PLANT AND SOIL NUTRIENTS IN YOUNG VERSUS MATURE CENTRAL APPALACHIAN HARDWOOD STANDS

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Abstract: Most models of forest succession and forest recovery following disturbance predict changes in nutrient availability. The purpose of this study was to compare soil and herbaceous layer plant nutrients between two young (~20 yr) and two mature (~80 yr) forest stands on Fernow Experimental Forest, Parsons, West Virginia. All sampling was carried out within 15 circular 0.04-ha sample plots per watershed, for a total of 30 plots for each age category. All vascular plants ≤1 m in height (herbaceous layer) were identified and estimated visually for cover in each of 10 circular 1-m^2 sub-plots. All above-ground portions of plants in the two sub-plots in each sample plot with the greatest herb layer cover were harvested and analyzed for nutrient content. In addition, a soil sample was taken to a 10-cm depth from each harvest sub-plot. Soils were analyzed for organic matter, texture, pH, and extractable nutrients. There were no significant differences related to stand age for soil pH, organic matter, cation exchange capacity, or any of the extractable nutrients. With the exception of significantly higher herb layer N for the young stands, there were few differences in herb layer tissue nutrients between young and mature stands. There were, however, differences in correlations among soil nutrients and other soil variables (e.g., texture and organic matter) which varied with stand age, with extractable nutrients more highly correlated with organic matter and texture in the young stands than in the mature stands. Furthermore, herb layer tissue nutrient concentrations were correlated significantly with soil organic matter for virtually all nutrients in young stands; in contrast, none were correlated with soil organic matter in mature stands. These results suggest minimal change in nutrient availability between 20 and 80 years of forest recovery from disturbance. Data in this study further emphasize the importance of soil organic matter decomposition as a source of available nutrients in these hardwood forests following disturbance and suggest that this importance might decrease with stand age. Finally, these results are consistent with the hypothesis that herb layer dynamics are controlled by nutrient availability early in succession, but that other factors, such as light, become more important later in succession.

INTRODUCTION

Most current models of secondary forest succession and forest response to disturbance predict measurable changes in nutrient availability over time (Bormann and Likens 1979, Vitousek and Reiners 1975). Although these patterns of change will vary among ecosystems and degrees of disturbance, it generally is accepted that nutrients will increase in availability and mobility immediately following a disturbance, such as forest harvesting, which usually results in ching increases and nutrient loss via streamflow. As regrowth occurs, however, plant root uptake increases rapidly, resulting in decreased nutrient leaching and increased nutrient storage in plant biomass. Thus, it is reasonable to generalize that nutrient availability increases for a short period following forest disturbance and that it decreases subsequently through time. Studies of stream chemistry response to forest harvests on montane watersheds of the eastern U.S. largely have supported these generalizations (Aubertin and Patric 1974, Bormann and Likens 1979, Kochenderfer and Wendel 1983, Swift and Swank 1981).

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Other research has focused on forest floor organic matter and its response to forest harvests (e.g., Covington 1981); fewer studies have looked directly at soil nutrients. Although forest successional changes in N are fairly well understood (Vitousek and others 1989), less is known about P and the base cations Ca, Mg, and K. These nutrients are not generally considered as frequently growth-limiting as is N, but limitations can occur, especially in forest soils developed from parent materials low in these nutrients (Jenny 1981), such as the highly weathered soils of the pine forests of the southeastern Coastal Plain (Gilliam 1991, Gilliam and Richter 1991), or the deep sands of the Adirondacks in New York (Stone and Kszystyniak 1977). In contrast to N change through time, which is tied into somewhat predictable changes in organic matter decomposition, it may be much more difficult to generalize about ecosystem changes in P and nutrient cations through succession because they are influenced both by decomposition rates of organic materials and by weathering rates of primary and secondary soil minerals.

Although difficult to assess empirically (Chapin and Van Cleve 1991), nutrient availability generally is defined in terms of amounts of nutrients present in the soil in chemical forms which allow for plant root uptake. Although N availability is often measured via incubation techniques, cation availability usually is measured as exchangeable amounts in soil extract solutions (Binkley and Vitousek 1991). Measurements of plant tissue concentrations also have been used to assess soil fertility and nutrient availability (Binkley and Vitousek 1991). This paper examines nutrient availability as both amounts of extractable nutrients from the mineral soil and tissue concentrations in plant material.

The herbaceous layer, defined here as vascular plants ≤ 1 m in height, is an important stratum of forest ecosystems, playing a significant role in initial competition among juveniles (seedlings and sprouts) of potential overstory canopy tree species (Gilliam and others 1994). Furthermore, the herb layer has been shown to be quite sensitive to a variety of forest disturbances, including gap openings (Moore and Vankat 1986) and forest management practices (Duffy and Meier 1992, Gilliam and Christensen 1986, Gilliam and Turrill 1993). Perhaps more important in the context of changes in nutrient availability, the herb layer also has been used as an indicator of edaphic factors and forest site quality (Cserep and others 1991, Pregitzer and Barnes 1982, Strong and others 1991). Reiners (1992) reported on 20 yr of vegetation recovery following deforestation and herbiciding on Watershed 2 at Hubbard Brook and found 6-8 fold increases in herb layer content of N, Ca, Mg, and K. In contrast, the shrub layer increased only 3-5 fold for these nutrients over the same 20-yr period (Reiners 1992).

The purpose of this study was to compare herbaceous layer and extractable soil nutrients (N, P, Ca, Mg, and K) between watersheds supporting young, clearcut (~20-yr old) vs. mature ~80-yr old) stands of central Appalachian mixed hardwood forests. We were also interested in examining soil-plant nutrient interactions and how these interactions might vary with stand age.

METHODS

Study Site

Research was done on four contiguous watersheds of the Fernow Experimental Forest (FEF), a 1900-ha area of montane hardwood forests within the unglaciated Allegheny Plateau, located in Tucker County, West Virginia (39°03'N, 79°49'W). WS7 and WS3 support stands which were approximately 20 yr old and even-aged (following clearcutting) at the time of sampling and will be referred to as "young." These stands are dominated primarily by black cherry (*Prunus serotina* Ehrh.) and yellow poplar (*Liriodendron tulipifera* L.). WS13 and WS4 support stands which were older than 75 yr at the time of sampling and will be referred to as "mature." They are mixed-age, being dominated by sugar maple (*Acer saccharum* Marsh.) and northern red oak (*Quercus rubra* L.), and originated from natural regeneration from the heavy cutting which characterized the period of railroad logging from ~1880 to 1930 (Marquis and Johnson 1989). Herbaceous layer species have been described in previous papers (Gilliam and Turrill 1993, Gilliam and others 1994).

Field Sampling

Fifteen semi-permanent circular plots were established within each of the study watersheds, for a total of 60 sample plots for the study. Plots were established by locating plot centers throughout each watershed to include the extremes of elevation and aspect. A radius of 11.3 m was measured from each plot center for a total area of 0.04 ha per plot.

Methods of herbaceous layer and soil sampling also has been described in those papers, but is summarized briefly here. Within each sample plot all vascular plants within 10 1-m^2 circular sub-plots were identified to species and estimated visually for cover (total of 600 sub-plots for the study) using the technique of Gilliam and Christensen (1986). This method has been shown to be both reproducible and capable of accurate prediction of herb layer biomass (Gilliam and Turrill 1993). The two sub-plots with the greatest percentage of herb layer cover in each were chosen as "harvest" sub-plots, within which all above-ground herb layer material was collected. Harvesting was confined to only the two high-cover sub-plots in each plot to ensure enough herb tissue biomass for nutrient analysis of individual species. Although this criterion potentially confounds cover-nutrient relationships among watersheds, it allowed for a full range of cover values (from 1 to ~80%) for harvested species (Gilliam and Turrill 1993). Furthermore, there was a good correlation between the mean cover of the two sub-plots per plot and mean cover of the entire plot (based on all 10 plots). In other words, relatively high-cover sample plots had relatively high-cover harvest sub-plots, and visa versa. Therefore, using high cover as a selection criterion for herb layer harvests does not appear to create problems for comparison among watersheds. Finally, a sample of mineral soil was taken to a 10-cm depth from each of the two harvest sub-plots following removal of organic forest floor material.

Sample Analysis

Herb layer samples from each of the 120 harvest sub-plots were separated into species, oven-dried at 50°C, weighed, and ground in a Wiley mill to pass a 1-mm screen. Plant tissue (and soil--see below) samples were shipped to the University of Maine (U. M.) Soil Testing Service and Analytical Laboratory for macronutrient analysis (N, P, Ca, Mg, and K). Total plant N was measured as Kjeldahl N. All other nutrients were measured with plasma emission spectrophotometry after dry-ashing plant material and extraction with HCl and HNO_3.

Mineral soil samples were sieved to pass a 2-mm screen, air-dried, and shipped to the U. M. laboratory for analysis, including pH (1:1 w/v, soil/H2O), 1N KCl-extractable Ca, K, Mg, and P (plasma emission), 1N KCl-extractable NO_3 and NH_4 (flow-injection colorimetry), and soil organic matter (loss-on-ignition). Particle-size (texture) was determined on each soil sample at the laboratory at Marshall University using the hydrometer method of Bouyoucos (1951).

Data Analysis

Data analysis for this study was based on mean plot values (i.e., not sub-plot values) of all soil and plant variables. Stand age class means of all variables were calculated as the average of 30 plots (15 plots in each of two watersheds per stand age class) and were compared (young vs. mature) using Student's t-test (SAS 1982, Zar 1984). Within each age class, relationships among soil and plant variables (soil vs. soil, plant vs. plant, and plant vs. soil) were determined with Pearson product-moment correlation analysis (SAS 1982).

RESULTS

There were no significant differences between stand age classes for any of the measured soil variables, including organic matter, cation exchange capacity, pH, and extractable nutrients (Table 1). There were also no differences between age classes for P, Ca, Mg, and K concentrations in the herbaceous layer (Table 2). However, the herb layer of the young stands was significantly higher ($P<0.01$) in N than that of mature stands (Table 2).

Table 1. T-test comparisons of soil variables of young vs. mature stands of the Fernow Experimental Forest, WV. OM=organic matter; CEC=cation exchange capacity. NS indicates no significant differences between stand age classes at P<0.05. Values in parentheses are one standard error of the mean.

Stand Age	OM (%)	CEC (meq/kg)	pH	NO_3	NH_4	P	Ca	Mg	K
				-----	-----	mg/kg	-----	-----	-----
Young	13.8	45.5	4.39	1.3	2.1	0.8	12.6	2.1	2.3
	(0.7)	(4.6)	(0.06)	(0.2)	(0.2)	(0.4)	(5.0)	(0.4)	(0.2)
	NS	NS	NS	NS	NS	NS	NS	NS	NS
Mature	12.6	40.1	4.32	0.9	1.9	0.4	6.4	2.4	2.2
	(0.4)	(1.2)	(0.05)	(0.1)	(0.1)	(0.0)	(1.1)	(0.7)	(0.1)

Table 2. T-test comparisons of herbaceous layer tissue nutrients of young vs. mature stands of the Fernow Experimental Forest, WV. Significant differences (P<0.01) between stand age classes indicated by *. NS indicates no significant difference between age classes at P<0.05. Values in parentheses are one standard error of the mean.

Stand Age	N	P	Ca	Mg	K
	-----	-----	mg/kg	-----	-----
Young	2.35	0.16	0.62	0.22	2.68
	(0.07)	(0.01)	(0.08)	(0.01)	(0.26)
	*	NS	NS	NS	NS
Mature	1.99	0.15	0.75	0.24	2.21
	(0.09)	(0.01)	(0.06)	(0.02)	(0.19)

Numerous significant correlations (nearly 60% of total possible combinations) existed among soil variables for the young stands (Table 3). Notable variables with which there were several significant correlations were texture classes (sand and silt) and organic matter. In contrast, neither extractable P nor extractable NH_4 were correlated with any other soil variables (Table 3). Soils of mature stands exhibited far fewer significant correlations (<20% of the total) compared to young stand soils (Table 4).

In contrast to differences between stand age classes in patterns of soil variable correlations, correlations among herb layer nutrient concentration were quite similar between young and mature stands. All plant nutrients were correlated significantly with each other for mature stands, and all but Ca:K were significant for young stands (Table 5).

In comparing plant vs. soil nutrients between stand ages, the young stand exhibited significant correlations for the nutrient cations, but neither N nor P; the mature stand had significant correlations for P, Ca, K, and plant N vs. soil NO_3 (Table 6). Finally, all plant nutrients except N were correlated significantly with soil organic matter in the young stands, whereas no plant nutrients were correlated with organic matter in mature stands.

Table 3. Correlations among soil variables of young stand plots. Values shown are Pearson product-moment correlation coefficients (r) significant at P<0.05.

	Sand	Silt	Clay	OM	Ca	K	Mg	P	NO_3	NH_4	pH
Silt	-0.89**										
Clay	-0.70**	---									
OM	0.56*	-0.41	-0.53*								
Ca	0.46	-0.42	---	0.66**							
K	0.56*	-0.42	-0.52*	0.77**	0.72**						
Mg	0.47*	-0.39	---	0.73**	0.97**	0.76**					
P	---	---	---	---	---	---	---				
NO3	0.50*	-0.44	---	0.78**	0.68**	0.76**	0.73**	---			
NH4	---	---	---	---	---	---	---	---	---		
pH	0.55*	-0.49*	-0.39	0.51*	0.75**	---	---	---	0.40	---	
CEC	0.44	-0.37	---	0.68**	0.98**	0.69**	0.98**	---	0.72**	---	0.61**

*indicates correlation coefficient significant at P<0.01.
**indicates correlation coefficient significant at P<0.001.

Table 4. Correlations among soil variables of mature stand plots. Values shown are Pearson product-moment correlation coefficients (r) significant at P<0.05.

	Sand	Silt	Clay	OM	Ca	K	Mg	P	NO_3	NH_4	pH
Silt	-0.82**										
Clay	-0.47*	---									
OM	0.38	-0.42	---								
Ca	---	---	---	---							
K	---	---	---	---	0.59**						
Mg	---	---	---	---	0.61**	---					
P	---	---	---	0.44	---	---	---				
NO3	---	---	---	---	---	---	---	0.67**			
NH4	---	---	---	---	---	---	---	---	---		
pH	---	---	---	---	0.42	0.48*	---	---	---	---	
CEC	---	---	---	---	0.74**	---	0.46*	---	---	---	---

*indicates correlation coefficient significant at P<0.01.
**indicates correlation coefficient significant at P<0.001.

Table 5. Correlations among herbaceous layer nutrient concentrations of young and mature stand plots. Values shown are Pearson product-moment correlation coefficients (r) significant at P<0.05.

	N	P	Ca	Mg
Young stands				
P	0.63**			
Ca	0.49*	0.62**		
Mg	0.71**	0.38	0.58**	
K	0.56*	0.38	---	0.67**
Mature stands				
P	0.83**			
Ca	0.53*	0.48*		
Mg	0.88**	0.64**	0.54*	
K	0.88**	0.67**	0.58**	0.89**

*indicates correlation coefficient significant at P<0.01.
**indicates correlation coefficient significant at P<0.001.

Table 6. Plant-soil nutrient interactions of young and mature stands of Fernow Experimental Forest, WV. Values shown are Pearson product-moment correlation coefficients (r) for indicated pairs significant at P<0.05.

Variables			Stand Age	
Plant	vs.	Soil	Young	Mature
N	vs.	NO_3	---	0.63**
N	vs.	NH_4	---	---
P	vs.	P	---	0.63**
Ca	vs.	Ca	0.78**	0.43
Mg	vs.	Mg	0.57*	---
K	vs.	K	0.44	0.42
N	vs.	OM	---	---
P	vs.	OM	0.48*	---
Ca	vs.	OM	0.75**	---
Mg	vs.	OM	0.50*	---
K	vs.	OM	0.37	---

*indicates correlation coefficient significant at P<0.01.
**indicates correlation coefficient significant at P<0.001.

DISCUSSION

Based on soil and plant tissue nutrient comparisons alone, there appears to have been little long-term change in nutrient availability over time following forest disturbance at this site. Soil variables were virtually identical between young and mature stands. In general these forest soils were acidic, with moderate levels of organic matter (~13%) and a relatively low cation exchange capacity (~42 meq/kg). It should be emphasized that the extractable N data represent pools of available N and not fluxes. Current research using in situ incubations ("buried bag" technique) on many of these same plots indicate that fluxes (e.g., uptake) are >10-fold higher than available N pools (Gilliam and Adams, submitted manuscript).

Herb layer tissue nutrient data are indicative of small decreases in N availability with stand development over time. Because these data are for the herb layer as an entire stratum (i.e., all species combined), the significant difference in plant N may have resulted from stand age-related differences in herb layer species. However, these stands are remarkably similar with respect to herb layer species composition, regardless of stand age (Gilliam and Turrill 1993, Gilliam and others, submitted manuscript), with the possible exception of higher fern cover on WS7 (Gilliam and others 1994). Herb layer nutrient concentrations for FEF were similar to other hardwood forests for N and P, but lower for Ca, Mg, and K (Grigal and Ohmann 1980, Peterson and Rolfe 1982, Siccama and others 1970). These differences may be related to the sandstone parent materials of the FEF watersheds. Concentrations of herb layer nutrients at FEF are well within the range of values reported as adequate for crop plants (Chapin and Van Cleve 1991).

Although correlation analysis is more appropriate for generating hypotheses than for testing them, such analyses can be useful in describing general patterns of relationships of soil and plant nutrients. For example, the numerous significant correlations among soil variables of the young stand plots suggest that there may a single factor determining, or controlling, overall soil fertility of these young stands. Furthermore, the general lack of correlations for the mature stand plots indicate that this factor is not as prevalent for the mature stands as it is for the young stands.

Soil organic matter is the variable which is consistently the most highly correlated with extractable soil nutrients in the young stands (Table 3), suggesting that organic matter is an important factor determining overall fertility of these soils. Indeed, it was significantly correlated ($P<0.01$) with all other young stand soil variables except extractable P and NH_4 (Table 3). Significant correlation ($P<0.001$) between organic matter and cation exchange capacity further support this contention, and indicate that exchange sites of these soils are dominated by organic colloids (Tate 1987). In sharp contrast in mature stand soils, among the nutrients organic matter was correlated only with extractable P, and it was not correlated with cation exchange capacity.

Surprisingly, there were numerous significant correlations among plant nutrients for both stand age classes. Other studies have reported fewer significant correlations among plant nutrients, but ones which suggest either biochemical or functional groups. For example, using nutrient data from 110 plant species, Garten (1978) found significant correlations for the following plant nutrient pairs: N:P, Mg:K, and Ca:Mg. He concluded that these pairings were related to biochemical functions within the plant, e.g., nucleic acids-proteins for N:P. Gilliam (1988) found significant correlations for most of these same nutrient pairs and for K:P. He concluded that the latter was the result of limitation of herb layer plant growth from both nutrients in the highly weathered soils of a southeastern U.S. pine forest. Thus, the numerous correlations found in the present study are certainly notable, though difficult to interpret.

Young and mature stands differed slightly from each other with respect to correlations between plant tissue nutrient concentrations and extractable forms of the same nutrients in mineral soil (Table 6). However, correlations between plant nutrients and soil organic matter varied greatly with stand age. Virtually all nutrients were correlated in young stands, whereas none were correlated in mature stands (Table 6). The numerous significant correlations in young stands further illustrates the importance of soil organic matter in mediating nutrient availability following forest disturbance. Organic matter serves both as a nutrient source via decomposition and a cation exchange source.

CONCLUSIONS

Although differences between stand age classes in soil organic matter/plant nutrient correlations might suggest that this importance decreases with stand age, this explanation is probably unlikely considering the nature of the soils of these watersheds (i.e., that they are derived from low-nutrient sandstone parent materials). Because soil organic matter plays such an important role in determining fertility of these sandy soils, stand age-related differences in correlations of herb layer nutrient concentration with organic matter may arise from successional changes in factors limiting herb layer dynamics. Significant correlations would suggest soil-mediated limitations (e.g., nutrient availability), whereas lack of correlation would suggest limitations from other sources. Gilliam and Turrill (1993) hypothesized that the herb layer of these forests are nutrient-limited early in succession when light availability is relatively high and uniform in the stand, and that the herb layer becomes more limited by light availability later in succession following canopy closure and stratification. Although certainly not conclusive, data presented in this paper are consistent with this hypothesis.

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