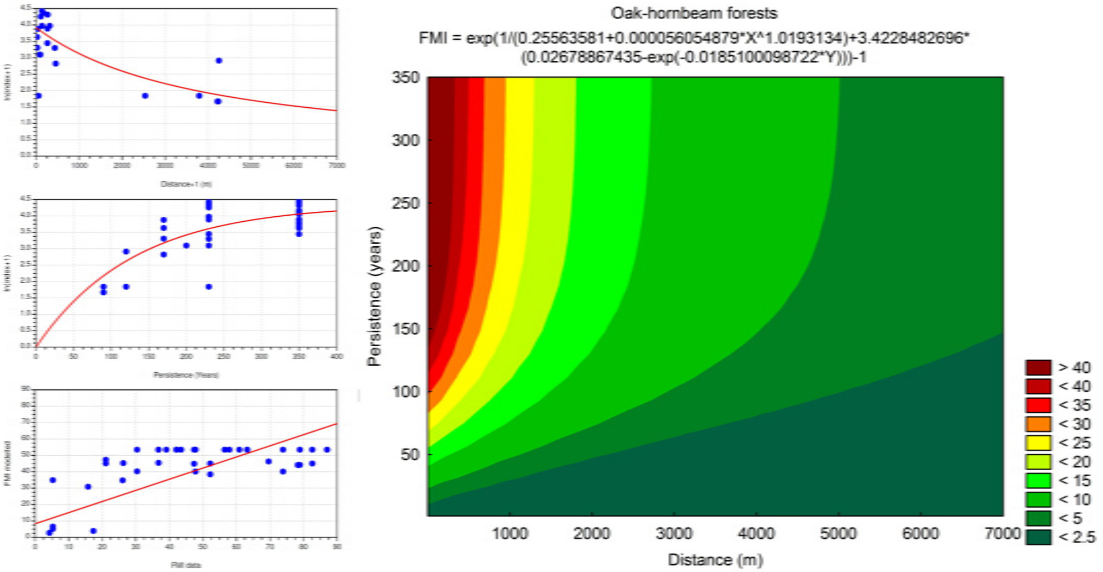


Fig. 157. Relationship between FMI and persistence and distance in oak-hornbeam forests (*Tilio-Carpinetum*). Left side from top to bottom - (a) regression curve for relation between the distance to the nearest ancient forest (expressed as Distance+1) and FMI expressed as ln(FMI+1); (b) regression curve for relation between persistence and FMI expressed as ln(FMI+1); (c) linear regression curve between observed FMI values and modeled values according to the model presented on the right side. Right side - two dimensional model of the relationship between FMI and persistence and distance. Parameters of regression curves are presented in Table 31.

Ryc. 157. Zależności między wskaźnikiem dojrzałości lasu (FMI), trwałością lasu i odległością od starego lasu w grądach (*Tilio-Carpinetum*). Lewa strona, z góry na dół - (a) krzywa regresji dla zależności pomiędzy odległością od starego lasu (oznaczoną jako Distance+1) i wskaźnikiem dojrzałości lasu oznaczonym jako ln(FMI+1); (b) krzywa regresji dla zależności pomiędzy trwałością lasu i FMI wskaźnikiem dojrzałości lasu oznaczonym jako ln(FMI+1); (c) liniowa krzywa regresji dla obserwowanych wartości wskaźnika FMI i wartości modelowych wg modelu przedstawionego z prawej strony. Prawa strona – dwuwymiarowy model zależności między wskaźnikiem dojrzałości lasu (FMI), trwałością lasu i odległością od starego lasu. Parametry krzywych regresji zamieszczone są w Tabeli 31.

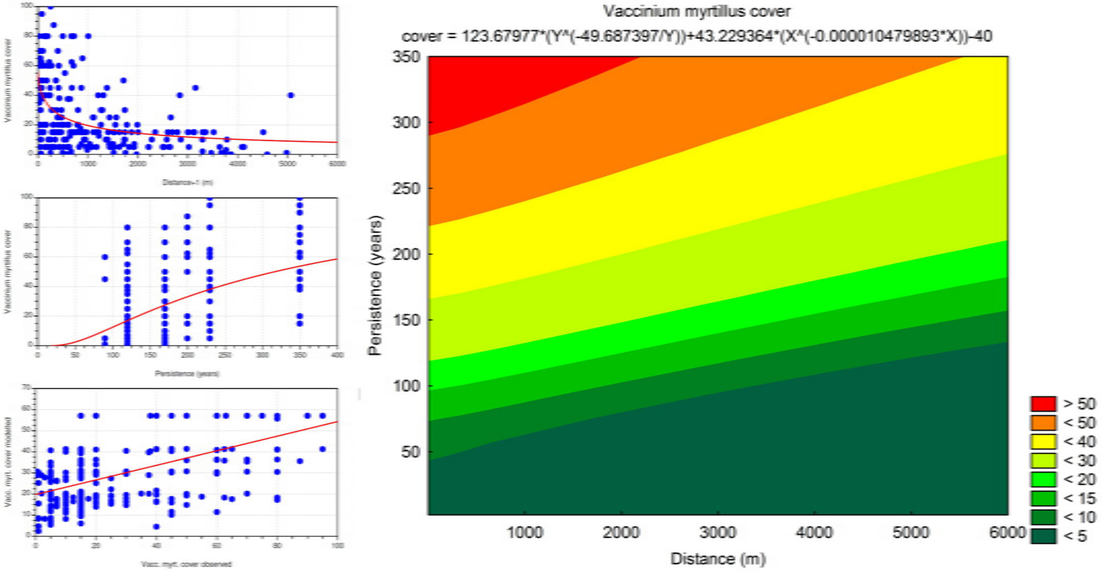


Fig. 158. Relationship between *Vaccinium myrtillus* cover and persistence and distance in pine forests (*Peucedano-Pinetum*). Left side from top to bottom - (a) regression curve for relation between the distance to the nearest ancient forest (expressed as Distance+1) and Vaccinium myrtillus cover; (b) regression curve for relation between persistence and *Vaccinium myrtillus* cover; (c) linear regression curve between observed *Vaccinium myrtillus* cover and modeled values according to the model presented on the right side. Right side - two dimensional model of the relationship between *Vaccinium myrtillus* cover and persistence and distance. Parameters of regression curves are presented in Table 31.

Ryc. 158. Zależności między pokryciem *Vaccinium myrtillus*, trwałością lasu i odległością od starego lasu w borach sosnowych (*Peucedano-Pinetum*). Lewa strona, z góry na dół - (a) krzywa regresji dla zależności pomiędzy odległością od starego lasu (oznaczoną jako Distance+1) i pokryciem *Vaccinium myrtillus*; (b) krzywa regresji dla zależności pomiędzy trwałością lasu i pokryciem *Vaccinium myrtillus*; (c) liniowa krzywa regresji dla obserwowanych wartości pokrycia *Vaccinium myrtillus* i wartości modelowych wg modelu przedstawionego z prawej strony. Prawa strona – dwuwymiarowy model zależności między pokryciem *Vaccinium myrtillus*, trwałością lasu i odległością od starego lasu. Parametry krzywych regresji zamieszczone są w Tabeli 31.

8.2.2. REGENERATION RATE OF *VACCINIUM MYRTILLUS* COVER IN PINE AND MIXED OAK-PINE FORESTS

One of species, whose appearance influences the value of FMI in the pine forests and mixed oak-pine forests is *Vaccinium myrtillus*. Relationship between the cover of *Vaccinium myrtillus* and distance is in the case of fresh pine forests best described by the Harris model, while in the mixed oak-pine forests – by the modified power model, with the correlation coefficients between data and models being equal, respectively, 0.59 and 0.57 (see Table 31, Figs. 158, 159). One should emphasise an important difference between the analysed forest types. In the fresh pine forests the model suggests the relatively fast changes of the *Vaccinium myrtillus* cover not far from the ancient forest, and then a very slow decrease (close to stabilisation) at bigger distances. On the other hand, in mixed oak-pine forests, a somewhat more regular decrease is observed, but leading to values close to zero at distances exceeding 4 km.

Relationship between the cover of *Vaccinium myrtillus* and the forest persistence in the fresh pine forests is best described by the modified geometric fit, while for the mixed oak-pine forests – by the exponential association model. The respective correlation coefficients between data and models are equal 0.52 and 0.56 and are only slightly lower than the corresponding coefficients of relations between the *Vaccinium myrtillus* cover and distance (Table 31, Figs. 158, 159). Comparison of models for two forest types suggests that in the case of fresh pine forests with short persistence values the rate of increase in the *Vaccinium myrtillus* cover is very slow, attaining maximum in the persistence interval of 70-230 years, to then slow down. Then, within the mixed oak-pine forests the maximum rate of increase in *Vaccinium myrtillus* cover is observed on the youngest forests (up to roughly 120 years), and then the rate of the cover increase gradually becomes lower.

The models presented of a combined dependence of the *Vaccinium myrtillus* cover upon persistence and distance describe sufficiently well the variability of actual data, as demonstrated by the values of correlation coefficients between data and models, equal approximately 0.55 in the fresh pine forests and approximately 0.53 in the mixed oak-pine forests.

The nonlinear interrelations between the *Vaccinium myrtillus* cover and distance, and between the *Vaccinium myrtillus* cover and persistence cause that the combined effect of these two variables on the values of *Vaccinium myrtillus* cover has quite a complex character, which is somewhat different in two analysed communities types (Table 31, Figs. 158, 159). It can be concluded on the basis of the models presented that at limited distances from the ancient forest (up to some 500 m) bilberry appears earlier in the mixed oak-pine forests and attains earlier high cover values, for instance – approximately 30% in forests having persisted for 60-70 years and more than 50% in

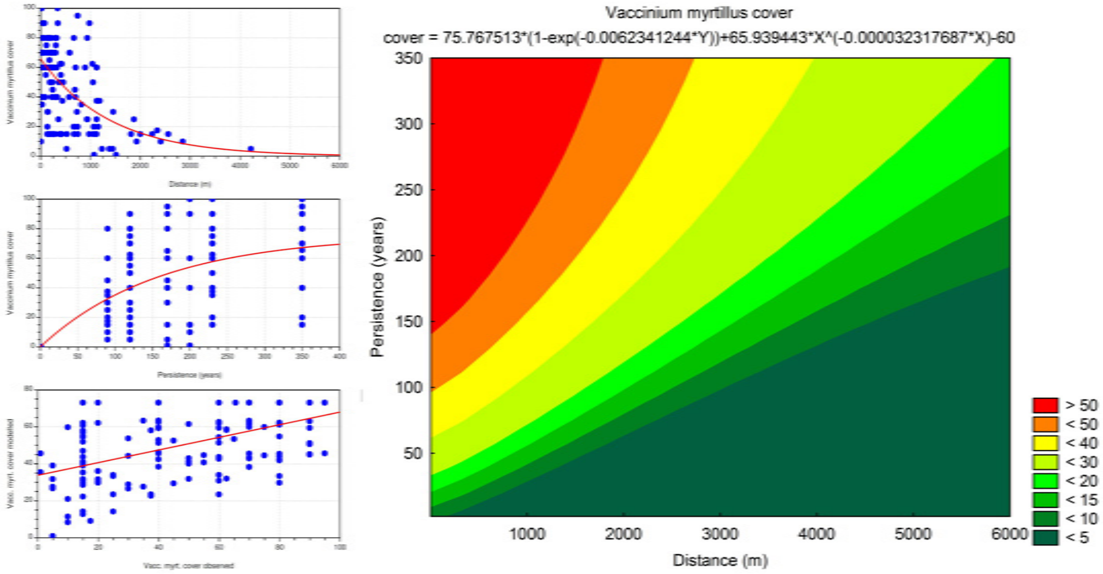


Fig. 159. Relationship between *Vaccinium myrtillus* cover and persistence and distance in mixed pine forests (*Querco roboris-Pinetum*). Left side from top to bottom - (a) regression curve for relation between the distance to the nearest ancient forest and *Vaccinium myrtillus* cover; (b) regression curve for relation between persistence and *Vaccinium myrtillus* cover; (c) linear regression curve between observed *Vaccinium myrtillus* cover and modeled values according to the model presented on the right side. Right side - two dimensional model of the relationship between *Vaccinium myrtillus* cover and persistence and distance. Parameters of regression curves are presented in Table 31.

Ryc. 159. Zależności między pokryciem *Vaccinium myrtillus*, trwałością lasu i odległością od starego lasu w borach mieszanych (*Querco roboris-Pinetum*). Lewa strona, z góry na dół - (a) krzywa regresji dla zależności pomiędzy odległością od starego lasu (oznaczoną jako Distance+1) i pokryciem *Vaccinium myrtillus*; (b) krzywa regresji dla zależności pomiędzy trwałością lasu i pokryciem *Vaccinium myrtillus*; (c) liniowa krzywa regresji dla obserwowanych wartości pokrycia *Vaccinium myrtillus* i wartości modelowych wg modelu przedstawionego z prawej strony. Prawa strona – dwuwymiarowy model zależności między pokryciem *Vaccinium myrtillus*, trwałością lasu i odległością od starego lasu. Parametry krzywych regresji zamieszczone są w Tabeli 31.

forests with persistence of around 150 years, while in the typical pine forest analogous cover values are attained, respectively, for the persistence periods of approximately 170 and 270 years, that is – roughly 100 years later. The second difference concerns the influence of distance. The decrease in the *Vaccinium myrtillus* cover along distance is much stronger in the case of mixed oak-pine forests than in the case of fresh pine forests. In pine forests having persisted for approximately 200 years the decrease in the cover by 10% occurs already at the distance of around 3 000 m, while in the mixed oak-pine forest the decrease over such a distance amounts to already more than 30%.

8.2.3. THE FREQUENCY OF *CONVALLARIA MAJALIS* IN PINE AND MIXED OAK-PINE FORESTS

Lily of the valley, *Convallaria majalis*, is another species included in the combination serving to determine the FMI of typical and mixed oak-pine forests. The relationship between the *Convallaria majalis* frequency and distance in the fresh pine forests is best described by the exponential association model, while in the mixed oak-pine forests – the Harris model, with the correlation coefficients between data and models equal, respectively, 0.57 and 0.79 (Table 31, Figs. 160, 161).

Relation between the frequency of *Convallaria majalis* and forest persistence is in the fresh pine forests best described by the MMF model, while in the mixed oak-pine forests – by the power fit model, with the correlation coefficient values between data and models being equal, respectively, 0.58 and 0.81, quite similar, therefore, to the corresponding coefficients of relations between the *Convallaria majalis* frequency and distance (Table 31, Figs. 160, 161). Comparison of models for two forest types suggests that in the case of the younger fresh pine forests (with persistence of up to 100-120 years) the frequency of *Convallaria maijalis* is very low (below 5%), to then increase almost regularly along the persistence growth. While, in the mixed oak-pine forests a regular increase is observed already starting with the youngest forests, although it is the fastest for the persistence exceeding 150 years.

The nonlinear interdependences between the *Convallaria majalis* frequency and distance, and between its frequency and persistence cause that the combined influence of two variables on the frequency values of lily of the valley has quite a complex character, which is somewhat different in two forest types analysed (Table 31, Figs. 160, 161). The models presented imply that at short distances from the ancient forest (up to roughly 100 m) frequencies of lily of the valley higher than 10% appear somewhat earlier in the fresh pine forests than in the mixed oak-pine forests, but older sites are characterised by almost identical frequencies. At the same time, irrespective of the persistence class, the influence of distance in the fresh pine forests stops to be significant for values exceeding 200-300 m, while in the mixed oak-pine forests a regular

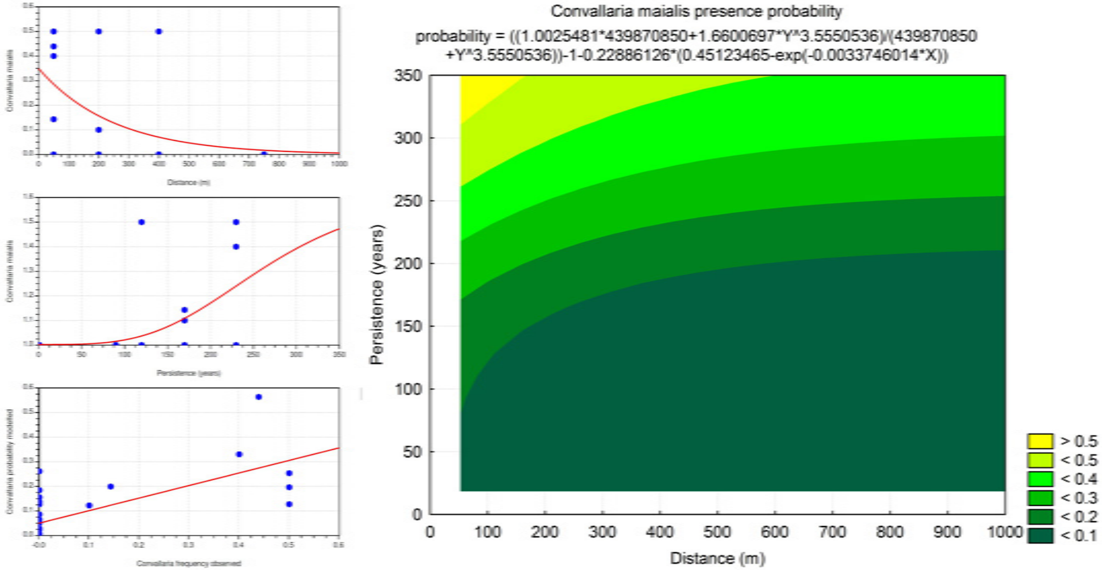


Fig. 160. Relationship between *Convallaria majalis* frequency and persistence and distance in pine forests (*Peucedano-Pinetum*). Left side from top to bottom - (a) regression curve for relation between the distance to the nearest ancient forest and *Convallaria majalis* frequency; (b) regression curve for relation between persistence and *Convallaria majalis* frequency; (c) linear regression curve between observed *Convallaria majalis* frequency and modeled probability values according to the model presented on the right side. Right side - two dimensional model of the relationship between *Convallaria majalis* frequency and persistence and distance. Parameters of regression curves are presented in Table 31.

Ryc. 160. Zależności między *Convallaria majalis*, trwałością lasu i odległością od starego lasu w borach sosnowych (*Peucedano-Pinetum*). Lewa strona, z góry na dół - (a) krzywa regresji dla zależności pomiędzy odległością od starego lasu (oznaczoną jako Distance+1) i frekwencją *Convallaria majalis*; (b) krzywa regresji dla zależności pomiędzy trwałością lasu i frekwencją *Convallaria majalis*; (c) liniowa krzywa regresji dla obserwowanych wartości frekwencji *Convallaria majalis* i wartości modelowych prawdopodobieństwa wg modelu przedstawionego z prawej strony. Prawa strona – dwuwymiarowy model zależności między frekwencją *Convallaria majalis*, trwałością lasu i odległością od starego lasu. Parametry krzywych regresji zamieszczone są w Tabeli 31.

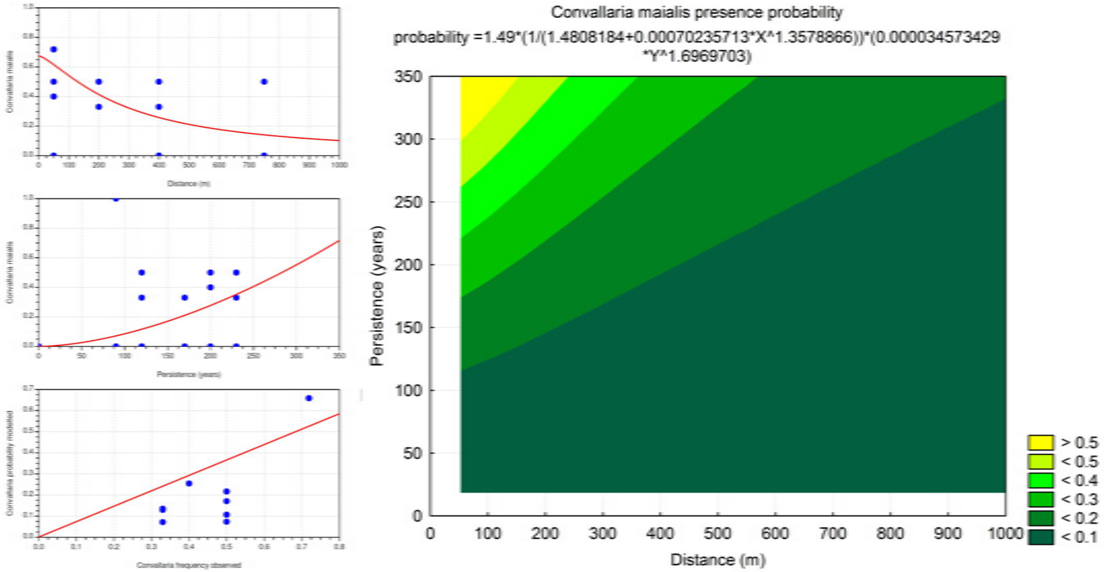


Fig. 161. Relationship between *Convallaria majalis* frequency and persistence and distance in mixed pine forests (*Querco roboris-Pinetum*). Left side from top to bottom - (a) regression curve for relation between the distance to the nearest ancient forest and *Convallaria majalis* frequency; (b) regression curve for relation between persistence and *Convallaria majalis* frequency; (c) linear regression curve between observed *Convallaria majalis* frequency and modeled probability values according to the model presented on the right side. Right side - two dimensional model of the relationship between *Convallaria majalis* frequency and persistence and distance. Parameters of regression curves are presented in Table 31.

Ryc. 161. Zależności między frekwencją *Convallaria majalis*, trwałością lasu i odległością od starego lasu w borach mieszanych (*Querco roboris-Pinetum*). Lewa strona, z góry na dół - (a) krzywa regresji dla zależności pomiędzy odległością od starego lasu (oznaczoną jako Distance+1) i frekwencją *Convallaria majalis*; (b) krzywa regresji dla zależności pomiędzy trwałością lasu i frekwencją *Convallaria majalis*; (c) liniowa krzywa regresji dla obserwowanych wartości frekwencji *Convallaria majalis* i wartości modelowych prawdopodobieństwa wg modelu przedstawionego z prawej strony. Prawa strona – dwuwymiarowy model zależności między frekwencją *Convallaria majalis*, trwałością lasu i odległością od starego lasu. Parametry krzywych regresji zamieszczone są w Tabeli 31.

decrease in the frequency of lily of the valley is observed along increasing distance.

The models presented of the joint dependence of *Convallaria majalis* frequency upon persistence and distance describe well the variability of actual data, as demonstrated by the values of correlation coefficient between data and models, equal approximately 0.65 in the fresh pine forests and approximately 0.83 in the mixed oak-pine forests.

8.3. SOIL PROPERTIES AND PHYTOINDICATORS IN THE COURSE OF THE RECENT FORESTS REGENERATION

During the process of recent post-agricultural forests regeneration, transformations occur with respect to the floristic composition and the structure as well as chemical characteristics of the soil. Changes in the species composition entail changes in the phytoindication values , which – at least in theory – ought to be linked with the changes in soil characteristics. At the same time, values of all these indicators (phytoindicators and soil characteristics) ought to undergo changes along with the development (regeneration) of the community. Relationships between these variables were analysed with the use of correlation analysis, while linkages to the regeneration process were assessed using partial correlations. The respective analyses accounted only for the soil characteristics related to Ae horizon.

Table 32 contains the values of correlation coefficients between selected phytoindication values and soil variables.

It can be concluded from this table that in the fresh pine forests all bioindicators considered are mutually strongly correlated, while their connections with soil characteristics are weaker. The pH value links two groups of variables, its value being significantly correlated with two phytoindicators and three soil variables.

In the case of mixed oak-pine forests one can also distinguish a group of strongly correlated phytoindicators, while the soil variables are much more dependent. Here, only the C:N ratio is correlated with the bioindicators and constitutes, at the same time, a part of slightly distinct group, which includes also total carbon and total nitrogen.

Situation is different in the lime-oak-hornbeam forests. Here, a group of strongly correlated phytoindicators is also observed, but it encompasses also the C:N ratio, which is not associated with the remaining soil variables. These remaining soil variables form the second internally well correlated group, a link between two groups being constituted by the Rmean variable.

An assessment of changes in the phytoindicators values and soil characteristics of the Ae horizon during the regeneration process can be based on correlations of these variables with those most strongly influencing the regeneration process, i.e. persistence and distance, as well as with the synthetic index of phytocoenosis maturity, FMI (see Chapters 8.1 and 8.2). Table 33 presents respective correlation values, including the partial correlations.

Table 32. Pearson's correlation coefficients for soil and bioindicative variables for three forest types. Statistically significant ($p<0.05$) correlations are shadowed

A - *Peucedano-Pinetum* (N=205)

	Rmean	Fmean	Lmean	Nmean	Total S	pH	Total C	C/N ratio	Total N
Rmean	1	0,224	-0,386	0,610	0,067	0,012	0,043	-0,063	0,079
Fmean	0,224	1	-0,141	0,180	0,084	-0,026	0,184	0,268	0,079
Lmean	-0,386	-0,141	1	-0,429	-0,288	0,255	-0,009	-0,081	-0,097
Nmean	0,610	0,180	-0,429	1	0,327	-0,227	0,104	0,068	0,147
Total S	0,067	0,084	-0,288	0,327	1	-0,272	0,288	0,132	0,128
pH	0,012	-0,026	0,255	-0,227	-0,272	1	-0,281	-0,276	-0,113
Total C	0,043	0,184	-0,009	0,104	0,288	-0,281	1	0,432	0,351
C/N ratio	-0,063	0,268	-0,081	0,068	0,132	-0,276	0,432	1	-0,372
Total N	0,079	0,079	-0,097	0,147	0,128	-0,113	0,351	-0,372	1

B - *Querco roboris-Pinetum* (N=94)

	Lmean	Rmean	Nmean	Fmean	C/N ratio	Total N	Total C	Total S	pH
Lmean	1	-0,406	-0,521	-0,411	0,089	0,106	0,128	-0,008	0,026
Rmean	-0,406	1	0,791	0,221	-0,148	-0,135	-0,164	-0,067	-0,034
Nmean	-0,521	0,791	1	0,204	-0,132	-0,220	-0,248	0,013	-0,027
Fmean	-0,411	0,221	0,204	1	-0,347	0,173	-0,090	-0,011	-0,029
C/N ratio	0,089	-0,148	-0,132	-0,347	1	-0,359	0,199	-0,035	-0,179
Total N	0,106	-0,135	-0,220	0,173	-0,359	1	0,801	0,121	-0,094
Total C	0,128	-0,164	-0,248	-0,090	0,199	0,801	1	0,096	-0,167
Total S	-0,008	-0,067	0,013	-0,011	-0,035	0,121	0,096	1	0,093
pH	0,026	-0,034	-0,027	-0,029	-0,179	-0,094	-0,167	0,093	1

C - *Tilio-Carpinetum* (N=29)

	C/N ratio	Lmean	Fmean	Nmean	Rmean	pH	Total C	Total S	Total N
C/N ratio	1	0,442	-0,544	-0,726	-0,618	-0,098	0,168	0,048	-0,190
Lmean	0,442	1	-0,568	-0,443	-0,590	0,004	0,154	0,041	0,054
Fmean	-0,544	-0,568	1	0,752	0,553	0,172	-0,059	0,017	0,033
Nmean	-0,726	-0,443	0,752	1	0,800	0,221	-0,274	-0,231	-0,091
Rmean	-0,618	-0,590	0,553	0,800	1	0,386	-0,444	-0,418	-0,275
pH	-0,098	0,004	0,172	0,221	0,386	1	-0,550	-0,534	-0,507
Total C	0,168	0,154	-0,059	-0,274	-0,444	-0,550	1	0,957	0,912
Total S	0,048	0,041	0,017	-0,231	-0,418	-0,534	0,957	1	0,923
Total N	-0,190	0,054	0,033	-0,091	-0,275	-0,507	0,912	0,923	1

Generally speaking, the level of statistically significant correlations is low, with persistence being somewhat stronger correlated with the soil characteristics than with the phytoindicators, while FMI is correlated quite strongly with the phytoindicators, not being correlated – or only slightly – with the majority of soil variables. It should also be emphasised that the significant correlations with distance are fewer and clearly weaker. Further, it is worthwhile to note that each type of community is characterised by a specific pattern of correlations with persistence and FMI.

The values of particular indicators and their changes are not only influenced by persistence and FMI, but also by a number of other factors. The influence of some of them can be observed by the analysis of partial correlations.

In the case of soil reaction (pH) a distinct negative correlation with persistence is observed in the fresh pine forests, meaning that the longer the forest persistence, the higher the acidity (lower pH). Additionally, correlation coefficient between pH and persistence decreases when the influence of tree stand age, FMI value and *Vaccinium myrtillus* cover is removed, which means that there is a slight, but analogously directed, influence of these variables on the pH values. Moreover, the degree of A, B and D layers cover does not exert a significant influence on the pH values.

The interrelations observed in the mixed oak-pine forests take a similar shape, with, additionally, an influence of the moss layer cover on soil pH being observed.

The relations observed in the lime-oak-hornbeam forests take a different shape. Here, though, in view of the sample size, the majority of correlations calculated are not statistically significant at the accepted significance level. First of all, pH is slightly negatively correlated with persistence, and the strength of this relation increases clearly with elimination of the FMI influence, which demonstrates the antagonistic kind of influence from persistence and FMI on the soils reaction. Other factors analysed do not exert any serious influence on the pH values. The observed correlation is insofar complicated as FMI increases, as well, with the increase of persistence. Such a double dependence can only be explained by the fact that there are frequently, on the lime-oak-hornbeam forest habitats (and that for many generations), artificially introduced pine stands (causing acidification), while the undergrowth is composed by species of a different ecological character and different kind of influence on soils.

The changes in carbon and nitrogen contents during the regeneration of communities take a clearly different shape in the analysed forest types. In the case of fresh pine forests and mixed oak-pine forests these variables display no significant correlations with persistence, distance and FMI. While, in the lime-oak-hornbeam forests a positive relation is observed between carbon content and persistence. A closer analysis of partial correlations points out, though, a more complex character of the relationship.

It turns out, namely, that in the mixed oak-pine forests elimination of the FMI influence brings about the statistically significant negative correlation between carbon content and persistence. It is, however, hard to make the interpretation of this observation. The situation in the lime-oak-hornbeam forests is even more complex. Elimination of the FMI influence causes an increase in the correlation coefficient between carbon content and persistence from 0.38 to 0.58, while elimination of the persistence influence brings about significant correlation between carbon content and FMI, its value being -0.49. It should be emphasised that a similar phenomenon (with, naturally, different values of correlation coefficients) is observed in the lime-oak-hornbeam forests for nitrogen and sulphur content. It appears that the above results, concerning the lime-oak-hornbeam forests should be interpreted as the effect of simultaneous appearance of two processes: carbon accumulation originating from the tree stand (the poorly decomposing lignified parts and the needles from coniferous trees artificially introduced onto the lime-oak-hornbeam forest areas), and activation of the carbon reserves, transferred to the biomass of undergrowth herbaceous plants, along with the losses caused by their respiration.

Side by side with the relationships, commented upon above, between the soil characteristics and persistence, distance and FMI, one should also consider the relation between the C:N ratio, on the one hand, and persistence and FMI on the other, observed within the fresh pine forests. Analysis of partial correlations suggests combined positive influence of both these variables on the value of C:N and lack of influence from other variables analysed.

The relationships of phytoindicators, most pronounced being those with the FMI, are quite obvious. As the FMI value increases, there is in all types of communities considered an increase of shading (decrease in Lmean value), nitrogen content, humidity, and decrease in soil reaction. This general image is most unambiguous in the case of mixed oak-pine forests, while in the case of fresh pine forests it is modified by the influence of persistence on the Rmean indicator value (negative correlation between persistence and Rmean).

When analysing the data of Table 33 one should pay attention to the fact that the variable *cover c* (cover of the undergrowth layer), as the variable controlling the correlations with persistence, distance and FMI, has not been accounted for. The calculations performed demonstrated, namely, that this variable does not play any role in the modification of correlations between analysed variables.

As mentioned already before, in the analyses carried out and reported above, the soil characteristics concerned the Ae horizon. A separate analysis has been performed for the same soil parameters, related to the plough horizon Ap, identified and described in numerous forest plots. Analogous correlation analysis, including partial correlations, demonstrated lack of any significant links with persistence, distance or FMI.

Table 33. Main partial correlations between soil and bioindicative variables and variables describing the ecosystem regeneration for three forest types. Statistically significant (p<0.05) correlations are shadowed.

Forest types	Variables	Correlation with Persistence								Correlation with Distance								Correlation with FMI							
			Partial correlations, controlling for:								Partial correlations, controlling for:								Partial correlations, controlling for:						
			Treestand age	A cover	B coner	D cover	Distance	FMI	*V.myrt.* cover		Treestand age	A cover	B coner	D cover	Persistence	FMI	*V.myrt.* cover		Treestand age	A cover	B coner	D cover	Persistence	Distance	*V.myrt.* cover
Peucedano-Pinetum	Lmean	-0,1038	-0,0783	-0,0559	-0,1041	-0,0955	-0,1092	0,1695	-0,0394	0,0233	0,0055	0,0163	0,0228	0,0109	-0,0412	-0,2049	-0,0468	-0,3325	-0,3173	-0,2766	-0,3338	-0,3288	-0,356	-0,384	-0,3382
	Fmean	0,2125	0,2369	0,211	0,2114	0,2037	0,1582	-0,0127	0,131	-0,1484	-0,1608	-0,1479	-0,1552	-0,1364	-0,0378	0,0443	-0,0635	0,3307	0,3556	0,3345	0,3268	0,3245	0,2596	0,3018	0,2761
	Rmean	-0,2064	-0,2158	-0,2269	-0,2083	-0,1905	-0,061	-0,3735	-0,1611	0,2848	0,2899	0,2888	0,2824	0,2687	0,2093	0,4134	0,2533	0,1039	0,1049	0,082	0,1005	0,1258	0,333	0,3279	0,2832
	Nmean	0,002	-0,0006	-0,029	0,0009	0,0208	0,1519	-0,2285	-0,017	0,2192	0,2237	0,2278	0,2173	0,2033	0,2646	0,4426	0,2664	0,2486	0,2533	0,213	0,2465	0,2714	0,3328	0,4555	0,3197
	pH	-0,3271	-0,3082	-0,3119	-0,3333	-0,3251	-0,23	-0,2128	-0,2407	0,2564	0,2416	0,2554	0,252	0,2536	0,0956	0,1393	0,1639	-0,2606	-0,2405	-0,2364	-0,2717	-0,2572	-0,0593	-0,1474	-0,1277
	Total N	0,111	0,1005	0,0947	0,1094	0,1245	0,1192	0,0845	-0,0154	-0,0211	-0,0126	-0,0185	-0,026	-0,0358	0,0487	0,0227	0,1069	0,0722	0,0613	0,0464	0,0672	0,0839	-0,0028	0,0727	-0,1375
	Total C	0,121	0,118	0,1175	0,1195	0,1	0,1387	0,0917	0,0014	-0,0099	-0,0056	-0,0091	-0,0148	0,0202	0,0691	0,041	0,1157	0,0793	0,075	0,0739	0,0742	0,0587	-0,0023	0,0886	-0,1193
	Total S	0,2384	0,2189	0,2222	0,2457	0,1949	0,2073	0,1254	0,1635	-0,1211	-0,1055	-0,1189	-0,1141	-0,0566	0,0135	0,0013	-0,0332	0,2204	0,2017	0,1962	0,2342	0,1793	0,0843	0,1856	0,1199
	C/N ratio	0,3422	0,335	0,331	0,3422	0,3221	0,2949	0,2118	0,3051	-0,1819	-0,1725	-0,1803	-0,1823	-0,1509	0,0097	-0,0295	-0,1199	0,2859	0,2767	0,2692	0,2862	0,2655	0,0814	0,2261	0,2438
Querco roboris-Pinetum	Lmean	-0,3306	-0,309	-0,2613	-0,3388	-0,2744	-0,2199	0,2025	-0,3372	0,278	0,2648	0,2095	0,279	0,2516	0,1189	-0,032	0,2761	-0,5926	-0,5697	-0,5379	-0,6036	-0,5222	-0,549	-0,5455	-0,6335
	Fmean	0,2465	0,2733	0,2063	0,2673	0,2112	0,1966	-0,0551	0,1892	-0,1527	-0,1688	-0,1115	-0,1568	-0,1298	-0,0184	0,0487	-0,104	0,3781	0,4288	0,3348	0,4006	0,3294	0,3005	0,3529	0,3288
	Rmean	0,0975	0,088	0,0782	0,0812	0,0316	0,1452	-0,3917	0,0934	0,0406	0,0479	0,0621	0,0445	0,0877	0,1154	0,3467	0,0501	0,4475	0,4439	0,4407	0,438	0,3743	0,5625	0,5433	0,4807
	Nmean	0,1366	0,126	0,0935	0,1313	0,0677	0,1691	-0,3669	0,1709	0,0064	0,0145	0,0523	0,0078	0,0561	0,1009	0,3259	-0,0106	0,4753	0,4702	0,4422	0,4744	0,3982	0,5633	0,5551	0,5549
	pH	-0,3234	-0,2952	-0,3601	-0,2976	-0,2975	-0,2892	-0,1189	-0,2584	0,1548	0,1321	0,183	0,152	0,1358	-0,0334	-0,0181	0,0945	-0,3346	-0,2808	-0,3873	-0,3101	-0,294	-0,149	-0,3007	-0,2609
	Total N	-0,1088	-0,096	-0,0757	-0,1063	-0,1105	-0,0375	-0,1794	-0,1615	0,1395	0,1314	0,1102	0,1388	0,1401	0,0954	0,1708	0,1772	0,0153	0,0399	0,0664	0,0193	0,0175	0,1442	0,1007	-0,0362
	Total C	-0,2257	-0,2365	-0,193	-0,2331	-0,2115	-0,2063	-0,3167	-0,247	0,0993	0,105	0,0644	0,1003	0,0886	-0,0335	0,1045	0,1065	-0,0182	-0,0321	0,0375	-0,0229	0,0161	0,2287	0,0374	-0,0261
	Total S	-0,0276	-0,0445	-0,0319	-0,0407	0,0034	-0,0686	0,0166	-0,0771	-0,0521	-0,0421	-0,0501	-0,0498	-0,0722	-0,0816	-0,0912	-0,0207	-0,0522	-0,0812	-0,0593	-0,0653	0,0008	-0,0473	-0,0913	-0,115
	C/N ratio	-0,2091	-0,2431	-0,2015	-0,2297	-0,1966	-0,2831	-0,1665	-0,189	-0,0451	-0,0282	-0,0585	-0,0421	-0,0562	-0,2001	-0,1316	-0,073	-0,1328	-0,1853	-0,1211	-0,1515	-0,1104	0,0343	-0,1807	-0,1035
Tilio-Carpinetum	Lmean	-0,3886	-0,3952	-0,2786	-0,2513	-0,3377	-0,2308	0,0066	==	0,357	0,3705	0,4491	0,1687	0,2518	0,1645	-0,0607	==	-0,6945	-0,7048	-0,6089	-0,6147	-0,626	-0,6248	-0,6395	==
	Fmean	0,1724	0,1786	0,0955	0,1651	0,1158	0,1752	-0,0061	==	-0,0554	-0,065	-0,0663	-0,0327	0,0561	0,0637	0,1559	==	0,3136	0,3117	0,2231	0,3263	0,205	0,266	0,3429	==
	Rmean	0,165	0,1982	0,0158	0,1834	0,0887	0,1902	-0,2628	==	-0,0233	-0,0714	-0,044	-0,0304	0,1356	0,0988	0,4782	==	0,5991	0,576	0,4923	0,679	0,5091	0,6217	0,7108	==
	Nmean	0,0319	0,0566	-0,127	0,1022	-0,0392	0,224	-0,146	==	0,231	0,1996	0,2454	0,1836	0,3861	0,3162	0,4768	==	0,2622	0,225	0,0821	0,3767	0,1349	0,2961	0,4898	==
	pH	-0,3425	-0,3271	-0,3491	-0,2931	-0,3542	-0,3566	-0,4891	==	0,1004	0,0408	0,1015	0,0013	0,1132	-0,1455	0,1943	==	0,1041	0,0298	0,1305	0,2243	0,1099	0,384	0,1961	==
	Total N	0,3326	0,3245	0,3084	0,2474	0,3217	0,4075	0,4707	==	-0,0159	0,0049	-0,0201	0,1545	0,0179	0,25	-0,0852	==	-0,0954	-0,0724	-0,1714	-0,2668	-0,1585	-0,3642	-0,1267	==
	Total C	0,3846	0,3748	0,3897	0,3171	0,3777	0,4515	0,5794	==	-0,0445	-0,0172	-0,0459	0,1024	-0,0179	0,2597	-0,1624	==	-0,1551	-0,1257	-0,1925	-0,3195	-0,2191	-0,489	-0,2188	==
	Total S	0,4012	0,3916	0,4073	0,3312	0,3923	0,4144	0,5504	==	-0,1233	-0,0982	-0,1248	0,0156	-0,0977	0,167	-0,2124	==	-0,0903	-0,0583	-0,1205	-0,2517	-0,1523	-0,4195	-0,1957	==
	C/N ratio	-0,0137	-0,0244	0,1429	-0,0062	0,0189	-0,1305	0,1828	==	-0,1454	-0,1303	-0,1482	-0,1802	-0,2137	-0,1939	-0,3841	==	-0,2803	-0,2665	-0,1106	-0,3062	-0,2414	-0,3305	-0,4445	==

The analyses, reported in this section and the results reported earlier, allow for the statement that both the value of FMI and the phytoindicators values are a derivative of the floristic composition, shaped by numerous factors, of which most important include persistence and distance. On the other hand, in the case of soil properties, the influence of persistence is much more limited, with decisive role being played by the local factors, associated with the character of substratum and the anthropogenic impacts. Besides, changes in the soil chemical properties require a different time scale than changes in species composition, which brings about the asynchronous character of these two ecosystem components regeneration.

8.4. MAIN CONCLUSIONS FROM THE MODELS

It can be concluded from the models presented that:

- The sequence of regeneration rate of recent post-agricultural forests is as follows: lime-oak-hornbeam forest, mixed oak-pine forest, typical pine forest. This sequence corresponds to the sequence of these types according to the habitat richness. This is also reflected in the regeneration rate of post-agricultural soils. This regularity can be shortly characterised as: 'the poorer the habitat, the slower the regeneration'.
- Poor habitats of the pine forests display very long periods of regeneration, despite the accordance of introduced tree stands with the potential vegetation community type. Spontaneous regeneration of the pine forests is so slow that it becomes unattainable within the time frame adopted for analysis and modelling.
- Models of pine and mixed oak-pine forests regeneration with regard to re-establishment of two important species, *Vaccinium myrtillus* and *Convallaria majalis*, even though they concern different characteristics (bilberry – cover, lily of the valley – frequency), demonstrate a surprisingly similar image. The domination of dependence upon persistence over that upon distance is visible. Higher regeneration rate in the somewhat richer mixed oak-pine forests than in the oligotrophic pine forests can also be seen. Likewise, the fact that dependence upon distance is more pronounced in the mixed oak-pine forests than in the pine forests, is visible. It should be noted that the influence of distance is perceptible especially at the smaller distances from the ancient forest. This may be the consequence of the fact that although both species are endozoochorous, in reality they spread mainly in the vegetative manner.

9. REGENERATION OF THREE FORESTS TYPES ON POST-AGRICULTURAL LAND – THE GENERAL SCHEME

It is possible to distinguish between three types of causes influencing the observed, current effects of forest regeneration processes:

- the natural tendency of phytocoenoses towards formation of the floristic composition and structure that are optimal for the given conditions, this leading from the disturbed, 'unnatural' communities to those in which human influence is insignificant;
- the reasons of incidental character, occurring now and in the past as the impacts from the outside of the system, disturbing its structure (disruption of the soil-and-vegetation cover by humans or animals, small fire or windbreak);
- the reasons that have their origins in the past conditions, not existing any more, which could have a natural character or – much more frequently anthropogenic character.

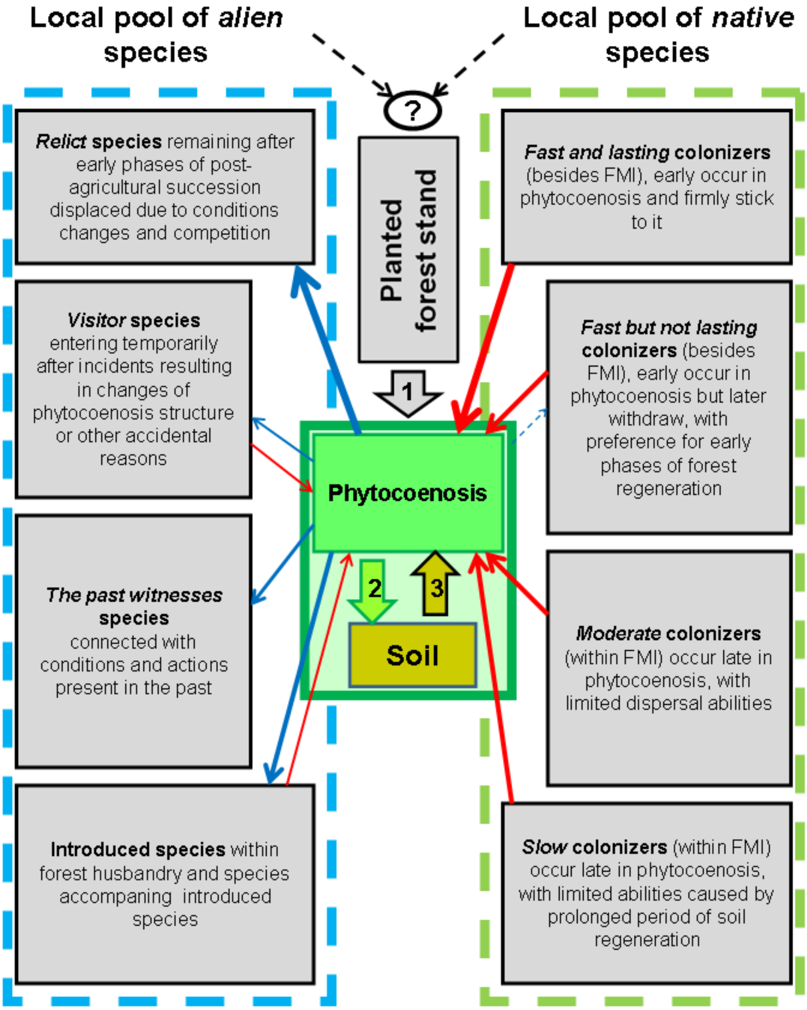
The relationships, identified in this study, taking place during the post-agricultural forests regeneration, might be considered as a specific case of formation of the 'ecological pool of species', conform to the concept of Balyea and Lancaster (1999), or of the 'community pool' according to Zobel et al. (1998), in the framework of the concept of 'limited membership' (Roughgarden, Diamond, 1986), presented, in particular, by Dzwonko (2007). These concepts refer to three constraints groups, which do eliminate definite species:

- constraints to the species dispersal, defining the 'geographical pool of species';
- environmental constraints, defining the 'habitat pool of species';
- internal biocoenotic processes, which produce, out of the ecological pool of species, resulting from the superposition of the geographical and habitat pools, the actual pool of species in the community.

Within the framework of the same concept, the 'geographical pool of species' is shaped not only by the local flora, but also by the distance between the regenerating forest and the refuge, that is – in our case – the ancient forest. Then, the 'habitat pool of species' is shaped not only by the substratum and moisture conditions etc., but also by the fine changes that occur to the soils in the course of regeneration. Since soil regeneration is in the evident way dependent upon the passing time, forest persistence exerts, as well, an influence on the shape of the ’habitat pool of species‘. The apparent dependence of the Ellenberg indicator values upon the recent forest categories, i.e. upon persistence, demonstrate plants reaction to the changes, linked with regeneration, and concerning habitat conditions. Change in the community structure is a particular form of habitat change, causing changes in the light conditions of the undergrowth layer. These changes are perceptible in consideration of the L indicator according to Ellenberg. (Such changes could also be considered as the biocoenotic influence, but in view of the disproportion between the trees causing shade and the herbaceous plants, depending upon this, it is simpler to describe the process as the change of habitat conditions for the undergrowth plants).

It is most difficult to point out the biocoenotic changes within the phytocoenosis, especially when the analysis is limited to the plants of a undergrowth layer. Without deeper considerations on this subject, it can be taken for granted that such influences must be present, even though we are not always capable of showing and documenting them.

The general scheme of the recent post-agricultural forest regeneration derived from our investigations is displayed in Fig. 162. It should be reminded at the beginning that the conversion from the arable land ecosystem to the forest ecosystem constitutes an essential change encompassing transformations concerning all ecosystem elements . The most important changes consist in the complete exchange of the floristic composition and development of an entirely different vegetation structure. It can be practically assumed that there are no forest species in a cultivated field. The forest regeneration, which would start after these or other transitory stages (grasslands, heathlands or other), with the controlling humans intervention (planting of young trees and other operations), or without it (spontaneous forest succession), consists in the return of species typical of forest appropriate type, with simultaneous (or asynchronous) elimination of species typical of a non-forest community. One should add to this scheme that the forests investigated are not the ‘wild primeval forest‘, but are managed forests, exploited intensively for many years, with recurring smaller and bigger felling areas. Thus, the normal cycle in such a forest goes from the felling clearing through the juvenile forest forms , the middle-aged forest, up to the mature forest, when (or earlier) felling takes place again, before the tree stand enters the late degradation phase. This cycle applies both to the ancient forests and to the recent ones, except for a few areas, put under protection. The latter, though, constitute a small part of the forests, and in the case of recent forests are indeed very rare. For this reason the regeneration process of recent post-agricultural forest ought to be seen as, at the same time, the directional process (post-agricultural regeneration) and the cyclic one (re-establishment of the forest community after felling). In the case of ancient forest one deals, on the other hand, only with the cyclical process, if we neglect the introduction of the tree stands having composition inconsistent with the natural one.



1 – Phytocoenosis formation by tree species over its lifespan.
2 – Soil formation by phytocoenosis.
3 – Floristic composition depending on soil characteristics.

Fig. 162. Post-agricultural forests regeneration as a replacement of alien species pool by native species pool.

Ryc. 162. Schemat regeneracji lasów wtórnych na gruntach porolnych jako zastępowanie puli gatunków „obcych" przez pulę gatunków „własnych"

It should be also noted that in the present work we do not deal with the early forest phases and conversion from the open habitat to the high forest. This concerns both the post-agricultural land and the ancient forests. The study concerns the developing phases of mature forest or, ultimately, close to maturity, that is – the ones in which the vegetation systems can be described as associations. When comparing – the study refers to adults, and not children. Thus, recent forests are analysed in the comparable phase of the tree stand age, but of a different regeneration period. This means, in practice, that the recent forests, featuring different persistence, do also feature a different number of trees generations having grown up on the given place since the post-agricultural land had been afforested. Considering this, it was assumed that the species participating in the regeneration process can be classified into two groups:

- the ʼnativeʻ species, that is – the ones that are typical of a given community; it could be admitted that this applies to all species, forming the so-called characteristic species combination in the association;
- the ʼalienʻ species, that is – the ones, which do not appear in the typical and natural biocoenoses of ancient forests, or appear there only incidentally.

Among the ʼnativeʻ species one can distinguish four slightly separated types, differing in the rate of colonization.

The ʼ**fast and lasting colonisers**ʻ are the species belonging to the characteristic combination of species (the characteristic, differential species and companions of high frequency), which have not been included in the Forest Maturity Index (FMI) because they appear relatively fast in the recent forests. Already in the recent forests aged 90-120 years, that is – in the first generation of tree stands, the frequency of these species does not differ significantly from that in ancient forests of the same type. In addition, in the particular categories of recent forests they feature similar frequencies, even though in many cases their actual role in the phytocoenoses may increase along with longer persistence. This means that the species in question return to the recent forests (in terms just of frequency, their quantitative contribution to the phytocoenosis put apart!) already within the first decades after afforestation, and then they continue to take part in the further regeneration stages, provided the forest has sufficiently old tree stand.

It can be stated that this category comprises:

- in the pine forests (*Peucedano-Pinetum*) – the species characteristic of the communities from the class of *Vaccinio-Piceetea*: *Dicranum scoparium*, *Dicranum polysetum*, *Lycopodium annotinum*, *Melampyrum pratense*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, as well as the companions: *Dryopteris carthusiana, Polytrichastrum formosum, Sorbus aucuparia*;
- in the mixed oak-pine forests (*Querco-Pinetum*) – the species characteristic of the communities from the class of *Vaccinio-Piceetea*: *Dicranum scoparium*, *Dicranum polysetum*, *Hylocomium splendens*, *Lycopodium annotinum*, *Melampyrum pratense*, *Pleurozium schreberi*, *Vaccinium vitis-idaea*, as well as the companions: *Calamagrostis arundinacea*, *Calluna vulgaris*, *Deschampsia flexuosa*, *Dryopteris carthusiana*, *Festuca ovina*, *Fragaria vesca*, *Frangula alnus*, *Juniperus communis*, *Rubus idaeus*, *Rubus saxatilis*, *Sorbus aucuparia*;

- in the lime-oak-hornbeam forests (*Tilio-Carpinetum*) – the species characteristic of the communities from the class of *Querco-Fagetea*: *Aegopodium podagraria*, *Athyrium filix-femina*, *Carex digitata*, *Dryopteris filix-mas*, *Melica nutans*, *Plagiomnium affine* (and perhaps also a number of other species, rarer, not sufficiently identified in the study), as well as the companions: *Dryopteris carthusiana*, *Geum urbanum*, *Hieracium lachenalii*, *Luzula pilosa*, *Maianthemum bifolium*, *Moehringia trinervia*, *Mycelis muralis*, *Oxalis acetosella*, *Polytrichastrum formosum*, *Rubus saxatilis*, *Sorbus aucuparia*, *Urtica dioica*.

The '**fast but not lasting colonisers**' are also constituted by the species classified as typical of a given association, which are present already in the recent forests of the first (mature) generation, displaying similar frequency as in the ancient forests. For this reason they are not included in the FMI. Yet, in distinction from the preceding group, their frequency of appearance is the highest not in the ancient forests but in the mature tree stands of recent forests. It appears that their development optimum takes place in the associations, whose structure has not been fully restored. It is highly probable that this may largely result from the limited regeneration degree of some ancient forests species, like, e.g. *Vaccinium myrtillus*. Under advanced regeneration these species remain, but their frequency in the patches is limited. It is possible that their development capacities become constrained.

The following species can be classified in this category:

- in the pine forests (*Peucedano-Pinetum*) – from among those characteristic of the class of *Vaccinio-Piceetea*: *Chimaphila umbellata*, *Monotropa hypopitys*, *Diphasiastrum complanatum*, *Orthilia secunda*, *Pyrola chlorantha*, and the companions: *Deschampsia flexuosa*, *Juniperus communis*;
- in the mixed oak-pine forests (*Querco-Pinetum*) – *Chimaphila umbellata*, *Diphasiastrum complanatum*, *Orthilia secunda*, *Ptilium crista-castrensis*, *Pyrola chlorantha*, *Pyrola rotundifolia* (all of them being characteristic of the *Vaccinio-Piceetea* class);
- in the lime-oak-hornbeam forests (*Tilio-Carpinetum*) – it is hard to indicate the respective species in view of the limited relevés number; most probably, one can classify in this category: *Dactylis polygama*, *Corylus avelana*, *Euonymus verrucosa*, *Pteridium aquilinum*.

The '**moderate colonisers**' comprise the species included in the characteristic combination of an association, which feature in the recent forests – at least in those of shorter persistence period – significantly lower frequency than in the ancient forests. They were included in the FMI on just this basis. The species in question return late to the recent forests, and the possibility of their return depends partly upon the distance to the refuge.

This category includes:

- in the pine forests (*Peucedano-Pinetum*) – from among the species characteristic of the class of *Vaccinio-Piceetea*: *Hylocomium splendens, Vaccinium vitis-idaea*, *Vaccinium myrtillus*, and from among the companions: *Calamagrostis arundinacea, Calluna vulgaris, Frangula alnus, Luzula pilosa, Molinia caerulea, Oxalis acetosella, Peucedanum oreoselinum, Scorzonera humilis*;
- in the mixed oak-pine forests (*Querco-Pinetum*) – from among the species characteristic of the class of *Vaccinio-Piceetea*: *Trientalis europaea, Vaccinium myrtillus*, and from among the companions: *Convallaria majalis, Luzula pilosa, Maianthemum bifolium, Molinia caerulea,* Oxalis acetosella, *Peucedanum oreoselinum, Polygonatum odoratum, Polytrichastrum formosum, Pteridium aquilinum*;
- in the lime-oak-hornbeam forests (*Tilio-Carpinetum*) – species characteristic of the class of *Querco-Fagetea*: *Anemone nemorosa*, *Carpinus betulus* (in the tree layer), *Galeobdolon luteum*, *Milium effusum*, *Polygonatum multiflorum*, *Scrophularia nodosa*, *Stellaria holostea*, *Viola reichenbachiana* (and most probably yet a number of other ones), as well as the companions: *Ajuga reptans*, *Calamagrostis arundinacea*, *Convallaria majalis*.

The '**slow colonisers'** are the species classified in the FMI, very slowly returning to the recent forests. This very slow return is probably caused by the soil conditions, transformed by agrotechnical measures. Soil regeneration, taking place generally much slower than the regeneration of floristic composition (at least regarding its basic pattern), influences return possibility of these species. It must be noted that distinction between this group and the preceding one is quite nominal and highly hypothetical, since usually the factors of regeneration period and distance to the refuge act in synergy, and are, additionally, correlated, because the recent forests with longer persistence are usually situated close to the ancient forests, while forests located far away from the ancient forests have usually been regenerating for a shorter time.

This category consists of:

- in the pine forests (*Peucedano-Pinetum*) - *Convallaria majalis, Trientalis europaea, Vaccinium uliginosum*;
- in the mixed oak-pine forests (*Querco-Pinetum*) - *Athyrium filix-femina, Sciuro-hypnum oedipodium, Scorzonera humilis*;
- in the lime-oak-hornbeam forests (*Tilio-Carpinetum*) - *Atrichum undulatum*, *Galium odoratum*, *Hepatica nobilis*, *Hypnum cupressiforme*, *Lathyrus vernus*, *Lilium martagon*, *Phyteuma spicatum*, *Ranunculus lanuginosus*.

Among the 'alien' species several categories can be distinguished. They are classified into four groups.

The **’relict‘ species** are the species typical of communities preceding forests in the secondary succession on post-agricultural land. These are usually the species, linked with the open habitats – arable lands, meadows, sandy grasslands, heathlands, fringe communities, as well as shrubs. Such species retreat in the course of regeneration, due to conditions changes (e.g. increasing shading, stabilisation of the soil cover) or through interaction with other species, gaining competitive advantage.

This category is seen as comprising:

- in the pine forests (*Peucedano-Pinetum*) – *Agrostis capillaris*, *Anthoxanthum odoratum*, *Hieracium lachenalii*, *Hieracium pilosella*, *Lycopodium clavatum*, *Polytrichum juniperinum*;
- in the mixed oak-pine forests (*Querco-Pinetum*) – *Anthoxanthum odoratum*, *Cytisus scoparius*, *Galium molugo*, *Lycopodium clavatum*, *Polytrichum juniperinum*, *Veronica officinalis*;
- in the lime-oak-hornbeam forests (*Tilio-Carpinetum*) the following speciess might perhaps be included in this category: *Frangula alnus*, *Fragaria vesca*, *Galium molugo*, *Geranium robertianum*, *Veronica chamaedrys*, *Veronica officinalis*.

The **’visitor’ species** are the ones that enter the recent forests transitorily in different periods of regeneration, and also the ancient forests, due to various random events, usually through disruption of the phytocoenosis or the soil structure. The species of this group are most often associated with clearings, grasslands of early succession stages or ruderal communities. In principle, these species enter sporadically, but actually they may be frequent additional components of phytocoenoses, given the frequency of respective events. *Rumex acetosella* is such a species in pine and mixed oak-pine forests, appearing in sites, where the vegetation cover was destroyed and bare soil got uncovered, like due to skidding or boar rooting. Another instance, under different circumstances, is *Calamagrostis epigeios*. Similarly – *Galeopsis tetrahit* in the lime-oak-hornbeam forests. A special kind of ’visitors‘ is constituted by invasive species, which do enter, but it is not known when they would leave. The unambiguously invasive species in the analysed communities of lime-oak-hornbeam forests is *Impatiens parviflora*.

The **introduced species** are the ones that entered the phytocoenosis due to the deliberate human activities or were their side-effects. This group includes, certainly, the species which are consciously introduced in the framework of forest management (mainly the tree species, and also the shrub species, like, e.g., *Padus serotina*). In the study, this group was also assumed to comprise these species, which accompany the species introduced into the stand (although they could have been classified separately). These are, in particular, the species associated with pine forests, appearing in the lime-oak-hornbeam woods in the effect of introduction of Scots pine or spruce into the stand, or, generally, owing to a community deformation (*Pleurozium schreberi*, *Trientalis europaea*, *Vaccinium vitis-idaea*, *Hylocomium splendens*, *Deschampsia flexuosa*, *Rubus idaeus*, *Juniperus communis*). Further, the species that appeared in connection with other human activities in forest, like, e.g. grasses and other grasslands species, whose seeds enter forests due to introduction of hay as a fodder for forest animals (*Holcus mollis*, *Galium molugo*).

The species being **'past witnesses species'** seem to have been connected with the conditions that existed in the past, and which do not exist anymore. This group was assumed to comprise the species thought to be linked with the ancient, nowadays practically extinct, forest pasturing. The authors think that in the period of forest pasturing, which lasted certainly until the middle of the 19th century, this happened either through the seeds supply or through limitation of competition from other species. It appears that in the pine forests this group may contain such species as *Festuca ovina* and the lichen species from the genus *Cladonia*, in particular – *Cladonia arbuscula*. In the lime-oak-hornbeam forests these species may belong to the 'companions of pine', which remain even when pine itself has been eliminated from the stand (without clear cut).

In the considerations on the paths of post-agricultural forest regeneration it is important what the species composition of re-established tree stands is. In the area studied the tree stands have been for a long time in a vast majority planted, and so their composition is the effect of forest manager decisions and only a definite part of changes occurred under the influence of spontaneous trees reproduction. This, however, has not always been the situation. It can be assumed that the tree stands before the middle of the 19th century could have had in their majority the character of spontaneous afforestations, while the later ones were in their majority planted, with domination of pine as the economically exploited species. The scheme, shown in Fig. 162 accounts for the variants, depending upon whether the introduced (or spontaneous) tree stand belongs to the pool of native species (e.g. Scots pine on the habitats of pine and mixed oak-pine forests, oak on the habitats of mixed oak-pine forest and of lime-oak-hornbeam forests), or to the pool of 'alien' species (e.g. Scots pine on the habitats of lime-oak-hornbeam forests). It can be assumed that the regeneration of recent forest is more effective and faster for the introduced tree stand from the pool of 'native' species, than in the case of tree stand inconsistent with the habitat. The tree stand from the pool of 'native' species improves the conditions for the return of other 'native' species, while the tree stand from the pool of the 'alien' species on the one hand creates conditions that are disadvantageous for the 'native' species (change in light conditions, humus type and the soil reaction), and on the other hand attracts the 'accompanying' species also from among the 'alien' ones. These accompanying species first enter and strengthen their position as the tree stand develops, and only afterwards are 'pushed out' by the species typical of a community. An instance is provided by the entry of *Vaccinium myrtillus* and other pine forest species into the forest with the pine stand on the habitat of lime-oak-hornbeam forest. These species appear in the recent forests at a definite age of pine stand, often even earlier than on the habitat of pine forest, appropriate for them. This is followed by the optimum phase of their development, and afterwards they start to be 'pushed out' by the returning species of lime-oak-hornbeam forest. The latter phase is often linked with the shading of the ground by shrubs and young individuals of deciduous trees, which eliminates photophilous pine forest species. Regeneration of the recent post-agricultural forest with the introduced tree stand from the pool of 'alien' species is obviously charged with the simultaneous processes, leading in diverse directions, even opposite to the direction of a potential community regeneration.

In our opinion, interactions between phytocoenosis and soil are crucial in the regeneration of recent forests . In natural conditions – that is, approximately, in the ancient forests, individual associations are related to more or less diversified soils. Agricultural use of soils evens out to a certain degree (although certainly not entirely) habitat conditions of the associations. This is implied by the specific features of segetal vegetation communities, mutually close – although usually not identical – on different habitats. For this reason the regeneration of phytocoenosis on post-agricultural land (as this was indicated in Chapter 4) is linked with slow regeneration of the soil (see Chapter 7). This is also constituted by changes in the floristic composition, perceived through the indicator values (see Chapter 6).

The here stated much slower regeneration of soils under the pine forests, when compared to the mixed oak-pine forests and the lime-oak-hornbeam forests, is just one side of the coin of slower regeneration of pine forests community. At the same time, in both pine and mixed oak-pine forest it is only the regeneration of *Vaccinius myrtillus* to the typical large cover that provides appropriate conditions for the re-establishment of humus and topsoil layers, typical of these forests. We are persuaded that the slow entry of *Vaccinium myrtillus* into pine and mixed oak-pine forests is first of all caused by the agricultural transformation of soils, while, at the same time – lack or hesitant development of *Vaccinium myrtillus* delays the soil regeneration.

10. CONCLUSIONS FOR THE FOREST MANAGEMENT PRACTICE

Based on the studies performed it is possible to formulate practical recommendations, that is – such ones that might be important for the forest management or nature protection and environmental improvement. Given the scope of the study, the practical recommendations concern only some forest communities: pine forests (*Peucedano-Pinetum* association), mixed oak-pine forests (*Querco-Pinetum* association) and, to a limited degree, the lime-oak-hornbeam forests (*Tilio-Carpinetum* association). They correspond to the forest habitat types: fresh pine forest, fresh mixed oak-pine forest, and, to a limited extent, fresh mixed forests and fresh forests.

The conclusions drawn from the study served to formulate the postulates, addressed at forest science and practice, which, in our opinion, ought to be considered and potentially fulfilled during restoration of disturbed forest communities.

10.1. PRACTICAL CONCLUSIONS

Ancient forest constitutes a richer ecosystem than the non-regenerated recent forest

This higher richness of the ancient forest is expressed through:

- appearance of specific forest species, which do not appear (or appear much less frequently) in the recent forests;
- richer structure of phytocoenosis and bigger productivity of the undergrowth layer,
- richer structure of forest soil.

A rich ecosystem is more advantageous as a managed forest than an impoverished ecosystem

The fully developed, natural structure of forest phytocoenosis provides conditions for the existence of an ecosystem that is stable and resistant to disturbances. Besides, the richer ecosystem is capable of providing broader ecosystem services.

Forests on post-agricultural land require long-lasting regeneration

Regeneration of forests on post-agricultural land is a process distributed over time. Spontaneous entry or intentional introduction of tree stands onto post-agricultural land, even if a composition of this stand is conform with the habitat type (i.e. corresponds to the potential natural vegetation), constitutes only a starting point for the regeneration of natural forest. Floristic composition regenerates unevenly – that is, some species return quicker, while other ones slower – and the structure of phytocoenosis, i.e. quantitative proportions, species distribution patterns, layers structure etc., regenerates even slower. Regeneration concerns all layers of the phytocoenosis, starting with trees and ending with the undergrowth and underground layers. In the temporal categories, resulting from the forest commercial use, this means that regeneration is not possible in the first generation of tree stand and must be perceived as a process taking place during several tree stand generations. The regeneration of forest soil is even longer. It should be noted that regeneration is understood here in terms of restoration of the floristic composition and the structure in their general outline. Some consequences of the agricultural land use may leave an indelible imprint in recent forests phytocoenoses, this applying particularly to soils.

The regeneration rate of post-agricultural forests depends upon their vicinity

The possibilities of regeneration are certainly dependent upon the distance between the regenerating patch and the refuge of species, which must return during the regeneration. This was demonstrated in the study results here reported. The particular species display different re-colonisation rates upon distance to ancient forest. Doubtless, side by side with the physical distance to the refuge, other factors may also influence the regeneration rate, either hampering the spread (various barriers) or helping in the propagulae dispersal.

Regeneration of post-agricultural forests is slower on poorer habitats

Comparison of the regeneration rates on the fresh habitats in pine forests, mixed oak-pine forests, mixed deciduous and fresh deciduous forests, shows that higher values are observed in forests on richer habitats. Particularly time-consuming is spontaneous regeneration on sandy habitats – i.e. those of pine forests. Observations made in the fresh pine forests indicate that within them the regularity also exists such that the regeneration rate of the floristic composition and structure is faster on the somewhat richer habitats (a bit more humid and richer, with less destroyed soil).

Table 34. The most probable disturbance degree of recent post-agricultural forests depending on: forest type, persistence and distance

Type	Distance [m]	Persistence												
		300	280	260	240	220	200	180	160	140	120	100	80	60
Peucedano-Pinetum	20	0	0	0	0	0	0	1	1	1	2	2	3	3
	200	0	0	0	0	1	1	1	2	2	2	3	3	3
	400	0	0	1	1	1	1	2	2	2	2	3	3	4
	600	1	1	1	1	2	2	2	2	3	3	3	3	4
	800	1	1	2	2	2	2	2	3	3	3	3	4	4
	1000	2	2	2	2	2	2	3	3	3	3	4	4	4
	1200	2	2	2	2	3	3	3	3	3	3	4	4	4
	1400	2	2	3	3	3	3	3	3	3	4	4	4	4
	1600	2	3	3	3	3	3	3	3	4	4	4	4	4
	1800	3	3	3	3	3	3	3	4	4	4	4	4	4
	2000	3	3	3	3	3	3	4	4	4	4	4	4	5
	2200	3	3	3	3	3	4	4	4	4	4	4	4	5
	2400	3	3	3	4	4	4	4	4	4	4	4	5	5
	2600	3	3	4	4	4	4	4	4	4	4	4	5	5
	2800	3	4	4	4	4	4	4	4	4	4	5	5	5
	3000	4	4	4	4	4	4	4	4	4	4	5	5	5
	3200	4	4	4	4	4	4	4	4	4	5	5	5	5
	3400	4	4	4	4	4	4	4	4	4	5	5	5	5
	3600	4	4	4	4	4	4	4	4	5	5	5	5	5
	3800	4	4	4	4	4	4	4	4	5	5	5	5	5
	4000	4	4	4	4	4	4	4	5	5	5	5	5	5
Querco-Pinetum	20	0	0	0	0	0	0	0	0	0	0	0	0	1
	200	0	0	0	0	0	0	1	1	1	1	2	2	2
	400	1	1	1	1	2	2	2	2	2	2	3	3	3
	600	2	2	2	2	3	3	3	3	3	3	3	4	4
	800	3	3	3	3	3	3	3	3	4	4	4	4	4
	1000	3	3	3	4	4	4	4	4	4	4	4	4	4
	1200	4	4	4	4	4	4	4	4	4	4	4	5	5
	1400	4	4	4	4	4	4	4	4	4	5	5	5	5
	1600	4	4	4	4	4	4	4	5	5	5	5	5	5
	1800	4	4	4	5	5	5	5	5	5	5	5	5	5
	2000	5	5	5	5	5	5	5	5	5	5	5	5	5
	2200	5	5	5	5	5	5	5	5	5	5	5	5	5
	2400	5	5	5	5	5	5	5	5	5	5	5	5	5
	2600	5	5	5	5	5	5	5	5	5	5	5	5	5
	2800	5	5	5	5	5	5	5	5	5	5	5	5	5
	3000	5	5	5	5	5	5	5	5	5	5	5	5	5
	3200	5	5	5	5	5	5	5	5	5	5	5	5	5
	3400	5	5	5	5	5	5	5	5	5	5	5	5	5
	3600	5	5	5	5	5	5	5	5	5	5	5	5	5
	3800	5	5	5	5	5	5	5	5	5	5	5	5	5
	4000	5	5	5	5	5	5	5	5	5	5	5	5	5
Tilio-Carpinetum	20	0	0	0	0	0	0	0	0	0	1	2	2	3
	200	0	0	0	0	0	0	1	1	1	2	2	3	4
	400	1	1	1	1	1	1	1	2	2	2	3	3	4
	600	2	2	2	2	2	2	2	2	2	3	3	4	4
	800	2	2	2	2	2	2	2	3	3	3	4	4	4
	1000	3	3	3	3	3	3	3	3	3	3	4	4	5
	1200	3	3	3	3	3	3	3	3	3	4	4	4	5
	1400	3	3	3	3	3	3	3	4	4	4	4	4	5
	1600	3	3	3	3	4	4	4	4	4	4	4	5	5
	1800	4	4	4	4	4	4	4	4	4	4	4	5	5
	2000	4	4	4	4	4	4	4	4	4	4	5	5	5
	2200	4	4	4	4	4	4	4	4	4	4	5	5	5
	2400	4	4	4	4	4	4	4	4	4	5	5	5	5
	2600	4	4	4	4	4	4	4	4	5	5	5	5	5
	2800	4	4	4	4	4	4	4	5	5	5	5	5	5
	3000	4	4	4	4	4	4	5	5	5	5	5	5	5
	3200	4	4	4	5	5	5	5	5	5	5	5	5	5
	3400	5	5	5	5	5	5	5	5	5	5	5	5	5
	3600	5	5	5	5	5	5	5	5	5	5	5	5	5
	3800	5	5	5	5	5	5	5	5	5	5	5	5	5
	4000	5	5	5	5	5	5	5	5	5	5	5	5	5

Degree of recent forest regeneration:
0 - regenerated recent forest
1-5 - recent forest not regenerated (disturbance degree)

For three types of forests regional (initial) tables were elaborated of the most probable regeneration degree of post-agricultural forests

The degree of patches regeneration was shown in dependence upon two variables: persistence (duration of regeneration) and distance to the ancient forest of the corresponding type (Table 34).

Bilberry (*Vaccinium myrtillus*) is an important element of pine or mixed oak-pine forests ecosystems, undergoing relatively slowly regeneration in the recent post-agricultural forests

Definitely, bilberry is in the typical fresh pine forests one of the most significant element of the undergrowth, its importance extending also to the mixed oak-pine forests. This species exerts a very significant influence on the litter accumulation and formation of humus layer in the soil, which, in particular, increases the capacity of accumulating precipitation water in the soil. Bilberry significantly enriches the spatial structure of phytocoenosis, providing the living conditions for various animal groups. It can be assumed that the enrichment of zoocoenosis is advantageous for the maintenance of ecological equilibrium of the entire ecosystem. This allows for the supposition that the pine forests with bilberry may be less susceptible to phytophagous gradations, and thus 'cheaper to maintain'. At the same time, bilberry belongs among these species, which slowly return to the recent forests on post-agricultural land.

Bilberry (*Vaccinium myrtillus*) is an important resource that can be exploited in the forest

Bilberry fruits are a valuable contribution to the human and animal diet. They feature high taste value and very advantageous health characteristics. The bilberry dwarf shrubs also represent an attractive food element for the forest fauna, significantly raising forest capacity in terms of wild game. The ecosystem services of forests with well developed populations of *Vaccinium myrtillus* are also much more valuable than of those deprived of this species, which is the case of numerous recent post-agricultural forests.

10.2. RECOMMENDATIONS

It is highly recommended to consider from the scientific and practical points of view the problems of recent post-agricultural forests in terms of the needs and possibilities of supporting their regeneration. It is necessary, in our opinion, to undertake research programmes that would provide answers to several fundamental, and also more detailed, questions. Among these questions the most important ones are:

- to what extent the recent forests are 'worse' in natural and economic terms (less productive, less ecologically advantageous, more susceptible to phytophagous gradations etc.) than the ancient ones?

- is it possible to accelerate spontaneous regeneration (restoration) of the post-agricultural forests?
- is restoration justified in environmental or economic terms?
- what are the detailed conditions for the restoration of particular forest types?
- which forests and where ought to be restored as the first ones?
- what are practical possibilities of introduction or support for spontaneous entry into the post-agricultural forests regarding the most important species, constitutive for the regeneration of the entire ecosystem, with special emphasis on bilberry (*Vaccinium myrtillus*) and some other species on the pine forests habitats?

It is recommended to develop a general restoration programme of the recent post-agricultural forests. In particular, such a programme (or regional programmes, adapted to the regional conditions) ought to be elaborated for fresh and dry pine forests. In the areas, where recent post-agricultural forests are broadly present, detailed programmes should be developed for their identification, inventorying, cognition of conditions for spontaneous regeneration and regeneration degree, as well as working programmes for restoration of post-agricultural forests.

The presence, reach and status of forest regeneration on post-agricultural lands ought to be defined in a detailed manner in the forest management documents. In the framework of forest departments description the respective documents should provide for the recognition of plough horizon traces in the soil, and in case it is identified, the appearance of plant species indicative of the regeneration degree of recent forest ought to be considered. On the basis of archival materials (cartographic or other) the forest persistence ought to be determined, i.e. the time period (approximate, but preferably as precise as possible) since the post-agricultural land had been afforested. Besides, distance ought to be determined between a given patch and the fragments of ancient forest of the same, or similar type. This should allow for determination of recommendations concerning the measures to be undertaken with the aim of forest restoration in the justified cases and adequately to the possibilities of spontaneous regeneration. Elaboration of appropriate instructions is necessary for carrying out these tasks.

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MODELE DŁUGOOKRESOWEJ EWOLUCJI FITOCENOZ LEŚNYCH REGENERUJĄCYCH NA TERENACH POROLNYCH

Streszczenie

Problematyka i cel badań

Jednym z głównych aspektów relacji „człowiek i środowisko” w ostatnich kilku tysiącach lat w Europie środkowej jest zamienianie lasów na pola orne. Proces ten nie jest jednak całkowicie jednokierunkowy. Obok odlesień często występują zalesienia gruntów wcześniej użytkowanych rolniczo. Dawniej był to głównie wynik zmian zaludnienia lub zmian władania terenu, od ponad wieku jest to także wyraz zmniejszającego się zapotrzebowania na ziemię orną jako podstawę bytu społeczności.

Samorzutne lub sztuczne zalesienie gruntu porolnego stanowi początek procesu regeneracji lasu, przy czym uzyskanie dojrzałego wieku przez drzewostan nie oznacza powrotu lasu do tej postaci, jaką miał on przed odlesieniem. Las taki różni się wyraźnie pod względem składu florystycznego gatunków spontanicznych od analogicznego lasu występującego w miejscu, które nigdy nie było trwale odlesione. Te obserwacje i pogłębione badania doprowadziły do powstania pojęcia **„starego lasu”** (Peterken 1974; 1977; 1996; Rackham 1980), a zagadnienie to stało się tematem wielu studiów (Hermy, Stieperaere 1981; Petersem 1994; Dzwonko, Loster 1988; 1989; 1992; De Frenne et al. 2011; Góras, Orczewska 2007; Orczewska 2009a; 2009b; 2009c; 2010a; 2010b; 2010c) oraz określenia list gatunków, które mają takie lasy wskazywać w Europie zachodniej (Peterken 1974; Honney et al. 1998; Hermy et al. 1999; Wulf 1997), jak również w Polsce (Dzwonko, Loster 2001). Stwierdzono, że warunkiem powrotu gatunków jest dostępność ich propagul, co w niektórych przypadkach związane jest z koniecznością obecności w niezbyt dużej odległości płatów „starego lasu”, jako refugium gatunków leśnych (Dzwonko 1993; 2001a, b; Dzwonko, Gawroński 1994; Matlack 1994; Bossuyt i in. 1999a; Bossuyt, Hermy 2000; Orczewska 2007; 2010; Orczewska, Fernes 2011).

Praca niniejsza podejmuje ważny zarówno z naukowego jak i praktycznego punktu widzenia problem regeneracji lasów na terenach, które w mniej lub bardziej odległej przeszłości były odlesione i wykorzystywane rolniczo. Przyjmujemy, że proces regeneracji w późniejszej fazie może być traktowany jako odtwarzanie się specyficznego pod względem struktury i składu florystycznego zbiorowiska potencjalnej roślinności naturalnej, a w tym także jako wymiana „**puli gatunków obcych**” (odpowiadających zbiorowiskom nieleśnym) przez „**pulę gatunków własnych**” lub inaczej „**pulę ekologiczną**” (Balyea, Lancaster 1999) lub „**pulę zbiorowiska**” (Zobel i in. 1998) odpowiadających charakterystycznej kombinacji gatunków danego zespołu.

Jednym z regionów, w których lasów wtórnych na gruntach porolnych jest stosunkowo wiele jest obszar wielkiego sandru przez stulecia podzielonego granicą o charakterze etniczno-politycznym. Na tym terenie obejmującym część Mazur oraz Kurpiów skupiliśmy nasze badania. Historyczna dokumentacja kartograficzna umożliwia analizę zalesienia na tym terenie na około 200-270 lat wstecz.

Na podstawie przeglądu literatury oraz prowadzonych wcześniej badań, można stwierdzić, że „stare lasy" różnią się pod względem składu florystycznego roślin runa od lasów wtórnych na gruntach porolnych. Wobec tego **postawiono hipotezę** w następującym brzmieniu.

Proces regeneracji lasów wtórnych trwa długo, dłużej niż dojście do wieku dojrzałego drzewostanu (wieku rębnego w leśnictwie) a stopień regeneracji jest zależny od stażu regeneracji oraz od szeregu innych czynników, w tym od rodzaju zbiorowiska i od odległości regenerującego płatu od trwałego płatu „starego lasu".

Głównym celem badań jest opracowanie modelu – odmiennego dla każdego z podstawowych typów zbiorowisk leśnych, który określać będzie tempo i przebieg procesu zaawansowanej regeneracji runa leśnego na gruncie porolnym oraz najważniejsze uwarunkowania mające na to wpływ.

Badania mają także szereg **celów podrzędnych**, a mianowicie:

– określenie różnic w zakresie składu florystycznego, struktury warstwy runa, specyfiki gleb pomiędzy „starymi lasami" a lasami wtórnymi o różnym stażu i ustalenie listy gatunków różnicujących,

– weryfikację w warunkach regionalnych znanej z literatury listy gatunków „starych lasów" (Hermy i in. 1999; Dzwonko, Loster 2001), jako narzędzia rozpoznawania stopnia regeneracji lasów wtórnych,

– opracowanie przydatnego dla badań regeneracji zbiorowisk wskaźnika zmian zachodzących w warstwie runa w trakcie regeneracji lasu wtórnego,

– rozpoznanie tych czynników, które w największym stopniu wpływają na tempo regeneracji lasu wtórnego, w tym szczególnie stwierdzenie, w jakim stopniu o regeneracji lasów wtórnych decydować może oprócz stażu regeneracji także odległość od starego lasu, jako ostoi gatunków typowo leśnych.

W celach badań mieszczą się także **cele praktyczne**, związane z doskonaleniem gospodarki leśnej w kierunku poszukiwania sposobów na prowadzenie „ekologicznego leśnictwa".

Charakterystyka postępowania badawczego: schemat i zakres badań.

Schemat badań

1. Budowa modelu wymaga zbioru danych (zdjęć fitosocjologicznych opisujących dojrzałe fitocenozy) reprezentujących 3 zespoły roślinne.

2. Dla określenia związku stopnia regeneracji każdego zespołu ze stażem regeneracji potrzeba zdjęć fitosocjologicznych opisujących dojrzałe fitocenozy „starych lasów" oraz lasów wtórnych o zróżnicowanych stażach regeneracji. Lokalizacja zdjęć powinna zapewnić odpowiednią reprezentację ilościową wszystkich kategorii w ramach typu (postulat często nie dający się w pełni zrealizować).

3. Określenie związku stopnia regeneracji wtórnych lasów z odległością od „starego lasu" wymaga zbioru zdjęć fitosocjologicznych opisujących dojrzałe fitocenozy określonych typów i kategorii położonych w zróżnicowanych odległościach od fragmentów „starych lasów", które mogły pełnić funkcję refugium. Wobec tego, poszukuje się wytypowanych z materiałów kartograficznych „starych lasów", a następnie dokonuje doboru punktów na zdjęcia w odpowiednich

lasach wtórnych w różnej odległości od "starego lasu:, najlepiej w układzie prostej linii i braku istotnych barier terenowych (spełnienie tego warunku w pełni okazało się niemożliwe, gdyż w części zdjęcia zastępowano danymi uproszczonymi).

4. Dla wstępnego uporządkowania materiału przeprowadza się podział zestawu zdjęć fitosocjologicznych na grupy wg typu zbiorowiska i stażu regeneracji, tak aby uzyskać odpowiednio liczne zestawy opisujące dojrzałe fitocenozy „starych lasów" oraz lasy wtórne o zróżnicowanym stażu regeneracji. Wykonuje się charakterystyki florystyczne (skład gatunkowy, frekwencja i pokrywanie) dla każdej kategorii trwałości i każdego zespołu. Określa się związek między stażem a charakterystykami florystycznymi.

5. Dla powiązania zmian fitosocjologicznych z siedliskiem przeprowadzane są analizy profili glebowych w specjalnie wytypowanych lokalizacjach, reprezentujących wszystkie analizowane typy lasu oraz wyróżnione kategorie stażu lasu.

6. Dla budowy modelu konieczne są odpowiednie miary. Wobec tego zostają opracowane podstawowe miary regeneracji lasu, obejmujące: (a) weryfikację listy „gatunków starych lasów" i przystosowanie jej do warunków lokalnych, (b) zdefiniowanie i obliczenie syntetycznego „wskaźnika dojrzałości lasu" (Forest Maturity Index - FMI), (c) sprawdzenie możliwości wykorzystania stanu populacji pojedynczych gatunków, jako wskaźników regeneracji, w tym w szczególności borówki czernicy (*Vaccinium myrtillus*)

7. Ostateczną budowę modelu poprzedza identyfikacja najważniejszych zależności między „wskaźnikiem dojrzałości lasu" a stażem regeneracji i odległością od „starego lasu".

8. Cel osiąga się poprzez: (a) opracowanie modeli tempa regeneracji lasów wtórnych dla poszczególnych typów zbiorowisk, (b) opis procesu regeneracji, jako procesu wymiany „pul gatunków" o różnej dynamice i charakterystyce ekologicznej, z uwzględnieniem specyfiki poszczególnych gatunków.

9. Cel praktyczny zostaje osiągnięty poprzez opracowanie uproszczonej wersji modeli regeneracji zbiorowisk dla ewentualnych potrzeb praktyki leśnej.

Zakres badań pod względem przedmiotowym obejmuje:

– zbiorowiska lasów zaliczane do trzech zespołów: *Peucedano-Pinetum*, *Querco-Pinetum*, *Tilio-Carpinetum* (patrz Matuszkiewicz J.M. 2001),

– skład florystyczny fitocenoz w zakresie roślin naczyniowych oraz naziemnych mszaków i porostów występujących w płatach lasów,

– udział ilościowy gatunków wyróżnianych w fitocenozach,

– charakterystykę wierzchnich poziomów gleb leśnych.

Zakres badań pod względem przestrzennym obejmuje:

– 6 nadleśnictw lasów państwowych: Jedwabno, Szczytno, Spychowo, Wielbark, Parciaki (bez fragmentu południowego) i Myszyniec, z niewielkimi fragmentami nadleśnictwa Korpele.

Materiały i metody

Materiały dla niniejszego opracowania obejmują dwie zasadnicze grupy:

– materiały obrazujące zróżnicowanie przestrzenne pokrywy roślinnej (w szczególności formacji leśnej) obecnie i w przeszłości, obejmujące głównie materiały kartograficzne,

– materiały dokumentujące charakterystyki roślinno-glebowe poszczególnych płatów lasów, wybranych jako reprezentatywne dla typów i kategorii, obejmujące głównie zdjęcia fitosocjologiczne i związane z nimi wyniki badań glebowych.

Najważniejszym materiałem dla niniejszego opracowania jest zbiór dokładnie zlokalizowanych 464 zdjęć fitosocjologicznych wykonywanych metodą Braun-Blanqueta (patrz: Wysocki, Sikorski 2009), prezentujących skład florystyczny i strukturę zbiorowiska roślinnego, uzupełniony dodatkowo zbiorem uproszczonych opisów płatów zbiorowisk roślinnych. W miejscach 202 zdjęć fitosocjologicznych przeprowadzono badania wierzchnich warstw gleby.

Zbiór zdjęć fitosocjologicznych ma charakter próby tendencyjnej. Wybór miejsc na wykonanie zdjęć dokonywany był w terenie, przy uwzględnieniu informacji zebranych na mapach o historii poszczególnych fragmentów terenu oraz aktualnym stanie lasu (przede wszystkim wieku drzewostanu). Przy wyborze kierowano się następującymi kryteriami:

– dojrzałości i ustabilizowanej struktury fitocenozy,

– rozpoznanej historii lasu na danym fragmencie terenu,

oraz dodatkowo:

– przynależnością typologiczną zbiorowiska pod względem potencjalnej roślinności naturalnej,

– położeniem punktu w stosunku do kompleksów leśnych obecnie i w przeszłości.

Do analizy wybierane były fragmenty lasu o drzewostanie dostatecznie dojrzałym, tj. od ok. 80-90 lat wzwyż oraz o strukturze w miarę możliwości mało zniekształconej przez aktualne oddziaływania zewnętrzne. Na podstawie map historycznych oraz terenowego rozpoznania istnienia lub braku **poziomu płużnego** w glebie przyjęto możliwość podziału współczesnych lasów na dwie zasadnicze kategorie: „lasy stare” (w rozumieniu jak wyżej) oraz lasy wtórne. Te ostatnie dzielone na kategorie w zależności od stażu regeneracji, czyli od momentu, kiedy dany fragment terenu użytkowanego rolniczo został zalesiony. Podział na kategorie i przyjęcie czasu stażu wynikało z analizy map historycznych. Ważnym czynnikiem było także położenie danego fragmentu lasu wtórnego od fragmentów „lasów starych” odpowiedniego typu.

Materiały fitosocjologiczne, zawierające dane o występowaniu gatunków oraz miarach ilościowego udziału niektórych z nich, poddawane były obróbce przy wykorzystaniu:

– klasycznej analizy tabel fitosocjologicznych, opartej na porównywaniu frekwencji gatunków w podzbiorach, z analizą różnic występowania gatunków charakterystycznych dla grup zbiorowisk,

– bioindykacyjnych metod wykorzystujących klasyfikacje biologiczne roślin, w tym tzw. liczby wskaźnikowe wg Ellenberga i innych (1991),

– miar podobieństwa w zakresie składu florystycznego pomiędzy częściami zbioru (kategoriami zbiorowisk),

– analizy frekwencji gatunków w podzbiorach zdjęć z wykorzystaniem programów statystycznych dla obliczania wartości średniej, ustalania istotności różnic (test Fishera) oraz wyróżniania na tej podstawie grup gatunków najczęściej występujących na różnych etapach regeneracji,

– analizy różnic pomiędzy zdjęciami i kategoriami pod względem syntetycznego „wskaźnika dojrzałości lasu” (FMI) obliczanego na podstawie występowania wyselekcjonowanych gatunków roślin,

– modelowania zmian wybranych charakterystyk fitocenoz w procesie regeneracji w zależności od dwóch zmiennych niezależnych: stażu regeneracji i odległości od „starego lasu”.

Rozpoznanie gleb w wierzchnich poziomach polegało na:

– diagnozie typu gleby oraz próchnicy,

– oznaczeniu kwasowości (pH w H_2O potencjometrycznie),

– oznaczeniu zawartości węgla organicznego i azotu ogółem (analizatorem TOCN FormacsTM) oraz obliczeniu stosunku C:N,

– oznaczeniu zawartości siarki (metodą Butters-Chenery).

Najważniejsze uzyskane wyniki

1. Badany teren, pod wieloma względami jednorodny, wykazuje wyraźne zróżnicowanie pod względem geomorfologicznym (wiek zlodowacenia), klimatycznym, geobotanicznym, a także społecznym i historycznym na część północną (Mazury) i południową (Kurpie).

2. Pod względem zalesienia badany teren przeszedł w ciągu 200 lat wielkie przemiany. Były one przy tym odmienne w obszarze Mazur i Kurpiów. Widoczne zróżnicowanie pomiędzy Mazurami i Kurpiami nie zmienia jednak ogólnej tendencji wzrostu zalesienia w porównaniu do minimum, jakie miało miejsce w połowie XIX (Mazury) lub w początku XX wieku (Kurpie).

3. Wzrost ogólnego zalesienia w ostatnich 100–150 latach, a także przesuwanie się niektórych kompleksów leśnych w minionych 200 latach, wpływają na zróżnicowany staż poszczególnych fragmentów współczesnych lasów. Wśród współczesnych lasów wyróżniono lasy „stare” oraz 5 kategorii lasów wtórnych o różnym stażu od zalesienia, minimum ok. 70–80 lat.

4. Lasy wtórne na gruntach porolnych, reprezentujące *Peucedano-Pinetum, Querco-Pinetum, Tilio-Carpinetum* wykazują istotne różnice pod względem składu florystycznego oraz udziału niektórych gatunków w porównaniu ze „starymi lasami”. Poszczególne gatunki mogą wykazywać preferencje dla różnych kategorii stażu regeneracji. Podobieństwo lasów wtórnych do właściwych im „starych lasów” jest tym większe im dłuższy jest czas od zalesienia gruntu porolnego.

5. W borach sosnowych a także w borach mieszanych gatunki charakterystyczne dla zbiorowisk z klasy *Vaccinio-Piceetea* wykazują podział na trzy grupy ze względu na występowanie w lasach „starych” i wtórnych. Wyraźną preferencję dla „lasów starych” wykazują: *Hylocomium splendens, Trientalis europaea, Vaccinium vitis-idaea*; także *Vaccinium myrtillus* pod względem ilościowości (w małym zakresie pod względem frekwencji). Umiarkowaną preferencję dla lasów wtórnych wykazują natomiast: *Chimaphila umbellata, Pyrola chlorantha, Orthilia secunda, Diphasiastrum complanatum, Monotropa hypopitys*. Trzecią grupę stanowią takie, które nie wykazują wyraźnych różnic w frekwencji pomiędzy lasami wtórnymi i starymi: *Melampyrum pratense, Pleurozium schreberi, Dicranum polysetum, Dicranum scoparium, Ptilium crista-castrensis, Lycopodium annotinum.*

6. W borach i borach mieszanych gatunki, które wykazują wyraźne preferencje dla lasów wtórnych, zwłaszcza tych o krótkim stażu regeneracji w zdecydowanej większości należą do charakterystycznych dla zbiorowisk terenów otwartych: muraw piaskowych (klasa *Koelerio glaucea-Corynephoretea canescentis*), muraw bliźniczkowych (klasa *Nardo-Callunetea*) i łąk (klasa *Molinio-Arrhenatheretea*).

7. W lasach grądowych zdecydowana większość gatunków charakterystycznych dla klasy *Querco-Fagetea* wykazuje słabszy lub mocniejszy związek z „lasami starymi", pojawiając się w lasach wtórnych rzadziej lub wcale. Są jednak takie gatunki uznawane za charakterystyczne dla wymienionej klasy, które w lasach wtórnych są równie częste jak w starych (*Dryopteris filix-mas*).

8. W zbiorowiskach wtórnych borów sosnowych, których początki sięgają pierwszej połowy XIX wieku frekwencja *Festuca ovina* i *Cladonia arbuscula* jest wyraźnie wyższa niż w „lasach starych" oraz wtórnych o krótszym stażu. Na tej podstawie domniemywać można, że jest to ślad po zanikłej już obecnie, ale dawniej powszechnej praktyce wypasu zwierząt domowych w lasach.

9. Nie wszystkie gatunki z listy „gatunków starych lasów" wg Hermy i in. (1999) oraz Dzwonko i Loster (2001) uzyskały potwierdzenie przy regionalnej weryfikacji. W części może to wynikać ze szczupłości materiałów (lasy dębowo-grabowe), ale w części można to traktować jako przejaw odrębności regionalnej.

10. Wartość wskaźnikową poszczególnych gatunków jako „gatunków starych lasów" należy odnosić do konkretnych typów siedlisk. Szereg gatunków, które spełniają to kryterium w jednym typie lasu (np. w borze sosnowym lub sosnowo-dębowym) może nie spełniać go w innym typie lasu (np. w grądzie), a nawet wręcz przeciwnie - może być wskaźnikiem lasu wtórnego.

11. Podczas weryfikacji regionalnej listy „gatunków starych lasów" (Hermy i in. 1999) w borach (*Peucedano-Pinetum*), potwierdzono status dwóch gatunków charakterystycznych dla klasy *Vaccinio-Piceetea* (*Vaccinium vitis-idaea* i *Trientalis europaea*) oraz dwóch często występujących gatunków towarzyszących (*Convallaria majalis* i *Luzula pilosa*), z których ten pierwszy uznawany jest za gatunek wyróżniający dla zespołu *Peucedano-Pinetum*, a także dwóch gatunków stosunkowo rzadkich: *Athyrium filix-femina* i *Oxalis acetosella*. Grupa gatunków, dla których wyniki analiz nie potwierdziły statusu „gatunków starych lasów" w borach obejmuje gatunek charakterystyczny dla klasy *Vaccinio-Piceetea* (*Melampyrum pratense*) oraz gatunek towarzyszący *Dryopteris carthusiana*. Szczególnym przypadkiem jest gatunek *Vaccinium myrtillus*. Gatunek ten nie wykazuje (lub wykazuje bardzo słabo) statusu „gatunku starych lasów" pod względem frekwencji, natomiast przy uwzględnieniu ilościowości pokazuje pozytywny i jednoznaczny związek.

12. W borach mieszanych (*Querco-Pinetum*) potwierdzono status „gatunków starych lasów" w odniesieniu do jednego gatunku charakterystycznego dla klasy *Vaccinio-Piceetea* (*Trientalis europaea*), jednego charakterystycznego dla klasy *Querco-Fagetea* (*Athyrium filix-femina*) oraz 4 gatunków ogólnoleśnych (*Convallaria majalis, Pteridium aquilinum, Luzula pilosa, Maianthemum bifolium*). Trzy gatunki z listy "gatunków starych lasów" (*Vaccinium vitis-idaea*, *Oxalis acetosella* i *Carex digitata)* mają status niejasny. Trzy gatunki z listy "gatunków starych lasów" (*Melampyrum pratense, Dryopteris filix-mas* i *Dryopteris carthusiana*) w badanych borach mieszanych nie wykazują w zakresie frekwencji różnic pomiędzy lasami

“starymi” a wtórnymi, co oznacza, że ich status został zanegowany. Podobnie jak w borach status *Vaccinum myrtillus* zależeć może od formy rejestrowania jego występowania (obecność czy udział ilościowy).

13. Gatunki z listy „gatunków starych lasów” stwierdzone w grądach (*Tilio-Carpinetum*) podzielić można na 5 grup: a – 10 gatunków o potwierdzonym statusie, wśród których można wyróżnić takie, które występują tylko w „lasach starych” i lasach wtórnych o najdłuższym stażu regeneracji („grupa Hepatica” należą do nich: *Hepatica nobilis, Galium odoratum, Lathyrus vernus*), oraz takie, które mogą występować w lasach wtórnych, ale w „starych” występują istotnie częściej („grupa Anemone” – *Anemone nemorosa, Convallaria majalis, Galeobdolon luteum, Milium effusum, Polygonatum multiflorum, Stellaria holostea, Viola reichenbachiana*); b – „grupa Melica” – 13 gatunków o statusie wątpliwym (być może z powodu zbyt małej liczby zdjęć): *Actea spicata, Athyrium filix-femina, Carex digitata, Festuca gigantea, Gymnocarpium dryopteris, Lilium martagon, Maianthemum bifolium, Melica nutans, Oxalis acetosella, Paris quadrifolia, Phyteuma spicatum, Ranunculus lanuginosus, Scrophularia nodosa*; c – „grupa Luzula” – 8 gatunków, których status został słabo zanegowany, należą do nich: *Dactylis polygama, Dryopteris carthusiana, Dryopteris filix-mas, Luzula pilosa, Melampyrum pratense, Pteridium aquilinum, Trientalis europaea, Vaccinium myrtillus*; d –*Vaccinium vitis-idaea* – gatunek, którego status został jednoznacznie zanegowany (wyraźnie częstszy w lasach wtórnych, różnica istotna*)*.

14. Odrębność florystyczną „starych lasów” od lasów wtórnych można mierzyć poprzez wyróżnienie zestawu gatunków jednoznacznie związanych z „lasami starymi” tworzących **wzorzec dla danego typu lasu**. Procent gatunków z listy „wzorca”, które w konkretnym płacie występują może stanowić „wskaźnik dojrzałości lasu” (Forest Maturity Index – FMI), czyli stopnia zregenerowania płatu.

15. Stopień zregenerowania płatów lasów wtórnych mierzony poprzez „wskaźnik dojrzałości lasu” (FMI) wykazuje zależność od dwu zmiennych niezależnych: stażu regeneracji i odległości od płatu „starego lasu” odpowiedniego typu.

16. Tempo regeneracji populacji *Vaccinium myrtillus* w sosnowych borach wtórnych na gruntach porolnych jest ogólnie rzecz biorąc powolne; nawet lasy o około 230 letnim stażu regeneracji wykazują jeszcze różnice w rozprzestrzenieniu tego gatunku w porównaniu ze „starymi lasami”. W borach mieszanych regeneracja *Vaccinium myrtillus* przebiega szybciej niż w typowych borach sosnowych. W borach i borach mieszanych na siedliskach świeżych możliwości regeneracji *Vaccinium myrtillus* w lasach wtórnych są tym lepsze im siedlisko jest zasobniejsze i wilgotniejsze.

17. Wyniki jednoznacznie wskazują na zależność pokrycia *Vaccinium myrtillus* w lasach wtórnych od odległości regenerującego płatu od fragmentów „starych lasów”, w których gatunek ten mógł przetrwać, a następnie skąd mógł się na powrót rozprzestrzeniać.

18. Wiele gatunków typowych dla „starych lasów” powraca do lasów wtórnych tym szybciej im dany płat lasu jest bliżej położony od ich ostoi w „starym lesie”. Jest to całkowicie jednoznaczne w przypadku gatunków rozmnażających się głównie wegetatywnie, ale dotyczy także gatunków o rozmaitych typach rozprzestrzeniania się nasion.

19. Staż regeneracji lasu wtórnego i odległość od ostoi gatunków, choć teoretycznie będące zmiennymi niezależnymi, w praktyce wykazują wyraźny związek (lasy wtórne o długim stażu są zwykle bliższe przestrzennie „starym lasom” niż lasy wtórne o krótkim stażu), przez co

oddziaływają w sposób skumulowany na powracające do lasów wtórnych gatunki „starych lasów".

20. Wśród gatunków tworzących zestawy FMI można wydzielić dwie grupy: **wstrzemięźliwych rekolonizatorów**: względnie szybki, które mogą pojawiać się już przy dość krótkim stażu regeneracji i nawet w dużej odległości od ostoi oraz **rekolonizatorów bardzo wstrzemięźliwych**, opornie wracających do lasów wtórnych, bardzo wyraźnie posuwając się od ostoi danego typu zbiorowiska. Są to gatunki o „krótkim kroku".

21. Jednym z najlepszych gatunków wskaźników „starych lasów" oraz warunków regeneracji lasów wtórnych w zależności od stażu regeneracji i odległości od „starego lasu" jest *Convallaria majalis*. Gatunek ten, choć jest gatunkiem uznawanym za endozoochoryczny i w związku z tym mógłby być przenoszony na duże odległości od ostoi, w praktyce rozprzestrzenia się tak, jakby głównie rozmnażał się wegetatywnie. Jego zaletą jako wskaźnika jest też i to, że taką rolę może pełnić dla trzech typów badanych zbiorowisk.

22. „Lasy stare" i lasy wtórne o różnym stażu regeneracji różnią się pod względem wartości średnich i rozkładu liczb wskaźnikowych Ellenberga oraz pod względem biologicznych charakterystyk gatunków. Niezależnie od typu zbiorowiska „lasy stare" przy porównaniu z lasami wtórnymi, odznaczają się stosunkowo wyższymi udziałami: geofitów, gatunków autochorycznych, gatunków tolerujących zacienienie. Dla lasów wtórnych (niezależnie od typu zbiorowiska) charakterystyczny jest stosunkowo wyższy niż w „starych lasach" udział gatunków typu konkurencyjnego „c".

23. Gleby pod „lasami starymi" (bielicowe, rdzawe ze śladami bielicowania, rdzawe typowe, brunatne i płowe) wykazują cechy, na podstawie których sądzi się, że odznaczają się większą równowagą biochemiczną niż analogiczne gleby porolne. Gleby porolne tego samego typu różnią się od gleb „naturalnych" właściwościami fizycznymi i chemicznymi zależnie od stażu regeneracji ekosystemów leśnych. W przypadku gleb rdzawych z borami mieszanymi oraz gleb płowych i brunatnych z roślinnością grądową istnieje zależność, że im dłużej występuje wtórny las na gruncie porolnym, tym bardziej wzrasta ich jakość i aktywność biologiczna. Natomiast najuboższe gleby bielicowe i rdzawe ze śladami bielicowania pod borami sosnowymi nie wykazują jednoznacznej zależności od stażu regeneracji. Jest to następstwem małych zdolności buforowych tych gleb oraz niskiej odporności na czynniki zewnętrzne.

24. Wyniki analizy korelacji częściowych, określających wpływ trzech czynników głównych: staż, odległość od „starego lasu" i wiek drzewostanu, przy uwzględnieniu szeregu zmiennych kontrolujących, na wartości wybranych cech fitocenoz borów sosnowych (*Peucedano-Pinetum*), wskazują, że:

– wskaźnik FMI oraz pokrycie *Vaccinium myrtillus*, *Calluna vulgaris* i *Vaccinium vitis-idaea* są zależne głównie i silnie od stażu i odległości,

– pokrycie *Convallaria maialis* oraz pokrycie *Hylocomium splendens*, zależy głównie i silnie od stażu, z niewielkim modyfikującym wpływem odległości i wieku drzewostanu,

– liczba gatunków „starych lasów" w płacie jest zależna głównie od stażu i odległości, ale z zauważalnym modyfikującym wpływem wieku drzewostanu,

– pokrycie *Luzula pilosa*, *Frangula alnus* i *Calamagrostis arundinacea* zależy istotnie, ale słabo od stażu, natomiast słaby modyfikujący wpływ wieku drzewostanu jest silniejszy od wpływu odległości,

– liczba gatunków mchów i porostów, wykazuje słabą, ale istotną statystycznie zależność od wieku drzewostanu, przy braku zauważalnego wpływu odległości i stażu,

– całkowita liczba gatunków, liczba gatunków mchów charakterystycznych dla *Vaccinio-Piceetea*, liczba gatunków krzewów, liczba gatunków ziół, liczba gatunków zielnych charakterystycznych dla klasy *Vaccinio-Piceetea*, liczba gatunków drzew nie wykazują istotnych korelacji ze stażem, odległością i wiekiem drzewostanu.

25. Szczegółowe modele zależności między FMI a odległością od „starego lasu" i stażem regeneracji w lasach wtórnych dla borów (*Peucedano-Pinetum*), borów mieszanych (*Querco-Pinetum*) i grądów (*Tilio-Carpinetum*) wskazują na nieliniowe zależności między FMI i odległością oraz między FMI i stażem. Łączne oddziaływanie obu zmiennych na kształtowanie się wartości FMI ma skomplikowany charakter. We wszystkich trzech typach zbiorowisk zmniejsza się tempo spadku wartości FMI wraz z rosnącą odległością, zarówno w przypadku powierzchni o wyższej trwałości jak i powierzchni niedawno zalesionych (ryc.: 155, 156, 157).

26. Szczegółowe modele zależności między pokryciem *Vaccinium myrtillus* a odległością i stażem w lasach wtórnych dla borów (*Peucedano-Pinetum*) i borów mieszanych (*Querco-Pinetum*) wskazują, że w niewielkich odległościach od starego lasu (do ok. 500 m) borówka czernica pojawia się wcześniej w borach mieszanych i wcześniej osiąga wysokie pokrycie, podczas gdy w borze typowym analogiczne pokrycia są osiągane odpowiednio około 100 lat później. Natomiast spadek pokrycia *V. myrtillus* wraz z odległością jest znacznie silniejszy w przypadku borów mieszanych niż borów świeżych (patrz ryc.: 158, 159).

27. Szczegółowe modele zależności między frekwencją *Convallaria majalis* a odległością i stażem w lasach wtórnych dla borów (*Peucedano-Pinetum*) i borów mieszanych (*Querco-Pinetum*) wskazują, że w niewielkich odległościach od starego lasu (do ok. 100 m) frekwencja konwalii powyżej 10 % pojawia się nieco wcześniej w borach świeżych niż w borach mieszanych, ale starsze powierzchnie charakteryzują się już prawie identyczną frekwencją. Jednocześnie, niezależnie od stażu w borach świeżych wpływ odległości od „starego lasu" przestaje być istotny przy wartościach przekraczających 200–300 m, podczas gdy w borach mieszanych obserwuje się regularny spadek frekwencji konwalii wraz ze wzrostem odległości (ryc.: 160, 161).

28. W ramach opracowanego schematu przebiegu regeneracji lasów wtórnych na gruntach porolnych dokonano podziału gatunków na „**pulę gatunków własnych**", a w niej grupy gatunków określane jako: **rekolonizatorzy szybcy i trwali**, **rekolonizatorzy szybcy lecz niestali**, **rekolonizatorzy wstrzemięźliwi**, **rekolonizatorzy bardzo wstrzemięźliwi**, oraz „**pulę gatunków obcych**", a w niej grupy: **gatunki „relikty", gatunki „goście", gatunki introdukowane, gatunki „świadkowie minionych czasów**" (ryc. 162).

29. Dla potrzeb praktyki leśnej opracowano tabelę prawdopodobnych stopni odkształcenia lasów wtórnych na skutek niepełnego zregenerowania w zależności od: typu zbiorowiska roślinnego (*Peucedano-Pinetum, Querco-Pinetum* i *Tilio-Carpinetum*) oraz stażu regeneracji i odległości od płatów „starego lasu" (tab. 34). Zaprezentowano uzyskane wyniki i sformułowano postulaty, które mają bezpośrednie przełożenie na sposoby gospodarowania w lasach w kierunku ich rewitalizacji. W szczególności zwrócono uwagę na potrzebę wspomożenia regeneracji *Vaccinium myrtillus* w lasach wtórnych położonych z dala od „starych" lub już zregenerowanych lasów.

Podstawowe wnioski

1. Najważniejszym czynnikiem dla regeneracji spontanicznej lasów na gruntach porolnych jest czas, określany tu jako staż regeneracji.

2. Dla badanych siedlisk świeżych o szybkości regeneracji, zarówno roślinności jak i gleby, decyduje w pewnym stopniu zasobność siedliska. Prawidłowość tę można opisać w uproszczeniu: „im uboższe siedlisko, tym wolniejsza regeneracja".

3. Na siedliskach najuboższych tempo regeneracji jest prawdopodobnie tak powolne, że pełna regeneracja, szczególnie w zakresie właściwości gleby, może trwać wiele set lat, tj. wykraczać poza „historyczny" horyzont czasowy państw i społeczeństw.

4. Do głównych czynników warunkujących tempo regeneracji lasów porolnych zaliczyć można odległość od ostoi gatunków z puli „gatunków własnych". Zależność ta ma charakter nieprostoliniowy, lecz w ogólnym zarysie zbliżony do funkcji logarytmicznej. Jest przy tym wysoce prawdopodobne, że nie chodzi tu o zależność „fizyczną", lecz „ekologiczną", uwzględniającą możliwości i drogi przenoszenia diaspor poszczególnych gatunków, oraz występowanie barier i korytarzy.

5. Szybkość regeneracji lasu wtórnego jest silnie uzależniona od gatunku drzewa jakie opanowało (na ogół przy pomocy człowieka) teren w początkowej fazie regeneracji.

6. Korelacja stażu regeneracji lasów wtórnych i odległości płatów od fragmentów „starych lasów" pokazuje złożoność uwarunkowań regeneracji lasów porolnych. Te uwarunkowania zależą w ogólnym zarysie od struktur krajobrazowych, tj. między innymi od elementów składowych (typu siedliska, formy i rodzaju zbiorowiska roślinnego), struktury przestrzennej (np. rozmieszczenia i struktury płatów „starych lasów") i historycznego rozwoju krajobrazu.

7. Modele regeneracji borów i borów mieszanych dotyczące ważnych gatunków *Vaccinium myrtillus* i *Convallaria majalis*, a także dane o innych gatunkach „starych lasów" mogą wskazywać, że rola wegetatywnego rozmnażania może być w przypadku wielu gatunków leśnych dominująca.

8. Wyniki wyraźnie wskazują, że odtworzenie się populacji *Vaccinium myrtillus* jest bardzo istotnym elementem regeneracji naturalnego składu florystycznego i struktury zbiorowisk borów i w mniejszym stopniu także borów mieszanych.

9. Złożony charakter zależności rozprzestrzenienia *Vaccinium myrtillus* i odległości od „starego lasu" wskazuje na zróżnicowanie rozmnażania na wegetatywne i generatywne oraz zróżnicowane strumienie przenoszenia diaspor tego gatunku. Jest to gatunek wybitnie endozoochoryczny, a jego roznosiciele mogą dzielić się na grupy o znacznie zróżnicowanej możliwości przemieszczania się. Możliwe jest, że za bliskie przenoszenie odpowiedzialne są małe zwierzęta poruszające się po ziemi, a za dalekie zwierzęta ruchliwe, takie jak ptaki i większe ssaki.

10. Na podstawie porównania danych z lasów wtórnych na gruntach porolnych ze zbadanymi przypadkami lasów wtórnych (czasowe odlesienie), ale bez użytkowania rolniczego połączonego z orką, można przyjąć, że istotne znaczenie dla powolnego powrotu *Vaccinium myrtillus* ma istnienie w glebie poziomu płużnego. Wskazuje na to wyższe pokrywanie *Vaccinium myrtillus* w lasach wtórnych bez poziomu płużnego w porównaniu z powierzchniami z poziomem płużnym przy tym samym stażu regeneracji.

11. Jako zdecydowanie wartą rozpatrzenia od strony praktycznej należy uznać możliwość wspomagania regeneracji lasów wtórnych na gruntach porolnych przez introdukcję istotnych dla regeneracji gatunków roślin, w pierwszej kolejności borówki czernicy (*Vaccinium myrtillus*) w borach.

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LIST OF PHOTO / LISTA FOTOGRFII

Photo. 1. Continental pine forest (*Peucedano-Pinetum*) in Masuria – ancient forest without plough horizon in the soil, economically used (Jedwabno forest division) – PP-1 category. Moss-dwarf shrub undergrowth dominated by *Vaccinium myrtillus*. (photo. J.M. Matuszkiewicz)

Fot. 1. Bór sosnowy (Peucedano-Pinetum) na Mazurach użytkowany gospodarczo (nadleśnictwo Jedwabno) – stary las bez śladów poziomu płużnego w glebie (kat. PP-1), z runem mszysto-krzewinkowym zdominowanym przez borówkę czernicę (*V. myrtillus*). (fot. J.M. Matuszkiewicz)

Photo. 2. Continental pine forest (*Peucedano-Pinetum*) in Kurpie, Czarnia reserve (Myszyniec forest division) – ancient forest without plough horizon in the soil (PP-1 category). Dwarf shrub-moss undergrowth destroyed by fire 50 years ago; in the aftermath lichens appeared and the community started to resemble *Cladonio-Pinetum* association. This was described by J.B. Falińskiego (1964). Since then, regeneration has started – lichen withdraw and dwarf shrubs appear, first *Vaccinium vitis-idaea*, and then *Vaccinium myrtillus*. (photo. A. Kowalska)

Fot. 2. Bór sosnowy (*Peucedano-Pinetum*) na Kurpiach, w rezerwacie Czarnia (nadleśnictwo Myszyniec), – stary las bez śladów poziomu płużnego w glebie (kat. PP-1) z runem krzewinkowo-mszystym. W runie, zniszczonym w pożarze przed 50ciu laty, pojawiło się wiele porostów powodując upodobnienie się do zespołu *Cladonio-Pinetum* (Faliński 1964). Regeneracja zbiorowiska polega na wycofywaniu się porostów i powrocie krzewinek, borówki brusznicy (*V. vitis-idaea*) i znacznie wolniej borówki czernicy (*V. myrtillus*). (fot. A. Kowalska)

Photo. 3. Continental pine forest (*Peucedano-Pinetum*) in Kurpie (Myszyniec forest division) - recent forest on post-agricultural grounds with long regeneration period (afforestation probably in 1830 – cat. PP-3 or PP-4) with moss or moss-dwarf shrub undergrowth. *Vaccinium myrtillus* in big, partly connected patches. Significant *Juniperus communis* share shows past pasture use. (photo. J.M. Matuszkiewicz)

Fot. 3. Bór sosnowy (*Peucedano-Pinetum*) na Kurpiach (nadleśnictwo Myszyniec) – las wtórny na gruncie porolnym o długim okresie regeneracji (zalesienie około 1830 roku – kat. PP-3 lub PP-4), z runem mszystym lub mszysto-krzewinkowym. Borówka czernica (*V. myrtillus*) w trakcie zaawansowanej regeneracji w dużych, częściowo łączących się płatach. Znaczny udział jałowca (*J. communis*) wskazuje na dawniejszą presję pasterską (fot. J.M. Matuszkiewicz)

Photo. 4. Continental pine forest (*Peucedano-Pinetum*) in Masuria (Wielbark forest division) – recent forest on post-agricultural grounds with moderate regeneration period (afforestation probably between 1830 and 1876 – PP-4 cat.). Undergrowth dominated by mosses with *Vaccinium myrtillus* in small and medium-sized, partly connected patches. (photo. J.M. Matuszkiewicz)

Fot. 4. Bór sosnowy (Peucedano-Pinetum) na Mazurach (nadleśnictwo Wielbark) – las wtórny na gruncie porolnym o umiarkowanym okresie regeneracji (zalesienie prawdopodobnie pomiędzy 1830 a 1876 rokiem - kat. PP-4), z runem w większości mszystym. Borówka czernica (*V. myrtillus*) w trakcie regeneracji w średnich i małych, niełączących się płatach. (fot. J.M. Matuszkiewicz)

Photo. 5. Continental pine forest (*Peucedano-Pinetum*) in Masuria (Szczytno forest division) - recent forest on post-agricultural grounds with short regeneration period (afforestation probably between 1876 and 1928 – PP-5 cat.). Undergrowth dominated by mosses and grasses with *Deschampsia flexuosa, Vaccinium myrtillus* in small patches. (photo. I. Zawiska)

Fot. 5. Bór sosnowy (*Peucedano-Pinetum*) na Mazurach (nadleśnictwo Szczytno) – las wtórny na gruncie porolnym o stosunkowo krótkim okresie regeneracji (zalesienie pomiędzy 1876 a 1928 rokiem – kat. PP 5). Runo w większości trawiasto-mszyste ze śmiałkiem pogiętym (*D. flexuosa*), borówka (*V. myrtillus*) w niewielkich skupieniach. (fot. I. Zawiska)

Photo. 6. Subcontinental mixed pine-oak forest (*Querco roboris-Pinetum*) in Kurpie (Parciaki forest division) – ancient forest without plough horizon in the soil, undergrowth dominated by *Vaccinium myrtillus* (QP-1 cat.). At present, cows grazing in forest is rare but in the past it was quite common practice. (photo. J.M. Matuszkiewicz)

Fot. 6. Bór mieszany sosnowo-dębowy (*Querco roboris-Pinetum*) na Kurpiach (nadleśnictwo Parciaki) - stary las bez śladów poziomu płużnego w glebie (kat. QP-1), z runem zdominowanym przez borówkę (*V. myrtillus*). Obecnie wypas krów w lesie ma charakter incydentalny, dawniej było to stałą praktyką. (fot. J.M. Matuszkiewicz)

Photo. 7. Subcontinental mixed pine-oak forest (*Querco roboris-Pinetum*) in Masuria (Jedwabno forest division) – recent forest on post-agricultural grounds with distinct plough horizon (QP-5 cat., see photo. 14). Undergrowth dominated by *Deschampsia flexuosa*; *Vaccinium myrtillus* in small patches. (photo. J.M. Matuszkiewicz)

Fot. 7. Bór mieszany sosnowo-dębowy (*Querco roboris-Pinetum*) na Mazurach (nadleśnictwo Jedwabno) – las wtórny (kat. QP-5) z wyraźnym poziomem płużnym w glebie (patrz fot. 14). W runie dominuje śmiałek (*D. flexuosa*); borówka (*V. myrtillus*) w niewielkich płatach. (fot. J.M. Matuszkiewicz)

Photo. 8. Lime-oak-hornbeam forest (*Tilio-Carpinetum calamagrostietosum*) in Masuria (Jedwabno forest division) – ancient forest without plough horizon in the soil (TC-1 cat., see photo. 15). Single, old *Quercus robur* trees in the stand. (photo. J. Solon)

Fot. 8. Las dębowo-grabowy (*Tilio-Carpinetum calamagrostietosum*) na Mazurach (nadleśnictwo Jedwabno) – stary las (kat. TC-1) bez śladów poziomu płużnego w glebie (patrz fot. 15). W drzewostanie pojedyncze okazy starych dębów (*Q. robur*). (fot. J. Solon)

Photo. 9. Lime-oak-hornbeam forest (*Tilio-Carpinetum typicum*) in Masuria (Szczytno forest division) – probably ancient forest without plough horizon in the soil (TC-1 cat.). (photo. J.M. Matuszkiewicz)

Fot. 9. Las dębowo-grabowy (*Tilio-Carpinetum typicum*) na Mazurach (nadleśnictwo Szczytno) będący prawdopodobnie *starym lasem*, bez zauważalnych śladów poziomu płużnego w glebie (kat. TC-1). (fot. J.M. Matuszkiewicz

Photo. 10. Lime-oak-hornbeam forest (*Tilio-Carpinetum calamagrostietosum*) in Masuria (Jedwabno forest division) - recent forest on post-agricultural grounds with long regeneration period, with *Pinus sylvestris* planted in the stand (TC-4 cat.). (photo. J.M. Matuszkiewicz)

Fot. 10. Las dębowo-grabowy (*Tilio-Carpinetum calamagrostietosum*) na Mazurach (nadleśnictwo Jedwabno) – las wtórny na terenie użytkowanym rolniczo w dość dawnej przeszłości, z sosną wprowadzoną do drzewostanu, obecnie regenerujący (kat. TC-4). (fot. J.M. Matuszkiewicz)

Photo. 11. Rusty podzolic soil without plough horizon in pine forest (*Peucedano-Pinetum*). (photo. I. Zawiska)

Fot. 11. Gleba rdzawa bielicowana bez śladów poziomu płużnego pod zbiorowiskiem boru sosnowego (*Peucedano-Pinetum*) (fot. I. Zawiska)

Photo. 12. Post-agricultural soil with traces of podzolisation and old plough horizon in pine forest (*Peucedano-Pinetum*). Post-agricultural area afforested before 1800. (photo. I. Zawiska)

Fot. 12. Gleba porolna z wtórnym bielicowaniem z bardzo przekształconym poziomem płużnym pod zbiorowiskiem boru sosnowego (*Peucedano-Pinetum*). Teren porolny zalesiony jeszcze przed 1800 rokiem. (fot. I. Zawiska)

Photo. 13. Post-agricultural soil with traces of podzolisation and very distinct plough horizon in pine forest (*Peucedano-Pinetum*). Post-agricultural area afforested at the turn of 19th and 20th centuries. (photo. I. Zawiska)

Fot. 13. Gleba porolna z wtórnym bielicowaniem z bardzo wyraźnym poziomem płużnym pod zbiorowiskiem boru sosnowego (*Peucedano-Pinetum*). Teren porolny zalesiony w końcu XIX lub początku XX wieku. (fot. I. Zawiska)

Photo. 14. Post-agricultural soil with faint traces of podzolisation and deep plough horizon in mixed oak-pine forest (*Querco roboris-Pinetum*). (photo. J.M. Matuszkiewicz)

Fot. 14. Gleba porolna ze słabo zaznaczonym wtórnym bielicowaniem i z głębokim poziomem płużnym pod zbiorowiskiem boru mieszanego sosnowo-dębowego (*Querco roboris-Pinetum*) (fot. J.M. Matuszkiewicz)

Photo. 15. Luvisols without plough horizon in lime-oak-hornbeam forest (*Tilio-Carpinetum calamagrostietosum*). (photo. J.M. Matuszkiewicz)

Fot. 15. Gleba płowa bez śladów rolniczego użytkowania pod zbiorowiskiem lasu dębowo-grabowego (*Tilio-Carpinetum calamagrostietosum*) (fot. J.M. Matuszkiewicz)

Photo. 16. Post-agricultural soil, with plough horizon in lime-oak-hornbeam forest (*Tilio-Carpinetum calamagrostietosum*). (photo. J.M. Matuszkiewicz)

Fot. 16. Gleba porolna pod zbiorowiskiem regenerującego lasu dębowo-grabowego (*Tilio-Carpinetum calamagrostietosum*) (fot. J.M. Matuszkiewicz)

Photo. 1

Photo 2

Photo 3

Photo 4

Photo 5

Photo 6

Photo 7

Photo 8

Photo 9

Photo 10

Photo 11

Photo 12

Photo 13

Photo 14

Photo 15

Photo 16

Deforestation due to agriculture development is one of the most important indication of human pressure on the environment. It results in significant vegetation changes as well as transformations in soil environment and other habitat elements. In Central Europe, for many centuries, any increase in human population led to a growing demand for food production followed by extensive clear-cutting and an increase in arable land cover. This, however, is not the only process observed in the landscape. Side by side with deforestation, there have been going on for a long time already the processes of the forest return onto the agricultural land, especially in the late 19th and 20th centuries. Changes in forest area can be observed on archival topographical maps documenting the existence of forests for at least the last 200 years.

The study was conducted in a region of former German-Polish borderland (East Prussia – Masuria and Kurpie) and resulted from an interest in a correlation between present floristic composition, the structure of forest communities and the history of the area – if it was afforested constantly (ancient forest) or was used for some time in agriculture (recent, post-agricultural forest). Having data on the range of ancient forests and probable date of afforestation in recent forests, phytosociological relevés and soil samples were collected with the aim of indicating differences between ancient and recent forests. The analysis was carried out in three associations: *Peucedano-Pinetum, Querco roboris-Pinetum* and *Tilio-Carpinetum*. A new indicator of forest maturity FMI useful for evaluation of recent forest regeneration degree and models which define the rate and the course of the advanced forest regeneration process on the post-agricultural land were developed.

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