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Effect of industrial pollution and spruce forest decline on the biocenoses of Karkonosze Mts. (south-western Poland)				

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CHANGES OF HERB-LAYER VEGETATION IN MOUNTAIN SPRUCE FORESTS UNDER THE INFLUENCE OF INDUSTRIAL POLLUTION AND THE FOREST DECLINE

ABSTRACT: The studies were carried out in the region of two peaks (Mumlawski Wierch 1219 m a.s.l. and Szrenica Mt. 1362 m a.s.l.) in the Karkonosze Mts (south-western Poland). As a consequence of deforestation of the area studied, herb-layer vegetation has been altered. This consists in e.g. changes in quantitative proportions among components of the plants, gradual diminishing of dicotyledonous forest species, and an increase in participation of grasses (*Deschampsia caespitosa* and *Calamagrostis villosa*) in the communities. Range of these changes depends on how long ago an area was devoid of forest. However, the effects of such transformations are not irreversible. Within the spruce saplings overgrowing the deforested areas, regeneration of typically forest herb-layer vegetation has been observed.

KEY WORDS: Industrial pollution, acid rain, mountain spruce forests, herb-layer vegetation, Karkonosze Mts.

1. INTRODUCTION

The Karkonosze Mts extending over the south-western part of Poland are the highest mountain range of Sudeten. It is about 35 km long and almost 3 km wide. Granite rocks prevail, though gneiss and metamorphic schist are also frequently found (Sachanbiński 1995).

Originally, the whole Karkonosze region was overgrown by forests. In the foothill zone extending to about 400 m a.s.l., forest communities from the alliances Carpinion and Dicrano-Pinion had occurred (Pawłowski 1959), in the lower montane zone (400–1000 m a.s.l.) – acid montane beech forests (Luzulo

-Fagetum) where beech stands dominated with an admixture of fir and sycamore (Pawłowski 1959, Matuszkiewicz W. and Matuszkiewicz A. 1967). The upper montane zone (1000–1250 m a.s.l.) is a habitat of spruce forests qualified phytosociologically as Plagiothecio-Piceetum hercynicum R. Tx. (1932) 1937 (Matuszkiewicz 1977, 1981). In phytocenoses belonging to this association, spruce is the dominant tree species, and woody mountain ash constitutes a small admixture.

For last 500 years, the forests of Karkonosze Mts. have been substantially altered, primarily due to human activity. Growing demands for pastures, agricultural fields and settlements had led to progressive deforestation of the mountainous regions. Moreover, wood for industrial purposes (mostly mining and smelting industry) was commonly harvested (Perina and Sanek 1958). As a consequence, the tree stands vanished almost completely from the foothill and lower montane zone. Since the beginning of the 17th century, Sudety Mts. had been reforested by introducing (mainly to the lower montane zone) spruce monocultures inadequate to the site. Such practices caused the forest ecosystems to have become less resistant to severe climatic conditions prevailing in the mountains (mainly heavy snowfalls and strong winds). For instance, only in 1966 did the wind destroy some 150 ha of the forests (Capecki and Zwoliński 1984). Establishing of spruce monocultures has also favoured outbreaks of insect pests and fungal pathogens.

For the last 20 years the above situation has been made even worse due to the effects of industrial pollution by dusts and gases, in particular. The pollutants have been carried from south-western Poland, as well as from the western part of the Czech Republik, south-eastern and central Germany and, most probably also from Westfaly and Saxony (Zwoździak et al. 1993). The region has typically high concentrations of sulphur compounds (SO_2 and sulphate aerosols) and ammonia in the air, and is highly contaminated by heavy metals, mostly cadmium and zinc. Concentrations of the gaseous pollutants exceed permissible levels for forest ecosystems, whereas cadmium and zinc are present in amounts exceeding by several times the levels typical of urban areas (Zwoździak et al 1995). The soils of the Karkonosze Mts. contain substantial amounts of lead, cadmium and zinc. Concentrations of these elements exceed to a high degree allowable levels (Skiba and Drewniak 1994, Skiba 1995, Gworek and Wasiłowska 1999). Moreover, the soils have been highly acidified as an effect of both natural shortages of many different elements neutralising the soil acidity (primarily calcium and magnesium) and self-acidifying strategy of spruce trees (Zimka and Stachurski 1996).

The pollutants may affect trees directly, primarily by damaging their foliage, and indirectly by changing site conditions, this being harmful to forest biocenoses (Wolak 1974, Sachanbinski 1995, Stachurski et al. 1994, Zimka et al. 1995, Zimka and Stachurski 1996).

Soil acidification results, among others, in leaching of most base metals, including elements necessary for plants to grow properly, i.e. calcium, magnesium and sodium cations. Moreover, soil acidification causes insoluble aluminium compounds to be converted into soluble forms that are toxic to plants. The changes in site conditions described above have led to transformations of natural herb-layer vegetation.

The main idea of this work was to characterise changes in herb-layer vegetation of spruce forests following destruction of the tree stands.

2. STUDY AREA

2.1. CHARACTERISTICS OF STUDY SITES

The studies were carried out in two areas of Karkonosze Mts.: on the slope of Mumlawski Wierch and in the valley of Kamienna river at the foothill of the mount (in the years 1992, 1993), as well as on the slope of Szrenica mount (1993) (Fig. 1).

Mumlawski Wierch (1219 m a.s.l.) is situated in the westward part of the Karkonosze Mts. According to Zwoździak et al. (1993), the area is particularly exposed to industrial pollutants derived most frequently from the west. Only in 60-ties, was the slope of Mumlawski Wierch covered by a spruce forest. Since early 70-ties, forest stands of that region have begun to decline. At present, the mount top and a large part of the slopes are devoid of trees. The only fragment of living spruce forest is partially declined. In the deforested sites, spruce saplings grow spontaneously (Fig. 1A).

Herb-layer vegetation was examined in five sites located on the north-western slope of Mumlawski Wierch, and in four

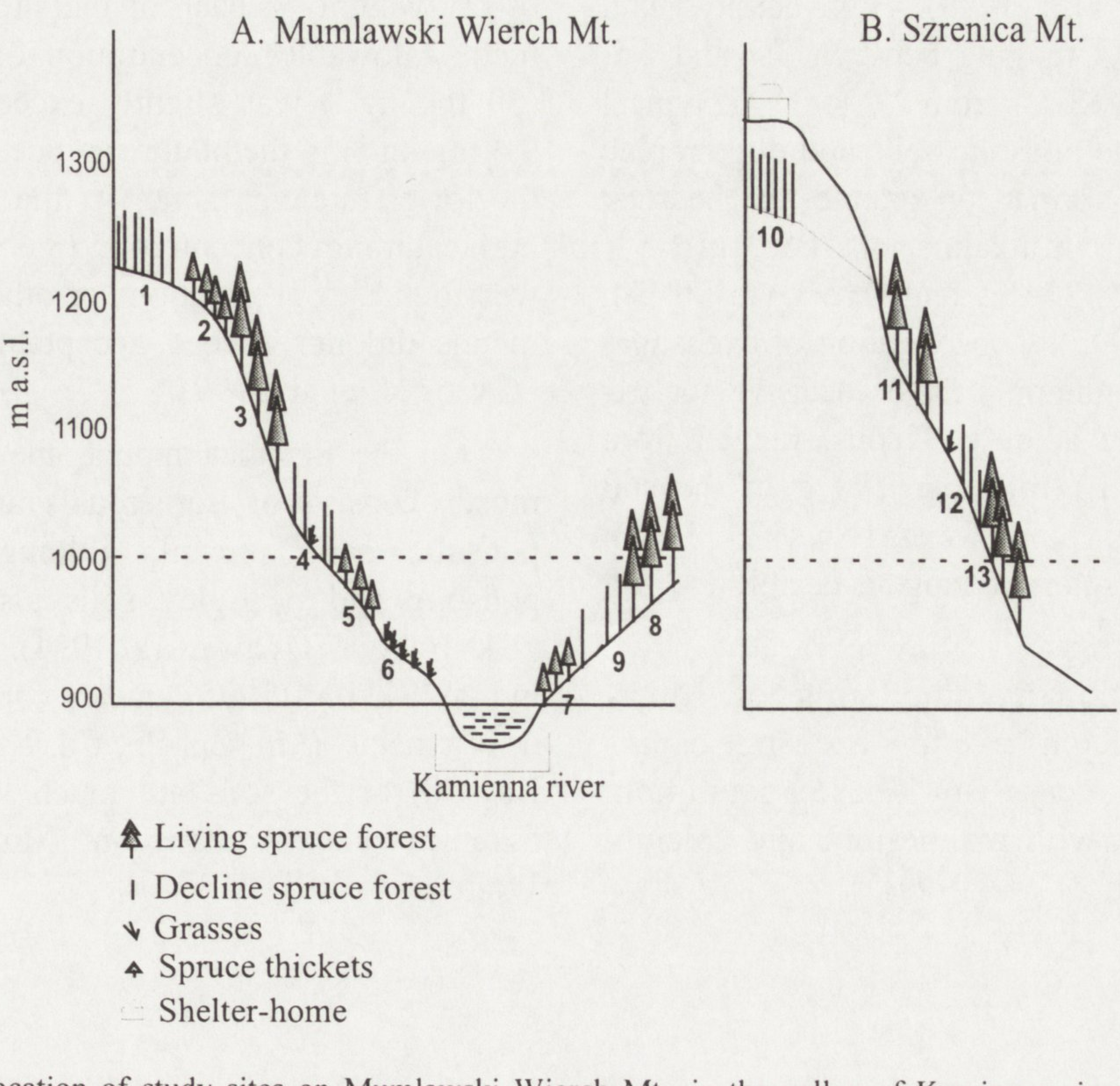

Fig. 1. Location of study sites on Mumlawski Wierch Mt., in the valley of Kamienna river, and on Szrenica Mt in Karkonosze Mts. The broken line denotes bordeline between the lower and upper montane zone. 1–13 – sample plots.

additional sites situated at the mount foothill, in the Kamienna river valley (Fig. 1A). The stations on Mumlawski Wierch numbered from 1 to 4 were situated in a spruce forest of the upper montane zone – Plagiothecio-Piceetum hercynicum R.Tx. (1932)1937, and the next sites (5–9) – in the lower montane zone in man-planted spruce stands. The trees were relatively healthy in only two sites: 3 and 8. At the stations 1, 4, 6 and 9, the tree stands were declined, whereas the sites 2, 5 and 7 were overgrown by spruce thickets (12, 15 and 20 year-old, respectively).

The Szrenica region with its highest peak (1362 m a.s.l.) belongs to the main ridge of the Karkonosze Mts. The area is typically mountainous with developed zone of alpine vegetation. At present, fairly large areas of the Szrenica slopes are devoid of forests. The studies performed on the mount were primarily concentrated in the upper montane zone. Forests of the sites 10 and 12 belonged to the association Plagiothecio-Piceetum hercynicum typicum in various phases of tree stand decline, and that of the site 11 – to Plagiothecio-Piceetum hercynicum filicetosum with partially declined tree stand. Station 13 was the only site located within a man-planted forest of the lower montane zone with still healthy trees.

2.2 SOIL PROPERTIES

In the region, mineral podsolic soils prevail with patches of organic soils: peat-mud and peat-gley soils (Gworek and Wasiłowska 1999). High acidity, with pH in H_2O ranging between 3.3 and 4.5, and pH in KCl – from 2.9 to 3.7, is typical of montane podsolic soils and oligotrophic peat soils formed on granite, the bedrock being poor in alkaline ions (Adamczyk et al. 1985, Skiba and Drewniak 1994, Skiba 1995). Concentration of exchangeable aluminium, a factor decisive for exchangeable acidity of soils, ranged from 4.38 to 83.1 me per 100 g of the soil (Gworek and Wasiłowska 1999), whereas its normal range is usually 1–3 mg 100 g^{-1} of the soil.

Additionally, the soils of Mumlawski Wierch have low exchange capacity and very low base saturation, especially with magnesium and calcium (Gworek et al. 1999).

Among heavy metals, lead was the only element, the concentrations of which exceeded permissible level (100 mg kg^{-1} of dry weight) in each of the sites examined. Allowable concentration of copper (50 mg kg^{-1}) was slightly exceeded (by 9.4 mg kg^{-1}) in the mature spruce forest of the lower montane zone. At the site 6, a high cadmium concentration (8.6 mg kg^{-1}) was found. Concentrations of other heavy metals did not exceed acceptable levels (Gworek et al. 1999).

On the Szrenica mount, the bedrock mostly consists of isomerous granite, and podsolic soils prevail, although peat-podsolic and peat-gley soils also occur (Skiba and Drewniak 1994). According to Skiba (1995), mean contents of heavy metals (Mn, Zn, Pb, Cd, Ni, Bi, Cr, Be, Cu) of the soils are much lower on Szrenica slopes than on Mumlawski Wierch.

3. METHODS

In order to assess transformations of herb-layer vegetation following deforestation, phytosociological records were made in the described sites characterised by different stages of the tree stand decline. Phytosociological studies were conducted by the Braun-Blanquet method, universally accepted in Middle Europe (Pawłowski 1972).

On the slope of Mumlawski Wierch and in the valley of river Kamienna, from 6 to 13 surveys were made at each site (in the years 1992 and 1993). Individual sample plots had 4 m^2 in area. The records were made in patches of plants growing on mineral soils, whereas waterlogged areas were not taken into account.

On Szrenica, 6 surveys were made at each station (1993). Dimensions of the plots and selection criteria were the same as in the case of Mumlawski Wierch.

In the studies, vascular plants (excluding planted ones) and mosses were only considered, whereas lichens and algae were ignored.

The following parameters were examined on each sample plot: total number of plants, number and coverage of species characteristic of coniferous forests (Ch. Vaccinio-Piceetea and Ch. Vaccinio-Piceetalia) (*Vaccinium myrtillus, Vaccinium vitis-idaea, Trientalis europea, Lycopodium annotinum, Homogyne alpina*), coverage by grasses (*Deschampsia flexuosa* and *Calamagrostis villosa*), and coverage by species typical of clearing areas (*Rubus idaeus, Chamaenerion angustifolium, Digitalis purpurea, Senecio fuschii*).

One-factor ANOVA (Statistica software) was used to assess significance of differences in the above parameters among the sites examined, taking into account the influence of:

– site location (lower or upper montane zone),

– tree layer status (living, dead, young trees),

– time since deforestation (living forests, forests declined shorter or longer time ago, younger and older thickets).

Furthermore, transformations of the herb-layer vegetation following tree stand destruction were examined by using indices commonly applied to phytosociological surveys:

1. the sum of coverage index values for species characteristic of coniferous forests and for grasses (Pawłowski 1972),

2. systematic group value of the species characteristic of coniferous forests (Pawłowski 1972),

3. similarity of vegetation between living and dead forests, assessed with use of Sorensen's index.

Each of the indices reflects a different feature of the transformations of herb-layer vegetation. Coverage indices inform about quantitative changes that are the first response to altered site conditions. Composition and floral richness of herb-layer vegetation, similarly to systematic group value of species, convey an idea of directions and rates of qualitative changes in herb layer affected by deforestation.

Because of slightly different floral composition of the herb layer occurring in the fern sub-association of high-elevation spruce forests (Plagiothecio-Piceetum hercynicum filicetosum), the site (station 11) was excluded from considerations on vegetation transformations.

Transformations of the herb layer in the examined spruce forests were analysed separately for the sites located in the upper and lower montane zones. Such an approach was principally dictated by different origin of the forests in the two zones. As mentioned previously, the spruce forests of the upper montane zone are potential communities that are adequate to the sites and represent the association of Plagiothecio-Piceetum hercynicum. By contrast, the spruce forests of the lower montane zone were planted on acid mountain beech forest sites (Luzulo-Fagetum). According to Matuszkiewicz W. and Matuszkiewicz A. (1967), introduction of spruce monocultures has led in many cases to irreversible site degradation. Moreover, a new equilibrum has been attained, in which a new potential community is the association Abieti-Piceetum montanum. Such a situation mainly relates to the upper primary range of beech forests, i.e. a transition zone between the lower and upper montane zones. At present, the area is covered by spruce forests very poor florally and sometimes even completely devoid of herb-layer plants.

In this connection, differences between the lower and upper montane zone regarding origin and species composition of the spruce forests that are primary communities subjected to transformations following tree stand destruction are sufficient reason to treat them separately in further analyses.

The sites examined in both upper and lower montane zones were classified into several groups depending on the status of tree layer that indirectly reflects time that had passed since first visible injuries that occurred in the stands. In the upper montane zone, there were six such classes singled out: living spruce forest (station 3), stand declined recently (few years ago) (station 10), stand declined not long ago (in late 80-ties) (station 1), stand declined long ago (in mid 80-ties) (station 12), stand declined very long ago (in late 70-ties) (station 4), young spruce stand (about 12-year-old) (station 2). In the lower montane zone there were five such classes: old-growth living spruce forests (stations 8 and 13), stand declined not long ago (in mid 80-ties) (station 9) , stand declined long ago (in 70-ties) (station 6), younger spruce thicket (about 15-year-old) (station 5), and older thicket (about 20-year-old) (station 7). The classes constituted a basis for further statistical analyses.

4. RESULTS

4.1. TRANSFORMATIONS OF HERB-LAYER VEGETATION IN SPRUCE FORESTS OF THE UPPER MONTANE ZONE

When compare composition, richness, and floral similarity of herb-layer vegetation between living and dead forest stands, it can be concluded that deforestation have not impoverished the vegetation much. This is testified by high values of similarity indices between the vegetation of deforested areas and that of living forests, the values being fairly high and ranging between 61% and 71%. According to the results of one-factor analysis of variance, the differences in the mean number of species among the sample plots located in the upper montane zone were not statistically significant (Fig. 2A). In a few stations located in tree

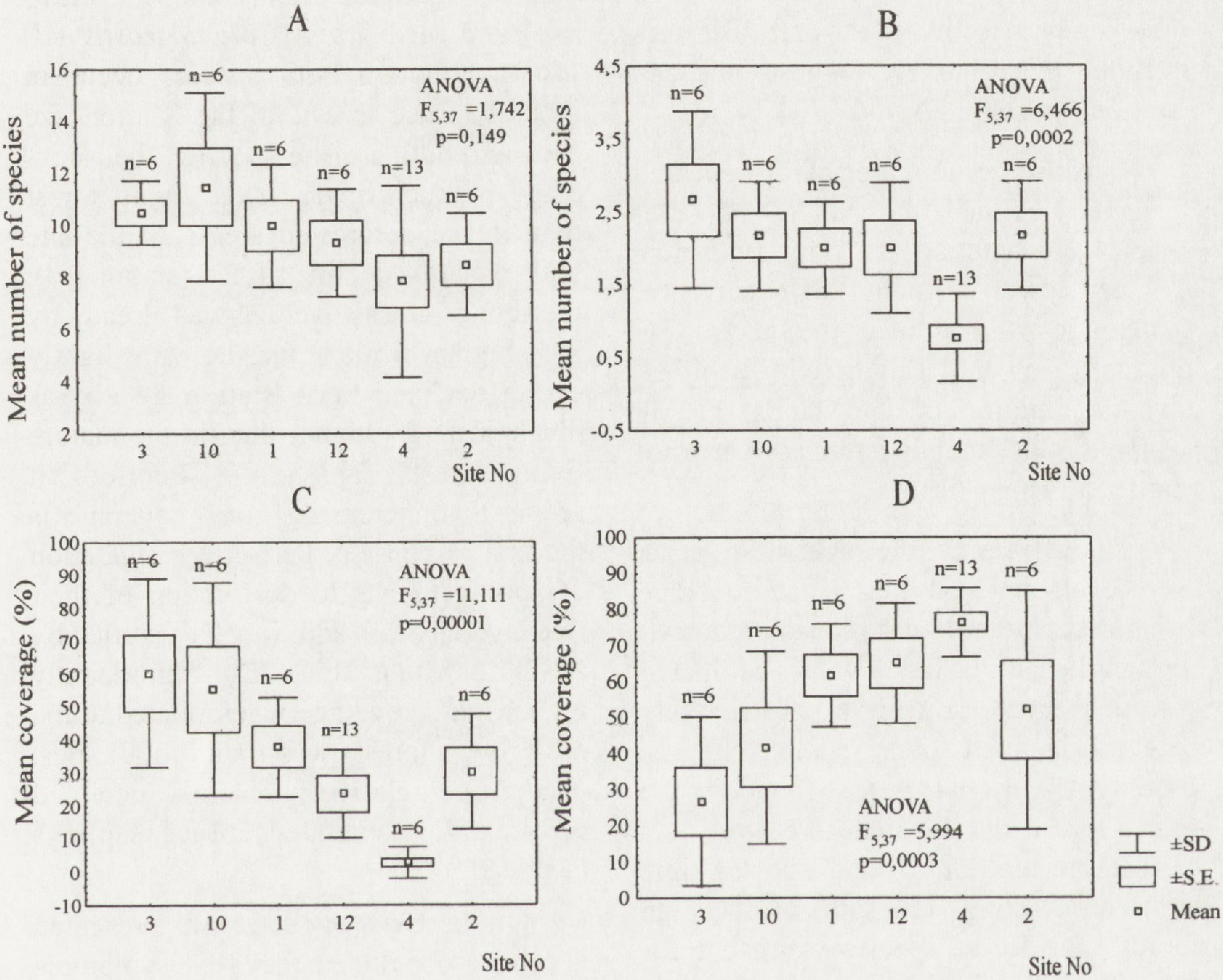

Fig. 2. Mean number and coverage of high-elevation forests by different groups of plant species (2-years data). A – mean number of plant species found on examined sites, B – mean number of species typical of coniferous forests, C – mean coverage of species typical of coniferous forests, D – mean coverage of grass species (*Deschampsia flexuosa* and *Calamagrostis villosa*). St. 3 – living spruce forest, st. 10 – the stand declined recently, st. 1 – the stand declined not long ago, st. 12 – the stand declined long ago, st. 4 – the stand declined very long ago, st. 2 – thicket. ANOVA results are given at confidence level of 0.95, n – number of samples plots (individual sample plot – $4m^2$). Note the different scale.

stands declined the relatively longest time ago (stations 4 and 12), occurrence of species typical of clearings (*Rubus idaeus, Chamaenerion angustifolium, Digitalis purpurea*) has been noticed. Nevertheless, floral richness of the sites has not been significantly affected.

At the sites with declined trees, many forest species typical of living spruce forests have survived. However, certain species, especially those having diagnostic value for syntaxonomic classification of a community (*Homogyne alpina, Vaccinium vitis-idaea, Lycopodium annotinum*), have already vanished from some of the deforested areas of Mumlawski Wierch (station 4). No records of *Lycopodium annotinum* were made in either of the two sites devoid of forest stand on Szrenica (stations 10 and 12). Differences in the mean species number per sample plot among the sites compared were statistically significant (Fig. 2B). A paired site-to-site comparison demonstrated that an area significantly different in this respect from the other ones was the site where the trees declined the relatively longest time ago (station 4) (Table 2A).

Because certain species disappeared from the declined tree stands, and other species characteristic of coniferous forests had lower constancy of occurrence, systematic group value of the species was gradually lowered (along with progressive degradation of the stands) (Table 1A) although the differences were not statistically significant.

The effects of tree layer destruction were even more obvious when coverage by forest species was considered. Although the sum of index values estimated for the species occurring in the relatively recently declined forest (station 10) was by only 4% lower than that found for the living forest, the differences between areas deforested longer and shorter time ago were striking. The sums of coverage indices for forest species estimated for the site with recently (station 10) and slightly earlier declined trees (station 1) were by about 3 and 2 times higher than for the site where only few and partially fallen trees were left (station 12), and by as many as 16 and 12 times higher than for the completely deforested site (station 4) (Table 1A). A site-to-site comparison with regard to the mean coverage of the species (in a sample plot) confirmed statistical significance of the differences (Fig. 2C). Values of the parameter did not differ among the old-growth forest (station 3), relatively recently declined forests (stations 1 and 10) and thickets (station 2), but the values differed significantly between the sites deforested long or very long time ago (stations 4 and 12) and the living forest (Table 2B).

The deforested areas are characterised by increased coverage by grasses: common hairgrass (*Deschampsia flexuosa*) and reed grass (*Calamagrostis villosa*). Although both species occur in natural spruce forests of the Karkonosze Mts. and both are site specific, their coverage is much lower in the living forest than in the deforested areas. At the site with recently declined trees (station 10), the sum of grass coverage was already by 35% higher, while at the site with slightly earlier declined trees (station 1) – by as much as 164% higher than in the mature living forest (Table 1A). Therefore, it seems that increasing grass coverage is the first response of herb-layer vegetation of spruce forests to destruction of their tree layer. This is additionally testified by ANOVA results (Fig. 2D). Significantly higher grass coverage when related to the old-growth forests was found in all sites, except the relatively recently declined forest and regenerated spruce saplings (Table 2C).

On the basis of the results presented it can be concluded that first symptoms of changes in herb-layer vegetation of spruce forests undergoing destruction of trees consist in expansion of two grass species (*D. flexuosa* and *C. villosa*). Recently declined stands were the only sites that did not differ from those with living tree cover. The next stage comprises gradual disappearing of species typical of coniferous forests. This is manifested by initially slight, then a very rapid decline in their coverage (significantly lower values for the stands that declined the relatively longest time ago compared to the mature living forests), and eventually their complete extinction (significant differences in number of such species were statistically confirmed only between the site deforested the longest time ago and the living forest).

The transformations of the herb layer as a consequence of forest decline are not

Table 1. Charactristics of herb-layer vegetation in Mumlawski Wierch (M) and Szrenica Mt. (S). Analysis based on systematic group values for species characteristic of coniferous forests, sums of their coverage values (%), and coverage index of a forest species *Vaccinium myrtillus* L. and two grass species (*D. flexuosa* and *C. villosa*)

A. UPPER MONTANE ZONE

PARAMETER	Living tree stand	Declined tree stand				Spruce thicket
		recently	Not long ago	Long ago	Very long ago	
Site number	3 M	10 S	1 M	12 S	4 M	2 M
Number of samples plots	6	6	6	6	13	6
Altitude (m a.s.l.)	1100–1080	1200–1160	1180–1120	1100–1020	1080–1000	1120–1100
Systematic group value of species typical of coniferos forests (%)	13.9	18.2	17.1	16.0	3.9	18.1
Sum of coverage index values of species typical of coniferous forests	3050	2922	2168	1093	186	2503
Sum of coverage index values of *Calamagrostis villosa* and *Deschampsia flexuosa*	1783	2420	4708	6913	7116	3500

B. LOWER MONTANE ZONE

PARAMETER	Living tree stands		Declined tree stands		Spruce thickets	
			not long ago	long ago	15-year-old	20-year-old
Site number	8 M	13 S	9 M	6 M	5 M	7 M
Number of samples plots	6	6	6	6	8	8
Altitude (m a.s.l.)	920–940	940–980	900–920	900	960–900	900
Systematic group value of species typical of coniferous forests (%)	15.7	11.5	10.0	7.0	10.9	14,5
Sum of coverage index values of species typical of coniferous forests	3750	2877	708	333	2446	3007
Sum of coverage index values of *Calamagrostis villosa* and *Deschampsia flexuosa*	2880	3272	6458	6666	3688	3100

Table 2. Differences among the high-elevation forest sites examined with regard to A – mean number of species characteristic of coniferous forests, B – mean coverage (%) of species characteristic of coniferous forests, C – mean coverage (%) of grass species, *C. villosa* and *D. flexuosa*

	Site	Old-growth forest st.3	The stand declined recently st.10	The stand declined not long ago st.1	The stand declined long ago st.12	The stand declined very long ago st.4
A	Old-growth forest st.3					
	The stand declined recently st.10	–				
	The stand declined not long ago st.1	–	–			
	The stand declined long ago st.12	–	–	–		
	The stand declined very long ago st.4	+	+	+	+	
	Sapling spruce stand st.2	–	–	–	–	+
B	Old-growth forest st.3					
	The stand declined recently st.10	–				
	The stand declined not long ago st.1	–	–			
	The stand declined long ago st.12	+	+	–		
	The stand declined very long ago st.4	+	+	+	+	
	Sapling spruce stand st.2	–	–	–	–	+
C	Old-growth forest st.3					
	The stand declined recently st.10	–				
	The stand declined not long ago st.1	+	–			
	The stand declined long ago st.12	+	+	–		
	The stand declined very long ago st.4	+	+	–	–	
	Sapling spruce stand st.2	–	–	–	–	+

+ significant difference; – insignificant difference

irreversible. In places where the tree stands have regenerated, proportions among components of the herb layer have changed, as well. Indices of coverage by species typical of coniferous forests and by grasses reach here intermediate values between those found for the mature spruce forests and deforested areas (Table 1A). Coefficient of vegetation similarity between the thickets and mature forests was as high as 93%, being much higher than similarity between the living and declined tree stands (on average 67.5%). The mean number of all species, mean number and coverage by species characteristic of coniferous forests, and mean grass coverage did not differ significantly among the sites (Fig. 2A, B, C, D).

4.2. TRANSFORMATIONS OF HERB-LAYER VEGETATION IN DECLINED TREE STANDS OF THE LOWER MONTANE ZONE

Similarly to the upper montane zone, the most distinct changes in herb-layer vegetation following deforestation of the lower montane zone included expansion

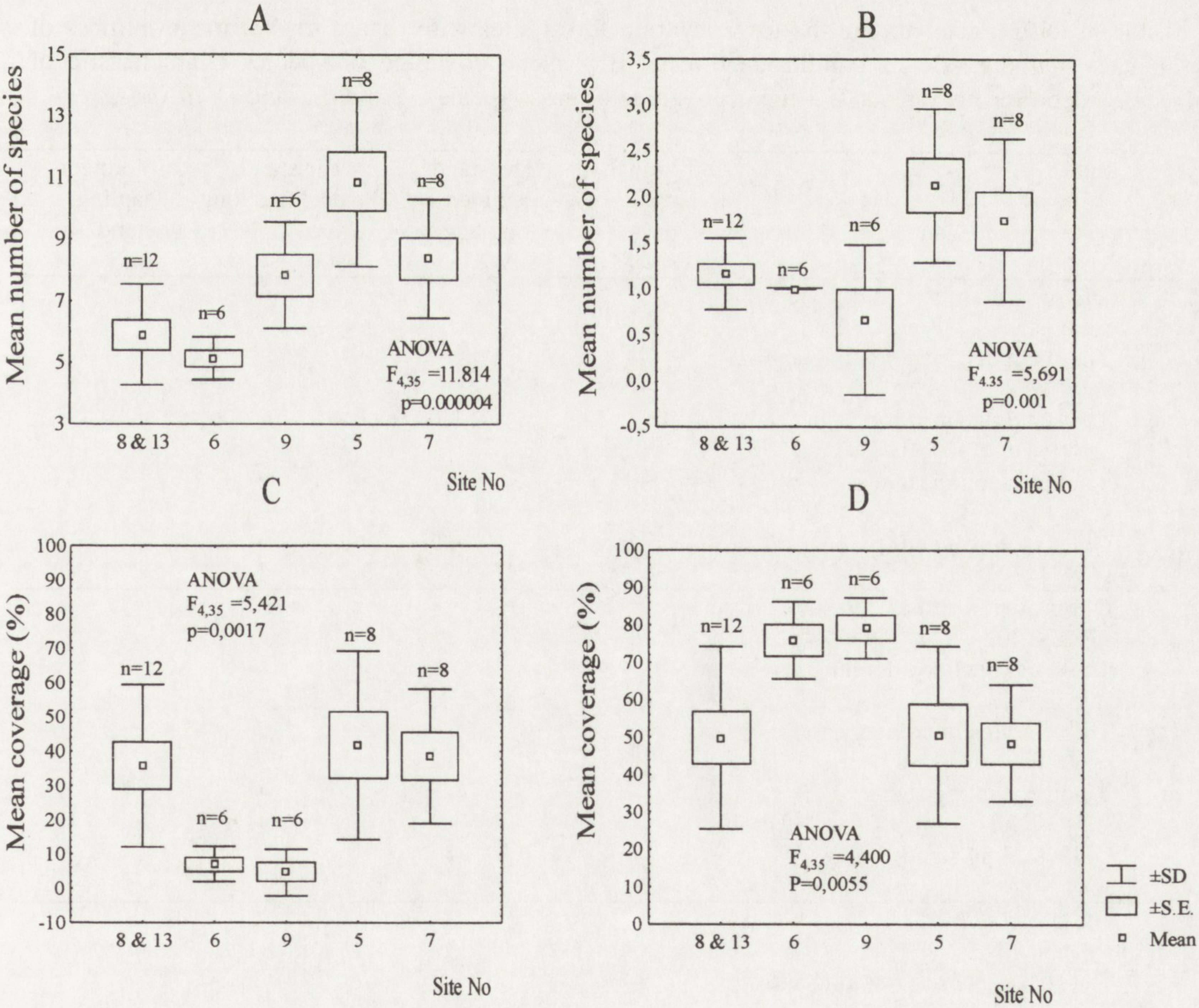

Fig. 3. Mean number and coverage of low-elevation forests by different groups of plant species (2-years data). A – mean number of plant species found on examined sites, B – mean number of species typical of coniferous forests, C – mean coverage of species typical of coniferous forests, D – mean coverage of grass species (*Deschampsia flexuosa* and *Calamagrostis villosa)*. St.8 and 13 – living spruce forest, st. 6 – the stand declined not long ago, st.9 – the stand declined long ago, st. 5 – the youger thicket, st. 7 – the older thicket. ANOVA results are given at confidence level of 0.95 n – numer of sample plots (individual sample plots – 4m^2). Note the different scale.

of grasses and lowered coverage by species typical of coniferous forests. This observation was confirmed by a comparison of coverage index sums and systematic group values for species characteristic of coniferous forests, as well as of coverage index sums for grasses (Table 1B).

The differences in mean coverage by species typical of coniferous forests and by grasses among the sites compared were statistically significant (Fig. 3C, D). A paired site-to-site comparison revealed that neither did spruce thickets differ from each other or from the mature living forest. No statistically significant differences were found between the sites deforested a shorter and longer time ago. All the remaining differences were proved to be significant (Table 3B, C).

Unlike in the upper montane zone, no decrease in number of species typical of coniferous forests was observed when move from the deforested areas to the living forests of the lower montane zone (Fig. 3B, Table 3A).

Table 3. Differences among the low-elevation forest sites with regard to A – mean number of species characteristic of coniferous forests, B – mean coverage of species characteristic of coniferous forests, C – mean coverage of grass species, *C. villosa* and *D. flexuosa*

	Site	Old-growth forests st3 & st.13	The stand declined not long ago st.9	The stand declined long ago st.6	Younger sapling stand st.5
A	Old-growth forests st3 & st.13				
	The stand declined not long ago st.9	–			
	The stand declined long ago st.6	–	–		
	Younger sapling stand st.5	+	+	+	
	Older sapling stand st.7	+	+	+	–
B	Old-growth forests st3 & st.13				
	The stand declined not long ago st.9	+			
	The stand declined long ago st.6	+	–		
	Younger sapling stand st.5	–	+	+	
	Older sapling stand st.7	–	+	+	–
C	Old-growth forests st3 & st.13				
	The stand declined not long ago st.9	+			
	The stand declined long ago st.6	+	–		
	Younger sapling stand st.5	–	+	+	
	Older sapling stand st.7	–	+	+	–

+ significant difference; – insignificant difference

By contrast, species richness of the herb layer changes with time since deforestation. A paired site-to-site comparison revealed that the forests that declined a long time ago, as well as thickets differed significantly from the living spruce forests with regard to the mean number of species in a sample plot (Fig. 3D, Table 4). This can be attributed to invasion of clearing species, such as *Rubus idaeus, Chamaenerion angustifolium, Digitalis purpurea, Senecio fuschii* to the areas covered with dead trees. In the spruce thickets many places are moist, and for this reason species associated with such environments have appeared, namely *Malachium aquaticum, Cardamine amara, Juncus conglomeratus, Juncus filiformis, Deschampsia caespitosa.* Participation of these species is so high that significantly influences floral richness of the sites considered.

It is especially interesting that a significantly higher number of species typical of coniferous forests was recorded within the thickets (Fig. 3B, Table 3A). There were two such species that were present in the thickets, while absent in the old-growth spruce forests, namely *Vaccinium vitis-idaea* and *Homogyne alpina*. Both species occurred in the older and younger thicket. Certain species typical of coniferous forests absent in the mature living forests colonised the spruce forests of the lower montane zone in the course of the regeneration process. Statistical analysis did not reveal any significant differences in the number nor coverage of the species between the thickets examined.

Table 4. Differences in species number among the low-elevation forest sites

Site	Old-growth forests st3 & st.13	The stand declined not long ago st.9	The stand declined long ago st.6	Younger sapling stand st.5
Old-growth forests st3 & st.13				
The stand declined not long ago st.9	+			
The stand declined long ago st.6	+	–		
Younger sapling stand st.5	+	+	+	
Older sapling stand st.7	+	+	–	+

+ significant difference; – insignificant difference

5. DISCUSSION AND SUMMARY

Decline of coniferous tree stands has been a phenomenon increasingly often observed (Schulze et al. 1989). Many studies have been dedicated to explain possible causes and consequences of the process. Atmospheric pollution by nitrogen and sulphur compounds and by heavy metals has affected the forest stands directly as well as indirectly by changing the site conditions. This is manifested by e.g. acidification of the soils, deficiency of nutrient elements

(Hauhs and Wright 1986, Kaupenjohann et al. 1989, Oren and Schulze 1989), aluminium toxicity (Ulrich 1987) and changes in communities of soil microorganisms (Paulus and Bresinsky 1989). Moreover, it is of importance that spruce monocultures inadequate to the sites were introduced to the lower montane zone, which has resulted in considerable susceptibility of the communities to severe climatic conditions, as well as to pests (Capecki and Zwoliński 1984).

As a consequence of deforestation of the Karkonosze region, further alterations of site conditions have taken place consisting in changes in microclimate (insolation, temperature, wind speed), soil moisture and acidity, organic matter content, erosion triggering (Skiba 1995), transformations of communities of bacterial microflora and mycorrhizal fungi (Pietr et al. 1995, Kasowska 1994) and subsequent transformations of herb-layer vegetation (Fabiszewski et al. 1993, Wasiłowska 1993, Żołnierz et al. 1994).

The results of these studies performed in the region of Mumlawski Wierch and on Szrenica slopes (Fig. 1) show that the transformations consist initially in a change in quantitative proportions among components of the herb layer. Magnitude of these changes depends on the time since deforestation. At the first stage, a rapid expansion of grasses: *Deschampsia flexuosa* and *Calamagrostis villosa*, occurs (Figs 2D and 3D, Tables 1A, B, 2C, 3C). Then, species typical of coniferous forests begin to disappear, which is manifested by reduced values of their coverage index (Figs 2 C and 3 C, Tables 1A, B, 2B, 3A).

Spatial structure of herb-layer vegetation of the spruce forests is patchy, and the patches are dominated by one or a few plant species at most. As being shade-tolerant (Zarzycki 1984), species typical of coniferous forests (e.g. *Vaccinium myrtillus* or *Homogyna alpina*) concentrate in the close vicinity of tree stems, while light-demanding species, such as grasses, grow in a further distance from the stems (Parusel and Holeksa 1991). Destruction of tree stands and related canopy opening can cause light-demanding species to grow up intensively. Fabiszewski et al. (1993) have found that an increase in coverage of *D. flexuosa* is positively correlated with the degree of spruce canopy destruction. By contrast, there was no relationship between the tree canopy opening and coverage of *Calamagrostis villosa* nor *Vaccinium myrtillus* – the most abundant coniferous forests' species occurring in that region. However, coverage index values for the two latter species appeared to be interrelated. As coverage of *C. villosa* increased, coverage of *V. myrtillus* decreased. This relationship reflects competition between the two species. Thus, a change in site conditions brought about by deforestation favours grasses over species typical of coniferous forests, the latter ones becoming outcompeted.

In the upper montane zone, in the habitat of naturally growing spruce forests of the association Plagiotecio-Piceetum hercynicum, the above changes have led to complete disappearance of many species typical of coniferous forests, e.g. *Lycopodium annotinum, Vaccinium vitis-idaea, Homogyne alpina*. Only two such species, namely *Vaccinium myrtillus* and *Trientalis europea*, have survived over a relatively longer period. As an effect, a significantly lower number of coniferous forests' species occurs in the areas deforested the longest time ago (Fig. 3B, Table 2A). Moreover, species typical of forest clearings have begun to colonise the areas, although their numbers and coverage are very low. These changes do not influence significantly the total number of species (Fig. 2A).

Deforestation in the lower montane zone does not bring about any reduction in the number of species typical of coniferous forests (Fig. 3B, Table 3A). This is because living spruce forests in the area are also poor in such species. The forest interia are commonly overgrown by only two species most resistant to environmental changes. These are *V. myrtilus* and *T. europea*. Transformations of floral composition of the low-elevation sites devoid of trees consist rather in ground vegetation enrichment with alien species, mainly those typical of clearings. Thus, the areas deforested a long time ago are florally richer than the living old-growth forests (Fig. 3A, Table 4).

The above tendencies in transformations of the herb-layer vegetation can be qualified as a form of forest ecosystem degeneration described by Olaczek (1974) termed cespitisation. This is manifested by extensively developing grasses at simultaneous diminishing of dicotyledons. Alterations of this type have been observed e.g. in riparian forests where domestic animals were fed, and this was associated with opening of the tree canopies and destruction of shrub and herb layers. Such transformations also occur in afforested farmlands or clearings.

Transformations of herb layer related to deforestation are not irreversible. At the sites where tree stands regenerate, grass species begin to vanish, and forest species gradually recolonise the area (Table 1). Floral composition, especially in the upper montane zone, begins to liken that of the living spruce forests. In spruce thickets of the lower montane zone, a larger number of species typical of coniferous forests have appeared than in the living mature forests (Fig. 3B, Table 3A). Moreover, presence of young generation of trees allows to re-establish many animal communities (Dąbrowska-Prot 1993, 1994, 1999a, 1999b, Sztrantowicz 1993, 1994, Łuczak 1994, Łuczak and Woźny 1999).

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