# Relationships Between Soil Properties and Community Structure of Soil Macroinvertebrates in Oak-Hickory forests along an Acidic Deposition Gradient

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**Abstract**

Soil macroinvertebrate communities were studied in ecologically analogous oak-hickory forests across a three-state atmospheric pollution gradient in Illinois, Indiana, and Ohio. The goal was to investigate changes in the community structure of soil fauna in study sites receiving different amounts of acidic deposition for several decades and the possible relationships between these changes and physico-chemical properties of soil. The study revealed significant differences in the numbers of soil animals among the three study sites. The sharply differentiated pattern of soil macroinvertebrate fauna seems closely linked to soil chemistry. Significant correlations of the abundance of soil macroinvertebrates with soil parameters suggest that their populations could have been affected by acidic deposition in the region. Abundance of total soil macroinvertebrates decreased with the increased cumulative loading of acidic deposition. Among the groups most sensitive to deposition were: earthworms, gastropods, dipteran larvae, termites, and predatory beetles. The results of the study support the hypothesis that chronic long-term acidic deposition could adversely affect the soil decomposer community which could cause lower organic matter turnover rates leading to an increase in soil organic matter content in high deposition sites.

**Introduction**

Soil-inhabiting invertebrates are essential components of the decomposer food web and nutrient cycling pathways in soil ecosystems (Crossley, 1977, Edwards et al., 1970, Seastedt, 1984). They are also important agents in the formation and maintenance of the biological, chemical and physical character of soil ecosystems. Several studies have shown that populations of soil invertebrates are potentially sensitive to acidic-deposition-mediated alterations of the soil chemical environment (Abrahamsen, 1983; Abrahamsen et al., 1980; Bääth et al., 1980; Hågvar, 1984; Hågvar, 1987; Hågvar, 1988; Hågvar, 1980; Hågvar and Kjøndal, 1981; Hågvar and Abrahamsen, 1984; Huhta, 1984; Huhta et al., 1986; Vilkamaa and Huhta, 1986). Given the short lifespan of most soil invertebrates, relative to the lifespan of trees, and the close relationship between the soil invertebrate community and soil chemical and physical properties, it is likely that acidic deposition-mediated changes in soil characteristics will be reflected in this community long before changes become apparent in the forest plant community. To the extent that changes in the soil invertebrate community reflect changes in soil characteristics detrimental to plant growth (e.g., acidification with increased Al in soil solution) or affect nutrient cycling processes critical to plant growth (e.g., N-cycling), such changes may be useful indicators of impending change in the forest community.

Most of the previous studies were conducted on experimental plots in the field or in laboratory microcosms over short periods of time using acidic solutions which were 10-20 times more concentrated than observed precipitation pH levels (see Kuperman and Edwards, 1994). Studies of long-term (more than ten years) effects of acidic deposition are few. They primarily include surveys along a point source pollution gradient (Kilham and Wainwright, 1981).

Although frequently conflicting, results of many studies demonstrated that soil acidification, in general, favors populations of soil invertebrates with already high numbers in naturally acidic environments. It is often difficult, however to use results from short-term experiments with unrealisticly high acidic input treatments to evaluate potential effects of chronic (several decades) exposure of ecosystems to moderate and low levels of acidic deposition. In addition, most current knowledge is based on studies conducted in Scandinavian coniferous forests, southeastern Canada, and in the southeastern United States. Conditions in these studies differ considerably in terms of climate, geology, soil characteristics, vegetation, and existing invertebrate community limiting the use of their results for evaluating effects of pollution in the Ohio River Valley region. The objectives of this investigation were to study changes in the soil macroinvertebrate community in ecologically analogous study sites in oak-hickory forests receiving different amounts of acidic deposition for several decades and the possible relationships between these changes and physico-chemical properties of soil.

## Materials and Methods

### *Site description*

Three study sites were selected in the Ohio River Valley to represent high, intermediate and low deposition sites. The Edge-of-Appalachia preserve in southern Ohio (OH) had high long-term levels of $SO_4^{2-}$ and $NO_3^-$ deposition. The Hoosier National Forest in Indiana (IND) had intermediate levels of deposition, and the Touch-of-Nature Preserve in southern Illinois (ILL) had low levels input. Study sites generally follow parallel climate isopleths resulting in a relatively uniform climate along the gradient. The estimated deposition chemistry in study sites is shown in Table 1.

All study sites represent a typical oak-hickory forest. The sampleable areas were selected on upper slopes with southerly aspect, underlain by sandstone and low-base shales and Berks soil association, or a closely related soil type. The tree stands in each area were predominantly 80-130 years old and free of observable disturbance. Consideration of the geology, climate, surface soils, forest composition and structure indicate generally analogous conditions within the capacity of several study plots to represent the sample universe at each study site along a three-state acidic deposition gradient (Loucks, 1990).

### *Sampling procedure*

Soil macroinvertebrates were sampled in May and August of 1989 and 1990. The sampling regime was designed to obtain peak densities in May and low densities in August when the effects of soil moisture deficit on the abundance of invertebrates would be greater.

Abundance of animals was estimated from soil cores taken with a soil sampler of 10.5 cm diameter and 20 cm deep. Twenty-four soil cores per sampling date were taken randomly in each of the three study sites. The combined depth of F and H layers was measured in each soil sample. Animals were extracted from samples by handsorting with an illuminated desk magnifier and preserved in ethyl alcohol for further identification. Abundance of soil macroinvertebrates was expressed as the number per square meter to a depth of 20 cm. In addition to soil cores, the abundance of earthworms in the study site was determined by randomly excavating 0.25 $m^2$ quadrats to a depth of 30 cm at 10 cm increments and hand sorting them on-site (n=20 per site/date). Sampling at all study sites was completed within ten days from the beginning of each sampling period to minimize phenological changes.

*Taxonomic and functional characterization of soil fauna*

Animals were sorted into the following categories: Isopoda, Lumbricidae, Gastropoda, Diplopoda, Lithobiomorpha, Geophilomorpha, Symphyla, Pseudoscorpionida, Aranea, Phalangida, Diplura, Machilidae, Acrididae, Gryllacrididae, Gryllidae, Blattoidea, Isoptera, Hemiptera, Cicadidae, Psocoptera, Cicindelidae, Carabidae, Staphylinidae, Scarabaeidae, Elateridae, Curculionidae, "other" coleoptera, Lepidoptera and Diptera (predatory species from genus *Asilidae* and *Rhagionidae* were counted separately). These levels of taxonomic identification were regarded sufficient for characterizing the response patterns of the soil macroinvertebrate community while providing adequate taxonomic resolution for determining functional characteristics of indigenous soil fauna. Based on the ecological characteristics of soil animals, particularly on feeding habits and their role in the decomposer subsystem, soil macroinvertebrates were placed in one of three functional groups: Decomposers (including saprophagous forms feeding on humus, decaying organic matter, litter, wood, carrion, dung, and fungivores), Predators, and Herbivores (primarily belowground herbivores). There may be considerable overlap however, between different functional groups and some taxa are difficult to classify unambiguously in either one or the other. Table 2 summarizes functional groups of soil macroinvertebrates extracted from soil samples.

*Soil Analyses*

Twenty samples of H/F layer material were collected in each study site to determine pH level and total N and S content. Samples were oven-dried (60°C) for 72 hours. Course woody debris and rocks were removed from the samples by hand-sorting. The remaining material was ground in a Wiley mill to pass a 40 mesh screen. Subsamples of ground material were ashed in a muffle furnace (5 hours at 500°C) to determine the percent ash-free dry mass (AFDM) which was used as an index of organic matter content. Mineral soil was analyzed for pH, exchangeable Al (weak acid extracted), C, N, S, P, B, K, Mg, Mn, Ca, Co, Cr, Cu, Fe, Ni, Pb, Zn, extractable $SO_4^{2-}$, BS (percent Base Saturation), CEC, SumB (sum of base cations normalized for %C), TSLR (total sulfate loading ratio, 3 year deposition data to 2.5 cm depth of soil), and TNLR (total nitrogen loading ratio, 3 year deposition data to 2.5 cm depth of soil). Loading ratios were calculated as the ratios of deposition inputs (sulfate or nitrogen)to the sum of bases (Ca, Mg, K, and Na in equivalents) in the top 2.5 cm of soil.

*Data analyses*

A three-way analysis of variance was used to test for overall significant differences in the numbers of the most abundant taxa and of the total macroinvertebrates among study sites and among sampling dates. A univariate procedure was performed to determine whether the error variation was homogenous and normally distributed. To comply with the assumptions of the ANOVA, macroinvertebrate numbers were transformed prior to statistical analysis using formula log (X+1). Bonferroni *t* tests were performed to determine where significant differences occurred.

Correlation and regression analyses were done to test for significant relationships between soil chemical parameters that are usually affected by acidic deposition and the numbers of macroinvertebrates across all sites. Statistical analyses was done using SAS (SAS Institute, 1985). Untransformed data are presented in tables and figures unless stated otherwise. All tests of significance were made at an $\alpha$ level of $P = 0.05$.

## Results

*Soil characteristics*

Changes in soil characteristics along the deposition gradient were indicative of acidic deposition effects. Parameters of the soil organic horizons are summarized in Table 3. The pH of combined H/F layer material was significantly ($P < 0.001$) lower in both high deposition sites in Indiana and Ohio (4.49 and 4.51 respectively) as compared with the Illinois reference site (pH 6.50). There was also a substantial increase in the accumulation of surface organic matter with increased cumulative loading of acidic inputs. The depth of H/F layer was significantly ($P < 0.0001$) different in all three study sites, increasing from 0.25 cm in Illinois to 1.30 cm in Indiana, and to 2.75 cm in Ohio. The H/F layer material in study sites along the deposition gradient was characterized by an increasing percentage of AFDM, total nitrogen and sulfur contents (Table 3). Changes in the soil chemistry in $A_1$ mineral horizons were also symptomatic of acidic deposition effects and were reported in detail by Somers et al. (1990). Mineral horizon site means are shown in Table 4. There were significant differences in soil pH, percent C, and extractable $SO_4^{2-}$ in samples of $A_1$ horizons across the three study sites. The Indiana and Ohio study sites which had the longest period of high level of acidic deposition and the greatest cumulative dose were characterized by significantly lower pH and a higher percentage of carbon in surface mineral horizon. Soil pH in the $A_1$ horizon decreased from 4.57 in the Illinois site to pH 3.9 in Indiana and Ohio sites. The percentage of carbon in the $A_1$ horizon increased from 2.08 in the Illinois low-dose site to 7.84 in Ohio. Water extractable sulfate increased from 33.4 mg/l in Illinois to 74.2 mg/l in Ohio. There was an increase in $H^+$ and $Al^{3+}$ on the exchange sites at the Ohio study site resulting in a higher cation exchange capacity as compared with the Illinois reference site. When differences in soil pH were evaluated in relation to total sulfate inputs and the exchangeable neutralizing cations (sum of exchangeable Ca, Mg, Na, and K) the Illinois site was found to be less sensitive to acidic inputs than the Indiana and Ohio sites.

*Soil fauna*

The number of soil macroinvertebrates averaged across all sampling dates are presented in Table 5. There were significant differences among the three study sites in the number of macroinvertebrates extracted from the top 20 cm. Abundance of total macroinvertebrates in sites across the deposition gradient were in order of highest to lowest: Illinois > Indiana > Ohio. Illinois, the low-dose site, was significantly ($P < .0001$) different from the other two study sites. The Indiana and Ohio sites were not significantly different from each other. The mean ($\pm$ SE) number of total soil macroinvertebrates averaged across all sampling dates ($n = 96$) was 1510.56 $\pm$ 144.29 per $m^{-2}$ in Illinois; 977.39 $\pm$ 109.63 per $m^{-2}$ in Indiana, and 834.55 $\pm$ 104.59 per $m^{-2}$ in the Ohio study site.

Abundance of all three functional groups of soil macroinvertebrates varied in study sites along the deposition gradient (Table 6). The number of decomposers in the Illinois study site, were significantly ($P < 0.0001$) higher than in the other two sites (Fig. 1, 2). Termites and larvae of Diptera made the greatest contribution (over 50%) to this functional group and to the observed trend. The number of both taxa were significantly ($P < 0.0001$) higher in Illinois than in the other two study sites.

In contrast to decomposers, the total number and relative abundance of belowground herbivores increased with increasing cumulative dose of acidic inputs (Table 6). The total number of herbivores in Illinois was significantly ($P < 0.0001$) lower when compared with the other two sites. The most abundant taxon in this functional group was Elateridae, followed by Curculionidae, Lepidoptera, and Cicadidae. The site significantly affected the number of adults and larvae of elaterids ($P < 0.0001$ and $P < 0.0008$, respectively), and adults of Curculionidae ($P < 0.0158$). The number of Elateridae were lower in Illinois than in both high deposition study sites, while the reverse was true for adults of Curculionidae.

The total number of soil predators was significantly ($P < 0.0001$) lower in both high-dose sites as compared with the Illinois study site (Table 6). Spiders and staphylinids made the greatest contribution (over 50%) to this functional group. The site, however, significantly affected only the numbers of staphylinids ($P < 0.0001$) among them. The observed difference in the abundance of staphylinid beetles was consistent throughout the study period. Besides staphylinids, a significant decrease in the abundance in high-dose sites was recorded for populations of Geophilomorpha ($P < 0.0001$), and Carabidae ($P < 0.0001$).

The abundance of populations of several soil macroinvertebrate taxa and their total abundance varied significantly from 1989 to 1990 in high deposition study sites, while remaining relatively unchanged in the low-dose site in Illinois. Overall, there was a significant site x year interaction effect ($P < 0.0001$) on the total abundance of soil animals because differences between sites occurred mostly in 1989 (Fig. 3 A) when all study sites were experiencing the consequences of the severe drought of the preceding year. The abundance of total macroinvertebrates in both years was not significantly different in the low deposition site, whereas in the high-dose sites in Indiana and Ohio it was significantly lower in 1989 than in 1990, following two years of normal precipitation (Fig. 3B). Specifically, the drought-deposition interaction had a significant effect on numbers of Lumbricidae ($P < 0.0044$), larvae of Diptera ($P < 0.0002$), Symphyla ($P < 0.0001$), Staphylinidae ($P < 0.0088$), Pseudoscorpionida ($P < 0.0454$), and Geophilomorpha ($P < 0.0454$). All soil macroinvertebrates which were significantly affected by the drought-deposition interaction belonged to either predator or decomposer functional groups and none to the functional group of belowground herbivores.

*Relations between macroinvertebrate community and soil characteristics*

Correlation analyses was performed to obtain a measure of the proportion of the variation in macroinvertebrate numbers determined by the variation of selected soil parameters which were affected by the long-term acidic inputs in the study region. Statistically significant correlation coefficients ($P < 0.05$) for soil parameters and the number of soil macroinvertebrates are summarized in Table 7. Correlation analysis indicated that soil pH significantly positively correlated with total number of macroinvertebrates ($P < 0.03$), numbers of earthworms ($P < 0.01$), Gastropoda ($P < 0.001$), Izoptera ($P < 0.024$), Carabidae ($P < 0.002$), Staphylinidae ($P < 0.0001$), Blattoidea ($P < 0.025$), and larvae of Diptera ($P < 0.003$). The same populations significantly negatively correlated with the amount of exchangeable Al. The percentage of AFDM of H/F layer negatively correlated only with taxa from the decomposer functional group including larvae of Diptera ($P < 0.032$), Lumbricidae ($P < 0.022$), and Gastropoda ($P < 0.004$). There was also a significant negative correlation between the total carbon content in $A_1$ horizon and the numbers of Lumbricidae ($P < 0.038$), Gastropoda ($P < 0.029$), Carabidae ($P < 0.009$), and Staphylinidae ($P < 0.001$). There was a significant negative correlation between concentrations of extractable sulfate in the $A_1$ mineral horizon and the numbers of Lumbricidae ($P < 0.04$), Gastropoda ($P < 0.016$), Carabidae ($P < 0.043$), Staphylinidae ($P < 0.003$), Blattoidea ($P < 0.034$), and the total number of macroinvertebrates ($P < 0.022$). The total numbers of macroinvertebrates also negatively correlated with both TSLR ($P < 0.034$) and TNLR ($P < 0.032$). There was no significant correlation between the two major contributors to the functional group of belowground herbivores (larvae of Elateridae and Curculionidae) and any of the mineral soil characteristics sensitive to the effects of acidic deposition.

Linear regression analyses were applied to the data to more accurately describe the relationship between soil pH, abundance of the macroinvertebrate decomposer community, and surface organic matter accumulation. The regression analyses showed a highly significant ($P < 0.0001$) relationship between soil pH and the total number of decomposers in study sites along the deposition gradient. Approximately 87% of the variation in numbers of decomposers was explained by the soil pH (Fig. 4). Furthermore, the relationship between the abundance of the macroinvertebrate decomposer community and the amount of surface organic matter accumulation along the deposition gradient was also highly significant ($P < 0.0005$), with approximately 71% of the variation in the amount of surface organic matter accumulation explained by the abundance of decomposers (Fig. 5).

**Discussion**

The results of the survey suggest that significant differences exist in several key characteristics of the soil macroinvertebrate community at study sites which were exposed to different amounts of acidic deposition throughout most of this century. These differences were particularly evident in the total abundance of soil macroinvertebrates and in the abundance of major taxonomic and functional groups of soil fauna. Among populations that had a gradual decrease in abundance along the gradient of increasing acidic deposition were earthworms, snails, dipteran larvae, termites, scarab, carabid, and staphylinid beetles and roaches. The number of symphylas, diplurans, wireworms and weevil larvae were higher in high-dose sites, while the abundance of diplopods, Lithobiomorpha, geophilids, pseudoscorpions, spiders, and lepidopteran larvae did not have any consistent trend.

The sharply differentiated pattern of soil macroinvertebrate fauna in sites along the long-term deposition gradient seems closely linked to soil chemistry. The study results show that the largest step in the abundance of soil macroinvertebrates is between Illinois and both high-dose sites in Indiana and Ohio. This step corresponds to similar steps in the chemical characteristics of soil organic and mineral horizons. Sites with higher current and long-term cumulative annual acidic inputs (Indiana and Ohio study sites) showed a significantly lower pH level, a higher level of exchangeable $Al^{3+}$ and extractable sulfate, and a greater total carbon content in the surface mineral horizon. In addition, the highest-dose site in Ohio was characterized by significantly lower total bases and a lower percentage of base saturation in the B horizon than the comparable low-dose site in Illinois (Loucks, 1992). Other indications of the effects of acidic deposition were the decrease in pH of soil organic horizon, increase in the organic matter content, and higher concentrations of total nitrogen and sulfur in the H/F layer material in high deposition sites. The important measures of soil acidification, such as pH, CEC, extractable $SO_4^{2-}$, and concentration of exchangeable $Al^{3+}$, significantly correlated with the number of total soil macroinvertebrates and the number of several taxa including earthworms, gastropods, staphylinids, carabids, and roaches. The number of termites significantly correlated with soil pH, aluminum, and potassium amounts. Dipteran larvae significantly correlated with soil pH, aluminum, potassium, and with total soil nitrogen and phosphorus content. The abundance of total macroinvertebrates also significantly correlated with TSLR and TNLR. These results suggest that the abundance of soil fauna in oak-hickory forests in the Ohio River Valley may be explained, in part, on the basis of soil pH, exchangeable $Al^{3+}$, CEC, extractable $SO_4^{2-}$, TSLR and TNLR. These variables, however, are sensitive to acidic deposition in soils with very low cation content suggesting that long-term acidic deposition in the region could have been an important factor directly or indirectly affecting the soil macroinvertebrate community in the region.

Little information is available on the effects of acidic deposition on soil macroinvertebrates because most of the earlier research focused on the responses of microarthropods and enchytraeids. In those few studies where the effects of acidic deposition on soil macroinvertebrates were investigated, treatments usually included short-term effects with unrealisticly high concentrations. The results of the present investigation concur with those reported by Craft and Webb (1984). They reported the significant effects of acidic and nonacidic $SO_4^{2-}$ treatments on the number of litter macroarthropods. Litter fungivores showed a more pronounced treatment effect than total litter populations, litter predators were affected in the same manner as the total macroarthropod populations. However, litter detritivores were unaffected by the treatments in their experiments.

The significant reduction in the abundance of earthworm populations observed in high-dose sites is in accord with the findings of several studies (Reynolds, 1971; Gates, 1978; Hågvar, 1980; Ma et al., 1990; Esher et al., 1992; Esher et al., 1993). Esher and coworkers (1993) reported striking effects of mild acid treatments on populations of earthworms. In their experiments, a single treatment with sulfuric acid (pH 3.0) was sufficient to reduce earthworm numbers significantly under a pine plantation. However, it was impossible to determine in this study whether the earthworms actually left the acid-treated plots or simply moved deeper into their tunnels, as authors pointed out. Several experiments have shown that many earthworms have special tolerance limits to soil acidity and that they can avoid unfavorable pH levels. In laboratory experiments with *Eisenia foetida*, 100% mortality was observed at pH < 5 or pH > 9 (Kaplan et al., 1980). Huhta et al. (1986), however, found no effect of pH manipulations on earthworm abundance in coniferous forest soils in Finland. The populations of earthworms at the study sites, however, were sparse.

Contrary to our results, Esher and coworkers (1993) reported that the total number of insects and diplopods was higher in plots treated with $H_2SO_4$ at a pH level of 3.0, than in plots treated with $H_2SO_4$ at a pH level of 4.0, or in plots treated with deionized water. However, when animals weighing less than 50 mg were excluded from these data, the differences largely disappeared. Edwards and Lofty (1975) reported that they did not find any direct correlation between myriapod populations and soil pH, although the numbers of Chilopoda and Symphyla were much larger between 5.0 and 6.0 than at higher or lower pH's and none of these animals were present at a pH below 4.0. Wireworms and other insects were more numerous in plots with a pH between 4.0 and 7.0, i.e. very acid or alkaline soils did not support large numbers of these arthropods in their study.

The central focus of the investigation was changes in functional groups of soil macroinvertebrates. These changes provide considerable information on the functioning of the soil invertebrate community especially regarding its role in controlling rates of organic matter turnover and patterns of nutrient dynamics, and regarding the possibility of belowground pest outbreaks effecting the vitality of the tree stand in the ecosystems exposed to acidic deposition.

The abundance of decomposers gradually declined along the deposition gradient. This decline was paralleled by an increase in the percentage of AFDM in the H/F layer (Table 3), by the increase in the overall depth of H/F layer, and by an increase in the soil carbon content in an $A_1$ mineral horizon (Table 4) without any evidence of differences in primary production in sites along the gradient (unpublished information from other cooperators in the project). Based on the results of regression analyses (Fig. 4, 5), the observed patterns of decreasing abundance of decomposers, increasing organic matter content, and the decrease in soil pH along the gradient in cumulative dose of acidic deposition seem to be related. They illustrate the complex interplay between acidic inputs, soil decomposer community dynamics and soil organic matter turnover in study sites along the deposition gradient. This interrelationship is further supported by the analyses of the historical pattern of changes in the soil C content in the research region over the last 30 years. Loucks and Somers (1990) used county soil survey reports for the 1960s-1970s that include data on the carbon content for the soil types sampled under natural forest conditions at the Ohio Corridor study sites in all states (the sample handling and laboratory analytic technique have not changed substantially from the 1960s into the late 1970s). They concluded that although no statistical test was appropriate, and the timing of early data was uncertain, the results gave little indication of a west to east pattern evident during these early years for the percentage of C, suggesting that the phenomenon was induced or strengthened during the past 25 years. This appears to support the hypothesis that chronic long-term acidic deposition could lead to an increase in soil organic matter content resulting from lower organic matter turnover rates by adversely affecting the soil invertebrate decomposer community in high deposition sites.

In contrast to decomposers and predators, the two major soil herbivore taxa, wireworms and weevil larvae did not correlate significantly with soil chemical characteristics, suggesting that factors other than acidic-deposition-mediated changes in soil chemistry could have influenced the abundance of this functional group. A significant increase in the numbers of belowground herbivores in sites with higher doses of acidic deposition could be a direct response to changes in plant characteristics resulting from the effects of acidic deposition. Several studies demonstrated that air pollution stress can induce a large array of biochemical, morphological, and physiological changes in forest trees (Malhotra and Sarkar, 1979; Kozlowski, 1980; 1986; Laurence and Weinstein, 1981; Kozlowski and Constantinidou, 1986). It is reasonable to suggest then, that stressed trees will be more nutritionally suitable to root-feeding insects and thus would support greater numbers of herbivores. The possibility that these changes could alter plant-insect interactions has been a topic of several reviews (Alstad et al., 1982; Hughes and Laurence, 1984; Baltensweiler, 1985; Hain, 1987). All of them suggested that pollution stress which increases plant nutrient levels will effectively increase the potential intrinsic rate of increase of many phytophagous insects. This could lead to higher injury to plants that exceed the plant's usual carrying capacity for the insect.

There is data from many studies (mostly correlative) on insect activity levels and proximity to a pollution source or on the effects of simulated acidic deposition on herbivory intensity (Alstad et al., 1982; Dohmen et al., 1984; Hughes et al., 1985; Neuvonen and Lindgren, 1987; Stinner et al., 1987). Overall, no correlation or a positive correlation was reported for most insects at low to intermediate levels of pollutant. Negative correlations were reported at very high levels (Hughes and Laurence, 1984). Information is lacking, however, on the effects of acidic deposition on soil herbivores in deciduous forests because, in most cases, the effects of atmospheric pollution were studied on defoliators. In a study of feeding preference by gypsy moth larvae, Haack (1990) demonstrated that larvae had a distinct preference for black oak and white oak foliage from both high deposition sites in Indiana and Ohio over that of a reference site in Illinois. It is not certain that similar responses will occur with belowground herbivores, however, the observed increase in the numbers of wire worms and Curculionidae larvae in the Indiana and Ohio sites suggest that this possibility should be further investigated because if greater preference can be demonstrated for roots from high deposition sites, it can be argued that insect outbreak potential would increase as acidic deposition levels increase.

The observed significant effect of interaction of drought and pollution stresses on the abundance of belowground herbivore populations suggest that the effects of chronic exposure of ecosystems to acidic deposition may not be evident during periods with normal precipitation. However, they can be expressed when this ecosystem is subjected to drought stress. Data indicates that drought stress can be an additional factor affecting the numbers of belowground herbivores with the potential of exacerbating the effect of pollution stress on the community. Both drought stress and mild to moderate pollution stress typically cause increased levels of soluble nitrogen and sugars in plant tissues (Kozlowski and Constantinidou, 1986) and many phytophagous insects are known to respond positively to increases in these key nutrients (Mattson, 1980; Mattson and Haack, 1987; White, 1984). Furthermore, drought often appears to initiate insect outbreaks (Mattson and Haack, 1987; Haack and Mattson, 1989). Therefore, it is not unreasonable to hypothesize that the interaction of these two stress factors which usually affect large geographic areas may alter normal tree-herbivore relationships on a wide scale. The possible result may be the promotion of larger belowground herbivore populations in more polluted areas.

The significant interaction of pollution and drought stresses was also observed for decomposers and predators. Similar results were reported by Craft and Webb (1983). They demonstrated that the negative effects of acidic and nonacidic $SO_4^{2-}$ on litter arthropod populations, particularly on litter fungivores and predators were apparent during the summer and early autumn when populations of litter organisms were most susceptible to drought. In our study, patterns of responses were not uniform for different taxonomic groups within the functional units. These differential response patterns reflect diversity of adaptive strategies of soil macroinvertebrates. Among decomposers the interaction effect was significant for earthworms, symphylas, and dipteran larvae. All three taxa are represented by the softbodied organisms which are susceptible to desiccation, although some (i.e. earthworms) may weather unfavorable conditions by burrowing deeper in soil and aestivating. The significant interaction effect for the whole group of decomposers was largely due to the Diptera larvae, which contributed 23% of all decomposers in the reference site and 19% in the highest dose site. Among predators, the significant interaction of pollution and drought stresses was observed for Staphylinidae, Carabidae, Pseudoscorpionida, and geophilids.

The mechanisms of response of populations of soil invertebrates to the pollution-drought interaction effect are probably indirect and result from complex changes in soil food chains beginning with soil microorganisms and with changes in their environment. Sulfate deposited to soil may be cycled by microorganisms and reduced to sulfides in waterlogged soils (Killham and Wainwright 1984). Germida et al. (1992) suggested that when this soil is then dried, any $S^{2-}$ that was formed is available for oxidation back to $SO_4^{2-}$. Thus a S reduction-oxidation cycle may operate in soils, depending upon their water status. Although such a cycle could operate in nonpolluted soils, it is more obvious in atmospherically polluted soils because of the elevated levels of $SO_4^{2-}$ present in them (Table 4). The authors conclude that, even though the total amount of S present would not change, the form in which it exists would alter and, as a result, potentially influence soil pH and the rate of cation leaching. These changes resulting from the pollution-drought interaction may then affect a large spectrum of changes in soils which in turn, could lead to alterations in the soil macroinvertebrate community. Such alterations may result from changes in vegetation, changes in predation pressure, changes in availability of food, changes in fecundity and population growth rate or competitive interactions between species.

Overall the interaction effect was highly significant for the total numbers of soil macroinvertebrates, supporting the hypothesis that pollution can exacerbate drought stress effects on the soil macroinvertebrate community. However, because it is practically impossible to control all factors affecting populations of soil invertebrates in the gradient study, this hypothesis remains speculative and should be further investigated in controlled microcosm experiments.

Results of the study show that the pattern of differences observed in communities of soil macroinvertebrates in study sites along the deposition gradient are consistent with the hypothesis relating acidic inputs to changes in the abundance of soil invertebrates populations. Correlation and regression analyses, as well as analysis of the historical soils data provided additional supporting evidence that long-term acidic deposition could have been an important factor directly or indirectly affecting the soil macroinvertebrate community in the region. Changes in the macroinvertebrate community in study sites along the spatial and temporal deposition gradients include decreased abundance of soil fauna with an increased amount of acidic inputs and changes in the abundance of functional groups of soil macroinvertebrates. It appears that chronic acidic deposition can adversely affect the soil macroinvertebrate decomposer community. This could result in lower organic matter turnover rates leading to an increase in organic matter content in the surface mineral horizon and an increase in both the percentage of AFDM and total depth of H/F layer in high deposition sites. The effect of interaction of pollution and drought stresses was highly significant for several taxa and the total number of soil macroinvertebrates, supporting the hypothesis that pollution can exacerbate the drought stress effects on the soil macroinvertebrate community. Interaction of these two stress factors which usually affect large geographic areas may alter normal tree-herbivore relationships on a wide scale, resulting in promotion of larger belowground herbivore populations in the more polluted areas.

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Table 1. Estimated deposition chemistry in study sites in oak-hickory forests of the Ohio River Valley across a three-state acidic deposition gradient. Source: Loucks (1990).

| DEPOSITION CHEMISTRY | ILLINOIS | INDIANA | OHIO |
|---|---|---|---|
| 86 yr cumulative (1900-1985) annual $SO_4^{2-}$ ($g/m^{-2}/yr^{-1}$) | 8.15 | 8.81 | 10.19 |
| 30 yr cumulative (1956-1985) annual $SO_4^{2-}$ ($g/m^{-2}/yr^{-1}$) | 5.52 | 6.23 | 7.21 |
| 30 yr cumulative (1956-1985) annual $NO_3$ ($g/m^2/yr^{-1}$) | 2.63 | 3.14 | 3.58 |
| 1988-1989 dry $SO_4^{2-}$ ($g/m^{-2}/yr^{-1}$) | 1.69 | 1.79 | 1.89 |
| % of wet | 60 | 58 | 69 |
| 1988-1989 all dry N as $NO_3$ equiv. ($g/m^{-2}/yr^{-1}$) | 1.20 | 1.42 | 1.72 |
| % of wet | 70 | 69 | 91 |
| 1988-1989 dry $NH_4^+$ ($g/m^{-2}/yr^{-1}$) | 0.062 | 0.080 | 0.120 |
| % of wet | 20 | 21 | 42 |

Table 2. Functional groups of soil macroinvertebrates in oak-hickory forests along an acidic deposition gradient in the Ohio River Valley.

| Taxa | Functional groups | | |
|---|---|---|---|
| | Decomposer | Predator | Herbivore |
| Isopoda | X | | |
| Lumbricidae | X | | |
| Gastropoda | X | | |
| Diplopoda | X | | |
| Lithobiomorpha | | X | |
| Geophilomorpha | | X | |
| Symphyla | X | | |
| Pseudoscorpionida | | X | |
| Aranea | | X | |
| Phalangida | | X | |
| Diplura | | X | |
| Machilidae | X | | |
| Gryllidae | | | X |
| Gryllacrididae | X | | |
| Blattoidea | X | | |
| Isoptera | X | | |
| Cicadidae | | | X |
| Psocoptera | X | | |
| Carabidae | | X | |
| Staphylinidae | | X | |
| Scarabaeidae (larvae) | X | | X |
| Elateridae | | | X |
| Curculionidae | | | X |
| Lepidoptera (larvae) | | | X |
| Diptera* (larvae) | X | | |

* Excluding *Asilidae* and *Rhagionidae*.

Sources: Borror et al., 1976, Craft and Webb, 1983, Dindal, 1990.

Table 3. Parameters of soil organic horizons in oak-hickory forests along an acidic deposition gradient in the Ohio River Valley.

| H/F layer Characteristics | ILLINOIS | INDIANA | OHIO |
|---|---|---|---|
| Thickness (cm) | 0.25 | 1.30 | 2.75 |
| $pH_{(water)}$ | 6.50 | 4.50 | 4.51 |
| AFDM (%) | 51.16 | 73.59 | 74.75 |
| Total N (%) | 1.30 | 1.45 | 1.80 |
| Total S (%) | 0.13 | 0.16 | 0.22 |

Table 4. Parameters of $A_1$ soil mineral horizon in oak-hickory forests along an acidic deposition gradient in the Ohio River Valley.

| $A_1$ Soil Horizon Characteristics | ILLINOIS | INDIANA | OHIO |
|---|---|---|---|
| Thickness (cm) | 5.9 | 2.9 | 4.4 |
| pH (water) | 4.57 | 3.93 | 3.95 |
| C (%) | 2.08 | 6.41 | 7.84 |
| Total N (%) | 0.105 | 0.190 | 0.317 |
| Total S (%) | 0.015 | 0.025 | 0.043 |
| Exchang. Al (ppm) | 433.73 | 1022.18 | 935.72 |
| Extractab. $SO_4^{2-}$ $mg/L^{-1}$ | 33.4 | 70.45 | 74.20 |
| CEC (meq/100 g) | 4.91 | 10.25 | 11.44 |
| Σ Bases (meq/100 g) | 1.88 | 2.84 | 4.07 |
| Base Saturat.(%) | 38.7 | 26.7 | 39.5 |
| TSLR 3 yr 2.5 cm | 0.191 | 0.406 | 0.580 |
| TNLR 3 yr 2.5 cm | 0.126 | 0.280 | 0.392 |

Table 5. Abundance of soil macroinvertebrates averaged across all sampling dates in oak-hickory forests along an acidic deposition gradient in the Ohio River Valley. Invertebrate abundance is expressed as number per $m^{-2}$ to a depth of 20 cm. Values are means ± S.E. (n = 96).

| TAXA | ILLINOIS | INDIANA | OHIO |
|---|---|---|---|
| Gastropoda | 32.39 ± 6.44[a] | 4.72 ± 2.73[b] | 9.44 ± 3.86[b] |
| Diplopoda | 33.97 ± 10.52 | 53.12 ± 11.33 | 33.05 ± 7.61 |
| Chilopoda | | | |
| Lithobiomorpha | 22.99 ± 6.62 | 18.89 ± 4.88 | 33.05 ± 9.20 |
| Geophilomorpha | 80.19 ± 20.43[a] | 14.17 ± 5.31[b] | 63.74 ± 11.93[a] |
| Symphyla | 54.80 ± 11.82[a] | 54.30 ± 20.39[a] | 142.83 ± 39.20[b] |
| Pseudoscorpionida | 14.89 ± 3.54[a] | 33.05 ± 9.68[b] | 3.54 ± 3.54[a] |
| Aranea | 130.35 ± 23.39 | 139.29 ± 17.82 | 128.67 ± 28.03 |
| Insecta | | | |
| Diplura | 63.78 ± 13.45[a] | 61.38 ± 16.40[a] | 102.70 ± 23.26[b] |
| Tipulidae | 7.22 ± 4.83 | 0.0 ± 0.0 | 7.08 ± 4.84 |
| Other Diptera | 203.85 ± 33.67[a] | 106.24 ± 26.76[b] | 62.56 ± 11.78[b] |
| Isoptera | 361.27 ± 113.76[a] | 140.47 ± 47.87[b] | 21.25 ± 13.67[b] |
| Elateridae A*+L** | 28.73 ± 8.60[a] | 106.24 ± 15.98[b] | 53.12 ± 10.66[b] |
| Scarabaeidae A | 25.21 ± 6.52[a] | 4.72 ± 2.73[b] | 5.90 ± 3.32[b] |
| Scarabaeidae L | 49.48 ± 8.93[a] | 8.26 ± 3.84[b] | 25.97 ± 6.65[b] |
| Curculionidae A | 9.26 ± 2.95[a] | 2.36 ± 1.61[b] | 3.54 ± 2.57[b] |
| Curculionidae L | 15.31 ± 3.94 | 29.51 ± 15.22 | 38.95 ± 19.54 |
| Carabidae A+L | 22.43 ± 6.27[a] | 8.26 ± 3.84[b] | 2.36 ± 2.36[b] |
| Staphylinidae A | 119.50 ± 11.03[a] | 36.59 ± 9.52[b] | 21.25 ± 8.06[b] |
| Other Coleoptera | 79.93 ± 13.20 | 55.48 ± 13.63 | 29.51 ± 5.96 |
| Cicadidae L | 8.42 ± 3.41 | 12.98 ± 3.32 | 2.36 ± 1.61 |
| Lepidoptera L | 10.20 ± 3.39 | 61.38 ± 49.02 | 18.89 ± 4.56 |
| Blattoidea | 18.43 ± 6.23[a] | 2.36 ± 1.61[b] | 1.18 ± 1.18[b] |
| Other*** | 117.96 ± 30.52 | 23.61 ± 7.99 | 23.61 ± 6.33 |
| TOTAL | 1510.56 ± 144.29[a] | 977.39 ± 109.63[b] | 834.55 ± 104.59[b] |

* Adult; ** Larva; *** Includes: Lumbricidae, Isopoda, Phalangida, Psocoptera, Gryllidae.
Means with the same latter are not significantly different at the 0.05 level.

Table 6. Total numbers and relative abundance of functional groups of soil macroinvertebrates in oak-hickory forests along an acidic deposition gradient in the Ohio River Valley.

| | ILLINOIS | | INDIANA | | OHIO | |
|---|---|---|---|---|---|---|
| Functional group | Total ind/$m^2$ | % | Total ind/$m^2$ | % | Total ind/$m^2$ | % |
| Decomposers | 879.4[a] | 58.2 | 393.1[b] | 40.2 | 327.0[b] | 39.2 |
| Predators | 454.2[a] | 30.1 | 311.6[b] | 31.9 | 355.0[b] | 42.6 |
| Herbivores | 71.9[a] | 4.8 | 212.4[b] | 21.7 | 116.9[b] | 14.0 |

Comparisons significant at the 0.05 level are indicated by different letters.

Table 7. Pearson correlation coefficients (*r*) with probability values $P < 0.05$ for soil characteristics and abundance of soil macroinvertebrates in oak-hickory forests along regional acidic deposition gradient from Illinois to Ohio.

| Taxa | pH | Al | %C | %N | %S | P | K | Mg | Mn | Ca |
|---|---|---|---|---|---|---|---|---|---|---|
| Lumbricidae | 0.422 | -0.402 | -0.347 | | | -0.337 | | | | |
| Gastropoda | 0.522 | -0.493 | -0.364 | | | | | | | |
| Diplura | | | | | | 0.423 | | 0.436 | 0.395 | 0.416 |
| Isoptera | 0.376 | -0.493 | | | | | -0.347 | | | |
| Carabidae | 0.497 | -0.479 | -0.427 | | -0.360 | -0.395 | -0.351 | | | |
| Staphylinidae | 0.690 | -0.708 | -0.529 | -0.585 | -0.534 | -0.522 | -0.613 | | | |
| Cicadidae (L) | | | | -0.415 | -0.347 | | | | | |
| Blattoidea | 0.495 | -0.465 | | -0.346 | | -0.371 | | | | |
| Diptera (L) | 0.487 | -0.493 | | -0.409 | | -0.348 | -0.367 | | | |
| Total | 0.362 | -0.383 | | -0.333 | | | | | | |

Table 7 (concluded).

| Taxa | B | Co | Cr | Cu | AFDM | Zn | CEC | $SO_4^{2-}$ | TSLR | TNLR |
|---|---|---|---|---|---|---|---|---|---|---|
| Lumbricidae | | | | | -0.379 | | -0.378 | -0.344 | | |
| Gastropoda | -0.331 | | | | -0.468 | | -0.429 | -0.398 | | |
| Symphyla | | 0.375 | 0.376 | | | 0.408 | | | | |
| Pseudoscorpionida | -0.423 | -0.485 | -0.465 | | | | | | | |
| Diplura | 0.391 | 0.456 | | | | 0.374 | | | | |
| Carabidae | | | | | | | -0.361 | -0.340 | | |
| Staphylinidae | -0.469 | | -0.356 | -0.438 | | -0.340 | -0.595 | -0.482 | | |
| Scarabaeidae (L) | 0.534* | 0.342 | | | | 0.334 | | | | |
| Cicadidae (L) | -0.350 | -0.335 | -0.336 | | | | | | | |
| Blattoidea | | | | | | | -0.368 | -0.355 | | |
| Diptera (L) | | | | | -0.358 | | -0.413 | | | |
| Total | | | | | | | -0.365 | -0.381 | -0.354 | -0.358 |

**Figure legends**

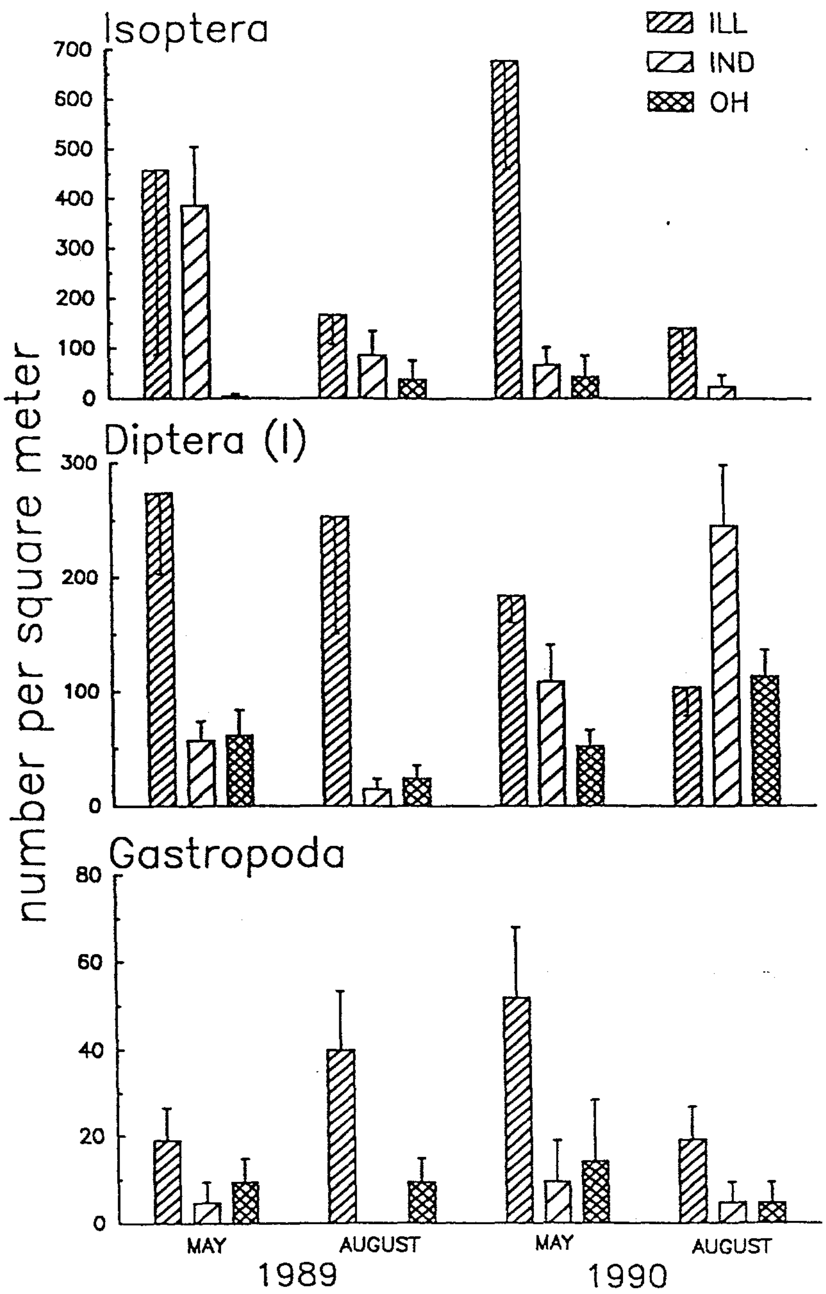
1. Total numbers of soil decomposers in the low-dose site in Illinois, in the intermediate-dose site in Indiana, and in the high deposition site in Ohio.

2. Total abundance of earthworms in the low-dose site in Illinois, in the intermediate-dose site in Indiana, and in the high deposition site in Ohio.

3. Abundance of soil macroinvertebrates in 1989 (one year after drought) and in 1990 (two years with normal precipitation after drought of 1988) in the low-dose site in Illinois, in the intermediate-dose site in Indiana, and in the high deposition site in Ohio.

4. Regression of the pH of H/F layer over abundance of soil decomposers across study sites in Illinois, Indiana, and Ohio.

5. Regression of the abundance of soil decomposers over depth of H/F layer across study sites in Illinois, Indiana, and Ohio



Isoptera
ILL
IND
OH
700
600
500
400
300
200
100
0
Diptera (l)
300
200
100
0
Gastropoda
80
60
40
20
0
number per square meter
MAY
AUGUST
MAY
AUGUST
1989
1990


Figure 1.

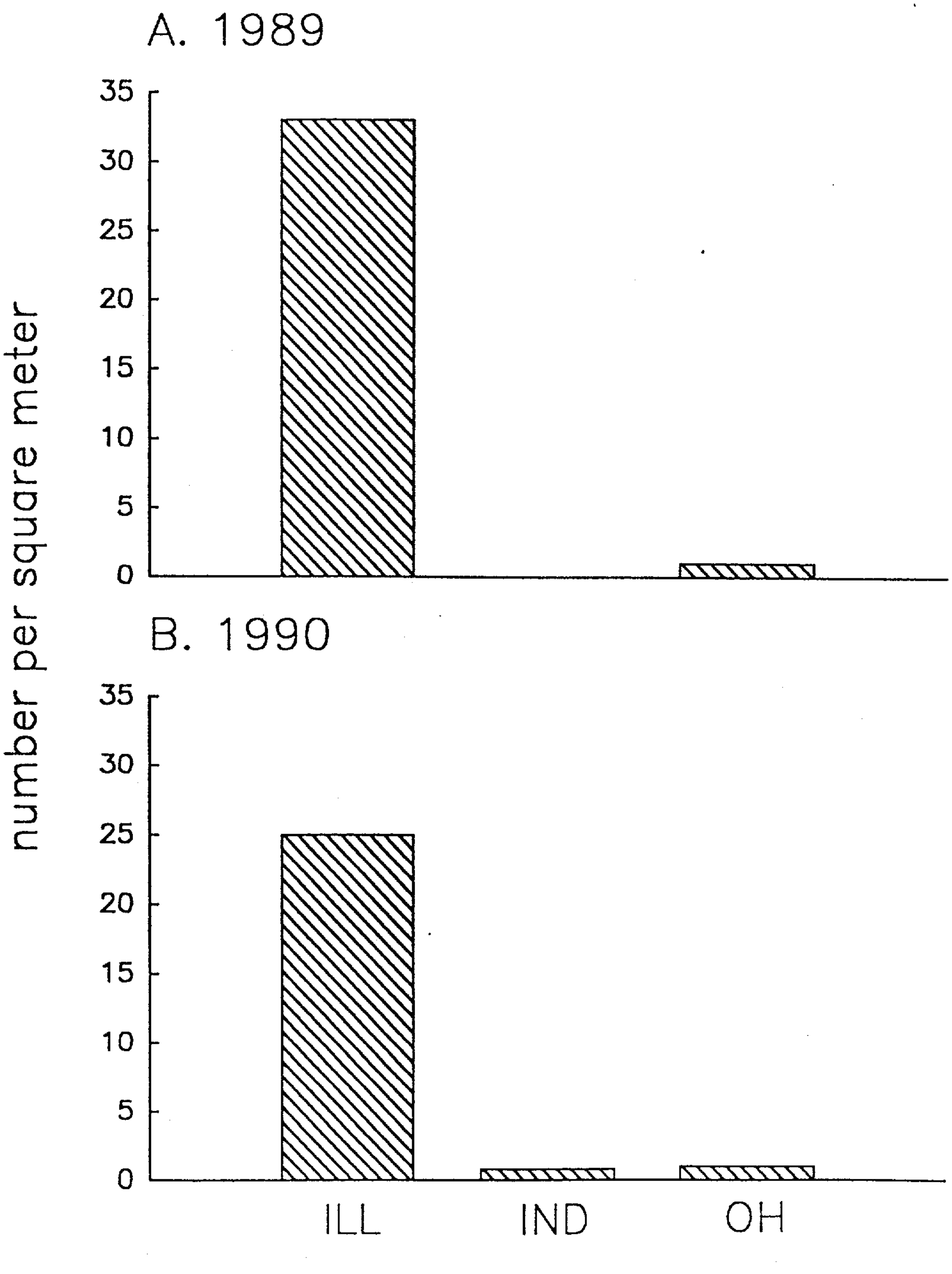
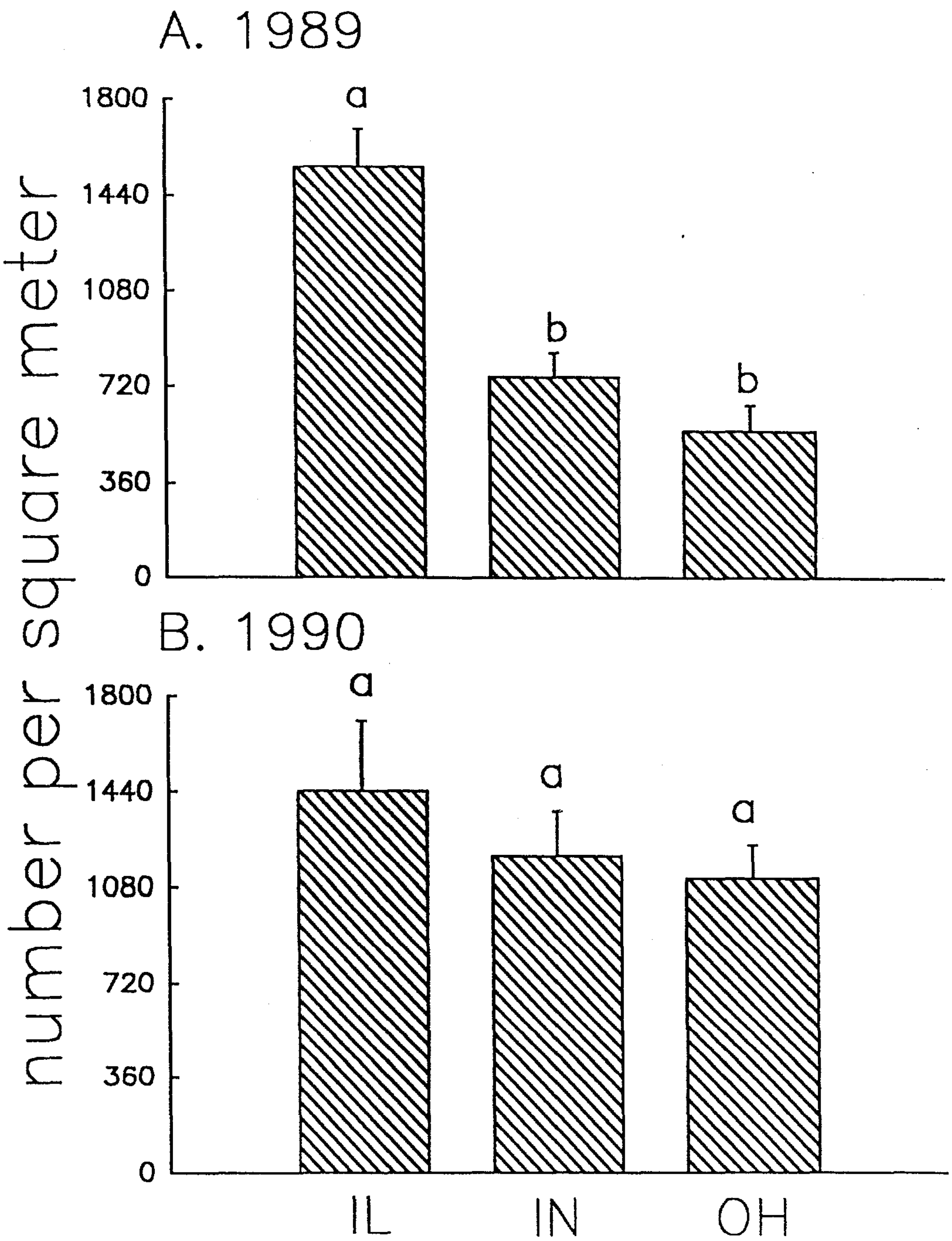
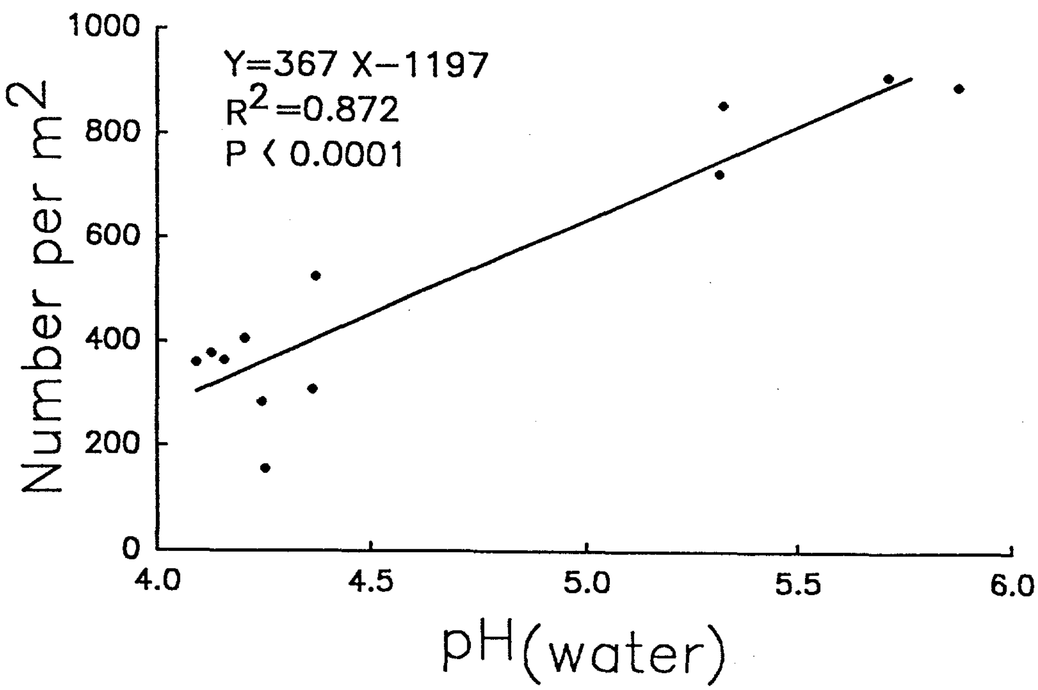

A. 1989
35
30
25
20
15
10
5
0
number per square meter
B. 1990
35
30
25
20
15
10
5
0
ILL
IND
OH

Figure 2.



A. 1989
B. 1990
number per square meter
1800
1440
1080
720
360
0
a
b
b
a
a
a
IL
IN
OH


Figure 3.



1000
800
600
400
200
0
Number per m2
Y=367 X-1197
R2 =0.872
P < 0.0001
4.0
4.5
5.0
5.5
6.0
pH(water)


Figure 4.

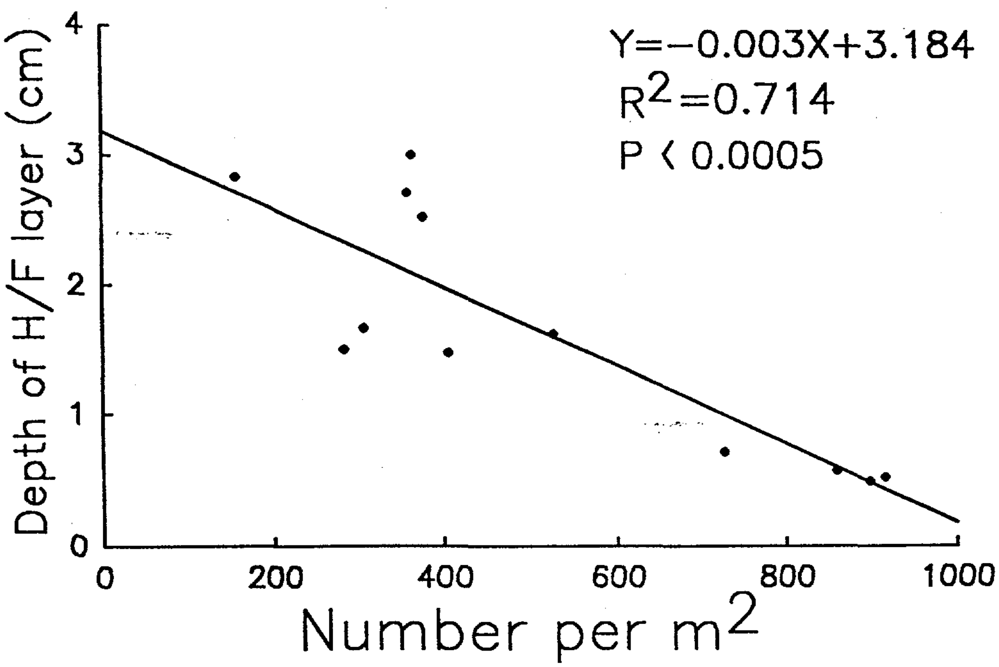

Y=-0.003X+3.184
R2=0.714
P < 0.0005
Depth of H/F layer (cm)
0
1
2
3
4
0
200
400
600
800
1000
Number per m2

Figure 5.