Patterns of Forest Invertebrates Along an Acidic Deposition Gradient in the Midwestern United States

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Abstract

The Ohio Corridor Study (OCS) was designed to detect possible effects of acidic deposition on oak-hickory (Quercus-Carya) forests in the midwestern United States. There was one study site in Arkansas, and two each in Illinois, Indiana, and Ohio. Estimates of total sulfate deposition have generally increased about two-fold from west (Arkansas) to east (Ohio) during the 1900s. Sites were broadly analogous in forest cover type, stand age, slope, aspect, mean annual temperature and rainfall, soil type (mostly poorly buffered soils derived from sandstone and shale), and disturbance history. The overall hypothesis was that for analogous stand conditions and soil types, differences in various forest response variables along a geographic acidic-deposition gradient would correspond to differences in pollutant dose. Response variables were correlated with the soil Ca:Al molar ratio, as an indicator of soil acidification, for the upper 50 cm of soil. In the OCS insect studies, as the soil Ca:Al ratio decreased, i.e., became more acidified, there tended to be an increase in (1) population densities of early season, canopy-feeding Lepidoptera larvae ($P = .19$); (2) foliage consumption by gypsy moth larvae, using a standardized feeding choice test with early season ($P = .01$) and late-season ($P = .16$) oak foliage; (3) attack densities of non-lethal, trunk-infesting, living oak borers in the families Cerambycidae and Cossidae on white oaks (Quercus alba) and black oaks (Quercus velutina) ($P = .003$); and (4) the probability of oak mortality being caused by the twolined chestnut borer, Agrilus bilineatus, a lethal cambial-feeding buprestid beetle ($P = .057$). Data from other OCS investigators indicated strong correlations between lower soil Ca:Al ratios and reduced tree growth, reduced soil pH, reduced soil invertebrate densities, and increased soil carbon levels. These results suggest that acidic inputs can alter forest ecosystem processes in oak-hickory forests growing on poorly buffered soils.

Introduction

Air pollution stress is known to induce a diverse array of biochemical, morphological, and physiological changes in forest trees (Heliövaara and Väisänen 1993, Koziol and Whatley 1984, Kozlowski and Constantinidou 1986a, 1986b, Malhotra and Khan 1984). The possibility that such changes in plants could alter plant-insect interactions was the topic of several recent reviews (Baltensweiler 1985, Führer 1985, Hain 1987, Heliövaara and Väisänen 1993, Hughes 1988, Hughes and Laurence 1984, Lechowicz 1987, Mattson and Witter 1990, Riemer and Whittaker 1989). In many of these studies, population size of tree-feeding insects increased at low to intermediate pollutant levels, but decreased at high pollutant levels. However, the exact relationship varied depending on factors such as pollutant type, pollutant dose, soil buffering capacity, insect species, and the insect's mode of feeding (*e.g.*, leaf-feeders, inner-bark feeders, wood borers).

The aim of the Ohio Corridor Study (OCS) was to examine possible effects of acidic deposition on oak-hickory (*Quercus-Carya*) forests in the lower midwestern United States (Haack and Blank 1991b, Kuperman 1993, LeBlanc 1993, Loucks 1992, Loucks *et al.* 1991). The OCS was designed to test the hypothesis that for analogous stand conditions and soil types, differences in forest response variables along the gradient could be explained by differences in pollutant dose. The soil calcium:aluminum (Ca:Al) molar ratio was used as an indicator of site acidification, given that it generally decreases with increasing soil acidification (Boudot *et al.* 1994).

The four major OCS insect projects described here examined the relationship between the deposition gradient and (1) population densities of leaf-feeding Lepidoptera, (2) larval feeding preference for oak foliage collected along the gradient, (3) attack densities of non-lethal trunk-infesting living oak borers, and (4) the probability that oak mortality resulted from *Agrilus bilineatus* attack, a lethal

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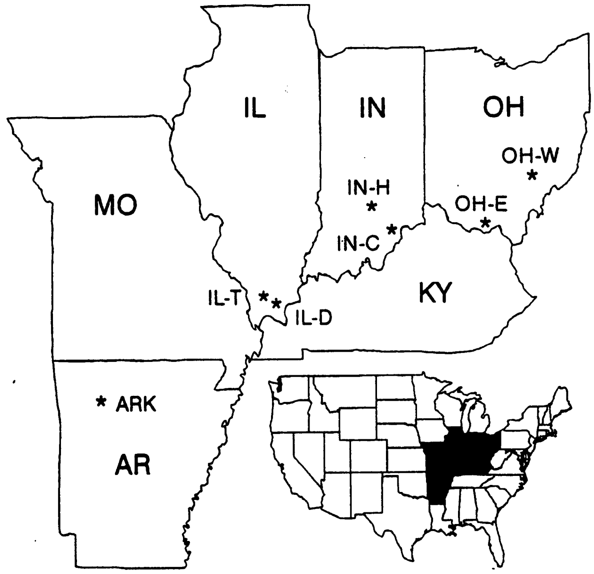

Figure 1. Map of the Ohio Corridor Study area and locations of study sites in the midwestern United States. States are: AR= Arkansas, IL=Illinois, IN=Indiana, KY=Kentucky, MO=Missouri, and OH=Ohio. Sites are: ARK=Fly Gap Mountain in AR; IL-D=Dixon Springs Agricultural Station in Illinois; IL-T=Touch of Nature Preserve in Illinois; IN-C= Clark State Forest in Indiana; IN-H=Hoosier National Forest, Deam Wilderness Unit, in Indiana; OH-E=Edge of Appalachia preserve in Ohio; and OH-W =Wayne National Forest, Athens Unit, in Ohio.

cambial borer of oaks. The insect studies concentrated on oaks because they were the dominant tree genus at all sites and because they are known to be sensitive to changes in soil aluminum levels (Joslin and Wolfe 1989).

Methods

Project description. **—** The OCS was conducted in oak-hickory forests in the midwestern United States. Seven study sites were selected: one in Arkansas and two each in Illinois, Indiana, and Ohio (Fig. 1). These sites were primarily situated in the Ohio River Valley, an area of regionally high sulfate emissions (Gschwandtner *et al.* 1986). Estimates of total annual sulfate deposition (wet + dry) increase about two-fold from Arkansas to Ohio (Table 1). In addition, the Ohio River Valley is recognized as an area of high ozone concentrations within the United States (Lefohn and Pinkerton 1988); however, no major ozone gradient was detected in the present study (Loucks 1992, Loucks *et al.* 1991). All study sites were south of the maximum glacial advance and north of areas where soils have high sulfate absorption capacities. Soils were stony, derived from sandstones and shales, and had low cation exchange capacity (Guillemette 1989, Loucks and Somers 1990, Loucks *et al.* 1991). Additional summary data for the sites can be found in Foster and LeBlanc (1993), Haack and Blank (1991a,b), LeBlanc (1993), Loucks *et al.* (1991), and Table 1.

At each site, three to five analogous forest stands were selected, and within these stands, seven to nine 0.04-ha circular plots were chosen. These sites were broadly analogous in forest cover type, stand age, slope, aspect, mean annual temperature and rainfall, soils, and lack of evidence of any fire or logging disturbance during the past several decades. Soil pits were dug near each study plot and detailed soil analyses were conducted (Loucks and Somers 1990). Each insect study was conducted at the plot or stand level. Although the seven OCS sites were selected to be highly analogous in 1987, subsequent detailed soil and stand-structure studies in 1988-89 indicated that the entire Arkansas site, and some stands at one Ohio site (OH-E) should be withdrawn from analyses when considering only the most narrowly

Table 1 OCS location data, mean growing-season (April 16 - October 15) temperature and precipitation (1900-1987; GS temp, GS precip), mean annual precipitation (1955-1986), mean stand age of dominant and co-dominant trees, percent of basal area consisting of *Quercus* and *Carya* species (trees ≥ 10 cm dbh), and estimated annual total (wet + dry) sulfate deposition for two time spans by site (Foster 1990, Foster and LeBlanc 1993, Haack and Blank 1991, LeBlanc 1993, Loucks *et al.* 1991)

Parameter	ARK	IL-D	IL-T	Site IN-C	IN-H	OH-E	OH-W
State	Arkansas	Illinois	Illinois	Indiana	Indiana	Ohio	Ohio
County	Franklin	Pope	Jackson	Scott	Jackson	Adams	Perry
Latitude	35°45'	37°25'	37°38'	38°30'	39°03'	38°40'	39°35'
Longitude	93°47'	88°40'	89°11'	85°50'	86°12'	83°27'	82°03'
Elevation (m)	685	145	170	275	260	315	270
GS temp (°C)	21	23	22	21	21	21	20
GS precip (cm)	69	65	64	63	64	63	62
Precip (cm)	120	118	120	109	113	106	105
Age (yr)	65	87	121	97	86	101	123
% *Quercus*	98	88	77	86	98	84	96
% *Carya*	1	9	20	6	1	13	1
% *Q + C*	99	97	97	92	99	97	97
Estimated total annual sulfate deposition (g/m/yr)							
1900-1985	5.51	8.64	7.66	8.68	8.80	9.99	9.89
1955-1986	3.85	6.73	5.97	6.14	6.23	7.16	7.08

analogous sites (Loucks *et al.* 1991). Therefore, data from these non-analogous locations will not be reported here. Results of the OCS insect studies are reported as means on a per site basis and correlated with the soil calcium:aluminum (Ca:Al) molar ratio for the upper 50 cm of soil. On average, the 50-cm depth included three soil horizons: A_1, E, and one or more B's. The 50-cm depth was chosen because it represented a less variable measure of the soil chemistry compared with the upper 2.5 or 5 cm of soil, and because it corresponded more closely to the soil rooting volume used by trees at these sites. For the insect studies conducted at the plot level (Studies 1 and 2), the soil Ca:Al ratio from each plot's corresponding soil pit was used to estimate a mean ratio for each study site. For studies conducted at the stand level (Studies 3 and 4), the soil Ca:Al ratio assigned to each stand was the average value for all soil pits dug within each particular stand; mean site ratios were obtained by averaging Ca:Al ratio values of each sampled stand.

Study 1: Defoliator density

There are many species of leaf-feeding insects in the oak-hickory forests of the eastern United States (Drooz 1985). Some are early-season defoliators, while others are late-season defoliators. Several methods have been devised to estimate populations of defoliating insects in tree canopies. I used an indirect method in which head capsules of lepidopteran larvae (caterpillars) were collected (Higashiura 1987, Paramonov 1959). In this method, larval densities were estimated from the number of head capsules collected in traps positioned on the forest floor. The head-capsule collection method is best suited for lepidopteran larvae because their head capsules are readily shed with each larval molt, easily identified, and resistant to decay.

To collect head capsules, 18 traps were placed at regular intervals around the outside perimeter of five study plots at each site in Illinois, Indiana, and Ohio (18 traps/plot x 5 plots/site x 6 sites = 540 traps). Each trap consisted of an inverted, 1-gallon plastic jug (ca. 15 x 15 cm in cross-section) from which the bottom was removed and four garden stakes were stapled to the sides to serve as "feet" (Haack and Blank 1991a). The trap's feet were pushed into the soil, making sure that the top remained horizontal. A fine-mesh, nylon bag was placed inside the trap and secured to the rim with paper clips.

Traps were placed in the field for 2 years, from April 1988 to April 1990. Site visits were made three times per year: June, September, and April. In June 1988, for example, all collection bags were removed from the traps and placed individually in labeled cartons. New nylon bags were then placed in each trap. This procedure was repeated for 2 years. In the laboratory, the contents of each carton were dried and sorted. Head capsules were detected with a dissecting microscope. Using the surface area of each trap, collection data were expressed as the number of head capsules collected per m^2 of forest floor for a given period of time, *e.g.*, April-June. Mean defoliator densities were calculated for each plot by averaging the collection data for the 18 traps at each plot. Site means were then obtained by averaging the plot values for mean head-capsule density. Data from OH-E were not included because subsequent soil analyses detected calcareous beds in the B horizon of the plots that were used to collect head capsules.

Study 2: Foliage choice test

Laboratory feeding preference studies were conducted in May and August 1989, using white oak (*Q. alba* L.) and black oak (*Q. velutina* Lam.) foliage and gypsy moth larvae [*Lymantria dispar* (L.)]. In the May study, oak foliage was collected from one site per state: ARK, IL-D, IN-H, OH-E. Although the Arkansas data were omitted from the final analyses, the OH-E data could be used because the foliage-collection trees were located on acceptable plots. In the August study, only foliage from IL-D, IN-H, and OH-E was used. At each site, foliage was collected from five white oaks and five black oaks that were dominant or co-dominant trees. Foliage was collected from the same trees in both studies. Separate field crews went to each site and all personnel used the same protocol. Branches were cut with pole-pruners from the lower crown on the south side of each tree. Foliage was collected between 8-10 a.m., placed on ice in labeled bags, and transported to our laboratory in Michigan. Undamaged leaves of similar phenological age were selected at all sites.

Feeding bioassays were initiated within 24 h following foliage collection. Gypsy moth larvae were obtained from a laboratory colony that was maintained on artificial diet at the U.S. Forest Service laboratory in Hamden, Connecticut. Recently molted second-instar larvae were used in the May study, while recently molted fourth-instars were used in the August study. Larvae were shipped from Hamden by overnight mail and arrived in Michigan on the same day that foliage was collected in the field.

Petri dishes, 10 cm in diameter, were used as the bioassay chambers. Forty leaf disks, 2.4 cm in diameter, were cut from the leaves of each tree, using a cork borer. In the May study, four leaf disks were placed in each dish, one disk per site. The disks were placed around the inside perimeter of each dish. Three second-instar larvae were placed in the middle of each dish and allowed to feed for 24 h. Overall, there were 200 bioassays with white oak foliage and 200 with black oak foliage. In the August study, six leaf disks were placed in each dish, two disks per site. Forty disks were cut from each tree's foliage to establish 100 bioassays with white oak foliage and 100 bioassays with black oak foliage. A single fourth-instar larva was placed in the middle of each dish and allowed to feed for 24 h.

In both studies, percent consumption was estimated visually at 6-h intervals during the 24-h feeding period. At termination of the study, percent consumption was calculated for each leaf disk, using a leaf-area meter. These values were then used to calculate mean consumption of black oak and white oak foliage for each site. For each study, surplus foliage from each tree was used to determine percent water content and mineral concentrations.

Study 3: Density of living oak borers

There are several wood borers in the families Cerambycidae (Coleoptera) and Cossidae (Lepidoptera) that attack living oaks in the eastern United States (Donley and Acciavatti 1980, Donley and Terry 1977, Drooz 1985, Galford 1983, Hay 1968, 1974, Hay and Morris 1970, Solomon 1972, 1977, Solomon and Donley 1983). These insects are commonly called "living oak borers" because they attack oaks without killing the host tree. Living oak borers produce signs of attack that are easily identified in the field, such as entrance holes, larval galleries, exit holes, frass, and stains. The entrance holes, galleries, and exit holes remain for many years after the insect has departed. In addition, living oak borers usually attack the lower trunk, facilitating inspection from the ground.

At each site, the lower 2 m of trunk of 22 to 60 white oaks and 42 to 61 black oaks were inspected in spring 1989 for borer attacks. Oak trees under 20-cm dbh (diameter at breast height, 1.4 m) were generally selected because this is the preferred tree diameter for many living oak borers. Tree species, dbh, and stump diameter at 30 cm were recorded for each tree. Each borer attack was categorized as being currently active (*i.e.*, where larval frass was evident) or inactive but successful, *i.e.*, where larval galleries and adult emergence holes were evident. Attacks by all species of living oak borers were pooled because it was not always possible to make positive species determinations. The surface area of each tree's lower 2 m of trunk was estimated as a cylinder after averaging trunk diameters at 30 cm and 1.4 m. Attack density was expressed as the number of attacks/m^2 of bark surface area. Mean attack density values were computed separately for black oaks and white oaks at each site, using only those trees with a dbh between 8-16 cm. Again, the oaks inspected at OH-E in this study were dropped from the analyses because calcareous beds were later found in the B horizon of the sampled stands.

Study 4: Incidence of *Agrilus bilineatus* attack

Several dead oak trees, both standing and fallen, were present in all stands at each site. Many of these trees had been attacked and killed by the twolined chestnut borer, *Agrilus bilineatus* (Weber), a buprestid beetle that is a common mortality agent of stressed oaks in eastern North America (Haack and Acciavatti 1992, Haack and Benjamin 1982, Wargo 1977). As is true for living oak borers, *Agrilus* attacks along the trunk near groundline and produces very distinctive larval galleries in the cambial region and adult exit holes on the bark surface that are evident for several years following tree death (Haack and Acciavatti 1992).

Details of the methods for this study are given in Haack and Blank (1991b). Briefly, all dead oaks ≥7 cm dbh, both standing and fallen, were inspected in each approved forest stand at all sites. When possible, dead oaks were categorized as belonging to either the red oak sub-genus *Erythrobalanus* or the white oak sub-genus *Lepidobalanus*. The presence of *A. bilineatus* larval galleries or adult exit holes was used as positive evidence of *Agrilus* attack. The data set was restricted to oaks that had likely died in the past 1-2 decades by using dead trees with trunks in condition categories 1-3 as given in Haack and Blank (1991b) and McCune *et al.* (1988). Percent incidence of *Agrilus* attack was calculated for each stand, and then these individual stand values were averaged to obtain a mean site value.

Statistical analyses

Two statistical tests were conducted for each study. First, a one-way ANOVA was used to detect significant differences among site means for each insect variable. If significant, mean separation analysis was conducted using Duncan's multiple range test. Percentage data were transformed prior to analysis, using arcsin square-root. Second, linear regression analysis was conducted between the mean site insect values and mean site soil Ca:Al ratio values.

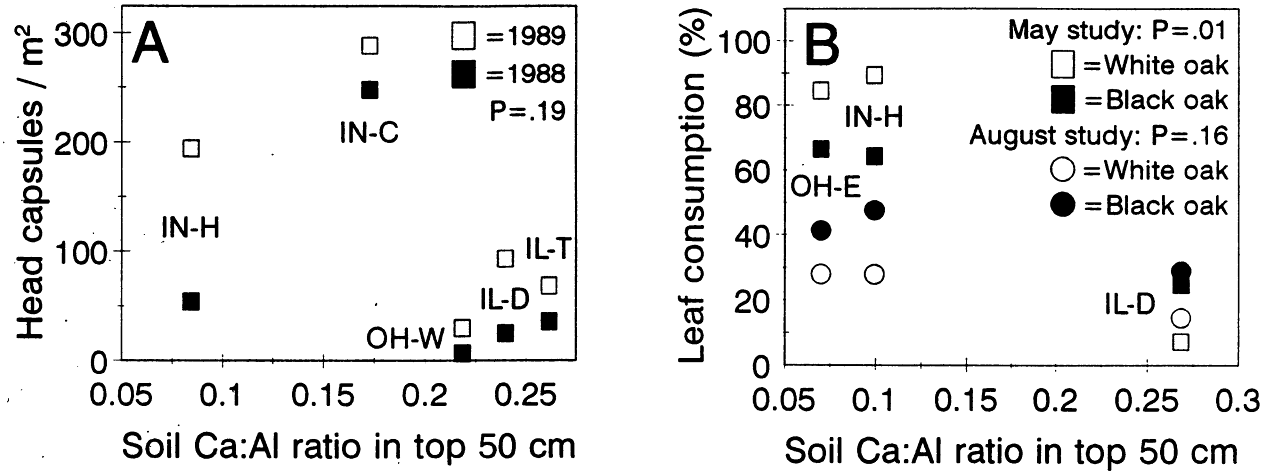

Figure 2 *(A) Mean number of lepidopteran larval head capsules collected per m of forest floor during the period April-June 1988 and 1989 at five sites along an acid-deposition gradient vs. soil Ca:Al molar ratio by site; and (B) mean percent consumption of leaf disks by gypsy moth larvae who were given a choice of black oak foliage or white oak foliage collected in May and again in August at three sites along an acid-deposition gradient vs. soil Ca:Al molar ratio by site. P values are based on linear regression analysis of the mean insect values vs. mean Ca:Al ratio by site (A: N=10; B: N=6 for both the May and August studies). See Fig. 1 for site locations*

Results and Discussion

Overall, most results tended to show greater insect activity with decreasing soil Ca:Al ratios. Assuming that these sites were broadly analogous except for historical acidic inputs and that soil Ca:Al ratio decreases as soils become more acidified, then the present studies indicate a strong correlation between greater insect activity and increased site acidification. Similar results could have been obtained if I had used pH of the A_1 soil horizon because soil pH and Ca:Al ratios were significantly correlated at the OCS sites (Loucks and Somers 1990). Specifics are presented below for each study.

Study 1: Defoliator density

Only the April-June collection data are presented because most defoliation occurred during that time. Overall, mean defoliator density increased in 1989 over 1988 at all sites (t-test, P = 0.03; N = 25 plots; Fig. 2a), with mean site values ranging from 24 to 264 head capsules/m^2 of forest floor in 1988 and from 44 to 305 in 1989. In both years, defoliator densities were significantly higher at one (IN-C) or both of the Indiana sites compared with the Illinois or Ohio sites (P = .0001 and N = 25 plots for both 1988 and 1989; Fig. 2a). Linear regression analysis indicated a slight tendency for mean defoliator density to increase with decreasing soil Ca:Al ratio (P = .19; N = 10 site-year combinations; Fig 2a).

It is not surprising that only a weak relationship was noted between defoliator density and soil Ca:Al ratio given the lack of refinement in this particular study. That is, (1) head capsules from all lepidopteran species and larval instars were pooled, (2) tree species composition changed somewhat between sites, which could influence species composition of phytophagous insects, especially monophagous species, and (3) the head-capsule data were not adjusted for variation in stand parameters such as basal area or percent crown cover. Possibly if the data set had been adjusted for one or more of the above parameters a stronger relationship would have been noted.

A significant positive relation between defoliator density and acidic inputs would not be unreasonable given that mild to moderate air pollution stress typically causes increased levels of soluble nitrogen and sugars in plant tissues (Heliövaara and Väisänen 1993, Hughes and Laurence 1984, Kozlowski and Constantinidou 1986a, Mattson and Haack 1987), and that many defoliating insects respond positively to increases in these key nutrients (Mattson and Haack 1987, Mattson and Scriber 1987).

In addition to changes in plant chemistry, populations of some phytophagous insects can increase due to negative impacts of pollutants on their natural enemies (Heliövaara and Väisänen 1993, Kataev *et al.* 1983, Saikkonen and Neuvonen 1992). In fact, as part of the OCS, Kuperman (1993) documented significantly lower densities of soil predatory invertebrates at the Indiana and Ohio sites compared with Illinois.

The increase in defoliator densities at all sites in 1989 compared with 1988 may reflect the severe regional drought in 1988 (Haack and Mattson 1989). That is, many defoliating insects experience faster larval development and greater survival during periods of drought because temperatures are typically elevated and they encounter less pressure from their natural enemies (Mattson and Haack 1987). It is interesting to note that the greatest 1988-to-1989 increase in defoliator density occurred at the site with the lowest soil Ca:Al ratio (IN-H; a threefold increase).

Study 2: Foliage choice test

In both the May and August studies, gypsy moth larvae preferentially ate more black oak and white oak foliage from Indiana and Ohio than from Illinois ($P = .0001$ and $N = 600$ leaf disks for each oak species in each study; Fig. 2b). Dropping the Arkansas data from the May study did not affect the final results because relatively little Arkansas foliage had been consumed: about 23% for each oak species.

When percent herbivory was estimated at 6 and 12 hours in the May test, larvae showed an early preference for Indiana foliage followed closely by Ohio foliage (Table 2); a similar pattern was recorded in the August study (data not shown). Percent water content for white oak foliage significantly increased from west (Illinois) to east (Ohio) in both the May and August studies, but no significant differences occurred for black oak foliage (Table 2). Similarly, in both the May and August studies, leaf nitrogen (N) content increased significantly from Illinois to Ohio for white oak foliage but less so for black oak foliage (Table 2).

Gypsy moth larvae preferred foliage from trees growing in soils with lower Ca:Al ratios. Using linear regression analysis, this inverse relationship was strongly significant for early season foliage (May study; $P = .0103$; $N = 6$ site-oak combinations; Fig 2b), but less so for late-season foliage (August study; $P = .16$; $N = 6$ site-oak combinations; Fig 2b).

This preference for Indiana and Ohio foliage can be partially explained in terms of differences in foliar water and N content, especially for the white oak foliage. It is well known that foliar water and N content greatly influence growth and survival of immature insects, and that many phytophagous insects discriminate among foods based on foliar water or N levels (Scriber and Slansky 1981). In foliage, water and N content decrease with leaf age (Mattson and Scriber 1987). The increase from Illinois to Ohio in water and N levels of May-collected white oak foliage at first suggested that we had used phenologically dissimilar foliage. But this same trend occurred in the August study, when levels of such nutrients remain rather constant. On the other hand, these differences could reflect among-site variation in microclimate, nitrate deposition, or 1989 rainfall and temperature patterns.

Study 3: Density of living oak borers

Attacks by four species of living oak borers were detected along the gradient: the cerambycids *Enaphalodes rufulus* (Haldeman) (red oak borer), *Goes pulverulentus* (Haldeman) (living beech borer), *Goes tigrinus* (DeGeer) (white oak borer), and the cossid *Prionoxystus robiniae* (Peck) (car-

Table 2. Mean (±1 SE) percent leaf-disk consumption by gypsy moth larvae after 6 or 12 hours of feeding in a foliage choice test, and mean percent foliar water and nitrogen content of white oak and black oak foliage collected from three sites along an acidic deposition gradient (see Methods for details).

Parameter	Site: IL-D	Site: IN-H	Site: OH-E	P=
	Estimated percent herbivory in the May study (%)			
White oaks (N=200 leaf disks/site)				
6 hours	2.7±0.19 **c***	16.8±0.64 a	12.3±0.54 **b**	0.0001
12 hours	4.0±0.47 **c**	38.0±1.42 **a**	23.1±1.15 b	0.0001
Black oaks (N=200 leaf disks/site)				
6 hours	6.9±0.25 **c**	11.9±0.40 **a**	9.3±0.34 **b**	0.0001
12 hours	9.8±0.47 **c**	27.3±1.19 **a**	19.2±0.69 **b**	0.0001
	Foliar water content (%)			
White oaks (N=5 trees/site)				
May study	67.0±1.4 **c**	72.0±0.4**b**	75.6±0.8 **a**	0.0001
August study	53.4±0.2**b**	54.8±0.2 **ab**	56.7±0.2**a**	0.006
Black oaks (N=5 trees/site)				
May study	71.6±0.4 **a**	70.1±1.4 **a**	70.6±0.4 **a**	0.48
August study	54.1±0.2 **a**	54.2±0.2 **a**	55.5±0.2 **a**	0.34
	Foliar nitrogen content (%)			
White oaks (N=5 trees/site)				
May study	2.03±.07 **b**	2.62±.19 **a**	2.87±.22 **a**	0.0147
August study	1.54±.04 **b**	1.62±.03 **b**	1.73±.02 **a**	0.0025
Black oaks (N=5 trees/site)				
May study	2.23±.07 **a**	2.24±.21 **a**	2.44±.13 **a**	0.546
August study	1.45±.06 **a**	1.67±.10 **a**	1.71±.08 **a**	0.0821

* *Means within the same row that are followed by the same letter are not significantly different at the $P < .05$ level using Duncan's multiple range test.*

penterworm). Mean attack density values by site, for both active and inactive attacks of all four species combined, ranged from 1.6 to 3.0 attacks/m^2 for black oaks and 1.3 to 4.0 for white oaks (Fig. 3a). On average, attack densities were higher in the Indiana and Ohio sites compared with the Illinois sites for both black oaks ($P = .02$; $N = 128$ trees) and white oaks ($P = .0001$; $N = 138$ trees; Fig. 3a). Linear regression analysis indicated that borer attack densities increased significantly with decreasing soil Ca:Al values ($P = .003$; $N = 10$ site-oak combinations; Fig 3a).

Attack rates by many species of bark- and wood-boring insects often increase on trees exposed to various environmental stresses, including air pollution (Heliövaara and Väisänen 1993, Kozlowski and Constantinidou 1986a, Mattson and Haack 1987, Stark *et al.* 1968). Likewise, the trend in the present study for attack density to increase with decreasing soil Ca:Al ratio suggests that oaks can become more susceptible to borer attack as site acidification progresses.

Larval survival of living oak borers is often enhanced during drought conditions. However, in the analysis of 1900-1987 climatic data for the OCS sites (Foster 1990), all sites had broadly similar growing-season climate variables, including temperature, rainfall, and drought history. Given Foster's (1990) results, it is not likely that the pattern of differential attack by living oak borers

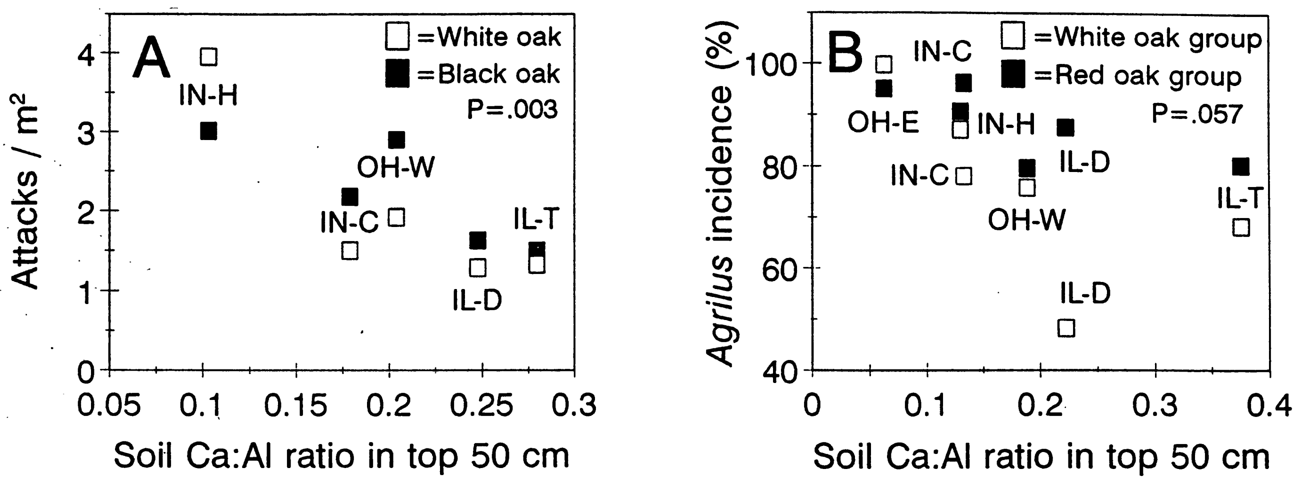

Figure 3 (A) Mean attack density of living oak borers along the lower trunks of white oak trees or black oak trees at five sites along an acid-deposition gradient vs. soil Ca:Al molar ratio by site; and (B) mean percent incidence of attack by Agrilus bilineatus on dead oaks in the red oak group or in the white oak group at six sites along an acid-deposition gradient. P values are based on linear regression analysis of the mean insect values vs. mean Ca:Al ratio by site (A: N=10; B: N=12). See Fig. 1 for site locations

among sites is due to differential rainfall patterns. Nevertheless, it is recognized that one environmental stress can predispose trees to a second stress (Chappelka and Freer-Smith 1995).

Study 4: Incidence of *Agrilus bilineatus* attack

A total of 534 dead oaks was examined at the six sites: 106 red oaks and 210 white oaks in Illinois, 50 red oaks and 99 white oaks in Indiana, and 42 red oaks and 27 white oaks in Ohio. Overall, mean incidence of *Agrilus bilineatus* attack at the site level ranged from 78 to 96% of the dead oaks in the red oak group and 48 to 100% of the dead oaks in the white oak group (Fig. 3b). Mean percent incidence of *Agrilus* attack tended to be higher in the Indiana and Ohio sites than in the Illinois sites for dead white oaks ($P = .011$; $N = 23$ forest stands) but not for dead red oaks ($P = .59$; $N = 23$ forest stands). With respect to soil Ca:Al ratio, linear regression indicated that incidence of *Agrilus* attack tended to increase with decreasing soil Ca:Al values ($P = .057$; $N = 12$ site-oak combinations; Fig 3b).

The above results suggest that as site acidification increases there is an increased likelihood that *Agrilus* will be the principal cause of oak death, especially among species of the white oak group. Likewise, in the Pennsylvania acidic deposition study (Nash *et al.* 1992), incidence of *A. bilineatus* was greatest at the high-deposition sites. Another possible explanation for the relatively low incidence of *Agrilus* attack on oaks in Illinois, especially for white oaks (Fig. 3b) could be due to changes in species composition of the white oaks along the gradient, *i.e.*, mostly post oak (*Quercus stellata* Wangenh.) in Illinois, but mostly chestnut oak (*Quercus prinus* L.) in Indiana and Ohio (Haack and Blank 1991b). It is not known whether *Agrilus* preferentially attacks chestnut oaks over post oaks. Nevertheless, signs of *Agrilus* attack were observed on all oak species encountered along the gradient (Haack and Blank 1991b).

Comparison with results of other OCS investigators

The OCS investigations by LeBlanc (1990) and Kuperman (1993) are the most relevant to the insect studies reported here. Briefly, LeBlanc (1990) showed an increase in the incidence of diameter growth decline for overstory black oaks and white oaks as soil Ca:Al ratios decreased. Perhaps this decline in oak diameter growth on sites with lower Ca:Al ratios partially explains why attack densities of living oak borers increased on these same sites, *i.e.*, slower growing trees were less able to resist attack by these wood-boring insects. Similarly, as the thickness of annual xylem growth rings declines in oaks there is increased vulnerability to girdling by *Agrilus* larvae. This is especially true for red oaks because they conduct fluids almost exclusively in the xylem's outermost annual ring, while conduction in white oaks can occur in the outer two to three annual rings (Haack and Blank 1991b).

In 1989 and 1990, Kuperman (1993) found significantly lower densities of soil invertebrate decomposers in the more acidified sites as measured by soil pH ($P = .0001$, $R = .87$). Earthworm densities appeared to be the most severely impacted. Moreover, as densities of soil decomposers declined there was a significant increase in percent carbon of the soil A_1 horizon: from about 2% in Illinois to 6-8% in Indiana and Ohio (Kuperman 1993, Loucks *et al.* 1991). In other recent studies (Ammer and Makeschin 1994, Edwards and Bohlen 1992), soil decomposers, and especially earthworms, have been shown to be negatively impacted by increased site acidification.

Conclusion

Overall, the pattern of results in the OCS insect studies and in the studies by other OCS investigators (Kuperman 1993, LeBlanc 1990, Loucks 1992, Loucks *et al.* 1991) suggests that increasing levels of acidic deposition can alter forest ecosystem processes. Loucks (1992) described these changes in terms of ecosystem destabilization. Of course, gradient-type studies like the OCS are correlative in nature and do not prove cause and effect. Furthermore, as stated earlier, the sites selected in gradient studies need to be highly analogous for the results to be meaningful. The OCS sampling universe was limited to poorly buffered soils that had been derived from sandstone and shale, and thus the results are most applicable to similar regions.

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Literature Cited

Ammer, S., and Makeschin, F. 1994. Effects of simulated acid precipitation and liming on earthworm fauna (Lumbricidae, Oligochaeta) and humus type in a mature stand of Norway spruce (Hoglwald experiment). Forstw. Cbl. 113: 70-85.

Baltensweiler, W. 1985. "Waldsterben": forest pests and air pollution. Z. Ang. Entomol. 99: 77-85.

Boudot, J.P., Becquer, T., Merlet, D., and Rouiller, J. 1994. Aluminium toxicity in declining forests: a general overview with a seasonal assessment in a silver fir forest in the Vosges Mountains (France). Ann. Sci. For. 51: 27-51.

Chappelka, A.H., and Freer-Smith, P.H. 1995. Predisposition of trees by air pollution to low temperatures and moisture stress. Environ. Pollut. 87: 105-117.

Donley, D.E., and Acciavatti, R.E. 1980. Red oak borer. USDA For. Serv., For. Insect & Disease Leaflet 163. 7 p.

Donley, D.E., and Terry, J.R. 1977. How to identify damage by major oak borers in the eastern United States. USDA For. Serv., Northeastern Area, Gen. Rept. NA-GR-12. 8 p.

Drooz, A.T., ed. 1985. Insects of eastern forests. USDA For. Serv., Misc. Publ. 1426. 608 p.

Edwards, C.A., and Bohlen, P.J. 1992. The effects of toxic chemicals on earthworms. Rev. Environ. Contam. Toxicol. 125: 23-99.

Foster, J.R. 1990. Historical growing-season climate in the lower Midwest, USA. *In* O.L. Loucks, *Ed.* Air pollutants and forest response: the Ohio Corridor Study year-3 annual report. Holcomb Research Institute Working Paper 134, Butler University, Indianapolis, Indiana. *pp.* 38-52.

Foster, J.R., and LeBlanc, D.C. 1993. A physiological approach to dendroclimatic modeling of oak radial growth in the midwestern United States. Can. J. For. Res. 23: 783-798.

Führer, E. 1985. Air pollution and the incidence of forest insect problems. Z. Ang. Entomol. 99: 371-377.

Galford, J.R. 1983. Life history of the red oak borer, *Enaphalodes rufulus* (Haldeman), in white oak (Coleoptera: Cerambycidae). Entomol. News 94: 7-10.

Gschwandtner, G., Gschwandtner, K., Eldridge, K., Mann, C., and Mobley, D. 1986. Historic emissions of sulfur and nitrogen oxides in the United States from 1900 to 1980. J. Air Pollut. Control Assoc. (JAPCA) 36: 139-149.

Guillemette, R.N. 1989. Reconnaissance survey of geological substrates at the study sites, Ohio Corridor Project. Holcomb Research Institute, Butler University, Indianapolis, Indiana. HRI Rept. 133. 43 p.

Haack, R.A. 1992. Forest insect trends along an acidic deposition gradient in the central United States. *In* S.B.J. Menken, J.H. Visser, and P. Harrewijn, *Eds.* Proc. 8th International Symposium on Insect-Plant Relationships, 9-13 March 1992, Wageningen, Netherlands. Kluwer, Dordrecht, Netherlands. *pp.* 55-56.

Haack, R.A., and Acciavatti, R.E. 1992. Twolined chestnut borer. USDA For. Serv., Forest Insect & Disease Leaflet No. 168. 12 p

Haack, R.A., and Benjamin, D.M. 1982. The biology and ecology of the twolined chestnut borer, *Agrilus bilineatus* (Coleoptera: Buprestidae), on oaks, *Quercus spp.*, in Wisconsin. Can. Entomol. 114: 385-396.

Haack, R.A., and Blank, R.W. 1991a. A simple ground-based trap for estimating densities of arboreal leaf-eating insects. USDA For. Serv., North Central For. Exp. Sta. Res. Note. NC-354. 4 p.

Haack, R.A., and Blank, R.W. 1991b. Incidence of twolined chestnut borer and *Hypoxylon atropunctatum* canker on dead oaks along an acidic deposition gradient from Arkansas to Ohio. *In* Proc. 8th Central Hardwood Conf. USDA For. Serv. Gen. Tech. Rept. NE-148. *pp.* 373-387.

Haack, R.A., and Mattson, W.J. 1989. They nibbled while the forests burned. Natural Hist. (January): 56-57.

Hain, F.P. 1987. Interactions of insects, trees and air pollutants. Tree Physiol. 3: 83-102.

Hay, C.J. 1968. Frass of some wood-boring insects in living oak (Coleoptera: Cerambycidae; Lepidoptera: Cossidae and Aegeriidae). Ann. Entomol. Soc. Am. 61: 255-258.

Hay, C.J. 1974. Survival and mortality of red oak borer larvae on black, scarlet, and northern red oak in eastern Kentucky. Ann. Entomol. Soc. Am. 67: 981-986.

Hay, C.J., and Morris, R.C. 1970. Carpenterworm. USDA For. Serv. For. Pest Leaflet 64. 8 p.

Heliövaara, K., and Väisänen, R. 1993. Insects and pollution. CRC Press, Boca Raton, Florida. 393 p.

Higashiura, Y. 1987. Larval densities and a life-table for the gypsy moth, *Lymantria dispar,* estimated using the headcapsule collection method. Ecol. Entomol. 12: 25-30.

Hughes, P.R. 1988. Insect populations on host plants subjected to air pollution. In E.A. Heinrichs, ed. Plant stress-insect interactions. Wiley, New York, NY. *pp.* 249-319.

Hughes, P.R., and Laurence, J.A. 1984. Relationship of biochemical effects of air pollutants on plants to environmental problems: Insect and microbial interactions. *In* M.J. Koziol and F.R. Whatley, *Eds*. Gaseous Air Pollutants and Plant Metabolism. Butterworths, London. *pp*. 361-377.

Joslin, J., and Wolfe, M.H. 1989. Aluminum effects on northern red oak seedling growth in six forest soil horizons. Soil Sci. Soc. Am. J. 53: 274-281.

Kataev, O.A., Golutvin, G.I., and Selikhovkin, A.V. 1983. Changes in arthropod communities of forest biocoenoses with atmospheric pollution. Entomol. Rev. 62: 20-29.

Koziol, M.J., and Whatley, F.R. *Eds*. 1984. Gaseous air pollutants and plant metabolism. Butterworths, London.

Kozlowski, T.T., and Constantinidou, H.A. 1986a. Environmental pollution and tree growth. For. Abst. 47: 105-132.

Kozlowski, T.T., and Constantinidou, H.A. 1986b. Responses of woody plants to environmental pollution. For. Abst. 47: 5-51.

Kuperman, R.G. 1993. Relationships between acidic deposition, soil invertebrate communities, microbial activity, and litter decomposition in oak-hickory forests. Ph.D. dissertation, Ohio State University, Columbus, Ohio. 353 p.

LeBlanc, D.C. 1990. A demographic analysis of vigor-change for white and black oak along the Ohio River corridor acidic deposition gradient. *In* O.L. Loucks, *Ed*. Air pollutants and forest response: the Ohio Corridor Study year-3 annual report. Holcomb Research Institute Working Paper 134, Butler University, Indianapolis, IN. *pp*. 219-241.

LeBlanc, D.C. 1993. Temporal and spatial variation of oak growth — climate relationships along a pollution gradient in the midwestern United States. Can. J. For. Res. 23: 772-782.

Lechowicz, M.J. 1987. Resource allocation by plants under air pollution stress: Implications for plant-pest-pathogen interactions. Bot. Rev. 53: 281-300.

Lefohn, A. S., and J. E. Pinkerton. 1988. High resolution characterization of ozone data for sites located in forested areas of the United States. J. Air Pollut. Control Assoc. (JAPCA) 38: 1504-1511.

Loucks, O.L. 1992. Forest response research in NAPAP: potentially successful linkage of policy and science. Ecol. Appl. 2: 117-123.

Loucks, O.L., and Somers, P.W. 1990. Evaluating potential effects of acidic deposition on soils along the Ohio Valley gradient. *In* O.L. Loucks, *Ed*. Air pollutants and forest response: the Ohio Corridor Study year-3 annual report. Holcomb Research Institute Working Paper 134, Butler University, Indianapolis, IN. *pp*. 151-170.

Loucks, O.L., Armentano, T.V., Foster, J.R., Fralish, J.S., Haack, R.A., Kuperman, R., LeBlanc, D.C., Loats, K.V., McCune, B., Pedersen, B., Robertson, P.A., Somers, P.W., and Varsa, E.C. 1991. Pattern of air pollutants and response of oak-hickory ecosystems in the Ohio Corridor. Summary report submitted to the U.S. Forest Service, Radnor, Pennsylvania. 42 p.

Malhotra, S.S., and Khan, A.A. 1984. Biochemical and physiological impact of major pollutants. *In* M. Treshow, *Ed*. Air pollution and plant life. Wiley, New York, NY. *pp*. 113-157.

Mattson, W.J., and Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. BioScience 37: 110-118.

Mattson, W.J., and Scriber, J.M. 1987. Nutritional ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral considerations. *In* F. Slansky and J.G. Rodriquez, *Eds*. Nutritional ecology of insects, mites, spiders, and related invertebrates. Wiley, New York, NY. *pp*. 105-146

Mattson, W.J., and Witter, J.A. 1990. Pollution induced changes in forest- insect relationships. *In* Proc. 19th IUFRO World Congress, Section 2, Montreal, Canada, August 5-11, 1990. *pp*. 152-163.

McCune, B., Cloonan, C.L., and Armentano, T.V. 1988. Tree mortality and vegetation dynamics in Hemmer Woods, Indiana. Amer. Midl. Natr. 120: 416-431.

Nash, B.L., Davis, D.D., and Skelly, J.M. 1992. Forest health along a wet sulfate/pH deposition gradient in north-central Pennsylvania. Environ. Toxicol. Chem. 11: 1095-1104.

Paramonov, A. 1959. A possible method of estimating larval numbers in tree crowns. Entomol. Mon. Mag. 95: 82-83.

Riemer, J., and Whittaker, J.B. 1989. Air pollution and insect herbivores: observed interactions and possible mechanisms. *In* E.A. Bernays, *Ed.* Insect-plant interactions. CRC Press, Boca Raton, Florida. *pp.* 73-105.

Saikkonen, K., and Neuvonen, S. 1992. Simulated acid rain and the susceptibility of the European pine sawfly (*Neodiprion sertifer*) larvae to nuclear polyhedrosis virus. *In* S.B.J. Menken, J.H. Visser, and P. Harrewijn, *Eds.* Proc. 8th International Symposium on Insect-Plant Relationships, 9-13 March 1992, Wageningen, Netherlands. Kluwer, Dordrecht, Netherlands. *pp.* 347-348.

Scriber, J.M., and Slansky, F. 1981. The nutritional ecology of immature insects. Annu. Rev. Entomol. 26: 183-211.

Solomon, J.D. 1972. Biology and habits of the living beech borer. J. Econ. Entomol. 65: 1307-1310.

Solomon, J.D. 1977. Frass characteristics for identifying insect borers (Lepidoptera: Cossidae and Sesiidae; Coleoptera: Cerambycidae) in living hardwoods. Can. Entomol. 109: 295-303.

Solomon, J.D., and Donley, D.E. 1983. Bionomics and control of the white oak borer. USDA For. Serv. Res. Pap. SO-198.

Stark, R.W., Miller, P.R., Cobb, F.W., Wood, D.L. and Parmeter, J.R. 1968. Incidence of bark beetle infestation in injured trees. Hilgardia 39: 121-152.

Wargo, P.M. 1977. *Armillariella mellea* and *Agrilus bilineatus* and mortality of defoliated oak trees. For. Sci. 23: 485-492.

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