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Bark-beetle parasitoids population surveys following storm damage in spruce stands in the Vosges region (France)

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Abstract

This paper presents the results of a long-term study designed to follow the population dynamics of hymenopteran parasitoids associated with *Ips typographus* L. (Coleoptera: Scolytidae) in northeastern France (Alsace and Vosges) in spruce stands devastated by the December 1999 storms. Population densities were estimated by periodic samplings in the pre-emerging insect populations developing under the bark of attacked trees. Data were collected between July 2000 and October 2001. *I. typographus* population density (per m^2) increased respectively by 28%, 105%, and 212% in one year in the three sites surveyed. Six hymenopteran ectoparasitoids were found: *Coeloides bostrichorum* Giraud and *Dendrosoter middendorffi* Ratzeburg (Hymenoptera: Braconidae); *Rhopalicus tutela* (Walker), *Roptrocerus xylophagorum* (Ratzeburg), *Roptrocerus mirus* (Walker) and *Dinotiscus eupterus* (Walker) (Hymenoptera: Pteromalidae). After two years, the parasitoid populations increased in terms of average density but parasitism rates remained at a relatively low level, ranging from 0% to 40%, with 60% of the trees having a parasitism rate below 5%. Data outlined the recurrent coexistence of competing parasitoid species.

Introduction

French forests were devastated on 26 and 28 December 1999 by storms that caused a nationwide estimated damage of 140 millions m^3 of wind-felled trees (Ministère de l'Agriculture et de la Forêt: http://www.agriculture.gouv.fr). Such catastrophic but natural events induce major changes in the forest entomofauna population dynamics. Uprooted and broken trees favour bark-beetle infestations and lead to spectacular outbreaks, causing new damage on healthy standing trees several years after the storm has struck. The spruce bark beetle, *Ips typographus* L. (Coleoptera: Scolytidae), an extremely harmful pest in Eurasian spruce forests, has been studied in this respect. Ravn (1985) described the changes in the abundance of this bark beetle following the hurricane that struck Denmark in 1981. The author observed bark beetle activity by pheromone trapping and recording the number of spruces killed by *I. typographus* for 2 years and observed that infestations were most comprehensive during the second year when standing trees were also attacked.

In Switzerland, Wermelinger *et al*. (1999) investigated the succession of the insect fauna in spruce forests damaged by the storm Vivian in 1990. During 4 years, those authors analysed window traps catches and observed that beetles densities reached their maximum

2 years after the storm and decline rapidly thereafter probably due to unfavourable weather conditions and regulation by antagonists (predators, parasitoids, and fungi). However, the population dynamics of natural enemies in such circumstances remains poorly explored. We do not know how *I. typographus* population growth affects these different species, or how differences in host-finding, dispersal, and competitive capacities determine parasitoid species impact on the bark-beetle populations and the way they share this common resource. Here, we report the first results of a long-term study on hymenopteran parasitoids associated with *I. typographus* in three spruce stands located in northeastern France (Alsace and Vosges), where bark beetle and parasitoid populations were allowed to develop freely.

Materials and Methods

Selection of sites and trees

Population density was estimated periodically on the basis of samples extracted from the pre-emerging insect populations developing underneath the bark of attacked trees. Sites were selected in July 2000 according to the following criteria: (1) regional coverage over a range of altitudes and stand conditions; (2) site accessibility; (3) site permanence: no sanitation measures planned; and (4) presence of two or more trees colonized by *I. typographus* and containing a majority of callow adults (see below). Six sites were originally selected; however, three of them were discarded after the attacked trees had been removed by foresters. The study was thus performed in three mature forest stands (Table 1), one located near Obersteinbach (forêt domaniale de Steinbach, Haut-Rhin), the second one near Guebwiller (forêt domaniale de Guebwiller, Bas-Rhin), the third one near Orbey (Forêt domaniale des Deux-Lacs, Bas-Rhin).

Periodicity

Sampling was repeated periodically at each new bark-beetle generation. Brood development and numbers of generations per year are principally governed by temperature in *I. typographus* (Annila 1969). At lower altitudes, *I. typographus* is bivoltine (Chararas 1962; Christiansen & Bakke 1988 and references therein): the first flight (overwintering population) occurs in April/May and the second, protracted flight (first generation of the year) takes place during the summer. At higher elevations (900–1400 m), several authors observed that a portion of the first generation of the year could disperse to produce a second generation (Chararas 1961; Abgrall & Schvester 1987). In our study, new attacks were observed in October 2000 in the higher elevation stands (1100 m) suggesting that a second flight took place, probably overlapping with a sister brood of the first flight. So we hypothesized the occurrence of two generations a year at all sites. As parasitoids usually produce two generations a year when the host is bivoltine (Krüger & Mills 1990), sampling was carried out twice a year.

Time of sampling

As the parasitoids concerned in this study attack the late larval instar of *I. typographus* and need some time to develop fully, sampling must occur when a majority of host have reached the callow adult stage. This is complicated by the fact that a great heterogeneity in development stages is very often observed on a tree attacked by *I. typographus*. Sampling was conducted in July and October for both years (Table 1). In 2000, almost all attacks occurred on windthrows, and sampling was carried out on windthrows only. In 2001, these windthrows had become largely unattractive to new bark-beetle generations, and the attacks started to shift to standing trees. A mixture of standing and

Table 1. Description of sites and number of windthrowns or *standing trees* sampled

Site	Location (department)	Elevation (m)	Slope	Age (year)	DBH (cm)	Species composition	July 2000	Oct. 2000	July 2001	Oct. 2001
ST	Steinbach (Haut-Rhin)	260	—	110	40	Spruce/pine	4	5	*5*	*2*
GU	Guebwiller (Bas-Rhin)	1100	S	150	60	Spruce/fir	3	4	5	*5*
2L	Deux lacs (Bas-Rhin)	1100	SE	125	45	Spruce	3	8	3 + *2*	*9*
Total							10	17	15	16

windthrown trees was therefore sampled. The standing trees had to be felled before sampling.

To check retrospectively the adequacy of the sampling time, the life cycle duration of successive *I. typographus* broods was subsequently estimated using the degree-days calculations of Abgrall & Juvy (1993), who established that 550 degree-days were necessary for the bark beetle to complete its development. A temperature logger (Waterproof Optic Stowaway Temperature Logger, Gempler's Inc.) was placed in each of the three surveyed sites from October 2000 onward (degree-days calculations were made for 2001 only). The start of the first flight was estimated by analysing the temperature data and the first day with temperatures above 18°C for more than 7 h was retained.

Sampling procedure

A total of 54 circular bark samples (1 dm^2) per tree were extracted using a metallic punch driven into the bark with a hammer. According to earlier studies (Gonzalez *et al*. 1996), this method presents a good balance between sampling effort and error (kept in this case around 15% of the mean). A higher variability in beetle density was observed by Gonzalez *et al*. (1996) in the lower ($<$15% of the standardized length) and upper ($>$80%) parts of the attacked portion of the tree, whilst attack density was fairly constant between these two levels. This suggested that sampling effort should be increased in the beginning part (0–20%), and in the terminal part (80–100%) of the attacked portion of the stems. At least nine samples were therefore taken at each of six levels, respectively, established at 5%, 15%, 35%, 65%, 85%, and 95% of the attacked portion of the stems. Groups of three contiguous samples were taken at each level, one group on the upper side of the trunk, and one group on each side. When the lower side was accessible, samples were also collected there. Bark thickness was measured at two diametrically opposite points of each sample disk and samples were then stored individually in a ventilated plastic box, brought back to the laboratory and kept until adult emergence for parasitoid identification. Additional measurements were taken on each sampled tree: total length (up to a diameter of 10 cm), diameter at breast height (1.5 m), orientation of each faces sampled (windfalls and standing trees), length of the attacked portion and trunk circumference at each sampling level.

Population estimates

Estimates of the pre-emergent insect populations on a tree were calculated as follows: the tree was divided into sections centered on the sampling level, the population observed in the sampled surface was extrapolated to the surface of the corresponding section, and all sections estimates were summed to obtain the estimate at the tree level.

Results and Discussion

Adequacy of sampling time

Fifty three to 78 days were probably necessary for the first brood to complete its development (Table 2). The longest development time was observed in the lowest site (Steinbach) due to bad weather conditions encountered that year in the northern part of the Vosges. Those estimates are in agreement with those of Chararas (1961) who observed a cycle duration of 42–55 days in the Forest of Sainte-Croix (Morvan, France; alt. 850 m) and those of Abgrall & Juvy (1993) who counted 54–74

Table 2. Estimation of life cycle duration in the three sites, according to Abgrall & Juvy (1993) (calculated for 2001)

Site Altitude	Steinbach 260 m	Guebwiller 1100 m	Deux Lacs 1100 m
First flight (overwintering population)	1 April	30 April	2 May
+ 550 day-degrees	17 June	22 June	6 July
Cycle duration	78 days	53 days	65 days
First sampling campaign	6 July	9 July	12 July
Second flight (1st generation of the year)	2 July	7 July	20 July
+ 550 day-degrees	15 Aug.	26 Aug.	25 Sept.
Cycle duration	44 days	50 days	67 days
Third flight (2nd generation of the year)	31 Aug.	10 Sept.	9 Oct.
Second sampling campaign	4 Oct.	8 Oct.	5 Oct.

days in sites located at 1100 m in Haute-Loire and Savoie (France). The dates that we calculated for the start of the first flight were also consistent with those observed by these authors in the sites they surveyed.

In Steinbach and Guebwiller, the first sampling campaign took place when the insects started to disperse (indeed some emergence holes were noticed at the bark surface of the sampled trees) but this timing is acceptable considering the heterogeneity of stage coexisting on a tree attacked by *I. typographus*. Sampling in Deux Lacs occurred before insect emergence.

The development of *I. typographus* was faster in the summer except in Deux Lacs, where the development time was nearly the same as in the spring. The date of emergence of a potential third flight was calculated but this brood would not have had enough time to reach the adult stage before the winter and would most probably have died (Abgrall & Juvy 1993).

The second sampling campaign occurred just before the winter. Only the population that would survive overwintering under the bark (or in the litter), i.e. the adults were counted in the estimates.

Host densities

Population densities increased regularly in Steinbach compared to the two others sites, probably because of the milder climatic conditions encountered in this altitude (Figure 1). From July 2000 to July 2001, population densities increased by 28%, 105%, and 212% in Guebwiller, Steinbach, and Deux Lacs, respectively.

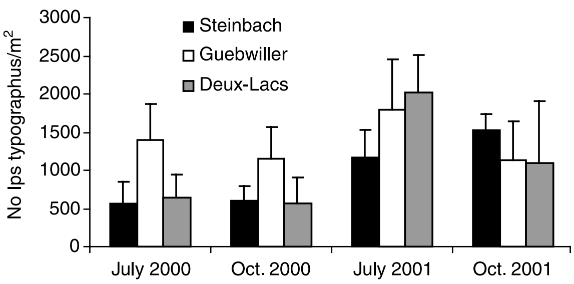

Figure 1. Variation in host density (No. of *I. typographus* /m^2) in Steinbach, Guebwiller, and Deux Lacs.

Population estimates in the Vosges were lower than those reported by Gonzalez *et al.* (1996) in Belgium, suggesting that *I. typographus* densities could still increase in France (Table 3). Although the population estimates presented in Table 3 were all made during outbreaks, the data reported by Gonzalez *et al.* (1996) are the most suitable for comparisons with our estimates because of the similar tree dimensions and the time of the sampling during the outbreak.

Parasitism rates

Six major hymenopteran ectoparasitoids were observed: *Coeloides bostrichorum* Giraud, *Dendrosoter middendorffi* Ratzeburg (both Hymenoptera: Braconidae), *Rhopalicus tutela* (Walker), *Roptrocerus xylophagorum* (Ratzeburg), *Roptrocerus mirus* (Walker), and *Dinotiscus eupterus* (Walker) (all Hymenoptera: Pteromalidae). The distinction between the two *Roptrocerus* species was only made from July 2001 onward, and the data related to both species were therefore merged in a single category '*Roptrocerus*'.

Total parasitism rates (estimated per tree) range from 0% to 40% (Table 4) but about 60% of the trees presented a low parasitism rate (below 5%). This proportion of poorly parasitized trees decreased with time: from 99% of the trees in July 2000, to 65% in October 2000, 67% in July 2001 and 30% in October 2001. In Germany, Eck (1990) found similar figures on *I. typographus*: parasitism rate varied from 0% to 70%, but for half the trees sampled, it was lower than 5%.

Average numbers of parasitoids per sample (all species and all sites together) increased with time

Table 3. Comparisons of mean number of beetles ± SD produced per tree (n = no. of trees) and per m^2 of attacked bark area. (a) Our data, (b) Weslien & Regnander (1990), (c) Gonzalez *et al.* (1996)

Source	Sampling date	No. of beetles produced/tree	No. of beetles produced/m^2	Mean DBH (cm)	Year after outbreak
(a)	July 2000	20 455 ± 20 843 (10)	1215 ± 582	38	1st year
	Oct. 2000	15 390 ± 11 822 (17)	833 ± 369	43	1st year
	July 2001	39 772 ± 17 674 (15)	1888 ± 840	54	2nd year
	Oct. 2001	21 236 ± 12 078 (16)	1525 ± 920	47	2nd year
(b)	July 1981	16 000 ± 3100 (4)	Unavailable	>30	4th year
(c)	Oct. 1991	48 470 ± 12 530 (8)	2267 ± 301	46	2nd year

Table 4. Total parasitism rates in % per tree (no. of samples)

	Steinbach	Guebwiller	Deux-Lacs
July 2000	0.4 (54)	1.7 (54)	1.0 (54)
	1.8 (54)	1 (54)	1.1 (72)
	0.4 (45)	2 (54)	25.0 (72)
	2.0 (54)		
Total	1.4 (207)	1.7 (162)	8.0 (198)
Oct 2000	23.3 (54)	3.1 (60)	1.7 (45)
	17.0 (69)	2.0 (54)	0.3 (66)
	29.3 (54)	2.1 (54)	7.5 (68)
	2.7 (54)	4.6 (54)	2.5 (54)
	2.5 (54)		6.4 (54)
			3.3 (54)
			1.9 (54)
			0.6 (54)
Total	14.6 (285)	2.8 (222)	2.5 (449)
July 2001	2.6 (54)	9.8 (54)	2.3 (54)
	0.6 (54)	0.6 (54)	2.5 (54)
	9.1 (54)	3.0 (54)	2.0 (54)
	2.7 (54)	14.1 (54)	2.0 (54)
	9.8 (54)	4.0 (54)	6.2 (54)
Total	4.5 (270)	5.9 (270)	2.8 (270)
October 2001	3.2 (132)	0.1 (54)	10.1 (54)
	5.3 (168)	1.7 (36)	8.4 (54)
		4.1 (54)	13.3 (54)
		3.1 (54)	40.4 (54)
		11.5 (54)	23.7 (54)
			12.4 (54)
			13.4 (54)
			16.0 (54)
			12.4 (54)
Total	4.2 (231)	3.3 (144)	15.0 (968)

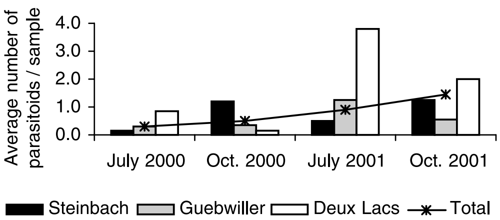

Figure 2. Average number of parasitoids (all species together) per sample in Steinbach, Guebwiller, and Deux Lacs at each sampling campaign.

(Figure 2). Percentage of samples colonised by parasitoids (all sites together) also increased with time (Figure 3), suggesting that parasitoids tend to spread more homogeneously between and within the attacked trees with time.

Mortality due to *C. bostrichorum* ranged from 0% to 22% per tree in our surveys. Mills (1983) reported that this species is the dominant parasitoid on *Ips amitinus* Eichh (Coleoptera: Scolytidae) and *I. typographus*

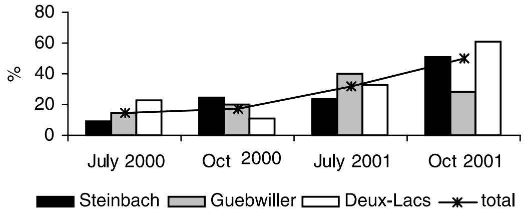

Figure 3. Percentage of samples colonized by parasitoids in Steinbach, Guebwiller, and Deux Lacs at each sampling campaign.

and that mortality could reach 50–95% on these host species. The other braconid, *D. middendorffi*, caused a maximum mortality rate of 2%. Among the Pteromalidae, *R. tutela* and *Roptrocerus* spp. showed the highest parasitism rates with 23% and 20%, respectively, while *D. eupterus* was only responsible for a maximum of 3.5% mortality. *Roptrocerus* spp. and *R. tutela* are widely distributed species found on several host species. *D. eupterus* seems to be a dominant parasitoid of *Pityogenes chalcographus* (L.) (Coleoptera: Scolytidae) (Mills 1983), another bark-beetle species very often associated with *I. typographus* and also present on the trees sampled.

Parasitoids relative abundance

Considering the relative abundance of parasitoids species in the three sites, *C. bostrichorum* dominated in Steinbach while *Roptrocerus* spp. were the most abundant species in Guebwiller and Orbey (Deux-Lacs) (Figure 4). This figure suggests that competing parasitoid species have developed long-term strategies allowing them to coexist. One or another species could be at one time favoured by climatic or stand-related conditions but this rarely leads to the exclusive presence of one species.

Conclusion

The population densities of *I. typographus* have increased in one year by 28–212%. This growth is bound to be limited by the carrying capacity of affected trees but, as local population levels are very high now, an unkown number of new trees (essentially standing spruces, as the windthrows have all been colonised or have become unsuitable), if available, can be attacked given favourable weather conditions. Wermelinger *et al*. (1999) reported that spruce bark-beetle densities peaked two years after the storm Vivian in

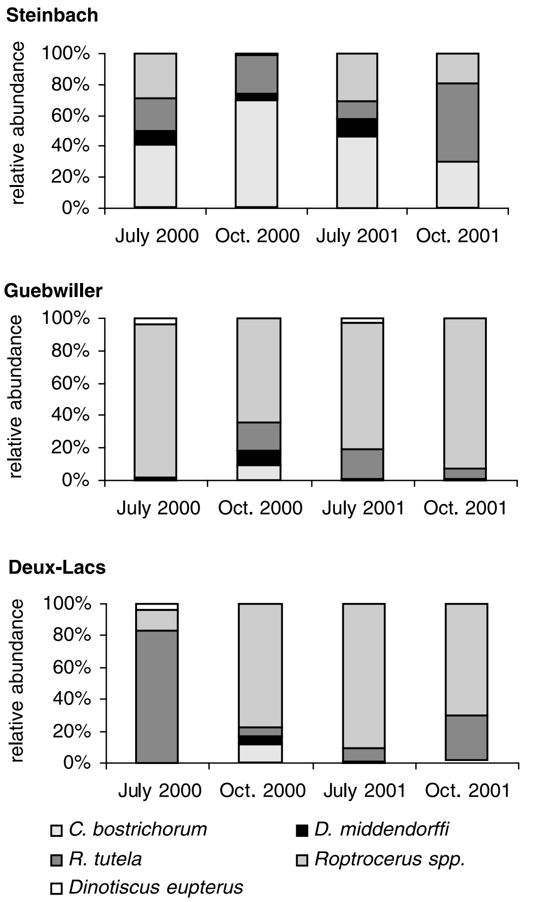

Figure 4. Specific relative abundance of parasitoids in Steinbach, Guebwiller, and Deux-Lacs.

February 1990 and then collapsed in the windthrow areas whilst in the adjacent stands the outbreak peaked one year later and continued for several years.

After two years and (probably) four host generations, the parasitoid populations in our study increased in terms of average density, but parasitism rates have remained at a relatively low level. Additional generations are probably needed before populations significantly increase and before efficient control of host population could be observed. The fact that this study started with low parasitoid numbers will provide a unique opportunity to follow population build-up in further generations.

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