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ORIGINAL ARTICLE

Changes in the structure of tree stands on bog habitats in the Białowieża forest

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Abstract

The analyses of 4 permanent study plots located in the Białowieża forest (NE Poland, at 52º43´ N, 23º50´ E) were carried out 4 times, first time in 1973 or 1974 and next in 1985, 1998, 2008. The paper presents the results of a long–term study on natural forest dynamics in two forest communities: raised-bog pine forest of the association *Ledo-Sphagnetum magellanici* Sukopp 1959 em. Neuhäusl 1969 and transitional bogs represented by the boreal spruce forest *Sphagno girgensohnii-Piceetum* Polak. 1962. On each measurement date the DBH of all trees were recognized. At the same time, stems of shrub species as well as tree species with the height lower than 1.3 m were counted within the experimental areas.

During the study period the structure of stands changed significantly. The major change observed on raised bog sites was an increase in numbers of *Betula spp., Picea abies* (L.) H. Karst. and *Quercus robur* L. After 34th-year of observations the boreal spruce forest stand partly passed the terminal phase and regenerated. New species occurred in the stands, especially in their lower layer, are typical for oak-lime-hornbeam forest, such as e.g. *Carpinus betulus* L.*, Q. robur, Acer platanoides* L. Rapid development of *Corylus avellana* L. was also observed. During last decades, the decrease in the number of *Pinus sylvestris* L. trees has been observed.

The results of analyses of stand data in four research periods show that the wetland habitat of the Białowieża forest has been a subject to the processes of succession conditioned by environmental changes such as desiccation through lowering of the water table as well as climatic changes entailing *inter alia* an increase of the air temperature and a decrease of precipitation.

Key words

bog forests, permanent plots, plant succession, stand structure

Introduction

The results of several studies carried out in permanently observed natural forest stands show that these forests are hardly ever compositionally stable (Bernadzki *et al.* 1998, Andrzejczyk and Brzeziecki 1995, Sokołowski 1999, Nygard *et al.* 1999). The results obtained by several authors led to conclusion that tree species with a dominant position in stands did not regenerate but were replaced by other species (Bernadzki *et al.* 1998, Foster and Tilman 2000). This applies also for the Białowieża forest. Kowalski (1993)

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and Bernadzki *et al.* (1998) found significant changes in tree species composition on permanently sampled plots established in 1936 in the Białowieża National Park. Generally, most essential feature observed was an increase of broadleaved tree species (*Tilia cordata* Mill.*, Carpinus betulus* L.*, Fraxinus excelsior* L.). Published later results of continuous studies on same plots confirmed these findings. The main habitats where these studies were conducted concerned fresh and wet sites from oligothrophic and euthrophic gradients (Bernadzki *et al.* 1998).

There has been considerable lack of studies on dynamics of forest stands on wetland sites which are relatively common in the Białowieża forest. The stands occurring on Białowieża bog sites were investigated by Sokołowski (1991, 1998, 1999). The results presented in this paper concern continuous studies conducted on the same stands with the aim to examine directions and nature of changes ongoing in tree stands on bog sites.

Methods

Investigated types of forest wetland

Raised bogs represented the most nutrient-poor habitat of all studied. They support two types of vegetation in the Białowieża forest (NE Poland, at 52º43′ N, 23º50′ E), i.e. raised-bog mossy vegetation of the association *Ledo-Sphagnetum magellanici* Sukopp 1959 em. Neuhäusl 1969, as well as the marshy pine forest *Vaccinio uliginosi-Pinetum* Kleist 1929. *Ledo-Spagnetum magellanici* is a raised-bog type of the class *Oxycocco--Sphagnetea* Br.-Bl. & R. Tx. 1943 in which tree stands of *Pinus sylvestris* reach the height of 10–12 m. The forest floor has a hummock-hollow structure and the understorey is developed very weakly, mainly consisting of *Sphagnum* mosses (especially *S. magellanicum* Brid. and *S. fallax* H. Linggr.). *Vaccinio uliginosi-Pinetum* differs from *Ledo-Spagnetum magellanici* in presence of the odd downy birch *Betula pubescens* Ehrh. or spruce *Picea abies* (L.) H. Karst, next to dominant *Pinus sylvestris.* The shrub layer is better developed, it has bigger cones and greater species composition. In the herb layer, there prevail coniferous-forest species, typical of the class *Vaccinio-Piceetea* Br.-Bl. 1939 (e.g. like *Pleurozium schreberi* Wild. Ex. Brid.*, Vaccinium myrtillus* L. and *V. uliginosum* L.) as opposed to raised-bog species of the class *Oxycocco-Sphagnetea* Br.-Bl. & R. Tx. 1943.

Transitional peatlands support the boreal spruce forest *Sphagno girgensohnii-Piceetum* Polak. 1962 representative of the class *Vaccinio-Piceetea*. A typical boreal-zone forest is characteristic for pure spruce stands, occasionally with the admixture of downy birch, as well as dwarf-shrub and herb layers. In contrast, the bryophyte layer is luxuriant there, and it comprises not only bog-mosses *Sphagnum girgensohnii* Russow*, S. palustre* L. and *S. fallax,* but also *P. schreberi*, *Hylocomnium splendens* Hedw. and *Bazzania trilobata* L. (Gray).

The first experimental plot was in the Michnówka nature reserve with *Ledo-Spagnetum magellanici* association. The reserve was established in 1979 and its area is 86 ha. The mainprotection target are bog forests abundant in the reserve (Sokołowski 1998).

The 3 experimental plots were located in the Wysokie Bagno nature reserve with *Sphagno girgensohnii-Piceetum* association. The reserve have existed since 1979 and its area is 79 ha (Sokołowski 1999).

The syntaxonomic names of vegetation units used in the paper are in accordance with those given by Matuszkiewicz (2001).

First measurements of the stand structure in the study area in the Michnówka nature reserve were carried out in 1973 and subsequently in the years: 1985, 1998 (Sokołowski 1991, 1998) and 2008. The size of experimental plot located in the nature reserve Michnówka was 50 × 150 m (Fig. 1).

The Wysokie Bagno reserve includes 3 experimental plots of the size 50 x 50 m (Fig. 2) which were initially surveyed in 1974 and the observations were repeated in the years 1985, 1998 (Sokołowski 1999) and 2008.

On all study areas there were applied the same methods of measurements. DBH of all trees was measured with 1 mm accuracy. The numbers of individual trees lower than 1.3 m as well as shrubs were assessed.

Results

Changes of stands in raised-bog pine forest *Ledo-Sphagnetum magellanici*

The results indicate that in raised-bog pine forest the stands have significantly changed their structure during last 35 (the Michnówka reserve) and 34 years (the

Fig. 1. Localization of sample plot in Michnówka reserve

Wysokie Bagno). The increase of numbers of *Betula spp., P. abies, Q. robur* with DBH, representing higher diameter classes was observed with time (Tab. 1). The same tendency was shown by the numbers of trees observed in the undergrowth which indicated the process of development of the lower layer of birch, oak and spruce trees. During the observations in 2008, individual specimen of shrubs *Corylus avellana* L. and *Frangula alnus* Mill. were noted. In the case of *Pinus sylvestris* L. more trees go through to the next diameter classes, but we could not observe supporting to young trees classes.

The Table 2 summarising data on stand structure changes shows a dramatic decrease of pine numbers:

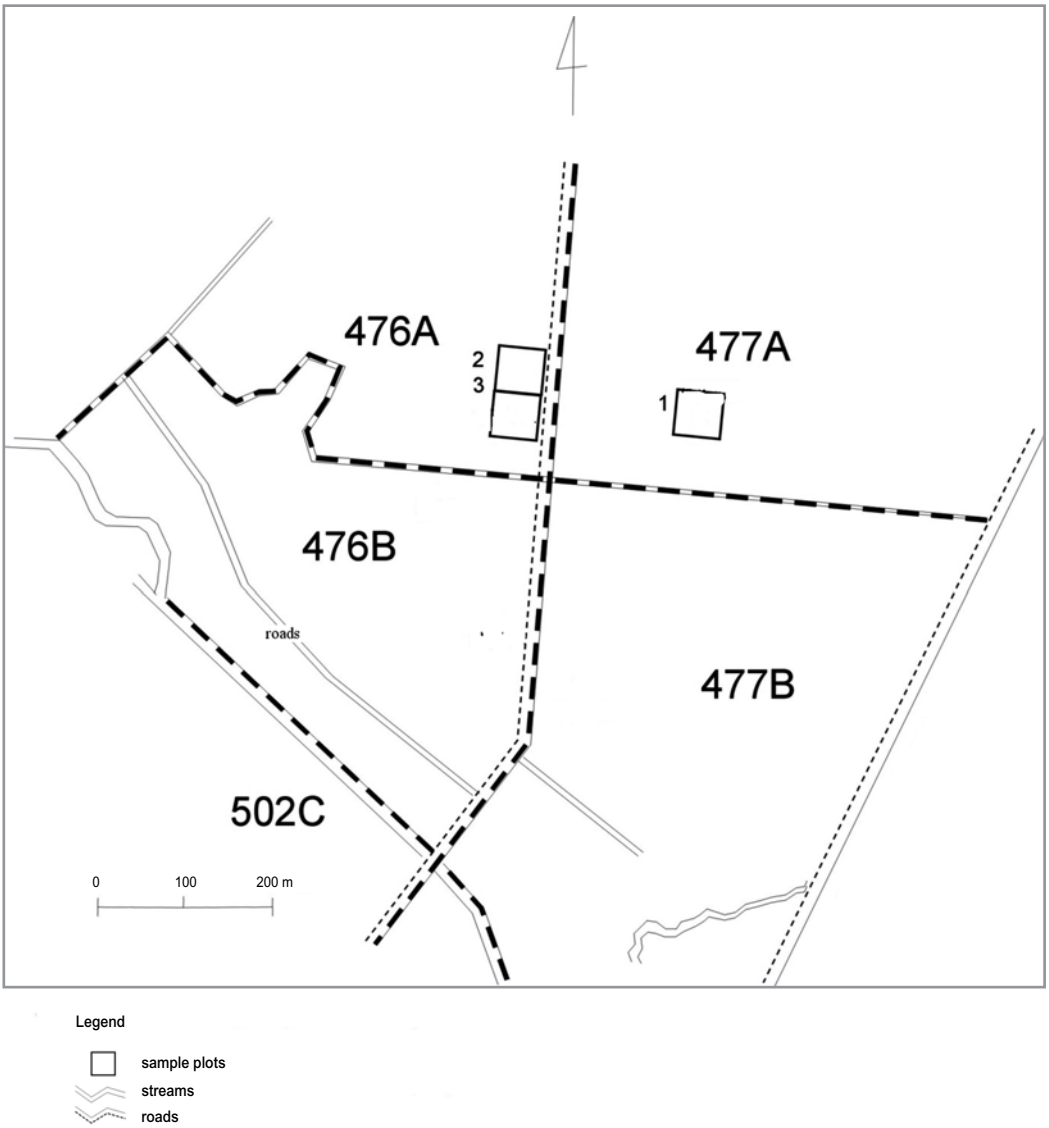

Fig. 2. Localization of sample plots in Wysokie Bagno reserve

in 1985 there were only 41% of pine trees recorded in 1973, whereas in 1998 and 2008 there were 28% and 24% trees respectively. Different results were obtained for the rest of studied tree species. The fastest increase of the number of trees as well as the share of basal area were observed for birches. In 1973 only 23 birch trees were recorded, however in 2008 there were 591 specimen per 1 ha. This indicates that in the first study year, the share of *Betula spp.* basal area was 0.07% and in the last study year it already amounted to 10%. The spruce also represents the species which during the whole study period systematically increased its share in terms of the number of trees and their basal area. The oak started occurring in the study stands from the year 1998, however the total number of oak trees decreased by 24% in the year 2008.

Changes of stands in boreal spruce forest *Sphagno girgensohnii-Piceetum*

On plot 1 in the Wysokie Bagno reserve in the period of 2003–2004, there was observed a collapse of mature spruce stands and in the year 2008 there was the beginning of regeneration processes on then open areas (Tab. 3). Rebuilding of tree species composition was

Tab. 1. Changes of stand species composition in *Ledo-Sphagnetum magellanici* association in the Wysokie Bagno nature reserve. Sampling area: 0.75 ha

Middle of diameter class [cm]	Species with DBH ≥ 130 cm															
	B. pendula and *B. pubescens*				*Picea abies*				*Pinus sylvestris*				*Quercus robur*			
	1973	1985	1998	2008	1973	1985	1998	2008	1973	1985	1998	2008	1973	1985	1998	2008
1.5	15	105	152	231	10	33	68	93	404	27	2	·	·	·	27	20
5	3	24	144	111	·	8	41	66	76	30	1	1	·	·	·	1
9	·	3	48	88	·	·	13	32	53	20	9	2	·	·	·	·
13	·	1	16	24	·	·	1	11	108	38	23	13	·	·	·	·
17	·	·	5	17	·	·	1	·	154	69	24	18	·	·	·	·
21	·	·	·	2	·	·	·	2	134	116	71	29	·	·	·	·
25	·	·	·	·	·	·	·	·	36	70	71	49	·	·	·	·
29	·	·	·	·	·	·	·	·	4	30	50	62	·	·	·	·
33	·	·	·	·	·	·	·	·	1	2	16	46	·	·	·	·
37	·	·	·	·	·	·	·	·	·	1	2	18	·	·	·	·
41	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·
undergrowth number with height < 130 cm	49	209	167	350	33	113	83	43	177	14	17	21	3	83	120	149

shrubs number in year	2008
Corylus avellana	1
Frangula alnus	1

Tab. 2. Changes of the total number of tree species and share of their basal area in stands of *Ledo-Sphagnetum magellanici* association. Sampling area: 0.75 ha

Tree species	Number of trees with height ≥ 1.3 per 1 ha				% of basal area			
	1973	1985	1998	2008	1973	1985	1998	2008
Pinus sylvestris	1213	504	338	298	99.92	99.01	91.12	86.59
B. pendula and *B. pubescens*	23	166	456	591	0.07	0.81	7.22	9.88
Picea abies	13	51	155	255	0.01	0.18	1.62	3.50
Quercus robur	0	0	34	26	0.00	0.00	0.04	0.03

manifested by new tree species, which started occurring in 1998. This was confirmed in 2008 when higher numbers of trees in young undergrowth were observed. The spruce started to regenerate from 1998. After the death of old stands in 2004, the regeneration process was evidently indicated in 2008. Alder and birch trees used to be an indicative species in old stands now they occur in young/thin age classes and its number have been increasing since 1998. The pine mainly occurred between the years 1974–98, but in 2008 only 6 trees remained in the thickest DBH classes. Several new tree species started occurring in 1998, and their

Tab. 3. Changes of stand species composition in *Sphagno girgensohnii-Piceetum* association in the Wysokie Bagno nature reserve on plot 1. Sampling area: 0.25ha

Middle of diameter class [cm]	Species with DBH ≥ 130 cm															
	1974	1985	1998	2008	1974	1985	1998	2008	1974	1985	1998	2008	1974	1985	1998	2008
	Alnus glutinosa				*B. pendula* and *B. pubescens*				*Picea abies*				*Pinus sylvestris*			
1.5	·	9	135	189	·	·	·	73	24	21	148	1511	·	·	·	·
5	3	·	32	68	·	·	·	1	18	5	18	279	·	·	·	·
9	2	1	·	21	3	·	·	·	23	2	1	10	·	·	·	·
13	3	2	·	3	9	1	·	·	39	17	8	3	2	·	·	·
17	1	2	·	·	8	·	·	·	38	17	9	5	1	·	·	·
21	·	·	1	·	6	1	1	·	27	18	10	3	1	2	·	·
25	3	1	1	·	1	·	1	1	26	28	16	4	7	2	1	·
29	·	2	2	1	·	·	·	·	11	15	18	5	7	4	1	·
33	·	·	1	2	·	·	·	·	10	16	7	4	7	4	·	·
37	·	·	·	·	1	·	·	·	2	8	12	2	6	2	1	·
41	·	·	·	·	·	·	·	·	·	3	9	5	3	4	5	5
45	·	·	·	·	·	·	·	·	·	1	4	2	1	2	·	·
49	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
53	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1
undergrowth number with height < 130 cm	4	142	26	9	·	482	332	42	309	145	1635	1015	·	·	1	·
	Fraxinus excelsior				*Populus tremula*				*Carpinus betulus*				*Tilia cordata*			
1.5	·	·	4	6	·	·	5	·	·	·	8	14	·	·	·	·
5	·	·	·	·	·	·	·	·	·	·	·	5	·	·	·	·
undergrowth number with height < 130 cm	·	3	5	2	·	4	19	·	·	6	18	7	·	·	·	1
	Sorbus aucuparia				*Quercus robur*				*Acer platanoides*				*Acer pseudoplatanus*			
1.5	·	·	23	86	·	·	2	24	·	·	·	5	·	·	·	2
5	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·
undergrowth number with height < 130 cm	12	194	207	44	8	62	105	29	1	·	4	1	·	·	·	1

shrubs number in years	1974	1985	1998	2008
Corylus avellana	3	45	168	671
Daphne mezereum	·	·	·	1
Euonymus verrucosus	·	·	2	·
Frangula alnus	69	236	391	303
Ribes nigrum	·	·	·	3
Ribes spicatum	·	·	7	1

Tab. 4. Changes of stand species composition in *Sphagno girgensohnii-Piceetum* association in the Wysokie Bagno nature reserve on plot 2. Sampling area: 0.25 ha

Middle of diameter class [cm]	Species with DBH ≥ 130 cm															
	1974	1985	1998	2008	1974	1985	1998	2008	1974	1985	1998	2008	1974	1985	1998	2008
	Alnus glutinosa				*B. pendula* and *B. pubescens*				*Picea abies*				*Pinus sylvestris*			
1.5	4	44	166	36	·	·	·	4	66	85	359	264	·	·	·	·
5	3	·	35	13	·	·	·	·	46	41	55	50	·	·	·	·
9	8	2	1	·	2	·	·	·	31	18	21	15	·	·	·	·
13	5	4	1	1	13	1	·	·	38	25	19	11	1	·	·	·
17	2	·	2	2	16	9	2	·	38	30	11	9	6	2	·	1
21	2	2	1	1	10	6	1	·	25	30	19	8	9	7	4	1
25	·	1	1	2	8	9	3	1	17	15	28	12	8	2	2	3
29	·	2	1	1	3	4	1	1	4	6	21	16	7	9	3	1
33	·	·	1	·	2	1	1	1	·	4	6	14	5	3	5	4
37	·	·	·	2	·	·	1	1	·	·	6	6	3	4	2	5
41	·	·	·	·	·	·	·	·	·	·	·	1	1	2	3	3
45	·	·	·	·	·	·	·	·	·	·	·	·	2	1	·	2
49	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·
undergrowth number with height < 130 cm	28	119	40	21	·	260	147	23	384	1468	638	1259	·	·	·	·
	Sorbus aucuparia				*Quercus robur*				*Acer platanoides*				*Fraxinus excelsior*			
1.5	1	7	63	59	·	·	25	22	·	1	2	7	·	·	·	5
5	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
undergrowth number with height < 130 cm	8	57	74	80	14	163	162	120	·	5	9	·	1	5	11	5
	Carpinus betulus				*U. campestris and U. glabra*				*Acer pseudoplatanus*				*Quercus rubra*			
1.5	·	·	5	16	·	·	·	1	·	·	·	·	·	·	·	·
5	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·
undergrowth number with height < 130 cm	·	10	3	17	·	·	1	1	·	·	·	6	·	·	·	2

shrubs number in years	1974	1985	1998	2008
Corylus avellana	8	32	103	232
Frangula alnus	64	296	296	148
Ribes spicatum	·	·	5	1
Ribes nigrum	·	·	3	14
Salix cinerea	·	10	·	·
Viburnum opulus	·	1	·	·

Tab. 5. Changes of stand species composition in *Sphagno girgensohnii-Piceetum* association in the Wysokie Bagno nature reserve on plot 3. Sampling area: 0.25 ha

Middle of diameter class [cm]	Species with DBH ≥ 130cm															
	1974	1985	1998	2008	1974	1985	1998	2008	1974	1985	1998	2008	1974	1985	1998	2008
	Alnus glutinosa				*B. pendula* and *B. pubescens*				*Picea abies*				*Pinus sylvestris*			
1.5	1	29	377	80	·	·	132	84	4	62	539	424	·	·	·	·
5	·	·	137	92	·	·	·	3	8	2	91	188	·	·	·	·
9	1	·	17	25	·	·	·	·	9	4	4	39	·	·	·	·
13	2	·	·	7	3	·	·	·	27	13	8	12	·	·	·	·
17	6	6	1	6	3	1	·	·	29	20	4	4	·	·	·	·
21	7	5	·	·	2	3	·	·	27	18	13	5	·	·	·	·
25	7	8	5	1	1	1	1	·	25	22	13	9	1	2	·	·
29	2	4	4	5	·	1	2	·	19	14	13	9	1	1	1	·
33	4	3	6	7	·	1	1	·	8	15	7	12	3	1	1	2
37	5	4	1	5	·	·	·	·	5	4	9	6	6	3	1	·
41	·	1	3	·	·	·	1	·	3	1	6	4	4	3	3	2
45	·	1	1	·	·	·	·	·	·	3	1	5	·	·	·	1
49	·	·	·	·	·	·	·	·	·	·	1	2	·	·	·	·
53	·	·	·	1	·	·	·	·	·	·	·	2	1	1	1	·
57	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1
undergrowth number with height < 130 cm	14	151	38	56	8	291	482	70	304	1538	727	731	·	·	·	·
	Sorbus aucuparia				*Quercus robur*				*Acer platanoides*				*Acer pseudoplatanus*			
1.5	2	30	74	136	·	·	66	37	·	·	2	4	·	·	·	1
5	·	·	·	6	·	·	·	7	·	·	·	1	·	·	·	·
33	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·
undergrowth number with height < 130 cm	41	199	98	147	8	139	56	59	·	2	8	6	·	·	·	·
	Fraxinus excelsior				*Populus tremula*				*Carpinus betulus*				*Salix caprea*			
1.5	·	2	23	·	·	·	3	1	·	·	4	8	·	·	3	1
5	·	·	·	·	·	·	·	1	·	·	·	3	·	·	·	·
9	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·
undergrowth number with height < 130 cm	3	18	6	2	·	1	2	·	·	6	5	6	·	·	8	·
	Malus sylvestris				*Fagus sylvatica*				*Quercus rubra*				*U. campestris* and *U. glabra*			
1.5	·	·	·	2	·	·	·	·	·	·	·	·	·	·	·	·
undergrowth number with height < 130 cm	·	·	·	1	·	·	·	1	·	·	·	1	·	1	1	2

shrubs number in years	1974	1985	1998	2008
Corylus avellana	8	32	55	66
Frangula alnus	64	296	459	419
Padus avium	·	·	·	5
Ribes spicatum	·	·	9	23
Sambucus racemosa	·	·	3	1
Salix cinerea	·	·	·	4
Viburnum opulus	·	1	4	10

numbers were increased in 2008. These were: *Sorbus aucuparia* L. em. Hedl., *Q. robur, C. betulus, F. excelsior, Acer platanoides* L., *Malus sylvestris* Mill, *Ulmus spp.* In many cases the above tree species occurred earlier in the undergrowth layer (< 1.3 m) and then passed the height of 1.3 m. *T. cordata* and *M. sylvestris* were noted in 2008, however there were 1 or 2 specimen in the undergrowth layer. The aspen was observed in 1985 and 1998, but its presence was not confirmed in 2008. Interesting changes in shrubs species composition are presented in Table 3. The dynamics of *C. avellana* is strongly marked. In 1974 there occurred only 3 specimen of this species. This number was systematically increasing to 671 individuals observed in 2008. The increase of the number of *F. alnus* in the developed shrub layer was also visible, however not as spectacularly as in the case of hazel. New shrub species which started to appear in the last years of this survey are as follows: *Daphne mezereum* L., *Euonymus verrucosus* Scop., *Ribes nigrum* L., *R. spicatum* E. Robson.

Plots 2 and 3 (the Wysokie Bagno reserve) indicated similar site conditions and development paths, thus the observed changes are described for both of them together (Tab. 4, 5). Significant indices of old growth stands are manifested by the regeneration processes of spruce shown by an increase of thin trees numbers. During the study period, the pine diameter increased. Otherwise the regeneration process of Scots pine does not exist. The alder was represented by more individuals in young classes of diameter, especially within plot 3 (Tab. 5). In this plot many trees of *Betula pendula* Roth. and *B. pubescens* were found in the undergrowth. Observations conducted in 1998 and 2008 indicated the beginning of development of the following tree species: oak, hornbeam, maple and willow. The ash lost trees higher than 1.3 m in 2008, and the rest exist only in undergrowth. The rowan decreased its numbers in thin classes. In the group of shrub species the hazel again indicated very active development, which is shown by the high numbers of its specimen observed since 1974. *F. alnus* increased its numbers along with increasing age of the stands. There was observed a growing trend for the number of currants in the years 1998 and 2008. Similar dynamics was observed in *Viburnum opulus* L., *Padus avium* Mill., *Sambucus racemosa* L. and *Salix cinerea* L..

The summary of observed changes in the stand structure positioned in *Sphagno girgensohnii-Piceetum* association is presented in Table 6. At all timings of measurements, within each of 3 sample plots there were indicated increased numbers of spruce, alder and rowan trees. Increased numbers of oak, hornbeam and maple trees were observed in the years 1998 and 2008. In 1974 there were 116 specimen of pine trees found and then this number started decreasing so that in 2008 there were

Tab. 6. Changes of the total number of tree species and share of their basal area in stands of *Sphagno girgensohnii-Piceetum* association. Sampling area: 0.75 ha

Tree species	Number of trees with height ≥ 1.3 per 1 ha				% of basal area			
	1974	1985	1998	2008	1974	1985	1998	2008
Picea abies	804	651	1219	3170	56.57	63.04	69.57	64.54
Pinus sylvestris	116	76	44	40	25.72	20.47	14.12	17.09
Alnus glutinosa	88	130	695	614	8.24	10.12	11.86	16.10
Betula pendula and *B. pubescens*	114	49	20	108	9.47	6.37	4.00	1.80
Sorbus aucuparia	1	9	109	189	0.00	0.00	0.42	0.18
Quercus robur	0	0	34	68	0.00	0.00	0.02	0.12
Carpinus betulus	0	0	16	50	0.00	0.00	0.01	0.14
Fraxinus excelsior	0	5	8	6	0.00	0.00	0.00	0.00
Acer platanoides and *A. pseudoplatanus*	0	1	3	19	0.00	0.00	0.00	0.02
Populus tremula and *Salix caprea*	0	0	6	1	0.00	0.00	0.00	0.01

only 40 pine trees observed. These structural changes had effects on the share of tree species in the stand basal area. The spruce began its percentage share in the basal area from 56% and until 1998 it was increased till 69% and then we observed decrease to 64%. The Scots pine seemingly lost its significance in stands, since its share in 1974 was more than 25% and in 2008 it was no more than 17%. The alder successively increased its share in the basal area, but the share of birch was decreased. The rest of observed tree species had very small basal area.

Discussion

The results of the study conducted for 35 years showed that the tree stands on bog sites changed their species composition and structure considerasbly. There was found no indication of pine regeneration. It seems that in the future there will be almost complete absence of Scots pine natural regeneration within these stands. Similar situation was observed in the Augustów forest (Andrzejczyk and Brzeziecki 1995), however then sampling was performed on stands localised on fresh sites. The stand of *Ledo-Sphagnetum magellanici* association changes noticeably in its lower layers. The development of birch and spruce trees in this typical bog forest, originally built by monotypic pine stands were also reported by other authors (Sokołowski 1991, Kloss 1996). Two-layer stands with well developed shrub layer observed today are not typical for natural vegetation. Naturally there should occur pine stands without any admixture (Sokołowski 1993). Observed changes in the undergrowth and raised bog site conditions were so deep, that in present studies there were found young oaks, which are alien elements for such habitats. This means substantial spontaneous transition of bog forest into another type of forest i.e. marshy pine forest *Vaccinio uliginosi-Pinetum* Kleist 1929.

The results of analyses of the stands connected with the boreal spruce forest *Sphagno girgensohnii-Piceetum* also indicated significant changes in composition dynamics. Previous studies from the Wysokie Bagno reserve related changes of stand structure to 1998 and in that time the old forest has existed on plot 1 (Sokołowski 1999). The observation in 2008 concerned time, when this stand collapsed and natural forest regeneration was started. It was possible to observe the development of young tree and shrub species which had occurred for the first time in 1998. We concluded, that broadleaved species which started occurring in 1998 were still developing and their share in the stand was not limited. These species (*Q. robur, C. betulus, A. platanoides*) were typical for oak-lime-hornbeam forest, especially wet subtypes (Bernadzki *et al.* 1998, Sokołowski 1999). The biggest increase in shrub layer was observed for *C. avellana*. The alder maintained its significant share in stands.

The above changes of site conditions on bog habitats show confirm that climate changes including the increase of air temperature and fall in precipitation totals have brought about lowering of the water table resulting in a decrease of habitat humidity in the Białowieża Primeval Forest (Ellis and Tallis 2000, Czerepko *et al.* 2007, Czerepko 2008). These environmental changes bring the vegetation changes including those in the stand structure.

Conclusions

Changes in tree stand species composition that were analysed in the present study allow the following conclusions:

- In the raised-bog pine forest *Ledo-Sphagnetum magellanici* association there was observed an increased share of *Betula spp., Picea abies and Quercus robur* with a parallel decrease of *Pinus silvestris*. In 2008 species composition and structure of stand are similar to the marshy pine forest *Vaccinio uliginosi-Pinetum*.
- The boreal spruce forest *Sphagno girgensohnii-Piceetum* association changed their tree stand composition by increasing numbers of broadleaved species typical for mesotrophic broadleaved forest such as: *Quercus robur, Carpinus betuluas* and *Acer platanoides*.
- The increasing share of *Corylus avellana* was observed in the shrub layer.
- Current (2008) boreal spruce stands are comparable to mixed broadleaved forest that occur on wet sites.

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