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Interactions among herbivores in three polluted pine stands

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TIIVISTELMÄ: TUHOHYÖNTEISTEN VUOROVAIKUTUSSUHTEISTA KOLMESSA SAASTUNEESSA MÄNNYNTAIMIKOSSA

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Succession of insect attacks on young Scots pines (*Pinus sylvestris* L.) was studied in heavily, moderately and slightly polluted pine stands within a 3-km distance from a prominent emission source in western Finland. The total number of pest species was highest in the moderately polluted stand but, unlike other herbivores, aphids were also abundant in the heavily polluted stand. A few positive but no negative interactions were detected between herbivores, which suggests that insect species may benefit from a previous occurrence of other species in the same tree.

Hyönteistuhoja tutkittiin voimakkaasti, kohtalaisesti ja vain vähän saastuneessa männyntaimikossa sadan metrin, kilometrin ja kolmen kilometrin etäisyydellä teollisuuslaitoksista Harjavallassa. Tuholaisten määrät olivat suurimmillaan kohtalaisesti saastuneella alueella, mutta kirvat olivat runsaita myös pahoin saastuneella alueella. Lajien välillä todettiin joitakin positiivisia, mutta ei negatiivisia vuorovaikutussuhteita. Tulosten mukaan tuhohyönteiset saattavat hyötyä toisten lajien aiemmasta esiintymisestä samassa puussa.

Keywords: *Pinus sylvestris*, insect pests, air pollution, Finland
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1. Introduction

Air pollution may decrease forest growth and, in extreme cases, may cause the death of trees and entire forests. The way in which the forest damage process develops is the question in dispute. It has been suggested that the process is primarily a direct consequence of abiotic factors, the pollutants themselves affecting the condition of the trees (e.g. Kozlowski 1980). Alternatively, the catalytic role of biotic factors such as insects and diseases may be decisive (e.g. Führer 1985). Trees stressed by pollutants are inevitably more susceptible to insect attack and some diseases, and the trees with an even more decreased resistance can in turn be more susceptible to new insect attacks and the effects of severe climatic conditions (Braun & Flückiger 1984, White 1984, Dohmen 1985, Führer 1985, Hain 1987). A *circulus vitiosus,* i.e. a positive feedback cycle of declining tree vigour (Loehle 1988), may result. If this scenario is of relevance to the forest decline syndrome, biotic factors may multiply the magnitude of forest damage caused by chemicals alone. On the other hand, some insects may be more sensitive to pollutants than trees, and this may counteract the damaging process (Alstad et al. 1982, Führer 1985).

There is ample evidence that herbivory induces chemical changes in plants (e.g. Haukioja & Niemelä 1979, Rhoades 1979, Ryan 1979, Baldwin & Schultz 1983, Leather et al. 1987). These changes may affect other phytophagous insects that later feed on the plant (Janzen 1973, Strong et al. 1984, Faeth 1986). Although these between-species interactions are usually negative (i.e. competitive, exclusive), it seems quite probable that, under certain circumstances, they may be positive as well (e.g. Hunter 1987; for the interrelationships between plant diseases and insects, see e.g. Kennedy 1951, Jayaraj & Seshadri 1967, Helms et al. 1971, Lewis 1979, White 1984). However, since these biotic relationships are complex and the interactions between pest species in polluted areas poorly known, their role in the forest decline syndrome has remained obscure.

This study concerns the results of insect attacks on young pines in heavily, moderately and slightly polluted pine stands in western Finland. The quantitative significance of different insect species on local forest damage is examined, and an attempt is made to determine whether there are any between-species interactions among pine herbivores and what is their role in the breakdown of pine resistance. This paper continues earlier studies on the interactions between air pollutants and insect outbreaks in the forest decline syndrome in Finland (Heliövaara 1986, Heliövaara & Väisänen 1986a, 1986b, and 1987, Heliövaara et al. 1987).

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2. Material and methods

3.1. Study area

The field work was carried out in the vicinity of the small industrial town of Harjavalta in western Finland (Finnish uniform grid 27°E 680:24). The study area lies on a wide ridge running in a northwest-southeast direction. The vegetation of the area consists of plant species typical to eskers and dry upland forest sites (*Calluna vulgaris, Empetrum nigrum, Vaccinium vitis-idaea, Arctostaphylos uva-ursi,* etc.). The most abundant tree species is Scots pine. Industrial activities in the area date back to the early 1940s. The pollutant load comes mainly from two factories: a metallurgical plant producing copper and nickel, and a chemical one producing sulphuric acid, aluminium sulphate and fertilizers. The annual mean of sulphur dioxide emission varied from 30 to 53 $\mu g/m^3$ during 1978–1985 (Kuokkanen 1986; for the heavy metal levels, see Hynninen 1986). A small amount of pollutants is derived from traffic and energy production. The prevailing winds are from the southwest (Hynninen & Lodenius 1986).

Three young pine stands, located at different distances from the factory complex, were selected to represent different stages in the forest damage process as follows:

Site A (Fig. 1 A). This site was situated about 100 metres from the factory complex, and represents an advanced state of damage. Many pines were dead or dying, most of the other ones had a very small annual growth, and the trunks had often divided to form several crooked, snake-like

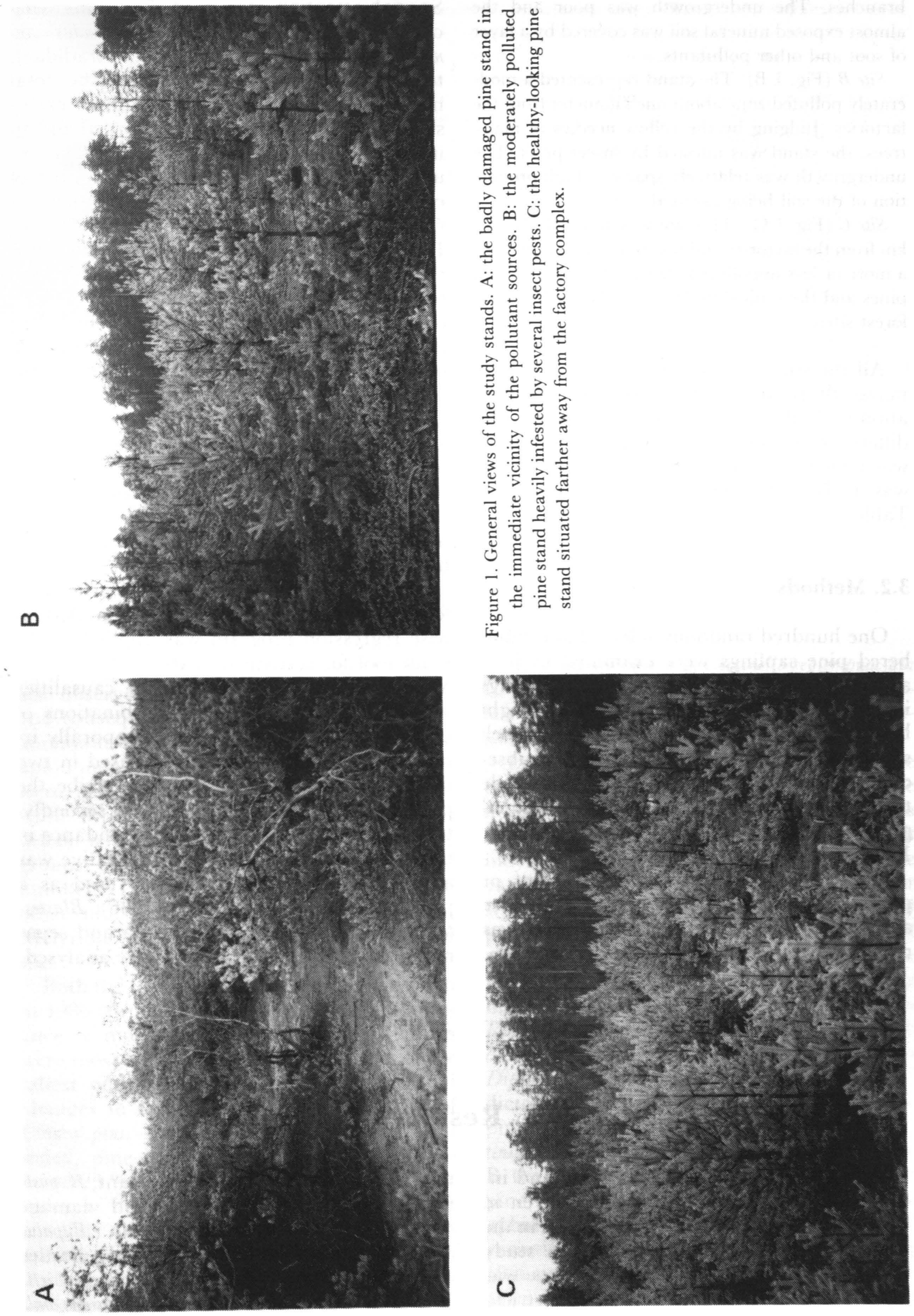

Figure 1. General views of the study stands. A: the badly damaged pine stand in the immediate vicinity of the pollutant sources. B: the moderately polluted pine stand heavily infested by several insect pests. C: the healthy-looking pine stand situated farther away from the factory complex.

branches. The undergrowth was poor and the almost exposed mineral soil was covered by a layer of soot and other pollutants.

Site B (Fig. 1 B). The stand represented a moderately polluted zone about one kilometer from the factories. Judging by the yellow needles of many trees, the stand was infested by insect pests. The undergrowth was relatively sparse, a high proportion of the soil being exposed.

Site C (Fig. 1 C). This site was situated about 3 km from the factories and was selected to represent a more or less unpolluted stand with well-growing pines and the typical undergrowth of *Calluna* type forest sites.

All the sites were edaphically similar pine monocultures originating from natural generation with about 3000 trees per hectare. The difference in the average height of the trees was relatively small, but the age of the stand was higher at site A than elsewhere (see Table 1).

3.2. Methods

One hundred randomly selected and numbered pine saplings were examined in June and August 1987 at each site. The saplings included in the investigation varied in height between 0.5 and 2.5 m. The first tree at each site was selected randomly, and the subsequent ones were those lying along a 2-m-wide transect. In addition to the height, the annual growth of the apical shoot in the years 1986, 1985, and 1984 was recorded for each pine.

Each sapling was examined for signs or presence of pests. Damage caused by moose and fungal diseases in the pine stands was negligible, but insect pests were common. Special attention was paid to aphids, coccinellids, the pine bark bug, *Aradus cinnamomeus* Panzer (Heteroptera, Aradidae), tortricid moths and diprionids. The total number of aphids, belonging almost exclusively to *Cinara pini* (L.), was recorded and an index of aphid abundance (as number per unit height) was calculated. The number of coccinellid predators was also recorded. In the case of *Aradus*, the maximum density per 100 cm^2 was determined (*Aradus* index; for the method, see Heliövaara 1982). In the tortricid moth species examined, the number of galls formed in 1984 and 1986 were counted for *Retinia resinella* (L.), the number of new, crooked shoots for *Rhyacionia pinicolana* (Doubleday), and the number of damaged shoots with pupae for *Blastesthia turionella* (L.) and *B. posticana* (Zetterstedt). It should be noted that *R. resinella* flies only in even years in the study area. The number of diprionid attacks, i.e. the feeding traces of larval groups in 1986, was recorded. Other insects were listed when encountered.

Parametric correlation analysis was used for preliminary statistical orientation. A stepwise regression program was applied as the main tool for statistical analysis of the data. Various biologically meaningful causalities were tested using different combinations of predictor variables, excluding temporally irrelevant ones. *Aradus* index was used in two quite different ways: firstly, to describe the present abundance of the bug, and secondly, to give a rough estimate for the abundance in the previous year. The latter alternative was applied when *Aradus* index was used as a predictor variable for *Retinia* (1986), *Blastesthia* and *Diprion*. The pooled data and separate data for sites A, B and C were analysed.

3. Results

Basic information about the pines and insect pests on sites A, B and C are given in Table 1. There were distinct differences in the pest infestation pattern among the study sites. The number of all pest insects was highest at site B. At this site, adult tortricid moths (*Blastesthia turionella*: abundant; *B. posticana*: 2 individuals), adults and damage caused by the geometrid moth *Bupalus piniarius* (L.), adult curculionid beetles *Brachyderes incanus* (L.) and *Hylobius abietis* (L.), and adult elaterid beetles *Ampedus balteatus* (L.) and *Cardiophorus ruficollis* (L.) were also observed on the pines at this site. Aphids and consequently also coccinellids were also abundant at site A (the highest value for the aphid index was due to the fact that the pines were more branched at site A than at B), while diprionids and tortricids, apart from *Retinia resinella*, were absent. All the studied groups were found at site C but in small numbers. In contrast to the situation on the other plots, *Dasytes niger* (L.) (Coleoptera, Melyridae) was common on the pines at this site.

Table 1. General information about the pines and herbivores per tree at study sites A, B and C. At each site, n = 100.

	Site A		Site B		Site C	
	$\bar{x}$	s.d.	$\bar{x}$	s.d.	$\bar{x}$	s.d.
Pinus height (cm)	184.8	47.0	179.9	41.8	157.1	31.5
Pinus growth in 1984 (cm)	4.0	2.4	21.5	8.7	19.0	5.7
Pinus growth in 1985 (cm)	3.7	2.3	20.6	9.1	23.8	6.8
Pinus growth in 1986 (cm)	3.8	2.8	19.6	8.5	21.2	5.9
No. of *Cinara*	13.05	24.58	15.91	20.56	1.93	3.72
Cinara index	2.67	4.40	0.95	1.45	0.09	0.18
No. of Coccinellidae	0.85	1.33	1.64	2.01	0.34	0.73
Aradus index	0.11	0.40	1.48	1.45	0.05	0.22
No. of *Diprion* attacks in 1986	0	0	0.24	0.51	0.02	0.14
No. of *Retinia* galls in 1984	0.09	0.38	0.24	0.59	0.05	0.22
No. of *Retinia* galls in 1986	0.07	0.26	0.26	0.52	0.16	0.42
No. of *Rhyacionia* shoots in 1987	0	0	0.27	0.57	0.13	0.44
No. of *Blastesthia* damage in 1986–1987	0	0	0.12	0.36	0.02	0.14

Both the height of the pine and pine growth in 1986 correlated positively with the abundance of most herbivores (Table 2). Aphids were most abundant on the new shoots of the tallest pines at sites A and B (for seasonal changes in the within-crown distribution of *Cinara pini*, see Larsson 1985). The *Aradus* index, pine height and growth in 1986 covered 23 % of the total variation in the aphid index at site B (Fig. 2). The number of coccinellids was associated with the number of aphids per pine at sites A, B and C, explaining about 27, 6 and 34 % of the observed variation respectively. The most abundant coccinellid species was *Coccinella septempunctata* L. Other species observed were *Adalia bipunctata* (L.), *Anatis ocellata* (L.), and *Calvia quattuordecimpunctata* (L.).

Diprion attacks were associated with the pine height and growth in 1985 at site B. The number of 1986 galls of *Retinia resinella* was dependent on pine height and the *Aradus* index, these predictors explaining 10 % of the variation at site B. Pooled data gave rather similar results. The number of galls in 1984 per tree had a statistically non-significant effect on the subsequent number in 1986. The amount of *Rhyacionia pinicolana* damage was highest in taller pines and on pines with new *Retinia* galls at site B. In the pooled data damage of this sort was also correlated to *Diprion* and *Blastesthia* attacks. The best predictors of the *Aradus* index at site A were the pine growth in 1986 and new attacks of *Retinia*, explaining 32 % of the variation. At site B the best predictors were respectively the pine height, new attacks of *Retinia* and the aphid index, these explaining 23 % of the variation, and at site C the pine growth in 1986.

Table 2. Correlation matrix of variables measured. *** = $p < 0.001$, ** = $0.001 < p < 0.01$, * = $0.01 < p < 0.05$. n = 100 per site.

Site A	*Aradus*	*Cinara*	*Ret.* (1986)	*Ret.* (1984)	*Blast.*	*Rhyac.*	*Diprion*	Growth	Height
Aradus	1.000								
Cinara	0.117	1.000							
Retinia (1986)	−0.076	0.000	1.000						
Retinia (1984)	0.067	0.060	0.143	1.000					
Blastesthia									
Rhyacionia									
Diprion									
Pinus									
Growth (1986)	0.541***	0.234*	0.147	0.171				1.000	
Height	0.138	0.187	−0.145	−0.013				0.092	1.000

Site B	*Aradus*	*Cinara*	*Ret.* (1986)	*Ret.* (1984)	*Blast.*	*Rhyac.*	*Diprion*	Growth	Height
Aradus	1.000								
Cinara	0.271**	1.000							
Retinia (1986)	0.207*	−0.005	1.000						
Retinia (1984)	0.196*	0.067	0.058	1.000					
Blastesthia	0.064	−0.807	−0.006	0.054	1.000				
Rhyacionia	0.038	−0.005	0.169	0.016	0.138	1.000			
Diprion	0.102	0.024	−0.084	0.375***	0.062	0.191*	1.000		
Pinus									
Growth (1986)	0.134	−0.213**	0.113	−0.082	0.099	0.049	0.180*	1.000	
Height	0.354***	0.253	−0.151	0.100	0.062	0.206**	0.311**	0.433***	1.000

Site C	*Aradus*	*Cinara*	*Ret.* (1986)	*Ret.* (1984)	*Blast.*	*Rhyac.*	*Diprion*	Growth	Height
Aradus	1.000								
Cinara	0.154	1.000							
Retinia (1986)	−0.088	0.085	1.000						
Retinia (1984)	−0.052	−0.120	−0.088	1.000					
Blastesthia	−0.033	0.033	−0.055	−0.033	1.000				
Rhyacionia	0.245*	0.204*	−0.113	−0.068	−0.042	1.000			
Diprion	−0.033	−0.074	−0.055	−0.033	−0.020	0.120	1.000		
Pinus									
Growth (1986)	0.257*	−0.044	0.007	−0.039	−0.078	−0.003	0.092	1.000	
Height	0.241*	0.044	−0.156	−0.067	−0.101	0.223*	0.082	0.652***	1.000

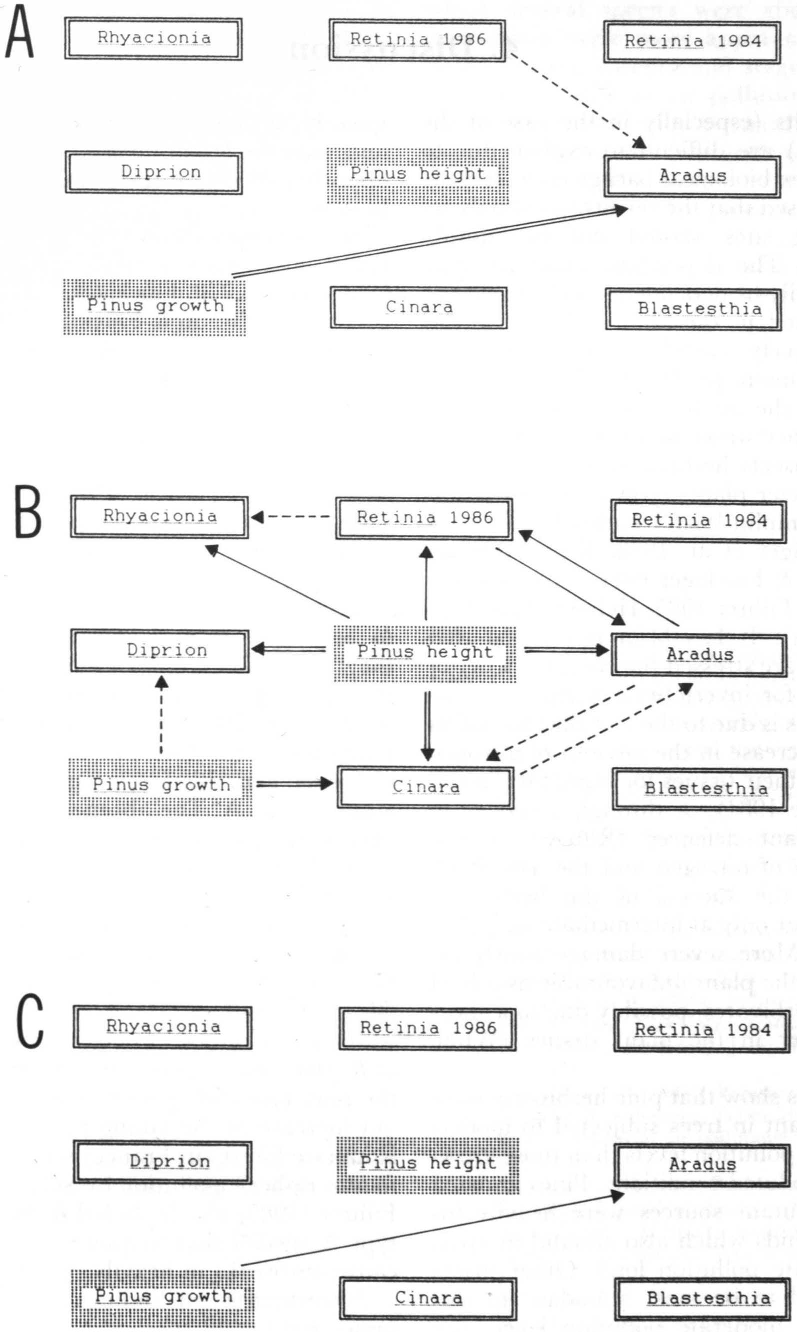

Figure 2. Between-species interactions of pine herbivores at sites A, B and C. Arrows are drawn from the predictor variables to the dependent variables in stepwise regression analyses. Partial correlation coefficients (r^2) are indicated by arrows as follows: broken – 1–4 %, solid – 5–9 %, double – 10- %. Only predictors with $r > 0.01$ are included. Note that *Aradus* index has been used in two alternative ways (see the text).

4. Discussion

The results (especially in the case of the pooled data) are difficult to explain due to their complex biological background. It must also be stressed that the results based only on three study sites should not be unduly generalized. The dependent variables may not necessarily be dependent on the predictor variables used in the analyses, but instead these positively correlated variables may have a common predictor which was not included in the analysis (e.g. nutrient deficiency or other stress factor of the pine).

Several insects herbivores have been suggested to prefer plants stressed by air pollution (e.g. Templin 1962, Charles & Villemant 1977, Flückiger et al. 1978, Katayev et al. 1983, Braun & Flückiger 1984, 1985, Baltensweiler 1985, Führer 1985, Heliövaara & Väisänen 1986a). It has been postulated that when plants are stressed they become a better food source for invertebrate herbivores. Assumably, this is due to the fact that the stress causes an increase in the amount of nitrogen available in their tissues for immature herbivores (White 1984), or through a decline in chemical plant defences (Rhoades 1983). Mobilization of nitrogen and the associated increase in the success of the herbivores seems to occur only at intermediate air pollution levels. More severe damage nearly always makes the plant unfavourable as a food source for herbivores, possibly due to a shortage of water in the plant tissues (White 1984).

Our results show that pine herbivores were more abundant in trees subjected to moderate and high pollution levels than those growing in less polluted conditions. Pines growing near to pollutant sources were heavily infested by aphids which also abound in areas with moderate pollution load. Other insect pests seemed to be most abundant in this zone with a moderate pollution level, and were absent or scarce at heavily and slightly polluted sites. We did not find any statistically significant relationships between aphids and other insect pests in the pooled data. This could be due to the fact that the stress caused by aphids to the pines and, consequently, the increased number of coccinellids and ants on aphid-infested pines may have opposing effects on the number of other herbivores.

Several papers have reported an increase in aphid infestions near pollutant sources (e.g. Wiackowski 1978, Flückiger et al. 1978, Przybylski 1979, Braun & Flückiger 1984). Furthermore, the increase in the numbers of *Aphis fabae* on bean plants has been reported to be mediated entirely via the host plant (Dohmen et al. 1984), thus supporting the stress hypothesis (White 1984). The results for *Aphis pomi* on *Crataegus* spp. (Braun & Flückiger 1985) also indicate that air pollution can alter the host plant-herbivore relationship so that the susceptibility of the plant is increased.

Aradus cinnamomeus and *Retinia resinella* seem to be relatively resistant to pollution since they were also present in small numbers in the heavily polluted areas (for more details on *Aradus*, see Heliövaara & Väisänen 1986a). Diprionids and tortricid species *Rhyacionia pinicolana* and *Blastesthia turionella* were not found at site A. The absence of these groups may be due to their poor tolerance to pollutants or a shortage of water in the plant tissues. These tortricids may also be absent simply because the slowly growing pine shoots are too short to maintain their larvae. However, Villemant (1980) reported that *Rhyacionia buoliana* (Denis & Schiffermüller), which has a rather similar life history to that of *R. pinicolana* (Bakke 1969, Scott 1972), was the only tortricid species showing a significant increase in the young pine stands in the Roumare forest (in France) which is exposed to atmospheric pollution by SO_2 and fluoride. Führer (1985) also included *R. buoliana* in his type A species that frequently or chronically cause outbreaks in heavily polluted areas.

According to our findings, the interactions between different species are not very strong. In most cases the potential effect of one species on another is only of the order of a few percent or less. A few positive interactions were detected between herbivores, especially at site B. No statistically significant negative between-species interactions were found. One herbivore is not likely to have a direct positive effect on another, but an intensive herbivore attack is likely to upset the metabolism of the plant (for the effect of defoliation on *Pinus*, see Wagner & Evans 1985, Leather et al. 1987) which, in turn, could favour other herbivores. The results thus seem to support the stress hypothesis (White 1984).

The study shows that insect outbreaks may cause serious local damage near pollutant sources, probably partially due to the indirect interactions between herbivore species. At sites A and C insect densities were so low that their interactions were weak, while at site B where several species were abundant their interactions were more apparent. This may be due to the successional stage of the pine stand in relation to air pollution. At site A pines were in too poor a condition to maintain dense herbivore populations, and at site C the insect pests were scarce due to the resistance of pines. In general, the role of insect pests in the forest damage syndrome may not necessarily be central if the pollutant level does not reach a relatively high level.

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