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STUDIES OF THE BIOLOGY, ECOLOGY, PHENOLOGY, AND ECONOMIC IMPORTANCE OF *IPS AMITINUS* (EICHH.) (*COL.*, *SCOLYTIDAE*) IN EXPERIMENTAL FORESTS OF KRYNICA (BESKID SĄDECKI, SOUTHERN POLAND)

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Abstract. From among 392 *Picea abies* trees growing at the height of 700-800 m above the sea level in the Beskid Sądecki mountain range of the Carpathians (49°35' N, 19°31' E, southern Poland), infested by cambio- and xylophagous insects, 110 (28.1%) were also attacked by *Ips amitinus* (Eichh.). This bark beetle infested most willingly the weakened standing trees of age classes III-V (i.e. 41-100 years old) as well as trees recently overthrown, broken, and felled. It was most abundant in the middle part of the stem where the bark was 2-3 mm thick, infesting 38.4% of its length on the average. On a single tree *I. amitinus* always occurred in associations of cambio- and xylophagous insects composed of 2-12 species. There was only one generation of *I. amitinus* in the year, composed of the main brood and the sister brood. Its life-cycle is presented against a background of phenology of forest plants. There were three larval instars. Dimensions of all developmental stages and individual components of brood galleries are also given. *I. amitinus* plays an important role in killing weakened *P. abies* trees. The trap trees commonly used against *Ips typographus* turned out to be very effective also in the control of *I. amitinus*.

Key words: *Ips amitinus*, biology, ecology, phenology, life-cycle, economic importance

INTRODUCTION

Ips amitinus (Eichh.), a species trophically associated with *Picea abies* (L.) Karst., occurs in countries of central Europe, i.e. Poland, Slovakia, the Czech Republic, Hungary, Rumania, Austria, and Germany as well as in the Balkans, northern Italy, Switzerland, western France, Spain, Belgium, Holland, southwestern Ukraine, central Russia, Lithuania, and Latvia [Pavlovskij 1955, Pfeffer 1955]. In the 20th century it extended its range northwards, and in the 1930s it appeared in northern Estonia, while in the early 1950s first specimens of this species were found in Finland [Annila and Nuorteva 1976,

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Biermann and Thalenhorst 1977]. Afterwards it reached Sweden [Grodzki 1998]. In Poland *I. amitinus* is one of the most common secondary pests of *P. abies* [Michalski and Mazur 1999] occurring more abundantly in the southwestern part of Poland, including mountains, than in the northeastern part [Bilczyński 1966]. This bark beetle belongs to a group of physiological secondary insect pests of *P. abies* in which *Ips typographus* (L.) and *Pityogenes chalcographus* (L.) play a leading role. The activity of these three species, together with other less abundant cambio- and xylophagous insects, may result in decline of whole stands.

In experimental forests of Krynica *I. amitinus* is a commonly occurring species, and it is one of cambio- and xylophagous insects reaching on *P. abies* the highest values of such indexes as dominance, frequency, constancy, and density of occurrence [Starzyk et al. 1987]. Taking this into consideration as well as the fact that there are many gaps in the knowledge concerning its biology and ecology, partly due to its similarity and co-occurrence with *Ips typographus* and accepting certain data to be true for both these species, the research was undertaken in Krynica forests with the aim to determine the biology, ecology, life-cycle, phenology, and economic importance of *Ips amitinus* in mountain forests. The results of this research are presented in this paper.

MATERIAL AND METHODS

Field studies were carried out in *Picea abies-Abies alba* stands with a small admixture of *Alnus incana* (L.) Moench, *Larix decidua* Mill, *Acer pseudoplatanus* L., *Fraxinus excelsior* L., *Fagus sylvatica* L., and *Betula verrucosa* Ehrh., growing at 700-800 m above the sea level. These stands were situated in Kopciowa forest division of Krynica experimental forests owned by the Agricultural University of Cracow (49°25’ N, 19°31’ E, Beskid Sądecki mountain range of the Carpathians, southern Poland).

Beskid Sądecki is the Carpathian range of rather low mountains with the highest summit of Radziejowa (1262 m above the sea level). The climate of Krynica surroundings is a typical climate of mountain valleys with mean annual temperature of 5.5°C and mean annual precipitation of 850 mm. This area belongs to the region of short summer, long winter, and a relatively short growing season (150-180 days). Prevailing northwestern and southern winds often cause damages in the forest. Also considerable damages are caused by snow formations on the branches of trees.

The mountain forest is the main forest site type (90% of area) in Krynica forests with the dominant phytosociological association *Dentario glandulosae-Fagetum.* The following tree species dominate in stands: *Abies alba* (36%), *Picea abies* (29%), and *Fagus sylvatica* (13%) [Plan... 1998]. Many *P. abies* stands have been established on unsuitable sites which in consequence led to the disappearance of older age classes of trees and the intensification of disease processes in stands of middle age classes. These stands have become the area of abundant occurrence of *Armillaria* spp. and *Fomes annosus* Fr. Weakened *P. abies* trees are readily attacked by secondary insect pests such as *Ips typographus* (L.), *Ips amitinus* (Eichh.), *Polygraphus poligraphus* (L.), *Pityogenes chalcographus* (L.), *Pityophthorus pityographus* (Ratz.), *Cryphalus abietis* (Ratz.), *Hylurgops palliatus* (Gyll.), *Xyloterus lineatus* (Ol.), *Pissodes harcyniae* (Herbst), *Tetropium* spp., *Monochamus* spp., and species from the family *Siricidae.* So far, the greatest role was played by *I. typographus*, but with decline of stands of older age classes the role of the hitherto less important species, including *I. amitinus*, is increasing. *I. amitinus* may attack trees which are not even 20 years old (age class Ib). In stands of age class II (21-40 years) it is more abundant than *I. typographus. P. chalcographus* in stands of age classes I (1-20 years) and IIa (21-30 years) kills weakened trees alone. *P. poligraphus* attacks *P. abies* stands of almost all age classes. *P. pityographus* often kills tops of *P. abies* trees weakened by *Armillaria* root rot thus initiating their dying process [Kisielowski and Tuteja 1980].

The main material of this study consisted of results of the detailed qualitative and quantitative entomological analyses of *P. abies* breeding material of cambio- and xylophagous insects, including *I. amitinus*, carried out in the forest by the staff of the Department of Forest Entomology, Agricultural University of Cracow during the period between 1980 and 1998. These analyses were conducted according to the method described by Starzyk [1987] and consisted of examination of entire tree stems after complete removal of the bark. The brood galleries of cambio- and xylophagous insects were counted in stem sections 1 m long. The examined trees included standing weakened, dying, and dead trees (they were felled just before the analysis) as well as trees broken, overthrown, or felled at an earlier date. In total, 392 *P. abies* trees were analysed, including 110 trees also infested by *I. amitinus.* On the basis of information concerning trees infested by *I. amitinus*, in respect of their age, dbh, height, length and width of the crown, quality of the stem, position in a vertical stand structure, conditions of shading, and causes of their weakening, confronted with characteristics of all examined *P. abies* trees, and also on the basis of information concerning stem sections colonized by *I. amitinus*, in respect of their number, position on the stem, diameter, bark thickness, and the degree of decomposition of phloem and xylem, it was possible to determine the trophic and ecological requirements of this bark beetle. The quantitative results of entomological analyses of trees infested by *I. amitinus* permitted to compute the ecological indexes of dominance and constancy, as well as the Agrell's index of species coexistence, [Kasprzak and Niedbała 1981] for all species of cambio- and xylophagous insects present on these trees. This in turn permitted to determine the position of *I. amitinus* in the structure of ecological associations (species occurring on trees of a given 20-year age class) and microenvironmental trophic communities (species colonizing individual trees) of cambio- and xylophagous insects. On the basis of this information the economic importance of *I. amitinus* in the investigated area was determined.

Insect specimens and brood galleries collected in the field were used to determine in the laboratory the body dimensions of individual developmental stages of *I. amitinus* as well as dimensions of individual elements of its brood galleries. In each case mean dimensions were computed on the basis of at least 50 measurements.

Between 1991 and 1998 field observations on the life-cycle of *I. amitinus* were made. The appearance of individual stages of its development was referred to phenology of forest herbaceous plants, trees, and shrubs. In the laboratory the width of the head capsule of larvae of different sizes was measured in order to determine the number of larval instars of *I. amitinus*, similarly as it was done by Lekander [1986] for several bark beetle species.

In early June of 1999 the entomological analysis of 15 trap trees prepared against *I. typographus* was carried out in order to determine their efficiency in respect of *I. amitinus.*

During the entire study period occasional observations on *I. amitinus* were carried out in the entire area of the Krynica experimental forests and in neighbouring forests.

RESULTS

Trophic and ecological requirements of *Ips amitinus*

During the entire study period *Ips amitinus* was found only on *Picea abies*. It was not found on *Abies alba* in spite of the fact that over 690 trees of this species were also analysed under the same research project concerning cambio- and xylophagous insects of these two coniferous tree species.

From among 392 *P. abies* trees 110 (28.1%) were infested by *I. amitionus*. This bark beetle occurred on standing much weakened and dying trees (sometimes on their heavier branches) as well as on trees felled, broken, and overthrown during the last winter and early spring. It was also present on heavier logging residuals.

Out of the investigated age classes (II-V) *I. amitinus* least willingly infested trees of age class II (21-40 years). Only 13.8% of trees of this age class were attacked by this bark beetle. The infestation of trees of age classes III (41-60 years), IV (61-80 years), and V (81-100 years) was similar i.e. 51.4%, 54.2%, and 53.3% respectively. In some measure *I. amitinus* preferred trees 21-30 cm in dbh infesting 40.9% of such trees. The infestation of trees of dbh classes 11-20 cm and 31-40 cm was 27.7% and 31.0% respectively.

The height of the analysed *P. abies* trees ranged from 5.1 to 30.0 m. *I. amitinus* most readily attacked trees above 15 m in height. It infested 42.5% of trees in height class 15.1-20.0 m, 49.0% of trees in height class 20.1-25.0 m, and 55.5% of trees in height class 25.1-30.0 m. Trees in height class 10.1-15.0 m were less willingly infested (18.6%), while trees of height below 10 m were not infested at all. Similar preferences were observed in the case of stand layers. *I. amitinus* decidedly preferred trees belonging to the upper stand layer (38.1% of trees infested). The infestation of trees in the middle stand layer was much lower (17.6%), while trees in the lower layer were attacked sporadically.

I. amitinus preferred trees little shaded or without a direct shading (26.5% and 26.4% respectively). The infestation of trees strongly shaded was considerably lower (15.0%). This species preferred trees with living crowns longer than 10 m. It infested 42.3% of trees with crowns 10.1-15.0 m long, and 64.7% of trees with crowns longer than 15 m. Trees having crowns shorter than 10 m were infested only in 8.6%. This bark beetle preferred trees with crowns wider than 4 m infesting 47.8% of such trees, while trees having crowns narrower than 4 m were infested in only 24.6%.

I. amitinus readily infested trees broken or overturned by wind and snow as well as trees felled some time ago. It infested 53.3% of trees of this category. Also standing dying trees, attacked earlier by *Armillaria* root rot, were willingly infested by this bark beetle (36.9%). On the other hand, suppressed trees were infested only sporadically (6.4%).

Taking all trees attacked by *I. amitinus* into consideration it was found that on the average 38.4% of their stem's length was colonized by this species. In the case of 35.2% of trees *I. amitinus* colonized more than a half of the stem's length. On trees of age class II this bark beetle was most abundant in the middle part of the stem (40.8% of brood galleries). It was, however, also quite numerous in the lower (28.0%) and upper (31.2%) parts. On trees of age class III over a half (56.8%) of galleries were situated in the upper part of the stem, considerably less (39.5%) in the middle part, and only 3.7% in the lower part. In the case of trees of age classes IV and V *I. amitinus* colonized only the middle (34.3% and 12.5% respectively) and upper (65.7% and 87.5%) parts of the stem.

Brood galleries of *I. amitinus* were found in 1-m stem sections 2-27 cm in diameter, but sections 8-15 cm in diameter were most frequently colonized by this species. It preferred sections with the bark 2-3 mm thick. *I. amitinus* colonized 67.2% of the total number of sections with the 2-mm bark, and 55.3% of the total number of sections with the 3-mm bark. However, often galleries of *I. amitinus* were found in sections with the 1-mm bark (39.4%), and less frequently in sections with the 4-mm bark (14.5%). In sections with the bark thicker than 4mm *I. amitinus* was very seldom present.

Coexistence of *Ips amitinus* with other species of cambio- and xylophagous insects

On all 110 trees infested by *I. amitinus* this species was accompanied by other species of cambio- and xylophagous insects. Values of the constancy index C, given in Tables 1-4, reflect the strength of these associations. In total, besides *I. amitinus*, 22 other species of cambio- and xylophagous insects were found on trees infested by this bark beetle. The constancy of occurrence of *I. typographus* on trees infested by *I. amitinus* increased with increase of tree age from C = 50.0% for trees of age class II to C = 100.0% for trees of age class V. Often, besides *I. typographus*, such species as *P. chalcographus*, *P. pityographus*, and *P. poligraphus* were occurring on trees of age classes II and III, while on trees of age classes IV and V also *Tetropium castaneum* was present. In all these cases the value of the index C was above 50% (Tables 1-4).

In respect of the number of brood galleries in the ecological community on trees of age class II *P. pityographus* was the dominant species (D = 33.36%), on trees of age class III *I. typographus* D = 29.56%, on trees of age class IV *P. poligraphus* (D = 58.04%), and on trees of age class V again *I. typographus* was decidedly the dominant species (D = 77.1%). The dominance index D for *I. amitinus* decreased from about 12% in the communities on trees of age classes II and III to about 5% on trees of age classes IV and V (Tables 1-4).

Almost on each analyzed *P. abies* tree the species composition of the microenvironmental-trophic association of cambio- and xylophagous insects was somewhat different. These associations were composed of 2-12 species. In associations on trees of age class II *P. pityographus* most often played the role of the superdominant or eudominant species. Beginning with trees of age class III this role was played by *I. typographus* (Tables 1-4).

Taking into account all distinguished associations *I. amitinus* was 8 times a superdominant species, but only in associations on trees of age classes II and III, 35 times an eudominant species, 18 times a dominant species, 16 times a subdominant species, 6 times a recedent species, and 11 times a subrecedent species (Tables 1-4).

Values of the index of species coexistence (Ag) in the same 1-m stem section showed that brood galleries of *I. amitinus* on stems of *P. abies* trees of all investigated age classes most often were situated in a direct neighborhood of galleries of *P. chalcographus* (Tables 1-4).

Table 1. Ecological community and microenvironmental-trophic associations of cambio- and xylophagous insects including *Ips amitinus* on *Picea abies* of age class II (21-40 years)

Tabela 1. Zgrupowanie ekologiczne i zespoły mikrośrodowiskowo-troficzne owadów kambio- i ksylofagicznych z udziałem *Ips amitinus* na *Picea abies* II klasy wieku (21-40 lat)

Community – Zgrupowanie						Associations – Zespoły									
Species – Gatunek	N	C	n	D	Ag										
Ips amitinus (Eichh.)	34	100.0	2 459	11.63	–	D3	D6	D4	D6	D5	D3	D3	D5	D4	D5
Pityophthorus pityographus (Ratz.)	29	85.3	7 055	33.36	0.29	D6		D6	D6	D4	D5	D6	D5	D3	D5
Pityogenes chalcographus (L.)	19	55.9	3 839	18.15	0.44		D6				D6		D5		
Polygraphus poligraphus (L.)	18	52.9	2 232	10.56	0.22			D3		D5			D5		
Ips typographus (L.)	17	50.0	2 381	11.26	0.29		D4			D6	D6		D6	D6	D6
Hylurgops palliatus (Gyll.)	15	44.1	1 177	5.56	0.16				D3			D3		D5	D2
Dryocoetes autographus (Ratz.)	12	35.3	999	4.72	0.11										
Cryphalus abietis (Ratz.)	9	26.5	59	0.28	0.12										
Tetropium castaneum (L.)	9	26.5	91	0.43	0.04										D4
Xyloterus lineatus (Ol.)	7	20.6	295	1.39	0.12									D5	
Molorchus minor (L.)	7	20.6	181	0.86	0.16										
Rhagium inquisitor (L.)	7	20.6	49	0.23	0.05										
Pissodes harcyniae (Herbst)	5	14.7	15	0.07	0.07				D3						
Xylechinus pilosus (Knoch.)	4	11.8	153	0.72	0.03										
Pityogenes quadridens (Hrtg.)	4	11.8	42	0.20	0.06							D1			
Urocerus gigas (L.)	3	8.8	61	0.29	0.01										
Monochamus sutor (L.)	2	5.9	24	0.11	0.07										
Pityogenes bidentatus (Hrbst.)	2	5.9	16	0.07	0.01										
Pogonocherus fasciculatus (Deg.)	2	5.9	5	0.02	0.01										
Monochamus sartor (Fabr.)	1	2.9	10	0.05	0.08										
Sirex juvencus (L.)	1	2.9	7	0.03	0.23										
Carilia virginea (L.)	1	2.9	1	0.01	0.01										

Table 1 – cont.

Species – Gatunek	Associations – Zespoły																							
Ips amitinus (Eichh.)	D4	D1	D4	D2	D5	D3	D5	D4	D5	D1	D3	D5	D4	D1	D5	D5	D5	D1	D3	D3	D1	D2	D4	D6
Pityophthorus pityographus (Ratz.)	D6	D6	D6	D2	D5	D6	D1	D5	D5	D6		D5	D6	D6	D6	D5			D4	D6	D5		D6	D5
Pityogenes chalcographus (L.)	D3		D6	D6			D5	D5	D6	D3			D4		D1	D5	D5	D6	D6	D3		D5	D5	
Polygraphus poligraphus (L.)					D5	D4	D6	D5	D6			D5		D5		D3	D2	D2	D6	D2		D3	D3	D5
Ips typographus (L.)			D3		D6		D5	D5			D6		D5		D5		D6	D6	D3	D1				
Hylurgops palliatus (Gyll.)		D3			D1	D2					D1	D6		D5		D4		D1		D6	D4			D4
Dryocoetes autographus (Ratz.)	D5			D5			D4			D6	D2	D1		D2				D2			D6	D6	D6	D4
Cryphalus abietis (Ratz.)										D1		D1	D1				D1	D2			D3	D1	D3	D2
Tetropium castaneum (L.)	D3				D4				D1						D1		D1			D1		D3	D2	
Xyloterus lineatus (Ol)													D1	D2				D2			D5	D5	D1	
Molorchus minor (L.)						D1							D2	D1		D5			D1				D1	D2
Rhagium inquisitor (L.)											D1				D1	D2	D1		D1				D1	D3
Pissodes harcyniae (Herbst)								D1									D2				D1	D1		
Xylechinus pilosus (Knoch.)		D1				D5															D2			
Pityogenes quadridens (Hrtg.)		D3							D1												D1			D1
Urocerus gigas (L.)												D4				D2				D2				
Monochamus sutor (L.)										D3												D3		
Pityogenes bidentatus (Hrbst.)			D1																D3					
Pogonocherus fasciculatus (Fabr.)				D1							D1													
Monochamus sartor (Fabr.)															D2									
Sirex juvencus (L.)																								D2
Carilia virginea (L.)																				D1				

N – number of infested trees, n – number of brood galleries, Ag – index of coexistence of *I. amitinus* with other insect species in trunk sections one metre long, C – constancy (%), D – dominance: D6 – superdominants (> 30.0%), D5 – eudominants (10.1-30.0%), D4 – dominants (5.1-10.0%), D3 – subdominants (2.1-5.0%), D2 – recedents (1.1-2.0%), D1 – subrecedents (≤ 1.0%).

N – liczba zasiedlonych drzew, n – liczba żerowisk owadów, Ag – wskaźnik współwystępowania *I. amitinus* z innymi gatunkami owadów w jednometrowych sekcjach strzały, C – stałość występowania (%), D – dominacja: D6 – superdominanty (> 30,0%), D5 – eudominanty (10,1-30,0%), D4 – dominanty (5,1-10,0%), D3 – subdominanty (2,1-5,0%), D2 – recedenty (1,1-2,0%), D1 – subrecedenty (≤ 1,0%).

Table 2. Ecological community and microenvironmental-trophic associations of cambio- and xylophagpous insects including *Ips amitinus* on *Picea abies* of age class III (41-60 years)

Tabela 2. Zgrupowanie ekologiczne i zespoły mikrośrodowiskowo-troficzne owadów kambio- i ksylofagicznych z udziałem *Ips amitinus* na *Picea abies* III klasy wieku (41-60 lat)

Community – Zgrupowanie						Associations – Zespoły																			
Species – Gatunek	N	C	n	D	Ag																				
Ips amitinus (Eichh.)	55	100.0	5 158	12.18	–	D5	D6	D5	D5	D1	D5	D4	D5	D5	D5	D2	D4	D3	D6	D3	D4	D5	D5	D4	D5
Ips typographus (L.)	48	87.3	12 513	29.56	0.15	D6	D6	D6	D5	D2	D5	D6	D6	D6	D6	D6	D6		D6	D6	D3	D2	D6	D6	D5
Pityogenes chalcographus (L.)	44	80.0	6 966	16.46	0.40	D6	D5		D6	D4	D4		D2	D3	D3	D3	D3		D6	D5	D2		D6	D6	
Pityophthorus pityographus (Ratz.)	42	76.4	6 315	14.93	0.34		D2	D5	D3		D6	D4	D6	D3	D6	D6	D5			D3	D2	D6	D1	D1	D5
Polygraphus poligraphus (L.)	32	58.2	7 169	16.93	0.22				D5	D6				D5				D6			D6	D5		D2	D3
Hylurgops palliatus (Gyll.)	18	32.7	571	1.35	0.02										D2					D6		D2	D4	D2	D4
Rhagium inquisitor (L.)	17	30.9	124	0.29	0.03					D1	D1						D2	D1						D1	
Molorchus minor (L.)	16	29.1	424	1.00	0.22													D3			D3	D2			
Cryphalus abietis (Ratz.)	15	27.3	1 021	2.41	0.24									D4									D1		D4
Tetropium castaneum (L.)	15	27.3	163	0.39	0.05							D1						D1							
Xyloterus lineatus (Ol.)	12	21.8	336	0.79	0.05															D1					
Dryocoetes autographus (Ratz.)	9	16.4	484	1.14	0.04							D1													D5
Monochamus sutor (L.)	9	16.4	103	0.24	0.11										D2			D4	D1						
Pissodes harcyniae (Herbst)	8	14.5	332	0.78	0.19			D1								D1									
Urocerus gigas (L.)	6	10.9	138	0.33	0.14								D1												
Sirex juvencus (L.)	5	9.1	153	0.36	0.06															D1					
Pityogenes quadridens (Hrtg.)	5	9.1	62	0.15	0.37																				
Monochamus sartor (Fabr.)	4	7.3	154	0.36	0.10								D1			D2	D1								
Xylechinus pilosus (Knoch.)	4	7.3	92	0.22	0.07																				
Pogonocherus fasciculatus (Deg.)	2	3.6	19	0.04	0.20															D2					
Carilia virginea (L.)	2	3.6	2	0.01	0.01																				
Pityogenes bidentatus (Hrbst.)	1	1.8	34	0.08	0.20																				

Table 2 – cont.

Species – Gatunek	Associations – Zespoły																										
Ips amitinus (Eichh.)	D3	D6	D4	D6	D5	D2	D3	D5	D1	D5	D2	D5	D5	D5	D5	D5	D1	D4	D6	D4	D2	D1	D1	D5	D2	D3	D4
Ips typographus (L.)		D3	D6	D4	D3	D1	D3	D5		D5	D6	D6	D6	D5	D6	D1	D6	D6	D3	D6	D2			D6			D5
Pityogenes chalcographus (L.)			D4	D5	D5	D5	D4	D5	D2	D1	D4	D6	D1	D5	D5	D6		D4		D2		D2	D1	D4		D5	D2
Pityophthorus pityographus (Ratz.)	D5	D6	D5	D6	D5	D4	D6	D5	D6	D4	D5				D3	D2	D1	D5	D4	D6	D2		D2			D3	D5
Polygraphus poligraphus (L.)	D6	D3			D5	D6	D5		D3	D5		D5	D5	D4		D5	D5		D5		D6	D6	D6	D1		D6	D6
Hylurgops palliatus (Gyll.)			D2	D1									D2		D2		D5	D5		D2			D5	D4		D2	D2
Rhagium inquisitor (L.)						D1		D1	D1		D2		D1	D1		D1			D3	D1			D2	D2			
Molorchus minor (L.)	D1	D5	D1						D4	D3	D5	D5			D5				D2		D3				D1	D5	D5
Cryphalus abietis (Ratz.)	D5				D5					D6	D4			D5				D2	D2		D2		D1	D2	D2		D1
Tetropium castaneum (L.)		D2	D1	D1			D1					D2		D1	D2	D3	D3			D2	D3	D3			D4		
Xyloterus lineatus (Ol.)				D3				D1	D1						D4					D2		D1	D5	D5	D4	D1	D2
Dryocoetes autographus (Ratz.)	D5															D1			D4		D2		D1		D6		D1
Monochamus sutor (L.)												D2						D2				D1		D1		D1	D1
Pissodes harcyniae (Herbst)	D1											D1	D4	D5								D3			D2		
Urocerus gigas (L.)		D1						D5											D1	D3		D2					
Sirex juvencus (L.)						D4	D2										D3										D1
Pityogenes quadridens (Hrtg.)																					D5		D1	D1	D2	D3	
Monochamus sartor (Fabr.)																	D4										
Xylechinus pilosus (Knoch.)													D2									D2			D2	D4	
Pogonocherus fasciculatus (Deg.)																		D2									
Carilia virginea (L.)																									D1	D1	
Pityogenes bidentatus (Hrbst.)					D3																						

Explanation of symbols as in Table 1.
Objaśnienia symboli jak w tabeli 1.

Table 3. Ecological community and microenvironmental-trophic associations of cambio- and xylophagous insects including *Ips amitinus* on *Picea abies* of age class IV (61-80 years)
Tabela 3. Zgrupowanie ekologiczne i zespoły mikrośrodowiskowo-troficzne owadów kambio- i ksylofagicznych z udziałem *Ips amitinus* na *Picea abies* IV klasy wieku (61-80 lat)

Species – Gatunek	Community – Zgrupowanie					Associations – Zespoły													
	N	C	n	D	Ag														
Ips amitinus (Eichh.)	13	100.0	688	4.91	–	D1	D5	D4	D5	D5	D4	D1	D1	D5	D3	D3	D5	D3	D4
Ips typographus (L.)	12	92.3	2 081	14.85	0.16	D6	D6	D6	D6	D6	D6	D4		D6	D2	D6	D6	D4	D4
Pityogenes chalcographus (L.)	11	84.6	1 762	12.57	0.28	D2		D6	D2		D6	D6	D3	D5	D3	D5	D5	D4	D5
Pityophthorus pityographus (Ratz.)	11	84.6	392	2.80	0.22	D2			D5	D5	D4	D2	D4	D5	D3	D2	D3		D4
Polygraphus poligraphus (L.)	7	53.8	8 135	58.04	0.25					D5		D6	D6	D5	D6			D6	D6
Tetropium castaneum (L.)	7	53.8	96	0.68	0.02							D1	D1	D3	D2	D3	D1		D2
Cryphalus abietis (Ratz.)	5	38.5	199	1.42	0.43				D5	D5						D2	D3	D3	
Xyloterus lineatus (Ol.)	4	30.8	478	3.41	0.01		D1					D1						D6	D3
Molorchus minor (L.)	4	30.8	15	0.11	0.09						D1					D1	D1		D2
Rhagium inquisitor (L.)	4	30.8	12	0.09	0.01			D2						D1				D1	D1
Pissodes harcyniae (Herbst)	3	23.1	34	0.24	0.08					D1			D3						D3
Hylurgops palliatus (Gyll.)	3	23.1	10	0.07	0.14											D1	D2	D1	
Monochamus sutor (L.)	3	23.1	12	0.09	0.17						D1				D1			D1	
Urocerus gigas (L.)	2	15.4	86	0.60	0.01												D3		D5
Sirex juvencus (L.)	1	0.8	17	0.12	0.01											D3			

Explanation of symbols as in Table 1.
Objaśnienia symboli jak w tabeli 1.

Table 4. Ecological community and microenvironmental-trophic associations of cambio- and xylophagous insects including *Ips amitinus* on *Picea abies* of age class V (81-100 years)
Tabela 4. Zgrupowanie ekologiczne i zespoły mikrośrodowiskowo-troficzne owadów kambio- i ksylofagicznych z udziałem *Ips amitinus* na *Picea abies* V klasy wieku (81-100 lat)

Community – Zgrupowanie						Associations – Zespoły					
Species – Gatunek	N	C	n	D	Ag						
1	2	3	4	5	6	7	8	9	10	11	12
Ips amitinus (Eichh.)	8	100.0	475	5.15	–	D1	D5	D4	D3	D3	D2
Ips typographus (L.)	8	100.0	7 109	77.11	0.05	D6	D5	D6	D6	D6	D6
Pityogenes chalcographus (L.)	6	75.0	1 289	14.00	0.44	D3	D6		D5	D3	D4
Pityophthorus pityographus (Ratz.)	5	62.5	66	0.71	0.33		D2	D4	D5		D1
Tetropium castaneum (L.)	4	50.0	82	0.89	0.01			D4	D5		D3
Hylurgops palliatus (Gyll.)	4	50.0	44	0.48	0.10		D1	D5		D2	

Table 4 – cont.

1	2	3	4	5	6	7	8	9	10	11	12
Cryphalus abietis (Ratz.)	3	37.5	64	0.69	0.31			D2		D5	
Polygraphus poligraphus (L.)	2	25.0	31	0.34	0.33					D4	D1
Rhagium inquisitor (L.)	2	25.0	6	0.06	0.01				D2		D1
Dryocoetes autographus (Ratz.)	1	12.5	6	0.06	0.01						D1
Monochamus sutor (L.)	1	12.5	1	0.01	0.16					D1	
Pityogenes bidentatus (Hrbst.)	1	12.5	46	0.50	0.22					D5	

Explanation of symbols as in Table 1.
Objaśnienia symboli jak w tabeli 1.

The life-cycle of *Ips amitinus* against a background of plant phenology, body dimensions, and characteristics of brood galleries

During six out of eight years of observations of the life-cycle of *I. amitinus* in the area under investigations this bark beetle produced only one generation in the year. It was composed of the main brood and the sister brood. In 1991 and 1995 summer and autumn were warmer than usually and *I. amitinus* attempted to initiate the second generation. In early September of these two years boring dust appeared on trees manifesting infestation of trees by beetles of the first generation. In the middle of this month larvae appeared in brood galleries remaining there for the winter. Unfortunately no observation was made whether these second generation larvae survived until spring.

The life-cycle of *I. amitinus* during "average" in respect of weather years is as follows (Fig. 1). After overwintering the adult beetles swarm and begin to colonize the breeding material in spring. Usually this takes place during the second decade of May when in the mountain forest *Petasites albus* (L.) ends to flower and flowers begin to appear on *Oxalis acetosella* L., while *Pinus sylvestris* L., *Larix decidua* Mill., *Acer pseudoplatanus* L., *Alnus incana* (L.) Moench, *Betula verrucosa* Ehrh., *Sorbus aucuparia* L., *Crataegus* spp., *Corylus avellana* L., *Sambucus racemosa* L., *Rosa canina* L., and *Lonicera nigra* L. begin to develop leaves. The male gets under the bark by boring a circular entrance hole, 2 mm in diameter. The presence of boring beetles is manifested by rusty-brown dust gathering on the bark surface. Next, the pairing chamber is quite deeply cut in the wood, and sometimes it leaves its imprint on the inner surface of the bark. The area of measured pairing chambers was 0.2-0.5 cm^2 (mean 0.35 cm^2).

I. amitinus is a polygamous species, and therefore the male attracts more than one female. Each female cuts its own egg-tunnel. In the brood galleries examined during this study the number of egg-tunnels in a single gallery varied from three (18% of galleries) to seven (1%). Most often a gallery had four egg-tunnels (53% of galleries). Five egg-tunnels were found in the case of 20% of galleries, and six in the case of 8%. Initially the egg-tunnels run from the pairing chamber in all directions, but soon they start to run in a wavy manner rather along the stem, cutting deeply into the wood. The breadth of measured egg-tunnels was 2 mm and their length 3.0-17.2 cm (mean 9.05 cm, most often 7.0-11.0 cm). The egg-tunnels are cleaned of the dust and have ventilating holes. On both sides of the egg-tunnel females cut egg-niches, 1 mm broad, into which they lay eggs, one in each niche. In the examined brood galleries the distance between

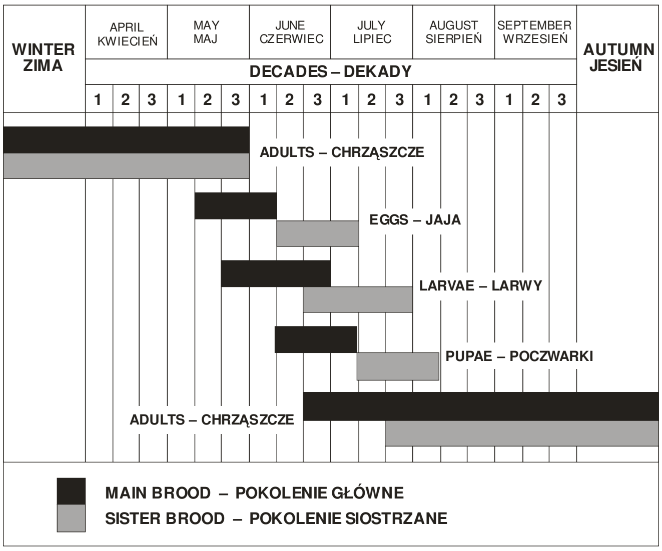

Fig. 1. The life-cycle of *Ips amitinus* (Eichh.) on *Picea abies* (L.) Karst. at 700-800 m above the sea level in experimental forests of Krynica (Beskid Sądecki mountain range of the Carpathians, southern Poland) during 1991-1998

Rys. 1. Cykl rozwojowy *Ips amitinus* (Eichh.) na *Picea abies* (L.) Karst. na wysokości 700-800 m n.p.m. w lasach doświadczalnych w Krynicy (Beskid Sądecki, południowa Polska) w latach 1991-1998

neighbouring egg-niches was 1.5-5 mm (mean 3.2 mm). This distance, however, concerns only egg-tunnel sections of which the side walls are almost continuously occupied by egg-niches. Often, on one or both side walls of the egg-tunnel, there are sections several centimeters long completely free of egg-niches. Sometimes egg-tunnels are so close to each other that egg-niches and subsequent larval tunnels occur on only one side of the egg-tunnel. There are cases that the egg-tunnel is completely devoid of egg-niches, or they are very scarce. In brood galleries examined during this study the number of egg-niches with eggs, and in consequence the number of larval tunnels, per a single egg-tunnel (i.e. per a single female) was 26.9 on the average. The eggs are 0.9 mm × 0.6 mm in size.

The intensive egg-laying takes place in the third decade of May when on *Abies alba*, *Picea abies*, *Acer pseudoplatanus*, *Sambucus racemosa*, and *Lonicera nigra* flowers begin to appear. Also at that time *Stellaria nemorum* L., *Homogyne alpina* (L.), *Ajuga reptans* L, *Asperulla odorata* L., *Lysymachia nemorum* L., and *Majanthemum bifolium* (L.) F.W. Schm. begin to produce flowers, while *Primula elator* (L.) Grufb., *Anemone nemorosa* L., *Oxalis acetosella* L., *Viccinium myrtillus* L., and *Symphytum cordatum* W.K. end their flowering.

The larvae appear in brood galleries in the first decade of June. At the same time the swarming and infestation of the material for development of the sister brood take place. This happens when *Sorbus aucuparia*, *Crataegus* spp., and *Rosa canina* as well as such herbaceous plants as *Rubus idaeus* L. and *Senecio nemoris* L. begin to bloom, while *Acer pseudoplatanus*, *Sambucus racemosa*, *Homogyne alpina*, and *Asperula odorata* terminate their flowering. Each larva cuts its own tunnel. The larval tunnels do not cut into the sapwood. In brood galleries examined the length of larval tunnels was 7-31 mm (mean 16.4 mm, most often 12-18 mm). Larval tunnels are filled with a compact dust. Larvae feed for about 2-3 weeks undergoing through three instars. The breadth of the head capsule of respective larval instars was: I – 0.50 mm, II – 0.70 mm, and III – 0.92 mm. The length of larvae just after hatching was 0.9-1.00 mm (mean 0.95 mm, most often 1.0 mm), and just before their pupation 4.0-6.0 mm (mean 5.15 mm, most often 5.0-5.1 mm).

In the second decade of June the larvae at the end of their tunnels cut the oval pupal chambers in which they pupate. In the examined galleries the breadth of the pupal chamber was 2.0-3.5 mm (mean 2.58 mm, most often 2.5-2.6 mm), while the length of pupae was 4.5-5.2 mm (mean 4.99 mm, most often 5.0 mm). At that time *Stachys silvatica* L. starts to flower, while *Crataegus* spp., *Sorbus aucuparia*, *Lonicera nigra*, *Majanthemum bifolium*, *Geum rivale* L., and *Stellaria nemorum* cease flowering.

The pupal stage lasts for about 10 days and in the third decade of June adult beetles begin to emerge in the galleries. At the same time in galleries of the sister brood females begin to lay eggs. In the forest *Rubus idaeus* and *Ajuga reptans* come out of bloom and fruits of *Vaccinium myrtillus* start to ripen. The maximum of young adult appearance takes place in the first decade of July. At that time larvae begin to appear in sister brood galleries. In the forest the beginning of flowering of *Chamaenerion angustifolium* (L.) may be observed. The length of adult beetles measured during this study was 3.0-5.0 mm (mean 4.8 mm, most often 4.0-4.1 mm). After attaining full color, and completing their maturation feeding in the place of birth, the young adults begin to cut their way out of tree stems. This lasts until the first decade of August when *Senecio Fuchsi* Gmel. and *Gentiana asclepiadea* L. begin to flower, while *Stachys silvatica* L. terminates this phenological phase, and fruits of *Sorbus aucuparia* become ripe.

In the second decade of July pupae appear in galleries of the sister brood and this coincides with appearance of flowers on *Hypericum maculatum* Cr. In the third decade of that month sister brood young adults begin to emerge, and at that time *Rubus hirtus* W.K. starts to flower, *Senecio nemorensis* ends to flower, and fruits of *Sambucus recemosa* and *Lonicera nigra* start to ripen. In the first decade of August, when adults of the main brood have already left their home galleries, in the galleries of the sister brood the maximum of appearance of young adults takes place. These young sister brood beetles leave their home galleries during the third decade of August when flowers begin to appear on *Carlina acaulis* L., and *Hipericum maculatum* cease blossoming. Some few adult beetles remain in their home galleries to overwinter.

The area of phloem damaged by a single brood gallery of *I. amitinus* was 0.3-1.9 dm^2 (mean 0.75 dm^2).

Economic importance

The results of qualitative and quantitative entomological analyses presented in this paper showed that *I. amitinus* in experimental forests of Krynica does not attack weakened and dying *P. abies* trees alone but it is an important member of associations of cambio- and xylophagous insects infesting and killing such trees. It was found that this bark beetle belongs to the group of five species playing the most important role in this respect. Besides *I. amitinus* this group includes *Ips typographus*, *Pityogenes chalcographus*, *Polygraphus poligraphus*, and *Pityophthorus pityographus.* On trees of age class II *I. amitinus* is often the dominant species, especially in the absence of *I. typographus* as it was the case on 38.2% of examined trees. Also *P. pitographus* plays a very important role in this age class of trees. However, it does not compete with *I. amitinus* for place on the tree stem since each of them colonizes a different stem's part. On the other hand there is a strong competition in this respect between *I. amitinus* and *P. chalcographus* as it was observed on trees of all four age classes investigated. On trees of age class III and older *I. typographus* gradually becomes a dominant species, and on trees of age class V it is an unquestionable superdominant species. Only on trees of age class IV this domination of *I. typographus* is somewhat weakened on trees abundantly infested by *P. poligraphus.*

Also the fact that *I. amitinus* infested 110 (28.1%) out of 392 *P. abies* trees examined during studies on cambio- and xylophagous insects conducted in experimental forests of Krynica showed its important role in killing trees weakened mainly by *Armillaria* root rot.

Efficiency of trap trees

The entomological analyses of trap trees felled in March to attract *I. typographus* showed their high efficiency also in attracting *I. amitinus*. In early June all 15 trap trees were colonized almost exclusively by four bark beetle species: *I. typographus*, *I. amitinus*, *P. chalcographus*, and *P. pityographus*. The stem section colonized by *I. amitinus* consisted of 50.6% of the stem's length on the average.

DISCUSSION

In experimental forests in Krynica brood galleries of *I. amitinus* were found only on *P. abies*. However, this species in its natural range may also occur on other tree species. According to Balachovsky [1949] this bark beetle may occur on trees of four genera, i.e. *Picea*, *Abies*, *Pinus*, and *Larix.* Pfeffer [1955] listed the following host trees of *I. amitinus*: *Picea abies*, *Pinus cembra*, *Pinus montana*, *Pinus uncinata*, and *Pinus nigra*. The list presented by Pavlovskij [1955] includes: *Picea abies*, *Pinus sylvestris*, *Pinus austriaca*, *Pinus leucodermis*, *Pinus nigricans*, *Pinus peuce*, *Abies pectinata*, and *Larix decidua.* In Finland *I. amitinus* breeds on *Picea abies* and *Pinus sylvestris* [Annila and Nuorteva 1976]. From among Polish authors Kozikowski [1922] mentioned *Picea abies* (main host), *Pinus cembra*, *Pinus montana*, and *Larix decidua* as hosts of *I. amitinus.* Bałazy and Michalski [1964] found this bark beetle on *Pinus sylvestris* growing in *Fagus sylvatica-Abies alba* stands in the Bieszczady range of the eastern Carpathians. Dominik [1972] during his observations of phytophagous insects of coniferous trees of foreign origin growing in Rogów (central Poland) found *I. amitinus* on *Picea sitchensis. I. amitinus* breeding in the central part of the Alps on *Pinus cembra* and *Pinus montana*, and less frequently on *Larix decidua*, was separated as a subspecies *Ips amitinus* var. *montana* Fuchs. This separation was made on the basis of slight morphological differences and preference of different hosts [Fuchs 1913]. Presently it is being questioned, also because of the chemical composition of the aggregation pheromones which turned out to be identical for both subspecies [Zuber et al. 1993].

It is difficult to compare results of this study concerning ecological requirements of *I. amitinus* with literature data because the latter ones treat this problem in general terms, and usually refer to *I. amitinus* and *I. typographus* together. However, in general they are in agreement with information found by the author in Polish and foreign literature. In Poland many details concerning ecology of *I. amitinus* in mountain forests may be found in the paper of Capecki [1978].

The conclusion in the present study that *I. amitinus* least willingly colonized *P. abies* trees of age class II seem to be contradictory to the fact that on trees of this age class it reached the highest values of the index of dominance. This contradiction seem to result from the fact that trees of age class II were little attacked by *I. typographus* and *I. amitinus* took advantage of that. Also Kisielowski and Tuteja [1980] found that on weakened *P. abies* trees of age class II *I. amitinus* was more abundant than *I. typographus.* It should also be remembered that relations presented in this paper concern only trees infested by *I. amitinus* and not all trees of *P. abies* examined during studies on cambio- and xylophagous insects in this area. Relationships between individual species of these insects were discussed in the paper of Starzyk et al. [1987].

It was found that *I. amitinus* under climatic conditions of the Beskid Sądecki mountain range above 700 m in altitude produces only one generation during the year including the main brood, and in addition, the sister brood. Only when summer and autumn were exceptionally warm it attempted to establish the second generation with larvae hatched before winter frosts. A similar life-cycle of *I. amitinus* was presented by Vasečko [1971] on trees growing above 750 m in altitude in the Ukrainian part of the Carpathians. The life-cycle of *I. amitinus* described in the present paper is also similar to the one presented by Annila and Nuorteva [1976] in Finland. Nevertheless, under slightly warmer climate *I. amitinus* may produce two full generations a year [Vasil'ev 1974, Capecki 1978].

For the first time the life-cycle of *I. amitinus* was described against a background of phenology of forest plants. Only Vasečko [1971] connected the swarming maximum of this bark beetle with appearance of foliage of *Betula verrucosa* and flowering of *Oxalis acetossella* and *Vaccinium myrtillus*. It seems that using plant phenology is a more dependable method of determination of dates of occurrence of individual insect developmental stages than calendar dates commonly used in literature. Earlier or later appearance of individual developmental stages of insects during the growing season more or less corresponded with earlier or later occurrence of plant phenological phases. This attempt to connect phenology of *I. amitinus* with phenology of plants was mainly based on moments of beginning and ending of plant flowering. These two phases are relatively easy to be observed in the forest. This may be of practical importance to foresters.

Results of this study showed another similarity between biology of *I. amitinus* and *I. typographus*. Three larval instars found in *I. amitinus* correspond to three instars found in *I. typographus* by Lekander [1986].

A high efficiency of trap trees used against *I. typographus* also in the case of *I. amitinus* showed that such trees may be used in the control of this species as well as in forecasting of its occurrence. The trap trees in the case of *I. amitinus* are important because there are no commercial pheromone preparations for the control of this bark beetle in spite of the fact that chemical composition of its pheromones is known [Francke et al. 1980].

CONCLUSIONS

1. In the area investigated during this study *I. amitinus* mainly threatened the weakened trees of *P. abies*, and together with other species of cambio- and xylophagous insects caused their premature death.

2. Stands above age class II are more endangered by *I. amitinus* than younger stands.

3. The accumulation of trees felled, broken, and overthrown during winter and early spring, and failing to remove them from the forest before spring swarming of *I. amitinus*, may stimulate its intensive reproduction because besides the weakened standing trees it readily infests trees lying on the ground.

4. Loose canopy of stands with numerous *P. abies* trees little shaded or without direct shading, having long and broad crowns, may aid the occurrence of higher numbers of *I. amitinus.*

5. *I. amitinus* most willingly colonized the material with relatively thin bark (2-3 mm), i.e. mainly the middle part of the stem.

6. In areas situated above 700 m in altitude development of only one *I. amitinus* generation in the year may be a factor limiting its excessive occurrence there.

7. By using the trap trees against *I. typographus* it is possible at the same time to control *I. amitinus.* Such trees may also be useful in forecasting of its occurrence.

8. Observations of individual phenological phases of plants (especially the beginning and end of flowering) seem to be a more dependable method of determination of dates of swarming of *I. amitinus* and appearance of its individual developmental stages than traditionally used calendar dates.

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BADANIA NAD BIOLOGIĄ, EKOLOGIĄ I ZNACZENIEM GOSPODARCZYM *IPS AMITINUS* (EICHH.) (*COL.*, *SCOLYTIDAE*) W LASACH DOŚWIADCZALNYCH W KRYNICY (BESKID SĄDECKI, POŁUDNIOWA POLSKA)

Streszczenie. Spośród 392 świerków rosnących na wysokości 700-800 m n.p.m. w Beskidzie Sądeckim (49°35' N, 19°31' E, południowa Polska), opanowanych przez owady kambio- i ksylofagiczne, 110 (28,1%) było również zaatakowanych przez *Ips amitinus*

(Eichh.). Kornik ten najchętniej zasiedlał osłabione drzewa stojące III-V klasy wieku oraz drzewa niedawno wywrócone, złamane i ścięte. Najliczniej występował w środkowej części strzały, gdzie grubość kory wynosiła 2-3 mm, zasiedlając średnio 38,4% jej długości. Na pojedynczym drzewie *I. amitinus* zawsze występował w zespołach owadów kambio- i ksylofagicznych składających się z 2-12 gatunków. Wyprowadzał on tylko jedno pokolenie w roku wraz z pokoleniem siostrzanym. Przebieg cyklu rozwojowego przedstawiono na tle fenologii roślin leśnych. Stwierdzono występowanie trzech stadiów larwalnych. Podano również wymiary ciała wszystkich stadiów rozwojowych i wymiary poszczególnych elementów żerowiska. *I. amitinus* odgrywa ważną rolę w dobijaniu osłabionych świerków. Stwierdzono dużą przydatność drzew pułapkowych wykładanych na *Ips typographus* również do zwalczania *I. amitinus.*

Słowa kluczowe: *Ips amitinus*, biologia, ekologia, fenologia, cykl rozwojowy, znaczenie gospodarcze

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