

Distinguishing the Effects of Environmental Stress and Forest Succession on Changes in the Forest Floor

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ABSTRACT: When interpreting change over time in forest ecosystems, distinguishing the effects of forest succession from the effects of environmental stress can be difficult. The result may be a simplistic interpretation, citing a specific successional or environmental cause of forest change when both types may be occurring. We present two case studies of changes in the forest floor in northern hardwoods. First, the belief that 50% of soil organic matter is lost in the first 20 years after logging was based on a study comparing northern hardwood stands of different ages. We resampled a series of 13 such stands after an interval of 15 years, and found that the young stands were not, in fact, losing organic matter as rapidly as predicted from the original chronosequence study. The pattern of higher organic matter content in the forest floors of older stands compared to young stands could be equally well explained by changes in logging practices over the last century as by the aging of the stand. The observed pattern of forest floor organic matter as a function of stand age was previously interpreted as a successional pattern, ignoring changes in treatment history. In the second case study, observed losses of base cations from the forest floor were attributed to cation depletion caused by acid rain and declining calcium deposition. We found that young stands were gaining base cations in the forest floor; losses of base cations were restricted to older stands. Differences in litter chemistry in stands of different ages may explain some of the pattern in cation gains and losses. In this case, the contribution of successional processes to cation loss had been overlooked in favor of environmental stress as the dominant mechanism behind the observed changes. Studies of environmental stress use repeated measures over time, but often don't consider stand age as a factor. Studies of successional change often assume that environmental factors remain constant. We were able to consider both forest succession and external factors because we repeatedly sampled stands of different ages.

Key Words: Calcium, Cation depletion, Chronosequence, Forest disturbance, Litterfall, Northern hardwood forest, Soil organic matter.

INTRODUCTION

Forest ecosystems change over time in response to external factors, such as environmental stress, and in response to biotic factors, such as forest succession. Distinguishing between the effects of environmental stress and forest succession in interpreting the cause of forest change can be difficult, particularly because we typically examine either the effects of stress or the effects of succession, but rarely both at the same time. For example, in studying forest succession, we hope to hold environmental factors, such as climate and air pollution, constant, despite the near impossibility of doing so. Similarly, in studying the effects of environmental stress, we hope to ignore changes in the ecosystem that are driven by intrinsic factors such as forest succession.

In this paper, we present two case studies of

changes in the forest floor in New Hampshire northern hardwoods. In one, differences between stands in forest floor organic matter, previously attributed to forest succession following logging, were instead due partly to historic changes in logging practices. In the second, losses of base cations from the forest floor, previously attributed to acid rain or declining Ca deposition, were instead due partly to forest succession. In both studies, we were able to consider forest succession and external factors because we sampled stands of different ages over time.

The northern hardwood forest accumulates a thick organic horizon called a mor-type forest floor (Green *et al.* 1993). In temperate forests, forest floor organic matter has been thought to decrease by fifty percent within 20 years after harvesting, and then to accumulate to pre-disturbance levels in about 60 years (Covington

1981). These predictions for change in soil organic matter have important implications for estimates of the effects of forest harvesting on carbon budgets (Harmon *et al.* 1990, Houghton *et al.* 1983). Explanations for a reduction in forest floor mass after harvesting include mechanical disturbance, increased moisture and temperature leading to greater rates of decomposition, and changes in litter inputs.

The idea that forest floor mass declines after harvesting in northern hardwood forests was based on a study of a chronosequence of forest stands in New Hampshire (Covington 1981). Using the organic mass data from 14 stands of different ages, Covington fitted a curve to predict organic mass as a function of stand age (Fig. 1). Federer (1984) sampled an additional 13 forest stands of different ages, and found higher organic mass in older stands, and the lowest in younger stands, consistent with Covington's observation (Fig. 1). By sampling forest floor in stands of varying ages, these studies suggested a degree of biotic control (related to stand age) over forest floor organic matter mass.

Alternatively, this pattern could be interpreted as a function of the date at which the stands were harvested (Fig. 2). Changes over time in the treatment of these stands include the degree of disturbance to the forest floor and the intensity of harvest removals, driven by changes in logging technology and markets for wood products. If forest floor mass is controlled by the differences in treatments applied to the stands, then we would not expect the equation fit by Covington to describe organic matter as a function of stand age to remain accurate. In

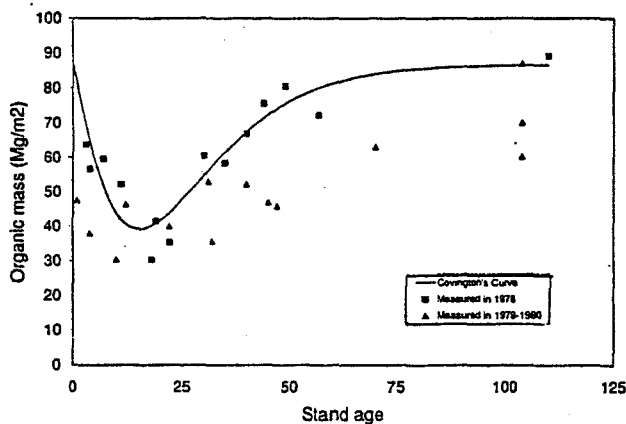


Fig. 1. Forest floor organic matter as a function of the date of stand age, as measured in 1976 by Covington (1981) and in 1979-80 by Federer (1984). The curve is that fit by Covington to describe organic matter content (Mg/ha) as a function of stand age: $-5.25 X^{1.24} \exp(-0.0649 X^{1.063}) + 86.75$, where X = time since logging (years).

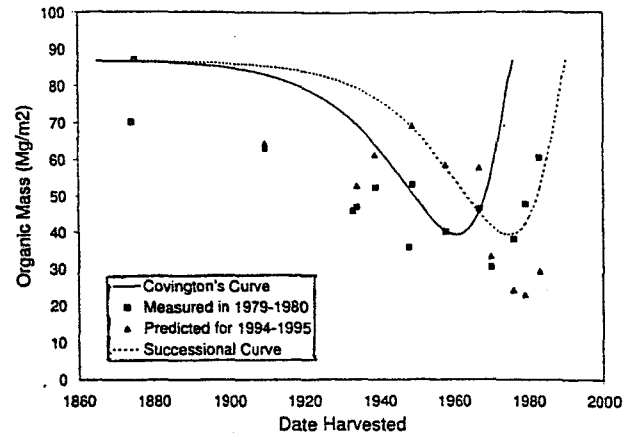


Fig. 2. Forest floor organic matter as a function of the date of forest harvest for our stands sampled in 1979-80 (Federer 1984) and the predicted values after 15 years. Covington's curve (Fig. 1) is shown for the ages of the stands at the time they were measured (solid line) and for their ages at the second sampling date (1994-95; dashed line). Predicted values were based on the proportional change in the Covington curve applied to the measured masses.

contrast, if forest floor mass is controlled by successional processes, then Covington's curve can be used to predict the mass we should find in those same stands, measured at a later date. The successional prediction is represented in Fig. 2 by a shift in the curve as the stands age by 15 years. The three stands cut most recently are predicted to decline by 28 to 56 percent, while the stands cut between 1930 and 1970 are predicted to increase by an average of 25 percent. Determining the accuracy of such predictions is important to assessing global C budgets as well as the sustainability of local harvesting practices.

There is growing concern that base cations are being lost from forest soils in the northeastern United States, as a result of acid rain and elevated nitrogen deposition (Baes and McLaughlin 1984, Shortle and Bondiotti 1992, Likens *et al.* 1996, Likens *et al.* 1998). The forest floor of the northern hardwood forest is an important substrate for rooting (Fahey and Hughes 1994) and an essential pool of available nutrients. The loss of base cations from forest soils may have important implications for productivity and forest health, as noted for eastern North America (Baes and McLaughlin 1984, Shortle and Bondiotti 1992) and Europe (Ulrich *et al.* 1980). Several recent studies have suggested dramatic declines in base cation concentrations from forest floor or soil (Johnson *et al.* 1994, Johnson *et al.* 1988, Knoepp and

wank 1994). However, studies that have identified a decline in cation concentrations in forest floor have generally been limited to repeated measures, usually two, within single stands. Without sampling across stand age, these studies cannot detect the effects of forest succession on forest floor cation concentrations.

To distinguish between the effects of forest succession and environmental factors on changes in the forest floor in the northern hardwood forest, we measured organic matter content and nutrient cation concentrations in the forest floor at a fifteen-year interval in thirteen forest stands of different ages. We also measured litter-fall mass and nutrient concentrations in the same chronosequence, because they may contribute to successional changes in the forest floor. This study was made possible by the foresight of previous researchers who archived forest floor samples, enabling us to simultaneously analyze archived and contemporary samples.

METHODS

This study was conducted in 13 northern hardwood stands in New Hampshire, USA. The stands ranged in age at the time of sampling in 1994-95 from 12 to more than 120 years. Important species in mature stands included *Fagus grandifolia* Ehrh., *Acer saccharum* Marsh., *A. rubrum* L., *Betula papyrifera* Marsh. and *B. alleghaniensis* Britton. Younger stands were dominated by *Prunus pensylvanica* L. The soils were coarse-loamy, mixed, frigid, Typic haplorthods. More detailed site descriptions are given by Yanai *et al.* (2000a).

We resampled the forest floor in the chronosequence of 13 northern hardwood stands measured by Federer (1984) in 1979-80. The stands were resampled after an interval of 15 years in 1994-95, according to the methods used by Federer (1984). Forest floor samples were collected quantitatively: each sample was a 10 × 10 cm block of forest floor collected to the top of the E or B horizon. Ten such samples were composited from 5 or 6 sampling lines in each stand. Forest floor samples from the 1979-80 sampling had been carefully stored for future use. Contemporary and archived samples were analyzed side by side. Detailed descriptions of sampling and analytical methods are given by Yanai *et al.* (2000b).

Samples were air dried and sieved. Organic matter was determined by loss on ignition at 500°C (Wilde *et al.* 1978). In preparation for cation analysis, ground subsamples were ashed and dissolved in 6 mol/L nitric acid. The resulting

solutions were analyzed for calcium (Ca) and magnesium (Mg) by inductively coupled plasma spectroscopy (ICP).

Successional changes in inputs of organic matter and nutrients to the forest floor in litterfall may contribute to change over time in the forest floor. We measured litterfall mass and nutrient inputs to the forest floor for three years in the chronosequence, from 1994 to 1996. Litter was collected in three baskets in each of five transects in each stand. Baskets were emptied two or three times per year. Litter was separated by species and weighed after drying at 60°C. The concentration of Ca and Mg in each stand for each species was measured in freshly collected leaves, to avoid changes due to leaching or decomposition after litter was deposited in the baskets.

RESULTS

Forest floor organic matter

The observed changes in forest floor organic matter in stands of different ages (Fig. 3) were significantly different from those predicted by Covington's curve (Fig. 2). Most importantly, the 50% decline in forest floor organic matter predicted to occur in recently harvested stands was not observed. Changes in forest floor organic matter in the three stands predicted to show losses were positive in two cases, and insignificant on average (Fig. 3). We did find that younger stands had less forest floor organic matter than older stands, but the observed pattern was equally well explained by the year in which the stand was logged as by the age of

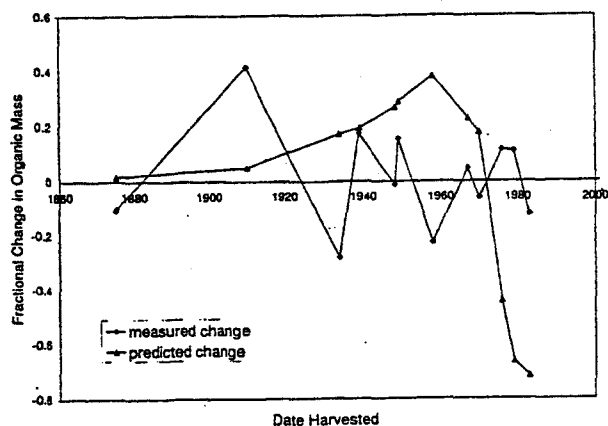


Fig. 3. Predicted and observed changes in forest floor organic matter over a fifteen-year interval as a function of the date of forest harvest. The predicted change is based on Covington's equation (Fig. 1). The observed change is based on the means of log-transformed organic masses.

the stand (Yanai *et al.* 2000b, Fig. 4). In other words, differences related to the year in which the stands were harvested, such as the degree of disturbance to the forest floor and the intensity of harvest removals, might be as important as successional change in explaining the observed pattern.

Changes in calcium and magnesium in the forest floor

Despite the high loadings of acid rain and N deposition to these ecosystems (EPA 1996), we did not find a systematic loss of base cations from the forest floor over the 15-year period from 1979–80 to 1994–95. Instead, we found that young stands gained Ca and Mg, while older stands were more likely to lose Ca and Mg (Yanai *et al.* 2000a; Fig. 5). This successional pattern suggests a degree of biotic control over cation losses from the forest floor.

Differences in litterfall cation concentrations as a function of stand age could contribute to the observed pattern of Ca accumulation in young stands and loss in old stands. We found that Ca concentrations in litterfall, averaged over three years (1994–1996) declined with stand age ($R^2=0.32$, $p=0.045$; Fig. 6A). There was a non-significant trend toward declining Mg in litterfall with stand age ($R^2=0.27$, $p=0.067$; Fig. 6B). Calcium and Mg contents of litterfall were constant across forest stands; greater litterfall mass in older stands compensated for higher concentrations in younger stands.

DISCUSSION

We were able to consider both forest succession and environmental stress as causes of change in the forest floor because we repeatedly sampled

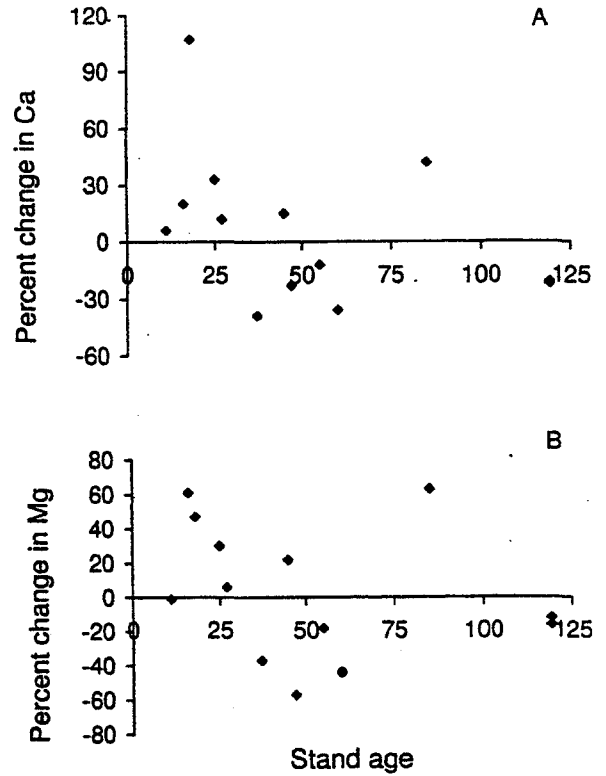


Fig. 5. Percent change in forest floor Ca (A) and Mg (B) concentrations over the 15 year sampling period.

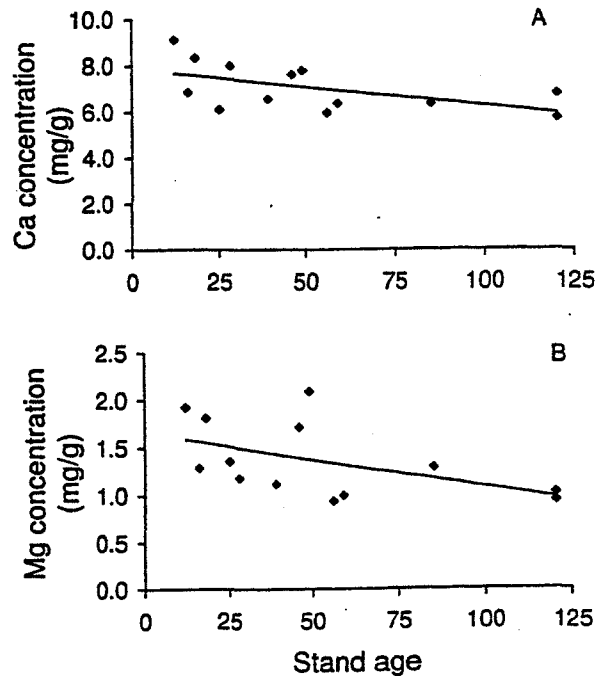


Fig. 6. Calcium and Mg concentrations in litterfall as a function of stand age. Lines are linear regression fits: for Ca, $R^2 = 0.32$, $p = 0.045$; for Mg, $R^2 = 0.27$, $p = 0.067$.

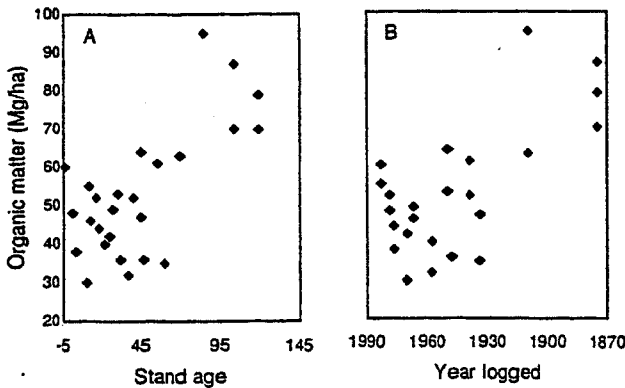


Fig. 4. Forest floor organic matter as a function of stand age (A) and year logged (B) for stands sampled in 1979–80 (Federer 1984) and in 1994–95 (Yanai *et al.* 2000b).

stands of different ages. In our first case study, the observed pattern of forest floor organic matter as a function of stand age was previously interpreted as a successional pattern, ignoring changes in treatment history. By resampling a chronosequence of forest stands, we were able to show that the loss of organic matter over time was not the same as that predicted from the one-time sampling of stands of different ages. Instead, we found that the date at which stands received a logging treatment was as good a predictor of the observed organic matter content as was the age of the stand. Horse logging, which was common until the 1940's, probably caused much less disturbance to the forest floor than mechanized logging. In addition, markets for hardwoods have changed dramatically during this century (Whitney 1994), resulting in increasingly intense biomass removals. Both of these changes could help to explain why the time of logging, as well as the time since logging, is an important predictor of forest floor organic matter content.

In our second case study, observed losses of base cations from the forest floor were previously attributed to acid rain. We found that young stands were gaining base cations in the forest floor; losses of base cations were restricted to older stands. In this case, the contributions of successional processes to cation loss were previously overlooked in favor of environmental stress as the dominant mechanism.

In studies examining successional change, researchers often use a chronosequence approach. This approach assumes that a series of stands share a soil type, climate, and forest history. However, changes in management practices or environmental stresses violate the assumption of a common history of development. With repeated sampling, the potential importance of differences in stand history or environmental conditions can be assessed.

Studies of environmental stress may use repeated measures over time, but often don't consider stand age as a factor. Studies that rely on repeated measures from a single or a few forest stands necessarily assume that stand age or forest succession are not important determinants of forest change. Combining the forest chronosequence approach with repeated measures on archived samples provides a powerful tool for distinguishing biotic and environmental control of forest floor dynamics.

LITERATURE CITED

- Baes, C.F., III. and S.B. McLaughlin. 1984. Trace elements in tree rings: evidence of recent and historical air pollution. *Science* 224: 494-497.
- Covington, W.W. 1981. Changes in the forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology* 62: 41-48.
- EPA (U.S. Environmental Protection Agency). 1996. National air pollutant emission trends, 1900-1995. EPA-454/R-96-007. U.S. Environmental Protection Agency, Research Triangle Park, North Carolina, USA.
- Fahey, T.J. and J.W. Hughes. 1994. Fine root dynamics in a northern-hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *Journal of Ecology* 82: 533-548.
- Federer, C.A. 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. *Canadian Journal of Forest Research* 14: 763-767.
- Green, R.N., R.L. Trowbridge and K.Klinka. 1993. Towards a taxonomic classification of humus forms. *Forest Science Monographs* 39: 1-48.
- Harmon, M.E., W.K. Ferrell, and J.F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247: 699-702.
- Houghton, R.A., J.E. Hobbie and J.M. Melillo. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: a net release of CO₂ to the atmosphere. *Ecological Monographs* 53: 235-262.
- Johnson, A.H., S.B. Andersen and T.G. Siccama. 1994. Acid rain and the soils of the Adirondacks. I. Changes in pH and available calcium, 1930-1984. *Canadian Journal of Forest Research* 24: 39-45.
- Johnson, D.W., G.S. Henderson and D.E. Todd. 1988. Changes in nutrient distribution in forests and soils of Walker Branch Watershed, Tennessee: roles of uptake and leaching in causing soil changes. *Journal of Environmental Quality* 19: 97-104.
- Knoepp, J.D. and W.T. Swank. 1994. Long-term soil chemistry changes in aggrading forest ecosystems. *Soil Science Society of America Journal* 58: 325-331.
- Likens, G.E., C.T. Driscoll and D.C. Buso. 1996. Long-term effects of acid rain: Response and recovery of a forest ecosystem. *Science* 272: 244-246.
- Likens, G.E., C.T. Driscoll, D.C. Buso, T.G. Siccama, C.E. Johnson, G.M. Lovett, T.J. Fahey, W.A. Reiners, D.F. Ryan, C.W. Martin and S.W. Bailey. 1998. The biogeochemistry of calcium at Hubbard Brook. *Biogeochemistry* 41: 89-173.
- Malmer, N. 1976. Chemical changes in the soil. *Ambio* 5: 231-234.
- Shortle, W.C. and E.A. Bondiotti. 1992. Timing, magnitude, and impact of acidic deposition on sensitive forest sites. *Water, Air, and Soil Pollution* 61: 253-267.
- Ulrich, B., R. Mayer and P.K. Khanna. 1980. Chemical changes due to acid precipitation in a loess-derived soil in central Europe. *Soil Science* 130: 193-199.
- Whitney, G.G. 1994. From coastal wilderness to fruited plain: a history of environmental change in tem-

- perate North America, 1500 to the present. Cambridge University Press. New York, 451 p.
- Wilde, S.A., R.B. Corey, J.G. Iyer and G.K. Voigt. 1978. Soil and Plant Analysis for Tree Culture. Oxford and IBH Publishing Co. Madison, Wisconsin, 224 p.
- Yanai, R.D., M.A. Arthur, T.G. Siccama and C.A. Federer. 2000a. Challenges of measuring forest floor organic matter dynamics: Repeated measures from a chronosequence. Forest Ecology and Management (In Press).
- Yanai, R.D., T.G. Siccama, M.A. Arthur, C.A. Federer and A.J. Friedland. 2000b. Accumulation and depletion of base cations in forest floors in the northeastern United States. Ecology (In Press).

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