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Processes of loss, recruitment, and increment in stands of a primeval character in selected areas of the Pieniny National Park (southern Poland)

A. Jaworski[1], R. Podlaski[2]

[1]*Department of Silviculture, Faculty of Forestry, Agricultural University of Cracow, Poland*
[2]*Division of General Biology and Nature Protection, Institute of Biology, University of Kielce, Poland*

ABSTRACT: Studies were carried out during 1987–1997 in four stands situated in the lower mountain zone, and representing the association *Carici-Fagetum abietetosum* (sample plots Facimiech and Walusiówka) and the community of a transitory character between *Dentario glandulosae-Fagetum* and *Carici-Fagetum* (sample plots Gródek and Przełęcz Sosnów). The greatest volume increment was found in a pure fir (*Abies alba*) stand of Facimiech (9.4 m^3/ha/year, i.e. 1.4% of actual stand volume determined in 1997) being in the optimum stage, phase of aging and regeneration, and the smallest one stand of Gródek (5.3 m^3/ha/year, i.e. 0.9% of actual stand volume) being in the growing up stage, phase of selection forest. The stand of Przełęcz Sosnów was characterized by the greatest mortality of trees (volume of loss, i.e. 13.5 m^3/ha/year). In this stand of a transitory character between the growing up and optimum stages, due to rapid mortality of fir the break up of the stand took place, and in consequence the growing up stage, phase of a little diversified stratified structure was developed. Volume of recruitment was the greatest in the stand of Facimiech, i.e. 0.05 m^3/ha/year. In three fir (*Abies alba*)-beech (*Fagus sylvatica*) stands the proportions of fir and beech in stand increment differed from their proportions in stand volume. The percentage of fir in volume increment was smaller, and that of beech greater, than their percentages in stand volume. Processes of increment and mortality of fir and beech pointed to a progressive process of changes taking place in stand species composition, expressed by the increase of beech and the decrease of fir. The knowledge about values of loss, recruitment, and increment, expressed by the number of trees and volume units, may be of help in determination of the amount of cut in productive and protective forests managed according to a close-to-nature silviculture.

Keywords: forest of a primeval character; developmental stages and phases; fir mortality; *Fagus sylvatica*; *Abies alba*

The volume increment is one of the more important elements characterizing the dynamics of the forest (Botkin 1993). The value of volume increment permits to determine the direction of changes taking place in biomass of the ecosystem in the layer of trees, and this is why it is taken into account in determination of stages and phases of development of the forest of a primeval character. The analysis of loss, recruitment, and increment renders a full determination of changes in volume of individual tree species, and this in turn permits, for example, to conclude on the progress in the process of mortality and recovery, the occurrence of disturbances, and the crop rotation taking place in the forest ecosystem (Runkle 1990).

The determination of the value of loss and recruitment, and calculation of increment, can be accomplished by two control measurements of the stand, one at the beginning and one at the end of the study period. Control measurements must render an unmistakable identification of all trees in sample plots, which is connected with great work consumption. This is one of the reasons why data on all three processes, mentioned above, may be found in not too many elaborations. In Poland, studies of this type were, for example, carried out in the Gorce and Pieniny Mountains (Dziewolski, Rutkowski 1987, 1991), on Mt. Babia Góra, and in the Bieszczady and Świętokrzyskie Mountains (Jaworski, Paluch

2001; Jaworski, Kołodziej 2002; Jaworski, Podlaski 2006).

The aims of this study were to determine loss, recruitment, and increment of the stand, and to characterize dead trees in beech-fir forests of a primeval character, representing different developmental stages and phases in the Pieniny National Park. The paper includes materials collected in four permanent sample plots in two control years: 1987 and 1997.

MATERIAL AND METHODS

Characteristics of sample plots

Characteristics of the study area and four sample plots are included in Table 1. There were favorable conditions for growth of beech (*Fagus sylvatica*) – fir (*Abies alba*) stands in sample plots established in the lower mountain zone. Under these conditions the association of the stenothermal beech forest *Carici-Fagetum abietetosum* (Walusiówka and Facimiech), and the community of a transitory character between the Carpathian beech forest (*Dentario glandulosae-Fagetum*) and the stenothermal beech forest (*Carici-Fagetum*) (Przełęcz Sosnów and Gródek) have developed (Table 1). Three stands (Walusiówka, Przełęcz Sosnów, and Gródek) represented the growing up stage in various stages, and the fourth one (Facimiech) the optimum stage, phase of aging and regeneration (Table 1).

METHODS

In 1987 and 1997 diameter measurements included all trees with dbh greater than 5.9 cm. Permanent numbering of trees (dbh ≥ 6 cm) and permanent marking of the place of dbh measurement in 1987, and repeated measurements in 1997 permitted to determine the loss. Trees which in 1997 passed the diameter threshold (dbh ≥ 8 cm) were considered as the recruitment, and trees of 6–7.9 cm in dbh were considered as the advanced upgrowth. Trees of dbh ≥ 8 cm were also classified according to the IUFRO classification (Leibundgut 1966) using its biological part:

a – height classes: 100 – upper layer, 200 – middle layer, 300 – lower layer;

b – vitality classes: 10 – luxuriant tree, 20 – tree normally developed, 30 – tree weakly developed;

c – classes of growth tendency: 1 – trees with an accelerated rate of growth, 2 – trees with a normal rate of growth, 3 – trees with a decelerated rate of growth.

Volume of trees was calculated according to a computer program Zasoby worked out by J. Ptak, and based on volume tables of Grundner and Schwappach (1952). To determine stand volume in 1987 and volume of loss during the period 1987–1997 the smoothed curve of stand height was plotted according to the Michailov function (Korf et al. 1972) on the basis of 1987 measurements, while stand volume per hectare in 1997 and volume of recruitment were determined on the basis of the curve for 1997 data.

Calculations comprised at first the control of the number of trees:

$$N_{97} - N_{87} + N_L - N_R = 0$$

where: N_{87} – number of trees at the beginning of the period (1987),

N_{97} – number of trees at the end of the period (1997),

N_L – number of trees which died (loss) during 1987–1997,

N_R – number of trees qualified as recruitment during 1987–1997.

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

Plot	Walusiówka	Przełęcz Sosnów	Gródek	Facimiech
Geographic coordinates	49°25´24´´N 20°25´39´´E	49°25´12´´N 20°26´15´´E	49°25´47´´N 20°25´40´´E	49°24´14´´N 20°25´47´´E
Location (compartment)	12h	10b	7c	24
Size (ha)	0.40	0.33	0.25	0.25
Exposure	SW	SW	S	S-SW
Slope	30°	37°	30°	30°
Altitude (m)	650	650	570	650
Plant association	*Carici-Fagetum abietetosum*	*Dentario glandulosae-Fagetum/Carici-Fagetum*	*Dentario glandulosae-Fagetum/Carici-Fagetum*	*Carici-Fagetum abietetosum*
Developmental stage and phase acc. to Korpeľ (1989, 1995) determined in 1997	growing up stage, phase of many-storied structure	growing up stage, phase of little diversified stratified structure	growing up stage, phase of selection forest and regeneration	optimum stage, phase of aging and regeneration

Table 2. Loss, recruitment, and volume increment in 1987–1997

Species	Number of trees N_{87}* (trees/ha)	Volume V_{87} (m^3/ha)	Number of trees N_{97} (trees/ha)	Volume V_{97} (m^3/ha)	Loss		Recruitment		Increment I_V (m^3/ha)
					number of trees N_L (trees/ha)	volume V_L (m^3/ha)	number of trees N_R (trees/ha)	volume V_R (m^3/ha)	
					per 10 years				
Walusiówka									
Fagus sylvatica and other broadleaves	155	408.06	147	440.57	12	28.77	4	0.08	61.20
Abies alba	223	226.16	183	219.88	48	21.23	8	0.07	14.88
Acer pseudoplatanus	32	17.36	22	15.48	10	3.89	–	–	2.01
Total	410	651.58	352	675.93	70	53.89	12	0.15	78.09
Przełęcz Sosnów									
Fagus sylvatica and other broadleaves	306	340.04	294	401.10	18	13.71	6	0.09	72.68
Abies alba	150	323.27	108	220.67	60	121.22	18	0.20	18.42
Total	456	665.31	402	621.77	78	134.93	24	0.29	91.10
Gródek									
Fagus sylvatica	200	406.08	192	438.93	12	8.40	4	0.04	41.21
Abies alba	228	162.28	172	143.09	60	30.36	4	0.04	11.13
Other	12	3.14	12	3.38	–	–	–	–	0.24
Total	440	571.50	376	585.40	72	38.76	8	0.08	52.58
Facimiech									
Abies alba	492	657.59	432	657.12	68	93.76	8	0.12	93.17
Other	24	2.20	44	3.60	–	–	20	0.36	1.04
Total	516	659.79	476	660.72	68	93.76	28	0.48	94.21

*See explanations in the text

Current periodic volume increment (I_V) was calculated according to the formula:

$$I_V = V_{97} - V_{87} + V_L - V_R \text{ (m}^3\text{/ha/10 years)}$$

where: V_{87} – volume at the beginning of the period (1987),
V_{97} – volume at the end of the period (1997),
V_L – volume of trees which died (loss) during 1987–1997,
V_R – volume of trees qualified as recruitment during 1987–1997.

The same method was used to calculate the basal area increment (I_G).

Mortality of trees was calculated as a ratio between the number of trees which died during 1987–1997 and the number of living trees in 1987.

RESULTS

Loss, recruitment, and increment

Walusiówka

During the control period 1987–1997 70 trees per hectare were lost, including 12 beech, 48 fir, and 10 sycamore maple trees. Their total volume was about 54 m^3/ha. Recruitment consisted of 12 trees per hectare, including 4 trees of beech and other broadleaf species, and 8 fir trees. Total volume of recruited trees was 0.15 m^3/ha (Table 2). The greatest annual loss in the number of trees in relation to the total number of trees of a given species in the stand in 1997 occurred in the case of sycamore maple (*Acer pseudoplatanus*) (4.5%), then fir (2.6%), and beech (0.8%) (Table 3). Also annual volume loss of sycamore maple in relation to total volume of this species in the stand (2.5%) was greater than that of fir (1.0%) and beech (0.7%) (Table 3). Stand volume increment reached about 7.8 m^3/ha/year (Table 2), while the ratio between annual volume loss and stand volume in 1997 was 0.8% (Table 3). Mean annual basal area increment during the period 1987–1997 was 0.41 m^2/ha (Table 4).

Przełęcz Sosnów

During 1987–1997 78 trees per hectare were lost (including 18 trees of beech and other broadleaf species, and 60 fir trees). Total volume of this loss was about 135 m^3/ha. Recruitment numbered 24 trees per hectare (6 trees of beech and other broadleaf species, and 18 fir trees) of total volume 0.29 m^3/ha (Table 2). A considerably greater annual loss in the number of trees in relation to the number of trees of this species in the stand was found in the case of fir (5.6%) than in the case of beech (0.6%). Also the

Table 3. Mean annual loss, recruitment and increment in relation to actual (1997) numbers or volume of living trees (%)

Species	Ratio of the number of dead trees to the number of living trees	Ratio of the volume of dead trees to the volume of living trees	Ratio of the number of recruited trees to the number of trees in stand	Ratio of volume increment to stand volume
Walusiówka				
Fagus sylvatica and other broadleaves	0.8	0.7	0.3	1.4
Abies alba	2.6	1.0	0.4	0.7
Acer pseudoplatanus	4.5	2.5	0.0	1.3
Total	2.0	0.8	0.3	1.2
Przełęcz Sosnów				
Fagus sylvatica and other broadleaves	0.6	0.3	0.2	1.8
Abies alba	5.6	5.5	1.7	0.8
Total	1.9	2.2	0.6	1.5
Gródek				
Fagus sylvatica	0.6	0.2	0.2	0.9
Abies alba	3.5	2.1	0.2	0.8
Other	0.0	0.0	0.0	0.7
Total	1.9	0.7	0.2	0.9
Facimiech				
Abies alba	1.6	1.4	0.2	1.4
Other	0.0	0.0	4.5	2.9
Total	1.4	1.4	0.6	1.4

Table 4. Loss, recruitment, and increment expressed in basal area units (m^2) in 1987–1997 (m^2/ha/10 years)

Species	Stand basal area		Loss	Recruitment	Increment
	G_{87}	G_{97}	G_L	G_R	I_G
Walusiówka					
Fagus sylvatica and other broadleaves	25.03	26.26	1.72	0.02	2.93
Abies alba	16.00	15.40	1.74	0.05	1.09
Acer pseudoplatanus	1.26	1.09	0.29	–	0.12
Total	42.29	42.75	3.75	0.07	4.14
Przełęcz Sosnów					
Fagus sylvatica and other broadleaves	23.56	25.82	0.99	0.03	3.22
Abies alba	20.75	13.71	7.76	0.10	0.62
Total	44.31	39.53	8.75	0.13	3.84
Gródek					
Fagus sylvatica	25.15	27.02	0.61	0.02	2.46
Abies alba	11.34	9.84	2.29	0.02	0.77
Other	0.27	0.30	–	–	0.03
Total	36.76	37.16	2.90	0.04	3.26
Facimiech					
Abies alba	45.22	45.01	6.31	0.05	6.05
Other	0.29	0.50	–	0.10	0.11
Total	45.51	45.51	6.31	0.15	6.16

value of annual volume loss of fir in relation to its volume in the stand (5.5%) was considerably greater than that of beech (0.3%) (Table 3). Average volume of a single dead beech tree (0.76 m^3) was smaller than that of a fir tree (2.02 m^3). Stand volume increment reached about 9.1 m^3/ha/year (Table 2), and the ratio between volume of annual loss and stand volume in 1997 was 2.2% (Table 3). Mean annual basal area increment during the control period was 0.38 m^2/ha (Table 4).

Gródek

In total 72 trees per hectare (including 12 beech and 60 fir trees) of total volume of about 39 m^3/ha were lost during the control period 1987–1997. Recruitment numbered 8 trees per hectare (4 beech and 4 fir trees) of total volume of 0.08 m^3/ha (Table 2). Fir showed a considerably higher annual loss in the number of trees (3.5%) in relation to its numbers in the stand in 1997 than beech (0.6%) (Table 3). Also the annual value of volume loss in fir in relation to its volume in the stand (2.1%) was greater than that found for beech (0.2%) (Table 3). Average volume of a dead beech tree (0.7 m^3) was greater than that of a fir tree (0.51 m^3). Volume increment reached about 5.3 m^3/ha/year (Table 2), while the ratio between volume of annual loss to stand volume in 1997 was 0.7% (Table 3). Mean annual basal area increment during 1987–1997 was 0.33 m^2/ha (Table 4).

Facimiech

During the period 1987–1997 68 fir trees per hectare of volume of about 94 m^3/ha were lost, while recruitment numbered 28 trees per hectare (8 trees of fir and 20 trees of other species) of total volume of 0.48 m^3/ha (Table 2). Annual loss of fir in the number of trees in relation to its numbers in the stand in 1997 was 1.6%, and its annual volume loss in relation to its volume in the stand was 1.4% (Table 3). Average volume of a dead fir tree was 1.38 m^3. Volume increment reached about 9.4 m^3/ha/year (Table 2), and the ratio between annual volume loss and stand volume in 1997 was 1.4% (Table 3). Mean annual basal area increment was 0.62 m^2/ha (Table 4).

Characteristics of trees which died

Walusiówka

Trees which died (70 trees per hectare) were growing in all stand layers. The greatest mortality occurred in the middle layer (40 trees per hectare, i.e. 57% of all dead trees) (Table 5). Mostly, these were weakened trees (96.6%) of a decelerated rate of growth (85.9%) (Table 6). Dead trees in the upper and lower layers comprised 10.1 and 32.8% of all dead trees respectively (Table 5). Mean dbh of dead beech trees was 34.8 cm, while that of fir 19.2 cm, and sycamore maple 18.4 cm (Table 6). Mortality of

trees expressed by the per cent of trees that died during 1987–1997 in the total number of living trees in 1987 was 17.1% (Table 5). Mortality of fir (21.5%) was almost three times as great as that of beech (7.7%).

Przełęcz Sosnów

The greatest number of trees died in the upper layer (42 trees per hectare, i.e. 53.9% of all dead trees), while 19.2% of trees which died were growing in the middle layer and 26.9% in the lower layer (Table 5). Among dead trees 19.2% represented IUFRO class 20, while 7.7 and 11.5% represented classes 1 and 2, respectively (Table 6). In this stand class 30 (weakly developed) and class 3 (with a decelerated rate of growth) were represented each by 80.8% of dead trees (Table 6). Mortality of all tree species together during 10 years was 17.1% (Table 5), that of fir (40%) being considerably greater than that of beech (5.9%). Mean dbh of dead beech trees was 23.8 cm, and of dead fir trees 36.4 cm (Table 6).

Gródek

Trees were dying in all stand layers (in total 72 trees per hectare), but their greatest number died in the middle layer (28 trees per hectare, i.e. 38.9% of all dead trees) (Table 5). Trees which died were weakly developed (IUFRO class 30) and of a decelerated rate of growth (class 3) (Table 6). Mean dbh of dead beech trees was 21.2 cm, while that of fir 20.7 cm (Table 6). Mortality of all tree species together was 16.4% (Table 5). Mortality of fir (26.3%) was over four times as great as that of beech (6.0%).

Facimiech

The greatest number of trees (only fir) died in the upper layer (40 fir trees per hectare, i.e. 58.8% of all dead trees). Trees which died in the middle layer comprised 29.4% of dead trees, and those in the lower layer 11.8% (Table 5). Majority of dead trees (82.4% and 70.6%) belonged respectively to the class 30 (weakly developed trees), and class 3 (a decelerated rate of growth) (Table 6). Mean dbh of dead fir trees was 31.8 cm (Table 6). Mortality of fir was 13.8% (Table 5).

DISCUSSION

The values of three processes: loss, recruitment, and increment, determined during this study, contain important information which may be interpreted from the ecological as well as from the economical point of view. In the case of primeval forests they provide a more detailed knowledge on stages and phases of development of the primeval forest described by Leibundgut (1959, 1982) and Korpeľ (1989, 1995). In the investigated forests of a primeval character the obtained values of current volume increment (increment of a period of 10 years) are the index of a potential site productivity (natural productive capacity) which may be compared with increment of managed forests of identical species composition and site conditions.

Generally, in natural and primeval forests, stands being in the growing up stage reach the highest increment (7.0–8.6 m^3/ha/y) (Korpeľ 1989; Jaworski, Paluch 2002; Jaworski, Kołodziej 2004), although in the Badin reserve, the stand in the advanced break up stage reached a higher increment (8.6 m^3/ha/y) that in the growing up stage (4.7 m^3 per ha/y). Among four stands of the Pieniny Mountains the highest periodic volume increment was found in the pure fir stand of Facimiech, showing features of the optimum stage, phase of aging. A slightly lower increment was found in the Przełęcz Sosnów stand being in the growing up stage, phase of a little diversified storied structure (Table 2). In 1974 this stand had a transitory character between the growing up and optimum stages, but due to mortality of fir of all generations (period 1974–1997), including the oldest trees, the rejuvenation of the stand took place, since in this stand beech trees of the growing up generation and optimum growth have survived. This way this stand, showing features of the growing up stage in transition to the optimum stage, returned to the growing up stage.

Stands of Facimiech and Przełęcz Sosnów reached the highest current annual volume increment (9.4 and 9.1 m^3/ha/y) among Polish Carpathian forests of a primeval character. It was also higher than in Badin (8.6 m^3/ha/y) (Korpeľ 1995) and Peručica (6.4–8.8 m^3/ha/y) reserves (Pintarič 1978), but smaller than in one of the plots in the Dobročský prales reserve (12.4 m^3/ha/y) (Korpeľ 1995) (compare Tables 2). In two remaining stands, Walusiówka and Gródek, current volume increment was the smallest among stands of the Pieniny Mountains, but in spite of the growing up stage, it was similar to increments in other Carpathian stands as well as in some sample plots in Badin, Dobročský prales (Korpeľ 1995), and Peručica reserves (Pintarič 1978).

For comparison, current volume increment in fir selection forests was 8–14 m^3/ha/y (Šmelko et al. 1992). In selection stands with predomination of beech it was 5–12 m^3/ha/y, and in beech stands 4.2–4.6 m^3/ha/y (Kramer 1988).

In three fir-beech stands (Walusiówka, Przełęcz Sosnów, Gródek), increment was not proportional to

Table 5. Number and percentage of living (1987) and dead trees (loss 1987–1997) in the respective stand layers

Stand layer acc. to IUFRO classification	Species	Living trees		Dead trees (loss)		Tree mortality – ratio of the number of dead trees (loss) to the number of living trees per layer (1987)	
						of a given species	of all species in total
		(trees/ha)	(%)	(trees/ha)	(%)	(%)	
Walusiówka							
100	*Fagus sylvatica* and other broadleaves	80	19.5	2	3.0	2.5	1.3
	Abies alba	63	15.4	5	7.1	7.9	3.3
	Acer pseudoplatanus	10	2.4	0	0.0	0.0	0.0
200	*Fagus sylvatica* and other broadleaves	60	14.6	5	7.1	8.3	3.0
	Abies alba	85	20.7	25	35.7	29.4	15.0
	Acer pseudoplatanus	22	5.4	10	14.3	45.5	6.0
300	*Fagus sylvatica* and other broadleaves	15	3.7	5	7.1	33.3	5.6
	Abies alba	75	18.3	18	25.7	24.0	20.0
	Acer pseudoplatanus	0	0.0	0	0.0	0.0	0.0
Total		410	100.0	70	100.0	–	17.1
Przełęcz Sosnów							
100	*Fagus sylvatica* and other broadleaves	147	32.2	6	7.7	4.1	2.5
	Abies alba	93	20.4	36	46.2	38.7	15.0
200	*Fagus sylvatica* and other broadleaves	102	22.4	6	7.7	5.9	5.3
	Abies alba	12	2.6	9	11.5	75.0	7.9
300	*Fagus sylvatica* and other broadleaves	57	12.5	6	7.7	10.5	5.9
	Abies alba	45	9.9	15	19.2	33.3	14.7
Total		456	100.0	78	100.0	–	17.1
Gródek							
100	*Fagus sylvatica*	128	29.0	4	5.6	3.1	1.9
	Abies alba	76	17.3	16	22.2	21.1	7.7
	Other	4	0.9	0	0.0	0.0	0.0
200	*Fagus sylvatica*	44	10.0	0	0.0	0.0	0.0
	Abies alba	72	16.4	28	38.9	38.9	22.6
	Other	8	1.8	0	0.0	0.0	0.0

Table 5 to be continued

300	*Fagus sylvatica*	28	6.4	8	11.1	28.6	7.4
	Abies alba	80	18.2	16	22.2	20.0	14.8
	Other	0	0.0	0	0.0	0.0	0.0
Total		440	100.0	72	100.0	–	16.4
Facimiech							
100	*Abies alba*	224	43.4	40	58.8	17.9	17.9
	Other	0	0.0	0	0.0	0.0	0.0
200	*Abies alba*	188	36.4	20	29.4	10.6	10.4
	Other	4	0.8	0	0.0	0.0	0.0
300	*Abies alba*	80	15.5	8	11.8	10.0	8.0
	Other	20	3.9	0	0.0	0.0	0.0
Total		516	100.0	68	100.0		13.2

Table 6. Characteristics of dead trees (loss) (measurements and classifications of 1987)

Species	Number of trees (trees/ha)	Mean		Stand layer (%)				Vitality index (%) according to IUFRO classification				Index of growth tendency (%)			
		dbh (cm)	height (m)	100	200	300	total	10	20	30	total	1	2	3	total
Walusiówka															
Fagus sylvatica	12	34.8	19.1	20.0	40.0	40.0	100.0	0	20.0	80.0	100.0	0	20.0	80.0	100.0
Abies alba	48	19.2	16.4	10.4	52.7	36.9	100.0	0	0	100.0	100.0	0	5.2	94.8	100.0
Acer pseudoplatanus	10	18.4	19.9	0	100.0	0	100.0	0	0	100.0	100.0	0	50.0	50.0	100.0
Total	70	21.9	17.4	10.6	57.3	32.1	100.0	0	3.4	96.6	100.0	0	14.1	85.9	100.0
Przełęcz Sosnów															
Fagus sylvatica	18	23.8	23.3	33.3	33.3	33.4	100.0	0	33.3	66.7	100.0	33.3	0	66.7	100.0
Abies alba	60	36.4	24.7	60.0	15.0	25.0	100.0	0	15.0	85.0	100.0	0	15.0	85.0	100.0
Total	78	33.4	24.5	53.9	19.2	26.9	100.0	0	19.2	80.8	100.0	7.7	11.5	80.8	100.0
Gródek															
Fagus sylvatica	12	21.2	11.5	33.3	0	66.7	100.0	0	0	100.0	100.0	0	0	100.0	100.0
Abies alba	60	20.7	17.8	26.7	46.6	26.7	100.0	0	0	100.0	100.0	0	0	100.0	100.0
Total	72	20.8	16.7	27..8	38.9	33.3	100.0	0	0	100.0	100.0	0	0	100.0	100.0
Facimiech															
Abies alba	68	31.8	25.1	58.8	29.4	11.8	100.0	0	17.6	82.4	100.0	0	29.4	70.6	100.0

stand species composition, i.e. fir share in volume increment was smaller (19, 20.2, 21.2%) and beech one was higher (78.4, 79.8, 78.4%) in comparison with their percentages in stand volume (fir: 32.5, 35.5, 24.4% and beech: 65.2, 64.5, 75.0%). The per cent of volume increment of beech and other broadleaf tree species was greater than that of fir (Table 3).

According to studies of Dziewolski and Rutkowski (1987), carried out in the Pieniny National Park during 1972–1974, 40% of increment (out of its total value of 7.64 m^3/ha/year) fell to broadleaf species (mainly beech, sycamore maple, and lime), volume of which made only 23% of total stand volume. In stands investigated by these authors the transformation of species composition was taking place, i.e. retreat of conifers (spruce and fir) in favor of broadleaf species (mainly beech, sycamore maple, and lime).

Dziewolski and Rutkowski (1987) were of the opinion that perhaps during 1972–1974 this was only a preliminary phase of these changes and therefore "their future progress is unknown". Our studies showed that during 1987–1997 beech percentage had increased, while that of fir had decreased (Table 2), and that beech proportion in increment was greater than it proportion in basal area and stand volume (Tables 2 and 4).

According to studies of Priesol and Hladík (1974) carried out in over 200 Slovak managed forests, composed of fir and beech, which reached age of 20–120 years, the greater was the percentage of fir in the stand the greater were the productivity indexes, including the average increment of total production.

Also Standovár and Kenderes (2003) showed that the increase of beech proportion at a simultaneous decrease of fir causes the drop in volume of stands composed of many species.

Due to a too small number of sample plots in the Pieniny the results of this study do not permit to make a far reaching generalizations. It may be supposed that a relatively greater increment of beech than that of fir in mixed stands is, beside predomination of beech in regeneration, an indicator of its high vitality in comparison with fir, which during the period from 1960 to 1980 showed a decreasing diameter increment (Jaworski et al. 1995), frequently as the result of high air pollution (Schöpfer, Hradetzky 1986; Pretzsch 1996).

It may also be supposed that a relatively high volume increment in beech, greater than in fir, may be an indicator of climate warming up, similarly as height growth in beech stands in Bavaria, where height growth of beech increases with increase of temperature, and in dry and warm areas these stands reach the greatest productivity (Felbermeier 1994).

In this discussion also the fact that beech stands later reach the growth culmination (Assmann 1961; Šmelko et al. 1992) should be taken into consideration. This, together with dying of many fir generations and survival of beech older generations in stands of the Pieniny Mountains, could have resulted in disproportionately greater increment of beech than that of fir in relation to their proportions in stand volume.

In fir-beech stands, fir showed not only a smaller productivity, but also greater mortality than beech. Mortality is often used to characterize the population dynamics of trees (Szwagrzyk, Szewczyk 2001; Battles et al. 2003). In the investigated stands of the Pieniny Mountains the mortality of all tree species during a 10-year period (Walusiówka and Przełęcz Sosnów 17.1, Gródek 16.4, Facimiech 13.2%) was greater than in the fir-beech stand on Mt. Babia Góra (12.5%) (Szwagrzyk, Szewczyk 2001), and also greater than tree mortality in the Gorce Mountains in the stand representing growing up stage, phase of selection structure (7.4%) and similar to that in the stand in the initial phase of the break up stage (16.9%), but smaller than that in the stand in the break up stage (21.8%) (Jaworski, Kołodziej – unpublished data). The authors are of the opinion that this index does not fully reflect the changes taking place in stands, and that it should be supplemented with volume or biomass of trees that died.

The process of natural mortality of trees in stands of a complex vertical structure resembles the removal of mature trees in the selection cutting system. It may be assumed that dead trees from the upper stand layer of dbh about 60–70 cm correspond to "crop harvesting" (Table 5). Dead smaller trees in this layer and in layers below correspond to a generally known method of conducting selection cuttings in all stand layers. This natural selection plays a function of a selection cutting (Schütz 2001), but mainly inclined towards a negative selection. It is, however, difficult to suppose that "cuttings" resulting from natural processes taking place in the stand could agree with aims of the forest manager.

Volume loss ("amount of cut") in the investigated plots was diversified (Table 2). In Walusiówka and Gródek stands the loss was smaller than the increment (Table 2), and therefore it was within the limits of a selection cut corresponding to current volume increment. It may be expected that these stands will be increasing their volume along with transition

from the growing up stage to the optimum stage. In the Facimiech stand during 1987–1997 the loss and increment were equal to each other (Table 2), and this is why this stand showed the equilibrium in volume, and its further development will depend on the progress of the aging process expressed by the value of loss. In the Przełęcz Sosnów stand the loss caused by intensive mortality of fir considerably exceeded the increment (Table 2), and thus an accelerated stand break up took place, having a transitory character between the growing up stage and the optimum stage, which in consequence impoverished a natural developmental cycle of the stand of a primeval character described by Korpeľ (1995).

In general, in the growing up stage mortality included fir trees of smaller diameters (mean dbh Walusiówka 19.2 cm and Gródek 20.7 cm) than in the optimum stage (Facimiech – 31.8 cm) and in the stand of an accelerated break up (Przełęcz Sosnów 36.4 cm). Similar results were presented by Jaworski and Kołodziej (2002) in their study concerning forests of the Bieszczady Mountains.

In the first place trees of the upper and middle layers of the investigated stands were dying. Among them there were also trees of a normal vitality and average and high growth tendency. The causes of this mortality were probably the disturbances connected with the process of fir receding (White, Pickett 1985; Splechtna et al. 2005). Dying of trees in the lower layer and individuals of low vitality and low growth tendency was in the first place caused by natural processes of tree mortality in the stand.

CONCLUSIONS

1. Processes of increment and loss of fir and beech indicated a progressive process of changes in species composition expressed by increased proportion of beech and decreased proportion of fir.
2. In three mixed stands proportions of fir and beech in stand increment were different from their proportions in stand volume: fir showed a smaller and beech a greater proportion in stand volume increment than their proportions in stand volume.
3. In the Pieniny National Park fir was characterized by a greater mortality than beech. The dying process of fir observed since the early 1970s was continued in the late 1990s.
4. Trees which died were characterized by a generally lower vitality and decreasing growth tendency, however, among them there were also individuals of a normal vitality and average growth tendency. The causes of death of latter trees were disturbances not associated with natural mortality of trees in the stand.
5. The knowledge on loss, recruitment, and increment, expressed by the number of trees and volume units, documented in a large number of experimental areas, may be of help in determination of the amount of cut in productive and protective forests managed according to a close-to-nature silviculture.

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Procesy ztráty, dorostu a přírůstu porostů pralesovitého charakteru ve vybraných územích Pieninského národního parku (jižní Polsko)

ABSTRAKT: Studie byla provedena během let 1987–1997 ve čtyřech porostech ležících v nižším horském stupni, které reprezentovaly rostlinnou asociaci *Carici-Fagetum abietetosum* (výzkumné plochy Facimiech a Walusiówka) a přechodné společenstvo mezi *Dentario glandulosae-Fagetum* a *Carici-Fagetum* (výzkumné plochy Gródek a Przełęcz Sosnów). Největší objemový přírůst byl zjištěn v nesmíšeném porostu jedle bělokoré (*Abies alba*) na ploše Facimiech (9,4 m^3/ha/rok, tj. 1,4 % objemu porostu zjištěného v roce 1997), který byl ve stadiu optima (fáze stárnutí a obnovy). Nejmenší objemový přírůst byl zjištěn v porostu Gródek (5,3 m^3/ha/rok, tj. 0,9 % aktuálního porostního objemu), který byl ve stadiu dorůstání, fázi výběrného lesa. Porost Przełęcz Sosnów byl charakteristický největší mortalitou stromů (objem odumřelých stromů 13,5 m^3/ha/rok). Tento porost se nacházel v přechodu mezi stadiem dorůstání a stadiem optima; díky intenzivnímu odumírání jedle se porost rozpadal a v důsledku toho se v rámci stadia dorůstání rozvinula fáze málo diverzifikované a vrstevnaté struktury. Objem dorostu do kmenoviny byl největší v porostu Facimiech (0,05 m^3/ha/rok). Podíl jedle a buku na porostním přírůstu se ve třech jedlo-bukových (*Abies alba, Fagus sylvatica*) porostech odlišoval od podílu těchto dřevin na objemu porostu. Ve srovnání s podílem těchto dřevin na objemu porostu byl podíl jedle na porostním přírůstu menší, zatímco podíl buku byl větší. Průběh přírůstu a mortality jedle a buku podmínil progresivní proces změny v druhové skladbě porostu, který se projevil nárůstem podílu buku a poklesem zastoupení jedle. Poznatky o hodnotách úbytku, dorostu a přírůstu, vyjádřené počtem stro-

mů a objemovými jednotkami, mohou být pomocí při determinaci velikosti těžby v hospodářských lesích a v lesích ochranných, obhospodařovaných podle zásad přírodě blízkého pěstování lesů.

Klíčová slova: lesy pralesovitého charakteru; vývojová stadia a fáze; odumíraní jedle; *Fagus sylvatica*; *Abies alba*

Corresponding author:

Prof. Dr. hab. Andrzej Jaworski, Agricultural University, Faculty of Forestry, Department of Silviculture,
ul. 29 Listopada 46, 31-425 Cracow, Poland
tel.: + 48 12 662 50 50, fax: + 48 12 411 97 15, e-mail: ajaworski@ar.krakow.pl