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Spruce windfalls and cambioxylophagous fauna in an area with the basic and outbreak state of *Ips typographus* (L.)

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ABSTRACT: In spruce windfalls incurred in the autumn and winter season the synusia of cambioxylophagous fauna was evaluated in the profile of a whole stem and crown branches according to the species spectrum, tree cover and intensity of attack. The fauna of windfalls in the area with the basic level of *Ips typographus* (L.) and in the gradation area differed by species diversity. In the gradation area, frequency of the occurrence of *Ips typographus* (L.) was higher by 20–40%. *Pityogenes chalcographus* (L.) showed decreased stem cover in the gradation area. In the area with the basic state of *Ips typographus* (L.), windfalls were intensively colonized by secondary species *Hylurgops palliatus* (Gyll.), *Isarthron fuscum* (Fabr.), *Monochamus* sp. With the increasing dbh (diameter at breast height) of windfalls the colonization of stems by *Ips typographus* (L.) was positively affected, *Hylurgops palliatus* (Gyll.), *Isarthron fuscum* (Fabr.), *Polygraphus poligraphus* (L.) responded the other way round.

Keywords: Norway spruce; the Beskids; windfalls; cambioxylophages; *Ips typographus*; *Pityogenes chalcographus*; *Ips amitinus*; *Polygraphus poligraphus*

Spruce windfalls incurred annually in a different extent make possible the reproduction of cambioxylophages and subsequent threat to living trees (Bakke 1989; Weslien, Schröter 1997; Schröter et al. 1998; Peltonen 1999b; Wermelinger et al. 2002; Hedgren et al. 2003). Even at the decreased population density *Ips typographus* (L.) is able to overcome heavily disturbed defensive mechanism of windfalls (Mulock, Christiansen 1986). However, it can be later affected by intense intraspecific and interspecific competition (Anderbrant 1990).

Attractiveness and availability of a windthrow incurred in the course of winter are particularly limited by the phloem quality and the procedure of its wilting. Unprocessed windfalls can be invaded throughout the growing season but also in the next year (Butovitsch 1971; Annila, Petäistö 1978; Göthlin et al. 2000; Eriksson et al. 2005). The cover of stems by feeding marks is higher at localities with the smaller concentration of windfalls (Eriksson et al. 2005). The attractiveness of sites increases with the extent of windbreak areas where the high production of volatile affects the aggregation of *I. typographus* (Austarå et al. 1986; Lindelöw, Risberg 1992; Franklin et al. 2000). Thus, mixed stands are of lower attractiveness. Schröder and Lindelöw (2002) determined significant correlation between the extent of windbreak and the number of standing trees killed by *I. typographus*.

The rate of attack of windfall wood is related to the density of population before the origin of a windbreak and on the regional and local heterogeneity of site conditions (Martikainen et al. 1999; Nageleisen 2001; Eriksson et al. 2005). Windbreaks are

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preferred on open and insolated places, along stand margins where the rate of phloem wilting influences the intensity of invasion, the rate of the development of *I. typographus* or the competition environment with other species (Göthlin et al. 2000; Jakuš 1998; Peltonen 1999a).

The aim of the paper is to complete missing data on the cambioxylophagous fauna of windfalls, its proportion in the stem profile and crown branches and the progress of invasion on spruce windfalls in areas with the basic and gradation level of *I. typographus.*

METHODS

In the area of the Beskids (Forest Districts Ostravice and Ujsoly), windfalls (211) which originated during one event in October 2002 and November 2004 were analyzed in consequential spring (June) and summer (September) aspects in 2003 and 2005. Each of the windfalls was characterized by mensurational parameters (diameter at breast height – dbh, crown length, crown height), health condition (drying up of phloem, rate of foliage), position in a stand (open area, stand shelter). Characteristics of particular stands result from data of forest management plans and include information on the stand age, altitude, aspect, stocking, species composition, forest type group and other information specifying site and stand conditions. Differentiated population density of *I. typographus* occurring in Forest District Ostravice in the basic state and in Forest District Ujsoly in the outbreak state is considered to be critical.

The occurrence of particular cambioxylophagous species was determined after barking the stem and branches in the whole windfall profile. In consequential one-meter sections following parameters were determined: cambioxylophagous species, developmental stage, the rate of attack (scattered – sporadic occurrence of feeding marks, increased – feeding marks occupy 1/3–2/3 of the section or branch surface, heavy – feeding marks occur on more than 2/3 of the section or branch surface) (Kula, Zábecki 1996).

Frequency of the occurrence of particular cambioxylophagous species was expressed by the percentage of the number of trees attacked by the given species on a stem and branches of the total number of analyzed windfalls not distinguishing place, extent and the degree of damage separately for the gradation area and the basic state area. The average extent of using the available profile and the degree of attack of a tree or branches was expressed by the percentage extent of the sum of lengths of stem and crown profiles attacked by the given species in relation to the total length of stems and crowns of all analyzed windfalls.

Description of the area of study

Forest District Ostravice

Spruce stands under evaluation are part of selected points of a 1 × 1 km monitoring network of the Šance reservoir basin (altitude 550–850 m a.s.l., balanced proportion of aspects, mostly on steep slopes 15–25 degrees), mean annual temperatures 4–7°C, total annual precipitation 700–1,000 mm. In spite of the occurrence of windbreaks (2001–2004) (Table 1) cambioxylophages remain in the basic state in the area for a long time and in the past 50 years, bark beetle gradations did not occur there.

Forest District Ujsoly

The gradation area of *I. typographus* of the Beskid Żywiecki is characterized by the decreasing stability of spruce stands where incidental felling induced by bark beetles represents 51–95%. In 2001 to 2004, incidental felling reached gradually 25,031; 31,436; 56,655 and 84,316 m^3 (Table 2). The dominant proportion of spruce (94.12%) mainly at altitudes 485–1,100 m a.s.l. is characterized by mean annual temperatures 4–7°C, total annual precipitation 700–1,400 mm.

RESULTS

Spruce windfalls incurred by the effect of abiotic harmful factors (snow – X. 2002, wind – XI. 2004)

Table 1. The extent of salvage felling in the area of Forest District Ostravice (2001–2004)

Year	Salvage felling (m^3)			
	natural disasters	insect pests	other	Sa
2001	21,254	340	1,434	23,028
2002	57,356	169	3,711	61,236
2003	48,022	979	4,744	53,745
2004	22,397	203	2,375	24,975

Table 2. The amount of salvage felling and felling induced by *I. typographus* attack in Forest District Ujsoly (1993–2004)

Year	Coniferous salvage felling (m^3)		
	total	bark beetles	(%)
1993/1994	27,961	18,197	65
1994/1995	36,770	19,144	52
1995/1996	38,840	22,030	57
1996/1997	38,686	19,872	51
1997/1998	44,882	27,095	60
1998/1999	54,881	26,445	48
1999/2000	47,110	26,985	57
2000/2001	36,826	25,031	68
2001/2002	43,565	31,436	72
2002/2003	83,671	56,655	68
2003/2004	88,987	84,316	95

became an available area for the development of cambioxylophagous fauna in the consequential growing season. In Forest District Ostravice, 133 (82 + 51) windfalls were analyzed in the spring and summer season and in Forest District Ujsoly 78 (41 + 37) windfalls.

The cambioxylophage fauna of windfalls out of the gradation area

Of 18 cambioxylophagous species registered on windfalls some 10 species were confirmed in the spring aspect while 18 species in the summer aspect. The highest occurrence was noted in *Pityogenes chalcographus* (L.) (95.1%) and *I. typographus* (75.6%) in spring. In one third of windfalls, *Ips amitinus* (Eichh.) (34.1%) and *Hylurgops palliatus* (Gyll.) (32.9%) were noted. *Xyloterus lineatus* (Ol.) attacked windfalls (17.1%) in the spring season (Table 3).

In the summer aspect, following economically important species occurred: *P. chalcographus*

Table 3. The frequency of the attack of windfall stems by cambioxylophages in an area with the various population density of *I. typographus*

Species/frequency	Outside outbreak (%)		Outbreak (%)	
	spring	summer	spring	summer
Cryphalus abietis		5.88		
Dryocoetes autographus	1.22	23.53		8.11
Hylastes ater		3.92		
Hylocoetes dermestoides		1.96		
Hylurgops glabratus		1.96		
Hylurgops palliatus	32.93	47.06	19.51	
Ips amitinus	34.15	33.33	68.29	13.51
Ips typographus	75.61	56.86	100.00	94.59
Isarthron fuscum	1.22	62.75		
Monochamus sp.	1.22	54.90		2.70
Pissodes harcyniae		5.88		
Pissodes scabricollis		11.76		
Pityogenes chalcographus	95.12	62.75	92.68	64.86
Pityophthorus pityographus	4.88	15.69	2.44	86.49
Pogonocherus fasciculatus		1.96		
Polygraphus poligraphus		27.45		
Rhagium sp.	1.22	1.96		2.70
Xyloterus lineatus	17.07	1.96	2.44	
Total of windfall stems	82	51	41	37

Table 4. The windfall stem cover by cambioxylophages in the spring and summer aspect in an area with various population density of *I. typographus*

Species/cover	Outside outbreak (%)		Outbreak (%)	
	spring	summer	spring	summer
Cryphalus abietis		3.61		
Dryocoetes autographus	2.70	29.69		8.62
Hylastes ater		7.94		
Hylocoetes dermestoides		21.62		
Hylurgops glabratus		5.41		
Hylurgops palliatus	41.69	35.28	21.15	
Ips amitinus	11.44	8.41	18.76	9.41
Ips typographus	38.83	46.88	60.06	64.57
Isarthron fuscum	3.13	19.30		6.67
Monochamus sp.	31.25	37.13		27.72
Pissodes harcyniae		18.39		
Pissodes scabricollis		16.58		
Pityogenes chalcographus	34.35	47.82	22.41	27.46
Pityophthorus pityographus	7.19	6.42	18.92	
Pogonocherus fasciculatus		0.27		
Polygraphus poligraphus		28.91		
Rhagium sp.	6.25	3.23		5.71
Xyloterus lineatus	45.81	86.49	62.86	

(62.7%), *I. typographus* (56.9%), *I. amitinus* (33.3%), *Polygraphus poligraphus* (L.) (27.5%). At the same time, the high proportion of secondary species was noted [*Isarthron fuscum* (Fabr.) 62.8%, *Monochamus* sp. 54.9%, *H. palliatus* 47.1%, *Dryocoetes autographus* (Ratz.) 23.5%] which, however, did not threaten standing trees even under outbreaks. Low frequency was noted in members of the genera of *Pissodes* and *Pityographus* (Table 3).

In some species, the stem cover of windfalls deviated from usual ecological requirements. *X. lineatus* attacked the longer profile of a stem (45.8%) climbing up to the undercrown section, thus occurring virtually in the whole stem profile under the crown. *I. typographus* and *P. chalcographus* show the same cover of the windfall profile which was lower in the spring aspect than in the summer aspect (38.8–46.9% and 34.4–47.8%). Similar response appeared also in later swarming species (*D. autographus* 2.8 × 29.7%, *I. fuscum* 3.1 × 19.3% and partly also in *Monochamus* sp. 31.2 × 37.1%). *I. amitinus* did not differ by its space niche in studied aspects. *P. chalcographus* showed the heavy degree of stem attack in the summer aspect. Less obvious shift was demonstrated by *I. typographus* while *H. palliatus* markedly increased its proportion in the low degree of attack (Table 4).

Of 133 analyzed windfalls 86 trees were situated in a stand and remaining trees occurred in an open area or in the open part of a stand thereby different conditions were created for drying up windfalls and the development of bark beetles. The open area microclimate was slightly preferred particularly by economically important cambiophages of spruce (*I. typographus* 65 × 74%, *P. chalcographus* 79 × 89%) and significantly by *I. amitinus* (28 × 45%). The increased occurrence frequency on windfalls in a stand can be demonstrated in *D. autographus, I. fuscum, Monochamus* sp., *H. palliatus* and *P. poligraphus* and *Pissodes* sp. (Table 5). *P. poligraphus* colonized a further section of the stem on windfalls of the open area and similarly also members of the genus *Monochamus.* Differences in the profile of the colonized stem niche under conditions of a stand and open area were not noted in *I. typographus, I. amitinus, P. chalcographus* even in species earlier activated (*H. palliatus, I. fuscum, X. lineatus*) (Table 6).

Table 5. The occurrence frequency of cambioxylophages according to the position in an area with the various population density of *I. typographus*

Species/frequency	Outside outbreak (%)		Outbreak (%)	
	forest	free site	forest	free site
Cryphalus abietis	3.49			
Dryocoetes autographus	13.95	2.13	6.67	3.17
Hylastes ater	2.33			
Hylocoetes dermestoides	1.16			
Hylurgops glabratus	1.16			
Hylurgops palliatus	43.02	29.79	13.33	9.52
Ips amitinus	27.91	44.68	26.67	46.03
Ips typographus	65.12	74.47	100.00	96.83
Isarthron fuscum	32.56	10.64		1.59
Monochamus sp.	25.58	14.89	46.67	26.98
Pissodes harcyniae	3.49			
Pissodes scabricollis	6.98			
Pityogenes chalcographus	79.07	89.36	93.33	88.89
Pityophthorus pityographus	8.14	10.64		1.59
Pogonocherus fasciculatus	1.16			
Polygraphus poligraphus	15.12	2.13		
Rhagium sp.	2.33			1.59
Xyloterus lineatus	10.47	12.77	6.67	
Total of windfall stems	86	47	15	63

Changes in the quality of windfalls in the course of the growing season became also evident in the degree of crown drying. In the spring aspect (VI), 81% windfalls showed green crowns and only in 6% trees, uniform and marked needle shedding occurred. In the summer aspect (IX), the majority of windfalls shows only partly live crown (81%) and only 7% windfalls showed green crown. Although the fauna of cambioxylophages of branches was relatively very manifold (13 species) as for the frequency of occurrence and the degree of attack it is possible to specify 9 species as sporadic. *P. chalcographus* showed generally the high frequency of occurrence on windfall branches in open areas as well as in the stand both in the spring (87.3 × 79.9%) and summer aspects (72.6 × 83.7%). *H. palliatus* which prefers the shaded environment of a stand to an open area in the spring aspect (51.7 × 36.1%) is not a typical species colonizing branches but it refers to a concomitant event when during the high degree of the attack of stem also phloem on large branches was colonized. *I. amitinus* proved similarly in case of more intense occurrence. *P. pityographus* showed the same occurrence in the open area both in the spring and summer aspect. *Cryphalus abietis* (Rtzb.) was found on windfalls in a stand only in the summer aspect.

Changes in the phloem quality of windfalls occurred throughout the growing season. In the spring aspect, there was increased homogenity and *I. typographus* showed a more marked shift in the development and attack on windfalls with die-back progressing from crown and live phloem in the lower part of the tree stem. The rate of phloem necrosis was a limiting factor for the repeated attack of windfalls by sister generations and the second generation of *I. typographus.* If *P. chalcographus* in the spring aspect did not respond more markedly to the phloem quality by the stem cover (20–35%), in the summer aspect differences were differentiated by the degree of phloem wilting (10–64%) and on dead windfalls up to a level of 55%. Balanced stem cover characterizes a species *P. pityographus* (3–7%) with the exception of dead trees with wilting phloem in the lower part of a stem. The stem cover by members of genera

Table 6. The windfall stem cover by cambioxylophages according to the position in an area with the various population density of *I. typographus*

Species/frequency	Outside outbreak (%)		Outbreak (%)	
	forest	free site	forest	free site
Cryphalus abietis	3.61			
Dryocoetes autographus	24.62	61.29	10.53	2.51
Hylastes ater	7.94			
Hylocoetes dermestoides	21.62			
Hylurgops glabratus	5.41			
Hylurgops palliatus	38.82	39.16	35.62	16.74
Ips amitinus	7.86	13.12	12.59	18.10
Ips typographus	38.39	45.54	66.67	60.85
Isarthron fuscum	19.37	15.28		6.67
Monochamus sp.	34.68	43.95	26.34	28.37
Pissodes harcyniae	18.39			
Pissodes scabricollis	16.58			
Pityogenes chalcographus	35.88	41.14	23.79	24.81
Pityophthorus pityographus	6.67	6.77		18.92
Pogonocherus fasciculatus	2.63			
Polygraphus poligraphus	28.49	34.62		
Rhagium sp.	4.76			5.71
Xyloterus lineatus	49.03	48.63	62.86	

Monochamus and *Isarthron* appears to be relatively independent and irregular.

Diameter at breast height (dbh) characterizes also the quality of a tree from the point of view of phloem thickness and the size of a windfall. In the group of 133 windfalls, dbh was specified by 13–67 cm. Determined frequency trends of the occurrence of particular species with changing dbh corresponded to ecological requirements of some species similarly as in standing trees. In *I. typographus*, the frequency of occurrence increased with the increasing dbh of windfalls. The species was noted even on windfalls with dbh < 30 cm (44%). Other categories were defined by dbh 31–46 cm (68–74%) and > 47cm (95–100%) (Table 7). *P. chalcographus* attacked stems of windfalls of all diameter categories. We noted a gradual and continual increase in the frequency of occurrence with the increasing diameter of a stem. *H. palliatus, I. fuscum, P. poligraphus* (Table 7) responded conversely. The stem cover decreased with the size of windfalls (*H. palliatus, P. chalcographus, Monochamus* sp., *Pissodes* sp.). *I. amitinus* preferred a medium category (31–38 cm) and *I. typographus* occupied the balanced part of the stem profile in all diameter categories under study (Table 8).

Fauna of the cambiophages of windfalls in the gradation area

Gradations of *I. typographus* in Forest District Ujsoly began in spruce stands in 1993 as a result of dry years and neglect of measures in forest protection. As for basic site conditions, the area does not differ from Forest District Ostravice. In November 2004, stands were damaged by a wind disaster (67,000 m^3). Compartment windbreaks were created and at the same time, particular windfalls occurred in stands.

Six of ten cambioxylophages were recorded in the spring aspect the highest frequency of them reached *I. typographus* (100%), *P. chalcographus* (92.7%) and *I. amitinus* (68.3%). *H. palliatus* noted insignificant position (19.5%). In the summer aspect, a persistent condition was proved in *I. typographus* (94.6%) and *P. chalcographus* (86.5%) and a marked decrease in *I. amitinus* (13.5%). *D. autographus* and members

Table 7. The occurrence frequency of cambioxylophages of the windfall stem in relation to dbh (in cm) in an area with the various population density of *I. typographus*

Species/frequency	Outside outbreak (%)						Outbreak (%)			
	13–21	22–30	31–38	39–46	47–54	55+	31–38	39–46	47–54	55–62
Cryphalus abietis		12.00								
Dryocoetes autographus	12.50		19.05	10.71		5.26		3.23	5.88	14.29
Hylastes ater			4.76							
Hylocoetes dermestoides				3.57						
Hylurgops palliatus	50.00	56.00	52.38	32.14	16.67	5.26	9.09	12.90	11.76	
Ips amitinus	12.50	44.00	28.57	32.14	50.00	31.58	36.36	51.61	47.06	14.29
Ips typographus		44.00	73.81	67.86	100.00	94.74	95.45	100.00	100.00	100.00
Isarthron fuscum	50.00	28.00	28.57	21.43	16.67	10.53				14.29
Monochamus sp.	12.50	32.00	28.57	10.71	25.00	10.53	36.36	35.48	23.53	14.29
Pissodes harcyniae	12.50		2.38	3.57						
Pissodes scabricollis			11.90		8.33					
Pityogenes chalcographus	62.50	72.00	76.19	89.29	100.00	94.74	95.45	90.32	88.24	85.71
Pityophthorus pityographus		8.00	2.38	17.86	8.33	15.79			5.88	
Pogonocherus fasciculatus						5.26				
Polygraphus poligraphus	50.00	28.00	4.76			5.26				
Rhagium sp.			4.76						5.88	
Xyloterus lineatus		12.00	19.05	14.29			4.55			
Total of windfall stems	8	25	42	28	12	19	22	31	17	7

of the genus *Monochamus* were ranked among important secondary species (Table 3).

No difference was determined in the attack of windfalls by *I. typographus* in a stand and in the open area (100 × 97%), *P. chalcographus* L. (93 × 89%) or *H. palliatus* (13 × 9.5%). *I. amitinus* preferred windfalls on released places (46 × 27%), members of the genus *Monochamus* responded the other way round (27 × 47%) (Table 5).

Intensity of the attack of windfalls showing the presence of the given species was unambiguously highest in *I. typographus* because the stem cover reached 60% at the 83% proportion of the heavy attack (spring aspect). In the consequential summer season, the stem cover remained preserved (65%) but the degree of attack was balanced (slight – 11%, increased – 24%, heavy – 30%). *P. chalcographus* colonized the same profile in the spring (22%) and summer (27%) aspect with the dominant proportion of heavy attack. In the spring season, *I. amitinus* corresponded with *P. chalcographus*, in the consequential stage decreased by half and also *H. palliatus* covered only one fifth of the stem profile. In the summer aspect, members of the genus *Monochamus* on windfalls were classified mainly in the slight degree of attack but the stem cover reached 27% (Table 4).

In the outbreak area, the behaviour of *I. typographus* was not affected by the position of windfalls. The stem cover (67 × 61%) and the distribution of degrees of attack were similar. A species *P. chalcographus* (24 × 25%) can be evaluated identically. *H. palliatus* and *D. autographus* showed partial preferences for shaded area in a stand (Table 6).

Changes in the foliage of windfalls occurred much more radically than in Forest District Ostravice. In the spring aspect, the decisive part of windfalls showed green crown (83%), however, in the summer aspect, we noted dead crowns in 67% windfalls and 14% crowns had dead tops. On branches, *P. chalcographus* (85–94%, heavy degree of attack) was accompanied by *I. amitinus*.

In the spring aspect, there were 56% living and 19.5% dead windfalls, in the summer aspect living windfalls did not occur. There were 42% dead windfalls and remaining ones occurred in the

Table 8. The windfall stem cover by cambioxylophages in relation to dbh (in cm) in an area with the various population density of *I. typographus*

Species/frequency	Outside outbreak (%)						Outbreak (%)			
	13–21	22–30	31–38	39–46	47–54	55+	31–38	39–46	47–54	55–62
Cryphalus abietis		3.61								
Dryocoetes autographus	4.35		36.19	16.50		10.53		3.03	10.53	11.11
Hylastes ater			7.94							
Hylocoetes dermestoides				21.62						
Hylurgops palliatus	63.33	35.70	42.60	33.54	11.54	12.82	35.62	13.21	23.75	
Ips amitinus	5.00	8.73	15.98	9.91	8.58	6.94	19.20	19.80	12.34	11.90
Ips typographus		37.50	34.67	48.91	37.96	46.78	69.76	63.26	57.76	48.79
Isarthron fuscum	9.89	9.60	21.22	21.74	35.62	14.47				6.67
Monochamus sp.	69.23	36.04	40.16	42.06	31.53	13.16	37.65	20.31	37.04	6.67
Pissodes harcyniae	40.00		18.18	5.88						
Pissodes scabricollis			14.81		24.32					
Pityogenes chalcographus	52.99	54.75	43.98	33.78	31.02	24.11	29.67	27.10	17.91	16.21
Pityophthorus pityographus		10.53	6.67	6.59	5.26	5.60			18.92	
Pogonocherus fasciculatus						2.63				
Polygraphus poligraphus	25.56	35.64	18.03			21.05				
Rhagium sp.			4.76						5.71	
Xyloterus lineatus		33.33	54.14	48.23			62.86			

various degree of dieback. In the spring aspect, *I. typographus* was in the lower degree of stem cover on living trees (56%). On windfalls with wilting and dead phloem where the development of the species was already finished, the stem cover reached 62–80%. In the summer aspect, the stem phloem was markedly differentiated and the degree of attack corresponded to the situation (50 to 82%). The high degree of diversity was demonstrated by windfalls with *P. chalcographus* (10–41%). It was rather difficult to specify the relationship between the occurrence of a bark beetle and the phloem structure quality. Attack of *I. amitinus* (14–27%) appears to be relatively homogeneous if we do not take into account dead trees with wilting phloem (55%).

dbh of windfalls (31–67 cm) was unambiguously available for *I. typographus* the frequency of which was highest (95–100%) in all categories. The high frequency of *P. chalcographus* with increasing dbh gradually receded (95–86%) the fall being significant also for the genus of *Monochamus.* Non-uniform distribution showed *I. amitinus* (Table 7). Decreased stem cover in the gradation area was noted in *P. chalcographus.* In *I. typographus*, the stem cover decreased with dbh (Table 8).

DISCUSSION

Frequency and extent of windbreak situations cannot be predicted. Windfalls occur every year and, therefore, it is inevitable to deal with this type of salvage felling not only as an area for reproduction of insect pests but also for use in checking cambioxylophagous species and control at localities with the low proportion of windfalls. At the same time, it is necessary to specify the response of cambioxylophages under conditions of the high concentration of windfalls at the various population density of *I. typographus* (Martikainen et al. 1999). This variance became evident in the different degree of colonization of windfalls and the cover and intensity of attack because the occurrence frequency was higher by 24.4% (100 × 75.6%) in *I. typographus* in the gradation area in the spring aspect and in the summer aspect by 37.7% (94.6 × 56.9%). Higher invasion by 34.2% (68.3 × 34.1%) was noted in *I. amitinus* in the gradation area in the spring aspect. In *P. chalcographus*, conformity in the spring season (92.7 × 95.1%) changed during the summer aspect in a decrease in the occurrence frequency outside the gradation area (86.5 × 62.8%).

The occurrence of secondary species related to decaying wood and not attacking living trees was differentiated. In the summer aspect in stands out of the species gradation (Forest District Ostravice), the frequency of the genus *Monochamus* was 10% lower while the occurrence frequency of *I. fuscum* (+ 60%) and *H. palliatus* (+ 47%) increased.

The decreased species diversity of cambioxylophages in the gradation area on windfalls conforms with deviations in the diversity of cambioxylophages in standing trees under these conditions (Kula et al. 2005a,b, 2006). Deviations were also proved between the fauna of standing trees and windfalls from the viewpoint of stem cover (e.g. *X. lineatus*, *H. palliatus*, *Monochamus*) (Kula, Ząbecki 2006b).

Differences between the fauna of windfalls of a gradation area and an area with the basic level of *I. typographus* result even more distinctly from the comparison of attacked sections of groups including all analyzed windfalls regardless of the presence of particular members. The competitive environment between species, rate of the stem colonization by early spring species (*H. palliatus*) before *I. typographus* can limit its available area similarly as it was under conditions of Forest District Ostravice. The occurrence of *P. chalcographus* on stems in the gradation area was restricted by *I. typographus.* Thus, some findings obtained by Økland and Bjornstad (2003) were corroborated. In the area under study, windfalls did not differ in the mean extent of interconnection of roots with soil. Differences consisted in the water table which was higher at studied sites of Forest District Ostravice.

Site conditions given by the position of a windfall in the stand shade or half-shade and on an open area affect aggressive species less markedly than species searching for moist phloem (*H. palliatus, D. autographus*) concentrating on windfalls in a stand often lying on the soil surface or under the layer of branches. Members of the genus *Monochamus* attacked windfalls throughout the stem profile at insolated, released locations particularly on windfalls with a decreased attack by *I. typographus*.

Similarly as in standing trees (Kula, Ząbecki 2000a; Göthlin et al. 2000; Butovitsch 1938, 1971; Weslien, Regnander 1990), dbh is a limiting factor for the structure of cambioxylophagous fauna also in windfalls. Preferences in colonizing larger dimensions by *I. typographus* was similar in both areas under study.

The gradation area differed by the phloem quality in the spring aspect (70% living sections) (Kula, Ząbecki 2006a) though the period of origin of windfalls agreed with Forest District Ostravice (100% living sections). The cause of the occurrence of dead and wilting phloem on windfalls (Forest District Ujsoly) as against exclusively living phloem in windfalls in Forest District Ostravice could consist in the more intensive attack and feeding of *I. typographus*, smaller number of windfalls at waterlogged localities, large open areas and different slope orientation.

In the course of the growing season, the degree of phloem necrosis generally increased. In both studied areas, the same extent of living sections (18–19%) as well as wilting sections occurred (10–11%). It follows that one third of the windfall profile (usually the lower part of a stem) is still available to the development of cambiophages and in the second year after the origin of a windfall, it is possible to expect invasion and development of *I. typographus* (Kula, Ząbecki 2006b). Eriksson et al. (2005) mention repeated colonization of windfalls in the second year, namely of 50%, but also only 12% of the initial extent. Göthlin et al. (2000) decrease attractiveness in the second year by 17%. Butovitsch (1971), Annila and Petäistö (1978) admit that *I. typographus* is able to use the material of windfalls during the second year after the autumnal damage to the stand.

It means that windfalls represent a long-term risk for the reproduction of *I. typographus*. An aspect of the rate of concentration of windfalls is also discussed because at the local small number of trees a deviation in the risk of damage did not become evident (Hengren et al. 2003). However, it is generally known that extensive areas with windfalls and snowfalls are subsequently threatened by gradations of *I. typographus* (Ravn 1985; Worrell 1983; Gregoire 1988; Schröder, Lindelöw 2002) which was also confirmed by the high spring population of *I. typographus* in 2006 in the Tatra Mts. after a wind disaster in November 2004. There is the high degree of correlation between the population density dynamics of *I. typographus* (Økland, Bjorustad 2003) and the number of attacked and killed standing trees (Økland, Berryman 2004; Gilbert et al. 2005). Therefore, it is not suitable to leave unprocessed felled wood in commercial forests although a critique can appear that the development of dead wood fauna is not possible as it is required by some authors (Esseen et al. 1977; Siitonen 2001).

A lying tree (windfall), living foliaged crown and living phloem and interconnection of roots with soil create quite different conditions when invasion of cambiophages occurs as compared with a standing tree characterized by the various length of dieback according to occurring stresses (from acute – lightning to chronic – air pollution,

competition, fungi etc.) or barked trap trees. The synusia of cambioxylophages was generally described by Pfeffer (1955), in relation to vegetation zones by Zumr (1984), in relation to the presence of fungal pathogens, social position of a tree, forest type group, lightning injury etc. by Kula and Ząbecki (1997a,b, 1999a,b, 2000a,b). On living windfalls particularly in the spring aspect, we noted partial departures from general regularities probably due to the progress of phloem necrosis. The culmination level of an attack by *I. typographus* occurred higher in the place of crowns at the expense of *I. amitinus* which used large branches under conditions of the shortage of area on a stem (Kula et al. 2006). Continual increase of the occurrence of *I. typographus* to the stage of culmination in the lower half of a crown (spring) and the centre of the crown (summer) (Kula, Ząbecki 2006b). The uniform distribution of *H. palliatus* in the stem profile or the retreat of *I. fuscum* from the stem foot to its centre appears to be characteristic. The microclimate of a lying tree which is often in contact with soil affects moisture conditions of phloem inducing changes in its quality and attractiveness.

CONCLUSION

The fauna of cambioxylophages of spruce windfalls in a gradation area is characterized by decreased species diversity as compared with an area with the basic state of *I. typographus*.

The occurrence frequency and the species spectrum of cambioxylophages are differentiated in the course of the growing season (spring and summer aspect) by the appearance of secondary species not threatening living trees (*Monochamus, Isarthron, Dryocoetes*).

A change in the phloem quality during the first growing season after uprooting the tree was faster in the gradation area during the spring season. At the end of the growing season living and wilting phloem occurred on one third of the available area of windfalls thereby conditions were created for the invasion and development of cambioxylophages also in the second growing season after the windbreak.

The increasing dbh of windfalls positively affected colonization by *I. typographus*; the response of *H. palliatus, I. fuscum, P. poligraphus* was opposite.

Windfalls in the gradation area show 20–40% higher attack by *I. typographus* at the balanced proportion of *P. chalcographus* which is characterized by a narrower stem niche in the gradation area. In an area with the basic state of *I. typographus*, windfalls were intensively occupied by *H. palliatus, I. fuscus* and *Monochamus* sp.

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Smrkové vývraty a kambioxylofágní fauna v území se základním a gradačním stavem lýkožrouta smrkového

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ABSTRAKT: Na smrkových vývratech vzniklých v podzimním a zimním období byla hodnocena synuzie kambioxylofágů v profilu celého kmene a větví koruny podle druhového spektra, pokryvnosti stromu a intenzity napadení. Fauna vývratů v území se základním stavem lýkožrouta smrkového a v gradačním území se lišila druhovou diverzitou. V gradačním území byla o 20–40 % vyšší četnost výskytu *Ips typographus* (L.). *Pityogenes chalcographus* (L.) měl sníženou pokryvnost kmene v gradačním území. V území se základním stavem lýkožrouta smrkového byly vývraty intenzivně osidlovány sekundárními druhy *Hylurgops palliatus* (Gyll.), *Isarthron fuscum* (Fabr.) a *Monochamus* sp. Narůstající výčetní tloušťkou vývratů bylo pozitivně ovlivněno osídlení kmene lýkožroutem smrkovým, opačně reagoval *H. palliatus, I. fuscum, Polygraphus poligraphus* (L.).

Klíčová slova: smrk ztepilý; Beskydy; vývraty; kambioxylofágové; *Ips typographus*; *Pityogenes chalcographus*; *Ips amitinus*; *Polygraphus poligraphus*

Smrkové vývraty, které vznikají každoročně v různém rozsahu, umožňují namnožení kambiofágů a následné ohrožení živých stromů. Nezpracované vývraty mohou být nalétány nejen v průběhu celého vegetačního období, ale i v navazujícím roce. Míra napadení polomové hmoty závisí na hustotě populace lýkožrouta smrkového před vznikem polomu, na regionální a lokální heterogenitě stanovištních podmínek.

Cílem práce je doplnit chybějící údaje o kambioxylofágní fauně vývratů, jejím zastoupení v profilu kmene a větví koruny, postupu nalétání na smrkové vývraty v oblastech se základním a gradačním stavem lýkožrouta smrkového.

V území Beskyd (LS Ostravice, LS Ujsoly) byly v navazujícím jarním (VI.) a letním (IX.) aspektu v r. 2003 a 2005 analyzovány vývraty (211), které vznikly jednorázově v říjnu r. 2002 a v listopadu 2004.

Četnost výskytu a pokryvnost kmene a větví jednotlivými druhy kambioxylofágní fauny byla stanovena po odkornění kmene a větví v celém profilu vývratu, kdy v navazujících metrových sekcích byl určen druh kambioxylofága, stadium vývoje a stupeň napadení odděleně pro gradační území a území se základním stavem (Kula, Ząbecki 1996).

LS Ostravice – hodnocené smrkové porosty jsou součástí monitorovací sítě povodí nádrže Šance. Přes výskyt polomů (tab. 1) zůstávají kambioxylofágové v této oblasti dlouhodobě v základním stavu a v uplynulých padesáti letech se zde nevyskytla kůrovcová gradace.

LS Ujsoly – gradační oblast lýkožrouta smrkového Beskidu Żywieckiego je charakterizována snižující se stabilitou smrkových porostů, v nichž se nahodilá kůrovcová těžba podílí 51–72 % (tab. 2). V letech 2001 až 2004 dosáhla nahodilá těžba postupně 25 až 84 tisíc m^3.

Smrkové vývraty vzniklé působením abiotických škodlivých činitelů (sníh v říjnu 2002, vítr v listopadu 2004) se staly disponibilním prostorem pro vývoj kambioxylofágní fauny v navazujícím vegetačním období. V LS Ostravice bylo analyzováno v jarním a letním období 133 vývratů (82 + 51) a v LS Ujsoly 78 vývratů (41 + 37).

Z 18 druhů kambioxylofágů registrovaných v mimogradačním území na vývratech bylo v jarním aspektu potvrzeno 10 druhů, zatímco v letním aspektu 18 druhů. Nejvyšší četnosti výskytu v jarním období dosáhl *Pityogenes chalcographus* (L.) (95,1 %), *Ips typographus* (L.) (75,6 %) (tab. 3). V letním aspektu se z hospodářsky významných druhů profiloval *P. chalcographus* (62,7 %), *I. typographus* (56,9 %), *I. amitinus* (33.3 %) a *Polygraphus poligraphus* (L.) (27,5 %). Souběžně bylo zaznamenáno vysoké zastoupení druhů sekundárních [*Isarthron fuscum* (Fabr.) 62,8 %, *Monochamus* sp. 54,9 %, *Hylurgops palliatus* (Gyll.) 47,1 %, *Dryocoetes autographus* (Ratz.) 23,5 %] (tab. 3). Pokryvnost kmene vývratu se u některých druhů odchýlila od běžných ekologických nároků. Druhy *I. typographus* a *P. chalcographus* se shodují v celkové pokryvnosti profilu vývratu, která byla v jarním aspektu nižší než v letním (38,8–46,9 % a 34,4–47,8 %) (tab. 4).

Mikroklima volné plochy bylo mírně preferováno především hospodářsky významnými kambiofágy smrku (*I. typographus, P. chalcographus*) a průkazně

druhem *Ips amitinus*. Zvýšenou četnost výskytu na vývratech v porostu lze prokázat u druhů *D. autographus, I. fuscum, Monochamus* sp., *H. palliatus* a *P. poligraphus* a *Pissodes* sp. (tab. 5). *P. poligraphus* obsadil delší úsek kmene na vývratech volné plochy, podobně i zástupci rodu *Monochamus.* Rozdíl v profilu obsazené niky kmene v podmínkách porostu a volné plochy nebyl zaznamenán u *I. typographus, I. amitinus, P. chalcographus* ani u druhů časněji aktivujících (*H. palliatus, I. fuscum, X. lineatus*) (tab. 6).

U lýkožrouta *I. typographus* se zvyšovala četnost výskytu s narůstající výčetní tloušťkou vývratu (tab. 7). *P. chalcographus* atakoval kmeny vývratů všech tloušťkových kategorií, přičemž jsme zaznamenali pozvolný a kontinuální nárůst četnosti výskytu se zvyšující se tloušťkou kmene. Opačně reagoval *H. palliatus, I. fuscum, P. poligraphus* (tab. 7).

Z deseti kambioxylofágů bylo v jarním aspektu gradační oblasti zachyceno šest, z nichž nejvyšší četnost výskytu dosáhl *I. typographus* (100 %), *P. chalcographus* (92,7 %) a *I. amitinus* (68,3 %) (tab. 3).

Pokryvnost vývratů byla jednoznačně nejvyšší u lýkožrouta smrkového, neboť dosáhla 60 % při 83% podílu silného stupně napadení (jarní aspekt). V navazujícím letním období zůstala pokryvnost kmene zachována (65 %). *P. chalcographus* osídlil shodný profil v jarním (22 %) i letním aspektu (27 %) s dominantním podílem silného stupně napadení. *I. amitinus* v jarním období byl ve shodě s lýkožroutem lesklým, v navazující etapě ustoupil na polovinu a rovněž *H. palliatus* pokrýval pouze pětinu profilu kmene. Zástupci r. *Monochamus* na vývratech v letním aspektu byli klasifikováni převážně ve slabém stupni napadení, ale pokryvnost kmene dosahovala 27 % (tab. 4).

Výčetní tloušťka vývratů (31–67 cm) byla jednoznačně disponibilní pro lýkožrouta smrkového, jehož četnost výskytu byla ve všech stanovených kategoriích nejvyšší (95–100 %). Vysoká četnost druhu *P. chalcographus* s narůstající výčetní tloušťkou pozvolna ustupovala (95–86 %), pokles byl průkazný i pro r. *Monochamus*. Nejednotné rozložení vykázal *I. amitinus* (tab. 7).

Fauna kambioxylofágů smrkových vývratů v gradačním území se vyznačuje sníženou druhovou diverzitou. Stoupající výčetní tloušťkou vývratů bylo pozitivně ovlivněno osídlení lýkožroutem smrkovým, opačně reagoval *H. palliatus, I. fuscum, P. poligraphus.* Vývraty v gradačním území vykazují o 20–40 % vyšší napadení lýkožroutem smrkovým při vyrovnaném zastoupení druhu *P. chalcographus,* který se v gradačním území vyznačuje užší kmenovou nikou. V území se základním stavem lýkožrouta smrkového byly vývraty intenzivně osidlovány druhy *H. palliatus, I. fuscum, Monochamus.*

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