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Development of the bark beetle (Scolytidae) fauna in windthrow areas in Switzerland

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In three windthrow areas in mountain spruce forests the succession of the insect fauna was investigated. Window traps were operated during the growing seasons from 1991 to 1994. The present contribution reports on the species composition and the dynamics of bark beetle population development. Two years after the storm, beetle densities reached their maximum and declined rapidly thereafter. Species numbers increased during the first two years and subsequently remained on an elevated level. A total of 34 species was found in the windthrow areas. The numbers of individuals as well as the species numbers reached higher levels in uncleared areas than both in cleared areas (timber removed) and in an adjacent intact spruce stand. The diversity index, however, varied more with location than with clearing treatment. During the first few years after the storm, species composition changed drastically: potential forest pests (*Pityogenes chalcographus*, *Ips typographus*) were dominant during the first two years. They were then replaced by secondary beetles such as *Crypturgus pusillus* and *Dryocoetes autographus*. After the storm Vivian the outbreak of the European spruce bark beetle (*I. typographus*) caused high mortality in standing spruce trees. In the windthrow areas spruce bark beetle densities peaked after two years and then collapsed. In the adjacent stands the outbreak peaked in 1993 and continued for several years.

Keywords: Scolytidae, bark beetles, outbreak, windthrow, storm, spruce, diversity

INTRODUCTION

In February 1990 the storm Vivian struck Central Europe and left behind large quantities of uprooted or broken trees. This event gave rise not only to enormous work dealing with clearing the damage but also to a controversy about the sense and purpose of clearing windthrows (BROGGI, 1990; SCHÖNENBERGER, 1993). The abundance of breeding material in Switzerland, 4.9 Mio. m^3 of timber (HOLENSTEIN, 1994), corresponding approximately to an annual cut, and the dry weather conditions led to the largest outbreak of the European spruce bark beetle (*Ips typographus*) in this century. This is reflected by the sanitation fellings due to *I. typographus* attack of another 2 Mio. m^3 between 1990 and 1995. All the sanitary measures during this period were subsidized by the Swiss federation with 350 Mio. Swiss francs (BFS, 1996). In addition, the storm triggered intensive research (SCHÖNENBERGER *et al.*, 1992, 1995; LÄSSIG *et al.*, 1995; KENTER *et al.*, 1997). Not only from economic and protective points of view but also from an ecological one, the development of bark beetle populations on windthrow areas is an important aspect in these long-term investigations. The present study was part of a faunistic monitoring program in windfall areas with two treatments, i.e. with (cleared) and without timber harvest (uncleared). Some results of this project were already published earlier (WER-

Tab. 1. Basic characteristics of the study sites.

Location	Altitude a.s.l. (m)	Size of experimental area (ha)	Timber volume in uncleared treatment (m^3)	Slope
Schwanden (GL)	1000	4	600	W
Pfäfers (SG)	1450	2	400	W
Disentis (GR)	1500	4	800	NW

MELINGER *et al.*, 1995). This article focuses on the composition and development of the Scolytid fauna during the first four years after the storm with respect to clearing treatments and weather conditions.

MATERIAL AND METHODS

Investigations were carried out in three windfall areas in mountain spruce forests in Switzerland. The locations are briefly characterized in Tab. 1 (see also SCHÖNENBERGER *et al.*, 1992). The windthrow areas were subdivided into a cleared and an uncleared part (two different treatments). In the former all the timber apart from the stumps was removed, while in the latter the fallen trees were left untouched. In addition, the location Schwanden included an adjacent intact spruce stand as a control plot. Every year from 1991 to 1994 three window (flight) traps were operated per treatment from the end of April until early October. They consisted of a wooden frame with a vertical glass pane (80x50 cm) 1.3 m above ground (a picture is given in WERMELINGER & DUELLI, 1994). The traps were regularly distributed across the study sites, and their orientation staggered by 60° each. The insects flying against the pane dropped and were caught in two plastic trays containing water and some traces of detergent and fungicide. The traps were emptied weekly during the whole season and the insects stored in 70 % alcohol until identification. Since the two species *Dryocoetes autographus* and *D. hectographus* were not distinguished from the beginning, they are treated as one single species in the multiseasonal analyses, namely as *D. autographus*. Both species, however, were observed in all three sites of investigation, with *D. hectographus* amounting to roughly 3 % of *D. autographus*. To test differences between the sites, treatments or years, analyses of variance (significance level 5 %) with subsequent Scheffe post-hoc tests were carried out (DataDesk, Data Description Inc.). For these analyses the numbers of individuals were log-transformed. Diversity was assessed by means of the Shannon-Weaver index (SOUTHWOOD, 1978). To evaluate climatic effects on the development of the spruce bark beetle (*I. typographus*), weather data from the Swiss Meteorological Institute were utilized from the stations closest to the study sites: Glarus (GL), Vättis (SG) and Disentis (GR). The heat sums relevant for the development of *I. typographus* were calculated as the sum of the daily accumulated heat degrees above the developmental threshold and expressed as day-degrees. According to WERMELINGER & SEIFERT (1998) this threshold amounts to 8.3°C.

Tab. 2. List of bark beetle (Scolytidae) catches in the three windthrow areas (both cleared and uncleared treatments. The control "forest" was excluded).

Species	1991	1992	1993	1994	Total
Cryphalus abietis (Ratzeburg)	852	1607	943	364	3766
Cryphalus intermedius Ferrari		11	6	1	18
Cryphalus piceae (Ratzeburg)		14	75	7	96
Cryphalus saltuarius Weise		24	21	8	53
Crypturgus cinereus (Herbst)		1			1
Crypturgus hispidulus Thomson		3	6	13	22
Crypturgus pusillus (Gyllenhal)	5	237	2016	1548	3806
Dendroctonus micans (Kugelann)	3	6	6	4	19
Dryocoetes alni (Georg)	5		3		8
Dryocoetes autographus (Ratzeburg) (incl. *D. hectographus* Reitter)	77	1424	2670	876	5047
Ernoporicus fagi (Fabricius)	3	1		12	16
Hylastes attenuatus Erichson		2			2
Hylastes cunicularius Erichson	183	883	718	338	2122
Hylastes opacus Erichson		1			1
Hylurgops glabratus (Zetterstedt)		8	1	4	13
Hylurgops palliatus (Gyllenhal)	29	351	464	32	876
Ips amitinus (Eichhoff)	6	96	28	9	139
Ips cembrae (Heer)		1		1	2
Ips typographus (Linné)	681	2461	1654	233	5029
Leperisinus fraxini (Panzer)	17		1	2	20
Orthotomicus laricis (Fabricius)	25	203	78	3	309
Phthorophloeus spinulosus Rey	38	36	46	61	181
Pityogenes bidentatus (Herbst)		1			1
Pityogenes chalcographus (Linné)	479	8475	4202	448	13604
Pityogenes conjunctus (Reitter)	33	126	203	47	409
Pityophthorus pityographus (Ratzeburg)	80	421	398	193	1092
Polygraphus poligraphus (Linné)	69	82	29	16	196
Tomicus minor (Hartig)			1		1
Trypodendron domesticum Stephens (=*Xyloterus domesticus* (Linné))		1		2	3
Trypodendron lineatum Eichhoff (=*Xyloterus lineatus* (Olivier))	404	1176	1578	82	3240
Xyleborus dispar (Fabricius)		26	43	121	190
Xyleborus germanus Blandford (=*Xylosandrus germanus* (Blanford))			2		2
Xylechinus pilosus (Ratzeburg)	8	4	3	5	20

RESULTS

Development of the number of species and individuals

A total of 34 species (including *D. hectographus*) with more than 40,000 individuals were caught in the windthrow areas (Tab. 2). The number of species markedly increased during the first years after the storm (Fig. 1A). It grew on average from 16 up to 21 species during the first two years and then remained at a constant high level. In the last two years (1993, 1994) species numbers were significantly higher than in 1991. While in Disentis and Pfäfers species numbers reached maximum values in the third year after the storm in most treatments, the value for Schwanden was an inexplicable outlier. Most of the species absent here were found in just small numbers at the other locations. *Orthotomicus laricis* and *Polygraphus poligraphus*, however, are the two species that are missing in Schwanden in 1993 but found in considerable numbers at the other locations.

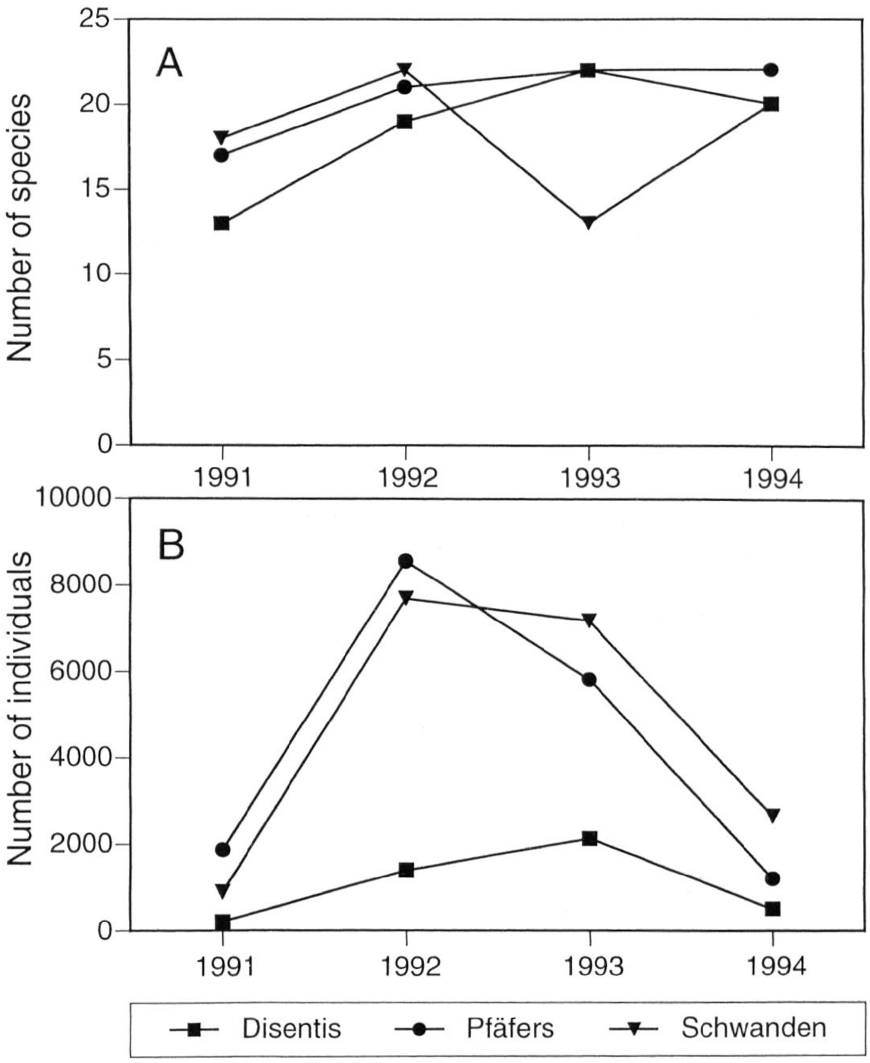

Fig. 1. Development of species numbers (A) and individual numbers (B) at three experimental sites during the first four years after the storm Vivian.

Tab. 3. Number of Scolytid species and individuals as well as the diversity index according to Shannon-Weaver (H) at the three experimental sites with two clearing treatments each and the control "forest" (Schwanden). For statistical significances see the text.

Location	Treatment	Year	Species	Individuals	H
Schwanden	uncleared	1991	18	644	1.653
		1992	18	5965	1.762
		1993	12	5359	1.565
		1994	18	2439	1.301
	cleared	1991	13	259	1.778
		1992	17	1736	1.445
		1993	12	1844	1.426
		1994	17	245	1.689
	forest	1991	12	208	1.522
		1992	15	4173	1.518
		1993	13	1646	1.721
		1994	17	908	1.463
Pfäfers	uncleared	1991	16	1459	1.902
		1992	19	7914	1.551
		1993	21	4539	1.965
		1994	19	934	2.120
	cleared	1991	13	418	1.542
		1992	16	661	1.846
		1993	18	1307	2.093
		1994	18	289	2.237
Disentis	uncleared	1991	10	111	1.658
		1992	18	730	1.943
		1993	21	1367	1.963
		1994	16	322	1.766
	cleared	1991	12	106	1.770
		1992	18	676	1.984
		1993	16	779	2.063
		1994	16	201	1.703

The Shannon index H (Tab. 3; large H = high diversity), calculated from the number of species and their abundance, is a measure of faunistic diversity. However, it reflects species number only up to a point because dominant single species depress the index. In Disentis the diversity index maximum in the uncleared treatment areas coincided in 1993 with the highest species number. In the cleared treatment areas species number in the same year was smaller, despite a maximal index. In Pfäfers H peaked only in 1994 and in Schwanden the indices showed no consistent pattern and remained at a lower level. No significant differences were found between years or clearing treatments, but there were differences between the experiment sites, namely between Schwanden (small index) and Pfäfers (large index).

The number of individuals developed in a different way from the number of species (Fig. 1B). After a sudden increase individual numbers peaked in 1992, i.e. two years after Vivian. Thereafter the numbers gradually declined. The densities of 1992 and 1993 significantly differ from those of 1991 and 1994 (cf. Tab. 3). This pattern is mainly determined by species relevant to forestry such as the European spruce bark beetle (*I. typographus*) and the six-toothed spruce bark beetle (*Pityogenes chalcographus*) (Tab. 2; Fig. 2) and is also reflected in the nationwide spruce bark beetle attack rates (cf. Fig. 4). Five years after the storm (1994) Scolytid abundance had returned to a low figure similar to the one in the first year, but still with elevated species diversity (Fig. 1). Bark beetle density depended on the location as well: Disentis showed significantly lower values than the two other locations (cf. section "European spruce bark beetle").

Clearing treatments

At each of the three experiment sites, the logs were not harvested in the uncleared treatment. The temporal development of the Scolytid fauna in the various treatments is shown in Tab. 3. While total species numbers in the different experiment sites developed in a more or less consistent manner (apart from Schwanden), the behavior of the two clearing treatments was less homogeneous. In both treatments the number of species started out low in 1991 and subsequently increased. In most cases, in uncleared areas both the number of species and the number of individuals clearly exceeded those on cleared areas. In general, the differences in individual numbers between the clearing treatments were highly significant with much higher beetle densities developing in uncleared areas. Furthermore, there were significant interactions between the factors treatment and location.

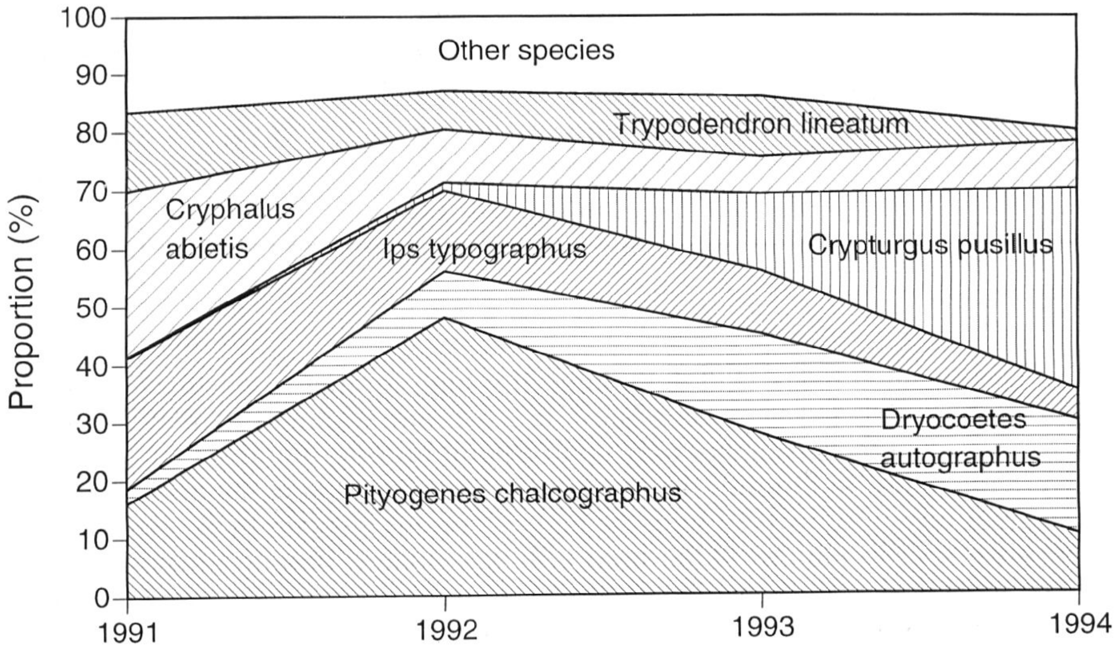

Fig. 2. Relative frequency of the six most abundant Scolytid species during the first four years after the storm Vivian (mean of the windthrows of three experimental sites).

In Schwanden, a control in the standing, intact forest can be compared (Tab. 3). It was in this stand that the lowest number of species was caught, although there were more individuals than in the cleared treatment. The bark beetle proliferation in the windthrow areas could be clearly discerned in the forest as well. From 1991 to 1992 the populations multiplied twentyfold. This might be attributed to endogenous populations developing in scattered windthrows in the stand, but it is also certainly the result of the migration of beetles away from the crowded windthrow areas into the adjacent forest stands (cf. DUELLI *et al.*, 1997). Migration might also explain the tendency towards an increase in the numbers of species.

Typical "forest species", i.e. species that were at least five times more abundant in the forest than in the windthrow areas and that were caught in substantial numbers, included mainly *Hylastes cunicularius* and *Xylechinus pilosus*. The latter was almost completely missing in the windthrows. The species that were virtually absent in the forest were *Crypturgus pusillus*, the two *Ips* species *I. typographus* and *I. amitinus* as well as *Xyleborus dispar*. The latter species colonizes broad leaf trees. Indeed, some beech and maple trees were present in the Schwanden windfall areas.

Succession of species

The 34 species found in this study correspond to approx. 30 % of the about 115 currently known Scolytid species in Switzerland (M. KNÍZEK, pers. comm.). Some of them were present only in small numbers (e.g. the species on deciduous trees). By far the most frequent species was the six-toothed spruce bark beetle (*P. chalcographus*), which formed 34 % of all specimens. Interestingly enough, this bark beetle species caused almost no lethal infestations of young living trees during this period. However, it did colonize the crowns of *I. typographus*-infested spruce trees. Over the years a succession of dominant species became evident. Fig. 2 depicts the relative frequency of the six most abundant species in the windthrow areas. The most frequent species at the beginning, namely *Cryphalus abietis*, was soon replaced by other species. This was primarily *P. chalcographus*, accounting for almost half of all Scolytids in 1992. Thereafter its proportion steadily declined, along with the European spruce bark beetle (*I. typographus*), which was the second most abundant species in 1992. They were replaced by *C. pusillus* whose population literally exploded, and by *D. autographus*. In 1994 *C. pusillus* contributed 35% of all individuals and will probably remain the dominant species for some time (KENTER *et al.*, 1997). These two species are pronounced secondary colonizers, as they are restricted to dead or strongly weakened trees. They replace the potentially damaging primary colonizers. The striped ambrosia beetle (*Trypodendron lineatum*), which is a potential pest in the sapwood, reached its numerical maximum in the third year (cf. Tab. 2). It may also be of interest that three specimens of *Xyleborus* (*Xylosandrus*) *germanus* were caught, a species which has been described in Switzerland only recently (MAKSYMOV, 1987). In the meantime it became a well-known pest on stored logs (JANSEN & FORSTER, 1991; GRAF & MANSER, 1996).

The European spruce bark beetle (I. typographus)

This species has been specially singled out as it is the most important from the forester's point of view. The development of its population parallels that of the total Scolytid numbers depicted in Fig. 1B. Fig. 3 shows in detail the seasonal swarming pattern at the three locations. Schwanden, the site with the lowest alti-

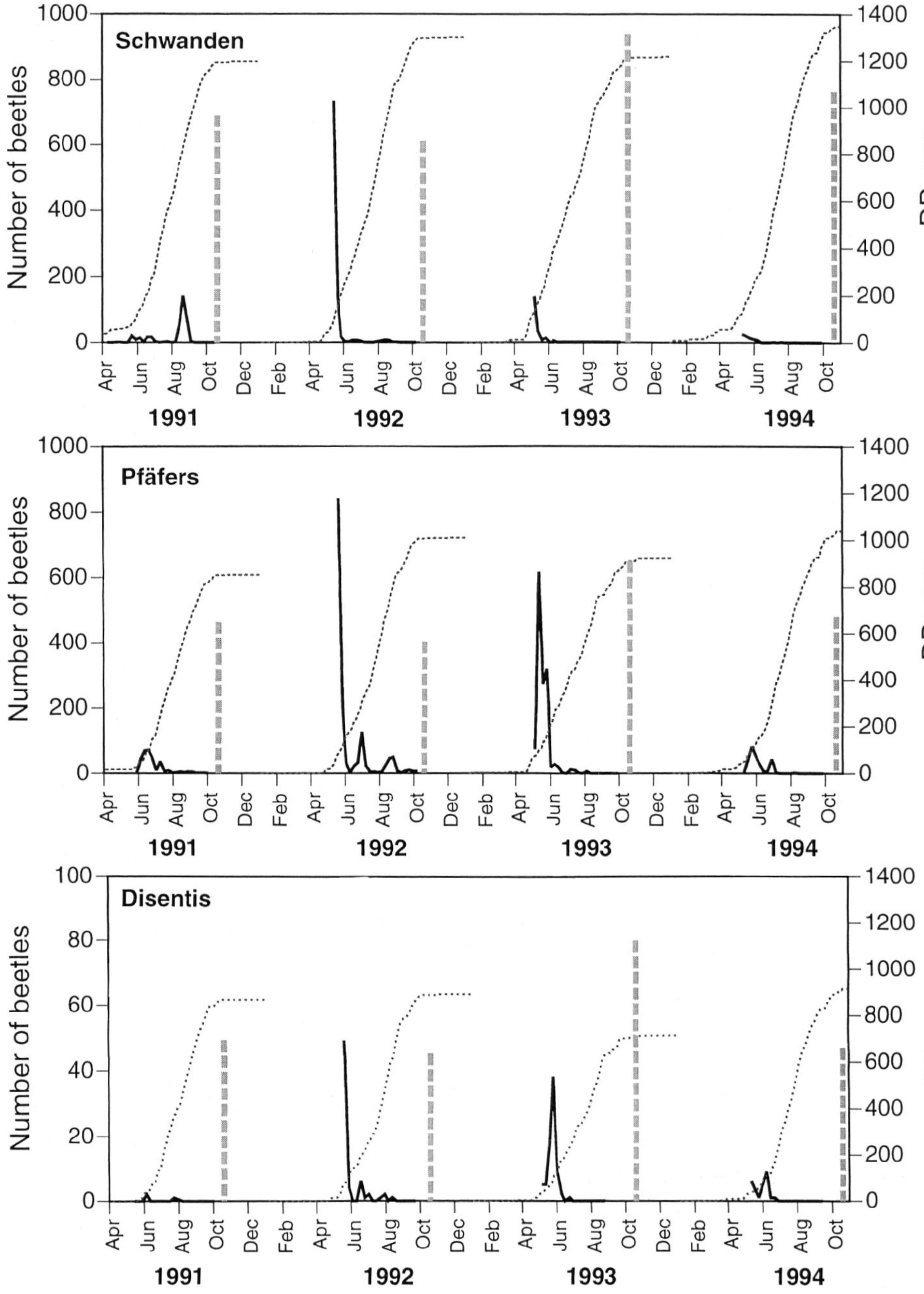

Fig. 3. Development of the densities of the European spruce bark beetle (*Ips typographus*) (solid line) during the first four years after the storm Vivian at three experimental sites (cf. Table 1). The dotted lines denote the heat sums above the developmental threshold of 8.3 °C in day-degrees (DD), the dashed bars represent total precipitation (mm) during the months April to October each year. Note that the scale of the y-axis for Disentis is different!

tude, was the only location in this study where two beetle generations, albeit in low numbers, were able to develop when there was a particularly warm spring in 1991. During the year 1991, the populations from the first to the second generation tripled, as they did from the second to next year's generation. The beetles emerging in August 1991 produced broods that must have almost completed their development in the same year. Evidence for this was the early swarming of their progeny in the spring of 1992. Out of the first three years after Vivian, it was the year 1992, which accumulated most day-degrees above the developmental threshold of *I. typographus* (Wermelinger & Seifert, 1998). Already one year later the *Ips*-densities in the windthrows had collapsed. The maximum in 1992 also holds for Pfäfers, but the outbreak did not stop as abruptly as it did in Schwanden. The small peaks in June and August 1992 were sister broods rather than true generations, i.e. broods that were established in other trees by the same parents after their first brood. Such sister generations may play a major role in the population dynamics in higher altitudes (Wermelinger & Seifert, 1999). The heat sums above the developmental threshold at the experimental sites in Pfäfers, 450 m higher than those in Schwanden, were approx. 20–30 % lower. Correspondingly, swarming in Pfäfers started later than in Schwanden. For the other years, especially for the warm year 1992, swarming could not be recorded when it first began because snow made the experimental areas inaccessible.

The location Disentis is a special case. Beetle densities were one or two orders of magnitude below those at the other locations (note the different scales of the y-axes in Fig. 3!). Not only was the site in Disentis at the highest altitude, but it was also located within Switzerland's largest windthrow area comprising 125 ha (Holenstein, 1994). This means that, in the vicinity of 500–1000 m, there were no more standing trees, from which *I. typographus* could have emigrated. The same is true, of course, for other bark beetle species. In addition, the latent population density must have been small before the storm: in 1991 just three individuals of spruce bark beetles were caught! Before these small numbers could develop into large populations, many of the sun-exposed logs in the large windthrow area were desiccated without being attacked by the spruce bark beetle. However, outbreaks of this beetle did occur in other windthrow areas and in remaining stands in the region of Disentis.

DISCUSSION

Scolytids form a guild that differs from most other saproxylic insect groups. While the adults of many other Coleoptera, Hymenoptera or Diptera that inhabit dead wood rely on, e.g. flowers as a food source, the food requirements of adults and larvae are for most bark beetles identical. For them the initially increased supply of blossom on cleared windthrows (Jehl, 1995) made no difference. This explains why almost all species were clearly more abundant on uncleared areas with much more dead wood than in the cleared treatments.

In the windthrows under study beetle densities peaked in the second year after the storm. Other investigations at lower altitudes have reported that peaks of species relevant to forestry (*I. typographus*, *P. chalcographus*, *T. lineatum*) occurred 1–2 years earlier (Kopf & Funke, 1998a, 1998b; Schröter *et al.*, 1998). Besides the numerical population development, a succession of bark beetle species took place. A windthrow provides a variety of bark humidities, bark thicknesses, sun expositions and other conditions which are exploited differently by various species.

First the pioneer species were those that colonized fresh bark or even living weakened trees, followed by those that were specialized in desiccated bark or were pure xylem dwellers. *C. pusillus* was a species characteristically found in windfalls that were more than two years old (cf. KOPF & FUNKE, 1998a). The list of the most common species coincides fairly well with those reported for the Bavarian Forest after windthrows (SCHOPF & KÖHLER, 1995). The initial increase in species numbers is a consequence of the availability of ample breeding facilities for numerous species. Thereafter, a large quantity of diverse substrates kept the species number at a high level (Fig. 1A).

The standing forest appears to have low numbers of both species and individuals. It was not until bark beetle populations in the adjacent windthrows had built up that the number of species in the forest began to increase. It is true, however, that some species found only in the windthrows were probably present in the forest as well, but in such low numbers that it was unlikely that they would be caught. Compared to windthrow areas the standing forest is also poor in other animal taxa (cf. OTTE, 1989a, 1989b; WERMELINGER *et al.*, 1995; DUELLI & OBRIST, 1999). The Shannon index, a measure of diversity, revealed no consistent tendencies. The patterns in its development over time were heterogeneous with respect to both regions and clearing treatments. The index varied more with location than with treatment or time.

The density peak in the second year after Vivian can be largely attributed to those species that are relevant to forestry such as *C. abietis*, *H. cunicularius*, *I. typographus*, *P. chalcographus* and *T. lineatum*. Living trees were attacked exclusively by *H. cunicularius* in young, planted or naturally regenerated spruce stands around Disentis (MEIER *et al.*, 1995a) and, of course, by *I. typographus* in older spruce stands. The latter caused pronounced damage all over Switzerland (cf. MEIER *et al.*, 1995b). Its rapid population growth was favored by the first two years after the storm

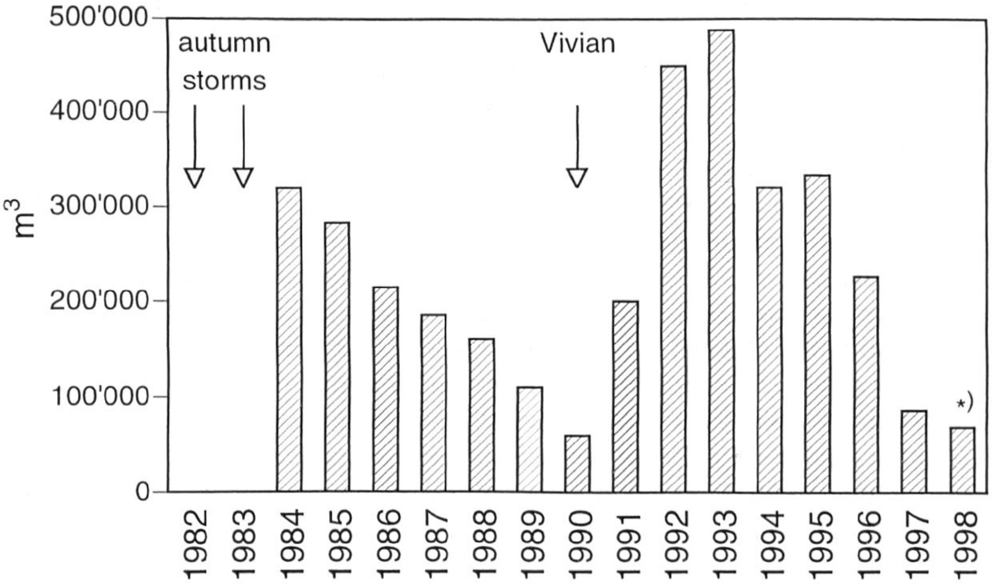

Fig. 4. Total sanitation fellings in Switzerland due to the European spruce bark beetle (*Ips typographus*). Data courtesy of the Forest Insect and Disease Survey PBMD/WSL.
*) Estimate based on summer fellings.

being warm and dry (cf. Fig. 3). The development of population densities in the windthrow areas is also reflected in the total Swiss sanitation fellings (Fig. 4). These are quantified as the timber volume of trees cut for phytosanitary reasons to eliminate *I. typographus* broods underneath the bark. Immediately after returning to "normal" minimum levels at the end of the outbreak in the eighties, which had been caused by storms and dry years, sanitation fellings sharply increased again after Vivian. The peak in population density in 1992 in the windthrow areas led to a large number of sanitation fellings in the surrounding spruce stands one year later. The enormous population pressure and the fact that breeding material in the windfalls had been desiccated in the meantime forced the beetles to switch over to weakened or even to apparently healthy trees. Fallen trees with their roots still partly in contact with the soil, or shaded scattered windthrows retained their attractiveness for beetle colonizers for a longer period (DEMLEITNER, 1964; FORSTER, 1993). Higher levels of precipitation during the following years enabled the weakened trees to recover and to resist the penetration attempts of the beetles better. The wet weather conditions probably also permitted the antagonists (parasitoids, predators, and fungi, cf. KOPF & FUNKE, 1998b) to control more effectively the bark beetles that lingered longer in their galleries. Eventually, these factors in combination led to the collapse of the spruce bark beetle outbreak. In spite of its extremely high population densities, *P. chalcographus* astonishingly did not create problems in younger stands.

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ZUSAMMENFASSUNG

Auf drei 1990 vom Sturm Vivian verursachten Windwurfflächen in Schweizer Gebirgsfichtenwäldern wurden von 1991 bis 1994 jeweils während der Vegetationsperiode regelmässig Insektenfallen betrieben. In diesem Beitrag werden die Zusammensetzung und Entwicklung der Scolytidenfauna diskutiert. Ein Maximum der Populationsdichten wurde 1992 zwei Jahre nach dem Sturm erreicht. Danach fielen die Käferzahlen schnell wieder ab. Die Artenzahl stieg in den ersten zwei Jahren an und blieb danach erhöht. Insgesamt wurden 34 Arten gefundenen. Sowohl die Individuenzahl als auch die Artenzahl war auf den nicht geräumten Teilflächen – infolge des grösseren Brutangebots – deutlich höher als auf den geräumten Flächen oder im stehenden Wald. Dies schlug sich jedoch nicht im Shannon-Weaver-Diversitätsindex nieder, der v.a. zwischen den Versuchsorten variierte. Die Artenzusammensetzung änderte sich im Laufe der Zeit stark: Dominierten zu Beginn noch die potentiellen Forstschädlinge (*Pityogenes chalcographus*, *Ips typographus*), wurde die austrocknende Rinde bald von Sekundärbewohnern wie *Crypturgus pusillus* und *Dryocoetes autographus* besiedelt. Der Buchdrucker (*I. typographus*) durchlief in den Jahren nach Vivian eine Massenvermehrung mit eindrücklichen Folgeschäden. Zwei Jahre nach dem Sturm erreichte er auf den untersuchten Windwurfflächen seine höchste Dichte, danach fiel sie schnell zusammen. In den angrenzenden Waldbeständen dauerte die Gradation jedoch länger an.

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