

J. Appl. Ent. 119, 9–15 (1995)
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 ISSN 0931-2048

Abundance and emergence of spruce cone insects in different parts of Switzerland

B. Wermelinger, J. v. Hirschheydt and B. Fecker

Swiss Federal Institute for Forest, Snow and Landscape Research, Department of Landscape Ecology, Birmensdorf, Switzerland

Abstract: In 1989 a total of 4471 spruce cones was harvested at 29 locations distributed over the five main geographic regions of Switzerland, i.e. Jura, Central Plateau, North, Central and South Alps. The cones were incubated in a controlled environment chamber and the emerging insects were collected and identified. This analysis excludes parasitoids except for the most abundant *Torymus* spp. Twelve insect species and some 14 000 individuals in total were identified. On the average, every cone was inhabited by three insects. The most numerous species were *Kaltenbachiola strobi* (Winn.), *Cydia strobilella* (L.), and *Torymus* spp., amounting together to 95% of the total insect number. Though the abundance peaks varied for different species, most insects were reared from cones from the alpine area. Vegetation type (alliance) was related to the abundance of several species but did not correlate with total infestation rate. For two species their number was related to sampling site altitude. Likewise, a positive, linear correlation was found between the frequencies of the parasitoid *Torymus* spp. and its host *K. strobi*, the ratio between the two species averaging 0.7. Cone setting did not correlate with infestation level, but tree age was positively related to total insect number per cone.

In the laboratory *C. strobilella* and *K. strobi* were the earliest species to emerge; they had the shortest emergence period as well. The percentage of *K. strobi* with prolonged diapause (emergence in second year after cone sampling) was 51%, while the corresponding values for all other species were lower than 20%. Neither sampling site elevation nor cone setting affected diapause length.

1 Introduction

From flower formation up to cone maturation reproductive organs of conifers are subject to attacks by numerous phytophagous insects which in turn are themselves the target of antagonists. A number of studies describes the insect fauna inhabiting spruce (*Picea abies* (L.) Karst.) cones. As far as Europe is concerned, extensive investigations have been made in Germany (HOLSTE, 1922), Norway (BAKKE 1955; SKRZYPCZYŃSKA 1987), France (ROQUES, 1977, 1983; DA ROS et al., 1993) and Poland (SKRZYPCZYŃSKA, 1982). For Switzerland MADZIARA-BORUSIEWICZ (1963) published a short, non-quantitative study. Most of the typical species living in spruce cones were found in all of these studies. Although insects can account for significant reduction of the reproductive capacity of conifers (MATTSON, 1978), seed losses caused by insects are, unlike in other countries (BARBOSA and WAGNER, 1989), not considered a significant problem in Switzerland. TURGEON et al. (1994) published a synopsis on ecology and management of cone insects.

The goals of this study were to investigate species spectrum, abundance, distribution and emergence dynamics of the cone inhabiting insect guild in Switzerland and to search for quantitative relations between infestation levels of conophagous species and site specific parameters such as altitude, phytosociological classification, tree age and cone setting. Parasitoids, except the most abundant *Torymus* spp., were excluded

from this report. An analysis of seed losses caused by insects will be published later.

1.1 Biology of some frequent cone insects

The biology of the three most common phytophagous cone insects and the most frequent parasitoid is briefly summarized below, basing mainly on BARNES (1951), BAKKE (1955, 1963) and ROQUES (1983).

Kaltenbachiola strobi (Winn.) (Cecidomyiidae, Dipt.) spruce cone gall midge, Fichtenzapfenschuppen-Gallmücke. The female gall midge deposits her eggs during the pollination period of the flowers (May/July) between the scales near the cone spindle. The hatched larvae penetrate into the scales and feed on the tissue moving in the direction of the cone axis. The last larval instar overwinters in a cocoon and, after pupation in May, the adults leave the scales by a hole previously prepared by the larvae. Larval diapause of several seasons may occur. The damage by this gall midge is restricted to the fact that the opening of the scales and therefore the release of the seeds may be hindered by excessive resin formation at high infestation levels.

Asynapta strobi (Kieff.) (Cecidomyiidae, Dipt.) (= *Camptomomyia strobi*, = *Rübsaamenia strobi*). Little is known on the biology of this phytosaprophagous species. It overwinters as larva, the adults emerge in May/June. The larvae develop in or on the cones and pupate in white cocoons. The larvae do not make galls or attack the seeds but may induce resin flow.

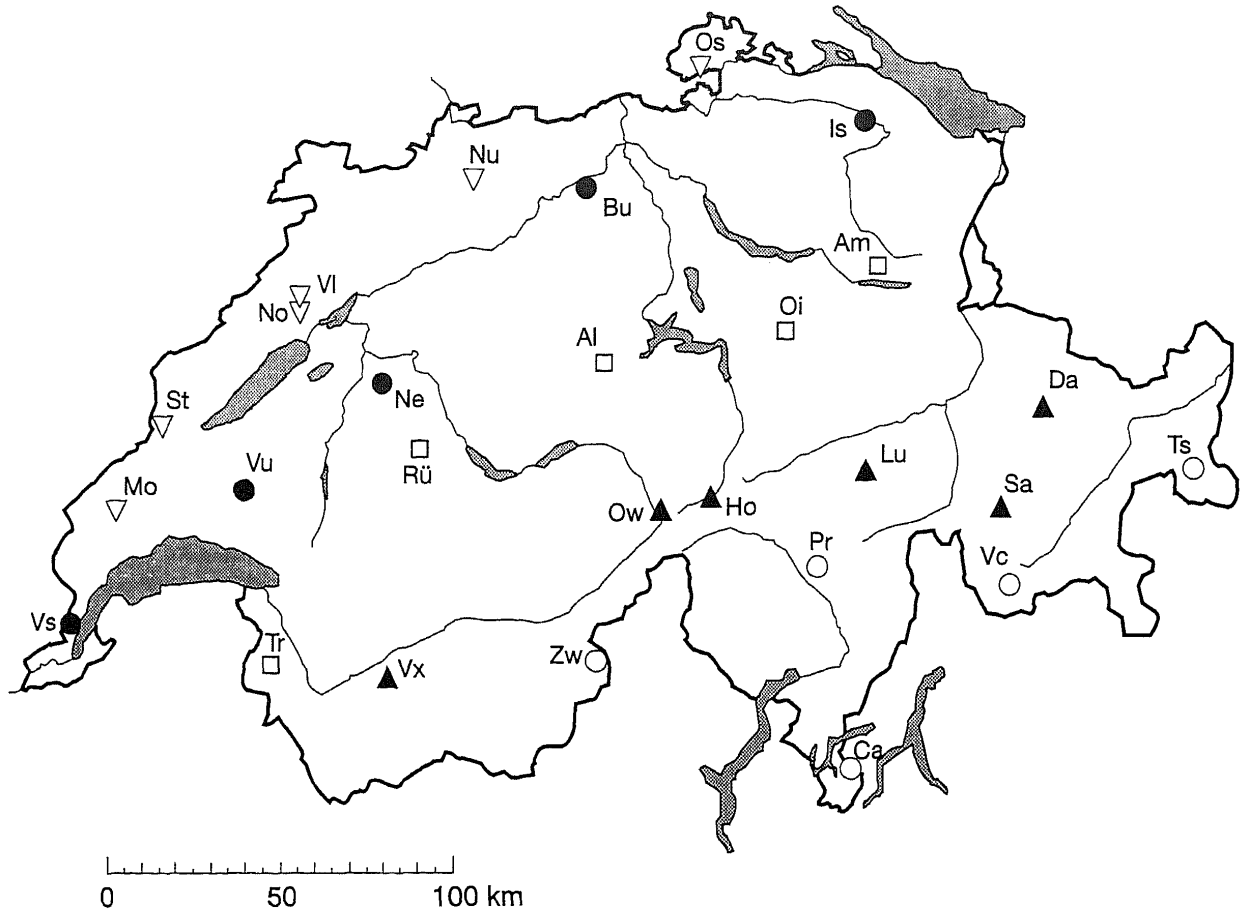


Fig. 1. Distribution of sampling sites in Switzerland; ∇ = Jura, \bullet = Central Plateau, \square = North Alps, \blacktriangle = Central Alps, \circ = South Alps, location abbreviations see table 1

Cydia strobilella (L.) (Tortricidae, Lep.) (*Laspeyresia strobilella*), spruce cone moth, spruce seed worm, Fichtenzapfenwickler. Eggs are laid at the scale basis at the end of the pollination period (June/July). After hatching, the first larval instar moves within the scale towards the cone axis, the next two instars feed on the seeds and the fourth instar develops and overwinters in the cone spindle. Pupation occurs in April/May and the adults leave the cones by holes prepared by the larvae in May/June. The last larval instar undergoes a diapause of 1–3 years. *C. strobilella* can significantly contribute to seed losses.

Torymus spp. (Torymidae, Hym.). The biology of *T. azureus* (Boh.) and *T. caudatus* (Boh.) is very similar and the following description is valid for both species (after DUMČIUS, 1986). *Torymus* is a significant parasitoid of *Kaltenbachiola strobi*. By means of her long ovipositor the female lays one egg into a host larva where the hatched parasitoid larva accomplishes its development. Pupation takes place in the host cocoon. The adults emerge later than *K. strobi*. Some larvae may diapause 1 or 2 years.

2 Materials and methods

From August to mid-October 1989 spruce cones were harvested at 29 locations distributed all over Switzerland. The sites were selected among pure, fructifying spruce stands of good vitality, evenly spread over the five major geographic regions, Jura Mountains, Central Plateau, North Alps, Central Alps and South Alps (fig. 1). They covered the cor-

responding altitudes of 600–1600, 370–740, 1190–1800, 1600–2000 and 1560–1900 m above sea level, respectively. From five spruce trees per location some 20% of their total cone number were harvested using a 'tree bicycle' (Baumvelo). Because of lacking cones in 1989 three places were harvested in 1990 which was a year of high spruce fructification (ANON. 1991, 1992). The number of harvested cones per tree varied between 9 and 170 (cf. table 1). At each site a vegetation relevé was conducted and the phytosociological association (forest community) determined. The associations were combined to alliances (Verbände) according to ELLENBERG and KLÖTZLI (1972). The most frequent alliances were 1) the Abieti-Fagion = fir-beech forests, 2) the Eu-Fagion = beech forests, 3) the Piceo-Abietion = spruce-fir forests, and 4) the Vaccinio-Piceion = blueberry-spruce forests. The harvest index of each tree was evaluated according to ROHMEDER (1972, p. 64). Wood core samples were taken from all trees and the age of each tree was determined.

The cones were stored in a sheltered place at outside temperatures up to next February. Subsequently, all cones of one tree were placed in photo-electors consisting of cardboard boxes with transparent plastic tubes. They were kept in an environmental chamber at 5°C. In May temperatures were gradually increased to 20°/10°C day/night at 75% rh. After the emergence period a chilling period of 2 weeks at –5°C was interposed and the same procedure was repeated in 1991 and 1992 to catch diapausing insects. The emerging adults were daily removed, recorded and subsequently identified. Because the males of *Torymus azureus* and *T. caudatus* are difficult to discriminate, they were analysed together. The boxes were checked after every annual emergence period for insects not trapped in the tubes. As a consequence of by harvest time, insects that had left the cones in summer were not caught.

Table 1. Specifications of sampling sites, average tree age, harvest index (100 = 600 cones/tree = heavy crop), number of cones harvested, numbers of insect species and individuals

Location	Altitude [m asl]	Slope	Phytosociological association ¹	Phytosoc. alliance ^{1,2}	Tree age [years]	Harvest index	Number of cones	Number of species	Number of insects	
Montricher VD	Mo	1600	SE	Dryopterido-Abietetum	P-A	168	30	200	6	192
Ste-Croix VD	St	1510	NNW	Sorbo-Aceretum	Til-Ac	98	20	120	6	599
Nods BE	No	1490	SE	Sorbo-Aceretum/Dryopterido-Abietetum	Til-Ac	148	20	170	5	219
Villeret BE	Vi	1460	NW	Aceri-Fagetum	A-B	131	10	120	4	298
Osterfingen SH	Os	600	NNE	Cardamino-Fagetum typicum	B	120	20	90	6	374
Nunningen SO	Nu	870	S	Abieti-Fagetum typicum	A-B	48	20	130	5	32
Jura							830	8	1714	
Neuenegg BE	Ne	640	N	Galio odorati-Fagetum typicum	B	105	20	109	6	807
Buchs AG	Bu	370	—	Galio odorati-Fagetum typicum	B	88	10	90	5	274
Istighofen TG	Is	450	NW	Galio odorati-Fagetum typicum	B	86	10	70	5	406
Versoix GE	Vs	450	—	Lathyro-Quercetum	Q	—	40	290	5	239
Vulliens VD	Vu	740	SW	Galio odorati-Fagetum typicum	B	—	40	280	5	284
Central Plateau							839	8	2010	
Troistorrents VS	Tr	1800	W	Adenostylo-Abietetum	P-A	109	30	150	6	564
Rüschegg1 BE	Rü	1680	S	Equiseto-Abietetum	P-A	130	10	90	7	611
Rüschegg2 BE	Rü	1190	—	Bazzanio-Abietetum	P-A	67	20	150	5	146
Alpnach OW	Al	1620	S	Sphagno-Piceetum calamagrost. vill.	V-P	121	20	150	7	188
Oberiberg SZ	Oi	1390	W	Aceri-Fagetum	A-B	65	10	60	8	427
Amden SG	Am	1510	WNW	Sphagno-Piceetum calamagrost. vill.	V-P	174	10	110	7	803
North Alps							710	8	2739	
Vex VS	Vx	1950	NE	Sphagno-Piceetum calamagrost. vill.	V-P	112	40	260	5	1127
Oberwald VS	Ow	1750	—	no forest community (playground)	—	89	50	281	4	187
Hospental UR	Ho	1580	NW	Adenostylo-Abietetum	P-A	92	10	110	5	229
Lumbrein GR	Lu	1900	SSE	Sphagno-Piceetum calamagrost. vill.	V-P	139	20	131	4	364
Savognin 1 GR	Sa	1800	NE	Adenostylo-Abietetum	P-A	155	50	310	7	1718
Savognin 2 GR	Sa	1600	NNE	Adenostylo-Abietetum	P-A	83	10	70	6	539
Davos GR	Da	2000	SW	Sphagno-Piceetum calamagrost. vill.	V-P	137	30	200	4	66
Central Alps							1362	9	4230	
Zwischbergen VS	Zw	1800	SW	Sphagno-Piceetum calamagrost. vill.	V-P	117	30	160	8	276
Castel San Pietro TI	Ca	1560	ESE	Calamagrostio villosae-Abietetum	P-A	81	20	100	5	37
Prugiasco TI	Pr	1750	E	Sphagno-Piceetum calamagrost. vill.	V-P	148	30	230	7	236
Vicosoprano GR	Vc	1620	SSO	Calamagrostio villosae-Abietetum	P-A	173	20	120	6	883
Tschierv GR	Ts	1900	NNO	Larici-Piceetum	V-P	335	20	120	8	1678
South Alps							730	10	3110	
Total							4471	12	13 803	

¹ After ELLENBERG and KLÖTZLI, 1972² A-B Abieti-Fagion; B Eu-Fagion; P-A Piceo-Abietion; Q Quercion pubescenti-petraeae; Til-Ac Tilio-Acerion; V-P Vaccinio-Piceion.

Results were calculated in terms of the number of insects per cone, except for the very rare species. The systematic terminology follows the taxonomic checklist of YATES (1986). Weighted data were analysed by the ANOVA procedure and means were separated by Tukey's test (SYSTAT[®] package).

3 Results

3.1 General

Table 1 lists all site-specific characteristics. The phytosociological association describes the habitat and its potential vegetation, but not the actual tree species composition. The harvest index, i.e. fructification of the spruce trees, was low to medium for all plots. A total of 11 conophagous and seminiphagous species was found plus one parasitoid (*Torymus* spp.) determined, amounting to almost 14 000 individuals. Insect species found in this study, besides the ones described in the introduction, were *Eupithecia abietaria* Goeze (Geometridae, Lep.; Zapfenspanner); *Dioryctria abietella* (Den. et Schiff.) (Pyralidae, Lep.; spruce cone pyralid, Fichten-

zapfenzünsler); *Cydia illutana* (H.-S.) (Tortricidae, Lep.); *Gastroles abietum* Berg. (Lygaeidae, Het.; Fichtenzapfenwanze); *Ernobius angusticollis* (Ratz.), *E. abietis* (F.), *E. abietinus* (Gyll.) (Anobiidae, Col.; Fichtenzapfennagekäfer), and *Plemeliella abietina* Seitr. (Cecidomyiidae, Dipt.; Fichtensamengallmücke). Most of the parasitoid complex is still unidentified (approx. 10–15 species).

3.2 Emergence dynamics

The emergence dynamics of the four most frequent species is depicted in fig. 2. Starting day is defined as the point in time when the temperature in the growth chamber reached 10°C in the 1-week course of the gradual temperature increase from 5°C to 20°C. This is 3 days before reaching the final day temperature of 20°C. The dynamics of the four most frequent species differed. The tortricid *Cydia strobilella* and the cecidomyid *Kaltenbachiola strobi* were the first to emerge, followed by the parasitoids *Torymus* spp. with a 2-week delay. These

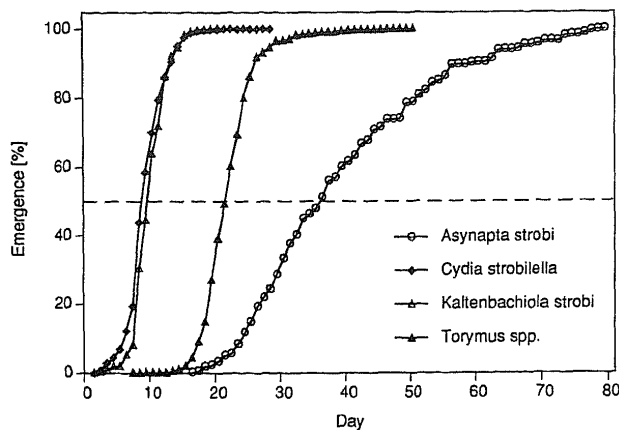


Fig. 2. Temporal dynamics of emergence of *Asynapta strobi*, *Cydia strobilella*, *Kaltenbachiola strobi*, and *Torymus* spp. in a growth chamber relative to an arbitrary starting day (see text)

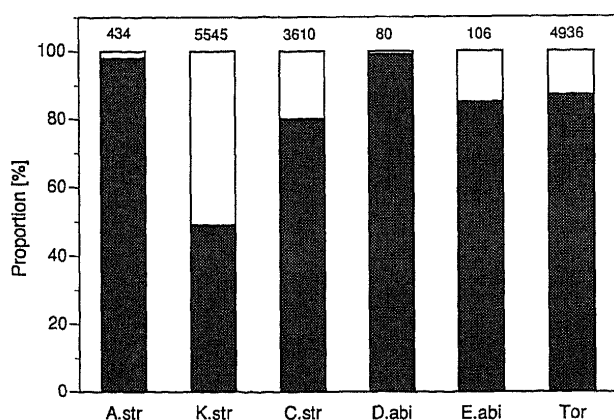


Fig. 3. Prolonged diapause: proportion of insects emerging after 1 (dark) or 2 (light) years; n = total number of insects (*A.str* *Asynapta strobi*, *K.str* *Kaltenbachiola strobi*, *C.str* *Cydia strobilella*, *D.abi* *Dioryctria abietella*, *E.abi* *Eupithecia abietaria*, *Tor* *Torymus* spp.)

three species showed a short emergence period of 4–6 weeks. In contrast, the cecidomyid *Asynapta strobi* appeared on average another 2 weeks later (50% level) and emergence was scattered over 9 weeks. For all species, there were only small, inconsistent differences of average emergence time between the five geographic regions.

Fig. 3 shows the proportion of insects diapausing 1 or 2 years, respectively (i.e. emergence in first or second year after cone sampling). 51% of *K. strobi* did not emerge before 2 years (prolonged diapause), whilst in the other species the proportion was notably smaller (*C. strobilella* 20%, *Eupithecia abietaria* 15%, *Torymus* 13%, *A. strobi* 2%, *Dioryctria abietella* 1%). Two individuals of *Torymus* did not appear before 3 years. For five species the rates did not differ between the geographic regions while *K. strobi* tended to have higher second-year emergences in the Central Plateau and Central Alps. The incidence of prolonged diapause did not significantly correlate with either plot altitude or cone setting.

3.3 Species abundance

The number of insects per cone summarized for the respective regions is listed in table 2. The two most

abundant species were *K. strobi* and *Torymus* spp., averaging more than one individual per cone. *K. strobi* made up 40% of the total insect number, *Torymus* 29%. The vast majority of *Torymus* spp. was *T. azureus*. Only a few individuals of the easily discriminated females of *T. caudatus* were found, most of them from the Central Plateau. Likewise *C. strobilella* was frequent (26% of total number), while *A. strobi*, *E. abietaria* and *D. abietella* were more sparse. Six further species were found only as isolated specimen. *Ernobius* spp. seem to attack shed cones rather than cones still attached to the trees. It has to be noted that the occurrence of only one single individual of *Plemeliella abietina* is an artefact (discussed below). The total infestation levels per cone ranged from 0.02–51.3 individuals.

The comparison of the insect abundance in different regions reveals a non-uniform pattern for the different species. Three species peaked in locations in the South Alps, and three species were lowest in the Central Plateau. Overall, the trees of the north and mainly the south parts of the Alps were more heavily infested by cone insects than the others. These areas possessed the highest number of species as well (table 1). On the average, every cone was inhabited by three individuals.

Furthermore, insect abundance was related to the phytosociological classification of the sites (table 3). The four most frequent alliances were compared with each other in terms of insect infestation levels. *C. strobilella* showed the highest numbers in the Eu-Fagion, which generally deviated most from all other alliances in terms of insect densities.

The parasitic behavior of *Torymus* on *K. strobi* is underpinned by the linear relationship between the log-transformed abundance of the two species (fig. 4). The correlation yielded an approximate parasitoid/host ratio of roughly 0.7. However, this relationship is the result of only a few data pairs at elevated insect numbers, mainly from the South Alps. No differences in parasitization rate between different regions were found.

A correlation was also found between the abundance of *K. strobi* and the altitude of the sampling site (fig. 5). Likewise a corresponding relationship goes for *Torymus*, while *C. strobilella* showed a slight negative dependence on altitude. The meaning of these findings is discussed below. The value from the plot 'Tschier' was identified as an outlier and discarded. There were no negative correlations (competition) between species abundance.

Tree age and infestation level were also interrelated. Older trees had a higher number of total insects per cone than younger ones [$(n = 0.053 * \text{age} - 2.10, R^2 = 2.39, \text{graph not shown})$].

The hypothesized correlation between cone setting and insect infestation level was tested and rejected. The visual trend of higher infestation levels in trees of a low cone crop could be confirmed neither for single species nor for total insect number.

4 Discussion

The temporal order of emergence found in this laboratory study confirms the field observations of BAKKE

Table 2. Species spectrum and number of conophagous insects and of one parasitoid reared from spruce cones from the five main geographic regions of Switzerland (individuals/cone and number of individuals (n), respectively)

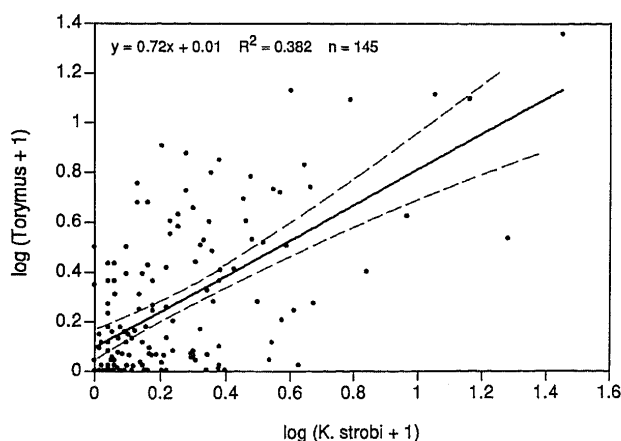
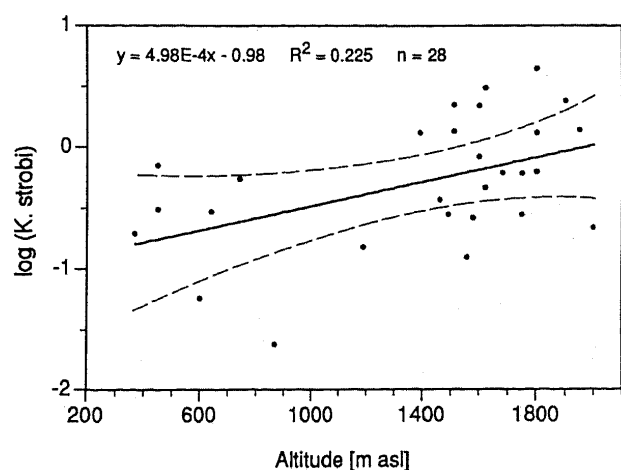
Species	Family	Jura	Central Plateau	N-Alps	C-Alps	S-Alps	All regions
<i>Asynapta strobi</i>	Cecidomyiidae	0.291 ^a	0.067 ^b	0.132 ^b	0.009 ^b	0.046 ^b	0.10
<i>Kaltenbachiola strobi</i>	Cecidomyiidae	0.50 ^a	0.50 ^a	0.91 ^{ac}	1.68 ^{bc}	2.45 ^b	1.24
<i>Cydia strobilella</i>	Tortricidae	0.44 ^a	1.31 ^b	0.78 ^{ab}	0.59 ^a	1.06 ^{ab}	0.81
<i>Dioryctria abietella</i>	Pyralidae	0.030 ^a	0.013 ^{ab}	0.021 ^{ab}	0.002 ^b	0.036 ^a	0.02
<i>Eupithecia abietaria</i>	Geometridae	0.026 ^{ac}	0.001 ^b	0.034 ^{ac}	0.018 ^{ab}	0.049 ^c	0.02
<i>Torymus</i> spp.	Torymidae	0.73 ^a	0.51 ^a	1.96 ^b	0.80 ^a	1.88 ^b	1.10
<i>Cydia illutana</i> [n]	Tortricidae	1	0	4	3	0	8
<i>Ernobius angusticollis</i> [n]	Anobiidae	1	4	0	0	2	7
<i>Ernobius abietis</i> [n]	Anobiidae	0	0	0	0	1	1
<i>Ernobius abietinus</i> [n]	Anobiidae	0	0	0	0	1	1
<i>Gastrodes abietum</i> [n]	Lygaeidae	0	3	2	1	0	6
<i>Plemeliella abietina</i> ¹ [n]	Cecidomyiidae					1	
Total insects		2.03 ^a	2.40 ^a	3.86 ^{ab}	3.11 ^a	5.52 ^b	3.09

^{a,b,c} Means with different letters within a row differ significantly from each other (P < 0.05%, ANOVA, Tukey's test);
¹ actually more abundant, cf. discussion in text

Table 3. Mean number/cone of the most abundant conophagous insects and of one parasitoid reared from spruce cones originating from different phytosociological alliances (A-B Abieti-Fagion; B Eu-Fagion; P-A Piceo-Abietion; V-P Vaccinio-Piceion)

Species	Family	A-B	B	P-A	V-P
<i>Asynapta strobi</i>	Cecidomyiidae	0.073 ^a	0.086 ^a	0.058 ^a	0.037 ^a
<i>Kaltenbachiola strobi</i>	Cecidomyiidae	0.395 ^{ab}	0.349 ^b	1.776 ^a	1.781 ^a
<i>Cydia strobilella</i>	Tortricidae	0.632 ^a	2.174 ^b	0.742 ^a	0.760 ^a
<i>Dioryctria abietella</i>	Pyralidae	0.013 ^{ab}	0.044 ^a	0.025 ^{ab}	0.009 ^b
<i>Eupithecia abietaria</i>	Geometridae	0.007 ^a	0.011 ^a	0.035 ^a	0.034 ^a
<i>Torymus</i> spp.	Torymidae	1.222 ^a	0.691 ^a	1.146 ^a	1.550 ^a
Total		2.352 ^a	3.364 ^a	3.784 ^a	4.177 ^a

^{a,b,c} Means with different letters within a row differ significantly from each other (P < 0.05%, ANOVA, Tukey's test).

**Fig. 4.** Relationship between the host *Kaltenbachiola strobi* and its parasitoids *Torymus* spp. (n/cone); confidence intervals 95% (non-log form: $y = 0.65 \times + 0.69$)**Fig. 5.** Relationship between number of *Kaltenbachiola strobi* (n/cone) and altitude of sampling site; confidence intervals 95% (non-log form: $y = 0.104 * e^{(1.15E - 3x)}$)

(1955, 1963). The delayed emergence of *Torymus* relative to that of *Kaltenbachiola strobi* makes biological sense in that newly emerged *Torymus* adults need young host larvae of *K. strobi* in the cones to deposit their eggs. In some species, the proportion of individuals terminating diapause is related to cone setting of the trees (BAKKE, 1963; ANNILA, 1984; BARBOSA and

WAGNER, 1989; HANSKI, 1989; TURGEON et al., 1994). Both insect life cycle and flower setting are driven by summer temperature. *Cydia strobilella*, for example, can diapause 3 or more years, thereby by-passing years of poor spruce flowering. Each year individuals from different cohorts emerge from the cones. Therefore, diapause percentages for one year are not very mean-

ingful. Relationships between cone setting and infestation levels have to be sought in multiseasonal studies rather than at locations of different settings from one year.

The dominance of *K. strobi* and *C. strobilella* has also been reported in other countries (SKRZYPCZYŃSKA, 1982, 1987). Although different species peaked at different geographic regions, insects in the alpine area outnumbered those at lower elevations. While the statistical analyses suggest significant differences of infestation levels among regions and vegetation types, one has to keep in mind the huge variation of the infestation levels. The standard error of low-level species can reach more than 500% of the mean. Moreover, these results are based on one single year. The relationships between insect frequencies and geographic regions, vegetation, tree age and, partly, altitude raises the question as to which one of these factors, if any, actually determines the abundance of a cone insect species. It seems obvious that a geographic classification of an area *per se* cannot be the cause for differences in infestation rates. Certainly, all parameters are interrelated, since geographic regions are connected with vegetation types as well as altitude. This is reflected by the comparison of infestation rates in different regions and vegetation alliances (tables 2 and 3): species with minima at low-elevation regions peak at vegetation types occurring in higher regions, and vice versa. For example, *C. strobilella* peaks in the low situated Central Plateau and in the corresponding Eu-Fagion. The alliance order with increasing altitude is: Eu-Fagion, Abieti-Fagion, Piceo-Abietion, Vaccinio-Piceion. Again, it needs to be pointed out that all plots consisted of natural or planted spruce stands while the definition of those alliances relies on herb and shrub layer composition. Insect species spectrum is also the result of the history of a spruce stand.

A common driving variable for insects as well as vegetation is temperature, thus determining the abundance of cone insects, together with other factors such as coincidence of host and antagonist biology. The varying abundance of certain species in different plant alliances may be governed by alternative food plants available either directly to the adult cone insects or indirectly to their antagonists. The elevated infestation level of older trees is possibly caused by their more numerous and larger seeds, thus supplying better resources to insects.

An investigation in Norway (BAKKE, 1963) confirms the occurrence of *C. strobilella* in lower areas, but contradicts our relationship between *K. strobi* and altitude. Presumably, temperature becomes too limiting at higher elevations in the high Norwegian latitudes. *C. illutana* is generally supposed to be rare. The low numbers found in our study (and probably in others too) is due to the fact that *C. illutana* leaves the cones in August (LOVÁSZY, 1942), i.e. partly before our harvest.

Some seed insects like *Megastigmus strobilobius* (Torymidae) and *Plemeliella abietina* (Cecidomyiidae) (c.f. MADZIARA-BORUSIEWICZ, 1963) did not emerge (one specimen of *P. abietina*, respectively) in our study, though their larvae were frequently found in the seeds of the dissected cones from all regions. This is possibly explained by too high humidity in the growth chamber,

as, for example, the scales of the cones did not open, or by insufficient chilling temperatures to break prolonged diapause. Other common species like *Strobilomyia (Lasiomma) anthracina* (Anthomyiidae) and *Assara (Cateremna) terebrella* (Pyrilidae) were not caught due to our cone sampling time since the maggots had left the cones, or the infested cones had dropped, before our harvest (SCHWENKE, 1982).

In this study the spectrum of the cone inhabiting insect fauna was investigated. However, long term studies are necessary to provide more insight into the dynamics of infestation rates, prolonged diapause and their relations to tree phenology.

Acknowledgements

The laborious work of the phytosociological relevés and their analyses was carried out by T. WOHLGEMUTH and is gratefully acknowledged. S. DECRISTOFORIS, M. SEIDL, P. SUTER and S. ZÜRCHER climbed the trees for cone harvest. J. KERN, D. SCHNEIDER and P. WIRZ helped to prepare the lab experiments; P. WIRZ determined the age of the tree core samples. Many thanks for insect identification and verification are due to Dr. M. SKUHRAVÁ (Cecidomyiidae), Prof. W. SAUTER (Lepidoptera), and Dr. B. MERZ (Anobiidae). Dr. C. HOFFMANN gave statistical assistance and Dr. A. ROQUES reviewed the manuscript and provided valuable suggestions.

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- Authors' address:** Dr. BEAT WERMELINGER, JOHANN VON HIRSCHHEYDT, BEAT FECKER, Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, CH-8903 Birmensdorf