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The ecological effects of acid deposition

Part II

Acid rain effects on soil and aquatic microbial processes

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1. Introduction

Microorganisms play a significant role in C, N, P, and S cycles in nature and are critical to ecosystem functioning. The type and abundance of microorganisms in terrestrial and aquatic ecosystems are influenced not only by the nature and the availability of carbon but also by several environmental factors. Microorganisms in general are sensitive to acidity. Microbial activity is inhibited by a direct H^+ effect, an indirect pH-induced effect such as increased toxic heavy metal availability, or both. A change in pH of the soil or aquatic systems due to acid deposition would be expected to affect microbial numbers and activities and thus to alter the biogeochemical processes brought about by them. The purpose of this paper is to discuss the effects of acid rain and acidity on terrestrial and aquatic microbial processes, with a review of pertinent literature.

2. Effects on soil microorganisms and microbial processes

Soil microorganisms play an important role in the cycling of nutrients in the terrestrial ecosystem. They are responsible for converting many organic forms of essential nutrient elements to the inorganic forms, and are known to solubilize several major and minor trace metals that are available for higher plants. If acidic precipitation has a significant impact on soil microbial processes such as organic matter decomposition, nitrogen transformation, and nutrient release, this creates a potential for reduced soil fertility and economic loss, primarily in unmanaged range and forest soils. In extremely sensitive ecosystems, the impact could be significant and long lasting, even perhaps irreversible. On the other hand, the capacity of most soils, especially agricultural soils, to buffer acid inputs, as well as the diversity and adaptability of microbes in the soil, contribute to resistance to acid rain effects. Experimental data provide evidence on the effects of acidic rain and soil acidity on the following important soil microbial processes: organic matter decomposition, nitrogen transformation (ammonification, nitrification, denitrification, nitrogen fixation by symbiotic and non-symbiotic associations), and soil enzymatic activities.

2.1 Effects of acidification on soil microbiota

Much of the impetus for studies on soil microflora is due to the need for a better understanding of the possible alterations in soil organic carbon and nutrient cycles resulting from acidic deposition. Microbial growth, activity and numbers are reduced by soil acidification. The normal functioning of soil biological communities is affected when a significant change in soil pH is brought about by acid precipitation. The effect of acid rain on soils has been recently reviewed[87]. Different soil types respond to acidic rain differently, and a change in soil pH may or may not be observed.

Bacteria in general are less acid tolerant than fungi, except for chemoautotrophic thiobacilli, which can survive under extreme acid environments. Fungi in general are less sensitive to acidity, whereas heterotrophic bacteria are far more sensitive to acidity[2]. Bryant et al.[20] reported that bacterial numbers were significantly reduced in acidified soils and that total soil biological activity was severely affected in an acid soil of pH 3.0. They also found that, when these acid soils were amended with organic substrates, certain physiological groups of organisms were severely inhibited by the acid condition. Wainwright[94] isolated fewer heterotrophic bacteria but more fungi from soils exposed to acid rain and heavy atmospheric pollution than from similar but unexposed soils. Baath et al.[6-8] reported that artificial acidification of field plots in a pine forest podzol decreased fungal biomass as well as bacteria numbers and cell size. They also reported significant changes in the functional characteristics of the bacterial population due to acid treatment, as determined by factor analyses[7]. They noted a shift towards spore-forming bacteria in soils receiving H_2SO_4 inputs for six years, compared with control soils[8]. They also observed that FDA (fluorescein diacetate) active fungal biomass decreased significantly with increasing severity of acid treatment[8].

Francis et al.[32] reported that the total number of bacteria and actinomycetes generally declined in soil acidified from pH 4.6 to 3.0 by the addition of H_2SO_4. Wainwright[93] reported that in a soil receiving rain of pH 3.0 and dry deposition, the bacterial numbers did not change significantly over a one-year period, even though the soil pH changed from 4.2 to 3.7. Over the long term, it is conceivable that only those organisms that can tolerate these conditions are able to grow and survive, and hence they become dominant because of less competition, so that the total population of microorganisms may represent the dominant organisms and not the natural overall community or species diversity. Studies by Francis[30] indicated that organisms involved in N-transformations were sensitive to soil acidity. The abundance of N-fixing free-living bacteria was low in acidic and acidified forest soils. Studies have indicated differential tolerance of algal species to soil acidity, and the dominance of fungi in acid soils compared with other groups of microorganisms. The microbial diversity of poorly buffered Adirondack soils has decreased, with *Phythium* and *Phytophthora*[45] becoming dominant. Wang et al.[96] studied the effect of acidic deposition on microbial populations in Adirondack forest soils. They examined the microbial community in soil and litter under a beech and maple stand, and red pine plantations. In the hardwoods the populations of bacteria, actinomycetes, and fungi closely paralleled changes in soil acidity. Microbial populations in softwood sites were not correlated with characteristics of the site. In soil microcosm studies, Wang et al. also found that acid treatments increased fungi and actinomycetes populations, which they suggested may be caused by reduced competition from bacterial populations. Alexander[2] also suggested decreased competition from other heterotrophs as a possible explanation for the relative abundance of fungi with decreased pH.

Four years after the last application of sulfuric acid, the fungal species composition in the humus layer of a coniferous forest in Sweden was found to have been altered by treatments of 100 and 150 kg/ha each year over six years. However, very few individual species were significantly affected by the experimental acidification; *Penicillium spinulosum* and *Oidiodendron* cf. *echinulatum* II increased with increasing acid application, but only small changes were found for other isolated fungal taxa[9].

Little is known of the response of mycorrhizal associations to acid rain. Since most fungi are able to proliferate under acidic conditions, one can expect minimal effects on survival or growth of mycorrhizal fungi and consequently their associations under acidic conditions. A reduction in the fungal mantle of spruce mycorrhizae receiving heavy atmospheric pollution, including acid rain, was noted by Sobotka[84]. However, Haines and Best[39] found no visible damage to endomycorrhizae of sweetgum exposed to pH 3.0 treatments.

2.2 Organic matter decomposition

A major concern regarding the effect of acidic deposition is the reduction in the rate of organic matter decomposition and release of essential nutrients. A diverse group of microorganisms participate in the decomposition of natural organic materials in soil and many of these organisms are sensitive to acidity. An increase in soil acidity due to acidic precipitation may enable only certain groups of organisms to proliferate. Some organisms either tolerate acidity and remain in a dormant state or are completely eliminated. Depending on the nature of the organic materials, soil type, pH, temperature, moisture, etc., one should expect differences in the rate and extent of organic matter decomposition.

Decomposition of materials subjected to acidic precipitation or acidification of soils either in the laboratory or in the field has been studied by several investigators. Acidification effects on leaf litter decomposition in forest soils vary with the type of material studied. Exposure to simulated acid rainfalls increased the rate of decomposition of pine needles[1,7,76] but had no detectable effect on that of spruce needles or aspen sticks[1]. Abrahamsen et al.[1] studied the decomposition of lodgepole pine needles, Norway spruce needles, and raw coniferous humus with various acid rain treatments. They found that lodgepole pine needles incubated in the field for 70–90 days at pH 5.6 and 3.0 showed an increase in decomposition (29%) at pH 3.0 over that at pH 5.6. Norway spruce needles given twice weekly waterings with pH 5.6, 3, or 2 at a rate of 100 mm/month or 200 mm/month for up to nine months showed relatively small effects from the acid treatments. At 100 mm/month, no significant effect was noted, and at 200 mm/month the pH 3 and 2 treatments decreased decomposition by $< 5\%$. In litterbag experiments, raw coniferous humus was given pH 5.3, 4.3, and 3.5 treatments. The pH 4.3 treatment decreased the rate of decomposition by 8% and the pH 3.5 treatment by 10%, respectively.

Roberts et al.[76] incubated litterbags for five months in field plots subjected to biweekly 5 mm applications of pH 3.1 and 2.7 acid rain. They observed no significant effect of acid treatments on respiration, but they found a significant increase (15%) in weight loss of the litterbags with increased acidity. Baath et al.[7] studied the decomposition of Scotspine needle litter in litterbags placed in field plots exposed to H_2SO_4 treatments at the rate of 50 and 150 kg/ha. Acid treatments lowered the decomposition rate of both needle and root litter.

Small effects on decomposition of Norway spruce needles in lysimeters exposed to pH 5.6, 3.0, and 2.0 solution at 100 and 200 mm/month were observed by Hovland et al.[47]. The pH 3 and 2 treatments at 100 mm/month initially increased the decomposition rate. With pH 3 and 2 treatments at 200 mm/month, after 38 weeks decomposition had decreased relative to that of controls. The effect of acid treatments on monosaccharide content was not consistent, but with pH 3 and 2 treatment at 200 mm/month, some indication of reduced lignin decomposition was seen. Abrahamsen et al.[1] suggested that decomposition of organic matter in acidic coniferous forest soils is apparently only slightly affected by acidification and that the decomposition of fresh litter and cellulose is influenced only at pH < 3.

Strayer and Alexander[85] studied ^{14}C-glucose mineralization in soils exposed to pH 4.1 and 3.2 acid rain treatments. The pH 4.1 treatment had no apparent effect on glucose mineralization, but the pH 3.2 treatment decreased the glucose mineralization rate by 30–66%. Acid rain treatments lowered pH values, increased total and exchangeable acidity, increased exchangeable Al, and decreased the heterotrophic microbial activity. Bewley and Stotzky[13] observed progressively decreasing amounts of mineralization of vanillin in montmorillonite-amended soil with increasing acidification with H_2SO_4 (pH 3.4, 2.8, 2.2, and 1.6), and complete inhibitions of mineralization at a soil pH of 1.6.

Acidic rain application has significantly reduced organic matter decomposition in forest soils where increases in soil acidity have been observed. Long-term acidification of a field soil severely retards its biological potential for degrading protein and complex polysaccharides[20]. Tamm et al.[88,90] found decreased CO_2 respiration with increased H_2SO_4 in coniferous samples from field plots given 0, 50, and 100 kg/ha/y applications of H_2SO_4. Lohm[62] exposed litter bags for two years in plots given 0, 50, and 150 kg/ha H_2SO_4 per year and found that acid treatments lowered the decomposition rate by 5–7%. With a slight decrease in soil pH after application of pH 2.5 rainfalls, rates of cellulose decomposition decreased; with increased acidification, the rate of humus decomposition decreased significantly; and finally changes in pH of the humus samples were observed[1].

Effects of acidity on microbial decomposition of oak leaves in naturally acid and acidified soils were studied by Francis[30]. Acid soil with pH adjusted to 3.5 showed a 52% decrease in total CO_2 production relative to that in natural control soil at pH 4.6. Highly significant differences ($p < 0.01$) in the rates of CO_2 production were observed among soils amended with organic material. A 37% reduction of total CO_2 evolution was observed in acidified (pH 3.5) soils.

The rate of organic matter decomposition in soils decreases as exchangeable H^+ increases. Among the soils tested (control and amended), there was a highly significant ($p < 0.01$) correlation ($y = 0.8160$) between the relative amount of CO_2 produced and exchangeable hydrogen ion content of the soil[30].

Simulated sulfuric acid rain (pH 3.0, 3.5, or 4.0) or control (pH 5.6) was applied to decomposing leaf packs of ten hardwood species. Changes in weight and chemical element concentrations were followed for 408 days. Leafpack weight decreased most rapidly under the intermediate acid treatments, especially at pH 3.5. The ratio of the decomposition rate of leaves at pH 3.5 to that of the control leaves varied from 1.10 for Garry oak *(Quercus garryana)* to 12.57 for pin oak *(Quercus palustris)*[61].

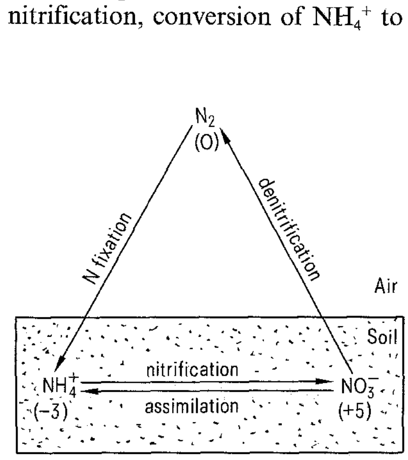
Moloney et al.[66] reported that in vitro studies on degradation of fir and spruce mixed needle litter showed reduction of microbial CO_2 evolution from litter under acidic conditions (pH 3 or 4) and further reduction in the presence of Pb and Zn but not Al or Cu. They found cellulose breakdown to be unaffected in acidic, metal-containing soils treated with water acidified to pH 3.8. They attribute the reduction in litter decomposition, which could adversely alter the rates of mineral cycling in natural ecosystems, to repression of the metabolism of litter-degrading microflora by precipitation acidity and metals present in soils and introduced by polluted rains.

Soils that had previously been subjected to long-term acidification or to liming were tested for microbial activity after three years. Total soil respiration was decreased by acidification; mineral N accumulation was not influenced, but the rate of microbial N turnover was markedly decreased[62a]. Klein et al.[57] observed significantly reduced rates of carbon and nitrogen mineralization in soil that had received simulated precipitation at pH 3.5.

Kelly and Strickland[54] used both field and laboratory measurements of CO_2 evolution as an index of decomposer activity. Forest microcosms were used to evaluate the impact of simulated acidic precipitation on decomposition. Treatments with annual average pH 5.7, 4.5, 4.0, and 3.5 were applied for a 30-month period. No statistically significant effect of treatment on decomposition could be found in the field measurements. When the microcosm was partitioned into 01 and 02 litter, mineral soil (A and B horizons), and roots within the mineral soil horizons for laboratory determination of CO_2 efflux, only the 02 litter exhibited a statistically significant decrease as a function of treatment. Efflux of CO_2 from the 02 layer was small compared with that from the other layers, and this may account for the failure to detect a significant response in field measurements. The inhibition effect observed in the 02 layer may be ecologically important since many plants derive a major portion of their nutritional requirements directly from the 02 litter layer.

2.3 Nitrogen transformation

Nitrogen is the major nutrient limiting plant growth in nature. Higher plants are known to assimilate nitrogen in the form of nitrate and ammonia. The nitrogen cycle can be very simply viewed as a triangle (fig.)[28]. Step 1 is N fixation in which N_2 in air is converted to NH_4^+ in soils. Step 2 is nitrification, conversion of NH_4^+ to NO_3. The



reverse of this reaction is nitrogen assimilation. Step 3 is denitrification, the conversion of NO_3 in soils to N_2 in air. First, two of the three steps on the triangle are not reversible reactions in biology. Second, all but the assimilatory reaction are brought about, for the most part, by bacteria. Third, the weakest link in the triangle (nitrification) is greatly affected by pH.

Ammonification, nitrification, nitrogen fixation, and denitrification (fig.) are affected by soil acidity to varying degrees. Although pH optima have been reported for pure cultures and cultures grown in sewage and in some soils, little information is available on diverse soils or on the performance of the organisms when the soil medium is subjected to prolonged exposure to acid precipitation.

2.3.1 Ammonification

The organic nitrogenous compounds in soil, sediments, and terrestrial and aquatic plants are converted to ammonium (ammonification) by a large group of heterotrophic bacteria, fungi, and actinomycetes. Several investigators have reported that acid inputs can slightly accelerate mineralization of organic nitrogen[86,89,93]. Ammonification in a pH-adjusted acid soil (pH 3.5) was about 50% less than in a naturally acidic soil (pH 4.6). Highest rates of ammonification were observed in the pH-adjusted neutral soil[30].

2.3.2 Nitrification

Nitrification is the sequential oxidation of ammonia to nitrite and then to nitrate by autotrophic and heterotrophic microbial communities. The autotrophic nitrification is principally accomplished by *Nitrosomonas* sp. and *Nitrobacter* sp. Members of the genus *Nitrosomonas* oxidize ammonia to nitrite only, and the genus *Nitrobacter* is limited to the oxidation of nitrite to nitrate. Inasmuch as nitrification, like all autotrophic processes, results in production of H^+ ions, it can be considered both as a source of acidity and as a process regulated by acidity. Unlike the sulfur-oxidizing chemolithotrophs, which are the most acid-tolerant forms of life known, the nitrifying bacteria have not evolved to become tolerant to acidity. Nitrification is the rate-controlling step not only in the oxidation of ammonium, but also in the generation of the product for its loss to the atmosphere through denitrification.

Nitrification occurs optimally at neutral to slightly alkaline pH. In acid environments, nitrification proceeds slowly even in the presence of an adequate supply of substrate, and the responsible species are rare or totally absent at high acidities. Typically, nitrification decreases markedly below pH 6.0 and becomes negligible below pH 5.0,[25] yet nitrate may occasionally be present in field soils of pH 4.0 or lower[3]. Some soils nitrify at pH 4.5; others do not. The difference is possibly attributable to acid-adapted strains or to chemical differences in the two habitats. Neutral to alkaline soils have the largest nitrifier populations. Accumulation of nitrate has been observed in acidic soils of pH as low as 3.9[50,51,99]. Walker and Wickramasinghe[95] isolated pure cultures of ammonium-oxidizing autotrophic, nitrifying bacteria from acid soils at pH 4.0 to 4.5. They detected nitrite-oxidizing bacteria in several of the acid soils but did not isolate pure cultures.

Application of acid rain (pH 4) reduced nitrification rates in a soil with pH 4.4[48]. In a beach forest soil (pH 3) very small numbers of nitrite- and nitrate-forming organisms were found and substantial amounts of nitrate were detected[69,77]. Formation of nitrate by heterotrophic nitrification in acid soils has been suggested by Abrahamsen et al.[1] and Ishaque and Cornfield[50]. Nitrification by heterotrophs might be of major importance in acidic soils and in highly alkaline, nitrogen-rich aqueous environments, where autotrophic nitrification is not detected[29,75]. Little autotrophic and heterotrophic nitrification in acidified soil (pH 3.5) was observed in a soil perfusion study[30].

Of particular concern are the rates of nitrification (autotrophic, and/or heterotrophic) in forest soils impacted with acidic pollutants because autotrophic nitrification is far more sensitive to acidity than are other steps in the nitrogen cycles. In natural ecosystems, however, the significance of nitrate formation by the heterotrophic nitrification process still remains small. Wainwright[93] reported that N mineralization was enhanced by exposing soil to atmospheric pollutants. Acidification of soil by addition of either powdered sulfur or sulfuric acid decreased CO_2 evolution (decomposition) by soils, whereas it increased the amount of mineral-N (ammonification) in the sample, but lowered the amount of nitrate[90]. Strayer et al.[86] found that nitrate formation from added ammonium, but not from native organic N, was inhibited following continuous exposure of several forest soils to simulated acid rain. In naturally acidic soils in which the pH was adjusted with H_2SO_4 or $Ca(OH)_2$, Francis[30] found that ammonium formation decreased as soil acidity increased. The data also indicated that nitrification is very sensitive to acidic conditions because little nitrate accumulated in acidified and naturally acid soils compared with soils adjusted to neutral pH. In studies of nitrate formation in three forest soils from the Adirondack Mountains of New York, Klein et al.[56] found that nitrate was formed when the soils were treated with artificial rain at pH 3.5, 4.1, or 5.6. Compared with simulated rain at pH 5.6, simulated rain at pH 3.5 enhanced nitrate formation in one soil and inhibited it in two others. The rates of N mineralization in acid forest soil exposed to the simulated precipitation were less for rain at pH 3.5 than at pH 5.6[72].

Inhibition of nitrification in acid forest soils and soils undergoing acidification due to acid precipitation would indeed result in the accumulation of NH_4^+ in soils, i.e., nitrogen conservation as opposed to nitrogen mineralization (nitrification) and loss of NO_3^- due to leaching and denitrification. Therefore, it would appear that the inhibition of nitrification in acid soils would result in conservation of N in forest soils and benefit forest growth in the long term. Whether such accumulation and increased availability of ammonium in forest soils can be attributed to forest dieback observed across vast areas of northern Europe and North America, is not clearly understood. It has been suggested that increased nitrogen compounds in acid rain could be an important factor involved in forest dieback[70]. Nevertheless, the significance of nitrification in forest soils needs to be critically examined. Furthermore, to what extent the natural processes, particularly nitrification in the watershed soils, contribute to surface water acidification is not clearly understood.

2.3.3 Denitrification

Soil bacteria are known to reduce nitrates to nitrogen gas under anoxic conditions in the presence of available carbon; the process is called denitrification. In acid soils, denitrification is inhibited so that N_2O instead of N_2 is released as the end product. Biological denitrification has received much attention because of its importance in the removal of nitrates from waste waters. Of particular interest to soil and atmospheric scientists is the biogenic evolution of N_2O and its subsequent effect in depleting atmospheric ozone. Soil pH is known to affect the evolution rate and the composition of the gaseous end products of denitrification. Denitrification is favored by relatively high pH values, and at pH values below 6 the reduction of N_2O is often strongly inhibited[16,18,30,58,71,97,101]. Francis[30] reported that the rate of denitrification was rapid at soil pH 6.5 with little N_2O detected, indicating further reduction to N_2, but in acid (pH 4.6) and acidified (pH 3.5) soils, the rate of denitrification was slow and N_2O was the major end product.

2.3.4 Nitrogen fixation

2.3.4.1 Asymbiotic N-fixation. Nitrogen-fixing microorganisms differ in tolerance to acidity. Among bacteria *Azotobacter, Beijerinckia,* and *Clostridium* have been extensively studied. Although the increase in N in soil by nonsymbiotic fixation is low, its ecological significance in the long term can be important. Environments more acidic than pH 6.0 contain few or no nitrogen-fixing bacteria. Nitrogen fixation by free-living bacteria in freshly collected forest soil (pH 4.6) was not detectable. Only soil samples of pH 5.7 amended with glucose and preincubated under aerobic or anaerobic conditions exhibited slight activity[30]. Blue-green algae, which also fix nitrogen, grow poorly and are found to be sparse in acid environments. Chang and Alexander[23] reported that the rates of nitrogen fixation in three forest soils exposed to acid precipitation were significantly lower if the pH of the simulated rain was 3.5 than if it was 5.6, and that CO_2 fixation also was significantly less in soils exposed to acid rain of pH 3.5. They suggest that algae in terrestrial ecosystems may be especially susceptible to acid precipitation.

2.3.4.2 Symbiotic N-fixation. Soil acidification affects symbiotic nitrogen fixation in legumes. Although several physical and chemical factors contribute to efficient nitrogen fixation in legume-Rhizobium symbiosis, soil acidity affects a) plant growth, b) survival of rhizobia, and c) the symbiotic relationship. Reductions in nodulation and plant growth due to reduced N fixation have been reported[24,26,68,81,82]. In some cases, the bacterial symbiont appears to be sensitive to acidity[19,63]. Toxicity resulting from iron or aluminum in acidified soils also has a profound effect upon nitrogen fixation. Effects on symbiotic nitrogen fixation by legumes in unmanaged range soils could be significant.

Little is known of the effects of acid rain on N fixation by actinomycetes associations with nonleguminous plants in forest soils. Alnus seedlings with *Frankia* were grown in soils of pH 3.6 to 7.6 to study the influence of acidity on nodulation of black alder used to revegetate acid mine soils[38]. In some of the soil types tested, nodulation was reduced at pH below 5.5, and there was evidence of decreased viability of the endophyte at pH below 4.5; root growth and root hair development were inhibited at pH below 5.0.

2.4 Soil enzymes

The activities of certain enzymes present in the soil provide a general indicator of the microbial activity. Reductions in many soil enzymes have been reported in acidified soils or soils treated with acid rain. Soil acidification studies[78,80,83,100] have in some cases shown decreased cellulolytic activity with decreasing pH.

Natural acid soils (pH 4.7), acidified soils (pH 3.5), and pH-adjusted neutral soils (pH 6.8) which had been preincubated under moist conditions for 60 and 270 days were assayed for urease and dehydrogenase activities[33]. These activities showed no apparent differences between the natural and pH-adjusted neutral soils, but they were much lower in the acidified soil. Surface samples of a brown earth soil exposed to heavy atmospheric pollution for one year resulting in a decrease in soil pH from 4.2 to 3.7 showed no significant change in the activities of soil enzymes such as arylsulfatase, cellulase, dehydrogenase, phosphatase, rhodanese, and urease[93]. Treatments of field plots with acid rain of pH 3.7 and 3.0 did not significantly alter enzyme activity, except protease activity, which increased at pH 3.0[15].

Norway spruce needle litter collected from field plots exposed to pH 6.1, 4.0, 3.0, and 2.5 rains over a 5-y period showed little effect on biological activity as measured by respiration and cellulase activity[46]. The lack of effect is probably due to a shift in the microbial community in the litter, as evidenced by enhanced growth of litter decomposing fungi, Basidiomycetes, mainly of the genera *Mycena* and *Marasmius*. Killham et al.[55] exposed a Sierran forest soil (pH 6.4) planted with Ponderosa pine seedlings to simulated rain (pH 2.0, 3.0, 4.0, and 5.6) with 15 cm of precipitation over a 12-week period. Changes in microbial activity were most significant in surface soils. Only the pH 2.0 rain caused inhibition both of respiration and of enzyme activities of urease, phosphatase, dehydrogenase, and arylsulfatase.

2.5 Degradation of pesticides

Information on the effects of acid precipitation or of acidity on biodegradation of xenobiotics is scanty. Biodegradation of pesticides would be affected by acid precipitation via changes in microbial populations or changes in pH levels in water and soil solutions which affect adsorption characteristics of pesticides by soil particulate matter and in some cases make them unavailable for biodegradation. Captan, Dicamba, Amitrole, Vernolate, Chloramben, Crotoxyphos[41], Metribuzin[59], 2,4-D and MCPA[91], and Prometryne[12] were reported to persist longer under acidic than under neutral conditions. Conversely, Diazinon and Diazoxan[41] were degraded more readily at lower pH levels. The effects of the pesticides 2,4-D, cacodylic acid, Dylox, methoxychlor, Sevin, and Paraquat on soil microbial activity and the fate of ^{14}C-labeled 2,4-D, Sevin, and Paraquat in naturally acid (pH 4.7) and pH-adjusted acid (pH 3.5) and neutral soils (pH 6.8) were studied (Francis, unpublished results). The data suggest that the addition of these compounds to soils did not have any effect on soil respiration. However, variations in the rate and degradation of 2,4-D, Sevin, and Paraquat were observed. Paraquat was not degraded in acid soils.

3. Effects on aquatic microorganisms and processes

Increasing acidity of precipitation has caused extinction of fish and other changes in species composition at all trophic levels in oligotrophic lakes in northern Europe and eastern North America. Microorganisms play an important role in the decomposition of organic matter (autochthonous, originating by primary production; and allochthonous, transported by inflowing water, airborne litter or rain) in lakes and streams and are responsible for the regeneration and cycling of nutrients in the aquatic ecosystem. Inhibition of microbial activity due to acid deposition in aquatic ecosystems can have profound effects. Detritus removal, conservation of energy, nutrient recycling, primary production, detritivore production and production at higher trophic levels can all be affected by changes in microbial activity. The effect of acidification on the mineralization of autochthonous and allochthonous organic carbon in lakes and streams is not fully determined. Furthermore, little is known about the effect of acid precipitation on the biogeochemical cycling of major and minor elements brought about primarily by the activities of microorganisms in oxic and anoxic environments.

3.1 Microbial population distribution and activity in acid lakes and streams

Reductions in microbial numbers and activity have been observed in water, sediment, and leaf litter samples in lakes and streams. Laboratory studies indicate lower decomposition rates of glucose, glutamic acid, and homogenized leaf litter at pH 4 than at pH 7. Fungi were the predominant organisms at pH 4, whereas bacteria and zooflagellates dominated at pH 7[92]. Bick and Drews[14] found that the microbial decomposition rate of peptone decreased with increasing acidity and observed no ammonium oxidation below pH 5. They also found that the total counts of bacteria decreased slowly within the pH range 7 to 5 but decreased rapidly as the acidity increased from pH 5 to 3.

Microbiological analysis of water, sediment, and leaf litter samples from lakes and streams indicates reductions in microbial numbers and activity with increases in acidity of water and/or sediment.

3.1.1 Microbial population in water

Traaen[92] compared numbers of planktonic bacteria in the waters of seven acidic lakes (pH $<$ 5) and less acidic lakes (pH $>$ 5). Three of the acidic lakes were humic (brown-water), and these lakes had three to four times as many bacteria per volume of water as did the others; however, the acidic and less acidic clear-water lakes did not differ in this respect. This difference is probably due to the presence of high levels of available carbon, which support microbial growth, in humic lakes. Nine high-altitude oligotrophic lakes in the Adirondack Mountains of New York with water pH ranging from 4.3 to 7.0 were surveyed for major representatives of the microbial community[17]. Heterotrophic bacterial numbers were low for most of the lakes, in the range of 10–1000 per ml. Sediment aerobic heterotrophs ranged from 1.4×10^4 to 1.3×10^6 per gram of sediment[17]. Acridine orange direct counts (AODC) were approximately two orders of magnitude higher than plate counts for each lake. Acidified enclosures placed in a Canadian lake showed no change in bacterial numbers before and after acidification[67]. Scheider et al.[79] found that the aerobic heterotrophic microbial populations in acidified lakes near Sudbury, Ontario, Canada, were markedly lower than in non-acidified lakes. Sediment microbial populations, however, were not different. When acidified lakes were chemically neutralized, the planktonic bacterial densities quickly responded and soon rose to resemble those in the non-acidic lakes.

Bacteriological and hydrological studies were conducted in lakes undergoing acidification by Fjerdingstad and Nilssen[27] in southern Norway. The numbers of bacteria, except for *Thiobacillus*, were much lower than in oligotrophic lakes in Denmark and Greenland. This is perhaps due to constant low acidity of the Norwegian lakes, heavy metal accumulation in the sediments, or biocides in the acid rain. The authors suggest that with increasing acidification, *Thiobacillus thioparus* and other *Thiobacillus* species may increase in numbers and, since they produce sulfuric acid, add to the acidity of the lakes. Rao and Dutka[73] investigated the relative abundance of total, respiring, aerobic heterotrophic, nitrogen cycle, and sulfur cycle bacteria in acid-stressed and non-acid stressed hard water lakes. They found that the bacterial populations and densities were nearly an order of magnitude less in acid-stressed waters than in non-acid-stressed waters. Nitrifying bacteria and some sulfur cycle bacteria (*Thiobacillus* sp.) were very sparse or absent in acid-stressed waters. Francis et al.[34] studied the distribution of bacterial populations in water samples from Woods Lake (pH $\sim$ 5), Sagamore Lake (pH $\sim$ 6), and Panther Lake (pH $\sim$ 7) during several seasons. Populations of bacteria as determined by acridine orange direct counts (AODC) in acid Woods Lake water were significantly lower than in moderately acid Sagamore Lake and neutral Panther Lake. Autotrophic ammonia-oxidizing and nitrite-oxidizing bacteria were not detected in Woods Lake water. Wassel and Mills[98] reported that the bacterial communities were stressed both in the surface water and, to a lesser extent, in the sediment in areas of a large impoundment near an inflowing acid mine stream. AODC of bacteria did not differ significantly among the sites; however, significantly fewer viable heterotrophs were observed by plate counts at the acid impacted station than at the uncontaminated site. The diversity of the communities was significantly lower at the sites receiving mine drainage than at the unaffected station, and comparisons of community similarity showed that collections from the impacted sites were more like each other than like those from the control sites[98].

Two acid-stressed lakes (pH 4.4–6.4, and pH 5.5–6.5) in the Pocono Mountains of Pennsylvania were surveyed for total numbers of heterotrophic, proteolytic, nitrogen cycle, and sulfur cycle bacteria in water and sediment samples by Majumdar et al.[64]. The numbers of heterotrophic and proteolytic bacteria recovered were low (10^4–10^5/ml). Nitrogen cycle and sulfur cycle bacteria were very sparse or absent in both acid-stressed lakes. The numbers of total bacterial flora in the two acid-stressed lakes in the Poconos were markedly lower than in non-acid-stressed lakes (1–5×10^6/ml).

3.1.2 Microbial population and activity in sediments

Surface sediments of acid stressed lakes in Norway contained three to four times as much organic matter as did those of the relatively more enriched lake. The rate of oxygen utilization at the surface of both natural lake sediment cores and artificial sediments composed of sand and organic materials indicated that heterotrophic microbial activity is reduced when the pH of the overlying water is lowered[60]. The utilization of radioactive glucose in the water just above the sediments was decreased by as much as 98% with an increase in acidity from pH 6 to pH 5. Furthermore, in the sediment samples, lower pH also led to a reduced rate of phosphorus cycling, as measured by the uptake of radioactive phosphate[60]. In sediment from Lake Gardsjon, Gahnstrom et al.[36] found that oxygen uptake was lower in littoral sediment (3 m depth) than in profundal sediment (18 m depth). In the profundal sediments, they found that 1) glucose turnover rate was low with no significant difference between sediments from acidified and non-acidified lakes, indicating low microbial activity, and 2) oxygen consumption of profundal sediments was of the same magnitude in acidified and non-acidified lakes. These results suggest that the buffering of the sediment is strong and the shallow, littoral sediment is affected by the overlying acid water to a greater extent than is the profundal sediment. Baker et al.[10,11] reported that the mineralization of ^{14}C-glucose, ^{14}C-glycine, and ^{14}C-glutamic acid was lower in sediments at pH 4 and 5 than at pH 7. The majority of the sediment bacterial populations were resistant to lead and selenium and a smaller proportion to mercury and arsenic. Many of the bacteria were resistant to more than one of the elements. Lead and mercury were more toxic to bacterial growth at pH 4.5 than at 7.5, whereas selenium and arsenic were slightly more toxic at the higher pH[10,11].

No significant differences were observed in the bacterial populations or pH values of the sediment samples from the three lakes, Woods (pH $\sim$ 6.6), Sagamore (pH $\sim$ 7.1), and Panther (pH $\sim$ 6.4)[34]. Sediment samples from Woods Lake contained no detectable ammonia oxidizers, but nitrite-oxidizing bacteria were present in all three lake sediments samples with little variation in populations among the lakes. A strong relationship between lake acidification and bacteria was observed in water and sediment cores from eight lakes near Sudbury, Ontario[74]. In the sediments the critical pH value for respiring and aerobic heterotrophic bacteria appears to be $\sim$ 5.5. In the sediments a relationship was found between pH, bacterial populations, sediment microbial activity, and total organic matter; in an acid-stressed lake (pH 3.8) the sediment respiration was 10–20% of that in a non-acid-stressed lake (pH 7.2).

In lakes affected by acid deposition, inputs of sulfate and nitrate increase, and reducing power normally going to methane production is expected to be diverted to nitrate and sulfate reduction, which, unlike methane production, can result in production of alkalinity. Kelly et al.[52] measured the rates of microbial reduction of O_2, Fe^{3+}, Mn^{4+}, NO_3^-, and SO_4^{2-} and total generation of CO_2 and CH_4 in the hypolimnia of three Canadian Shield lakes. Methanogenesis accounted for 72–80% of anoxic carbon generation, sulfate reduction contributed 16–20%, and the remainder (2–8%) originated from all the other processes combined, such as nitrate, iron, and manganese reduction. The authors developed a model which showed that the hypolimnia of two lakes which have been made eutrophic artificially could potentially produce enough persistent alkalinity to neutralize 'typical' acid deposition, while the lake that was not eutrophic could not[52].

3.2 Decomposition of organic matter in acid lakes and streams

Swedish investigators[37] found abnormal accumulation of litter in six lakes in which the pH had decreased by 1.4–1.6 units during the preceding three to four decades. Furthermore, dense felts of organic debris and algal filaments covered up to 85% of the shallow bottom area of Lake Gardsjon (this is the material erroneously reported to be fungal hyphae) and were observed in several other lakes. These findings led to investigations of litter decomposition in lake and stream waters at different pH values and in laboratory experiments. Large accumulations of organic debris have also been found in acid mine drainage waters in South Africa[42].

In Norway, litterbags containing birch leaves were placed in flowthrough tanks at the Tovdal field station[92]. The pH levels of these tanks were adjusted to approximately 4, 4.5 to 5.2, and 6. Weight losses after one year were approximately 45%, 48%, and 52% at the respective pH treatments (all significantly different: $p > 0.05$). Two other tests, in which birch litterbags were exposed for two years in Norwegian lakes and brooks at differing pH, showed leaf decomposition to be inhibited by low pH.

Breakdown of leaf litter in leaf packs was much slower in an acidic Swedish stream (pH 4.3 to 5.9) than in a very similar non-acidic stream (pH 6.5 to 7.3). The densities of invertebrates associated with these leaf packs were greater in the non-acidic stream. Among the functional groups of invertebrates, species that specialize in shredding material such as leaf litter were by far the most abundant in the acidic stream, and species that scrape material such as attached growths of algae, bacteria, etc., were greatly reduced, compared with their numbers in the non-acidic stream[35].

When Norris Brook, a small forest stream in New Hampshire, was acidified from about pH 6 to pH 4, dense growths of basidiomycete fungus appeared on submerged mosses and tree roots, covering about 1% of the acidified study area[40]. Fungal hyphae grew as a thin layer over 70% of the stream bottom near the site of acid addition, but the species diversity of fungi was reduced in the acidified area[40]. Burton et al.[21] studied the decomposition of white birch *(Betula papyrifera)* and sugar maple *(Acer saccharum)* leaves in artificial streams acidified to pH 4 with sulfuric acid. They found significant reductions in the decomposition of the leaves in the acidified streams and also substantial decreases in the invertebrate populations.

Heavy growths of filamentous algae and mosses have also been reported in streams in Norway affected by acidification. In experiments in artificial stream channels using water and the naturally seeded algae from an acidified brook (pH 4.3 to 5.5), an increase in the acidity to pH 4 by addition of sulfuric acid led to an increased accumulation of algae compared with that in an unmodified control[43]. An experimental acidification to pH 4.0 of a natural stream in the Hubbard Brook Experimental Forest also resulted in extensive growths of filamentous algae[40].

The effects of acid on the microbial decomposition of the dominant aquatic macrophyte (*Carex* spp.) in oligotrophic Toolik Lake, Alaska, were studied in microcosms by McKinley and Vestal[65] during the ice-free season of 1980. Microbial activities (as determined by ^{14}C-acetate incorporation into extractable lipids) associated with *Carex* litter were significantly reduced ($p < 0.01$) at pH 3.0, but not at the other pH levels tested. After 18 days, microbial activity was significantly correlated with weight loss, nitrogen content, and C/N ratios of the litter, but not with ATP levels. Analysis of the litter surface by scanning electron microscopy revealed that the fungi present at ambient pH after 18 days did not become dominant at pH values below 5.5, diatoms were absent below pH 4.0, and bacterial numbers and extracellular slime were greatly reduced at pH 4.0 and below. Decomposition of *Carex* ^{14}C-(lignin)- and ^{14}C-(cellulose)-lignocellulose was reduced at pH 2.0 but not at pH 4.0, 5.0 or 6.0, compared with that in controls (pH 7.1). The authors concluded that, if the pH of the water was sufficiently reduced, rates of litter decomposition would be significantly reduced. Carpenter et al.[22] compared the effects of acid mine drainage on the decomposition of vascular plant material in a reservoir at three locations: 1) a control site with no acid mine drainage (pH 6.3), 2) an experimental site with dilute acid mine drainage (pH 5.7), and 3) an experimental site near the acid mine drainage source (pH 3.7). They found that both microbial activity and the process of leaf decomposition were inhibited in a region close to the source of contamination, and that the degree of inhibition decreased with distance from the source as the acid mine drainage was diluted. The decomposition rate of leaves from three types of trees and a rush differed significantly between leaf species and between sites. For all leaf species, the decay rate coefficient (k) for the control site was at least twice that for the most severely affected site. Heterotrophic activity, measured with ^{14}C-glucose, was depressed at both experimental sites compared with that at the control site. Numbers of bacteria were about 10^{10} cells per gram dry detritus, and did not differ significantly between control and experimental sites.

Decomposition of leaf litter in Woods Lake (pH ~ 5.0), Sagamore Lake (pH ~ 6.0), and Panther Lake (pH ~ 7.0) in the Adirondack Mountains, a region heavily impacted by acid deposition, was studied by Francis et al.[31,34] Litterbags containing leaves of American beech, sugar maple, red maple, leather leaf, and red spruce were incubated at various depths in the lakes. Samples were removed periodically over a two-year period and analyzed for loss in weight, changes in leaf surface area, carbon and nitrogen contents and bacterial populations. The rate of decomposition of litter depended on the leaf species tested as well as on the lake water in which they were incubated. Of the five leaf species tested, red maple had the highest rate of decomposition and red spruce the lowest: i.e., red maple > sugar maple > beech > leather leaf > and red spruce. The rate differed among the lakes in the order Woods (pH ~ 5) < Sagamore (pH ~ 6) < Panther (pH ~ 7).

The decay rate constant (k_2) for red maple, which decomposed fastest, was higher than for the other leaf species tested and showed a direct relationship with the type of lake studied: i.e., Woods (pH ~ 5) = 0.206 < Sagamore (pH ~ 6) = 0.436 < Panther (pH ~ 7) = 0.584. Sugar maple followed more or less the same trend as red maple but at an intermediate rate. The k_2 values for beech, leather leaf, and red spruce were very low, suggesting that these leaves may remain for a longer time and accumulate in the lakes.

No significant difference in decomposition of the beech leaves due to incubation depth within Woods or Panther lakes was observed. In Sagamore, the leaves at 5-m depth were found buried in the sediment, where conditions were probably anaerobic, and the extent of decomposition at this depth was significantly less than at the other two depths.

The population of bacteria in the litter after two years' incubation was 3×10^9 to 2×10^{10} bacteria per gram dry weight of leaf material, a range similar to that found in sediments. The population varied with leaf species with maximum counts found in red maple, the most rapidly decomposing one.

In acidic lakes, lime treatment caused rapid decomposition of the organic litter as well as great reductions of algal mats and *Sphagnum*, indicating that bacterial activities had been inhibited at low pH[4,5,37,49,79]. Winter and summer measurements, in experimentally acidified Lake 223 in the Canadian Shield, suggest that the in situ decomposition rates in sediments were unaffected by acidification over an epilimnetic pH range of 6.7 to 5.1. In laboratory experiments, however, decomposition rates of newly sedimented material began to decrease at pH 5.25 to 5.0. In general, basic processes (such as primary production, organic matter decomposition, nutrient regeneration) apparently would not be seriously impaired until lake pH dropped well below values that would severely affect the growth and reproduction of higher life forms[53]. The aquatic ecosystem is seen as a complex association of interdependent organisms, in this case linked together by the processes of decomposition. Perturbations to communities of these decomposer organisms will quite likely have ramifications throughout the system, i.e., such as reduced mineral cycling, accumulation of litter, and lowered nutrient supply to plants and food source to invertebrates[44].

4. Conclusion

Further acidification of acid forest soils by acidic rain is perhaps a very slow process – it may take many years for acidic rain to change the soil pH. Rapid adaptability of microbial populations to changing physical and chemical environments and substantial differences between the measured soil pH and the actual pH in the microsite environments make it difficult to monitor accurately short-term changes that might be caused by acidic precipitation. Slow acidification may have effects on soil microbial communities which may gradually result in the selection of acid-resistant or tolerant organisms or in the total elimination of certain species. On a long-term basis, acidic rain may affect certain key processes catalyzed by soil microorganisms such as organic matter decomposition and nitrogen transformation, and ultimately the nutrient cycling in the forest ecosystem. To date, studies with simulated acidic rain indicate overall reductions in several soil microbial processes. Stimulatory effects on microbial activities observed in some cases have been assumed to be temporary. The physical and chemical characteristics of the soil and its response to environmental pollutants significantly affect the type, abundance, and activities of soil microorganisms. No generalizations can be made because of the diversity and complex nature of these systems.

Many of the available data on the effects of acidic rain on soil microbiological processes have been obtained through laboratory studies[20,30,32,55,85,86]. Little is known, however, about the effects of acidic rain on nitrogen transformation (e.g., ammonification, nitrification and denitrification) under field conditions, or microbial contribution to the acidification of surface waters. Therefore, on the basis of existing data, it is not clear to what extent and at what rate the current acidic precipitation is affecting soil microbial processes.

The literature reviewed above makes it clear that increasingly acidic conditions inhibit microbial activity in the aquatic environment. Observations to date of acidified lakes and streams demonstrate that acidification inhibits the processes of decomposition. Only limited studies deal with the effects of acidity on microbial populations and activities in lakes and streams located in sensitive areas receiving acid rain. Furthermore, there is still a large gap in the knowledge of the effects of acidic precipitation on microorganisms and particularly on microbial processes important in the biogeochemical cycles of the lake and stream ecosystem. Future studies should focus on obtaining quantitative information about the various microbial processes critical to ecosystem function by standardized methods so that results from various studies can be compared and evaluated for usefulness in long-term prediction.

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Vegetation structure and primary production in acidified lakes in southwestern Sweden

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Summary. Research during the last two decades has clearly pointed out that dramatic ecosystem changes have occured in lakes due to deposition of acid substances and decreased pH. Today a large number of lakes and running waters in Scandinavia are suffering biological damage with disappearing fish populations, overgrowth of the bottom by mosses and filamentous algae, reduced invertebrate fauna, increased transparency etc. – Of all documented biological changes the effect on macrophyte succession, in particular that of *Sphagnum,* is the most striking effect. Along with the growth of filamentous algae, these changes have brought about major shifts in the composition of the primary producers. The biomass in one lake was estimated to be 6.5 t (dry wt) corresponding to about 24 g m^{-2}, the relevant proportions being 52% for *Sphagnum,* 34% for *Lobelia* and 15% for *Isoetes.* Percentage production in the whole lake is 54% for *Sphagnum,* 29% for *Lobelia* and 17% for *Isoetes,* which gives an estimated production of 2.9 t yr^{-1} or 9 g m^{-2} yr^{-1}. *Sphagnum* is a recent flora element and its occurrence is related to the acidification of the lakes. The investigations also show that the growth of *Lobelia* is reduced in acid lakes compared to other oligotrophic lakes due to shading by the benthic mat of filamentous algae, detritus and *Sphagnum* debris. – One can conclude that there are several quantitative and qualitative changes in the macrophyte community which are related to acidification. One can also conclude that liming of lakes cause elimination of *Sphagnum* and some increase in the production of *Isoetids.*
Key words. Acidification; macrophytes; aquatic mosses; primary production.