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THE EFFECTS OF SIMULATED ACID RAIN ON GROWTH AND SUSCEPTIBILITY TO PREDATION OF *Phratora polaris* (Col., Chrysomelidae)

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Abstract

*The effects of long-term simulated acid rain on tritrophic interactions between mountain birch, a leaf beetle (*Phratora polaris*) and its predators were studied. Leaf beetle larvae were fed on foliage treated during 6–7 years with simulated acid rain of pH 3 (both H_2SO_4 and HNO_3) or with spring water of pH 6 (irrigated controls). There were significant differences between treatments in the susceptibility of* P. polaris *to predators. Generally, beetles reared on acid treated birches were more susceptible to predators than those reared on irrigated control trees. This effect was present over several stages in the life cycle of the beetle and for several types of predators: ants preying on larvae, carabids attacking pupae and birds feeding on adult beetles. However, host plant treatment did not have consistent effects on the growth of larvae. This suggests that the defensive ability of leaf beetles is more sensitive to pollution induced variation in host foliage than larval growth.*

INTRODUCTION

Air pollution may affect quality of the host plant foliage for herbivorous insects or change the susceptibility of herbivores to their natural enemies (Riemer & Whittaker, 1989). The importance of these mechanisms varies from case to case depending, for example, on feeding guild, host plant species, defence systems and predators of herbivores. Some studies have suggested that herbivores benefit from feeding on plants moderately stressed by air pollution (e.g. Neuvonen & Lindgren, 1987; Houlden *et al.*, 1990; Koricheva & Haukioja, 1992) or by other abiotic factors (e.g. McCullough & Wagner, 1987; Coleman & Jones, 1988). Stressed plants are considered to be more susceptible to herbivory because of increased nutritional value and/or reduced defences (White, 1974, 1984; Rhoades, 1979; Waring & Pitman, 1985; Mattson & Haack, 1987; Larsson, 1989).

The quality of mountain birch (*Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman) foliage for some insect species was enhanced by short term (1–3 years) simulated acid rain treatments but other insect species did not show any significant response (Neuvonen *et al.*, 1990*a*). The net effects of acid rain cannot be predicted by examining only the growth and fecundity of herbivores, because concomitant changes in their mortality may enhance or mitigate the growth responses. The effects of acid rain on the natural enemies of herbivores have been little studied. The efficacy of the nucleopolyhedrosis virus disease of the European pine sawfly (*Neodiprion sertifer* (Geoffr.)) was reduced on pine foliage treated with simulated acid rain (Neuvonen *et al.*, 1990*b*; Saikkonen & Neuvonen, 1993). Field studies have demonstrated changes in the number of some predator species in polluted areas (e.g. Galecka, 1980; Stary & Kublznakova, 1987), but we are not aware of experiments testing how simulated acid rain effects the susceptibility of herbivores to predation.

In this paper, we studied the influence of simulated acid rain on tritrophic interactions between mountain birch (*Betula pubescens* ssp. *tortuosa*), *Phratora polaris* (Schneid.) (Col. Chrysomelidae) and its predators. *P. polaris* is a common herbivore on mountain birch in northern Fennoscandia (Tenow, 1963; Nuorteva, 1966; Koponen, 1973). Chrysomelid beetles are convenient for studies on the effects of air pollution on tritrophic interactions, because of their well developed chemical defences (e.g. Pasteels *et al.*, 1988; Palokangas & Neuvonen, 1992; Palokangas *et al.*, 1995). We pose the following question: does simulated acid rain treatment of host-plant foliage affect the growth of leaf-beetle larvae and/or the susceptibility of larvae, pupae or adults to predation? Effects on beetle susceptibility were tested by exposing larvae to crab spiders (*Xysticus obscurus* (Collett) and *X. audax* (Schrank)) and ants (*Formica aquilonia* (Yarrow)), pupae to ground beetles (*Pterostichus adstrictus* (Pk.)) and adults to willow warblers (*Phylloscopus trochilus* (L.)).

MATERIALS AND METHODS

The experiments were carried out during the summers of 1991–1992 at the Kevo Subarctic Research Institute (69° 45' N, 27° 01' E) in northernmost Finland. Larvae and adults of *P. polaris* were fed leaves from mountain birches treated with simulated acid rain or irrigated with water since 1985. The study area consisted of 80 experimental plots grouped into 20 blocks of four plots. Plots within each block were randomly allocated to four treatments, two of which were used in the present study: (IC) irrigated controls, with additional 60 mm/month simulated rain (sprinkled over the canopy and a 5 × 5 m area of ground) of pH 6; and (A3) treatment with simulated acid rain of pH 3 (both sulphuric and nitric acids; S:N mass ratio 1·9 : 1). The acidity of simulated acid rain was adjusted by adding both sulphuric and nitric acids to the control water. The amount of sulphur added by the simulated acid rain treatment was 2·0–2·5 g m^{-2} per season, while the ambient sulphur deposition at Kevo is 0·35 g m^{-2} $year^{-1}$ (Laurila *et al.*, 1991). The plots were further grouped into four sub-areas, of which only sub-areas I and IV were used in this study. Detailed descriptions of the experimental design and treatments at the study site are given by Neuvonen *et al.* (1990*a,b*) and Neuvonen and Suomela (1990).

Growth of larvae on acid- and control-treated foliage

In 1991 and 1992 *P. polaris* larvae were reared on detached control- and acid-treated mountain birch leaves. The larvae were reared from second instar onwards in groups of three in plastic vials (diameter 3·2 cm, height 6 cm). Freshly collected leaves were given to larvae every second day. Vials were kept outdoors in natural light and temperature. Since it was necessary to use larvae for other experiments, the number of replicate vials varied from 3–5 per tree. The mean weight of larvae after 10 days (1991) or 12 days (1992) was used as the response variable.

Spider and ant predation of third instar larvae

Larvae were exposed to spiders on Petri dishes which had two similar untreated mountain birch leaves for larvae to feed on and wet paper on the bottom to keep the leaves fresh. A pair of larvae reared on acid- and control-treated foliage was set on the leaves. We painted a small spot with a brush on the back of each larva, using acrylic colours (Teranishi Chemical Industry Co., Ltd.). The side of larvae (left/right) and the colour of the distinguishing spot (yellow/orange) painted was randomized. A crab spider (*Xysticus obscurus* or *X. audax*) was released in the Petri dish. Surviving larvae were counted after 24 h. Each experimental tree (10 in both treatments) was represented by three replicate trials.

Ant (*Formica aquilonia*) predation experiments were conducted in summer 1991 and 1992. After the larvae had been reared for one week on acid- or control-treated foliage, small twigs (10 cm) with leaves were taken from experimental birches and third instar larvae (9 per twig) were placed on them. Larvae were set on twigs from the same tree on which they had been reared. Pairs of twigs with the cut ends in plastic vials filled with water were placed into the ground close to each other near an ant mound. During two day exposure, we observed predation every third hour and counted the number of larvae that disappeared. In several cases, the removal of larvae by ants was observed, but not all disappearances were witnessed. We surmised predation to be the only cause of disappearance.

Pupal predation by carabids

The experiment on pupal predation by ground beetles (*Pterostichus adstrictus*) was done in transparent plastic tubes (diameter 20 cm, height 50 cm) in the laboratory. Carabids used in the experiment were collected in pitfall-traps from mountain birch woodland. The 20 trials were arranged in a randomized block design. A 1·5 cm layer of litter was placed on the bottom of each tube. The bottom was divided into quarters with small blue sticks. One pupa was placed on the surface of the litter on either side of each stick, making a total of eight pupae. Alternate pupae had eaten acid- and control-treated leaves, respectively, during larval stages. One carabid was placed into each plastic tube. There were 1–4 replicates of each pair of trees (IC and A3). The proportion of surviving pupae after 8 h was used as the response variable.

Avian predation on adult beetles

Adult leaf beetles were exposed to willow warblers (*Phylloscopus trochilus*), one of the most common insect feeding birds in Europe. In Finland, 70% of its food consists of adult insects, mostly different species of beetles, dipterans and sawflies (Haartman von *et al.*, 1963). Birds were attracted with recorded willow warbler song, then trapped with nets. They were taken to an aviary and fed meal worms in Petri dishes to accustom them to eating in captivity and to allow them to recover from possible stress of capture. Willow warblers were allowed to feed for 1 h. Petri dishes and uneaten meal worms were then removed and birds were starved for 1 h before the choice trials. The aviary was a 2·5 × 2·5 × 2·0 m wooden house with artificial lights (60 W). Inside the house there were four small (1·0 × 1·2 × 1·0 m) chambers, one for each warbler, so four trials could be run simultaneously. In the door of each room there was a 5 × 10 cm one-way window for observation. Choice trials lasted up to 150 min, depending on how fast the choice was made. Adult birds made their choice quickly, but juveniles were slower to decide. Adult leaf beetles were offered to warblers on cold petri dishes, so that beetles moved slowly and could not escape during the experiment. During the trials birds were observed every 15 min. After the tests, the birds were aged (Svensson, 1976) and released.

A total of 68 beetles from acid- and control-treated leaves (i.e. 34 per treatment) were offered to 19 juvenile and 5 adult willow warblers. Leaf beetles were marked with paint pens (Snowman, Permanent marker) to facilitate the identification of their feeding treatment. A golden, silver or white dot was painted on the elytra of beetles. The colours were changed for each replicate to avoid possible colour induced biases.

Statistics

All experiments were arranged as a randomized block design and tested by analysis of variance for randomized blocks (Zar, 1984). Tree-specific means were used to avoid pseudoreplication (Hurlbert, 1984). The number of experimental trees was 10 in both treatments (IC

Table 1. (A) Weight (mg) of *P. polaris* larvae reared on mountain birch leaves treated with simulated acid rain (A3) or control leaves (IC) in two separate sub-areas in 1991 and 1992. (B) ANOVA testing the significance of differences between treatments (control vs simulated acid rain), between trees from two separate sub-areas, and the sub-area–treatment interaction

Sub-area	Treatment	Larval weight (1991)			Larval weight (1992)		
		N	Mean	SE	N	Mean	SE
A							
I	IC	5	4·09	0·368	5	3·79	0·819
I	A3	3	5·28	0·733	4	3·97	1·051
IV	IC	5	4·80	0·661	5	3·01	0·531
IV	A3	5	4·62	0·987	4	5·57	0·732
Source		DF	F	p	DF	F	p
B							
Sub-area		1	0·00	0·976	1	0·28	0·605
Treatment		1	0·45	0·515	1	3·06	0·101
Sub-area–Treatment		1	0·83	0·378	1	2·33	0·148
Error		14	MSE = 2·44		15	MSE = 2·87	

N = number of trees; SE = standard error; DF = degrees of freedom; MSE = mean square error. Multiplying F-values by respective MSE gives mean squares for each source of variation.

Table 3. (A) The survival of leaf beetle larvae on acid treated (A3) and control (IC) leaves in ant predation experiments. (B) ANOVA testing the significance of differences between treatments (control vs simulated acid rain), between trees from two separate sub-areas, and the sub-area–treatment interaction

Sub-area	Treatment	Survival 1991 (%)			Survival 1992 (%)		
		N	Mean	SE	N	Mean	SE
A							
I	IC	4	35	9	3	67	19
I	A3	4	38	13	3	22	11
IV	IC	5	28	9	5	53	17
IV	A3	5	40	17	4	25	16
Source		Experiment 1991			Experiment 1992		
		DF	F	p	DF	F	p
B							
Sub-area		1	0·02	0·891	1	0·12	0·745
Pair (sub-area)		7	0·86	0·579	6	4·35	0·064
Treatment		1	0·29	0·608	1	10·89	0·022
Sub-area–Treatment		1	0·13	0·728	1	0·85	0·398
Error		7	MSE = 0·09		5	MSE = 0·04	

The term 'pair (sub-area)' refers to the positioning of experimental twigs in pairs in the ant predation assay. Definitions as in Table 1.

and A3) but in some trials there were not enough beetles to test every experimental tree, which reduced the power of the tests. The analyses were performed with SAS statistical software, procedure GLM and type III sums of squares were used (SAS, 1985).

RESULTS

Growth performance of *P. polaris* larvae

In the 1991 experiment, the body mass of larvae reared on acid-treated foliage was higher than that of larvae on control foliage in sub-area I, but there was almost no difference in sub-area IV (Table 1). However, in 1992, acid-reared larvae were heavier than control larvae in sub-area IV, but there were only slight differences in sub-area I. The variation among trees within treatments was high in both years and, consequently, the differences due to treatment were not significant (Table 1).

Table 2. (A) The survival of leaf beetle larvae on acid treated (A3) and control (IC) leaves in the spider predation experiment. (B) ANOVA testing the significance of differences between treatments (control vs simulated acid rain), between trees from two separate sub-areas, and the sub-area–treatment interaction

Sub-area	Treatment	Survival (%)		
		N	Mean	SE
A				
I	IC	5	57	12
I	A3	4	50	10
IV	IC	5	67	12
IV	A3	5	47	6
Source	DF	F	p	
B				
Sub-area	1	0·10	0·755	
Treatment	1	1·61	0·223	
Sub-area–Treatment	1	0·40	0·535	
Error	15	MSE = 518·60		

Definitions as in Table 1.

Susceptibility of *P. polaris* to predation

There were no significant differences between larvae reared on acid- or control-treated birch foliage in their susceptibility to predation by crab spiders (Table 2).

The results of the ant predation experiments varied between years. In 1991 there were no significant differences between treatments, but in 1992 the survival of larvae reared on acid-treated foliage was significantly smaller than that of control larvae (Table 3). The difference was similar on trees from both sub-areas: ants on average had 83% higher predation of acid- than control-reared larvae by the end of the experiment (predation on IC-treatment scaled to 100%; Table 3).

After 8 h, carabids had consumed 79% more *Phratora* pupae from acid-treated trees than control pupae (predation on IC-treatment scaled to 100%) (Table 4). This difference was significant and consistent in both sub-areas.

There was a significant difference due to host plant treatment ($F_{1,11}$ = 6·57, p = 0·0264) in the survival of adult leaf beetles from bird predation. Willow warblers ate, on average, about 60% more leaf beetles reared on acid-treated host trees than those from control trees (Fig. 1).

Table 4. (A)The survival of *P. polaris* pupae reared on mountain birch leaves treated with simulated acid rain (A3) or control leaves (IC) from carabid predation. (B) ANOVA testing the significance of differences between treatments (control vs simulated acid rain), between trees from two separate sub-areas, and the sub-area–treatment interaction

Sub-area	Treatment	Survival (%)		
		N	Mean	SE
A				
I	IC	5	67	9
I	A3	5	47	7
IV	IC	4	83	9
IV	A3	4	62	14
Source		DF	*F*	*p*
B				
Sub-area		1	6·16	0·042
Pair (sub-area)		7	3·98	0·045
Treatment		1	10·30	0·015
Sub-area–Treatment		1	0·02	0·906
Error		7	MSE = 0·02	

The term 'pair (sub-area)' refers to pairing of experimental trees in the predation assay. Definitions as in Table 1.

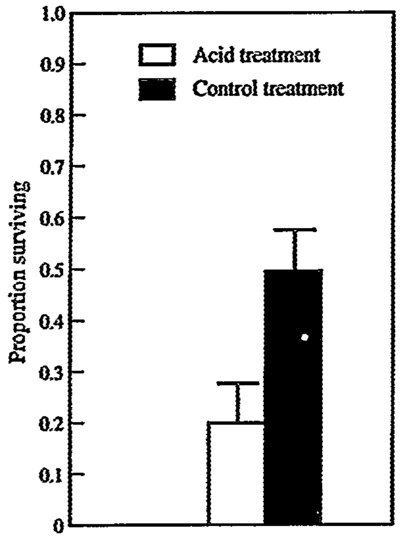

Fig. 1. Survival (mean ± SE) of adult *P. polaris* leaf beetles reared on acid- and control-treated leaves subjected to willow warbler predation.

DISCUSSION

Insect species with different feeding habits may respond to changes in leaf quality differently (Larsson, 1989). The performance of sawflies (*Arge fuscinervis* (Lindqvist), *Dineura viridiorsata* (Retzius)) and geometrid moths (*Erannis defoliaria* (Clerk), *Epirrita autumnata* (Bkh.)) chewing on mountain birch foliage did not show consistent differences between acid- and control-treated mountain birches during a three-year experiment (Neuvonen *et al.*, 1990*b*). When clear responses are not found in short-term experiments, the question remains as to whether an experiment of longer duration might have revealed some effects. In the present study, we found no consistent effects of acid rain on larval growth of *P. polaris*, even though the trees had been treated for over six years with simulated acid rain and there were significant treatment effects on soil chemistry (Neuvonen & Fritze, unpublished). If there was any difference, there was a trend for simulated acid rain to enhance growth of *P. polaris* larvae.

In addition to direct host-plant effects, the net performance of herbivorous insects depends on the number and efficacy of natural enemies and on how changes in host foliage modify these interactions. There were significant differences in the susceptibility of acid- and control-reared *P. polaris* to several predators. Generally, herbivores reared on acid-treated foliage were more susceptible to predators than those fed on control foliage. This effect was present over several stages in the life cycle of the beetle and for several types of predators: ants, carabids, and birds. There was, however, variation in the results of predation trials: crab spiders and ants in one of the two trials preyed equally on larvae from different treatments. Further studies are necessary to reveal whether this is due to differences between the type of predator or to variation in experimental conditions. Neuvonen and Lindgren (1987), for example, found that the reproduction of the aphid *Euceraphis betulae* (Koch) was significantly enhanced when ambient precipitation during the trial was below the long-term average but not when the precipitation was higher than average.

The results suggest that variation in food-plant quality may cause variation in the efficacy of defence in leaf beetles. It is not exactly known what kind of defensive compounds *P. polaris* contains. Probably the adults produce isoxazolinone derivatives and nitropropanolic acid, and the larvae produce monoterpenes, as other *Phratora* species do (Pasteels *et al.*, 1988 and personal communication). The mechanism increasing the susceptibility to predation on acid-treated foliage is unclear. An explanation may be that beetles on acid foliage produce less defensive secretion. This could occur even if their growth is not reduced, suggesting that the defensive ability is more sensitive than larval growth to pollution-induced variation in host foliage.

Is it possible to generalize the results of this study to all tritrophic interactions? Obviously not. The growth performance of the European pine sawfly (*Neodiprion sertifer*) was not directly affected by the simulated acid-rain treatment of its host tree (Neuvonen *et al.*, 1990*b*) but its susceptibility to a viral disease was decreased (Neuvonen *et al.*, 1990*b*, Saikkonen & Neuvonen, 1993). In the present study, the effects in relation to the third trophic level were opposite: the susceptibility of birch feeding *P. polaris* to predators was increased by simulated acid rain. Also, experiments with raised CO_2 levels have shown very inconsistent changes in interactions between plants, herbivores and their predators (Lincoln *et al.*, 1986).

The results of this and other recent studies (Neuvonen *et al.*, 1990*b*; Saikkonen & Neuvonen, 1993) show that, in evaluating the effects of acid rain on the performance and population dynamics of herbivorous insects, one should not concentrate only on insect growth. More manipulative experiments are needed to clarify the effects of pollutants on the susceptibility of herbivores to natural enemies. These studies should include different types of plants and herbivore–natural enemy complexes and they should be complemented by integrating results from field and modelling studies (cf. Bell *et al.*, 1993) so that generalized patterns (if any) can be identified in these complex interactions.

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REFERENCES

SAS (1985). The GLM precedure. In *SAS User's Guide: Statistics (Version 5 Edition)*. SAS Institute Inc., Cary, NC, pp. 432–506.

Bell, J. N. B., McNeill, S., Houlden, G., Brown, V. C. & Mansfield, P. J. (1993). Atmospheric change: Effect on plant pests and diseases. *Parasitol.*, **106**, 811–24.

Coleman, J. S. & Jones, C. G. (1988). Acute ozone stress on eastern cotton wood (*Populus deltoides* Batrtr.) and the pest potential of the aphid, *Chaitophorus populicola* Thomas (Homoptera: Aphidae). *Environ. Entomol.*, **17**, 207–12.

Galecka, B. (1980). Structure and functioning of community of Coccinellidae (Coleoptera) in industrial and agricultural-forest regions. *Pol. Ecol. Stud.*, **6**, 717.

Haartman von, L., Hilden, O., Linkola, P., Suomalainen, P. & Tenovuo, R. (1963). *Pohjolan Linnut värikuvin II*. Otava, Helsinki, pp. 867–71.

Houlden, G., McNeill, S., Aminu-Kano, M. & Bell, J. N. B. (1990). Air pollution and agricultural aphid pests. I. Fumigation experiments with SO_2 and NO_2. *Environ. Pollut.*, **67**, 305–14.

Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.*, **54**, 187–211.

Koponen, S. (1973). Herbivorous invertebrates of the mountain birch at Kevo, Finnish Lapland. *Rep. Kevo Subarctic Res. Stat.*, **10**, 20–8.

Koricheva, J. & Haukioja, E. (1992). Effects of air pollution on host plant quality, individual performance, and population density of *Eriocrania* miners (Lepidoptera: Eriocraniidae). *Environ. Entomol.*, **21**, 1386–92.

Larsson, S. (1989). Stressful times for the plant stress — insect performance hypothesis. *Oikos*, **56**, 277–83.

Laurila, T., Tuovinen, J.-P. & Lättilä, H. (1991). *Lapin ilmansaasteet*. Ilmatieteen laitos, Helsinki (in Finnish).

Lincoln, D. E., Couvet, D. & Sinoit, N. (1986). Responses of an insect herbivore to host plants grown in carbon dioxide rich atmospheres. *Oecologia*, **69**, 556–60.

Mattson, W. J. & Haack, R. A. (1987). The role of drought stress in provoking outbreaks of phytophagous insects. In *Insect Outbreaks*, ed. P. Barbosa & J. C. Schultz. Academic Press, San Diego, pp. 365–407.

McCullough, D. G. & Wagner, M. R. (1987). Influence of watering and trenching ponderosa pine on a pine sawfly. *Oecologia*, **71**, 382–7.

Neuvonen, S. & Lindgren, M. (1987). The effects of simulated acid rain on performance of the aphid *Euceraphis betulae* (Koch) on silver birch. *Oecologia*, **74**, 77–80.

Neuvonen, S. & Suomela, J. (1990). The effect of simulated acid rain on pine needle and birch leaf litter decomposition. *J. Appl. Ecol.*, **27**, 857–72.

Neuvonen, S., Suomela, J., Haukioja, E., Lindgren, M. & Ruohomäki, K. (1990*a*). Ecological effects of simulated acid rain in a subarctic area with low ambient sulphur deposition. In *Acidification in Finland*, ed. P. Kauppi, K. Kenttämies & P. Anttila. Springer-Verlag, Berlin, pp. 477–93.

Neuvonen, S., Saikkonen, K. & Haukioja, E. (1990*b*). Simulated acid rain reduces the susceptibility of the European pine sawfly (*Neodiprion sertifer*) to its nuclear polyhedrosis virus. *Oecologia*, **83**, 209–12.

Nuorteva, P. (1966). Leaf development and leaf pathogens on subarctic birches after a calamity of *Oporinia autumnata* (Bkh.) (Lep., Geometridae). *Ann. Zool. Fennici*, **3**, 270–86.

Palokangas, P. & Neuvonen, S. (1992). Differences between species and instars of leaf beetles in the probability to be preyed on. *Ann. Zool. Fennici*, **29**, 273–8.

Palokangas, P., Neuvonen, S. & Halonen, M. (in press). Interspecific differences in susceptibility of adult leaf beetles (Col., Chrysomelidae) to predation by Willow warblers (*Phylloscopus trochilus*). *Rep. Kevo Subarctic Res. Stat.*

Pasteels, J. M., Braekman, J. C. & Daloze, D. (1988). Chemical defence in the Chrysomelidae. In *The Ecology of Chrysomelidae*, ed. P. Jolivet, T. H. Hsiao & E. Petitpierre. Junk, Dordrecht, pp. 231–50.

Rhoades, D. F. (1979). Evolution of plant chemical defense against herbivores. In *Herbivores: Their Interaction with Secondary Plant Metabolites*, ed. G. A. Rosenthal & D. H. Janzen. Academic Press, London, pp. 3–54.

Riemer, J. & Whittaker, J. B. (1989). Air pollution and insect herbivores: Observed interactions and possible mechanisms. In *Insect–Plant Interactions*, ed. E. A. Bernays. CRC, Boca Raton, FL, pp. 73–105.

Saikkonen, K. T. & Neuvonen, S. (1993). Effects of larval age and prolonged simulated acid rain on the susceptibility of European pine sawfly to virus infection. *Oecologia*, **95**, 134–9.

Stary, P. & Kublznakova, J. (1987). Content and transfer of heavy metal air pollutants in populations of *Formica* spp. wood ants (Hym., Formicidae). *J. Appl. Entomol.*, **104**, 1–10.

Svensson, L. (1976). *European Varpuslinnut, Sukupuolen ja iän Määritys*. Suomen Lintutieteellinen Yhdistys r.y, Helsinki, pp. 99–100 (in Finnish).

Tenow, O. (1963). Leaf-eating insects on the mountain birch at Abisko (Swedish Lapland) with notes on bionomics and parasites. *Zool. Bidr. Uppsala*, **35**, 545–67.

Waring, R. H. & Pitman, G. B. (1985). Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology*, **70**, 578–9.

White, T. C. R. (1974). A hypothesis to explain outbreaks of looper caterpillars, with special reference to population of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. *Oecologia*, **22**, 119–34.

White, T. C. R. (1984). The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia*, **63**, 90–105.

Zar, J. H. (1984). *Biostatistical Analysis*. 2nd edn, Prentice-Hall, Inc., Englewood Cliffs, NJ, 718 pp.