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Effect of exposure to fluoride, nitrogen compounds and SO_2 on the numbers of spruce shoot aphids on Norway spruce seedlings

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Summary. Development of spruce shoot aphid (*Cinara pilicornis* Hartig) populations was monitored in natural and artificial infestations of Norway spruce (*Picea abies* Karst.) seedlings, exposed to air pollutants in an experimental field. The pollutants, applied both singly and in mixtures, were gaseous sulphur dioxide, NaF (30 mg l^{-1} F) and $Ca(NO_3)_2$ or $(NH_4)_2SO_4$ in aqueous solutions (200 mg l^{-1} N). Aphid numbers on 10 seedlings in each treatment and two control plots were counted at 2-week intervals. At the beginning of the experiment aphid numbers did not differ between treatments. Aphid populations peaked in late June and early July. All the pollutants and their combinations significantly increased the numbers of aphids per seedling. Four apterous females were transferred to spruce seedlings which were growing in containers in the same plots. After 4–5 weeks aphid numbers were significantly higher in the fluoride treatment and in the combined treatment of fluoride, nitrogen and SO_2. The pollution treatments did not have a significant effect on shoot growth. Concentrations of F and S in needles were higher in treatments involving these pollutants. There were no significant differences in the concentrations of free amino acids in shoot stems between control and fluoride treatment. However, the relatively low concentration of arginine in the F treatment at the end of the growing season might indicate disturbances in the nitrogen metabolism of spruce seedlings.

Key words: *Picea abies* – *Cinara pilicornis* – Air pollution – Amino acids – Plant-insect interactions

The effect of air pollution on plant-insect relationships has on many occasions been favourable to insect herbivores (Przybylski 1979; Dohmen et al. 1984; Hughes et al. 1985; Heliövaara and Väisänen 1986a, b; Trumble el al. 1987; Warrington 1987; Spencer and Port 1988). In addition insect damage may increase the susceptibility of plants to atmospheric pollutants (Warrington et al. 1989). The mechanism involved in alterations of the success of the insect is suspected to be mediated via the host plant (Dohmen et al. 1984; Lechowicz 1987). However, exposure to high levels of NO_2 and SO_2 singly (Feir and Hale 1983b) or in mixtures (Feir and Hale 1983a) can directly enhance growth and reproduction of seed-eating plant bugs.

Increased development of aphid populations in woody plants stressed by air pollutants has been reported in several studies (e.g. Dohmen 1985; Neuvonen and Lindgren 1987; Bolsinger and Fluckiger 1989; Braun and Fluckiger 1989). On Scots pine (*Pinus sylvestris* L.) exposed to fluoride and sulphur pollution, Villemant (1981) found increases in aphid populations of *Cinara pini*, *C. pinea* and *Protolachnus agilis*, but the opposite trend was observed for *Schizolachnus tomentosus* and *Pineus pini*. On the contrary, Wiackowski (1978) found *S. tomentosus* to be common around factories emitting sulphur and dust. *Cinara* spp. were also more numerous in heavily and moderately polluted pine stands than in slightly polluted ones near factories emitting sulphur and heavy metals (Heliövaara and Väisänen 1988). On Norway spruce (*Picea abies* (L.) Karst.), a gall aphid *Sacchiphantes abietis* L. (Thalenhorst 1975; Sierpinski 1985) and spruce shoot aphid (*Cinara pilicornis* Hartig) are common in polluted areas. We report observations of spruce shoot aphids on Norway spruce seedlings experimentally exposed to some air pollutants.

Materials and methods

Field exposure

Experiments were carried out in an experimental field where 30 5-year-old Norway spruce *(Piced abies)* seedlings (average height 0.63 m in spring) together with 30 Scots pine *(Pinus sylvestris)* seedlings (average height 0.70 m) were growing in 9 circular plots of diameter ca. 5 m. Each plot was surrounded by a 1-m high polycarbonate fence to decrease the dilution of SO_2, and the plots were 5–10 m apart. Deposition of pollutants on seedlings was

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Table 1. Simulated air pollutants and their concentrations

Treatment	Compound	Form	pH	Concentration
S	SO_2	gaseous		430(627)–90(106) $\mu g m^{-3}$ at 0.8 m[a] 325(522)–75(117) $\mu g m^{-3}$ at 1.6 m
F	NaF	aqueous	6.1	30 mg l^{-1} F
N	$Ca(NO_3)_2$	aqueous	5.7	200 mg l^{-1} N
N	$(NH_4)_2SO_4$	aqueous	5.7	200 mg l^{-1} N

[a] At both distances from the pipe opening the values indicate hourly means (maxima in brackets) of four measurement points around the center at heights of 0.2 m and 0.8 m, respectively, during SO_2 fumigation

simulated by spraying NaF and nitrogen compounds in aqueous solution and fumigating plants with gaseous SO_2 separately and in mixtures between 9 June and 11 November 1986 (Table 1).

SO_2 was released from a pipe opening in the center of each fumigated plot. The fumigation period was 7 h per day between 9 a.m. and 4 p.m. on weekdays. The concentration of SO_2 was measured with a Thermo Electron Fluorescence SO_2 analyzer (Model 43) from eight points 0.8 and 1.6 m from the center. At each point the measurements were carried out at 0.2 m and 0.8 m above the soil surface. The concentration among the seedlings fluctuated depending on the distance from the plot center and the soil surface and velocity and direction of wind. The maximum concentration measured directly at the gas releasing point was 7100 $\mu g\ m^{-3}$, but due to dilution the gas concentration decreased rapidly with increasing distance from the plot center (Table 1). The ambient background level of SO_2 was less than 5 $\mu g\ m^{-3}$.

Two plots were used as controls without any treatments. All the plots received ambient rain. Mean daily rainfall was 0.3 mm, 2.4 mm and 3 mm in June, July and August, respectively.

Occurrence of the spruce shoot aphid (*Cinara pilicornis* Hartig) on 10 randomly selected spruce seedlings was monitored at about 2-week intervals between 9 June and 23 September. However, the numbers of aphids fell to a very low level after 14 August and the data after that date were not analysed. Few aphid predators (syrphid larvae, coccinellids) were observed during the decline period of aphid populations and their numbers were not analysed. The number of eggs of the aphids on the needles of these same seedlings were counted at the end of September.

In the other control plot and the plots with F, N, S, N+S, and F+N+S treatments, eight 3-year-old nursery-grown spruce seedlings (average height 0.24 m) were planted in fertilised sand-peat mixture in 1.5–l containers and they received the same pollutant treatments as the other seedlings in the plot. Four apterous females collected from spruce seedlings growing outside the experimental plots were transferred onto the leader shoot of each seedling on 17 June. To allow free access of gaseous and sprayed pollutants to needles the aphids were not protected from natural enemies with mesh bags. The aphid numbers per seedling were counted weekly until the end of August. At the end of the growing season the length of the leader shoot of each seedling was measured.

Chemical analysis

For fluoride, nitrogen and sulphur analyses the needles of artificially infested spruce seedlings were washed and oven-dried at 60° C for 24 h and milled. The material from four seedlings was pooled to form one sample and so two separate samples from each treatment were analysed. Fluoride content in the needles of seedlings was analysed by a microdiffusion method using an F-selective electrode (Kari et al. 1978), nitrogen by the Kjeldahl method, and sulphur by ion chromatography after combustion in oxygen in a calorimetric bomb where all sulphur was oxidized to sulphate (e.g. Small et al. 1975).

At the end of the following growing season, the numbers of eggs in control and F treatments were counted, and the free amino acids from the stems of the current year's shoots of the naturally infested seedlings in control and F-treatments were analysed. Amino acids were analysed with an automatic amino acid analyzer (LKB Alpha Plus 4151) using a standard programme for the separation of amino acids. Before analysis, the samples were homogenised, sulphosalicylic acid was added to precipitate the proteins and norleusine was added as a reference compound. After centrifugation at 3000 rpm for 15 min, the samples were frozen and kept at −25° C. Before analysis the pH of the melted samples was adjusted to 2.2.

Data analysis

The data from measurements of shoot growth were subjected to one-way analysis of variance and means were compared by Duncan's Multiple Range Test. Means from chemical analyses were compared by the Mann-Whitney *U* Test. The numbers of all stages of aphid nymphs and adults were pooled for analyses. The data from aphid counts in the artificially infested seedlings and from egg counts were subjected to one-way analysis of variance after log-transformation. Statistical analyses were accomplished with the SPSS/PC+ system (SPSS Inc. Chicago, Illinois).

The data from natural aphid infestation were analysed as a generalized linear model (McCullagh and Nelder 1983) using the GLIM package (Payne 1986). The treatments (F, N, S) were specified as two-level factors. The aphid abundances were counts, but they were clearly overdispersed to the Poisson distribution. Of the various available contagious distributions (Kemp 1987) we used the negative binomial, for which moment estimates can be easily found in GLIM (Breslow 1984; Lawless 1987; Oksanen et al. 1990). The aggregation parameter of the negative binomial distribution was estimated from the full model (with two-way interaction F.N.S) and it was kept fixed in reduced models. The model was reduced by backward elimination following the guidelines given for structured models by McCullagh and Nelder (1983). The significance of the removed terms was estimated by assuming that the deviances followed the Chi-squared distribution. As a link function relating fitted values to linear predictor, we used identity. This makes the effect of interaction terms additive and so the model inspection is comfortable. The fit was as good as or better than when using logarithmic link which would make the model multiplicative.

Results

In naturally infested seedlings, all exposure treatments resulted in significant increases of aphid numbers (Fig. 1). Fluoride had a stronger effect on aphid numbers than SO_2 or nitrogen. During the population peak on 26 June, fluoride, SO_2 and nitrogen produced increases of about 300%, 200% and 100%, respectively, in the numbers of aphids per seedling. The highest interactive effect during the population peak was found between nitrogen and

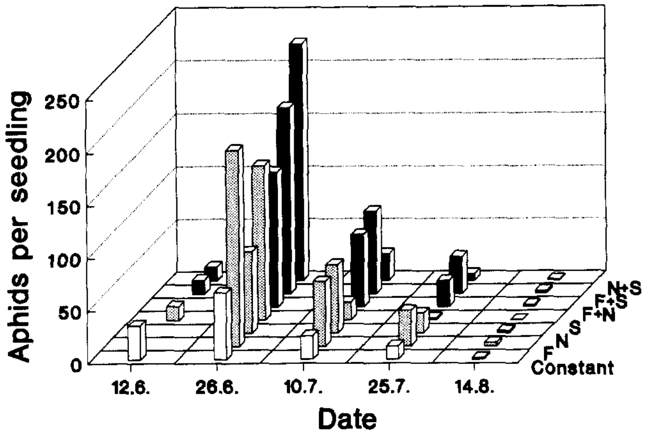

Fig. 1. The additive effects of pollutants singly and in combination on aphid numbers per 5-year-old naturally infested spruce seedlings. *Constant* shows the natural level of aphid numbers and it should be added to other bars for final number of aphids. Only significant effects are included

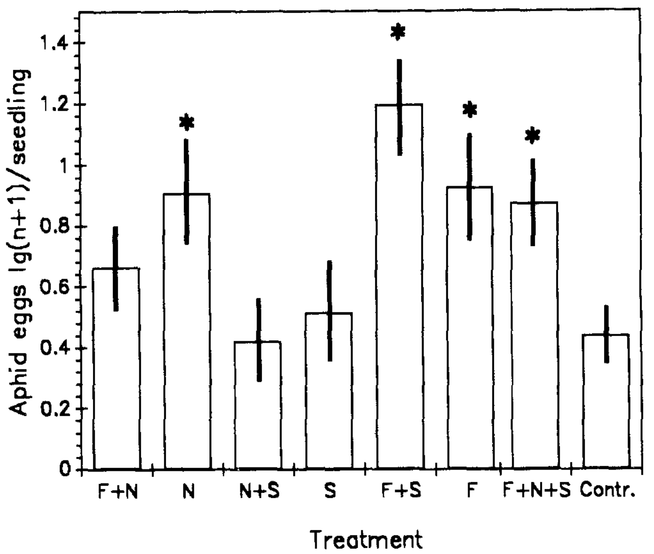

Fig. 2. Mean number of *Cinara pilicornis* eggs per 5-year-old naturally infested seedling at the end of growing season in 1986. The *black bar* indicates SD and *asterisks* indicate significant ($P < 0.05$) differences from control treatment

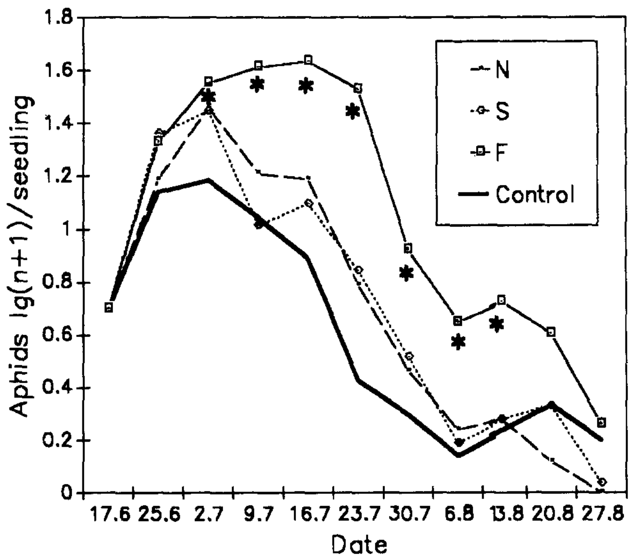

Fig. 3. Mean number of aphids per artificially infested 3-year-old spruce seedlings in single-pollutant treatments. *Asterisks* indicate significant ($P < 0.05$) differences from control treatment

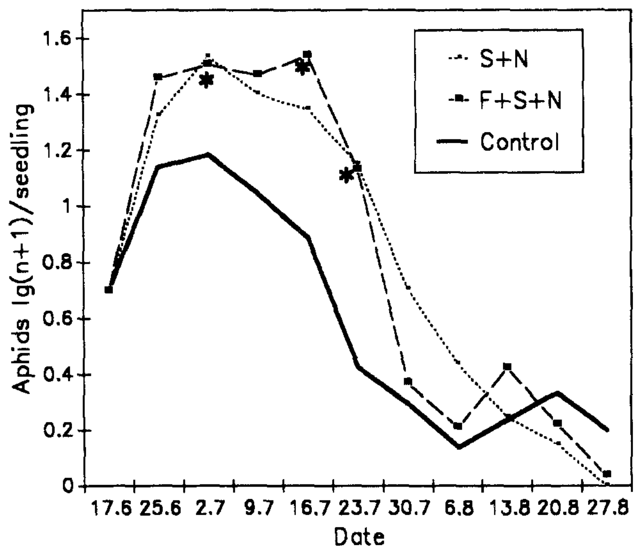

Fig. 4. Mean number of aphids per artificially infested 3-year-old spruce seedlings in combined pollutant treatments. *Asterisks* indicate significant ($P < 0.05$) differences from control treatment

Table 2. The mean length (mm) of the current-year leader shoot in spruce seedlings naturally (5-year-old) or artificially (3-year-old) infested by *Cinara pilicornis*

Treatment	5-year-old seedlings		3-year-old seedlings	
	n	Mean ± SD	*n*	Mean ± SD
F+N	10	305.0 (95.0)		no data
N	10	273.5 (89.2)	8	85.0 (25.6)
N+S	10	273.0 (50.2)	8	83.8 (23.7)
S	10	319.5 (61.6)	8	88.1 (16.9)
F+S	10	353.5 (93.6)		no data
F	10	273.0 (84.2)	8	77.5 (28.4)
F+N+F	10	286.5 (91.5)	8	84.4 (28.7)
Control	20	306.8 (80.4)	8	91.3 (20.1)

Table 3. Concentration (±SD) of F, N and S in the needles of 3-year-old pine seedlings at the end of the growing season. ($n=2$)

Treatment	F µg g⁻¹ DW	S µg g⁻¹ DW	N mg g⁻¹ DW
1. N	7.8 (0.7)	1019 (210)	10.8 (0.4)
2. N+S	7.7 (3.4)	1825 (199)	13.6 (1.1)
3. S	5.7 (1.2)	1972 (42)	13.8 (0.8)
4. F	22.8 (4.5)	1591 (28)	13.1 (0.6)
5. F+N+S	23.1 (4.3)	1668 (18)	15.6 (0.5)
6. Control	5.2 (0.4)	1240 (255)	11.6 (2.6)
F treat. (4+5)	23.0 (3.4)**		
F contr. (1+2+3+6)	6.6 (1.9)		
S treat. (2+3+5)		1822 (162)**	
S contr. (1+4+6)		1283 (298)	
N treat. (1+2+5)			13.3 (2.2)
N contr. (3+4+6)			12.7 (1.6)

** = Significant difference (P<0.01)

Table 4. Levels of free amino acids in the current-year twigs of 6-year-old pine seedlings at the end of growing season in 1987

Amino acid	Free amino acids Control ($n=6$) $\bar{x}$ (SD)	(µmol/10 g FW) F treatment ($n=6$) $\bar{x}$ (SD)
Aspartic acid	8.6 (3.81)	6.8 (1.63)
Threonine	1.9 (0.60)	2.0 (0.26)
Serine	7.5 (2.00)	7.2 (0.99)
Asparagine	2.8 (2.64)	1.8 (0.27)
Glutamic acid	16.7 (5.35)	15.9 (1.19)
Glutamine	59.4 (48.99)	38.4 (9.69)
Glycine	1.1 (0.31)	1.6 (0.69)
Alanine	8.3 (2.06)	8.1 (1.48)
Isoleucine	1.2 (0.56)	1.0 (0.23)
Leucine	1.2 (0.39)	1.1 (0.21)
Tyrosine	0.4 (0.45)	0.8 (0.42)
Phenylalanine	0.7 (0.42)	0.8 (0.42)
Ornithine	0.7 (0.62)	1.1 (0.26)
Lysine	2.5 (1.77)	1.7 (0.66)
Histidine	1.6 (2.33)	2.4 (1.00)
Arginine	38.7 (38.20)	14.2 (3.94)
Proline	0.7 (1.72)	3.0 (3.31)
Total	153.8 (99.00)	107.7 (14.18)

SO_2. The numbers of aphid eggs per seedling at the end of the growing season were significantly ($P<0.05$) higher in F, F+S, F+N+S and N treatments than in the control treatment (Fig. 2).

With artificial aphid infestation, significantly increased aphid populations were observed especially in the fluoride treatment (Fig. 3) but also in combination treatments (S+N and S+N+F) (Fig. 4).

Neither aphid infestation nor exposure to pollutants had any significant effect on the growth of the current-year shoot in naturally infested ($F_{7,82}=1.22$, $P=0.305$) or artificially infested seedlings ($F_{5,42}=0.29$, $P=0.916$) (Table 2).

At the end of the growing season the concentrations of fluoride and sulphur in the needles of 3-year-old pine seedlings were significantly ($P<0.01$) increased in the treatments in which these compounds were included but nitrogen applications had no observable effect on N levels in the needles (Table 3).

At the end of the following growing season the numbers of aphid eggs per seedling were significantly ($P=0.001$, t-test) higher (61.24 ± 8.6 SE, $n=29$) in F treatments than in control treatment (25.76 ± 5.6, $n=29$). There were no significant differences in the concentrations of free amino acids in shoot stems between control and fluoride treatments (Table 4).

Discussion

Our results show that all the pollutants studied or their combinations had a stimulating effect on aphid numbers. One explanation could be the additional precipitation on the seedlings which might increase seedling vigour and suitability for aphids during very dry periods in June. The sudden drop of aphid numbers in the SO_2 treatment in container-grown seedlings on 9 July might partly be explained by increased water loss from needles due to stomatal opening stimulated by SO_2 (Malhotra and Khan 1984) resulting in decreased availability of phloem sap. Yet in combination treatments, SO_2 and spraying of aqueous pollutants seemed to have a synergetic effect on aphid success. Neuvonen and Lindgren (1987) also observed that dry periods and pollution stress have interacting effects on aphid reproduction. According to their results simulated acid rain increased aphid reproduction on birch when the weather was drier than normal, but no effect was observed when the precipitation was above normal.

In the naturally infested, taller spruce seedlings, gaseous SO_2 alone had a stimulating effect on aphid numbers. According to Warrington (1987) there is a positive linear relationship between the percentage change in the mean relative growth rate (MRGR) of the pea aphid *(Acyrtosiphum pisum)* and SO_2 concentration, MRGR being highest when SO_2 concentration was 260 µg m^{-3} (100 nl l^{-1}). In the present study most of the spruce seedlings in SO_2 treatments were exposed to concentrations which stimulated the growth of aphids in Warrington's (1987) experiments.

The results of this study are consistent with earlier observations (Villemant 1981; Thalenhorst 1974) where fluoride pollution particularly promoted the growth of aphids on conifers. According to Thalenhorst (1975), *P. abies* has a histologically visible defensive reaction against gall aphids and fluoride exposure reduces this reaction thus improving aphid survival. In this study, fluoride alone or in combination treatments caused brown and chlorotic needle tips, indicating strong physiological response to fluoride, while SO_2 and nitrogen alone caused only a few visible symptoms (Wulff et al. 1990).

Increase of free amino acids in the needles of *P. abies* with HF induced injury has been reported by Jäger and Grill (1975). In plants subjected to other air pollutants (Malhotra and Sankar 1979; Bolsinger and Fluckiger 1987, 1989; Braun and Fluckiger 1989) or to other environmental stresses (White 1984), the concentration of free amino acids has also increased. Translocation of free amino acids as a result of degradation of leaf protein, and also alteration of amino acid metabolism (Lechowicz 1987) increases available nitrogen in the phloem, and this has been proposed as a mechanism to explain the increase of sucking insects on stressed plants (Cockfield 1988).

We did not observe an increase of free amino acids in the stems of the current year's shoots in F treatments after two growing seasons. However, we do not know whether the levels of free amino acids were increased in F-treated seedlings during active growth in June. The relatively low concentration of arginine in F treatments at the end of the growing season might indicate disturbances in the nitrogen metabolism of spruce seedlings. Normally arginine concentrations are lower during active growth than during dormancy (Durzan 1968). According to Wellings and Dixon (1987), arginine is more abundant in sycamore leaves previously infested with sycamore aphids than in uninfested leaves. On the other hand, Fisher (1987) found lower concentration of this essential amino acid in spruce foliage infested by aphids than in uninfested foliage. According to our unpublished laboratory observations, *C. pilicornis* does not reproduce on spruce cuttings, which have high concentrations (about 750 μmol per 10 g FW) of arginine. This amino acid may be an indicator of the nutritive value of the host plant for conifer aphids.

Secondary plant compounds may act as feeding deterrents for needle-eating herbivores (Niemelä et al. 1982; Cates et al. 1983) on conifers. In grasses terpenes (Rose et al. 1981) and phenolics (Dreyer and Jones 1981) are feeding deterrents for aphids, but their role in aphid resistance in conifers has not been studied. Alterations in terpene production of conifers have been observed in environments polluted by F and SO_2 by Lehtiö (1981) who suggested that the increased emissions of monoterpenes might be due to degradation of lipids in needles damaged by air pollution. The composition of lipids in conifer needles is strongly influenced by fluoride compounds (Zwiazek and Shay 1988; Anttonen and Kärenlampi, unpubl.), but their influence on plant secondary compounds is not known. More detailed studies of the alterations in nutritive value and defence chemistry in plants are needed to understand the air pollution-induced alterations in insect-plant relationships.

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References

Bolsinger M, Fluckiger W (1987) Enhanced aphid infestation at motorways: the role of ambient air pollution. Entomol Exp Appl 45:237–243

Bolsinger M, Fluckiger W (1989) Ambient air pollution induced changes in amino acid pattern of phloem sap in host plants – relevance to aphid infestation. Environ Poll 56:209–216

Braun S, Fluckiger W (1989) Effect of ambient ozone and acid mist on aphid development. Environ Poll 56:177–187

Breslow NE (1984) Extra-Poisson variation in log-linear models. Appl Statist 33:38–44

Cates RG, Redak RA, Henderson CB (1983) Patterns in defensive natural product chemistry within and among populations of Douglas-fir affecting western spruce budworm success. In: Hedin PA (ed) Plant Resistance to Insects, American Chemical Society Symposium 208. American Chemical Society, Washington, DC, pp 3–20

Cockfield SD (1988) Relative availibility of nitrogen in host plants of invertebrate herbivores: three possible nutritional and physiological conditions. Oecologia 77:91–94

Dohmen GP (1985) Secondary effects of air pollution: Enhanced aphid growth. Environ Poll 39:227–234

Dohmen GP, McNeill S, Bell JN (1984) Air pollution increases *Aphis fabae* pest potential. Nature 307:52–53

Dreyer DL, Jones KG (1981) Feeding deterrency of flavonoids and related phenolics towards *Schizaphis graminum* and *Myzus persicae:* aphid feeding deterrents in wheat. Phytochem 20:2489–2493

Durzan DJ (1968) Nitrogen metabolism of *Picea glauca*. II. Diurnal changes of free amino acids, amides, and guanidino compounds in roots, buds, and leaves during the onset of dormancy of white spruce saplings. Can J Bot 46:921–937

Feir D, Hale R (1983a) Growth and reproduction of an insect model in controlled mixtures of air pollutants. Int J Environ Stud 20:223–228

Feir D, Hale R (1983b) Responses of the large milkweed bug, *Oncopeltus fasciatus* (Hemiptera: Lygaeidae) to high levels of air pollutants. Int J Environ Stud 20:269–273

Fisher M (1987) The effect of previously infested spruce needles on the growth of the green spruce aphid, *Elatobium abietinum,* and the effect of the aphid on the amino acid balance of the host plant. Ann Appl Biol 111:33–41

Heliövaara K, Väisänen R (1986a) Parasitization in *Petrova resinella* (Lepidoptera, Torticidae) galls in relation to industrial air pollutants. Silva Fenn 20:233–236

Heliövaara K, Väisänen R (1986b) Industrial air pollution and the pine bark bug, *Aradus cinnamomeus* Panz. (Het., Aradidae). J Appl Ent 101:469–478

Heliövaara K, Väisänen R (1988) Interactions among herbivores in three polluted pine stands. Silva Fenn 22:283–292

Hughes PR, Chiment JJ, Dickie AI (1985) Effect of pollutant dose on the response of Mexican bean beetle (Coleoptera: Coccinellidae) to SO_2-induced changes in soybean. Environ Entomol 14:718–721

Jäger HJ, Grill D (1975) Einfluss von SO_2 und HF auf freie Aminosäuren der Fichte (*Picea abies*, Karsten). Eur J For Path 5:279–286

Kari T, Kauranen P, Alhava E (1976) Effect of drinking water fluoridation on the fluoride content of human bone in and around Kuopio, Central Finland. Analytical study. Publ Univ Kuopio, Commun Health Ser, Orig Rep 1:1–15

Kemp AW (1987) Families of discrete distributions satisfying Taylor's power law. Biometrics 43:693–699

Lawless JF (1987) Negative binomial and mixed Poisson regression. Can J Statist 15:209–225

Lechowicz MJ (1987) Resource allocation by plants under air pollution stress. Implications for plant-pest-pathogen interactions. Bot Rev 53:281–300

Lehtiö H (1981) Effect of air pollution on the volatile oil in needles of Scots pine (*Pinus sylvestris* L.) Silva Fenn 15:122–129

Malhotra SS, Khan AA (1984) Biochemical and physiological impact of major pollutants. In: Treshow M (ed) Air pollution and plant life. John Wiley and Sons, New York, London, Sydney, Toronto pp 113–157

Malhotra SS, Sankar SK (1979) Effects of sulphur dioxide on sugar and free amino-acid content of pine seedlings. Physiol Plant 47:223–228

McCullagh P, Nelder JA (1983) Generalized linear models. Chapman and Hall, London

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

Niemelä P, Mannila R, Mäntsälä P (1982) Deterrent in Scots pine, *Pinus sylvestris,* influencing feeding behaviour of the larvae of *Neodiprion sertifer* (Hymenoptera, Diprionidae). Ann Ent Fenn 48:57–59

Oksanen J, Läärä E, Huttunen P, Meriläinen J (1990) Maximum likelihood prediction of lake pH according to sedimented diatoms, and an analysis of its performance. J Veget Sci 1: 49–56

Payne CD (ed) (1986) The GLIM system release 3.77 manual. Numerical Algorithms Group, Oxford

Przybylski Z (1979) The effects of automobile exhaust gases on the arthropods of cultivated plants, meadows and orchards. Environ Pollut 19:157–161

Rose AF, Jones KC, Haddon WF, Dreyer DL (1981) Grindelane diterpene acids from *Grindelia humilis*: feeding deterrency of diterpene acids towards aphids. Phytochem 20:2249–2253

Sierpinski Z (1985) Luftverunreinigungen und Forstschädlinge. Z Ang Entomol 99:1–6

Small H, Stevens TS, Bauman WC (1975) A novel ion exchange chromatographic method using conductimetric detection. Anal Chem 47:1801–1809

Spencer HJ, Port GR (1988) Effects of roadside conditions on plants and insects. II. Soil conditions. J Appl Ecol 25:709–715

Thalenhorst W (1974) Untersuchungen uber den Einfluss fluorhaltiger Abgase auf die Disposition der Fichte für den befall Durch die Gallenlaus *Sacchiphantes abietis* (L.) Z Pflkrankh Pflschuz 81:717–727

Trumble JT, Hare JD, Musselman RG, McCool PM (1987) Ozone-induced changes in host-plant suitability: Interactions of *Keiferia lycopersicella* and *Lycopersicon esculentum.* J Chem Ecol 13:203–218

Villemant C (1981) Influence de la pollution atmosphérique sur les populations d'aphides du pin sylvestre en forêt de Roumare (Seine-Maritime). Environ Pollut (Ser A) 24:245–262

Warrington S (1987) Relationship between sulphur dioxide dose and growth of the pea aphid, *Acyrthosiphon pisum,* on peas. Environ Pollut 43:155–162

Warrington S, Cottam DA, Whittaker JB (1989) Effects of insect damage on photosynthesis, transpiration and SO_2 uptake by sycamore. Oecologia 80:136–139

Wellings PW, Dixon AFG (1987) Sycamore aphid numbers and population density. III. The role of aphid induced changes in plant quality. J Anim Ecol 56:161–170

White TCR (1984) The abundance of invertebrate herbivores in relation to the avaibility of nitrogen in stressed food plants. Oecologia 63:90–105

Wiackowski SK (1978) Wplyw przemyslowych zanieczyszczen powietrza na entomofagi skosnika tuzinka (*Exoteleia dodecella* L.) i mszyc oraz na inne owady wystepujace na sosnie w okolicy Tomaszowa Maz. Folia For Polon A 23:175–187

Wulff A, Ropponen L, Kärenlampi L (1990) Causes of conifer injuries in some industrial environments. In: Kauppi P, Kenttämies K, Anttila P (eds) Acidification in Finland. Springer-Verlag, Berlin, pp 669–690

Zwiazek JJ, Shay JM (1988) The effects of sodium fluoride on cytoplasmic leakage and the lipid and fatty acid composition of jack pine *(Pinus banksiana)* seedlings. Can J Bot 66:535–541