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Andrzej Jaworski, Zbigniew Kołodziej, Mariusz Łapka

Mortality, recruitment, and increment of trees in the *Fagus-Abies-Picea* stands of a primeval character in the lower mountain zone

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Abstract: From among three stands, situated in the lower mountain zone, and representing the association *Dentario-glandulosae Fagetum,* the Łopuszna I stand, being in the growing up stage and phase of selection forest, reached the highest increment (8.5 m^3/ha/year, i.e. 1.3% of actual stand volume/ha measured at the end of the control period). Stands, Łopuszna II, being in the stage of an intensive break-up, and Łopuszna III, being in the stage of an initial break-up, reached smaller increments (5.4 and 6.3 m^3/ha/year respectively, i.e. each 0.9% of actual stand volume/ha). The greatest tree mortality occurred in stands Łopuszna II and III (14.1 and 10.5 m^3/ha/year respectively), and the smallest in the stand Łopuszna I (4.8 m^3/ha/year). The knowledge about the value of mortality, recruitment, and increment, expressed in the number of trees and in volume units, may greatly help in planning the amount of cut which would secure sustainability of the forest ecosystem in the layer of trees in the economic as well as in the protection forests, under similar stand and site conditions, managed by the selection cutting permitting to realize the conception of a close-to-nature silviculture.

Additional key words: *Abies alba, Fagus sylvatica,* development stages and phases, close-to-nature silviculture

Address: A. Jaworski, K. Kołodziej, M. Łapka: Departament of Silviculture, Agricultural University of Cracow, 29 Listopada 46, 31-425 Kraków, e-mail: ajaworski@ar.krakow.pl

Introduction

A constant amount of organic substance of the over-ground part in the phase of a relative equilibrium is a feature of forests of a primeval character (Bormann and Likens 1979). This equilibrium, expressed by stand volume, is associated with three natural, separate, and partly antagonistic processes: tree mortality, recruitment, and increment (Dziewolski and Rutkowski 1987).

There are three basic causes of tree dying in primeval forests. The first cause consists of unfavorable light conditions and inadequate space for growth of trees from the lower, and possibly middle layer. This results in the process of natural stand thinning. The second cause, typical for primeval forests, is dying of trees due to physiological old age, i.e. reaching natural death by trees. The third cause is closely connected with the second one, because the trees reaching old age are frequently overturned or broken (Korpel 1989).

The process of recruitment is associated with reaching by trees of the young generation of a definite size, and passing over a certain d.b.h. threshold. Thus, including a part of tree population into the recruitment is of a conventional character.

While the volume increment of the stem of a single tree is the result of the increase in its height and diameter, and change of its form, the volume increment of a stand is connected not only with all these changes in tree dimensions, but also with changes in the number of trees forming the stand (mortality and recruitment). The process of increment and its value in primeval forests depends on several factors: species and condition of individual trees, site quality, age and structure of the stand, being characteristic for definite stages and phases of development.

The determination of mortality, recruitment, and increment is possible, in the first place, by carrying out two stand measurements in assumed control periods on permanent experimental plots. Data, also concerning the stand increment, for primeval stands of Bosnia (Peručica) were presented by Pintarič (1978), and of Slovakia by Korpel (1995). In stands of a primeval character in the Polish part of the Eastern Carpathians (the Bieszczady range) this problem was studied by Jaworski and Kołodziej (2002), who also determined the tree mortality. Data concerning exclusively the increment of the lower mountain zone natural stands of the Western Carpathians are a little more numerous. Similar studies were carried out by Dziewolski and Rutkowski (1987) in the Pieniny Mountains, and Jaworski and Paluch (2002) on Mt. Babia Góra. In the Gorce range this problem was studied by Dziewolski and Rutkowski (1991), and also by Przybylska et al. (1995). Outside the Carpathians the dynamics of changes in forest resources was investigated by other authors, e.g. Poznański (1998) in the Świętokrzyski National Park.

The purpose of this study was to determine the value of mortality (with description of dead trees), recruitment, and increment of stands, and to relate them to stages of stand development.

Materials and methods

The study plots were established in 1981 in the upper part of the lower mountain zone, in the "Dolina Łopusznej" reserve situated in the Gorce National Park (Fabijanowski and Jaworski 1989). This part of the reserve, representing the association *Dentario glandulosae-Fagetum,* was quite diversified in structure of stands. Taking into account the degree of human interference, the forest complexes investigated during this study were of a primeval, and in some places of a natural character, which was concordant with the definition of Schuck et al. (1994). The stages and phases of stand development in 1991 and 2001 are presented in table 1.

The initial measurements were completed in the field in August of 1991 (Jaworski and Skrzyszewski 1995), while the control measurements were carried out in 2001. They included the measurement of d.b.h ($\geq$6 cm) and height of all trees, with an exception of slanting ones. Trees with d.b.h. $\geq$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

Table 1. Location and general characteristics of study plots established in the "Dolina Łopusznej" reserve

Study plot		Łopuszna I (s.p.I)	Łopuszna II (s.p.II)	Łopuszna III (s.p.III)
Geographic coordinates		49°32'21''N 20°07'54''E	49°32'14''N 20°08'12''E	49°39'17''N 20°07'56E
Location (compartment)		72	71	72
Size (ha)		0.6	0.5	0.5
Exposure		SW	S	SW
Slope (°)		12–15	15–20	19
Altitude (m)		1025	990	1020
Species composition by volume 2001 (%)				
Abies alba		8.1	23.7	12.7
Fagus sylvatica		83.6	23.6	81.0
Picea abies		8.3	52.7	6.3
Volume in 2001 (m^3/ha)		641.58	601.78	714.01
Plant association		*Dentario glandulosae-Fagetum*		
Forest site type		Mountain forest		
Stage and phase of development	1991	growing up stage phase of selection forest	optimum stage phase of aging advanced phase of regeneration	optimum stage initiation of phase of aging
	2001	growing up stage phase of selection forest	intensive break-up stage advanced phase of regeneration	initiation of break-up stage advanced phase of aging and regeneration

growth. In each plot the stage and phase of stand development was determined, using criteria assumed by Korpel (1989, 1995).

The stand volume and basal area per hectare were calculated using a computer program "Zasoby", which was worked out by J. Ptak, and based on volume tables of Grundner – Schwappach (1952). Only trees of d.b.h. ≥8 cm were taken into account in this study.

To calculate stand volume in 1991 and volume of dead trees the height curve plotted on the basis of 1991 measurements was used, while stand volume in 2001 and volume of recruitment were calculated using the height curve plotted on the basis of 2001 measurements.

Calculations of the 10-year current volume increment comprised at first the control of the number of trees:

$$N_{01} - N_{91} + N_L - N_R = 0$$

where:
N_{91} – number of trees at the beginning of the period (1991),
N_{01} – number of trees at the end of the period (2001).
N_L – number of trees that died (loss) during 1991–2001,
N_R – number of trees qualified as recruitment during 1991–2001.

Volume increment (I_V) during 1991 – 2001 was calculated according to the formula:

$$I_V = V_{01} - V_{91} + V_L - V_R \text{ (m}^3\text{/ha/10 years)}$$

where:
V_{91} – volume at the beginning of the period (1991),
V_{01} – volume at the end of the period (2001),
V_L – volume of trees that died (loss) during 1991–2001,
V_R – volume of trees qualified as the recruitment during 1991–2001.

According to the same method the increment of basal area $I_{(G)}$ was calculated.

The calculated values of stand increment and volume were used to calculate the mean annual mortality, recruitment, and increment in relation to the number and volume of living trees in the stand in 2001.

Results

Mortality, recruitment, and increment

Łopuszna I

In this stand during the control period 32 trees per hectare (15 beeches, 15 firs, and 2 spruces) were lost due to mortality. Their volume was 48.39 m^3/ha. There were 12 firs per hectare which grew up to d.b.h. ≥8 cm. Their volume was 0.19 m^3/ha (Table 2). The greatest annual mortality in relation to the number of trees of a given species was found for fir (1.2%), then for beech (0.7%) and spruce (0.4%) (Table 3). Also the annual mortality expressed by volume in relation to volume of a given species was grater for fir (2.8%) than for beech (0.6%) and spruce (0.6%) (Table 3). The mean annual volume increment during the pe-

Table 2. Mortality, recruitment, and volume increment in 1991–2001

Species	1991		2001		Mortality 1991–2001		Recruitment 1991–2001		Increment 1991–2001	
	Number of trees N	Volume V	Number of trees N	Volume V	Number of trees N_L	Volume V_L	Number of trees N_R	Volume V_R	$I_V = V_{01} - V_{91} + V_L - V_R$	
	No. trees/ha	m^3/ha	No. trees/ha	m^3/ha	No. trees/ha	m^3/ha	No. trees/ha	m^3/ha	m^3/ha/10 years	%
Łopuszna I										
Fagus sylvatica	243	496.91	228	536.52	15	30.92	–	–	70.53	82.9
Abies alba	132	56.25	129	52.11	15	14.37	12	0.19	10.04	11.8
Picea abies	55	51.54	53	52.95	2	3.10	–	–	4.51	5.3
Total	430	604.70	410	641.58	32	48.39	12	0.19	85.08	100.0
Łopuszna II										
Fagus sylvatica	68	162.71	88	142.15	8	29.82	28	0.80	8.46	15.7
Abies alba	48	139.93	50	142.38	2	12.04	4	0.13	14.36	26.6
Picea abies	196	384.92	144	317.25	58	99.01	6	0.15	31.19	57.7
Total	312	687.56	282	601.78	68	140.87	38	1.08	54.01	100.0
Łopuszna III										
Fagus sylvatica	170	601.15	156	578.39	16	75.05	2	0.02	52.27	82.5
Abies alba	92	86.88	82	90.93	14	7.00	4	0.04	11.01	17.4
Picea abies	58	67.41	38	44.69	24	22.83	4	0.05	0.06	0.1
Total	320	755.44	276	714.01	54	104.88	10	0.11	63.34	100.0

Table 3. Mean annual mortality, recruitment, and increment in relation to actual (2001) numbers or volume of living trees

Species	Ratio between the number of dead trees and the number of living trees	Ratio between the volume of dead trees and the volume of living trees	Ratio between the number of recruitment trees and the number of trees in stand	Ratio between the volume increment and the stand volume
	%			
Łopuszna I				
Fagus sylvatica	0.7	0.6	–	1.3
Abies alba	1.2	2.8	0.9	1.9
Picea abies	0.4	0.6	–	0.9
Total	0.8	0.8	0.3	1.3
Łopuszna II				
Fagus sylvatica	0.9	2.1	3.2	0.6
Abies alba	0.4	0.8	0.8	1.0
Picea abies	4.0	3.1	0.4	1.0
Total	2.4	2.3	1.3	0.9
Łopuszna III				
Fagus sylvatica	1.0	1.3	0.1	0.9
Abies alba	1.7	0.8	0.5	1.2
Picea abies	6.3	5.1	1.1	0.03
Total	2.0	1.5	0.4	0.9

riod of 10 years was 8.51 m^3/ha (Table 2), which was 1.3% in relation to stand volume in 2001 (Table 3). The mean annual basal area increment during the control period reached 0.39 m^2/ha (Table 4).

Łopuszna II

During 1991–2001 mortality amounted to 68 trees per hectare, mostly spruce (58 trees/ha). In recruitment (38 trees/ha) beech dominated (28 trees/ha) (Table 2). The greatest mean annual loss in the number of trees in relation to the number of living trees in 2001 occurred in the case of spruce (4.0%), then beech (0.9%) and fir (0.4%) (Table 3).

During the period of 10 years volume of mortality was 140.87 m^3/ha, and volume of recruitment 1.08 m^3/ha (Table 2). The ratio between volume of mortality of trees of all species and the stand volume in 2001 was 0.8% (Table 4). Volume increment reached the value of 5.40 m^3/ha/year, including almost 58% of spruce (Table 2). The annual stand volume increment was 0.9% (Table 3), and increment of fir and spruce was mainly responsible for this result. Basal area increment reached 0.38 m^2/ha/year (Table 4).

Łopuszna III

In the analyzed 10-year period 54 trees died per hectare, predominantly spruce (24 trees/ha) (Table 2).

In this stand the ratio between the number of dead trees per year and the number of trees in the stand was 2.0%. The greatest annual loss in the number of trees in relation to the number of trees of a given species was found for spruce (6.3%), while that for fir was 1.7%, and for beech 1.0% (Table 3). The number of trees in recruitment reached 10 trees/ha (4 spruces, 4 firs, and 2 beeches) (Table 2).

Volume of mortality during the control period was 104.88 m^3/ha, while that of recruitment only 0.11 m^3/ha. Volume increment reached 6.33 m^3/ha/year (Table 2), while that of basal area 0.34 m^2/ha/year (Table 4). Mainly beech decided about increment (almost 83% in volume increment). The annual per cent of stand volume increment during 1991–2001 reached the value of 0.9 (Table 3).

Characteristics of dead trees

Łopuszna I

Among dead trees (32 trees/ha) (Table 2), trees of diameter class I prevailed (37%) (Table 5). In the case of beech, these were usually the trees growing in the middle layer of the stand (56%), and among them specimens of a lowered vitality (67%) and a lower rate of growth (67%) prevailed. Among dead firs the majority was from the lower stand layer (56%), of a normal (44%) and lowered vitality (56%) and a lowered rate of growth (67%) (Table 5). The ratio between the number of dead beech trees (during 1991–2001) and the number of living ones was the greatest in the lower layer (23.1%), while in the case of fir and spruce it was the greatest in the upper layer (29.4% and 18.2% respectively) (Table 6).

Łopuszna II

In this stand, spruce dominated among dead trees (58 from among 68 trees/ha) (Table 2). Among dead spruces the trees of d.b.h. ≥36 cm prevailed (59%), and they were mainly from the upper stand layer

Table 4. Mortality, recruitment, and increment expressed in m^2/ha of basal area during 1991–2001

Species	Stand basal area		Mortality 1991–2001 G_L*	Recruitment 1991–2001 G_R*	Increment 1991–2001 $I_G^* = G_{01}–G_{91}+ G_L–G_R$	
	1991 G_{91}*	2001 G_{01}*				
	m^2/ha		m^2/ha/10 years			%
			Łopuszna I			
Fagus sylvatica	34.26	34.96	2.22	–	2.92	75.3
Abies alba	5.67	5.01	1.38	0.08	0.64	16.5
Picea abies	4.62	4.69	0.25	–	0.32	8.2
Total	44.55	44.66	3.85	0.08	3.88	100.0
			Łopuszna II			
Fagus sylvatica	11.12	10.27	2.00	0.21	0.94	24.9
Abies alba	8.92	9.25	0.73	0.03	1.03	27.2
Picea abies	26.14	21.12	6.88	0.05	1.81	47.9
Total	46.18	40.64	9.61	0.29	3.78	100.0
			Łopuszna III			
Fagus sylvatica	38.02	35.63	4.60	0.01	2.20	64.3
Abies alba	7.16	7.50	0.68	0.02	1.00	29.3
Picea abies	5.36	3.61	1.99	0.02	0.22	6.4
Total	50.54	46.74	7.27	0.05	3.42	100.0

*See explanations in the text

(66%). These trees were chiefly of a normal (55%) and lowered (41%) vitality, and a normal (41%) and lowered (38%) rate of growth (Table 5).

The ratio between the number of dead beeches and spruces and the number of living ones was the highest in the middle stand layer (33.3% and 66.7% respectively), while dead firs occurred only in the upper layer, and their ratio between dead and living trees was 6.7% (Table 6).

Łopuszna III

During the control period spruce prevailed among dead trees (24 out of 54 trees/ha), while mortality of beech (16 trees/ha) and fir (14 trees/ha) was smaller (Table 2). Dead spruce trees were mostly from the diameter class IV (42%) and classes I and II (50% in total), from the upper (42%) and middle (33%) stand layers, of a normal (58%) and lowered (42%) vitality, and a normal (42%) and lowered (58%) growth tendency. Dead beech trees were from higher diameter classes (IV–VII) (75%), middle and upper stand layers (50% each), mainly of a lowered vitality (75%), and of a normal and lowered growth rate (50 and 38% respectively). Among firs, trees from the diameter class II (57%), from the lower and middle stand layer (43% each) prevailed, and all of them were of a lowered vitality and a lowered rate of growth (Table 5).

The ratio between the number of dead beeches and spruces and the number of living trees of these species was the greatest in the middle stand layer (36.4% and 133.3% respectively), while that for fir in the lower layer (25%) (Table 6).

Discussion

Processes of the mortality, recruitment, and increment of trees in the forest community correspond to the processes of death, birth, and growth of basic factors of the development of every complex ecological system (Dziewolski and Rutkowski 1987). The description of these phenomena and estimation of their value are the subject of research concerning natural forest ecosystems, and they constitute a measurable index of their stability. They may also have a significant importance for forestry based on principles of a close-to-nature silviculture (Vezina 1959, Leibundgut 1982, Schütz 1994). A quantitative expression of the processes taking place also permits to obtain a more detailed knowledge about stages and phases of development of the primeval forest described by Leibundgut (1959, 1982) and Korpel (1989, 1995).

It has been accepted that processes of natural mortality, recruitment, and increment in the investigated stands of the lower mountain zone were related to the stage and phase of stand development. The mortality process concerned trees of all diameter classes (Table 5, Figs. 1–4).

Tree mortality in our investigations had the smallest value in the growing up stage (plot I – 4.8 m^3/ha/year), and the greatest in the stage of advanced break up (plot II – 14.1 m^3/ha/year). In the study carried out in the Bieszczady Mountains the mortality of the smallest value occurred in the growing up stage, phase of a many-storied structure with symptoms of

Table 5. Characteristics of dead trees

Species		Diameter class*								Stand layer				Vitality index				Index of growth tendency			
										according to IUFRO classification **											
		I	II	III	IV	V	VI	VII	Σ	100	200	300	Σ	10	20	30	Σ	1	2	3	Σ
Łopuszna I (0,6 ha)																					
Fagus sylvatica	No.trees	2	1	2	2	2	–	–	9	2	5	2	9	–	3	6	9	1	2	6	9
	%	22.2	11.2	22.2	22.2	22.2	–	–	100	22.2	55.6	22.2	100	–	33.3	66.7	100	11.1	22.2	66.7	100
Abies alba	No.trees	5	–	1	1	2	–	–	9	3	1	5	9	–	4	5	9	–	3	6	9
	%	55.6	–	11.1	11.1	22.2	–	–	100	33.3	11.1	55.6	100	–	44.4	55.6	100	–	33.3	66.7	100
Picea abies	No.trees	–	–	–	1	–	–	–	1	1	–	–	1	–	1	–	1	–	1	–	1
	%	–	–	–	100	–	–	–	100	100	–	–	100	–	100	–	100	–	100	–	100
Total	No.trees	7	1	3	4	4	–	–	19	6	6	7	19	–	8	11	19	1	6	12	19
	%	36.8	5.2	15.8	21.1	21.1	–	–	100	31.6	31.6	36.8	100	–	42.1	57.9	100	5.2	31.6	63.2	100
Łopuszna II (0,5 ha)																					
Fagus sylvatica	No.trees	–	–	–	2	2	–	–	4	1	3	–	4	–	–	4	4	–	2	2	4
	%	–	–	–	50	50	–	–	100	25	–	–	100	–	–	100	100	–	50	50	100
Abies alba	No.trees	–	–	–	–	1	–	–	1	1	–	–	1	–	1	–	1	–	–	1	1
	%	–	–	–		100	–	–	100	100	–	–	100	–	–	–	100	–	–	100	100
Picea abies	No.trees	–	4	8	13	4	–	–	29	19	10	–	29	1	16	12	29	6	12	11	29
	%	–	13.8	27.6	44.8	13.8	–	–	100	65.6	34.4	–	100	3.4	55.2	41.4	100	20.7	41.3	38.0	100
Total	No.trees	–	4	8	15	7	–	–	34	21	13	–	34	1	17	16	34	6	14	14	34
	%	–	11.7	23.6	44.1	20.6	–	–	100	61.8	38.2	–	100	2.9	50	47.1	100	17.6	41.2	41.2	100
Łopuszna III (0,5 ha)																					
Fagus sylvatica	No.trees	–	1	1	2	2	1	1	8	4	4	–	8	–	2	6	8	1	4	3	8
	%	–	12.5	12.5	25.0	25.0	12.5	12.5	100	50.0	50.0	–	100	–	25.0	75.0	100	12.5	50.0	37.5	100
Abies alba	No.trees	1	4	–	2	–	–	–	7	1	3	3	7	–	–	7	7	–	–	7	7
	%	14.2	57.2	–	28.6	–	–	–	100	14.2	42.8	42.8	100	–	–	100	100	–	–	100	100
Picea abies	No.trees	3	3	1	5	–	–	–	12	5	4	3	12	–	7	5	12	–	5	7	12
	%	25.0	25.0	8.3	41.7	–	–	–	100	41.7	33.3	25.0	100	–	58.3	41.7	100	–	41.7	58.3	100
Total	No.trees	4	8	2	9	2	1	1	27	10	11	6	27	–	9	18	27	1	9	17	27
	%	14.8	29.7	7.4	33.3	7.4	3.7	3.7	100	37.0	40.8	22.2	100	–	33.3	66.6	100	3.7	33.3	63.0	100

*Diameter classes: I – 8.0–15.9 cm, II –16.0–23.9 cm, III – 24.0–35.9 cm, IV – 36.0–51.9 cm; V– 52.0–71.9 cm; VI –72.0–91.9 cm; VII ≥92 cm,
** See explanations in the text

aging (5.8 m³/ha/year), and of the greatest value also in the growing up stage, phase of a many-storied structure, but on another plot (7.6 m³/ha/year), while in the optimum stage, phase of aging, it was 7.1 m³/ha/year (Jaworski and Kołodziej 2002).

The above data indicate how diversified are the values expressing mortality of trees growing in different forest complexes.

The results, mentioned above, were based on a sample, too small to draw a far reaching conclusions concerning the relationship between the developmental stage and the value of tree mortality. Nevertheless, it may be concluded with a considerable probability that in order to fully describe a natural stand it is not enough to state the stage of its development, but also the phase and degree of its advancement should be given. Besides, the loss of trees does not only consist of their death due to reaching a physiological old age, which decides about the stage of break up, but it also is caused by biotic and abiotic factors that may disturb a natural cycle of development described by Korpel (1995) or Leibundgut (1959).

In studies on the dynamics of natural forests the mortality of trees may also be expressed by the ratio between the number of trees which died during the study period (control period) and the number of living trees at the end of the period (Table 3) or the number of trees at the beginning of the period (Szwagrzyk and Szewczyk 2001).

The annual tree mortality in our study calculated by the latter method was the smallest in the growing up stage (plot I – 0.7%), intermediate in the initial phase of the break up stage (plot III – 1.7%), and the greatest in the advanced stage of intensive break up (plot II – 2.2%). In a stable beech-fir-spruce stand of the lower mountain zone of Mt. Babia Góra the annual tree mortality was 1.25% (Szwagrzyk and Szewczyk 2001). The data presented above indicate that

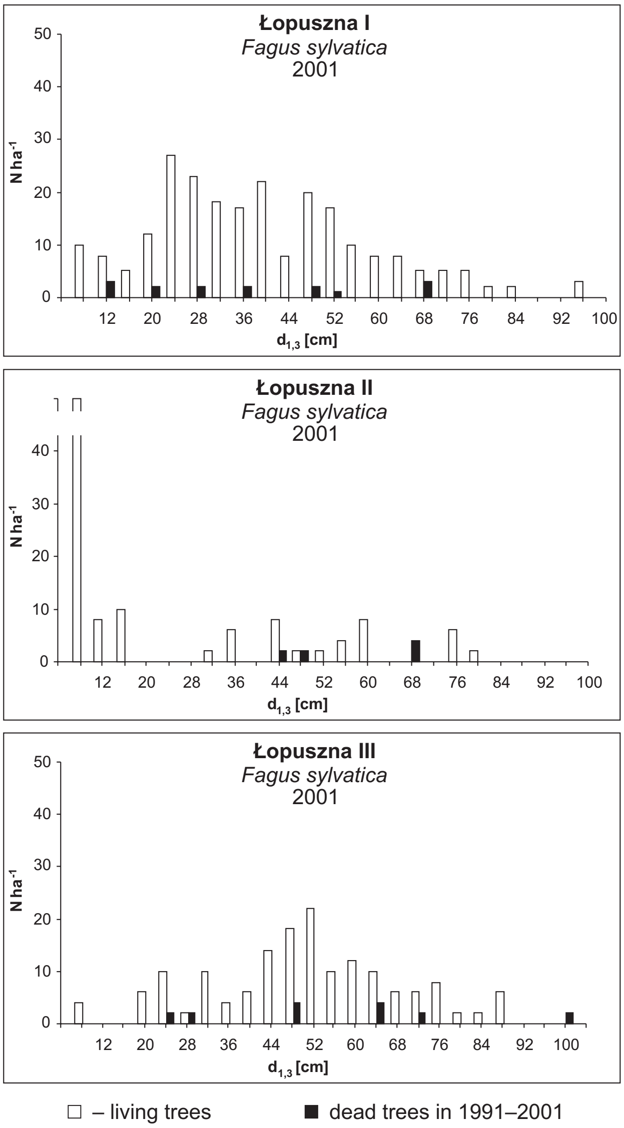

Fig. 1. D.b.h. distribution of living and dead trees for common beech

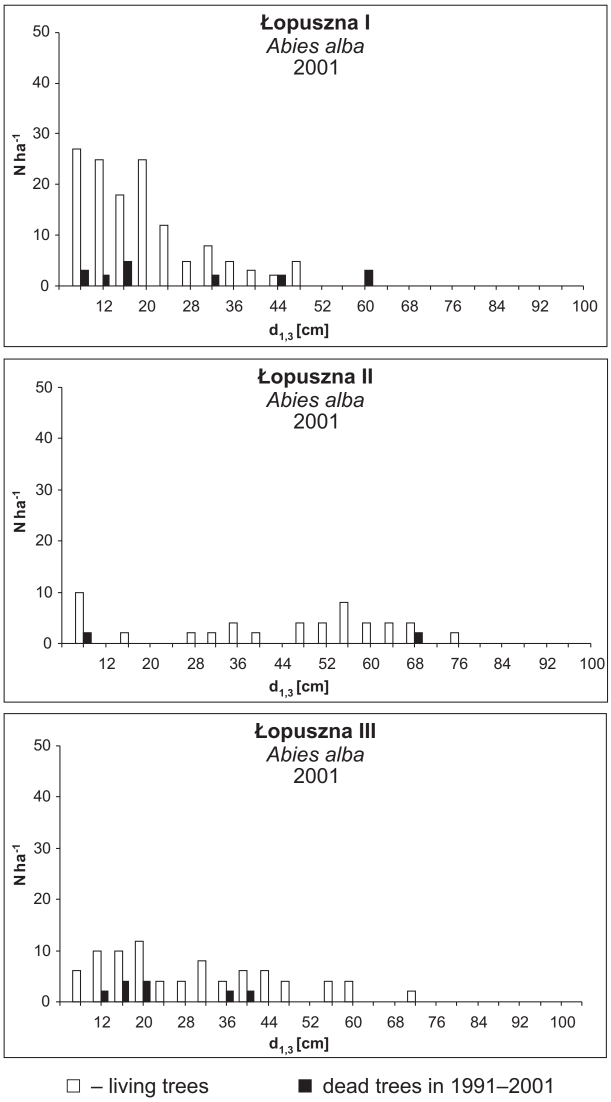

Fig. 2. D.b.h. distribution of living and dead trees for silver fir

the stand is stable when tree mortality is about 1%, while if this index reaches 2% its break up begins. Authors of this paper are of the opinion, however, that mortality expressed by the per cent of dead trees alone (without giving their volume) does not fully characterize the processes taking place.

The study presented in this paper showed that the greatest increment was reached by the stand in the growing up stage, and the smallest in the break up stage (Table 2). Similar conclusions were drawn from studies carried out in the Bieszczady Mountains, Mt. Babia Góra, and Slovakia (Jaworski and Kołodziej 2002, Jaworski and Paluch 2002, Korpel 1995). While in the Pieniny Mountains the greatest current volume increment was found in a fir stand showing characters of the optimum stage, phase of aging, and a smaller one, although very diversified, was found in three fir-beech stands in the growing up stage (Jaworski and Podlaski – unpublished data). It may be supposed that increment depends on the developmental stage and phase to a lesser degree than on vitality of large trees, considerably contributing to volume and occupying much space in the stand. This to a certain degree was indicated by studies of Jaworski and Paluch (2002).

The investigated stands reached the annual volume increment close to the increments of stands of a primeval character in the Babia Góra National Park, Pieniny National Park and Gorce National Park (Władysław Orkan and Dolina Łopusznej reserves, as well as in the Peručica reserve (Sutjeska National Park of Bosnia), but it was smaller than in the Dobročsky Prales reserve in Slovakia (Table 7).

Fir in sample plot I and spruce in plots II and III was most severely affected by tree mortality during the period 1991–2001. This was expressed by the ratio between the number of dead trees and the number of living trees, and the ratio between volume lost due

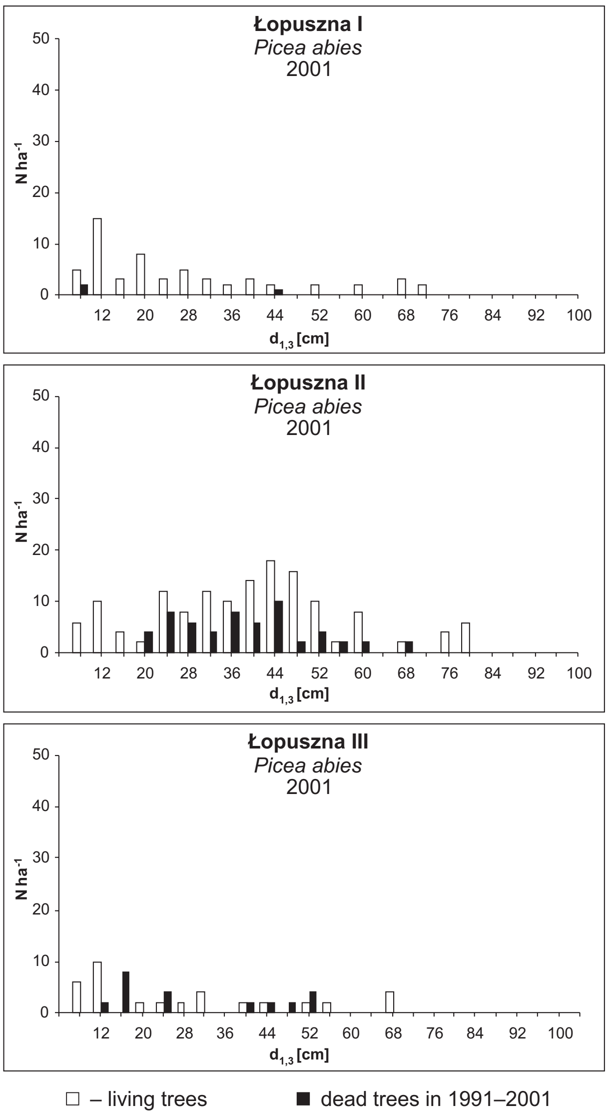

Fig. 3. D.b.h. distribution of living and dead trees for Norway spruce

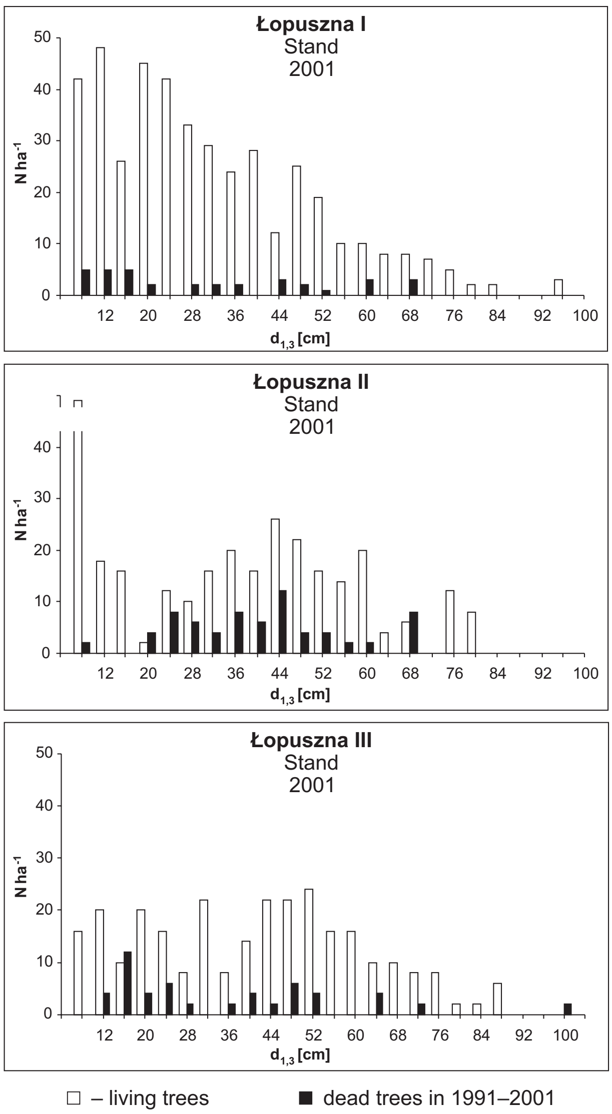

Fig. 4. D.b.h. distribution of living and dead trees in the stand

Table 6. Number and percentage of living and dead trees in respective stand layers

Stand layer acc. to IUFRO classification	Species	Number of living trees 2001		Number of dead trees 1991–2001		Ratio between the number of dead trees of a given species and the number of living trees of this species (2001) in a layer
		trees/ha	%	trees/ha	%	%
			Łopuszna I			
100	*Fagus sylvatica*	150	36.6	3	9.4	2.0
	Abies alba	17	4.1	5	15.6	29.4
	Picea abies	11	2.7	2	6.2	18.2
	Total	178	43.4	10	31.2	5.6
200	*Fagus sylvatica*	65	15.8	9	28.2	13.8
	Abies alba	50	12.2	2	6.2	4.0
	Picea abies	22	5.4	0	0	0
	Total	137	33.4	11	34.4	8.0
300	*Fagus sylvatica*	13	3.2	3	9.4	23.1
	Abies alba	62	15.1	8	25.0	12.9
	Picea abies	20	4.9	0	0	0
	Total	95	23.2	11	34.4	11.6
Total		410	100.0	32	100.0	7.8
			Łopuszna II			
100	*Fagus sylvatica*	22	7.8	2	2.9	9.1
	Abies alba	30	10.6	2	2.9	6.7
	Picea abies	94	33.3	38	56.0	40.4
	Total	146	51.7	42	61.8	28.8
200	*Fagus sylvatica*	18	6.4	6	8.8	33.3
	Abies alba	10	3.6	0	0	0
	Picea abies	30	10.6	20	29.4	66.7
	Total	58	20.6	26	38.2	44.8
300	*Fagus sylvatica*	48	17.0	0	0	0
	Abies alba	10	3.6	0	0	0
	Picea abies	20	7.1	0	0	0
	Total	78	27.7	0	0	0
Total		282	100.0	68	100.0	24.1
			Łopuszna III			
100	*Fagus sylvatica*	130	47.1	8	14.8	6.2
	Abies alba	28	10.1	2	3.7	7.1
	Picea abies	16	5.8	10	18.6	62.5
	Total	174	63.0	20	37.1	15.0
200	*Fagus sylvatica*	22	8.0	8	14.8	36.4
	Abies alba	30	10.9	6	11.1	20.0
	Picea abies	6	2.2	8	14.8	133.3
	Total	58	21.1	22	40.7	37.9
300	*Fagus sylvatica*	4	1.4	0	0	0
	Abies alba	24	8.7	6	11.1	25.0
	Picea abies	16	5.8	6	11.1	37.5
	Total	44	15.9	12	22.2	27.3
Total		276	100.0	54	100.0	19.6

Table 7. Current volume increment of selected stands of a primeval character in Poland, Slovakia, and Bosnia

Area	Volume increment m^3/ha/year	Stage and phase of development acc. to Korpel (1989, 1995)	Author
		Babia Góra National Park	
Orawski Chodnik I	6.3	optimum stage	Jaworski and Paluch 2002
Orawski Chodnik II	4.3	Break-up stage, phase of regeneration	
Pod Sokolicą	3.5	growing up stage phase of selection forest	
Dolny Płaj III	4.1	Break-up stage, phase of aging and regeneration	
Dolny Płaj IIIB	7.0	growing up stage, phase of selection forest	
Jałowiecki Potok	8.6	growing up stage, phase of selection forest	
Czarna Hala	4.3	Break-up stage, phase of regeneration	
		Gorce National Park	
Turbacz – Forest reserve Wł. Orkana	5.3	no data	Dziewolski and Rutkowski 1991
Dolina Łopusznej	6.9	initiation of break-up stage, phase of aging and regeneration	Przybylska et al. 1995
Łopuszna I	8.5	growing up stage, phase of selection forest	Data from Table 2
Łopuszna II	5.4	intensive break-up stage, advanced phase of regeneration	
Łopuszna III	6.3	iniciation of break-up stage, phase of advanced aging and regeneration	
		Pieniny National Park	
Trzy Korony	7.6	no data	Dziewolski and Rutkowski 1987
		Slovakia	
Dobročsky Prales	7.1–12.4	no data	Korpel 1995
Badin	4.7 8.6	growing up stage advanced break-up stage	
		Bosnia	
Perućica	6.4–8.8	no data	Pintarič 1978

to mortality and volume of living trees (Table 3). In other Carpathian stands of a primeval character the greatest value of mortality was estimated for fir (Szwagrzyk et al. 1995, Jaworski 2004).

The results of this study may have a great practical importance.

The value of the current volume increment, determined in this study, is the index of a potential site productivity, and it may be used when this increment is being compared with increments of managed stands of the same species composition and growing under the same site conditions.

The natural mortality process in stands of a complex vertical structure seem to be similar, to a certain degree, to tree removal during selection cutting. It may be assumed that dead trees from the upper stand layer of 60–70 cm in d.b.h. correspond to "harvesting of the crop" (Table 5). The dead trees of smaller d.b.h. from this layer, and from lower layers, correspond with selection cuttings performed in all stand layers. The natural selection taking place in such stands somehow plays a role of selection cutting (Schütz 2001), but is mainly directed toward a negative selection. However, it is difficult to suppose that "cutting" performed by natural processes taking place in the stand could agree with aims of the forestry practice..

The volume loss due to mortality in the investigated stands was diversified (Table 2). In Łopuszna I (growing up stage, phase of selection forest) it was a little over 48 m^3/ha/ 10 years (i.e. about 8% in relation to stand volume in 2001). This is a much smaller value than the value of volume increment (about 85 m^3/ha/10 years) (Table 2). This volume loss, because it is smaller than increment, is comparable to volume harvested in selection cutting corresponding to a current volume increment. It is to be expected that this stand will be increasing its volume per hectare during transition from the growing up stage to the optimum stage.

In plots Łopuszna II and III the "cutting value" was 141 and 105 m^3/ha/10 years (i.e. 23% and 15% of volume per hectare) respectively (Table 3), and it much exceeded allowable "harvesting", which should not be greater than increment during the same period (54 and 63 m^3/ha/10 years respectively). Such a volume loss disturbed the equilibrium of both stands, and this is why the break-up stage was reached there. Thus these "cuttings" were too strong to maintain a stable complex structure similar to the selection forest structure.

The stand break up found in plots II and III occurred over small areas, comprising only fragments of the plot area, and corresponded to a gap model (Shuggart 1984), where gaps, in the opinion of many ecologists, decide about regeneration and formation of structure and dynamics of forest communities (Drõssler and Lüpke 2005, Zeibig et al. 2005, Nagel et al. 2006). However, plots I and III, adjoining each other, and representing the growing up stage, the phase of a selection structure and the initial phase of the break up stage (Table 1), indicated that in the "Dolina Łopusznej" reserve the developmental stages of the primeval forest make a mosaic, which confirmed the correctness of conceptions of Leibundgut (1959) and Korpel (1995), concerning the development of the primeval forest, and based on developmental stages and phases.

Conclusions

1. The tree mortality process in the investigated stands of a primeval character included trees of all diameter and height classes.
2. In the investigated forests of a primeval character values of tree mortality and increment are connected with a stage of stand development. The growing up stage was characterized by a greater volume increment than increment in the break-up stage. The greatest loss due to mortality was found in the break-up stage.
3. The knowledge about mortality, recruitment, and increment, observed on a sufficiently large number of sample plots, and expressed in the number of trees and volume units, may be of help in planning of cutting extent in economic and protection forests managed according to the conception of a close-to-nature silviculture.

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