Feeding ecology of pine shoot beetles (*Tomicus* spp.) in tree crowns of Scots pine (*Pinus sylvestris* L.) stands under one-year outbreak

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ABSTRACT: Studies were carried out in southern Poland during 2002–2006 in Scots pine stands under the effect of an outbreak of pine shoot beetles. The qualitative aspects of beetle feeding in tree crowns, studied on the basis of fallen shoots collected on experimental plots, are presented in this paper. The beetle numbers affected the age distribution of damaged shoots and the proportion of multiple attacks. The proportions of one-year-old shoots and the numbers of shoots with more than two attacks increased in the marginal part of the stand in the year of intensive feeding of beetles and in the subsequent year. A similar proportion of shoots with two attacks in both stands under investigations in individual study periods, with no relation to beetle numbers, does not permit to use this characteristic for forecasting purposes. The average length of tunnels in shoots attacked once reached 20 mm at maximum. The average length of tunnels (measured from the place of shoot disruption) was greater in shoots with two attacks than in shoots with a single one ($P < 0.0001$). The difference was not significant ($P = 0.3429$) only in stand B during the study season 2004–2005. The majority of the tunnels made in apical portions of shoots with two attacks damaged the tissue of apical shoots. The distance between the base of the second tunnel and the shoot apex in shoots with two attacks, and its significant ($P < 0.01$) linear relationship with the length of beetle tunnels, indicated a high nutritional quality of apical portions of shoots.

Keywords: *Tomicus piniperda*; *T. minor*; *Pinus sylvestris*; needle drop; shoot damage

Pine shoot beetles, *Tomicus piniperda* (L.) and *T. minor* (Hart) (Coleoptera: Scolytinae), are widely distributed in the Palaearctic Region infesting various pine species within their natural ranges (Nunberg 1947; Lekander et al. 1977). In the early 1990s *T. piniperda* was introduced into North America. It was detected for the first time near Cleveland, Ohio (Haack, Kucera 1993). One of the methods of evaluating the population size of the pine shoot beetles is the estimation of numbers of shoots damaged by adult feeding in pine crowns. This is accomplished either by counting damaged shoots in crowns of standing or felled sample trees (Långström, Hellqvist 1991; McCullough, Smitley 1995; Haack et al. 2001; Långström et al. 2002; Lieutier et al. 2003) or by collecting on sample plots the shoots pruned by adult beetles and fallen onto the ground under infested trees (Michalski, Witkowski 1962; Lottyniemi 1978; Långström 1983; Långström, Hellqvist 1990; Annila, Heikkila 1991; Borkowski 2001, 2006a,b; Långström et al. 2001; Cedervind et al. 2003; Martikainen et al. 2006). The number of damaged shoots is the basis for estimating losses in tree increments (Michalski, Witkowski 1962; Nilson 1974; Långström, Hellqvist 1990, 1991; Czokajlo et al. 1997; Borkowski 2001, 2006a,b). In forestry, it is also the basis for prediction of the occurrence of pine shoot beetles. In Poland, besides the number of dying trees, the number of collected fallen shoots is used to estimate the degree of threat to Scots pine stands (Anonymous 2004).

The ecology of feeding of pine shoot beetles in crowns of healthy pine trees has been studied in many scientific centres around the world (Eidman, Nuorteva 1968; Šrot 1968; Salonen 1973; Beaver 1974; Långström 1980, 1983; Ericsson et al. 1985; Ye, Zhao 1995; Ye 1996; Petrice et al. 2002; Eager et al. 2004). Results of studies have indicated that some quantitative aspects of beetle feeding in pine crowns may be useful for the estimation of density and population dynamics of pine shoot beetles (Långström 1983; Haack et al. 2001). For example, the number of multiple attacks as a result of beetle competition for a limited number of shoots suitable for colonization or the number of shoots damaged by a single attack are important characteristics.

This paper presents ecological aspects of pine shoot beetle feeding in crown shoots of Scots pine in stands situated at different distances from sawmill timber yards. A 4-year study period, comprising a year of pine shoot beetle outbreak, permitted to compare and verify the results obtained. This study has been justified by a lack of elaborations of this type concerning stands of older age classes which were growing during their entire life within the influence of a source of the reproduction of these insects.

MATERIALS AND METHODS

Study site

The study site was located in Zagnańsk in southeastern Poland (longitude 20°45´E; latitude 50°55´N; altitude 350 m). Studies were carried out in 2002 to 2006 on experimental plots established in pure Scots pine stands situated 50 m (Stand A) and 500 m (Stand B) away from sawmill timber yards existing without break since 1916. In summer 2002, there were over 500 m^3 of unpeeled pine timber stored in the yards. This caused a mass migration of young adults into surrounding stands which resulted in severe damage in tree crowns reflected by a high amount of tunnelled shoots found on the ground in marginal parts of stands (Borkowski 2003).

Characteristics of the investigated stands:

Stand A: 90-years-old Scots pine stand, growing on a fresh coniferous forest site, of a moderate crown closure, mean dbh of 17.4 cm and mean height of 9.9 m. The canopy of trees was severely damaged by beetle feeding in shoots repeated every year. The top section of the crown, 1–2 m in length, was either dead or heavily deformed.

Stand B: 90-years-old Scots pine stand, growing on a fresh coniferous forest site, of an open crown closure, mean dbh of 22.8 cm and mean height of 18.5 m.

Shoot survey

The amount of fallen shoots was estimated on permanent experimental plots. Shoots were collected from the ground once a month from August to December, and once more in March of the next year after snow disappearance (this time span represents the study season).

In 2002–2003 and 2003–2004 study seasons, a sample consisted of shoots collected on four strips, 25 m long and 1 m wide, running in four cardinal directions from sample tree No. 1, centrally situated in an experimental plot. In stand A in 2002 one sample was collected. In stand B in 2002 as well as in both stands in 2003, due to a low level of shoot fall, three samples were collected in each stand. The additional samples were collected around trees No. 2 and No. 3 situated S–E and N–W from sample tree No. 1.

In 2004–2005 and 2005–2006 study seasons, a sample consisted of shoots collected on a plot 0.2 ha in size (40 × 50 m) laid out around sample tree No. 1.

In the case of shoots found on the border of a sampling plot every second shoot was taken.

Field measurements

On shoot collecting plots the following measurements were carried out during 2004–2006 study seasons: (*i*) age of stand was calculated as an arithmetic mean of ages of 31 sample trees selected at random (every tenth tree according to the existing tree numbering) and cored at the base of their trunks; (*ii*) height of all pine trees was measured to the nearest 0.25 m; (*iii*) dbh of all pine trees was measured outside bark in N–S and E–W directions to the nearest 0.5 cm.

Laboratory procedures

In the laboratory, the density of the shoot fall, the age of shoots with separation into current growth and one-year-old shoots, and the percentage of multiple attacks were determined for stands A and B in the respective years. A multiple attack is the situation when there are more than one beetle entrance holes in a shoot in a given year. For shoots collected during 2004–2006 the following elements were measured to the nearest 1 mm:

(*i*) shoot diameter at the place of break;
(*ii*) length of the beetle tunnel from the place of break to its end (first tunnel);
(*iii*) distance of the second entrance hole from the shoot apex in shoots with two attacks;
(*iv*) length of the beetle tunnel from the second entrance hole to its end (second tunnel).

Data processing

Shoot diameter measurements were analyzed using the Levene's test for homogeneity of variance.

Before the statistical analysis the data were log-transformed. Then, shoot diameter data were processed by the factor analysis of variance (ANOVA) assuming the stand and study season as classification factors. The post-hoc comparison was carried out on the basis of the Tukey's multiple range test.

Using Student's *t*-test for unpaired samples, the differences between the mean lengths of the first tunnel with one and two attacks were checked.

To determine the relationship between the distance of the entrance hole of the second tunnel from the shoot apex and its length the analysis of correlation was used. The coefficients of rectilinear correlation (r_n) were computed and zero hypotheses H_0, according to which they are equal to zero, were checked (Fisz 1963; Sokal, Rohlf 1981).

The analyses were carried out using the package Statistica 6.1 (STATSOFT Inc. 2004).

RESULTS

Feeding of beetles in pine shoots in 2002–2006

During the study period a total of 4,838 shoots damaged by adult feeding fell on experimental plots. The mean shoot fall in individual years indicated a high intensity of beetle feeding in pine crowns in 2002 in the marginal part of the stand (Table 1). During the remaining study seasons the shoot density dropped below 1 shoot per 1 m^2 of ground. In stand B, the mean shoot fall was below 0.5 shoots per m^2, which is characteristic of stands situated outside the range of the reproduction centres of these insects.

The shoots damaged in the current growth part dominated among damaged shoots found on experimental plots (Table 1). The remaining fallen shoots were the one-year-old shoots. No evidence of feeding was found on two-years-old shoots and older. The highest percentage of one-year-old shoots was found in stand A during the year of intensive beetle feeding (31.6%), and also during the next year (22%). In subsequent years the percentage of one-year-old shoots was below 10%. In stand B, the percentage of one-year-old shoots during all study periods was below 20%.

Among the collected shoots, the shoots with single attacks dominated, while among shoots with multiple attacks the shoots with two attacks prevailed (Table 1). Shoots with more than two attacks (maximum 6) were found in stand A. Their proportion was the highest in a year of intensive beetle feeding in pine shoots (15.9%). In individual years the percentage of shoots with two attacks was similar in both investigated stands ranging from 11.2 to 21.6%.

Qualitative aspects of beetle feeding in pine shoots in 2004–2006

The analysis of variance showed the influence of the study season (F = 27.08, d.f. = 1,1,1947, P < 0.0001) and did not confirm differences between the two stands (F = 3.10, d.f. = 1,1,1947, P = 0.0784) in respect of shoot diameter. The mean diameter of fallen shoots in stand A during both study seasons was similar, about 3.2 mm (range 2–9 mm). In stand B during the study season 2004–2005 the mean diameter of shoots was 3.6 mm (range 1–6 mm), and it was greater than during the season 2005–2006 (3.1 mm, range 2–7 mm).

The mean length of beetle tunnels in shoots was below 20 mm (range 1–108 mm) (Table 2). In stands under investigations (with the exception of stand B during the season 2004–2005) the mean length of the first tunnel in a shoot with two attacks was greater than in the case of shoots with single attacks (*t*-test; P < 0.05) (Table 2).

The mean distance between the base of the second tunnel and the shoot apex was 20 mm (range 4–86 mm)

Table 1. Characteristics of fallen shoots collected in stands under investigations

Stand and study season		No. of shoots fallen per m^2	Current shoots (%)	Per cent frequency of the number of entrance holes per attacked shoot						n
				1	2	3	4	5	6	
A	2002–2003	26.4	68.4	65.3	18.8	7.6	5.2	2.3	0.8	2,640
	2003–2004	0.73	78.0	71.1	18.9	6.8	2.3	0.9		219
	2004–2005	0.38	92.7	77.7	21.6	0.4	0.3			768
	2005–2006	0.37	96.5	86.7	13.3					742
B	2002–2003	0.35	82.3	79.2	20.8					105
	2003–2004	0.23	86.1	81.2	19.8					69
	2004–2005	0.11	81.8	80.0	20.0					210
	2005–2006	0.12	94.8	88.8	11.2					231

Table 2. Length of the first tunnel in shoots with one (1) and two (2) attacks

Stand and study season		Number of entrance holes	Mean ± SEM (mm)	n	$P_{(t)}$
A	2004–2005	1	12.96 ± 0.51	603	< 0.0001
		2	19.14 ± 1.14	165	
	2005–2006	1	11.59 ± 0.44	643	< 0.0001
		2	18.49 ± 1.42	99	
B	2004–2005	1	13.71 ± 0.84	168	0.3429
		2	15.59 ± 2.07	42	
	2005–2006	1	9.05 ± 0.49	205	< 0.0001
		2	16.57 ± 2.31	26	

Student's t-test, $P < 0.05$ indicates statistically significant differences

Table 3. Relationship between the distance of the entrance hole of the second tunnel from the shoot apex and its length

Stand and study season		Mean ± SEM (range)		Coefficients of correlation	
		distance between entrance hole and shoot apex	tunnel length	r_n	P for r_n
A	2004–2005	17.98 ± 0.54 (7–86)	10.55 ± 0.41 (3–57)	0.8009	< 0.0001
	2005–2006	17.29 ± 0.92 (4–76)	9.61 ± 0.71 (2–63)	0.6662	< 0.0001
B	2004–2005	17.45 ± 1.32 (8–60)	9.35 ± 0.59 (3–18)	0.4224	0.0053
	2005–2006	17.07 ± 0.76 (9–27)	8.92 ± 1.11 (3–23)	0.6888	0.0001

(Table 3). The mean length of the tunnels was about 10 mm (range 3–57 mm). The results of correlation analysis indicated that there were statistically significant linear relationships between the distance of the base of the second tunnel from the shoot apex and the length of this tunnel. The coefficients of linear correlation were statistically significant ($P < 0.01$) ranging from 0.4224 to 0.8009 (Table 3).

DISCUSSION

Characteristics of fallen shoots, pruned by pine shoot beetles, during the study period including a year of their outbreak, permitted to explain many important aspects of beetle feeding in shoots of Scots pine crowns.

Feeding of beetles in pine shoots in 2002–2006

Scots pine unpeeled timber stored in the amount of 500 m^3 became a source of the mass reproduction of pine shoot beetles. Their adults migrated from sawmill timber yards into surrounding pine stands where they made feeding in tree crowns. Their high numbers were manifested by the amount of falling pruned shoots in the marginal part of the stand (Table 1). The distribution of fallen shoots during the study season 2002–2003 resembled rather a distribution during a strong 1-year attack or attack of several years in duration (Michalski, Witkowski 1962; Sauvard et al. 1987; Långström, Hellqvist 1991) than the distribution during a long-term outbreak characterized by a significant number of fallen shoots at the distance of 1,000 m from sawmill timber yards (Långström, Hellqvist 1990). Shoot fall in the marginal part of the stand during the study season 2002–2003, accounting for 26.4 shoots per m^2, was much lower than the estimates of Långström and Hellqvist (1990, 1991), i.e. 60 to 100 shoots/m^2.

The age distribution of fallen shoots in the investigated stands indicated a higher proportion of one-year-old shoots in the marginal part of the stand during a year of intensive beetle feeding (Table 1). This probably resulted from a limited amount of current growth shoots suitable for beetle feeding in relation to a large number of beetles of young generation migrating from sawmill timber yards. A low proportion of current growth shoots a year after an outbreak resulted from severe shoot damage a year earlier. This is in agreement with results obtained by Långström (1980) in Sweden, where the proportion of current growth shoots was even smaller (about 40%) and beetles were feeding on 2-years-old shoots and older. The age distribution of fallen shoots during the growing seasons 2004–2006 in stand A, and during the entire study period in stand B, characterized by a low and similar level of shoot fall, probably reflected fluctuations in beetle numbers at the age structure of the local population of pine shoot beetles, i.e. mutual relations between adults of old and young generation. Probably the majority of maturation feedings are conducted in current growth shoots, and in the case of their shortage, feeding takes place in older shoots, although the study results did not confirm this directly. This was also pointed out by results of other studies (Šrot 1968; Salonen 1973; Långström 1980).

The distribution of multiple attacks in stands under discussion indicated that shoots with more than two attacks, resulting from competition for a limited number of shoots suitable for colonization, could be of help in forecasting the population size of pine shoot beetles. Their higher proportion a year after an outbreak could have been caused by a limited number of shoots suitable for colonization, which was also indicated by a higher proportion of one-year-old shoots during this study season. This was also indicated by results of other studies. In Sweden, in uneven-aged stands, shoots with more than two attacks accounted for about 6% (Långström 1980), in the United States in Christmas tree plantations for about 12% (Haack et al. 2001), and for a few per cent in China on *Pinus yunnanensis* Fr. (Ye 1996). The predominance of shoots with two attacks among shoots with multiple attacks in stands of the present study, irrespective of the distance from a source of the reproduction of pine shoot beetles, during years of low beetle feeding, makes their use in forecasting impossible.

Quantitative aspects of beetle feeding in pine shoots in 2004–2006

The mean length of the tunnel in shoots with a single attack and the first tunnel in shoots with two attacks was not over 20 mm. It was highly variable in the range of 1 to 108 mm (Table 2). This is in agreement with results of other authors. In studies of Šrot (1968) the mean tunnel length was 16–23 mm, in those of Långström (1983) it was 20 mm, and Haack et al. (2001) 23 mm. The weak activity of pine shoot beetles during the study seasons 2004–2006 does not permit to explain the fact of making longer tunnels in shoots attacked earlier (with the exception of stand B during the study season 2004–2005) (Table 2). A similar proportion of shoots with two attacks in both stands indicated that making longer tunnels is connected rather with the nutritional quality of shoots than with their shortage. As it has been indicated by studies carried out in crowns of felled trees, beetles prefer the apical parts of shoots. In Scandinavia, the majority of single attacks took place at the distance of 10 mm from the base of the apical bud (Långström 1983). In the United States this distance was 4–6 cm (McCullough, Smitley 1995; Haack et al. 2001) and in China 3–4 cm (Ye 1996). The results of this study also indicated a high nutritional quality of apical portions of shoots. Haack et al. (2001) observed that in shoots with multiple attacks the subsequent attacks were made below the earlier ones. This study showed that the first attacks in shoots with two attacks took place at a distance of about 20 mm from the shoot apex (Table 3). The analysis of correlation showed a significant relationship between the distance of the entrance hole of the second tunnel from the shoot apex and the length of this tunnel (Table 3). Beetles when making tunnels attempted to reach the apical buds. The majority of the tunnels more or less damaged the tissue of the apical bud.

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Ekologie žíru lýkohubů (*Tomicus* spp.) v korunách porostů borovice lesní (*Pinus sylvestris* L.) v podmínkách jednoročního přemnožení

ABSTRAKT: Výzkum byl prováděn v jižním Polsku v období let 2002–2006 v porostech borovice lesní v podmínkách přemnožení borových lýkohubů. V článku jsou prezentovány kvalitativní aspekty žíru brouků v korunách stromů, které byly studovány na základě opadu výhonů sbíraných na pokusných plochách. Četnost brouků ovlivňovala věkové složení poškozených výhonů a podíl jejich vícenásobných napadení. Podíl jednoletých výhonů a počet výhonů s více než dvěma napadeními vzrostl v okrajové části porostu v roce intenzivního žíru brouků a v následujícím roce. Podíl výhonů se dvěma napadeními byl podobný na obou studovaných místech v průběhu studovaného období a nevykazoval žádný vztah k četnosti brouků, což nedovoluje využívat tento znak pro účely prognózy. Průměrná délka požerků ve výhonech napadených jednou dosáhla maximálně 20 mm. Průměrná délka požerků (měřených z místa ulomení výhonu) byla větší na výhonech se dvěma požerky než na výhonech s jedním požerkem ($P < 0.0001$). Rozdíl nebyl signifikantní ($P = 0{,}3429$) jenom na ploše B v průběhu sezony 2004–2005. Většina požerků vyvrtaných v koncové části výhonů se dvěma požerky poškodila pletiva apikálních výhonů. Vzdálenost mezi základnou druhého požerku a apexem výhonu u výhonů se dvěma požerky a její signifikantní ($P < 0.01$) lineární vztah s délkou požerku indikuje vysokou nutriční kvalitu apikálních částí výhonů.

Klíčová slova: *Tomicus piniperda*; *T. minor*; *Pinus sylvestris*; opad jehličí; poškození výhonů

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