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Effects of Acid on Plant Litter Decomposition in an Arctic Lake

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The effects of acid on the microbial decomposition of the dominant aquatic macrophyte (*Carex* sp.) in Toolik Lake, Alaska were studied in microcosms during the ice-free season of 1980. Toolik Lake is slightly buffered, deep, and very oligotrophic. Microbial activities, as determined by ^{14}C-acetate incorporation into extractable lipids, associated with *Carex* litter were significantly ($P < 0.01$) reduced within 2 days at pHs of 3.0 and 4.0, but not 5.0, 5.5, or 6.0, as compared with ambient controls (pH 7.4). ATP levels were significantly reduced at pH 3.0, but not at the other pHs tested. After 18 days, microbial activity significantly correlated with weight loss ($P < 0.05$), nitrogen content ($P < 0.01$), and C/N ratios ($P < 0.01$) of the litter, but did not correlate with ATP levels. Scanning electron microscopy of the litter surface revealed that the fungi present at ambient pH did not become dominant at pHs 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. Mineralization of *Carex* ^{14}C-lignin-labeled or ^{14}C-cellulose-labeled lignocellulose was reduced at pH 2.0, but not at pH 4.0, 5.0, or 6.0, compared with controls (pH 7). We concluded that if the pH of the water from this slightly buffered lake was sufficiently reduced, rates of litter decomposition would be significantly reduced.

Acid precipitation formed from atmospheric sulfur and nitrogen oxides originating primarily from industrial sources has been blamed for the acidification of many lakes in Scandinavia (1, 16, 24, 28), Canada (2, 7, 30, 33), and the United States (6, 25, 31). Recent air samplings near Barrow, Alaska and Mould Bay, Canada have shown that industrial pollutants, including sulfate, carbon, and trace elements, are transported to the arctic, particularly during the winter and spring (22, 29). Such pollutants tend to accumulate in snow packs during the winter, and cause rapid pH shocks to lakes and streams because of the highly acidic (pH 3.0; 32) runoff during the initial spring melt in Norway (14, 18, 19) and Canada (17). In addition, freshwater ecosystems in northern regions are particularly susceptible to the effects of acid precipitation since these waters commonly have little buffering capacity because of the composition of the underlying bedrock (10, 32).

Previous observations of acidified lakes and streams in Sweden (11–13), England (35), and New Hampshire (15) have suggested that decomposition rates in these systems were greatly reduced, as indicated by an increase in the accumulation of organic matter at the sediment surface. In some acidified lakes, the sediments have also become overgrown with dense mats of fungal hyphae (13). Low pH values decreased the rate of decomposition of birch leaves, oak leaves, and grasses in natural streams in Norway (37) and England (27), although no direct assessment of microbial activity was made. In laboratory experiments with inocula from natural waters, Bick and Drews (3) have found that the decomposition of peptone decreased with pH, that bacterial numbers declined slowly from pH 7 to 5 and rapidly from pH 5 to 3, and that the number of fungi increased at pH 4 and below. Traaen (36) has also found that dominance shifted from bacteria to fungi at pH 3.5 in laboratory respirometry experiments with glucose and glutamic acid as substrates.

The effects of acidic pH on the microbial decomposition of plant litter were studied during the summer of 1980 in microcosms from Toolik Lake, Alaska. Toolik Lake is a large, deep-water lake on the north slope of the Brooks Range of mountains within the Trans-Alaska Pipeline corridor (68° 38′N; 149° 38′W) (8, 9, 26). Like most other arctic lakes, it is very oligotrophic (9, 26), and its waters have very little buffering capacity (ca. 22 μg of $CaCO_3$ per liter total alkalinity). The microbial colonization and decomposition of *Carex aquatilis* (the dominant emergent macrophyte) in this lake have been described (8). Microbial decomposition of *Carex* in response to acidification was evaluated directly by determinations of weight loss and changes

in C/N ratios of the litter over time. Microbial biomass and activity associated with the litter were evaluated by the measurement of ATP concentrations and by determination of the rates of acetate incorporation into microbial lipids, respectively. In addition, the community structure of the microbiota on the litter surface was examined with scanning electron microscopy (SEM). The effects of acid on the mineralization of *Carex* lignocellulose were also examined.

MATERIALS AND METHODS

Preparation of plant litter. *Carex* leaves were collected from live green plants at the margins of Toolik Lake, Alaska, cut into 4-cm segments, and dried to constant weight at 60°C. For weight loss and chemical analyses, leaf segments were randomly selected, and 300- to 400-mg samples were sewn into litter bags (8 by 8 cm) constructed of 1.5-mm mesh fiber glass window screening. For microbiological analyses, leaf segments were selected for uniformity in width, thickness, and weight, and 20 such segments were placed into a litter bag.

Incubation and sampling. Clear plastic aquaria (29 by 19 by 13 cm) were filled with 4.0 liters of water taken from the surface of Toolik Lake and inoculated with 30 ml of a 2% (wt/vol) suspension of littoral sediments from Toolik Lake. Six litter bags were placed into each aquarium and allowed to colonize for 5 days before the start of the experiment. The aquaria were kept in an outdoor circulating water bath with water from Toolik Lake continuously pumped through the bath to maintain the aquaria at temperatures near those of the lake. The ambient littoral water temperatures ranged from 10 to 21°C.

At the start of the experiment, the litter bags were removed from these colonization aquaria and three litter bags (two for weight loss determinations and one for microbiological analyses) were randomly placed into each experimental aquarium containing 4.0 liters of water from Toolik Lake. The water in each aquarium was adjusted to one of the following pH values by using sulfuric acid: 6.0, 5.5, 5.0, 4.0, or 3.0. One aquarium received no additions of acid and served as an ambient (pH 7.1) control. All determinations of pH were made by means of a Digi-Sense LCD portable pH meter, model no. 5994-10 (Cole-Palmer Instrument Co., Chicago, Ill.). The incubation period was 2 days in one experiment and 18 days in another. During the 2-day experiment, the pH of each aquarium was monitored at 2- to 4-h intervals, except for one period of 14 h, and the pH in each aquarium was readjusted to its starting value if necessary (except for the ambient control). During the 18-day experiment, the pH was monitored on a daily basis, but no subsequent adjustments were made. Microbiological analyses were also made after the first 2 days of the 18-day experiment. Table 1 shows a comparison of the initial, 2-day, final (18-day), and mean pH values for this experiment.

At the conclusion of each of the pH experiments, the litter bags were rinsed briefly in lake water. For weight determination, litter bags were dried to constant weight at 60°C and reweighed. Litter for microbiological analyses was immediately cut into 1-cm segments, which were held in filter-sterilized (0.45 μm; Millipore Corp., Bedford, Mass.) lake water until analysis (not more than 15 min).

TABLE 1. Comparisons of pH values of lake water in experimental microcosms during 18 days of litter incubation at Toolik Lake, Alaska

Initial pH	pH value after 2 days	pH value after 18 days	Mean ± SD[a]
3.00	3.17	3.79	3.40 ± 0.23
4.00	4.42	4.78	4.51 ± 0.16
5.00	6.38	7.33	6.84 ± 0.49
5.50	6.74	7.40	7.00 ± 0.36
6.00	7.00	7.60	7.10 ± 0.30
7.10[b]	6.76	7.60	7.38 ± 0.27

[a] Calculated from daily pH determinations. Significant differences between the means of the pH treatments as determined by Tukey's honestly significant difference procedure (34):

ambient > 6.0 5.5 5.0 > 4.0 > 3.0.

Treatments not underlined are significantly ($P < 0.01$) different from each other.

[b] Untreated ambient control.

Microbiological and chemical analyses. (i) Acetate incorporation into microbial lipids. Ten 1-cm leaf segments were placed in 2.0 ml of filter-sterilized (0.45 μm) lakewater in a 20-ml glass scintillation vial and incubated with 0.1 ml of sodium [1-^{14}C]acetate (1.11 μCi; 0.036 μmol) for 2 h. Lipids were extracted by a modification of the method of Bligh and Dyer (4) in 5 ml of methanol and 2.5 ml of chloroform as described previously (26). Radioactivity in the lipid fraction was counted by liquid scintillation counting. Values are reported as dpm [^{14}C]acetate incorporated per hour per 1-cm leaf segment. Data were analyzed by a *t*-test and analysis of variance.

(ii) ATP. Extraction of ATP was conducted by the method of Bulleid (5), which was adapted for use with plant litter as described previously (26). Twelve 1-cm leaf segments were extracted in 8 ml of boiling McIlvaine buffer (0.04 M Na_2HPO_3 adjusted to pH 7.70 with 0.02 M citric acid) for 1 min. ATP was quantified by the luciferin-luciferase bioluminescence assay (21). ATP content, expressed as nanograms per 4-cm segment, was calculated based on an ATP (FF-ATP; Sigma Chemical Co., St. Louis, Mo.) standard curve and the subtraction of blanks, which were extracted and analyzed concurrently with each set of samples. Internal ATP standards were used to estimate the efficiency of ATP recovery and quantification, which was approximately 70 to 90%. Data were evaluated with a *t*-test and analysis of variance.

(iii) SEM. Replicate leaf segments were fixed for 60 min in 3% glutaraldehyde (Eastman Kodak Co., Rochester, N.Y.) in 0.1 M phosphate buffer (pH 7.4). The litter was then washed three times in buffer and in distilled water, dehydrated sequentially in 30, 50, 70, 90, 95, and 100% ethanol, and washed two more times in 100% ethanol (10 min per wash). The litter was fixed and dehydrated in the field immediately after sampling and was stored at −20°C until further preparation. Dehydrated samples were dried at the critical point with liquid carbon dioxide in a pressure bomb (Parr Instruments, Moline, Ill.) or in a critical-point drying

apparatus (Penton Vacuum, model DCP-1), mounted onto SEM stubs with silver conducting paint, and coated with 50 nm of gold by direct-current sputtering (ISI PE-5000 sputter coater; International Scientific Instruments, Mountain View, Calif.). Samples were examined and photographed on an ISI Mini-SEM, model MSM-2. The entire ventral surface of each leaf segment was examined under low power (100 to 200 ×), and several representative areas were examined at higher powers. Micrographs were taken with Polaroid film, type 665. Conclusions about the microbial community were based on the examination of multiple leaf segments, and the areas photographed were determined to be representative of the overall community structure.

(iv) Carbon and nitrogen. Approximately 1 to 2 mg of dried *Carex* leaf litter were ground to a fine powder, combusted, and analysed in a Carlo Erba element analyzer with cysteine as the standard. Values reported are a mean of three replicates.

Lignocellulose mineralization. The cellulose and lignin components of *Carex* lignocellulose were specifically labeled with D-[*U*-^{14}C]glucose or L-[*U*-^{14}C]phenylalanine, respectively, as described by Federle and Vestal (9). The labeled substrates (10 mg) were placed into 38-ml glass serum vials and incubated with 5.0 ml of a 2% (wt/vol) suspension of littoral sediments from Toolik Lake. To determine the effects of pH, triplicate samples were adjusted to pH 6.0, 5.0, 4.0, or 2.0. Abiotic controls contained 20% (vol/vol) formaldehyde. The volume of the head space in the vials (33 ml) was adequate to prevent the aqueous layer from becoming anaerobic during the incubation period (9), although this could not be determined directly. After 21 days of incubation in the dark at 10°C, $^{14}CO_2$ was collected and quantified as previously described (9). Values are reported as the percentage of ^{14}C-lignin-labeled or ^{14}C-cellulose-labeled lignocellulose mineralized to $^{14}CO_2$. Statistical significance was determined by the *t* test.

RESULTS

Microbial activities on leaf litter. Differences in percent weight loss were found among the various pH treatments after 18 days, with weight loss generally declining with pH (Fig. 1). No differences could be detected after only 2 days of incubation, however. The *Carex* leaf litter exposed to pH 3.0 for 18 days exhibited significantly ($P < 0.05$) less weight loss than did litter incubated in ambient pH (pH 7.4) lake water. The maximum difference in weight loss was that between pH 3.0 and the ambient pH (20%). The C/N ratios of the litter also declined with decreasing pH (Fig. 1), with those of the litter incubated at pH 3.0, 4.0, and 5.0 being significantly ($P < 0.01$) lower than that of the ambient control. The C/N ratios were significantly ($P < 0.02$) correlated with weight loss ($r = 0.8256$). C/N ratios also correlated significantly ($P < 0.01$) with the nitrogen content of the litter ($r = -0.9936$), whereas the carbon content remained relatively unchanged.

Significant ($P < 0.01$) reduction in activity was seen only at pH 4.0 or 3.0 after 2 days of incubation, whether the pH was adjusted only initially (Fig. 2) or at more frequent intervals. The rate of acetate incorporation into lipids was significantly less ($P < 0.05$) on litter incubated in lake water adjusted to pH 5.0 or less than at the

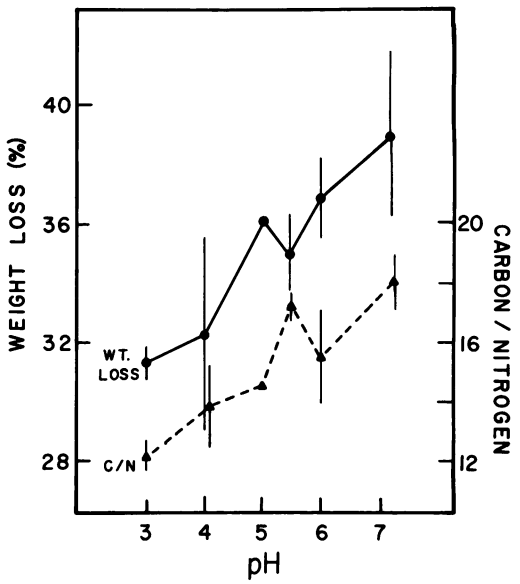

FIG. 1. Weight loss and C/N ratios of *Carex* litter after 18 days of incubation in water from Toolik Lake initially adjusted to various pH values with sulfuric acid. Values shown are a mean ± one standard deviation ($n = 2$ for weight loss, $n = 3$ for C/N ratios).

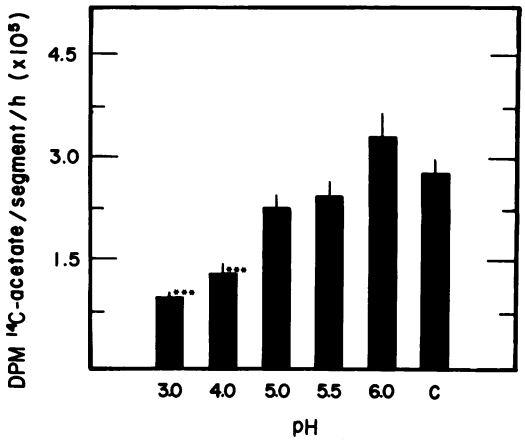

FIG. 2. Metabolic activity of the *Carex* litter microbiota measured as the rate of acetate incorporation into lipids after incubation for 2 days in water from Toolik Lake initially adjusted to various pH values. Values shown are a mean ± one standard deviation ($n = 3$). ***, $P < 0.01$ compared with ambient (pH 7.1) controls (C).

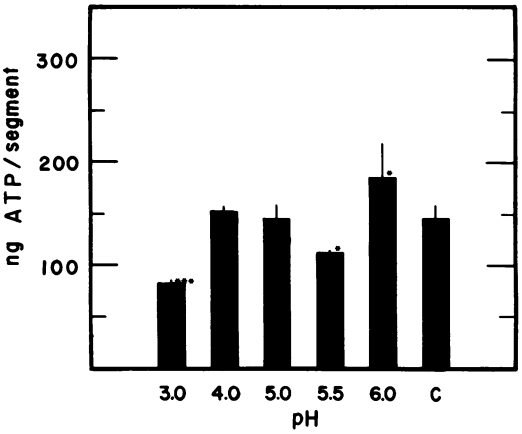

FIG. 3. ATP extracted from *Carex* leaf litter after incubation for 2 days in water from Toolik Lake initially adjusted to various pH values. Data shown are a mean ± one standard deviation. *, $P < 0.05$; ***, $P < 0.01$ compared with ambient (pH 7.1) controls (C).

ambient pH (7.1) after 18 days of incubation. The pH 5.0 treatment showed 36% less activity than did the ambient control, whereas the activity of the pH 4.0 and 3.0 treatments were reduced by 61 and 73%, respectively. No significant differences in activity were seen between pH treatments of 5.5 or 6.0 and the ambient levels after 18 days.

After 2 or 18 days of incubation at various pH values, the ATP concentrations associated with decomposing *Carex* litter showed no regular pattern with pH. From pH 7.1 to 4.0, levels of ATP fluctuated with decreasing pH after 2 days, but at pH 3.0 ATP was significantly ($P < 0.01$) reduced compared with ambient pH controls when the pH was adjusted only initially (Fig. 3) and when it was adjusted at frequent intervals. After 18 days of incubation, litter exposed to lake water initially adjusted to pH 6.0, 5.5, or 5.0 showed no significant differences in ATP levels between treatments, but litter exposed to pH 4.0 had significantly ($P < 0.05$) less ATP than did these treatments.

A correlation analysis revealed that the changes in weight loss and C/N were correlated with microbial activity. Acetate incorporation into microbial lipids significantly correlated with weight loss ($P < 0.05$; $r = 0.8541$), C/N ratios ($P < 0.01$; $r = 0.9805$), and nitrogen content ($P < 0.01$; $r = -0.9831$) of the litter. ATP levels, however, did not significantly correlate with any of these measurements.

SEM. SEM of the litter after 18 days of incubation under various pH regimes revealed differences in apparent numbers and types of organisms associated with the litter. The samples incubated under ambient pH conditions (Fig. 4, B and C) appeared to be heavily colonized with a variety of types of microorganisms, including bacteria, large filaments and spores or spore-bearing bodies, smaller filaments, some of which appeared to be actinomycete-like, and a variety of large and small pennate and centric diatoms. The surface of the leaf was largely obscured in many areas by dense accumulations of extracellular slime. Samples incubated in lake water that was initially adjusted to pH 6.0 showed no obvious differences in colonization compared with the ambient pH samples. In samples from the pH 5.0 microcosm (Fig. 5A), the litter was also heavily colonized, but the overall abundance of large filaments and diatoms relative to bacteria appeared to be less than in the ambient pH samples. Several smaller fungal- and actinomycete-like filaments were apparent, and the extracellular slime material was also present. The litter exposed to the pH 5.5 treatment looked very similar to the pH 5.0 samples. The surface of the litter that was incubated in lake water initially adjusted to pH 4.0 (Fig. 5B and C) or 3.0 (Fig. 5D) was, however, strikingly different in appearance. The litter in these treatments supported relatively little microbial growth compared with all other samples. The pH 4.0 samples had fewer fungal- and actinomycete-like filaments, although some fungal spores were present, primarily concentrated in localized areas on the litter surface. Far fewer bacteria could be seen than on the previously described samples, and very little of the extracellular slime was present (Fig. 5C) compared with the samples incubated in ambient-pH lake water (Fig. 4C). The pH 3.0 samples appeared to be even less colonized than the pH 4.0 samples, with fewer bacteria and only very rare, short filaments present. No diatoms were seen on either the pH 4.0 or 3.0 samples.

Lignocellulose mineralization. Only the pH 2.0 treatment had a significant ($P < 0.01$) effect on the rate of mineralization of ^{14}C-lignin-labeled or ^{14}C-cellulose-labeled lignocellulose. There were no significant differences between the rates of mineralization of lignocellulose labeled with [^{14}C]lignin when the sediment suspensions were initially adjusted to pH 6.0, 5.0, or 4.0 or were not adjusted (control). In the pH 2.0 treatment, however, only 0.41% of the label appeared as $^{14}CO_2$ after 21 days of incubation, a reduction of 94% compared with controls. This value was comparable with an inhibition of 94% in the abiotic controls.

Similarly, only the pH 2.0 treatment had a significant effect on the rate of mineralization of lignocellulose labeled with [^{14}C]cellulose ($P < 0.01$). At pH 2.0, only 1.94% of the label appeared as $^{14}CO_2$, representing an inhibition of 88% compared with controls. In this case, abiot-

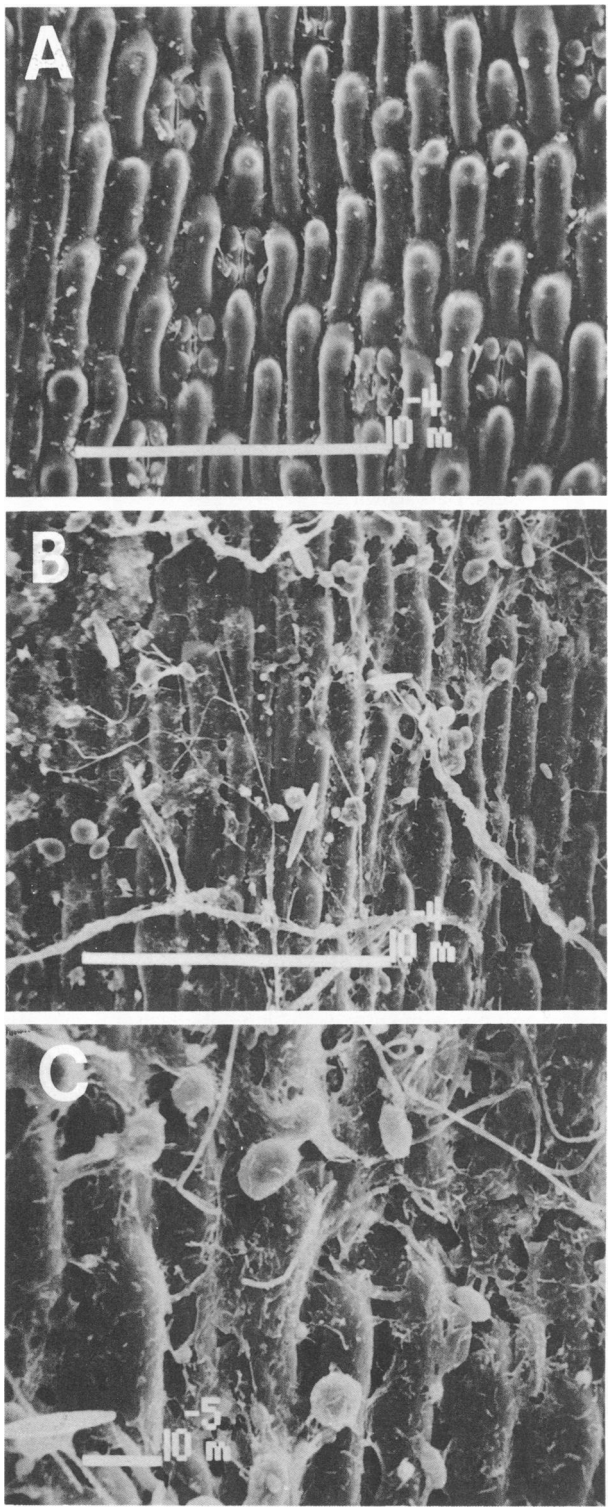

FIG. 4. Scanning electron micrographs of *Carex* leaf litter (A) at the beginning of the incubation and (B and C) after 18 days in water from Toolik Lake at ambient pH (7.4).

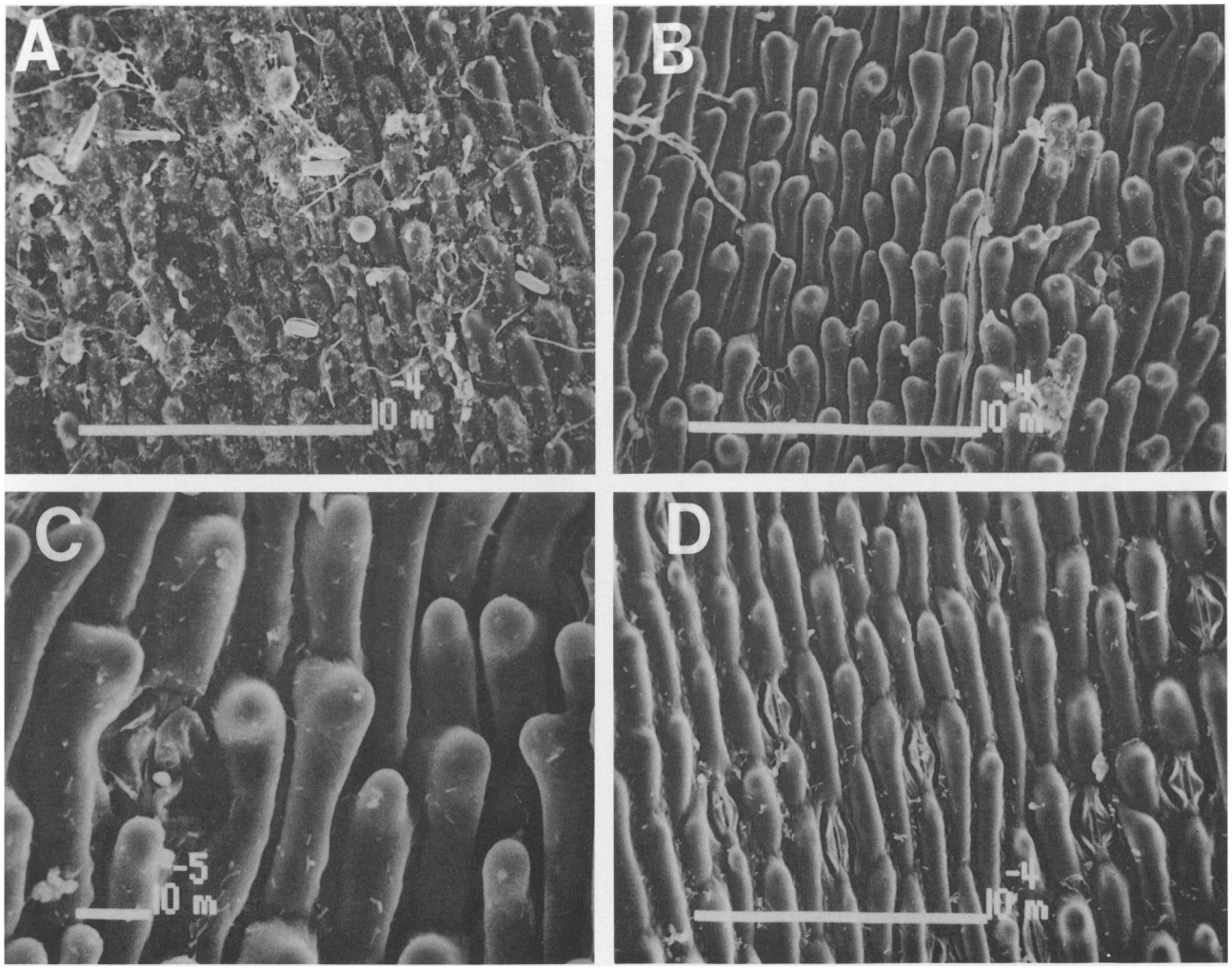

FIG. 5. Scanning electron micrographs of *Carex* leaf litter incubated for 18 days in water from Toolik Lake initially adjusted to pH 5.0 (A), 4.0 (B and C), or 3.0 (D).

ic controls were inhibited by 98% compared with untreated controls.

DISCUSSION

In these microcosm experiments, reductions below pH 5.0 in the pH of lake water were shown to have increasingly dramatic effects on the microbial colonization and decomposition of *Carex* leaf litter. Microbial activity, measured as the rate of acetate incorporation into microbial lipid, was significantly inhibited at pH 4.0 or 3.0 after 2 days of incubation and at pH 5.0, 4.0, or 3.0 after 18 days of incubation. Likewise, Laake (23) has found glucose utilization over sediment cores to be inhibited by as much as 98% as the pH was lowered from 6 to 5. No regular trends in biomass, as measured by ATP concentrations, could be associated with decreasing pH, however. Determinations of percent weight loss, C/N, and examination by SEM revealed dramatic differences in the characteristics of the litter and its associated microbiota after 18 days of incubation in acidic lake water as opposed to untreated lake water.

It appears, on the basis of trends in percent weight loss and C/N ratios, that *Carex* litter was degraded at a slower rate at low pH than under ambient pH conditions. Weight loss was significantly ($P < 0.05$) less at pH 3.0 than at ambient pH levels, as has been found by Traaen (36) in litter bag and laboratory experiments. In addition, C/N ratios at pH 5.0 and below were significantly ($P < 0.01$) lower than those for the ambient controls.

A correlation analysis revealed that these decompositional changes in the litter with pH were related to differences in microbial activity. The C/N ratios were highly correlated with %N, whereas %C remained fairly constant with varying pH. The observed differences in C/N ratios can therefore be attributed primarily to changes in nitrogen content. However, as also indicated in work with hydrocarbons (26), ATP does not appear to be a good indicator of microbial biomass or activity when the microbial community is undergoing certain environmental perturbations or other types of stress (20). Although weight loss was significantly less at pH 3.0 than at ambient pH, microbial activity appears to be a more sensitive indicator of perturbational effects on the microbial community, especially during short periods of time when no differences in weight loss between treatments can be detected. Qualitative differences in the microbial community structure were observed by SEM. On the ambient-pH and pH 6.0 samples incubated for 18 days, an abundant and diverse microbial community was observed. Fungi and diatoms appeared to gradually decline in numbers at pH 5.5 and 5.0 and were almost totally absent at pH 4.0 and 3.0. It was surprising that fungal forms did not come to dominate the community at low pH, as has been reported by other investigators (3, 15, 36). These investigators were, however, studying the decomposition of simple substrates in laboratory systems (3, 36) or surfaces in a stream (15), rather than a complex substrate such as leaf litter. Only bacteria and a few very rare fungal or actinomycete filament fragments were seen at pH 3.0 on *Carex* leaf litter.

Lignocellulose mineralization was also found to be sensitive to the effects of acidification. The lignin component of the lignocellulose was apparently more sensitive to these perturbational effects than the cellulose component. Mineralization of ^{14}C-lignin-labeled or ^{14}C-cellulose-labeled lignocellulose was not significantly affected by changes in pH until the pH was lowered to 2.0. However, no samples were tested between pH 4.0 and 2.0, so the actual pH limit for these effects may be within this range. Once again, it should be considered that in this experiment the pH values of each of the treatments were adjusted only at the beginning of the 21-day incubation period, and are likely to have undergone some changes during this period.

The effects of acidification on microbial activity and colonization in these microcosm experiments seem to be rapid. Significant differences in activity (acetate incorporation) and colonization (as seen by SEM) were found within 2 days after the pH was lowered to below 5.0, whether the pH was readjusted frequently or whether it was adjusted only at the start of the experiment. After 18 days of incubation, little or no recovery of microbial activity and colonization was seen at pHs of 3.0 or 4.0. Acid appeared to have little or no effect on the microbial community in the pH 5.0, 5.5, and 6.0 treatments, probably because of the rapid recovery of the lake water to near ambient pH levels in these treatments (Table 1). This can be particularly seen in the scanning electron micrographs, where the pH 3.0 and 4.0 treatments exhibited relatively little microbial biomass on the leaf surface compared with the pH 5.0, 5.5, 6.0, and ambient-pH treatments, which were similar in degrees of colonization. Thus, the effects of acidification on the microbial community associated with plant litter and its decomposition appeared to be manifested rapidly, and if any recovery took place, it must have been slow. Although it is precarious to extrapolate data from microcosm experiments to whole lake systems, it seems quite possible that similar effects could occur in the lake if it became acidified. However, in the lake itself, there could be a greater opportunity for the selection of an acid-tolerant microbiota derived from allochthonous sources that could carry out decomposition at low pH. The findings reported

here take on importance when the effects of short-term, rapid influxes of acidic waters to natural aquatic systems, which frequently occur in many areas during the first flush of the spring snowmelt, are considered. Bicarbonate has a very long turnover time in poorly buffered lakes. Once the buffering capacity is exhausted, which in this experiment occurred only in the pH 3.0 and 4.0 treatments, it may take many years for the system to return to normal, even without additional acid perturbations.

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