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Production potential and ecological stability of mixed forest stands in uplands – III. A single tree mixed stand with Douglas fir on an eutrophic site of the Křtiny Training Forest Enterprise

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ABSTRACT: The paper deals with the growth, development, production and stability of a mixed stand with a rich species composition (Scots pine, European larch, Douglas fir, oak, beech, hornbeam, lime). The stand (age 68 years) is situated at an altitude of 430 m. Since 1961, thinning measures are not applied and the stand is intentionally left to its natural development. In the course of 38 years (1961–1999), particularly Douglas fir showed exceedingly high production parameters in the given mixture (species participation increased from 16 to 28% and volume increased from 52 to 232 m³/ha). The species together with larch and beech form the basis of production and stability of the forest ecosystem. With respect to the fact it is possible to recommend, as an alternative target species composition for rich sites of the 3rd and 4th forest vegetation zones, the following species composition: larch 20–40%, Douglas fir 20–40% and beech 30–50%.

Keywords: Douglas fir; mixed stands; natural development; production; ecological stability

The project *Ecological stability and production potential of mixed forest stands in anthropically changed conditions of uplands as a background for the proposal of a target species composition* is one of the pivotal research projects conducted at the Department of Forest Establishment and Silviculture (DFES), Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry, Brno. The project is systematically carried out since the beginning of the 90s, and since 1993, it is continuously supported by the Grant Agency of the Czech Republic (Project Nos. 504/93/0793, 526/96/0649 and 526/99/1302) and since 1999 partly by the National Agency for Agricultural Research (Project No. EP9299).

The contents and main objectives of the project are evident from its title. The professional and scientific public was acquainted with it in the scientific journal *Lesnictví-Forestry*, No. 5, Vol. 43 (KANTOR 1997).

The project is based on the evaluation of a series of precisely established (in 1959–1963) and regularly monitored permanent experiment plots in mixed stands of the 2nd and 3rd forest vegetation zones. It is a case of long-term thinning trial plots where low thinning and crown thinning plots are compared with control plots. In total,

10 experimental stands are available for the Department of Forest Establishment and Silviculture (DFES) – from simple stand mixtures of beech and larch up to mixed stands with ten tree species. The areas are situated particularly in the region of the Křtiny Training Forest Enterprise (TFE). A list of the stands is given in the paper mentioned above (*Lesnictví-Forestry*, No. 5, Vol. 43, 1997).

The first, and according to our opinion particularly valuable phase of evaluation of our research is based on the analysis of time series of *control plots* which are entirely left to their natural development since the time of the establishment of experiments (in principle from the origin of the stands) being without intentional thinning measures and only dead trees are removed from them.

The long-term series of monitoring (35–40 years), extent and preciseness of plot establishment make possible to evaluate changes in species composition due to natural development, to compile the scale of mortality and vitality of particular species, to assess competition relations of trees, production potential of various mixtures and their ecological stability. These data will then serve as an exact background for the proposal of target species composition in particular site conditions of upland regions.

The paper is based on the results of a project conducted with a financial support of the Grant Agency of the Czech Republic – Grant No. 526/99/1302, National Agency for Agricultural Research (NAZV) – Grant No. EP9299 and within the Research Plan of the Faculty of Forestry and Wood Technology, Brno No. MSM 434100005.

In the Journal of Forest Science, production potential and stability of all 10 experimental stands will be gradually analysed. The first two reports were published in Vol. 44 (KANTOR, PAŘÍK 1998) and Vol. 46 (KNOTT, KANTOR 2000). Thus, the paper presented appears to be the third scientific contribution where results are given of another naturally developing stand No. 41D7 (without intentional thinning measures) in the Vranov Forest District, Třešňov. It concerns a single tree mixture with a very rich species composition consisting of 7 main species (Scots pine, larch, Douglas fir, oak, beech, hornbeam, lime). A special attention is paid to Douglas fir which attains remarkable parameters in the mixture. The compilatory part of the paper – a brief outline of the problem – deals with the production potential of Douglas fir.

BRIEF OUTLINE OF THE PROBLEM: PRODUCTION POTENTIAL OF DOUGLAS FIR

According to the recent General forest management plan for 1997, there are only 4,122 ha of Douglas fir stands in the Czech Republic (less than 0.2% of forests in the CR), i.e. for example, markedly less than in mountain pine (6,737 ha), blue spruce (13,608 ha) and locust (about 13,000 ha). Nevertheless, it is very probably a species which exhibits the highest production potential from all commercially important introduced species in the Czech Republic or even Central Europe. It is also documented by papers of German authors (e.g. TEUFFEL, KASTRUP 1998; PETERS 1997) which show that the percentage of Douglas fir in Germany was 1.1% in 1970 but in 1995 already 3.3% of forest land (about 300 thousand ha). However, an increase up to 5% of forest area is expected in the species in the future. The percentage of Douglas fir in particular Districts of the Czech Republic is illustrated in Fig. 1. Comprehensive data on the natural range, history of introduction into Europe and Czech lands but also on the production potential of Douglas fir can be found e.g. in monographs of HOFMAN (1964) and OTTO (1984).

In the country of its origin, in North America, Douglas fir grows on extensive areas from the coast of the Pacific Ocean up to alpine locations of the Cascade Range, in the south from northern Mexico and in the north up to 56° of

northern latitude. It is generally known that there are two basic subspecies, viz. var. *glauca* which grows slowly and comes from mountain continental regions of America and var. *viridis* which is a coastal fast-growing form. From the viewpoint of forestry, particularly important is var. *viridis* which is often introduced into Europe. According to HOFMAN (1964), the first consignment of Douglas fir seed to Europe was sent in 1826. The seed was sown in southern and central Britain. Our oldest planting in the Chudcnice park comes from 1843. The 70s of the 19th century are the period of the first plantations in the Czech lands. At the beginning of the 20th century, the first trial plots with Douglas fir were established. The selection of suitable Douglas fir provenances for our country was published by ŠIKA (1981) at the beginning of the 80s.

In the paper of HOFMAN (1964), a problem is analysed of the production of pure and mixed Douglas fir stands under conditions of Europe. German tables show high growing stock of timber to the top of 7 cm o.b ('Derbholz') of the principal crop of Douglas fir of the 1st site class in 50 years of age – 536 m³/ha and of the secondary crop 296 m³/ha (total volume production 832 m³/ha, i.e. mean volume increment 16.6 m³/ha per year). Even higher production show Swiss experimental stands at an altitude of 590–760 m where the growing stock at an age of 40–50 years amounted to 911–1,164 m³/ha under conditions of high stand density (700 trees per ha in 51 years). Production of our Douglas fir stands, according to HOFMAN (1964), can even exceed growing stocks in German stands nearing those in French and British stands (with more oceanic climate). Of interest are also comparisons of production possibilities of Douglas fir with those of domestic species. None of them can match with Douglas fir either in growth or production (HOFMAN 1964).

The production potential of Douglas fir has been recently intensively studied particularly in Germany (e.g. HUSS 1996; BURGBACHER, GREVE 1996; KENK, EHRING 1995; ROHLE, HEISS 1988). HUSS (1996), for example, mentions that the oldest stands of Douglas fir in forests of Freiburg reach a height of 55 m being even in this age considerably vital. Based on the fact, he concludes that Douglas fir, similarly as in America, can grow up to a height of 70–80 m. In sample plots, annual increase in

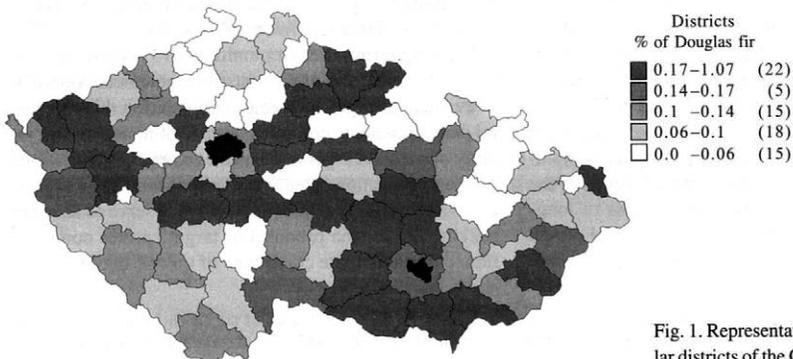


Fig. 1. Representation of Douglas fir in particular districts of the Czech Republic (SLHP 1997)

Table 1. Basic mensurational data of the control plot in the period of plot establishment (1961)

Species	Number of trees per hectare	Mean tree			Growing stock (m ³ /ha)	Stand basal area (b.a.) (m ² /ha)	Stand density	Species composition (%)
		<i>h</i> (m)	d.b.h. (cm)	<i>v</i> (m ³)				
Spruce	75	10.5	10.0	0.055	4.1	0.676	0.03	2.0
Pine	410	13.9	14.6	0.117	48.1	7.389	0.24	19.0
Larch	495	15.0	16.2	0.163	80.8	11.037	0.36	28.9
Douglas fir	325	13.0	12.8	0.159	51.7	5.614	0.20	16.3
Oak	495	10.5	7.3	0.024	12.0	2.439	0.12	9.7
Beech	730	7.4	4.7	0.015	10.8	2.076	0.12	9.8
Hornbeam	680	6.4	3.4	0.005	3.4	0.917	0.07	5.4
Lime	425	8.0	6.2	0.026	11.0	2.028	0.10	8.8
Total	3,635				221.9	32.176	1.25	100.0

standing volume amounted to 15 m³/ha exceeding all other species two-fold. BURGBACHER and GREVE (1996) mention results of research from the same region. They found that a 55-year-old Douglas fir stand reached a mean height of 31.4 m and standing volume 574 m³/ha. At an age of 75 years, mean height amounted to 40.6 m and standing volume 820 m³/ha and at 85 years, Douglas fir reached a mean height of 45.4 m and standing volume 891 m³/ha. Even higher parameters of Douglas fir stands are mentioned by KENK and EHRING (1995) from the northern part of the German Black Forest (Schwarzwald). The stand was established in 1891 being monitored from 1949 when with a mean height of 37 m the stand reached a standing volume of 703 m³/ha. In 100 years of the stand age, i.e. in 1991, mean height of the stand amounted to 50 m and standing volume 1,387 m³/ha. In addition, Douglas fir showed a high degree of stability. While during last 40 years, 23% of spruce and 35% of silver fir died particularly due to drought and snow damage, losses in Douglas fir did not exceed 3%.

With respect to the fact that volume increment in Douglas fir culminates later than in domestic conifers, it is recommended in Germany to increase rotation age to 120 years in stands with a higher percentage of the species (BURGBACHER, GREVE 1996). According to the authors, Douglas fir wood is more appreciated (on average 140 DM per m³)

on the German market at present than that of Norway spruce and silver fir (on average 110 DM per m³).

In Slovakia, production potential of Douglas fir was assessed for example by GREGUŠ (1996). He evaluated trial plots with a series of introduced species in an arboretum near Banská Štiavnica established in 1900–1913. He reports a standing volume of 1,463 m³/ha for 88-year-old Douglas fir. WOLF (1998a,b) mentions particularly high production potential of Douglas fir in Czech lands in the region of Písek. A young pure Douglas fir stand growing on a site poor in minerals in the Hůrky Training Forest District (forest type group 3K) showed a total volume production of 619 m³/ha in 31 years and in 1993–1997, the stand exhibited even 23 m³/ha per year. According to all parameters, it is a stand which markedly exceeds the 1st site class of all yield tables. Also in another stand growing on a similar poor site (forest type group 2K), mean volume increment amounted to 21 m³/ha per year (WOLF 1998a) in last 8 years. In another study, WOLF (1998b) assessed the production of a mature 113-year-old Douglas fir stand on a rich site (forest type group 4B). In 1997, 50 trees taller than 45 m were measured and 15 of them exhibited volume higher than 10 m³. Total growing stock of the stand amounted to 716 m³/ha at stand density 0.6–0.7 and volume increment reached 12 m³/ha per year.

Table 2. The development of stand density (trees/ha) and mortality (%)

Species	1961	1966	26.7 (%)	25	54.5 (%)	10	60.0 (%)	10	5	50.0 (%)	100.0 (%)	Total mortality					
												to 1961		to 1966			
												<i>N</i>	(%)	<i>N</i>	(%)		
Spruce	75	55	26.7	25	54.5	10	60.0	10	5	50.0	100.0	75	100.0	55	100.0		
Pine	410	310	24.4	225	27.4	135	40.0	110	18.5	60	45.5	55	8.3	355	86.6	255	82.3
Larch	495	435	12.1	415	4.6	360	13.3	325	9.7	245	24.6	225	8.2	270	54.5	210	48.3
Douglas fir	325	255	21.5	220	13.7	180	18.2	165	8.3	140	15.2	140		185	56.9	115	45.1
Oak	495	300	39.4	225	25.0	140	37.8	100	28.6	40	60.0	40		455	91.9	260	86.7
Beech	730	595	18.5	480	19.3	390	18.8	360	7.7	285	20.8	285		445	61.0	310	52.1
Hornbeam	680	435	36.0	305	29.9	185	39.3	170	8.1	100	41.2	90	10.0	590	86.8	345	79.3
Lime	425	285	32.9	190	33.3	145	23.7	135	6.9	110	18.5	105	4.5	320	75.3	180	63.2
Total	3,635	2,670	26.5	2,085	21.9	1,545	25.9	1,375	11.0	985	28.4	940	4.6	2,695	74.1	1,730	64.8

Analysis of the production of Douglas fir in mixed stands is much more difficult than in pure stands. In the region of its origin, Douglas fir grows in pure as well as mixed conifer stands with Sitka spruce, hemlock and grand fir. With respect to the fact and based on previous studies, HOFMAN (1964) considers spruce to be the best temporary admixture in Douglas fir groups and stands. Similar silvicultural measures are also recommended by WOLF (1998b) for the purpose of economic benefits. However, it is not quite evident that the productive mixture ensures sustainable yield.

In addition to this, stand mixtures of Douglas fir with broadleaves (usually beech) do not have to fulfil production expectations with respect to different growth dynamics. It is true particularly in those cases when sufficient silvicultural care is not applied to broadleaved species (HOFMAN 1964; BURSCHEL 1987). Problems of growing single tree mixtures of Douglas fir, beech, silver fir and Norway spruce in Baden-Württemberg were analysed in detail by TEUFFEL and KASTRUP (1998) and in urban forests of Freiburg by HUSS (1996). It is emphasized here that Douglas fir occurs as a co-dominant and dominant species in these mixtures so that sufficient space and light appear to be inevitable preconditions.

As a matter of fact, the survey presented is not quite exhaustive, however, it allows to obtain a general view of production possibilities of the species under conditions of this republic and Central Europe.

EXPERIMENTAL STAND

The stand 41D7 in the Vranov Forest District, Forest Enterprise Křtiny, originated by the natural regeneration of a variety of species (only Douglas fir was artificially supplied) in the course of about 20 years. In the period of establishing thinning plots in 1961, mean age was 30 years and the control area of 0.20 ha (5 plots 20 × 20 m) left to its natural development without any intentional felling measures was characterized by basic parameters given in Table 1. The stand is situated on a flat area with a slight SW slope at an altitude of 430 m (49°15'34" N lat.; 16°37'06" E long.). The stand ranks among the forest type 3B₂, i.e. nutrient rich *Querceto-Fagetum* with *Asperula odorata*.

METHODS OF FIELD MEASUREMENTS AND RESULT EVALUATION

Methods of assessing the growth and development of particular experimental stands are uniform within the whole experimental project being already published in the journal *Lesnictví-Forestry* (KANTOR 1997; KANTOR, PAŘÍK 1998). Therefore, we shall discuss here only basic information.

In regular 5-year intervals (with the exception of a period 1982–1994), tree height, d.b.h., crown height, crown length and crown cover were measured in each of the trees. Every tree was assessed according to the classification scale of the Department of Silviculture.

In a 38-year time series (1961–1999), the following parameters were evaluated in each of the species under study:

- total number and tree mortality;
- frequency in height and diameter classes;
- mean stand height;
- mean d.b.h.;
- stand basal area;
- growing stock;
- stand density and species composition.

Particular species in the stand have been recorded and summarized from the height class 1 m (from height 1.3 m) and d.b.h. 1 cm.

In compiling and assessing evaluation criteria the following procedures were used:

Mortality (expressed as a percentage of died trees) in particular intervals of 5-year investigations is always related to the frequency of the previous measurement.

Data on the top height are of orientation importance. The height was determined in each of the species as a mean of 10 highest trees (at $n > 20$). At $n < 20$, the height was determined from 5 trees only.

Standing volume and the periodic volume increment derived from it are related particularly to the main crop, the volume of dead trees is included in Table 9 only.

Stand density was calculated according to the routine mensurational practices from the ratio of actual stand basal areas of particular species and table data. Species composition was derived from the reduced areas determined in such a way. Tabular stand basal areas were determined using *Growth and mensurational tables of principal species of the Czech Republic* (ČERNÝ et al. 1996) and graphical *Mensurational tables* (Taxační tabulky, 1990 – effective from the 1 Jan. 1990).

Based on this evaluation, the importance and proportion were assessed of particular species on the production potential and ecological stability of the mixed stand under study. At the same time, background data were obtained to fulfil the strategic goal of the whole project: specification and presentation of alternative proposals (variants) of target species composition in the most important management groups of stands in upland regions, in the given case for HS 45.

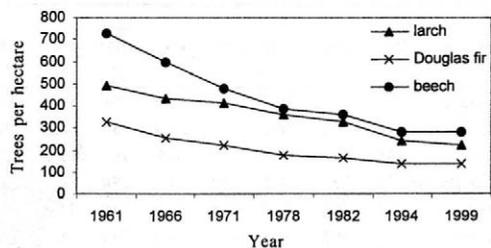


Fig. 2. Development of the number of European larch, Douglas fir and beech (trees/ha)

**RESULTS OF THE STUDY: ANALYSIS OF THE
NATURAL DEVELOPMENT OF STAND 41D7**

Basic characteristics of the control plot in stand 41D7 are given in Table 1. The table shows that it is a case of a mixed stand extraordinarily rich in species. The initial numbers of 7 species (Scots pine, European larch, Douglas fir, oak, beech, hornbeam, lime) were comparable (325–720 trees per ha); Norway spruce occurred as an interspersed species and birch, mountain ash and field maple were neglectable (these species were classified together with lime).

**THE DEVELOPMENT OF STAND DENSITY
AND MORTALITY**

High initial density of the stand (3,635 trees per ha) decreased by the year 1978 owing to competition relations in the age-differentiated stand (20–40 years) to 1,545 trees/ha (in total by 57%). In further five-year periods, the total mortality amounted to about 10%, i.e. in

limits of the natural development. According to the last investigation in 1999, at an age of 68 years some 940 trees per ha remained in the control plot (Table 2).

In assessing particular species in the given mixture, the lowest mortality was shown in European larch and Douglas fir and as for broadleaves in beech (Fig. 2). The mortality gradually increased in lime, Scots pine and hornbeam up to extreme values in oak (92%) the values being evidently affected by the mass occurrence of tracheomycosis in the 80s. The interspersed spruce totally died in a period 1994–1999.

**FREQUENCY OF SPECIES IN PARTICULAR HEIGHT
CLASSES**

Age differences up to 20 years and obviously also insufficient tending measures in young-growth stands were the reason for the extraordinary range of heights in the period of establishing the experimental plots. The unusually broad range of height classes (2–20 m!) was recorded particularly in Douglas fir (Table 3b). Light-demanding

Table 3a. The development of European larch frequency in height classes (m) and mortality in the control plot (0.20 ha)

Height class (m)	1961	1966	1971	1978	1982	1988	1994	1999					
1													
2													
3													
4													
5													
6													
7													
8													
9													
10													
11	5	5											
12	10	4											
13	9	3	1										
14	11	4	1										
15	21	8	1	3	3								
16	26	8	1	6	5								
17	14	20	1	6	1	2	1						
18	1	25		8	1	6	1	2					
19	2	14		15	1	8	1						
20		5		16		9	2	6	4	1			
21		2		15	1	15	1	6	3		1		
22				10		13	1	8	1				
23						6		9	1	3	1		
24				3		4		10	1	4		1	
25				1		9		9	1	6	2	2	
26								7	1	9	1	4	
27								3		7		6	
28								1		8		7	
29										7		9	
30										3		5	
31										1		6	
32												3	
33												1	
34													
Total	99	12	87	4	83	11	72	7	65	16	49	4	45
Per hectare	495	60	435	20	415	55	360	35	325	80	245	20	225
Mean height	15.0	11.9	17.5	15.5	19.6	16.3	21.3	19.6	23.1	21.1	26.8	24.9	28.6
Standard deviation	1.83	0.87	1.66	1.41	2.19	1.32	2.16	1.64	2.43	2.37	2.19	0.89	2.35

Table 3b. The development of Douglas fir frequency in height classes (m) and mortality in the control plot (0.20 ha)

Height class (m)	1961		1966		1971		1978		1982		1994		1999	
	1961	1966	1966	1971	1971	1978	1978	1982	1982	1982	1994	1994	1999	1999
1														
2	1	1												
3	1	1												
4	3	1	2	1	1	1								
5	4	3	1		1	1								
6	6	3	2	2										
7	2	1	1											
8	1		2	1	2	1	1	1						
9	3	1												
10	4	2	3		3	1	2	2						
11	1		1											
12	1		1	1	1	1								
13	4	1	1		1		1		1	1				
14	2		2	1	1	1								
15	2		1											
16	6		1		2	1								
17	6		3		1		2				1			
18	6		2		1				1	1				1
19	5		5		3	1	1							
20	7		8		3		1		1	1				
21			8		3		2							
22			5	1	4		5		1					
23			1		5		2		6	2				
24					6		5		1		1			
25					5		7		4		2			1
26			1				4		8		1			2
27					1		2		4		1			1
28							1		2		1			
29									3		7			1
30											4			4
31											7			5
32											2			3
33														6
34											1			4
Total	65	14	51	7	44	8	36	3	33	5	28			28
Per hectare	325	70	255	35	220	40	180	15	165	25	140			140
Mean height	13.0	6.5	16.6	10.4	19.1	11.1	22.1	9.6	24.7	19.4	29.1			30.6
Standard deviation	5.68	3.01	5.72	5.79	5.92	4.98	4.82	1.02	3.52	3.72	3.13			3.55

Scots pine and larch virtually did not occur in the height classes to 10 m in 1961 and, vice-versa, mean height of hornbeam did not exceed 6.5 m and of beech 7.5 m.

Considerable losses due to mortality in the first 5 years were found not only in subdominant and suppressed trees but in Scots pine, oak and hornbeam also in co-dominant and dominant trees.

In the course of further years, losses in conifers were particularly concentrated on suppressed and intermediate trees. As for Scots pine, also co-dominant trees died.

In broadleaves, particularly suppressed trees died and in height classes up to 10 m, only beech occurred in 1999.

Conifers gradually predominated as co-dominant and dominant trees and, in the last year of evaluation, heights up to 34 m were recorded in Scots pine, larch and Douglas fir.

In competition with conifers, all broadleaved species lagged behind so that in 1999, only 20 trees in the control plot occurred as intermediate ones (100 trees per ha).

Lime and hornbeam occupied the limits between 10 and 20 m and even 46% of beech survived in the height classes 2–10 m!

FREQUENCY OF SPECIES IN DIAMETER CLASSES

Similarly as in heights, the control plot was characterized by the marked diameter differentiation of all species, particularly in conifers (Scots pine 6–24 cm, larch 8–26 cm, Douglas fir 2–29 cm). Initial diameter at breast height (d.b.h.) of broadleaved species was 2–16 cm, only 9 trees exhibited d.b.h. > 16 cm.

In larch and Douglas fir, the high mortality of all species in 1961–1978 was concentrated on the smallest diameters, however, in Scots pine, it affected even trees of an above-average d.b.h. In broadleaves with the exception of oak, only smallwood (2–8 cm) died in the period.

In the course of next years, again trees with the lowest d.b.h. were doomed to extinction. Only in Scots pine and oak (in this case evidently due to tracheomycosis), also trees of higher diameter classes died.

The initial broad diameter distribution in conifers increased more and more and in 1999, limit values of 16–46 cm were recorded in larch, and in Douglas fir even 14–50 cm (Tab. 4b). From the viewpoint of the distribution

Table 3c. The development of beech frequency in height classes (m) and mortality in the control plot (0.20 ha)

Height class (m)	1961		1966		1971		1978		1982		1994		1999	
	1961	1966	1966	1971	1971	1978	1978	1982	1982	1994	1994	1999	1999	
1	1	1												
2	8	6	1		1		1		1		2		1	
3	13	6	3		1	1								
4	19	2	19	4	17	7	7	1	5	2	2		6	
5	14	2	9		8	1	10	1	7	1	4		3	
6	18	3	12	2	10	5	4		6		3		2	
7	12	1	13	3	8		8	2	5	1	5		3	
8	12		11	6	7	1	5	1	5	1	5		5	
9	2		4	1	3		3		4	2	3		5	
10	15	5	7	1	6	1	6		6	1	3		1	
11	11	1	6	1	4	1	3		1	1	3		2	
12	2		3		3		3		3		2		4	
13	6		8	5	3		3	1	3				1	
14	7		4		4		4		2	1	2		2	
15	6		7		5		5		6	1	7		1	
16			5		3	1	3		4	1	1		5	
17			5		4		3		3	2	4		4	
18			1		3		2		2		1		2	
19			1		3						2		3	
20					3		4		1				1	
21							3		3					
22							1		2	1	2			
23														
24									3		1			
25											1			
26											3		1	
27													2	
28													2	
29											1			
30													1	
31														
32														
33														
34														
Total	146	27	119	23	96	18	78	6	72	15	57		57	
Per hectare	730	135	595	115	480	90	390	30	360	75	285		285	
Mean height	7.4	5.0	9.0	8.3	9.6	6.3	10.7	7.4	11.5	11.2	12.6		12.8	
Standard deviation	3.76	3.20	4.33	3.00	5.04	3.12	5.33	2.99	5.82	5.26	6.72		7.00	

of these species in height classes, it is evident that extremely slender trees with unfavourable slenderness ratio (h/d ratio) survive in the stand. However, there are also larch and Douglas fir trees with markedly above-average d.b.h. and dynamic volume increment.

The distribution of broadleaved species in diameter classes in the last year of evaluation corresponds to their height position in the stand. Lime is differentiated uniformly (4–42 cm), hornbeam is concentrated in diameter classes 4–22 cm and beech largely in diameter classes 2–18 cm (only 5 trees are markedly above-average with d.b.h. 30–42 cm).

MEAN STAND HEIGHT AND D.B.H.

The development of mean heights (Table 5) shows that, in principle, two storeys occur in the stand 41D7: upper storey formed particularly by conifers and lower storey with broadleaved species (beech, hornbeam and lime).

The high mean height of oak was affected by the absence of subdominant trees.

Regular and remarkable height increment of Scots pine and larch in the course of the whole period and gradual dying of subdominant and suppressed trees ranked both species among the +1st site class of yield tables (in 68 years, mean height of Scots pine and larch 28.8 and 28.6 m, respectively). In Douglas fir, mean height was even 2 m larger in last 15 years.

Data in Fig. 3 clearly proved that Douglas fir and larch predominated in the mixture of 7 species and occurred as dominant trees.

The development of mean d.b.h. in particular species corresponds to their height distribution. In the course of the whole period 1961–1999, all three conifers were characterized by a dynamic diameter increment (Table 7). Remarkable are particularly parameters of Douglas fir in the last two measurements (in 1994 and 1999 d.b.h. was 33.6 and 35.8 cm, respectively). On the other hand, broadleaved species (particularly beech and hornbeam) with respect to the high proportion of trees in the subdominant layer show markedly lower mean d.b.h. values.

Table 4a. The development of European larch frequency in diameter classes (cm) and mortality in the control plot (0.20 ha)

Diameter class (cm)	1961	1961 - 1966	1966	1966 - 1971	1971	1971 - 1978	1978	1978 - 1982	1982	1982 - 1994	1994	1994 - 1999	1999
0													
2													
4													
6													
8	8	6	2		2	2							
10	3	2	1		1	1							
12	18	2	15	3	10	6	2	1	1	1			
14	10	1	7		6	1	6	4	1	1			
16	14	1	13	1	9	6	6	1	6	3	3	1	1
18	19		11		9	1	10	1	7	5	1	1	1
20	10		14		10	8	8	8	8	4	1		
22	8		13		13	13	13	6	6		6	1	4
24	4		4		11	11	11	13	2	4	4	1	3
26	5		3		4	5	5	10		7	7		6
28			4		2	4	4	3		11			8
30					4	2	2	3		1	7		7
32					2	4	4	3		6	2		2
34							1	3		2	5		5
36								1		2	2		2
38										3	2		2
40										1	3		3
42										1			
44													
46													
48													1
50													
Total	99	12	87	4	83	11	72	7	65	16	49	4	45
Per hectare	495	60	435	20	415	55	360	35	325	80	245	20	225
Mean d.b.h.	16.2	10.1	18.0	13.3	19.5	11.7	21.7	14.3	23.5	18.3	27.9	20.8	29.6
Standard deviation	4.66	2.59	4.75	1.96	5.54	2.51	5.22	1.48	5.28	3.09	6.02	3.01	6.18

Table 4b. The development of Douglas fir frequency in diameter classes (cm) and mortality in the control plot (0.20 ha)

Diameter class (cm)	1961	1961 - 1966	1966	1966 - 1971	1971	1971 - 1978	1978	1978 - 1982	1982	1982 - 1994	1994	1994 - 1999	1999
0													
2	6	5											
4	7	5	3	1	2	2							
6	5		5	3	2	1	1	1					
8	8	2	5	1	4	2	2	2					
10	4	1	2		2	1	1		1	1			
12	6	1	5	1	4	1	2		2	2			
14	3		2				1		1		1		1
16	4		4		4	1							
18	5		3		3		2		2	1			
20	5		4		4		6				1		1
22	4		5		1		1		7	1	2		
24	5		5		3		1				1		3
26	2		3	1	6		6		3		1		
28	1		3		3		3		4		3		2
30			2		2		3		2		1		3
32					2		2		4		3		
34					2		4		2		1		3
36									3		2		1
38							1		1		4		
40									1		2		5
42											1		2
44											4		2
46											1		1
48													3
50													1
Total	65	14	51	7	44	8	36	3	33	5	28		28
Per hectare	325	70	255	35	220	40	180	15	165	25	140		140
Mean d.b.h.	12.8	5.2	16.5	9.7	19.4	8.6	23.4	7.4	26.5	15.0	33.6		35.8
Standard deviation	7.42	2.92	7.86	7.12	8.61	3.65	8.35	0.78	7.77	4.21	8.44		9.45

Table 4c. The development of beech frequency in diameter classes (cm) and mortality in the control plot (0.20 ha)

Diameter class (cm)	1961	1961	1966	1966	1971	1971	1978	1978	1982	1982	1994	1994	1999
		-		-		-		-		-		-	
		1966		1971		1978		1982		1994		1999	
0	9	6	2	1	1	1							
2	51	13	37	7	25	9	15	2	8	2	5		4
4	40	4	36	10	27	5	21	3	20	4	9		8
6	17	4	12	4	11	1	10	1	9	3	9		9
8	10		11		11	1	10		10	1	9		7
10	6		4	1	4	1	4		5	1	4		8
12	6		9		6		7		8	2	8		8
14	2		2		3		3		4	1	4		3
16	3		2		2						2		2
18	2		2		2		3		1		1		2
20			1				1		2	1			
22			1		2						1		
24					1		1		1				1
26					1		2		1				
28							1		2		1		
30											1		1
32									1		1		1
34											1		2
36													
38													
40											1		
42													1
44													
46													
48													
50													
Total	146	27	119	23	96	18	78	6	72	15	57		57
Per hectare	730	135	595	115	480	90	390	30	360	75	285		285
Mean d.b.h.	4.7	2.6	5.7	4.1	6.5	3.4	7.7	4.1	8.7	7.6	10.6		11.1
Standard deviation	3.71	1.76	4.36	1.95	5.26	2.22	6.01	1.45	6.57	4.65	8.14		8.53

STAND BASAL AREA

Dynamics of the increase in the stand basal area (b.a.) is evidently the most objective criterion for evaluating the production potential of particular species in mixed stands developing naturally without intentional felling measures. The course of the development of b.a. both in

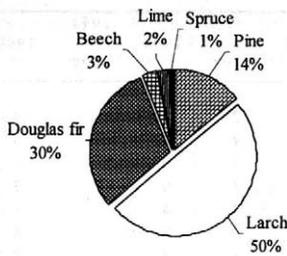
particular species and the whole stand 41D7 is evident from Table 8. The initial b.a. 32.18 m² increased by 42% to 45.85 m² during 38 years of monitoring. Two species, viz. larch (increment 5.12 m²) and Douglas fir (increment 9.48 m²) markedly participated in the increase.

If we accept the premise mentioned above, i.e. that the development of b.a. is one of the most objective criteria of

Table 5. The development of mean height and dead tree height (all in m)

Species	1961	1961	1966	1966	1971	1971	1978	1978	1982	1982	1994	1994	1999
		-		-		-		-		-		-	
		1966		1971		1978		1982		1994		1999	
Spruce	10.5	6.8	13.2	11.0	17.6	17.3	19.9		21.0	18.0	24.0		24.0
Pine	13.9	12.0	16.3	15.1	18.8	17.9	20.3	19.1	22.2	20.9	28.2		31.0
Larch	15.0	11.9	17.5	15.5	19.6	16.3	21.3	19.6	23.1	21.1	26.8		24.9
Douglas fir	13.0	6.5	16.6	10.4	19.1	11.1	22.1	9.6	24.7	19.4	29.1		30.6
Oak	10.5	8.5	13.5	12.1	15.6	13.7	17.8	16.0	20.4	19.2	25.0		27.4
Beech	7.4	5.0	9.0	8.3	9.6	6.3	10.7	7.4	11.5	11.2	12.6		12.8
Hornbeam	6.4	5.1	8.2	7.2	9.1	6.5	11.1	6.3	11.8	9.6	13.7	6.2	14.8
Lime	8.0	5.3	11.1	8.3	13.5	10.2	15.2	10.5	16.5	14.8	18.0	16.0	19.0
Total	10.0	7.1	12.6	10.0	14.6	11.5	16.5	13.8	17.9	16.3	20.7	20.3	21.7

1961



1999

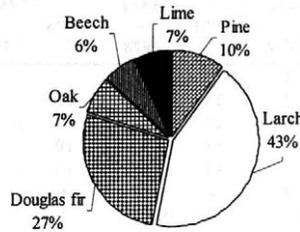


Fig. 3. 100 of the tallest trees in the control plot of 0.20 ha

Table 6. The development of top height (m)

Species	1961	1966	1971	1978	1982	1994	1999
Spruce	14.0	15.7	17.6	19.0	21.0	24.0	
Pine	16.4	18.5	21.2	21.9	23.9	30.8	31.2
Larch	17.7	20.0	23.1	25.0	26.6	29.6	31.4
Douglas fir	19.9	22.3	24.7	26.1	27.9	31.8	33.4
Oak	14.5	17.0	19.8	20.4	22.7	26.0	29.0
Beech	14.9	17.1	19.0	20.1	21.8	23.9	24.3
Hornbeam	12.3	13.8	14.9	15.4	15.9	17.1	19.9
Lime	13.7	16.8	19.1	20.1	21.3	24.0	26.1

the production potential and ecological stability of particular species in mixed stands then it is possible to compile two basic groups for the stand:

- (1) European larch,
Douglas fir, beech, lime stable increase of G
- (2) Scots pine, oak,
hornbeam stagnation or decrease of G.

GROWING STOCK OF THE PRINCIPAL CROP AND THE SECONDARY CROP

The total growing stock of the stand increased from the original 221 m³/ha in 1961 to 631 m³/ha in 1999. During the

stand development, 57% of trees died naturally. Standing volume of the trees amounted to 152.9 m³/ha (Table 9).

Production and volume increment in the mixture are based on two species, viz. larch and Douglas fir. These species amounted to 73% of the growing stock in stand 41D7 in 1999. On the other hand, Scots pine did not increase its volume due to high mortality in the course of 38 years. Four broadleaved species initially participated in the total growing stock by 16%, at the last investigation after 38 years by 20%. Volume production of oak was affected by tracheomycosis in the 80s. Standing volume of oak and lime increased in relative values dynamically (increase by 335 or 340%, respectively), absolute increment was, however, low with respect to the initial social position of both species.

On the basis of all evaluative criteria, the mixture of species can be considered to be highly productive. It is documented particularly by the periodic volume increment of the main stand which amounted to 9.8 m³/ha per year in 1982–1994 and in the last five years even 15.6 m³/ha per year.

With respect to the present development of the stand, the development of growing stock in next years was estimated using extrapolation. Providing the preservation of the dynamics of stand volume increment it is possible to expect that the main crop growing stock will reach about

Table 7. The development of mean diameter (d.b.h.) and dead tree diameter (all in cm)

Species	1961	1966	1966	1971	1971	1978	1978	1982	1982	1994	1994	1999	
	1961	1966	1971	1978	1978	1982	1994	1994	1999	1999	1999	1999	
Spruce	10.0	6.3	12.0	9.6	16.3	16.1	17.4	18.1	18.7	17.5	17.5		
Pine	14.6	11.6	16.5	14.0	18.3	15.6	21.0	18.6	22.4	17.9	28.0	22.2	29.4
Larch	16.2	10.1	18.0	13.3	19.5	11.7	21.7	14.3	23.5	18.3	27.9	20.8	29.6
Douglas fir	12.8	5.2	16.5	9.7	19.4	8.6	23.4	7.4	26.5	15.0	33.6		35.8
Oak	7.3	5.1	9.8	8.7	11.0	8.2	13.5	8.9	16.1	14.3	21.6		22.2
Beech	4.7	2.6	5.7	4.1	6.5	3.4	7.7	4.1	8.7	7.6	10.6		11.1
Hornbeam	3.4	2.3	4.4	3.2	5.1	3.1	6.6	3.1	7.2	5.2	9.4	5.8	10.1
Lime	6.2	3.1	8.2	4.7	10.8	5.6	13.1	6.9	14.6	12.1	17.5	11.1	19.3
Total	8.5	4.8	10.6	7.0	12.5	7.9	14.9	9.7	16.4	12.6	20.4	16.2	21.6

Table 8. The development of stand basal area (m²/ha) and its increase in per cent

Species	1961	1966	(%)	1971	(%)	1978	(%)	1982	(%)	1994	(%)	1999	(%)	Total increase to 1961	(%)	Total increase to 1966	(%)
Spruce	0.676	0.676		0.543	-19.7	0.238	-56.2	0.258	8.3	0.120	-53.3		-100.0	-0.676	-100.0	-0.676	-100.0
Pine	7.389	6.993	-5.4	6.273	-10.3	4.904	-21.8	4.523	-7.8	3.738	-17.4	3.784	1.2	-3.605	-48.8	-3.209	-45.9
Larch	11.037	11.808	7.0	13.451	13.9	14.071	4.6	14.788	5.1	15.724	6.3	16.156	2.7	5.119	46.4	4.348	36.8
Douglas fir	5.614	6.697	19.3	7.765	16.0	8.749	12.7	9.856	12.7	13.223	34.2	15.094	14.1	9.480	168.9	8.397	125.4
Oak	2.439	2.544	4.3	2.377	-6.5	2.166	-8.9	2.141	-1.2	1.485	-30.6	1.578	6.2	-0.862	-35.3	-0.966	-38.0
Beech	2.076	2.402	15.7	2.655	10.5	2.938	10.7	3.345	13.9	3.979	18.9	4.409	10.8	2.333	112.4	2.007	83.6
Hornbeam	0.917	0.911	-0.6	0.854	-6.3	0.785	-8.2	0.844	7.6	0.820	-2.8	0.861	4.9	-0.056	-6.1	-0.051	-5.6
Lime	2.028	2.180	7.5	2.396	9.9	2.558	6.8	2.885	12.8	3.424	18.7	3.976	16.1	1.949	96.1	1.797	82.4
Total	32.176	34.210	6.3	36.315	6.2	36.408	0.3	38.640	6.1	42.513	10.0	45.856	7.9	13.681	42.5	11.646	34.0

1,020 m³/ha at an age of 100 years and at an age of 110 years even 1,120 m³/ha. Although the estimated values are very high it is probable that the stand will reach the growing stock values.

Information on the potential production of Douglas fir can be also obtained from Fig. 4 where the development of 3 trees of the highest volume is illustrated (at an age of 68 years the volume amounted to as much as 2.8 m³).

STOCKING AND SPECIES COMPOSITION

A certain disadvantage of stocking as a criterion for assessing the production potential of mixed stands can be documented on the mixed stand 41D7. In the course of a period 1961-1999, the mensurational value ranged between 1.13 and 1.25 so that it should be a case of an 'overstocked stand'. As a matter of fact, the main cause of these high values is considerable proportion of surviving subdominant beech and lime trees of high reduced area (partial stocking) amounting to 0.22-0.33.

Therefore, from silvicultural and production aspects, of greater importance is rather comparison of the development of reduced areas (partial stocking) of particular species (Table 10). In the given case, of interest is decrease of values in Scots pine and oak and also a certain 'aggressiveness' in Douglas fir where partial stocking increased from the initial value of 0.20 to the final value of 0.34.

Species composition representing transformed data of the partial stocking is given in Table 11.

CONCLUSION

The unusually rich mixture of 7 species (Scots pine, larch, Douglas fir, oak, beech, hornbeam, and lime) from natural regeneration with additional planting of Douglas fir is particularly productive on the given site. Based on present studies, it is possible to assume that it exhibits also high ecological stability. Basic mensurational data on the stand obtained during a period 1961-1999 are given in Table 12.

Due to growth performance and competition relations, conifers prevailed as dominant trees. The dominant position obtained Douglas fir and larch, Norway spruce with its negligible initial proportion totally disappeared and pines occurred only as the highest trees of largest diameter.

Broadleaved species survive for the whole period of investigation largely as subdominant trees. In 1999, only 6 beeches, 7 limes and 7 oaks (i.e. 100 trees/ha) occurred as intermediate trees (height ≥ 25 m). With a rather similar number of trees (conifers 420 trees/ha, broadleaves 520 trees/ha) in the last year of investigation, broadleaved species (32%) participated in the growing stock by 20% only. These species are, however, irreplaceable from the viewpoint of soil improvement (litterfall) and silviculture (natural pruning of dominant and co-dominant trees). Once again, the extraordinary capacity of beech to survive for a number of decades as subdominant and suppressed trees was proved (31% of beech trees aged 68 years was assessed as smallwood).

IX. The development of growing stock and standing volume of dead trees (all in m³/ha)

Species	1961	1966	1966	1971	1971	1978	1978	1982	1982	1982	1994	1994	1999
	1961	1966	1971	1971	1978	1978	1982	1982	1994	1994	1999	1999	
Spruce	4.1	0.3	5.0	1.3	5.1	3.1	2.5	2.8	1.3	1.5	1.5		
Pine	48.1	6.2	52.5	9.5	53.9	14.4	44.8	6.0	45.0	11.8	45.6	2.5	47.7
Larch	80.8	2.7	101.8	2.3	133.9	5.1	151.9	5.9	174.1	24.7	208.5	9.2	229.6
Douglas fir	51.7	0.9	71.1	3.7	91.4	2.2	109.7	0.2	131.7	5.5	196.5		232.1
Oak	12.0	1.8	16.4	2.8	18.7	3.2	19.4	1.7	22.0	9.5	18.6		21.6
Beech	10.8	0.4	14.7	0.7	19.2	0.5	23.1	0.2	28.2	3.4	40.4		47.0
Hornbeam	3.4	0.6	3.5	0.6	3.6	0.5	3.5	0.0	3.9	0.6	4.4	0.1	5.1
Lime	11.0	0.9	14.6	0.9	19.7	0.6	23.0	0.2	27.9	3.4	38.1	0.3	48.5
Total	221.9	13.8	279.5	21.7	345.5	29.4	377.9	14.2	435.6	60.2	553.5	13.6	631.6

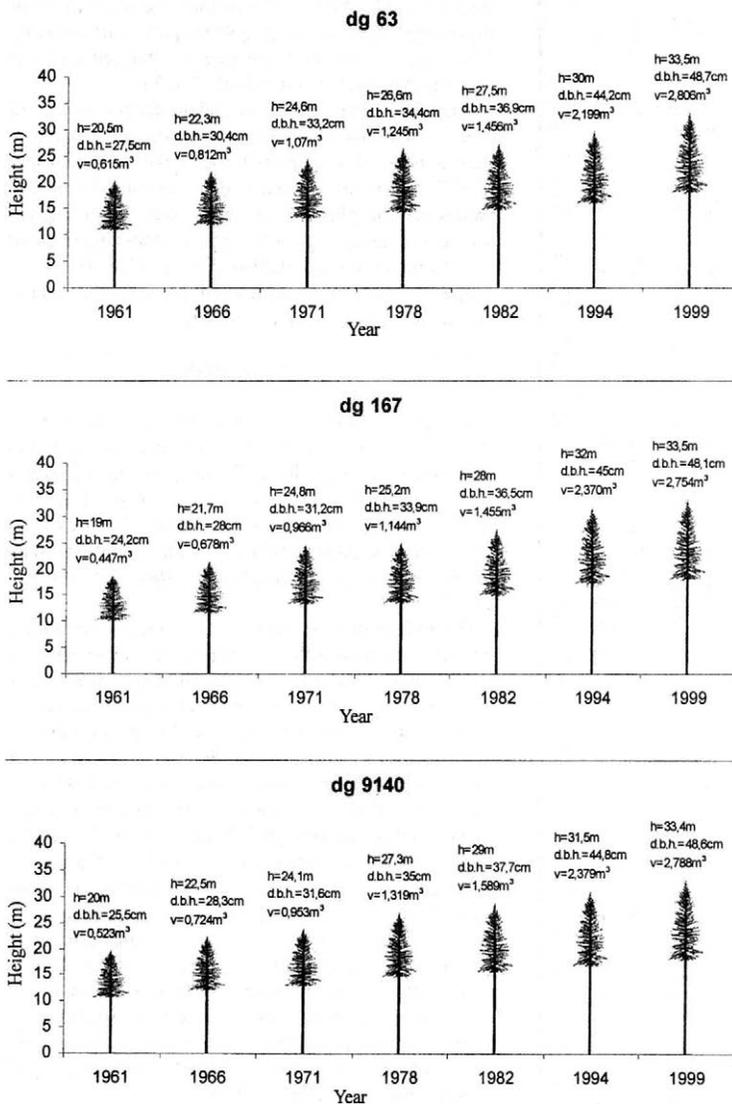


Fig. 4. The development of Douglas firs with the largest volume in 1961–1999

Table 10. Development of stand density

Species	1961	1966	1971	1978	1982	1994	1999
Spruce	0.03	0.02	0.02	0.01	0.01	0.00	
Pine	0.24	0.21	0.17	0.13	0.11	0.08	0.08
Larch	0.36	0.36	0.39	0.39	0.39	0.38	0.38
Douglas fir	0.20	0.22	0.23	0.24	0.25	0.31	0.34
Oak	0.12	0.12	0.10	0.09	0.08	0.05	0.05
Beech	0.12	0.13	0.14	0.14	0.16	0.18	0.19
Hornbeam	0.07	0.06	0.05	0.04	0.04	0.04	0.04
Lime	0.10	0.10	0.10	0.10	0.11	0.13	0.14
Total	1.25	1.22	1.19	1.13	1.15	1.16	1.22

Table 11. Development of species composition (in %)

Species	1961	1966	1971	1978	1982	1994	1999
Spruce	2.0	1.8	1.3	0.6	0.6	0.3	0.0
Pine	19.0	17.1	14.4	11.3	9.7	7.1	6.7
Larch	28.9	29.8	32.6	34.6	33.9	32.4	30.8
Douglas fir	16.3	18.0	18.8	20.8	21.9	26.7	28.1
Oak	9.7	9.5	8.5	7.7	6.8	4.2	4.0
Beech	9.8	10.4	11.4	12.5	13.6	15.2	15.5
Hornbeam	5.4	4.7	4.3	3.7	3.8	3.2	3.2
Lime	8.8	8.5	8.6	8.9	9.6	10.9	11.7
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 12. The development of stand basic data in 1961–1999

Species	Number of trees per hectare	Mean tree			Growing stock (m ³ /ha)	Stand basal area (b.a.) (m ² /ha)	Stand density	Species composition (%)
		<i>h</i> (m)	d.b.h. (cm)	<i>v</i> (m ³)				
1961								
Spruce	75	10.5	10.0	0.055	4.1	0.676	0.03	2.0
Pine	410	13.9	14.6	0.117	48.1	7.389	0.24	19.0
Larch	495	15.0	16.2	0.163	80.8	11.037	0.36	28.9
Douglas fir	325	13.0	12.8	0.159	51.7	5.614	0.20	16.3
Oak	495	10.5	7.3	0.024	12.0	2.439	0.12	9.7
Beech	730	7.4	4.7	0.015	10.8	2.076	0.12	9.8
Hornbeam	680	6.4	3.4	0.005	3.4	0.917	0.07	5.4
Lime	425	8.0	6.2	0.026	11.0	2.028	0.10	8.8
Total	3,635				221.9	32.176	1.25	100.0
1971								
Spruce	25	17.6	16.3	0.204	5.1	0.543	0.02	1.3
Pine	225	18.8	18.3	0.240	53.9	6.273	0.17	14.4
Larch	415	19.6	19.5	0.323	133.9	13.451	0.39	32.6
Douglas fir	220	19.1	19.4	0.415	91.4	7.765	0.23	18.8
Oak	225	15.6	11.0	0.083	18.7	2.377	0.10	8.5
Beech	480	9.6	6.5	0.040	19.2	2.655	0.14	11.4
Hornbeam	305	9.1	5.1	0.012	3.6	0.854	0.05	4.3
Lime	190	13.5	10.8	0.104	19.7	2.396	0.10	8.6
Total	2,085				345.5	36.315	1.19	100.0
1982								
Spruce	10	21.0	18.1	0.280	2.8	0.258	0.01	0.6
Pine	110	22.2	22.4	0.410	45.0	4.523	0.11	9.7
Larch	325	23.1	23.5	0.536	174.1	14.788	0.39	33.9
Douglas fir	165	24.7	26.5	0.798	131.7	9.856	0.25	21.9
Oak	100	20.4	16.1	0.220	22.0	2.141	0.08	6.8
Beech	360	11.5	8.7	0.078	28.2	3.345	0.16	13.6
Hornbeam	170	11.8	7.2	0.023	3.9	0.844	0.04	3.8
Lime	135	16.5	14.8	0.206	27.9	2.885	0.11	9.6
Total	1,375				435.6	38.640	1.15	100.0
1999								
Pine	55	28.8	29.4	0.867	47.7	3.784	0.08	6.7
Larch	225	28.6	29.6	1.020	229.6	16.156	0.38	30.8
Douglas fir	140	30.6	35.8	1.658	232.1	15.094	0.34	28.1
Oak	40	27.4	22.2	0.541	21.6	1.578	0.05	4.0
Beech	285	12.8	11.1	0.165	47.0	4.409	0.19	15.5
Hornbeam	90	14.8	10.1	0.056	5.1	0.861	0.04	3.2
Lime	105	19.0	19.3	0.462	48.5	3.976	0.14	11.7
Total	940				631.6	45.856	1.22	100.0

The indisputable advantage of single tree mixtures rich in species consist in their high ecological stability. Even the dieback of one or several species does not necessarily result in stand disintegration. The fact is also proved by findings from the stand 41D7 with an extremely high dieback of oak and Scots pine.

Of course, stands with such rich mixtures will not be artificially established. However, it is possible to say that:

– in natural regeneration, it is highly useful and effective to try to regenerate even interspersed species of the target species composition;

– in the natural regeneration of beech stands in the 3rd–5th vegetation zones, it is possible to recommend improvement planting with Douglas fir and larch in gappy advance regeneration (usually only about 300–500 trees per ha).

The basic mixture of larch, Douglas fir and beech which has been stabilized during its natural development in stand 41D7 (originally markedly richer in species composition) shows particularly high production parameters and, at the same time, ensures ecological stability to such an extent that it is possible to recommend it as an alternative target species composition in the 'management set of stands' No. 45. The following species composition can be recommended: larch 20–40%, Douglas fir 20–40% and beech 30–50%.

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Produkční potenciál a ekologická stabilita smíšených lesních porostů v pahorkatinách III. Jednotlivě smíšený porost s douglaskou na živném stanovišti ŠLP Křtiny

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ABSTRAKT: Ve studii je posuzován růst, vývoj, produkce a stabilita jednotlivě smíšeného porostu s pestrá druhovou skladbou (borovice, modřín, douglaska, dub, buk, habr, lípa). Porost (věk 68 let) leží v nadmořské výšce 430 m a je záměrně od roku 1961 ponechán přirozenému vývoji bez úmyslných probírkových zásahů. V průběhu časové řady 38 let (1961–1999)

vykazovala v dané směsi mimořádně vysoké produkční parametry zejména douglaska (nárůst zastoupení ze 16 % na 28 % a objemu z 52 m³/ha na 232 m³/ha). Tato dřevina společně s modřínem a bukem tvoří kostru produkce i stability posuzovaného lesního ekosystému. Z tohoto pohledu lze doporučit jako alternativní cílovou skladbu pro bohatá stanoviště 3. a 4. lesního vegetačního stupně toto rámcové zastoupení dřevin: modřín 20–40 %, douglaska 20–40 %, buk 30–50 %.

Klíčová slova: douglaska; smíšené porosty; přirozený vývoj; produkce; ekologická stabilita

Studie je v pořadí třetím sdělením v rámci širokého výzkumného projektu *Produkce a ekologická stabilita smíšených lesních porostů v antropicky se měnících podmínkách pahorkatin jako podklad pro návrh cílové skladby dřevin* (KANTOR 1997; KANTOR, PAŘÍK 1998; KNOTT, KANTOR 2000), který se řeší na Lesnické a dřevařské fakultě MZLU v Brně.

Příspěvek má výstupy charakteru aplikovaného výzkumu a hodnotí přirozený vývoj, růst, produkci a ekologickou stabilitu jednotlivě smíšeného porostu s pestrou druhovou skladbou (borovice, modřín, douglaska, dub, buk, habr, lípa) v letech 1961–1999. V celém tomto období byl porost záměrně ponechán přirozenému vývoji bez úmyslných probírkových zásahů a byly z něj odstraňovány pouze odumřelé stromy.

Porost leží na plošině mírně skloněné k jihozápadu v nadmořské výšce 430 m (zeměpisné souřadnice 49°15'34" s.š. 16°37'06" v.d.). Jeho dendrometrické parametry v době založení experimentu v roce 1961 (věk 30 let) jsou sestaveny v tab. I. Z tab. 2–9 vyplývá řada dalších významných údajů o ekologické stabilitě i produkci jednotlivých dřevin hodnoceného porostu do roku 1999.

Specifická pozornost je záměrně věnována douglasce, která v této směsi dosahuje pozoruhodných parametrů. Její počáteční zásoba 52 m³/ha v roce 1961 (při zastoupení 16 %) se za 38 let pozorování zvýšila na 232 m³/ha (zastoupení 28 %). Ve věku 68 let byla její průměrná výška 30,6 m a průměrná výčetní tloušťka 35,8 cm. U nejobjemnějších douglasek byl při posledním měření v roce 1999 zjištěn objem přesahující 2,7 m³.

Nezvykle pestrá směs sedmi druhů dřevin, vzniklá vesměs z přirozené obnovy s dosadbou douglasky, je na daném stanovišti mimořádně produktivní a na základě dosavadního šetření lze předpokládat, že vykazuje i vysokou ekologickou stabilitu.

V důsledku růstových schopností, konkurenčních a kompetičních vztahů obsadily nadúrovňový prostor jehličnany. Dominantní postavení zde získaly douglaska a modřín, smrk s nepodstatným původním zastoupením zcela uhynul, u borovice neodumřely pouze nejvyšší stromy největších tloušťkových dimenzí.

Listnaté dřeviny přežívají po celou dobu výzkumných šetření v rozhodující míře v podúrovni; v r. 1999 vrůstalo do úrovně porostu (25 m a výše) pouze 6 buků, 7 lip a 7 dubů (tj. 100 stromů na ha). Při nepřilíš rozdílném počtu stromů (jehličnany 420 ks/ha, listnáče 520 ks/ha) v posledním hodnoceném roce 1999 se tak listnáče při celkovém zastoupení 32 % podílely na zásobě porostu pouze 20 %. Byla opět potvrzena mimořádná schopnost buku přežívat dlouhá desetiletí v hluboké podúrovni (v daném porostu bylo 31 % buků ve věku 68 let hodnoceno jako nehroubí).

Nespornou výhodou druhově pestrých jednotlivě smíšených porostů je již naznačený vysoký předpoklad ekologické stability. Ani kalamitní úhyn jedné nebo několika dřevin nemusí znamenat rozpad porostu. To potvrzují i poznatky z posuzovaného porostu 41D7 s extrémně vysokým až kalamitním úhynem dubu a borovice.

Základní směs modřínu, douglasky a buku, která se přirozeným vývojem stabilizovala v původně druhově výrazně pestřejším porostu 41D7, vykazuje mimořádně vysoké produkční parametry při souběžném zabezpečení ekologické stability do té míry, že ji lze doporučit jako alternativní cílovou skladbu v hospodářském souboru 45. V širokém průměru lze zde doporučit zastoupení modřínu v rozpětí 20–40 %, douglasky rovněž v rozpětí 20–40 % a buku v rozsahu 30–50 %.

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Structure and dynamics of the lower mountain zone forests of primeval character in the Babia Góra Mt. National Park

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ABSTRACT: The d.b.h. and height of living and dead trees were measured on three study plots in 1976–1986, and on four plots in 1986–1996. The proportion of fir was 15–58%, and that of spruce 12–71% of the stand volume. The stand volume ranged from 442 to 793 m³/ha, and the numbers of trees from 140 to 346 trees/ha. The proportion of fir decreased by 1–24% of the number of trees. The volume of dead firs amounted to 63–104% of the volume of living trees.

Keywords: *Abies alba*; *Fagus sylvatica*; *Picea abies*; fir regression; changes in species composition; developmental stages and phases

Studies concerning forests of a primeval character are of great importance for the knowledge of the dynamics of natural forest ecosystems which under temperate zone conditions are the most complex ecological structures. Spruce, fir and beech are the main arborescent species of the lower mountain zone in the Western Carpathians. These forests are characterized by a slow rate of changes taking place there, and a complex space-time structure resulting from a different length of the developmental cycles of component species, and their great plasticity.

The fluctuations in numbers of trees are not synchronized in time and space, which leads to the formation of a characteristic mosaic structure of community. Spatial separateness of the units, differing in size and direction of biomass changes and frequency of individuals representing various phases of ontogenesis, is the basis for the distinguishing of the developmental stages of primeval forests (LEIBUNDGUT 1978; KORPEL 1995). In the situation of a relative stability of the environmental conditions, the communities of the Carpathian lower mountain zone reach stability on areas 40–50 hectares in size. This stability is characterized by a constant area proportion of the developmental stages, constant species composition, and the stand volume oscillations below 10% (KORPEL 1995). On the basis of simulation of area proportion of the regeneration phase, some authors are of the opinion that the area mentioned above is larger (HOLEKSA 1997). SHUGART (1984), when modelling the dynamics of natural forests, concluded that they reach the stage close to equilibrium on an area 50–100 times larger than the size of an average disturbance in the tree layer. Such an area should secure a stability of the opening size distribution. In the

Carpathian lower mountain zone forests, where small area disturbances up to 2,500 m² prevail, this area would be 25 hectares in size.

The identification of ecological processes taking place in a community, and distinguishing the degeneration or degradation caused by external factors from the oscillatory changes characteristic for communities (FALIŃSKI 1991), require detailed knowledge of their dynamics. Only then the forests of a primeval character, excluded from a direct effect of human activity, may fulfil the role of biological monitoring, making an excellent comparative material for the forests remaining under an anthropogenic stress, and in many cases making possible to determine the causes of the disturbances taking place.

The Babia Góra Mt. National Park was established in 1954, but the protection of its resources was initiated in 1933, when a newly created reserve included its considerable area. At the present moment 61% of the Park's area is under strict protection, out of which 22% is covered by the lower mountain zone forests (KALWA 1983). High scientific value of this area was recognized in 1978, when the Park was included in an international network of biosphere reserves.

The first permanent study plots of the Department of Silviculture at the Agricultural University of Cracow were established in the Babia Góra Mt. National Park in 1976. The results of studies carried out in 1976–1986 were published earlier (JAWORSKI, KARZYMARSKI 1990a,b). This paper contains a summary of investigations into the structure and dynamics of forest stands conducted in 1976–1996. The growth characteristics of the forests of Babia Góra Mt., taking into account the ingrowth, volume

losses, and tree increment variability, will be presented in a separate publication.

CHARACTERISTICS OF THE AREA AND STUDY PLOTS

The Babia Góra Mt. National Park occupies the upper part of the massif of Babia Góra Mt. (1,725 m above sea level), being the highest range of the Beskid Wysoki Mts. in the Western Carpathians. This range is mainly built of the Magura sandstones, and to a lesser extent of the hieroglyph layers with marl inserts. Acid brown, brown podzolic, and leached brown soils prevail in the lower mountain zone (ADAMCZYK 1983). The mean annual temperature is 5°C, and the total annual precipitation is 200 mm with a maximum in June–July, while the snow cover is present for 110–120 days on an average during a year (OBREBSKA-STARKLOWA 1983).

The first series of experimental plots was established in 1976 (Czarna Hala, Jałowiecki Potok, and Dolny Płaj III), and the second one in 1986 (Pod Sokolicą, Orawski Chodnik I, Orawski Chodnik II, and Dolny Płaj IIIB). Their location is shown in Fig. 1, and site characteristics are listed in Table 1.

FIELD STUDY METHODS AND PROCESSING OF RESULTS

The height and d.b.h. of all living trees, 6 cm in d.b.h. and above, and also the large timber of dead standing trees were measured, and the developmental generations were determined according to ŘEHÁK's classification (1964). In 1976, exceptionally, the height of some trees (57–84%) was measured. In the study plots Dolny Płaj IIIB, Orawski Chodnik I, and Pod Sokolicą, the large tim-

ber of dead trees lying on the ground was measured, taking into account the degree of wood decomposition (A – hard wood with bark on, B – partially decomposed wood permitting identification of species, C – strongly decomposed wood without any possibility of visual species identification), and the regeneration was counted: the upgrowth of over 0.5 m in height and below 5.9 cm in d.b.h. in a plot 10 × 60 m, and the young natural reproduction up to 0.5 m in height in a belt 2 × 60 m.

Knowing the d.b.h. and height of each tree, the volume of stands in 1986 and 1996 was determined on the basis of Grundner and Schwappach volume tables (GRUNDNER, SCHWAPPACH 1952). The stand volume in 1976, when the height of only some trees was measured, was computed using a method of smoothed height curves according to Michajlov's equation (KORF et al. 1978).

RESULTS

OPTIMUM STAGE

Orawski Chodnik I

It was found that in 1986–1996 the stand volume increased from 536 to 571 m³/ha, and the numbers of trees decreased from 202 to 188 trees/ha (Table 2). During the same period of time a proportion of large diameter trees (d.b.h. ≥ 52 cm) increased by 7% of the total number of trees (Fig. 2). The d.b.h. distribution was characterized by symmetry and strong flatness, and a small number of trees up to 16 cm in d.b.h. (Fig. 3). The coefficient of variation of d.b.h. for 1986–1996 remained at a low level of 43–46%. The structure of the growing stock was characterized by a distinct domination of the 52–71.9 cm diameter class, and a small percentage of trees over 72 cm d.b.h. The low stand volume, as for this developmental stage, resulted

Table 1. Characteristics of the study plots

Study plot	Czarna Hala	Dolny Płaj III	Dolny Płaj IIIB	Jałowiecki Potok	Orawski Chodnik I	Orawski Chodnik II	Pod Sokolicą
Location (compartment)	16	7	7	16	6	6	18
Size (ha)	0.2	0.25	0.5	0.2	0.5	0.2	0.5
Altitude (m)	1,010	970	920	890	940	940	1,045
Slope (°)	5	10	9–21	10–15	18–32	2.5	5–32
Exposition	NNW	N	NNW	NE	NNW	NNW	NNW
Association	<i>Dentario glandulosae-Fagetum festucetosum sylvaticae</i>	<i>Dentario glandulosae-Fagetum poor variant</i>	<i>Dentario glandulosae-Fagetum</i>	<i>Abieti-Piceetum montanum</i>	<i>Dentario glandulosae-Fagetum</i>	<i>Dentario glandulosae-Fagetum</i>	<i>Abieti-Piceetum montanum</i>
Composition ¹	49F 39A 12P	57A 27F 16P	54F 32A 14P	58A 26P 16F	54F 29A 17P	43F 35A 22P	71P 15A 14F
Maximum age of trees	270	240	–	270	–	–	–
Stage and phase of development	break-up stage regeneration phase	break-up stage aging and regeneration phases	growing up stage selection phase	growing up stage selection phase	optimum stage aging phase	break-up stage regeneration phase	growing up stage selection phase

¹according to volume percentage of the species at the first measurement (A – *Abies*, F – *Fagus*, P – *Picea*)



Fig. 1. Localization of Babia Góra National Park
Black rectangles – the research plots

from a high proportion of beech (60%) in the class of trees over 52 cm d.b.h. (Fig. 4).

On the basis of a high frequency of beech in the 52–71.9 cm diameter class one may expect a shortening of the aging phase and a fast break-up of the stand, being actually a repetition of a scenario of the previous cycle. The shortening of the break-up stage of the previous generation favoured the regeneration of beech, while it had a negative effect on fir, which in the 48–64 cm d.b.h. interval

showed a distinct depression in its numbers (Fig. 4). A high mortality of firs of the growing up generation was observed in 1986–1996.

The tree height distribution was characterized by a left-sided asymmetry with distinct tendency to increase (from 55 to 64% of standard deviation). The strongest asymmetry was shown by beech (Fig. 5). The percentage of trees in the upper stand layer increased from 48 to 54% in 1986–1996. In the middle and lower layers beech (39%) and spruce (33%) were most numerously represented in 1996.

The fluctuations of the upgrowth numbers in 1986–1996 showed its considerable lability (Table 4). The proportion of beech in the layer of younger upgrowth (up to 5.9 cm d.b.h.) exceeded 90%. A low frequency of beech in the lowest diameter class (Fig. 4), and a considerable amount of the upgrowth in 1986 gave evidence of a periodic appearance of its regeneration. No fir upgrowth was found in spite of abundant young natural reproduction.

In 1996, the volume of dead trees reached 329 m³/ha (58% of the volume of living trees), including 214 m³/ha of timber lying on the ground (Table 5). The rate of its decomposition in relation to the volume at the beginning of the period was 29%. Fir wood had the highest proportion in the volume of timber lying on the ground, as well as that of dead standing trees (Table 5). The comparison between the d.b.h. distribution of living trees with that of dead standing trees showed a higher mortality in the lower diameter classes, which is characteristic for the optimum stage (Figs. 3, 6).

BREAK-UP STAGE

This stage was represented by the study plots: Czarna Hala, Dolny Plaj III, and Orawski Chodnik II.

Table 2. Changes in the numbers of trees, arithmetic means of d.b.h., height and stand volume in 1986–1996

Sample plot	Species	1986						1996					
		<i>N</i>		d.b.h.	\bar{h}	<i>V</i>		<i>N</i>		d.b.h.	\bar{h}	<i>V</i>	
		(No./ha)	(%)	(cm)	(m)	(m ³ /ha)	(%)	(No./ha)	(%)	(cm)	(m)	(m ³ /ha)	(%)
Dolny Plaj IIIB	<i>Abies</i>	56	21	45.9	24.8	177.70	32	56	20	48.4	25.1	196.01	34
	<i>Fagus</i>	128	48	39.6	23.8	295.49	54	146	52	36.8	22.3	308.84	54
	<i>Picea</i>	82	31	27.1	17.0	78.49	14	78	28	26.8	16.5	70.89	12
	Total	266	100	37.1	21.9	551.68	100	280	100	36.4	21.3	575.74	100
Orawski Chodnik I	<i>Abies</i>	54	27	44.3	27.0	154.57	29	46	24	47.1	28.5	145.50	25
	<i>Fagus</i>	94	46	46.5	26.2	289.93	54	94	50	48.6	26.3	325.75	58
	<i>Picea</i>	54	27	34.0	22.0	91.94	17	48	26	38.6	23.7	99.92	17
	Total	202	100	42.5	25.3	536.44	100	188	100	45.7	26.2	571.17	100
Orawski Chodnik II	<i>Abies</i>	40	17	50.7	24.9	198.25	35	35	13	57.3	28.2	202.34	34
	<i>Fagus</i>	140	60	31.9	20.2	242.76	43	170	66	28.1	17.9	252.15	43
	<i>Picea</i>	55	23	38.4	22.7	125.35	22	55	21	40.1	23.3	133.48	23
	Total	235	100	36.6	21.6	566.36	100	260	100	34.5	20.4	587.97	100
Pod Sokolica	<i>Abies</i>	18	6	47.8	24.1	67.92	15	16	5	49.7	23.3	69.21	15
	<i>Fagus</i>	64	20	25.1	14.8	61.22	14	92	27	21.5	13.6	68.73	15
	<i>Picea</i>	242	74	32.4	20.4	312.57	71	238	68	33.5	20.4	326.07	70
	Total	324	100	31.7	19.5	441.71	100	346	100	31.0	18.8	464.01	100

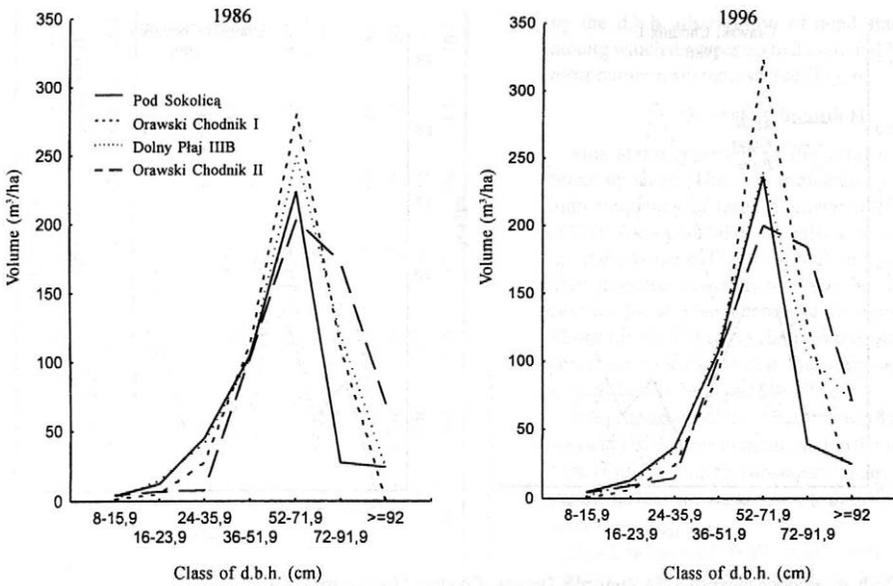


Fig. 2. Growing stock structure in the study plots Pod Sokolica, Dolny Plaj IIIB, Orawski Chodnik I and II in 1986 and 1996

Czarna Hala

In 1976–1986, the volume of this stand decreased by 28%, from 793 to 571 m³/ha, mainly as a result of the mortality of fir (138 m³/ha and 40% of the number of trees) and spruce (over 84 m³/ha and 67% of the number of trees), and then in 1986–1996 it slightly increased up to the level of 586 m³/ha (Table 3). This rapid decrease of the stand volume was accompanied by a drop of tree numbers from 215 to 140 trees/ha, and by a change in species composition, i.e. a distinct increase of the beech percentage from

49 to 66% of the stand volume, and a decrease in the percentage of spruce and fir, from 12 to 2%, and from 39 to 32%, respectively. A high proportion of trees over 72 cm d.b.h. (21% of the number of trees) (Fig. 7) indicates that the process of stand break-up has not been finished. Intensive mortality of beech, a dominant species among the largest diameter trees, should be expected (Fig. 8).

Among the trees up to 36 cm in d.b.h., fir (55%) and spruce (33%) predominated (Fig. 8).

The volume of dead standing trees in 1996 was 249 m³/ha (43% of stand volume), and the basal area of these trees

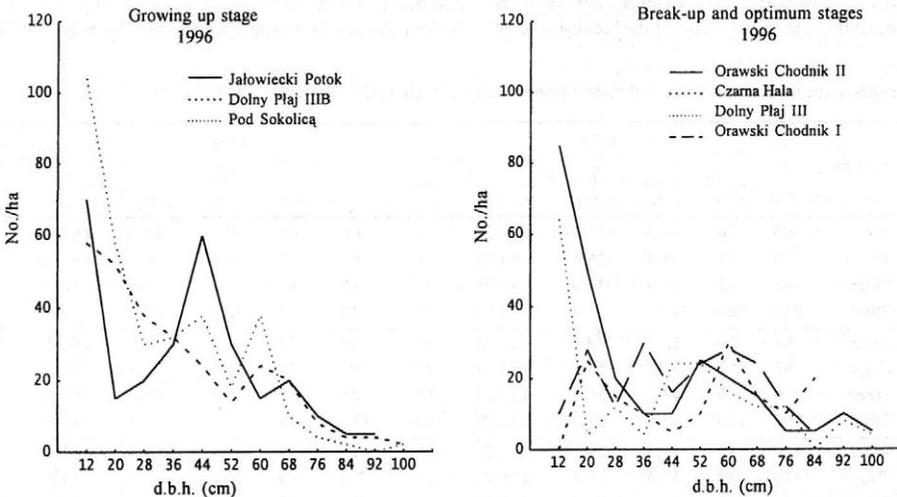


Fig. 3. Stand d.b.h. distribution curves (1996)

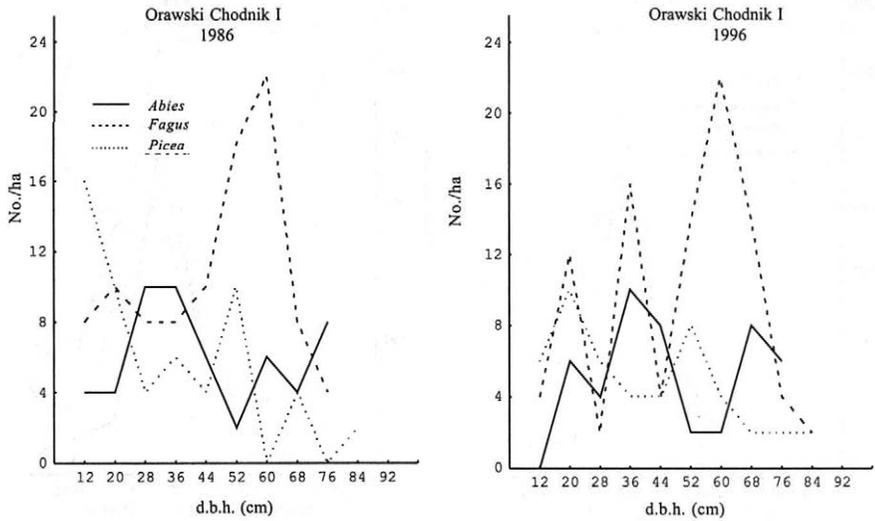


Fig. 4. Tree d.b.h. distribution curves for the study plot Orawski Chodnik I (optimum stage)

was 94% of the basal area of living trees (Table 6). These are the highest values recorded in Babia Góra Mt. experimental plots. Trees below 32 cm and over 56 cm in d.b.h. dominated among the dead standing trees (Fig. 6), which corresponded with the diameter structure of living trees.

Dolny Płaj III

In 1976–1996, the volume of this stand decreased by 33%, from almost 722 to 505 m³/ha (Table 3). This rapid change was mainly the result of fir mortality, the volume of which decreased by 38%, and to a lesser degree of the mortality of beech and spruce.

The structure of the growing stock was characterized by a relatively high proportion of very large diameter trees (> 92 cm) indicating the initial phase of the break-up stage

(Fig. 7). The stand volume in this cycle should not drop below 450 m³/ha.

The dissolution of the old stand rendered an ample regeneration and transition to a beech stand. In 1996, beech made 94% of all trees in the lower layer (Fig. 5). Under strong expansion of this species the regeneration of fir and spruce is difficult.

In 1976, the trees of medium diameter were the most numerous ones (Fig. 9). A low percentage of trees up to 24 cm d.b.h. indicated the final phase of the optimum stage. In 1996, the d.b.h. distribution was already bimodal, with modes in the diameter classes: up to 16 cm and 40–56 cm (Fig. 3). A low frequency of trees 16–40 cm d.b.h. reflected an increased mortality of small diameter trees and decreased intensity of the growing up process. Both is characteristic for the optimum stage. This was confirmed

Table 3. Changes in the numbers of trees, arithmetic means of d.b.h., height and stand volume in 1976–1996

Sample plot	Species	1976						1996					
		N		d.b.h.	\bar{h}	V		N		d.b.h.	\bar{h}	V	
		(No./ha)	(%)	(cm)	(m)	(m ³ /ha)	(%)	(No./ha)	(%)	(cm)	(m)	(m ³ /ha)	(%)
Czarna Hala	<i>Abies</i>	100	46	43.5	29.9	311.24	39	60	43	45.6	25.6	185.43	32
	<i>Fagus</i>	70	33	64.6	26.8	388.80	49	65	46	64.1	30.1	389.33	66
	<i>Picea</i>	45	21	39.0	25.8	93.05	12	15	11	29.0	19.8	11.05	2
	Total	215	100	49.4	27.9	793.09	100	140	100	52.4	27.0	585.81	100
Dolny Płaj III	<i>Abies</i>	104	54	53.2	29.9	414.75	57	56	30	59.1	31.0	256.76	50
	<i>Fagus</i>	52	27	51.2	26.8	194.70	27	100	55	26.9	15.9	149.21	30
	<i>Picea</i>	36	19	47.3	25.8	112.33	16	28	15	51.6	24.4	98.99	20
	Total	192	100	51.6	27.9	721.78	100	184	100	40.5	21.8	504.96	100
Jałowiecki Potok	<i>Abies</i>	110	39	48.5	29.1	391.21	58	75	27	57.0	34.6	369.60	53
	<i>Fagus</i>	120	43	28.3	21.5	105.43	16	170	60	26.7	19.7	173.91	25
	<i>Picea</i>	50	18	52.6	32.5	172.00	26	35	13	58.9	36.3	149.10	22
	Total	280	100	40.6	26.7	668.64	100	280	100	38.9	25.7	692.61	100

Table 4. Numbers and structure of regeneration in 1986 and 1996

Year	Species	Dolny Plaj IIIB						Orawski Chodnik						Pod Sokolica					
		Young natural reproduction ¹		Upgrowth I ²		Upgrowth II ³		Young natural reproduction		Upgrowth I		Upgrowth II		Young natural reproduction		Upgrowth I		Upgrowth II	
		(No./ha)	(%)	(No./ha)	(%)	(No./ha)	(%)	(No./ha)	(%)	(No./ha)	(%)	(No./ha)	(%)	(No./ha)	(%)	(No./ha)	(%)	(No./ha)	(%)
1986	<i>Abies</i>	5,900	50	-	-	-	-	10,083	77	-	-	-	-	1,000	18	-	-	2	5
	<i>Acer</i>	86	1	-	-	-	-	167	1	-	-	-	-	143	3	-	-	-	-
	<i>Fagus</i>	5,314	45	7,276	99	14	78	2,750	21	5,131	96	2	50	571	10	1,057	61	24	54
	<i>Picea</i>	357	3	10	0	4	22	167	1	31	1	2	50	1,071	19	114	7	18	41
	<i>Sorbus</i>	114	1	43	1	-	-	-	-	167	3	-	-	2,857	50	571	32	-	-
	Total	11,771	100	7,329	100	18	100	13,167	100	5,329	100	4	100	5,642	100	1,742	100	44	100
1996	<i>Abies</i>	254	13	-	-	-	-	184	6	-	-	-	-	84	3	2	1	-	-
	<i>Acer</i>	-	-	8	1	-	-	2	0	6	1	-	-	118	4	-	-	-	-
	<i>Fagus</i>	1,718	85	538	96	60	81	3,146	94	560	99	36	95	1,204	41	154	40	22	50
	<i>Picea</i>	48	2	6	1	14	19	10	0	-	-	2	5	1,290	44	20	5	22	50
	<i>Sorbus</i>	6	0	6	1	-	-	2	0	-	-	-	-	206	7	216	55	-	-
	Total	2,026	100	558	100	74	100	3,344	100	566	100	38	100	2,902	100	390	100	44	100

¹up to 0.5 m in height in a belt 2 × 60 m; ²from 0.5 m in height to 5.9 cm in d.b.h. in a plot 10 × 60 m; ³6.0-7.9 cm in d.b.h. counted in the whole plot

by the d.b.h. distribution of dead standing trees, among which the trees up to 32 cm in d.b.h. were the most numerous/ly represented (Fig. 6).

Orawski Chodnik II

This stand represented the final phase of the break-up stage. This was indicated by a relatively high frequency of large diameter trees (> 72 cm) (43%). Their gradual dying will cause a reduction in the stand volume (Fig. 2). A high proportion of medium diameter trees indicated that the break-up process was slow. The decrease in the number of trees 32-48 cm d.b.h. (Fig. 3), defining the optimum stage, permitted to suppose that the break-up stage had already lasted for about 60-70 years.

The proportion of trees in the lower layer in 1986 was 42% of the tree number, and in the middle layer 15% (Fig. 5). During subsequent years one should expect further increase in the proportion of middle layer trees.

Beech dominated in all stand layers, and its proportions in the lower, middle, and upper layer were 75%, 70%, and 50% of the tree number, respectively (Fig. 5). Firs above 72 cm d.b.h. made 43% of the number of trees of this species. There was no fir in the 24-64 cm d.b.h. interval, in which beech dominated (Fig. 10).

The medium and large diameter trees prevailed among dead standing trees (Fig. 6). A low frequency of small diameter trees indicated low mortality among the trees up to 24 cm d.b.h.

GROWING UP STAGE

Jalowiecki Potok

This stand represented an advanced phase of the growing up stage, as was indicated by high stand volume (693 m³/ha) (Table 3), high volume proportion of medium diameter trees (Fig. 7), well developed middle layer (Fig. 5), and a high percentage of trees in the old age generation (11%). Also a small number of trees 16-32 cm d.b.h. indicated that this stand was in transition to the optimum stage.

A large volume of this stand resulted from a high proportion of spruce and fir which, however, decreased from 84 to 75% during 1976-1996 (Table 2). Beech was a dominated species (91%) among the trees up to 36 cm d.b.h. (Fig. 11).

The d.b.h. distribution was right-side asymmetric, bimodal, with modes in the diameter classes: up to 16 cm and 40-48 cm, and in form it was closest to the beech distribution (Figs. 3, 11).

The proportion of middle layer trees was very high (39%). There were only 25% of trees in the lower layer (Fig. 5).

High mortality of trees in the lower layer was indicated by their high frequency in dead standing timber (Fig. 6), which was also reflected in a small basal area of dead standing trees (Table 6).

Table 5. Volume of dead trees, standing and lying on the ground, according to the species and decomposition degree

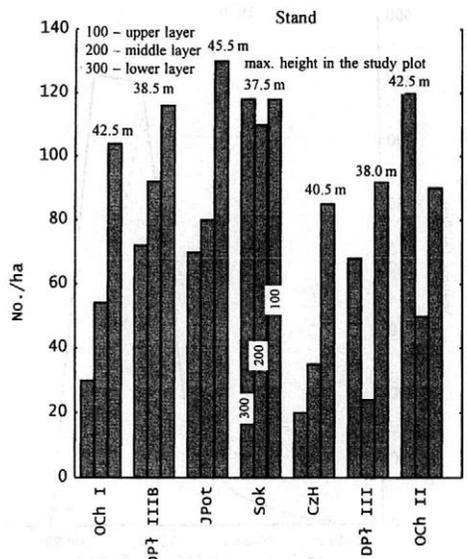
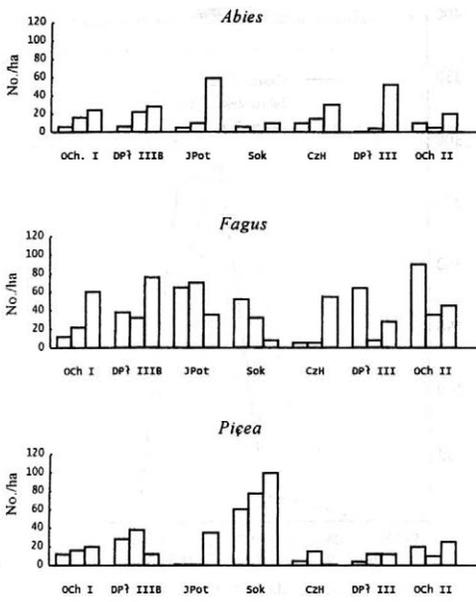
Plot	Species	1986									1996						Decomposition rate ⁶ $I_{(86-96)}$ (%)			
		Standing dead trees			Lying dead trees			Dead trees – total			Standing dead trees			Lying dead trees				Dead trees – total		
		V_{SD}^1 (m ³ /ha)	G_{SD}^2 (m ² /ha)	G_{SD}/G_T^3 (%)	V_{LA}^4 (m ³ /ha)	V_{LB}^4 (m ³ /ha)	V_{LC}^4 (m ³ /ha)	V_{L-SD} (m ³ /ha)	V_{L-SD}/V_T^5 (%)	V_{L-SD}^1 (m ³ /ha)	G_{SD}^2 (m ² /ha)	G_{SD}/G_T^3 (%)	V_{LA}^4 (m ³ /ha)	V_{LB}^4 (m ³ /ha)	V_{LC}^4 (m ³ /ha)	V_{L-SD} (m ³ /ha)		V_{L-SD}/V_T^5 (%)	V_{L-SD}^1 (m ³ /ha)	G_{SD}^2 (m ² /ha)
Orawski	<i>Abies</i>	142.2	18.8	188	5.4	97.7	x	245.3	68	159	97.8	13.8	148	–	53.7	x	151.5	46	104	–
Chodnik I	<i>Fagus</i>	–	–	–	3.4	33.4	x	36.8	10	13	–	–	–	–	25.5	x	25.5	8	8	–
	<i>Picea</i>	11.6	2.0	29	–	12.3	x	23.9	7	26	15.0	3.0	41	–	29.3	x	44.3	13	400	–
	Unknown	–	–	–	x	x	53.7	53.7	15	x	1.9	0.7	x	x	x	105.4	107.3	33	x	–
	Total	153.8	20.8	59	8.8	143.4	53.7	359.7	100	67	114.7	17.5	48	–	108.5	105.4	328.6	100	58	29
Pod Sokolica	<i>Abies</i>	52.2	5.7	125	–	5.5	x	57.7	33	85	29.8	3.9	85	–	13.8	x	43.6	27	63	–
	<i>Fagus</i>	–	–	–	–	–	x	0.0	–	–	–	–	–	0.5	x	0.5	0	1	–	
	<i>Picea</i>	32.2	3.2	12	21.6	21.7	x	75.5	42	24	36.4	4.2	16	–	28.5	x	64.9	40	20	–
	Unknown	–	–	–	x	x	43.8	43.8	25	x	1.8	0.9	x	x	x	50.9	52.7	33	x	–
	Total	84.4	8.9	25	21.6	27.2	43.8	177.0	100	40	68.0	9.0	24	–	42.8	50.9	161.7	100	35	31
Dolny Plaj IIIB	<i>Abies</i>	111.1	16.6	139	–	104.0	x	215.1	74	121	93.0	15.2	115	–	90.6	x	183.6	59	94	–
	<i>Fagus</i>	10.1	0.2	1	21.7	–	x	31.8	11	11	6.3	1.3	6	–	37.5	x	43.8	14	14	–
	<i>Picea</i>	5.8	0.6	9	11.0	2.2	x	19.0	6	24	15.7	1.5	24	–	12.6	x	28.3	9	40	–
	Unknown	–	–	–	–	x	27.3	27.3	9	x	0.1	0.1	x	x	x	56.8	56.9	18	x	–
	Total	126.0	17.4	46	32.7	106.2	27.3	292.2	100	53	115.1	18.1	45	–	140.7	56.8	312.6	100	54	16

Explanations:

¹ V_{SD} – volume of standing dead trees² G_{SD} – basal area of standing dead trees³ G_T – basal area of living trees⁴ $V_{LA, LB, LC}$ – volume of lying dead trees according to decomposition degrees A, B, C⁵ V_T – volume of living trees⁶Intensity of wood decomposition ($I_{(86-96)}$) was determined according to the formula:

$$I_{(86-96)} = [(V_{L86} - V_{L96} - V_{SD86-96} - V_{SD86-96} + V_{SD96}) / V_{L86}] \times 100$$

where: $V_{SD(86-96)}$ – volume of standing dead trees which died in 1986–1996



Explanation: Och I – Orawski Chodnik I, DP I III B – Dolny Płaj III B, JPot – Jאלowiecki Potok, Sok – Pod Sokolicą, CzH – Czarna Hala, DP I III – Dolny Płaj III, Och II – Orawski Chodnik II

Fig. 5. Storeyed structure of stands according to tree participation in IUFRO classes (1996)

Dolny Płaj III B

A well developed middle layer indicated the advancement of the growing up stage. The proportions of trees in the lower and middle layers were 26 and 33%, respectively (Fig. 5).

The d.b.h. structures of fir, beech and spruce were characterized by high coefficients of variation (53, 58, and 66%, respectively), and a single-armed form of the distribution curve with right-side asymmetry (Fig. 12). From among all tree species fir showed the highest proportion of trees above 52 cm d.b.h. (36%) (Fig. 12). Among the

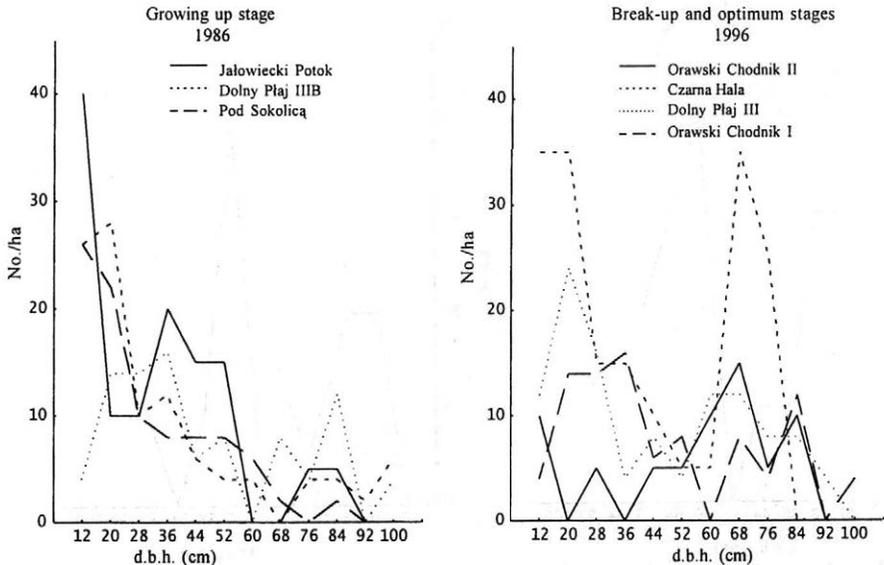


Fig. 6. D.b.h. distribution curves for dead standing trees (1986)

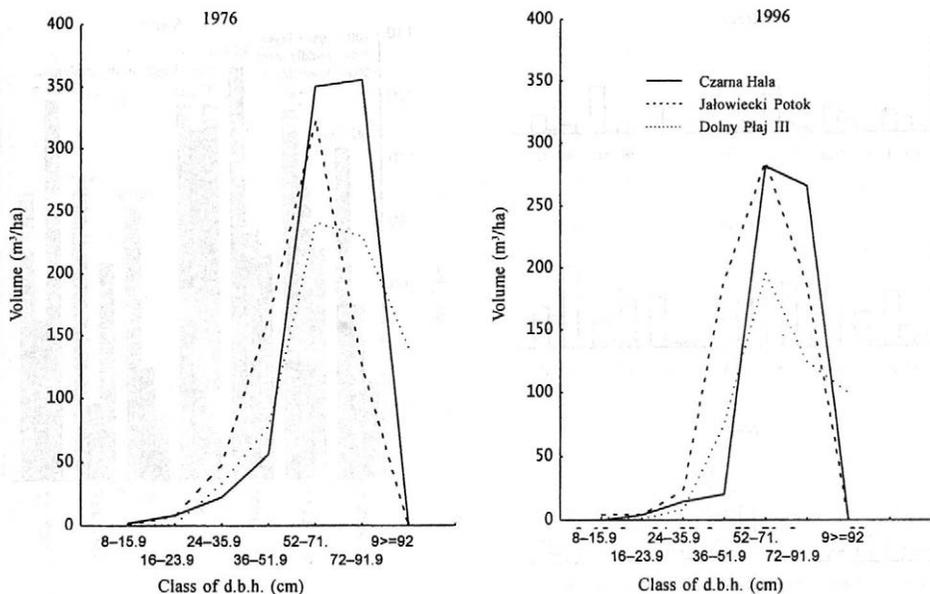


Fig. 7. Growing stock structure in the study plots Czarna Hala, Dolny Plaj III, and Jałowiecki Potok in 1976 and 1996

trees up to 24 cm d.b.h. beech (49%) and spruce (41%) dominated. Spruce, because of a high frequency of individuals of the growing up generation (72%), represented the most progressive type in respect of the number dynamics.

There was no fir in the upgrowth during the period 1986–1996 in spite of the presence of young natural reproduction of this species (Table 4). Beech was the most stable species in the regeneration.

The volume of dead trees in 1996 was 313 m³/ha (54% of stand volume), out of which 63% was made by the timber lying on the ground. The rate of its decomposition was 16%, and it was lower than that in the study plots Orawski Chodnik and Pod Sokolica.

On the basis of the d.b.h. distribution curve for dead standing trees it may be concluded that the mortality of trees up to 40 cm d.b.h. was intensive (Fig 6), and corre-

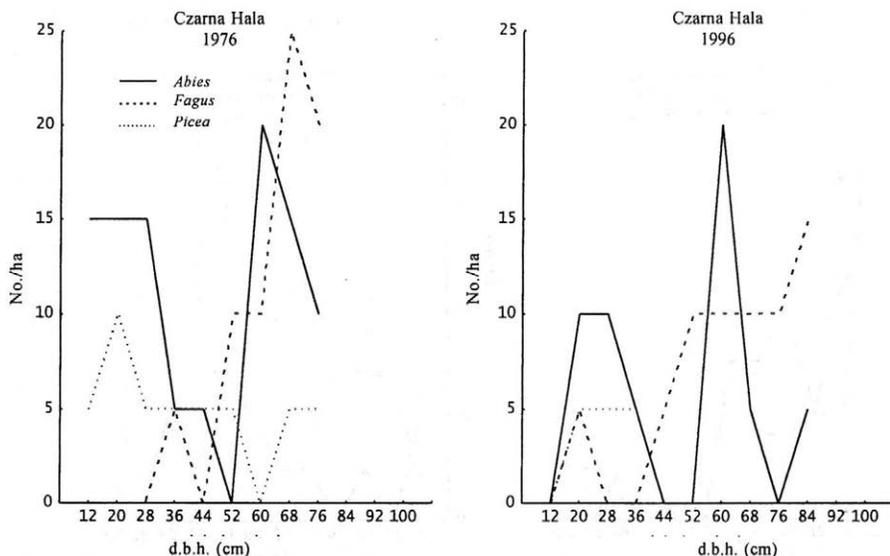


Fig. 8. Tree d.b.h. distribution curves for the study plot Czarna Hala (break-up stage)

Table 6. Basal area and volume of dead standing trees

Plot	Species	1986		1996			
		G_{SD} (m ² /ha)	G_{SD}/G_T (%)	G_{SD} (m ² /ha)	G_{SD}/G_T (%)	V_{SD} (m ³ /ha)	V_{SD}/V_T (%)
Jałowiecki Potok	<i>Abies</i>	14.5	68	9.3	44	92.1	25
	<i>Fagus</i>	—	—	—	—	—	—
	<i>Picea</i>	—	—	3.2	32	50.9	34
	Unknown	—	x	1.0	x	6.5	x
	Total	14.5	33	13.5	31	149.5	22
Orawski Chodnik II	<i>Abies</i>	16.6	136	11.9	97	82.0	41
	<i>Fagus</i>	—	—	1.8	11	6.0	2
	<i>Picea</i>	0.4	5	0.1	1	0.6	0
	Unknown	2.3	x	5.5	x	9.6	x
	Total	19.3	53	19.3	50	98.2	17
Czarna Hala	<i>Abies</i>	18.0	160	21.3	175	160.8	87
	<i>Fagus</i>	8.2	37	5.2	23	36.3	9
	<i>Picea</i>	5.2	594	5.5	533	48.2	436
	Unknown	—	x	1.8	x	3.8	x
	Total	31.4	91	33.8	94	249.1	43
Dolny Płaj III	<i>Abies</i>	17.2	45	14.9	89	120.7	47
	<i>Fagus</i>	3.2	8	5.7	57	44.2	30
	<i>Picea</i>	1.7	4	1.6	20	15.0	15
	Unknown	—	x	0.7	x	5.1	x
	Total	22.1	58	22.8	66	185.0	37

Explanations see Table 5

sponded with a high frequency of living trees in this diameter interval (Fig. 3).

Pod Sokolicą

This study plot was characterized by a predominance of spruce (71% of stand volume), highest numbers of trees (346 trees/ha in 1996), and vertical stand structure with

even proportions of trees in the upper, middle, and lower layers (32, 35, and 33%, respectively) (Fig. 5). In the case of the latter characteristic a certain importance may be ascribed to the amplitude of the height above sea level and the variability of orographic conditions within this plot, deciding upon the maximum heights attained by trees.

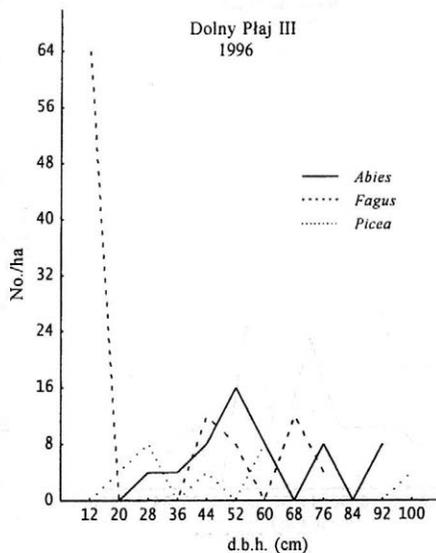
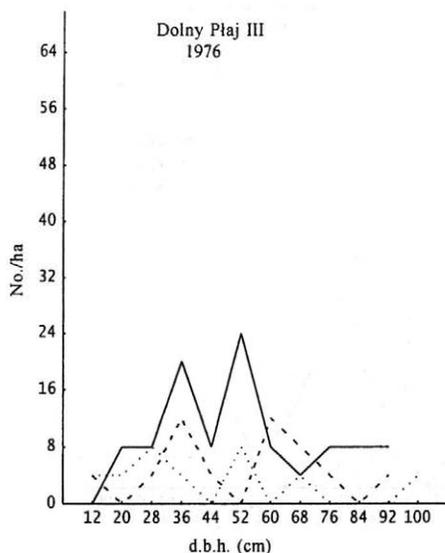


Fig. 9. Tree d.b.h. distribution curves for the study plot Dolny Płaj III (break-up stage)

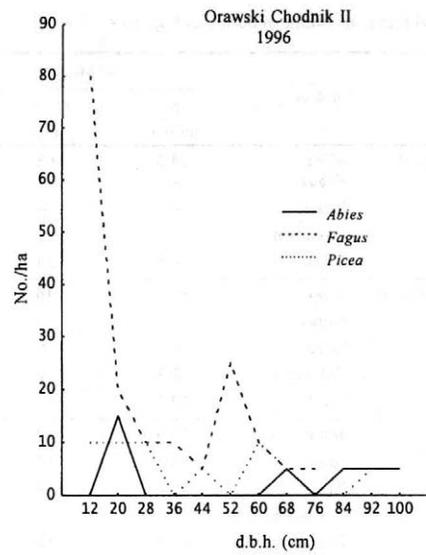
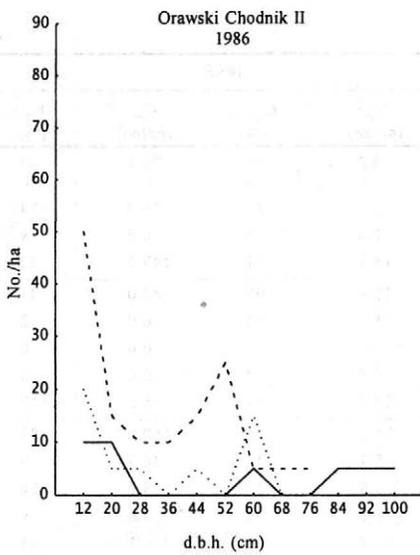


Fig. 10. Tree d.b.h. distribution curves for the study plot Orawski Chodnik II (break-up stage)

A distinct increase in percentage of beech was observed during this study. Its proportion among the trees up to 16 cm d.b.h. increased to 51% (Table 2). The tree diameter distribution of this species was characterized by a distinct domination of trees with smallest diameters, thus indicating its progressive character. Under these conditions the trees of the greatest diameters reached d.b.h. over 70 cm and height of 30 m, and therefore, an increase of their proportion in the middle and upper layers is quite realistic in future.

The proportion of fir in the diameter interval up to 52 cm was only 2%. The trees of the old age generation made 50% of the number of trees of this species, which indicated its regressive character. The diameter distribution of spruce was represented by a single-armed curve showing its demographic stability (Fig. 13).

From among the analysed study plots this stand was characterized by the lowest fluctuation in the regeneration numbers indicating a continuous occurrence of favourable conditions for its creation (Table 4). The spe-

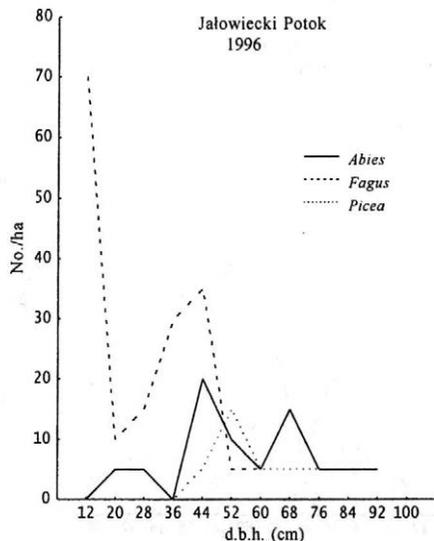
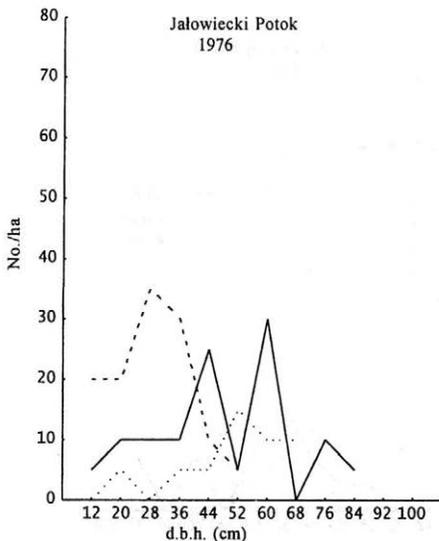


Fig. 11. Tree d.b.h. distribution curves for the study plot Jałowicki Potok (growing up stage)

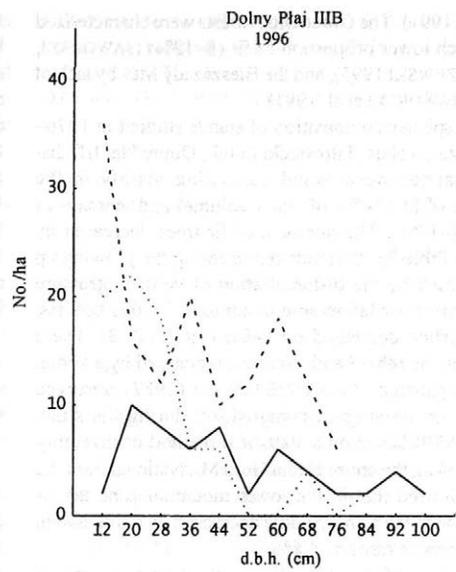
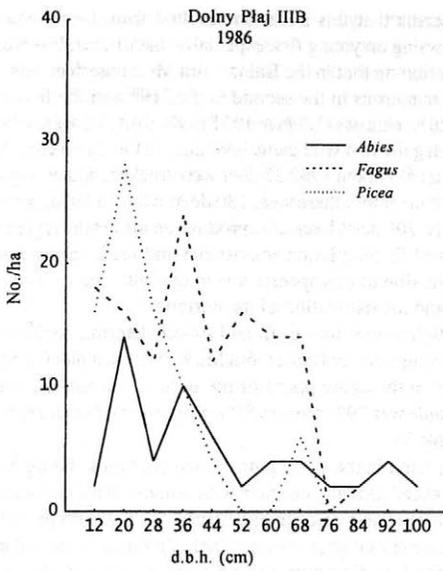


Fig. 12. Tree d.b.h. distribution curves for the study plot Dolny Plaj IIIB (growing up stage)

cies composition of the young natural reproduction was subjected to strong changes mainly conditioned by the occurrence of good seed years. Periodically, however, all species participated in the composition which showed a potential possibility of their presence in the species composition of the stand. The highest proportion in the species composition of the upgrowth was attained by beech, while fir was almost absent (Table 4).

In 1996, the volume of dead trees was $162 \text{ m}^3/\text{ha}$ (35% of stand volume), out of which 58% was made by trees lying on the ground (Table 5).

DISCUSSION

Among the forests of a primeval character in the lower mountain zone of the Western Carpathians, included in the studies of the Department of Silviculture at the Agricultural University of Cracow in 1970s, the Babia Góra Mt. forest stands were distinguished by a high proportion of fir, from 39 to 58%, and a considerable percentage of spruce, from 12 to 26%. In respect of species composition these stands were most similar to the Pieniny Mts. forests (43–58% of fir, no spruce) (JAWORSKI, KARZ-

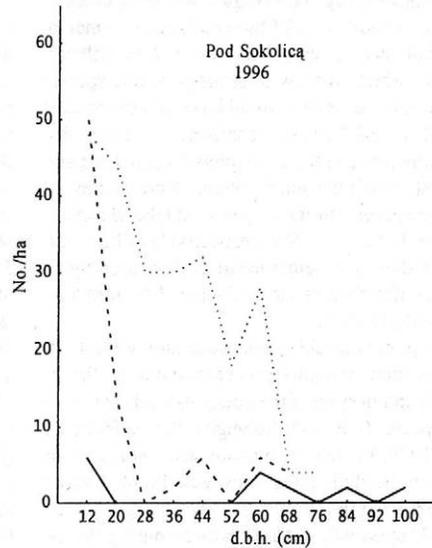
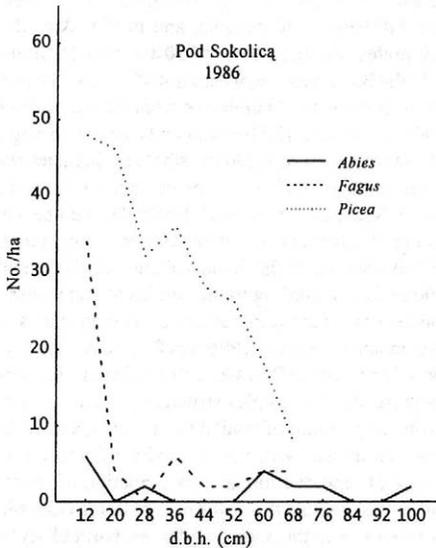


Fig. 13. Tree d.b.h. distribution curves for the study plot Pod Sokolica (growing up stage)

MARSKI 1991). The Gorce Mts. forests were characterized by a much lower proportion of fir (8–12%) (JAWORSKI, SKRZYSEWSKI 1995), and the Bieszczady Mts. by lack of spruce (JAWORSKI et al. 1991).

In the species composition of stands studied in 1976–1996 (Czarna Hala, Jałowiecki Potok, Dolny Płaj III) distinct changes were found consisting mainly in the decrease of fir (5–7% of stand volume) and increase of beech (3–17%). The numbers of fir trees decreased by 1–24% (Table 2). In stands representing the growing up stage, which by the differentiation of vertical structure creates the most favourable conditions for this species, its proportion decreased by 1–8% (Tables 2, 3). These stands, on the other hand, were characterized by a strong beech expansion. Also DZIEWOLSKI (1987) observed changes in the species composition during his study (1960–1979) based on a statistical method of inventory and including the entire Babia Góra Mt. National Park. Its results showed that in the lower mountain zone the fir proportion in the stand volume decreased by 6.8%, and in the numbers of trees by 4.8%.

A decrease of fir and spruce proportion in favour of beech was also recorded in the Pieniny Mts. National Park in 1972–1987 (DZIEWOLSKI 1991).

Fir is a species characterized by a very high ratio of dead to living trees. Taking into account the fact that the decomposition of fir wood under conditions of the lower mountain zone takes 4–6 times less time than its accumulation (KORPEL 1993) this ratio at normal mortality should range from 15 to 25%. Much higher values found in the investigated stands (63–104%) indicate the intensification of mortality of trees of this species which occurred before 1970. Similar conclusions were drawn from studies on fir vitality in the Carpathian forests (JAWORSKI, SKRZYSEWSKI 1986; JAWORSKI et al. 1995). The weakness of fir could have contributed to a shortening of the break-up and growing up stages (aging and dying phases), and therefore, a shortening of the whole developmental cycle, especially in fragments characterized by a high percentage of fir, which in view of strategy of this species was unfavourable, while this would have rather favoured the beech. This hypothesis was confirmed by a very fast break-up taking place in the study plots Czarna Hala and Dolny Płaj III, where the stand volume decreased by 28 and 26%, respectively, during 10 years, and the fir mortality was highest (62 and 76%, respectively) (Table 2). Symptoms of shorter developmental cycle caused by fir mortality were also observed in the Pieniny Mts. (JAWORSKI, KARZMARSKI 1991).

In the study plots Orawski Chodnik and Dolny Płaj IIIB, where regeneration inventory was carried out, no fir upgrowth was found in spite of the young natural reproduction of this species (Table 4). No upgrowth was found by JAWORSKI (1979a) either, who conducted a study on fir regeneration in the study plots Jałowiecki Potok, Czarna Hala, and Dolny Płaj III.

A lack of fir upgrowth was also noticed during the inventory of stands carried out in 1979 (DZIEWOLSKI 1987).

It seems that this situation resulted from heavy animal browsing on young firs, especially that of deer. It is worth mentioning that in the Babia Góra Mt. range deer was not too numerous in the second half of 19th and the first half of 20th centuries (LILPOP 1931 in KAŁWA, TOMEK 1983). During the first wild game inventory in the Babia Góra Mt. National Park in 1960 23 deer were tracked, and during the 1970 inventory there were 130 deer, while in 1976, periodically, 200 deer. Lack of reproduction makes the regeneration of fir population impossible and leads to increased regression of this species due to the lowering of its vitality and intensification of its mortality.

High proportions of fir and spruce determined the high growing stock of Babia Góra Mt. forests. In a plot 0.2 ha in size, in the aging phase of the optimum stage, the stand volume was 793 m³/ha at 51% proportion of fir and spruce (Table 3).

A stand in the study plot Jałowiecki Potok, being in an advanced growing up stage with volume of 693 m³/ha and joined proportion of fir and spruce of 75 %, will probably reach even a higher volume (Table 3). A maximum volume reached by investigated stands in the Gorce Mts. was 739 m³/ha (optimum stage, 47% of fir and spruce) (JAWORSKI, SKRZYSEWSKI 1995), in the Pieniny Mts. – 702 m³/ha (advanced growing up optimum stage, 46% of fir) (JAWORSKI, KARZMARSKI 1991), in the Beskid Sądecki Mts. – 671 m³/ha (optimum stage, aging phase, 42% of fir) (JAWORSKI et al. 1994), and in the Bieszczady Mts. – 618 m³/ha (growing up stage, 5% of fir) (JAWORSKI et al. 1991). There are primeval forests of lower mountain zone in Slovakia reaching the stand volume of 1,366 m³/ha (Dobročský prales reserve, optimum stage, 70% of fir and spruce) (KORPEL 1995).

A low number of trees, ranging from 140 (break-up stage with no regeneration) to 280 trees/ha (growing up stage) is evident in the investigated stands. In stands of the Beskid Mts. of similar species composition this number does not fall below 300 trees/ha, and in Slovakia (Dobročský prales, Stuzica) below 250 trees/ha (KORPEL 1995). In the Badin reserve, where in 1957–1987 the proportion of fir in the total number of trees decreased from 65 to 18%, there were 126 trees/ha in the optimum stage. Similar low numbers (160–290 trees/ha) are characteristic of the beech stands with a low percentage of fir in the Bieszczady Mts. (JAWORSKI et al. 1991). The numbers of trees in the Slovakian primeval beech forests range from 350 to 550 trees/ha, at the stand volume oscillations of 400–600 m³/ha. According to the studies of Dzewolski, mentioned above, the mean number of trees in stands of the lower mountain zone in 1996 was 803 trees/ha, and in 1979 only 555 trees/ha (DZIEWOLSKI 1987). The numbers of trees in stands of a complex structure are mainly associated with the presence of small diameter trees, and therefore are connected with the intensity of upgrowth, appearance of reproduction, and participation of shade-tolerant fir. It is possible that in the case of Babia Góra Mt. forests a decrease in the numbers of trees, particularly in plots representing the break-up stage, resulted from a

strong stress caused by wild game through limiting the ingrowths and eliminating fir from the upgrowth.

The fluctuations in the growing stock and numbers of trees during the developmental cycle depend on an assumed spatial scale, and they increase with a decrease in sample plot size. The differences in structure of the investigated stands were mainly manifested by the differences in the numbers of trees up to 32 cm d.b.h. These stands differed little in respect of tree frequency in the higher diameter classes and volume, while the existing differences may have resulted from the species composition (e.g. prevalence of fir and spruce or beech), or site conditions. SZWAGRZYK et al. (1995), conducting investigations in a plot 1 ha in size, situated in a close neighbourhood of stands under discussion, found surprising similarity in respect of the volume (553 m³/ha) and numbers of trees (220 trees/ha). KORPEL (1995), in the Dobročský praes reserve, did not find a single fragment, 0.5 ha in size, with volume below 500 m³/ha. All these facts appear to show a great homogeneity of the structure of primeval forests in the lower mountain zone, and induce to undertake further studies in order to become better acquainted with its spatial variability.

A stand in the study plot Pod Sokolicą in respect of the species composition, developmental stage and phase somewhat resembled that in the study plot Górny Płaj, which is already situated in the upper mountain zone (1,150–1,170 m above sea level) (JAWORSKI, KARCZMARSKI 1995). The latter, however, was characterized by a higher stand volume (561 m³/ha in 1986) and smaller numbers of trees (246 trees/ha).

The following conclusions may be drawn on the basis of this study:

1. The lower mountain zone stands of Babia Góra Mt. are under strong stress created by deer, which makes the reproduction of fir and regeneration of its population impossible.
2. Increased mortality of fir observed in the 1960s, in stands with a high percentage of this species, was the cause of shorter aging and dying phases which promoted reproduction and expansion of beech. Present domination of beech among the trees of the growing up generation points to a possibility of change in the species composition.
3. The range of the numbers of trees in the investigated beech-fir stands, representing the full spectrum of developmental stages, was from 140 to 280 trees/ha, and the range of stand volume from 504 to 793 m³/ha. These amplitudes resulted not only from the regularities connected with the developmental cycle, but also from the trends of fir recession and beech expansion.

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Struktura a dynamika lesů pralesního charakteru v nižší horské zóně v Národním parku Babia Góra

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ABSTRAKT: Výčetní tloušťku a výšku živých i odumřelých stromů jsme měřili na třech pokusných plochách v letech 1976–1986 a na čtyřech plochách v letech 1986–1996. Podíl jedle činil 15–58 % a podíl smrku 12–71 % porostní zásoby. Porostní zásoba se pohybovala mezi 442 a 793 m³/ha a počet stromů kolísal od 140 do 346 jedinců/ha. Podíl jedle se snížil o 1–24 % z počtu stromů. Objem odumřelých stromů jedle dosáhl 63–104 % objemu živých stromů.

Klíčová slova: *Abies alba*; *Fagus sylvatica*; *Picea abies*; ústup jedle; změny v druhovém složení; vývojová stadia a fáze

Výzkum byl prováděn v zachovalých partiích bukojedlových a smrkových porostů pralesního charakteru v nižší horské zóně Národního parku Babia Góra. V období 1976–1986 výzkum probíhal na třech plochách, v období 1986–1996 na čtyřech plochách. Vybrané porosty reprezentovaly stadium optima, dorůstání a rozpadu (tab. 1). U všech živých i mrtvých stromů s výčetní tloušťkou nad 6 cm byl měřen výčetní průměr. Na plochách Pod Sokolicą, Orawski Chodnik I a Dolny Płaj IIIB bylo navíc měřeno velké množství ležících stromů, jedinců starších nárůstů (na ploše 10 × 60 m) a nejmladších stadií přirozené obnovy (v pásu 2 × 60 m).

Zastoupení jedle se v porostní zásobě pohybovalo v rozmezí 15–58 %, smrku 12–71 % (tab. 1). Během doby sledování se snížil počet jedlí o 1–24 % (tab. 2 a 3). Objem ve sledovaných bukojedlových porostech kolísal od 504 m³/ha (stadium rozpadu) do 793 m³/ha (stadium optima, stárnutí), počet stromů kolísal od 140 (stadium rozpa-

du bez obnovy) do 280 stromů/ha (stadium dorůstání) (tab. 2 a 3). Ve smrkovém porostu v období 1986–1996 objem dosahoval 442–464 m³/ha a počet stromů 324 až 346 ks/ha (stadium dorůstání, fáze výběrného lesa). Počty přirozené obnovy kolísaly od 2 000 do 13 000 semenáčků/ha, nárost od 400 do 7 300 ks/ha (tab. 4). V obnově převažoval buk. Přestože se jedle vyskytovala v přirozené obnově, chyběla ve starších nárostech. Tato situace je způsobena intenzivním okusem zvěře, jejíž početní stavy se v sedmdesátých letech výrazně zvýšily. Objem mrtvého jedlového dřeva dosahoval 63–104 % objemu živých jedlí. Zvýšená mortalita jedle v porostech s jejím vysokým podílem, zjištěná v průběhu této studie, vyústila ve zkrácení fáze stárnutí a odumírání, což podpořilo obnovu a expanzi buku. Početní převaha buku v přirozené obnově zjištěná v současné době ukazuje na možnost změny druhové skladby a vyloučení jedle z porostního zastoupení.

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Terrestrial single-image photogrammetry for measuring standing trees, as applied in the Dobroč virgin forest

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ABSTRACT: For about one century, terrestrial photogrammetry has been applied in forestry. Especially, the development of electronic data processing, as well as the production of high-quality amateur cameras, facilitated an extensive and economical use of this technology. Measuring the stem form of standing trees does not normally require stereo photogrammetry, a simple single-image photogrammetry is sufficient. Such a method is described here in detail, both in theory and in practice. Error studies showed that the standard deviation of the diameter and the height measurement errors becomes greater with increasing measurement height and camera distance. At a distance of 22 m and at a height of 32 m, the diameter error-related standard deviation $s_{\Delta d}$ is 0.8 cm and that of the height error $s_{\Delta h}$ is 0.4 m. At a height of 23 m, $s_{\Delta d}$ is 0.6 cm at a distance of 25 m and 1.0 cm at a distance of 50 m. Simulations revealed that especially errors due to incorrect handling of the scale pole, while capturing the image, and measurement errors of the pass points of the pole result in systematic deviations of diameter and height, both increasing by measurement height. This error study was performed in connection with measurements of some of the greatest trees in the Dobroč primeval forest of Slovakia: the principal suitability of terrestrial photogrammetry for assessing objects with heights of 50 m and more should be checked.

Keywords: terrestrial photogrammetry; stem form measurement; Dobroč virgin forest

One of the main tasks of forestry is estimating the wood volume of single trees, especially of the stem, as reliably as possible. In addition, the prognosis of assortments, into which a stem can be classified, requires exact information on the stem taper. Therefore, methods for measuring standing trees were developed a relatively long time ago (see, e.g., PRODAN 1965), and photogrammetry technology was introduced to forestry later in the last century (WEBER 1902). But it was not before electronic data processing and the substitution of aerial cameras by less expensive amateur cameras that photogrammetry could be carried out economically (KREIBIG 1967a, 1968; DEHN et al. 1985; DEHN 1987). Sufficient accuracy has been proven for this simplified measurement technique, too, but studies were performed only on objects with maximum heights up to 30 m. However, in practice, trees with heights of 50 m and more exist and have been measured (e.g., GAFFREY 1996). Photogrammetric analyses of some of the largest trees in the Slovakian Dobroč primeval forest in the year 1998 gave reason to present possibilities, as well as constraints, of the terrestrial single-image photogrammetry used, with a special focus on the achievable accuracy.

DEVELOPMENT OF TERRESTRIAL PHOTOGRAMMETRY

One of the pioneers of forestry-related photogrammetry is WEBER (1902). He used a plate camera of which the plates were adjusted parallel to the stem axis, resulting in a single scale for the complete image. The mathematical definition under this condition of projection is very easy, but the great disadvantage is that only the lower part of the stem can be captured. Around the turn of the century, stereo photogrammetry, too, was introduced and intensively used in forestry, e.g., in Austria (lit. see MÜLLER 1931) or in Russia (lit. see KREIBIG 1967a). Stereo technology was considerably refined by MÜLLER (1931), who used professional cameras. But, in normal cases, images were still taken with the image plane parallel to the stem axis. Apart from normally oriented exposures, MARSH (1952) experimented with tilted ones which show a perspective distortion, but the obtained precision was poor.

For the first time, the development of electronic data processing offered the possibility of considerable time-saving during the process of image analysis. But an economical application of photogrammetry for remotely

sensing tree stems, moreover, required a method which permitted a simple and flexible use in the field, with equipment being available at a reasonable price. Confronted with these demands, KREIBIG (1964) realised a system based on a standard medium-format camera, being tilted to assess the whole stem with one single exposure (1967a,b, 1968). A linear scale, a pole with three pass points, attached to the stem parallel to its axis, served for determining the parameter of the transformation equation. In such a case, distance and inclination angle of the camera need not be measured and the camera location can be chosen under conditions being optimal for taking photos. Independently of Kreibig's work*, in the early eighties, the same solution for the challenge of developing an economical technology for remotely measuring standing stems, the application of a terrestrial single-image photogrammetry, was invented by DEHN et al. (1985; DEHN 1987). At that time, advanced data processing indeed allowed a comfortable, interactive image analysis and, with the improvement of film materials and amateur cameras, the chosen low-cost 35-mm reflex camera met the desired accuracy. A comparable method, equal in mean characteristics including the use of a 35-mm camera, was also presented by ASHLEY and ROGER (1969), but their system was tested only under laboratory conditions.

Contrary to taking only a single photo per tree, BRADSHAW (1972) preferred separate photos for each stem location where a diameter was to be measured. Therefore, he chose a 35-mm camera combined with a 135-mm telescopic lens. Each picture taken must be accompanied by recording the camera tilt angle and its distance to the tree. On account of the greater image scale, CROSBY et al. (1983), NOSENZO (1993) and TAKAHASHI et al. (1997), too, take a sequence of pictures per tree, using long-focus lenses. CROSBY et al. (1983) additionally use a pole with a scale which permits measuring several diameters within one exposure, but their method is restricted to a height of about 10 m. TAKAHASHI et al. (1997) have a special camera prototype, optionally displaying the object distance or a measuring scale. In combination with externally determined camera inclination angles, scanned images can be analysed photogrammetrically.

The latest development is characterised by the application of digital photography (CLARK 1998; CLARK et al. 1998). Savings in costs and time, as well as the possibility of digital image processing are notable advantages. CLARK et al. (1998) chose four camera stations per tree, positioned in steps of 90° around the stem, for assessing tree lean and asymmetric stem cross-sections. As no scale is used, the camera's outer orientation, distance and inclination, must be measured.

Though producing much more effort and costs than single-image photogrammetry, terrestrial stereo photogrammetry is still represented in forestry because it offers the only way of spatial information acquisition. Unlike in the early past, tilted photographing is standard today.

Professional double-measuring cameras (e.g., LEBRUN 1974; RAČKO 1983; OLENDEREK 1992), medium-format cameras (RAČKO 1983) and 35-mm cameras (NAKAYAMA, NAGASHIMA 1963; FIRTH et al. 2000) are in use. Image analysis is performed by conventional stereo comparators or by specially developed hard and software solutions (e.g., BARTORELLI 1978; HENGL et al. 1997).

METHOD OF TERRESTRIAL SINGLE-IMAGE PHOTOGRAMMETRY

In the following section, the method of terrestrial photogrammetry, in the manner developed by DEHN et al. (1985; DEHN 1987) in Göttingen, is described. As ever, it is intensely used at the Institute of Forest Biometry and Informatics in Göttingen. It primarily serves to acquire information on the stem form of standing trees, with the aim to derive species-specific, local and regional taper curve models (GAFFREY 1994; SLOBODA et al. 1998; GAFFREY, NAGEL 1998). For this purpose, relatively extensive surveys are indispensable (the measurement of about 10–20 trees per species and per stand is necessary for constructing taper curve models; up to now over 2,000 trees have been analysed), the method must guarantee in particular a simple and fast work flow in the field. This is achieved by taking only a single picture per tree, using a 35-mm camera (CANON AE1) equipped with a 28-mm wide-angle lens, and attaching a linear scale of 4 or 5 m length (aluminium pole with 3 pass points) at the stem (Fig. 1), making measurements of parameters of the outer orientation unnecessary.

Field work requires two persons: the cameraman and another person responsible for handling the pole. Choosing a location for the camera must take into account unimpaired visibility of the complete stem, and the tip of the crown must be identifiable for determining the tree height. Simultaneously, photographing against the light must be avoided and, in the case of appreciable slope inclination, the camera must be directed downhill. The horizontal camera distance normally equals the height of the tree; at least, it must be two thirds of the tree length. The camera, mounted on a tripod, is tilted by an angle ω (Fig. 1) until the complete tree is centred in the view-finder. Rotations on the other two axes, especially on the y -axis, must be avoided. Measuring the horizontal camera distance to the tree or the camera inclination angle is not necessary. The pass-point pole is fixed at the side of the tree (by hanging it on a branch or by hammering the pole with an attached pin into the bark). The exact parallel orientation to the tree axis as well as the visibility of all three pass points, must be controlled by the cameraman. Lastly, the distance from the foot of the stem, defined as the origin of the object coordinate system, to the first pass point must be measured and noted on a board, together with an identification code. Due to unfavourable light conditions in a stand (very wide density range from the ground to the sky),

*At that time, the literature of Eastern Europe was not often accessible and therefore unknown.



Fig. 1. Application of single-image terrestrial photogrammetry for assessing the stem form of standing trees

generally three pictures are taken by varying the shutter speed, to ensure at least one satisfying exposure for the image analysis. As a black-and-white film with a very fine grain and thus, with a low speed, is preferred (AGFAPAN APX 25, ISO 25/15°), a remote or a cable shutter release is required to avoid blurred images. Moreover, the tree must remain more or less motionless during the exposure. Fur-

ther details concerning photo acquisition can be inferred from the treatise of DEHN (1987) and KREIBIG (1967a).

The analysis of the photo negatives is performed in the laboratory using a PC-controlled 2-axis industry controller, supplemented with a 3rd axis, a rotary plate, illuminated from below (Fig. 2). A macroscope, combined with a CCD camera, resolves continuously up to 80 times. The software for controlling the comparator and for measur-

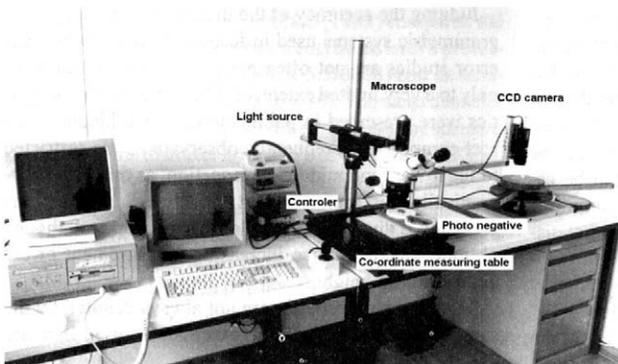


Fig. 2. Digital analysis of photo negatives using an individually optimised measuring equipment

ing tree diameter and heights was developed at the institute. The best-exposed negative is fixed flat on the rotary plate and it is oriented by joystick control, so that the pass point pole is parallel to the y -axis of the measuring table. (By doing so, a possible rotation of the camera around its z -axis [Fig. 1] during the image capture can be corrected.) As the 35-mm negatives do not have any fiducial marks, the principal point, of which the exact location is needed for the distortion correction (see below), is approximately determined by the intersection of the image diagonals. The image corners are normally more or less rounded and hence, they must be defined by the intersection points of four straight lines representing the image edges. For this purpose, two image points for each edge are measured. This way of calculating the principal point is very robust: minor measurement errors of recognising the edge points are negligible (DEHN 1987). By contrast, as the precise localisation of the image pass points is of extreme importance (DEHN et al. 1985; DEHN 1987), this step must be performed twice. The identification of the image co-ordinates (x'_{pp}, y'_{pp}) of the three pass points, combined with the corresponding object co-ordinates (X'_{pp}, Y'_{pp}), allows the determination of the three unknown parameters $\hat{e}_1, \hat{e}_2, \hat{e}_3$ of the perspective transformation equation. Then, measured image co-ordinates (x_p, y_p) of any image point p can be converted into object co-ordinates (X_p, Y_p) of the corresponding object point P , by

$$Y_p = \frac{y_p \cdot \hat{e}_1 + \hat{e}_3}{y_p \cdot \hat{e}_2 + 1}, \quad X_p = \frac{x_p \cdot D_h / \cos(\omega \cdot c)}{y_p \cdot \hat{e}_2 + 1}$$

The required parameters of the outer orientation, the camera inclination ω , the horizontal distance D_h from the perspective projection centre to the object plane and the vertical distance D_v of the projection centre relative to the origin of the object co-ordinate system (Fig. 1), are given by the relations:

$$\omega = \arctan(c \cdot \hat{e}_2), \quad D_v = \frac{\hat{e}_3 + (c \cdot \hat{e}_1 \cdot \tan \omega)}{\tan^2 \omega + 1}, \quad D_h = \frac{\hat{e}_3 - D_v}{-\tan \omega}$$

c is the focal length, the distance of the projection centre to the image plane.

The correction of the distortion of the radial image distances must precede any calculation of object co-ordinates. According to the principle of the perspective projection, any object radius R is projected on an image radius r with $r = c \cdot \tan \tau$. But a photographic projection will result in a distorted radius r' , rather than r . The radial distortion Δr is given by $\Delta r = r - r'$. As normally the distortion of amateur cameras, depending on the used lens, is unknown, the camera-lens system must first be calibrated. In approximation, the distortion can be assumed symmetrical to the principal point. This simplifies the determination of the distortion function, a radial distortion polynomial starting in the principal point (supposed to be free of distortion) and which depends on r' only. It is practical to explain the relative distortion $\Delta r'/r'$ rather than the absolute deviations. The correction of the distorted image radii is done by the correction function

$$\varphi(r'): r' \rightarrow r = r' + r' \cdot \sum_{i=0}^n a_i \cdot (r')^i$$

with a_i being the polynomial coefficients of the distortion function.

The CANON camera used with a 28-mm wide-angle objective showed a relative distortion, which increased approximately linearly, with maximum values of about 2.5%. The graph of the distortion of another calibrated camera (Minolta X300, 28-mm lens) was similar, but the absolute values were a bit lower. Ten years later, the CANON camera was re-calibrated and the resulting distortion function showed only marginal differences, which lie in the error scale of the calibration process. This means that repeated removal and fixation of the lens do not affect the inner orientation of the camera because the bayonet mount guarantees a well-defined lens positioning.

The photogrammetric analysis of a tree stem is performed interactively, i.e., after measuring a pair of image points of the stem, its diameter and height position is displayed. In principle, non-horizontal distances can also be assessed. At any time of the measuring process, image points can be re-identified, controlled and, if necessary, corrected or deleted.

Terrestrial single-image photogrammetry has methodically been optimised so far that within one day of photographing, about 40–50 trees in two or three stands are achievable. These are rough guide numbers, and it has to be considered that, apart from the distance of the locations of the stand, the characteristics of the stands (density, undergrowth) and the terrain (slope) as well as the weather conditions have considerable influence on the performance. Especially during field work of several weeks, down times caused by rainfall or heavy wind must be planned. Laboratory performance of the image analysis is about four to five trees per hour, but working four hours or more per day, done by the same person, is not advisable because of the necessary high concentration. Lastly, it must be underlined that the accuracy of the resulting data extremely depends on very conscientiously performed field and laboratory work.

ACCURACY OF PHOTOGRAMMETRIC MEASUREMENTS

Judging the accuracy of the different terrestrial photogrammetric systems used in forestry is difficult because error studies are not often performed systematically, or only to a very limited extent, or different error characteristics were presented in publications, which hinders a direct comparison. Frequently, observations are restricted to the lower- and middle-stem section, as this is the economically most important part of the tree. Sometimes, the precision is given for the whole length of the stem, though oblique images induce increasing measurement errors depending on height.

As error characteristics are not always denoted by the same terms in literature, the expressions, used here are defined as follows:

The measurement error

$$\Delta x = \bar{x} - x$$

is the deviation of a photogrammetrically determined value \bar{x} of a distinct variable (e.g., diameter or height) related to a measured reference value x (calliper diameter, height determined by a measuring tape).

The average error $\overline{\Delta x}$ is defined by

$$\overline{\Delta x} = \frac{1}{n} \sum_{i=1}^n (\bar{x}_i - x_i)$$

and the average absolute error $\overline{\Delta x}_{\pm}$ by

$$\overline{\Delta x}_{\pm} = \frac{1}{n} \sum_{i=1}^n |(\bar{x}_i - x_i)|$$

The standard deviation of the measurement error $s_{\Delta x}$ is

$$s_{\Delta x} = \sqrt{\frac{1}{n} \sum_{i=1}^n (\Delta x_i - \overline{\Delta x})^2}$$

and the root mean square error (RMSE) s_x , often simplified to mean error, is

$$s_x = \sqrt{\frac{1}{n} \sum_{i=1}^n (\bar{x}_i - x_i)^2}$$

Measurement errors in practical use — published data

Concerning the accuracy of one of the first photogrammetric plate images by WEBER (1902), it is stated (quoted from MÜLLER 1931, p. 16, translated): "88% of all diameter measurements range between error limits from 0 to 1.0 cm." Due to a non-oblique plate orientation, stem diameters could be assessed only up to height of 14 m. MÜLLER (1931) found for his normally oriented stereo images (stereometer camera, type Hegershoff) a mean diameter error s_d of 0.35 cm for spruce, and for pine, a range from 0.38 to 0.48 cm. Concerning oblique images, he mentioned, without differentiating between the measurement heights, a mean error s_d of 0.44 cm. LEBRUN (1974) observed for tilted stereo photos (stereo camera Zeiss SMK 120) a mean diameter error s_d for pine from 0.4 to 0.9 cm and for spruce from 0.4 to 1.4 cm. The mean height error s_h was 0.39 m (pine) and 0.16 m (spruce). RAČKO (1983) compared the precision of stereo images (oak trees) taken with a professional stereo camera (Zeiss SMK 5.5/0808) and an amateur medium-format camera (KIEV 80). The mean diameter error s_d was 0.6 cm (SMK) vs. 0.4 cm (KIEV), the standard deviation of the diameter error $s_{\Delta d}$ was 0.42 cm (SMK) vs. 0.57 cm (KIEV). Concerning the height (the mean height of the oaks was 19.6 m), the mean height error s_h of 0.19 m (SMK) and of 0.08 m (KIEV) respectively, and standard deviation $s_{\Delta h}$ of 0.32 m (SMK) were determined.

KREIBIG (1964, 1967a,b, 1968, 1972) proved the principal suitability of amateur cameras (medium-format camera Praktisix with Flektogon 4/50 lens) for terrestrial single-

image photogrammetry in forestry. For spruce, the mean diameter error s_d of 0.35–0.6 cm was calculated in the interval from 2 to 15 m. Whereas from 2 to 10 m, the error remained relatively constant, it increased up to a height of 20 m, reaching the value of 1.0 cm. Of similar order was the mean error in the region of the bud swell. With an average tree height of 23.8 m, the mean height error s_h was 0.8 m (KREIBIG, 1967a). BRADSHAW (1972), who took a sequence of images per tree (135-mm lens) where each picture served for only a single diameter measurement, mentioned an average diameter error $\overline{\Delta d}$ of 0.07 cm within the range from 1.3 to 28 m, and a standard error (not clear whether s_x or $s_{\Delta x}$ was meant) of 1.0 cm. Concerning the height, $\overline{\Delta h}$ was 0.09 m and s_h (or $s_{\Delta h}$) was 0.15 m. DEHN (1987) investigated in detail measurement errors resulting from images of firs, taken with a 35-mm camera (CANON AE1 with 28 mm lens). For about the whole length of the stem (measurement distances 1 m), the average diameter error $\overline{\Delta d}$ ranged from 0 to ± 0.2 cm, but the top region showed a slight systematic underestimation by -0.3 cm. The tendency of the standard deviation of the measurement error $s_{\Delta d}$ is comparable with the tendency which is described by KREIBIG for the mean error. In the stem section from 2 to 20 m, $s_{\Delta d}$ varies between 0.4 and 0.6 cm, increases in the region above and reaches the values between 1.0 and 1.3 cm. Using the same photogrammetric method, but applying a modified aerial camera (AFP 21 K with 50-mm and 200-mm lenses), PERLWITZ (1994) determined for pine – averaged for all height positions – the mean error s_d of 0.7 (200 mm lens) and 1.2 cm (50 mm lens), respectively.

TAKAHASHI et al. (1997) could use a measuring camera prototype (Minolta MC-100 with 500-mm lens). Photogramming separate stem sectors, the average diameter error $\overline{\Delta d}$ for *Chamaecyparis obtusa* (35 years old, measuring height 1.2 m) was +0.16 cm and the mean error s_d was 0.46 cm. Measurements of *Cryptomeria japonica* at different heights (1.2, 3.2 and 5.2 m) resulted in +0.02 cm for the average error $\overline{\Delta d}$ and in 0.05 cm for s_d . Concerning the height errors (tree heights ranging from 15 to 21 m), $\overline{\Delta h}$ was found to be +0.25 m (+1.3%) and s_h was 0.62 m.

The attainable precision of digital cameras depends essentially on the pixel number of the CCD elements. The camera used by CLARK et al. (1998), a Kodak DC-120 (1,280 × 960 pixels), permitted an optical resolution of not more than about 7 mm per 10-m distance to the object plane. Measurements performed on several deciduous trees at stem heights of 1.4 to 21 m (camera distance ranging from 6 to 21 m and tilt angle from 3 to 63 degrees) contain an average error $\overline{\Delta d}$ of +0.97 cm. The single-error interval ranges from -5.8 to 8.4 cm. Depending on height, the spread of error increases considerably.

Answering the question about acceptable error limits for diameter measurements necessitates judging of the effect of diameter errors on volume estimation, in relation to the total stem or to assortment volumes. If the mean diameter error s_d is known, the mean volume error s_v of a stem section with length l and diameter d is given by

$s_v = \pi/2 \times l \times d \times s_p$ assuming a cylindrical form of the section. As the diameter error increases depending on height, and the diameter itself becomes smaller, the relative volume error in the uppermost stem regions can reach immense values. But this *random* error is of little importance and can generally be neglected if the estimation of the total stem volume is of interest, especially if the measured values are interpolated (e.g., by spline functions: SLOBODA et al. 1998). Not negligible are *systematic* errors, but they can be avoided – at least in the lower and middle part of the stem – if the photogrammetric method is applied correctly. In the upper part, in the case of backlit conditions or of highly reflecting radiation caused by clouds, the edges of the stem are inundated with radiation, leading to a systematic underestimation of stem diameters. KREIBIG (1967a,b) mentions deviations of –1.5 to –3.0 cm. Though this effect can cause a great relative volume error in the uppermost stem section, due to its little absolute volume, it is of minor significance for the estimation of the total stem volume (DEHN 1987).

Errors of the Göttinger photogrammetric system – control measurements

The principal suitability of low-cost 35-mm cameras for photogrammetric purposes has been proven, but all measurement equipment must be controlled carefully so that possible system-inherent systematic errors can be corrected. Control measurements require the analysis of geometrically exactly defined objects under optimal conditions.

The test of our own CANON camera was performed in 1984 and 1992 in Göttingen, as well as in 1999 in Zvolen (Slovakia). Several pairs of marks were attached at multi-storey houses in well-defined vertical distances (measured using a steel tape). The photo scale used was a 5-m aluminium pole with pass points distances of 2.5 m. In 1992, the horizontal distances of the marks were about 30 cm, the vertical ones about 4.5 m, with the highest mark at 32 m. The camera distance to the house was chosen as

Table 1. First control of the “Göttinger photogrammetric equipment”. Influence of the height positions of the measured marks on systematic and random diameter and height errors (width of the marks: 30.0 cm)

Control measurements – Göttingen 1992				
Height (m)	Diameter error (cm)		Height error (m)	
	Mean	Std. dev.	Mean	Std. dev.
	Δd	$s_{\Delta d}$	Δh	$s_{\Delta h}$
5.26	0.05	0.26	0.00	0.00
9.78	0.48	0.10	–0.01	0.02
14.25	0.18	0.40	–0.01	0.06
18.74	0.44	0.26	0.00	0.12
23.24	0.58	0.27	–0.02	0.19
27.75	–0.06	0.60	–0.03	0.29
32.22	–0.58	0.80	–0.09	0.40
Mean	0.16		–0.02	

close as possible (about 22 m) and thus, requiring in consequence a great camera tilt (about 25°), with the aim to increase the potentially existing systematic error. The best-exposed photo negative was measured in triple replication. The results (Table 1) do not show any systematic diameter or height errors (Δd and Δh). The standard deviation of the height error $s_{\Delta h}$ starts with 0.0 m at a height of 5 m, increases continuously, and reaches 0.4 m at 32 m. In respect to the diameter, below a height of 23 m, $s_{\Delta d}$ revealed variation ranging from 0.1 to 0.4 cm, then increasing to 0.8 cm at the height of 32 m.

Table 2. Second control of the “Göttinger photogrammetric equipment”. Influence of camera distance and width of the measured marks on systematic and random diameter errors (height positions of the marks about 23 m)

Diameter (cm)	Control measurements – Zvolen 1999			
	Diameter error (cm)			
	Camera distance 25 m		Camera distance 50 m	
Mean	Std. dev.	Mean	Std. dev.	
Δd	$s_{\Delta d}$	Δd	$s_{\Delta d}$	
5.0	0.14	0.06	0.84	0.41
10.0	–0.13	0.96	–0.29	0.65
20.0	–0.49	0.12	1.08	0.76
25.0	0.90	0.33	0.08	0.86
40.0	0.03	0.18	–0.98	1.07
60.0	0.36	0.09	–0.24	0.58
Mean	0.14		0.08	
Std. dev.	0.57		0.96	

In 1999, in Zvolen, control measurements were repeated with the intention of testing for systematic errors once more. The influence of different widths of the measured marks on the resulting precision was to be studied, as well as the effect of doubling the camera distance. The marks were then positioned at a height of about 23 m and the camera locations were chosen at distances of 25 and 50 m from the object plane. The measurements of each exposure were repeated three times. Again no systematic error could be found (Table 2).

The average diameter error or its standard deviation does not depend on the width of the marks. But the camera distance influences the random error noticeably: $s_{\Delta d} = 0.57$ cm at a distance of 25 m vs. $s_{\Delta d} = 0.96$ cm at a distance of 50 m. Just like in the increasing dispersion of the measurement error at higher positions, the reason is the same: a greater camera distance results in a smaller image scale. Thus, the edges of the marks are more blurred and their identification becomes more vague. This is valid for the pass points, too. The influence of random deviations of measured pass points on calculated object co-ordinates was investigated by simulations.

Error simulations

DEHN (1987; DEHN et al. 1985) calculated theoretical diameter and height errors for the Göttinger photogram-

metric system. He determined maximum values for the tilt angle of the pass point pole with reference to the object axis (0.2°), for the standard deviation of the identification error of the edges of the photo negative ($50 \mu\text{m}$), of the pass points ($2 \mu\text{m}$) and of the object points ($3 \mu\text{m}$). Running multiple computer simulations, with all errors randomly varying from zero up to the given upper limit, the results were obtained (Table 3) which are comparable to those of the control measurements (Table 2).

Normally, working under field conditions, the assumed maximum tilt angle of the scale pole of 0.2° (equivalent to a deviation of 1.7 cm for the 5-m pole) is more or less frequently exceeded. Moreover, in the simulation studies,

Table 3. Error study by simulating the "Göttinger photogrammetric method". Influence on random diameter and height errors by differentiating three height ranges

Height range (m)	Error simulation – DEHN et al. (1985)	
	Diameter error (cm)	Height error (m)
	Std. dev. $s_{\Delta d}$	Std. dev. $s_{\Delta h}$
0–10	0.26	0.009
10–20	0.36	0.058
20–30	0.51	0.152

errors at heights over 30 m were not examined, but in old stands trees regularly exceed this value. Therefore, exemplarily taking into account such typical conditions, the effect of incorrect handling of the photogrammetric equip-

ment – and certain other factors – will be calculated (Table 4).

The *basic variant (V1)* is given by a 50-m object. The camera distance D_v is relatively close (25 m) and, with a camera tilt ω of 30° , the object will approximately fill the film format in longitudinal direction. Rotations on the other image axis do not exist. The terrain is not inclined and thus, the vertical distance D_v of the projection centre of the camera with reference to the object co-ordinate system is defined as 1.5 m. The first pass point is located at a height of 1 m. The *pass point pole* lies in the object plane, with distance D_p from the camera, but *parallelism to the tree axis will not be assumed*. The fulcrum lies in the third pass point with a rotation angle of 0.5° (equivalent to a deviation of 4.4 cm at the first pass point). (To facilitate comparisons, calculated systematic diameter and height measurement errors of this and of the following variants are given in per cent, related to the corresponding variable value.) The tilt of the pole causes comparable errors $\Delta D\%$ and $\Delta H\%$, which increase depending on height, reaching 1.6% and 1.5% respectively, at a height of 50 m. *Doubling the tilt (V2):* 1.0° equiv. to 8.8 cm) doubles the errors, too. *By increasing the camera distance (35 m) and reducing the camera inclination (25°) both errors will be decreased by about 30% (V3).* Further distance enlargement (50 m) and camera tilt reduction (20°) reduces the errors once again by about 30% (V4). The influence of *rotating the camera around its vertical axis (y-axis, see*

Table 4. Error study of the significance of different variants of systematic errors on measured diameters and heights, calculated for different height positions

	Theoretical measurement errors																	
	V1	V2	V3	V4	V5	V6	V7	V8	V9									
	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)		
Camera distance D_h (m)	25	25	35	50	25	25	25	40	25									
1. Camera tilt angle ω^1	30°	30°	25°	20°	30°	30°	30°	10°	30°									
2. Camera tilt angle ²	0°	0°	0°	0°	0.5°	0°	0°	0°	0°									
PPS ³ tilt angle	0.5°	1.0°	1.0°	1.0°	0.5°	0°	0.5°	1.0	0°									
PPS distance error (m)	0	0	0	0	0	0.5	0	0	0									
Height 1. PP ⁴ (m)	1	1	1	1	1	1	2	1	1									
Slope	0°	0°	0°	0°	0°	0°	0°	20°	0°									
Camera height D_v (m)	1.5	1.5	1.5	1.5	1.5	1.5	1.5	19.7	1.5									
Meas. error 2. PP (mm)	0	0	0	0	0	0	0	0	0.01									
Height (m)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	ΔH (%)	ΔD (%)	
5	0.0	0.0	-0.1	-0.1	-0.1	0.0	0.0	0.0	0.03	0.08	-2.0	-1.4	-0.1	-0.1	0.0	0.1	-0.1	-0.1
10	0.1	0.1	0.3	0.2	0.2	0.2	0.1	0.1	0.03	0.08	-2.0	-1.7	0.1	0.1	0.1	-0.1	0.4	0.4
15	0.3	0.3	0.6	0.6	0.5	0.4	0.3	0.3	0.03	0.08	-2.0	-1.8	0.3	0.2	0.2	-0.1	0.9	0.8
20	0.5	0.5	1.0	0.9	0.7	0.7	0.5	0.5	0.04	0.08	-2.0	-1.9	0.4	0.4	0.3	0.0	1.4	1.3
25	0.7	0.6	1.4	1.3	1.0	0.9	0.7	0.6	0.04	0.08	-2.0	-1.9	0.6	0.6	0.4	0.1	1.9	1.8
30	0.9	0.8	1.7	1.6	1.2	1.2	0.8	0.8	0.04	0.08	-2.0	-1.9	0.8	0.7	0.5	0.2	2.4	2.3
35	1.0	1.0	2.1	2.0	1.5	1.4	1.0	1.0	0.04	0.08	-2.0	-1.9	1.0	0.9	0.6	0.3	2.9	2.8
40	1.2	1.2	2.4	2.4	1.7	1.7	1.2	1.2	0.04	0.08	-2.0	-1.9	1.1	1.1	0.7	0.4	3.5	3.4
45	1.4	1.3	2.8	2.7	2.0	1.9	1.4	1.3	0.04	0.08	-2.0	-1.9	1.4	1.3	0.9	0.5	4.0	3.9
50	1.6	1.5	3.2	3.1	2.3	2.2	1.6	1.5	0.04	0.08	-2.0	-1.9	1.5	1.4	1.0	0.6	4.5	4.4

Note: ¹inclination angle and ²angle related to the y-axis (Fig. 1), ³pass point system, ⁴pass point

Fig. 1), here by an angle of 0.5° , is totally insignificant (V5). A distance error of the pole (V6: located 0.5 m in front of the object plane of the tree, simulating a pole hanging up on a branch somewhat far from the stem) results in a diameter error $\Delta D\% = -2.0\%$, which does not depend on height. To the contrary, the height error $\Delta H\%$ increases with the height (-1.4 to -1.9%), but the change rate slows down considerably. Halving the distance error will reduce the measurement errors by the same amount. Hanging the pole higher by 1 m has only a marginal effect (V7). In the case of a significant slope (20°), the camera tilt can be reduced considerably (10°). With a horizontal distance of 40 m, the vertical distance D_v will be about 19.7 m (V8). While, in comparison to distances of 40 m in a flat terrain and with a camera inclination of 25° , there is no improvement concerning the diameter error, the height error is 0% at a height of about 20 m. Below this height, the error is very small, above, it slightly increases, reaching 1.2% at a height of 50 m.

Lastly, the effect of incorrectly measuring the image pass points will be examined: the y -co-ordinate of, e.g., only the second pass point is assumed to be overestimated by $10 \mu\text{m}$ (V9). The standard deviation for this pass point measurement error was found to be $2.0 \mu\text{m}$ (DEHN 1987); the mean error is $3.0 \mu\text{m}$ (KREIBIG 1967a). The resulting systematic diameter and height errors depend on height and, at 50 m, they are 4.5 and 4.4%, respectively.

The above simulations confirm the experience of DEHN (1987; DEHN et al. 1985): avoiding systematic diameter and height errors requires – in the stand – taking special care in orienting the pass point pole parallel to the tree axis and – in the laboratory – of measuring the pass points. Moreover, the pass point pole must hang within the object plane, as KREIBIG (1967a) already underlined.

MEASUREMENT RESULTS IN THE DOBROČ VIRGIN FOREST

The renewed testing of the calibrated CANON camera in 1999 in Zvolen was considered to be advisable due to

the results of preceding photogrammetric analyses of photographs taken in the Dobroč virgin forest. In April 1998, 27 of the largest trees of the species fir (14), beech (7) and spruce (6) were assessed for estimating yield data (height, volume, etc.). The analyses of the photo negatives were performed with triple replications, with the aim of reducing the influence of random measurement errors. Additionally, for control purposes, seven of these trees were measured with a theodolite. It turned out that the volumes V_p , based on taper curves which were photogrammetrically derived, were significantly smaller (on average 13%) than those which were based on theodolite measurements (Table 5).

One of the possible explanations could be a systematic error due to an inexact positioning and orientation of the pass point pole. In such a case, the determined heights H_p must contain a negative error, too. But the difference of -0.2 m (-0.5%) on average is insignificant. In regard to single trees, the situation is different in some cases: the photogrammetrically measured height of, e.g., beech No. 5 is lower by -2.8% . If this was caused by false handling of the scale pole, the consequence would be – as shown by the error simulation (Table 4, V2, V9) – diameter errors of a similar order in the uppermost stem part. The stem cross-sectional error would be about twice the size, but this error would diminish downward the stem, reaching zero at the base, so that the total volume error would be clearly smaller than the determined one. Hence, it must be stated that a possible systematic error of the pole orientation cannot be the (single) reason for the high volume differences.

Graphs of single trees showing stem diameter over height reveal further information. For beech No. 3, the diameters, obtained by the photo and the theodolite method respectively, largely coincide (Fig. 3). (Take note that in the case of stem forks of beech trees the largest of the two stems was always measured. Therefore, the calculated volumes do not represent the total "stem" volume.)

Using the theodolite for this tree and most of the others, too, stem positions very close to the ground were

Table 5. Comparison of height (H) and volume (V) data on seven trees from the Dobroč virgin forest, acquired by theodolite (T) and photogrammetric (P) measurements

Tree measurements in the Dobroč virgin forest											
No.	Species	d.b.h. (cm)	Circ. (m)	Theodolite		Terrestrial photogrammetry					
				H_T (m)	V_T (m ³)	H_p (m)	$\Delta H = H_p - H_T$ (m)	$\Delta H = H_p - H_T$ (%)	V_p (m ³)	$\Delta V = V_p - V_T$ (m ³)	$\Delta V = V_p - V_T$ (%)
2	Fir	117.7	3.70	53.5	26.8	54.7	1.2	2.1	26.0	-0.8	-2.9
3	Beech	104.3	3.28	44.3	16.2	45.7	1.5	3.3	16.0	-0.1	-0.9
4	Fir	120.8	3.80	50.3	21.5	50.1	-0.2	-0.4	19.6	-1.9	-8.7
5	Beech	88.4	2.78	38.6	10.3	37.5	-1.1	-2.9	8.6	-1.7	-16.3
6	Fir	131.6	4.13	54.7	34.1	54.1	-0.6	-1.1	27.7	-6.4	-18.8
10	Spruce	96.8	3.04	53.0	17.6	51.6	-1.3	-2.5	14.4	-3.2	-18.2
13	Spruce	81.2	2.55	45.4	10.0	44.4	-1.0	-2.1	8.6	-1.3	-13.5
	Mean	105.8	3.32	48.5	19.5	48.3	-0.2	-0.5	17.3	-2.2	-12.8

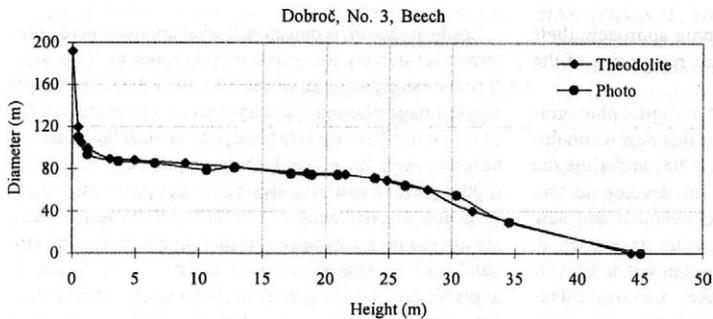


Fig. 3. Comparison of stem profiles of a beech, derived by theodolite and photogrammetric methods: relatively good congruence

assessed. In contrast, the photogrammetric method did not often allow clear identification of the borders of the stem at such a low height and, thus, in most cases, the strongly developed butt swelling could not be represented to its full extent. The importance of this effect was estimated by omitting all those diameter values of the theodolite data, which were situated below the position of the first recorded photo value. Then, the volume differences are reduced to 1.4 m³ or 4.2% (tree No. 6), 0.8 m³ or 4.4% (No. 10) and 0.6 m³ or 5.6% (No. 13), i.e., the different butt swell representation only partially accounts for the deviations. A further fundamental reason is the diameter differences in the middle and upper stem parts. Regarding spruce No. 10, the deviations in the region from 30 to 40 m are about 10 cm (Fig. 4).

This is much more than could be explained by a possible flare effect (1.5–3.0 cm: KREIBIG 1967b). But the pictures were taken under quite favourable light conditions and, therefore, the photo negatives contain, if any, only minor rimlighting. In regard to the theodolite measurements, on the other hand, a systematic error of the instrument itself can be denied, too, as control measurements show. Moreover, it must be stressed that there is, on average, a sound coincidence of the heights determined by both methods. The one-sided deviations of the diameters within entire stem parts of several trees exclude random errors. Random errors should be very small: theodolite measurements on pine (maximum heights of about 26 m) showed the mean diameter error s_d of 0.2 cm (PERLWITZ 1994). Another aspect is the non-identical position of the camera and theodolite. But, with approximately the same

viewing direction, possible asymmetries of stem cross sections should be of secondary importance. Another potential error may have occurred during targeting at the borders of the stem. The pertinent stem regions of the conifers were more or less hidden by great needled branches and as for the beech, it cannot be excluded that, within the crown, the same branching stems were not measured. Lastly, possible stem movements due to wind might have caused errors, but it must be stated that the theodolite measurements (as well as the photographing) were performed by experienced persons.

Therefore, unfortunately, it must be concluded that, in retrospect, the final, satisfying explanation for the volume differences is not possible. On account of the great interest in exact yield data on the Dobroč forest reserve, it is proposed to repeat the measurements using both methods (or, additionally, another, e.g., laser-based one) at the next possible opportunity.

DISCUSSION

The given results demonstrate that terrestrial single-image photogrammetry, based on 35-mm commercially available cameras, can principally provide reliable measurement data, even in the case of exceptional tree heights of 50 m or more. Of course, with greater camera distances and inclination angles, the random errors and, if any, the systematic ones, will increase. But these shortcomings, as well as the general problem of recognising stem contours of conifer trees in the crown region, are inherent in alternative methods (theodolite, laser, etc.), too. Addi-

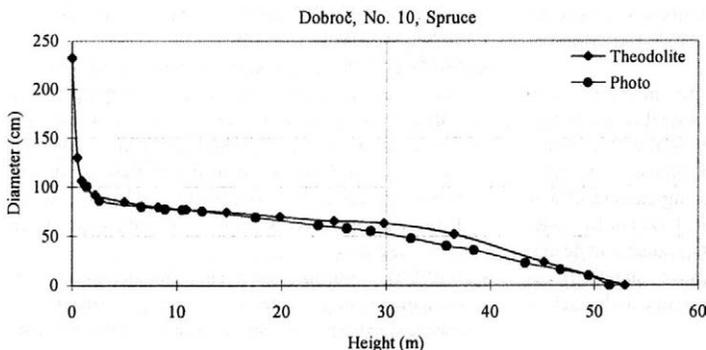


Fig. 4. Comparison of stem profiles of a spruce, derived by theodolite and photogrammetric method: great differences for the stem swelling due to missing photo values, and inexplicable divergence in the upper part of the stem

tionally, compared to the photographic approach, their disadvantage is that the simultaneous registering of the complete object is not possible.

With the progressive development of digital photography, the question arises as to whether this new technology is to be preferred. CLARK et al. (1998) underline the advantages: costs and time delay in film development no longer exist, data storage is more convenient and new perspectives of digital image processing have opened. The financial argument may be of importance if, as CLARK et al. did, eight images per tree are taken. Our own calculations show that film and film-processing costs (three photos per tree) account for only a small part (not more than 10%) of the total costs. Saving huge quantities of data (by choosing a resolution of $2,240 \times 1,500$ pixels with the Kodak DC290, 20 images will require a capacity of 20 MB) and today, a rapid data access is no longer a problem for CD or DVD media. Unintentional data damage must be prevented by adequate safety strategies, whereas photo negatives, stored in special sheets, will not normally suffer any loss of information. By digitising the analogue images with very high-resolving, special scanners, principally, digital data processing is possible, too.

The strongest argument contra digital imaging is the resolving power of today's matrix cameras which do not come up to films with very fine grain. Direct comparisons are difficult because the film resolution depends on the object contrast and, concerning the CCD cameras, such technical information is not usually given. Besides, differences in vertical and horizontal resolution exist. For the Kodak DC-120 ($1,280 \times 960$ pixel), adjusting the lowest focus of 7 mm, CLARK et al. (1998) experimentally determined a maximum vertical resolution of 0.7 cm at an object distance of 10 m. With the top-of-the-range camera of today, the Kodak DC290, an improvement obtained through the higher pixel number would be achievable. In comparison, an extremely fine-grained film, the AGFAPAN APX 25, has a resolution of 200 lines per mm at a contrast of 1:1,000. In combination with a 35-mm camera and a 28-mm wide-angle lens, the mathematical object resolution is 0.18 cm at a distance of 10 m. If the contrast is considerably lower, as is the case for the lower part of a tree stem in stand, the resolving power may be reduced by the half. However, this applies to the digital technique, too (CLARK 1998). As the development of CCD elements takes place much faster than the refinement of film emulsions, it is to be expected that terrestrial photogrammetry based on digital imaging has a future ahead.

Regardless whether future photogrammetry will use analogue or digital technology, most probably, the necessity of developing a measuring system itself will continue. Commercial solutions do not seem to come to the market. Moreover, e.g., the prototype measuring camera of Minolta, the MC-100 (TAKAHASHI et al. 1997) or MacARBOR, a project of Regent Instruments, Canada, to design a hard- and software package for measuring standing trees (Regent, pers. commun.), were given up due to the lack of profitability perspectives.

Lastly, it should be questioned what application requires terrestrial stereo photogrammetry in forestry. If the stem form is merely the aim of interest, then the more simple single-image photogrammetry proved successful. In the case of considerable stem bend, which must be taken into account, e.g., for estimating assortments, FIRTH et al. (2000) prefer a spatial analysis of image pairs. Measuring branches, for calculating their volume (OLENDEREK 1992), always requires 3-dimensional photogrammetry. Unfortunately, the associated analysis effort as well as the general problem of visibility of branches and of assignment of branches within the crown of trees, standing in more or less dense stands (NODA 1992), does not permit an extensive use of this type of application.

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Terestrická jednoobrazová fotogrametria ako prostriedok zamerania stojacích stromov s modelovou aplikáciou v pralese Dobroč

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ABSTRAKT: Terestrická fotogrametria sa v lesníctve používa už takmer jedno storočie. Predovšetkým vývoj výpočtovej techniky ako aj produkcia vysokohodnotných amatérskych kamier umožnila rozsiahle a racionálne nasadenie tejto techniky. Pre zmeranie morfolologickej krivky stojacích stromov nie je spravidla použitie stereofotogrametrie potrebné, jednoducho jednoobrazová fotogrametria je postačujúca. Teória a praktické použitie metódy jej nasadenia je popísaná v príspevku. Analýza chýb ukázala, že smerodajná odchýlka priemeru a výšky stromov s výškou merania a vzdialenosti od meraného

stromu rastie. Pri vzdialenosti cca 22 m a pri výške cca 32 m činí táto pre priemer stromu $s_{\Delta d} = 0,8$ cm a pre výšku $s_{\Delta h} = 0,4$ m. Pri výške merania 23 m a vzdialenosti 25 m $s_{\Delta d} = 0,6$ cm a pri vzdialenosti 50 m $s_{\Delta d} = 1,0$ cm. Systémové systematické chyby neboli zistené. Simulácie ukazujú, že predovšetkým chyby držania výškovej laty ako aj zmerania jej vličovacích bodov vedú k tomu, že hodnoty priemeru a výšky stromov sú zaťažené systematickou chybou, ktorá s výškou merania rastie. Príležitosťou k analýze chýb boli merania na niektorých najvyšších stromoch v pralese Dobroč v Slovenskej republike: cieľom analýzy bolo zhodnotiť vhodnosť terestrickej fotogrametrie aj pri objektoch s výškou 50 m a viac.

KLúčové slová: terestrická fotogrametria; meranie morfolologickej krivky; prales Dobroč

Terestrická fotogrametria bola v lesníctve použitá už koncom 19. storočia na zmerania stojacich stromov, spočiatku s pomocou jednoduchých platňových kamier (WEBER 1902). Táto technika bola pomocou profesionálnych meračských kamier podstatne rozvinutá ako stereofotogrametria (MÜLLER 1931). Rozsiahlejšie a ekonomické nasadenie terestrickej fotogrametrie bolo umožnené až pokročilým vývojom výpočtovej techniky, ktorá umožňuje racionálne vyhodnotenie dát, a voľnou dostupnosťou hodnotných a cenovo prístupných amatérskych kamier. Na základe strednoformátovej kamery vyvinul KREIBIG (1967a,b, 1968) postup, pri ktorom je strom zobrazený spolu s lineárnou mierkou na jednom obraze a kedy je pozícia kamery flexibilne voliteľná a parametre vonkajšej orientácie (sklon kamery, jej vzdialenosť k objektu) nemusia byť zmerané. Začiatkom osemdesiatych rokov bol navrhnutý a v praxi použitý analógový postup nezávisle od DEHNA et al. (1985, DEHN 1987) pre 35mm kameru. Na rozdiel od postupu, pri ktorom je vyhotovený len jeden obraz z každého stromu, ponúkajú – pri použití teleobjektívu – snímky z jednotlivých častí stromu väčšiu mierku, ale umožňujú spraviť iba jedno meranie na snímke (BRADSHAW 1972; CROSBY et al. 1983; NOSENZO 1993; TAKAHASHI et al. 1997). Náročná stereofotogrametria je naďalej vhodná všade tam, kde je priestorová informácia požadovaná alebo nevyhnutná. Aj v tejto oblasti boli vyvinuté paralelne k profesionálnym dvojkomorovým kamerám (napr. LEBRUN 1974; RAČKO 1983; OLENDEREK 1992) meračské systémy pre použitie strednoformátových (RAČKO 1983) a maloformátových kamier (NAKAYAMA, NAGASHIMA 1963; FIRTH et al. 2000).

Terestrická jednoobrazová fotogrametria, ktorú vyvinuli DEHN et al. (1985; DEHN, 1987) v Göttingene, je používaná doteraz a bola aplikovaná aj v tejto práci v pralese Dobroč. Jej použitie je možné predovšetkým na zmeranie tvaru kmeňov pre zhotovenie morfolologickej krivky (SLOBODA et al. 1998; GAFFREY, NAGEL 1998). Potrebné vybavenie pozostáva z chachovanej zrkadlovky a 5 m dlhej laty s tromi vličovacími bodmi a jedného meracieho stola pre vyhodnotenie obrazu riadeného pomocou PC. Pre fotografovanie sú potrebné dve osoby. Zatiaľ čo kameraman hľadá vhodnú polohu (s dobrou viditeľnosťou celého stromu vrátane vrcholu a dobrými svetlostnými pomermi), priloží druhá osoba vličovaciu latu paralelne k stromovej osi (obr. 1). Identifikácia vličovacích bodov na negatíve a určenie ich súradnicových bodov umožňuje výpočet troch neznámych parametrov perspektívneho zobrazenia a tým transformáciu ľubovoľných obrazových

súradnicových bodov do objektových súradnicových bodov. Meračské zariadenie disponuje optikou s možnosťou voľného až 80-násobného zväčšenia, takže body objektu pre zmeranie priemeru môžu byť identifikované pri vyššom rozlíšení interaktívne na obrazovke (obr. 2).

Akceptácia fotogrametricky zistených hodnôt vyžaduje schopnosť metodiky dosiahnuť požadovanej presnosti a vylúčenie systematickej chyby individuálne použitého meračského systému. V literatúre o chybách merania priemeru stromu nie sú žiadne informácie o závislosti chyby od výšky merania. Pri fotografovaní s vhodnou kamerou je však tento vplyv veľmi významný (KREIBIG 1967a). Väčšina doterajších skúmaní sa okrem toho obmedzuje na stromy s výškou menšou ako 20 m (zriedka do 30 m – DEHN 1987), hoci je potrebné zmerať aj stromy s výškou 50 m a viac (ako aj v pralese Dobroč) (GAFFREY 1996). Z týchto dôvodov boli vykonané kontroly náhodných a systematických chýb vlastného vybavenia ako aj simulácie chýb v závislosti od rôznych vplyvov. Systémové chyby neboli zistené (tab. 1 a 2). Smerodajná odchýlka chýb priemeru stromu vykazuje pomimo závislosti od výšky merania aj rast so vzdialenosťou zmerania (tab. 1 a 2). Dôvodom tohto javu sú ťažkosti rozoznania meraných bodov objektu so znižujúcou sa mierkou zobrazenia. Zjednodušene možno povedať, že pri výške merania 30 m a približne rovnakej vzdialenosti od meraného stromu smerodajná odchýlka chyby priemeru neprekračuje hodnotu 1 cm, ktorú odporúča KREIBIG (1967b) ako hornú hranicu. Simuláciou je skúmaný vplyv rôznych chýb počas fotografovania ako aj počas vyhodnotenia obrazu (tab. 4). Ukázalo sa, že veľmi významná je správna orientácia vličovacej laty (paralelne k stromovej osi so vzdialenosťou ku kamere zodpovedajúcej vzdialenosti stromovej osi ku kamere) ako aj určenie obrazových súradnicových bodov vličovacích bodov.

V roku 1999 bolo v pralese Dobroč fotogrametricky zmeraných 27 najväčších stromov (14 jedlí, 7 bukov a 6 smrekov). Ako kontrola nasledovali merania teodolitom na siedmich týchto stromoch. Ukázalo sa, že objem stromov vypočítaný na základe fotogrametricky meraných hodnôt (konštrukcia morfolologickej krivky pomocou spline funkcie – SLOBODA et al. 1998 – a výpočet rotačného objemu) bol v priemere o 13 % menší. Keďže vypočítané výšky boli takmer identické, systematické chyby meracieho zariadenia a jeho obsluhy môžu byť vylúčené. Časť odchýlok je možné vysvetliť spravidla extrémnym priebehom kmeňa, ktorý nebol zohľadnený. Hlavný dôvod je však možné vidieť vo výrazne menších hodnotách priemeru

stromov vo vyšších kmeňových častiach. Presvetlenie stromových hrán protisvetlom ako dôvod týchto chýb je možné vylúčiť. Ďalšie dôvody mohli byť pohyby stromov zapríčinené vetrom počas merania teodolitom, alebo merania na rôznych stanovištiach a tým diferencovaným (vo viacetážových porastoch veľmi ťažkým) určením hraníc kmeňa v korunovej oblasti. Záverečné jednoznačné vysvetlenie žiaľ nebolo možné.

Ukázalo sa, že terestrická fotogrametria je principiálne vhodná aj pre zameranie veľmi vysokých stromov, keď je tento postup aplikovaný s potrebnou dôkladnosťou. Základné problémy pri rozoznaní stromových kontúr v koru-

novej časti vykazujú aj iné techniky zamerania stojacích stromov. V budúcom vývoji fotogrametrie ponúka veľký potenciál digitálna fotografia (CLARK 1998; CLARK et al. 1998). Momentálne však digitálne dosiahnuteľné rozlíšenie ešte nedosahuje potenciál jemnozrnných filmov. Málo pravdepodobné je, že sa v blízkej budúcnosti nájde výrobca integrovaného systému fotogrametrického zmerania stromov. Vzhľadom na nedostatočný trh boli aj doterajšie pokusy vyvinutia napr. špeciálnych meračských kamier (Minolta) alebo kompletných systémov (Regent Instruments) zastavené.

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Attractiveness of spruce for cambioxylophages as related to stand age

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ABSTRACT: Attractiveness and stem and crown niches of cambioxylophages in relation to stand age were assessed in trees attacked and killed by bark beetles in Norway spruce stands aged 55–115 years and situated in the monitoring network of the Šance reservoir watershed (the Beskids). The study area was characterized by the basic level of bark insects. The age range was optimum for the occurrence of *Ips typographus*. A positive response in relation to the increasing stand age was determined in accompanying species *Callidium aeneum* and *Phthorophloeus spinulosus*. Decreased attractiveness was characteristic of *Molorchus minor*, *Cryphalus abietis* and *Pissodes harcyniae*. The stem niche extended with stand age in *Ips amitinus*, *Dryocoetes autographus* and receded in *I. typographus* (intermediate trees), *M. minor* and *Pogonochaerus fasciculatus* while an opposite response was found in *Polygraphus poligraphus* and *Pityogenes chalcographus*. *C. abietis* disappeared from branches and the longer crown profile was occupied by *C. aeneum* and *Pityophthorus pityographus*.

Keywords: cambioxylophagous fauna; *Picea abies*; stand age; the Beskids

The cambioxylophagous insect constitutes typical synusiae particularly on coniferous trees (PFEFFER 1955). Species composition is conditioned by their ecological requirements influenced by body size, food requirements, developmental cycle, rate of aggressiveness and competition. Food quality (predisposition resulting from tree weakening), phloem and bark thickness and its surface structure are important factors for the infestation of certain stand age categories. Within the profile of especially older trees, the colonization of stem and crown niches is differentiated. *Polygraphus poligraphus* L. occupies stems along their whole length (ZUMR 1984). From the territory of the Polish Beskids, KWAPIS and MATUSZCZYK (1991) report intensive occurrence of this species particularly on trees with honey fungus (*Armillaria* spp.). Attractiveness of a tree is affected by site and growth conditions (KULA, ZABECKI 2000), social status of the tree (KULA, ZABECKI 1997a,b,c), lightning stress (KULA, ZABECKI 1997b), stand age (PRICE 1975; GRÜN WALD 1986). *P. poligraphus* with its abundance and stem infestation extent belongs to important cambioxylophages causing the subdominant tree mortality. Potentially, it passes to co-dominant or dominant trees in the case of closed stands of smaller d.b.h. It does not create any foci but it afflicts individual trees. However, it is able to attack healthy trees along their whole stem profile (KULA, ZABECKI 1997c). It is considered to be a primary harmful insect in air-polluted stands. KISIEŁOWSKI (1978) reports

that it develops, first of all, on spruces infested by honey fungus (*Armillaria* spp.) which also occurred abundantly in sample trees analyzed in the area of the Beskids (KULA, ZABECKI 1998, 1999a,b). For the development of synusiae, temperature and humidity conditions of the microclimate given by the standing tree exposure seem to be important (ZUMR 1984) as well as stand structure (stand density, canopy closure), the stage of the mortality process and time of tree death, tree infestation predisposition (KANGAS 1952; SCHWERTFEGER 1955), swarming period, number of generations per year (BAKKE et al. 1977) and weather conditions particularly during swarming.

An important role in the development of cambioxylophages is played by the stand, stem and crown microclimate of individual trees. Subdominant trees do not satisfy more thermophilic species requiring bark insolation. These species can appear there during later periods of time when even in the subdominant stratum favourable temperature conditions (normally found in co-dominant and dominant trees) occur. Therefore, we could deduce that the existing species preferred quality trees in the stand rather than suppressed ones (*Ips amitinus* Eichh., *Xyloterus lineatus* Oliv., *Hylurgops palliatus* Gyll., *Ips typographus* L., *Tetropium fuscum* F., *Pityogenes chalcographus* L.) and that important harmful species in spruce stands in the Beskids are concerned (KULA, ZABECKI 1997a,c). The stem niche occupation is also affected by natural natality particularly in bark beetles from the tribe *Ipini*. During

warm and dry weather at an altitude of up to 700 m, the natality is characterized by repeated laying of higher egg numbers and creation of 'sister generations' whereas at higher elevations, with the increasing drop of temperature the frequency of repeated oviposition decreases.

The stand age is reflected in bark quality and, first of all, in bark thickness. *P. chalcographus* being of half body length as compared with *I. typographus* is concentrated in bark of less than 2.5 mm in thickness, however, it reaches high population density also in phloem which is *suboptimum* for *I. typographus*. Thus, the species becomes an important competitor for *P. chalcographus* (PRICE 1975). In spite of this, the coexistence of these species is possible with respect to the fact that the small *P. chalcographus* uses for its development bark remainders between feeding marks of *I. typographus*. According to GRÜNWARD (1986), the high proportion of *P. chalcographus* in 5mm thick bark, where *I. typographus* is missing, can result from pheromone information preventing another species to enter. If SAALAS (1917), ESCHERICH (1923), KRÄMER (1953) and POSTNER (1974) described differences in the vertical distribution of bark beetles on tree stems the distribution being in correlation with phloem and bark thickness which changed with stem age and height, then it is possible to say that it is not the height on a stem but quality of the material which are important for the development of the bark beetle.

X. lineatus occurs in standing dead trees on lower parts of their stems (ZUMR 1984). Even though the decisive infestation was observed on lower parts of their stems, its occurrence was registered up to the tree undercrown part (KULA, ZABECKI 1999c).

T. fuscum develops in the thick rough bark in the lower part of middle age and maturity age spruce trees usually infested by *Armillaria* spp. and red rot (KUDELA 1970). *Pissodes harcyniae* Herbst prefers stems with thinner bark in stands aged 15–120 years often damaged by air pollution. It develops in the upper part of the stem (LOUŽIL

1961). According to ZAHRADNÍK (1974), it attacks trees from their lower part upwards. Infested trees occur in forest stands individually. The species is often accompanied by *P. poligraphus*. According to KUDELA and WOLF (1963), *P. harcyniae* prefers subdominant (9.8%) rather than suppressed (6.6%), co-dominant (2.7%) and dominant (0.5%) trees.

The aim of the paper is to evaluate the effect of stand age on spruce attractiveness and colonization of the stem and branch niche by cambioxylophages.

MATERIAL AND METHODS

Within the monitoring network established in the Šance reservoir watershed (the Beskids) including 140 monitoring points, 51 Norway spruce stands were selected representing from the viewpoint of their age (60–100 years) those stands in which a major part of spruce cambioxylophages develops. The analysis was carried out in 476 dead standing trees 1–2 years old. After felling, each of the sample trees was debarked along the whole stem and branch profile. According to feeding marks or imagoes, the cambioxylophage abundance was determined in 1m sections (KULA, ZABECKI 1997a). At the same time, the sample tree was characterized by mensurational parameters, habitat conditions and social status of the tree. The niche mean length of tree stem and crown branches was derived from the sum of stem or crown length profiles infested by particular species, related to the stem or crown lengths of those trees where the species occurred.

The age of the stands ranging from 55 to 115 years (in the Kněhyně Reserve up to 200 years) was assessed in age categories of < 60, 60–70, 71–80, 81–90, 91–100, and > 100. At the same time, the relation of spruce cambioxylophages to altitude (KULA, ZABECKI 1999c) and forest type groups (KULA, ZABECKI 2000) was evaluated. The proportion of the stands from the viewpoint of age and altitude was balanced.

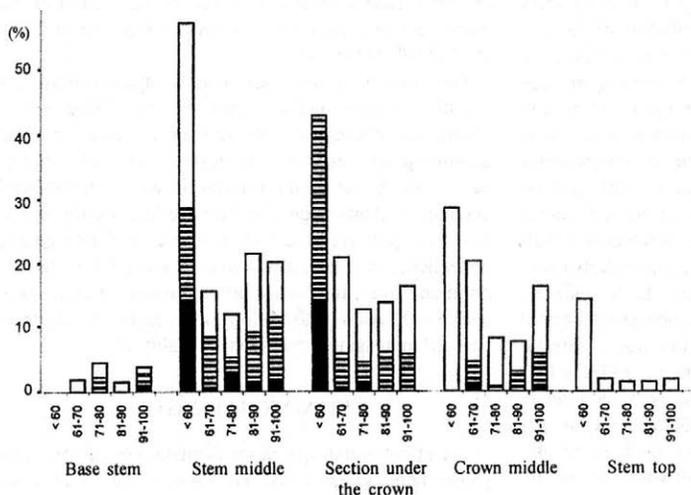


Fig. 1. Spruce attractiveness for *Molorchus minor* in relation to stand age (the Beskids) in comparative stem sections (infestation: ■ – heavy, ▨ – increased, □ – scattered)

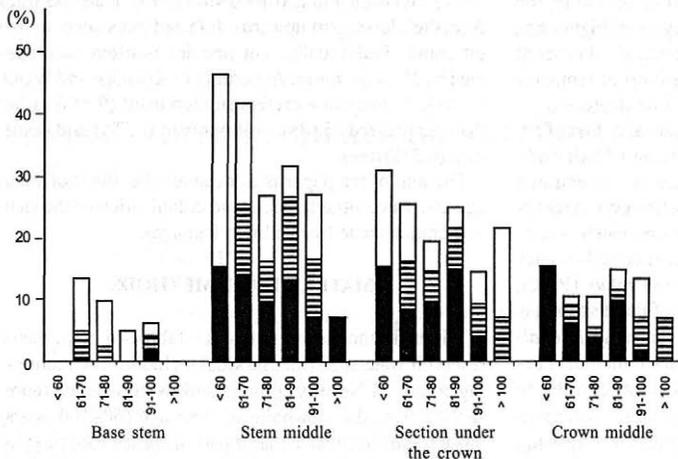


Fig. 2. Spruce attractiveness for *Polygraphus polygraphus* in relation to stand age (the Beskids) in comparative stem sections (infestation: ■ – heavy, ▨ – increased, □ – scattered)

Spruce stands in the Šance reservoir watershed are part of the Ostravice working-plan area in the Moravian-Silesian Beskids. They occur at an altitude of 500–1,200 m mostly on steep slopes of 15–25°. In this area, cambioxylophages occur in their latent status for a long time.

RESULTS AND DISCUSSION

SPRUCE ATTRACTIVENESS

The limited spruce stand age (60–100 years) is an optimum for *I. typographus* and accompanying species. Except for the set of trees younger than 60 years (7 trees) and older than 100 years (15 trees), the remaining categories were represented by sufficiently large sets of sample trees (65–153 trees).

With increasing tree age, the attractiveness increased for *Callidium aeneum* Deg. (0–6.7%) and *Phthorophloeus spinulosus* Rey. (28.6–54.0%), however, *Cryphalus abietis* Rtz. (24.8–6.7%), *Molorchus minor* L. (71–20%) and *P. harcyniae* (28.6–6.7%) attacking in general subdominant trees responded conversely. *M. minor* prefers trees younger than 60 years, the distribution of the species being balanced (Fig. 1) along the tree profile from mid-stem to mid-crown. Although *P. polygraphus* appeared to be less dependent on tree age in relation to attractiveness, according to its proportion in the most typical part of its niche (from mid-stem to mid-crown), a decreasing infestation intensity of spruce with increasing age can be deduced in spite of certain unbalance (Fig. 2). In older trees, their attractiveness was well-balanced, increasing moderately with age, particularly in co-dominant trees, for *Rhagium inquisitor* L. *H. palliatus* reached increased occurrence only in the age category of 81–90 years, otherwise showing the low rate of infestation (13–18%) in all remaining age categories (Table 1).

Low proportions in all age categories were recorded in *Dryocoetes autographus* Rtz. (0–7.8%) without any specific age dependence. On the contrary, the high infestation rate (46.7–71.4%) was associated with *Pityophtho-*

rus pityographus Rtz. particularly in trees younger than 60 years. In stands aged 60–100 years, its distribution was well-balanced (Fig. 3).

The sawyer beetle *Obrium brunneum* F. preferred trees aged 81–100 years. In *I. amitinus* (particularly in co-dominant trees), the attractiveness increased from trees younger than 60 years (28.6%) to the age category of 71–90 years (46.6–44.6%) with subsequent decrease in the oldest stands (20%). The species was clearly differentiated along the stem profile with culmination in the crown centre and the highest infestation in stands aged 81–90 years (Fig. 4). *I. typographus* attacked most frequently dominant and co-dominant trees aged 61–80 years (35%) and trees older than 100 years without any general age dependence for the assessed categories of < 60 and > 100 years (Table 1, Fig. 5).

P. chalcographus is affected by the social status of a tree and its dominant incidence occurred in stands aged 71–80 years (73%), the degree of infestation being distributed in the same manner in comparative sections with the total maximum of occurrence in the section of the crown centre (Fig. 6). Every second tree was infested (51.6–53.8%) (Table 1).

The wood wasp *Sirex juvencus* L. attacked most frequently younger trees and with their increasing age its abundance decreased. The sawyer *T. fuscum* ranked among the species with smaller deviations between age categories, however, the infestation was well-balanced and independent of age. The bark beetle *Xylechinus pilosus* Rtz. preferred the youngest trees and its tree age dependence was low. *X. lineatus* is a species preferring dominant trees, the lowest attractiveness being in trees aged 81–90 years (9%) while younger and also older trees showed increasing attractiveness (Table 1).

STEM NICHE LENGTH

The effect of tree age on the formation of cambioxylophage niche was assessed regardless of the social status

Table 1. Attractiveness of spruce for cambioxylophages as related to stand age (left), stem niche length (middle), crown niche length (right)

Species/age	< 60	61-70	71-80	81-90	91-100	> 100	< 60	61-70	71-80	81-90	91-100	> 100	< 60	61-70	71-80	81-90	91-100	> 100	
<i>Antaxia quadripunctata</i>	0	0	1	0	1	0	0	0	58	0	5	0							
<i>Callidium aeneum</i>	0	2	5	5	5	7	0	23	0	3	34	0	0	0	10	17	10	31	
<i>Camponotus herculeanus</i>	0	1	0	0	1	0	0	9	0	0	4	0							
<i>Cryphalus abietis</i>	14	25	17	17	13	7	0	22	20	10	20	54	78	39	41	41	32	29	
<i>Crypturgus</i> sp.	14	0	1	0	0	0	4	0	5	0	0	0							
<i>Dryocoetes autographus</i>	0	8	5	3	4	7	0	8	7	8	14	22							
<i>Hylastes cunicularius</i>	0	1	0	0	0	0	0	3	0	0	0	0							
<i>Hylcoetes dermestoides</i>	0	2	1	3	1	0	0	7	7	4	10	0							
<i>Hylurgops glabratus</i>	0	1	1	2	0	0	0	14	21	3	0	0							
<i>Hylurgops palliatus</i>	14	18	17	31	17	13	33	28	19	25	26	20							
<i>Ips amitinus</i>	29	37	47	45	36	20	19	27	26	32	23	9	0	21	23	28	15	15	
<i>Ips typographus</i>	0	27	35	20	24	73	0	47	57	45	43	72	0	11	0	0	0	0	
<i>Molorchus minor</i>	71	46	41	51	43	20	52	45	42	35	46	0	47	25	25	19	21	18	
<i>Monochamus sutor</i>	0	3	2	2	2	0	0	11	3	12	9	0							
<i>Obrium brunneum</i>	29	34	29	40	40	20	5	22	16	12	37	3	33	20	17	23	25	23	
<i>Orthotomicus starki</i>	0	1	0	0	0	0	0	8	0	0	0	0							
<i>Phthorophloeus spinulosus</i>	29	39	34	54	52	40	0	9	8	0	5	0	35	24	17	23	24	29	
<i>Pissodes harcyniae</i>	29	19	13	9	13	7	17	33	21	11	19	26							
<i>Pissodes scabricollis</i>	0	1	1	2	1	0	0	15	7	7	3	0							
<i>Pityogenes chalcographus</i>	29	52	73	54	53	80	67	62	53	50	49	27	35	65	68	73	61	45	
<i>Pityophthorus exsculptus</i>	0	3	1	3	2	7	0	90	0	0	16	0	0	19	17	11	13	17	
<i>Pityophthorus pityographus</i>	71	63	70	72	75	47	23	17	14	18	17	14	58	48	52	58	50	33	
<i>Pogonocherus fasciculatus</i>	14	20	14	3	21	0	0	12	8	3	16	0	22	28	16	13	16	0	
<i>Polygraphus poligraphus</i>	43	52	47	49	44	40	51	44	40	42	36	40	0	30	29	10	6	55	
<i>Polygraphus punctifrons</i>	0	0	0	2	2	7	0	0	0	0	4	0							
<i>Rhagium inquisitor</i>	57	20	19	22	22	27	6	9	7	6	7	7							
<i>Sirex juvencus</i>	14	7	6	5	9	0	4	22	21	11	21	0							
<i>Tetropium fuscum</i>	14	10	18	9	19	13	13	14	6	9	18	41							
<i>Xylechinus pilosus</i>	43	12	15	22	14	0	7	26	20	20	23	0	10	13	15	0	0	0	
<i>Xyloterus lineatus</i>	0	23	17	9	16	27	0	28	18	25	25	21							
Tree number	7	153	133	65	104	15	7	153	133	65	104	15	7	153	133	65	104	15	

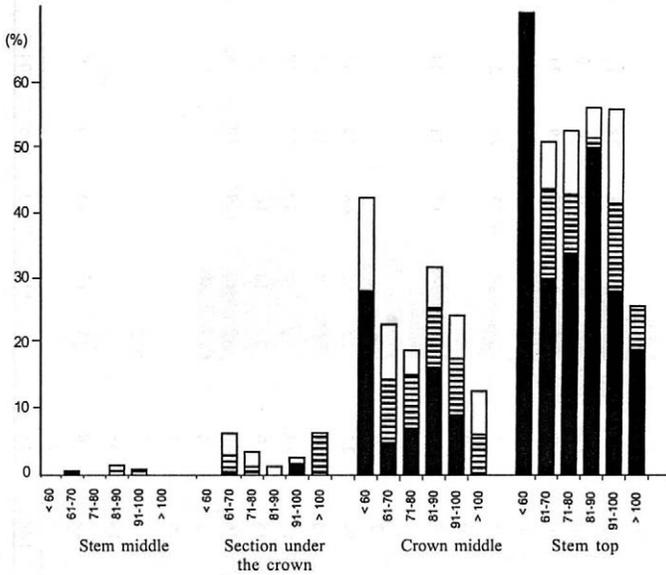


Fig. 3. Spruce attractiveness for *Pityophthorus pityographus* in relation to stand age (the Beskids) in comparative stem sections (infestation: ■ – heavy, ▨ – increased, □ – scattered)

of the tree. *D. autographus* is a species where the stem niche increased with tree age (0–21.9%) being longest in co-dominant trees. *I. amitinus* showed an increasing niche in the interval of <60–90 years (19.1–31.9%) followed by niche shortening in older stands. *P. chalcographus* limited continuously the occupied stem niche profile with increasing tree age. Within the social status of the tree, the longest niche was formed by *P. chalcographus* in subdominant trees. *M. minor* showed shortening the niche in age categories of <60–90 years. In subdominant trees, a longer stem niche (46%) was created than in co-dominant trees (26.5%). Also *P. poligraphus* showed a gradual decrease in niche length with tree age (<60–100 years) 50.8–36% regardless of the social status of the tree. *T. fuscum* shortened its niche length in the interval of <60–80 years (12.5–6%) and then its niche increased in stands aged 70–100 years (6–41.3%). Independent of age, the niche was formed in the species *Rh. inquisitor*, being relatively

narrow (5.5–8.6%), but in dominant trees, its decrease was registered with increasing tree age. *X. lineatus* occupying mostly 1/5–1/4 of a stem can be characterized similarly. Although in the youngest trees (<60 years), lengthened niche was registered in *H. palliatus* (33.3%), however, in older stands the stem occupation seems to be balanced in 1/4–1/5 stem length. Moderate increase of the niche occurred in subdominant trees (16–25–27.5%). *X. pilosus*, whose niche was narrowed in stands younger than 60 years (7.1%), can be assessed similarly. *I. typographus* covered the stem to the extent of 43–57% in the age category of 61–100 years and 72% stem niche deviation in trees older than 100 years was affected by sample trees from the Kněhyně Reserve. The niche total length decreased towards subdominant trees. *C. abietis* deviated from the stem mean niche covering 1/5 stem in the age category of 81–90 years (9.7%) and in stands older than 100 years (53.8%) (Table 1).

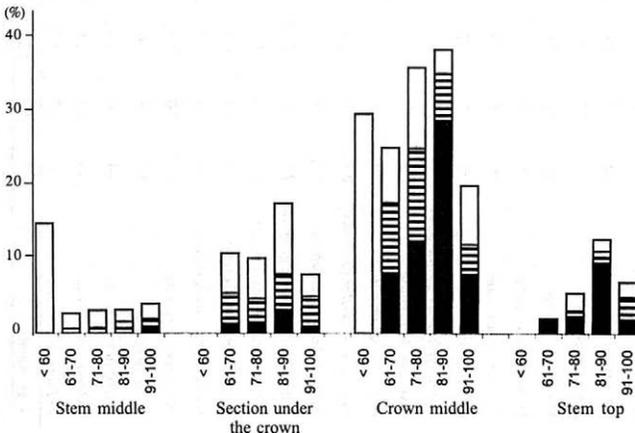


Fig. 4. Spruce attractiveness for *Ips amitinus* in relation to stand age (the Beskids) in comparative stem sections (infestation: ■ – heavy, ▨ – increased, □ – scattered)

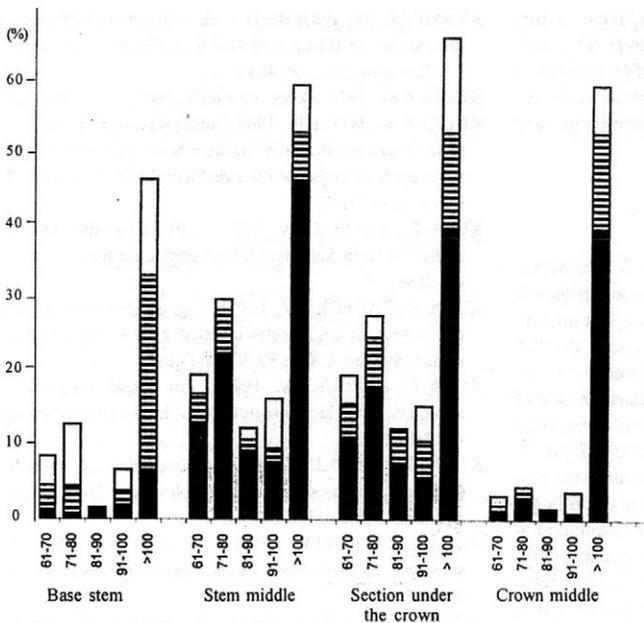


Fig. 5. Spruce attractiveness for *Ips typographus* in relation to stand age (the Beskids) in comparative stem sections (infestation: ■ – scattered, ▨ – increased, □ – heavy)

Non-uniform niche with respect to the stand age was registered in *O. brunneum*, *P. harnycinae*, *Pogonocherus fasciculatus* Deg. and *S. juvenis*.

CROWN NICHE LENGTH

C. aeneum (0–30.7%) and *X. pilosus* (10–15%) rank among the species affected positively by increasing tree

age but only within the age spectrum of <60–80 years. On the contrary, crown branch occupation decreased in *C. abietis* (77.8–28.6%) which attacked particularly subdominant spruces. In *I. amitinus* and *P. chalcographus*, the niche length culminated in the age category of 81–90 years and decreased towards subdominant trees. *P. pityographus* exhibited increased niche in subdominant trees in stands aged 60–90 years, however, within a social group,

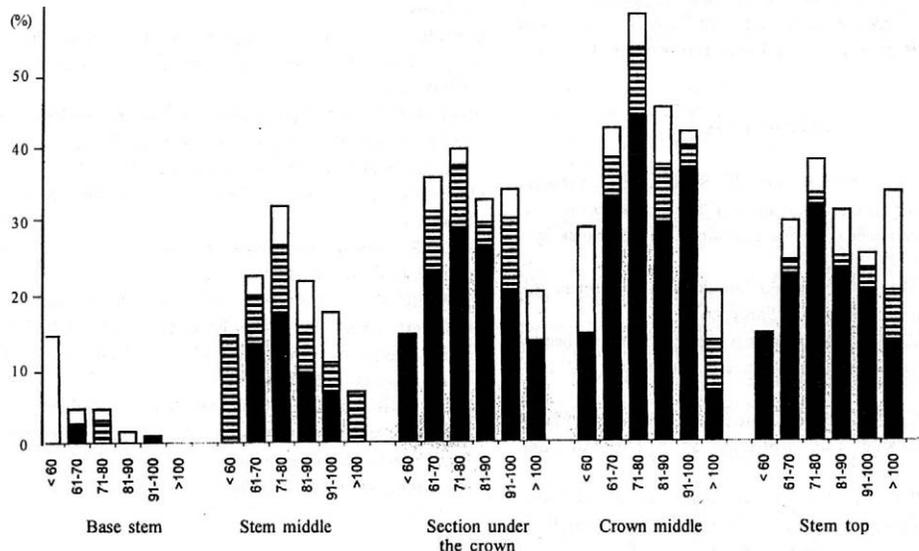


Fig. 6. Spruce attractiveness for *Pityogenes chalcographus* in relation to stand age (the Beskids) in comparative stem sections (infestation: ■ – heavy, ▨ – increased, □ – scattered)

the crown niche was balanced and independent of tree age. With the exception of the youngest trees (< 60 years), it is possible to classify the branch niche of *O. brunneum* and *Ph. spinulosus* as increasing with age in subdominant trees and as decreasing with age in dominant trees (Table 1).

CONCLUSION

The stand age of 55–115 years is decisive for the occurrence of *I. typographus* and associated spruce cambioxylophages. As it is the case of a certain optimum, no general attractiveness dependence on tree age occurred in the most important cambioxylophages except for *P. poligraphus*. An increased occurrence was characteristic of accompanying members *C. aeneum* and *Ph. spinulosus* whereas *C. abietis*, *M. minor*, *P. harcyniae* and *S. juvenis* responded conversely decreasing with the host tree age. Stands of these age classes were endangered in the same way. *I. amitinus* and *D. autographus* responded to increasing tree age by lengthening their niche and *I. typographus*, *M. minor* and *P. fasciculatus* receded from the stem profile in dependence on the social status of a tree. An opposite response was registered in *P. poligraphus* and *P. chalcographus*. *C. abietis* disappeared from branches and *C. aeneum* and *P. pityographus* increased the occupation of branches. The most attractive age category was that of 81–90 years for *I. amitinus* and *P. chalcographus*.

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Atraktivita smrku pro kambioxylofágy v závislosti na stáří porostu

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ABSTRAKT: Atraktivita a kmenová a korunová nika kambioxylofágů v závislosti na stáří porostu byly hodnoceny na stromech napadených a usmrčených kůrovci ve smrkových porostech o stáří 55–115 let situovaných v monitorovací síti povodí nádrže Šance (Beskydy). Studovaná oblast se vyznačovala základním stavem podkorního hmyzu. Věkové rozpětí bylo optimální pro výskyt druhu *Ips typographus*. Pozitivní reakce na zvyšující se věk porostu byla zjištěna u doprovodných zástupců *Callidium aeneum* a *Phthorophloeus spinulosus* a sníženou atraktivitou se vyznačovaly druhy *Molorchus minor*, *Cryphalus abietis* a *Pissodes harcyniae*. Kmenová nika se prodlužovala s věkem porostu u druhů *Ips amitinus* a *Dryocoetes autographus* a ustupovala u druhů *I. typographus* (stromy podúrovňové), *M. minor* a *Pogonochaerus fasciculatus*; opačně reagovaly druhy *Polygraphus poligraphus* a *Pityogenes chalcographus*. Z větví mizel *C. abietis* a delší profil koruny obsažovaly druhy *C. aeneum* a *Pityophthorus pityographus*.

Klíčová slova: kambioxylofágní fauna; *Picea abies*; stáří porostu; Beskydy

Podkorní a dřevokazný hmyz vytváří typické synuzie zvláště na jehličnanech (PFEFFER 1955). Zastoupení jednotlivých druhů je dáno jejich ekologickými nároky, které jsou ovlivněny velikostí těla, přijímanou potravou, vývojovým cyklem, mírou agresivity a konkurencí. Atraktivitu stromu ovlivňují stanovištní a růstové podmínky (KULA, ZABECKI 2000), sociální postavení stromu (KULA, ZABECKI 1997a,b,c), stres bleskem (KULA, ZABECKI 1997b), věk porostu (PRICE 1975; GRÜNWARD, 1986). Jako významné se jeví i utváření synuzie teplotní a vlhkostní poměry mikroklimatu dané expozicí stojících stromů (ZUMR 1984), porostní výstavba (zakmenění, zápoj), ale i stadium procesu odumírání a délka odumření stromu, predispozice napadení stromu (KANGAS 1952; SCHWERTFEGGER 1955), období rojení, počet generací do roka (BAKKE et al. 1977) a počasí zvláště v průběhu rojení. Stáří porostu se promítá do kvality a především síly borky stromu.

Cílem příspěvku je zhodnotit vliv stáří porostu na atraktivitu smrku a obsazení niky kmene a větví kambioxylofágy.

Analýza se uskutečnila u 476 stojících kůrovcových souší starých 1–2 roky. Každý vzorníkový strom byl po vytěžení v celém profilu kmene a větví odkorněn. Podle požerků, případně imag byl postupně v jednodetových sekcích stanoven výskyt kambioxylofágů (KULA, ZABECKI 1997a).

Věk sledovaných porostů s rozpětím 55–115 let (rezervace Kněhyně až 200 let) byl hodnocen v kategoriích < 60, 60–70, 71–80, 81–90, 91–100, > 100 let.

Smrkové porosty povodí nádrže Šance jsou součástí LHC Ostravice v Moravskoslezských Beskydech. Nacházejí se v nadmořské výšce 500–1 200 m, většinou na příkrých svazích 15–25°. Kambioxylofágové jsou v této oblasti dlouhodobě v základním stavu.

K druhům částečně prodlužujícím kmenovou niku vlivem zvýšené atraktivity hostitele s narůstajícím věkem se řadily druhy *Callidium aeneum* Deg. (0–6,7 %) a *Phtho-*

rophloeus spinulosus Rey. (28,6–54 %). Dilším snížením atraktivity se smrky vyznačovaly pro druhy *Cryphalus abietis* Rtzb. (24,8–6,7 %), *Molorchus minor* L. (71–20 %) a *P. harcyniae* (28,6–6,7 %), které obecně atakují stromy podúrovňové. *M. minor* preferuje jednoznačně stromy mladší 60 let, přičemž v profilu stromu od poloviny kmene do poloviny koruny bylo zastoupení vyrovnané (obr. 1). I když málo závislý na věku smrku se z hlediska atraktivity projevil *P. poligraphus*, podle zastoupení v nejtypičtější části své niky od středu kmene do středu koruny lze i přes určitou nevyrovnanost odvodit snižující se stupeň napadení smrku s narůstajícím věkem (obr. 2). Zvláště u stromů úrovnňových se zvyšovala atraktivita od jedinců mladších 60 let (28,6 %) k věkové kategorii 71–90 let (46,6–44,6 %) s následným ústupem v nejstarších porostech (20 %) pro *I. amitinus*. Tento druh byl zřetelně diferencován v profilu kmene s kulminací ve středu koruny a s vyšším napadením porostů 81–90letých (obr. 4). *I. typographus* atakoval nejčastěji stromy nadúrovňové a úrovnňové ve věku 61–80 let (35 %) a stromy starší 100 let bez obecné závislosti na věku v rozpětí hodnocených kategorií < 60 a > 100 let (tab. 1, obr. 5).

I. amitinus měl prodlužující se niku v intervalu < 60–90 let (19,1–31,9 %) a poté následoval pokles ve starších porostech. *P. chalcographus* kontinuálně omezoval obsazený profil kmenové niky s narůstajícím stářím stromu. *M. minor* se projevil zkracující se nikou ve věkových kategoriích porostů mladších 60 let až do 90 let. Podobně se i *P. poligraphus* vyznačoval postupným ústupem délky niky s věkem (< 60–100 let) 50,8–36 % bez vlivu sociálního postavení stromu.

K druhům pozitivně ovlivněným narůstajícím stářím stromu se řadilo *C. aeneum* (0–30,7 %) a *X. pilosus* (10–15 %) pouze ve věkovém spektru < 60–80 let. Naproti tomu k poklesu obsazení větví profilu koruny došlo u druhu *C. abietis* (77,8–28,6 %), který atakoval především podúrovňové smrky.

Věk porostu 55–115 let je rozhodující pro výskyt lýko-žrouta smrkového a jeho doprovodných kambioxylofágů smrku. Protože se jedná o určité optimum, neprojevila se zde žádná obecná závislost atraktivity na věku nejvýznamnějších kambiofágů s výjimkou druhu *P. poligraphus*. Zvýšený výskyt charakterizoval doprovodné zástupce *C. aeneum* a *Ph. spinulosus*, opačně reagovaly druhy *C. abietis*, *M. minor*, *P. harcyniae* a *S. juvencus*, které ustupovaly s věkem hostitelské dřeviny. Porosty v těchto vě-

kových třídách jsou ohroženy shodně. Na narůstající věk prodlužující se kmenovou nikou reagovaly druhy *I. amitinus*, *D. autographus* a v závislosti na sociálním postavení stromu ustupovaly druhy *I. typographus*, *M. minor* a *P. fasciculatus* z profilu kmene. Opačnou reakci jsme zaznamenali u *P. poligraphus* a *P. chalcographus*. Z větví mizel *C. abietis* a narůstalo obsazení větví druhu *C. aeneum* a *P. pityographus*; nejatraktivnější věkovou kategorií bylo 81–90 let pro *I. amitinus* a *P. chalcographus*.

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