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FOREWORD

The Northern Global Change Program meeting was held March 14-16, 1995, in Pittsburgh, Pennsylvania. Its purpose was to chronicle the research activities of the Northern Global Change Program over the past five years, and outline the implications of these research results for natural resource management. We thank the authors for their participation and for promptly submitting their papers in both paper and electronic form.

THE HOWLAND INTEGRATED FOREST STUDY (HIFS) - ECOSYSTEM RESEARCH ON ATMOSPHERIC
INFLUENCES GOVERNING FOREST FUNCTION

Ivan J. Fernandez, Lindsey E. Rustad, Jeffrey A. Simmons, and James W. McLaughlin¹

The Howland Integrated Forest Study (HIFS) was developed in a low elevation, commercial spruce-fir forest in east-central Maine, USA at approximately 60 m elevation on level topography. The site was established in the 1980's to evaluate the effects of atmospherically derived N and S on this important forest type through intensive studies of biogeochemical cycling. Since 1990 the program has developed a suite of studies designed to evaluate the influence of both the chemical and physical climate on Maine forests, including an ecosystem manipulation component. The current program includes (a) long-term intensive biogeochemical cycling measurements of major ecosystem pools and fluxes of elements, (b) a landscape-scale gradient study that examines the relationship between modern gradients in climate and ecosystem function, (c) an ecosystem manipulation that experimentally warms the forest floor to determine the effects of warming on critical soil processes, and (d) a modelling component to describe atmosphere-canopy interactions. Emphasis is on soil processes controlling carbon and nutrient cycling that include decomposition, nitrification, soil respiration, and fine root biomass production.

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BIOGEOCHEMICAL CYCLING OF CARBON, NITROGEN, AND SULFUR AT THE HOWLAND
INTEGRATED FOREST STUDY SITE, HOWLAND, MAINE

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Abstract: The biogeochemistry of C, N, and S was studied for six years at the Howland Integrated Forest Study (HIFS) site by measuring those constituents in major above- and below-ground pools and fluxes. Leaching losses of C from the solum were much less than CO₂ efflux, with a mean annual leaching rate of 31.2 kg ha⁻¹ yr⁻¹. Carbon return to the forest floor via litterfall and outputs via CO₂ efflux were relatively equal. Mean annual total (wet+plus) atmospheric deposition inputs were 5.51 kg ha⁻¹ yr⁻¹ for NO₃⁻-N, 2.64 kg ha⁻¹ yr⁻¹ for NH₄⁺-N, and 8.09 kg ha⁻¹ yr⁻¹ for SO₄²⁻-S; wet deposition inputs for C were 6.67 kg ha⁻¹ yr⁻¹. Sulfur-deposition, in the form of SO₂ dry deposition, and SO₄²⁻ in wet deposition showed significant decreasing temporal trends during the six year study period. There were no significant temporal trends for NO₃⁻ in neither dry nor wet deposition. Wet deposition of NH₄⁺, however, showed a significant decreasing pattern through the study period. Decreases in precipitation chemical flux was likely the result of decreases in precipitation volume through the study period because no significant decreases in concentration of SO₄²⁻ or NH₄⁺ occurred. There was a net ecosystem retention of NO₃⁻ and NH₄⁺, attributable to the N-deficiency of this forest. Mean annual input-output for SO₄²⁻, however, was near zero for the study period, indicating the conservative behavior of that ion in this ecosystem. Ongoing research is attempting to further define the temporal trends in C, N, and S cycling, and to determine the mechanisms controlling these characteristics including the effects of temperature and moisture.

INTRODUCTION

We have witnessed at least two areas of concern regarding forest ecosystem structure and function during the past two decades; acidic deposition from the 1970's through the 1980's, and global change from the mid 1980's through the present. While nitrogen (N) and sulfur (S) represent the clearest examples of an altered chemical climate to which forest ecosystems are now exposed, the past decade has also witnessed the emergence of widespread concern for the potential of global climate change to simultaneously alter the physical environment of forest ecosystems. Pastor and Post (1988) discussed various models that predict 2° to 4°C increases in global temperatures, and how this change may shift forest distribution and character depending upon related ecosystem conditions, such as water balance and N availability. In Maine, this could result in a northward migration of the southern extent of the spruce-fir forest type. Numerous key soil processes may be influenced by climate change that include organic matter decomposition, N mineralization, and nitrification that have been discussed in the literature (Anderson 1991; Van Cleve et al. 1990; McGuire et al. 1992; Rastetter et al. 1991, 1992).

The Howland Integrated Forest Study (HIFS) has been developed to examine the influences of N and S deposition, and climatic variations, on biogeochemical cycling in a representative, low elevation, commercial coniferous forest ecosystem of northern New England. The program has focused on the role of soil processes in ecosystem function, but includes a wide range of ecological investigations within the practical limits of time and resources.

The HIFS site originally served as the only low-elevation commercial spruce-fir forest site of the six sites in the Spruce-Fir Research Cooperative (SFRC) that was part of the national Forest Response Program (FRP) in the U.S. during the 1980's (Eager and Adams 1992). The HIFS program was also a non-funded cooperating site in the Electric Power Research Institute/Oak Ridge National Laboratory (EPRI/ORNL) Integrated Forest Study (IFS) during this period (Johnson and Lindberg 1992), and part of the U.S. Environmental Protection Agency's Mountain

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Cloud Chemistry Program (MCCP) for the intensive measurement of the chemical and physical climate exposures to forests. Numerous investigators from various institutions have utilized HIFS as part of their research programs, including the National Oceanic and Atmospheric Administration (NOAA), the U.S. Geological Survey (USGS), the USDA Forest Service (USDA FS), and the US Environmental Protection Agency (US EPA), as well as other universities. The National Aeronautics and Space Administration's (NASA) FIFE, FED, and BOREAS field campaigns have also included the HIFS site. During the 1990's a number of new research initiatives were developed as part of the USDA Forest Service's Northern Global Change Research Program (NGCRP) that were built on the foundation of the HIFS program. The purpose of this paper is to present some of the highlights of the biogeochemistry of C, N, and S cycling at the HIFS site from January, 1988 through December, 1993.

MATERIALS AND METHODS

Study Site: The HIFS site is located in east-central Maine within International Paper's Northern Experimental Forest (Fig. 1). The site includes two, 0.2-ha biogeochemical study plots and a 27 m tower that extends above the canopy equipped with meteorological and air pollution monitoring instrumentation. Selected stand characteristics are given in Table 1.

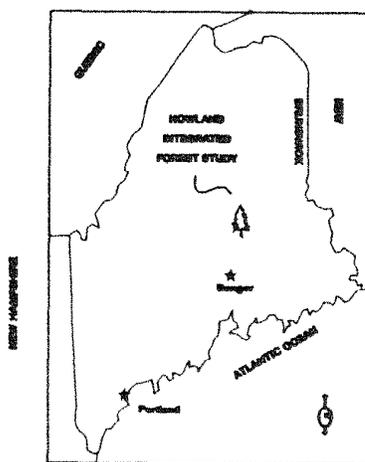


Figure 1.

Sample Collection: Precipitation was sampled weekly from January, 1988 through December, 1993 with a single wet-only Aerochem Metric® collector located in a forest clearing approximately 2 km east of the study site, in accordance with National Atmospheric Deposition Program protocol (Bigelow and Dossett 1988). Throughfall was sampled using two Aerochem Metric® collectors weekly and composited monthly. Chemical fluxes for incident precipitation were estimated as the product of weekly volume-weighted concentrations and hydrologic flux. Chemical fluxes in throughfall were estimated as the product of monthly volume-weighted concentrations and hydrologic flux. Further description of the sampling protocols are given in Lawrence and Fernandez (1991) and McLaughlin *et al.* (1995).

Air concentrations for vapor-phase SO_2 and HNO_3 , and fine-particle SO_4^{2-} and NO_3^- , were measured continuously from January, 1988 through December, 1993 on the meteorological tower 10 m above the forest canopy using filter packs consisting of three sequential filters (Teflon, nylon, and carbonate-treated cellulose) (Meyers *et al.* 1991). Dry deposition fluxes were estimated as the product of air concentrations and deposition velocities (V_d). Deposition velocities for vapors were estimated using the big-leaf model of Hicks *et al.* (1987) based on site-specific hourly meteorological measurements and canopy structure and physiological data. Deposition velocities for particles were

derived from site specific canopy structure data using the submicron radionuclide tracer methods of Bondietti et al. (1984).

Table 1. Selected stand characteristics for the HIFS site.

Location	45°10'N, 68°40'W
Growing Season (days)	120 to 160
Mean Annual Precipitation (mm)	1063
Mean January Temperature (°C)	-8.9
Mean July Temperature (°C)	20.1
Total Basal Area (m ²)	85
Overstory Vegetation (% basal area)	
Red spruce	50
White pine	22
Hemlock	13
Soils	Aquic Haplorthods Aeric Haplaquods

Soil solution was collected beneath the Oa horizon and from the middle of the Bs horizon using zero-tension lysimetry from six lysimeter stations on each plot. At each sampling station, three lysimeters (23.3 x 12.5 cm-pans) drained into one collection bottle for each horizon. Samples were collected monthly from January, 1988 through December, 1993. Chemical fluxes in the Bs horizon solution were calculated by multiplying monthly solution concentrations by the mean monthly water flux. Monthly water flux was estimated using the Priestly-Taylor equation modified for interception losses (Shuttleworth and Calder 1979; Spittlehouse 1985). Further description of the sample design are given in Fernandez et al. (1995)

Soil CO₂ efflux was measured every three weeks using the soda-lime technique (Edwards and Ross-Todd 1983) at three locations at each plot. Further description is given in Fernandez et al. (1993b). Soil sampling was conducted during 1987 and 1988 using quantitative pits. Twelve 71 cm x 71 cm x 1 m pits were excavated in 1987 (six per plot) and 12 in 1988 (six per plot) for a total of 24 pits (Fernandez et al. 1993a).

Analytical Procedures: Solutions were analyzed for pH, SO₄²⁻, NO₃⁻, NH₄⁺, and dissolved organic carbon (DOC). Prior to chemical analyses, solutions were passed through Whatman #42 filter paper. In addition, solutions for DOC analysis were passed through Whatman GF/F glass fiber filters. Sulfate and NO₃⁻ were measured using a Dionex Model 2000i/SP ion chromatograph. pH was measured potentiometrically using an Orion Model 701A pH meter. NH₄⁺ was measured by automated colorimetric phenate (American Public Health association 1981) using a Bran-Lubbe Traacs Model 800 autoanalyzer, and DOC was measured by ultraviolet (UV)/persulfate oxidation with infrared detection of liberated CO₂ (EPA 1992) using an Oceanographic Instrument (OI) Model 700 Total Organic Carbon Analyzer.

Soils were analyzed for total C and N using a Carlo-Erba CHN elemental analyzer, total S on a Leco Sulfur Determinator (SC 132), and phosphate-extractable ("adsorbed") SO₄²⁻ using ion chromatography.

Experimental Design and Statistical Analyses: The intent of this research is to provide an intensive case study of biogeochemical processes at the HIFS site, and to study the interactions of the soil-plant system with its chemical and physical climate. Temporal trends for the chemical constituents of precipitation, dry deposition, and throughfall were analyzed using the Mann-Kendall test for trend analysis (Gilbert 1987).

RESULTS AND DISCUSSION

Total C and N contents were greater in the mineral soil than the forest floor (Table 2), but the reverse was true for total S at the HIFS site. Total C, N, and S generally decreased with depth in the soil profile, with the exception of the albic horizon (E), whereas soil pH increased (Fig. 2). Adsorbed SO_4^{2-} , however, increased from the E to the Bs horizon, but then decreased in the BC and C horizons (Fig. 2). The vertical trends of total C, N, and S, are largely governed by organic matter (Fernandez *et al.* 1993a). Comparing the quantitative pit method with that of standard morphological sampling suggests that the latter tends to underestimate total C (Fernandez *et al.* 1993a), which may have important implications in evaluating the sequestering of C in forest soils of the northeastern U.S. Every 1 percent change in the soil coarse fragment estimate at the HIFS site is equivalent to approximately 1 metric ton of C and 31 kg of N per ha. Litterfall C return to the forest floor was 1,300 $\text{kg ha}^{-1} \text{ yr}^{-1}$, and was about 40-fold higher than C returned via throughfall DOC.

Table 2. Soil carbon, nitrogen, and sulfur contents at the HIFS site.

Constituent	Forest Floor	Mineral Soil
	kg ha^{-1}	
Total carbon	44,000	68,000
Total nitrogen	1,034	2,270
Total sulfur	130	840
Adsorbed sulfate	4	34

Fernandez *et al.* (1993b) reported that CO_2 efflux from the forest floor at the HIFS was surprisingly similar to that for selected deciduous or harvested forest sites in Maine, being roughly 2000 $\text{kg CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$. Carbon efflux as CO_2 was much greater than that lost through leaching. Carbon output through CO_2 and DOC flux was slightly greater than the amount of C returned to the soil through litterfall and throughfall DOC. These differences, however, are likely not significant.

Dry deposition of SO_4 , NO_3 , and NH_4 was comparable to wet deposition, suggesting that a simple doubling of wet deposition is a reasonable estimate of total deposition to the forest canopy for these ionic species (Table 3). There was a significant ($p < 0.05$) decreasing trend for SO_2 -S flux, but no significant ($p > 0.05$) pattern occurred for fine-particle SO_4^{2-} (Fig. 3a). Decreasing SO_2 deposition suggests that local S-emissions are probably declining since it is likely that long-range transported SO_2 would be oxidized to SO_4 in transit. Mean annual dry deposition of NO_3^- -N was $1.69 \pm 0.05 \text{ kg ha}^{-1} \text{ yr}^{-1}$ with HNO_3 vapors accounting for over 99% of the flux. Neither HNO_3 or fine-particle NO_3^- dry deposition showed significant ($p > 0.05$) temporal trends for the study period (Fig. 3a).

Table 3. Carbon, nitrogen, and sulfur fluxes for dry deposition, precipitation, throughfall, and soil solution in the Bs horizon at the HIFS site.

Constituent	Dry Deposition	Wet Deposition	Throughfall	Net Canopy Exchange	Bs Horizon Solution
	kg ha^{-1}				
SO_4^{2-} -S	3.45	4.64	8.96	0.87	8.74
NO_3^- -N	2.70	2.81	0.52	-4.99	0.04
NH_4^+ -N	1.54	1.26	0.26	-2.52	0.41
DOC-C	-	6.67	103	99	31.16

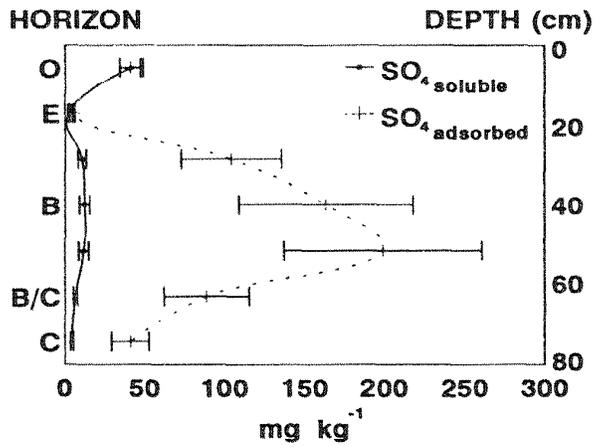
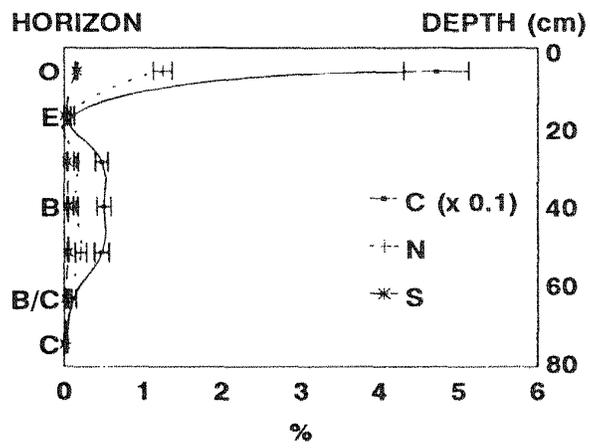
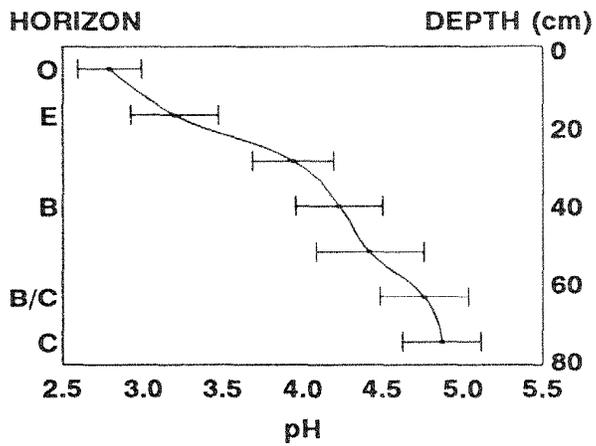


Figure 2. Vertical distribution of soil C, N, S, and pH at the HIFS site.

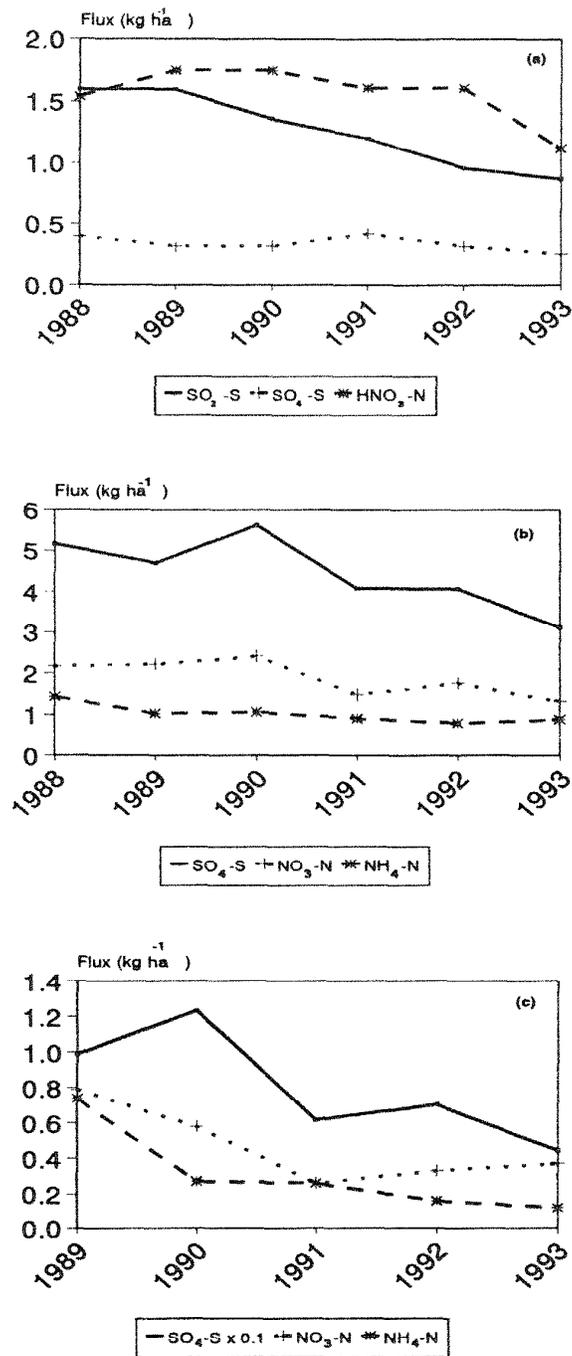


Figure 3. Temporal trends in atmospheric deposition of N and S at HIFS: (a) Dry Deposition, (b) Precipitation, (c) Throughfall. Data adapted from McLaughlin et al. (1995).

Mean annual wet deposition of SO_4^{2-} -S, NO_3^- -N, and NH_4^+ -N are shown in Table 3. Precipitation flux for SO_4^{2-} and NH_4^+ showed significant ($p < 0.05$) decreasing trends, while NO_3^- showed no significant ($p > 0.05$) temporal pattern (Fig. 3b). The decrease in flux for precipitation SO_4^{2-} , NH_4^+ , and H^+ was likely due to decreases in precipitation amount during the study period (Fig. 3b). McLaughlin et al. (1995) reported that there were no significant temporal patterns for precipitation SO_4^{2-} or NH_4^+ concentrations during the study period.

Sulfate and NH_4^+ throughfall deposition decreased significantly ($p < 0.05$) throughout the study period, while no significant trends occurred for NO_3^- (Fig. 3c). McLaughlin et al. (1995) also reported significant decreasing trends for throughfall concentrations of SO_4^{2-} , but not for NO_3^- nor NH_4^+ . Therefore, the decreasing NH_4^+ flux probably reflects decreasing throughfall amounts, whereas SO_4^{2-} decreases are likely the result of interactions between concentrations of those ions and throughfall amounts.

Mean annual net canopy exchange (NCE) for the study period indicated canopy uptake of N (Table 3) which is attributable to the N-deficiency of the HIFS site as suggested by Fernandez et al. (1990) based on foliar chemistry. Mean annual NCE of SO_4^{2-} , however, was near zero (Table 3) which is similar to other forest ecosystems in the United States.

Monomeric Al was 0.38 and 0.32 mg L^{-1} in the Oa and Bs horizon solutions, respectively. Organic Al was 0.30 and 0.16 mg L^{-1} in the Oa and Bs horizon solutions, respectively (Fernandez et al. 1995). Aluminum concentrations at the HIFS site are lower than that reported for other sites in the eastern U.S., and Ca/Al ratios do not suggest inhibition of Ca uptake by roots (Fernandez et al. 1995).

There was a net ecosystem retention of N at the HIFS site for the six-year study period (Fig. 4). Mean annual input-output for SO_4^{2-} , however, was near zero for the study period (Fig. 4), indicating the conservative behavior of SO_4^{2-} at HIFS (Lawrence and Fernandez 1991). The relatively high N-retention indicates efficient immobilization by vegetation and soil microflora. However, there were differences between the behavior of NO_3^- and NH_4^+ , although both ions showed net retention (Fig. 4). Total output of NO_3^- was only 1 percent of the total atmospheric deposition, with approximately 90 percent retained within the forest canopy. Ninety percent of the NO_3^- that reached the forest floor as throughfall was also retained within the soil. In contrast to NO_3^- , NH_4^+ had approximately a 1.5-fold higher flux from the Bs horizon as opposed to throughfall flux. However, the canopy retained about 90 percent of the total atmospheric NH_4^+ that was deposited to the canopy. The lack of a net retention of SO_4^{2-} at HIFS is also a common occurrence in a number of forest ecosystems in the U.S. Outputs of SO_4^{2-} from the Bs horizon decreased temporally (Fernandez et al. 1995), similarly as dry, wet, and throughfall fluxes reported in this study.

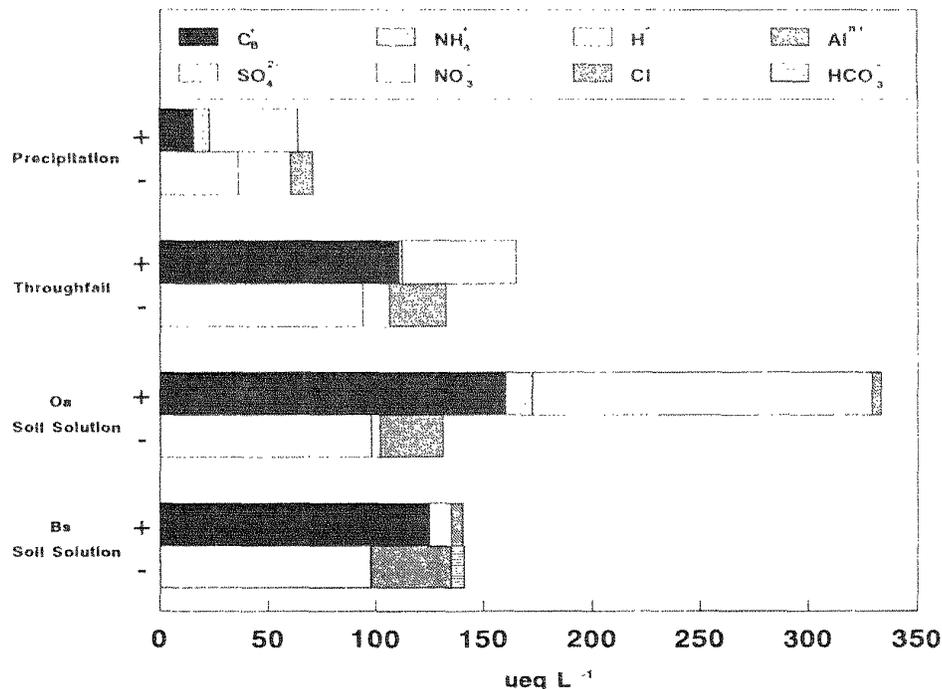


Figure 4. Solution migration through the forest canopy and soil at the HIFS (Lawrence and Fernandez 1991).

SUMMARY

Carbon and N contents were greater in the mineral soil compared to the forest floor. Total C, N, and S decreased with depth, in relation to organic matter, whereas adsorbed SO_4^{2-} increased with depth. Carbon return to the forest floor was greater for litterfall than that from throughfall DOC. Carbon dioxide represented the major C flux from the HIFS site.

There was a decline in S-loading, but not N-loading, to the HIFS site between 1988 and 1993. Declining S-loading was due to decreasing SO_2 , and may reflect trends in local SO_2 emissions for the state and region. Although little evidence of SO_4^{2-} net ecosystem retention was found, biological immobilization in the canopy and soil removed most atmospherically deposited inorganic N. Only through long-term, intensive investigations of biogeochemical processes at the HIFS site is it possible to define mechanisms controlling temporal trends in atmospheric deposition and their effects on forest biogeochemistry.

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ELEMENTAL CYCLING RESPONSE OF AN ADIRONDACK SUBALPINE SPRUCE-FIR FOREST TO ATMOSPHERIC AND ENVIRONMENTAL CHANGE

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Abstract: Patterns and trends in forest elemental cycling can become more apparent in the presence of atmospheric perturbations. High-elevation forests of the northeastern United States have received large amounts of atmospheric deposition of pollutants, which have altered natural elemental cycling and retention rates in a variety of ways. This study examined atmospheric deposition of nitrogen, sulfur and base cations, and their interactions in a high-elevation forest on Whiteface Mountain, New York. Eight years of elemental cycling data (1986-1993) have shown that at our main study site (1050-m elevation), atmospheric deposition of N was approximately $16.7 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, with 32 percent contributed by cloud water. Atmospheric deposition of S was $16.3 \text{ kg S ha}^{-1} \text{ yr}^{-1}$, with 37 percent contributed by cloud water. Total atmospheric inputs of nitrogen and sulfur to the forest canopy increased by a factor of four and five, respectively, over the elevational range of 600 to 1275 m, largely due to the increased importance of cloud water deposition at high elevations. At 1050-m elevation, analyses of total ecosystem inventories and cycling revealed that nitrogen and potassium are conserved or retained in the ecosystem while sulfur, calcium and magnesium show losses in a relatively undisturbed spruce-fir-birch ecosystem.

INTRODUCTION

High elevation forests in the northeastern USA currently receive higher pollutant deposition inputs than most other locations in the country (Lovett 1994). Deposition rates were much lower earlier in this century, increased in the 1950s through 1980s, and have begun to decrease over the last ten years or so, depending on the element (NAS, 1986; Hedin et al. 1994; Miller and Friedland 1994). Atmospheric deposition has been shown and has been hypothesized to cause a variety of direct and indirect effects on forested ecosystems (Taylor et al. 1994). Given that elemental deposition rates will continue to change over the coming decades (EPA 1995), it is important to understand the role of atmospheric deposition in elemental cycling in forested ecosystems. A high-elevation site in the Adirondacks is an ideal location to study these projected changes and the potential effects of such changes because these types of sites: (1) receive relatively large pollutant inputs (Miller et al. 1993b); (2) already show some signs of assimilating atmospheric pollutants (Friedland et al. 1991; McNulty et al. 1991); and (3) have undergone significant red spruce decline, partly as a result of air pollution (Eagar and Adams 1992) which has changed the composition of the forest (Scott et al. 1984; Friedland 1989; Battles et al. 1992).

In order to ascertain the effects of atmospheric deposition of pollutants on a high-elevation forested ecosystem, we have established atmospheric deposition and nutrient cycling monitoring plots on Whiteface Mountain, New York. These include two towers for atmospheric measurements, four 0.1 hectare permanent plots and two adjacent monitoring plots where litterfall, throughfall and soil water collectors have been installed. This project is the core effort of a series of projects funded by the USDA Forest Service Northern Global Change Research Program, NSF and the Andrew W. Mellon Foundation. As such, a primary objective of this project has been to provide a comprehensive evaluation of atmospheric deposition and nutrient cycling in high-elevation forests that can serve as a foundation for other process-level research, including branch and tree fertilizations.

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RESULTS AND DISCUSSION

Ecosystem Mass Balance

An eight-year average of wet (a combination of rain, snow and cloud water) and dry input delivered to the forest illustrates that input is dominated by hydrogen ion, ammonium, nitrate and sulfate (Fig. 1). This is similar to deposition in many forests in the Northeast, but total deposition amounts are higher here because the site is at a higher elevation and is immersed in clouds as much as 10 percent of the year (Miller et al. 1993c). No element shows constant input and output during the eight years of measurements (Fig. 1). Calcium and magnesium inputs are fairly constant during the eight years of our study, although there is a long-term trend of decreasing calcium inputs in the Northeast (Hedin et al. 1994). Hydrogen ion and ammonium outputs are nearly constant during the study, and ammonium outputs are virtually zero. Nitrate output varies from year to year but is definitely greater than zero. High ammonium output is thought to be one indication of the later stages of excess nitrogen storage in an ecosystem, also called nitrogen saturation (Aber et al. 1989). Apparently, this site is not in the later stages of nitrogen saturation. But the continual loss of nitrate suggests that the site might be in early stages of nitrogen saturation (Aber et al. 1989). Hedin et al. (1995) suggest that the loss of nitrate is an indicator of a polluted system.

Elements can be grouped into three categories based on their behavior: (1) sulfate and potassium outputs appear to be sensitive to inputs of sulfate and potassium, respectively; (2) hydrogen, ammonium and nitrate outputs appear to be insensitive to inputs of these same ions; and (3) the outputs of calcium and sulfate appear to be linked to one another (Fig. 1). These patterns suggest that the outputs of sulfate and potassium are in part regulated by inputs of those ions and of hydrogen ion. Both calcium and sulfate outputs are greatest in the 1989 water year, when water deposition is approximately 60 percent greater than any other year of the study and hydrogen ion input is greatest. Apparently, leaching of calcium and sulfate pools is at least partially dependent on water flow. This pattern of increased leaching with increased water flow is seen for nitrate but not sulfate in streams in the Catskills in 1989 (Murdoch and Stoddard 1992), and suggests there is a relatively labile pool of exchangeable sulfate and calcium (e.g. Johnson et al. 1991). Outputs of ammonium and nitrate are apparently insensitive to the size of the input presumably because they are in relatively high biological demand. However, nitrate output was high in at least one year, 1987 (Fig. 1B), and is significantly higher during the non growing season (data not shown), suggesting that plants are using most of the nitrogen available during the growing season but that atmospheric deposition provides excess nitrate to the system at other times of the year.

In a previous study (Johnson et al. 1994), we presented hydrogen ion and calcium budgets for this forest and suggested that current calcium loss rates are higher than historical loss rates. However, the same article suggests that hydrogen ion accumulation will be offset by mineral soil weathering (which consumes hydrogen ion). The only pool that is questionable in terms of sustainability is the forest floor calcium pool.

In Miller et al. (1993a), we show that as much as 60 percent of the forest floor calcium pool is derived from atmospheric calcium. Given that calcium outputs appear to be influenced by inputs of hydrogen and outputs of sulfate (Fig. 1A,E,G), and since calcium deposition to the northeast has been decreasing (Hedin et al. 1994), it is reasonable to be concerned about calcium limitations in the future. This situation could be exacerbated by increased nitrogen deposition, which may occur; and it could be partially ameliorated by reductions in sulfur deposition. The effect of increased temperature is much more difficult to predict. Thus, the specific nature of the environmental change over the next few decades will be critical in determining the future health of high elevation spruce-fir-birch forests.

Atmospheric Deposition

Inputs of elements such as sulfur and nitrogen increase by a factor of four and five, respectively, over the elevational range of 600 to 1275 m (Fig. 2; for nitrogen, data not shown). Steep gradients in wind speed and cloud immersions contribute to a nearly exponential increase in ion deposition by cloud water interception. Deposition rates are for simulations based on wind speeds representative of topographically sheltered inter-montane areas below 1000-m elevation (Miller et al. 1993b). Atmospheric inputs can vary significantly from year to year (Fig. 1) in forests subject to significant cloud water deposition; therefore, atmospheric influences on the nutrient cycling can be dynamic as well as chronic.

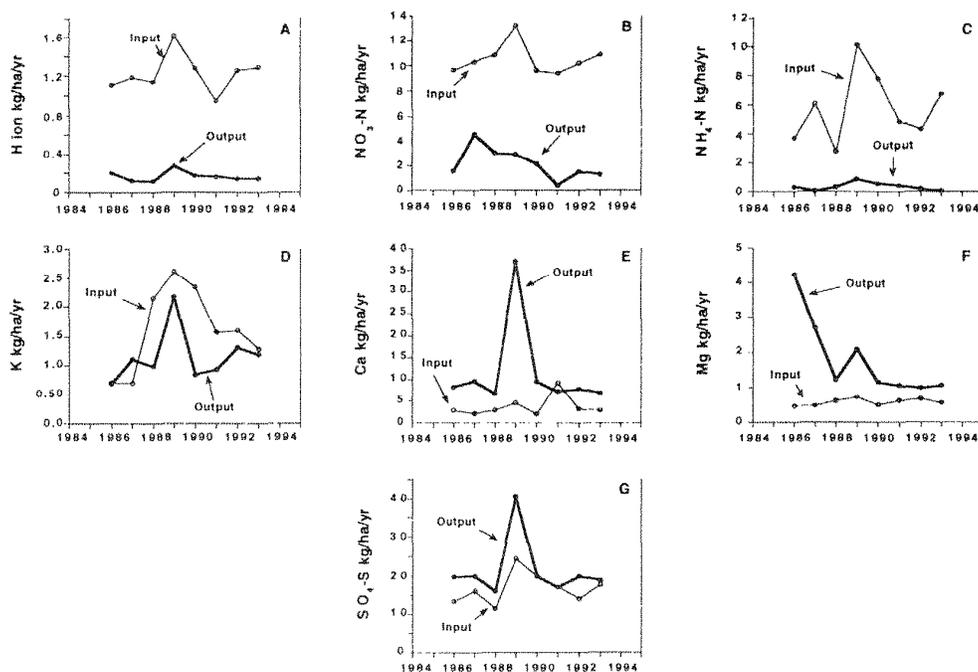


Fig. 1. Yearly mean inputs (precipitation + cloud water + dry deposition) and outputs (Bw horizon soil water) from 1025-m elevation on Whiteface Mountain, New York between 1986 and 1993. A given year (i.e., 1986) represents Water Year 1986 (June 1, 1986-May 31, 1987). Source: A.J. Friedland and E.K. Miller, unpublished data.

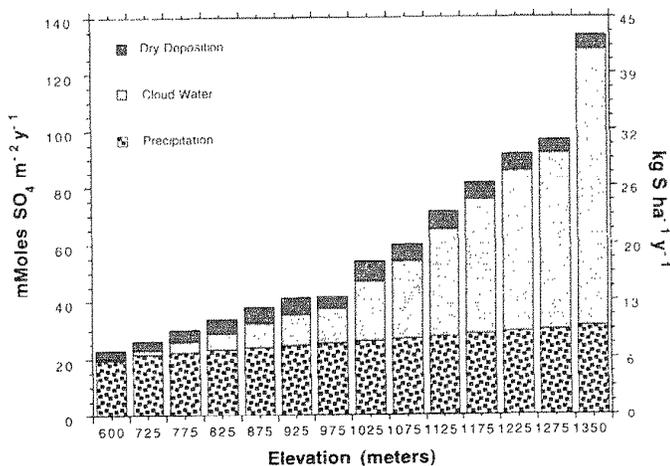


Fig. 2. Model estimates of the total annual deposition of sulfur to the forest canopy on Whiteface Mt., NY. Deposition rates are for model simulations based on wind speeds representative of topographically sheltered inter-montane areas below 1000 m. Estimates of deposition rates to low elevation forests on more exposed mountain slopes and in the low elevation terrain surrounding the high peak region are indicated by the open bars. Source: Miller et al. 1993b.

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INTERNAL UPTAKE AND ASSIMILATION OF GASEOUS NITRIC ACID BY WESTERN FOREST TREE
SPECIES

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A nitric acid gas analysis system was designed, tested, and calibrated to measure nitric acid deposition to forest tree species. Two modified Monitor Labs 8440 NO, NO_x, NO₂ analyzers were used in parallel to measure the nitric acid deposited onto leaf surfaces of ponderosa pine (*Pinus ponderosa*) and California black oak (*Quercus kelloggii*) seedlings. Measurements were made during 24 hr exposures in which plants were kept in dark, temperature controlled growth chambers. The broadleaf oaks had much higher rates of deposition than pines on a leaf area basis: 4.7 nmoles HNO₃ m⁻² s⁻¹ for oaks, and 0.6 nmoles HNO₃ m⁻² s⁻¹ for pines. There was good agreement in HNO₃ deposition calculated from the nitric acid gas analysis system and that measured by nitrate analysis of leaf washings.

Alternate light with dark period experiments (48 hr fumigation) showed that nitric acid deposition was about 2X greater than fumigation under darkness calculated by gas analysis and ¹⁵N labeling methods. Nitrate reductase activity was used as an indicator of internal uptake and assimilation of HNO₃ into the leaf foliage. The enzyme activity increased in the alternate light/dark fumigated plants 10X greater than the unfumigated control. Preliminary experiments on the epicuticular waxes showed increases in the proportion of free fatty acids and alkyl esters, while estolide fractions decreased. These results indicate that nitric acid vapor may decrease the cuticular resistance to the nitric acid uptake into the leaf.

This HNO₃ analysis system is a significant advancement into nitric acid research and has the potential to measure the physiological response of plants to nitric acid exposures.

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CLIMATIC AND POLLUTION INFLUENCES ON ECOSYSTEM PROCESSES IN NORTHERN HARDWOOD FORESTS

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OVERVIEW AND OBJECTIVES

The Michigan gradient study was established in 1987 to examine the effects of climate and atmospheric deposition on forest productivity and ecosystem processes in the Great Lakes region. Four intensively-monitored northern hardwood study sites are located along a climatic and pollutant gradient extending from southern lower Michigan to northwestern upper Michigan. The project continues today, with the following overall objectives: (1) to continue measuring key ecosystem variables at four sites; (2) to understand how carbon allocation, nutrient cycling, and forest productivity respond to differing levels of temperature, moisture availability, and atmospheric deposition; and (3) to quantify sources of temporal and spatial variability in ecosystem processes for use in regional modeling efforts. Additional research designed to investigate the effects of soil temperature and N availability on belowground processes was initiated at the sites in 1993. Objectives of this research are: (1) to quantify relationships between soil temperature and fine root longevity, and root system construction and maintenance costs; (2) to determine how soil nitrogen supply affects fine root construction and maintenance costs, and lifespan; (3) to understand the effects of soil temperature and nitrogen availability on soil respiration; and (4) to quantify the contributions of root and microbial respiration to respiratory flux from the soil.

GENERAL APPROACH

The four study sites extend across a 600 km climate/pollutant gradient in Michigan (Figure 1). All sites are 80 year old second-growth northern hardwood stands dominated by sugar maple (*Acer saccharum* Marsh.). Mean annual temperature increases from 4.2°C at Site 1 to 7.6°C at Site 4. Total annual wet plus dry deposition of NO₃-N increases from 4 kg ha⁻¹ to 8 kg ha⁻¹ between Sites 1 and 4 (MacDonald et al. 1992), with similar gradients existing for SO₄ and H⁺. At each site, three 30 m by 30 m study plots were established in 1987.



Figure 1. Study site locations.

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The influence of climate on ecosystem processes is being assessed by determining the effects of yearly variation in precipitation and temperature within sites. As length of record becomes sufficient, individual sites are compared to determine if they respond in the same way to climatic variation. The impact of pollutant deposition along the gradient is addressed by comparing rates of ecosystem processes at sites receiving historically different levels of pollutants. Our long-term records of key variables along the climatic/pollutant gradient give us a unique opportunity to study ecosystem processes under real-world environmental stress in an area that is predicted to be greatly affected should global change occur.

Our long-term data base includes the following parameters: forest productivity (basal area growth, height growth, biomass increment, individual tree vigor and mortality), wet deposition, soil solution chemistry, soil and air temperature, soil moisture availability, above and below-ground litter inputs, seed production, leaf and fine root nutrient contents, leaf area index, canopy transmittance, insect defoliation, and soil chemical and physical properties. Variables are measured on different time steps ranging from hourly measurements of soil temperature to annual measurements of tree diameter growth. Some measurements have been continuously recorded since 1987. In many instances, six to eight years of data exist. Measurements of soil and root respiration, soil gas fluxes, leaf and root nitrate reductase activity, microbial biomass, N mineralization, nitrification, and fine root turnover were initiated in the fall of 1993.

PROJECT STATUS

When we began our study, many believed that the substitution of space for time would be confounded by geographic differences in climate and soil, and temporal variation in variables such as leaf area and N flux in litterfall. Measurements along the gradient of insect defoliation, stand leaf area, foliar litter production, net primary productivity, production of flowers and seeds, and nutrient flux since 1987 have, in fact, demonstrated significant year-to-year variability within and among sites (Burton et al. 1991a; Pregitzer and Burton 1991; Pregitzer et al. 1992; Burton et al. 1993; Reed et al. 1994c). Fluxes of reproductive litter and foliar litter were negatively correlated at the stand level, suggesting a direct tradeoff between production of leaf biomass and reproductive biomass (Pregitzer and Burton 1991). Bumper sugar maple seed crops and insect defoliation had large impacts on nutrient cycling, (Pregitzer and Burton 1991, Burton et al. 1993). But in spite of such spatial and temporal variation, there was clear evidence that pollutant deposition had altered vegetation and soil processes along the gradient. MacDonald et al. (1992, 1994) documented a direct relationship between soil solution SO_4^{2-} concentration and flux and SO_4^{2-} deposition. Leaching losses of Ca^{2+} and Mg^{2+} exceeded inputs for all sites along the gradient. Elevated losses of Ca^{2+} and preferential leaching of Mg^{2+} from high deposition sites with coarse textured soils suggest that depletion of cation reserves at poorly buffered sites remain a likely consequence of pollutant deposition. Liechty et al. (1993) measured increased foliar leaching of Ca and Mg at sites receiving higher H^+ deposition, and foliar concentrations of S and Al were positively correlated with increasing SO_4^{2-} deposition along the gradient (Pregitzer and Burton 1992, Burton et al. 1993).

Several effects of climatic conditions on ecosystem processes have been demonstrated at the sites. Lane et al. (1993) studied sugar maple diameter growth over the past fifty years at the sites and showed that productivity was affected by temperature to some degree at all sites, with precipitation increasing in importance at the southern sites. Climatic conditions in the prior growing season affected current season sugar maple growth. Reed et al. (1994c) showed that growth efficiency measures may differ by an order of magnitude in successive years on a site due to natural factors affecting the accumulation of woody biomass. Production dynamics of the northern hardwood forests studied were driven by complex interactions among climatic factors affecting energy storage, insect defoliation, and seed crop production. Year-to-year changes in crown condition largely reflected the gradual decline and mortality of suppressed and intermediate trees, apparently the result of severe drought in 1988 in combination with other stress factors such as defoliation.

Contents of many nutrients in midsummer foliage and litterfall increased from north to south, largely as a consequence of higher foliar biomass production and litter fall at the more southern sites (Pregitzer et al. 1992, Burton et al. 1993). This increase in foliar biomass may be a consequence of increasing temperature and length of

growing season, but also is consistent with the hypothesized effects of chronic N deposition at the southern, higher deposition sites (Pregitzer et al. 1992).

Studies of fine root dynamics were performed at two sites and have shown that fine roots (< 2 mm) dominate total biomass and N litter inputs to soil, accounting for over 55 percent of total biomass and nearly 50 percent of total N returns (Hendrick and Pregitzer 1993a). Rates of fine root turnover were different for the two sites, and it appears that rates of fine root "turnover" (longevity) may be related to soil temperature (Hendrick and Pregitzer, 1993b), a possibility that has not been considered in current models of the effects of global warming on forest ecosystems.

Soils from the sites were incubated for 32 weeks over a range of temperatures to quantify the effects of temperature on kinetics of microbial respiration and mineralization of N and S (MacDonald et al. 1995). Microbial respiration and the net mineralization of N and S increased with temperature at all sites. Rate constants estimated for each site and temperature from these models were not consistently related to temperature. In contrast, estimates of labile C and N pools were strongly temperature dependent. These results suggest the commonly accepted assumptions of constant pool sizes and temperature-dependent rate constants may not be tenable (MacDonald et al. 1995), leading to possible errors in predictions of soil C storage and N availability in response to global warming.

We continue to examine the interacting effects of climate, defoliation, pollutant deposition and seed production on forest productivity and health, fine root dynamics, microbial dynamics, soil solution chemistry, foliar nutrient status, and leaf area. We are now entering a stage where sufficient years of record exist to allow us to assess the relative impacts of these multiple stressing factors on ecosystem processes in northern hardwoods, an important biome type, widely distributed in North America.

MICHIGAN GRADIENT PUBLICATIONS

1995

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EFFECTS OF ELEVATED CO₂ AND SHADE ON THE DECOMPOSITION OF SENESCED TREE FOLIAGE:
IMPACTS ON MICROBIAL ACTIVITY

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Abstract: We examined microbial respiration and carbon/nitrogen content of decomposing leaf material in microcosms used for growth studies of the treehole mosquito, *Aedes triseriatus*. Leaf material originated from birch and oak trees exposed to conditions of shade/sun and elevated/ambient levels of CO₂. Microbial respiration as measured by CO₂ production was generally greatest on birch leaves grown under shaded conditions, however, ANOVA indicated possible light X CO₂ interactions. There were also strong interactions between species of leaf and CO₂ levels, but oak leaves grown under elevated CO₂ supported significantly higher microbial respiration rates than oak leaves grown in an ambient CO₂ atmosphere. Birch leaves grown under elevated CO₂ also generally supported higher rates of microbial respiration. However, light effects were much more pronounced and birch leaves grown under full sun and elevated CO₂ conditions supported relatively low microbial respiration. Microbial respiration varied inversely with leaf carbon:nitrogen ratio and directly with nitrogen content across treatments, however, initial carbon and nitrogen content of leaf material was not a consistent predictor of microbial respiration. In general, mosquito production paralleled microbial respiration, suggesting a tight link between the two trophic levels. These data indicate that interactions between available light and CO₂ on parent plant material could have variable, species-dependent effects on microorganisms and secondary consumers in aquatic, detritus-based systems.

INTRODUCTION

Most investigations of the potential effects of elevated atmospheric CO₂ levels on ecosystems have been directed toward plant growth in terrestrial environments. Repercussions from atmospheric perturbations, however, will also be seen in the indirect effects on other trophic levels (Field et al. 1992). The majority of vascular plant production ultimately enters the detrital pool in both terrestrial and aquatic systems, yet little is known about how atmospheric CO₂ changes might affect organisms involved in processing of detritus. Presumably, biochemical characteristics of litter produced under elevated CO₂ will be the key factors in detritus decomposition and a knowledge thereof should allow predictions of what may happen to detritus processing as atmospheric CO₂ concentrations increase (Mooney et al. 1991, Field et al. 1992, Meyer and Pulliam 1991). This assumption has not been consistently met, however (e.g. Norby et al. 1986), and there is a conspicuous lack of investigation of this question in aquatic systems that depend upon terrestrial leaf litter as a major carbon source (Carpenter et al. 1992).

Larvae of most mosquitoes are detritivores in aquatic environments and many species are thought to be dependent upon terrestrial plant litter and associated decomposer microorganisms for nutrition. One such species in North

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America is the treehole mosquito *Aedes triseriatus*. Previous studies have suggested that *Ae. triseriatus* growth and development are directly related to the quantity and quality of plant material available to larvae (Carpenter 1983, Fish and Carpenter 1982, Walker and Merritt 1988, Walker et al. 1991). Although not well-documented at present, larvae are presumed to feed mainly on microorganisms that metabolize senescent leaf material in the treehole habitat (Fish and Carpenter 1982). Therefore, factors that affect the abundance, activity, and/or composition of microbial communities in the habitat would be expected to influence mosquito production.

In this study, we investigated the effects of parent-plant growth conditions on the microbial respiration associated with the decomposition of senescent leaf material in simulated larval *Ae. triseriatus* habitats. Overall microbial respiration was significantly affected by leaf species, light conditions, and CO₂ levels. These results were related to leaf carbon and nitrogen content, and linked to mosquito growth and development.

METHODS

Experimental treatments and conditions

Senescent leaf material was obtained from one-year-old seedlings of paper birch (*Betula papyrifera* Marsh) and red oak (*Quercus rubra* L.) after growth under light and CO₂ conditions described by Kubiske and Pregitzer (1995). The conditions were either full sun (sun) or 26 percent of full sun (shade), and ambient CO₂ levels (350 ppm) or approximately twice ambient levels (714 ppm). These treatments were administered via open top chambers.

Microcosms were set up in parallel to those described by Strand et al. (this volume). 600 mg of dry leaf material was added to 300 ml of a weak solution containing inorganic nutrients (Na₂HPO₄, Na₂SO₄, KNO₃) and a microbial inoculum from natural treeholes. Nitrate (152 μM), sulfate (68 μM), and phosphate (33 μM) ion concentrations in the solution were within ranges found in stemflow and treeholes (Walker et al. 1991, Carpenter 1982a). Leaf material was incubated in the microcosm solution for one week at room temperature (23 - 25°C) prior to the first sampling. Mosquito larvae were added to half of the microcosms in the same proportion (one larva per 50 mg dry wt. leaf material) used by Strand et al. (this volume).

Microbial respiration and elemental analyses

On days 0 (coinciding with addition of larvae), 3, and 10, two subsamples of approximately 100 mg each of leaf material were removed, weighed, and placed into 38 ml serum vials. Serum vials were then capped and the headspace was sampled at approximately six hours (exact times recorded and used for rate calculations) after incubation at room temperature (24 - 25°C). Preliminary studies had shown CO₂ production from leaf material was linear for up to 18 hours under these conditions. Headspace gas was analyzed for CO₂ content with a Beckman® (#865, Beckman Instruments, Inc., Fullerton, CA) Infrared Analyzer. Remaining leaf material was dried, weighed, and analyzed for total carbon (C) and nitrogen (N) content with a Carlo Erba Nitrogen Analyzer® (#1500, Series 2, Carlo Erba, Milan, Italy).

Statistics

There was insufficient material for a complete leaf X light X CO₂ factorial ANOVA (no leaves from the oak shade treatment). Consequently, birch sun and birch shade treatments were analyzed as a two-way, repeated measures, fully factorial ANOVA (®Systat, Inc.). The birch sun and oak sun data were analyzed in another two-way, repeated measures ANOVA. Data were transformed as necessary with log or square root functions to reduce variance heteroscedasticity as determined with Bartlett's test (Sokal and Rohlf 1969, ®Systat, Inc.). Initial analyses revealed no significant effects of larvae within any treatment or on any leaf parameter measured. Consequently, replicates from microcosms with and without larvae were combined within treatments for all analyses. Relationships between microbial respiration and leaf percent nitrogen, percent carbon, and carbon:nitrogen ratio (C/N) were analyzed with Pearson correlation and standard regression techniques. Relationships between grand means of total adult mosquito biomass (from Strand et al., this volume) and grand means of microbial respiration (averaged across all sampling dates), initial (prior to water addition) senescent leaf percent N, percent C, and C/N were similarly analyzed.

RESULTS AND DISCUSSION

Microbial respiration

Microbial respiration as indicated by CO₂ production rate varied greatly with time, leaf species, light, and CO₂ treatment (Fig. 1, Tables 1 and 2). Leaf X CO₂ comparisons (Table 1) showed significant interaction between all main factors, reflecting the more pronounced effect of growth-condition CO₂ levels on senescent oak leaf decomposition vs. birch leaf decomposition. Additionally, differences between treatments were less distinguishable as decay progressed. In contrast, the light X CO₂ comparison of birch leaves showed significant increases in microbial respiration rates on leaves from the shaded treatment and fewer interactions with other factors (Table 2). There was no evidence of a direct CO₂ effect in the birch-only comparison, however, significant interaction of light with time and CO₂ suggests elevated CO₂ history may have influenced microbial respiration during a portion of the decay process. As in the leaf X CO₂ comparison, differences between treatments became attenuated over time.

The convergence of respiration values on day 10 in both comparisons indicates that differences in leaf chemistry due to growth conditions were in the relatively labile fraction. This fraction would be utilized more readily in earlier stages of decomposition and remaining leaf material of all types would be similar in its refractory nature. Although mass loss was not determined in this study, decay curves for different deciduous leaves in aquatic and terrestrial habitats typically show the most pronounced divergence early in the process (Willoughby, 1974, Jensen 1974, Carpenter 1982b, Aber et al. 1990). Additionally, the overall decline of respiration rates with time may reflect depletion of initial inorganic nutrient sources that would normally be replenished by stemflow (Carpenter 1982a, Walker et al. 1991).

Carbon and nitrogen content

Nitrogen (N) content and carbon:nitrogen (C/N) ratios of leaf material also varied considerably with time and treatment (Figs. 2 and 3, Tables 2 - 6). Nitrogen concentration in birch leaf material generally increased with time (Figure 2, Table 4), however, this trend was not obvious in the oak leaf material during the sampling period (Figure 2). An increase in N content during decay is characteristic of most litter and is presumably due to microbial immobilization and humification (Willoughby, 1974, Suberkropp et al. 1976, Melillo et al. 1982). Percent leaf N was significantly lower in decomposing oak than birch, but this was dependent upon growth-condition CO₂ level (Table 3). However, there was no overall main effect of plant growth-condition CO₂ on N content.

In general, C/N ratios in the leaf material reflected trends in nitrogen content; C/N declined with time as nitrogen increased and the trend was most obvious in the birch treatments. In contrast to percent N, however, analysis of C/N ratios showed significant light and CO₂ main effects (Tables 5 and 6). These main effects must be cautiously interpreted along with significant interaction terms, however, results from ANOVA of C/N ratios more closely parallel those found for microbial respiration (compare Tables 1 and 2 with 5 and 6). This suggests that carbon content and/or quality, not nitrogen content or quality, during decay was most affected by parent-plant treatment conditions and that carbon sources in the leaf material influenced microbial respiration more directly.

Relationships between microbial respiration, leaf carbon:nitrogen content, and adult mosquito biomass

That the relationship between microbial respiration, and carbon and nitrogen content is complex is illustrated in Figure 4. Microbial respiration varied directly with percent N, but inversely with percent C and C/N ratio. Although correlations are all significant, only 5 - 8 percent of the variance can be explained by any factor. This would further suggest that other factors, including carbon quality of the leaf material, may have the strongest overall influence on microbial respiration. Carbon quality, for example, has been shown to be the major limiting factor for microbial decomposer activity in many terrestrial systems (e.g. Collins et al. 1990, Melillo et al. 1982).

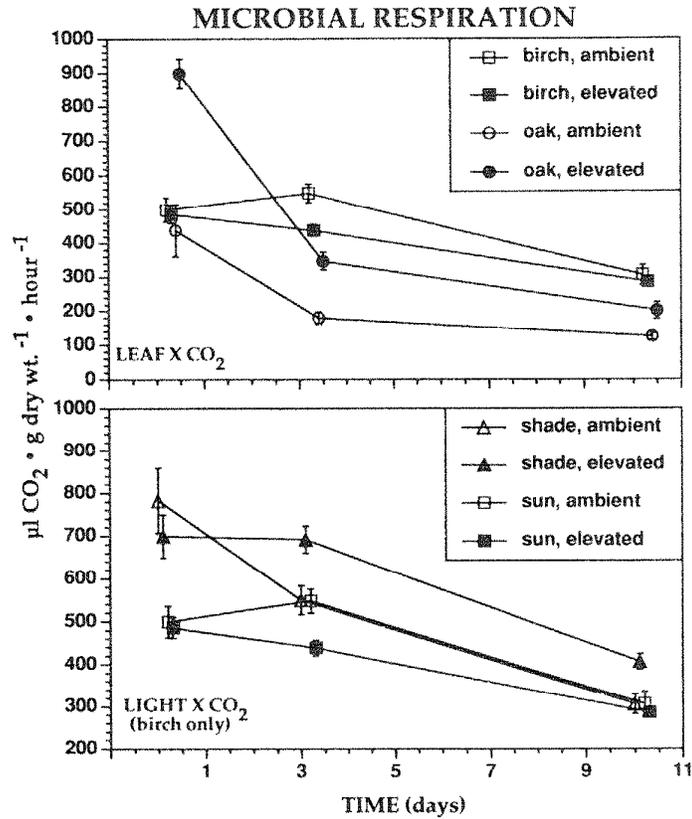


Figure 1. Microbial respiration on decomposing, senescent leaf material in *Ae. triseriatus* microcosms. Values are mean \pm S.E. n = 6 in all cases. Initial values (day 0) correspond to addition of larvae in parallel microcosms.

Table 1. Repeated measures ANOVA results comparing microbial respiration on decomposing, senescent birch and oak leaf material grown under ambient and elevated CO₂ levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
LEAF	68930.641	1	68930.641	5.962	0.024
CO ₂	156967.476	1	156967.476	13.576	0.001
LEAF*CO ₂	359770.118	1	359770.118	31.116	0.000
ERROR	231246.895	20	11562.345		
WITHIN SUBJECTS					
TIME	1490252.429	2	745126.214	111.552	0.000
TIME*LEAF	538468.305	2	269234.153	40.307	0.000
TIME*CO ₂	152280.638	2	76140.319	11.399	0.000
TIME*LEAF*CO ₂	107048.693	2	53524.346	8.013	0.001
ERROR	267184.288	40	6679.607		

Table 2. Repeated measures ANOVA results comparing microbial respiration on decomposing, senescent birch leaf material grown under ambient and elevated CO₂ levels, and two light levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
CO ₂	98.467	1	98.467	0.007	0.934
LIGHT	381763.220	1	381763.220	26.881	0.000
CO ₂ *LIGHT	45612.067	1	45612.067	3.212	0.088
ERROR	284043.486	20	14202.174		
WITHIN SUBJECTS					
TIME	1134588.130	2	567294.065	73.464	0.000
TIME*CO ₂	25508.008	2	12754.004	1.652	0.205
TIME*LIGHT	109450.810	2	54725.405	7.087	0.002
TIME*CO ₂ *LIGHT	78295.658	2	39147.829	5.070	0.011
ERROR	308880.754	40	7722.019		

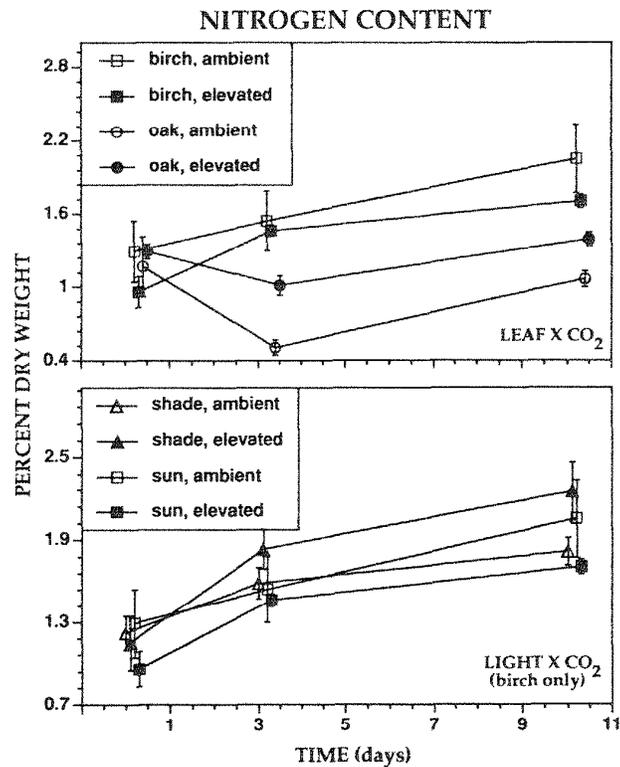


Figure 2. Nitrogen content of decomposing, senescent leaf material in *Ae. triseriatus* microcosms. Values are mean \pm S.E. n = 6 in all cases. Initial values (day 0) correspond to addition of larvae in parallel microcosms.

Table 3. Repeated measures ANOVA results comparing nitrogen concentration of decomposing, senescent birch and oak leaf material grown under ambient and elevated CO₂ levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
LEAF	2.171	1	2.171	15.372	0.001
CO ₂	0.307	1	0.307	2.173	0.156
LEAF*CO ₂	1.278	1	1.278	9.053	0.007
ERROR	2.824	20	0.141		
WITHIN SUBJECTS					
TIME	2.011	2	1.005	19.280	0.000
TIME*LEAF	2.171	2	1.085	20.813	0.000
TIME*CO ₂	0.514	2	0.257	4.929	0.012
TIME*LEAF*CO ₂	0.071	2	0.036	0.681	0.512
ERROR	2.086	40	0.052		

Table 4. Repeated measures ANOVA results comparing nitrogen concentration of decomposing, senescent birch leaf material grown under ambient and elevated CO₂ levels, and two light levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
CO ₂	0.003	1	0.003	0.064	0.803
LIGHT	0.062	1	0.062	1.375	0.255
CO ₂ *LIGHT	0.109	1	0.109	2.404	0.137
ERROR	0.908	20	0.045		
WITHIN SUBJECTS					
TIME	1.341	2	0.670	33.714	0.000
TIME*CO ₂	0.064	2	0.032	1.611	0.212
TIME*LIGHT	0.008	2	0.004	0.212	0.810
TIME*CO ₂ *LIGHT	0.024	2	0.012	0.596	0.556
ERROR	0.795	40	0.020		

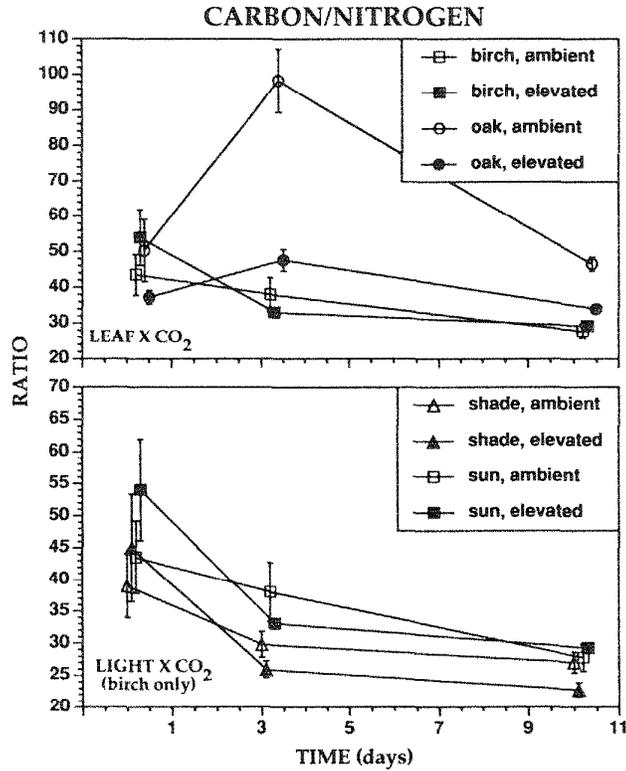


Figure 3. Carbon:nitrogen ratios (percent carbon/percent nitrogen) of decomposing, senescent leaf material in *Ae. triseriatus* microcosms. Values are mean \pm S.E. n = 6 in all cases. Initial values (day 0) correspond to addition of larvae in parallel microcosms.

Table 5. Repeated measures ANOVA results comparing carbon:nitrogen ratio of decomposing, senescent birch and oak leaf material grown under ambient and elevated CO₂ levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
LEAF	1.731	1	1.731	14.287	0.001
CO ₂	0.558	1	0.558	4.605	0.044
LEAF*CO ₂	1.141	1	1.141	9.415	0.006
ERROR	2.423	20	0.121		
WITHIN SUBJECTS					
TIME	1.802	2	0.901	17.551	0.000
TIME*LEAF	1.919	2	0.959	18.691	0.000
TIME*CO ₂	0.565	2	0.283	5.504	0.008
TIME*LEAF*CO ₂	0.064	2	0.032	0.625	0.540
ERROR	2.053	40	0.051		

Table 6. Repeated measures ANOVA results comparing carbon:nitrogen ratio of decomposing, senescent birch leaf material grown under ambient and elevated CO₂ levels, and two light levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
CO ₂	0.001	1	0.001	0.006	0.938
LIGHT	0.528	1	0.528	4.361	0.050
CO ₂ *LIGHT	0.086	1	0.086	0.712	0.409
ERROR	2.422	20	0.121		
WITHIN SUBJECTS					
TIME	3.028	2	1.514	27.720	0.000
TIME*CO ₂	0.237	2	0.118	2.169	0.128
TIME*LIGHT	0.037	2	0.018	0.337	0.716
TIME*CO ₂ *LIGHT	0.037	2	0.019	0.340	0.714
ERROR	2.184	40	0.055		

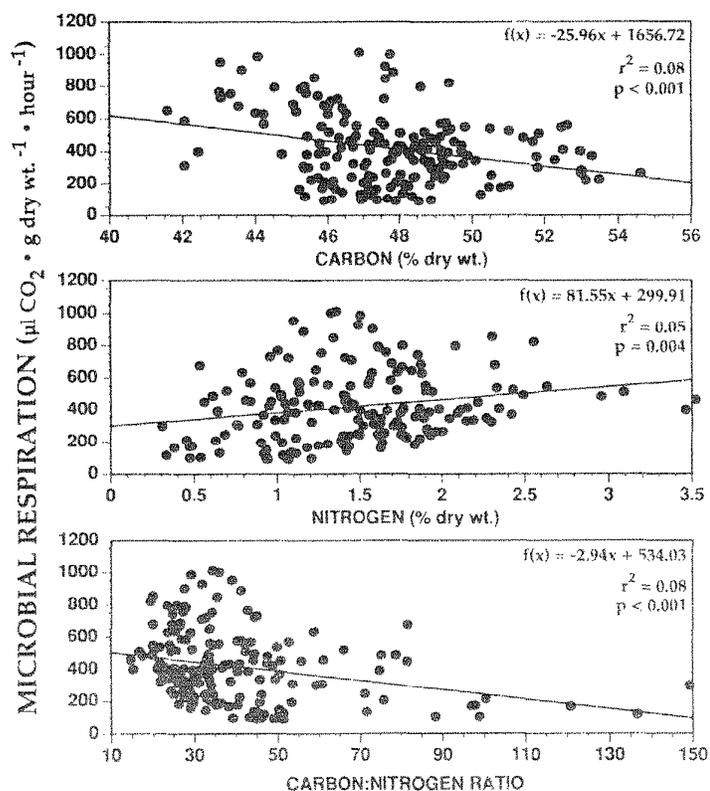


Figure 4. Correlation between microbial respiration and percent carbon, percent nitrogen, and carbon:nitrogen ratios of decomposing, senescent leaf material in *l.c. triseriatus* microcosms. Data from all leaf types and all three sampling dates are illustrated in each panel.

The initial carbon and nitrogen content of the senescent leaf material (Table 7) is likely to be a poor predictor of microbial respiration during decay or of adult mosquito biomass produced (Table 8). Only the relationship between initial percent N and mosquito adult biomass produced was significant, although the analysis also suggested a possible relationship between initial percent N and microbial respiration (Table 8). The negative relationships between percent N and mosquito biomass, and between percent N and microbial respiration are surprising in that nitrogen content of leaf detritus often is positively correlated with decomposition rates and detritivore growth in aquatic systems (Anderson and Sedell 1979 and references therein). These data must be viewed cautiously, however, since correlations based upon grand means simply reflect the relationships of general trends in the data set. Nevertheless, in contrast to earlier studies (see Park 1975, Jensen 1974) initial leaf N and C/N were not broad indicators of microbial respiration or detrital processing potential in these microcosms. Elevated CO₂ is generally thought to decrease overall percent N and increase C/N in terrestrial leaf litter, resulting in lower decomposition rates (Mooney et al. 1991, Field et al. 1992). However, excess carbon content of leaf litter from CO₂-enhanced parent plants is mostly in the form of sugars and starches, not lignin (Mooney et al. 1991). Therefore, decomposition rates of the litter could conceivably be increased provided other nutrients (e.g., N) are in adequate supply from external sources. It has been recognized more recently that percent N and C/N in detritus may be inadequate predictors of decomposition since other factors such as lignin content have a more pronounced influence on decay processes in aquatic habitats (Gessner and Chautier 1994, Boulton and Boon 1991, Stout 1989, Polunin 1984, Suberkropp et al. 1976). This further underscores the need to investigate specific carbon sources in treehole systems.

Table 7. Initial (before water addition and incubation) nitrogen (N), carbon (C), and carbon:nitrogen ratios (C/N) of senescent leaf material in *Ae triseriatus* microcosms. Values are mean \pm S.E. of subsamples from pooled and homogenized material. n = 4 in all cases. BSHA = birch, shade, ambient CO₂; BSHE = birch, shade, elevated CO₂; BSA = birch, sun, ambient CO₂; BSE = birch, sun, elevated CO₂; OSA = oak, sun, ambient CO₂; OSE = oak, sun, elevated CO₂.

Treatment	N (% dry wt.)	C (% dry wt.)	C/N
BSHA	1.25 \pm 0.05	32.86 \pm 1.12	26.41 \pm 0.80
BSHE	1.09 \pm 0.02	44.67 \pm 0.08	41.00 \pm 0.81
BSA	1.27 \pm 0.03	48.78 \pm 0.10	38.63 \pm 1.03
BSE	1.70 \pm 0.03	47.70 \pm 0.14	28.09 \pm 0.47
OSA	1.56 \pm 0.06	47.13 \pm 0.11	30.56 \pm 1.24
OSE	1.49 \pm 0.02	46.88 \pm 0.12	31.47 \pm 0.33

Table 8. Pearson correlation analysis of initial (before water addition and incubation) carbon (C) and nitrogen (N) content of senescent leaf material vs. grand means of microbial respiration and total adult mosquito biomass. n = 6 in all cases.

Leaf content vs.	Pearson Correlation			
	Microbial Respiration		Mosquito Biomass	
	Coeff.	p value	Coeff.	p value
% N	-0.780	0.067	-0.842	0.038
% C	-0.381	0.456	-0.729	0.103
C:N	0.474	0.343	0.688	0.211

Although leaf biochemical characters that may influence microbial respiration and decay processes are complex and incompletely-addressed in this study, microbial respiration appears to be a good predictor of larval *Ae. triseriatus* production in the microcosms. Figure 5 illustrates the relationship between grand means of adult mosquito biomass and microbial respiration. Such a relationship has been shown for other detritivore/microbe systems (e.g. Ward and Cummins 1979), but this study represents the first such evidence for larval mosquitoes. The positive relationship supports our contention that mosquito larvae in treehole habitats are limited by microbial biomass and/or respiration. The results also reinforce the idea of a tight link between trophic levels in the system and that microorganisms are the key intermediates. Higher microbial respiration measurements have been associated with higher microbial biomass in detritus (Ward and Cummins, 1979). Since observations indicate that *Ae. triseriatus* larvae feed directly upon leaf surface-associated microorganisms (Fish and Carpenter 1982, Walker and Merritt 1991, Kaufman unpub. obs.), the higher biomass of emerging adults in some treatments is potentially attributable to a higher biomass of microbes. Alternatively, higher microbial respiration may be acting to release more leaf material for larval consumption. Since we presently have no data on microbial turnover rates or microbial biomass/vs. leaf material contributions to larval growth, additional experimentation will be required to address the details of the linkage. Further examination of this linkage will allow more detailed predictions of the effects of atmospheric changes on small, aquatic, detritus-based systems.

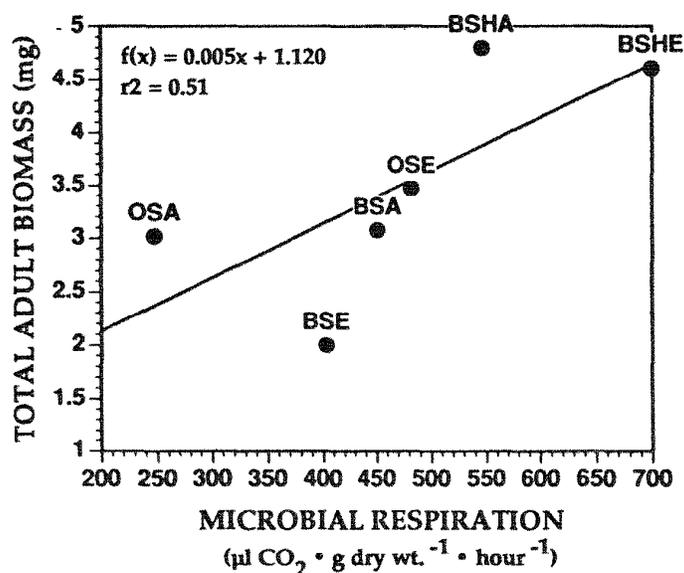


Figure 5. Correlation between mean total mosquito biomass and mean respiration values of decomposing, senescent leaf material in *Ae. triseriatus* microcosms. Mean respiration values are the average of mean respiration rates over the three sampling dates. Treatments are indicated as BSHA = birch, shade, ambient CO₂; BSHE = birch, shade, elevated CO₂; BSA = birch, sun, ambient CO₂; BSE = birch, sun, elevated CO₂; OSA = oak, sun, ambient CO₂; OSE = oak, sun, elevated CO₂.

SUMMARY AND CONCLUSIONS

Microbial respiration on decaying leaves in *Ae. triseriatus* microcosms was affected by leaf species and CO₂ conditions during growth of the parent plant. However, both of the effects changed significantly with time. Microbial respiration on oak was enhanced by growth-condition elevated CO₂ while birch leaves showed the opposite trend.

Microbial respiration on decomposing senescent birch leaves was affected most by parent-plant light conditions and this effect was more pronounced in earlier stages. Leaves from plants grown in shade supported higher levels of

respiration than those produced in full sun. Elevated CO₂ conditions during parent-plant growth enhanced microbial respiration on decomposing, senescent leaves only when the leaves originated from plants grown under shaded conditions.

Nitrogen content and carbon-nitrogen ratios, both of which are known to be altered by microbial biomass and respiration, were significantly correlated with microbial respiration. Senescent leaf material with higher nitrogen content had lower C/N values and higher microbial respiration. Carbon content or quality, however, appeared to have a more direct influence on microbial respiration.

Initial values for percent nitrogen and carbon-nitrogen ratios in the senescent leaf material were not good indicators of either microbial respiration or mosquito production. This warrants further investigation, however, it also points out that over simplistic models of decomposition may not adequately predict the flow of carbon and nitrogen in plant material through decomposer and detritivore communities.

Adult mosquito production was directly and positively related to microbial respiration, suggesting a tight trophic link between mosquito larvae and decomposer microorganisms. Effects of elevated CO₂ and light on senescent leaf material will likely have complex repercussions for detritivores in aquatic systems and will depend upon the microbial mediation of the detritus-detritivore interactions.

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EFFECTS OF ELEVATED CO₂ AND SHADE ON THE DECOMPOSITION OF SENESCED TREE FOLIAGE:
IMPACTS ON THE GROWTH AND SURVIVAL OF TREEHOLE MOSQUITOES

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Abstract: We tested the hypothesis that growth, survival, and reproductive capacity of treehole mosquitoes can be affected by alterations of forest sunlight and CO₂ levels. Larval *Aedes triseriatus* were fed naturally senesced, abscised foliage from red oak (*Quercus rubra*) and paper birch (*Betula papyrifera*) seedlings grown in ambient and elevated CO₂ atmospheres. Oak seedlings were grown in full sunlight. Birch were grown in full sun and partial shade. Females fed birch leaves grown in elevated CO₂ were larger than those fed birch grown in ambient CO₂. However, fewer females emerged from microcosms containing birch foliage grown in elevated CO₂, which significantly lowered estimates of microcosm total egg production. Elevated CO₂ did not affect the performance of mosquitoes reared on leaves of either species grown in full sunlight. Shading birch foliage led to the production of more mosquitoes of both sexes. Males fed shaded foliage were larger and survivorship was higher for males and females, which led to a significantly higher estimate of microcosm egg potential. Birch diets produced larger females and a larger quantity of smaller males than did diets of oak. Mosquitoes of both sexes took significantly longer to develop on birch. Our results indicate that *A. triseriatus* larvae are more sensitive to forest light intensity and tree species composition than they would be to a doubling of atmospheric CO₂ elevation.

INTRODUCTION

Aedes triseriatus is a common inhabitant of water-filled treeholes in eastern North America wherein larvae graze on allochthonous foliage and the microbes that decompose it. In the Great Lakes region, the *A. triseriatus* life cycle begins in early spring as eggs break winter diapause to hatch. Mosquitoes that complete development pass through four larval instars and a pupal stage prior to adult emergence. Development from egg to adult typically requires two weeks to two months depending on growing conditions. Adult females live only long enough to mate, obtain a blood meal, and oviposit in cavities. Males are similarly ephemeral. Cohorts are univoltine in the northern part of the range and bivoltine elsewhere when habitat requirements are met (Walker et al. 1991).

Water-filled treeholes are distinct ecosystems fueled almost exclusively by organic carbon derived from allochthonous foliage and inorganic nutrients that enter the system via stemflow (Carpenter 1983, Walker et al. 1991). Treehole communities are predominantly comprised of decomposer microbes and larval insects that consume decomposing foliage. Like other aquatic insect detritivores (Cummins and Klug 1979), *A. triseriatus* larvae are known to be sensitive to quantitative and qualitative changes in microbially conditioned, senesced-leaf diets

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(Carpenter 1983, Walker et al. 1991). Therefore, alteration of any environmental variable that affects the quantity or quality of foliage inputs could affect all biological processes occurring in a treehole.

Qualitative changes in leaf chemical composition and quantitative changes in total leaf production can result from forest CO₂ and sunlight alteration (Kubiske and Pregitzer 1995). Such changes in leaf chemistry can affect the performance of decomposer microbes (Kaufman et al. this issue) and the insects that feed on leaves (Herms et al. this issue). In this study, we examine the effects of forest sunlight and CO₂ alteration on the development time, adult mass, survivorship, and reproductive capacity of a detritivorous insect common to the Great Lakes region.

MATERIALS AND METHODS

Leaves

Senesced leaves were collected following autumn abscission from one-year-old paper birch and red oak seedlings grown in 350 ppm and 750 ppm CO₂ atmospheres in full sunlight and from birch seedlings grown in both CO₂ levels under a simulated forest canopy (26 percent full sunlight) (see Kubiske and Pregitzer 1995).

Leaf material was sufficient to establish 42 microcosms: eight oak-sun-ambient CO₂, five oak-sun-elevated CO₂, nine birch-sun-ambient CO₂, eight birch-sun-elevated CO₂, seven birch-shade-ambient CO₂, and five birch-shade-elevated CO₂ microcosms.

Mosquitoes

Eggs were collected from automobile tire oviposition traps that were placed in woodlots on the Michigan State University campus (47°N, 84°W, 244-274 m altitude). Eggs were hatched in deoxygenated water and immediately added to microcosms. Each 500 ml plastic microcosm contained 20 larvae and 1 g of leaves conditioned for seven days in 300 ml of deionized water and a 5 ml inoculum of microbes in an inorganic ion solution derived from field-collected stemflow (see Kaufman et al. this issue). The experiment was conducted in a walk-in growth chamber. Temperature was held constant at 23 °C. Microcosms were shaded. Upon emergence, adults were aspirated from microcosms and immediately frozen at -20 °C. At the end of the experiment, they were dried for 12 hours at 65 °C and weighed on a Cahn model 27 microbalance.

Fecundity was estimated with Livdahl's (1982) regression equation for *A. triseriatus* egg production potential (fecundity = 7.13 + 45.85 mg dry mass). Total microcosm egg production was calculated by summing fecundity estimates for each surviving female, thereby providing an estimate of the potential of treatment effects to influence *A. triseriatus* population dynamics.

Statistical Analysis

Effects of the six treatment combinations on development time, adult mass, and estimated fecundity were determined with the use of two ANOVA models. The first tested the effects of CO₂, sunlight, and their interaction on the development time, adult mass, and estimated egg production potential of mosquitoes reared on birch leaves. The second model tested the effect of CO₂, tree species, and their interaction on the development time, adult mass, and estimated potential egg production of mosquitoes reared on oak and birch grown in full sunlight. All data are reported as untransformed means except microcosm fecundity estimates which were square-root transformed to reduce variance heteroscedasticity.

RESULTS AND DISCUSSION

Effects of Elevated CO₂

Females fed birch leaves grown in elevated CO₂ were larger, and therefore more fecund, than those fed birch grown in ambient CO₂ (Table 1, Figure 1). This positive response by a detritivore to elevated CO₂ is in direct contrast to previously observed and predicted effects of CO₂ elevation on foliage decomposition (Lambers 1993, Cotrufo et al 1994).

Elevated CO₂ is predicted to decrease decomposition rate because it increases leaf C:N ratios and the concentration of lignin and other decomposition-inhibiting secondary metabolites (Lambers 1993). However, it is generally thought that the key component of the *A. triseriatus* larval diet is not leaves, but the microorganisms that decompose leaves (Walker and Merritt 1988, Walker 1991, Kaufman et al. this issue). Kaufman et al. (this issue) observed that elevated CO₂ slows decomposition by microbes. Therefore, females, which take longer to develop than males, may achieve greater mass due to increased substrate permanence as would result from delayed nutrient availability for microbes.

Table 1. F values from ANOVA of mosquito performance on senesced birch leaves exposed to two levels of CO₂ and sunlight (* denotes P < 0.10, ** < 0.05, *** < 0.01).

	CO ₂	SOURCE Light	CO ₂ * Light
females per microcosm	6.9 ***	4.2 **	1.7
males per microcosm	0.1	6.5 ***	0.2
female development time	0.3	17.9 ***	2.2
male development time	0.7	94.4 ***	0.0
female mass	3.3 *	2.6	1.6
male mass	0.1	43.5 ***	1.5
microcosm fecundity	3.4 *	2.9 *	0.3

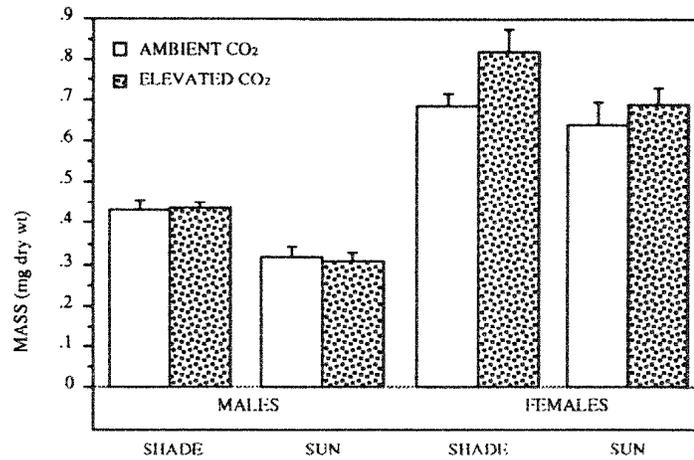


Figure 1. Effects of sunlight intensity and CO₂ level on *A. triseriatus* mass (± 1 S.E.).

Females that survived to adulthood on diets of elevated CO₂-treated leaves were more fecund, but fewer survived per microcosm, which led to lower estimates of potential microcosm egg production (Figures 2 and 3). Therefore, we observed no potential positive population-level responses to elevated CO₂.

Male development time and adult mass were unaffected by CO₂-elevation effects on birch leaves grown at either light level. Elevated CO₂ had no discernible effect on the performance of males or females reared on leaves of either species grown in full sunlight (Figures 6-10).

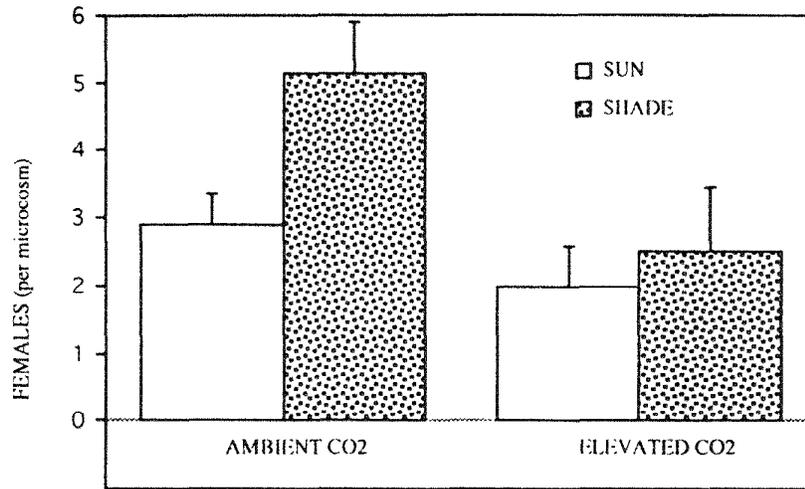


Figure 2. Effects of sunlight intensity and CO₂ level on *A. triseriatus* female survival (± 1 S.E.).

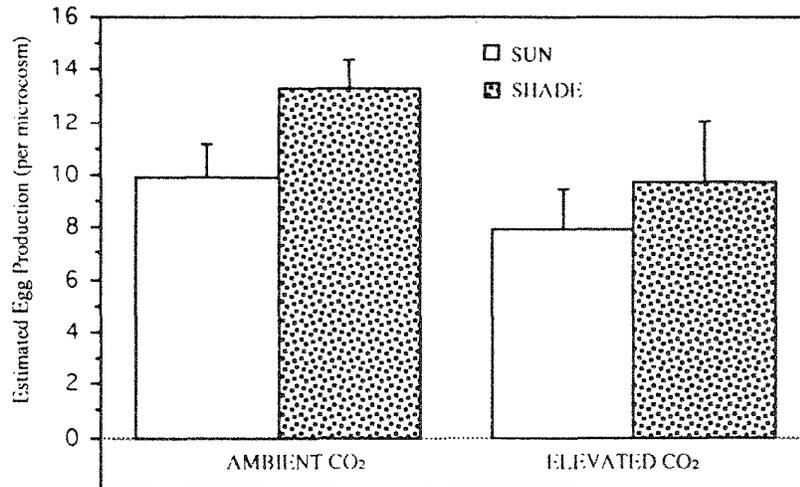


Figure 3. Effects of sunlight intensity and CO₂ level on *A. triseriatus* fecundity (square root mean ± 1 S.E.).

Effects of Shade

Mosquito performance was greatly enhanced by the effects of shade on birch (Table 1). Shading led to the production of a larger number of more-rapidly developing mosquitoes of both sexes (Figures 2, 4, and 5). Also, microcosms containing shaded foliage had a higher potential egg production than did those containing foliage grown in full sunlight. This was attributable to enhanced female survival (Figure 3).

Like the effects of elevated CO₂ on mosquito performance, those of shading may be caused by alterations of leaf chemistry and structural integrity. Typical plant responses to shade include decreased C:N ratios and lowered concentrations of carbon-based allelochemicals such as lignin, tannins, and phenolics (Herms and Mattson 1992). These reductions would be expected to increase decomposition by microbes, as observed by Kaufman et al. (this issue). Decomposition of shaded foliage may, therefore, progress too rapidly to allow for the complete development of some female mosquitoes. Males were able to gain more mass on leaves grown in shade (Figure 1), presumably due to their relatively rapid development time (Figure 5).

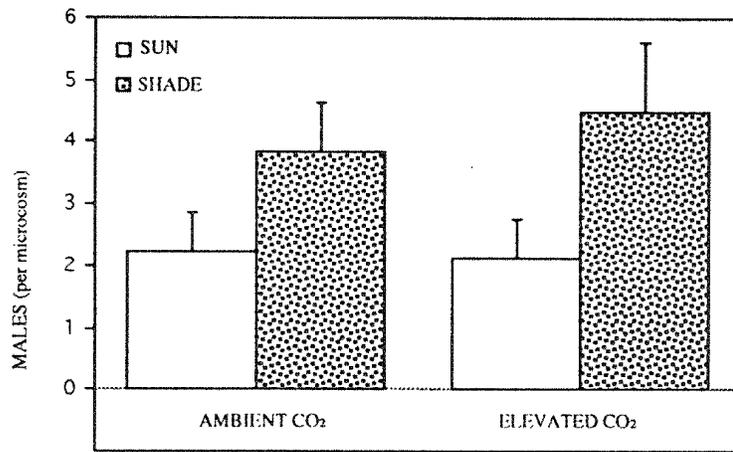


Figure 4. Effects of sunlight intensity and CO₂ level on *A. triseriatus* male survival (± 1 S.E.)

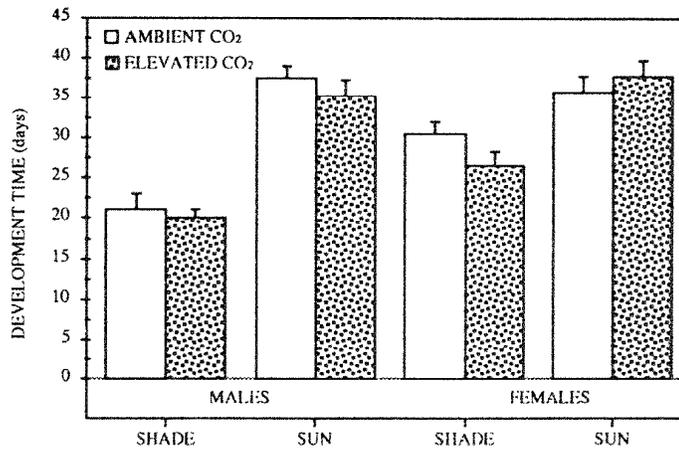


Figure 5. Effects of sunlight intensity and CO₂ level on *A. triseriatus* development time (± 1 S.E.).

Birch responses to shade apparently caused the observed effects on mosquito performance. Light intensity reduction can affect tree species differentially, which could alter forest vegetation composition. Therefore, changes in light intensity may be predicted to generate effects that cascade through an ecosystem from producers to detritivores.

Effects of Tree Species

Females fed birch leaves were larger than those fed oak, but they required much more time to complete development (Table 2, Figures 6 and 7). Males fed birch also took longer to develop and they were more numerous, but smaller than those fed oak (Table 2, Figures 8, 6, and 7). Any positive population-level effects caused by increased female mass and male survivorship would likely be counteracted in natural systems by the increased rates of death by predation, disease, and habitat drying that would result from prolonged development time.

Females reared on birch were larger, and therefore more fecund, than those fed oak. However, this increase did not lead to differential estimated total egg production per microcosm, due, in part, to slightly lower female survivorship on birch relative to oak (Table 2, Figures 9 and 10).

Table 2. F values from ANOVA of mosquito performance on senesced oak and birch leaves exposed to two levels of CO₂ (* denotes P ≤ 0.10, ** ≤ 0.05, *** ≤ 0.01).

	SOURCE		
	CO ₂	Tree Species	CO ₂ *Species
females per microcosm	0.8	0.3	0.2
males per microcosm	0.6	10.4 ***	0.7
female development time	0.0	65.4 ***	0.7
male development time	1.9	294.9 ***	0.0
female mass	0.2	11.0 ***	0.9
male mass	0.1	2.9 ***	1.9
microcosm fecundity	0.1	0.1	1.2

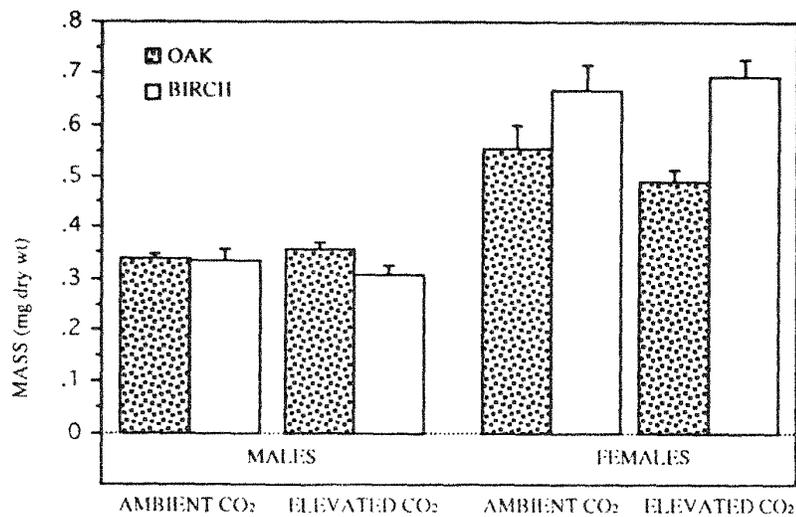


Figure 6. Effects of tree species and two levels CO₂ on *A. triseriatus* mass (± 1 S.E.).

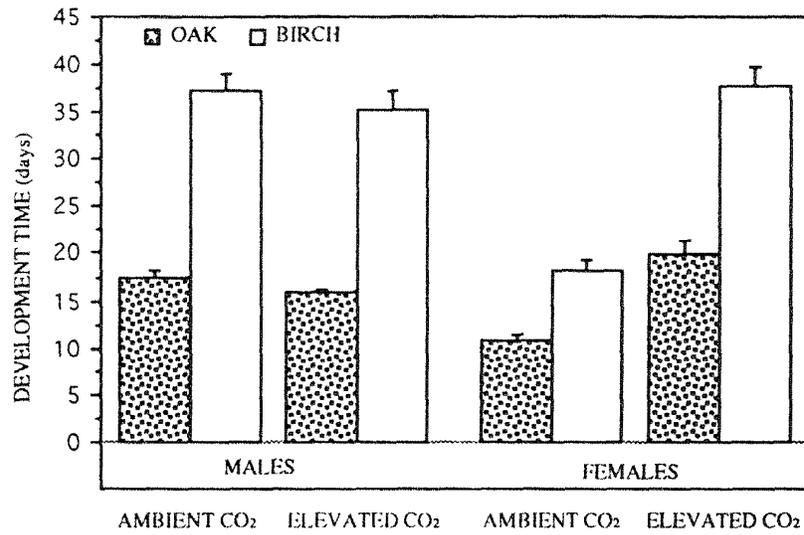


Figure 7. Effects of tree species and two levels CO₂ on *A. triseriatus* development time (± 1 S.E.).

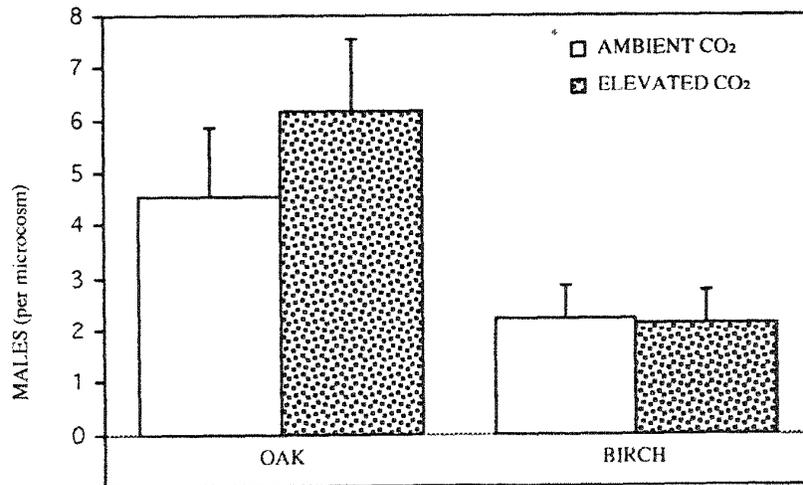


Figure 8. Effects of tree species and two levels CO₂ on *A. triseriatus* male survival (± 1 S.E.).

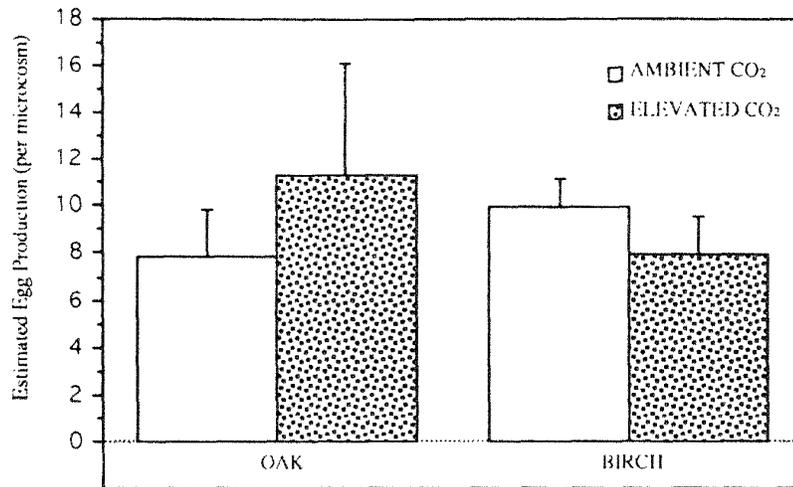


Figure 9. Effects of tree species and two levels CO₂ on *A. triseriatus* fecundity (square root mean \pm 1 S.E.).

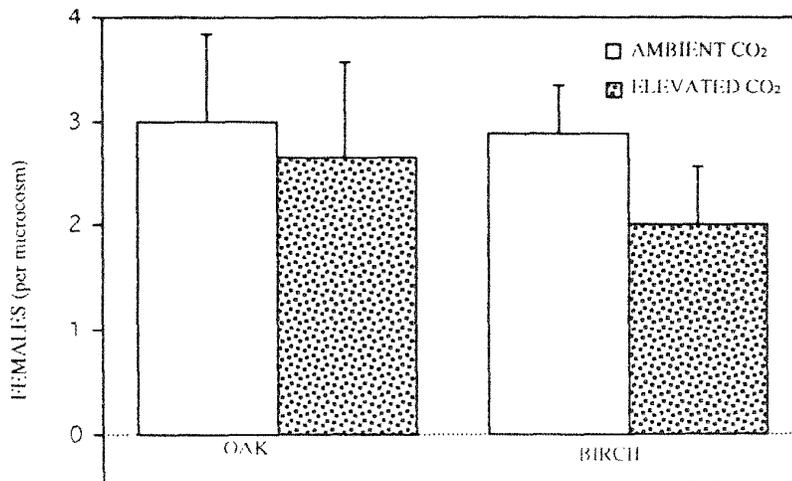


Figure 10. Effects of tree species and two-levels CO₂ on *A. triseriatus* female survival (\pm 1 S.E.).

The relative dominance of any tree species is determined by a variety of abiotic conditions including ambient light and CO₂ levels (Herms and Mattson 1992). Trees respond differentially, both inter- and intraspecifically, to changes in these parameters (Kubiske and Pregitzer 1995). Therefore, ambient light intensity and CO₂ level could independently and in concert, shape forest vegetation composition. Our results suggest that such an effect would ultimately affect detritivorous insect populations

SUMMARY

Differences in light intensity and atmospheric CO₂ level can generate effects that cascade through an ecosystem from producer to detritivore. The effects of elevated CO₂ observed here (increased female mass and decreased female survival and potential egg production per microcosm) were generally small compared to those of sunlight (increased male and female survival and estimated potential egg production per microcosm and decreased male and female development time) and tree species (increased size and development time of females fed birch, prolonged development time and decreased mass of males fed birch, and decreased estimated egg production for microcosms containing birch). These results suggest that elevated CO₂ impacts on *A. triseriatus* may be difficult to detect against the backdrop of environmental variation already experienced by this insect in the forests of the Great Lakes region.

Further study is required to establish whether or not the patterns observed here for treehole mosquitoes also apply to other detritivores in heterotrophic aquatic systems or elsewhere. However, the reliance of detritivores on abscised foliage does lend support to the supposition that change of any environmental variable that alters leaves qualitatively, will likely impact ecosystem detritivory processes.

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CATION DEPLETION IN NEW ENGLAND FORESTS

Richard Hallett¹ and James Hornbeck²

Preliminary results are presented from a case study designed to evaluate the potential for cation depletion in low-elevation forest soils of northern New England and New York. Samples of foliage, wood, and soils were collected in August, 1993 from plots with deep sandy soils that had previously been cleared or harvested and are now dominated by mature stands of either red oak or white pine. Plots were located in New York, Vermont, New Hampshire, Maine, and Massachusetts. Planned and/or completed analyses include extractable and total nutrients for soils, total nutrients in foliage, and extractable nutrients in wood. Nutrients include Ca, Mg, K, Fe, Mn, Al, N, and P. Results presented here include nutrient values in green foliage sampled from upper and middle layers of the canopy.

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ALUMINUM MOBILIZATION AND CALCIUM DEPLETION IN THE FOREST FLOOR OF RED SPRUCE
FORESTS IN THE NORTHEASTERN UNITED STATES

Gregory B. Lawrence¹, Mark B. David² and Walter C. Shortle³

Abstract: Mechanisms of Ca depletion were investigated as part of a regional study of relations among acidic deposition, soil chemistry and red spruce decline. Comparison with results from studies in the Adirondack Mountains of New York and the White Mountains of New Hampshire indicates that current acid-extractable Ca concentrations in the Oa horizon are less than one-half the average measured in the 1930's. A statistically significant decrease of similar magnitude was also observed for both exchangeable and acid-extractable Ca, over the past two decades, in archived Oa horizon samples collected in red spruce stands at the Hubbard Brook Experimental Forest, N. H. The same samples indicated increases in exchangeable and acid-extractable Al concentrations over this period. Our results indicated no relation between concentrations of exchangeable Ca and exchangeable H in the forest floor, whereas a strong inverse relation was observed between concentrations of exchangeable Ca and exchangeable Al. We also found that exchangeable Al concentrations were related to the concentrations of acid-extractable Al (mostly organically complexed Al), but unrelated to mineral Al concentrations. Furthermore, the exchangeable Al content of the forest floor was positively correlated with the molar ratio of inorganic Al to Ca in the soil solution of the B horizon. We propose that Al mobilized within the mineral soil by acidic deposition is an important contributor to the pools of exchangeable and acid-extractable Al in the forest floor. Once mobilized in the mineral soil, Al is transported by water movement and root uptake into the forest floor, where it can replace Ca on exchange sites through its strong affinity for organic functional groups.

INTRODUCTION

Concern about the effects of acidic deposition on forest soils has led to numerous investigations in both Europe and North America, as summarized by Johnson et al. 1991. The underlying hypothesis of these studies is that acidic deposition enhances leaching of base cations, increases soil acidity and reduces soil fertility. Decline and dieback of red spruce forests (Shortle and Smith 1988), acidification of surface-water (van Breemen et al. 1984), and decreases in forest productivity (Federer et al. 1989) have all been linked to increased soil acidity resulting from acidic deposition.

Investigations of soil acidification have shown that measurable increases in soil acidity can occur in as little as two decades and that both acidic deposition and natural growth processes can cause significant soil acidification (Johnson et al. 1991). Despite the progress that has been made, however, no consensus has been reached on whether acidic deposition has significantly increased soil acidity in declining red spruce forests of the northeastern United States. Varying interpretations of the effects of acidic deposition on soil chemistry in red spruce forests result from difficulties in quantifying processes such as plant uptake, weathering and leaching by organic acids, and also from a lack of data that characterizes the regional variability of these processes.

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With support from the Northern Global Change Research Program, a joint project was begun by the U.S. Geological Survey, the USDA Forest Service, the University of Illinois, and Yale University to investigate relations between acidic deposition and the health of northeastern red spruce forests. A primary goal of this project was to determine if acidic deposition has caused measurable changes in soil chemistry in these forests. This report summarizes data on Ca and Al concentrations in soil and soil-solution samples from 12 red spruce forests in the northeastern U.S., and compares these data to results reported by Heimburger, 1934 and Lunt, 1932 for the same region.

METHODS

Sites were selected to include the four physiographic regions in the Northeast where spruce forests are common; the Adirondack Mountains of New York, Green Mountains of Vermont, White Mountains of New Hampshire and low-to-mid elevation areas in Maine. The sites were selected to encompass the range of conditions found in red spruce forests in the Northeast with respect to elevation, climate, bedrock, mineral weathering characteristics, acidic deposition, and forest-stand condition. Each site was sampled either two or four times during 1992 and 1993.

Soil samples were collected from the Oa horizon and top 10 cm of the B horizon from the faces of nine soil pits during each sampling. Exchangeable-Ca concentrations were measured by NH_4Cl extraction, and mineral-matter concentrations were measured by loss-on-ignition, by the methods of Blume et al. (1990). Exchangeable-Al concentrations were measured by the method of Thomas (1982). Acid-extractable Ca concentrations were measured by the methods of Friedland et al. (1984), and total Ca concentrations were analyzed by neutron activation (Parry, 1991). Mineral Ca concentrations were calculated as the difference between total Ca concentrations and acid-extractable Ca concentrations.

Soil solutions were collected by a new method developed for this project, termed solution expulsion (Lawrence, et al. 1992). The solution-expulsion method was specifically designed to avoid the effort and expense required for lysimeter installations and to enable collection of soil solutions at a large number of sites regardless of soil moisture conditions before or at the time of sampling. In this method a soil sample is collected and then compressed in a PVC cylinder to increase bulk density by about 40 percent. A solution chemically similar to throughfall is then added to saturate the soil. Water not held by the soil is allowed to drain by gravity and is discarded. Positive air pressure is then applied to expel the remaining soil solution, which can then be chemically analyzed. Extensive experimentation has shown that the technique gives reproducible results that are insensitive to moderate changes in bulk density, duration of contact between soil and solution, and chemical concentrations of the added solution. Soil solutions were expelled from all Oa and B horizon samples and were chemically analyzed by the methods cited in Lawrence and Fernandez, (1991).

A literature search on the past and present status of available Ca in soils of northeastern red spruce forests, was also conducted to locate all data collected since 1980 that could be directly related to our study, plus any comparable data that was collected before the onset of acidic deposition in the region (assumed to be 1950).

RESULTS AND DISCUSSION

Samples from all 12 sites indicated that exchangeable Ca concentrations varied between 2.1 and 21.6 $\text{cmol}_c \text{ kg}^{-1}$ in Oa horizons and 0.41 to 0.68 $\text{cmol}_c \text{ kg}^{-1}$ in the upper B horizon. All comparable data on exchangeable Ca concentrations from other studies in northeastern red spruce stands were within these concentration ranges, except for the concentration reported for the O2 horizon by Mollitor and Raynal (1982), of 1.07 $\text{cmol}_c \text{ kg}^{-1}$, which was about half the concentration we measured at Mt. Abraham, Vermont, our lowest value. At most sites, exchangeable Ca was the largest fraction of total Ca in the forest floor; exceptions were sites with the highest mineral matter concentrations, where mineral Ca was 55 to 70 percent of total Ca.

Concentrations of acid-extractable Ca measured in our study ranged from 13.9 mmol kg^{-1} at Mt. Abraham, Vermont, to 102.6 mmol kg^{-1} at Sleepers River, Vermont. Comparison of these values to those of Heimburger (1934) and Lunt (1932) for the White Mountains of New Hampshire and Adirondack Mountains of New York, indicates a highly

probable regional decrease in acid-extractable Ca concentrations since the 1930's (Fig. 1). Concentrations were less than the value we measured at Sleepers River (the site with the highest concentration in our study), at only nine of 38 sites sampled in the previous studies.

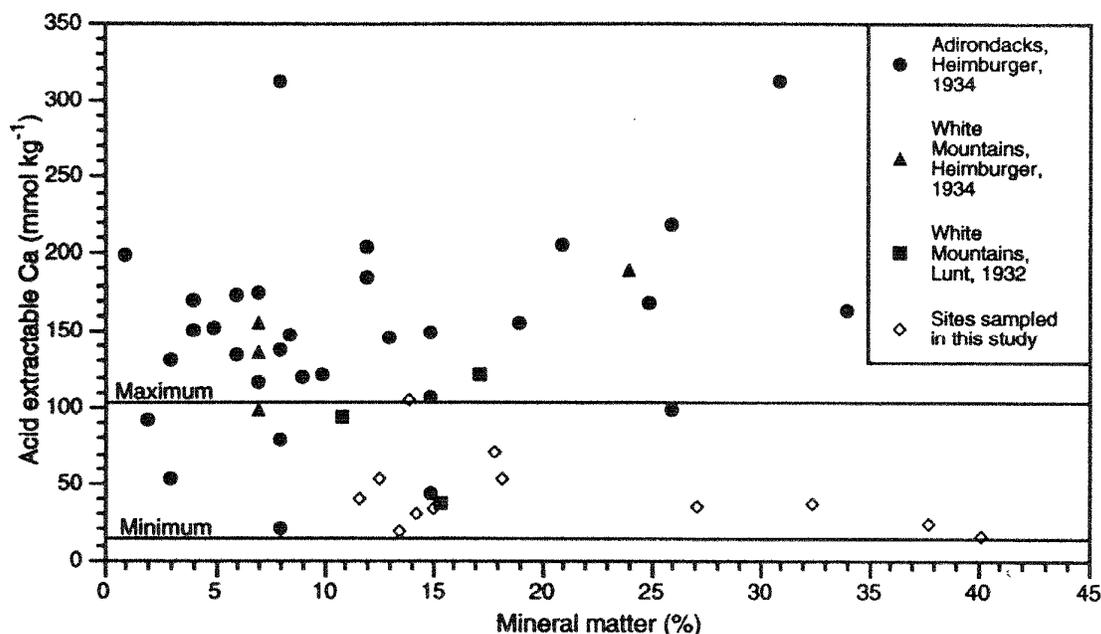


Figure 1. Acid-extractable Ca concentrations in Oa horizons of red spruce stands as a function of mineral matter concentrations (measured by loss-on-ignition), as determined by Heimburger (1934), Lunt (1932), and this study. Maximum and minimum lines represent the highest and lowest concentrations measured at the 12 sites we sampled.

Results of this study indicated, however, that concentrations of exchangeable Ca in the Oa horizon were correlated with neither exchangeable-H concentrations nor with soil pH ($p > 0.1$), but were inversely related to concentrations of exchangeable Al. Although an inverse relation between exchangeable Ca and Al concentrations in the mineral soil has been frequently observed (Johnson and Fernandez, 1992), this study is the first to identify the same relation in the forest floor, over a wide range of sites. This finding led to the hypothesis that the documented decreases of root-available Ca concentrations were associated with increases in concentrations of reactive forms of Al. No data from previous studies were available from which to evaluate temporal trends of forest-floor Al concentrations, but analysis of archived Oa-horizon soil samples collected from red spruce-balsam fir (*Abies balsamea* (L.) Mill) stands at the Hubbard Brook Experimental Forest (HBEF), New Hampshire suggested that, over the past two decades, concentrations of exchangeable and acid-extractable Al have increased, while concentrations of exchangeable and acid-extractable Ca have decreased, although the increase for exchangeable Al was not statistically significant.

The primary mechanism for incorporating Al into the forest floor has been hypothesized to be mixing of mineral soil with the forest floor through tree uprooting (Rustad, 1988), and a strong relation found between total Al and mineral content in this study ($p < 0.01$; $R^2 = 0.79$) supports this hypothesis. Once in the forest floor, mineral forms of Al can be mobilized by naturally derived organic acids, although dissolved Al is typically undersaturated with respect to mineral solubility in this horizon (Walker et al. 1990). Acidic deposition provides an additional source of H^+ that could possibly enhance Al mobilization and result in an increase in concentrations such as those observed at the HBEF. Results also showed, however, that in the forest floor, neither exchangeable- nor reactive-nonexchangeable Al (acid-extractable Al minus exchangeable Al) concentrations were related to mineral Al (total Al minus acid-extractable Al) concentrations, although exchangeable and reactive-nonexchangeable Al concentrations were positively correlated with each other ($p < 0.01$; $R^2=0.60$).

Table 1. Mean concentrations of exchangeable and acid-extractable Al and Ca in Oa-horizon soil samples collected in spruce-fir stands at the Hubbard Brook Experimental Forest, New Hampshire. Samples collected in 1969 and 1970 were averaged together, as were samples collected in 1987 and 1992. Means are based on nine to 14 samples. Statistically significant differences ($p < 0.05$) between sampling periods, determined from the Wilcoxon nonparametric test and the Tukey means separation test, are indicated by differing superscripts. Standard deviations are given in parentheses.

Sampling period	Exchangeable ($\text{cmol}_c \cdot \text{kg}^{-1}$)		Acid Extractable ($\text{cmol}_c \cdot \text{kg}^{-1}$)	
	Al	Ca	Al	Ca
1969-70	2.5 ^a (1.1)	8.3 ^a (4.4)	19.3 ^a (10.2)	9.9 ^a (6.4)
1987, 1992	3.7 ^a (2.9)	3.5 ^b (2.1)	37.0 ^b (21.6)	4.6 ^b (2.9)

An alternate mechanism that could potentially increase exchangeable- and reactive- nonexchangeable Al concentrations in the forest floor is transport of mobile Al from the mineral soil through both biocycling (Rustad and Cronan, 1989) and movement of soil water (Mulder et al. 1991). Soil-solution data from our study indicated that inorganic Al was being mobilized in the B horizon at all sites. Soil-solution pH values were in the range in which Al is readily soluble (4.1 to 4.8), and the ratios of inorganic Al to Ca in mineral-soil solution (1.5 to 16.4) exceeded 1.0, above which numerous experiments indicate that Al can effectively compete with Ca for root exchange sites (Cronan and Grigal, 1995). The role of mineral-soil solution as a control of the size of the exchangeable-Al pool in the forest floor is corroborated by the strong positive relation between the Al-to-Ca ratio in mineral soil solution and the exchangeable-Al content in the forest floor (Fig. 2).

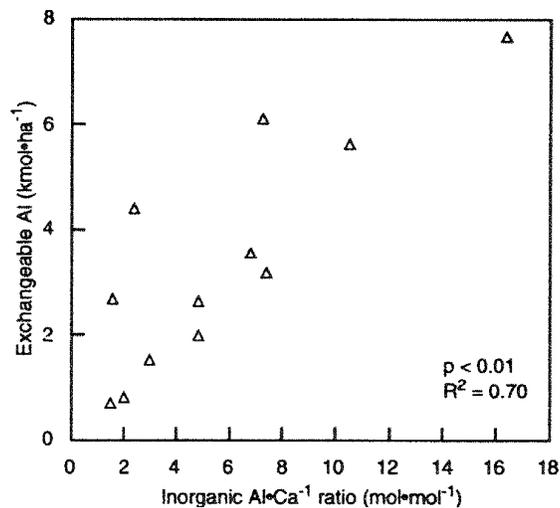


Figure 2. Exchangeable-Al content in Oa horizons of red spruce stands as a function of the molar inorganic Al-to-Ca ratio in B horizon soil solution. Exchangeable Al was expressed as content to normalize the data for varying forest-floor thicknesses. Each triangle represents the mean of 15 to 18 soil and soil-solution samples (combined into five to six samples before analysis) collected at each of 12 sites. One of the 13 sites was omitted because there was insufficient B horizon soil to sample.

We propose that Al mobilization in mineral-soil horizons, brought about by acid deposition, has significantly contributed to the documented decrease of root-available Ca in the forest floor of red spruce forests. Acidic deposition also might have enhanced Al mobilization from mineral matter within the forest floor, but the mechanisms of this process are currently unknown. In either case, mobile Al can exchange with Ca through its strong affinity for organic exchange sites (Deconink, 1980), increasing the susceptibility of Ca to leaching and also increasing the chemical similarity between the forest floor and the mineral soil.

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CALCIUM STATUS OF THE FOREST FLOOR IN RED SPRUCE FORESTS OF THE
NORTHEASTERN U.S. - PAST, PRESENT AND FUTURE

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Dieback and growth decline of red spruce (*Picea rubens*) in the eastern U.S. coincides with the period of acidic deposition, and has led to much speculation as to whether this decline is caused by decreased root-available Ca in the soil. Results of intensive research at several sites have led to conflicting conclusions as to whether acidic deposition has depleted Ca concentrations in the rooting zone to the degree that would cause growth decline in red spruce. Regional evaluations of the current status of soil Ca in red spruce forests have been limited by the small number of sites at which soil and soil solution Ca concentrations have been measured with comparable methods. Comparisons with historical data have also been limited by a lack of current data that is directly relatable. To obtain the additional data necessary for a regional analysis of soil Ca in red spruce forests, either 18 or 36 soil and soil solution samples were collected in 1992-93 from 12 sites in New York, Vermont, New Hampshire and Maine in a study supported by the USDA Forest Service Global Change Research Program. These sites represent the range of environmental conditions and stand health for red spruce in the northeastern U.S. Comparison with results from separate studies by Heimburger and Lunt in the 1930s indicate that current acid-extractable Ca concentrations in the Oa horizon are less than one-half the average measured in the 1930's. A statistically significant decrease of similar magnitude was also observed for both exchangeable and acid-extractable Ca, over the past two decades, in archived samples collected in red spruce stands at the Hubbard Brook Experimental Forest, N.H. The average ratio of inorganic Al to Ca in mineral-soil solution for the 12 sites was 5.0, indicating that inhibition of Ca uptake by Al in the mineral soil may have contributed to the decline of Ca concentrations in the forest floor. A Ca budget, developed through the use of Sr isotope ratios to estimate weathering rates, suggests that root-available Ca in the northeastern U.S. will likely continue to decline.

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