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Structure and dynamics of selected stands of primeval character in the Pieniny National Park

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Abstract: The purpose of this study was to determine changes which occurred during 23 years (1974–1997) in four stands in respect of species composition, structure, developmental stages and phases. In 1997 the Walusiówka stand represented the growing up stage, phase of a multistory structure, and during the study period its volume decreased from 698 to 676 m^3/ha. The Przełęcz Sosnów stand was in the growing up stage, phase of a little diversified storied structure and regeneration, and its volume decreased from 696 to 622 m^3/ha. The Gródek stand during the entire study period was in the growing up stage, phase of the selection forest structure and regeneration, and its volume increased from 529 to 585 m^3/ha. The Facimiech stand in 1997 was in the optimum stage, phase of aging and regeneration, and its volume decreased from 688 to 661 m^3/ha. During 1974–1997 the percentage of fir (*Abies alba*) considerably decreased in three stands (Walusiówka from 46 to 33%, Przełęcz Sosnów from 58 to 36%, Gródek from 42 to 24%). The Facimiech stand was almost a pure fir stand during the entire control period. In the Przełęcz Sosnów stand, due to a rapid mortality of fir and presence of vital trees of beech (*Fagus sylvatica*) of the growing up and optimum growth generations, the break up stage did not take place but the growing up stage had developed, which indicated the disturbance of the natural cycle of the primeval forest described by Korpel'. A scarce presence of fir upgrowth and prevalence of beech in stands composed of these two species permits to suppose that fir will be retreating in favor of beech.

Additional key words: *Abies alba, Fagus sylvatica,* developmental stages and phases, fir regression

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Introduction

Studies on virgin and natural Carpathian forests have been conducted since the first half of the 20th century (e.g. Mauve 1931; Roth 1932; Korsuň 1938; Frõhlich 1954). Usually they concerned productivity and structure of stands. Long-term investigations on natural forests and forests of a primeval character, with fir (*Abies alba*) and beech (*Fagus sylvatica*) in their composition, carried out in Central Europe, including the Carpathians, in the second half of the 20th century, yielded knowledge on their dynamics usually described as a sequence of successive stages and phases of the forest development cycle (e.g. Leibundgut 1979; Koop 1989; Korpel' 1995; Standovár and Kenderes 2003). The developmental cycle of Central European mountain forests presented by Korpel' (1982, 1995) is of a special interest. It is the result of his almost 40-year studies conducted on permanent plots in the Carpathians.

Present investigations in the lower mountain zone of the Carpathians concern not only the structure and dynamics of primeval forests (e.g. Szwagrzyk et al. 1995; Saniga 1999a, b; Jaworski and Paluch 2001; Chernyavsky 2005; Jaworski et al. 2005), their regeneration (Szwagrzyk et al. 1996; Szewczyk and Szwagrzyk 2001), productivity (e.g. Smaglyuk 1969; Saniga 1999a, b; Jaworski and Paluch 2002), mortality of fir and beech (Dziewolski and Rutkowski 1991), and fir, beech and spruce (*Picea abies*) competition (Szewczyk and Szwagrzyk 2001), but they also include studies concerning the comparison between virgin and managed forests (Commarmot et al. 2005), which is connected with the development of a close-to-nature silviculture (Schütz 1986, 1990; Thomasius 1997; Brang 2005). Also simulations, forecasting changes in species composition of uneven-aged spruce-fir-beech stands during next 400 years, are being carried out (Kozak et al. 2005). All these studies are conducted in national parks and forest reserves. The Pieniny National Park belongs to the oldest parks in the Carpathians. It was established in 1932, and in 1960 it was recognized by the International Union of Nature Protection as one of the most valuable natural objects in Europe. In 1932 the Pieniny National Park, together with the Czechoslovak (since 1967 Slovak) National Park in the Pieniny, was the first in Europe and the second in the world national park situated across the border of two countries. Presently its total area is 6096 ha, including 2346 ha on the Polish side. In the first place this area has been of interest of phytosociologists (e.g. Kulczyński 1928; Pancer-Koteja 1973; Bodziarczyk and Pancer-Koteja 2004). Taking into account forest communities, Carpathian beech forest *Dentario glandulosae-Fagetum* and stenothermal fir-beech forests *Carici albae-Fagetum* (Bodziarczyk and Pancer-Koteja 2004), the Pieniny mountains are much different from the Tatra and the Beskids.

The oldest data on stands of the Pieniny came from forest inventory of 1936. They permitted to reconstruct the species composition, structure, and volume of some stands of the Park (Dziewolski 1972).They did not, however, contain information on stages and phases of forest development, in the form presented later by Korpel' (1995). For this reason the authors of the present paper have established in 1974 four permanent experimental plots situated in fragments of the natural forest. Measurements were repeated in 1987 and 1997. These investigations were carried out during the period of high fir mortality in the Carpathians (Zawada 1984; Jaworski 1991).

The purpose of the study was to determine changes in the species composition, volume, dbh distribution, vertical structure, and developmental stages and phases of stands which occurred during 1974–1997.

The results of this study should also give answers to the following questions:

– did the fir mortality process affected the developmental cycle of the primeval forest?
– did a relatively short observation period (about 25 years) indicated the tendency which could confirm simulations forecasting changes in the species composition in the case of climatic warming up?
– what conclusions for forest management in the lower mountain zone of the Carpathians arise from the processes observed in natural forests of the Pieniny?

The analysis of recruitment, loss, and increment in these stands is presented in another paper (Jaworski and Podlaski 2007).

Material and methods

Characteristics of the area and study plots

The Pieniny is a range of low mountains (up to 982 m above sea level) with favorable site conditions for fir and beech. These mountains are built of carbonate rocks represented by limestones and marls, clastic rocks of a high carbonate content, and also sandstones and shales with a slight admixture of a carbonate binder (Niemyska-Łukaszuk et al. 2004).

The Pieniny clearly differ from neighboring mountain ranges in respect of climate, which is relatively mild here. The mean annual temperature ranges from 4°C (Wysokie Skałki) to 6.3°C (Dunajec valley). The highest mean temperatures occur in July (17°C) and August (16.2°C). January (–6.7°C) and February (–5.2°C) are the coldest months. Annual total precipitation amounts to only 690–850 mm (Perzanowska 2004).

The phythosociological characteristics of the investigated stands are very interesting. Two study plots (Walusiówka and Facimiech) represent the stenothermal beech forest association (*Carici-Fagetum abietetosum*), rare in the Carpathians (Table 1). Stands growing in Przełęcz Sosnów and Gródek plots are of a transitory nature, between the Carpathian beech forest (*Dentario glandulosae-Fagetum*) and the stenothermal beech forest (*Carici-Fagetum*) (Table 1).

Methods

On each plot (with permanently numbered trees and the place of dbh measurement marked on each tree) dbh of all living trees (dbh$\geq$6 cm) was measured. In 1974 height of over 20% of trees was measured on each plot. In 1987 and 1997 height of all trees on the Walusiówka plot was measured, while on the remaining three plots (Przełęcz Sosnów, Gródek, and Facimiech), due to steep slopes, height measurement included 40–90% of trees (Table 1).

Table 1. Location of study plots, their site and stand characteristics

Plot	Walusiówka	Przełęcz Sosnów	Gródek	Facimiech
Geographic coordinates	49°25'24'' 20°25'38.6'	49°25'11.8'' 20°26'15.1''	49°25'46.6'' 20°25'40''	49°24'13.7'' 20°25'46.9''
Location (compartment)	12h	10b	7c	25j
Size (ha)	0.40	0.33	0.25	0.25
Exposure	SW	SW	S	SSW
Slope	30°	37°	30°	30°
Altitude (m)	650	650	570	650
Soil	*Rendzic – Humic Leptosols*	*Calcaric – Humic Leptosols*	*Rendzic Leptosols*	*Calcaric – Humic Leptosols*
Plant association	*Carici-Fagetum abietetosum*	*Dentario glandulosae-Fagetum / Carici-Fagetum*	*Dentario glandulosae-Fagetum / Carici-Fagetum*	*Carici-Fagetum abietetosum*
Developmental stage and phase acc. to Korpel' (1989, 1995) determined in 1997	Growing up stage, phase of a multistory structure	Growing up stage, phase of a little diversified storied structure	Growing up stage, phase of the selection forest and regeneration	Optimum stage, phase of aging and regeneration

Also dbh and height of all standing dead trees, and length and diameter (in the middle of the stem) of dead trees lying on the ground were measured.

The number of trees in the young natural regeneration (1-year-old seedlings and trees up to 50 cm in height) was determined on strips two meters wide, while the number of trees in the upgrowth (>50 cm in height to 5.9 cm in dbh) on strips ten meters wide. The strips were 30–66 meters long, and run through the middle of plots, perpendicularly to contour lines and parallel to one of the plot sides.

The measurements of trees carried out (dbh≥8 cm) permitted to compute: parameters of Pearson's dbh distribution (Zieliński 1972), stand volume (using the computer program "Zasoby" elaborated by J. Ptak on the basis of Czuraj (1991) tables), volume of necromass (dead trees), and numbers of trees in young natural regeneration and upgrowth in distinguished classes. Trees with dbh 6.0–7.9 cm were included in the class of an advanced upgrowth.

The methods are described in detail in papers published earlier and concerning Carpathian forests of a primeval character (Jaworski and Skrzyszewski 1995, Jaworski et al. 2002).

On the basis of stand structure and criteria assumed by Korpel' (1995) the developmental stages and phases of the primeval forest were determined. Below are their characteristics.

Growing up stage

This is an initial stage of primeval forest development in which trees, usually of the young (growing up) generation, use their growth potential. They are of medium size and high vitality. Tree mortality is low. Stand volume is gradually increasing. Stands are of a specific structure, e.g. one-storied, two-storied, many-storied, or of a selection structure, which corresponds to the following phases: one-storied, two-storied, many-storied, and selection.

Optimum stage

In this stage stands are usually one-storied or two-storied, but they are uneven-aged. There is usually no regeneration, and the number of trees is relatively small. Stand volume and volume of individual trees are at their maximum. There is no height growth, and trees are of a low vitality and small current volume increment. This stage is terminated by the aging phase.

Break up stage

This is the final stage in the developmental cycle of the primeval forest. Most of trees of the old generation have reached their natural life termination. Volume of stands rapidly decreases and their structure is irregular. There are groups of dying trees (dying phase), and forest regeneration occurs in gaps (regeneration phase). The stand break up may be slow. As the years go by the regeneration forms the selection phase, e.g. in forests of the lower mountain zone. Also the stand break up may be rapid, and may occur over large areas, e.g. in Norway spruce stands of the upper mountain zone.

Results

Volume, number of trees, and species composition

Walusiówka. During 1974–1987 stand volume decreased from 698 to 652 m^3/ha, while during 1987–1997 increased, reaching 676 m^3/ha in 1997. In the control period the number of trees considerably decreased (by 44%). The species composition determined by volume changed. The percentage of beech increased during 1974–1987 as well as during 1987–1997, while that of fir decreased (Table 2).

Przełęcz Sosnów. During the first control period (1974–1987) stand volume decreased from 696 to

Table 2. Number of trees, stand volume, basal area and species composition (by volume and basal area) of stands investigated in 1974, 1987 and 1997

Species	Number of trees (trees/ha)			Volume (m^3/ha)			Basal area (m^2/ha)			Species composition (%)					
	N			V			G			V			G		
	1974	1987	1997	1974	1987	1997	1974	1987	1997	1974	1987	1997	1974	1987	1997
Walusiówka															
Fagus sylvatica	173	148	137	351.65	407.41	440.08	22.13	24.93	26.14	50.4	62.5	65.1	48.0	59.0	61.2
Abies alba	408	223	183	323.83	226.16	219.88	22.18	16.00	15.40	46.4	34.7	32.5	48.1	37.8	36.0
Acer pseudoplatanus	37	32	22	14.02	17.36	15.48	1.10	1.26	1.09	2.0	2.7	2.3	2.4	3.0	2.5
Other	12	7	10	8.50	0.65	0.49	0.65	0.10	0.12	1.2	0.1	0.1	1.5	0.2	0.3
Total	630	410	352	698.00	651.58	675.93	46.06	42.29	42.75	100.0	100.0	100.0	100.0	100.0	100.0
Przełęcz Sosnów															
Fagus sylvatica	309	300	288	290.52	339.60	398.68	20.32	23.36	25.62	41.7	51.0	64.1	44.3	52.7	64.8
Abies alba	216	150	108	403.08	323.27	220.67	25.37	20.75	13.71	57.9	48.6	35.5	55.2	46.8	34.7
Other	9	6	6	2.89	2.44	2.42	0.25	0.20	0.20	0.4	0.4	0.4	0.5	0.5	0.5
Total	534	456	402	696.49	665.31	621.77	45.94	44.31	39.53	100.0	100.0	100.0	100.0	100.0	100.0
Gródek															
Fagus sylvatica	212	200	192	301.80	406.08	438.93	21.58	25.15	27.02	57.0	71.1	75.0	56.2	68.5	72.7
Abies alba	472	228	172	223.92	162.28	143.09	16.46	11.34	9.84	42.3	28.4	24.4	42.9	30.8	26.5
Other	16	12	12	3.72	3.14	3.38	0.34	0.27	0.30	0.7	0.5	0.6	0.9	0.7	0.8
Total	700	440	376	529.44	571.50	585.40	38.38	36.76	37.16	100.0	100.0	100.0	100.0	100.0	100.0
Facimiech															
Abies alba	556	492	432	680.40	657.59	657.12	45.34	45.22	45.01	98.9	99.7	99.5	98.7	99.4	98.9
Other	12	24	44	7.60	2.20	3.60	0.61	0.29	0.50	1.1	0.3	0.5	1.3	0.6	1.1
Total	568	516	476	688.00	659.79	660.72	45.95	45.51	45.51	100.0	100.0	100.0	100.0	100.0	100.0

665 m^3/ha, and in the second period (1987–1997) it again decreased to 622 m^3/ha in 1997. During the investigated period the number of trees decreased by 25%. The species composition determined by volume changed. The percentage of beech increased, while that of fir decreased (Table 2).

Gródek. During 1974–1987 stand volume increased from 529 to 572 m^3/ha, and during 1987–1997 it increased again reaching 585 m^3/ha in 1997. During the control period the number of trees decreased by 46%. The species composition determined by volume changed. The percentage of beech increased, while that of fir decreased (Table 2).

Facimiech. During the first control period (1974–1987) the stand volume decreased from 688 to 660 m^3/ha, while during the second period (1987–1997) it slightly increased reaching 661m^3/ha in 1997. During 23 years the number of trees decreased by 16%. The species composition determined by volume underwent little changes. During 1974–1987 the percentage of fir increased, while during 1987–1997 decreased (Table 2).

Diameter structure

Walusiówka. In 1974, 1987 and 1997 the dbh distribution of all tree species together was conformable to the Pearson's type *I(J)*, that of beech to the type *I*, and that of fir to the type *I(J)* (Fig. 1). During the control period the mean dbh of all tree species together, as well as that of beech and fir separately, increased (Table 3).

Przełęcz Sosnów. In all three control periods the dbh distribution of all tree species together was conformable to the Pearson's type *I* (Fig. 1). The type of beech dbh distribution at first changed from *I* to *II*, and then to *I*, while that of fir from *I(J)* to *I(U)*. During 1974–1997 the mean dbh of all tree species investigated increased (Table 3).

Gródek. In 1974, 1987, and 1997 the dbh. distribution of all tree species together was conformable to the type *I(J)*, while that of beech to the type *I* (Fig. 1). The type of fir dbh distribution at first changed from *VI* to *I*, and then to *I(J)*. The mean dbh of the investigated tree species increased (Table 3).

Facimiech. The dbh distribution of all tree species together, as well as that of fir, in 1974 and 1987 was conformable to the Pearson's type *I*, while in 1997 it was of a transitional character between types *I* and *I(J)* (Fig. 1). The mean dbh of fir and beech increased (Table 3).

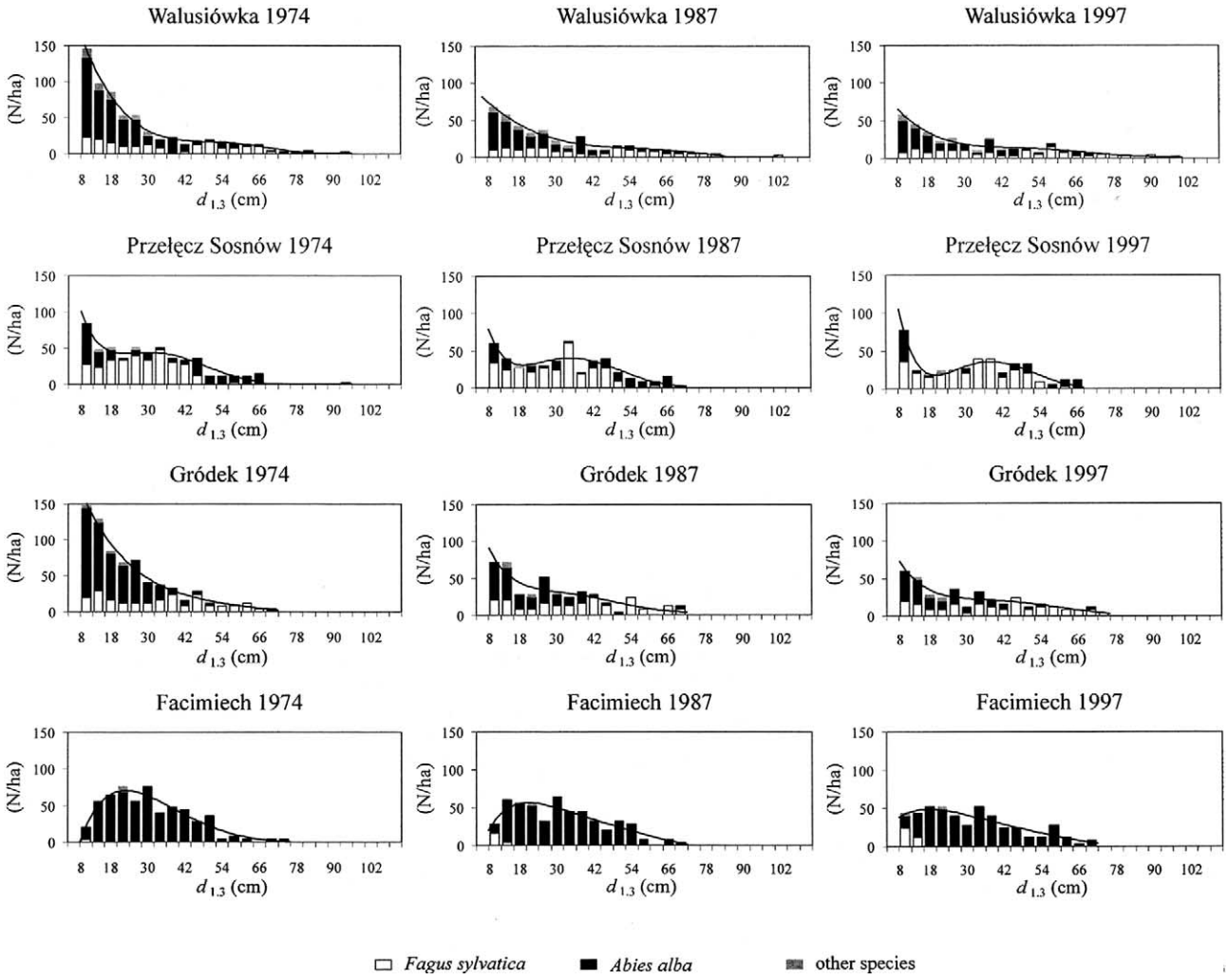

Fig. 1. D.b.h. distribution in the investigated stands in 1974, 1987 and 1998

Vertical structure

Walusiówka. The analysis of proportions of the number of trees in distinguished stand stories indicated that over 23 years there was a change in stand structure. In 1974 the middle story predominated. The percentage of trees in the lower and upper stories was considerably lower. The middle story was made up of beech, fir, and sycamore maple (*Acer pseudoplatanus*). In 1987 and 1997 the upper story predominated with about a half of the total number of trees (Table 4).

Przełęcz Sosnów. The analysis of the number of trees in respective stand stories indicated that the stand structure remained similar over the period of 23 years. In 1974 the upper story predominated comprising 46% of the total number of trees, while the proportions of the number of trees in the middle and lower stories were considerably smaller. The upper story was made up of beech and fir. In 1987 and 1997 also the upper story predominated, comprising about 60% of the total number of trees (Table 4).

Gródek. The number of trees in individual stand stories in 1974, 1987, and 1997 indicated a change of forest structure. In 1974 the middle story predominated comprising about 45% of the total number of trees, while the lower and upper stories comprised about 17% less trees each. The middle story was made up of beech and fir. In 1987 and 1997 the upper story predominated in respect of the number of trees comprising almost a half of their total number (Table 4).

Facimiech. During the entire study period the proportions of the number of trees in respective stand stories were similar. In 1974 the upper story slightly predominated. It comprised about 44% of the total number of trees, while trees in middle and lower stories comprised about 43 and 13% respectively. Also in 1987 and 1997 the upper story predominated comprising over a half of the total number of trees (Table 4).

Volume of necromass (dead standing trees and wood lying on the ground)

Walusiówka. Fir predominated among trees lying on the ground in 1987 as well as in 1997. Also fir pre-

Table 3. Characteristics of d.b.h. distributions in 1974, 1987 and 1997

Species	Number of trees in sample	D.b.h. (cm)			Coefficient of variation	Pearson distribution type
		min.	max.	mean		
			Walusiówka 1974			
Fagus sylvatica	69	8.0	92.0	34.6	0.605	*I*
Abies alba	163	8.0	80.0	21.5	0.711	*I(J)*
Acer pseudoplatanus	15	10.0	30.0	18.1	0.370	*I(J)*
Pinus sylvestris	1	–	–	–	–	–
Tilia cordata	4	8.0	18.0	–	–	–
Total	252	8.0	92.0	24.8	0.712	*I(J)*
			Walusiówka 1987			
Fagus sylvatica	59	10.0	101.5	40.6	0.553	*I*
Abies alba	88	8.0	82.0	25.0	0.671	*I(J)*
Acer pseudoplatanus	13	11.0	33.5	–	–	–
Tilia cordata	3	8.0	18.0	–	–	–
Total	163	8.0	101.5	30.1	0.668	*I(J)*
			Walusiówka 1997			
Fagus sylvatica	54	8.0	99.0	43.2	0.554	*I*
Abies alba	69	8.0	82.0	27.4	0.690	*I(J)*
Acer pseudoplatanus	9	11.0	36.0	–	–	–
Tilia cordata	3	8.0	18.0	–	–	–
Total	135	8.0	99.0	33.1	0.667	*I(J)*
			Przełęcz Sosnów 1974			
Fagus sylvatica	103	8.0	58.5	26.9	0.399	*I*
Abies alba	72	8.0	94.0	32.2	0.665	*I(J)*
Acer pseudoplatanus	2	16.0	24.0	–	–	–
Ulmus glabra	1	–	–	–	–	–
Total	178	8.0	94.0	28.9	0.558	*I*
			Przełęcz Sosnów 1987			
Fagus sylvatica	100	8.0	60.5	29.0	0.421	*II*
Abies alba	48	8.0	68.5	36.6	0.555	*I(U)*
Acer pseudoplatanus	1	–	–	–	–	–
Ulmus glabra	1	–	–	–	–	–
Total	150	8.0	68.5	31.3	0.499	*I*
			Przełęcz Sosnów 1997			
Fagus sylvatica	96	8.0	63.5	30.8	0.439	*I*
Abies alba	34	8.0	67.0	34.1	0.670	*I(U)*
Acer pseudoplatanus	1	–	–	–	–	–
Ulmus glabra	1	–	–	–	–	–
Total	132	8.0	67.0	31.5	0.521	*I*

vailed among dead standing trees. The volume of necromass was 4 and 5 times smaller than the stand volume respectively (Table 5).

Przełęcz Sosnów. Fir was a prevailing species in wood lying on the ground. Fir in both control periods dominated among dead standing trees (nearly 100%).The necromass volume in 1987 and 1997 was 3 and 2 times smaller than the stand volume (Table 5).

Gródek. Fir prevailed among wood lying on the ground. Also fir decidedly dominated among dead standing trees (near 100%). The necromass volume in 1987 and 1997 was 7 and 5 times smaller than the stand volume respectively (Table 5).

Facimiech. Fir prevailed in wood lying on the ground in both control periods. Also the proportion of unidentified wood was high. Taking into account species composition of the stand this unidentified wood was probably also fir**.** Dead standing trees were also in almost 100% firs. The necromass volume in 1987 and 1997 was 5 and 4 times smaller than the stand volume respectively (Table 5).

Table 3. cont.

Species	Number of trees in sample	D.b.h. (cm)			Coefficient of variation	Pearson distribution type
		min.	max.	mean		
			Gródek 1974			
Fagus sylvatica	53	8.0	66.0	32.0	0.513	*I*
Abies alba	118	8.0	68.0	18.5	0.541	*VI*
Picea abies	2	18.0	22.0	–	–	–
Acer pseudoplatanus	2	11.0	13.0	–	–	–
Total	175	8.0	68.0	22.6	0.609	*I(J)*
			Gródek 1987			
Fagus sylvatica	50	8.5	70.0	35.8	0.501	*I*
Abies alba	57	8.0	70.5	22.1	0.549	*I*
Picea abies	1	–	–	–	–	–
Acer pseudoplatanus	2	13.0	15.0	–	–	–
Total	110	8.0	70.5	28.1	0.585	*I(J)*
			Gródek 1997			
Fagus sylvatica	46	8.0	74.0	38.8	0.482	*I*
Abies alba	38	8.0	71.0	23.9	0.600	*I(J)*
Picea abies	1	–	–	–	–	–
Acer pseudoplatanus	1	–	–	–	–	–
Total	86	8.0	74.0	31.8	0.574	*I(J)*
			Facimiech 1974			
Fagus sylvatica	1	–	–	–	–	–
Abies alba	139	8.0	72.0	29.5	0.438	*I*
Picea abies	2	20.0	38.0	–	–	–
Total	142	8.0	72.0	29.4	0.437	*I*
			Facimiech 1987			
Fagus sylvatica	5	8.5	12.0	–	–	–
Abies alba	115	8.0	69.5	31.5	0.450	*I*
Picea abies	1	–	–	–	–	–
Total	121	8.0	69.5	30.5	0.475	*I*
			Facimiech 1997			
Fagus sylvatica	9	8.0	14.0	–	–	–
Abies alba	96	8.0	71.0	33.9	0.465	*I*
Picea abies	1	–	–	–	–	–
Ulmus glabra	1	–	–	–	–	–
Total	107	8.0	71.0	31.6	0.516	*I/I(J)*

Regeneration

Walusiówka. At the beginning of the control period in 1987 fir and ash (*Fraxinus excelsior*) prevailed among young natural regeneration (without seedlings) (Table 6), while after 10 years beech prevailed (Table 7). In the upgrowth in 1987 beech percentage was greater than that of ash (Table 6). In 1997 percentages of beech and sycamore maple were close amounting to about 45% in each case (Table 7). The number of trees in the advanced upgrowth was systematically decreasing, from 68 in 1974, to 53 in 1987, and 46 trees/ha in 1997. In all control years fir prevailed in the advanced upgrowth (about 74% in 1974, 66% in 1987, and 61% in 1997).

Przełęcz Sosnów. In 1987 and 1997 beech prevailed in young regeneration (without seedlings) (Tables 6 and 7). At the beginning and end of the control period also beech prevailed in the upgrowth. The number of trees in the advanced upgrowth decreased from 90 trees/ha in 1974 to 78 trees/ha in 1987 and 1997. In all three control years fir prevailed in the advanced upgrowth (about 90% in 1974, 85% in 1987, and 77% in 1997).

Gródek. In 1987 and 1997 beech prevailed in young regeneration as well as in upgrowth (Tables 6 and 7). The number of trees in the advanced upgrowth decreased from 84 (1974) to 28 trees/ha (1987), and then increased to 36 trees/ha (1997). In

Table 4. Distribution of number of trees in individual stand stories in 1974, 1987 and 1997

Stand stories (m)	Species						Other		Total	
	Fagus sylvatica		*Abies alba*		*Acer pseudoplatanus*					
	trees/ha	%	trees/ha	%	trees/ha	%	trees/ha	%	trees/ha	%
					Walusiówka 1974					
<12.7	12	7.0	161	39.4	–	–	2	18.2	175	27.8
12.7–25.1	60	34.9	152	37.3	32	86.5	8	63.6	252	40.0
>25.1	101	58.1	95	23.3	5	13.5	2	18.2	203	32.2
Total	173	100.0	408	100.0	37	100.0	12	100.0	630	100.0
					Walusiówka 1987					
<12.1	–	–	72	32.4	–	–	5	71.4	77	18.9
12.1–24.0	42	28.6	79	35.2	15	46.9	2	28.6	138	33.6
>24.0	106	71.4	72	32.4	17	53.1	–	–	195	47.5
Total	148	100.0	223	100.0	32	100.0	7	100.0	410	100.0
					Walusiówka 1997					
<12.2	2	1.5	62	34.1	–	–	10	100.0	74	21.1
12.2–24.1	37	27.0	55	30.2	7	31.8	–	–	99	28.2
>24.1	98	71.5	66	35.7	15	68.2	–	–	179	50.7
Total	137	100.0	183	100.0	22	100.0	10	100.0	352	100.0
					Przełęcz Sosnów 1974					
<13.4	27	8.7	78	36.1	–	–	–	–	105	19.7
13.4–26.5	138	44.7	36	16.7	–	–	9	100.0	183	34.3
>26.5	144	46.6	102	47.2	–	–	–	–	246	46.0
Total	309	100.0	216	100.0	–	–	9	100.0	534	100.0
					Przełęcz Sosnów 1987					
<12.3	36	12.0	33	22.0	–	–	–	–	69	15.1
12.3–24.3	96	32.0	27	18.0	–	–	3	50.0	126	27.6
>24.3	168	56.0	90	60.0	–	–	3	50.0	261	57.3
Total	300	100.0	150	100.0	–	–	6	100.0	456	100.0
					Przełęcz Sosnów 1997					
<12.4	36	12.5	42	38.9	–	–	–	–	78	19.4
12.4–24.5	69	24.0	9	8.3	–	–	3	50.0	81	20.1
>24.5	183	63.5	57	52.8	–	–	3	50.0	243	60.5
Total	288	100.0	108	100.0	–	–	6	100.0	402	100.0

the advanced upgrowth in 1974 and 1987 fir prevailed (81 and 57% respectively), while beech prevailed in 1997 (56%).

Facimiech. In 1987 and 1997 practically only fir occurred in young regeneration (without seedlings) (Tables 6 and 7). In upgrowth beech prevailed in 1987 (44%) and in 1997 (67%) (Tables 6 and 7). The number of trees in the advanced upgrowth increased from 36 in 1974 to 48 in 1987, and 60 trees/ha in 1997. Fir prevailed in 1974 (78% of the total number of trees in the advanced up growth), 1987 (58%), and 1997 (53%).

Developmental stages and phases

Walusiówka. In 1974 this stand exhibited characters of the growing up stage (in places in transition to the optimum stage), the phase of a selection structure. During 1974–1987 a violent process of fir mortality (Table 2) caused a drop in volume (from 698 to 652 m^3/ha), which disturbed the growing up stage. However, in 1987 a complex structure also pointed to the growing up stage, the phase of a many-storied structure.

In 1997 the stand still showed characters of the growing up stage and the phase of a selection structure with symptoms of volume reconstruction (Figs. 1 and 2). The following characteristics indicated this state:

– volume increase from 652 in 1987 to 676 m^3/ha in 1997 (Table 2),
– decreasing volume of necromass, and increasing stand volume, which was expressed by the ratios 1:4.2 in 1987 and 1:5.1 in 1997 (Table 5),
– complex vertical structure expressed by a relatively large percentage of trees in the lower (21%) and middle (28%) stories (Table 4),

Table 4. cont.

Stand stories (m)	Species						Other		Total	
	Fagus sylvatica		*Abies alba*		*Acer pseudoplatanus*					
	trees/ha	%	trees/ha	%	trees/ha	%	trees/ha	%	trees/ha	%
					Gródek 1974					
<12.9	16	7.5	176	37.3	–	–	–	–	192	27.4
12.9–25.7	100	47.2	196	41.5	–	–	16	100.0	312	44.6
>25.7	96	45.3	100	21.2	–	–	–	–	196	28.0
Total	212	100.0	472	100.0	–	–	16	100.0	700	100.0
					Gródek 1987					
<12.5	20	10.0	52	22.8	–	–	–	–	72	16.4
12.5–24.8	52	26.0	108	47.4	–	–	12	100.0	172	39.1
>24.8	128	64.0	68	29.8	–	–	–	–	196	44.5
Total	200	100.0	228	100.0	–	–	12	100.0	440	100.0
					Gródek 1997					
<12.8	24	12.5	60	34.9	–	–	–	–	84	22.3
12.8–25.3	44	22.9	60	34.9	–	–	8	66.7	112	29.8
>25.3	124	64.6	52	30.2	–	–	4	33.3	180	47.9
Total	192	100.0	172	100.0	–	–	12	100.0	376	100.0
					Facimiech 1974					
<12.9	–	–	72	12.9	–	–	4	33.3	76	13.4
12.9–25.6	–	–	240	43.2	–	–	4	33.3	244	43.0
>25.6	–	–	244	43.9	–	–	4	33.3	248	43.6
Total	–	–	556	100.0	–	–	12	100.0	568	100.0
					Facimiech 1987					
<11.8	–	–	24	4.9	–	–	20	83.3	44	8.5
11.8–23.5	–	–	188	38.2	–	–	4	16.7	192	37.2
>23.5	–	–	280	56.9	–	–	–	–	280	54.3
Total	–	–	492	100.0	–	–	24	100.0	516	100.0
					Facimiech 1997					
<11.9	–	–	20	4.6	–	–	32	72.7	52	10.9
11.9–23.7	–	–	172	39.8	–	–	8	18.2	180	37.8
>23.7	–	–	240	55.6	–	–	4	9.1	244	51.3
Total	–	–	432	100.0	–	–	44	100.0	476	100.0

– single-armed dbh distribution; dominant type *I(J)* according to Pearson (Fig.1,Table 3),
– increased coefficient of variation of height of all tree species (from 0.33 in 1974 to 0.43 in 1987, and 0.44 in 1997 (data not included in the table),
– prevalence of trees of the growing up generation (57%),
– relatively high volume increment (7.81 m^3/ha/year) (Jaworski and Podlaski 2007).

Przełęcz Sosnów. In 1974 this stand showed a transitional phase between the growing up stage and the optimum stage. During 1974–1987 the process of fir mortality resulted in decrease of stand volume from 696 to 665 m^3/ha (Table 2) and accumulation of a great quantity of necromass which in 1987 amounted to 235 m^3/ha. During 1987–1997 mortality of fir was especially high in the highest stand story (Table 4) This caused further decrease of stand volume (from 665 to 622 m^3/ha) which resembled the process of stand break up to a greater degree than in Walusiówka and Gródek stands (Table 2). Beech of growing up and optimum growth generations was liberated, and favorable conditions were created for regeneration and growth of trees in the upgrowth. Thus, a stand with beech prevalence was created, being in the growing up stage of relatively little diversified storied structure (Tables 2 and 4). Processes which occurred during 1974–1997 indicated the disturbance of a natural developmental cycle of a primeval forest (Korpel 1995). In this stand the growing up stage was formed instead of the optimum stage.

Gródek. The stand during the entire study period, in spite of intensive fir mortality, exhibited traits of the growing up stage, the phase of a selection structure, with the still continued phase of regeneration. This was indicated by processes taking place during

Table 5. Volume of dead trees (necromass), and its ratio to the volume of living trees (stand)

Species	Volume of dead trees (necromass)				Total necromass $V_L + V_P$		Ratio between necromass volume ($V_L + V_P = 1$) and stand volume V^*
	wood lying on ground V_L		standing dead trees V_P				
	m^3/ha	%	m^3/ha	%	m^3/ha	%	
			Walusiówka 1987				
Fagus sylvatica	1.75	2.3	0.67	0.9	2.42	1.6	1 : 168.4
Abies alba	28.22	37.8	71.53	90.7	99.75	65.0	1 : 2.3
Pinus sylvestris	–	–	5.56	7.1	5.56	3.6	–
Tilia cordata	–	–	0.27	0.3	0.27	0.2	1 : 2.4
Picea abies	–	–	0.77	1.0	0.77	0.5	–
Unidentified	44.65	59.9	–	–	44.65	29.1	–
Total	74.62	100.0	78.8	100.0	153.42	100.0	1 : 4.2
			Walusiówka 1997				
Fagus sylvatica	21.45	29.8	1.07	1.8	22.52	17.0	1 : 19.5
Abies alba	33.22	46.1	51.50	85.0	84.72	63.9	1 : 2.6
Acer pseudoplatanus	–	–	2.40	4.0	2.40	1.8	1 : 6.5
Pinus sylvestris	–	–	5.44	9.0	5.44	4.1	–
Tilia cordata	–	–	0.15	0.2	0.15	0.1	1 : 3.3
Unidentified	17.40	24.1	–	–	17.40	13.1	–
Total	72.07	100.0	60.55	100.0	132.62	100.0	1 : 5.1
			Przełęcz Sosnów 1987				
Fagus sylvatica	3.73	3.0	1.31	1.2	5.04	2.1	1 : 67.4
Abies alba	107.48	86.7	110.13	98.8	217.61	92.5	1 : 1.5
Acer pseudoplatanus	0.30	0.2	–	–	0.30	0.1	1 : 6.4
Unidentified	12.51	10.1	–	–	12.51	5.3	–
Total	124.02	100.0	111.44	100.0	235.46	100.0	1 : 2.8
			Przełęcz Sosnów 1997				
Fagus sylvatica	8.96	6.8	4.22	2.6	13.18	4.5	1 : 30.3
Abies alba	51.36	38.7	156.66	97.4	208.02	70.9	1 : 1.1
Unidentified	72.36	54.5	–	–	72.36	24.6	–
Total	132.68	100.0	160.87	100.0	293.55	100.0	1 : 2.1
			Gródek 1987				
Fagus sylvatica	7.52	45.6	1.86	2.9	9.38	11.6	1 : 43.3
Abies alba	6.40	38.8	62.22	97.1	68.62	85.2	1 : 2.4
Unidentified	2.56	15.6	–	–	2.56	3.2	–
Total	16.48	100.0	64.08	100.0	80.56	100.0	1 : 7.1
			Gródek 1997				
Fagus sylvatica	18.00	21.5	–	–	18.00	14.5	1 : 24.4
Abies alba	38.00	45.4	40.41	100.0	78.41	63.2	1 : 1.8
Unidentified	27.68	33.1	–	–	27.68	22.3	–
Total	83.68	100.0	40.41	100.0	124.09	100.0	1 : 4.7
			Facimiech 1987				
Abies alba	47.60	68.7	54.72	98.0	102.32	81.8	1 : 6.4
Picea abies	1.24	1.8	1.13	2.0	2.37	1.9	1 : 0.7
Unidentified	20.40	29.5	–	–	20.40	16.3	–
Total	69.24	100.0	55.84	100.0	125.08	100.0	1 : 5.3
			Facimiech 1997				
Abies alba	30.92	47.0	99.91	99.1	130.83	78.6	1 : 5.0
Picea abies	–	–	0.90	0.9	0.90	0.5	1 : 2.1
Unidentified	34.86	53.0	–	–	34.86	20.9	–
Total	65.78	100.0	100.81	100.0	166.58	100.0	1 : 4.0

* See Table 2

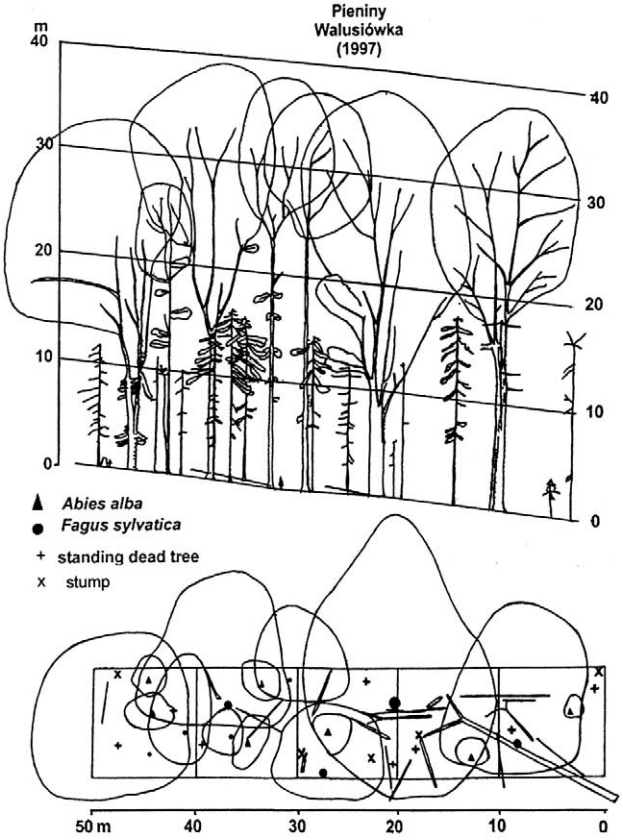

Fig. 2. Walusiówka stand profile

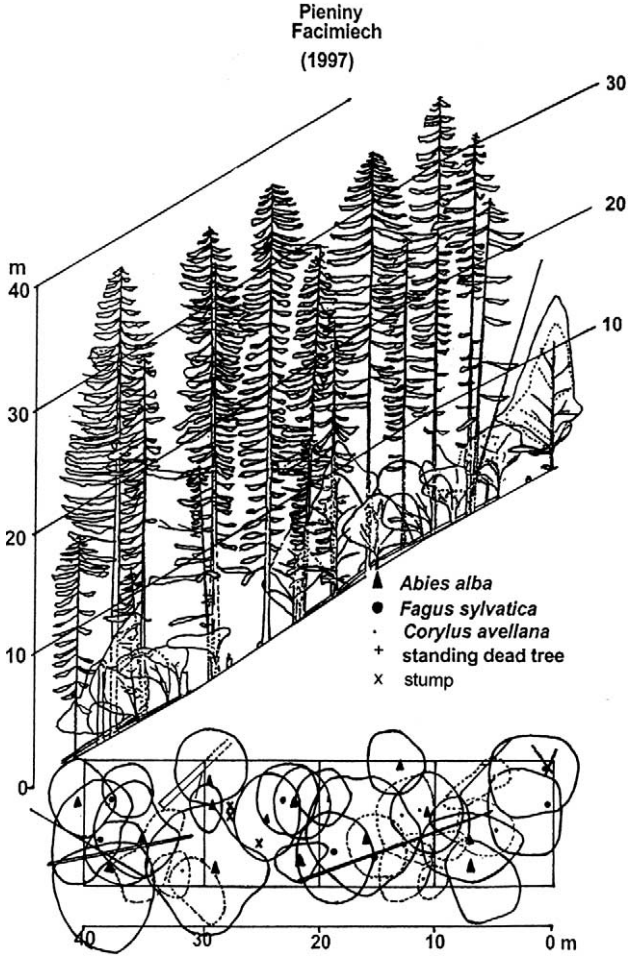

Fig. 3. Facimiech stand profile

1974–1997, as well as the condition of the stand in 1997:

- increase in volume from 529 in 1974 to 572 in 1987 and 585 m^3/ha in 1997 (Table 2),
- single-armed dbh distribution of all tree species-Pearson type *I(J)* (Table 3, Fig. 1),
- the greatest percentage of trees in diameter class 8.0–15.9 cm (Fig. 2),
- high value of the coefficient of variation of height of all tree species together (0.43 in 1997) (data not included in the table),
- intensive regeneration process (expressed by increased number of trees in the natural young regeneration from 44000 to about 84000 trees/ha, and a doubled number of trees in the upgrowth from about 3300 to 6600 trees/ha) (Tables 6 and 7),
- prevalence of trees in the growing up generation (57%).

Facimiech. In 1974 the stand exhibited traits of the optimum stage. In subsequent years this stage was retained in spite of an intensive process of fir mortality

(Table 2, Fig. 3). In 1997 the optimum stage, the phases of aging and regeneration were observed. This was indicated by:

- changes in stand volume: from 688 in 1974 to 660 in 1987 and 661 m^3/ha in 1997 (Table 2),
- increase in necromass volume from 125 m^3/ha in 1987 to 167 m^3/ha in 1997 (Table 5),
- increase in number of trees in regeneration from 3500 in 1987 to 57400 trees/ha in 1997 (Tables 6 and 7),
- increase in number of trees in the advanced upgrowth from 36 in 1974 to 60 trees/ha in 1997, -asymmetric, two-armed dbh distribution with frequency maximum in the interval 24.0–35.9 cm, Pearson type *I* (Table 3, Fig.1),
- relatively low value of the coefficient of variation of height of all tree species (0.37 in 1997) (data not included in the table),
- relatively high volume increment (9.42 m^3/ha/year) (Jaworski and Podlaski 2007).

Discussion

Results of the study presented in this paper show that the Pieniny fir-beech forests of a primeval character attain a relatively high stand volume (622–676 m^3/ha) and a complex (multistory phase) structure in the growing up stage. A similar stand volume (505–693 m^3/ha) was reached by fir, beech and spruce forests in the lower mountain zone of the Babia Góra National Park (Jaworski and Paluch 2002), but smaller than in Slovak Carpathians

Table. 6. Numbers and percentage of regeneration on study plots in 1987

Species	Young regeneration				Upgrowth height > 50 cm to d.b.h. 5.9 cm	
	one–year–old seedlings		young trees of height ≤ 50 cm			
	trees/ha	%	trees/ha	%	trees/ha	%
			Walusiówka			
Fagus sylvatica	–	–	1200	7.4	50	48.6
Abies alba	5800	77.3	6000	37.0	13	12.6
Acer pseudoplatanus	800	10.7	4000	24.7	–	–
Tilia cordata	300	4.0	–	–	–	–
Fraxinus excelsior	600	8.0	4900	30.3	40	38.8
Carpinus betulus	–	–	100	0.6	–	–
Total	7500	100.0	16200	100.0	103	100.0
			Przełęcz Sosnów			
Fagus sylvatica	303	7.7	35379	80.9	781	68.6
Abies alba	3561	90.4	4697	10.8	357	31.4
Acer pseudoplatanus	76	1.9	3031	6.9	–	–
Tilia cordata	–	–	228	0.5	–	–
Fraxinus excelsior	–	–	227	0.5	–	–
Carpinus betulus	–	–	152	0.4	–	–
Total	3940	100.0	43714	100.0	1138	100.0
			Gródek			
Fagus sylvatica	1000	9.7	34666	78.5	2744	84.1
Abies alba	9167	88.7	5667	12.8	49	1.5
Acer pseudoplatanus	167	1.6	2667	6.0	367	11.3
Tilia cordata	–	–	167	0.4	–	–
Carpinus betulus	–	–	1000	2.3	100	3.1
Total	10334	100.0	44167	100.0	3260	100.0
			Facimiech			
Fagus sylvatica	–	–	–	–	170	43.6
Abies alba	42625	100.0	3500	100.0	45	11.5
Acer pseudoplatanus	–	–	–	–	25	6.4
Tilia cordata	–	–	–	–	100	25.7
Ulmus glabra	–	–	–	–	25	6.4
Sorbus aucuparia	–	–	–	–	25	6.4
Total	42625	100.0	3500	100.0	390	100.0

(540–840 (1000) m^3/ha) (Korpel' 1995). The highest volume is reached by one-storied stands being in the optimum stage. Their volume may reach about 1400 m^3/ha (Korpel' 1995). Similar relationships occur in managed forests (Assmann 1968).

In stands of the Pieniny Mountains, investigated during this study, a distinct tendency of fir regression was observed (Table 2). These changes were connected with the process of fir retreat in the Western Carpathians which started in the 1960s (Jaworski et al. 1995; Zawada 2001). Studies carried out in the Pieniny (Jaworski and Skrzyszewski 1986; Dziewolski and Rutkowski 1987) showed that since 1960 there was a distinct decrease of diameter increment in fir, and not sooner than during 1980–1990 the increase of diameter increment in trees of this species was observed (Jaworski et al. 1995). The increment drop, initiated in 1960 and intensified during 1960–1970, caused an excessive mortality of fir during 1972–1974 (Dziewolski and Rutkowski 1987), and a very high (mass) mortality during 1974–1987 (Jaworski and Karczmarski 1991). In the Carpathians the restrained diameter increment preceded the process of fir dying by about 10–20 years (Jaworski and Skrzyszewski 1986; Jaworski and Karczmarski 1991), as it was the case in Switzerland (Schweingruber et al. 1983). Similar processes have been observed in other Polish mountain ranges, e.g. in the Gorce and the Góry Świętokrzyskie (Jaworski and Skrzyszewski 1995; Jaworski and Podlaski 2006). Also studies of Paulenka et al (1996), Spiecker et al. (1996a, b), and Saniga (1999a, b) showed the expansion of beech, often forcing out fir from mixed stands of the lower mountain zone in central Europe.

Table 7. Numbers and percentage of regeneration on study plots in 1997

Species	Young regeneration				Upgrowth height > 50 cm to d.b.h. 5.9 cm	
	one–year–old seedlings		young trees of height ≤ 50 cm			
	trees/ha	%	trees/ha	%	trees/ha	%
			Walusiówka			
Fagus sylvatica	–	–	19500	46.2	43	47.2
Abies alba	–	–	11900	28.2	8	8.8
Acer pseudoplatanus	300	6.8	8500	20.1	40	44.0
Tilia cordata	1900	43.2	–	–	–	–
Fraxinus excelsior	1000	22.7	1600	3.8	–	–
Carpinus betulus	1200	27.3	500	1.2	–	–
Picea abies	–	–	200	0.5	–	–
Total	4400	100.0	42200	100.0	91	100.0
			Przełącz Sosnów			
Fagus sylvatica	–	–	71591	87.2	2030	88.0
Abies alba	–	–	7954	9.7	220	9.5
Acer pseudoplatanus	–	–	1591	1.9	–	–
Tilia cordata	–	–	379	0.5	–	–
Fraxinus excelsior	–	–	–	–	45	1.9
Carpinus betulus	379	100.0	606	0.7	15	0.6
Total	379	100.0	82121	100.0	2310	100.0
			Gródek			
Fagus sylvatica	–	–	74667	89.4	6166	93.8
Abies alba	167	100.0	4500	5.4	41	0.6
Acer pseudoplatanus	–	–	2833	3.4	267	4.1
Tilia cordata	–	–	167	0.2	–	–
Carpinus betulus	–	–	1000	1.2	100	1.5
Cerasus avium	–	–	333	0.4	–	–
Total	167	100.0	83500	100.0	6574	100.0
			Facimiech			
Fagus sylvatica	–	–	125	0.2	208	66.7
Abies alba	2000	89.0	57250	99.8	29	9.3
Tilia cordata	125	5.5	–		50	16.0
Ulmus glabra	–	–	–		25	8.0
Sorbus aucuparia	125	5.5	–		–	–
Total	2250	100.0	57375	100.0	312	100.0

The weakening of fir, followed by intensive mortality, could had been caused by air pollution, since studies of Sawicka (1991) in the Pieniny showed a considerable amount of sulfur in one-year-old (0.12%) and two-year-old (0.14%) needles..

The intensive fir mortality, especially of trees of the older generation from the upper story, most likely associated with a greater amount of sulfur reaching crowns of the oldest, usually the highest trees (Roether 1979; Fabijanowski 1986; Keller and Imhof 1987) created gaps dynamically regenerated by beech.

The recession of fir and the increased percentage of beech in the area under investigations suggest the question whether these processes will alter the developmental cycle of the forest of a primeval character presented by Korpel' (1989).

The process of fir mortality of all generations (Fig. 1), including the highest and largest (dbh. above 72 cm) trees in the Przełęcz Sosnów stand resulted in drop of stand volume (Table 2) and production of a large quantity of necromass (Table 5). This resembled a small-area break up of the stand which, however, thanks to the presence of vital beech trees of the growing up and optimum growth generation and favorable conditions for beech regeneration, did not terminate the developmental cycle in the break up stage, phase of living up (Korpel'1995), but caused the formation of the growing up stage, phase of the diversified vertical structure. Due to disturbances the developmental cycle of the Przełęcz Sosnów stand differed from the model described by Korpel'(1995).

The growing up stage in the phase of diversified vertical structure is characterized by high stability of stands due to the occurrence of many generations of trees. Such diversification of structure and age of the stand with high percentage of beech prevents the large area stand break up, characteristic, for example, to Norway spruce stands of the higher mountain zone (Leibundgut 1979; Korpel' 1989, 1995).

From the above short considerations the following significant conclusion may be drawn for practical silviculture: it is necessary to diversify the structure and age of stands in managed forests. This may be attained through a close-to-nature silviculture which would not only manage the production but also raise the ecological stability of the biotop (Holling 1973). This stability is understood as the ability of the ecosystem to attain equilibrium after disturbances, as soon as possible (Schütz 1986).

In areas where disturbances associated with intensive mortality of fir were even more severe a lack of the optimum stage was observed. For example in the Świętokrzyski National Park in 1994 in near-natural beech-fir stands no optimum stage was found on 206 sample plots randomly distributed over the area of 2100 ha (Podlaski 2004).

The dynamic encroachment of beech may also be associated with warming up of the climate which causes changes in European forests (Thomasius 1991; Fabian and Menzel 1998) and favors the development of this tree species (Felbermeier 1994).

The computer simulation of the dynamics of uneven-aged spruce-fir-beech virgin stands in the Ukrainian Carpathians showed that the climatic warming up (increase of mean annual temperature by 2°C) will cause during the next 400 years the supremacy of beech, a considerable decrease in fir percentage, and a complete disappearance of spruce. However, if the mean annual temperature will drop by 2°C spruce and fir will dominate in stands (Kozak et al. 2005). In the Pieniny the first scenario will probably occur, because a general increase of temperature in the foreland of the Carpathians during 1881–1990 was 0.9–1.3°C (Obrębska-Starklowa et al. 1994). This study, although based on not large material, confirmed forecasts about beech expansion and fir recession in stands of the lower mountain zone. Also in other parts of Poland, e.g. Białowieża Forest, the retreat of conifers, e.g. spruce, in favor of broadleaf trees, including stenothermal species such as hornbeam and lime, is observed. The cause of these changes is associated with warming up of the climate (Kowalski 1991, 1994).

A high vitality of beech was also shown by data of two forest inventories in Bavaria in 1970/1971 and 1987. They showed the 10–20% increase in volume of stands, and surpassing of table data concerning the current annual volume increment by 10–40% (Pretzsch 1996). A similar level of productivity of beech stands was found in other parts of Germany (Untheim 1996). These results, among other things, are associated with climatic warming up, although its effect on tree growth has not been fully explained as yet (Spiecker et al. 1996a; Zingg 1996).

Regeneration of fir and beech has a crucial importance for the formation of future species composition of stands investigated during this study. Data of 1997 showed that due to prevalence of beech young regeneration and upgrowth (Tables 5 and 6), a small amount of an advanced upgrowth (fir 16–60, beech 10–20 trees/ha), and only a slight prevalence of fir in the lower story (Table 4), beech will have a deciding influence on formation of species composition of investigated stands in future. This phenomenon has also been observed in other Carpathian fir-beech stands (Saniga 1999a, b) and stands in the Dinaric Alps (Diaci et al. 2005; Nagel et al. 2006).

What will be the future development of the investigated stands? It seems that it will depend on the occurrence of factors causing weakening of fir vitality and its premature death. In the case of absence of these disturbances stands being in the growing up stage should increase their volume, simplify their structure, and after a certain period of time they should reach the optimum stage. In the case of the presence of such disturbances stands in the growing up stage and/or in the transitional phase between the growing up stage and the optimum stage, and of a complex storied structure (presence of trees in the middle and lower stories), mainly composed of beech which did not reach the age of the living up generation (Řehák 1964), may develop in a similar way as the Przełęcz Sosnów stand described above. On the other hand, one-storied stands, where a rapid mortality of trees of the optimum growth generation occurs, will be gradually passing through a regeneration phase in the growing up stage, thus initiating a new developmental cycle of the stand. Such cycles will be considerably shorter (faster) because tree mortality will not permit to reach the optimum stage.

The answers to these questions will be provided by observations carried out in stands under investigations during the next decades.

The retreat of fir and its dynamic replacement by beech, as well as overlapping of several generations of trees forming a complex stand structure is an example of self-regulation processes occurring in natural ecosystems (Schütz 1999). Science, as well as practice, shows that processes in forest ecosystems are determined in their basic tendency, but in addition they are modified by accidental influences (Thomasius 1997). In natural forests of a primeval character the changes in species composition and stand structure are the result of internal dynamics of the biocoenosis (stand), and also the result of adap-

tive processes caused by the change in the environment (Bernadzki et al. 1998).

Conclusions

1. During periods 1974–1987 and 1987–1997 stands studied in the Pieniny National Park showed dynamic changes in volume and species composition, i.e. decrease of fir and increase of beech proportions. These changes resulted from intensive fir mortality in all diameter classes, as well as the expansion of beech. Similar changes take place in most of forests of a primeval character in the lower mountain zone of the Carpathians.
2. In the Pieniny National Park the intermediate-scale disturbances, associated with fir mortality, caused the drop in volume of stands being in various developmental stages and phases, and led to deformation of the developmental cycle presented by Korpel' (1995).
3. When forming managed forests of species composition similar to that of primeval forests, and in agreement with processes occurring in natural forests, the increased proportion of beech should be foreseen when formulating silvicultural objectives. In stand characterized by site conditions optimal for fir and a high dynamics of regeneration, silvicultural treatments should be directed towards retaining of this highly productive tree species in composition of stands in the lower mountain zone.

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