Merocoenoses of cambioxylophagous insect fauna of Norway spruce (*Picea abies* [L.] Karst.) with focus on bark beetles (Coleoptera: Scolytidae) and types of tree damage in different gradation conditions

E. Kula[1], W. Ząbecki[2]

[1]*Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic*
[2]*Faculty of Forestry, Agricultural University of Cracow, Cracow, Poland*

ABSTRACT: Research on merocoenoses of cambioxylophagous insect fauna of Norway spruce (*Picea abies* [L.] Karst.) was carried out in spruce stands of different age in the area with an endemic population (Moravian-Silesian Beskids, Czech Republic) and in the area with an epidemic population (Beskid Żywiecki, Poland) of the eight-toothed spruce bark beetle *Ips typographus* (L.). The structure of merocoenoses was characterized separately for standing trees attacked by bark beetles, trees struck by lightning, trees affected by fungal pathogens and wind-felling and trees in the form of snags and fragments. The occurrence of cambioxylophagous insects, mostly bark beetles (Coleoptera: Scolytidae), was compared between the study areas with emphasis on dominant facultative primary bark beetles and types of damage to spruce trees.

Keywords: bark beetles; the Beskids; Central Europe; merocoenoses; Norway spruce, *Picea abies*; tree damage

The bark beetle fauna of the Central and Western Palaearctic region consists of a total of 308 species and 53 genera. A total of 56 bark beetle species feed on *Picea* spp., and a total of 39 species depend on Norway spruce as their host (Pfeffer 1995). Of a total of 111 bark beetle species known to occur in the Czech Republic (Pfeffer, Knížek 1993), a total of 31 species are the associates of Norway spruce (*Picea abies* [L.] Karst.) (Pfeffer 1995). Knížek (2004) reported the danger of spreading new species of bark beetles. Regarding the distribution of bark beetles and their ability to attack and kill also living spruce trees the following several species are economically important: *Ips typographus* (L.), *Ips amitinus* (Eich.), *Ips duplicatus* (Sahl.), *Pityogenes chalcographus* (L.), *Pityophthorus pityographus* (Ratz.) and *Polygraphus poligraphus* (L.). Among temporal secondary species, which do not attack living trees, the ambrosia bark beetle *Xyloterus lineatus* (Oliv.), a technical pest of spruce, is most important.

Like other forest tree species, Norway spruce is a host for bark beetles (Scolytidae) and numerous other representatives of cambioxylophagous insect fauna (Pfeffer 1955) which co-exist in species and space specific merocoenoses. Pfeffer (1932, 1955), Capecki (1978) and Zumr (1984) characterized the merocoenosis of bark beetle associates of Norway spruce in Central Europe. The merocoenosis structure depends on the habitat and habitat requirements of particular bark beetle species which reflect their biology, ecology and behaviour at particular sites and in particular areas. Therefore it is impossible to set the exact limits for the occurrence of bark beetles in spruce stems and branches. Some bark beetle species may develop together (e.g. *I. typographus* × *P. chalcographus, I. amitinus* × *P. chalcographus*), whereas the habitats of other species show

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only slight overlap (*I. typographus* × *I. amitinus*) or no overlap at all (*I. typographus* × *P. poligraphus*).

Orientation to attractants (Wood 1982), social position of a tree (Kula, Ząbecki 1997a), tree age, phloem and bark quality (Price 1975; Grünwald 1986; Kula, Ząbecki 2001, 2002), meso- and microclimate, the process of tree dieback and its duration, predisposition of a tree to bark beetle attack (Schwerdtfeger 1955; Kula, Ząbecki 2001), species gradology (Bakke et al. 1977), intensity of physiologically or mechanically acting stress factors such as fungal tree pathogens (Kisielowski 1978; Christiansen, Huse 1980; Kula, Ząbecki 1999a, 1999b), drought (Rudinski 1966; Renwick, Vité 1972; Mauer et al. 2005), lightning stroke (Bednarz 2005; Kula, Ząbecki 1997b, 2007), air pollution (Kudela, Wolf 1963), wind and snow (Schröter et al. 1998, Wermelinger et al. 2002, Kula, Ząbecki 2004) rank among the key factors affecting the occurrence and population densities of bark beetles on Norway spruce.

The study aims to evaluate the position (occurrence, role) of economically important bark beetles in the merocoenosis of cambioxylophagous insect fauna associated with stems of standing spruce trees attacked by bark beetles, in the merocoenosis of trees affected by fungal tree pathogens, lightning and wind-felling, and in the merocoenosis of snags and fragments (tree parts), in spruce stands of different age and in different situations with regard to the occurrence and population dynamics of *I. typographus*.

MATERIAL AND METHODS

Data on cambioxylophagous insect fauna associated with different types of spruce damage were collected in study plots situated in spruce stands of the Šance reservoir in the Moravian-Silesian Beskids, Czech Republic, over the period 1994 to 2007. Simultaneously, research was carried out in study plots located in spruce stands of the Beskid Żywiecki, Poland, between 2004 and 2007 (Kula, Ząbecki 2003; Kula, Kajfosz 2005). The study plots in the Czech Republic and Poland markedly differ from each other by the occurrence of *I. typographus* (see below).

According to methods and approaches employed in the study (for more information see Kula, Ząbecki 1996a, 1996b), damage to phloem by cambioxylophagous insect fauna (mostly by bark beetles) was documented in the area with an endemic (low) population of *Ips typographus* – endemic situation (Forest District Ostravice, CR) by evaluating a total of 1,536 spruce stems, the total length of which was 44,396 m. Of this, a total of 826 stems (21,853 m long altogether) were standing trees attacked by bark beetles, 194 stems (6,751 m) were trees struck by lightning, 140 stems (4,667 m) were trees afflicted by wind-felling (windfalls), 100 stems (5,202 m) were trees in the form of snags and fragments in mature spruce stands, 276 stems (5,923 m) were trees in the form of snags and fragments in pole-stage stands. The area was characterized by a small proportion (0.5–2%) of bark beetle salvage felling over the period 2001–2007.

Further, a total of 496 spruce stems (16,188 m) were checked for the presence of cambioxylophagous insect fauna in the area with an epidemic (high) population of *Ips typographus* – epidemic situation (Forest District Ujsoly, Jelesnia, Poland). In this particular area, a total of 381 stems (12,010 m long altogether) were the standing trees attacked by bark beetles, followed by 80 stems (2,854 m) of wind-felled trees, 35 stems (1,324 m) were checked in the form of snags and tree fragments (tree parts). A high proportion (37–97%) of annual bark beetle salvage felling in the area between 1993 and 2007 was typical.

RESULTS

A total of 34 species of cambioxylophagous fauna of spruce were recorded over the study period: Buprestidae (l), Cerambycidae (9), Curculionidae (2), Lymexylonidae (1), Scolytidae (18), Formicidae (1) and Siricidae (2 species). In the species spectrum the following trophic groups were distinguished: xylophages (3), cambioxylophages (8), mycetophages (2) and cambiophages (21 species). They were categorized as facultative primary pests (10), latent secondary pests (8) and temporal secondary pests (16 species).

Merocoenoses of cambioxylophagous insects with regard to the social position of a tree

In the study area with an endemic population of *I. typographus* (non-epidemic situation) a continuous decline of the frequency of occurrence of *I. typographus,* and *X. lineatus* from dominant to subordinate trees was documented. Bark beetle species preferring dominant and co-dominant trees to subordinate ones (*P. chalcographus, I. amitinus*), and also species attacking particularly dominant trees (*Hylurgops palliatus* /Gyll./), rank among cambioxylophages. Subordinate trees were more frequently colonized by *Xylechinus pilosus* (Ratz.), *P. poligraphus* (Scolytidae), *Molorchus minor* (L.), *Pogonocherus fasciculatus* (De Geer) (Cerambycidae) and *Pissodes harcyniae* /Herbst/) (Curculionidae) (Table 1).

The merocoenosis structure of cambioxylophages in standing trees in the area with an epidemic population of *I. typographus* (epidemic situation) was partly affected by a decrease in tree density (lower stocking). The effect of the social position of a tree, documented by the frequency of occurrence of particular species, was not evident in *P. chalcographus* and *I. amitinus*. In the case of subordinate trees, the frequency of occurrence of *I. typographus* was lower (compared to dominant and co-dominant trees), whereas in *Pityophthorus pityographus* (Ratz.) it was higher (Table 1).

In the study area with an endemic population of *I. typographus* the cover (exploitation) of stems by cambioxylophages markedly decreased only in subordinate trees (*P. chalcographus, I. amitinus*) or was lowering continuously from dominant trees (*I. typographus, X. lineatus*). Different response was seen in species preferring subordinate trees. Their attack was increasing continuously (*P. poligraphus*) or became more evident only in subordinate trees (*P. pityographus, M. minor*) (Table 1).

In the area with an epidemic population of *I. typographus*, only *P. chalcographus* occurred

Table 1. Frequency of occurrence of some cambioxylophagous insects in standing trees related to the social position of a tree (%)

Population density	Endemic situation						Epidemic situation					
Social position of a tree	D	CoD	ST	D	CoD	ST	D	CoD	ST	D	CoD	ST
Scolytidae		*N*			(%)			*N*			(%)	
I. typographus	83	56	6	43.4	25.5	2.0	100	92	77	58.8	51.6	38.9
I. amitinus	70	63	23	16.0	15.9	6.8	73	69	74	22.1	23.2	24.9
P. chalcographus	92	82	45	42.5	43.3	24.2	95	93	92	38.2	47.1	51.2
P. poligraphus	32	45	55	9.8	19.0	24.4	26	13	28	7.6	4.5	9.2
P. pityographus	62	61	75	4.3	5.0	12.8	17	21	44	0.7	1.2	3.3
C. abietis	11	9	18	0.8	0.6	2.1	0	0	0	0	0	0
X. lineatus	43	24	12	10.2	6.3	2.8	3	2	3	0.6	0.4	0.2
H. palliatus	34	23	23	8.0	5.8	5.7	6	5	3	1.0	0.8	0.2
X. pilosus	4	4	21	0.1	0.4	4.7	0	0	3	0	0	0.1
D. autographus	9	6	5	0.8	0.6	0.8	0	0	0	0	0	0
P. spinulosus	26	34	44	0	0	0.2	0	0	1	0	0	0
Curculionidae												
P. harcyniae	11	13	22	2.3	2.9	5.5	2	1	4	0.1	0.2	0.3
Cerambycidae												
M. minor	26	33	49	1.6	2.6	17.2	0	1	8	0	0.2	1.8
I. fuscum	26	27	5	3.2	4.2	0.6	9	5	5	2.1	0.5	0.5
R. inquisitor	36	24	22	3.0	2.1	1.7	6	3	3	0.6	0.4	0.1
Monochamus sp.		2	3	0	0.3	0.4	0	2	4	0	0.2	0.5
O. brunneum	25	26	25	0	0.2	1.4	0	1	0	0	0	0
P. fasciculatus	6	12	17	0.2	0.2	0.9	0	0	1	0	0	0
Number of trees	53	247	525				66	237	78			
Number of sections (m)				1,709	6,995	13,115				2,420	7,485	2,105

D – dominant, CoD – co-dominant, ST – subordinate tree, *N* – number of individuals frequently on co-dominant and subordinate trees. *P. poligraphus* and *I. amitinus* did not respond to the social position tree of a tree by the stem cover (exploitation) and a decrease in the population of *I. typographus* was evident in subordinate trees only (Table 1).

Merocoenoses of cambioxylophagous insects in standing trees attacked by bark beetles

The study area with an endemic population of *I. typographus* was characterized by high species richness and diversity of cambioxylophagous and wood-inhabiting insects (33), but only 18 species were more abundant. Considering the frequency of occurrence of cambioxylophagous insects in standing trees attacked by bark beetles, the frequencies exceeding 50% were found in the case of *P. pityographus* (69.7%), *P. chalcographus* (59.1%) and *P. poligraphus* (50.2%). Frequencies in the range of 25–50% were found in five species, of which *I. typographus* (26.3%) and *I. amitinus* (37.8%) were economically important (facultative primary pests). Frequencies ranging from 10 to 25% were documented in eight species (Table 2).

In the area with an endemic population of *I. typographus*, species richness was much lower (18 species). The highest frequency of occurrence was found in *P. chalcographus* (93.2%), *I. typographus* (90%) and *I. amitinus* (70.6%). Only *P. pityographus* (24.7%) and *P. poligraphus* (18.1%), the two species which do not occur together with *Ips typographus* under spruce bark and thus do not compete with it, ranked among relatively frequent accompanying species (Table 2).

Standing trees struck by lightning in the area with an endemic population of *I. typographus* were characterized by a specific merocoenosis in which

Table 2. Frequency of occurrence of some cambioxylophagous insects (three categories) in spruce stems depending on stem damage and gradation conditions of *Ips typographus* (%)

	Species/ Type of damage	Endemic situation						Epidemic situation			
		bark-beetles	lightning	windfall	stem breaks-snags	broken-off part (fragments)	sum	bark-beetles	windfall	stem breaks-snags	broken-off part (fragments)
Facultative-primary	*I. typographus*	26.3	35.7	66.4	1.0	27.7	32.7	90.0	98.8	2.9	91.4
	I. amitinus	37.8	59.7	32.9	1.0	15.8	40.9	70.6	43.8	0.0	74.3
	P. chalcographus	59.1	86.2	88.6	4.0	66.3	67.2	93.2	91.3	0.0	97.1
	P. poligraphus	50.2	83.7	10.7	34.3	38.6	51.1	18.1	0.0	0.0	0.0
	P. pityographus	69.7	40.3	16.4	0.0	32.7	58.3	24.7	1.3	0.0	2.9
	C. abietis	14.6	4.1	4.3	0.0	19.8	11.6	0.3	0.0	0.0	0.0
	P. harcyniae	19.1	4.6	7.2	11.1	9.9	15.2	1.8	0.0	0.0	0.0
	Number of trees	826	196	140	99	101	1,162	381	80	35	35
Temporal-secondary	*X. lineatus*	17.6	63.8	11.4	27.3	2.0	24.6	2.4	1.3	37.1	0.0
	H. palliatus	23.6	74.5	39.3	20.2	30.7	34.1	4.5	11.3	20.0	45.7
	X. pilosus	14.4	0.5	0.0	0.0	0.0	10.3	0.5	0.0	0.0	0.0
	D. autographus	5.2	2.0	9.3	9.1	4.0	5.2	0.0	3.8	0.0	0.0
	M. minor	42.7	11.7	2.1	0.0	1.0	32.6	2.1	0.0	0.0	0.0
	I. fuscum	13.0	28.6	25.7	22.2	5.0	17.1	5.5	1.3	0.0	0.0
	R. inquisitor	23.1	9.2	0.7	4.0	3.0	18.1	3.4	1.3	0.0	0.0
	Monochamus sp.	2.9	2.6	22.1	5.1	20.8	7.2	2.1	30.0	0.0	0.0
	Number of trees	826	196	140	99	101	1,162	381	80	35	35
Latent-secondary	*P. spinulosus*	40.1	13.8	3.6	0.0	0.0	31.2	0.3	0.0	0.0	28.6
	O. brunneum	25.2	8.7	0.7	0.0	0.0	19.4	0.5	0.0	0.0	0.0
	P. fasciculatus	14.9	2.0	2.1	0.0	3.0	11.2	0.3	0.0	0.0	0.0
	Number of trees	826	196	140	99	101	1,162	381	80	35	35

facultative primary species like *P. chalcographus*, *P. poligraphus* and *I. amitinus* played the most important roles (see the high frequency of occurrence), whereas the importance of *I. typographus* only slightly increased as compared to standing trees not affected by lightning (Table 2).

As for temporal secondary species, the frequency of occurrence of *X. lineatus* on standing trees greatly increases in trees affected by lightning stroke (Table 2). Changes in wood moisture and the rate of tree dieback suit the ecological requirements of the ambrosia bark beetle. It attacks trees struck by lightning which can have green crowns showing no visible signs of dying. Also, *H. palliatus* preferred the fermented moist phloem of trees affected by lightning (Table 2).

In the case of standing trees killed by cambioxylophagous insect species in the area with an endem-

Table 3. Stem cover of some cambioxylophagous insects (three categories) depending on stem damage and gradation conditions of Ips typographus (%)

Species/ Type of damage		Endemic population						Epidemic population			
		bark-beetles	lightning	windfall	stem breaks-snags	broken-off part (fragments)	sum	bark-beetles	windfall	stem breaks-snags	broken-off part (fragments)
Facultative-primary	*I. typographus*	12.8	8.8	29.7	0.1	20.0	14.37	50.84	60.16	2.04	65.3
	I. amitinus	10.4	9.5	3.5	0.2	2.9	9.28	23.26	8.20	0	15.8
	P. chalcographus	31.8	25.7	32.1	2.9	43.6	30.60	46.01	23.93	0	23.8
	P. poligraphus	21.5	36.0	2.4	27.7	16.4	21.75	5.92	0	0	0
	P. pityographus	9.6	2.1	0.7	0	3.8	6.83	1.47	0.25	0	0.1
	C. abietis	1.5	0.1	0.1	0	1.8	1.00	0	0	0	0
	P. harcyniae	4.5	0.4	0.7	5.1	0.9	3.25	0.22	0	0	0
	Number of sections (m)	21,853	6,751	4,667	1,030	1,831	33,271	12,010	2,854	49	1,275
Temporal-secondary	*X. lineatus*	4.5	15.3	5.4	6.6	0.9	6.79	0.41	0.77	26.53	4.1
	H. palliatus	5.9	20.5	15.2	6.0	11.4	10.20	0.71	2.52	14.29	9.2
	X. pilosus	2.9	0.0	0.0	0	0	1.93	0.02	0	0	0
	D. autographus	0.7	0.1	2.5	3.0	1.4	0.85	0	0.35	0	0
	M. minor	11.3	0.2	0.0	0	0.1	7.48	0.42	0	0	0
	I. fuscum	2.1	4.4	4.4	7.0	1.7	2.87	0.74	0.11	0	0
	R. inquisitor	1.9	1.4	0.0	0.4	0.3	1.54	0.40	0.07	0	0
	Monochamus sp.	0.3	0.3	7.6	1.7	6.7	1.27	0.21	7.95	0	0
	Number of sections (m)	21,853	6,751	4,667	1,030	1,831	33,271	12,010	2,854	49	1,275
Latent-secondary	*P. spinulosus*	0	0	0	0	0	0	0	0	0	0
	O. brunneum	0.9	0	0	0	0	0.57	0.02	0	0	0
	P. fasciculatus	0.6	0	0	0	0.2	0.42	0	0	0	0
	Number of sections (m)	21,853	6,751	4,667	1,030	1,831	33,271	12,010	2,854	49	1,275

ic population of *I. typographus*, the major part of a stem was exploited by *P. chalcographus* (32%) and *P. poligraphus* (21.5%), followed by relatively low densities of *I. typographus, I. amitinus, P. pityographus* and *M. minor* (10–13%). The temporal secondary species *X. lineatus* and *H. palliatus* (4.5–6%) were of marginal importance (Table 3). In the area with an epidemic population of *I. typographus*, standing trees were heavily colonized by *I. typographus* (51%), *P. chalcographus* (46%) and *I. amitinus* (23%) (Table 3). The magnitude of colonization was approaching the carrying capacity of trees.

In the case of trees struck by lightning in the area with an endemic population of *I. typographus*, *P. poligraphus* (36%) and *P. chalcographus* (26%) were most important with regard to the magnitude of stem cover, whereas *I. typographus* (9%) and *I. amitinus* (9.5%) were less important. On the other hand, a marked response occurred in temporal secondary pests *H. palliatus* (20.5%) and *X. lineatus* (15%) (Table 3).

Merocoenoses of cambioxylophagous insects affected by fungal tree pathogens

The fungal tree pathogens *Armillaria* spp. and *Heterobasidion annosum* Fr. represent important biotic stress factors affecting spruce health. In the area of the Šance reservoir, 27.2% of trees checked for the presence of cambioxylophagous insects were attacked by *Armillaria* spp., 17.7% by *H. annosum* and 33.9% by both pathogens (N = 825 trees colonized by bark beetles). Interestingly, a much lower proportion of fungal pathogens was found in trees affected by lightning (*H. annosum* – 14%, *Armillaria* spp. – 4%, N = 194).

The trees not attacked by fungi typically hosted facultative primary species (*P. chalcographus*, *I. typographus* and *I. amitinus*) and also temporal secondary species (*X. lineatus*) (Table 4). Fungal tree pathogens supported the presence of some cambioxylophagous insects in the study area. For example, the trees infested by *Armillaria* spp. showed the highest frequency of occurrence of *P. pityogra-*

Table 4. The frequency of occurrence and stem cover of some cambioxylophagous insects (%) in standing spruce trees non-infested and infested by fungal pathogens in the area of Forest District Ostravice.

Cambioxylophage/ Pathogen	Frequency of occurrence				Stem cover			
	0	Am	Ha	A+H	0	Am	Ha	A+H
Scolytidae								
C. abietis	8.3	16.4	14.5	17.1	3.0	4.3	5.7	4.6
D. autographus	0.0	0.0	0.0	0.0	0.8	0.4	0.7	1.0
H. palliatus	26.8	21.1	24.1	23.5	6.2	6.2	6.3	5.4
I. amitinus	52.4	36.2	35.9	31.3	11.2	10.9	9.7	10.0
I. typographus	58.9	15.1	25.5	16.4	31.8	6.5	11.3	7.1
P. chalcographus	76.2	56.9	53.1	53.7	35.9	31.9	31.0	29.6
P. pityographus	60.1	79.7	57.9	73.3	5.6	11.9	7.9	11.0
P. poligraphus	34.5	50.9	48.3	60.1	12.8	21.6	22.5	26.2
P. spinulosus	29.8	38.8	43.4	45.6	0.0	0.0	0.0	0.0
X. lineatus	27.4	17.2	16.6	12.5	5.7	5.2	4.8	3.0
X. pilosus	7.7	21.1	11.7	14.2	2.0	4.6	2.2	2.6
Curculionidae								
P. harcyniae	13.7	19.4	20.0	19.2	0.0	0.0	0.0	0.0
Cerambycidae								
I. fuscum	23.2	7.3	15.9	10.0	3.2	0.9	2.7	2.1
M. minor	29.8	46.1	38.6	49.8	6.5	16.3	9.1	11.3
Monochamus sp.	0.0	1.3	0.7	0.0	0.2	0.2	0.3	0.4
O. brunneum	20.2	25.9	19.3	30.6	0.0	0.0	0.0	0.0
P. fasciculatus	12.5	15.5	13.8	16.4	0.0	0.0	0.0	0.0
R. inquisitor	24.4	18.5	24.1	25.6	2.0	1.4	2.2	2.1
Number of sections (m)					4,601	6,118	3,615	7,519
Number of trees	168	232	145	281				

0 – healthy trees, Am – *Armillaria* sp., Ha – *Heterobasidion annosum*, A+H – the concurrence of pathogens

phus, whereas the trees free of pathogenic fungi or infested by *H. annosum* only hosted a smaller but still remarkable proportion of the species (Table 4). *P. poligraphus* also attacked trees infested by tree pathogenic fungi more often than uninfested trees. *M. minor* and *C. abietis* showed identical responses (Table 4).

The supportive effects of fungal tree pathogens on tree colonization by bark beetles were not evident in the case of *P. chalcographus, I. amitinus* and *X. lineatus*. However, both *P. pityographus* and *P. poligraphus* exploited a broader niche in trees stressed by pathogenic fungi compared to those without these fungi. In the trees infested by *Armillaria* spp. the niche width was extremely narrowed, particularly in the case of *I. typographus* (Table 4).

Merocoenoses of cambioxylophagous insects in wind-felled trees, breaks and fragments

The trees felled by the wind in autumn were checked for the presence of cambioxylophagous insects in next spring and autumn. Merocoenoses of cambioxylophagous insects in wind-felled trees in the area with an endemic population of *I. typographus* differed from those in standing trees. Among the species *P. chalcographus* (88.6%) and *I. typographus* (66.4%) were the most frequent. *I. amitinus* (32.9%) and the two temporal secondary representatives, *H. palliatus* (39.3 %) and the long-horned beetle *I. fuscum* (25.7%), were also relatively frequent (Table 2). Interestingly, lower tree attack was documented in *X. lineatus*, contrasting with the high frequency of occurrence of *Monochamus* species (Cerambycidae) (Table 2).

In the area with an epidemic population of *I. typographus*, much lower species richness was found (10 species recorded). The species composition reflected the presence of insect species typical of wind-felled trees. Two species may be considered as widely distributed, namely *I. typographus* (99%) and *P. chalcographus* (91%). A relatively high frequency of occurrence was also found in *I. amitinus* (44%) and *Monochamus* species (30%) (Table 2).

There are other special habitats of subcortical insect species in spruce forests. They are snags (standing, partly or completely dead trees, often missing the top or most of smaller branches) and tree fragments usually resulting from frequent wind and snow disturbances, mostly in autumn and winter. In the area with an endemic population of *I. typographus*, the merocoenosis of cambioxylophagous insects in snags was rather poor than rich. The facultative primary species, *P. poligraphus* (34%), gained from these specific conditions (the phloem retaining high water content, gradually dying). The relatively high frequency of occurrence of the temporal secondary species *X. lineatus* (27.3%), *I. fuscum* (22.2%) and *H. palliatus* (20.2%) cannot be overlooked (Table 2).

Wood fragments originating from snagged trees apparently showed differences in the frequency of attack by cambioxylophagous insects and in merocoenosis structure. In the area with an endemic population of *I. typographus*, a total of 15 species were recorded in fragments, of which the high frequency of occurrence of *P. chalcographus* (66.3%) and other species developing in the upper parts of stems and branches (*P. pityographus, I. amitinus, C. abietis*) was typical (Table 2). *I. typographus* was frequently found in long fragments. Similarly like in snags, *P. poligraphus*, *H. palliatus* and *Monochamus sutor* (L.) also occurred in tree fragments on the forest floor (Table 2).

In the area with an epidemic population of *I. typographus*, a total of 35 snags and fragments hosted a total of 6 species of cambioxylophagous insects. Low snags (up to 2 m high) supported three species only. *X. lineatus* (37%) and *H. palliatus* (20%) were the most frequent representatives of temporal secondary species in snags. In very long fragments a merocoenosis was established near the standing and wind-felled trees, *P. chalcographus* (97.1%), *I. typographus* (91.4%) and *I. amitinus* (74.3%) being the most frequent species. The records of *H. palliatus* (45.7%) were also frequent (Table 2).

The attractiveness of wind-felled trees for cambioxylophages differed from that of standing trees by the extent of stem cover (exploitation) by particular species. In the area with an endemic population of *I. typographus*, the exploitation of stems by *I. typographus* and *P. chalcographus* was balanced (30–32%). The stem cover was 15% in the case of *H. palliatus* and almost 8% in the case of *Monochamus* species (temporal secondary species). However, in the area with an epidemic population of *I. typographus* the exploitation of stem by *I. typographus* was as high as 60%, reflecting the aggressiveness of the beetle. *P. chalcographus* (24%) and long-horned beetles of the genus *Monochamus* (8%) were less important (Table 3).

Cambioxylophagous insects are affected by the length (size) of snags and other tree fragments. In the area with an endemic population of *I. typographus*, stem fragments were mostly exploited by *P. chalcographus* (stem cover 44%), *I. typographus, P. poligraphus* and *H. palliatus* (11–20%) (Table 2). In the epidemic situation, the intensive exploitation of stem fragments by *I. typographus* (65%)

was documented. The exploitation of stems by *P. chalcographus* (24%) and *I. amitinus* (16%) was less important (Table 3).

DISCUSSION

The study area in the Moravian-Silesian Beskids (Forest District Ostravice, Czech Republic) markedly differs from that in the Beskid Żywiecki (Ujsoly, Poland) with regard to the occurrence and population dynamics of *I. typographus*. In the Moravian-Silesian Beskids, in spite of the long-term instability of spruce stands, bark beetle outbreaks were noticed only infrequently, e.g. in 1917 and 1950 (Nosek 1952). The increase in bark beetle salvage felling after 2007 had much to do with snow and wind disturbances and unfavourable weather conditions (Kříštek et al. 2008). The outbreak of *I. typographus* in the area of the Beskid Żywiecki has lasted for more than 10 years and is associated with the decline of spruce forests adversely affected by abiotic and biotic factors, air pollution included.

The species rich spectrum of cambioxylophagous insects (34 species recorded in the study, bark beetles predominating among them) is related to the fact that the research was conducted in the area with endemic populations of facultative primary bark beetles where the structure of merocoenoses was more balanced compared to the area representing epidemic populations of bark beetles, of which a highly competitive environment of several predominating bark beetle species, mostly *I. typographus* and *P. chalcographus,* was typical.

The attractiveness of spruce to cambioxylophagous insects is largely affected by the rate of the tree dieback and changes in phloem quality as well as production of food attractants. A great differences in attractiveness to subcortical insects between standing spruce trees gradually dying due to drought, infrared radiation (insolation), pathogenic fungi, air pollution, etc. and spruce trees killed suddenly, e.g. by lightning, is apparent.

Moist and fermented phloem dries up and loses its moisture as a result of high temperatures, especially in open habitats. This is accompanied with changes in the contents of phenolic substances α and β pinene, generally after an intensive resin production in the crown area of a stem (horizontal lightning). Such habitat is not attractive to *I. typographus* (Kula, Ząbecki 1997b). On the other hand, the bark beetle *P. poligraphus,* which prefers shaded subordinate trees stressed by fungal tree pathogens, is exploiting the phloem of spruce trees affected by lightning much more often. A similar response is seen in *H. palliatus*, *X. lineatus* and *I. fuscum*. "Lightning circles" in spruce stands are a frequent phenomenon in the Beskids region. They create favourable conditions for *P. poligraphus* to outbreak locally, especially at places where timber removal and wood processing were delayed or impossible for some reasons. The bark beetle, after its outbreak, is able to kill even weakened co-dominant trees.

The ambrosia beetle *X. lineatus* is common in spruce trees struck by lightning. It may be the first species (in species succession) colonizing such trees. The trees colonized by it may have green crowns, without any visible signs of the bark beetle attack. As further survival of such trees is impossible, they should be removed from forest stands. The lower intensity of attack by *I. typographus* can be explained by the early occurrence of *H. palliatus,* an important food competitor in spruce stems. Particularly in trees affected by horizontal lightning, species typical of the crown area (*P. chalcographus*, *I. amitinus*) are present. High rates of their development inhibit the occurrence of *I. typographus*.

In the Czech Republic today approximately one third of spruce stands is threatened by pathogenic fungi of the genus *Armillaria*. Standing trees with roots infested by tree fungal pathogens are a subject of disturbance through physiological stress. This leads to changes in the quality and quantity of bark and phloem (Rudinski 1966; Renwick, Vité 1972; Madziara-Borusiewicz, Strzelecka 1977) and consequent negative impacts on tree health and stability of forest stands. The Beskids region is characterized by the frequent occurrence of fungal pathogens associated with spruce, species of the genus *Armillaria* being the most important among them. In the Polish part of the Beskids, the presence of *Armillaria* spp. was documented in 53% of analysed spruce trees (N = 381). Tree pathogenic fungi on spruce stems mostly affect the occurrence of cambioxylophagous insects typical of branches of the lower part of the crown. Also, the effect of physiological stress on the process of branch dying is highly likely and cannot be overlooked. Of cambioxylophagous species associated with spruce stems, only *P. poligraphus* was apparently gaining from the presence of fungi (*Armillaria* spp.) as shown by high frequency of occurrence and great magnitude of stem exploitation by the species (see results). The ecological requirements and response of *I. typographus* are quite different. The bark beetle prefers dominant spruce trees, also healthy ones, with optimum slenderness ratio and crown percentage (Kula, Ząbecki 2000). It is also attracted to trap trees infested by *Armillaria* spp., although there is a great deal of variation in such colonization. Nevertheless, trap trees infested by tree pathogenic fungi can be used for forest pest inventory purposes (Holuša et al. 2009).

The structure of merocoenoses of cambiophagous insects in lying (wind-felled) trees differs from that of standing trees (in endemic situation) in the high attack by *I. typographus* and *P. poligraphus*. Also, *H. palliatus*, *I. amitinus, I. fuscum* and *M. sartor* may compete with *I. typographus*. Snags are also a special habitat for cambiophagous insects. Qualitative changes are related to the position (location) of the break. Particularly trees snagged under the top host specific insect species which, except for *P. poligraphus*, are not harmful to spruce stands, namely *H. palliatus* and *I. fuscum*. The phloem with a high amount of water in the tissues increases the attractiveness of stems to some cambioxylophagous species (Kula, Ząbecki 2004). Processing damaged parts of trees can be delayed at the expense of lying fragments, where the proportion of species is balanced (with the exception of *P. chalcographus*) but differs from standing and wind-felled trees. The fragment length (fragment size) can be considered as a key factor structuring the merocoenoses of subcortical insect associates of spruce (Kula, Ząbecki 2005).

The bark beetle *P. chalcographus* ranks among broadly adaptive cambiophages with high ecological plasticity. It exploits most stem types (with the exception of snags). In spruce stands it is often responsible for the drying up of tree crowns and tree weakening. It may also cause the tree death.

The area with an epidemic population of *I. typographus* is characterized by a much narrower species spectrum compared to that with an endemic population of the beetle. It is composed of main facultative primary species like *I. typographus, I. amitinus* and *P. chalcographus*. Their rapid colonization of spruce stems and consequent loss of food sources due to their development are the main cause that *P. poligraphus, H. palliatus, X. lineatus* and *P. pityographus* are rather missing than present in standing trees. *P. chalcographus* is a frequent and harmful pest of subordinate trees. In the study area it frequently attacks the longest section of the stem and it also colonizes branches in the wide area of spruce crown. This agrees with the results of Kudela and Wolf (1963), who found the beetle to be a predominating species in prematurely shaded spruce trees in an area affected by air pollution. The beetle weakens spruce crowns and gradually moves down the stem to the middle part. In air-polluted areas, it colonizes the entire surface of spruce stems replacing *I. typographus* there (Moritz, Führer 1988).

The structure of merocoenoses of cambioxylophagous species differs among subordinate, co-dominant and dominant spruce trees. The weakening of a tree by the particular insect species depends on the social position of a tree. Novák (1962) did not consider the tree crown health to be a factor responsible for the attacks by cambioxylophagous species and wood-destroying insect associates of spruce, not even in cases where the needle loss was documented. According to Novák (1962), the phloem quality in the swarming period of the particular bark beetle species is crucially important for it to locate and colonize the host. In subordinate trees, shading associated with the resulting limited assimilatory activity and other stress factors are also responsible for the reduced vigour of a tree. In addition, the effects of tree fungal pathogens and diseases they cause can be associated with mechanical damage to trees, deer barking or specific weather conditions (drought, etc.).

There were bark beetle species in the study area preferring high-quality trees, suppressed ones again (*I. amitinus, X. lineatus, I. typographus, P. chalcographus*). They rank among the most important pests of spruce. Subordinate trees were preferred by *C. abietis, X. pilosus, M. minor* and *P. fasciculatus*. These species are of no economic importance and represent a number of numerous decomposing insect species. Moderate preference of subordinate trees, documented in *P. poligraphus* and *P. pityographus*, may indicate a potential threat to suppressed and/or co-dominant trees in dense spruce stands.

Wind-felled trees, when fresh enough, are highly attractive to *I. typographus* as shown by the high frequency of occurrence and large magnitude of stem exploitation by the bark beetle, especially in an epidemic situation. The critical amount of timber in the form of wind-felled trees which can remain in a spruce forest in the area with an endemic population of *I. typographus* is unknown. The more frequent use of wind-felled trees as trap trees for cambiophagous insects, especially bark beetles, is recommended.

CONCLUSIONS

The study was carried out in the area with an endemic population (Moravian-Silesian Beskids, Forest District Ostravice, Czech Republic) and in the area with and epidemic population of *I. typographus* (Beskid Żywiecki, Forest District Ujsoly, Jelesnia, Poland). A total of 34 species of cambioxylophagous insect fauna, representing merocoenoses of Norway spruce in the Beskids, were recorded from a total of 2,032 trees in the form of standing trees attacked by bark beetles, trees affected by lightning and tree fungal pathogens, wind-felled trees, snags and tree fragments.

The stability of spruce stands in the area with an endemic population of *I. typographus* is endangered by the following facultative primary cambioxylophagous species:

Standing bark beetle trees: heavily by *P. chalcographus,* moderately by *I. typographus, I. amitinus, P. poligraphus,* slightly by *P. pityographus*;

Trees struck by lightning: heavily by *P. poligraphus*, *P. chalcographus*, *X. lineatus*, *H. palliatus*, moderately by *I. amitinus,* slightly by *I. typographus*, *P. pityographus*;

Wind-felled trees: heavily by *I. typographus*, *P. chalcographus*, *H. palliatus*, moderately by long-horn beetles *Monochamus* sp. and *I. fuscum*, slightly by *I. amitinus*, *P. pityographus*;

Snags in mature spruce stands: heavily by *P. poligraphus*, slightly by *X. lineatus*, *H. palliatus*;

Fragments in mature stands: heavily by *P. chalcographus*, *I. typographus*, moderately by *P. poligraphus*, *H. palliatus*, slightly by *I. amitinus*, *P. pityographus*, long-horn beetles of the genus *Monochamus*; in stands up to 40 years: heavily by *P. chalcographus* and *H. palliatus*;

Trees infested by the fungal pathogens *Armillaria* spp. and *Heterobasidion annosum* show only low attractiveness to *I. typographus, P. chalcographus* and *I. amitinus*. However, their attractiveness to *P. poligraphus* is high.

In the area with an epidemic population of *I. typographus* the merocoenosis of cambioxylophages of spruce is species-poor. *I. typographus* and *P. chalcographus* are most frequent on standing trees, wind-felled trees, and in tree fragments.

In the area with an endemic population of *I. typographus*, the social position of a tree strongly affects the frequency of occurrence and exploitation of spruce stems by bark beetles: dominant trees (*I. typographus*, *X. lineatus*, *H. palliatus*), co-dominant trees (*P. chalcographus*, *I. amitinus*) and subordinate trees (*P. poligraphus*).

In the area with an epidemic population of *I. typographus*, no marked differences are evident with respect to the degree of tree attack by bark beetles.

References

Bakke A., Austarå Ö., Pettersen H. (1977): Seasonal flight activity and attack pattern of *Ips typographus* in Norway under epidemic conditions. Meddelelser fra Det Norske Skogforsöksvesen, ***33***: 253–268.

Bednarz B. (2005): Insects inhabiting stumps after trees lightning. Acta Scientiarum Polonorum - Silvarum Colendarum Ratio et Industria Lignaria, ***4***: 3–10. (in Polish)

Capecki Z. (1978): Untersuchungen über kambio- und xylophage Insekten in durch Wind und Wächte beschädigten Fichtenbeständen im Gebirge. In: Prace Institutu Badawczego Lešnictva, Warszawa, ***563***: 37–117.

Christiansen E., Huse K. J. (1980): Infestation ability of *Ips typographus* in Norway spruce in relation to butt rot, tree vitality and increment. Norsk Skogforskning, ***35***: 473–482.

Gründwald M. (1986): Ecological segregation of bark beetles (*Coleoptera, Scolytidae*) of spruce. Journal of Applied Entomology, ***101***: 176–187.

Holuša J., Kula E., Knížek M., Kozák D., Ząbecki W. (2009): Attractiveness of trap trees. Grantová Služba LČR, ***03***: 43. (in Czech)

Kisielowski S. (1978): The four-eyed spruce bark beetle (*Polygraphus poligraphus* L.) in montane forest stands attacked by the honey-fungus. Sylwan, ***CXXII*** (7): 25–29.

Knížek M. (2004): Bark beetles in quarantine. Zpravodaj ochrany lesa, ***10***: 20–22. (in Czech)

Křístek Š., Samec P., Rychtecká P., Holuša J. (2008): Numerical analysis of the time and spatial distribution of snow cover in the Ostravice river watershed /the Moravian-Silesian Beskids/ in winters 2005/2006 and 2006/2007. Meteorologický časopis, ***11***: 107–117. (in Czech)

Kudela M., Wolf R. (1963): The proportion of cambioxylophagous and wood-destroying insects in the dieback of spruce and pine in stands damaged by air pollution. Sborník lesnické fakulty VŠZ Praha, ***6***: 157–187. (in Czech)

Kula E., Kajfosz R. (2005): Site characteristics and salvage felling in the region of the Beskids. In: Hlaváč P. (ed.): Proceedings Uplatňovanie nových metód v ochrane lesa a ochrane krajiny. Zvolen-Kováčová, 8.–9. September 2005. Zvolen, Technicka univerzita vo Zvolene: 5–10. (in Czech)

Kula E., Ząbecki W. (1996a): The synusia of cambioxylophages on subordinate spruce trees. Zpravodaj Beskydy, ***8***: 213–220. (in Czech)

Kula E., Ząbecki W. (1996b): What danger is represented by cambioxylophages of subordinate spruce trees. Les - Lesnická práce, ***8***: 284–285. (in Czech)

Kula E., Ząbecki W. (1997a): Impacts of tree social position on the cambioxylophagous fauna of spruce trees. Lesnictví-Forestry, ***43***: 269–278. (in Czech)

Kula E., Ząbecki W. (1997b): Lightning-stroken areas as the centres of bark-beetle-infested patches within spruce stands. Sylwan, ***CXLI*** (8): 89–97.

Kula E., Ząbecki W. (1999a): Cambioxylophagous fauna of spruce-trees under stress of honey fungus and wood decay. Journal of Forest Science, ***45***: 457–466.(in Czech)

Kula E., Ząbecki W. (1999b): Cambioxylophagous niche on spruce-trees affected by the stress of root fungal pathogens. Journal of Forest Science, ***45***: 348–357. (in Czech)

Kula E., Ząbecki W. (2000): Slenderness coefficient and cambioxylophages fauna of Norway spruce. Zpravodaj Beskydy, ***13:*** 171–176. (in Czech)

Kula E., Ząbecki W. (2001): Attractiveness of spruce for cambioxylophages as related to stand age. Journal of Forest Science, ***47***: 88–96.

Kula E., Ząbecki W. (2002): Relationship between synusia of spruce cambioxylophages and extent of phloem dieback. Beskydy, ***15***: 113–118. (in Czech)

Kula E., Ząbecki W. (2003): The effect of some biotic and weather conditions on spruce (*Picea abies* [L.] Karst.) tree mortality in stands of the Beskid Slasko-Morawski Mts. Beskydy, ***16***: 137–143 (in Polish).

Kula E., Ząbecki W. (2004): Relationship between synusia of spruce cambioxylophages and extent of phloem dieback. Beskydy, ***17***: 149–154. (in Czech)

Kula E., Ząbecki W. (2005): Cambioxylophagous fauna of the broken-off parts of Norway spruce trees in the area of low population density of *Ips typographus*. Beskydy, ***18***: 145–150. (in Czech)

Kula E., Ząbecki W. (2007): Lightening and cambioxylophages. Lesnická práce, ***86*** (7): 28–29. (in Czech)

Madziara-Borusiewicz K., Strzelecka H. (1977): Conditions of spruce (*Picea excelsa* Lk.) infestation by the engraver beetle (*Ips typographus* L.) in mountains of Poland. I. Chemical composition of volatile oils from healthy trees and those infested with the honey fungus (*Armillaria mellea* [Vahl] Quél.). Zeitschrift für Angewandte Entomologie, ***83***: 409–415.

Mauer O., Palátová E., Rychnovská A., Peterka T. (2005): Regional decline of Norway spruce (*Picea abies* [L.] Karst.) in the Czech Republic. In: Proccedings Obnova lesních porostů v imisní oblasti východního Krušnohoří. Hora sv. Šebestiána, 2. June 2005. Brno, Mendlova zemědělská a lesnická univerzita v Brně: 47–59. (in Czech)

Moritz B., Führer E. (1988): Rindeninhaltstoffe der Fichte (*Picea abies*): Analysen an Borkenkäfer-Fangbäumen. Journal of Applied Entomology***, 105***: 502–509.

Nosek J. (1952): Biocoenology of the fauna of bark beeles in the Beskids. Zoologické a entomologické listy, ***2***: 95–110. (in Czech)

Novák V. (1962): Research into the succession of cambioxylophagous insect on trees declining due to industrial air pollution in the Krušné hory Mts. Lesnictví-Forestry, ***8***: 329–341. (in Czech)

Pfeffer A. (1932): The bark beetles in the forest of the High Tatra Mts. Lesnická práce, ***11***: 246–268. (in Czech)

Pfeffer A. (1955): Fauna of the CSR – Scolytoidea. Praha, ČSAV: 324. (in Czech)

Pfeffer A., Knížek M. (1993). Scolytidae. In: Jelínek J. (ed.): Check-List of Czechoslovak Insects IV (Coleoptera). Folia Heyrovskyana Supplementum, ***1***: 153–158.

Pfeffer A. (1995): Zentral- und Westpaläarktische Borken- und Kernkäfer (Coleoptera: Scolytidae, Platypodidae). Basel, Pro Entomologia, c/o Naturhistorisches Museum: 310.

Price P.W. (1975): Insect Ecology. New York, Wiley & Sons, 514.

Renwick J. A., Vité J. P. (1972): Pheromones and host odors governing the aggregating of the six-spinned engraver beetle *Ips calligraphus.* Journal of Insect Physiology, ***18***: 1215–1219.

Rudinski J. A. (1966): Host selection and invasion by the Douglas fir beetle *Dendroctonus pseudotsugae* Hopkins in coastal Douglas fir forests. Canadian Entomologist, ***98***: 98–111.

Schröter H., Becker T., Schelshorn H. (1998): Die Bedeutung der Sturmwurfflächen als Borkenkäferquellen für umliegende Wirtschaftswälder. In: Fischer A. (ed.): The Development of Biotic Communities after Windthrow. Landsberg, Ecomed: 292–314.

Schwerdtfeger F. (1955): Pathogenese der Borkenkäfer-Epidemie 1946–1950 in Nordwest-deutschland. Schriftenreihe der Forstlichen Fakultät der Universitet Göttingen, ***13/14***: 1–135.

Wermelinger B., Duelli P., Obrist M.K. (2002): Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. Forest Snow and Landscape Research, ***77*****:** 133–148.

Wood D.L. (1982): The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annual Review of Entomology, ***27***: 411–446.

Zumr V. (1984): Spaital distribution of bark beetles (*Scolytidae*) in Norway spruce (*Picea excelsa* L.) and their indifference in relation to forest belts. Lesnictví-Forestry, ***30***: 509–522.

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Corresponding author:

Prof. ing. Emanuel Kula, CSc., Mendlova Univerzita v Brně, Lesnická a dřevařská fakulta,
Zemědělská 3, 613 00 Brno
tel: + 420 604 731 516, e-mail: kula@mendelu.cz