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ORIGINAL RESEARCH ARTICLE

Rate and direction of changes in tree species composition of natural stands in selected forest associations in the Białowieża Forest

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Abstract. The main aim of the study was to determine changes in the species composition and structure of natural tree stands in the Białowieża Forest (BF), which occurred in the years 1975–2012, as well as to evaluate their trends, directions and rate. The study was carried out on 121 permanent research plots (50 × 50 m), which represented the most important forest phytocenoses in BF, i.e. fresh pine-whortleberry forest *Vaccinio vitis-idaeae-Pinetum* Sokoł. 1980, fresh mixed spruce-reed grass forest *Calamagrostio-Piceetum* Sokoł. 1968, oligotrophic form of hornbeam - bastard balm forest *Melitti-Carpinetum* Sokoł. 1976, different forms of linden-hornbeam forest: *Tilio-Carpinetum* Tracz. 1962, alder-ash forest *Fraxino-Alnetum* W. Mat. 1952 and sub-boreal spruce forest on bog moss *Sphagno girgenshonii-Piceetum* Polak. 1962. On the plots selected, there was measured the diameter at breast height (DBH) of all trees, as well as every tree and shrub up to 1.3 m high was counted and described with reference to species. The measurements and observations were regularly repeated every 10–15 years. The results showed that over the last period of nearly 40 years, there has increased a share of common hornbeam *Carpinus betulus* L. in the structure of forest stands in numerous BF associations. This tree species has expanded into different forest habitats including poor, medium fertile and wetland sites. The results obtained indicate a trend towards formation of linden-hornbeam forests in BF phytocenoses. The most evident changes were recorded in hornbeam – bastard balm forest. In natural conditions of the majority of forest associations analysed, there prevailed hornbeam trees in forest regeneration, except for the stands in fresh mixed pine forest and spruce forest on bog moss. In the latter two cases, hornbeam showed signs of its presence in the last observation period. Norway spruce (*Picea abies* L.) retreated into oligotrophic forest associations. In the recent decades, spruce populations have been dramatically reduced in the stands in mixed coniferous and different kinds of broadleaved forests. There have also decreased a share of light-demanding tree species, such as Scots pine (*Pinus silvestris* L.), pedunculate oak (*Quercus robur* L.) and silver birch (*Betula pendula* L.) in BF tree stands, including their regeneration-layer. Especially, Scots pine regeneration has not been successful.

In the short period of time (about 15 years) there has been observed rapid and outsized reduction of ash *Fraxinus excelsior* L. populations in natural conditions of alder-ash forests. All through the last 10–15 years, there has been also observed increased rate of change in stand species composition. The trend and rate of change in stand species composition point out to a possibility of human intervention towards stimulation of natural regeneration so as to preserve valuable populations of threatened tree species in the Białowieża Forest.

Key words: hornbeam expansion, natural stands, permanent study plots, Białowieża Forest, ash dieback

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1. Introduction and study aims

The Białowieża Forest (BF) is among the largest and best preserved woodlands in the East-Central European lowland. The woodland is dominated by eutrophic sites where the total share of deciduous forest sites amounts up to 60%. Coniferous forests account for several percent of the area only, and mixed coniferous–deciduous forests take a little more than 30% (Sokołowski 2004).

Nearly a half of the BF areas have recently been set aside and taken out of any direct human intervention, including the Białowieża National Park, nature reserves, and zones established to protect birds, fungi and other organisms. Moreover, all stands over 100 years old have been excluded from all silvicultural and protective practices. The areas set aside for conservation provide an excellent opportunity to study natural ecological processes. Forest habitats of EU importance, protected under Council Directive 92/43/EEC, take almost 80% of the BF and encompass the subcontinental linden–hornbeam forests (9170) as well as priority habitats such as bog woodland (91D0) and alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (91E0).

Long-term analyses of stand development in the BF show that there have been considerable changes in tree species composition over the last several decades, leading to, among others, the absence of pine regeneration and an increase in the frequency of hornbeam and linden (Kowalski 1982; Brzeziecki 2008; Drozdowski et al. 2012). Analogous observations (no pine regeneration, expansion of hornbeam) were also reported from other locations in the BF (Sokołowski 2004).

Results of systematic phytosociological study conducted in northeastern Poland as well as in the BF point out to a high dynamics of vegetation changes, including changes in stand composition (Sokołowski 1991, 2004; Paluch 2001, 2003; Czerepko and Sokołowski 2006).

A robust archive of relevant material has been gathered at the Forest Research Institute, encompassing phytosociological records, stand measurement data and results of long-term vegetation monitoring in permanent study plots, which were first set up as early as in 1975, mainly in northeastern Poland. The present study was undertaken with the aim to maintain uninterrupted vegetation monitoring as continuation of the work initiated by a team headed by Professor A.W. Sokołowski

The following aims of study were adopted:

1) To identify changes in stand structure and species composition in the permanent study plots over the last three to four decades,

2) To assess trends, directions and rates of the changes,

3) To evaluate how the consequences of vegetation changes identified would affect the long-term silvicultural planning and needs for its modification.

2. Methods and scope of study

Nearly 300 permanent study plots (structural) have been established in a variety of forest communities in northeastern Poland since 1970s up to now. The plots sized generally 50 × 50 m, were set up with the aim to analyse changes in stand structure and species composition (Sokołowski 2004). Oakwood rods were used to mark plot boundaries. Within the plots, the tree diameter at breast height (DBH) was measured in thickness classes and young trees and shrubs <1.3 m tall were counted by species. Measurements were repeated every 10–15 yr.

The continuation study in the BF was conducted in 121 permanent plots (Fig. 1), which originally represented:

– fresh pine–whortleberry forest *Vaccinio vitis-idaeae-Pinetum* Sokoł. 1980,

– fresh mixed spruce reed grass forest *Calamagrostio-Piceetum* Sokoł. 1968,

– oligotrophic hornbeam–bastard balm forest *Melitti-Carpinetum* (MC) Sokoł. 1976,

– various forms of linden–hornbeam forest *Tilio-Carpinetum* Tracz. 1962,

– alder-ash forest *Fraxino-Alnetum* W.Mat. 1952,

– sub-boreal spruce forest on bog moss *Sphagno girgensohnii-Piceetum* (S) Polak. 1962,

The study methods were based on those applied in the earlier works by Sokołowski (1960–2004, 1991 and 2004). Geographical coordinates of study plot boundaries were determined with the use of GPS receiver (Table 1).

Based on the measurements of stand density and DBH cross sections (stand basal area) by tree species, the species composition of the stands was determined in the respective investigation years. To compare proportions of individual tree species in the stand species composition between the respective study periods, a similarity coefficient was used (Brzeziecki 2008 after Bodeck et al. 2001), which was calculated using the following formula:

$$S = 1 - \frac{\sum_{i=1}^{n} \left| f_{1,i} - f_{2,i} \right|}{200}$$

where:

$f_{1,i}$ and $f_{2,i}$ – percent proportion of *i*-th species in the study periods compared,

n – total number of species in both study periods compared.

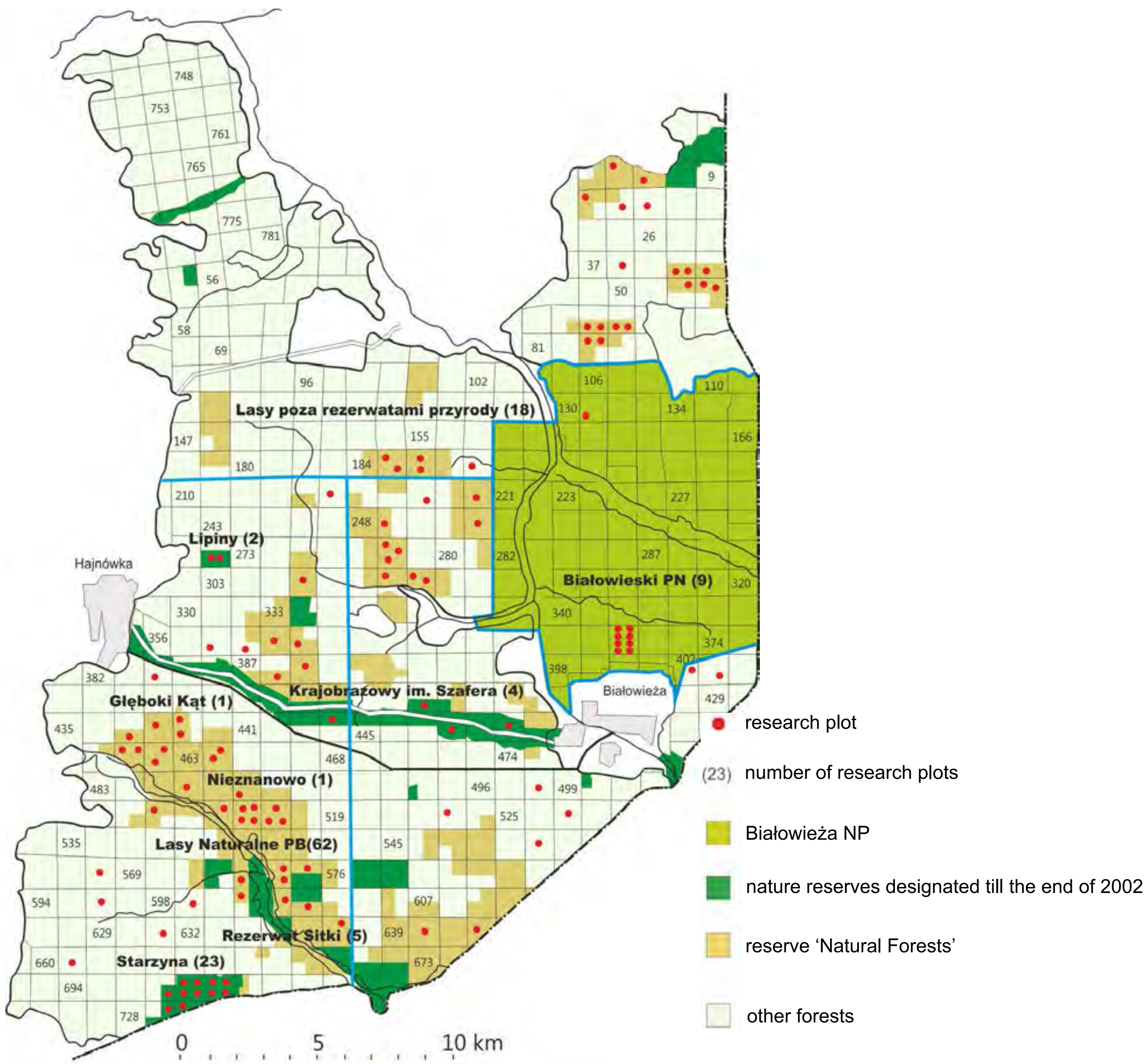

Figure 1. Permanent research plots of the Forest Research Institute and protected areas in the Białowieża Forest

The S coefficient fluctuated within a range from 0 to 1, where zero denotes a total lack of similarity while 1 – full similarity. The coefficient was calculated using tree number as the contribution of an individual tree species.

In order to present clearly the most important changes in the stand structure and species composition over the last nearly four decades, graphic visualisation of selected stands was made using BWINPro 6.2 mathematical model of forest dynamics (Nagel 1999).

3. Results of studies

Fresh pine–whortleberry forest *Vaccinium vitis-idaea-Pinetum* Sokoł. 1980

The proportions and numbers of the two main stand building tree species, that is Scots pine and Norway spruce were found to undergo significant changes over the last nearly four decades of the investigation. Changes in stand

Table 1. Location of permanent study plots of the Forest Research Institute in the Białowieża Forest

Nr.	Forest district	Sector (Item)	Year of plot establishment	Forest code	Forest site type*	Forest association	Compartement	GPS coordinates
1	Hajnówka	Sitki	1975	V1	Bśw	*Vaccinio vitis-idaeae-Pinetum* Sokoł. 1980	667Bh	N52.62401 E23.66780
2	Hajnówka	Sitki	1973	V2	Bśw	*Vaccinio vitis-idaeae-Pinetum* Sokoł. 1980	668Ac	N52.62281 E23.67379
3	Hajnówka	Sitki	1985	V3	Bśw	*Vaccinio vitis-idaeae-Pinetum* Sokoł. 1980	668Ac	N52.62510 E23.66967
4	Białowieski PN	Hwoźna	1999	V4	Bśw	*Vaccinio vitis-idaeae-Pinetum* Sokoł. 1980	131Cc	N52.80370 E23.84432
5	Hajnówka	Sitki	1973	V5	Bśw	*Vaccinio vitis-idaeae-Pinetum* Sokoł. 1980	667Bh	N52.62411 E23.66802
6	Hajnówka	Sitki	1973	V6	Bśw	*Vaccinio vitis-idaeae-Pinetum* Sokoł. 1980	668Ac	N52.62381 E23.67679
7	Białowieski PN	Hwoźna	1999	V7	Bśw	*Vaccinio vitis-idaeae-Pinetum* Sokoł. 1980	131C	N52.80170 E23.84632
8	Hajnówka	Starzyna	1975	CP1	BMśw	*Calamagrostio arundinaceae-Piceetum* Sokoł. 1968	699Bb	N52.61554 E23.65067
9	Hajnówka	Starzyna	1975	CP2	BMśw	*Calamagrostio arundinaceae-Piceetum* Sokoł. 1968	699Bg	N52.61386 E23.64845
10	Białowieża	Zwierzyniec	1975	CP3	BMśw	*Calamagrostio arundinaceae-Piceetum* Sokoł. 1968	448B	N52.70107 E23.77588
11	Białowieża	Zwierzyniec	1975	CP4	BMśw	*Calamagrostio arundinaceae-Piceetum* Sokoł. 1968	448C	N52.69855 E23.77082
12	Białowieża	Zwierzyniec	1975	CP5	BMśw	*Calamagrostio arundinaceae-Piceetum* Sokoł. 1968	448D	N52.69857 E23.77844
13	Hajnówka	Sitki	1994	CP6	BMśw	*Calamagrostio arundinaceae-Piceetum* Sokoł. 1968	668A	N52.62175 E23.67206
14	Hajnówka	Sitki	1994	CP7	BMśw	*Calamagrostio arundinaceae-Piceetum* Sokoł. 1968	668C	N52.62099 E23.67335
15	Hajnówka	Sitki	1994	CP8	BMśw	*Calamagrostio arundinaceae-Piceetum* Sokoł. 1968	668B	N52.62175 E23.67207
16	Hajnówka	Sitki	1994	CP9	BMśw	*Calamagrostio arundinaceae-Piceetum* Sokoł. 1968	668C	N52.62519 E23.67336
17	Hajnówka	Starzyna	1975	CP10	BMśw	*Calamagrostio arundinaceae-Piceetum* Sokoł. 1968	699Bb	N52.61597 E23.65267
18	Hajnówka	Leśna	1985	S1	BMb	*Sphagno girgensohnii-Piceetum* Polak. 1962	517Ba	N52.67482 E23.68486
19	Hajnówka	Leśna	1975	S2	BMb	*Sphagno girgensohnii-Piceetum* Polak. 1962	439Aa	N52.70336 E23.63043
20	Hajnówka	Leśna	1985	S3	BMb	*Sphagno girgensohnii-Piceetum* Polak. 1962	517Ba	N52.67445 E23.68497
21	Browsk	Narewka	1998	MC1	LMśw	*Melitti-Carpinetum* Sokoł. 1976	186Dh	N52.78115 E23.75698
22	Hajnówka	Starzyna	1996	MC2	LMśw	*Melitti-Carpinetum* Sokoł. 1976	663Ab	N52.62512 E23.59103
23	Hajnówka	Starzyna	1974	MC3	LMśw	*Melitti-Carpinetum* Sokoł. 1976	698Cd	N52.61135 E23.62219
24	Hajnówka	Starzyna	1974	MC4	LMśw	*Melitti-Carpinetum* Sokoł. 1976	697Db	N52.61173 E23.61918
25	Hajnówka	Starzyna	1975	MC5	LMśw	*Melitti-Carpinetum* Sokoł. 1976	697Db	N52.60967 E23.62028
26	Hajnówka	Starzyna	1975	MC6	LMśw	*Melitti-Carpinetum* Sokoł. 1976	700Bd	N52.61515 E23.66457
27	Hajnówka	Starzyna	1974	MC7	LMśw	*Melitti-Carpinetum* Sokoł. 1976	729Bb	N52.60464 E23.61797
28	Białowieża	Zwierzyniec	1986	MC8	LMśw	*Melitti-Carpinetum* Sokoł. 1976	422Cj	N52.70380 E23.74962
29	Hajnówka	Starzyna	1974	MC9	LMśw	*Melitti-Carpinetum* Sokoł. 1976	730Af	N52.60703 E23.62302
30	Hajnówka	Starzyna	1974	MC10	LMśw	*Melitti-Carpinetum* Sokoł. 1976	730Af	N52.60431 E23.62537
31	Hajnówka	Starzyna	1974	MC11	LMśw	*Melitti-Carpinetum* Sokoł. 1976	730Af	N52.60407 E23.62190
32	Hajnówka	Starzyna	1975	MC12	LMśw	*Melitti-Carpinetum* Sokoł. 1976	416B	N52.70889 E23.66929

33	Białowieża	Zwierzyniec	1998	MC13	LMśw	*Melitti-Carpinetum* Sokoł. 1976	472Cb	N52.68752 E23.76677
34	Hajnówka	Lipiny	1985	MC14	LMśw	*Melitti-Carpinetum* Sokoł. 1976	272D2	N52.75478 E23.64858
35	Hajnówka	Lipiny	1985	MC15	LMśw	*Melitti-Carpinetum* Sokoł. 1976	272D1	N52.75562 E23.64555
36	Hajnówka	Starzyna	1974	MC16	LMśw	*Melitti-Carpinetum* Sokoł. 1976	697Dh	N52.60816 E23.61557
37	Hajnówka	Lipiny	1985	MC17	LMśw	*Melitti-Carpinetum* Sokoł. 1976	272Da	N52.75278 E23.64633
38	Hajnówka	Starzyna	1975	MC18	LMśw	*Melitti-Carpinetum* Sokoł. 1976	416C	N52.70289 E23.66980
39	Hajnówka	Starzyna	1974	MC19	LMśw	*Melitti-Carpinetum* Sokoł. 1976	729Bb	N52.60464 E23.61597
40	Hajnówka	Hajnówka	1975	MC20	LMśw	*Melitti-Carpinetum* Sokoł. 1976	419Ca	N52.70830 E23.70523
41	Hajnówka	Leśna	1996	Tk1	LMw	*Tilio-Carpinetum calamagrostietosum*	604Cb	N52.63968 E23.70245
42	Hajnówka	Starzyna	1996	Tk2	LMw	*Tilio-Carpinetum calamagrostietosum*	569Bb	N52.65509 E23.60078
43	Białowieża	Białowieża	1997	Tk3	LMw	*Tilio-Carpinetum calamagrostietosum*	607Dc	N52.63737 E23.75822
44	Białowieża	Białowieża	1998	Tk4	LMw	*Tilio-Carpinetum calamagrostietosum*	640Aa	N52.63586 E23.75473
45	Browsk	Browsk	1998	Tk5	LMw	*Tilio-Carpinetum calamagrostietosum*	38Dg	N52.84803 E23.87292
46	Hajnówka	Leśna	1996	Tk6	LMw	*Tilio-Carpinetum calamagrostietosum*	575Bd	N52.65430 E23.70035
47	Browsk	Browsk	1998	Tk7	LMw	*Tilio-Carpinetum calamagrostietosum*	25Dd	N52.86142 E23.86895
48	Białowieża	Białowieża	1998	Tk8	LMw	*Tilio-Carpinetum calamagrostietosum*	546Bb	N52.66379 E23.76216
49	Białowieża	Białowieża	1996	Tk9	LMw	*Tilio-Carpinetum calamagrostietosum*	548Ag	N52.66189 E23.78300
50	Hajnówka	Hajnówka	1996	Tk10	LMw	*Tilio-Carpinetum calamagrostietosum*	418Af	N52.70921 E23.68593
51	Browsk	Browsk	1998	Tk11	LMw	*Tilio-Carpinetum calamagrostietosum*	38D	N52.84603 E23.87192
52	Białowieski PN	Orłówka	1985	TCt1	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	371C	N52.72767 E23.86735
53	Białowieski PN	Orłówka	1985	TCt2	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	371C	N52.72710 E23.86733
54	Białowieski PN	Orłówka	1985	TCt3	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	371C	N52.72681 E23.86716
55	Białowieski PN	Orłówka	1985	TCt4	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	371C	N52.72627 E23.86727
56	Białowieski PN	Orłówka	1985	TCt5	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	371C	N52.72765 E23.86656
57	Białowieski PN	Orłówka	1985	TCt6	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	371C	N52.72721 E23.86657
58	Białowieski PN	Orłówka	1985	TCt7	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	371C	N52.72678 E23.86659
59	Białowieski PN	Orłówka	1985	TCt8	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	371C	N52.72632 E23.86642
60	Browsk	Browsk	1998	TCt9	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	39Db	N52.84735 E23.88874
61	Browsk	Narewka	1998	TCt10	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	188Cb	N52.78151 E23.78051
62	Białowieża	Zwierzyniec	1998	TCt11	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	310Ac	N52.74937 E23.74897
63	Białowieża	Zwierzyniec	1998	TCt12	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	220Ac	N52.77877 E23.78070
64	Białowieża	Białowieża	1997	TCt13	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	524Dd2	N52.66695 E23.79347
65	Hajnówka	Hajnówka	1996	TCt14	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	360Cc	N52.72356 E23.67509
66	Hajnówka	Hajnówka	1996	TCt15	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	390Ab	N52.72168 E23.68506
67	Hajnówka	Hajnówka	1996	TCt16	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	418Bc	N52.71241 E23.69658
68	Hajnówka	Hajnówka	1996	TCt17	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	419Ac	N52.70877 E23.70224

Nr.	Forest district	Sector (Item)	Year of plot establishment	Forest code	Forest site type*	Forest association	Compartement	GPS coordinates
69	Białowieża	Zwierzyniec	1998	TCt18	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	451Ad	N52.69930 E23.81214
70	Białowieża	Białowieża	1997	TCt19	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	524D	N52.66795 E23.79328
71	Browsk	Browsk	1975	TCt20	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	38Bd	N52.85570 E23.86960
72	Browsk	Browsk	1998	TCt21	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	51Bb	N52.84371 E23.89000
73	Browsk	Narewka	1998	TCt22	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	186Af	N52.78709 E23.74882
74	Hajnówka	Starzyna	1996	TCt23	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	536Bo	N52.66040 E23.58273
75	Hajnówka	Starzyna	1996	TCt24	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	599Dd	N52.63806 E23.63230
76	Hajnówka	Starzyna	1996	TCt25	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	613Dc	N52.62935 E23.62130
77	Hajnówka	Starzyna	1996	TCt26	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	695Bc	N52.61297 E23.58811
78	Białowieża	Zwierzyniec	1998	TCt27	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	217Ac	N52.77769 E23.73339
79	Białowieża	Zwierzyniec	1998	TCt28	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	218Cb	N52.77593 E23.75167
80	Białowieża	Białowieża	1998	TCt29	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	403Cd	N52.71638 E23.90882
81	Białowieża	Białowieża	1997	TCt30	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	580Bc	N52.65124 E23.77940
82	Białowieża	Białowieża	1997	TCt31	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	582Af	N52.65532 E23.79900
83	Hajnówka	Hajnówka	1996	TCt32	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	360Ca	N52.72742 E23.66935
84	Hajnówka	Hajnówka	1996	TCt33	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	418Ad	N52.70987 E23.68549
85	Hajnówka	Hajnówka	1975	TCt34	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	443A	N52.70105 E23.69279
86	Hajnówka	Hajnówka	1996	TCt35	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	443Ca	N52.69917 E23.68745
87	Browsk	Narewka	1998	TCt36	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	185Ca	N52.78153 E23.73922
88	Browsk	Narewka	1998	TCt37	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	185Db	N52.78096 E23.74090
89	Białowieża	Zwierzyniec	1998	TCt38	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	251Db	N52.76169 E23.77414
90	Białowieża	Zwierzyniec	1975	TCt39	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	445B	N52.70139 E23.73211
91	Białowieża	Zwierzyniec	1975	TCt40	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	447B	N52.7002 E23.760025
92	Białowieża	Zwierzyniec	1975	TCt41	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	449A	N52.70087 E23.78319
93	Białowieża	Zwierzyniec	1975	TCt42	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	449B	N52.69969 E23.79213
94	Białowieża	Zwierzyniec	1974	TCt43	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	451D	N52.69544 E23.82160
95	Białowieża	Zwierzyniec	1974	TCt44	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	475A	N52.69338 E23.81602
96	Browsk	Narewka	1997	TCt45	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	186Aa	N52.78809 E23.74802
97	Hajnówka	Starzyna	1975	TCt46	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	536Bb	N52.66040 E23.58273
98	Hajnówka	Starzyna	1975	TCt47	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	599Dd	N52.63806 E23.63230
99	Hajnówka	Starzyna	1975	TCt48	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	613Cc	N52.62935 E23.62130
100	Hajnówka	Starzyna	1975	TCt49	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	695Ba	N52.61157 E23.58845
101	Białowieża	Białowieża	1997	TCt50	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	582B	N52.65932 E23.79912

102	Białowieża	Zwierzyniec	1998	TCt51	Lśw	*Tilio-Carpinetum typicum* Tracz. 1962	218D	N52.77993 E23.75197
103	Browsk	Browsk	1998	F1	OlJ	*Fraxino-Alnetum* W.Mat. 1952	16Aa	N52.87199 E23.88423
104	Browsk	Browsk	1998	F2	OlJ	*Fraxino-Alnetum* W.Mat. 1952	17Bg	N52.87151 E23.90194
105	Browsk	Narewka	1998	F3	OlJ	*Fraxino-Alnetum* W.Mat. 1952	185Ac	N52.78605 E23.74025
106	Browsk	Narewka	1998	F4	OlJ	*Fraxino-Alnetum* W.Mat. 1952	185Bd	N52.78628 E23.74093
107	Białowieża	Białowieża	1997	F5	OlJ	*Fraxino-Alnetum* W.Mat. 1952	524Cc	N52.66579 E23.78738
108	Białowieża	Białowieża	1997	F6	OlJ	*Fraxino-Alnetum* W.Mat. 1952	524Dd1	N52.66550 E23.79209
109	Białowieża	Białowieża	1997	F7	OlJ	*Fraxino-Alnetum* W.Mat. 1952	547Bd	N52.66084 E23.77672
110	Białowieża	Białowieża	1997	F8	OlJ	*Fraxino-Alnetum* W.Mat. 1952	610Af	N52.64366 E23.79618
111	Białowieża	Białowieża	1998	F9	OlJ	*Fraxino-Alnetum* W.Mat. 1952	641Af	N52.63430 E23.76480
112	Hajnówka	Hajnówka	1996	F10	OlJ	*Fraxino-Alnetum* W.Mat. 1952	360Cb	N52.72452 E23.66938
113	Hajnówka	Leśna	1996	F11	OlJ	*Fraxino-Alnetum* W.Mat. 1952	518Ad	N52.67219 E23.68685
114	Hajnówka	Leśna	1996	F12	OlJ	*Fraxino-Alnetum* W.Mat. 1952	518Cb	N52.66607 E23.68688
115	Białowieża	Zwierzyniec	1997	F13	OlJ	*Fraxino-Alnetum* W.Mat. 1952	249Cf	N52.76186 E23.73282
116	Białowieża	Zwierzyniec	1998	F14	OlJ	*Fraxino-Alnetum* W.Mat. 1952	277Da	N52.75377 E23.73112
117	Browsk	Narewka	1998	F15	OlJ	*Fraxino-Alnetum* W.Mat. 1952	185Bd	N52.78628 E23.74499
118	Białowieża	Białowieża	1997	F16	OlJ	*Fraxino-Alnetum* W.Mat. 1952	547Bd	N52.66084 E23.77972
119	Białowieża	Białowieża	1997	F17	OlJ	*Fraxino-Alnetum* W.Mat. 1952	610Af	N52.64366 E23.79618
120	Hajnówka	Leśna	1996	F18	OlJ	*Fraxino-Alnetum* W.Mat. 1952	518Ad	N52.67331 E23.68715
121	Białowieża	Zwierzyniec	1998	F19	OlJ	*Fraxino-Alnetum* W.Mat. 1952	277Da	N52.75154 E23.73268

Bśw – fresh coniferous forest, BMśw – fresh mixed coniferous forest, BMb – boogy mixed coniferous forest, LMśw – fresh mixed broadleaved forest, LMw – moist mixed breadleaved forest, Lśw – fresh broadleaved forest, OIJ – alder-ash forest

Table 2. Changes in species composition and structure in V1 stand (see Table 1) in fresh pine-whortleberry forest (*Vaccinio vitis-idaeae-Pinetum*)

DBH [cm]	*Pinus sylvestris*				*Picea abies*				*Betula pendula*				*Quercus robur*				*Populus tremula*				*Sorbus aucuparia*			
	1975	1986	1997	2012	1975	1986	1997	2012	1975	1986	1997	2012	1975	1986	1997	2012	1975	1986	1997	2012	1975	1986	1997	2012
	Tree number per hectare																							
0–3	92	-	-	-	80	156	220	216	148	96	20	-	8	-	108	44	-	-	4	-	-	-	44	-
3.1–7	-	-	-	-	120	188	172	148	44	92	28	-	4	8	12	8	4	-	-	-	-	-	-	-
Σ	92	-	-	-	200	344	392	364	192	188	48	-	12	8	120	52	4	-	4	-	-	-	44	-
7.1–11	16	12	-	-	20	100	104	132	-	8	36	24	4	4	-	-	-	4	-	-	-	-	-	-
11.1–15	36	4	12	-	4	112	124	112	-	-	8	8	-	4	4	-	-	-	-	-	-	-	-	-
15.1–19	44	12	16	12	-	12	84	96	-	-	4	4	-	-	-	4	-	-	-	-	-	-	-	-
19.1–23	52	40	20	16	-	-	20	56	-	-	-	-	-	-	4	4	-	-	-	-	-	-	-	-
Σ	148	68	48	28	24	224	332	396	-	8	48	36	4	8	8	8	-	4	-	-	-	-	-	-
23.1–27	60	36	12	8	-	4	8	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27.1–31	116	52	20	20	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31.1–35	44	80	72	28	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35.1–39	24	40	72	48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
39.1–43	20	12	28	60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Σ	264	220	204	164	-	4	8	28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
43.1–47	4	24	16	28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
47.1–51	4	8	16	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
51.1–55	4	4	8	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
55.1–59	-	-	4	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Σ	12	36	44	68	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Undergrowth $h < 130$ cm	228	-	12	-	240	180	116	64	224	124	168	-	88	344	564	192	16	16	36	-	64	272	420	-

species composition and DBH structure in one of the permanent research plots are presented in Table 2. Pine was found to withdraw entirely from the understory layers. At the time of the study onset, there were encountered pine trees with lower DBH values, while at the time being, only thick and medium-sized pine trees were present. Neither was the recruitment of Scots pine noted in the years 1986–2012 nor did it appear in inconspicuous number (Table 2), what testifies to a complete halt of the process of natural regeneration of the species. Notwithstanding the abovementioned lack of recruitment, for which a variety of causes can be held accountable, it is noteworthy to turn attention to a significant increase in the regeneration of understory spruce (trees of DBH <7 cm). Norway spruce is a major competitor for Scots pine in the forest community surveyed. In the year 1975, pine dominated both in numbers and stand basal area (Fig. 2), or else it was the most important component in all of the stand strata, and hence – in the whole forest community. The proportion of pine in stand species composition exceeded 60%, while that of spruce 25%. The proportions were reversed in 2012 when spruce was found to be overwhelmingly dominating in terms of tree density (Fig. 2). Over the same period, the share of birch also declined from 20% to a few percent, whereas pedunculate oak, which provided for a constant element of understory in the past, was not able to make it to the upper tier of the canopy over the last 40 years (Table 2). The

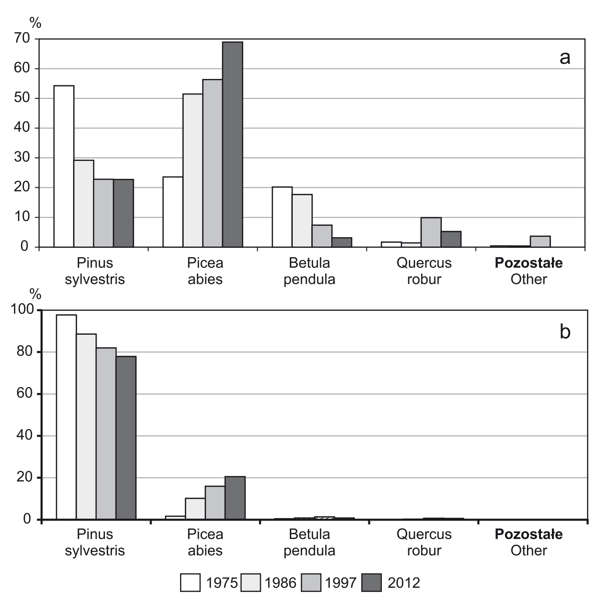

Figure 2. Tree species share (according to: a – density, b – basal area) in 1975–2012, based on permanent V1 research plot (see Table 1) in fresh pine-whortleberry forest (*Vaccinio vitis-idaeae-Pinetum*). Other tree species: *Populus tremula*. *Sorbus aucuparia*

participation of oak in the stand species composition was small and accounted for a few percent (Fig. 2). Though the pine contribution decreased from almost 100% down to 80%, it still remained the dominant species in the community. On the other hand, spruce was observed to increase its contribution by several times, both in terms of tree number and stand basal area. The participation of Scots pine and silver birch was considerably reduced: in the first of the abovementioned species by almost 40%, while in the second – down to a marginal value of a few percent (Fig. 2).

Fresh mixed spruce reed grass forest *Calamagrostio arundinaceae-Piceetum* Sokoł. 1968

In the mixed forest community, the density of both codominant species: Norway spruce and Scots pine was reduced significantly, which was, especially evident in the case of the second of the two species (Table 3). There was a decline in the density of young trees <7 cm DBH. No natural regeneration of pine, neither seedlings or saplings <1.3 m tall nor any older recruitment (7 cm DBH) could be observed in all research plots located in the above community type throughout the whole study period. In the year 2012, only thick and medium-sized pine trees (> 20 cm DBH) were present. Young spruce trees including low spruce undergrowth were found in every research plot and in all measurement periods; however, their numbers heavily depended on the density of old spruce trees (Table 3). Over the last four decades, no silver birch has been noted in any of DBH classes, except for the thinnest trees. At the onset of the study in 1975, the density of hornbeam population did not exceed a few trees per 1 ha. In 2012, there were significant numbers of hornbeam in the DBH class up to 3 cm (> 400/ha), and some individuals were even able to strengthen their position in the stand, advancing to higher DBH classes.

The most noticeable changes in the tree species density were registered in the years 1997–2012. The density of hornbeam, classified in the lowest DBH class, increased by about 10 times (Table 3). The hornbeam regeneration was observed to increasingly dominate in the understory, competing strongly with other tree species including Norway spruce (Fig. 3). Some hornbeam trees gained about 25 cm in DBH, which testifies to a high dynamics of the species and its expansion to mesotrophic sites outside its ecological optimum. Spruce, pine and birch diminished markedly in their their participation, calculated based on the species densities, while the proportion of hornbeam significantly increased (Fig. 4).

Things seemed different when analysing the stand basal area in respective tree species. The stand basal area in spruce and pine fluctuated only slightly – DBH incre-

Table 3. Changes in species composition and structure in CP1stand (see Table 1) in mixed fresh forest (*Calamagrostio arundinaceae-Piceetum)*

DBH classes [cm]	*Picea abies*				*Pinus sylvestris*				*Quercus robur*				*Betula pendula*				*Carpinus betulus*				Other			
	1975	1986	1997	2012	1975	1986	1997	2012	1975	1986	1997	2012	1975	1986	1997	2012	1975	1986	1997	2012	1975	1986	1997	2012
	Tree number per hectare																							
0–3	76	240	292	404	-	-	-	-	12	4	36	248	-	-	-	116	4	12	56	492	-	40	84	-
3.1–7	72	48	120	164	-	-	-	-	8	8	4	4	-	-	-	-	4	8	4	40	-	-	-	-
Σ	148	288	412	568	-	-	-	-	20	12	40	252	-	-	-	116	8	20	60	532	-	40	84	4
7.1–11	48	44	28	32	-	-	-	-	4	-	-	-	-	-	-	-	-	4	4	8	-	-	-	-
11.1–15	52	28	16	20	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	4	-	-	-	-
15.1–19	32	24	28	16	-	-	-	-	-	-	-	-	-	8	-	-	-	-	4	-	-	-	-	-
19.1–23	40	16	4	8	4	4	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-
Σ	172	112	76	76	4	4	-	-	4	-	-	-	8	8	-	-	-	4	8	12	-	-	-	-
23.1–27	36	32	16	8	4	-	-	-	4	-	-	-	16	8	-	-	-	-	-	4	-	-	-	-
27.1–31	40	12	16	24	4	8	-	-	-	4	4	4	8	-	-	-	-	-	-	-	-	-	-	-
31.1–35	4	44	28	12	12	4	8	-	-	-	-	-	16	8	-	-	-	-	-	-	-	-	-	-
35.1–39	12	8	12	16	8	12	8	4	-	-	-	-	4	8	-	-	-	-	-	-	-	-	-	-
39.1–43	16	16	20	24	12	16	8	4	-	-	-	-	4	4	-	-	-	-	-	-	-	-	-	-
Σ	108	112	92	84	40	40	24	8	4	4	4	4	48	28	-	-	-	-	-	4	-	-	-	-
43.1–47	12	12	12	12	8	12	12	8	-	-	-	-	8	8	-	-	-	-	-	-	-	-	-	-
47.1–51	-	4	4	16	12	8	16	20	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-
51.1–55	8	12	8	8	8	4	-	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
55.1–59	8	4	4	4	-	-	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
59.1–63	-	-	4	4	8	12	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
63.1–67	4	8	-	8	4	-	4	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
71.1–75	-	-	-	-	-	-	8	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
75.1–79	-	-	4	4	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Σ	32	40	36	56	40	36	52	56	-	-	-	-	8	8	4	-	-	-	-	-	-	-	-	-
Under-growth *h* < 130 cm	376	1092	304	248	-	-	-	-	228	560	292	248	24	4	260	-	8	128	132	492	32	1124	1176	-

Other: *Sorbus aucuparia, Acer platanoides, Populus tremula, Malus sylvestris, Salix caprea*

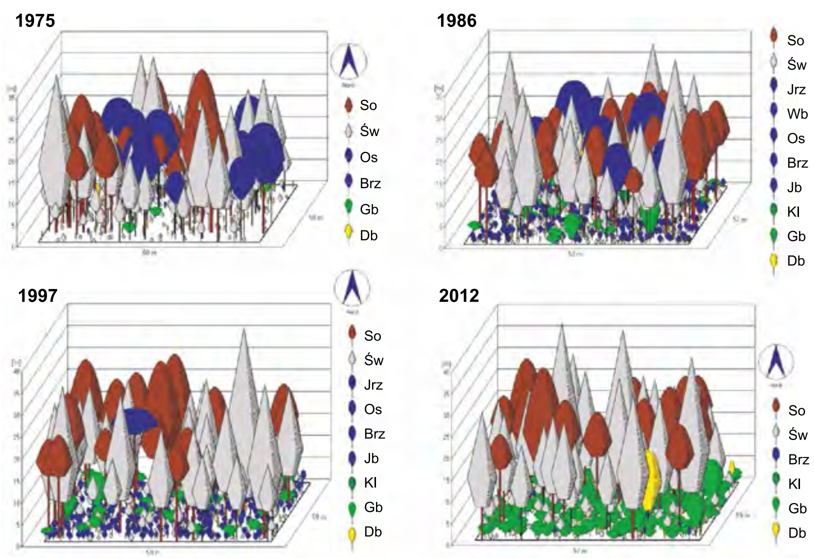

Figure 3. Visualisation of tree species composition in C1 stand in fresh mixed spruce-reed grass forest *Calamagrostio arundinaceae-Piceetum* in the period 1975–2012: So – *Pinus sylvestris*, Św – *Picea abies*, Jrz – *Sorbus aucuparia*, Wb – *Salix caprea*, Os – *Populus tremula*, Brz – *Betula pendula*, Jb – *Malus sylvestris*, Kl – *Acer platanoides*, Gb – *Carpinus betulus*, Db – *Quercus robur*

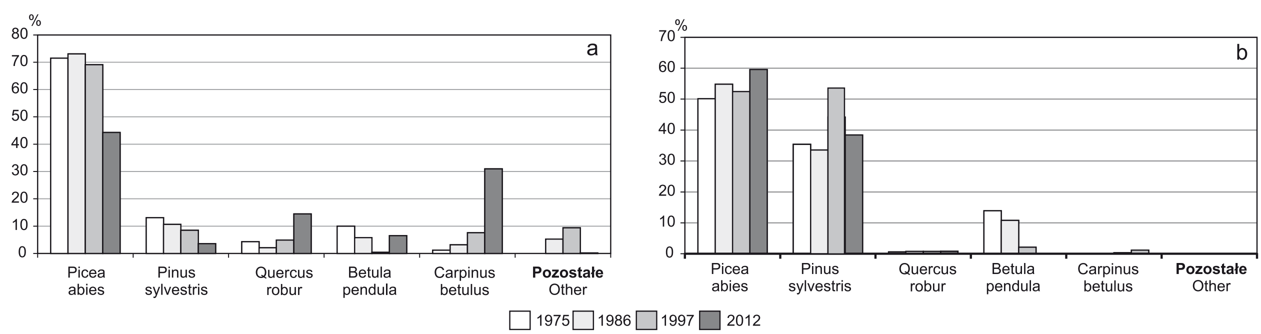

Figure 4. Tree species share (according to: a – density, b – basal area) in 1975–2012, based on permanent C1 research plot (see Table 1) in fresh mixed forest (*Calamagrostio arundinaceae-Piceetum*). Other tree species: *Sorbus aucuparia*. *Acer platanoides*

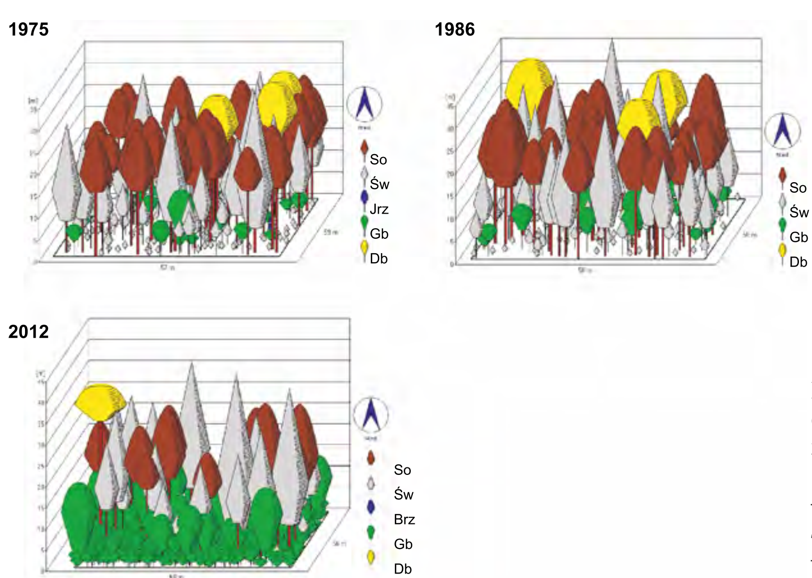

Figure 5. Visualisation of tree species composition in M6 stand (see Table 1) in hornbeam-bastard balm forest *Melitti-Carpinetum* in the period 1975–2012: So – *Pinus sylvestris*, Św – *Picea abies*, Jrz – *Sorbus aucuparia*, Gb – *Carpinus betulus*, Db – *Quercus robur*

ment provided compensation for declining tree numbers of the above species. The participation of hornbeam in the stand was observed to be significantly increased, while a reverse trend was noted in the case of birch (Fig. 4).

Oligotrophic hornbeam–bastard balm forest MC Sokoł. 1976

In this forest community, an exceptionally huge expansion of common hornbeam was observed in the lower understory. The number of hornbeam trees in the lowest DBH class (<3 cm) increased from several tens per 1 ha in 1986 to 3.3 thousand in 2012. The species dominated the entire lower understory creating a thick second tier of the stand (Fig. 5), thus making it impossible for other tree species to regenerate. Hornbeam maintained its domination among the undergrowth lower than 1.3 m, while its density in this group attained about 250 individuals/ha. Abundant recruitment of common spruce was already evident at the study onset in the 1970s. Ultimately, hornbeam was observed to replace Norway spruce in the lower understory. In the higher stand layers, a marked decline was noted in the participation of pedunculate oak, pine and spruce. Owing to the abundance of appearing young hornbeams, the participation of this species, calculated based on its numbers, increased significantly, while that of the remaining species largely declined (Fig. 6).

Over the nearly four decades long study period, the participation of pine in the stand basal area substantially declined, while inverse trends were observed for hornbeam and spruce. The parcticipation of oak stayed at the same level (Fig. 6).

Typical linden–hornbeam forest *Tilio-Carpinetum typicum* Tracz.1962

The most typical changes in stand structure and species composition in this forest type are shown in the example of TCt20 plot (Table 5, see also Table 1). Generally, the following species were found to withdraw from the linden–hornbeam stands: silver birch, Scots pine, Norway spruce and penduncalate oak, while in some stands the first three species were not encountered right from the onset of the study. The density of hornbeam, an important component of linden–hornbeam forest, steadily increased and the species became dominant in the lower and middle layers of the stand. In the year 2012, there were 1.3 thousand hornbeams in the <1.3 cm DBH class per 1 ha. It was the only species effectively regenerating in numbers up to 3.3 thousand per 1 ha in the recruitment and low growth (<1.3 m) story. The recruitment of linden with a small density was also observed (Table 5).

Owing to the abundance of appearing young hornbeam trees, participation of this species, calculated based on its numbers, substantially increased (Fig. 7), while that of other species largely declined. This can be explained also by the withdrawal of respective tree species from various stand layers.

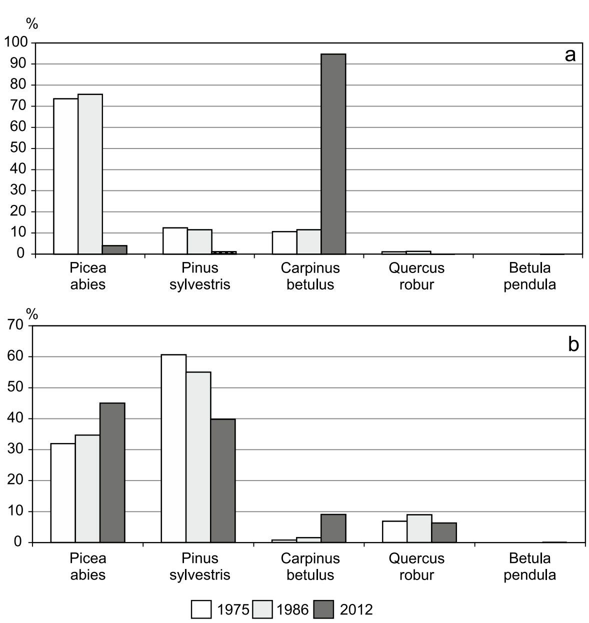

Figure 6. Tree species share (according to: a – density, b – basal area) in 1975–2012 based on permanent M6 research plot (see Table 1) in fresh mixed forest

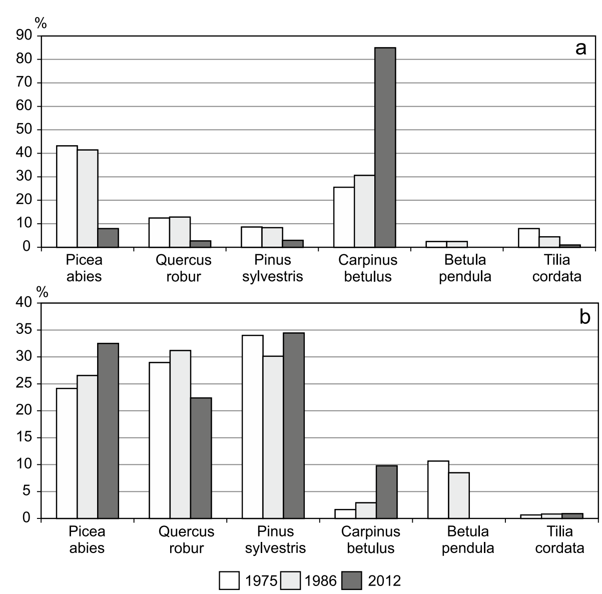

Figure 7. Tree species share (according to: a – density, b – basal area) in 1975–2012 based on permanent TCt20 research plot (see Table 1) in typical linden–hornbeam forest (*Tilio-Carpinetum typicum*)

Table 4. Changes in species composition and structure in M6 stand (see Table 1) in hornbeam-bastard balm forest (*Melitti-Carpinetum)*

DBH classes [cm]	*Picea abies*			*Pinus sylvestris*			*Carpinus betulus*			*Quercus rubra*			*Sorbus aucuparia*			*Betula pendula*		
	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012
	Tree number per hectare																	
0–3	484	292	12	-	-	-	32	8	3324	-	-	-	28	-	-	-	-	4
3.1–7	80	164	24	-	-	-	64	52	160	-	-	-	-	-	-	-	-	-
Σ	564	456	36	-	-	-	96	60	3484	-	-	-	28	-	-	-	-	4
7.1–11	48	44	12	-	-	-	16	20	40	-	-	-	-	-	-	-	-	-
11.1–15	40	28	8	-	-	-	4	8	8	-	-	-	-	-	-	-	-	-
15.1–19	28	12	16	-	-	-	4	16	16	-	-	-	-	-	-	-	-	-
19.1–23	24	28	4	-	-	-	-	-	12	-	-	-	-	-	-	-	-	-
Σ	140	112	40	-	-	-	24	44	76	-	-	-	-	-	-	-	-	-
23.1–27	32	16	4	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-
27.1–31	28	20	8	-	4	-	-	-	8	-	-	-	-	-	-	-	-	-
31.1–35	16	20	4	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35.1–39	12	16	8	4	4	-	-	-	-	-	-	-	-	-	-	-	-	-
39.1–43	8	4	16	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Σ	96	76	40	20	8	-	-	-	16	-	-	-	-	-	-	-	-	-
43–47	8	8	4	12	12	4	-	-	-	-	-	-	-	-	-	-	-	-
47–51	12	8	8	20	8	-	-	-	-	-	-	-	-	-	-	-	-	-
51–55	4	8	12	20	20	4	-	-	-	-	-	-	-	-	-	-	-	-
55–59	4	8	-	28	12	12	-	-	-	-	-	-	-	-	-	-	-	-
59–63	-	-	-	36	28	4	-	-	-	12	4	-	-	-	-	-	-	-
63–67	4	4	-	4	8	8	-	-	-	-	4	-	-	-	-	-	-	-
67–71	-	-	4	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-
71–75	-	-	4	-	8	4	-	-	-	-	4	-	-	-	-	-	-	-
79–83	-	-	4	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-
Σ	32	36	36	120	96	44	-	-	-	12	12	4	-	-	-	-	-	-
Undergrowth *h* < 130 cm	-	-	128	-	-	-	-	-	992	-	-	36	-	-	-	-	-	12

Table 5. Changes in species composition and structure in TCt20 stand (see Table 1) in typical linden–hornbeam forest (*Tilio-Carpinetum typicum*)

DBH classes [cm]	*Picea abies*			*Quercus robur*			*Pinus sylvestris*			*Carpinus betulus*			*Betula pendula*			*Tilia cordata*		
	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012
	Tree number per hectare																	
0–3	68	52	-	-	-	-	-	-	-	124	92	1224	-	-	-	40	8	4
3.1–7	124	24	-	4	-	-	-	-	-	128	64	24	-	-	-	32	8	4
Σ	192	76	-	4	-	-	-	-	-	252	156	1248	-	-	-	72	16	8
7.1–11	92	40	-	4	-	-	-	-	-	40	52	32	-	-	-	16	4	-
11.1–15	72	56	-	20	4	-	-	-	-	4	36	20	-	-	-	4	12	4
15.1–19	56	36	24	32	16	4	-	-	-	-	4	40	4	-	-	-	4	-
19.1–23	32	60	16	4	8	-	8	-	-	-	-	20	8	8	-	-	-	-
Σ	252	192	40	60	28	4	8	-	-	44	92	112	12	8	-	20	20	4
23.1–27	20	20	20	12	4	-	12	-	-	-	-	-	-	-	-	-	-	4
27.1–31	16	12	28	28	16	-	-	4	-	-	-	8	-	-	-	-	-	-
31.1–35	4	20	16	12	12	-	16	4	-	-	-	-	-	-	-	-	-	-
35.1–39	12	4	8	4	12	8	8	4	-	-	-	-	4	4	-	-	-	-
39.1–43	-	8	-	4	8	8	24	16	8	-	-	-	-	-	-	-	-	-
Σ	52	64	72	60	52	16	60	28	8	-	-	8	4	4	-	-	-	4
43.1–47	4	4	8	-	4	8	12	8	4	-	-	-	-	-	-	-	-	-
47.1–51	-	-	4	8	-	8	20	20	12	-	-	-	4	-	-	-	-	-
51.1–55	-	-	-	4	4	8	-	12	-	-	-	-	-	-	-	-	-	-
55.1–59	-	-	-	4	8	-	-	-	24	-	-	-	4	-	-	-	-	-
59.1–63	-	-	-	4	8	-	-	-	-	-	-	-	4	8	-	-	-	-
63.1–67	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Σ	4	4	16	20	24	24	32	40	40	-	-	-	12	8	-	-	-	-
Undergrowth $h < 130$ cm	36	-	-	64	8	4	-	-	-	356	432	3288	-	-	-	116	72	132

Participation of respective tree species defined on the basis of the stand basal area (Fig. 7) changed as well. There was an increase in the contribution of hornbeam from a few to 10%, and spruce to about 10% as well. The participation of pine in the stand composition was quite alike in all the study periods, whereas birch withdrew entirely from the stand.

Reedgrass oak–hornbeam forest *Tilio-Carpinetum calamagrostietosum* Tracz. 1962

Table 6 illustrates changes in stand structure and species composition registered in one of the permanent research plots – Tk8 (Fig. 1). In this plot, the density of hornbeam increased enormously in the lower and middle layers of the stand as was the case with specimens of littleleaf linden classified to the <3 cm DBH class. Hornbeam gained, in terms of numbers, a marked dominance in the stand composition (Table 6). Its participation increased distinctly in the year 2012, and attained more than 70%. At the same time, a trend was observed towards withdrawal of spruce, the density of which was halved in the respective DBH classes (Table 6). Its participation was markedly reduced, in terms of both tree numbers and stand basal area (Fig. 8) as old growth spruce trees died out and young individuals were lacking (Table 6). The share (determined on the basis of tree density) of the remaining species, such as oak, alder, linden and birch was also reduced (Fig. 8).

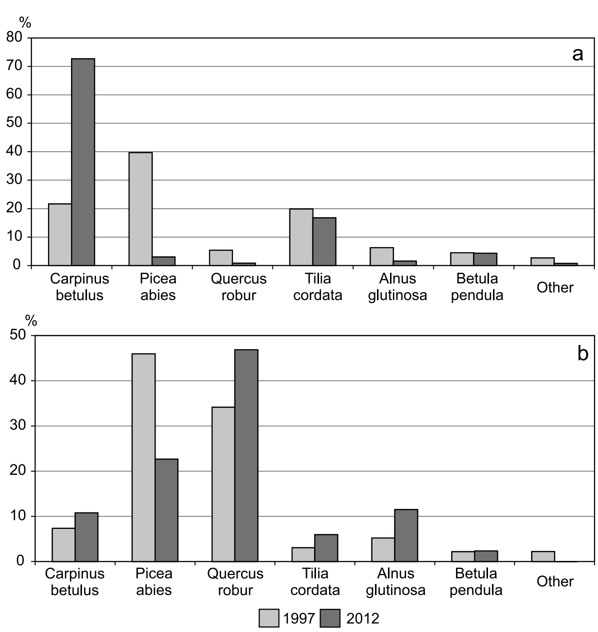

Figure 8. Tree species share (according to: a – density, b – basal area) in 1998–2011 based on TCt20 research plot (see Table 1) in typical linden-hornbeam forest (*Tilio-Carpinetum calamagrostietosum*). Other tree species: *Acer platanoides, Fraxinus excelsior, Sorbus aucuparia, Ulmus glabra*

On the other hand, there was an increase in the participation (defined on the basis of the stand basal area) of such species as hornbeam, oak, linden and alder, whereas a rapid decline in the participation of spruce was observed (Fig. 8).

Sub-boreal spruce forest on bog moss *Sphagno girgensohnii-Piceetum* Polak. 1962

Stages of forest stand development were totally changed in the years 1987–2012, that is when the stand after the optimal development stage entered via destruction stage the regeneration stage with intense tree regeneration. Three decades earlier, there dominated Norway spruce with little contribution of Scots pine and single deciduous species, including European ash, black alder, penduncuate oak and birches building the undergrowth (Table 7). All the spruce and pine trees observed in the earlier study periods died out in 2012. At that time, all of the main stand components, except for pine, regenerated, including spruce and hornbeam in the undergrowth (Table 7). Spruce contribution was then highest in the lower understory. Its density attained about 700 trees/ha in the DBH class <7 cm, and 2 thousand individuals per 1 ha in the recruitment and lower understory.

Despite the seemingly substantial change in the development stage of the stand surveyed (see Table 7), the participation of spruce, calculated by using various methods, remained fairly unchanged (Fig. 9). Only in the years 1997–2012, this participation, calculated on the basis of tree number, increased up to about 15%. In the same way, the participation of hornbeam increased from the level of a few to 10% (Fig. 9). Throughout the period analysed, the share of individual species in the stand basal area fluctuated only marginally, that is, it oscillated within the limits of 77–84% for spruce, 10–20%, for pine, while for the remaining species – a lump change amounted to a few percent. In 2012, the participation of hornbeam in the stand basal area reached 2% (Fig. 9).

Alder-ash forest *Fraxino-Alnetum* W. Mat. 1952

In the years 1997–2012, the numbers of ash trees were dramatically reduced in all the stand layers in the research plot F13 (Tables 1, 8). Whereas in the year 1997, almost 800 ash trees in the DBH class <7 cm could be counted per one hectare. In the year 2012, this number reduced to about 50. The density of ash trees in the remaining DBH classes was also substantially reduced, which was particularly evident among the thickest trees (Table 8). Ash is considered

Table 6. Changes in species composition and structure in Tk8 stand (see Table 1) in typical linden-hornbeam forest (*Tilio-Carpinetum calamagrostietosum*)

DBH classes [cm]	*Carpinus betulus*		*Picea abies*		*Quercus robur*		*Tilia cordata*		*Alnus glutinosa*		*Betula pendula*		*Sorbus aucuparia*		*Acer platanoides*		*Fraxinus excelsior*		*Ulmus glabra*	
	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012
	Tree number per hectare																			
0–3	24	1912	-	-	-	-	-	388	4	8	4	104	4	12	-	4	-	4	-	4
3.1–7	28	36	-	-	-	-	28	8	-	4	-	4	-	-	-	-	-	-	-	-
Σ	52	1948	-	-	-	-	28	396	4	12	4	108	4	12	-	4	-	4	-	4
7.1–11	8	8	12	4	-	-	20	8	-	-	-	-	-	-	-	-	-	-	-	-
11.1–15	12	20	12	12	-	-	16	24	-	-	-	-	-	-	-	-	-	-	-	-
15.1–19	4	8	12	4	-	-	4	12	-	-	4	4	-	-	-	-	-	-	-	-
19.1–23	4	4	12	8	-	-	12	4	4	-	-	-	-	-	-	-	-	-	-	-
Σ	28	40	48	28	-	-	52	48	4	-	4	4	-	-	-	-	-	-	-	-
23.1–27	4	12	16	4	-	-	4	8	-	4	4	-	-	-	-	-	-	-	-	-
27.1–31	-	4	8	4	-	-	4	12	8	4	-	-	-	-	-	-	-	-	-	-
31.1–35	4	-	12	20	-	-	-	-	4	4	8	8	-	-	4	-	-	-	-	-
35.1–39	-	4	4	12	-	-	-	-	4	8	-	-	-	-	-	-	-	-	-	-
39.1–43	-	-	28	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-
Σ	8	20	68	40	-	-	8	20	16	24	12	8	-	-	4	-	-	-	-	-
43.1–47	-	4	12	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-
47.1–51	4	4	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
51.1–55	-	-	4	8	-	-	-	-	4	8	-	-	-	-	-	-	-	-	-	-
55.1–59	-	-	12	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
59.1–63	-	-	4	-	4	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
67.1–71	4	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
71.1–75	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
75.1–79	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
91.1–95	-	-	-	-	4	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
95.1–99	-	-	-	-	8	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
99.1–103	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
111.1–115	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
115.1–119	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Σ	8	8	60	16	24	24	-	-	4	8	-	-	4	-	-	-	-	-	-	-

Table 7. Changes in species composition and structure in S1 stand (see Table 1) in spruce-bog moss association (*Sphagno girgensohnii-Piceetum*)

DBH classes [cm]	*Picea abies*			*Pinus sylvestris*			*Acer platanoides*			*Carpinus betulus*			*Sorbus aucuparia*			*Betula pendula*			*Fraxinus excelsior*			*Quercus robur*			Other		
	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012	1975	1986	2012
	Tree number per hectare																										
0–3	600	1332	552	-	-	4	4	4	-	52	48	104	28	8	8	288	16	4	24	16	-	60	12	4	-	-	4
3.1–7	24	88	112	-	-	36	4	-	-	8	16	-	-	-	-	4	24	-	8	8	-	4	8	-	12	-	-
Σ	624	1420	664	-	-	40	8	4	-	60	64	104	28	8	8	292	40	4	32	24	-	64	20	4	412	-	4
7.1–11	36	24	4	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	4	4	-	-	-	-	8	-	-
11.1–15	40	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15.1–19	48	40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	4	-
19.1–23	72	40	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Σ	196	124	4	4	-	-	-	-	-	-	4	-	-	-	-	-	-	-	4	8	-	-	-	-	48	4	-
23.1–27	92	36	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27.1–31	76	64	-	12	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31.1–35	88	36	-	44	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
35.1–39	20	80	-	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
39.1–43	20	36	-	8	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Σ	296	252	-	88	60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
43.1–47	4	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
47.1–51	4	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
51.1–55	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
55.1–59	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
59.1–63	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Σ	12	36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Undergrowth $h < 130$ cm	6392	2668	-	-	-	-	20	8	-	24	20	-	92	72	-	116	16	-	44	16	-	132	96	-	4	-	-

Shrubs	Shrubs per hectare		
	1975	1986	2012
Populus tremula	-	8	-
Corylus avellana	644	4140	-
Frangula alnus	40	12	-
Ribes rubrum	16	-	-
Lonicera xylosteum	4	8	-
Daphne mezereum	-	-	4
Ribes alpinum	-	40	-

Other: *Alnus glutinosa, Salix caprea, Tilia cordata, Ulmus glabra*

* as in Table 1

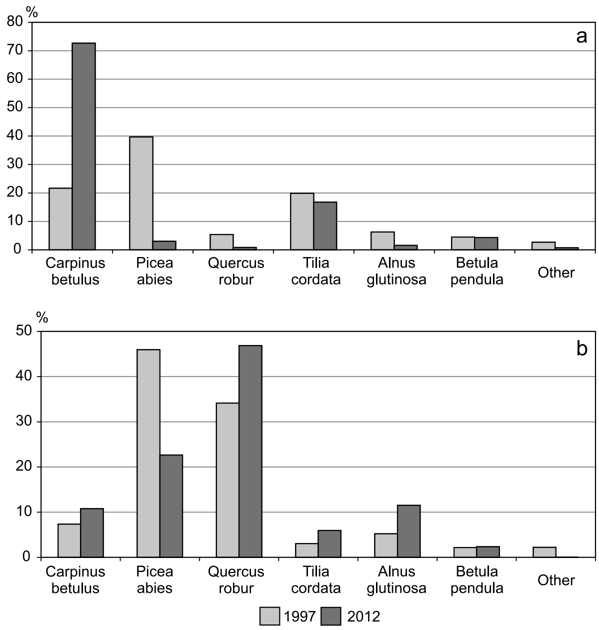

Figure 9. Tree species share (according to: a – density, b – basal area) in 1998–2011 based on permanent S1 research plot (see Table 1) in spruce-bog moss association (*Sphagno girgensohnii-Piceetum*). Other tree species: *Acer platanoides, Tilia cordata, Alnus glutinosa, Fraxinus excelsior, Salix caprea, Ulmus glabra, Sorbus aucuparia*

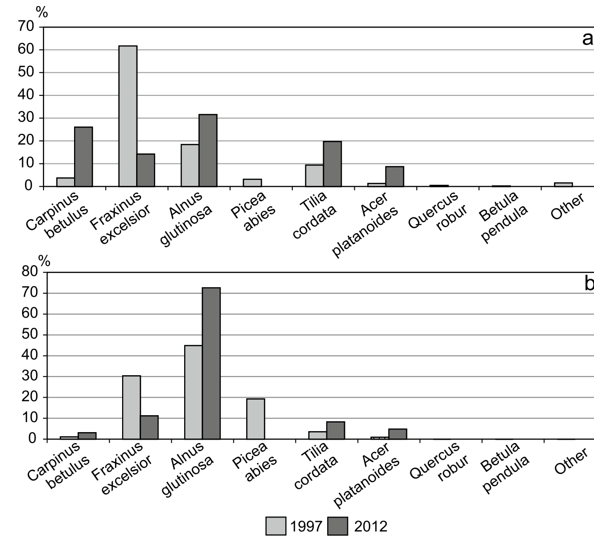

Figure 10. Tree species share (according to: a – density, b – basal area) in 1998–2012 based on permanent research plot F13 (see Table 1) in alder-ash forest *(Fraxino-Alnetum)*. Other tree species: *Quercus robur, Betula pendula*, *Sorbus aucuparia*, *Ulmus glabra*

to be a very important component of the community, but withdrew entirely from the stand species composition in some of the study plots (about 20%). There was no natural regeneration of ash; therefore, its future raises concerns. In a 15-year investigation period, there was observed most significant ash dieback (70% of trees died).

The participation of ash was radically reduced in terms of both tree numbers and stand basal area (Fig. 10). The most significant changes were noted in the density of ash, as its share was reduced from 60% to a little more than 10% (Fig. 10). It should be emphasised that all the spruce trees died out (Table 8), though not long ago, the participation of spruce in the stand basal area was 20%. Significant expansion of hornbeam was noted in this forest community, in particular in the understory (Table 8). Hornbeam participation, calculated based on tree numbers, increased by several times, from a few percent to 20% (Fig. 10), although its share in the stand basal area increased only insignificantly. This was because in the year 2012, there dominated trees of <7 cm DBH (Table 8). Black alder was observed to increase its participation notably in the stand basal area. This participation amounted to as much as 70% in 2012 and was similar to that of ash in the year 1998 (Fig. 10). Thus black alder replaced ash as a dominant component of the tree stand.

Similarity coefficient of species participation in the surveyed forest communities

A high average similarity (the value above 0.8) of stand species composition, determined based on tree numbers, was found in the mixed spruce-reed grass community *Calamagrostio arundinaceae-Piceetum* (CP) only for the years 1975 and 1986. In all the remaining cases, the similarity coefficient attained average values (0.5–0.79) (Fig. 11). Some of the surveyed forest communities showed a steady decrease in similarity in the subsequent study periods. This was evident, in particular, in the mixed spruce reed grass forest community CP, and in the hornbeam-bastard balm forest MC (Fig. 11). This testifies to a considerable rate of changes in species composition in the above forest communities. On the other hand, a considerable similarity of species composition was observed in all of the study periods in both forms of oak–hornbeam forests: *Tilio-Carpinetum typicum (*TCt) and *Tilio-Carpinetum calamagrostietosum* (Tk) as well as sub-boreal spruce forest on bog moss S. In only one period, similarity in alder-ash forest *(Fraxino-Alnetum)* was 0.6. w confirms significant changes in tree species composition defined based on the number of trees (Fig. 11). The lowest average similarity of stand species composition between the onset and end of the study (S4) was found in the hornbeam–bastard balm forest (MC). The similarity value was low (less than 0.5), which means that stand species composition underwent a significant change. The

Table 8. Changes in species composition and structure in F13 stand (see Table 1) in alder-ash forest *(Fraxino-Alnetum)*

DBH classes [cm]	*Carpinus betulus*		*Fraxinus excelsior*		*Alnus glutinosa*		*Picea abies y*		*Tilia cordata*		*Sorbus aucuparia*		*Ulmus glabra*		*Acer platanoides*		*Quercus robur*		*Betula pendula*	
	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012	1997	2012
	Tree number per hectare																			
0–3	36	88	776	40	152	4	-	-	88	40	16	-	8	-	16	32	8	-	4	-
3.1–7	-	16	12	8	36	40	-	-	20	20	-	-	-	-	-	-	-	-	-	-
Σ	36	104	788	48	188	44	-	-	108	60	16	-	8	-	16	32	8	-	4	-
7.1–11	-	8	8	-	8	20	-	-	4	-	-	-	-	-	-	-	-	-	-	-
11.1–15	4	-	12	-	4	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-
15.1–19	16	-	20	4	-	4	-	-	4	4	-	-	-	-	-	-	-	-	-	-
19.1–23	-	4	32	4	-	4	-	-	-	12	-	-	-	-	-	-	-	-	-	-
Σ	20	12	72	8	12	28	-	-	12	16	-	-	-	-	-	-	-	-	-	-
23.1–27	-	16	20	4	-	4	-	-	12	4	-	-	-	-	-	-	-	-	-	-
27.1–31	-	-	12	-	-	-	4	-	8	-	-	-	-	-	-	-	-	-	-	-
31.1–35	-	-	4	-	4	-	-	-	-	8	-	-	-	-	4	-	-	-	-	-
35.1–39	-	-	12	-	12	-	4	-	-	12	-	-	-	-	-	4	-	-	-	-
39.1–43	-	-	4	4	8	16	16	-	-	-	-	-	-	-	-	4	-	-	-	-
Σ	-	16	52	8	24	20	24	-	20	24	-	-	-	-	4	8	-	-	-	-
43.1–47	-	-	-	4	-	4	8	-	-	-	-	-	-	-	-	4	-	-	-	-
47.1–51	-	-	-	-	12	-	12	-	-	-	-	-	-	-	-	-	-	-	-	-
51.1–55	-	-	4	-	8	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
55.1–59	-	-	-	-	8	20	4	-	-	-	-	-	-	-	-	-	-	-	-	-
59.1–63	-	-	-	-	12	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
63.1–67	-	-	4	-	4	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-
67.1–71	-	-	-	-	4	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
71.1–75	-	-	4	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
75.1–79	-	-	4	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
79.1–83	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
87.1–91	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Σ	-	-	16	8	52	68	24	-	-	-	-	-	-	-	-	4	-	-	-	-

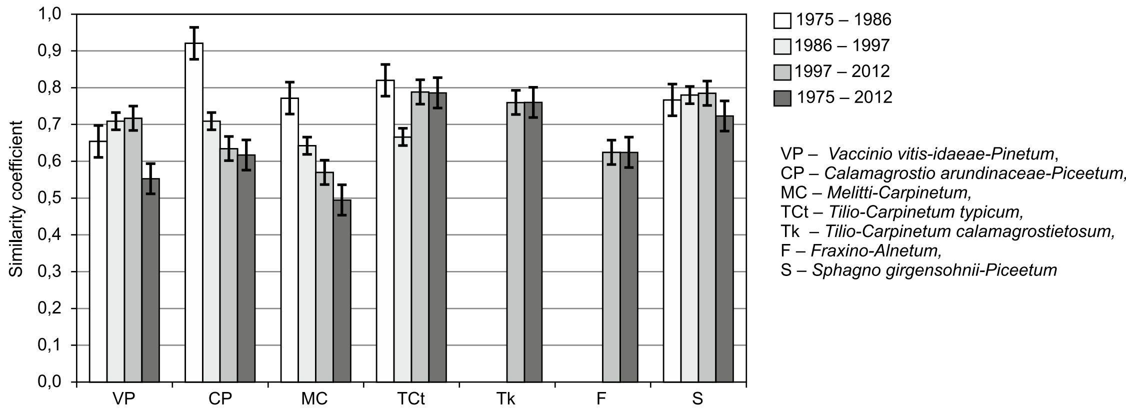

Figure 11. Similarities in tree species composition determined based on tree density in investigated forest associations during subsequent observation periods in 1975–2012

forest communities surveyed over the whole study period may be aligned along the axis of increasing similarity in the following way: hornbeam–bastard balm forest (MC), fresh pine-whortleberry forest (V), fresh mixed spruce reed grass forest (CP), alder-ash forest (F), sub-boreal spruce forest on bog moss (S), reedgrass oak–hornbeam forest (Tk) and typical linden–hornbeam forest (TCt) (Fig. 11). The smallest changes in the stand species composition were observed in the oak hornbeam forests, while the largest in the mixed hornbeam–bastard balm forests (MC).

4. Discussion

Significant changes in the stand species composition were observed over the study period (15–40 years) in all the forest communities surveyed. The abovementioned period of the study is but a little a fragment of the forest development history, and this makes it difficult to provide a reliable forecast. The present work basically corroborates the regularities of multiannual changes in species composition of natural stands in the BF, reported by such authors as Bernadzki et al. (1998); Brzeziecki (2008); Brzeziecki et al. (2010); Brzeziecki et al. (2012); Drozdowski et al. (2012) and Drozdowski (2014), and additionally provides new information on the issue concerning a variety of forest sites including some relatively rare in the Polish part of the BF, such as sub-boreal spruce forest on bog moss. The study results presented may be regarded as an addition to unique observations of natural forest stand development, systematically conducted over almost 80 years by successive generations of researchers from the Chair of Silviculture (KHL) at the Warsaw University of Life Sciences. The changes occurring in stands affect entire forest phytocoenoses. The stand, ecologically speaking, shapes the remaining forest strata (Obmiński 1977). The stand is a key component of forest community. By creating specific microclimate, it determines the habitat for organisms, which require definite ecological conditions to live. Moreover, the stand largely dominates the soil development processes, not only by adding litter, which influences the conditions of the soil upper layers, but also through its own living activities. The stand species composition, canopy closure, age, structure and many other attributes control ecological conditions of the forest interior. It seems that the high dynamics of stand species composition resulted from hornbeam expansion with coincident decrease in the spruce participation. Such scenario of stand development was observed in all the forest communities analysed in this study, except for mixed coniferous–deciduous forest and sub-boreal spruce forest on bog moss. In the two above communities, spruce was observed to dominate the stand, while hornbeam appeared in the lower tiers as an admixture only. Hornbeam is a key element of the oak–linden–hornbeam forests giving these multitier communities their specific appearance. The closed canopy of hornbeam in full foliage lets only minimum sunlight to the forest floor. Hornbeam litter, rich in mineral elements, decomposes more rapidly than that of the remaining Poland's native tree species, and its structure enables the appearance of numerous geophyte species. The presence of hornbeam in the oak–linden–hornbeam forests plays a major role in maintaining appropriate structure, species composition, environmental conditions and, above all, seasonal rhythms of the community (Faliński and Pawlaczyk 1993). The expansion of hornbeam may result, even on oligotrophic sites, in an increased homogeneity of a variety of forest communities, which may become more or less similar to an oak-hornbeam forest (Sokołowski 1991; Paluch 2001). Hornbeam is a species of competitive life strategy, which consist in monopolisation of the access to environmental resources, that is, in preventing other species from regeneration, growing and developing under the hornbeam canopy. The species ensures its large life space, thanks to the development of a wide and low-framed crown, which strongly shadows the forest floor, especially on oligotrophic sites (Brzeziecki 2000). An umbrella-shaped crown enhances the effect of hornbeams on microclimate in the forest interior. The hornbeam expansion may be regarded as one of the reasons for changes in the species composition of forest communities. Evidence of changes was so compelling that it justified the necessity for updating earlier phytosociological and habitat diagnoses (Sokołowski 1991, 2004; Paluch 2002). The works cited above reported changes in the vegetation of foremost mesotrophic and thermophilic plant communities. Based on this study, it can be demonstrated that changes of analogous character were noted in some eutrophic and swamp communities. Similar results were obtained by Czerepko and Sokołowski (2006) and Czerepko (2011) on permanent study plots established in northeastern Poland.

Based on the study carried out on the permanent plot established in the Białowieża National Park (1959–1998), Paluch (2001, 2003) indicated that floristic changes in wet habitats were considerably less pronounced. The author suggested that specific situation of wet habitats results from the fact that these sites developed on semihydrogenic and/ or hydrogenic soils, where water plays a major soil-forming role. Hence, the communities encountered in these sites were of relatively stable and close to climax character. A high groundwater level assured the survival, but only of a limited group of tree species best adapted to such conditions. Moreover, swamp habitats usually develop on fertile soils with high-buffering capacity (Brzeziecki and Żybura 1998; Bernadzki et al. 1998; Paluch 2003).

The withdrawal of ash from the stand species composition is not a phenomenon restricted to the BF. Massive dieback of ash trees, and generally ash in forest stands, was first noted on a large scale in Poland and in throughout Europe at the beginning of 20th century (Gil et al. 2011), and this phenomenon has continued up to now. The studies performed indicate that ash disappeared from all the stand strata under natural conditions as well. No ash regeneration can be observed any longer. In several cases, ash was found to disappear entirely from the study plots over just a 15-year-long period. It is not known when ash will start to regenerate, at the moment, there is no indication whatsoever as to when it may occur. Surely, the present health status of ash raises concerns since the condition of the still living individuals is bad.

The expansion of hornbeam is not yet over (Bernadzki et al. 1998; Brzeziecki (2008); Brzeziecki et al. (2012). Brzeziecki (2008), when analysing the multiannual study material collected from the permanent study plots in the Białowieża National Park, considered what should happen for hornbeam to withdraw. Paluch (2001) claimed that trends to establish hornbeam stands in a variety of habitats would be more pronounced, and this forecast works after 10-year period. Depletion of vital, productive tree species, such as pine, spruce, oak and ash under close to natural conditions, and simultaneous increase in the participation of species having a substantially lower significance for productivity purposes, are of great importance for long-term sylvicultural planning. Taking into account the trends of changes recognised and the acceleration of these changes in the BF, human intervention would be advisable in order to maintain valuable populations of vulnerable species and stimulate their natural regeneration. Setting aside more and more areas and excluding them from any human intervention does not and will not support the achievement of the abovementioned goals. Within this context, an important general question arises: how close our silvicultural activities may get to the natural ecological processes without failing to achieve economic and protective goals, evaluated from the human viewpoint (wind protection, soil protection, landscape protection and the like).

5. Statements and conclusions

Over a period of the last nearly four decades, there occurred an increase in the participation of common hornbeam in the stand species composition in many forest communities of the BF. Hornbeam was found to expand into a variety of habitats including oligotrophic, moderately fertile and wet sites.

Under natural conditions, hornbeam dominated in the regeneration in the majority of forest communities surveyed, except for mixed coniferous–deciduous forest and sub-boreal spruce forest on bog moss, though in the latter study period, it marked its presence also in the two abovementioned communities.

Spruce was found to withdraw to oligotrophic forest communities. Its numbers were drmatically reduced in stands of mixed coniferous-deciduous forests and oak–linden–hornbeam forests.

The participation of highly light demanding species such as pine, oak and birch in stand composition was markedly reduced in the stands of the BF, including also the regeneration layer. Pine is not regenerating effectively.

Over a short period of the last 15 years, there occurred a rapid and dramatic reduction of ash participation under optimal condition of ash-alder forest.

The rate of changes in the stand species composition accelerated over the last 10–15 years.

The trends towards changing the stand species composition and acceleration of these changes suggest that human intervention is needed in order to preserve valuable populations of vulnerable species in the BF with the aim to support natural regeneration of the withdrawing species.

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