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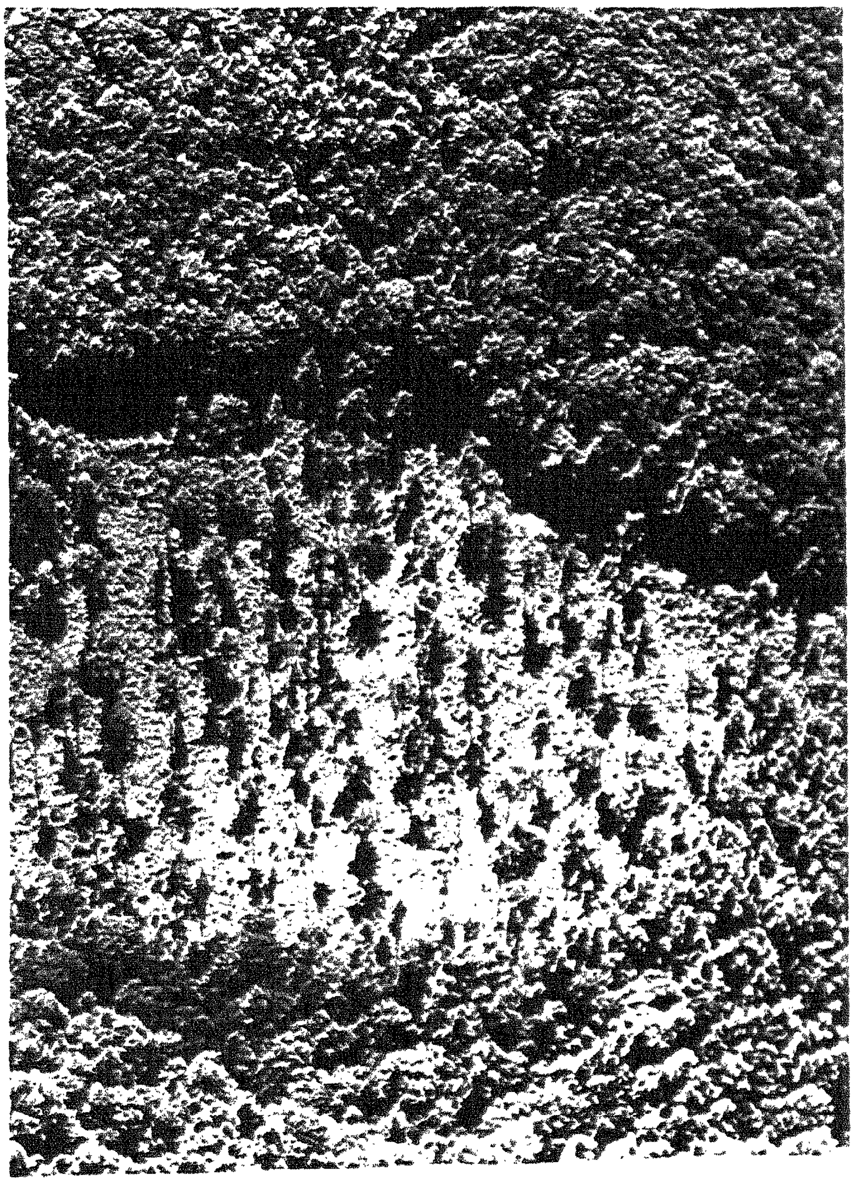

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For attending this conference, each registrant was eligible for 12 hours of Continuing Forestry Education (CFE) credit offered by the Society of American Foresters.

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ACKNOWLEDGMENTS

The editors would like to acknowledge and thank all of the people who served as manuscript reviewers for the Proceedings. The quality of the Proceedings has been improved due to your efforts. We would like to thank Becky Rosenberger for her assistance in typing the program, preparation of the table of contents, typing abstracts, proofreading, and in managing the manuscripts, reviews, and letters associated with the Proceedings. We thank Gary Miller for providing the cover photograph.

Cover Photo: This 1984 aerial photograph was taken from a helicopter three years after deferment cutting in 80-year-old central Appalachian hardwoods on the Fernow Experimental Forest near Parsons, West Virginia. (Photo by James N. Kochenderfer, USDA Forest Service.)

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Edited by

Kurt W. Gottschalk and Sandra L. C. Fosbroke

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FOREWORD

This conference is the tenth in a series of biennial meetings that began in 1976 at Southern Illinois University. Other conferences have been hosted by Purdue University, University of Missouri, University of Kentucky, University of Illinois, University of Tennessee, Southern Illinois University with the North Central Forest Experiment Station (NCFES), Pennsylvania State University with the Northeastern Forest Experiment Station, and Purdue University with NCFES. The purpose of these conferences has remained the same: to provide a forum for the exchange of information concerning the biology and management of central hardwoods by forest scientists from throughout the Central Hardwood Region of the eastern United States. As with previous Proceedings, a wide range of topics that represent the broad array of research programs in this area is represented.

The social and biological characteristics of the Central Hardwood Region make it unique in comparison with other forest regions of the United States. For example, one-fourth of the United States human population resides in this region. Approximately 90% of the land is in private ownership and public lands tend to be small and fragmented with private inholdings. These and related conditions play critical roles in the practice of forestry in this region. The information presented in this Proceedings is important to the long-term management of the forest resources of this unique region.

REVIEW PROCEDURES

Each manuscript published in these proceedings was critically reviewed by at least two (usually three) scientists with expertise in disciplines closely aligned to the subject of the manuscript. Reviews were returned to the senior author, who revised the manuscript appropriately and resubmitted it in a diskette format suitable for printing by the Northeastern Forest Experiment Station, USDA Forest Service where they were edited to a uniform format and type style. Manuscript authors are responsible for the accuracy and content of their papers.

TABLE OF CONTENTS

POSTER SESSION

FOREST FLOOR CO_2 FLUX FROM TWO CONTRASTING ECOSYSTEMS IN THE SOUTHERN APPALACHIANS

James M. Vose[1], Barton D. Clinton[1], and Verl Emrick[2]

Abstract: We measured forest floor CO_2 flux in two contrasting ecosystems (white pine plantation and northern hardwood ecosystems at low and high elevations, respectively) in May and September 1993 to quantify differences and determine factors regulating CO_2 fluxes. An automated, IRGA based, flow through system was used with chambers inserted into the soil. This approach allowed quantification of diurnal flux patterns which were subsequently averaged to estimate daily mean flux rates ($u$mol m^{-2} s^{-1}). Mean flux rates were 60 percent greater in the white pine ecosystem (8.9 $u$mole m^{-2} s^{-1}) than in the northern hardwood ecosystem (5.6 $u$mole m^{-2} s^{-1}). Across ecosystems and sample dates, the most important regulating factor was soil temperature ($r^2 = 0.70$; $p < 0.0001$). Mean (24-hr) soil temperature (at 5 cm depth) was 2.5 °C lower in the northern hardwood stand relative to the white pine stand. All other parameters considered (i.e., soil C:N, root mass, root C:N, litter C:N, litter mass) did not explain the differences in flux rates between sites, but variation in fine root mass and litter C:N did explain spatial and temporal variation within the northern hardwood site. These results indicated that at large spatial scales, variation in soil temperature was more important in regulating forest floor CO_2 flux than factors more closely associated with the species composition and productivity of the sites (e.g., litter and root mass and quality).

INTRODUCTION

Carbon dioxide (CO_2) evolution from the forest floor is due to the metabolic activity of roots, mycorrhizae, and soil micro- and macro-organisms. Although precise estimates of carbon (C) recycled to the atmosphere from belowground sources are unavailable, Raich and Schlesinger (1992) propose that the belowground contribution exceeds 70 Pg $year^{-1}$ globally. This represents a major component of C flux in the global C cycle. Belowground C cycling processes and subsequent forest floor CO_2 fluxes are equally important at ecosystem scales; however, we have limited knowledge of the magnitude of fluxes within and across ecosystems. Increased knowledge of the magnitude of C fluxes, as well as the factors which regulate these fluxes is critical for understanding ecosystem C cycling and potential effects of forest management or other factors such as climatic change. In this study, we quantified forest floor CO_2 flux in two contrasting ecosystems: a low elevation 36-yr-old white pine plantation and a high elevation mature northern hardwood stand.

Separating the contributing sources (i.e., roots vs. microbes) of forest floor CO_2 flux has proven difficult. The relative contribution of roots versus other soil components has been estimated to vary between 35 to 65% of the total CO_2 evolved (Edwards and Harris 1977, Ewel and others 1987, Bowden and others 1993). Factors influencing the rate of CO_2 evolution include soil temperature and moisture (through their influence on metabolic activity of both roots and microbes) (Edwards 1975, Schlentner and Van Cleve 1985, Weber 1985), soil organic matter (Ewel and others 1987), soil and root nitrogen (N) levels (Söderström and others 1983, Ryan 1991), and root biomass (Behera and others 1990).

Several techniques are available for measuring CO_2 evolution from the forest floor. Static chamber methods include soda lime or bases (KOH or NaOH) which measure CO_2 "trapped" over the measurement interval (see Cropper and others 1985). Static measures of CO_2 evolution may also be made by gas chromatograph analysis of air samples collected from sealed chambers on the soil surface (Raich and others 1990). de Jong and Schappert (1972) describe a

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variation of the static method by using a chamberless technique based on CO_2 profiles (pCO_2) in the soil. Dynamic chamber methods quantify CO_2 evolution by continuously monitoring CO_2 levels in chambers with either a closed or flow-through system and an infrared gas analyzer (IRGA). Studies comparing measurement techniques have found wide disparity between static chamber, static chamberless, and dynamic chamber methods (Edwards and Sollins 1973, Cropper and others 1985, Raich and others 1990, Rochette and others 1992, Norman and others 1992). In general, static chamber techniques provide lower estimates of CO_2 evolution than dynamic chamber techniques, while pCO_2 techniques provide higher CO_2 evolution estimates than dynamic chamber techniques (de Jong and others 1979). Although more difficult and expensive to conduct, dynamic, IRGA based techniques are considered more reliable (Ewel and others 1987) and they can be configured to quantify diurnal patterns.

The objectives of our study were: (1) to quantify and contrast forest floor CO_2 evolution in two ecosystems in late spring and summer using a dynamic, IRGA based measurement system, and (2) to qualitatively assess the importance of regulating factors such as, fine and coarse root biomass and C:N, soil temperature, litter mass and C:N, and soil C:N.

METHODS

Site Description

The study was conducted at the Coweeta Hydrologic Laboratory in the southern Appalachians of western North Carolina, USA. Two sites were selected for the present study (Table 1). Watershed one (WS1) is a 16.1 ha, 36-year-old white pine plantation (*Pinus strobus* L.). The watershed has a southerly aspect and spans an elevation range of 705 to 988 m. The site selected for study was located in the lower portion (≈715 m) of the watershed. Watershed 27 (WS27) is a 39 ha, ≈85-year-old mixed hardwood watershed. The watershed has a northeast aspect and spans an elevation range of 1061 to 1454 m. The site selected for study is in the upper portion (≈1375 m) of the watershed and contains a northern hardwood forest type.

The range in elevation and aspect between the two watersheds results in differences in climatology. At lower elevations, mean annual precipitation averages ≈1800 mm, while at higher elevations mean annual precipitation averages ≈2200 mm (Swift et al. 1988). Air temperature is also substantially lower (10-15%) at higher elevation sites (Swift et al. 1988).

Table 1. Summary of stand and site characteristics for the white pine and northern hardwood study sites.

Variable	White Pine	Northern Hardwood
elevation (m)	715	1375
stand age (years)	36	≈85
aspect	S	NE
trees ha^{-1}	1015	405
basal area (m^2 ha^{-1})	53.2	32.1
major species	*Pinus strobus* L.	*Quercus rubra* L. *Quercus prinus* L. *Acer rubrum* L.

Forest Floor CO_2 Flux Measurements

Sampling was conducted on four consecutive days in May and September 1993. In the southern Appalachians, May is a period where biological activity is beginning to occur and September is a period of active biological activity. Soil CO_2 flux was measured for 20-22 hrs (i.e., a diurnal cycle) using an automated, flow-through, IRGA based measurement system. Data were averaged to provide an average flux rate (μmol m^{-2} s^{-1}) over the entire sampling interval. The system measured flux sequentially from five soil chambers (10 cm diameter, 10 cm height, 785 cm^3 volume) constructed of PVC pipe. Soil chamber edges were sharpened on the open end and driven approximately 2 cm into the soil surface (at random locations) with a rubber mallet. All tubing was 5 mm (i.d.) flexible PVC. Air was passed through the chambers via inlet and outlet fittings attached to the upper sides of the chamber. Air flow through the chambers was regulated with a dual-sided air pump (Spec-Trex Corp.) which balanced flow into and out of the chambers. Actual flow rate (ml min^{-1}) was controlled by varying voltage (0-12 VDC) supplied to the pump and was measured and logged electronically with a flow meter and data logger (Campbell 21X). An air flow rate of 800 to 1000 ml min^{-1} provided stable readings within 7 to 8 minutes. Chamber sampling was controlled with a multiplexer, data logger, and solenoids which opened sequentially (chambers 1 - 5) at ten minute intervals. Carbon dioxide concentrations of air entering and exiting the chambers was measured and logged electronically with an IRGA (ADC LCA3) operating in differential mode and a data logger (Campbell 21X), respectively. Forest floor CO_2 flux (μmole CO_2 m^{-2} s^{-1}) was calculated based on the difference in CO_2 entering and exiting the chamber, the soil area sampled beneath the chamber, and the flow rate. Only data from the last minute of sampling were used in flux calculations.

Litter and Humus Measurements

Litter and humus were removed from beneath the chambers after flux measurements, dried, weighed, ground, and analyzed for N and C concentration (Perkin-Elmer 2400 CHN Analyzer).

Root Biomass Measurements

Root biomass, separated into fine (< 2 mm) and coarse (>2 mm) fractions, was determined using coring. After flux measurements, a 10 cm diameter metal pipe was placed in the exact chamber location and driven to a 30 cm depth with a mallet. The core was removed and the contents were placed in paper bags, transported to the laboratory, and washed over a fine mesh screen where live and dead roots were visually separated. Roots were dried, weighed, ground, and analyzed for N and C concentration (Perkin-Elmer 2400 CHN Analyzer).

Soil Measurements

Soil N and C (Perkin-Elmer 2400 CHN Analyzer) were determined on a sub-sample of soil from the cores. Soil temperature (5 cm depth) was measured with Type-T thermocouples and a datalogger (Campbell 21X). Soil moisture was not measured.

Statistical Analyses

Differences in temporal and spatial site means of average flux rates were determined with analysis of variance (SAS 1987). Stepwise regression analyses were used to relate between and within site variation (spatial and temporal) in average flux rates to soil temperature, litter mass, fine and coarse root mass, and the quality (i.e., C:N ratio) of soil, roots, and litter (SAS 1987). In all cases, $\alpha = 0.05$ was used for statistical significance and selection of significant parameters in multiple regression analyses.

RESULTS AND DISCUSSION

Forest Floor CO_2 Flux

The magnitude of forest floor CO_2 flux varied considerably between ecosystems and sample dates (Table 2). For example, averaged across sample dates, the flux rate for the white pine stand was 8.9 μmole m^{-2} s^{-1} versus 5.6 μmole m^{-2} s^{-1} for the northern hardwood stand (differences significant at $p<0.05$). Averaged across sites, May flux rates were also significantly ($p < 0.01$) lower than September flux rates (Table 2). Variation in flux rates within and between ecosystems has been observed in other studies (Garrett and Cox 1973, Hanson and others 1993). For example, Hanson and others (1993) found a maximum 2-fold variation in forest floor flux rates between ridge and valley locations within the same watershed. The values obtained in our study are in the upper range of those observed for many ecosystems (e.g., Weber 1985, Hanson and others 1993); however, comparison of rates with studies using other measurement techniques should be done with caution. Where measurement techniques were similar, our rates are in the range of values obtained by others (e.g., Edwards and Sollins 1973, Ewel and others 1987).

Table 2. Forest floor CO_2 flux by site and date (n = 5 for each sample date and site; † indicates significant [$p < 0.05$] difference between sites for mean flux rate; ‡ indicates significant [$p < 0.05$] difference between sample dates within a site).

Site	Date		Forest Floor CO_2 Flux (standard error)
White Pine	May		5.20(1.28)
	September		11.80(1.59)‡
		Mean =	8.87(1.52)
Northern Hardwood	May		3.22(0.12)
	September		7.46(1.61)‡
		Mean =	5.57(1.13)†

Regulating Abiotic and Biotic Factors

There was substantial variation in most abiotic and biotic factors between and within sites (Table 3). Coefficients of variation ranged from 12 to 118% for the northern hardwood ecosystem and from 19 to 87% for the white pine ecosystem. Based on the results from previous studies, higher forest floor CO_2 flux rates should occur in conjunction with warmer soils, lower C:N ratios in soil and litter, higher root biomass (especially fine roots). Regression analyses using data from both sites and sample periods indicated that temperature was the primary factor regulating spatial and temporal variation in forest floor CO_2 flux across ecosystems (Table 4). This emphasizes the importance of temperature in regulating heterotrophic and autotrophic activity in these ecosystems and indicates that temperature regulation may override variation in biotic factors at large spatial scales (i.e., between ecosystem types occurring at different climatic regimes). In our study, this was true even when the variation in ecosystem type (i.e., pine vs. hardwood ecosystems) and corresponding biotic components was quite large (Table 3). Other studies have also demonstrated the importance of temperature in determining forest floor CO_2 flux (Hanson and others 1993, Peterjohn others 1993). Soil and litter moisture has been shown to influence CO_2 flux in some studies (e.g., Hanson and others

Table 3. Means (n = 10), standard errors (SE), and coefficients of variation for ecosystem parameters used in regression analyses relating forest floor CO_2 flux to abiotic and biotic parameters across and within ecosystem types.

	White Pine		Northern Hardwood	
Parameter	Mean (SE)	Coefficient of Variation %	Mean (SE)	Coefficient of Variation %
Fine Root Mass ($g\ m^{-2}$)	432.4(72.3)	50.2	517.4(102.5)	59.4
Coarse Root Mass ($g\ m^{-2}$)	491.7(151.2)	87.0	762.0(299.9)	118.1
Fine Root C:N	63.9(4.1)	19.1	55.1(2.6)	14.3
Coarse Root C:N	110.6(10.7)	27.3	92.6(9.7)	31.4
Litter Mass ($g\ m^{-2}$)	1018.7(201.8)	59.4	938.0(114.8)	36.7
Litter C:N	40.1(2.5)	18.7	37.4(2.5)	20.0
Soil C:N	23.6(2.9)	36.3	21.2(0.9)	12.4
Soil Temperature (°C)	17.4(1.1)	18.8	15.6(0.7)	13.9

Table 4. Regression equations relating forest floor CO_2 flux to abiotic and biotic driving variables. All variables are significant at $P < 0.05$.

Model Type	Model	r^2	F	P>F
Across Ecosystems	Flux = -14.211 + 1.321 (soil temperature)	0.70	34.6	0.0001
w/in Northern Hardwood	Flux = 13.884 + 0.0099 (fine root biomass) -0.3604 (litter C:N ratio)	0.90	26.7	0.0010
w/in White Pine	Flux = -13.381 + 1.325 (soil temperature)	0.84	32.3	0.0013

1993). While we did not measure soil moisture, litter moisture in our study was always greater than 50%. In addition, we explained from 70 to 90% (see below) of the variation in forests floor CO_2 flux without accounting for variation in soil moisture. This suggests that soil moisture was not a dominant factor regulating spatial and temporal variation in forest floor CO_2 flux in our study.

Within the northern hardwood ecosystem, spatial and temporal variation in fine root mass and litter C:N ratio were important regulators of forest floor CO_2 flux (Table 4). Roots can contribute as much as 60% to forest floor CO_2 flux so it is not surprising that fine root mass is significantly and positively related to forest floor CO_2 flux. Litter quality (i.e., C:N ratio) is an important parameter regulating decomposition rate and the negative regression coefficient indicates less forest floor CO_2 flux (i.e., decomposition) as litter quality decreases. These results contrast with those found across ecosystems, where only soil temperature was related to spatial and temporal variation in forest floor CO_2 flux. Hence, during late spring and summer, within site variation in forest floor CO_2 flux was driven primarily by variation in biological components (i.e., root mass and litter quality) rather than soil temperature. We are reasonably certain, however, that temporal variation in soil temperature within the northern hardwood ecosystem would be an important variable if measurements in winter months were also included.

In the pine ecosystem, soil temperature was the only statistically significant factor regulating temporal and spatial variation in forest floor CO_2 flux (Table 4). It is noteworthy that some of the other parameters (i.e., soil C:N, coarse root C:N, and coarse root mass) were marginally significant ($p < 0.10$) when included in multivariable regressions. This indicates that while temperature is the most important factor, other factors may also be important and larger sample sizes are required to detect statistical significance.

SUMMARY AND CONCLUSIONS

Based on measurements in early spring and summer, forest floor CO_2 flux rates varied considerably (60 percent) between the white pine and northern hardwood ecosystems. Flux rates are a function of multiple and complex abiotic and biotic factors which vary in time and space. Between ecosystems, temperature was the most important driving variable; however, within the hardwood ecosystem, variation in fine root mass and litter quality were important. Hence, the relative importance of driving variables depends on the scale of study and the magnitude of variation in climatic, edaphic, and biological parameters within and between ecosystems. The short-term study presented here provides some interesting preliminary insights, however a more complete understanding of these relationships will require a much more intensive and extensive study. Our current research is focusing on including more ecosystem types and more intensive measurements (i.e., monthly sampling intervals).

LITERATURE CITED

Behera, N., S.K. Joshi, and D. Pati. 1990. Root contribution to total soil metabolism in a tropical soil from Orissa, India. For. Ecol. Manage. 36:125-134.

Bowden, R.D., K.J. Nadelhoffer, R.D. Boone, J.M. Melillo, and J.B. Garrison. 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. Can J. For. Res. 23:1402-1407.

Cropper, W.P. Jr., K.C. Ewel, and J.W. Raich. 1985. The measurement of soil CO_2 evolution in situ. Pedobio. 28:35-40.

de Jong, E., and H.J.V. Schappert. 1972. Calculation of soil respiration and activity from CO_2 profiles in the soil. Soil Sci. 113:328-333.

de Jong, E., R.E. Redmann, and E.A. Ripley. 1979. A comparison of methods to measure soil respiration. Soil Sci. 127(5): 300-306.

Edwards, N.T., 1975. Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. Soil Sci. Soc. Am. J. 39:361-365.

Edwards, N.T., and W.F. Harris. 1977. Carbon cycling in a mixed deciduous forest floor. Ecology 58:431-437.

Edwards, N.T., and P. Sollins. 1973. Continuous measurement of carbon dioxide from partitioned forest floor components. Ecology 54:406-412.

Ewel, K.C., W.P. Cropper, Jr., and H.L. Gholz. 1987. Soil CO_2 evolution in Florida slash pine plantations. I. Importance of root respiration. Can. J. For. Res. 17:325-329.

Garrett, H.E., and G.S. Cox. 1973. Carbon dioxide evolution from the forest floor of an oak-hickory forest. Soil Sci. Soc. Am. J. 37:641-644.

Hanson, P.J., S.D. Wullschleger, S.A. Bohlman, and D.E. Todd. 1993. Seasonal and topographic patterns of forest floor CO_2 flux from an upland oak forest. Tree Phys. 13:1-15.

Norman, J.M., R. Garcia, and S.B. Verma. 1992. Soil surface CO_2 fluxes and the carbon budget of a grassland. J. Geophysical Res. 97:18845-18853.

Peterjohn, W.T., J.M., Melillo, F.P. Bowles, and P.A. Steudler. 1993. Soil warming and trace gas fluxes: experimental design and preliminary results. Oecologia 93:18-24.

Raich, J.W., R.D. Bowden, and P.A. Steudler. 1990. Comparison of two static chamber techniques for determining carbon dioxide efflux from forest soils. Soil Sci. Soc. Am. J. 54:1754-1757.

Raich, J.W., and W.S. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B:81-99.

Rochette, P., E.G. Gregorich, and R.L. Des Jardins. 1992. Comparison of static and dynamic closed chambers for measurement of soil respiration under field conditions. Can. J. Soil Sci. 72:605-609.

Ryan, M.G. 1991. The effect of climate change on plant respiration. Ecol. App. 1:157-167.

SAS Institute. 1987. SAS/STAT guide for personal computers, version 6. SAS Institute Inc., Cary, NC.

Schlentner, R.E., and K. Van Cleve. 1985. Relationships between CO_2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. Can. J. For. Res. 15:97-106.

Söderström, B., E. Bääth, and B. Lundgren. 1983. Decrease in soil microbial activity and biomasses owing to nitrogen amendments. Can J. Microbiol. 29:1500-1506.

Swift, L.W., G.B. Cunningham, and J.E. Douglass. 1988. Climate and hydrology. pp. 335-55 In W.T. Swank and D.A. Crossley, Jr. Forest Hydrology and Ecology at Coweeta. Ecological Studies, Vol. 66. Springer-Verlag, New York.

Weber, M.G. 1985. Forest soil respiration in eastern Ontario jack pine ecosystems. Can. J. For. Res. 15:1069-1073.

ACID-BASE STATUS OF UPPER ROOTING ZONE SOIL IN DECLINING AND NON-DECLINING SUGAR MAPLE (*ACER SACCHARUM* MARSH) STANDS IN PENNSYLVANIA

William E. Sharpe and Troy L. Sunderland[1]

Abstract: Sugar maple (*Acer saccharum* Marsh) is an important commercial tree species of the central hardwood region which is valued for its wood and maple sugar products. High elevation sugar maple stands in northcentral Pennsylvania have been in serious decline for about the last 15 years with more than 1,200 hectares of maple forest affected. The decline appears to be largely irreversible, leading to the death of the affected trees. Stands at lower slope positions remain generally healthy. The objective of this study was to investigate the role of soil conditions in causing sugar maple decline by studying the acid-base status of soils, plant available soil aluminum and the relative differences in soil Al toxicity to maple seedling roots in declining (47-79 percent mortality) and non-declining (<10% mortality) stands. The acid-base status comparisons for the upper rooting zone (A, B1, B21 horizons) of soils of the sugar maple stands under study are reported here. Five declining and five non-declining stands in close proximity to one another were sampled with soil samples taken from the side walls of hand-excavated shallow soil pits in each stand. The samples were analyzed at the Agricultural Analytical Services Laboratory at The Pennsylvania State University for pH (water paste), and exchangeable Ca, Mg, K and P. Percent base saturation was also calculated. Results indicated that soils from the declining stands had significantly lower exchangeable Ca, Mg and K than the non-declining stands. pH and base saturation were also consistently lower in the declining stands while P was higher. The significance of these differences in acid-base status as a predisposing factor in the observed sugar maple decline requires additional study.

INTRODUCTION

Sugar maple decline is not a new phenomenon. Sugar maple declines have been reported in eastern North America since the early 1950's (Hendershot and Jones 1989). In most cases unusual weather events such as droughts and early frosts or episodes of insect defoliation have been cited as factors contributing to or causing declines (Bauce and Allen 1991, Kolb and McCormick 1993). However, recent severe declines of sugar maple in the Canadian provinces of Ontario and Quebec have prompted investigations into the likelihood that soil acidification and its concomitant suite of potential nutrient deficiencies and imbalances may be a contributing or predisposing factor in sugar maple decline (Kinch 1989, Hendershot and Jones 1989, Bernier and Brazeau 1988a and 1988b). Aluminum is also a potential contributor to these problems through direct toxicity to fine roots (Thornton and others 1986), by interference with nutrient uptake (Thornton and others 1986, Kelly and others 1990), and by causing precipitation of phosphorus to nonavailable forms (Kinch 1989). Liming and fertilization of declining sugar maple stands in Canada with P and K has been shown to improve decline symptoms (Adams and Hutchinson 1992, Hendershot 1991, Kinch 1989, Ouimet and Fortin 1992).

The purpose of this study was to test the hypothesis that the soils of declining ridge-top sugar maple stands were more acidic than those of the non-declining stands and that this condition has resulted in nutrient deficiencies, reduced radial growth and root development. We report here on the acid-base status of the upper rooting zone (A, B1, and B21 horizons) of soils from the ten stands under study.

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METHODS

Study Area

Ten sugar maple stands were chosen for study based on the severity of decline within each stand (Table 1). All of the stands were located within a 10 km^2 area along Rock Ridge Road in southern Potter County, Pennsylvania (Figure 1). The study area is part of the Susquehannock State Forest. The declining stands are located at elevations around 700 m. The non-declining stands were located at elevations around 560 m. Stands that had been salvage logged were not included in the study. This made selection of declining stands more difficult since extensive salvage logging of declining sugar maple stands has occurred along Rock Ridge Road.

Five stands with presently identifiable mortality of dominant and co-dominant sugar maples ranging from 47 to 79 percent were characterized as declining. Five additional stands with estimated mortality of 0 to 8 percent were characterized as non-declining. Mortality was assessed based on the mean number of dead sugar maples on three 0.1 ha plots within each stand. Any tree with a living branch, no matter how small, was considered living. Any dead standing or down tree with sufficient attached bark to allow for field identification was counted as dead. Mortality was no doubt underestimated particularly in the declining stands because many trees had been lost in years previous to this study that could no longer be identified as sugar maple and thus were not included in the tally. This fact was evident both from the number of stems on the ground and the very poor stocking of stands exhibiting the worst decline.

Trees with greater than 50 percent crown loss were also tallied. If these trees are added to the dead trees in each stand, the declining stands would have 76 to 89 percent of sugar maples in this category and the non-declining stands would have 0 to 11 percent.

Soils

Soils are classified according to the Soil Survey of Potter County (SCS 1953). The non-declining stands based on their plotted locations on the soil survey map are mostly of the Lackawanna Soil Series. These are for the most part channery silt loams. Declining stands are mapped primarily as Leetonia, Wharton, Bath or Nolo Soil Series. These are stony loamy sands and silt loams.

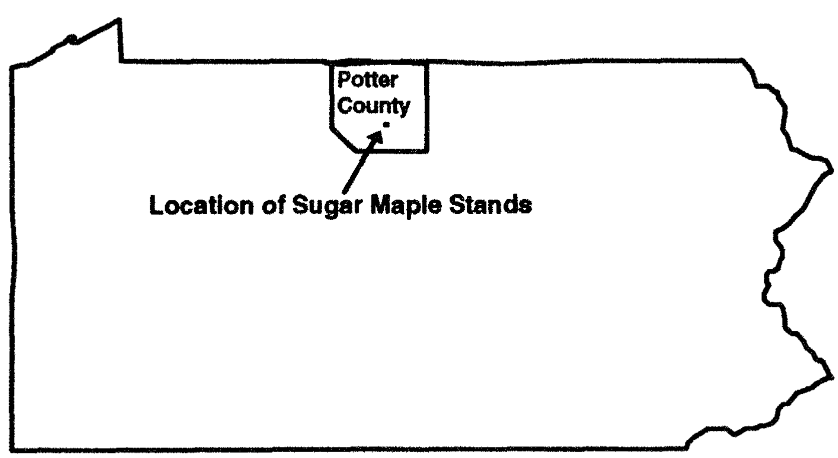

Figure 1. Location of the sugar maple stands within the Susquehannock State Forest in Potter County, Pennsylvania.

Table 1. Sugar maple mortality in the stands under study.

Stand	Mean % dead trees	Mean % dead and >50% crown dead trees
Declining		
D7	78.9[1]	89.0
D8	74.9	88.6
D4	63.8	85.2
D5	53.1	84.8
D6	47.4	76.2
Non-declining		
ND6	8.3	11.0
ND7	7.0	7.0
ND2	2.2	4.3
ND5	0.0	0.0
ND1	4.5	4.5

[1]Mean percentages of all declining vs. non-declining stands in both dead and dead plus >50% crown dead categories were significantly different at $\alpha \leq 0.05$.

Soil samples were obtained from the face of hand-excavated shallow soil pits. Samples were collected by individuals wearing plastic gloves by scraping soil from a clean pit face with a large plastic spoon. Soil descriptions for the soils mapped on each site were used to determine soil profiles in the field. Composite samples were collected from the A, B1, and B21 horizons in each soil pit. A total of 15 samples were collected from each stand. All samples were collected near living sugar maple trees. Samples were placed in plastic bags and transported to the Agricultural Analytical Services Laboratory where they were analyzed for pH, CEC, exchangeable Ca, Mg, K, and P, and acidity by the methods described in NDSU (1988). A percent base saturation was also calculated.

Statistical Analysis

Soil chemistry data were analyzed using the SAS mainframe computer package (SAS 1985). Summary statistics, including means, standard deviations, and standard errors, were calculated for each soil chemical parameter in each forest stand using the MEANS procedure. Significant differences in soil chemistry between declining and non-declining stands were determined using a two-factor nested analysis of variance (PROC NESTED in SAS). Significant differences were determined at $\alpha \leq 0.05$ unless otherwise noted. The Tukey Studentized Range Test was used to test for significant differences in mortality between stands.

RESULTS AND DISCUSSION

The results of the soil chemical analysis are presented in Table 2. The pH of the soils for the declining stands was lower than that of the non-declining stands but the difference was not significant (P=0.29). Base saturation was also lower on the declining stands but was also not significant (P=0.14). The mean base saturation of the soils in declining stand 5 was 10.2 percent while the mean of the other four declining stands was only 5.25 percent. Without stand 5 the difference in base saturation between declining and non-declining stands was significant. There were very few live trees remaining in stand 5 and most of these were at the edge of the former stand; consequently, it is possible that sampling near these trees in this stand biased the results toward more favorable soil chemistry.

Table 2. Comparisons of mean soil chemistry for declining and non-declining stands.

	Declining	Non-declining	P-value[1]
pH	4.24	4.46	0.29
exch. Ca (meq/100 g)	0.56	1.04	0.03
exch. Mg (meq/100 g)	0.17	0.25	0.05
exch. K (meq/100 g)	0.09	0.14	0.04
exch. P (lbs/acre)	50.6	18.9	0.06
% base sat.	6.36	9.39	0.14

[1]Probability that the means are not significantly different.

Base saturation values for forest soils of less than 10 percent are problematic with respect to aluminum availability (Cronan and others 1989). Both the declining and non-declining stands had base saturation values of less than 10 percent although the non-declining mean was 9.39 percent. Our estimates of exchangeable Al (0.01 M $SrCl_2$ extractable) are not complete as of this writing, but it is expected that they will be high in both declining and non-declining stands.

Estimates of exchangeable Ca, Mg and K indicate significant differences between declining and non-declining stands (Figures 2, 3 and 4). All of these essential nutrients are less available in the declining stands.

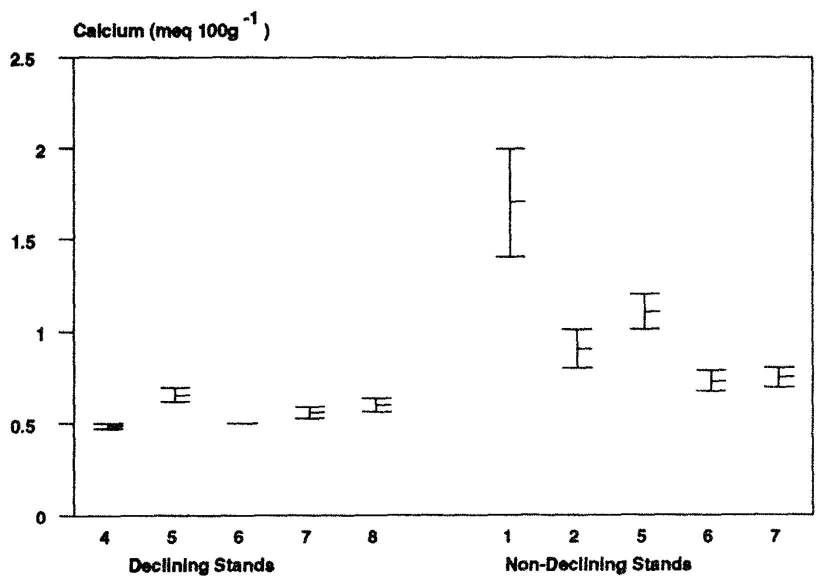

Figure 2. Mean calcium concentrations in soil from each of five declining and five non-declining stands studied. Bars around each mean indicate ± one standard error.

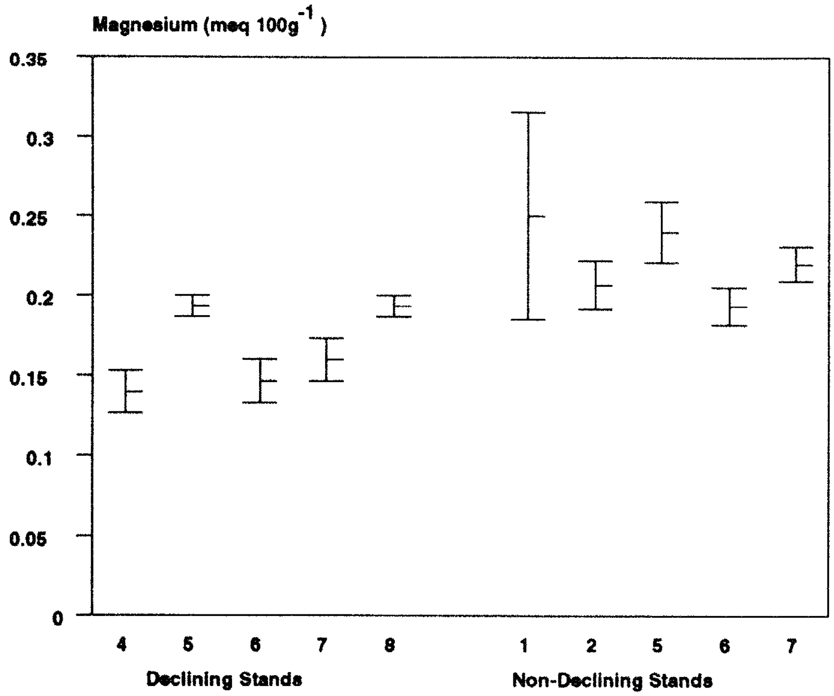

Figure 3. Mean magnesium concentrations in soil from each of the five declining and five non-declining stands studied. Bars around each mean indicate ± one standard error.

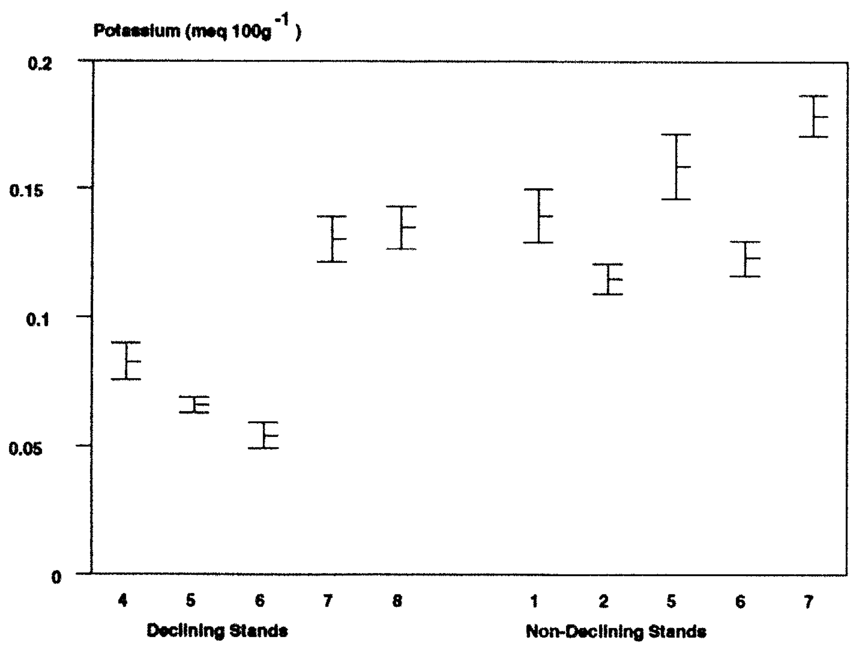

Figure 4. Mean potassium concentrations in soil from each of the five declining and five non-declining stands studied. Bars around each mean indicate ± one standard error.

This condition alone could be sufficient to explain the difference in decline severity between the stands studied. Kolb and McCormick (1993) reported Mg and possibly Ca deficiencies in the foliage of our declining stand 4 and an additional declining stand on the Susquehannock State Forest. Kinch (1989) reported that Ca, Mg and P were potentially deficient in sugar maples growing in declining stands and that the foliar concentrations of these elements were strongly predicted by soil Al and Ca concentrations and pH. Similarly Roy and others (1985) reported that declining sugar maple stands were often deficient in soil Ca and Mg.

The declining stands had higher exchangeable P than the non-declining stands (P=0.06). We tested whether or not this was a consequence of the extraction procedure (Mehlich III) utilized by the Agricultural Analytical Services Laboratory versus a water extraction method suggested by Bingham (1966). Estimated available P was much lower with water extraction. However, declining stands still had higher P although the difference betweeen declining and non-declining stands was not significant. Precipitation of insoluble aluminum phosphate in the presence of high concentrations of available soil Al and low soil pH (<pH 6) has been reported (Cole and Stewart 1982, Cook 1983, Hsu and Bates 1964). If insoluble P were extracted along with available P, as may be the case with the Mehlich III procedure, acidic soils with high P values would have the most fixed, unavailable P; consequently, they could test high for available P but be P limited. Data presented by Kolb and McCormick (1993) did not indicate a P deficiency in our declining stand 4. Foliar analysis currently underway should also indicate whether or not there may be less P available in the declining vs. non-declining sugar maple stands in this study.

SUMMARY AND CONCLUSIONS

The acid-base chemistry of the upper rooting zone soil from five declining and five non-declining sugar maple stands was evaluated. Upper rooting zone soil from the declining stands had lower pH and base saturation, higher exchangeable P and significantly lower exchangeable Ca, Mg and K. This finding is consistent with the results of other studies of soil chemistry in declining sugar maple stands and with the hypothesis that reduced availability of Ca, Mg and K is a potential predisposing factor in the observed decline. Addition of Ca, Mg and K in proper balance should be attempted as a remedy for decline and as a way to encourage sugar maple reproduction in the damaged stands in this area.

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LITERATURE CITED

Adams, C.M., and T.C. Hutchinson. 1992. Fine-root growth and chemical composition in declining Central Ontario sugar maple stands. Can. J. For. Res. 22:1489-1503.

Bauce, E., and Allen, D.C. 1991. Etiology of a sugar maple decline. Can. J. For. Res. 21:686-693.

Bernier, B., and M. Brazeau. 1988a. Nutrient deficiency associated with sugar maple dieback and decline in the Quebec Appalachians. Can. J. For. Res. 18:762-767.

Bernier, B., and M. Brazeau. 1988b. Magnesium deficiency symptoms associated with sugar maple dieback in a lower Laurentians site in southeastern Quebec. Can. J. For. Res. 18:1265-1269.

Bingham, F.T. 1966. Phosphorus. In: Diagnostic criteria for plants and soils. H.D. Chapman, Ed. University of California. p. 324-361.

Cole, C.V., and J.W.B. Stewart. 1982. Impact of acid deposition on P cycling. In: Response of agricultural soils to acid deposition. M.F. Arthur and C.K. Wagner, Eds. Battelle Columbus Laboratories, Columbus, Ohio: 2-63.

Cook, R.B. 1983. The impact of acid deposition on the cycles of C, N, P and S. In: The major biogeochemical cycles and their interactions. B. Bolin and R.B. Cook, eds. Chitchester, U.K.: 345-364.

Cronan, C.S., R. April, R.J. Bartlett, P.R. Bloom, C.T. Driscoll, S.A. Gherini, G.S. Henderson, J.O. Joslin, J.M. Kelly, R.M. Newton, R.A. Parnell, H.H. Patterson, D.J. Raynal, M. Schaedle, C.L. Schofield, E.I. Sucoff, H.B. Tepper, and F.C. Thornton. 1989. Aluminum toxicity in forests exposed to acidic deposition: The Albios results. Water, Air, and Soil Pollution 48:181-192.

Hendershot, W.H. 1991. Fertilization of sugar maple showing dieback symptoms in the Quebec Appalachians. Canada Fert. Res. 27:63-70.

Hendershot, W.H., and A.R.C. Jones. 1989. The sugar maple decline in Quebec: a discussion of probable causes and the use of fertilizers to limit damage. For. Chron. 65:280-287.

Hsu, P.H., and T.F. Bates. 1964. Formation of x-ray amorphous and crystalline aluminum hydroxides. Mineral Mag. 33:749-768.

Kelly, J.M., M. Schaedle, F.C. Thornton, and J.D. Joslin. 1990. Sensitivity of tree seedlings to aluminum: II. Red oak, sugar maple and European beech. J. Environ. Qual. 19:172-179.

Kinch, J.C. 1989. The relationships between soil and foliar chemistry and the decline of Acer saccharum in Ontario. M.S. Thesis, University of Toronto, Toronto, Ontario: 188 p.

Kolb, T.E., and L.H. McCormick. 1993. Etiology of sugar maple decline in four Pennsylvania stands. Can. J. For. Res. 23:2395-2401.

North Dakota State Univ. 1988. Recommended chemical soil test procedures for the north-central region. North Dakota Ag. Exp. Sta., NDSU, Bull. No. 499 (revised): 37 p.

Ouimet, R., and J.M. Fortin. 1992. Growth and foliar nutrient status of sugar maple: Incidence of forest decline and reaction to fertilization. Can. J. For. Res. 22:699-706.

Roy, G., L. Robitaille, and G. Gagnon. 1985. Etude des principaux facteurs du deperissement des erablieres au Quebec. Phytoprotection 66:91-99.

SAS Institute, Inc. 1985. SAS User's Guide: Statistics, Version 5 Edition, SAS Inst., Inc. Cary, N.C. p

Soil Survey of Potter County, Pennsylvania. 1953. USDA Soil Conservation Service. 108 p.

Thorton, F.C., M. Schaedle, and D.J. Raynal. 1986. Effect of Al on the growth of sugar maple in solution culture. Can. J. Forest Res. 16(5):892-896.

TREE-RING CHEMISTRY RESPONSE IN BLACK CHERRY TO AMMONIUM SULFATE FERTILIZATION AT TWO WEST VIRGINIA SITES

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Abstract: The chemical element content of black cherry (*Prunus serotina* Ehrh.) tree rings showed significant changes related to annual ammonium sulfate treatments on one watershed (Fernow WS-3) which exhibited a significant increase in streamflow N export due to treatment. However, tree-ring, soil and streamflow chemistry did not respond to the same treatment on another watershed (Clover Run WS-9). On WS-3, tree-ring concentrations of P, K, Ca, Mg, B, Zn, S and Sr were higher and concentrations of Mn, Fe, Cu and Al were lower in wood formed either before or after treatment. Lack of response to treatment on WS-9 was largely due to soil retention of N, lack of nitrate leaching and possibly the location of the sampled trees near the watershed mouth. Overall, black cherry tree-ring chemistry was consistent with streamflow chemistry changes caused by treatment and the method shows promise as an index to soil chemistry changes. Sapflow in rings formed prior to treatment and/or radial translocation prevented an exact determination of the year of treatment initiation.

INTRODUCTION

Study of the chemical element content of tree rings, or dendrochemistry, is receiving increased attention as a method of determining changes in the soil chemical environment. Several studies have been conducted which showed, or attempted to show, a link between tree-ring chemistry and soil chemistry. A study by Bondietti and others (1990) with red spruce (*Picea rubens* Sarg.) suggested a link between atmospheric deposition and altered soil chemistry. The relationship between soil pH and tree-ring chemistry was examined by Guyette and others (1992) with Eastern redcedar (*Juniperus virginiana* L.) and DeWalle and others (1991) with a variety of species. Effects of liming were studied by Kashuba-Hockenberry and DeWalle (1994) with scarlet oak (*Quercus coccinea* Muenchh.), DeWalle and others (in press) with red oak (*Q. rubra* L.) and McClenahan and others (1988) with tulip-tree (*Liriodendron tulipifera* L.). No known studies have focused on tree-ring response to soil treatment with known quantities of ammonium sulfate. In addition, concern about the effects of radial translocation or sapflow in xylem raises doubt about the utility of using tree rings to measure the timing of soil changes.

Experiments at two research watersheds maintained by the USDA Forest Service, Northeastern Forest Experiment Station in north central West Virginia (Adams and others 1993) provided an opportunity to determine the dendrochemical response to soil fertilization with ammonium sulfate in black cherry (*Prunus serotina* Ehrh.) trees. In earlier studies with black cherry, DeWalle and others (1991) showed that cation concentrations, such as Mn and Sr, in sapwood were sensitive to soil pH variations. In this paper, we compare the black cherry tree ring chemistry on control and treated areas and in wood formed before and after treatment to determine possible effects of ammonium sulfate treatment and radial translocation/sapflow.

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STUDY AREAS

Experiments were conducted on watersheds maintained by the USDA Forest Service, Northeastern Forest Experiment Station on or near the Fernow Experimental Forest near Parsons in north central West Virginia (39°3'15"N, 79°41'15"W). Treatment and control watersheds on the Fernow were WS-3 and WS-7, respectively. In the Clover Run area, watershed WS-9 and a nearby control area were sampled. WS-9 and the control area are on the Monongahela National Forest near Parsons. At both the Fernow and Clover Run sites, the treatment and control areas are adjacent to one another. Land use, current and past experimental treatments, and dominant vegetation are described for each watershed in Table 1.

Table 1. Comparison of treatments and land use history for watersheds WS-3, WS-7 and WS-9.

Watershed	Treatments	Dates	Area (ha)	Dominant Vegetation
WS-3	Weir Installation	5/51	34.3	*Prunus serotina*
	Intensive selection cut	10/58-2/59		*Acer rubrum*
	Repeated cut	9/63-10/63		*Betula lenta*
	Patch cuttings w/herbicide	7/68-8/68		*Fagus grandifolia*
	Clearcut, left stream buffer	7/69-5/70		
	Cut buffer, clear channel	11/72		
	Begin ammonium sulfate treatment	1/89		
WS-7	Weir Installation	11/56	24.2	*Acer saccharum*
	Upper 12.1 ha clearcut	11/63-3/64		
	Herbicide upper cut	5/64-10/69		*Betula lenta*
	Lower 12.1 ha clearcut	10/66-3/67		*Liriodendron tulipifera*
	Herbicide lower cut	5/67-10/69		*Prunus serotina*
WS-9	Farmed	1800s to 1920s	11.6	*Larix leptolepis*
	Weir Installation	1957		*Quercus rubra**
	Bulldozed forest regrowth, left stream buffer	11/83		*Prunus serotina**
	Planted to Japanese larch	Spring 1984		*Smilax rotundifolia*
	Began ammonium sulfate treatment	4/87		*Rubus* spp.

*buffer zone along stream.

Chemical applications on the two treatment watersheds for this study, WS-3 and WS-9, consisted of aerial applications of granular ammonium sulfate fertilizer (21:0:0:24= N:P:K:S) three times per year to give an annual total application of 167 kg ha^{-1}. Treatments were designed to double the seasonal and annual inputs of N and S occurring in throughfall on these watersheds. Applications varied seasonally with 33 kg ha^{-1} added generally in March and November and 101 kg ha^{-1} added in July on each watershed. Applications began in April 1987 on WS-9 and in January 1989 on WS-3. Details of the treatment are given by Adams and others (1993).

The region is part of the Allegheny Plateau with steep slopes and shallow soils. Soils are predominantly loamy-skeletal, mixed mesic Typic Dystrochrepts of Calvin channery silt loam type derived from shale and sandstone from the Hampshire formation. Precipitation averages about 145 cm per year with even seasonal distribution. Mean monthly air temperatures average about -1 to 5° C in January to about 25° C in July. Adams and others (1994) give a detailed description of the hydrometeorology of the Fernow Experimental Forest region.

METHODS

Wood samples were taken from trees growing on two pairs of treated and control areas using different methods due to size of trees. On WS-3 and WS-7, 3-cm thick wood disks taken at breast height were harvested from five pole-sized black cherry trees felled at each site on July 29, 1992. On July 2-3, 1992, 4-mm diameter increment cores were collected with a standard increment borer at breast height at four locations around the circumference of five mature black cherry trees in the streamside buffer zone on WS-9 and the control area. Other species also were sampled, but black cherry was the only species sampled that occurred at Fernow and Clover Run sites.

Wood disks from WS-3 and WS-7 were sanded, then a band saw was used to cut the wood disks into quadrants and quadrants into radial strips. Radial strips were separated into age-class sections using a utility knife under low power magnification. Wood from each quadrant was divided into the following sections according to the years in which wood was formed:

Treatment Period	1989-1992
Pre-treatment I	1986-1988
Pre-treatment II	1981-1985

The sanded edges were removed prior to chemical analysis with a stainless-steel chisel to avoid chemical contamination by the sand paper. Samples from each quadrant were analyzed separately, but for the purposes of this paper data for all quadrants were combined.

For Clover Run sites, increment cores also were separated by hand with a scalpel under low magnification into three sections based on ring age:

Treatment Period	1987-1992
Pre-treatment I	1982-1986
Pre-treatment II	1977-1981

Wood from each of the four cores per tree was combined by sections for each tree to give enough mass for chemical analysis.

Sterile laboratory rubber gloves were used for all sample collection, handling and preparation. Samples were rinsed with deionized water several times during processing and were stored frozen until submitted for analysis. Wood samples were analyzed for P, K, Ca, Mg, Mn, Fe, Cu, B, Al, Zn, Na, Sr, N and S at the Agricultural Analytical Services Laboratory operated by the College of Agricultural Sciences at Penn State University, University Park, PA. Nitrogen analysis was conducted using the Dumas method (Campbell 1991) and sulfur analysis using ICP emission spectroscopy (Huang and Schulte 1985). Analysis for the other elements was also by ICP emission spectroscopy (Dahlquist and Knoll 1978).

Soil samples were collected in spring 1994 at rooting depth (0-15 cm) around sample trees on WS-9 and its control area. Samples were collected around black cherry (n=5) and red oak trees (n=5) in the treated and control areas. Soil chemical analyses were performed at the Agricultural Analytical Services Laboratory at Penn State using standard soil tests (North Dakota State Univ. 1988). Since soil chemistry did not vary between species at a site, soil data were grouped for later comparisons between treatment and control areas. Statistical analysis involved simple t-tests to determine significant differences between treatment and control areas in soil data and tree-ring data by age classes.

RESULTS AND DISCUSSION

Treatment Effects at Each Site

Black cherry tree-ring chemistry changes in response to ammonium sulfate additions on WS-3 were quite pronounced (Table 2). Wood formed during the period 1989-1992, after initiation of treatment on WS-3, showed significant increases in P, K, Ca, B, Sr and S and significant decreases in Mn concentrations relative to WS-7. Pre-treatment wood on WS-3 formed during the 1986-88 (Pre-treatment I) period showed significant increases in P, K, Ca, Mg, B, Zn, Sr, and S and significant decreases in Al, Cu, Fe, and Mn concentrations. For the 1981-85 (Pre-treatment II) period, wood on WS-3 also showed significantly higher Ca, Mg, and Sr and significantly lower Mn, Cu, and Na relative to WS-7. Interestingly, more numerous and generally larger significant differences occurred in wood formed immediately prior to initiation of treatment (Pre-treatment I) than in wood formed after treatment. Nearly all of the differences between WS-3 and WS-7 were significant at the $p \leq 0.01$ level.

Table 2. Mean tree-ring element concentrations (mg/kg) for five black cherry trees on watersheds WS-3 (T=treated) and WS-7 (C=control) for periods of wood formation after and before initiation of soil ammonium sulfate treatments.

Element	Treatment 1989-92		Pre-treatment I 1986-88		Pre-treatment II 1981-85	
	C	T	C	T	C	T
P	122	146.0**	50.5	66.0**	20.0	29.5
K	1015	1213.0*	356	421.0**	225	234
Ca	431	502.0**	331.5	504.0**	171	320.0**
Mg	103	113	65	98.0**	27.5	57.0**
Mn	76.3	22.4**	66.4	22.5**	29.0	14.0**
Fe	10.9	10.9	8.1	5.25*	6.25	8.4
Cu	1.87	1.78	1.5	1.29*	1.76	0.98*
B	3.45	3.73*	2.72	2.98*	2.62	2.73
Al	8.6	1.7	2.9	1.30*	1.1	1.1
Zn	2.65	5.7	1.72	3.49*	2.49	2.06
Na	11.15	10	9.85	8.3	7.35	5.85*
Sr	3.91	5.22*	3.47	5.36*	2.78	4.08*
N	1273	1321	897	950	743	722
S	82.3	90.4*	60.0	64.4*	61.8	53.9

* = significant difference between C and T at alpha $\leq$ 0.05 level, ** at alpha $\leq$ 0.01 level

In contrast, mean black cherry tree-ring chemistry at WS-9 showed relatively minor response to ammonium sulfate applications (Table 3). Tree rings on WS-9 formed during the 1987-92 period, after treatment initiation, showed significant increases in only Ca and Fe concentrations relative to the control area. Wood formed for the five-year period immediately prior to treatment (1982-86) also showed Fe and Na increases and a decrease in S concentrations.

Table 3. Mean tree-ring element concentrations (mg/kg) for five black cherry trees on watershed WS-9 (T=treated) and a nearby control area (C) for periods of wood formation after and before initiation of soil ammonium sulfate treatments.

Elements	Treatment 1987-92		Pre-treatment I 1982-86		Pre-treatment II 1977-81	
	C	T	C	T	C	T
P	90	80	60	50	20	20
K	670	700	460	420	230	290
Ca	390	430.0*	390	390	200	250
Mg	120	130	110	90	40	50
Mn	49.2	56.4	45.6	46.8	18.6	24.6
Fe	49.8	97.8*	27.6	84.2*	27.4	94.8
Cu	2.1	1.8	1.7	1.4	1.5	1.4
B	3.4	3.4	3.0	2.9	2.9	2.7
Al	3.8	4.4	2.9	3.3	2.9	2.4
Zn	154.0	30.2	112.2	17.6	68.0	22.0
Na	17.2	11.4	13.0	9.4*	11.0	7.4
Sr	3.6	3.6	3.6	3.5	2.7	2.9
N	840	910	640	610	520	570
S	460	460	440	430.0*	440	440

* = significant difference between control and treatment at alpha $\leq$ 0.05 level

All of these changes were significant at the $p \leq 0.05$ level. Lowering $p \leq 0.1$ would only have added significant changes in Zn and Na in Pre-treatment II samples and in Zn in Post-treatment samples, respectively. Pre-treatment wood formed during the 1977-1981 period showed no significant differences relative to the control area.

Causes of Treatment Differences between Sites

Large differences in tree-ring response to ammonium sulfate treatment occurred between watersheds WS-3 and WS-9. Increased base cation concentrations in wood on WS-3 are consistent with the mobilization of base cations in soil solution to maintain a charge balance with the anions added by treatment. Sulfate anions were added directly in the ammonium sulfate treatment and nitrification of added ammonium would produce NO_3 anions. Nitrogen fertilization from the added ammonium also may have increased rates of decomposition of soil organic matter which increased the overall supply of base cations. Sulfur increases in wood are most likely a direct result of the soil treatment. Reductions in trace metal concentrations (Al, Cu, Fe, Mn) may have been caused by increased base cation availability. Tree-ring trace metal concentration reductions on WS-3 also imply that soil acidification due to three years of treatment has not occurred yet, since soil acidification should generally lead to increased availability of trace metals.

In contrast to WS-3 results, six years of ammonium sulfate treatment on WS-9 produced very small to negligible tree-ring chemistry effects. Lower site fertility caused by years of mountain farming on Clover Run WS-9 (Adams and others 1993) may have depleted available soil base cations and produced low soil N pools. Consequently, N may be very limiting on WS-9 and more strongly retained. Data for treated watersheds show lower tree-ring Ca and N content on WS-9 than WS-3 in all years (Tables 2 and 3), supporting the suggestion of lower site fertility on WS-9 as a cause of reduced treatment response in tree rings. However, trees sampled on WS-9 were located in a streamside buffer zone near the mouth of the watershed and may reflect soil conditions in this zone only. Helicopter additions of ammonium sulfate included the streamside buffer zone.

Increases in tree-ring Fe concentrations in wood formed during the 1987-92 and 1982-86 periods on WS-9 may signal initial stages of soil acidification caused by treatment. Treatment and control area differences in tree-ring Na and S at Clover Run cannot be related directly to treatment and may be due to natural site differences.

Soil chemistry data were used to test the hypothesis that ammonium sulfate treatments have affected soil properties near sampled trees at the Clover Run sites. Mean chemistry for 10 soil samples around sampled trees in the streamside buffer zone on WS-9 and the control area (Table 4) showed no significant differences at either the $p \leq 0.05$ or $p \leq 0.1$ levels. No significant change in measured soil properties had occurred due to treatment around sample trees in the buffer zone on WS-9.

Table 4. Comparison of root-zone soil chemical properties around sample trees in the streamside buffer zone on watershed WS-9 and nearby control site.

Parameter	Control	WS-9
pH	4.57	4.43
P (kg/ha)	17.3	11.4
Acidity (meq/100g)	8.37	9.59
K "	0.075	0.084
Mg "	0.16	0.18
Ca "	0.63	0.61
CEC "	9.24	10.44

* indicates significant difference at the 0.05 level

Published streamflow chemical export data provide some checks on the tree-ring results for both sites. Differences in black cherry wood chemistry response to ammonium sulfate treatment between watersheds WS-3 and WS-9 were consistent with differences in NO_3 and Ca export in streamflow in response to treatment on these watersheds (Adams and others 1993). On WS-3, where tree-ring chemistry was markedly changed by treatment, large increases in NO_3 and Ca export were noted. On WS-9, where little tree-ring response was found, no significant increases in NO_3 or Ca were found. No significant increases in streamflow export of SO_4 were found on either watershed. Soil sulfate adsorption probably is responsible. Increased export on WS-3 indicates that treatment indeed did mobilize cations and tree-ring chemistry was able to record those changes. Lack of streamflow export changes on WS-9 also is consistent with no soil chemical changes and limited tree-ring chemistry changes in response to treatment on this watershed.

Some soils data do exist to help interpret dendrochemical results. Gilliam and others (1994) found that inorganic soil NO_3-N concentrations at the 0-10 cm depth were significantly higher on WS-3 than on WS-7 after 3 years of treatment in support of the stream chemistry differences. Mean soil calcium concentrations on WS-3 were also much greater than on WS-7 but the differences were not significant due to high soil Ca variability on WS-3. Differences in soil K, Mg, P, NH_4-N, Cu, Fe, Mn, and Zn between WS-3 and WS-7 were not significant. The authors do cite unpublished data for the 0-5 cm soil depth which showed that soil on WS-3 was significantly more acidic than on WS-7. Although these soil data show NO_3 changes on WS-3 due to treatment, large changes in base cation availability as suggested by tree-ring chemistry data are not supported.

On the Clover Run WS-9 basin, Pickens and others (1995) present soils data which show that significant changes in soil Al, Mn, N, S, Ca, Mg, and pH occurred due to ammonium sulfate treatments. Only small tree-ring Ca increases could be attributed to treatment on WS-9. Tree ring samples were collected in the streamside buffer zone near the mouth of the watershed on WS-9, while soils data from Pickens and others (1995) were collected in the uplands portion of this basin. Considering that both tree-ring and stream chemistry data (Adams and others 1994) do not indicate acidification of WS-9 due to ammonium sulfate treatments, soils data presented by Pickens and others (1995) suggest a gradual acidification of soils on WS-9 from the uplands to the lowlands which has not yet affected the tree-rings, soils and water at the mouth of the basin.

Apparently, cation mobilization is largely due to NO_3 rather than SO_4 anions on WS-3. No significant changes in tree-wood N concentrations were found, even though NO_3 concentrations were increased in soil solution. Kashuba (1992) also found that scarlet oak tree-ring chemistry did not change in response to soil N fertilization. Tree-ring chemistry is more sensitive to base cation element availability changes, than N changes, since base cations can bind to pectic compounds in the cell wall of xylem. (Ferguson and Bollard 1976; Tomlinson and Tomlinson 1990). Nitrogen is not similarly adsorbed.

Radial Variations of Treatment Effects

Contrary to expectations, wood formed prior to, rather than following, treatment appeared to be affected most on WS-3. A larger number of significant differences were observed for the 1986-88 period, just prior to treatment, than for wood from the 1989-92 period occurring after treatment. Several explanations can be given for this occurrence: 1) radial translocation of elements could have occurred which would redistribute elements from post-treatment to pre-treatment wood, 2) previous watershed treatments could have affected tree rings on WS-3 or WS-7 in such a way that wood formed before ammonium sulfate treatment was inherently different between watersheds, and 3) ammonium sulfate treatment effects on WS-3 may be changing gradually over time.

Radial Translocation/Sapflow. Radial translocation of elements in xylem often has been suggested as an explanation of a treatment response in tree rings formed in years prior to treatment (McClenahen and others 1988). Parenchyma cells in wood rays represent living tissue, and radial translocation of carbohydrate in rays has been documented. Thus, radial translocation of chemicals could have occurred from rings affected by treatment to rings formed before treatment. However, this issue is controversial since tree rings formed in years just prior to treatment can also be affected by treatment, if those rings were participating in vertical sapflow at the time of treatment. In tree species with diffuse porous wood, such as black cherry, sapflow occurs in a band of sapwood of indeterminate thickness. By definition, sapflow cannot occur in heartwood. The number of annual rings involved in sapflow during treatments in this experiment is not known, but observations of sapwood thickness can at least be used to indicate the number of rings potentially available for sapflow.

Sapwood included most if not all of the wood analyzed on the two watersheds. The heartwood/sapwood boundary observed when the wood samples were cut in 1992 was located between 4-9 annual rings from the bark (mean 6.1 years) on WS-7 and 7-11 annual rings from the bark (mean 8.5 years) on WS-3. Since wood only up to 11 years of age at the time of sampling was considered in this study and the sapwood/heartwood boundary probably migrated toward the bark after treatment, sapflow probably could have occurred at some time after treatment was initiated in most, if not all, of the 11 annual rings analyzed.

Response to ammonium sulfate treatment in wood formed immediately prior to the treatment period (1986-88) could be easily explained by sapflow at treatment time in these three rings. Treatment effects on wood formed during the 1981-85 period implies that one or more annual rings formed 4-8 years prior to treatment also contributed to sapflow when treatments were initiated. Sapflow in at least some of these rings cannot be ruled out.

Effects of Past Treatments. Experimental treatments on Fernow watersheds WS-3 and WS-7 prior to the time of ammonium sulfate treatment may have contributed to differences in the chemistry of black cherry wood, but this is not considered likely. These watersheds were subjected to different forest cutting and herbicide treatments as part of earlier experiments (Table 1); however, the trees on each basin had been allowed to regrow naturally for at least 19 years prior to ammonium sulfate treatments. Wood formed only up to 8 years prior to ammonium sulfate treatment was analyzed in this study. This wood probably was not affected significantly by prior experimental treatment, but this can not be established with certainty.

Changing Treatment Effects. Since ammonium sulfate treatments were applied each year from 1989 through 1992 on WS-3, gradually changing soil response to treatments also could have influenced radial variations. Continued ammonium sulfate treatments are expected eventually to deplete base cations, cause soil acidification, and increase availability of trace metals. Timing of such base cation depletion/acidification cannot be predicted. That wood formed after treatment showed fewer and smaller significant differences than wood formed before treatment suggests that base cation depletion had begun after only three years of treatment, although no direct evidence for soil acidification was found. As treatment of WS-3 continues, tree-ring chemistry may eventually show soil acidification effects.

CONCLUSIONS

The chemical element content of black cherry tree rings is an indicator to the effects of ammonium sulfate fertilization on the soil which is at least as sensitive as measurements of streamflow or soil chemistry. Sapflow and/or radial translocation in black cherry wood may interfere with the detection of the precise timing of soil changes using dendrochemistry.

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LITERATURE CITED

Adams, M. B., P. J. Edwards, F. Wood, and J. N. Kochenderfer. 1993. Artificial watershed acidification on the Fernow Experimental Forest, USA. J. Hydrol. 150(1993):505-519.

Adams, M. B., J. N. Kochenderfer, F. Wood, T. R. Angradi, and P. Edwards. 1994. Forty years of hydrometeorological data from the Fernow Experimental Forest, West Virginia. USDA, Forest Service, Northeastern Forest Experiment Station. General Tech. Rpt. NE-184. 24 p.

Bondietti, E. A., N. Momoshima, W. C. Shortle, and K. T. Smith. 1990. A historical perspective on divalent cation trends in red spruce stemwood and the hypothetical relationship to acidic deposition. Can. J. For. Res. 20: 1850-1858.

Campbell, C.R. 1991. Determinization of total nitrogen in plant tissue by combustion p. 21-23 In Plank, C.O. (ed.). Plant Analysis Reference Procedures for the Southern Region of the United States. Southern Coop. Series Bull. 368 Georgia Ag. Exp. Sta., Univ. GA, Athens.

Dahlquist, R. L. and J. W. Knoll. 1978. Inductively coupled plasma atomic emission spectrometer: analysis of biological materials and major, trace, and ultra-trace elements. Appl. Spectr. 39(1): 1-29.

DeWalle, D. R., B. R. Swistock, R. G. Sayre, and W. E. Sharpe. 1991. Spatial variations of sapwood chemistry with soil acidity in Appalachian forests. J. Environ. Qual. 19:504-508.

DeWalle, D. R., W. E. Sharpe and B. R. Swistock. In press. Dendrochemistry and the soil chemical environment. In. Tree Rings as Indicators of Ecosystem Health. CRC Press, Inc.

Ferguson, I.B. and E.G. Bollard. 1976. The movement of calcium in woody stems. Annals of Botany 40:1057-1065.

Gilliam, F.S., N.L. Turrill, S.D. Aulick, D.K. Evans, M.B. Adams. 1994. Herbaceous layer and soil response to experimental acidification in a Central Appalachian hardwood forest. J. Environ. Qual. 23:835-844.

Guyette, R. P., G. S. Henderson, and B. E. Cutter. 1992. Reconstructing soil pH from manganese concentrations in tree-rings. For. Sci. 38(4):727-737.

Huang, C. L. and E. E. Schulte. 1985. Digestion of plant tissue for analysis by ICP emission spectroscopy. Commun. in Soil Sci. Plant Anal. 16(9):943-958.

Kashuba-Hockenberry, L. A. and D. R. DeWalle. 1994. Dendrochemical response to soil liming in scarlet oak. Can. J. For. Res. 24(3):564-567.

Kashuba, L. A. 1992. Using scarlet oak (*Quercus coccinea* Muenchh.) tree-ring chemistry to trace changes in soil chemistry caused by calcium, nitrogen, and phosphorus fertilization. School of For. Resour., Penn. St. Univ., Undergraduate Honors Thesis. 42 p.

McClenahen, J. R., J. P. Vimmerstedt and A. J. Scherzer. 1988. Elemental concentrations in tree rings by PIXE: statistical variability, mobility and effects of altered soil chemistry. Can. J. For. Res. 19:880-888.

North Dakota State Univ. 1988. Recommended chemical soil test procedures for the North Central Region. North Dakota Ag. Exp. Sta., NDSV, Bulletin No. 49 (revised), 37 p.

Pickens, C.J., W.E. Sharpe, P.J. Edwards. 1995. The effects of doubling annual N and S deposition on foliage and soil chemistry and growth of Japanese larch (*Larix leptolepis* Sieb and Zucc.) in north central West Virginia. Proc., 10th Central Hardwood Forest Conf., Morgantown, WV.

Tomlinson, G.H. and F.L. Tomlinson. 1990. Effects of Acid Deposition on the Forests of Europe and North America. CRC Press, Boca Raton, FL. 281 p.

ELEMENTAL CONCENTRATIONS IN FOLIAGE OF RED MAPLE, RED OAK, AND WHITE OAK IN RELATION TO ATMOSPHERIC DEPOSITION IN PENNSYLVANIA

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Abstract: Foliage was sampled in June and late August-early September in 1988 and 1989 from the outer crowns of codominant red maple (*Acer rubrum* L.), northern red oak (*Quercus rubra* L.), and white oak (*Q. alba* L.) trees in forest stands along an atmospheric deposition gradient in north-central Pennsylvania. Leaf samples from approximately 480 trees were analyzed for concentration of macroelements N, P, K, Ca, Mg, and S, as well as microelements Al, B, Cu, Fe, Mn, Mo, Na, Pb, Si, Sr, V and Zn. Foliar concentrations of Fe, S, and Sr were generally greater in the high deposition portion of the gradient. Concentrations of other foliar elements generally were not related to the spatial pattern of atmospheric input.

INTRODUCTION

Concentrations of specific elements (e.g. sulfur and trace elements) in plant tissue have been used to indicate the magnitude of atmospheric pollutant input to forest ecosystems. Several studies have been conducted in the oak forests of Pennsylvania USA which indicate that certain elements accumulate in plant tissues subjected to elevated pollution levels. For example, the sulfur content of tree foliage in woodlands of western Pennsylvania was related to distance and direction from a complex of large coal-fired power plants (Hutnik and others, 1989). Strontium concentrations of white oak (*Quercus alba* L.) xylem in a mixed-oak forest of central Pennsylvania were related to distance from a small coal-fired power plant (Long and Davis, 1989). In addition to these point-source studies, Lynch (1990) documented the existence of an atmospheric deposition gradient in north-central Pennsylvania based on precipitation monitoring conducted since 1982. He reported that pH, sulfate, nitrate, ammonium, and calcium ions in precipitation generally followed a west-to-east pattern of decreasing concentrations. The westernmost part of this forested gradient receives high sulfate loadings, as well as some of the most acidic rainfall in the USA (Figs. 1, 2). Lynch (1990) reported that wet $SO4^{=}$ deposition varied from 38 Kg.ha-1.yr-1 in study area 1 in the west to 30 Kg.ha-1.yr-1 in study area 4 in the east. Likewise, wet $NO3^{-}$ deposition varied from 23 to 20 Kg.ha-1.yr-1 across this gradient, and mean annual precipitation pH varied from 4.07 to 4.14. Historical seasonal mean temperatures have not varied significantly across the region of this study (Kingsley, 1985), but annual precipitation varies from 109.2 cm.yr-1 in study area 1 to 96.5 in study area 4 (Davis and others, 1990). Physiographic and soil factors along the gradient have been characterized (McClenahen and Long, 1993), but have not been analyzed with respect to atmospheric deposition. Variation in heavy metal burdens within vegetation may also occur along this gradient, as evidenced by Showman and Long (1990) who reported that concentrations of Al, Cr, Cu, and Fe in lichen thalli were significantly greater in the western, more polluted part of this deposition gradient.

A multi-disciplinary research project was initiated in 1986 to examine forest health along this deposition gradient (Davis and others, 1990). Using a rigorous statistical procedure, Long and others (1991) identified 13 ecologically analogous forest stands, clustered in four distinct "core areas" on the gradient (Fig. 1). These core areas served as focal points for a series of multi-faceted studies. At or near these four core areas, elemental analyses were conducted on samples of rainfall, soils, and plant tissue collected from both the herb-layer and canopy-layer. This report deals

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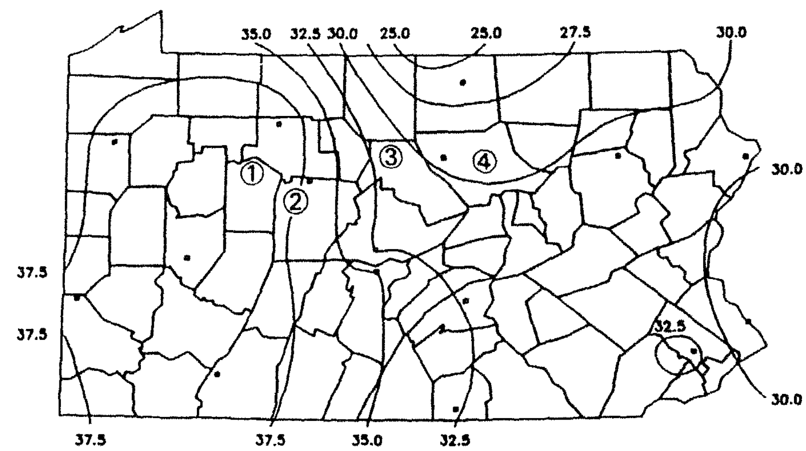

Figure 1. Spatial distribution of multiannual wet sulfate ion deposition (kg/ha) in Pennsylvania from 1982 - 1988. Numbers 1 - 4 indicate approximate location of the four core areas which served as focal points for the Pennsylvania Deposition Gradient research. The small squares represent atmospheric monitoring locations (Lynch, 1990).

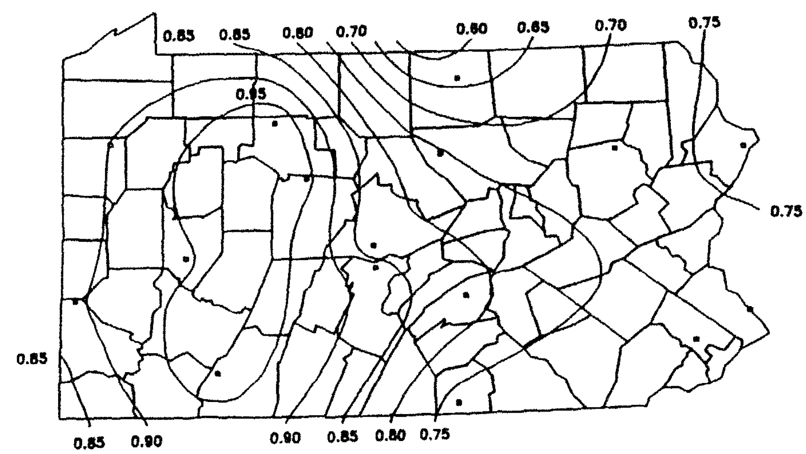

Figure 2. Spatial distribution of multiannual mean wet hydrogen ion deposition (kg/ha) in Pennsylvania from 1982 - 1988 (Lynch, 1990).

with the elemental content of the canopy-layer foliage of three native tree species. The primary objective of this study was to determine if elemental concentrations of foliage differ between the western and eastern forest stands receiving different levels of atmospheric deposition loadings. A secondary objective was to establish a database which would allow interpretation of future trends in changing elemental concentrations in forest tree foliage subjected to anthropogenic inputs.

METHODS

Four ecologically analogous forest stands, one per core area (Fig. 1), were sampled in 1988 and 1989. For this paper, "stand number" and "core area number" are identical. Ten dominant or co-dominant northern red oaks, white oak, and red maple trees growing within each stand were randomly located and tagged. Ten trees per species were tagged in all areas except in the easternmost stand, where 10 red maples, 9 red oaks and 8 white oaks were located in 1988; 10, 10, and 7 trees of each species, respectively, were tagged in stand 4 in 1989. Ten trees per species were not always present because the number of oak trees in each stand was restricted due to the number of individual trees being utilized in previously established research plots. These restrictions resulted in a total of 117 trees sampled in the four areas in each of the two years. Two samplings were conducted per year . Due to personnel constraints and inclement weather, sampling could not be done on the same dates each year. In 1988 the trees were sampled during June 21-30 and August 30 - September 2. In 1989 a different set of trees were sampled during June 27 - July 10 and August 21-25. The location of each sample tree relative to other sample trees, as well as height, and diameter of each sample tree was recorded.

Four 1-m long branches (one branch per cardinal direction) were cut from the outer canopy of each tree by a climber positioned within the crown. On the ground, excised branches were placed in plastic bags for transport to the laboratory, where 30 leaves per branch were randomly selected and removed. Leaves were not washed in order to retain external contaminants entrapped as dry (or wet) deposition. Foliage from each tree was air dried, composited per tree, ground, and sent to Micro-Macro International (Athens, GA 30607) for determination of the macroelements N, P, K, Ca, Mg, and S, as well as microelements Al, B, Cu, Fe, Mn, Mo, Na, Pb, Si, Sr, V and Zn.. Total N was analyzed using Kjeldahl digestion with generated ammonium determined by automated colorimetry. Sulfur content was determined using a LECO (LECO Corp., St. Louis, MO) sulfur analyzer. Concentrations of remaining elements were determined using dry ashing of tissue with remaining ash dissolved in dilute aqua regia, and assayed by inductively coupled plasma (ICP) emission spectrometry.

The general approach to the statistical analysis was based on results of on-going, intensive atmospheric deposition monitoring and lichen studies. The historical deposition trends (Fig. 1) are based on regional network data from Pennsylvania and adjacent states. However, intensive monitoring conducted during this study at approximately 16-km intervals along the east-west gradient revealed that depositon values at study areas 1 and 2, characterized by greater pollutant deposition loadings, were similar and were different from those monitored at 3 and 4, which in turn were similar to each other (Lynch, 1990). In complementary studies, Showman and Long (1992) concluded that lichen richness values did not form a continuum along the deposition gradient, but rather separated into two distinct groups. The lichen communities growing in study areas 1 and 2 were significantly less rich compared to those communities in study areas 3 and 4, and had significantly greater concentrations of Al, Cr, Cu, and Fe in their thalli.

Therefore, we calculated a mean concentration for each element per tree species within study areas 1 and 2, as well as within study areas 3 and 4. Significant differences between the mean concentration per element for the two areas were then tested. A GLM (Ray, 1982) analysis of variance was conducted separately for each element, tree species, and year of sampling using a factorial design, with sampling "month" (two levels = June and August-September samplings) and location (two levels = "Low" and "High" deposition portions of the gradient) as factors. Mean separation tests (Scheffe) were conducted if main effects were significant and if significant month x location interactions did not occur. Results from the two sampling times per year were combined and presented as annual means. Significance tests were conducted at $p < 0.05$.

RESULTS AND DISCUSSION

Although considerable variation existed in the data, foliar Fe, S and Sr concentrations were often directly related to the atmospheric deposition pattern, especially in red oak and red maple (Table 1). These three elements likely are emitted from the numerous anthropogenic sources such as coal-fired power plants or heavy industries located upwind in the Ohio River Valley, other states west of Pennsylvania and/or in southwestern Pennsylvania. Atmospheric S from these sources may enter Pennsylvania as gaseous sulfur dioxide (Fig. 3), or in the case of long-range transport, as sulfate. Trace metals, especially heavy metals, are most commonly associated with fine particles in contaminated atmospheres (Smith, 1981). Prevailing southwesterly winds during the growing season carry these industrial pollutants to the northeast, until they reach the front of the Allegheny Plateau in western Pennsylvania. As the pollutant-laden air masses rise up the plateau, Fe, S, and Sr are transferred from the atmosphere to the forest ecosystem through absorption by vegetation and soils as wet or dry deposition, with the greatest pollutant loadings occurring in forest stands located in the western end of the gradient (Lynch, 1990).

The use of increased foliar sulfur as a marker for delineating general polluted areas supports previous findings in Pennsylvania (Hutnik and others, 1989), in southeastern Ontario (Linzon and others, 1979), and Minnesota (Krupa and others, 1980). However, these cited studies were all conducted near point sources such as coal-fired power plants or smelters. Shriner and others (1980) reported that 82% of the sulfate deposited in Tennessee forest ecosystems, distant from point sources, was dissolved in rainfall, whereas only 18% occurred as dry particulate fallout. Similarly, it is likely that the majority of S input into the Pennsylvania forests occurs as wet sulfate, with lesser amounts occurring as gaseous sulfur dioxide. Whatever the form of deposited S, the primary available form of S in the soil solution is the sulfate anion, most of which is found in the subsoil (Jones and others, 1991). In our study, the sulfate-S of the B1 and B2 soil horizons were fairly uniform across the gradient (Davis and others, 1990). This would indicate that the greater S content of foliage in the western end of the gradient may have been due to greater foliar adsorption or absorption of wet or dry deposition.

Heavy metals are deposited in rainfall (Lindberg, 1982) but were not measured by Lynch and co-workers in precipitation sampling conducted across the study area. Likewise, Fe and Sr content of soils along the gradient were not measured. The elevated concentrations of Fe and Sr in tree foliage in the western end of the gradient could have been deposited as wet or dry deposition. Since the leaves were not washed, the Fe and Sr could have existed as particulates on the external leaf surfaces. Alternatively, soluble forms of Fe and Sr could have been directly absorbed by foliage. If deposited onto the soil, metal activity and subsequent uptake by the plant, is affected strongly by soil pH, in addition to metal equilibria among clay mineral, organic matter, hydrous oxides of Fe, Mn, Al, and soluble chelators (Adriano, 1986). Iron and Sr are more readily available in the soil solution at an acidic pH (Friedland and others, 1984). However, since the soils across the gradient were rather uniform in acidity with no east-to-west pattern (Davis and others, 1990; McClenahen and Long 1993), the ions should have been relatively available at all four stands. Soil acidity probably did not play a major role in the observed patterns of Fe, S, and Sr accumulation.

Total (Kjeldahl) N concentrations in red maple (only) foliage were significantly greater in the high deposition part of the gradient (Table 1). It has been hypothesized that elevated nitrogen inputs could promote succulent twig growth and delay hardening-off in the fall, which might lead to twig and crown dieback, and ultimately to decline (Friedland and others, 1984). We did not observe elevated twig dieback in the high deposition end of the gradient, based on observations of tree crowns (Nash and others, 1992). Perhaps the increases were not great enough to induce succulent growth. However, more detailed studies related to N accumulation and twig dieback in red maple are warranted. Alao, accumulation of N in red maple foliage may be useful as a sensitive indicator of N deposition.

The general values for elements reported herein are within the range reported in comparable studies for foliage of red and white oak (Majumdar and others, 1989) and red maple trees (Lea and others, 1980) growing in other parts of the Northeast. Thus, although the concentrations in foliage were relatively elevated in the western end of the gradient, and/or were relatively less in the eastern part of the gradient, there is no reason to suspect toxicity nor deficiency symptoms to occur in either section of the gradient. Indeed, our field observations of crowns (Nash and others,

Table 1. Concentration of elements in foliage of three species collected from the High vs Low deposition portions of the Pennsylvania gradient.

	Quercus rubra				*Quercus alba*				*Acer rubrum*			
	1988		1989		1988		1989		1988		1989	
Element	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low
%												
N	2.23[a]	2.26	2.24	2.32	2.24	2.31	2.40	2.37	1.62	1.53[b]	1.66	1.54
P	0.16	0.16	0.16	0.16	0.16	0.17	0.17	0.18	0.15	0.14	0.14	0.14
K	0.85	0.84	0.75	0.72	0.77	0.82	0.71	0.71	0.71	0.75	0.62	0.55
Ca	0.39	0.44	0.46	0.43	0.43	0.55	0.41	0.53	0.37	0.37	0.37	0.34
Mg	0.08	0.09	0.11	0.10	0.10	0.10	0.11	0.09	0.09	0.09	0.09	0.08
S	0.21	0.19	0.22	0.19	0.22	0.21	0.25	0.20	0.15	0.14	0.14	0.13
ppm												
Al	52	51	44	48	42	43	42	49	34	26	24	19
B	-[c]	-	35	33	31	29	26	27	24	22	22	18
Cu	-	-	4.2	3.9	-	-	5.2	5.8	4.6	4.4	4.2	3.7
Fe	105	102	100	94	97	92	95	92	110	100	84	78
Mn	2396	2526	2240	2333	2264	2446	2184	2569	1690	1676	1565	1521
Mo	-	-	-	-	-	-	0.17[d]	0.20	-	-	0.16	0.15
Na	49	47	61	51	36	42	48	36	37	28	36	28
Pb	-	-	2.9	3.1	1.6	2.1	2.7	3.0	1.6	1.7	1.7	1.5
Si	145	132	111	112	238	259	222	252	357	358	339	278
Sr	5.1	3.8	7.6	5.4	7.0	7.1	7.9	7.8	7.6	5.9	11.7	7.2
V	0.36	0.43	0.95	0.96	0.54	0.74	0.87	0.89	0.61	0.64	0.56	0.49
Zn	18	21	27	25	13	14	18	17	17	20	23	18

[a] each mean is based on approximately 40 samples averaged across the two sampling months within a year.
[b] underline indicates a significant difference (p=.05) between mean values from "High" (core areas 1 and 2) and "Low" (core areas 3 and 4) deposition portions of the gradient.
[c] - indicates no data.
[d] significance not tested between these two means.

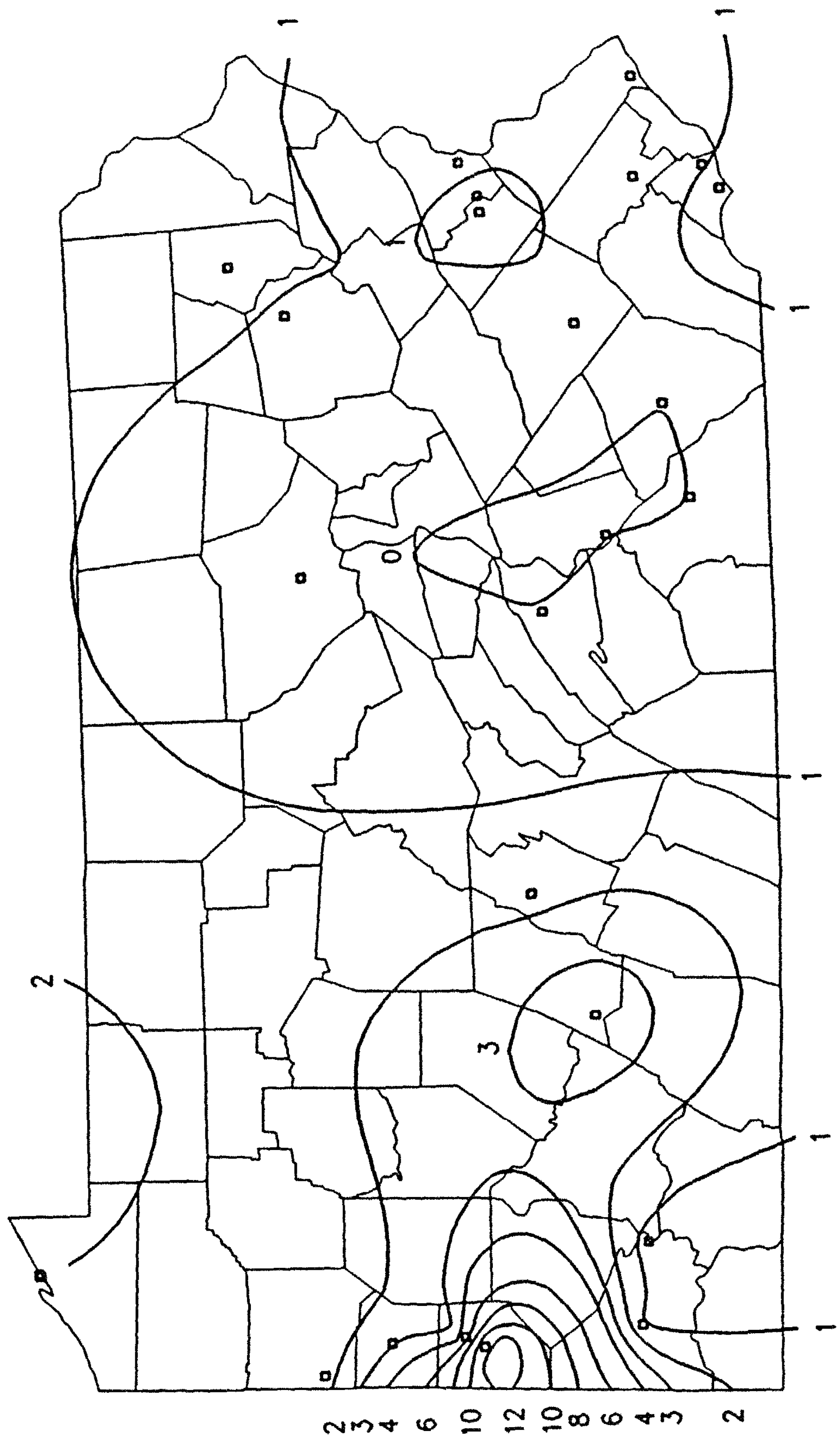

Figure 3. Percentage of hrs in 1988 that hourly-average SO2 concentrations exceeded 0.04 ppm in Pennsylvania (Data from PA Dept. Environ. Res., Bur. Air Qual. Map drawn by J. A. Lynch)

1992), as well as yet-unpublished laboratory evaluation of approximately 40,000 individual leaves indicated no apparent toxicity or deficiency symptoms.

In summary, our findings complement those of other researchers (Hutnik and others, 1989; Linzon and others, 1979; Krupa and others, 1980) who reported that S content of the foliage can be used to indicate areas affected by emissions from point sources such as coal-fired power plants and industries. Our findings extend the use of foliar S content as a marker of more widespread S or sulfate pollution. These results also complement the findings of others who reported that increased Sr content of white oak xylem (Long and Davis, 1989), sagebrush foliage (Connor and others, 1976) and grass (Wangen and Turner, 1980) as well as increased levels of Fe in grass, maple leaves, and pine needles (Klein and Russell, 1973) were increased immediately downwind from point sources such as coal-fired power plants. Since our unpublished data indicate that Fe, S, and Sr show an apparent increase during the growing season, late season collections should be utilized to ensure that concentrations of these three elements are great enough to delineate among areas of concern, and that levels are above the threshold limit for chemical analysis.

Thus, it appears that accumulations of Fe, S, and Sr may be indicative of ecosystems being subjected to atmospheric deposition originating as emissions from nearby point sources, or from pollutants which have undergone long range transport. Biological relationships between these long-term accumulations and forest health and productivity remain to be determined. In addition, the data set reported herein serves as a baseline from which future comparisons can be made as the Amended Clean Air Act goes into effect in the United States and industries reduce their emissions.

LITERATURE CITED

Adriano, D.C. 1986. Trace elements in the terrestrial ecosystem. Springer-Verlag, NY, 533 pp.

Connor, J.J., J.R. Keith, and B.M. Anderson. 1976. Trace metal variation in soils and sagebrush in the Powder River Basin, Wyoming and Montana. U.S. Geol. Survey 4:49-59.

Davis, D.D., J.M. Skelly, J.A. Lynch, and J.R. McClenahen. 1990. Measurement of forest condition and response along the Pennsylvania atmospheric deposition gradient. The Pennsylvania State University and Ohio State University, University Park, PA, 59 pp.

Friedland, A.J., R.A. Gregory, L. Karenlampi, and A.H Johnson. 1984. Winter damage to foliage as a factor in red spruce decline. Can. J. For. Res. 14: 963-5.

Hutnik, R.J., D.D. Davis, and J.R. McClenahen. 1989. Evaluation of vegetation near coal-burning power plants in southwestern Pennsylvania. I. Sulfur content of foliage. J. Air Pollut. Control Assoc. 39:1440-3.

Jones, J.B., B. Wolf, and H.A.Mills. 1991. Plant Analysis Handbook. Micro-Macro Pub., Athens, GA, 213 pp.

Kingsley, N.P. 1985. A forester's atlas of the northeast. USDA Forest Service Gen. Tech. Rpt. NE-95, NE For. Exp. Sta., Broomall, PA

Klein, D. H. and P. Russell. 1973. Heavy metals: fallout around a power plant. Environ. Sci. Technol. 7:357-8.

Krupa, S.V., B.I. Chevone, J.L. Bechthold, and J.L. Wolf. 1980. Vegetation: effects of sulfur deposition by dry-fall process. In Atmospheric Sulfur Deposition, ed D. S. Shriner, C. R. Richmond, and S. E. Lindberg, Ann Arbor Sci. Pub., Ann Arbor, MI, pp 309-20.

Lea, R., W.C. Tierson, B.H. Bicklehaupt, and A.L. Leaf. 1980. Differential foliar responses of northern hardwoods to fertilization. Plant and Soil 54:419-39.

Lindberg, S.E. 1982. Factors influencing trace metal, sulfate, and hydrogen ion concentrations in rain. Atmos. Environ. 16: 1701-09.

Linzon, S.N., P.J. Temple, and R.G. Pearson. 1979. Sulfur concentrations in plant foliage and related effects. J. Air Pollut. Control Assoc. 29:520-25.

Long, R.P. and D.D. Davis. 1989. Major and trace element concentrations in surface organic layers, mineral soil, and white oak xylem downwind from a coal-fired power plant. Can. J. For. Res. 19:1603-15.

Long, R.P., J.R. McClenahen, and K.A. Dwire. 1991. Selecting ecologically analogous stands: a rigorous method for studies of atmospheric deposition effects. OARDC Res. Circ 293, Ohio Agricultural Research and Development Center, Wooster, OH, 37 pp.

Lynch, J.A. 1990. Spatial and temporal variability in atmospheric deposition overview: A Pennsylvania prospectus. In Proceedings of Conference on Atmospheric Deposition in Pennsylvania: A Critical Assessment, ed. J. A. Lynch, E. S. Corbett, and J. W. Grimm. Sept. 11-14, 1989, The Pennsylvania State University, University Park, PA, pp 50-62.

Majumdar, S.K., S.W. Cline, and R.W. Zelnik. 1989. Chemical analyses of soils and oak tree tissues from two forest habitats in Pennsylvania differing in their sensitivity to acid precipitation. Environ. Tech. Letters 10:1019-26.

McClenahen, J.R. and R.P. Long. 1993. Height growth of northern red oak in relation to site and atmospheric deposition in Pennsylvania. Environ. Pollut. 80:105-114.

Nash, B.L., D.D. Davis, and J.M. Skelly. 1992. Forest health along a wet sulfate/pH deposition gradient in north-central Pennsylvania. J. Environ. Tox. Chem. 11:1095-1104.

Ray, E.E. (Ed.). 1982. SAS User's Guide: Statistics, 1982 Edition. SAS Institute, Gary, NC.

Showman, R.E. and R.P. Long. 1992. Lichen studies along a wet sulfate deposition gradient in Pennsylvania. The Bryologist 95:166-70.

Shriner, D.S., C.R. Richmond, and S.E. Lindberg (eds.). 1980. Atmospheric Sulfur Deposition. Ann Arbor Sci. Pub., Ann Arbor, MI, 568 pp.

Smith, W.H. 1981. Air Pollution and Forests. Springer-Verlag, NY, 379 pp.

Wangen, L. E. and F.B. Turner. 1980. Trace elements in vegetation downwind of a coal-fired power plant. Water, Air, and Soil Pollut. 13:99-108.

LANDSCAPE-LEVEL REGENERATION ADEQUACY FOR NATIVE HARDWOOD FORESTS OF PENNSYLVANIA

William H. McWilliams, Todd W. Bowersox, David A. Gansner, Larry H. McCormick, and Susan L. Stout[1]

Abstract: Studies of advance regeneration and post-disturbance regeneration adequacy were conducted during the recent USDA Forest Service inventory of forest resources in Pennsylvania. The first study examined advance tree-seedling regeneration in stands where stocking levels would suggest that advance regeneration should be abundant. A range of metrics was used to describe regeneration adequacy. Findings indicate that advance regeneration is generally lacking in the State. The results ranged from only 4% to 40% of the sample locations being adequately stocked (based on the most and least stringent metric, respectively). Levels of fern and grass cover were sufficient to make treatment to control herbaceous vegetation an option at 54% of the sample locations. The second study focused on mixed-oak (*Quercus* spp.) stands that had undergone significant disturbance since the time of the previous inventory. Results indicate that 92% of the mixed-oak stands were adequately stocked with woody species. Stocking of oak species was far below what it was before disturbance. The least stringent metric of oak regeneration showed that only 16% of the sample locations were adequately stocked with oak species.

INTRODUCTION

At a time when many within the environmental community are concerned about regeneration of native hardwood forests, there is little information that describes regeneration adequacy at large geographic scales. Practicing foresters need information on regeneration adequacy to aid decisions about silvicultural investments and future markets for timber products. Studies of advance tree-seedling regeneration and post-disturbance regeneration were carried out as part of a recent inventory of forest conditions in Pennsylvania (Alerich 1993). The inventory was conducted by the USDA Forest Service, Forest Inventory and Analysis Unit of the Northeastern Forest Experiment Station (NE-FIA). The advance regeneration study evaluated tree-seedling abundance in a variety of forest types. The post-disturbance study focused on heavily disturbed mixed-oak stands.

METHODS

Advance Tree-Seedling and Herbaceous Cover Sample

Measurements of tree seedlings and herbaceous cover were adapted from the understory sampling procedure of Marquis et al. (1992) and added to the standard NE-FIA inventory procedures. The design for each sample location consisted of two nested circular plots--a 6-foot-radius plot and a 16-foot-radius plot located at each of five satellite points. On the 6-foot plot, tree seedlings (more than 2 in. in height and less than 1 in. in diameter) were tallied by species and height. On the 16-foot plot, percent cover was estimated for four classes of herbaceous vegetation: bracken fern (*Pteridium aquilinum* L.) , hayscented fern (*Dennstaedtia punctilobula* Michx.), and New York fern

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(*Thelypteris noveboracensis* L.); other fern; grass; and blackberry (*Rubus* spp.). Sample locations were screened for the range of stand-level stocking (or relative density) where advance tree-seedling regeneration should be abundant, that is, in stands with overstory stocking of 40- to 75-percent. Stands in this stocking range have a significant overstory, but available light is not likely to limit the establishment and growth of tree seedlings. The screening resulted in 499 sample locations. Six metrics were developed to represent a range of expectations about future conditions for seedling development. The metrics assess the adequacy of advance tree-seedling regeneration for three species groups: woody, commercial, and desirable; and two levels of stocking: high and low. The specifics of deriving the metrics are described in the Appendix. The low-density measures follow the guidelines of Sander et al. (1976) and Leak (1988). The more conservative high-density measures parallel the recommendations of Marquis and Bjorkbom (1982) and reflect regeneration needs under conditions that are unfavorable for seedling development, i.e., high deer (*Odocoileus virginianus* L.) impact.

Post-Disturbance Sample

When the statewide inventory was completed, information on disturbance, species composition, and relative density (Ernst, R.L. and W. Knapp 1985) were used to identify heavily disturbed mixed-oak sample locations. The decision to focus on mixed-oak stands was in response to concern over oak regeneration (Loftis and McGee 1993). Three criteria were used to select sample stands. First, candidate stands must have had at least 50% of total density in oak species at the time of previous measurement. Second, the stand must have been at least 60% stocked at the time of previous measurement (or above B-level stocking). Third, the stand must have been reduced to below 40% stocking at the most recent measurement (or below C-level stocking). Stands in this range are considered to be in need of regeneration (Ginrich 1967). These selection criteria yielded a total of 49 sample locations which were then revisited, and a grid of twenty 6-foot-radius circular plots was installed. At each plot, stem counts were conducted by species and height class. To reduce collection cost, stem counts were limited to the number of stems needed to satisfy the most conservative of two guidelines for determining if the plot was adequately stocked with regeneration. Various stand disturbances were encountered, but most involved heavy cutting and (or) overstory mortality resulting from gypsy moth (*Lymantria dispar* L.) defoliation, drought, or other factors. For most of the sampled stands, 10 to 15 years had elapsed since disturbance. Sample locations were located across the State with highest concentrations in southcentral counties where gypsy moth defoliation had a strong impact.

Measurements were taken to gauge whether these mixed-oak stands were adequately stocked with woody, commercial, or oak species following disturbance. A high-density metric was adapted from the work of Marquis and Bjorkbom (1982). A low-density metric of roughly half the high-density guideline was used to provide a range for analyzing the results. The number of stems required for adequate stocking are:

	Stocking Level	
	Low	High
Tree-Size	# of stems/plot	
5 inches dbh and larger	1	1
>= 5 feet tall and < 5 inches dbh	1	2
>= 3 feet tall and < 5 feet tall	3	5
>= 2 inches tall and < 3 feet tall	15	25

Sample locations were considered adequately stocked if at least 50% of the satellite plots satisfied a given metric. The 50% rule was used because most of the sampled stands had established forest cover of sufficient age to assume that stocking of satellite plots provides a good representation of stocking once the stand reaches merchantable size--the typical objective of post-disturbance regeneration inventories.

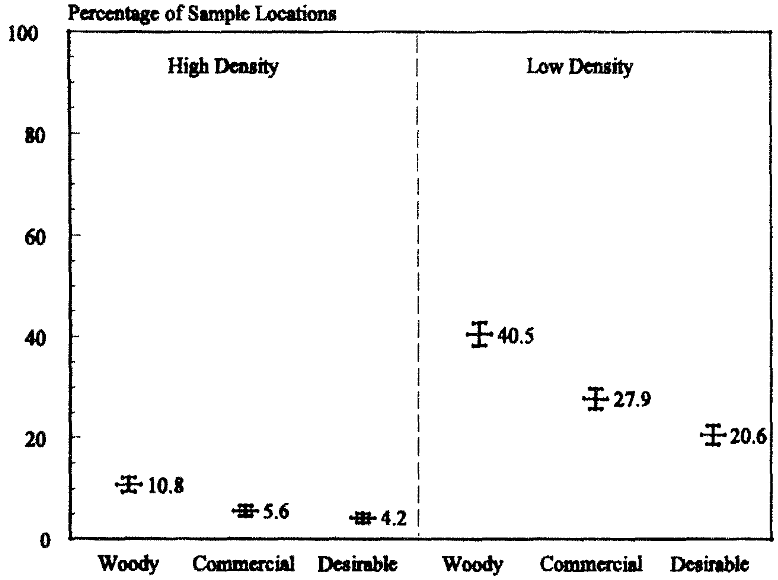

Figure 1. Mean percentage of sample locations adequately stocked with tree seedlings, by species group and density measure. (Brackets indicate the 95% confidence interval.)

RESULTS

Advance Tree-Seedling Regeneration and Herbaceous Cover

The data suggest that existing advance tree-seedling regeneration is an inadequate source for new stand establishment across most of Pennsylvania's forested landscape. Using the least stringent metric (a low density of woody stems) results in only 40% of the sample locations being adequately stocked (Fig. 1). When a high density of woody species is used, the estimate of adequacy is reduced to 11%. The woody-species measures assess the outlook for establishing woody cover following removal of the overstory without regard to how desirable the species may be for timber management. The success rates using the commercial-species measures of stocking adequacy are 28% for the low-density measure and 6% for the high-density measure. The commercial species group excludes species that contribute little to the stand's commodity value. The desirable group contains species most favored for timber production and, in general, offers more vigorous growth and a higher probability of developing a canopy of large well-formed stems that satisfy aesthetic objectives. The percentage of sample locations that were adequately stocked with desirable stems was 21 with the low-density measure and 4 with the high-density measure.

A search for statistically significant relationships between stocking adequacy and other variables collected by NE-FIA was conducted to find factors that might explain why advance tree-seedling regeneration so often is lacking in the forest understory. The variables of interest were: physiographic section (after Fenneman 1938), forest-type group, terrain position, aspect, stocking level, county-level deer density, and percentage of county-level land area occupied by forest. Continuous variables were grouped into discrete classes. Significance tests were conducted for all classes of variables and combinations of classes with at least 25 sample locations using SAS's categorical data modeling procedure (SAS Institute 1989). Of all categories tested, the only significant differences were between the oak-hickory and northern hardwoods forest-type groups. For all density measures, oak-hickory forests were associated with a higher abundance of advance tree-seedling regeneration than northern hardwood forests. This and the

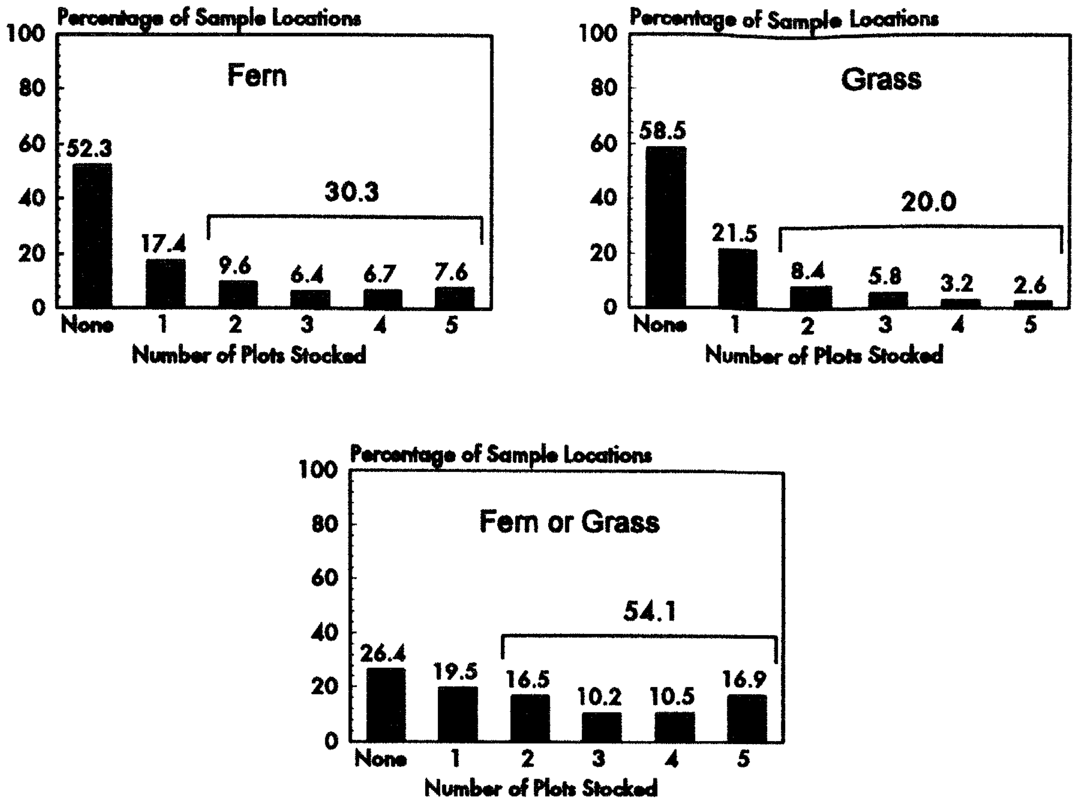

Figure 2. Mean percentage of sample locations and number of herbaceous cover plots stocked with at least 30% herbaceous plant cover, by type of vegetation.

finding that other variables and combinations were not significant suggest that poor advance regeneration is perhaps more wide ranging than was suspected.

The impact of herbaceous vegetation on regeneration ultimately depends on the abundance of advance regeneration because this determines the harvest options available (Marquis et al. 1992). In stands with sufficient regeneration for a final removal cut, the silvicultural guidelines recommend controlling herbaceous vegetation if at least 70% of the inventory plots are stocked with interfering herbaceous plants. (A herbaceous plot is considered stocked if 30% or more of the plot is covered.) If sufficient regeneration is lacking and a shelterwood seed cut is recommended, herbaceous control is considered if 30% of the plots are stocked. If the more conservative 30% threshold is used, over half of the sample locations would be potential candidates for herbaceous control due to the presence of fern, grass, or both in combination (Fig. 2). In the presence of fern alone, nearly one-third of the sample locations would qualify for treatment.

The sample also provides a general measure of the abundance of fern in Pennsylvania. Forty-eight percent of the sample locations had at least one herbaceous-cover plot stocked with 30% or more fern. The fern sample was collected for two species groups: species that have potential to spread through elongation of a perennial rhizome (bracken, hayscented, and New York fern) and other fern species. The former group is an aggressive invader of forest sites (Horsley 1988). Bracken, hayscented, and New York fern accounted for 70% of the total abundance of fern found in the sample.

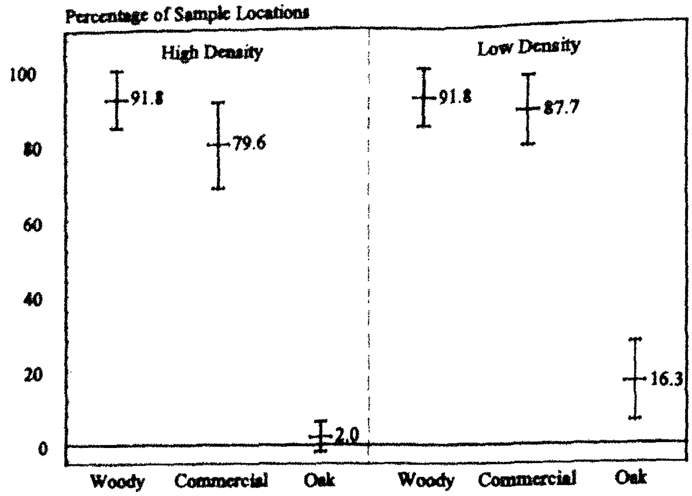

Figure 3. Mean percentage of sample locations adequately stocked with tree species following disturbance in oak-dominated stands by species group and density measure. (Brackets indicate the 95% confidence interval.)

Post-Disturbance Regeneration

The post-disturbance sample of mixed-oak stands was designed to answer two questions: 1)are stands regenerating with an adequate stocking of tree species and, 2)what is the status of oak species in the new stand? The results indicate that mixed-oak stands are regenerating adequately with tree species following heavy disturbance. Ninety-two percent of the sample locations were stocked with woody species using both the high- and low-density metrics (Fig. 3). For commercial species, 80% of the sample locations satisfied the high-density metric and 88% satisfied the low-density metric.

The findings show that the oak component is generally lacking following heavy disturbance in mixed-oak stands. When the high-density metric was used, oak regeneration was virtually non-existent. Only 2% of the sample locations were adequately stocked and this estimate was not significantly different from zero. When the low density metric was used, 16% of the sample locations were adequately stocked with oak. The low-density metric is probably a good indicator of adequacy for the oak component because of general stand conditions encountered on sample locations. Although evidence of deer was abundant on nearly all of the sample locations, most of the stands had developed to a point where sample trees were above 5 feet in height. Also, most of the oak regeneration encountered was found to be superior in terms of height, dominance, and vigor. In stands where oak regeneration was lacking, the most common species of the regeneration component were sweet birch (*Betula lenta* L.), red maple (*Acer rubrum* L.), and black cherry (*Prunus serotina* Ehrh.). As all of the stands in the study were at least 50% oak prior to disturbance, the results suggest a shift to forest types other than oak for most of the sample locations in the study. Further investigation of the data are planned to compare species composition before and after disturbance and the impact of disturbance on species diversity.

DISCUSSION

The results of these two studies have documented some significant regeneration challenges that exist across Pennsylvania's forested landscape. The advance regeneration study focused on stands where stocking levels would suggest that advance regeneration should be abundant. The most optimistic measure of advance regeneration adequacy was satisfied at only 40% of the sample locations. Fern and grass competition was significant at 54% of the sample locations. The impact of deer was not measured directly in the study, but Pennsylvania's deer herd has been a significant factor affecting understory conditions (Tilghman 1989). Other factors include soil and site characteristics, drought, stresses from diseases and insects, and other herbivores. The study of regeneration following heavy disturbance of mixed-oak stands found that regeneration was abundant, but species composition had changed due to poor regeneration of oak. The oak regeneration component was found to be inadequate in all but 16% of the sample locations. These findings are similar to those of Allen and Bowersox (1990).

It is interesting to compare the results of these two studies of regeneration adequacy even though they were conducted independently. The basic message of the advance tree-seedling study was that very few stands in Pennsylvania contained enough advance regeneration to adequately regenerate following harvest. The study of mixed-oak stands found that most stands had regenerated, but the composition tended to contain a new suite of species. The new stands typically contained light-seeded intolerant species such as black cherry and sweet birch. Black cherry and sweet birch are not preferred food sources for deer. The other prevalent species was red maple, which is very common throughout Pennsylvania and is a prolific producer of wind disseminated seed. Although not observed as part of this study, these invader species were likely not part of the advance seedling component of the sampled stands. This suggests that we need to know more about how well advance regeneration stocking guides predict future stand-level stocking and how forest composition changes as stands evolve over time.

LITERATURE CITED

Allen, David and Todd Bowersox. 1990. Regeneration in oak stands following gypsy moth defoliations. In Proceedings of the seventh central hardwoods forest conference, 1989 March 5-8, Carbondale, IL.

Alerich, Carol L. 1993. Forest Statistics for Pennsylvania-1978 and 1989. Res. Bull. NE-126. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 244 p.

Ernst, R.L. and W. Knapp. 1985. Forest stand density and stocking: concepts, terms, and the use of stocking guides. Gen. Tech. Rep. WO-44. Washington, DC: U.S. Department of Agriculture, Forest Service. 8 p.

Fenneman, Nevin M. 1938. Physiography of the eastern United States (1st edition). New York: McGraw-Hill. 714 p.

Ginrich [Gingrich], S.F. 1967. Measuring and evaluating stand density in upland hardwood forests in the Central States. For. Sci. 13:38-53.

Horsley, Stephen B. 1988. How vegetation can influence regeneration. P. 38-55 in Proceedings of guidelines for regenerating Appalachian hardwood stands, SAF Publ. 88-03. Bethesda, MD: Soc. Am. For.

Leak, William B. 1988. Effects of weed species on northern hardwood regeneration in New Hampshire. North. J. Appl. For. 5:237-240.

Loftis, David and Charles E. McGee. 1993. Oak regeneration: serious problems, practical recommendations. Symposium Proceedings. Gen. Tech. Rep. SE-84. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station 319 p.

Marquis, David A., Richard L Ernst, and Susan L. Stout. 1992. Prescribing silvicultural treatments in hardwood stands of the Alleghenies (revised). Gen. Tech. Rep. NE-96. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 101 p.

Marquis, David A. and John C. Bjorkbom. 1982. Guidelines for evaluating regeneration before and after clearcutting Allegheny hardwoods. Res. Note NE-307. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 4 p.

Sander, Ivan L., Paul S. Johnson, and Richard F. Watt. 1976. A guide for evaluating the adequacy of oak advance reproduction. Gen. Tech. Rep. NC-23. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 7 p.

SAS Institute, Inc. 1989. SAS/STAT user's guide, version 6, 4th ed., volume 1. Cary, NC: SAS Institute. 943 p.

Tilghman, Nancy G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildl. Manage. 53(3):524-532.

APPENDIX

Guidelines for determining the adequacy of advance tree-seedling regeneration.

Species Group

Desirable: Black cherry, oak, sugar maple (*Acer saccharum* Marsh.), red maple, conifer (*Juniperus virginiana* L., *Larix* spp., *Pinus* spp., *Tsuga canadensis* L.), hickory (*Carya* spp.), yellow-poplar (*Liriodendron tulipifera* L.), ash (*Fraxinus* spp.), basswood (*Tilia americana* L.), cucumbertree (*Liriodendron acuminata* L.), walnut (*Juglans nigra* L.), and butternut (*Juglans cinerea* L.).

Commercial: All desirable species and birch (*Betula* spp.), beech (*Fagus grandifolia* Ehrh.), blackgum (*Nyssa sylvatica* Marsh.), elm (*Ulmus* spp.), black locust (*Robinia pseudoacacia* L.), willow (*Salix* spp.), hackberry (*Celtis occidentalis* L.), and aspen (*Populus* spp.).

Woody: All desirable species, commercial species, and honey locust (*Gleditsia triacanthos* L.), sassafras (*Sassafras albidum* (Nutt.) Nees), ironwood (*Ostrya virginiana* (Mill.) K. Koch.), ailanthus (*Ailanthus altissima* (Mill.) Swingle), mountain ash (*Sorbus americana* Marsh.), blue beech (*Carpinus caroliniana* Walt.), hawthorn (*Crataegus* spp.), dogwood (*Cornus* spp.), redbud (*Cercis canadensis* L.), pin cherry (*Prunus pensylvanica* L.), striped maple (*Acer pensylvanicum* L.), hercules club (*Zanthoxylum clava-herculis* L.), scrub oak (*Q. ilicifolia* Wangenh.), chokecherry (*Prunus virginiana* L.), and shadbush (*Amelanchier arborea* (Michx f.) Fern.).

Satellite Plot Stocking

Seedling density	Minimum number of seedlings per plot
High	100
Low	25

To account for different seedling survival by height class, seedlings were weighted as follows:

Height	Weight
2 inches to 1 foot	1
1 to 3 feet	2
3 to 5 feet	20
5 feet and larger	50

Any combination of weighted stems that meets or exceeds the minimum number required is considered stocked. For example, a plot is considered to meet the high-density requirement for desirable species if it contains at least two stems at least 5 feet tall. Similarly, a plot is stocked with a low density of woody species if it contains 20 stems 6 inches tall and 3 stems 2 feet tall.

Sample Location Stocking

A sample location is considered stocked if at least four of the satellite plots (or at least 70%) contain the minimum number of seedlings.

LANDSCAPE VARIATION IN SPECIES DIVERSITY AND SUCCESSION AS RELATED TO TOPOGRAPHY, SOILS AND HUMAN DISTURBANCE[1]

Jeffrey N. Pearcy[2], David M. Hix[2], and Stacy A. Drury[3]

Abstract: Three hundred and thirty-two plots have been sampled on the Wayne National Forest of southeastern Ohio, for the purpose of developing an ecological classification system (ECS). The ECS will be based on the herbaceous and woody vegetation, soils and topography of mature (80-140 year-old), relatively-undisturbed forests. Species diversity changes little across this landscape. Forty-eight woody tree species were identified among all plots and species richness (R) varied from two to thirteen on individual plots. Although variable within landform type, R varied similarly across landform type, with slightly greater variability on moderately steep slopes (3-13) than on steep slopes (3-10). Ridgetops (4-11) were comparable to sideslopes while ravines generally had fewer species (2-9) than other landforms. Again, although variable, R and species diversity (H) were not highly different across areas with differing soils characteristics. However, higher values of R and H were associated with severe, xeric sites having sandy soils; and mesic to dry-mesic sites that had evidence of nearby disturbance.

Species composition did vary predictably across the landscape. Northerly aspect and lower slope positions had more mesic communities than did southerly aspect and upper slope positions which were typically more xeric. Compositional stability of stands was determined by calculating a composition index (CI, after Fralish et al., 1993) for overstory, sub-canopy, sapling and seedling layers of woody vegetation. CI was based on the sum of the product between each species importance value (IV) and environmental adaptation value (AV). IV was the average of the relative density and the relative dominance of each species, and AV was compiled from several previously published studies (Buell et al., 1965; Curtis and McIntosh, 1951; Fralish et al, 1993; and Wells, 1976). Differences between strata of less than 100 units were considered to be fairly stable. Compositionally stable stands (based on four vegetational layers) were generally restricted to very mesic sites, xeric sites, and sites with unstable soil/slope conditions that prevent successional climax. Compositional stability on dry-mesic sites that are dominated by oak-hickory overstory is related to subcanopy and sapling layers that are predominately *Acer rubrum* (L.) and other non-oak species with AVs similar to oaks.

LITERATURE CITED

Buell, M. F., A. N. Langford, D. W. Davidson, and L. F. Ohmann. 1966. The upland forest continuum in northern New Jersey. Ecology 47:416-432.

Curtis, J. T., and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32:476-496.

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Fralish, J. S., S. B. Franklin, P. A. Robertson, S. M. Kettler, and F. B. Crooks. 1993. An ordination of compositionally stable and unstable forest communities at Land Between The Lakes, Kentucky and Tennessee. *In*: [Fralish, J. S., R. P. McIntosh, and O. L. Loucks; eds.] Fifty Years of Wisconsin Plant Ecology. The Wisconsin Academy of Sciences, Arts, and Letters. pp. 247-267.

Well, P. V. 1976. A climax index for broadleaf forest: An n-dimensional, ecomorphological model of succession. *In*: [Fralish, J. S., G. T. Weaver, and R. C. Schlesinger; eds.] Proc: Central Hardwoods Forest Conf., Carbondale, Ill. Oct. 17-19, 1976. pp 131-175. North Central Forest Exp. Sta., 1992 Folwell Ave., St. Paul, MN 55108

CANOPY OPENINGS AND WHITE-TAILED DEER INFLUENCE THE UNDERSTORY VEGETATION IN MIXED OAK WOODLOTS[1]

Todd W. Bowersox, Gerald L. Storm, and Walter M. Tzilkowski[2]

Abstract: Effects of canopy opening and white-tailed deer on ground level vegetation are being assessed in south-central Pennsylvania. Herbaceous plants and woody seedlings are being monitored in three unevenaged, mixed oak woodlots at Gettysburg National Military Park. Canopy opening levels on 0.20 ha treatment units were closed (~100% canopy), small (50-60% canopy) and large (0% canopy). Number of white-tailed deer during April have averaged about 0.40 deer per ha since 1992. Overstory treatments were conducted in March 1993. Fences to exclude deer were installed on one-half of the understory inventory plots. Before treatment inventories (1992) of the July herbaceous vegetation indicated 30% of the ground was covered by broadleafs, grasses and vines. Total herbaceous coverage increased to 54% of the area in the first growing season after treatment. Woodlot, canopy opening and fencing significantly influenced the coverage of herbaceous vegetation. Overall, total herbaceous coverage increased from 38% in the closed canopy treatment to 50% and 75% in the small and large canopy treatments, respectively. Compared to before treatment values, overall total herbaceous coverage in the first growing season after treatment increased 19% on all unfenced plots and 30% on all fenced plots. Before treatment inventories of the woody vegetation recorded an average of 5.6 shrub and 4.0 tree species seedlings per m^2. In the first growing season after treatment, number of shrub and tree seedlings increased to 6.7 and 8.6 stems per m^2, respectively. Ash dominated the tree species with an average of 2.0 seedlings per m^2 before treatment and 2.5 seedlings per m^2 after treatment. Average number of oak seedling in the first growing season after treatment (0.9 per m^2) was the same as before treatment. Woodlot was the only factor that consistently influenced the number of before and after treatment seedlings. Before treatment average numbers of shrub and tree seedlings were 12.3, 6.9 and 9.5 per m^2 for Bushman Hill, Herr Ridge and Powers Hill woodlots, respectively. In the first growing season after treatment, average number of shrub and tree seedlings for Bushman Hill, Herr Ridge and Powers Hill increased to 15.2, 7.8 and 13.1 per m^2, respectively. Overall, there were 2.1 shrub species and 3.7 tree species germinates in the first growing season after treatment. Most abundant germinates were ash (0.6/m^2), grape (1.7/m^2), redbud (0.2/m^2) and yellow-poplar (2.9/m^2). Canopy treatment and litter conditions, but not fencing, significantly influenced the abundance and species composition of the germinates.

INTRODUCTION

Gettysburg National Military Park (GNMP) was established in 1895 to commemorate the July 1863 Civil War battle. Originally established under the US War Department, GNMP was transferred to the National Park Service in 1933. GNMP presently covers about 1560 ha, with 643 ha occupied by woodlots. These woodlots range in size from 2 to 24 ha.

Before the battle, the woodlots were important cultural resources for the residents. Historic photographs and documents, and recent research reports (Fairweather and Cavanaugh 1990, Storm and others 1994) suggest a general pattern to the 1863 condition and subsequent development of these woodlots. Open-grown white oak (*Quercus*

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alba L.) trees were the dominant vegetation in 1863. In 1993, there were about 15 residual white oak trees per ha that were >135 years old. These trees typically had rapidly tapering boles with wide spreading crowns that had large diameter branches originating near the ground. Their diameters at 1.4 m above ground (DBH) generally were >60 cm. A second group of trees became established around 1900 (±25 years) when the understocked woodlots were retired from active agriculture. This group of trees was mainly northern red oak (*Quercus rubra* L.), black oak (*Quercus velutina* Lam.) white oak, bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch.), mockernut hickory (*Carya tomentosa* Nutt.) and shagbark hickory (*Carya ovata* (Mill.) K. Koch). These trees were generally between 30 and 60 cm in diameter in 1993, with closed stand architecture of slowly tapering boles with narrow crowns. A third group of trees developed in response to occasional openings in the canopy. These trees were mainly black cherry (*Prunus serotina* Ehrh.), flowering dogwood (*Cornus florida* L.), mazzard cherry (*Prunus avium* L.), white ash (*Fraxinus americana* L.) and hickories. In 1993, the third group of trees was generally between 3 and 30 cm in diameter.

Storm and others (1994) evaluated the overstory and understory of six GNMP woodlots. They concluded that the species composition, number and size of the trees >12 cm in diameter should be capable of maintaining an acceptable woodlot appearance for at least 25 years. They also concluded that there was a variety of tree species present in the seedling and sapling sizes (stems<12 cm in diameter). Overall there was an adequate number of seedlings (average of 23,584 per ha) but the number of saplings (826 per ha) was about one half the number needed to sustain the woodlots. Furthermore, oak species accounted for 44% of the number of trees in the overstory but only 6% of the sapling-sized stems.

White-tailed deer (*Odocoileus virginianus*) browsing and woodlot management practices may be influencing the height growth and species composition of the understory at GNMP (Bowersox and others 1993, Tzilkowski and others 1993). Average number of white-tailed deer on GNMP during April have increased from 0.25 deer per ha in 1987 to about 0.40 deer per ha since 1992. These deer densities far exceed the Pennsylvania Game Commission management goal of 0.08 deer per ha for the surrounding county. Shrub and tree seedlings recorded in 1987 on demonstration plots located in five GNMP woodlots averaged 7.1 per m^2 in the fenced plots and 7.3 per m^2 in the unfenced plots. By 1991, densities dropped to 6.1 in the fenced areas and 4.2 in the unfenced areas. Loss of seedlings between 1987 and 1991 was substantial for white oak, which dropped from 2.6 to 0.8 per m^2 in the fenced areas and from 3.7 to 0.5 per m^2 in the unfenced areas.

Maintaining these woodlot areas as tree-dominated communities is important to the park's mission to preserve the historic scene. Resource managers want to manage these woodlots to sustain an unevenaged structure. However, the current conditions have raised a concern for the future of these woodlots. They were created under frequent partial cutting practices before 1863 and a change in land use about 1900. There has been no tree cutting activity since 1895. The canopy trees are at or are approaching maturity. The existing woodlots were established at a time when there were no deer. Today's deer density is very high and may be influencing the understory vegetation. A research project has been developed and is being conducted to provide a basis for actively managing these woodlots. This project was designed to evaluate the effects of various size openings in the canopy, with and without white-tailed deer, on understory vegetation. This paper reports on the first growing season responses to these treatments.

PROCEDURES

The gently rolling topography of GNMP is in the Piedmont physiographic region (Lull 1968) of south-central Pennsylvania. Regeneration potential is being evaluated in three mixed oak woodlots. These woodlots are Bushman Hill (22 ha), Herr Ridge (17 ha) and Powers Hill (21 ha). Site quality was about average, and if occupied by evenaged stands the site index for oak would be ≥ 70. A more complete description of the site, soil and vegetation conditions was presented by Bowersox and others (1993).

Locations of the three replications of three canopy treatments in each of the woodlots were selected in April 1992 (Bowersox and others 1993). Felling of the canopy trees was conducted in March 1993. Directional felling was used to uniformly distribute the residual over the 0.20 ha circular plot. Boles and branches were cut to place all material within 1 meter of the ground. No material was removed from the treatment units. Canopy treatments to the 0.20 ha areas were:

1. Closed. No changes in the overstory. Average stocking levels (based on standards developed for upland central hardwoods by Roach and Gingrich 1968) were 115, 100 and 99% for Bushman Hill, Herr Ridge and Powers Hill, respectively.

2. Small. Overstory canopies were reduced by single tree removals to achieve a modified structure (Bowersox and others 1993) goal at 50 to 60% of fully stocked level. Average stocking levels after tree felling were 53, 55 and 52% for Bushman Hill, Herr Ridge and Powers Hill, respectively.

3. Large. All stems >2 cm DBH were felled.

Wire fences 1.2 m high to exclude white-tailed deer were installed in August 1992. Estimates of the free-ranging white-tailed deer April densities for the unfenced areas have been based on actual counts since 1987 (Storm and others 1989, Storm and Tzilkowski 1992). These annual April counts are scheduled to be continued through 1997.

Abundance, composition and structure of understory vegetation were measured before and after the canopy treatments were executed. All understory inventory plots were randomly located in the central 314 m^2 of each 0.20 ha treatment unit to minimize the effect of adjacent community and site conditions. Three pairs of fenced and unfenced 2.0 m^2 circular plots were established in each 0.20 ha treatment unit to inventory the naturally established herbaceous and woody plant community. There were 27 pairs of fenced and unfenced natural regeneration plots per canopy treatment for all study woodlots. July coverage of broadleaf plants, grasses and vines on each plot was ocularly estimated to the nearest 5%. Similarly, coverage by individual herbaceous species was inventoried on a subset (n=9) of the plots. Total herbaceous was the summation of inventory categories, which due to layering, overlap and inclusions, may exceed 100%. Size and number of stems per woody species that were $\leq$ 1.50 cm in height were inventoried in August. Species were placed in Oak, Other Tree, Shrub or Total groups for some analyses. A list of species within each group is presented in Table 2.

A second set of plots was established to measure the abundance and species composition of new woody species germinates. To preserve known and unknown archeological resources in each woodlot, no disturbance to the soil was permitted when the canopy trees were felled. Seedbed conditions of no litter removed and litter removed were established to evaluate the effect of an undisturbed litter layer on the abundance and species composition of the new germinates. New woody species germinates were recorded in a set of two paired fenced and unfenced 4.0 m^2 circular plots per treatment unit. Each set of plots were randomly located within the central 314 m^2 of each treatment unit. One half of each plot was randomly assigned to each litter condition. Litter-removed treatments were conducted in May 1993 with all identifiable leaf and twig material manually removed to expose the humus or mineral soil surface. There were 18 pairs of fenced and unfenced germination plots (each with a 2.0 m^2 sub-plot for no litter removed and a 2.0 m^2 sub-plot for litter removed) per canopy treatment and a total of 54 paired plots for the study. Number of new germinates by species were recorded in August.

Analysis of variance was used to test for significant main and appropriate interaction factors on herbaceous coverage, number of seedlings and number of germinates. Mean separations were performed on those parameters which showed significant treatment effects with Tukey's method of Multiple Comparisons. Significance at the 0.05 level was used in all cases.

RESULTS

Before treatment inventories indicated 43 species of broadleaf plants, 6 species of grasses and 6 species of vines present in the three woodlots. In the first growing season after treatment, there were no overall changes in the presence of specific species on specific plots. Individual plots had an average of 8 species of broadleaf plants (1 to 14 species per plot), 1 species of grass (1 to 3 species per plot) and 3 species of vines (1 to 5 species per plot). Overall, herbaceous vegetation coverage averaged 2% for grasses, 6% for vines, 23% for broadleaf plants and 31% for total herbaceous. There was a significant difference in coverage of broadleaf plants and total herbaceous among the woodlots, and total herbaceous for canopy treatment. Bushman Hill and Powers Hill had significantly greater total herbaceous coverage (41%) than was measured at Herr Ridge (11%). Treatment units designated to receive small canopy and large canopy treatment had total herbaceous coverage of 33 and 37%, respectively. These values were significantly different from the total herbaceous coverage of 21% for those units designated for closed canopy treatment. There was no significant difference between the units designated for small and large canopy treatment. Otherwise, coverage values for all herbaceous vegetation groups were similar among the inventory plots. When averaged over woodlots, before treatment coverage values for non-fenced and fenced plots by canopy treatment ranged from 0 to 6% for grasses, 16 to 26% for broadleaf plants, 2 to 8% for vines and 18 to 37% for total herbaceous (Table 1).

Table 1. Average[1] coverage of herbaceous plant groupings by non-fenced and fenced plots, for before and after canopy treatments.

Canopy Treatment		Grasses Fenced No	Grasses Fenced Yes	Broadleaf Plants Fenced No	Broadleaf Plants Fenced Yes	Vines Fenced No	Vines Fenced Yes	Total Fenced No	Total Fenced Yes
		(%							)
Closed	Before	0	1	16	22	2	4	18	27
	After	1	2	21	27	12	14	34	42
Small	Before	1	2	24	26	5	8	30	36
	After	3	2	26	44	10	14	39	60
Large	Before	4	6	25	22	7	8	36	37
	After	11	7	31	55	23	22	65	84

[1] Based on 27 plots per canopy - fence condition.

As compared to before treatment values, canopy treatment resulted in significant increases in the first growing season coverage values for broadleaf plants, vines and total herbaceous. Overall, large canopy treatment had coverage increases of 19% for broadleaf plants, 15% for vines and 38% for total herbaceous. These increases were significantly greater than the 5 to 10% increases for broadleaf plants and vines in the closed and small canopy treatments. Overall, coverage of broadleaf plants and total herbaceous increases were significantly greater on the fenced plots than on the non-fenced plots. Broadleaf plant coverage increased by 5% on the non-fenced plots and 18% for the fenced plots. The increase in total herbaceous coverage was 18% for non-fenced plots and 29% for fenced plots.

Total herbaceous coverage in the first growing season after treatment was significantly different among the woodlots. Overall, total herbaceous coverage at Bushman Hill (58%) and Powers Hill (64%) were significantly different from the coverage at Herr Ridge (41%). Total herbaceous coverage at Bushman Hill and Powers Hill were not significantly different from each other. Coverage values for all groups of herbaceous vegetation were significantly different among canopy treatments. In all cases and when averaged over woodlots and fencing treatments, closed and small canopy treatment coverage values were not significantly different from each other but they were significantly different from the values for the large canopy treatment. Total herbaceous coverage averaged 38, 49 and 75% for closed, small and large canopy treatments, respectively. Fencing resulted in significantly different coverage values for broadleaf plants and total herbaceous. Unfenced plot coverage averaged 26% for broadleaf plants and 42% for total herbaceous whereas fenced plot coverage averaged 42 and 62%, respectively. Averaged over woodlots, first growing season after treatment coverage values for non-fenced and fenced plots by canopy treatment ranged from 1 to 11% for grasses, 21 to 55% for broadleaf plants, 10 to 23% for vines and 34 to 84% for total herbaceous (Table 1).

Total number of before treatment shrubs and tree species of stems >2 cm DBH was 24 for all woodlots. Individual woodlots ranged from 17 to 24 species. On the individual treatment plots, there was an average of 4.8 species in the before treatment inventories. There was an average of 5.6 shrub seedlings per m^2 and 4.0 tree seedlings per m^2 for the three woodlots (Table 2). ***Rubus*** spp. with 2.3 stems per m^2 and spicebush (*Lindera benzoin* L.) with 1.6 seedlings per m^2 accounted for a majority of the shrub seedlings. Ash dominated the tree species with an average of 2.0 seedlings per m^2. There was an average of 0.9 Oak seedlings per m^2. The seedlings were dominated by stems in the $\leq$ 25 cm height class. Oak, Other Tree and Shrub species groups had 2, 9 and 20%, respectively, of the Total in the >25 cm height classes. There were no significant differences in the number of Oak, Other Tree, Shrub and Total seedlings between the plots assigned to be fenced and those to be unfenced. Overall, average Total seedlings per m^2 were significantly different for Bushman Hill (12.3), Herr Ridge (6.9) and Powers Hill (9.5) (Table 2). The average number of Oak seedlings per m^2 at Bushman Hill of 2.1 was significantly different from the 0.2 and 0.3 per m^2 seedlings at Herr Ridge and Powers Hill, respectively.

Table 2. Average[1] before and after treatment number of seedlings per m^2 for the three woodlots, by species group[2].

Species-Time		Bushman Hill	Herr Ridge	Power Hill	Overall
		(----------------------Number of Stems per Square Meter		--------------------)	
Oak	Before	2.1a	0.2b	0.3b	0.9
	After	2.1a	.2b	.3b	.9
Other Tree	Before	4.4a	1.0b	3.9a	3.1
	After	6.4a	1.2b	6.0a	4.6
Shrub	Before	5.8a	5.6a	5.3a	5.6
	After	6.6a	6.3a	6.9a	6.6
Total	Before	12.3a	6.9c	9.5b	9.6
	After	15.2a	7.8b	13.1a	12.1

[1] Based on 54 plots per woodlot - time of inventory. Woodlot means within species group, by time, with the same letter were not significantly different at the 5% level.

[2] Oak included black, chestnut, northern red, scarlet and white.

Other Tree included American elm, bitternut hickory, black cherry, black gum, black walnut, eastern red cedar, hackberry, mazzard cherry, mockernut hickory, Norway maple, pignut hickory, red maple, shagbark hickory, sugar maple, white ash and yellow-poplar.

Shrub included blackhaw, euonymous, flowering dogwood, grape spp., Japanese barberry, redbud, rose spp., rubus spp., sassafras, serviceberry, spicebush and witch-hazel.

Over all woodlots, there was an increase in the average number of species and seedlings per plot in the first growing season after overstory treatment. There was an after treatment average of 5.4 species per plot, and 6.6 shrub species seedlings and 8.6 tree species seedlings per m^2. For the Shrub group, spicebush and *Rubus* spp. continued to have the most abundant seedlings with 1.8 and 2.6 stems per m^2, respectively. The Other Tree group continued to be dominated by ash which increased to 2.5 stems per m^2 but there was a notable gain with yellow-poplar (*Liriodendron tulipifera* L.). Yellow-poplar increased from 0 seedlings before treatment to 0.9 seedlings per m^2 after treatment. There was no change in the average number of Oak seedlings. There was an increase in the relative number of seedlings in the >25 cm height classes but none of the increases were significantly related to any of the treatments. Oak, Other Tree and Shrub groups had 3, 14 and 34% of the Total seedlings in the >25 cm height classes.

As with before overstory treatment values, woodlot continued to be a significant factor in the number of seedlings present after treatment in the Oak, Other Tree and Total groups. Average woody species seedlings per m^2 of 7.8, 13.1 and 15.2 for Herr Ridge, Powers Hill and Bushman Hill, respectively, were significantly different from each other (Table 2). Average Oak seedlings per m^2 at Bushman Hill (2.1) were significantly different from those at Herr Ridge (0.2) and Powers Hill (0.3). Average Other Tree seedlings per m^2 at Bushman Hill (6.4) and Powers Hill (6.0) were significantly different from those at Herr Ridge (1.2). There were no significant differences in the number of Oak seedlings at Herr Ridge and Powers Hill and the number of Other Tree group seedlings at Bushman Hill and Powers Hill. The only other significant treatment effect was with canopy opening for Other Tree. Average number of Other Tree seedlings per m^2 in the closed canopy (1.8), small canopy (2.7) and large canopy (2.3) treatments were significantly different from each other. This response was mainly due to the number of ash seedlings.

There was an average of 2.1 shrub germinates and 3.7 tree germinates per m^2 in the first growing season after treatment. There were seven shrub species that produced a least one germinate. Redbud (*Cercis canadensis* L.) and grape (*Vitis* spp.) had the most abundant shrub species germinates with 0.2 and 1.7 per m^2, respectively. Overall, 11 tree species produced at least one germinate. Ash and yellow-poplar had the most abundant tree species germinates with an average of 0.6 and 2.9 per m^2, respectively. Number of ash, grape, redbud, yellow-poplar, Total Tree, Total Shrub and Total germinates were significantly affected by woodlot, canopy treatment and litter treatment but not by fencing. Except for ash and yellow-poplar, all of these species groups also had significant canopy x litter interaction effects.

Ash was the most abundant before-treatment tree species in the understory of the woodlots. The number of germinates was greatest for the intact litter condition and for the small canopy opening condition (Table 3). In contrast, yellow-poplar seedlings were not present in the before treatment woodlot conditions. However, as the size of canopy opening increased and particularly when the litter was removed, the number of yellow-poplar germinates increased substantially (Table 3). Number of germinates for redbud and grape were differentially influenced by canopy and litter treatment. Litter retained or removed had little effect on germination when the canopy was closed (Table 3). However when openings were made in the canopy, the number of germinates was greater when the litter was removed.

SUMMARY AND CONCLUSIONS

Canopy opening and fencing to exclude deer treatments have been applied in previously unmanaged, unevenaged mixed oak woodlots at GNMP. Abundance, composition and structure of understory herbaceous and woody vegetation was inventoried before treatment and in the first growing season after treatment. Herbaceous vegetation in the first growing season after treatment was responsive to size of opening in the canopy and fencing. Broadleaf plants and vines were more responsive to treatments than were the grasses. Broadleaf plants and vines also had substantial after treatment increases in coverage with increased canopy removal. In addition, broadleaf plants had greater coverage where white-tailed deer were excluded.

Richness of shrub and tree species in the before and after treatment inventories indicated that the conditions were favorable for establishing natural regeneration. In addition, canopy opening and litter conditions could be adjusted to

Table 3. Average[1] number of germinates in the first growing season after treatment for ash, yellow-poplar, grape, redbud, all tree, all shrub and total, by canopy opening and litter treatment.

	Closed Canopy Litter Removed		Small Canopy Litter Removed		Large Canopy Litter Removed	
Species	No	Yes	No	Yes	No	Yes
	(------------------Number of Germinates per Square Meter--------------------)					
Ash	0.4	0.3	1.3	0.8	0.7	0.3
Yellow-poplar	.3	.3	1.5	5.0	3.2	7.2
Grape	.1	.4	.4	4.4	.8	3.8
Redbud	.1	.0	.2	.4	.1	.6
Total Tree	.8	.6	3.1	5.8	4.1	7.6
Total Shrub	.6	.4	.9	5.0	1.1	4.6
Total	1.4	1.0	3.9	10.8	5.3	12.2

[1] Based on 18 plots per canopy - litter condition.

influence the abundance and species mixture of new germinates from natural seed sources. However, the initial size and apparent height growth of the seedlings were of major concern. There was some increase in the relative number of seedlings >25 cm tall in the first growing season after treatment but the increase was small even where the seedlings were protected from white-tailed deer. Before treatment overstory interference on the seedlings' opportunity to grow, and frequent foraging by white-tailed deer may have resulted in seedlings with low energy reserves and poor vigor. The slow height growth of the tree seedlings combined with the rapid response in coverage by the herbaceous vegetation raises a concern about the potential application of large canopy openings to regenerate these woodlots.

Abundance, composition and structure of herbaceous vegetation, shrub and tree seedlings in the second growing season after treatment have been inventoried in 1994. Additional germinates in the second growing season have been recorded. These data and additional data to be collected in the fourth growing season after treatment (1996) will be used to develop management recommendations for the unevenaged mixed oak woodlots at GNMP.

LITERATURE CITED

Bowersox, T. W., G. L. Storm and W. M. Tzilkowski. 1993. Developing regeneration in woodlots at Gettysburg National Military Park. In 9th Central Hardwood Conference. USDA Forest Service General Technical Report NC-161. pp. 409-417.

Fairweather, S. E. and C. M. Cavanaugh. 1990. Identification, restoration, and maintenance of historic woodlots at Gettysburg National Military Park. U. S. Department of Interior, National Park Service, Technical Report NPS/MAR/NRTR - 90/049, Philadelphia, PA. 123 p.

Lull, H. W. 1968. A forest atlas of the northeast. U. S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 46 p.

Roach, B. A. and S. F. Gingrich. 1968. Evenaged silviculture for upland central hardwoods. U. S. Department of Agriculture, Forest Service Handbook 335. 39 p.

Storm, G. L., R. H. Yahner, D. F. Cottam, and G. M. Vecello. 1989. Population status, movements, habitat use, and impact of white-tailed deer at Gettysburg National Historic Site, Pennsylvania. U. S. Department of Interior, National Park Service, Technical Report NPS/MAR/NRTR - 89/043, Philadelphia, PA. 513 p.

Storm, G. L. and W. M. Tzilkowski. 1992. Plant community development in historic woodlots in Gettysburg National Military Park. U. S. Department of Interior, National Park Service and Penn State University Cooperative Agreement 4000-9-8004. 5 p.

Storm, G. L., W. M. Tzilkowski, T. W. Bowersox , S. E. Fairweather and R. Loughlin. 1994. Plant community development in historic woodlots at Gettysburg National Military Park. U. S. Department of Interior, National Park Service, Technical Report Philadelphia, PA. In press.

Tzilkowski, W. M., S. E. Fairweather, G. L. Storm and T. W. Bowersox. 1993. Forest regeneration and white-tailed deer at Gettysburg National Military Park. In Proceedings of 7th Conference on Research and Resource Management in Parks and on Public Lands, Hancock, MI. pp. 86-95.

HISTORY OF DEER POPULATION TRENDS AND FOREST CUTTING ON THE ALLEGHENY NATIONAL FOREST

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Abstract: The forests of the Allegheny Plateau section of northwestern Pennsylvania have been severely impacted for more than 70 years by selective browsing by white-tailed deer (*Odocoileus virginianus*). Historical and ecological interactions of deer and the forest ecosystem in this region from pre-settlement times to the present are presented based on data from the Allegheny National Forest area. The data suggest that deer impacts on forested ecosystems can be controlled through a combination of increased, sustained deer harvests and increased forage production through timber harvesting.

INTRODUCTION

As the second-growth forests on the Allegheny Plateau began to mature in the mid-1960's, foresters attempted to regenerate new stands by clearcutting, anticipating that species composition of the new stands would be similar to the second-growth forest that originated near the turn of the century. However, these harvest cuts resulted in a complete failure of woody species to regenerate or in understocked stands that lacked the hardwood species diversity of the second-growth forest.

Concern about the inability to obtain regeneration success led to the establishment of a regeneration research project conducted at the Northeastern Forest Experiment Station's Forestry Sciences Laboratory at Warren, Pennsylvania. Grisez and Peace (1973) showed that nearly half of all regeneration cuts in the 1960's failed to regenerate to woody species. The half that did regenerate successfully had well-established advance regeneration prior to cutting. Deer browsing was suspected as a primary cause of most regeneration failures. A series of deer exclosure studies was installed to test this hypothesis. Exclosures placed in recently failed clearcuts demonstrated that in 87 percent of the stands sampled, regeneration was satisfactory inside the fences but not outside (Marquis and Brenneman 1981). This finding supported the hypothesis that deer browsing was a direct factor in causing regeneration failures in the 1960's. But there were other indirect effects of deer browsing and other ecological factors that changed the entire dynamics of the regeneration process.

Four major components of the ecosystem had changed dramatically since the turn of the century, leading to the complex situation for regeneration that exists today. First, deer were nearly extinct in Pennsylvania at the turn of the century but at record levels in the 1960's (Horsley 1992). Second, species composition of the overstory and understory was different in second-growth forests than in the original forest. Much of the original forest contained overstories of large white pine (*Pinus strobus*), hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and chestnut (*Castanea dentata*), and small quantities of black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), oaks (*Quercus* spp.), and red maple (*Acer rubrum*) (Marquis 1975; Whitney 1990). The understories in the original forest contained many well-established advanced seedlings which were absent in the 1960's (Marquis 1973). The second-growth forest contained higher proportions of shade-intolerant species such as black cherry, white ash, and yellow-poplar (*Liriodendron tulipifera*) in the main crown canopy, with very shade-tolerant species such as American beech and sugar maple relegated to the lower canopy unless left as residual trees from the original forest (Marquis 1981). Species of intermediate tolerance such as red maple, basswood (*Tilia americana*), and cucumber (*Magnolia acuminata*) were in a third layer just below the main crown level.

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Third, the second-growth forest contained a species-altered and less diverse understory of shrubs and herbaceous plants because of decades of preferential browsing by an exceptionally large deer herd (Leopold 1943; Whitney 1984). Many of the shrub species that were abundant in the original forest, for example, greenbrier (*Smilax rotundifolia*), hobblebush (*Viburnum alnifolium*), wild raisin (*Viburnum cassinoides*), and other viburnums, were nearly lacking from the second-growth forest (Leopold 1943; Whitney 1984). Instead, the understory is dominated by species such as striped maple (*Acer pennsylvanicum*), root suckers of American beech, or by fern and grass. Fourth, seedbed conditions in the 1960's were different due to long periods without fire, years of heavy browsing, and a lack of dead and down course woody debris that had been present at the turn of the century (Mladenoff and Sterns 1993).

A look at long-term trends in deer densities and forage production suggests a strong relationship between the two (Whitney 1990; Marquis 1975). In this paper I have made the assumption that timber harvest can be used as a surrogate for forage production. This assumption is made with the knowledge that not all silvicultural treatments create the same quantity and quality of forage, and that forage production can vary within treatments. With these assumptions in mind, I present an historical overview of events from pre-settlement times to the present that shows how deer populations and forage availability have combined to create a deer impact on all forest communities on the Allegheny Plateau in Northwestern Pennsylvania.

Actual data for estimates of the deer population taken in Warren, Forest, McKean, and Elk Counties, that encompass the Allegheny National Forest, are presented. These data were used rather than statewide averages because actual timber harvesting figures are available for the Allegheny since 1923. Comparing deer population and forage production levels reveal some important relationships that are not apparent when looking at the two separately.

The 4-county area encompassing the Allegheny National Forest is a part of the larger Allegheny Plateau region. Elevations on the Plateau range from about 1,500 to 2,500 feet (Hough 1959). The climate is generally cool and moist with precipitation well distributed throughout the summer months (Whitney 1990). Nearly all of the soils in the area are podzols derived from acid sandstone and shale. The forests of the area are primarily second-growth cherry-maple mixed hardwood forests and are listed as SAF type 28 (Marquis 1975).

Human influence on ecological processes in the Allegheny region has been divided into 6 distinct periods[2]. I add a 7th period to reflect changes in forest management from 1980 to the present. Each period is discussed separately and summarized to show trends.

ECOLOGICAL PERIODS INFLUENCED BY HUMAN ACTIVITY

Pre-settlement Period: Pre-1800

Native Americans occupied northwestern Pennsylvania for many centuries prior to the arrival of the European settlers. The Allegheny River, Clarion River, and Conewango Creek served as major travelways and the rich river valleys provided sites for major Indian villages.

Vegetation conditions. Pre-settlement forests were a mosaic of forest stands in various stages of successional development. The largest share of the forest was mature or overmature hemlock-beech and beech-sugar maple (Illick 1923; Marquis 1975). There were scattered meadows and rough mountaintops void of forest cover but also vast stretches of unbroken timber (Whitney 1990). Areas of early successional ecosystems were created by natural disturbances such as hurricanes and tornadoes. A large area of blowdown was reported in what is now Alleghany State Park, just north of the present Allegheny National Forest, by a surveyor for the Holland Land Company in June 1805 (Gordon 1940). Understory conditions probably were variable due to human activity and periodic windstorms.

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[2]Bennett, A. 1969. History of Allegheny Plateau Forest. Unpublished talk at Regeneration Conference on Allegheny Plateau Hardwoods, Bradford, PA.

Native Americans periodically burned forest understories near their villages to increase berry production and enhance hunting opportunities (Marquis 1973; McCabe and McCabe 1984). Shrub species such as the viburnums likely were present during pre-settlement times as they were noted in early surveys of the area in the late 1700's.

Forage availability. The amount and quality of forage used by white-tailed deer were highly variable, spatially and temporally, due to periodicity of windstorms and the abandonment of Indian villages as resources were depleted (Marquis 1973). Agricultural crops grown in or near these villages provided quality forage as did early successional ecosystems, for example, areas burned by Native Americans and those created by tornadoes.

Predation. Predators of deer included wolves (*Canis lupus*), mountain lions (*Felis concolor*), bobcats (*Felis rufus*), and bears (*Ursus americanus*). It is believed that these predators accounted for half of the annual deer mortality (McCabe and McCabe 1984). The remaining mortality was caused by hunting by Native Americans, disease, starvation and weather events.

Weather. Due to cyclic patterns of weather and the length of the pre-settlement period, the entire range of weather conditions was experienced.

Deer densities. Estimates cited from the literature of deer densities during pre-settlement times are for the entire range of white-tailed deer, which extends beyond northwestern Pennsylvania. Findings from numerous archeological middens show that deer were an important source of protein in the diets of Native Americans (McCabe and McCabe 1984). Using population models developed by Severinghaus and Maguire, estimates of deer densities were made using sex ratios and age-class structures of the population harvested by Native Americans (Severinghaus and Maguire 1955). These estimates in the range of 20 deer/square mile for the region, agrees with those of Seton based on suitable habitat within the range of eastern white-tailed deer(Seton 1909).

It is likely that deer populations in the 4-county area of this report differed from place to place and year to year. Populations likely were higher near Native American villages where agricultural crops were available and firewood cuttings and burned areas produced browse. Also, populations probably were higher in and around areas of early successional forest created by periodic weather events. Most of the four-county area was inaccessible and heavily forested resulting in low deer browse production during this period so the best estimate of average deer density is 10 to 15 per square mile.

Pioneer Period: 1800-1860

The first record of Europeans in northwestern Pennsylvania was an English trading post established in 1750 at Buckaloons along the Allegheny River near Warren, Pennsylvania[3]. The first permanent European settlers traveled from Susquehanna County to Warren County in 1795. Settlement of the area progressed slowly at first but then increased rapidly in the latter part of the 19th century. Warren County, for example, had a population of only 26 in 1810 (Marquis 1973). The last half of this period saw rapid growth in human populations.

Vegetation conditions. Overall, vegetation changed little from pre-settlement times. The impact of humans on vegetation was restricted to the major drainages as most of the Plateau remained much as it was for centuries prior to settlement. A slight increase in agricultural land and timber harvesting resulted in modest increases in early successional vegetation along the drainages.

Forage availability. During the first 20 years of this period, little timber cutting took place. The few European settlers there were cut small quantities of wood for cabins, barns, and firewood, and cleared land for gardens. Forage availability during this time likely was similar to that of pre-settlement times.

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[3]Stotz, L. 1973. A country supposed uninhabitable, Senecas and Settlers on the Allegheny National Forest. In: Allegheny Nat. For. Spec. 50th Anniversary Pub. Article #3. Schuler, N. (ed.)

After 1820, water-powered mills were common and there was some commercial timber cutting along the major drainages where logs could be floated easily to the mill. During the last half of this period, forage production increased as timber cutting accelerated to meet the demands of an expanding population.

Predation. There was a gradual, continuing decline of major deer predators during this period, culminating in the near extirpation of some natural species toward the latter portion. Predators such as the gray wolf, wolverine, mountain lion, and lynx were not extirpated, but their numbers declined steadily as human populations increased (Merritt 1987). Deer populations also were reduced by Native Americans and European settlers.

Weather. The only major documented event was a large tornado that occurred in what is now the Tionesta Scenic and Research Natural Area in 1808 (Bjorkbom and Larson 1977). Winters likely were much as they are today.

Deer Density. During the first 20 years of this period, deer densities likely were similar to those of pre-settlement times as human populations increased little and timber harvesting remained about the same and were restricted to lands along the major drainages. As the period progressed, human populations and timber harvesting increased while natural predators decreased, resulting in a probable increase in deer populations. Speculative estimates of deer densities for this period are 10 to 15 per square mile early in the period and 25 to 35 per square mile toward the end of the period.

Steampower Period: 1860-1890

The 1860's saw the beginning of industrialization of the Allegheny Plateau. Steam replaced water as the major source of power. Steam-powered sawmills, railroads, log loaders, and other logging equipment became common during this period (Marquis 1975). This equipment was capable of processing huge quantities of timber. Tanneries were common during this time and used large quantities of hemlock bark for tannin.

Vegetation conditions. Major changes in vegetation began to take place. White pine was the major species being harvested by 1875,and was almost gone by 1892. Pine and hemlock were replaced with shade-intolerant, early successional hardwood species. Once the pine was depleted, hemlock became the major species harvested, for its bark for the tanning industry and for sawlogs cut into construction lumber. Most of the pine and hemlock harvests was small patchy cuts that were heaviest along the major drainages. Most of the forest remained intact.

Forage availability. Forage production resulting from the harvest cuts along the major drainages increased greatly. Encroachment by white settlers increased with better access to the region afforded by railroads, and more land was cleared for agriculture. But forage on the plateau top remained essentially unchanged.

Predation. By the end of this period, all of the major natural predators were extirpated. Wolverines, mountain lions, and lynx were gone by the late 1800's (Merritt 1987), and the last gray wolf was reported in 1892 in Clearfield County, southeast of the Allegheny region (Merritt 1987). Humans continued to play a large role in the annual mortality as there were no laws to protect deer..

Weather. There are no detailed records for this period. A large tornado was recorded in 1870 in the Tionesta Scenic and Research Natural Area (Bjorkbom and Larson 1977).

Deer Density. Although forage was increasing, especially near the major drainages, so too was human harvest of the deer herd as year-round hunting prevented the herd from becoming excessive. Knowing what we know about forage availability and the effects of hunting, I estimate the deer population was 20 to 25 deer/square mile during this period.

Chemical Wood Clearcutting Period: 1890-1930

Until this time, steam locomotives were used primarily for transportation. During this period specially designed narrow gauge locomotives were developed to traverse the most rugged terrain, and were located in nearly every drainage making nearly all of the Plateau accessible. Chemical wood plants utilized wood of all species, quality, and size to produce charcoal, acetic acid, wood alcohol, and other distillation products (Marquis 1975). The combination of markets utilizing trees of all species and quality, and the heightened access afforded by logging railroads resulted in an extremely high degree of utilization of the wood resource. Most of the area was clearcut down to stems 1 or 2 inches in diameter, resulting in a species conversion from true northern hardwoods to the second-growth cherry-maple forests that cover the area today. Along major drainages, stands of pine, chestnut, and oak, were converted to chestnut-oak-red maple.

Vegetation conditions. Nearly the entire area was in early successional stage vegetation consisting of a mixture of species of various tolerance to shade. Many shrub species such as hobblebush were abundant. By the late 1920's, about half of the cut areas had grown into sapling or small poletimber trees.

Forage availability. Vast quantities of forage were available to deer throughout this period. The midpoint of the period provided the most forage. By the late 1920's, many stands were growing out of the reach of deer.

Predation. All natural predators were absent during this period. From 1890 to 1900, deer were hunted for venison and hides and to supply meat for logging camps. By 1900, deer were all but extirpated from the entire state. The Pennsylvania Game Commission was established in 1896 primarily to establish laws to protect what few deer remained (Winecoff 1930). Salt licks and the use of dogs for hunting deer were prohibited after 1898. The first game refuge, known as State Gamelands today, was established in 1905. A "bucks only" law was enacted in 1907 and remained in effect for the next 16 years. A hunting license law was enacted in 1913 to raise money to restock deer from other states. During the period, 700 deer were purchased and restocked in Pennsylvania.

Weather. No unusual or extreme weather events are recorded for this period.

Deer density. Deer densities went from near extinction at the turn of the century to near record highs at the end of this period. Laws to protect deer, a lack of natural predators, and vast forage production resulting from chemical wood cuts led to an irruption of the deer population. Densities increased from nearly zero to more than 40 deer/square mile by the end of this period.

Figure 1 shows the pattern of timber harvest and deer density on the Allegheny National Forest from 1900 to 1992. Forage production was greatest during the chemical wood harvest and sawtimber-modern eras. Circles mark actual data points listed in Table 1, and are connected by arbitrary straight lines. Timber harvest data are actual annual figures for the Allegheny National Forest for 1941-92. The crashes in deer densities in the early 1940's and again in the late 1970's occurred after successive severe winters and a sharp decrease in forage production (timber cut).

Second-Growth Poletimber Period: 1930-1950

By the early 1930's, trees on the chemical wood clearcuts had grown into the large sapling-small pole size classes. Much of the land in the 4-county area was under protection and management by the USDA Forest Service. Although the Allegheny National Forest was established in 1923, little management other than fire protection took place until the 1950's.

Vegetation conditions. Much of the shrub layer of vegetation began to decline in number during the early part of this period and many species were absent by 1950. Fern, grass, striped maple seedlings, and small root suckers of American beech made up a large portion of the understory toward the end of this period. The overstory consisted of dense sapling and poletimber stands composed of shade-intolerant species such as black cherry, yellow-poplar, and white ash, with red maple poles growing in the intermediate canopy. Sugar maple and American beech saplings were found beneath the main canopy. By 1942, nearly all of the hemlock advance regeneration had been eliminated from the Tionesta Natural Area by deer browsing (Hough 1965). Most of the hemlock in the second-growth forest was left as residual trees from the original forest. Stems of sugar maple and American beech in the same crown layer as the shade intolerants also were residuals from the original forest and represented an older age class.

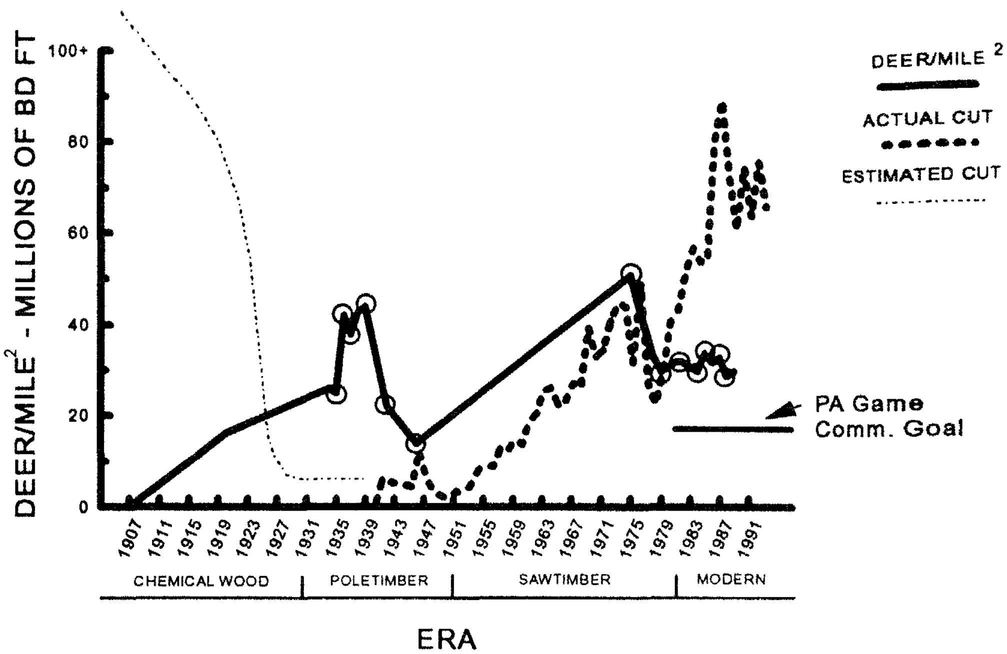

Figure 1. Deer population and timber cutting trends on the Allegheny National Forest.

Table 1. Data sources reported in Figure 1.

Source	Date	Deer/square mile
McCain	1935	23
McCain	1936	27
McCain	1937	34
McCain	1938	23
Hough	1936	29
Hough	1938	42
Hough	1946	14
Jordan	1974	15[a]
Jordan	1975	43
Jordan	1976	35
Jordan	1977	29
PA Game Comm.	1980 - 1992	30
deCalesta	1992	31

[a] Jordan's 1974 estimate was reduced by 30 percent due to consistent error found in the sampling technique used.

Forage availability. Due to the young age class of most of the forest, there was little timber cutting during this period (Fig. 1). Some selection cutting removed sawtimber left during the chemical wood cuts and some stands were thinned for pulpwood in the late 1940's. Little browse or mast was being produced during the period.

Predation. The natural predators that became extinct before the turn of the century remained absent during this period. Doe seasons were introduced periodically to reduce the deer herd which had irrupted before this time and remained high. Concerns for orchards and agricultural crops led to public pressure to control the deer population. The first concern in the forestry community was for plantation failures presumably caused by heavy deer browsing. The deer herd had become so large that hunting mortality no longer kept pace with recruitment.

Weather. Weather in the form of severe winters coupled with declining forage availability caused massive starvation of deer in the late 1930's and early 1940's (Fig. 1).

Deer density. This period witnessed the first attempts to quantify deer density. Deer drives were conducted using Civilian Conservation Corps crews; actual counts of deer on known areas were made in four consecutive years. In total, 8,124 acres of the Allegheny National Forest were driven, resulting in estimates of deer density for 1935 through 1938 of 23, 27, 34, and 23 per square mile, respectively (McCain 1939).

Estimates of carrying capacity during the mid-1930's indicated that the forest could support no more than 18 deer/square mile, and that many areas of the forest were overstocked by as much as 220 percent (Clepper 1931). As a result of too many deer, forage growing out of their reach, and successive severe winters in the late 1930's and early 1940's, mass starvation reduced population levels to a 20th century low (Fig 1). In one drainage alone, more than 200 deer were found starved to death[4].

Second-growth Sawtimber Period: 1950-1980

By 1950, some of the stands that regenerated around the turn of the century, though not yet mature, were yielding sawlog-size black cherry, white ash, and yellow-poplar. The timber industry, which had left the area during the 1930's, was small in 1950 but beginning to grow. Stands were managed using the single-tree selection system until 1960. A change to even-age systems of management was initiated in 1960; clearcuts were not to exceed 1 percent per year of all operable timber stands, and no single cut was to exceed 50 acres[5].

A new deer management era in Pennsylvania was initiated during the 1950's. Deer and habitat management were placed on a scientific basis, and food plots were established on the Allegheny National Forest by the Pennsylvania Game Commission under cooperative agreement. Sex ratios and age structure of the harvested deer were used to assess the condition of the herd and antlerless seasons became an annual occurrence.

Vegetation conditions. By the early 1950's, many of the second-growth stands that regenerated from cuttings between 1890 and 1910 had grown to sawtimber size. Individual trees were selectively harvested for sawtimber. Gaps created by these single-tree selection cuts generally were filled by beech, striped maple, or ferns. Understories remained fairly sparse throughout the forest. With a switch to even-age management in 1960, some stands regenerated to early successional stages of woody vegetation consisting primarily of black cherry and red maple. About half of these regeneration cuts regenerated to savannah stands of herbaceous cover along with isolated black cherry and red maple trees (Marquis 1973).

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[4]Curnutt, W.C. 1973. More than 1000 acres a year, the "new look" in reforestation on Allegheny National Forest. In: National Forest Special 50th Anniversary Pub. Warren, PA. Schuler, N. (ed.). Article #8

[5]Stotz, L. 1973. Crosscut'n doublebit, timber sales and timber utilization on the Allegheny National Forest. In: National Forest Special 50th Anniversary Pub. Warren, PA. Schuler, N. (ed.). Article #7

Forage availability. As a result of a steady increase in timber harvesting, forage production increased throughout the period as a whole (Fig. 1). An exception occurred during the early 1970's when there was a drop in timber harvesting due to a lack of stands with adequate advanced regeneration. Techniques for establishing adequate advanced seedlings were being developed at the Forestry Sciences Laboratory at Warren and not yet available. The sharp increase in harvest from 1976 through 1980 initially was the result of a large tornado salvage in 1976-78. By 1980, the use of guidelines for establishing advance reproduction using an herbicide-shelterwood technique made more stands eligible for final harvest. Both the quantity and quality of forage produced by regeneration and intermediate cuts was much less than that produced by cuttings at the turn of the century. Forage produced during this period tended to be of a single species such as black cherry or fern, both of which are low in nutrition and in preference by deer. Species of higher nutritional quality such as sugar maple, white ash, and yellow-poplar were preferentially browsed and eliminated or greatly reduced in abundance by white-tailed deer.

Predation. Hunting and highway accidents involving deer were the major causes of mortality during this period.

Weather. Severe winter weather played a major role in reducing deer numbers during this period. The winters of 1976 and 1977 were long and cold and characterized by heavy snowfall. A series of tornadoes occurred on the Allegheny National Forest during the summer of 1976.

Deer density. From 1950 through 1976, deer populations increased steadily as forage availability increased due to increased final harvest cuts (Fig 1.). In the mid-1970's pre-fawn estimates were made on 2154 acres of the Allegheny National Forest during 1974 through 1977 (Jordan 1977). These estimates, made using the belt-transect pellet-group method, were 50, 43, 35, and 29 deer/square mile, respectively. Three additional National Forest areas totaling 48 square miles that were sampled in 1974 had population estimates of 28, 35, and 41 deer/square mile (Jordan 1977). The deer population declined drastically during the late 1970's due to 2 consecutive severe winters and a sharp decrease in the annual cut on the Forest (Fig. 1).

Modern Period: 1980-Present

In response to an increasing deer herd the Pennsylvania Game Commission adopted a system of issuing doe permits in 1979 that was based on the overwinter carrying capacity of each county. Carrying capacity was determined by a formula involving amount of woodland in the seedling-sapling, poletimber, and sawtimber stage. This resulted in an increase in antlerless permits. A saturation point of 500,000 to 550,000 antlerless licenses annually was not enough to reduce populations to a goal of 18 deer/square mile on the Forest (Pa. Game Comm. 1991). To increase harvests, a bonus deer program was initiated in 1988 to allow hunters to harvest more that one deer. During this period, the Allegheny National Forest was increasing its annual timber harvest substantially due to the maturing of the forest. Annual cuts in the 1980's and early 1990's were more than double those of the 1970's.

Studies by Forest Service scientists at Warren showed that deer also could influence other portions of the ecosystem--songbirds, wildflowers, and other herbaceous plants (deCalesta 1992). Public awareness of the impact of deer on the entire ecosystem has been heightened as a result of these studies.

Vegetation conditions. Salvage from the 1985 tornadoes coincided with increased harvest levels when the Allegheny National Forest Land and Resource Management Plan was implemented in 1986 (USDA For. Serv. 1986). This increased the proportion of the land area in early successional stages, usually in communities dominated by one or several tree species. Partial cutting also increased and was supplemented by a series of insect and disease infestations, including invasion by the gypsy moth (*Porthetria dispar*), elm spanworm (*Ennomos subsignarius*), pear thrips (*Taeniothrips inconsequens*), beech bark disease complex, and a sugar maple decline complex. In understories exposed to increased light as a result of these forces, fern, grass, striped maple, and root suckers of beech often increased in dominance. Toward the end of the period there was increasing anecdotal evidence of increases in the regeneration of birch and of the limited recovery of at least one shrub species (hobblebush).

Forage availability. Although the quantity of forage has increased since the 1970's, quality has remained about the same. Regeneration cuts are restricted to stands with adequate advanced regeneration, generally black cherry. As a result, harvest cuts tend to regenerate to pure black cherry stands. In areas where there are insufficient advance seedlings, the understories generally are occupied by species not preferred by deer, for example fern, grass, striped maple, and beech. Forage availability increased substantially following a number of large tornadoes that struck the region in May 1985.

Predation. As mentioned previously, the Pennsylvania Game Commission attempted to reduce deer populations through increased antlerless license allocation and bonus tags. Road kills continue to be a major source of mortality in the state. In 1992, more deer were killed by motor vehicles on Pennsylvania highways (43,000) than were harvested through hunting in Vermont, Massachusetts Connecticut, and Rhode Island combined (38,520) (David S. deCalesta, pers. commun., 1994).

Weather. Winters during the early 1980's were more severe than normal; these were followed by 8 winters that were much milder and more snow free than normal. The winter of 1994 was the most severe snowfall for the period. As mentioned, tornadoes swept the region in 1985.

Deer density. Deer densities for the Allegheny plateau have remained fairly constant throughout the period. Estimates by the Pennsylvania Game Commission for the 4-county area remained at about 30 deer/square mile for the entire period (Palmer,Wm. Pa. Game Comm. pers.commun.1994). In 1992, data from 11 sites on the Allegheny National Forest obtained by the transect/pellet method showed a range across the forest of 19 to 49 deer/square mile, averaging 29 deer/square mile, which agrees with the Pennsylvania Game Commission's 1990 estimate (Pers. Comm. D.deCalesta 1994).

CONCLUSION

Human activity in northwestern Pennsylvania has shaped and influenced factors that affect species composition, age, and structure of plant communities from pre-settlement time to the present. Pre-settlement forests were characterized by vast expanses of unbroken mature forests intermixed with early successional stages created by natural disturbances such as tornados, hurricanes, and natural fires, and by Native Americans who cleared land for villages and agriculture, and burned the woods repeatedly for berry production and to facilitate hunting and travel.

Since the arrival of European settlers in the region around 1800, man, has manipulated the forests of northwestern Pennsylvania changing their character at an accelerated pace. In particular, human activity has altered the conditions under which forests of the region regenerate. Timber harvesting has increased forage availability for deer which, in turn, have increased from near extinction at the turn of the century to record levels during the mid-1970's (Fig. 1). Laws to protect deer, seasons and bag limits, and a lack of natural predators also have contributed to the overpopulation of deer. With deer densities well above ecological carrying capacity for more than 70 years, all forest communities have been affected as animal-plant, and plant-plant interactions have been influenced. The result is a less diverse ecosystem.

Through the first 6 historical periods reviewed in this paper, there was a tight link between forage availability, as represented by timber harvesting and deer density. The experience of the modern period suggests that this link is not unbreakable. Although current deer densities are well above goal levels, the herd has been stabilized at about 30 deer/square mile throughout the modern period due to Pennsylvania Game Commission's program of antlerless deer harvest and despite a dramatic increase in forage availability.

The experience of the modern period also allows us to focus on the challenge of managing deer and forested ecosystems on a landscape scale. We can anticipate cyclic fluctuations in forage availability as forest and ecosystem managers attempt to achieve a balance in age classes. At the same time, both the number of hunters have declined steadily since peaking in 1982 and the number of new hunters as reflected by the number of people taking huntertraining has also experienced a steady drop in numbers (deCalesta and Whitmer 1992). Careful coordination of management of both forage and deer density will be required if the region's forests are to recover from decades of overbrowsing during this century. The best short-term solution is to maintain high forage production through sustainable harvest levels while increasing hunting pressure to reduce density to 18 deer/square mile in the Allegheny region.

LITERATURE CITED

Bjorkbom, J.C.; Larson, R.G. 1977. The Tionesta Scenic and Research Natural Areas. Gen. Tech. Rep. NE-31. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 24p.

Gordon, R.B. 1940. The primeval forest types of southwestern New York. Bull No. 321. New York State Museum. 102 p.

Grisez, T.J.; Peace, M.R. 1973. Requirements for advance reproduction in Allegheny hardwoods--an interim guide. Res. Note NE-180. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 5 p.

Horsley, S.B. 1992. Historical and contemporary herbivore by deer in a temperate forest ecosystem: the Allegheny hardwood forest. Bulletin of the Ecological Society of America. 73(2):212

Hough, A.F.. 1959. Zoning for the management of black cherry on the Allegheny Plateau. Journal of Forestry. 57:353-357.

Illick, Joseph S. 1923. The forest situation in Pennsylvania. Bull. 30. Harrisburg, PA: Pennsylvania Bureau of Forestry. 14 p.

Jordan, James S. 1977. Deer populations on the Allegheny National Forest, 1974-1977. In: A seminar on the problem of deer and forest regeneration. Ridgway, PA: Society of American Foresters, Plateau and Hardwood Chapter: 40 .

Leopold, A. 1943. Deer irruptions. Wisconsin Conservation Bulletin. 8(8):3-11.

McCabe, R.E.; McCabe, T.R. 1984. Of slings and arrows: an historical retrospection. In: Halls, L.K., ed. White-tailed deer: ecology and management. Harrisburg, PA: Stackpole Books. pp 19-72.

Merritt, J.F. 1987. Guide to the mammals of Pennsylvania. Pittsburgh, PA: University of Pittsburgh. 408 p.

Mladenoff, D.J.; Sterns, F. 1993. Eastern hemlock regeneration and deer browsing in the northern great lakes region: a re-examination and model simulation. Conservation Biology. 7:889-900.

Marquis, D.A. 1973. Pennsylvania's Allegheny hardwood forests. Pennsylvania Forests. 63(430):88,89, 108-112.

Marquis, D.A. 1975. The Allegheny Hardwood Forest. Gen. Tech. Rep. NE-15. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 32 p.

Marquis, D.A. 1981. Effect of deer browsing on timber production in Allegheny hardwood forests of northwestern Pennsylvania. Res. Pap. NE-475. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 10 p.

Marquis, D.A.; Brenneman, R. 1981. The impact of deer on forest vegetation in Pennsylvania. Gen. Tech. Rep. NE-65. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, 7 p.

McCain, R. 1939. The development and use of game drives for determining whitetail deer populations on Allegheny National Forest. In: Proceedings of the North American wildlife conference: 221-230.

Pennsylvania Game Commission, 1991. Pennsylvania deer management, Harrisburg, PA: PennsylvaniaGame Commission. 4 p.

Seton, E.T. 1909. Life histories of northern mammals. Vol. I. New York: Chas. Scribner's Sons. 673 pp.

Severinghaus, C.W. and H.F. Maguire. 1955. Use of age compositiondata for determining sex ratios among adult deer. N.Y. Fish and Game J. 2(2):242-246.

U.S. Department of Agriculture, Forest Service. 1986. The Allegheny National Forest land and resource management plan. [Place of publication unknown]: U.S. Department of Agriculture, Forest Service, Eastern Region.

Whitmer,G.W; deCalesta, D.S. 1992. The need and difficulty of bringing the Pennsylvania deer herd under control. Proceedings of the eastern wildlife damage control conference. 5:130-137.

Whitney, G.G. 1984. Fifty years of change in the arboreal vegetation of Heart's Content, an old-growth hemlock-white pine-northern hardwood stand. Ecology. 65:403-408.

Whitney, G.G. 1990. The history and status of the hemlock-hardwood forests of the Allegheny plateau. Journal of Ecology.78:443-450.

Winecoff, T.E. 1930. The Pennsylvania deer problem. Bull. 12. Harrisburg, PA: Pennsylvania Game Commission. 66 p.

EFFECTS OF TWO-AGE MANAGEMENT AND CLEARCUTTING ON SONGBIRD DENSITY

AND REPRODUCTIVE SUCCESS

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Abstract: We examined density and reproductive success of passerine species on 7 uncut forest stands and on 12 stands harvested 10-14 years ago on the Monongahela National Forest of West Virginia (6 clearcut stands and 6 stands harvested using 2-age management). In 2-age management, stands resemble a shelterwood cut with 10-30 overstory trees/acre left uncut. Uncut periphery areas adjacent to treatments were used to examine edge effects. All stands and periphery areas were censused 5 times, May-July 1993 and 1994, with the variable-circular plot technique and were thoroughly searched for nests. Two-age treatment stands had higher densities (650 birds/40 ha) than all other treatment and periphery stands ($F = 19.08$, $\underline{P} = 0.0001$). Clearcut treatment stands averaged 522 birds/40 ha, no-harvest (341 birds/40 ha). Uncut periphery stands of two-age and clearcut treatments did not differ significantly from no-harvest stands. Intensive nest searching of all plots and periphery areas yielded complete nest histories of 90 nests representing 23 species. Nest success, calculated using the Mayfield method, was as follows: two-age treatment stands 49.8%, two-age periphery 61.2%, clearcut treatment 53.9%, clearcut periphery 48.2%, and no-harvest stands 59.6%.

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