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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.

## PUTRESCINE: A MARKER OF STRESS IN RED SPRUCE TREES

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**Abstract:** Aluminum (Al) has been suggested to be an important stress factor in forest decline due to its mobilization in soil following atmospheric deposition of acidic pollutants. A major goal of our research is to develop physiological and biochemical markers of stress in trees using cell cultures and whole plants. Needles of red spruce (*Picea rubens*) collected from several sites in the northeastern United States and red spruce cells grown in suspension cultures were examined for polyamine and inorganic-ion content. The cells in culture were exposed to various concentrations of Al for different lengths of time. Exposure to Al increased putrescine biosynthesis and lowered the concentrations of cellular Ca, Mg, Mn, and K. No treatments were applied to the trees but some of the sites were known to be under "general environmental stress" as indicated by a large number of dead and dying red spruce trees. All of the sites, while differing in geochemistry, had a soil pH value below 4.0. Data collected from field studies enabled us to categorize these sites on the basis of cellular levels of putrescine and soil chemistry. Needles from trees growing on Ca-rich soils (organic horizon) with low exchangeable Al:Ca ratios had lower levels of putrescine than those from trees growing on Ca-poor soils with high Al:Ca ratios.

### INTRODUCTION

The negative effects of acidic deposition on soil fertility, possibly due to the mobilization of Aluminum (Al) and leaching of bases, are of major concern because such processes can impact forest growth over large areas. Although exposure to low levels of pollutants under natural conditions may not result in immediate visible injury, subtle physiological and biochemical changes may still be quantifiable. The ability to detect these changes at an early stage would enable us to predict future forest damage and may suggest means to reduce the severity of such damage. Therefore, it is necessary to develop a set of early physiological and biochemical indicators to assess possible adverse effects of soil Al and Calcium (Ca) concentrations on forest growth.

Changes in the Al:Ca ratio of the soil solutions are correlated with Al stress and nutrient imbalances in sensitive tree species (Cronan and Grigal 1995). Among the effects of Al on plants are inhibition of cell division, DNA synthesis, needle biomass, root growth, and seedling height (McQuattie and Schier 1990, Schier et al. 1990). Al also affects the uptake of Ca and other inorganic ions (Minocha et al. 1992, Zhou et al. 1995). Earlier work by our group suggests that changes in the Al:Ca ratio in fine roots of red spruce growing under stress may be linked to increased vulnerability and mortality of trees (Shortle and Smith 1988). However, the primary sites of Al toxicity and the chain of biochemical and molecular events through which Al exerts its toxic effects are not well understood (Delhaize and Ryan 1995).

Recently, considerable attention has been focused on the study of changes in the metabolism of aliphatic polyamines (putrescine, spermidine, and spermine) in plants subjected to various kinds of environmental stress. The cellular polyamine content is highly regulated and stimuli such as Ca and magnesium (Mg) deprivation, high salinity, sulfur dioxide (SO<sub>2</sub>) fumigation, pathogenesis, osmotic stress, ozone, and acid stress lead to an accumulation of one or more of the polyamines (Galston 1989, Flores 1991). This increase in polyamines generally is accompanied by

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increased activity of their biosynthetic enzymes. Studies with cell cultures of a woody plant, *Catharanthus roseus*, showed that treatments with Al caused changes in cellular polyamines, particularly putrescine, while also causing inverse effects on cellular Ca levels (Minocha et al. 1992, Zhou et al. 1995). Therefore, we hypothesized that changes in levels of cellular putrescine or putrescine/spermidine ratios could be used as an early indicator of the stress response not only in cell cultures but also in mature forest trees.

The objectives of this study were to: 1) analyze changes in putrescine and putrescine/spermidine molar ratios in response to Al stress using cell cultures of red spruce; 2) determine cellular polyamine levels in needles of mature red spruce trees growing under stress; and 3) determine if there is a correlation between putrescine in needles of mature red spruce trees and Ca levels in soil solutions of the Oa and B horizons or exchangeable Al:Ca charge ratios in the Oa horizon.

## MATERIALS AND METHODS

### Cell Culture Studies

**Culture conditions.** Suspension cultures of *Picea rubens* were obtained from Dr. Krystyna Klimaszewska, Petawawa National Forestry Institute, Chalk River, ON, and maintained in half-strength Litvay's medium (Litvay et al. 1981) as modified by Klimaszewska (personal commun.). Modifications included the addition of 0.5 g/L glutamine, 1.0 g/L casein hydrolysate, 2 percent sucrose (rather than 3 percent), 9.05  $\mu\text{M}$  2,4-D, and 4.44  $\mu\text{M}$  BA. In addition, iron-EDTA was replaced by 40 mg/L of a plant product called sequestrine containing 7 percent iron chelate (Plant Products Co., Brampton, Ontario L6T1). The medium was adjusted to pH 5.7 before it was autoclaved. Cells were subcultured at intervals of seven days by transferring 15 ml of cell suspension into 45 ml of fresh medium in 250-ml Erlenmeyer flasks. The flasks were kept in darkness at 25 °C  $\pm$  2 on a gyratory shaker at 120 rpm.

The Al levels (0.2, 0.5, and 1.0 mM of  $\text{AlCl}_3$ ) used in cell-culture experiments were based on earlier work on the effects of Al on growth. The pH of the medium at the time of Al addition was 4.2 or lower. To study Al speciation in this medium Al was added to the cell-free medium or to three-day-old cell cultures. In either case, about half of the added  $\text{AlCl}_3$  was found to be precipitated. Before analysis for monomeric Al, the precipitate was removed by centrifuging the medium.

For experimental treatments, filter-sterilized  $\text{AlCl}_3$  was added to a final concentration of 0.2, 0.5, or 1.0 mM to 20 ml of three-day-old cells maintained in 50-ml flasks. The flasks were kept on a gyratory shaker at 120 rpm until analysis. The pH of the medium, which remained around 4.2  $\pm$  0.3 after 24 h of subculture, was not adjusted during the incubation period. Each treatment was run in triplicate and each experiment was run at least three times. At the end of the treatment period, cells were collected and analyzed for polyamines and inorganic ions by methods described in the section that follows.

**Inorganic ion analysis.** Cells were collected on Miracloth by vacuum filtration, washed thoroughly with deionized distilled water, and weighed. One hundred mg of cells were frozen and thawed (3X) in 10 ml of 0.01 N HCl (Minocha et al. 1994). Extracts were centrifuged at 18,000 g for 20 min at 4 °C or filtered through a 45- $\mu\text{m}$  nylon syringe filter. The supernatant solutions or the filtrates were analyzed for inorganic ion content with a Beckman Spectrospan V ARL DCP (Direct Current Plasma Emission Spectrometer, Beckman Instruments, Inc., Fullerton, CA) using the Environmental Protection Agency's method number 66-AE0029 (1986).

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<sup>5</sup>The use of trade, firm, or corporation names in this publication is for the information of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture or the Forest Service of any product or service to the exclusion of others that may be suitable.

Polyamine analysis. Cells were collected and extracted in 5 percent perchloric acid (PCA) in the manner described for inorganic ions. Extracts were centrifuged at 18,000 g for 20 min at 4 °C. The supernatant fractions were used for dansylation and quantification of polyamines by high performance liquid chromatography (HPLC) (Minocha et al. 1990).

## Whole-Plant Studies

### Sites

Six sites from the northeastern United States were selected for collection of soil, root, wood-core, and needle samples, as part of a collaborative effort funded under the USDA Forest Service Global Change Program. The sites were located at Howland, Lead Mountain, and Kossuth, ME; Crawford Notch, NH; Groton, VT; and Big Moose, NY. Seventy-two red spruce trees were selected randomly and tagged at each site at the beginning of the study. Each site was sampled twice a year for two years except for needle samples from Kossuth and Big Moose, which were sampled once a year. Soil and needle samples were collected within one year of each other. Visual observations at each site indicated that Howland, Kossuth, and Groton had no dieback or unusual mortality but that stands at the Big Moose and Crawford Notch were experiencing dieback. The stand at Lead Mountain, also known as Bear Brook, is relatively younger and did not exhibit dieback.

### Needle Samples

Extraction of acid soluble polyamines and inorganic cations. Ten of the 72 flagged trees were selected from each site for collection of needle samples. In some instances, because of difficulty in reaching branches of tall trees, untagged trees in the vicinity of tagged trees in the same stand were selected for needle samples. Needles from current- and previous-year growth were collected from freshly cut branches in the field and immediately placed in individual preweighed microfuge tubes containing 1 ml of 5 percent PCA. The tubes were kept on ice during transportation to the laboratory. The tubes were stored at -20 °C until they were processed. The samples were weighed, frozen and thawed (3X), and centrifuged at 14,000 rpm for 10 min. The supernatant was used directly for polyamine analysis or for inorganic-ion analysis after proper dilution with distilled, deionized water (final concentration of PCA 0.01 or 0.02 N) by the procedures described earlier.

### Soil Samples

At each sampling time, three clusters of three trees each were selected from the 72 tagged trees. Soil samples were collected from the Oa horizon and upper 10 cm of the B horizon near each of the nine selected trees and combined for each cluster. Thus, 12 pooled samples from the Oa and B horizons were collected at each site over the four sampling periods.

Analysis of exchangeable Ca and Al in soil. Soil samples were extracted with 1 M ammonium chloride and the extracts were analyzed for Ca by the procedure of Blume et al (1990). Exchangeable Al was determined in 1 M KCl extracts (Thomas 1982).

Ca in soil solution. Each soil sample was placed in a sealed cylinder and an artificial throughfall (chemically similar to Howland site throughfall) was added to attain a moisture content that approximated field capacity. The soil solution was expelled by positive air pressure from the soil that was placed in the sealed cylinder. This procedure for extraction of soil solution was developed by Lawrence et al. The soil solution was analyzed for aqueous Al species and other ions according to the procedures of Driscoll (1984) and Lawrence et al. (1995).

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<sup>6</sup>Lawrence, G. B. and M. B. David. A new method for collecting soil-solution in forest soils. In preparation.

## RESULTS

### Cell Culture Studies

Adding  $\text{AlCl}_3$  to the cell-free medium or cell cultures resulted in precipitation of 50 to 60 percent of the added Al even when the medium pH was 4.2 or lower. This medium contains a nursery product called "sequestrine", which has 7 percent iron-EDTA. The remaining undefined component(s) of sequestrine in half-strength Litvay's medium was largely responsible for the precipitation of Al (data not presented). All of the soluble Al was present in monomeric form at final concentrations of 0.085, 0.22, and 0.510 mM, respectively for the 0.2, 0.5, and 1.0 mM  $\text{AlCl}_3$  added to the cultures. More than 75 percent of this total monomeric Al was present as inorganic monomeric Al.

A significant negative growth effect was observed with the 1.0 mM Al treatment, as early as one day after the addition of Al. The 0.2 mM Al treatment had no significant effect on growth for the first three days. A dose-dependent inhibition of growth increased with increasing incubation time for treatments after four days (Fig. 1).

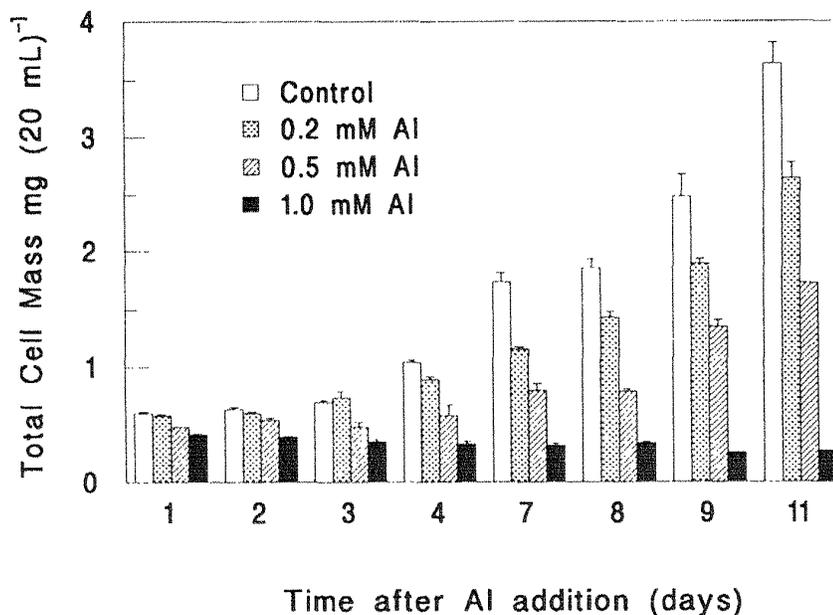


Figure 1. Effects of aluminum chloride on total cell mass in three-day-old cell cultures of red spruce (data are mean  $\pm$  SE of three replications).

Effects of Al on cellular putrescine metabolism were observed as early as 4 h after treatment (Fig. 2). In general, Al caused a dose-dependent elevation of cellular putrescine in these cells at all times ( $\alpha = 0.05$  for 0.5 and 1.0 mM Al). Spermidine levels were not affected or showed a slight increase (Fig. 3). This effect was not always dose-dependent.

There was an increase in cellular concentrations of Al and P in response to Al additions at all times tested (Fig. 4). This increase always was dose-dependent for Al. There was no change in cellular levels of Al between 4 and 48 h when cultures were incubated with 0.2 mM Al. However, the concentration of Al in 1.0 mM Al-treated cells increased from  $11.4 \mu\text{mol (g FW)}^{-1}$  at 4 h to  $23.94 \mu\text{mol (g FW)}^{-1}$  at 24 h after incubation. The content of cellular potassium (K) showed a dose-dependent decrease with all concentrations of Al. Both manganese (Mn) and Mg decreased following treatment with 0.5 and 1.0 mM Al, while Ca was significantly reduced only by 1.0 mM Al.

A comparison of putrescine/spermidine ratios showed a significant increase in these ratios with Al treatment (Fig. 5). This increase generally was dose-dependent.

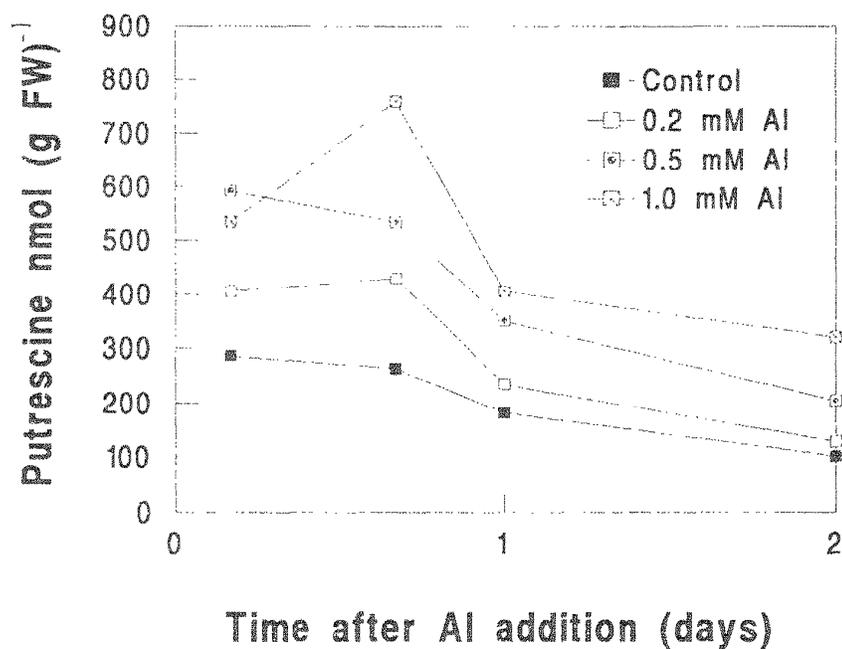


Figure 2. Effects of aluminum on cellular levels of putrescine in three-day-old cell cultures of red spruce (data are mean  $\pm$  SE of three replications).

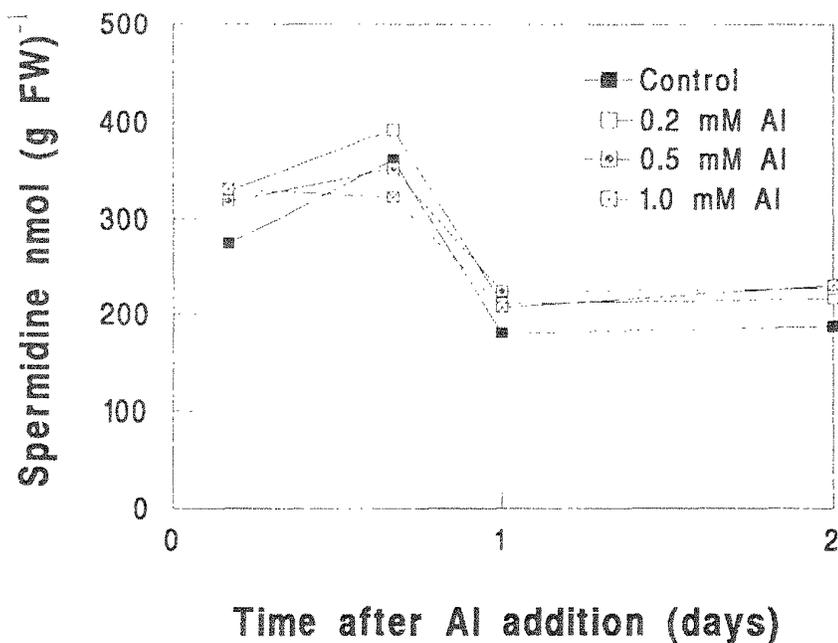


Figure 3. Effects of aluminum on cellular levels of spermidine in three-day-old cell cultures of red spruce (data are mean  $\pm$  SE of three replications).

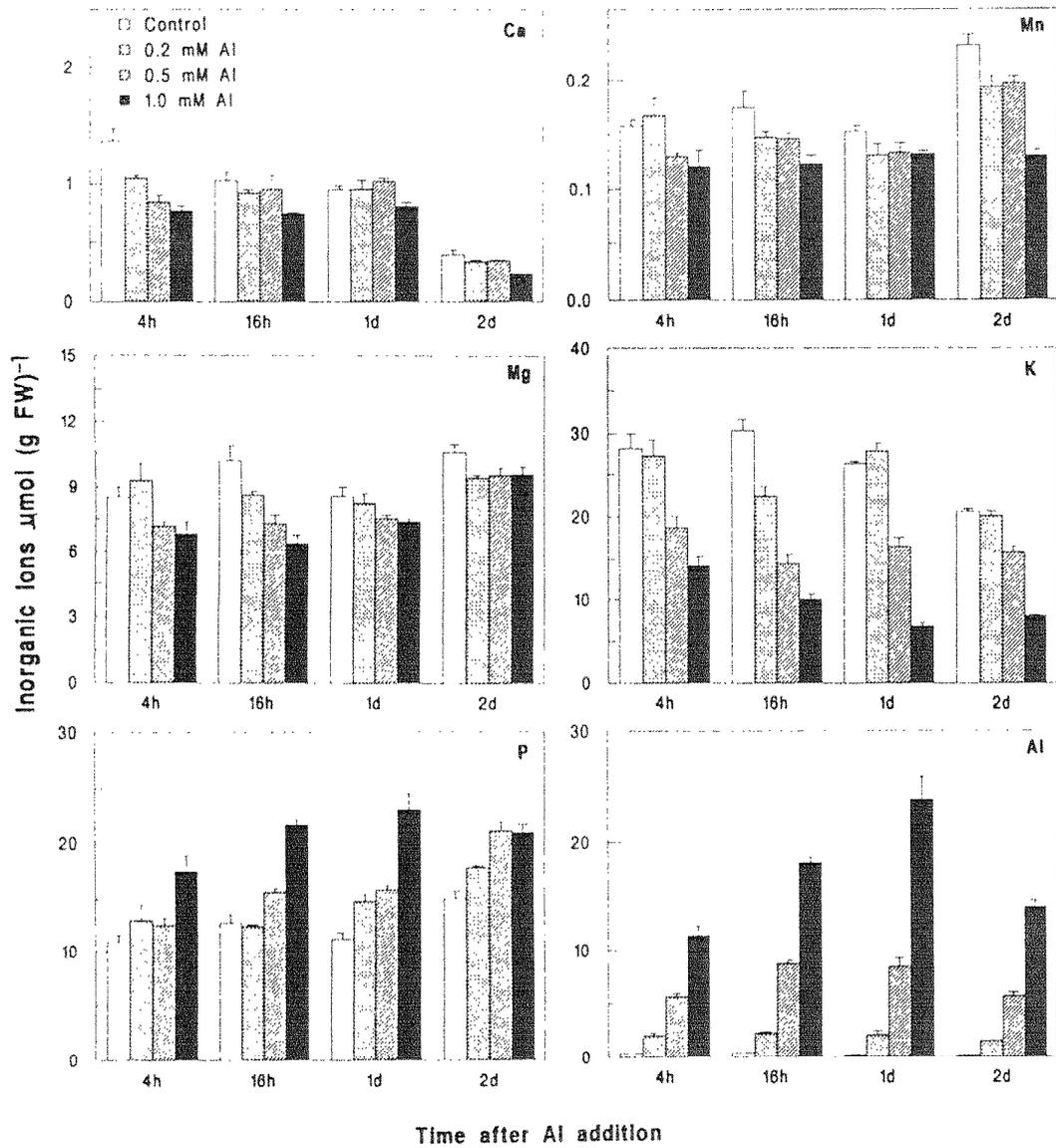


Figure 4. Effects of aluminum on cellular levels of inorganic ions in three-day-old cell cultures of red spruce (data are mean  $\pm$  SE of three replications).

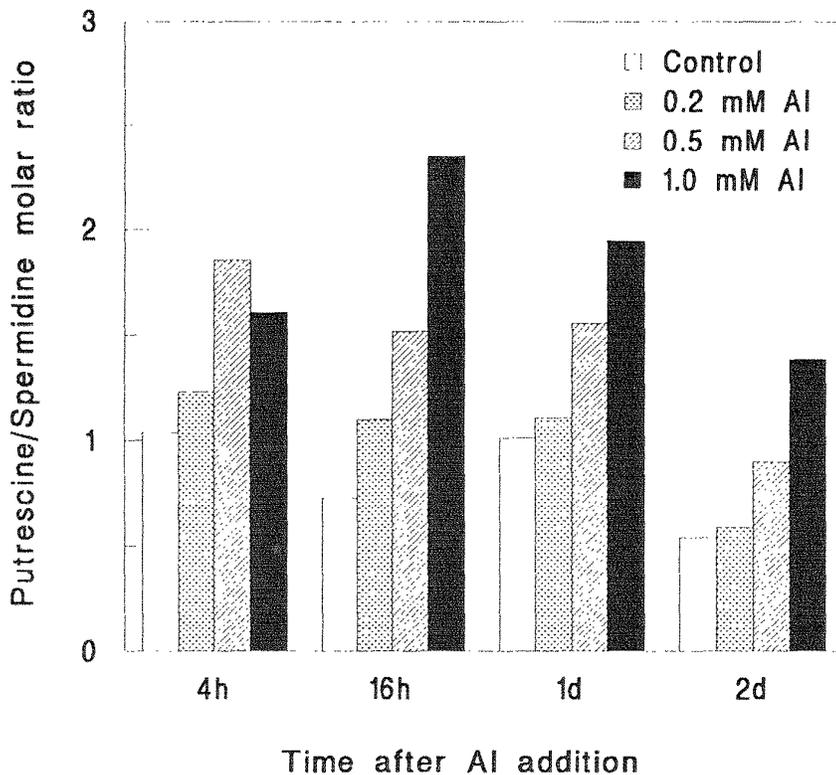


Figure 5. Effects of aluminum on putrescine/spermidine molar ratio in three-day-old cell cultures of red spruce (data are mean  $\pm$  SE of three replications).

#### Whole-Plant Studies

All field sites sampled had a soil pH (measured in 0.01 M CaCl<sub>2</sub>) of 2.56 to 3.11 and 3.58 to 4.46 for the Oa and B horizons, respectively. However, these sites differed in soil Ca and Al levels as well as general tree stress. While Groton and Howland showed no obvious signs of dieback, Crawford Notch and Big Moose exhibited higher general stress as indicated by a high rate of dieback and mortality. Levels of cellular putrescine generally were higher in needles of red spruce trees growing at sites with higher exchangeable Al:Ca ratios (Fig. 6). Differences in putrescine levels between sites were statistically significant ( $P < 0.01$ ). Putrescine levels in the needles were significantly correlated to the charge ratio of exchangeable Al:Ca in the Oa horizon of the forest floor ( $r^2 = 0.68$ ,  $P = < 0.02$ ) (Fig. 6). Whereas putrescine levels in the needles showed a significant correlation with Ca in the soil solution of the Oa horizon of the forest floor ( $r^2 = 0.58$ ,  $P = < 0.05$ ), there was no correlation with the Ca concentration in the soil solution of the upper 10 cm of the B horizon of the mineral soil ( $r^2 = .03$ ) (Table 1).

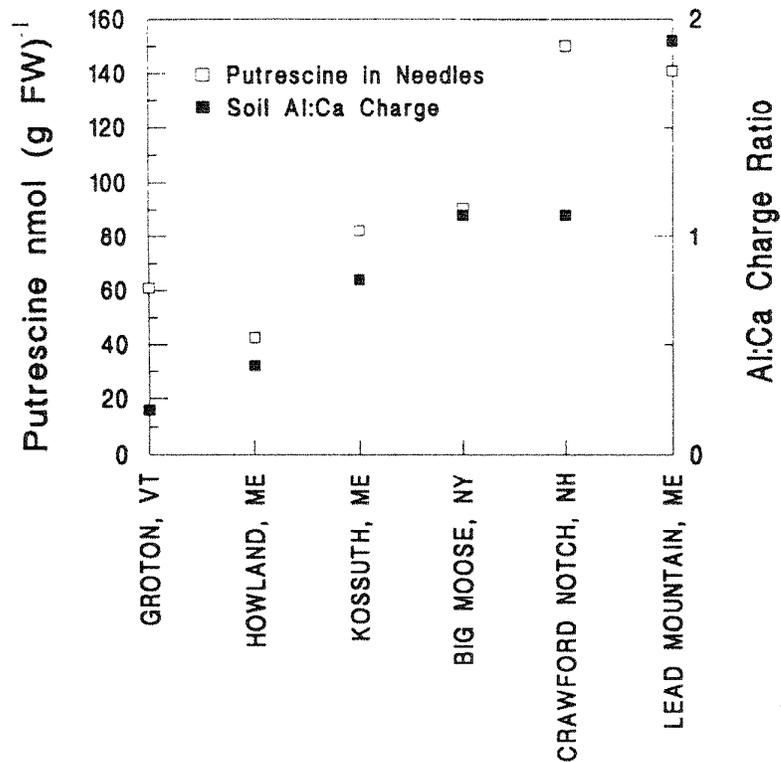


Figure 6. Comparison of putrescine in needles of red spruce trees and charge ratio of exchangeable Al:Ca in Oa horizon of the forest floor for the six sites studied. Data for putrescine are mean of 80 replicate analyses (except for Kossuth, ME, and Big Moose, NY, for which n = 40). Each value for soil data represents 36 samples collected individually and combined into 12 samples for analysis. (Data for Al:Ca are a mean of 12 replicate analyses).

Table 1. Comparison of putrescine in needles of red spruce trees, Ca in soil solution of Oa horizon of forest floor, and Ca in soil solution of upper 10 cm of B horizon of mineral soil for six sites studied. Data for putrescine are mean  $\pm$  SE of 80 replicate analyses (except for Kossuth, ME; and Big Moose, NY; for which n = 40). Each value for soil data represents 36 samples collected individually and combined into 12 samples for analysis (data for Ca are mean  $\pm$  SE of 12 replicate analyses).

Site	Putrescine in needles (nmole/g FW)	Ca in soil solution of Oa -----( $\mu$ mol/L)-----	Ca in soil solution of B
Groton, VT	60.9 $\pm$ 5.2	182 $\pm$ 43	6 $\pm$ 1
Howland, ME	42.6 $\pm$ 3.3	143 $\pm$ 28	5 $\pm$ 1
Kossuth, ME	82.3 $\pm$ 7.7	85 $\pm$ 27	5 $\pm$ 1
Big Moose, NY	90.4 $\pm$ 7.1	22 $\pm$ 2.9	5 $\pm$ 1
Crawford Notch, NH	150.2 $\pm$ 12.3	47 $\pm$ 13	4 $\pm$ 1
Lead Mountain, ME	140.9 $\pm$ 13.1	30 $\pm$ 3.9	8 $\pm$ 1

## DISCUSSION

Joslin and Wolfe (1988) reported a significant reduction in root and foliar biomass with an increase in the levels of inorganic monomeric Al in the soils, and Ohno et al. (1988) found a negative correlation between biomass of needles and concentration of Al in the needles of red spruce. The data presented here using suspension cultures of red spruce are consistent with these reports. The inhibition of DNA synthesis and cell division had been previously associated with a reduction in the growth of Al-treated cells or plants (Maniwaki et al. 1992, Ulrich and Clarkson 1992).

While the effects of Al on K uptake vary with plant species (Cummings et al. 1985, Godbold et al. 1988, Ohno et al. 1988, Schier et al. 1990); Al often causes a reduction in Mg and Ca in needles, roots, or shoots of spruce and pine seedlings (Asp et al. 1988, Ohno et al. 1988, Schroder et al. 1988, Schier et al. 1990, Jentschke et al. 1991). In our study with red spruce cultures, a decrease in accumulation of Ca, Mg, Mn, and K was coincident with an increase in putrescine. The observed decrease in K uptake in response to Al may be related to the efflux of malate and K, as seen in the root apices of wheat (Ryan et al. 1995). This has been suggested as a mechanism for Al detoxification (by chelation) around the critical growth region of the root (Delhaize and Ryan 1995). The observed increase of P in Al-treated cells is consistent with previous studies (Asp et al. 1988, Bengtsson et al. 1988, Maniwaki et al. 1992). See Zhou et al. (1995) for a discussion of the interaction between Al and P.

Various biological and chemical agents induce the accumulation of cellular putrescine in several plant species (Dohmen et al. 1990, Santerre et al. 1990, Flores 1991). The increase in putrescine generally was accompanied by an increase in arginine decarboxylase activity (Flores 1991). Treatment with Al also resulted in an increase in cellular putrescine in our study. This effect generally was dose-dependent and could be observed as early as 4 h after treatment. In most plants, while levels of both putrescine and spermidine change in response to growth, it is only putrescine that changes in response to stress. Thus, a molar ratio of putrescine/spermidine might be a better indicator of stress than putrescine concentration alone. In this study, the level of cellular putrescine was significantly higher in the needles of red spruce growing in areas of higher general stress such as Big Moose and Crawford Notch. An exception was at Lead Mountain, despite the higher level of cellular putrescine in needles at that site, the trees did not show any visible signs of stress. However, these trees are much younger than those at Crawford Notch and Big Moose, so they may be better able to cope with stress.

The data from Lead Mountain also indicate that along with high reactive Al concentrations, soil solutions at this site contain high concentrations of nitrate. In healthy coniferous stands nitrogen generally is expected to be growth limiting. This results in low to undetectable concentrations of nitrate in soil solutions. High concentrations of nitrate in soil solutions suggest that the trees at this site may be under early stages of stress that have not yet produced visible symptoms but this stress is detectable by changes in putrescine metabolism. These results are consistent with other studies with Norway spruce (*Picea abies*) that show that cellular putrescine levels and putrescine/spermidine ratios are higher in needles collected from trees growing in polluted areas (Tenter and Wild 1991, Villanueva and Santerre 1989).

An inverse correlation between cellular putrescine and Ca in *Catharanthus roseus* cell cultures treated with Al was reported by Maniwaki et al. (1992) and Zhou et al. (1995). A similar response was seen with the cell cultures of red spruce. This observation supports the view that under stress, putrescine production (a divalent organic cation) may substitute for Ca and Mg deficiency (Cohen and Zalik 1978, Cho 1983). Further analysis showed that there was a significant inverse correlation between putrescine levels of needles and Ca concentration in soil solution and between putrescine levels and exchangeable Al:Ca charge ratio of the Oa horizon of the forest floor at all six sites. The reason for the lack of a correlation between putrescine levels and Ca in the soil solution of the B horizon may be that most roots of red spruce grow only in the Oa horizon. As a consequence the soil chemistry of only this horizon primarily affects the health of the species. Our data also suggest that all parts of a tree need not be exposed to high levels of Al to respond to stress.

The Al/Ca ratio of the soil solution is one of several tools that can be used in assessing and predicting forest health (Cronan and Grigal 1995). Likewise, the molar ratio of Al/Ca rather than absolute amounts of these ions in root tips of spruce has been suggested as being important in determining the level of Al toxicity (Shortle and Smith 1988,

Schroder et al. 1988). Several studies have been reported where an Al/Ca molar ratio of greater than 1.0 in the soil solution, growth medium, or inside the cells had inhibitory effects on growth (Schier 1985, Stienen and Bauch 1988, Kruger and Sucoff 1989, Schulze 1989). On the basis of a critical review of the literature on Al stress, Cronan and Grigal (1995) estimated that there may be a 50, 75 and 100 percent risk of adverse impacts on tree growth or nutrition with molar Al:Ca ratios of 1, 2 and 5, respectively. We demonstrate here that an increase in cellular putrescine level in response to direct or indirect stress imposed on trees by Al exposure may be considered as another type of tool for assessing and predicting forest health. Further, the similarity of our results (on Al effects on growth and inorganic-ion uptake) using cell cultures of red spruce with the results obtained by others using seedlings of red spruce indicates that the cell cultures grown in vitro are highly suitable for studies of the mechanisms of Al effects on the metabolic processes of cells.

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LONG-TERM CHANGES IN THE ACIDITY OF A DEKALB FOREST SOIL IN THE MID-REGION OF THE  
SUSQUEHANNA RIVER WATERSHED

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Forest soil acidification has been reported to result in reduced forest productivity and forest decline. Soil acidification and forest decline may trigger changes in nutrient cycling in forest ecosystems with important consequences for drainage water chemistry and aquatic biota. In an attempt to determine whether or not Pennsylvania forest soils are becoming more acidic, soil samples were collected at six forested sites in Clinton County, Pennsylvania in 1993. Soil chemistry data obtained through two previous studies conducted in 1957 and 1961 were available for each of these sites. Soils were analyzed for pH and exchangeable calcium and magnesium, and results compared to the results obtained in the earlier studies. Soil analysis methods were evaluated to ensure that values obtained in the 1993 sampling were comparable to those of the original investigators. Results indicated significant decreases in pH and exchangeable Mg content at all sites. Exchangeable Ca decreased on the undisturbed sites and increased on the disturbed sites. Significant acidification of these soils has taken place over the past 32-36 years. Comparisons of disturbed and undisturbed sites indicated that at least part of the observed increase in acidification was the result of acid deposition.

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EXPERIMENTAL SOIL WARMING EFFECTS ON C, N, AND MAJOR ELEMENT CYCLING IN A LOW  
ELEVATION SPRUCE-FIR FOREST SOIL

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**Abstract:** The effect of global warming on north temperate and boreal forest soils has been the subject of much recent debate. These soils serve as major reservoirs for C, N, and other nutrients necessary for forest growth and productivity. Given the uncertainties in estimates of organic matter turnover rates and storage, it is unclear whether these soils will serve as short or longer-term net sources or sinks for C and N if mean air and soil temperatures increase over time. In light of these information needs, a thermal manipulation study was initiated in 1991 at the Howland Integrated Forest Study (HIFS) site to investigate the effect of a 5 °C increase in soil temperature on C and N dynamics in a low elevation spruce-fir forest soil. Elevated soil temperatures have been successfully maintained in replicated 15x15 m plots for two field seasons (1993 and 1994) using heat resistance cables buried 2-3 cm from the soil surface at 20 cm spacings. Replicated unheated plots with cables installed ("cabled control") and with no cable installation ("control") serve as the controls. Results to date indicate significantly increased rates of litter decay, fine root production, and CO<sub>2</sub> evolution in the heated plots relative to the controls as well as decreased concentrations of base cations and Mn in buried mineral soil bags. Soil moisture showed a slight but significant decrease in the O horizon in response to the thermal manipulations and no change in the upper B horizon. Although no statistically significant effect of the thermal manipulation has been observed on N mineralization rates during the first two years of this study, the cumulative amount of NH<sub>4</sub>-N mineralized over this period was greater in the heated plots relative to the control plots. No net nitrification has been observed at this site to date. Taken together, results from this thermal manipulation study indicate that modest changes in temperature can significantly alter C, N, and major nutrient dynamics at this site.

## INTRODUCTION

Considerable scientific uncertainty is associated with both the current predictions of climate change as well as the expected effects of this climate change on forest ecosystems. However, it is well documented that tropospheric concentrations of CO<sub>2</sub> are increasing at a rate of ~ 0.5 percent per year (Houghton et al. 1990, Denmead 1991, Keeling and Whorf 1992) and it is commonly agreed that this increase in CO<sub>2</sub> (as well as other "greenhouse" gases) could raise mean global temperature by 2-5 °C or more in the next 50-100 years, with a greater warming occurring in the higher latitudes than at the equator (Bolin et al. 1986, Hansen et al. 1988, IPCC 1990). Changes of this type would undoubtedly have an effect on the growth and character of northern temperate and boreal forests. The soils in these forests serve as major reservoirs for C, N, and nutrients necessary for forest growth and productivity, as well as sinks for "pollutants" ranging from metals to N to various organic compounds. Given the uncertainties in estimates of turnover rates and storage, it is unclear whether these soils will serve as a short or longer-term net source or sink for C and other materials if mean air and soil temperatures increase over time.

To address these information needs, a field study was initiated in 1991 at the Howland Integrated Forest Study site to investigate the effects of a 5 °C increase in soil temperature on processes controlling C and N dynamics in a representative low elevation spruce-fir forest soil in Maine. Specifically, we evaluated the response of CO<sub>2</sub> evolution, soil air CO<sub>2</sub> concentrations, N mineralization and nitrification, soil and soil solution chemistry, litter decay, fine root dynamics, and overstory foliar chemistry to *in situ* experimental manipulations of soil temperature.

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## METHODS

**Study Site.** The study site is located in a low elevation (60 m) commercial spruce-fir forest in east-central Maine (45° 10' N, 68° 40' W), adjacent to the Howland Integrated Forest Study (HIFS) site. The vegetation is dominated by red spruce (*Picea rubens* Sarg.) (~50 percent of live basal area), with occasional co-dominant white pine (*Pinus strobus* L., ~22 percent) and eastern hemlock (*Tsuga canadensis* Carr., 13 percent). Few balsam fir (*Abies balsamea* Mill.) over 4 cm dbh remain from the last spruce budworm infestation. Soils at the site are classified as Aquic Haplorthods developed from an underlying layer of dense basal till. The climate is continental with mean temperature between 5 and 6 °C and mean precipitation slightly more than 100 cm yr<sup>-1</sup> (Lautzenheizer, 1972).

**Experimental Design.** Three 15×15 m plots were established in each of two locations in the study area (separated by ~300 m) in the spring and summer of 1992. One thermal treatment (5 °C above ambient) and two controls (the undisturbed "control" which has no disturbance from cable installation and the "cabled control" in which subsurface cables were installed but not heated) were assigned to one plot in each location in a blocked design. A buried cable method, in which heat resistance cables are installed 2-3 cm below the soil surface at 20 cm intervals, is used to experimentally increase soil temperatures in the heated plots.

**Analytical Methods.** Soil air CO<sub>2</sub> concentrations were measured by extracting gas samples from soil air access tubes and determining CO<sub>2</sub> concentrations on a Gow-Mac 750P chromatograph (Erikson et al. 1990). Carbon dioxide flux was measured using a static chamber technique (modified from Steudler et al. 1989). Nitrogen mineralization and nitrification rates were measured using an on-site buried bag approach (Pastor et al. 1984). Change in mineral soil chemistry was evaluated using a buried mineral bag approach (David et al. 1990) with subsequent analysis for pH (0.01 CaCl<sub>2</sub>), exchangeable Ca, Mg, K, Na, extractable P, exchangeable acidity and Al, and total C, N, and S following the methods of Robarge and Fernandez (1986). Soil solutions were sampled with ceramic cup tension lysimeters and analyzed for major chemical constituents following the methods of Hillman et al. (1985). Litter decay rates were determined using the mesh bag technique (Bocock, 1964). Litter element concentrations were determined using a HCl digest followed by ICP analysis for Ca, Mg, K, P, Fe, Mn and Zn (Munter and Grande, 1981); C and N were determined on a Carlo Erba NA1500 CN Analyzer. Changes in fine root biomass were assessed using root ingrowth cores (modified from Persson, 1984). Fine root and overstory foliage samples were analyzed for total nutrient content using methods identical to those described for litter chemistry.

## RESULTS AND DISCUSSION

Results from the initial two years of this experiment indicate that the buried cable method is highly effective at maintaining surface soil temperatures at 5 °C above ambient at this site (Fig. 1). It is noteworthy that this temperature differential is maintained to a depth of 30-50 cm in the mineral soil (Fig. 2).

Both the summers of 1993 and 1994 were relatively dry when compared with previous years' data at the HIFS. Soil moisture tension was inversely related to throughfall volume, with peak moisture tensions occurring in early September. Soil moisture was slightly but significantly ( $P < 0.05$ ) decreased in the O horizon in the heated plots relative to the control plots. A similar decrease in soil moisture in response to soil warming was observed by Peterjohn et al. (1994) in a hardwood forest in Massachusetts.

Carbon dioxide evolution from the soil surface and soil air CO<sub>2</sub> concentrations both showed significant ( $P < 0.0001$ ) positive exponential relationships with soil temperature. These results are consistent with data from other temperate forests and reflect an increase in microbial decomposition and/or root respiration with increasing temperature (Edwards 1975, Crill 1991, Peterjohn et al. 1994, MacDonald et al. 1995). Carbon dioxide evolution rates in the heated plots were significantly ( $P < 0.05$ ) greater than in the control plots (Fig. 3).

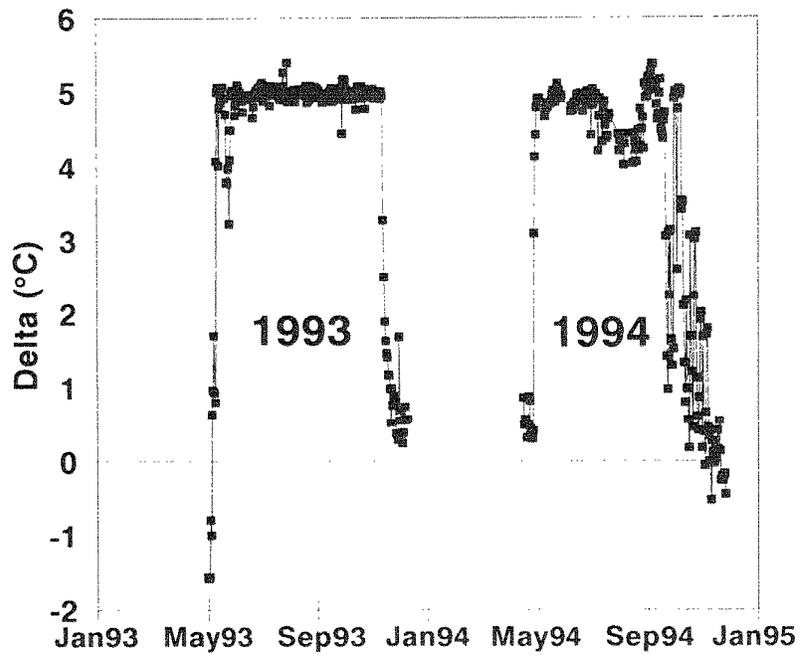


Fig. 1. Mean Temperature Deltas for 1993 and 1994 Field Seasons.

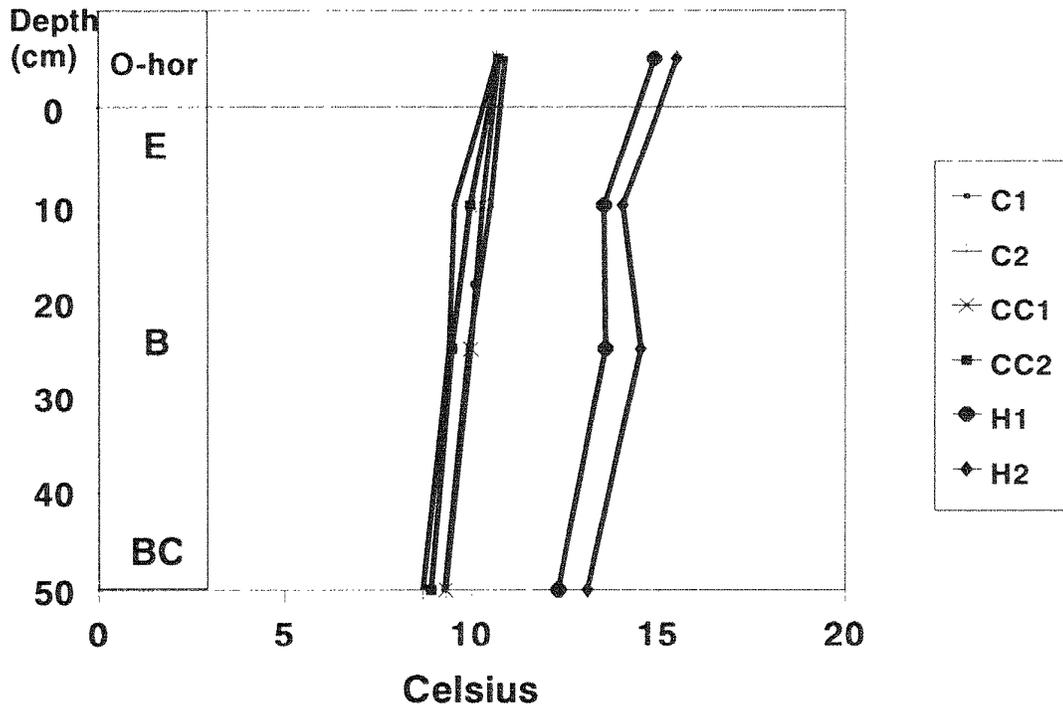


Fig. 2. Average Profile Temperatures for TeMP, 1993.

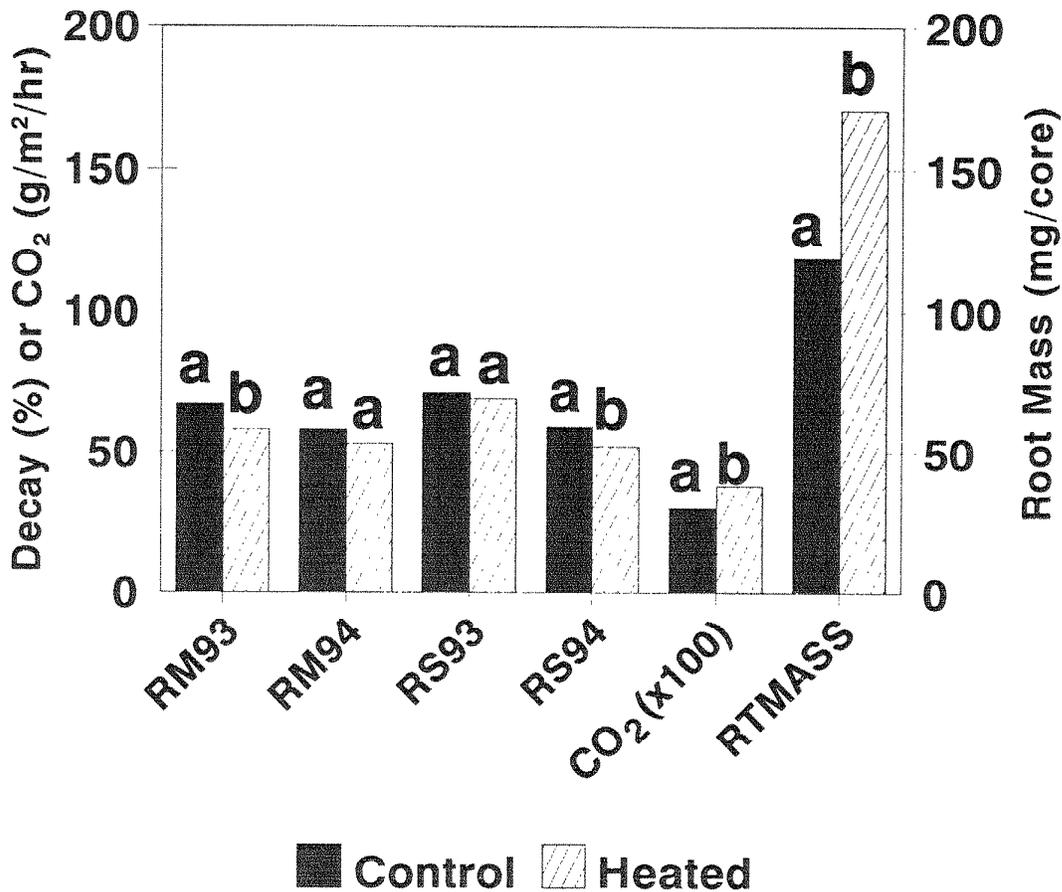


Fig. 3. The response of litter decay, CO<sub>2</sub> evolution, and fine root growth to a 5 °C increase in soil temperature. 'RM93' and 'RM94' are 1993 and 1994 red maple litter, respectively; 'RS93' and 'RS94' are 1993 and 1994 red spruce litter, respectively; 'CO<sub>2</sub>' is CO<sub>2</sub> evolution; and 'RTMASS' is soil core fine root mass. Units are percent original mass for litter decay, mg CO<sub>2</sub> m<sup>-2</sup> hr<sup>-1</sup> for CO<sub>2</sub> evolution, and mg/core for root mass.

We presume that a large portion of the CO<sub>2</sub> released from these soils is from the O horizon, where both roots and labile organic materials are most abundant. Neither O horizon nor mineral soil PCO<sub>2</sub> showed a response to heating. We attribute this to rapid gas diffusion in the O horizon toward equilibrium with the atmosphere and to minimal biological response to heating in the mineral soils.

Red maple and red spruce litter decay rates were both significantly increased ( $P < 0.05$ ) by thermal treatments (see RM93 and RS94, Fig.3). These results are consistent with other studies showing an increase in litter decomposition with increasing air and soil temperature (Witkamp 1966, Meentemeyer 1978, Jansson and Berg 1984, Moore 1986, Ruark 1993). Corresponding to first year mass loss, total red maple litter C, N, and S content were significantly lower ( $P < 0.05$ ) in the heated plots relative to the control plots. Red maple litter Ca, Mg, K, P, and Mn concentrations, however, were generally greater in heated plot litter relative to control plot litter, resulting in no significant differences in the *total content* of these elements between the treatments. Red spruce litter showed only minor differences in chemistry between the heated and control plots after the first year of decay, which reflects its more recalcitrant mass loss patterns.

First year growth of fine roots in O horizon root cores was significantly greater ( $P < 0.05$ ) in the heated plots relative to the control plots (Fig. 3), and root Ca, Mg, K, and Mn concentrations were significantly lower ( $P < 0.05$ ). This chemical "dilution effect" may be due to an export of these mobile nutrients out of the fine roots to other sinks within the plants or to insufficient supply of available nutrients to compensate for the increased growth. Second year fine root biomass (not shown), however, was significantly lower ( $P < 0.05$ ) in the heated plots relative to the controls, suggesting that the longevity of fine roots decreases with increasing temperature. This has been shown previously by Marshall and Waring (1985) and Hendrick and Pregitzer (1993), and is attributed to a greater root respiratory maintenance demands at higher temperatures.

The total N content of the soils at this site was low and the corresponding C:N ratio was high (e.g., O Horizon C:N = 44; Fernandez et al., 1993) relative to other sites in Maine, particularly hardwood sites. Nitrogen mineralization rates are also low compared to other nearby hardwood sites, suggesting a slower turnover rate of this nutrient. Overall, no statistically significant effects of the thermal manipulation have been observed on N mineralization rates during the first two years of this experiment. However, the cumulative amount of  $\text{NH}_4\text{-N}$  mineralized over this period was greater in the heated plots relative to the control plots. This trend was driven primarily by spikes of  $\text{NH}_4\text{-N}$  that were observed in many buried soil bags in the heated plots during the second summer. No net nitrification has been observed at this site during the two field seasons of study.

Preliminary data on the nutrient elements Ca, Mg, K, and Mn indicate decreased leaching losses in soil solutions, decreased abundance on soil exchange sites, and decreased storage in aboveground live foliage (for Ca and Mg) in the heated plots relative to the controls. We hypothesize that the sink for these nutrients is in microbial biomass.

Although we observed numerous responses to the thermal manipulations, we believe that the unusually dry conditions that characterized both the 1993 and 1994 field seasons precluded more dramatic biological effects of the temperature manipulation. This hypothesis is supported by a laboratory incubation study in which microbial biomass, microbial activity, and N mineralization showed no response to increasing temperatures (in the range of 5 to 25 °C) at low moisture, but showed a significant response to elevated temperatures at higher moisture contents (as shown for N mineralization in Fig. 4). Both field and laboratory studies at this site have underscored the importance of understanding the *interaction* between temperature and moisture on ecosystem processes.

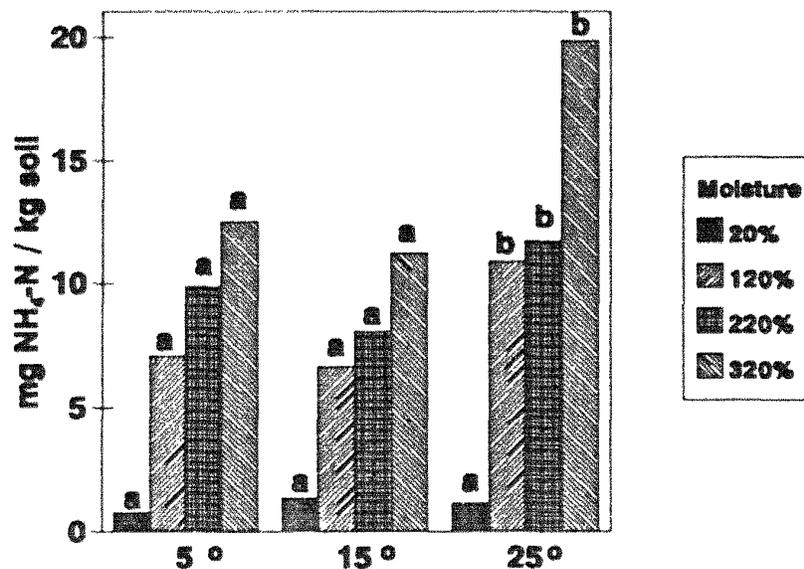


Fig. 4.  $\text{NH}_4\text{-N}$  mineralized after four weeks incubation at three temperatures and four moisture regimes.

## CONCLUSIONS

The use of heat resistance cable has proven to be an effective technique for *in situ* experimental warming of forest soils. Results from this study to date indicate that some parameters are responding to the thermal manipulations, e.g. CO<sub>2</sub> efflux, litter decay, and fineroot growth and turnover (as measured by root ingrowth cores) are all greater in the heated plots than the control plots. For other parameters, such as soil air PCO<sub>2</sub>, significant relationships were observed with temperature over a range of 0 ° to 20 °C range, although differences were not significant over the narrower range of 5 °C. Although these results suggest that there is a more rapid release of C from the soil-plant system to the atmosphere with increasing temperatures, increases in temperature alone are not sufficient to alter certain parameters. Soil moisture must also be adequate to support biological activity. Ideal available moisture conditions will optimize the biological responses to temperature whereas decreasing available moisture will minimize temperature responses. Thus, a dryer future climate scenario, as has been predicted for some regions, might offset some of the potential effects of a warmer climate. Taken together, results from this thermal manipulation study indicate that modest changes in temperature can significantly alter C, N, and major nutrient dynamics at this site.

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## SOIL RESPIRATION AND NET N MINERALIZATION ALONG A CLIMATE GRADIENT IN MAINE

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**Abstract:** Our objective was to determine the influence of temperature and moisture on soil respiration and net N mineralization in northeastern forests. The study consisted of sixteen deciduous stands located along a regional climate gradient within Maine. A significant portion of the variance in net N mineralization (41 percent) and respiration (33 percent) was predicted by temperature. The fraction of explained variance ( $r^2$ ) was much higher when data were partitioned by region or by individual sites (as high as 80 percent). This suggests that temperature is a strong predictor of respiration and net N mineralization within climate zones, but additional environmental factors become important at a larger landscape scale. The slope of the relationship between respiration and temperature was significantly greater in the Northern and Central regions than in the Southern and Coastal regions, suggesting that soil biota are more sensitive to temperature in the former. Soil moisture was a poor predictor, probably because moisture is infrequently and transiently limiting in these forests.

### INTRODUCTION

The continuing accumulation of greenhouse gases has led scientists to predict a global warming of 2 to 4 °C (Hansen et al. 1988). Because New England is at a relatively high latitude, this climate effect should be amplified, resulting in a 4 to 8 °C increase in mean annual air temperature in that region (Hengeveld and Skinner 1993). Changes in precipitation patterns are less certain but significant increases or decreases could occur (Manabe and Wetherald 1986). New England forests will be subject to potentially significant effects of these projected climatic shifts, ranging from almost immediate changes in biogeochemical cycling and phenology, to longer term changes in forest composition and productivity across the Northeast landscape.

The ability of forest vegetation to respond to changes in climate, such as increased temperatures, will depend upon the resources available to them, such as water and nutrients (Luxmoore et al. 1993, Pastor and Post 1988). Thus, it is essential that we understand how climate change will affect nutrient availability in forests. In order to predict the potential effects of climate change, we must first understand how climate currently influences soil nutrients. The Maine Gradient Study was initiated in 1993 to evaluate the effects of temperature and moisture on carbon (C) and nitrogen (N) mineralization, which are indicators of nutrient availability. We established a network of sixteen sites across the four climate regions of Maine (Briggs and Lemin 1992) and measured soil respiration, soil air CO<sub>2</sub> concentration, net N mineralization and nitrification, litterfall mass and chemistry, foliar chemistry and litter decomposition (Delaney et al. 1995). In this paper we focus on the soil respiration and net N mineralization results.

### METHODS

#### Study Sites

In order to make comparisons among sites in the Gradient Study, we tried to minimize differences among sites in terms of soil and vegetation characteristics. Thus, all sites had to satisfy a set of criteria. Candidate sites were identified along a transect within each of the four climate regions (Figure 1). An extensive site selection procedure was used to reduce the over 300 candidate sites to the chosen 16 sites. Soils at all sites are moderately well-drained to well-drained Spodosols (Typic or Lithic Haplorthods) with well-developed, mor-type forest floor. Stands are dominated by a combination of sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), American beech

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(*Fagus grandifolia* Ehrh.) or red oak (*Quercus rubra* L.). Mean age of the overstory is between 80 - 150 years old and basal area is between 25 and 35 m<sup>2</sup> ha<sup>-1</sup>.

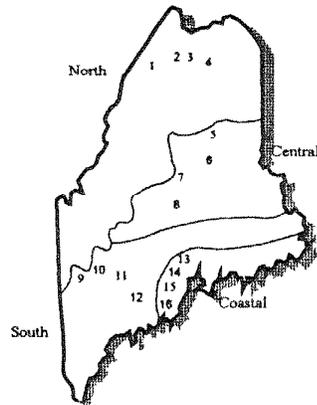


Figure 1. Location of Maine Gradient Study sites.

### Sampling

At each of the 16 sites three 15 x 15 m study plots were established. Automated weather stations at central locations in half the sites continuously recorded air temperature, soil temperature at 5 and 35 cm soil depth, and throughfall volume. Linear interpolation was used to estimate these parameters at the remaining sites. Each of the sites was visited monthly from May through November in 1993 and 1994. During each visit air temperature, soil temperature, soil water content, and soil respiration (Zibilske 1995) were measured in each plot. At the same time, N mineralization was estimated using buried bags (Hart et al. 1995). Ammonium and nitrate were extracted for 30 hours in 1N KCl before determination by phenol nitroprusside and cadmium reduction, respectively.

### Statistical Analysis

Least-squares linear regression and Pearson's correlation were performed on log-transformed data. Temperature and moisture were the independent variables and soil respiration and net N mineralization were the dependent variables. Temperature response curves of soil from each site were compared using analysis of variance with a significance level of 0.05 (Meredith and Stehman 1991).

## RESULTS AND DISCUSSION

Data from the eight weather station sites confirmed that our experimental design successfully captured a broad range of climate conditions (Figure 2). Mean annual precipitation ranged from 90.1 cm at site 1 to 139.6 cm at site 16. Mean annual air temperature ranged from 2.0 °C at site 1 to 6.2 °C at sites 12 and 16. This 4 °C difference is within the projected range of temperature increase from global warming (Hengeveld and Skinner 1993).

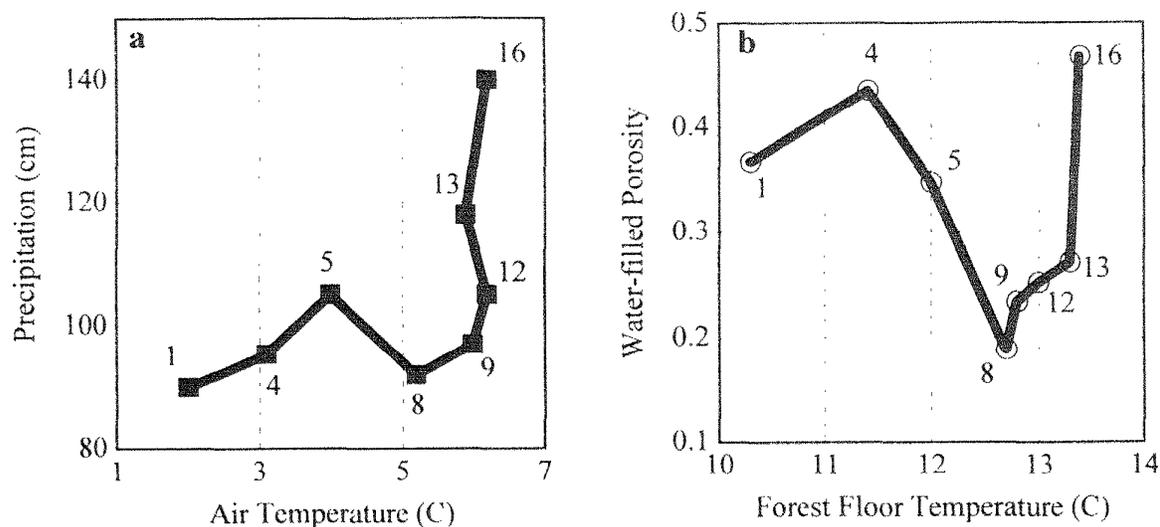


Figure 2. The location of the eight weather station sites on a climate surface. The surfaces are (a) annual precipitation vs. mean annual air temperature, and (b) mean annual water-filled porosity (% of saturation) vs. mean growing-season (May - Oct.) soil temperature at 5 cm below the surface of the Oe.

Although precipitation and air temperature define the regional climate conditions of each of the sites, soil biota will be most responsive to soil environmental factors, such as soil temperature and water content. Water-filled porosity, the fraction of pore space that is water-filled, was greater than 0.3 in sites 1, 4, 5 and 16 and less than 0.3 in sites 8, 9, 12 and 13. Note that the two northern sites exhibited a high water-filled porosity even though precipitation inputs were relatively low. This may be a result of cooler temperatures in the northern region limiting evapotranspiration of soil moisture. Mean growing season forest floor temperature (May through October at 5 cm below the surface of the Oe) increased from 10.3 to 13.4 °C from site 1 to site 16

Soil respiration values ranged from 0.034 to 0.557 g CO<sub>2</sub> m<sup>-2</sup> hr<sup>-1</sup> with the highest rates in July and August and the lowest rates in November. Soil respiration from all sites and all dates was significantly correlated with soil temperature (Figure 3a;  $r^2 = 0.33$ ;  $p < 0.01$ ), but not with water-filled porosity ( $r^2 = 0.03$ ; data not shown). Thus, temperature apparently influenced soil respiration at these sites, whereas soil moisture did not within the range of moistures we observed.

One of the unique aspects of this data set is that it represents the response of soil respiration over a wide geographic and climatic range. Most other soil respiration studies have used only a single site or adjacent sites (Reiners 1968; Bowden et al. 1993; Hanson et al. 1993; Peterjohn et al. 1994; Toland and Zak 1994). Performing correlations on data subdivided by region or by site revealed a noteworthy trend (Table 1). With a few exceptions, the strength of the correlations between temperature and either soil respiration or net N mineralization decreased as the spatial scale of the measurements increased. This suggests that temperature can be a strong predictor of soil respiration at individual sites, but is weaker at the landscape scale. Thus, at larger scales additional environmental parameters may be required.

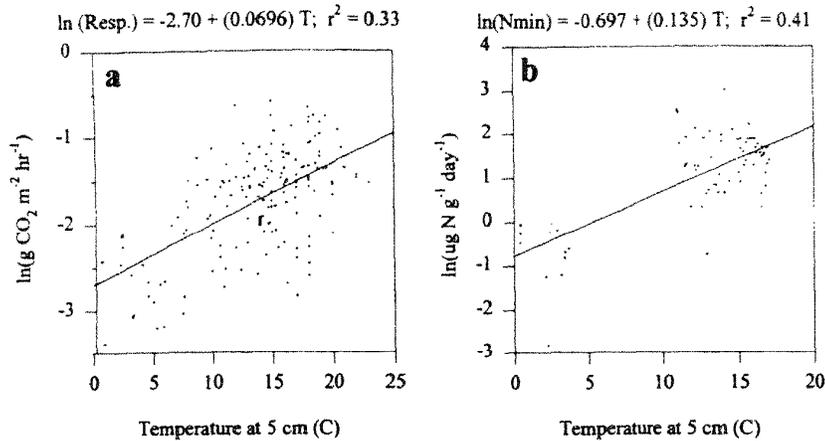


Figure 3. Linear regressions of (a) ln(soil respiration, g CO<sub>2</sub> m<sup>-2</sup> hr<sup>-1</sup>) and (b) ln(net N mineralization, μg N g<sup>-1</sup> day<sup>-1</sup>) versus forest floor temperature. Both regressions are significant (p < 0.01). Soil respiration data is for 1993-94 whereas net N mineralization data is for 1993 only.

Table 1. Adjusted-r<sup>2</sup> values from linear regressions of ln (soil respiration) and ln (net N mineralization) vs. forest floor temperature for the entire data set and for data grouped by region or site.

	Soil Respiration	Net N Mineralization
All points	0.33	0.41
By Region		
Northern	0.49	0.54
Central	0.53	0.46
Southern	0.27	0.80
Coastal	0.11	0.56
By Site		
1 through 16	0.20 to 0.74	nsd*

\*nsd = not sufficient data

The slopes and y-intercepts of the ln (respiration)-vs-temperature curves from each of the four climate regions were compared using analysis of variance to determine if the soil biota in each region responded to temperature changes in the same way. In other words, we wanted to know if the temperature response of soil biota from each region was governed by a unique equation or if there was one equation that can be applied to all regions. There were no significant differences in either y-intercept or slope among the four regions (p = 0.11; n = 4). However, when the North and Central regions were combined and compared to the combined South and Coastal regions, there was a significant difference in slope (p < 0.05; n = 8). Apparently soil biota in the North/Central regions are more sensitive to temperature (have a steeper slope) than soil biota from the South/Coastal regions (Figure 4). Peterjohn et al. (1994) combined data from a number of soil respiration studies in temperate deciduous forests (most of which were at lower latitudes) and reported a higher slope (0.113 compared to 0.0862 and 0.0627 in our study) and a lower y-intercept value (-3.89 compared to -2.84 and -2.52 in our study).

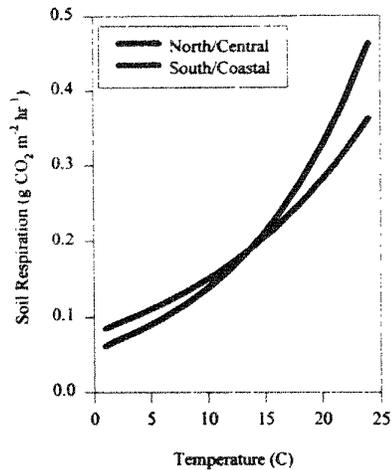


Figure 4. Soil respiration as a function of temperature {North/Central =  $\exp(-2.84 + 0.0862*T)$ ; South/Coastal =  $\exp(-2.52 + 0.0627*T)$ }.

Net N mineralization ranged from  $-1.56$  to  $12.79 \mu\text{g N g}^{-1} \text{ day}^{-1}$  in 1993 and was significantly correlated with temperature (Figure 3b;  $r^2 = 0.41$ ;  $p < 0.01$ ). This range of N mineralization rates is typical for northern hardwood forests ( $0.5$  to  $16 \mu\text{g N g}^{-1} \text{ day}^{-1}$ ; Zak and Pregitzer 1990; Simmons et al. 1995). Correlation with water-filled porosity was not significant. However, when measurements from November were omitted (a period when soil activity is not expected to be limited by water because of very low temperatures), then a weak correlation became apparent ( $r^2 = 0.10$ ;  $p < 0.05$ ; data not shown). Thus, it appears that temperature had a significant effect on net N mineralization and soil water content had a weak effect during the relatively drier growing season.

Similar to soil respiration, the strength of the correlation of net N mineralization with temperature was greater within regions than in the combined data set (Table 1). This suggests that additional environmental parameters may be required to more accurately predict net N mineralization at the landscape scale. Correlations for each site were not attempted because there was not a large enough number of data points for each site in 1993.

## SUMMARY AND CONCLUSIONS

Temperature was significantly correlated with soil respiration and net N mineralization at the regional level. Together with supporting evidence from laboratory studies by other researchers, this suggests that both C and N mineralization of northern hardwood forests in Maine have the potential to increase in response to global warming. The actual response of C and N mineralization will depend on a number of interacting factors including the response of foliar C:N ratios, litter C:N ratios, soil nutrient availability and soil C inputs. At the same time plants and soil biota will be exposed to elevated atmospheric  $\text{CO}_2$  concentrations and continued inputs of N from atmospheric deposition. Regional differences in the relationship between soil respiration and temperature exist and should be investigated further in other locations. Moisture was not an important limiting factor for C or N mineralization in these forests, probably because the forest floor remained moist most of the year.

## ACKNOWLEDGEMENTS

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# INCREASING SOIL TEMPERATURE IN A NORTHERN HARDWOOD FOREST: EFFECTS ON ELEMENTAL DYNAMICS AND PRIMARY PRODUCTIVITY

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**Abstract:** To investigate the effects of elevated soil temperatures on a forest ecosystem, heating cables were buried at a depth of 5 cm within the forest floor of a northern hardwood forest at the Huntington Wildlife Forest (Adirondack Mountains, New York). Temperature was elevated 2.5, 5.0 and 7.5°C above ambient, during May - September in both 1993 and 1994. Various aspects of forest ecosystem dynamics were studied, including soil solution chemistry (lysimeters at 15 and 50 cm depths), trace gas flux (closed box technique), decomposition of maple and American beech litter, and tree seed germination. A preliminary experiment showed that there was less effect on soil solution chemistry when cables were buried at 5 versus 15 cm depths. The soil warming plots experienced negligible disturbance effects associated with installation of heating cables. Nitrate concentrations were elevated in the highest temperature treatment. Carbon dioxide flux was positively correlated with soil temperature, as was the decomposition rate for American beech litter. In heated plots, germination of *Pinus strobus* (white pine) was positively correlated with soil temperature.

## INTRODUCTION

The mean global temperature (MGT) has been increasing for the past 150 years (Houghton et al., 1990), giving possible evidence of the phenomenon of global warming. Current general circulation models (GCMs) suggest that the MGT will continue to rise and could increase 1.5-5.0°C over the next 100 years (Houghton et al., 1990). Global warming is considered to be induced by increasing concentrations of atmospheric water vapor (H<sub>2</sub>O), carbon dioxide (CO<sub>2</sub>) and other trace gases, including methane (CH<sub>4</sub>), nitrous oxide (N<sub>2</sub>O) and chlorofluorocarbons (CFCs). Concentrations of CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O have been steadily increasing since the mid-1800s (Houghton and Woodwell, 1989). Various predictions have been made as to how regional climates will change if the earth continues to warm (Graham et al. 1990; Houghton et al. 1990). Climate change is likely to occur on a regional scale. For instance, northern latitudes (temperate and boreal) are expected to become warmer and wetter in the future (Houghton et al., 1990). Thus, it is important to understand how different ecosystems may respond to climate change, both biotically and abiotically.

## METHODS

### Site Description

The study site is located in a 100 year-old birch-beech-maple stand at the Anna and Archer Huntington Wildlife Forest (HF). This northern hardwood forest is located in the central Adirondack mountains of New York State (43°59'N, 74°14'W) near Newcomb. The site is underlain by Spodosols, specifically coarse-loamy, mixed frigid, Typic Haplorthods in the Becket-Mundal association (Somers, 1986). The research area was chosen because of the availability of electrical power, which was required for heating the plots, and additionally, it lies within close proximity to a nearby access road. The biogeochemistry and productivity of HF have also been well characterized by previous studies (Mollitor and Raynal, 1982; David et al., 1982; Shepard et al., 1989).

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## Experimental Design

Heating cables were buried in the forest floor to a depth of approximately 5 cm, at 20 cm spacing within four (10 m x 10 m) plots. At 5 cm, three heated plots had soil temperatures of 2.5, 5.0 and 7.5°C, respectively, above ambient (reference plot). Elevated soil temperatures were maintained throughout the field season from approximately mid-May to September 30 for both 1993 and 1994.

## Field and Laboratory Methods

Field sampling included measurements of nutrient cycling parameters identified as important to carbon and nitrogen dynamics within a forest ecosystem, and included solid phase (buried soil bags) and soil solution chemistry (lysimetry), trace gases fluxes (CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O), decomposition (litter bags), primary productivity (foliage/litter collection and germination) and soil moisture and soil temperature. Preliminary results from some of these analyses will be presented. Nitrate concentration was determined by ion chromatography, while calcium and magnesium concentrations were obtained by inductively coupled plasma emission (ICP) and potassium by atomic absorption spectrophotometry (AA), respectively (Standard Methods, 1992). Trace gas samples were collected and analyzed according to the methods of Richey (1994). Litter bags containing either maple or American beech leaves were installed in plots during October 1992 and collected at one and two years following installation. After collection, the bags were dried and weighed. A comparison of the weights at collection to the original bag weight was used to determine percent mass remaining. An *in situ* germination experiment, where seeds of *Pinus strobus* (white pine) and *Tsuga canadensis* (eastern hemlock) were planted in the litter layer (Oa horizon), began in May 1994. A total of fifteen wire mesh boxes were randomly located along a transect one meter from one edge of each plot. Twenty seeds per species were planted in a box, and each species was planted in a total of five boxes per plot (100 seeds/species/plot) with five additional boxes per plot as controls. The box design and planting methods were similar to those described by Dustin (1986).

## Disturbance Study

Preceding the soil-warming study, a preliminary experiment was implemented in order to assess the influence of disturbance on soil solution chemistry associated with installing heating cables (McHale and Mitchell, 1995). The study was conducted near the soil-warming site (within 500 m). The main difference between the two studies was that the cables were installed during fall 1991 for the disturbance experiment, whereas installation of heating cables occurred during spring 1992 for the soil warming study. Further details can be found in Mchale and Mitchell (1995).

# RESULTS AND DISCUSSION

## Disturbance

Results of the disturbance experiment showed that simulated cables buried at 15 cm initially produced elevated ion concentrations commonly associated with soil disturbance (Likens et al., 1970; Vitousek et al., 1979; Hornbeck et al., 1986), compared to simulated cables at 5 cm, which exhibited less disruption of elemental cycles due to cable burial (Fig. 1). Plots with no cable installation generally had the lowest ion concentration levels during the disturbance experiment. In comparison, the soil warming reference plot, which had heating cables installed at 5 cm, displayed no evidence of disturbance effects despite cable burial. Mchale and Mitchell (1995) suggested that the lack of disturbance effects in the soil warming reference plot could be attributed to the timing of cable installation.

## Temperature Treatments

Mean temperatures at 5 cm depth were monitored and recorded continuously throughout the 1993 and 1994 field seasons (Fig. 2). Heated plots were maintained at the specified temperatures, except the 7.5°C plot. At the 7.5°C treatment there was notable deterioration of the heating cables by the end of the 1993 field season and heat treatment was terminated approximately one month before the field season ended in 1994.

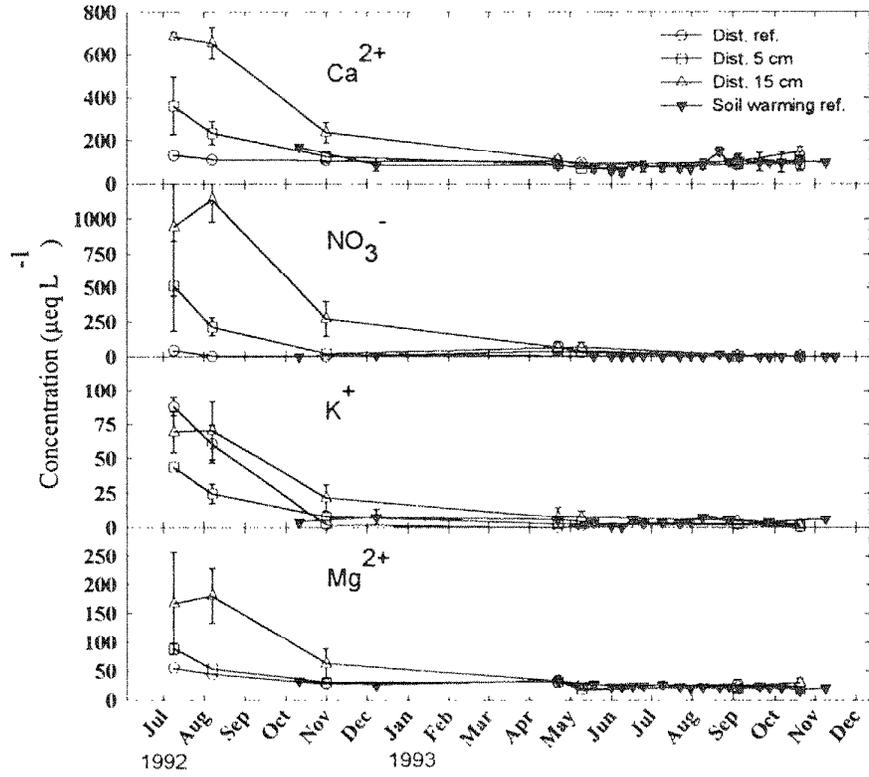


Figure 1. Soil solution chemistry from disturbance plots and soil warming reference plot.

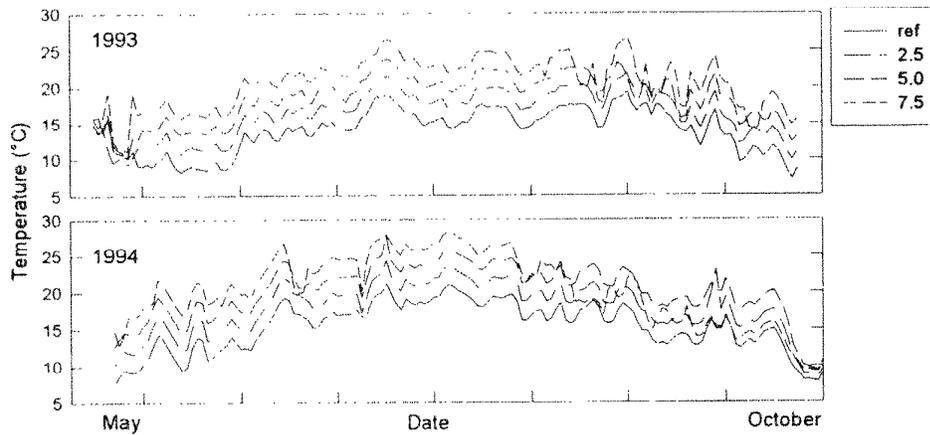


Figure 2. Mean temperatures at 5 cm depth for 1993 and 1994 field seasons

## Soil Solution Chemistry

It was anticipated that raising the soil temperature could produce important alterations of elemental cycles, specifically, soil solution chemistry. Nitrate levels at 15 cm (Bh horizon) and 50 cm (Bs2 horizon) from the 7.5°C plot exceeded all other plot concentrations during early summer and again in late fall of both 1993 and 1994 (Fig. 3). These results suggest that increased soil temperatures increased N mineralization.

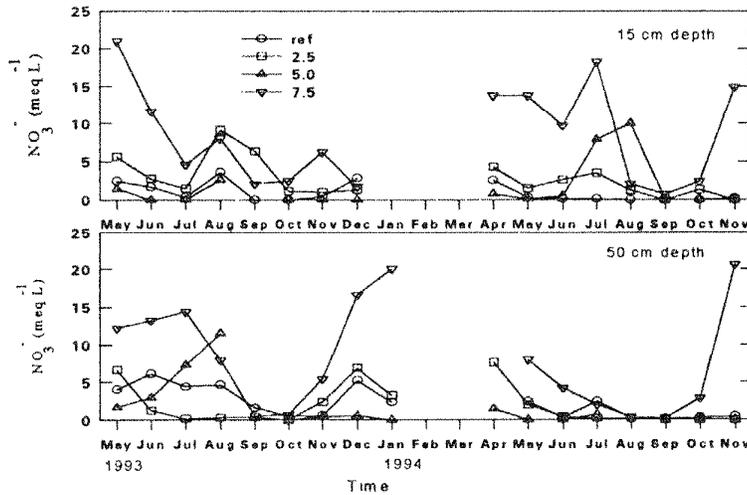


Figure 3. Mean monthly nitrate concentrations from soil warming plots at 15 and 50 cm depth.

## Carbon Dioxide Flux

Carbon dioxide flux showed the strongest correlation to soil temperature of the three gases analyzed (Fig. 4). The relationship was stronger in 1993 ( $r^2 = 0.41$ ,  $p \leq 0.05$ ) than in 1994 ( $r^2 = 0.23$ ,  $p < 0.05$ ). The relationship was linear and weaker than a similar soil warming study at Harvard Forest (Peterjohn et al., 1993) where the relationship was exponential and explained 72 percent of the variability. Methane and nitrous oxide fluxes failed to show any significant relationship to soil temperature.

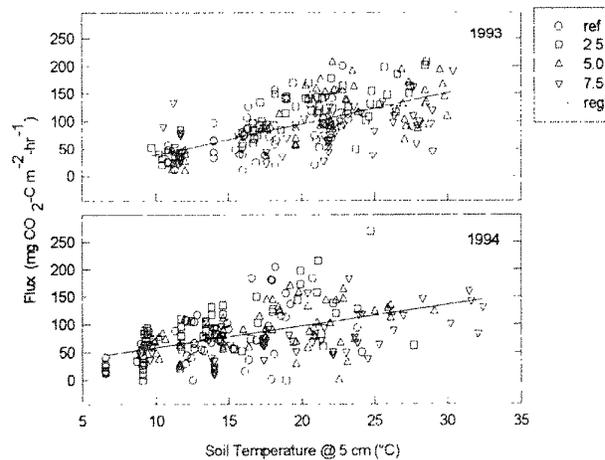


Figure 4. Carbon Dioxide flux verses soil temperature at 5 cm depth.

## Decomposition

One-way ANOVA showed that percent mass remaining in maple versus American beech litter bags was statistically significantly lower both one ( $p = 0.005$ ,  $n = 48$ ) and two ( $p = 0.0003$ ,  $n = 93$ ) years after heat treatments began (Fig. 5), which would be expected since the latter has higher lignin content (Melillo et al. 1982) and thus is more resistant to decay. Maple did not exhibit any statistically significant differences between treatments in either year one or year two. In comparison, percent mass remaining after one year for American beech litter bags in the two highest heat treatments was statistically lower ( $p = 0.001$ ,  $n = 24$ ) than the reference and 2.5°C plots. After two years *in situ*, mass remaining was significantly lower in the 7.5°C plot than both the reference and 2.5°C plots ( $p = 0.0001$ ,  $n = 48$ ). These results suggest that elevated soil temperatures increased the decomposition rate for American beech litter.

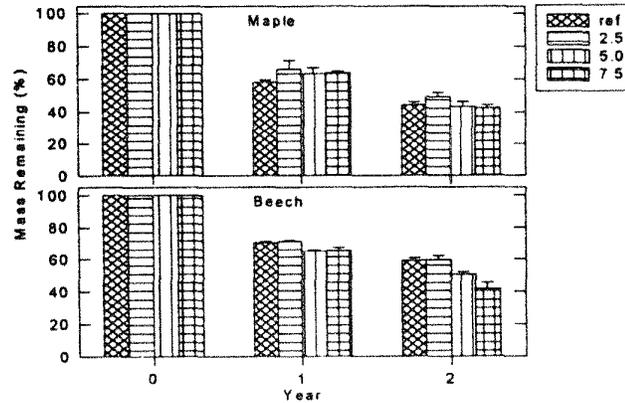


Figure 5. Percent mass remaining in litter bags since time of installation (year = 0), (vertical lines are S.E.).

## Seed Germination

Cumulative germination of planted eastern hemlock seeds failed to display a pattern of stimulation with increasing plot temperatures (Fig. 6) and was low in all plots. The reference plot had the highest germination rates for the entire study period. White pine seeds germinated faster with increasing temperatures in heated plots. The results of this experiment are consistent with the growth requirements of both species. Eastern hemlock is adapted to cool, moist conditions; white pine is more drought tolerant (Burns and Hondala 1990). Hemlock germination was more influenced by soil moisture than soil temperature. In comparison, white pine germination was strongly affected by soil temperature differences among the experimental plots.

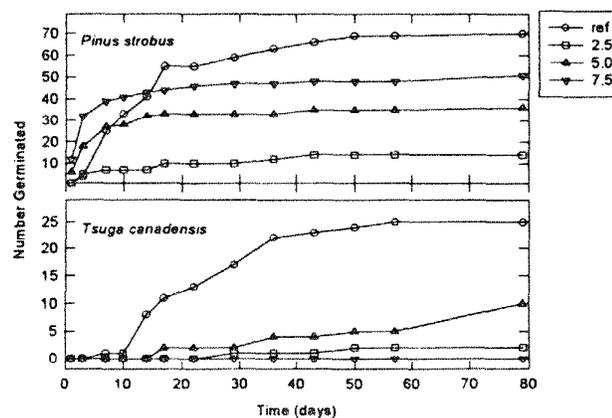


Figure 6. Cumulative germination of tree seeds planted in soil warming plots.

## CONCLUSIONS

Experimental manipulation of soil temperature is feasible and can be maintained throughout an entire field season. Experimentally heating a northern hardwood forest soil showed that elevated temperature can influence solute chemistry. Of the trace gases analyzed (CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O), carbon dioxide exhibited the strongest correlation to soil temperature. Elevated soil temperature showed differential effects on litter decomposition and seed germination. These results will be further evaluated using various biogeochemical simulation models.

## ACKNOWLEDGMENTS

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MICROHABITAT EFFECTS OF LITTER TEMPERATURE AND MOISTURE ON FOREST-FLOOR  
INVERTEBRATE COMMUNITIES

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Litter temperature and moisture may be altered due to changes in global climate. We investigated the effect of small changes in litter temperature and moisture on forest-floor communities in West Virginia. We altered litter temperature and moisture in 6 x 6 m plots covered with landscape cloth. The study sites were in six watersheds (three north-facing and three south-facing aspects) in the Fernow Experimental Forest and in the West Virginia University Forest from April 1992 - April 1993. We measured microbial biomass (ATP), invertebrate density, and invertebrate composition. In covered blocks, litter temperature increased by 0.01 °C, -2.1 °C and litter moisture increased by 0.01 - 4.2 percent.

We identified 134 litter invertebrate species in nine orders. Overall invertebrate density was not associated with changes in temperature and moisture; however, both richness and evenness were associated with changes in temperature and moisture. Density and richness of springtails (*Collembola*) were higher in covered blocks, which had higher temperature and moisture values as compared with reference blocks. Densities of 20 invertebrate species were correlated with changes in mean daily temperature, mean moisture, or changes in the range of temperature and moisture. Maximum and minimum values for both temperature and moisture increased in covered blocks, and there were more significant associations of invertebrate density and richness with changes in range (maximum and minimum values) than with changes in the average temperature or moisture values. Litter ATP decreased in covered study blocks.

Temporal (month and season) and spatial (forest, watershed, aspect, and location on slope) variables had an effect on invertebrate density, richness, and evenness, as well as on litter temperature and litter moisture. Results from this study indicate that small changes in litter temperature and moisture can effect forest-floor invertebrate communities.

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EFFECTS OF ACIDIC PRECIPITATION ON LEAF DECOMPOSITION RATES, MICROBIAL BIOMASS, AND  
LEAF PACK MACROINVERTEBRATES IN SIX STREAMS ON THE ALLEGHENY PLATEAU OF WEST  
VIRGINIA

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**Abstract:** We studied the effects of acidification on leaf litter decomposition in six headwater streams in the Monongahela National Forest. These streams differed in underlying geology and mean baseflow pH (3.99, 4.24, 6.13, 6.47, 6.59, and 7.52). We placed 10-gram leaf packs of white oak, red maple, and yellow poplar in each stream, and retrieved them after two days, two weeks, and then at 4-week intervals from November 1993 to February 1994. Leaf packs were analyzed to determine changes through time in leaf decay rate, invertebrate composition, density, and biomass, and microbial biomass (ATP concentration). The mass loss rate coefficient, *k*, ranged from -0.0128 to -0.0052 for poplar, -0.0120 to -0.0047 for maple, and -0.0059 to -0.0018 for oak. The acidic streams had significantly lower decay rates. The acidic streams had higher invertebrate densities but lower biomass than the more alkaline streams. ATP concentrations were lower in the acidic streams than in the more alkaline streams. In streams that are vulnerable to acidification, pH depression may reduce energy and material availability to stream macroconsumers.

#### INTRODUCTION

Allochthonous leaf litter may constitute as much as 90 percent of a stream's energy budget (Anderson & Sedell 1979; Fisher & Likens 1973). Decreased leaf litter processing rates have been observed in acidified aquatic systems (Burton et al. 1985; Griffith & Perry 1993; Mulholland et al. 1987). Decreases in processing rates have been attributed to direct toxicological effects of high H<sup>+</sup> concentrations, increased solubility of metals, particularly aluminum, and decreased microbial activity.

We placed three species of leaf packs in six streams of different mean pH. Mass loss rates, invertebrate community structure, and ATP concentration (microbial biomass) from each stream were compared in order to determine the effects of acidification on detrital processing.

#### METHODS

##### Site Descriptions

We sampled six streams: Freeland Run (FR), Engine Run (ER), South Fork of Red Run (SFR), Wilson Hollow (WH), Hickman Slide Hollow (HSH), and Camp Hollow (CH). All are in or near the Monongahela National Forest, Tucker County, West Virginia. Mean baseflow pH for the streams were 3.99 (ER), 4.24 (SFR), 6.13 (WH), 6.47 (FR), 6.59 (CH) and 7.52 (HSH).

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## Field Procedures

Nylon mesh bags (3-mm) were filled with 10g of either white oak, red maple or yellow poplar leaves. During the first week in November 1993, we placed 42 bags of each species in the center of each stream channel. After 2, 14, 28, 56, and 84 days, five bags of each species were randomly selected and removed. On each sampling day, stream pH and conductivity were measured, and a grab sample for measuring water chemistry was collected. Water temperature was continuously monitored with a Ryan model J thermograph in a pool of each stream.

## Laboratory Procedures

Three replicates of five leaf disks were cut from each leaf pack using a 10-mm diameter cork borer, two for ATP analysis, and one for ash-free dry weight determination.

Invertebrates in the leaf packs were separated from the organic matter, identified to the lowest possible taxa, and enumerated. They were then dried, and weighed to estimate biomass. ATP was extracted from two replicates from each leaf pack using  $H_2SO_4$ , and assayed using a luciferin-luciferase bioluminescence assay (Suberkropp & Klug 1976).

## RESULTS

### Water chemistry and temperature

Streamwater pH was highest in HSH (7.52), lowest in ER (3.99) and SFR (4.24), and intermediate in WH (6.13), FR (6.47) and CH (6.59). Daily mean stream temperatures decreased as the study progressed from 7°C at the start of the study to 2°C at the end.

### Leaf pack processing rates

During the 12-week study, AFDW of the leaves decreased from a mean initial weight of 8.60 g/bag at all sites for all species to values ranging from 3.02 g/bag to 7.25 g/bag. Decay rate coefficients ranged from -0.0018 for oak in ER to -0.0128 for poplar in CH. The decay rates for the acidic streams were significantly lower than both the neutral and alkaline streams for all leaf species ( $p < 0.01$ ). The decay rate for the alkaline stream was not different from the circumneutral streams for oak and poplar, but was significantly lower for maple ( $p < 0.01$ ).

### Microbial biomass

ATP concentrations were significantly lower in the acidic streams than in the neutral or alkaline streams for maple ( $p < 0.01$ ) and for oak ( $p < 0.05$ ). There were no significant differences in ATP concentrations on poplar leaves among streams.

### Shredder densities and biomass

The acidic streams supported significantly higher densities of invertebrate shredders than the neutral streams, which in turn supported significantly higher numbers than the alkaline stream. Based on ANOVA results, there were no significant differences in shredder biomass among the three pH groups. The shredder communities of the two acidic streams (ER and SFR) tended to be dominated by *Leuctra* and *Amphinemura*, and the communities of the other streams included significant numbers of *Pycnopsyche*, *Peltoperla*, *Paracapnia*, *Lepidostoma*, and *Gammarus*.

## DISCUSSION

The AFDW loss rates measured in this study, were lower in the low pH streams than in the more alkaline systems. This has been demonstrated by other investigators (Burton et al. 1985; Kimmel et al. 1985; Mackay & Kersey 1985;

Mulholland et al. 1987; Griffith & Perry 1993). The lower rates of decomposition in ER and SFR appear to be at least partially the result of lower microbial biomass. Our analysis of ATP concentrations showed that the acidic streams supported significantly less microbial biomass than the higher pH streams. This is consistent with the results of other studies which have examined the microbial communities of acidified systems. Rao and Dutka (1983) found that bacteria populations and densities were nearly an order of magnitude less in acidified lakes than in neutral lakes. Palumbo et al. (1987) found that epilithic microbial biomass was significantly correlated with pH in Tennessee and North Carolina streams. We found a trend towards larger numbers of smaller species of macroinvertebrates in acidified waters and fewer numbers of larger species in neutral waters. Other researchers have found similar results at sites with low pH (Hildrew et al. 1984; Mackay & Kersey 1985; Mulholland et al. 1987).

In summary, our results suggest lower rates of leaf mass loss in streams with pH <4.0. The lower rate of leaf mass loss was accompanied by significantly lower ATP levels, significantly higher shredder densities, and lower shredder biomass. This suggests that decomposition rates in these acidic streams are depressed by a decrease in microbial biomass and the altered shredder community. Continued acidification of headwater streams in this area may result in further reductions in decomposition rates, less microbial biomass, and altered macroinvertebrate communities.

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# LEAF LITTER PROCESSING IN WEST VIRGINIA MOUNTAIN STREAMS: EFFECTS OF TEMPERATURE AND STREAM CHEMISTRY

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**Abstract:** Climate change has the potential to alter detrital processing in headwater streams, which receive the majority of their nutrient input as terrestrial leaf litter. Early placement of experimental leaf packs in streams, one month prior to most abscission, was used as an experimental manipulation to increase stream temperature during leaf pack breakdown. We studied leaf litter processing in three second-order, mid-Appalachian streams along a pH gradient (mean pH = 4.2, 6.5, 7.5). Leaf pack processing rate coefficients ( $k$ ) were calculated for single species leaf packs of red maple, white oak, and yellow poplar retrieved from each stream at regular intervals over two 12-week study periods: October to January, average total degree days = 442.0; and November to February, average total degree days = 271.3. Processing rates for all leaf species in both study periods were highest in the most alkaline stream. Within each stream, processing rates were not significantly higher during either study period. Invertebrate density was higher during the earlier, warmer study period, but shredder biomass showed no significant trends. ATP concentrations on leaf material were generally higher during the earlier study period, indicating higher microbial biomass. Overall, leaf litter processing in this study was influenced by a combination of factors including temperature, water chemistry, invertebrate community, and microbial processing.

## INTRODUCTION

Potential global climate change over the next century may alter regional climate and precipitation patterns (Levine 1991). The probable effects of climate change on stream ecosystems include altered flow and temperature, which in turn can affect ecosystem energy flow, individual species distributions, and interspecific interactions (Carpenter *et al.* 1992). Forested headwater streams receive the majority of their nutrient input in the form of terrestrial leaf litter (Fisher and Likens 1973, Vannote *et al.* 1980). By altering the temperature and flow regimes of these forested headwater streams, climate change may affect rates of leaf litter breakdown in streams and also the life histories of stream-dwelling invertebrates that consume leaf litter, known as shredders.

Typically, researchers have studied detrital processing in streams by placing small packs of leaves in streams to coincide with the timing of maximum natural leaf input (e.g., Petersen and Cummins 1974, Benfield and Webster 1985, Griffith and Perry 1993). We used early placement of leaf packs in streams, one month prior to most abscission, in this study to increase the accumulation of degree-days over the processing period. This was done in order to investigate the role of increased temperature during leaf pack breakdown.

## STUDY SITES

This study was conducted from October 1993 to February 1994 in three second-order streams of different pH: South Fork of Red Run (SFR, mean pH = 4.2), Freeland Run (FR, pH = 6.5), and Hickman Slide Hollow (HSH, pH = 7.5).

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The streams are located in (HSH) or near (SFR, FR) the Fernow Experimental Forest, Monongahela National Forest, Tucker County, WV.

## METHODS

Water temperature was recorded by continuous recording thermographs in each stream. Water quality variables, including pH and total aluminum, were measured from grab samples analyzed by the USFS Timber and Watershed Lab, Parsons WV, and PKC Environmental, Morgantown, WV. Single species leaf packs (red maple, white oak, yellow poplar) were constructed by placing 10 g of dried abscised leaves in mesh bags, which were then attached to bricks and placed in the streams. Five packs of each species were removed from each stream at predetermined intervals: approximately two days, two weeks, four weeks, eight weeks, and 12 weeks after the packs were originally placed in the stream. Early leaf packs were in place from October to January, and normal leaf packs were in place from November to February.

In the laboratory, ash free dry weight remaining was determined. Invertebrates were separated from the leaf matter, preserved, and later identified, counted, and weighed to determine invertebrate biomass. Microbial biomass was estimated by determining ATP concentration on leaf discs cut from the leaf packs, using acid-extraction techniques (Suberkropp and Klug 1976). Rates of leaf pack decomposition were calculated as the rate coefficient ( $k$ ) of a negative exponential model of leaf pack decay (Petersen and Cummins 1974). Separate calculations of  $k$  were made using either days or degree days as the independent variable, in an attempt to account for temperature differences between the two sampling periods (Griffith and Perry 1993, Irons *et al.* 1994). Degree days accumulated at each sample date were calculated as the cumulative sum of the mean daily temperatures from the beginning of the study to that sample date. The General Linear Models (GLM) procedure of SAS was used to contrast decay rate coefficients between the study periods and streams. Invertebrate shredder density and biomass and ATP concentrations were also compared between study periods and streams using the GLM procedure and Duncan's Multiple Range Test as a multiple comparison procedure, with  $\alpha = 0.05$ .

## RESULTS

Degree-day accumulation during the early study period was highest in HSH, the lowest elevation stream (533 degree days), intermediate in SFR (410), and lowest in FR (384). Over the normally timed experiments, the three streams accumulated 367 degree days (HSH), 234 degree days (SFR), and 213 degree days (FR).

Mass loss rate coefficients are reported in two ways: from the regression of time in days versus  $\ln$  AFDW remaining ( $k$ ), and from the regression of degree-days versus  $\ln$  AFDW remaining ( $k_d$ ). Values of  $k$  were highest in HSH, intermediate in FR, and lowest in SFR, and also varied by leaf species. In general, yellow poplar leaves broke down the fastest, red maple leaves broke down at an intermediate rate, and white oak leaves broke down the slowest. No significant differences were seen when  $k$  was contrasted between early and normally-timed experiments within the same stream.

Values of  $k_d$  were calculated as a means of incorporating variation in temperature into the leaf litter breakdown rate. Values of  $k_d$  were highest in FR or HSH, and lower in SFR. These rate coefficients ( $k_d$ ) were significantly higher during the normally-timed experiments in HSH for all leaf species, and in FR for oak leaves.

Invertebrate density differed among the three study streams. Density was generally highest in either SFR or FR, and lower in HSH, for both study periods. Density was significantly higher in the early study period for all leaf species in HSR and FR. In SFR, densities were higher during the normal study period for red maple and white oak leaf packs. Invertebrate biomass also differed among the three streams. Biomass was highest in FR, intermediate in HSH, and lowest in SFR. This indicates that the shredder community in SFR was composed of many small individuals. Shredder biomass was higher during the normal study period, particularly on the last two sample dates. However, no statistically significant differences in biomass could be detected between study periods when considering all sample dates of both studies.

ATP concentrations, approximations of microbial biomass on leaf material, were significantly higher in the early study period for red maple and yellow poplar leaves. ATP concentrations were generally higher in FR and HSH, and low in SFR.

## DISCUSSION

Stream temperature has a recognized role in leaf litter breakdown and related stream processes such as invertebrate and microbial metabolism. Processing rates have been shown by some researchers to increase directly with temperature; yet in this study, the warmer study period generally had similar or even slower breakdown rates. In other studies that compared processing in streams with different temperature regimes, faster processing rates in cooler streams have often been attributed to more abundant shredders in the cooler streams (Triska and Sedell 1975, Short *et al.* 1980). However, still other studies comparing processing rates in the same stream during different study periods have found no significant differences in breakdown rate between study periods (Petersen and Cummins 1974), as was the case in the present study.

The differences in processing rates between early and normal study periods seen with the inclusion of degree-days in the breakdown rate calculation may indicate that temperature is a factor. Still, this method of rate calculation may not fully account for temperature differences between streams and study periods. The temperature differences in our two study periods may have been too slight to produce the expected effect of higher rates at higher temperatures, since temperature effects appear to have been confounded by other factors, particularly the biomass and life histories of shredding invertebrates.

Major effects of climate change on organic matter processing in streams may result over much longer time scales, as the range of tree species, timing of leaf abscission, and invertebrate life histories are affected. Future work may be directed toward exploring the impact of yearly variation in various climatic factors on leaf litter processing and the overall energy budget of streams in forested ecosystems.

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LEAF LITTER DECOMPOSITION AND ELEMENTAL CHANGE IN THREE APPALACHIAN MOUNTAIN  
STREAMS OF DIFFERENT PH

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**Abstract:** The decomposition of leaf litter provides the primary nutrient source for many of the headwater mountain streams in forested catchments. An investigation of factors affected by global change that influence organic matter decomposition, such as temperature and pH, is important in understanding the dynamics of these systems. We conducted a study of leaf litter elemental change during decomposition in three headwater mountain streams within or near the Fernow Experimental Forest, Monongahela National Forest, West Virginia. Three leaf species, placed in individual leaf bags, were placed in three streams that had mean pH values of 4.2, 6.2, and 7.5. Nitrogen, expressed as percent of initial concentration, was conserved in leaf litter in all three streams. Nitrogen concentrations were not significantly different in the acidic stream as compared with the more neutral streams. In contrast, phosphorus was lost more rapidly from the leaf detritus in the acidic stream (45.9 percent), than in the more neutral streams (52.0 percent and 63.1 percent). The rates of decomposition for white oak and red maple were significantly lower ( $k = 0.0062$  for red maple) in the acidic stream as compared with the more neutral streams, WSH and HSH ( $k = 0.0128$  and  $0.0072$ , respectively). Although no differences in final nitrogen content were observed, detrital decomposition, microbial biomass, and the accumulation of phosphorus, calcium, and magnesium were inhibited in the low pH stream. These results suggest that acidification may significantly reduce the rate of leaf detrital breakdown, which may result in a reduction of the nutrient base for aquatic consumers.

INTRODUCTION

The trophic structure and secondary production in stream ecosystems is controlled by both the quality and quantity of leaf litter. Decomposition is often the major source of nutrients to both microconsumers and macroconsumers in headwater streams. Mobilization of nutrients from leaf detritus during decomposition is regulated by environmental factors such as stream water chemistry, temperature, and stream biota, as well as by the physical and chemical composition of the detrital substrate (Gosz et al., 1973; Melillo et al., 1984; Rustad, 1994).

Changes in precipitation chemistry may affect detrital-based ecosystems that are otherwise unaffected by land use in a watershed. Acidification of streams as a result of atmospheric inputs may introduce changes in water chemistry, particularly depression of pH. These changes in water chemistry may, in turn affect detrital decomposition and the associated biogeochemical processes that influence every trophic level (Haines, 1981).

The goal of our research was to compare detrital processing rates and temporal changes in detrital nutrients among streams with different pH. We measured changes in mass loss rates, microbial biomass, and elemental composition of leaf litter to provide insight into the effects of stream acidification on detrital processing and detrital quality.

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## STUDY SITES

This study was conducted in three streams within or near the Fernow Experimental Forest, Monongahela National Forest, West Virginia. The study sites are within the physiographic region of the central Appalachian Mountains known as the Allegheny Plateau. Headwater streams of this region tend to form dendritic stream patterns common in landscapes originating from an elevated plateau that was previously level.

The South Fork of Red Run (SFR) is a second-order stream (mean pH = 4.2) draining approximately 230 hectares underlain by silicate sandstones and conglomerate of the Pottsville formation. The riparian forest is dominated by red maple (*Acer rubrum* L.), yellow poplar (*Liriodendron tulipifera*), eastern hemlock (*Tsuga canadensis* L.), and rhododendron (*Rhododendron maximum* L.).

Wilson Hollow (WH) is a third-order stream (mean pH = 6.2) which drains approximately 128 hectares underlain by shales and siltstones of the Hampshire formation. The riparian forest consists of red oak (*Quercus rubra* Michx.), eastern hemlock (*Tsuga canadensis*), and sugar maple (*Acer saccharum*).

The North Fork of Hickman Slide Hollow (HSH), also in the Fernow Experimental Forest, is a second-order stream (mean pH = 7.5) draining a 72 hectare catchment underlain by the Mauch Chunk formation. The Mauch Chunk consists of shales and sandstones, as well as heavily jointed limestones of the Greenbriar member. The riparian vegetation is similar to that of Wilson Hollow.

## METHODS

Three leaf species, white oak (*Quercus alba*), red maple (*Acer rubrum*), and yellow poplar (*Liriodendron tulipifera*) were selected. These species represent leaves that decompose at relatively slow, medium, and fast rates, respectively. Thirty-five leaf packs of each leaf species were placed in each of the three streams in November 1992. Five leaf packs of each species were retrieved from each stream after two days, two weeks, four weeks, and then at four-week intervals until March 1993. To measure the ash-free dry weight (AFDW), random subsamples of ten leaf disks were taken from the rinsed leaf pack material using a 1 cm diameter cork borer. Remaining leaf pack dry weight was then multiplied by the percent AFDW to estimate the remaining leaf pack AFDW. Microbial biomass estimations were made using ATP extraction and analysis with luciferin-luciferase enzyme system (Suberkropp et al. 1976).

A random experimental design was employed to examine the effects of stream, leaf species, and the interaction on rates of decomposition and elemental change. Both stream and leaf species were considered fixed effects. Differences in mean nutrient content after 112 days of incubation were evaluated using analysis of variance (ANOVA). Because sample sizes were unequal for some of the parameters that were measured, the general linear models and least-squares means procedures were used. Analysis of covariance was used to compare changes in mass loss among streams.

## RESULTS

In terms of mass loss of the detritus, the rates of decomposition were significantly lower ( $k = 0.0062$ , for red maple) in the acidic stream, SFR, as compared with the more neutral streams, WH and HSH ( $k = 0.0128$  and  $0.0072$ , respectively). This trend was also observed in white oak but not in yellow poplar.

Following a decline in nitrogen concentration during the first 20 days, nitrogen was conserved in all three leaf species. No significant difference in final nitrogen content of the detritus was observed among the three streams. Similarly, phosphorus and calcium were conserved in detritus from the two neutral streams, but were lost from detritus in the acidic stream. The final content of phosphorus was significantly lower in the acid stream SFR (45.9 percent for red maple), than in either of the two neutral streams WSH (52.0 percent) and HSH (63.1 percent), which

were not significantly different from each other. Calcium in detritus was also conserved, but only during the first 20 days in the alkaline stream, HSH. Calcium was lost by detritus by both SFR and WH.

Magnesium was lost by the detritus in all three species. Magnesium in SFR was significantly lower (4.09 percent for red maple) than WH and HSH, 25.3 percent and 25.7 percent respectively, which were not significantly different. Potassium was rapidly leached from detritus in all three streams.

Microbial biomass on the detritus was significantly lower in the acidic stream, SFR (38.2 ng ATP/g for red maple), in comparison with the more neutral streams, WH (201.5 ng ATP/g) and HSH (145.2 ng ATP/g).

## DISCUSSION

We concluded that litter decomposition and elemental accumulation or loss in aquatic detrital material was strongly influenced by water chemistry. Of the water quality variables measured, pH appeared to be the most important in determining decomposition rates. Decomposition rates and microbial colonization are significantly reduced in acidic conditions.

Nitrogen was conserved in the detrital material over time. However, no significant differences in net nitrogen concentration were observed among the three streams. This suggests that decomposition is not controlled by nitrogen alone in our study streams. Nitrogen conservation was most likely the result of loss of more labile leaf litter components such as potassium.

Phosphorus was conserved in the two neutral streams but was lost in the acidic stream. Phosphorus may be accumulating on detritus in the two neutral streams as a result of contributions of phosphorus by the microbial community. Mulholland et al. (1984) suggested that phosphorus accumulation in decomposing leaf detritus is a function of microbial biomass and activity within the detritus. Phosphorus loss in the acidic stream may be the result of the reduced microbial biomass.

Elemental changes in calcium and magnesium may be the result of the location of these components within the detritus or the presence of refractory materials. Potassium, the most mobile element measured, was rapidly leached from the detritus.

Our results indicate that, with the exception of nitrogen, detrital elements are lost more rapidly in the acidic stream than in the more neutral streams. In addition, both decomposition rate and microbial biomass were also lower in the acidic stream. This suggests that elemental content of detritus was more rapidly depleted under acidic conditions, reducing quality for macroconsumers. In addition, lower microbial biomass in detritus in acidic systems may result in slower conditioning rates which may also contribute to lower detrital quality, an important factor in detrital-macroconsumer relationships.

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## METHANE EVOLUTION FROM MINNESOTA PEATLANDS

Elon S. Verry<sup>1</sup>

Peatlands in the northern hemisphere ( $346 \times 10^8$  ha) store large amounts of carbon, estimated at 455 petagrams (Pg) ( $=10^{15}$ ) (Gorham 1991). This is about 30% of the world's pool of soil carbon (excluding peat), about 64% of the atmospheric pool (Bolin 1983), and about 55% of total plant biomass. This stored organic matter is passed to the atmosphere as both carbon dioxide ( $\text{CO}_2$ ) and methane ( $\text{CH}_4$ ) through aerobic or anaerobic decomposition, respectively. This review summarizes the annual evolution of methane from peatlands in north central Minnesota (1990-1993), its seasonal variance, its variance with air pressure, and its dependence on active transport through the stems of peatland emergents. Soil temperature, and water table position are major factors correlated with methane evolution. Modeling studies of possible climate changes (associated with 2X changes in  $\text{CO}_2$  concentrations in the atmosphere) show that methane in the Lake Region will not change water levels. However, extended growing seasons and elevated peat temperatures will lead to additional methane evolution at rates 50 to 80 % higher than currently experienced. In this scenario, warming begets warming. However, field studies in 1994 testing the impact of elevated ammonium sulfate loading on peatlands, show that methane evolution is suppressed under atmospheric loading rates typical of Europe today.

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NUTRIENT CYCLING IN AGGRADING FORESTS: 50 YEARS OF RESEARCH AT PACK FOREST, NEW  
YORK

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The Charles Lathrop Pack Demonstration Forest, Warrensburg, New York, has been the site of long-term forest fertilization and biogeochemical ecosystem research for over 50 years. It is by far the longest ongoing examination of trends in nutrient cycling in North America. Plots of red pine that were fertilized 50 years ago with potassium were reexamined to determine the changes in forest soil properties after exposure to acid deposition. Subsoil uptake of nutrients by plantation red pine was confirmed by experimental use of tracer techniques with  $\text{SrCl}_2$  and Rb/K ratios as a mechanism for improving the soil. K levels in the unfertilized sites did show improved levels of K relative to fertilized stands, improving at approximately twice the rate of the fertilized stand. The pH of unfertilized plots remained the same over time, while the pH of the fertilized plots significantly declined over the 50 years, attributed primarily to initial increase in pH due to the addition of KCl as fertilizer and the increase in forest soil organic matter buildup over time. The results of historical biogeochemical trends, in conjunction with the analysis of lateral fertilizer transport and significant subsoil uptake each clarify distinct aspects of nutrient dynamics in the K-deficient soils of the Pack Forest Plain under fertilized and unfertilized red pine over time. Combined, the pieces of the story tell a greater tale of nutritional improvement of degraded surface soils mediated by the long-term effects of human management practices such as reforestation and forest fertilization, and by the nutrient uptake, conservation and distribution abilities of aggrading forests. The data provides new insights into understanding and modeling the interaction of developing forest ecosystems with subsoil nutrient pools and the dynamics of lateral transport and conservation of nutrients that need to be recognized in assessing impacts of global change on forest ecosystem sustainability.

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RELATIVE NITROGEN MINERALIZATION AND NITRIFICATION POTENTIALS IN RELATION TO SOIL  
CHEMISTRY IN OAK FOREST SOILS ALONG A HISTORICAL DEPOSITION GRADIENT

Ralph E.J. Boerner<sup>1</sup> and Elaine Kennedy Sutherland<sup>2</sup>

This study quantified soil nutrient status and N mineralization/nitrification potentials in soils of oak-dominated, unmanaged forest stands in seven USDA Forest Service experimental forests (EF) ranging along a historical and current acidic deposition gradient from southern Illinois to central West Virginia. Among these seven sites (that spanned 8.5 ° of longitude) soil pH and Ca<sup>2+</sup> decreased and soil organic C and soluble Al<sup>3+</sup> increased from west to east. In general, initial soil solution NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup> was uncorrelated with longitude. The Fernow EF (WV), the easternmost site, was the exception to this trend. Soils from the Fernow had the highest concentrations of both NO<sub>3</sub><sup>-</sup> accumulation, and the greatest N mineralization potential. Stepwise regressions of N mineralization rate, net NO<sub>3</sub><sup>-</sup> accumulation, and proportional nitrification on initial soil properties produced models with overall r<sup>2</sup> of 0.705, 0.772, and 0.708, respectively. Rates of N turnover were positively correlated with initial NO<sub>3</sub><sup>-</sup>, pH, and Ca:Al ratio and negatively correlated with soil solution Al<sup>3+</sup> concentrations. Differences in oak growth and mortality may be related to the differences in soil chemical status and soil N dynamics along these seven experimental forests.

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## MORTALITY PATTERNS IN OAK FORESTS ALONG A CLIMATIC AND ACID DEPOSITION GRADIENT

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The cause or causes of recently observed mortality and changes in forest composition in eastern mixed-oak forests has been a controversial topic. Causes discussed in the literature include air pollution (ozone, acid deposition), drought-induced decline, insect infestation, or simply stand age. The objective of this study was to relate patterns of mortality and stand composition changes to edaphic characteristics, soil parameters, and records of drought. We compare individual tree records from seven experimental forests (EF) in the Ohio River Valley ranging along a historical and current acidic deposition gradient from southern Illinois to central West Virginia (Kaskasia EF, Illinois; McKee EF, KY; Bald Rock EF, KY; Robinson EF, KY; Mead EF, OH; Raccoon EF, OH; and Fernow EF, WV). To determine similarities among the sites, we performed multivariate analyses relating species composition to an integrated moisture index (IMI), soil elemental concentrations, Ca/Al ratios, and nitrogen turnover rates. We characterized patterns of mortality as a function of species, tree size, and time. We used logistic regression approaches to model mortality as a function of the Palmer Drought Severity Index (PDSI), IMI, and the abovementioned soil parameters.

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