9-1-2009

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Peter Kenlan

G. B. Wiersma

A. S. White

I. J. Fernandez

ISSN 1070–1524

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Technical Bulletin 202 September 2009

MAINE AGRICULTURAL AND FOREST EXPERIMENT STATION
THE UNIVERSITY OF MAINE

Composition and Biomass of Forest Floor Vegetation in Experimentally Acidified Paired Watersheds at the Bear Brook Watershed in Maine

Peter Kenlan
School of Forest Resources
University of Maine

G. B. Wiersma
Center for Research on Sustainable Forests
University of Maine

A. S. White
School of Forest Resources
University of Maine

and

I. J. Fernandez
Department of Plant, Soil and Environmental Sciences
University of Maine

Maine Agricultural & Forest Experiment Station
University of Maine
5782 Winslow Hall
Orono, Maine, 04469

ABSTRACT

The percent cover (abundance), frequency of occurrence, biomass, species richness, and species diversity of understory herbs was measured on a paired watershed ecosystem in eastern Maine, USA. This paired watershed site (Bear Brook Watershed in Maine, BBWM) has had the West Bear Brook Watershed treated bi-monthly with granular ammonium sulfate at a rate of 28.8 kg S ha^{-1} yr^{-1} and 25.2 kg N ha^{-1} yr^{-1} since 1989. East Bear Brook Watershed serves as the reference site. More than 100 plots were randomly located across the two watersheds. The data suggest that there is generally a lower frequency of occurrence of understory plants on the treated watershed. In addition there was a significant difference in species richness with the treated watershed (West Bear) being lower than the reference watershed (East Bear). Biomass measures generally followed this same trend although there were not significant differences detected. These differences reflect treatment effects in light of biogeochemical changes shown to be occurring in other studies due to treatments.

INTRODUCTION

Acidic deposition results primarily from the atmospheric input of sulfur (S) and nitrogen (N) compounds from the burning of fossil fuels. Deposition of acidic compounds in forests has the potential to cause substantial effects on forest vegetation by direct effects of this deposition on plant tissue and by causing biogeochemical changes in the soil that affect fertility and toxicity. The Bear Brook Watershed in Maine (BBWM) is a paired, forested, first-order stream watershed experiment site, which was designed to investigate the effects of acidification and nitrogen enrichment on forest ecosystems. The study area consists of two watersheds of similar size, soil type, forest composition, slope and aspect. The West Bear Brook Watershed is treated with granular ammonium sulfate to simulate elevated acidic deposition, and the East Bear Brook Watershed serves as a reference. Early research at BBWM focused on surface water chemistry with later research focusing on soil chemistry and effects on vegetation (e.g., Fernandez et al. 1999; Kahl et al. 1999; Norton et al. 1999b; White et al. 1999; Elvir et al. 2003; Fernandez et al. 2003; Norton et al. 2004). These studies have shown that the foliar chemistry of mature trees reflects some of the soil and surface water changes induced by treatments that include base cation depletion, aluminum (Al) mobilization, an acceleration of N cycling, and changes in carbon (C) dynamics.

We expect that geochemical changes from chemical treatments will be evident quickly, but over time these alterations will begin to increasingly influence whole-ecosystem function by altering biota, including alterations to the composition and structure of plant communities at the site. These changes should be detectable over time among herbaceous understory plants and tree seedlings. Previous vegetation studies at BBWM have focused mainly on mature trees (e.g., White et al. 1999; Elvir et al. 2003). Eckhoff's (2000) study included measurements of understory plants, and the results from her study will provide some basis for general comparison.

The purposes of this study are twofold. The first purpose is to determine whether there are differences in the abundance and frequency of occurrence of understory plant species between the treated watershed and the reference watershed. The second purpose is for the results of this study to provide a baseline for understory plant community composition at BBWM that can be used to study additional response to the continuing treatment program in the future.

Statement of Null Hypothesis

The cover (abundance), frequency, biomass, and diversity of species of herbaceous understory plant and tree seedlings will not vary significantly between the treated and reference watersheds. Soil pH and nutrient availability are important factors influencing forest vegetation, and treatments at BBWM influence both. Treatment at BBWM is done with ammonium sulfate, an acidifying fertilizer. Low-pH forest soils are commonly associated with low populations of understory plants due to lowered nutrient availability (Lodhi 1982; Falkengren-Grerup 1986; Lucassen et al. 2002; Økland et al, 2004). Accordingly, it is expected that the treated watershed will exhibit a lower frequency of occurrence, lower abundance, lower total biomass, and lower diversity than the reference watershed.

MATERIALS AND METHODS

Site Description

The study site is located in eastern Maine (44°52'15" N, 68°06'25" W) on the upper southeast slope of Lead Mountain (475m) (Norton et al. 1999a). Two contiguous forested watersheds, West Bear (WB) and East Bear (EB), comprise the BBWM with areas of 10.3 ha and 11.0 ha, respectively (Fernandez et al. 2003). Each of the watersheds is drained by a first-order stream, and they have highly similar soil and forest composition and topography (Uddameri et al. 1995). Climate at the BBWM site is temperate with temperatures ranging from -30°C to 35°C and mean annual precipitation of 1.4 m, approximately 25% of which is in the form of snow (Norton et al. 1999a). Five tree species constitute the majority of vegetation at BBWM: Picea rubens (red spruce), Fagus grandifolia (American beech), Acer rubrum (red maple), Acer saccharum (sugar maple), and Betula alleghaniensis (yellow birch). These species are distributed among three forest cover types: softwood (SW), mixedwood (MW) and hardwood (HW) (Elvir et al. 2003). A grid overlays the site with lines spaced at 30 m and aligned to geodetic north.

Treatment

Experimental manipulation at BBWM began in 1989 and consists of bimonthly applications of granular ammonium sulfate $[(NH_4)^2SO_4]$ to WB by helicopter at a rate of 28.8 kg S ha^{-1} yr^{-1} and 25.2 kg N ha^{-1} yr^{-1} (Fernandez et al. 2003). The added deposition is equivalent to approximately twice the ambient rate for S and three times the ambient rate for N deposition at this site (Norton et al. 1999a). The total deposition rate in the treated watershed is comparable to the areas of the U.S. with the highest observed deposition rates (Rustad et al. 1994).

Experimental Design

Grid-line intersections served as the source of a sampling population for this study. Intersection points were classified according to forest cover type. Cover types were classified based on a visual estimate of canopy cover with hardwoods (HW) having >75% hardwood canopy cover, softwoods (SW) having >75% softwood cover, and mixedwoods (MW) having neither hardwoods nor softwoods with >75% cover. Points were considered ineligible for inclusion if they were located less than 15 m from a cover type boundary or the boundary between EB and WB. An equal number of points were randomly selected within each watershed and their numbers distributed between cover types in proportion to the relative dominance of each cover type within each watershed. Plots were established a fixed distance and direction from each selected point and eliminated without replacement if they fell in an unsuitable area (e.g., road, streambed, or an unrelated study plot). When a point was selected multiple times, additional plots were established in different directions than the first, up to four plots per point.

It is worth noting that the design of this study could be considered pseudoreplication (Hurlbert 1984) because each watershed represents a treatment with only one sample. Though pseudoreplication has the potential to cause some difficulties with the interpretation of statistical results, it is a common characteristic of watershed studies due to practical limitations.

Plot Design

Plots were designed to assess characteristics of understory plant communities. This vegetation survey estimated the same parameters as the forest health monitoring (FHM) protocols used by Eckhoff (2000) at BBWM described in the Forest Health Monitoring 1994 Field Methods Guide (Tallent-Halsell 1994). In addition to abundance (% cover) estimates and frequency of occurrence measurements used by Eckhoff (2000), this study added measurements of total plant biomass and species richness. Total biomass measurements were included because cover estimates, while useful, are not always a perfect proxy for estimating this parameter (Chiarucci et al. 1999). FHM protocols divide vegetation structure measurements into four strata. This study used only the lowest level of those strata, from ground level to 0.6 m in height.

Though the measurements made were similar, the physical design of plots in this study was different from that used by Eckhoff (2000). Therefore, modifications were made to maximize both the number of plots that could be measured and the area covered by each plot (Jalonen et al. 1998). This was best accomplished by using a collapsible frame to divide the plot area (2 m square) into 1-m2 compartments. The advantage of the smaller plot area is that a greater number of plots were measured, increasing the usefulness of the frequency of occurrence estimates.

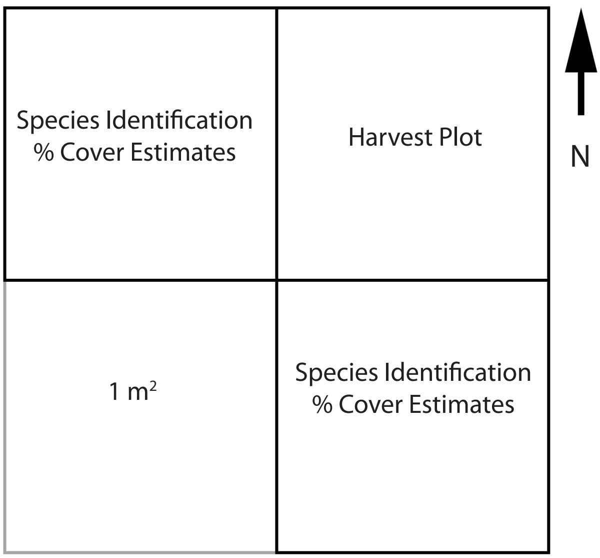

Figure 1. Illustration of plot design

Each plot consisted of a 2-m-by-2-m square divided into four 1-m^2 subplots and aligned with the grid lines (Figure 1). All plants less than 0.6 m in height in the northwest and southeast subplots were identified, and cover estimates were made to the nearest 5%. For measurements of species abundance, the mean estimated percent cover of the two subplots was reported as the value for the plot. To estimate frequency of occurrence, a species was considered to occur in a plot if it appeared in at least one of the two subplots used for cover estimates. In the northeastern subplot, all plants less than 0.6 m in height were harvested by cutting the stem at ground level to measure total biomass. The plant material harvested from each plot was placed in a paper bag and dried until a constant weight was reached. For this study, the southwest subplot was ignored. The total number of plots was 101 with 53 located in EB and 48 in WB. All of the plots used in this study were measured between July 5, 2005, and September 1, 2005.

Statistical Methods

Data for abundance and frequency of occurrence were analyzed by permutation testing of resampled data. Resampling takes data that already exist and reshuffles them many times to experimentally determine the probability that the observed result would occur by chance. A p-value is obtained by calculating the fraction of times that a test statistic calculated for each iteration was equal to, or more extreme than, the observed result. For abundance, the test statistic used was the difference between means because it was an equivalent test statistic to t in this instance and was more efficient to compute over many iterations. For frequency of occurrence, chi-square was used as a test statistic on permuted data. Randomization was necessary for the chi-square test because in many instances the number of observations in the reference watershed was low. These tests are a means of directly determining the probability that an observed result is due to random chance. Hypothesis testing done by this method requires no assumptions be made about population distribution because the probability of obtaining an extreme test statistic is based on permutations of randomized data (Crowley 1992; Edgington 1995; Eckhoff 2000).

The randomization test algorithms used in this study were developed in 2006. Using the original data as input, the algorithm randomly ranked and then ordered these data, thereby reassigning each observation to one of the two test categories (treated or untreated watershed). The test statistic was calculated for each of 10,000 iterations and the distribution of these statistics determined whether there was a statistically significant difference.

Linear regression equations were computed using the R statistical package. Total biomass and species count data were analyzed using one-way ANOVA tests in R. Where conclusions of statistical significance are reported, $\alpha = 0.05$ was used to confer significance. Log transformations were used when necessary to meet assumptions of normality.

Sorensen's community similarity index was calculated with the equation $Cs=2a/(b+c)$ where a = the total number of species in common to WB and EB, b = the number of species in WB and c =

the number of species in EB (Barbour et al. 1987). Simpson's index (D) was used as an index of diversity with the equation

$$D = \sum_{i=1}^{S} p_i^2$$

and subsequently converted to effective species by Simpson's reciprocal index (1/D) (Jost 2006).

To assess whether the observed differences in species abundance and frequency are meaningful in aggregate, we used a scatter plot of frequency and abundance with the reference watershed along the x-axis and the treated watershed on the y-axis, similar to the technique employed by Gilliam et al. (1994). Each point (x, y) represents the frequency or abundance of a single species in both watersheds. If treatment has no effect on frequency or abundance of understory plants, then a line fitted to plots of mean species frequency or abundance should have a slope of one (y = x), meaning that the species are equally abundant on both watershed. Points that fall below a 1:1 reference line are more abundant or frequent in the reference watershed, while those that fall above the line are more abundant or frequent in the treated watershed. For these plots, only species that had a presence on both watersheds were part of the analysis.

RESULTS

Species Frequency and Abundance

Most plants were identified and counted at the species level, but in certain instances, multiple species were grouped at a higher taxonomic level, as in the case of ferns and graminoids. For simplicity, when "species" are referred to broadly, it will be understood to include these higher-taxa groupings in addition to individual species. A total of 26 species was found within plots on EB and WB. Of these 26 species, 25 were found in EB and 20 in WB. There were seven species (*Fragaria virginiana, Cypripedium* spp., *Viola* spp., *Medeola virginiana, Cornus canadensis, Pinus strobus,* and *Lycopodium* spp.) that occurred in EB but not in WB, and two species (*Polygonum convolvulus* and *Vaccinium* spp.) that occurred in WB but not in EB. Sorensen's community similarity index gave a value of 0.80 for the two watersheds. A comparison of the relative diversity of the two watersheds using Simpson's reciprocal index gave a value of 13 for each of the two watersheds.

Statistical comparisons of abundance and frequency of occurrence were performed on aggregations of the observations from the mixedwood and hardwood cover types. Plots that fell in pure softwood stands had very little in the way of herbaceous ground cover and seedlings while plots that fell in the hardwood and mixedwood cover types were similar in the amount of ground cover present. Combining plots from the mixedwood and hardwood cover types resulted in 33 plots from WB and 45 plots from EB. Frequency of occurrence was calculated as the number of plots in which a species was found divided by the total number of plots in the watershed. Abundance was calculated as the mean percent cover of each species in all the plots in each watershed.

Statistical comparisons of the abundance and frequency data were made by permutation testing of the results (Table 1). In the deciduous forest types (a combination of HW and MW plots) at BBWM both *Acer pensylvanicum* and *Aster* spp. were significantly more abundant and had a significantly greater frequency of occurrence in EB compared to WB. Two species, Trientalis borealis and the ferns, were more abundant in EB than in WB, with p-values between 0.05 and 0.1. And one species, *Maianthemum canadense,* was more frequent in EB, with a p-value of 0.09.

Regression of mean species frequency in the reference watershed against mean species frequency in the treated watershed resulted in the equation $y = 0.45x + 0.05$, $R2 = 0.67$, which was significant with a p-value <0.0001 ($H0:\beta = 1$). This indicates a significant and relatively strong relationship, with the species measured having consistently lower frequency of occurrence in WB than in EB. Figure 2 shows the 95% confidence interval of this regression equation (dashed lines) compared with a 1:1 reference line (dotted line) representing the condition where there is no difference in species frequency between watersheds.

Regression of mean percent cover by species in the reference watershed against mean percent cover by species in the treated watershed result in the equation $y = 0.26x + 0.27$, $R2 = 0.21$ (Figure 3). This result was significant with a p-value of <0.0001 when $H0:\beta = 1$, but the p-value was only 0.07 when $H0:\beta = 0$. The relationship was weaker than the frequency plot, with an R2 of 0.21. One of the reasons that this relationship is different from the frequency relationship is that there is more variance in percent cover measurements while frequency is calculated based on presence alone. For the region of the line where most of the points are concentrated, the 1:1 reference line (dotted line) falls within the 95% confidence interval (dashed line). These results are interpreted with caution because there remains the possibility of bias in the sample. The hardwood forest type plots combine the mixedwood plots with the

Table 1. Frequency and abundance of plant species <0.6 m in height in the deciduous forest types at Bear Brook Watershed in Maine in 2005.

	Abundance (avg % cover)			Frequency (% of plots)		
Species	EB	WB	p-value	EB	WB	p-value
Abies balsamea	0.16	0.00	0.187	7	0	0.184
Aralia nudicalis	0.60	0.97	0.276	13	15	0.530
Acer pensylvanicum	1.11	0.24	0.001*	58	24	0.002*
Acer rubrum	0.71	0.48	0.203	53	36	0.101
Acer saccharum	0.49	0.55	0.443	31	18	0.147
Aster spp.	1.53	0.45	0.029*	40	15	0.015*
Betula alleghaniensis	0.49	0.27	0.248	22	15	0.144
Cornus canadensis	0.02	0.00	0.572	2	0	0.582
Cypripedium spp.	0.13	0.00	0.317	4	0	0.325
Fern	7.29	1.15	0.066	24	18	0.351
Fagus grandifolia	0.40	0.27	0.341	22	15	0.320
Fragaria virginiana	0.04	0.00	0.324	4	0	0.323
Graminoids	0.22	0.39	0.358	13	12	0.591
Hamamelis virginiana	0.36	0.64	0.316	7	9	0.499
Lycopodium spp.	0.33	0.00	0.331	4	0	0.324
Maianthemum canadensis	0.36	0.24	0.339	27	12	0.097
Medeola virginiana	0.11	0.00	0.587	2	0	0.570
Polygonatum pubescens	0.02	0.06	0.384	2	6	0.392
Picea rubens	0.58	0.67	0.424	31	27	0.449
Pinus strobus	0.02	0.00	0.580	2	0	0.584
Rubus spp.	0.07	0.61	0.427	7	3	0.426
Sorbus americana	0.02	0.06	0.389	2	6	0.384
Trientalis borealis	0.27	0.06	0.098	18	6	0.115
Uvularia sessilifolia	1.76	0.91	0.123	31	27	0.456
Viola spp.	0.13	0.00	0.326	4	0	0.332
Vaccinium spp.	0.00	0.15	0.423	0	3	0.421

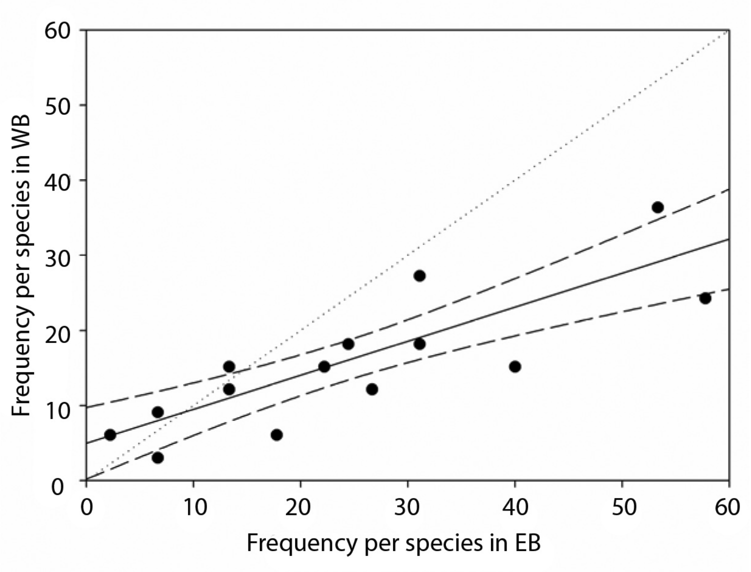

Figure 2. Frequency of species in EB vs frequency of species in WB in deciduous forest types.

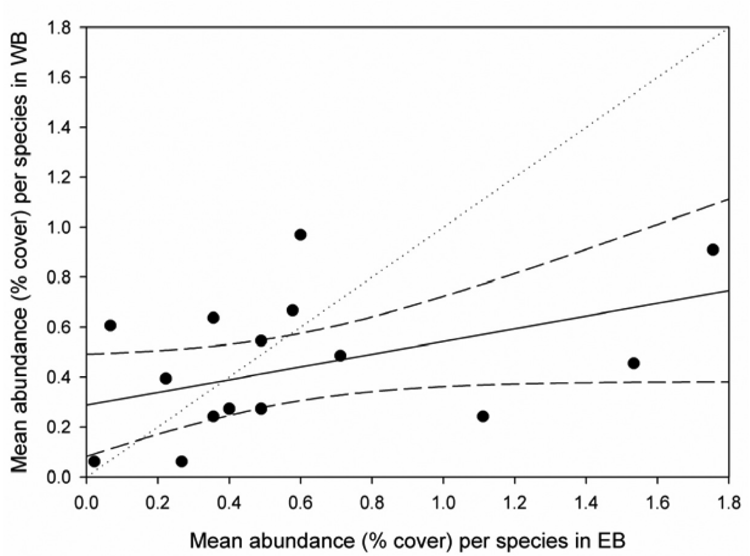

Figure 3. Abundance of species in EB vs abundance of species in WB in deciduous forest types.

hardwood plots to calculate mean frequency and percent cover. In addition to the fact that the total number of these plots from WB is smaller than the number from EB, hardwood plots constitute a greater fraction of the plots from WB. Nevertheless, combining mixedwood and hardwood plots to make comparisons between the watersheds is necessary because not only does the relative disparity between sample sizes become much larger when comparisons are reduced to a single cover type, the absolute size of these samples is too small to make credible statistical assertions.

Mean Biomass

The total dry biomass for each plot was measured and means were calculated separately for mixedwoods and hardwoods and their combination (Table 2). There was a numerical trend for the mean understory plant biomass per plot to be numerically greater in the untreated watershed for each cover type. The distribution of these data was highly non-normal and log transformation was required to normalize the data.

Table 2. Mean biomass per plot for all species combined

	Biomass (dry g/m^2)		Biomass (dry g/m^2)		
Cover Type	EB[a]	WB[a]	EB[b]	WB[b]	p-value[b]
Mixedwood	2.62	2.02	0.35	0.10	0.141
Hardwood	3.13	2.09	0.92	0.24	0.262
Combined	2.74	2.05	0.43	0.15	0.107

[a]Arithmetic means calculated from untransformed data.

[b]Geometric means and significance tests following log transformation to correct non-normal data.

Species Density

Means for the number of distinct species per plot were calculated separately for each of the hardwood forest types and for both types combined (Table 3). Each of the hardwood forest types had greater mean species per plot in the reference watershed compared to the treated watershed.

Table 3. Mean number of species per plot

Cover Type	Species per plot		
	EB	WB	p-value
Mixedwood	4.00	2.89	0.094
Hardwood	5.30	2.38	0.001*
Combined	4.30	2.68	0.0002*

DISCUSSION

Species Composition

The primary ecological issue addressed by this study was whether there were differences in biodiversity or species composition that could be attributed to the treatment. There were several species that were only recorded in one of the two watersheds. These species, however, were all relatively rare, occurring in only one or two plots, and therefore their presence is not likely a test of treatment effects. The community coefficient for the watersheds overall, computed by Sorensen's presence-only calculation was 0.80, which represents a strong similarity in the species composition of the two watersheds (a community coefficient greater than 0.50 generally indicates the same association). However, the Sorensen calculation is only a measure of similarity, not of biodiversity. Biodiversity was calculated with Simpson's diversity index, and the index was converted to effective species (Jost 2006). The Simpson's index for EB and WB were 0.923 and 0.920, respectively, which translates to 13 effective species in each watershed. Simpson's index of diversity incorporates relative species abundance but not similarity like Sorensen's. These measures suggest equal diversity and a high degree of similarity between the two watersheds

Density

The results from biomass, species count, and individual species' frequency and percent cover measurements indicate a greater dominance of understory plants in the untreated watershed. In each category, plots from the untreated EB watershed had greater total mean biomass and a greater number of mean species per plot. Even though there were a greater number of species on any given plot, however, the species found in both watersheds were largely the same, with the notable exceptions of the few species that occurred rarely in the plots of only one watershed or the other. None of the observed differences was statistically significant, but they did follow the same numerical pattern as the other measurements, with higher values appearing in the plots from EB. In addition, the significant differences in individual species' percent cover (*A. pensylvanicum* and *Aster* spp.) indicated a greater abundance of these species in the reference watershed compared to the treated watershed. The same was true for the significant differences in individual species frequency of occurrence (*A. pensylvanicum* and *Aster* spp.) where all of the significant differences indicated a greater frequency of occurrence in the reference watershed. This is best illustrated in the linear regression plots, which produce equations with a slope <1 for both frequency of occurrence and percent cover of individual species. The regression analyses taken together with the significant differences in percent cover and frequency of several individual species is evidence that, generally, there is a lesser mean abundance and a lower frequency of occurrence of understory plant species in the treated watershed.

There are several plausible hypotheses to explain this pattern. The first is that treatment with ammonium sulfate is directly responsible for a decrease in the abundance and frequency of certain species in the treated watershed. Given what is known about how the treatment affects soils, it is possible that since the treatment began in 1989, base cation depletion has progressed to the point where it negatively affects plant growth, Al mobilization has increased to a toxic level with the same negative effect, or soil pH has become too acidic for certain species (Andersson 1988; Houdijk et al. 1993; Thomas et al. 1999; Roem et al. 2002).

Two species, *A. pensylvanicum* and *Aster* spp., were significantly less frequent and had a significantly lower percent cover in the treated watershed, and seven species occurred in the reference watershed but did not occur at all in the treated watershed. While all the evidence supports the assertion that there are real differences between the plant communities in the two watersheds, what is less clear is whether the observed differences were due to experimental manipulation. It is possible that the two watersheds have always had different abundances of understory plants for undefined reasons, and the treatments have not altered that condition.

While N is typically the most limiting plant nutrient on terrestrial sites, the increased export of nutrients observed in stream chemistry—particularly Ca and Mg—may have reduced the plant-available pools of these nutrients such that they are now the dominant factors limiting growth (Kirchner and Lydersen 1995; Gbondo-Tugbawa and Driscoll 2003). The results of chemical analyses of plants from

BBWM lend some support for an assertion that the observed plant community composition results are due to a chemical change (Elvir et al. 2005; Kenlan 2006; Bethers et al. 2007).

A second possibility is that ammonium sulfate treatment indirectly results in a reduction of understory plant abundance and frequency by altering the amount of available light at the forest floor. Based on the results of Elvir's (2003) tree growth study, it is possible that the effect of the treatment resulted in a flush of tree seedling growth that has reached sapling stage. Qualitative field observations during this study were that the abundance of sapling-stage *F. grandifolia* and *A. pensylvanicum* was greater in the treated watershed. Several plots in the treated watershed had no forest floor plants at all, presumably due to very dense tree saplings observed near these plots, which reduced the amount of available light to the forest floor. A factor such as this could be the major cause of the observed differences, or it could interact with and compound the direct effects of acidification on understory plants.

Another possibility is that the two watersheds have different forest floor vegetation communities because of the stochastic effects of a disturbance such as the 1998 ice storm that disproportionately affected the available light at ground level on one of the watersheds. A report on the storm (Miller-Weeks and Eagar 1999) indicated that it affected approximately 11 million acres in Maine, including the BBWM research site. Hardwood stands were considerably more damaged than softwood stands. Another source of bias could be that the most severely affected portions of WB were oversampled—the sample from WB contains a greater fraction of hardwood plots than the sample from EB—and that crown damage in the most severely affected hardwood plots resulted in a flush of sapling-stage trees that reduced available light at ground level and inhibited understory plant growth as described above. Within-watershed differences between cover types were not analyzed because certain sample sizes became too small when plots were separated by cover type.

Because this is an unreplicated paired watershed study, the best way to determine the influence of treatments on forest floor vegetation would be to do a longitudinal study with careful attention to consistency of methods. The first measurements of forest floor vegetation at BBWM were made in a study done in 1997 and 1998 by Eckhoff (2000). However, the methodology of that study was different enough from this study so that it precluded valid statistical comparisons. Eckhoff's study measured a small number of plots that covered a large area, whereas this study measured a larger number of plots each covering a smaller area. Individual tests for significant differences between percent cover and frequency were not done in the Eckhoff study. Randomization tests were performed to test the significance of a difference in total abundance of understory plants, but no significant differences were found (Eckhoff 2000). That differences were observed in this study but not Eckhoff's could be because those differences did not exist in 1999, or because of differences in the precision of each of the experimental designs.

The results from this study add to a body of literature about the effects on understory and forest floor vegetation of acid deposition that have varied results (Falkengren-Grerup and Tyler 1993; Gilliam et al. 1994; Hallbäcken et al. 1998; Hurd et al. 1998). Gilliam et al. (1994) found no differences in understory plants in a West Virginia forest. Falkengren-Grerup and Tyler (1993) found increases in some species and decreases in others. Hurd et al. (1998) found minor decreases, and Hallbäcken et al. (1998) found decreases in understory plant abundance and the number of species present. The design of this study was most similar to that employed by Gilliam et al. (1994) though the measurements in the present study were made considerably longer after treatment commenced than in Gilliam's study.

CONCLUSIONS

Based on all of the evidence including biomass, species density, species frequency, and percent cover, it is likely that there is a difference between the treated and reference watersheds with respect to species frequency and percent cover within the hardwood forest types. The data suggest that there is a generally lower frequency and percent cover of understory plants in the treated watershed. Furthermore, a significant difference in species richness in the treated watershed per plot was detected. The differences in total mean biomass per square meter were not significant although the amount measured was lower in the treated watershed. Species composition was, in general, similar, but there were several species that occurred only in the reference watershed. All of this evidence collectively leads to a rejection of the original null hypothesis: that there would be no difference in species abundance, frequency, biomass, or diversity.

In the absence of comparable baseline data and data regarding light conditions and sapling abundance, it is difficult to draw any further conclusions about the observed differences between the watersheds. The continuous and ongoing bimonthly treatment schedule at BBWM simulates chronic acidic deposition, as opposed to a single deposition event, and it is expected that the effects of treatment will evolve and progress over time. The ecology of understory plants at BBWM remains an area of interest because it is likely that changes that may eventually alter the composition of these plant communities—including their overstory component—will first be visible in the understory. Further study will be needed to assess how these communities continue to change and to determine more definitively what the cause of the observed differences is.

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Maine Agricultural and Forest Experiment Station
5782 Winslow Hall
Orono ME 04469-5782

5-5-38900

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