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Forest Nutrient and Carbon Pools at Walker Branch Watershed: Changes during a 21-Year Period

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ABSTRACT

A 21-yr perspective on changes in nutrient and C pools on undisturbed upland forest sites is provided. Plots originally representing four cover types have been sampled three times. On each plot, forest biomass, forest floor, and soil, to a depth of 60 cm, were measured, sampled, and analyzed for Ca, Mg, C, N, and P. Exchangeable soil Ca and Mg have declined in most soils. Despite the low exchangeable Ca, cumulative sequestration in the biomass has exceeded the soil pool, suggesting that soil supplies below 60 cm are satisfying the biomass demand. Extractable soil P also declined, with means ranging from 4.2 to 18.2 kg ha^{-1}, as a result of reductions in the mineral soil and Oi horizon. The loss of extractable soil P exceeded biomass sequestration in all but one plot, suggesting abiotic soil processes as the removal mechanism. Soil C and N were either stable, although highly variable, or declined, which was unexpected in these undisturbed sites. The net C balance of these sites was controlled by aboveground sequestration, which offset changes in the soil and forest floor. Soil parent material and geomorphic setting strongly influenced the changes in soil properties during the 21-yr period, reflecting the importance of those factors in assessing soil nutrient and C cycles over that of forest cover type. The variability encountered in the periodic soil measurements highlights the difficulty in detecting temporal changes in soil chemical properties.

SHORT-TERM STUDIES have provided the bulk of the information about the structure and function of forested ecosystems. Inadequate temporal scales in those studies preclude assessment of the interactions of biological, chemical, and physical processes within the ecosystem, especially the contributions of anthropogenic factors. Long-term studies are instrumental to understanding nutrient cycling in forests and identifying potential limitations to sustainable production as a result of management practices or climate change.

In contrast to suggestions that soil nutrient pools are buffered from short-term changes, several recent, long-term studies have shown that soil change can occur on a scale of decades or even on a seasonal basis under certain conditions (reviewed by Johnson et al., 1991). Significant reductions in the pools of exchangeable base cations for instance, have been noted during periods of one to three decades in European and North American forests (Ahokas, 1997; Binkley et al., 1989; Drohan and Sharpe, 1997; Johnson et al., 1994, 1988; Falkengen-Grerup and Eriksson, 1990; Falkengen-Grerup and Tyler, 1992; Hallbäcken and Tamm, 1986; Knoepp and Swank, 1994; Mandersheid et al., 1995; Richter et al., 1994). Surface soil concentrations may vary on a seasonal basis (Haines and Cleveland, 1981; Johnson et al., 1988). These changes were attributed to sequestration of base cations (especially Ca) in biomass and to leaching, the latter of which is often accelerated by acid deposition.

A long-term study of soils on the Walker Branch Watershed (WBW), in Tennessee, was among the first to suggest that soil Ca depletion from uptake could be a major factor constraining sustainable production if stands were harvested without regard to conserving nutrients (Johnson et al., 1988). Other work on those soils showed that cation leaching was also a major factor affecting the soil cation balance (Johnson and Todd, 1990). Long-term studies on the Coweeta watersheds and a South Carolina piedmont soil have also shown uptake and leaching to result in reductions in soil nutrients (Knoepp and Swank, 1994; Richter et al., 1994). Long-term, chronosequence studies have also been important for understanding changes in soil processes following disturbance such as agriculture. Those studies have typically found a reduction in nutrients and C on managed sites, and then a "recovery" following reversion of the sites to trees. The control or reference sites are typically "undisturbed" forests, with the assumption that the soil conditions are relatively constant. Studies at the Walker Branch and Coweeta watersheds as well as elsewhere (e.g., Haines and Cleveland, 1981) have demonstrated that soil chemical properties are not constant in undisturbed stands; accordingly, understanding the inherent temporal dynamics of soil conditions is fundamental to assessing long-term changes as a result of external stressors (e.g., management or climate change).

We present an assessment of nutrients and C in soils and vegetation within eight sites for a 21-yr period on the WBW. Our objective is to characterize the temporal changes in the distribution of nutrients and C within the sites and to consider the changes with respect to forest type, soils, and geomorphic position. An earlier study of the WBW established the potential for nutrient depletion in these undisturbed forests, and considered the implications of assessing long-term soil changes at the landscape level following 10 yr of observation (Johnson et al., 1988). This study reinforces the findings from the previous work on the watershed and offers evidence to suggest that interactions of soil moisture regime and deep rooting may affect interpretations of nutrient cycling based on characterization of the surface soils. We also confirm that parent material and geomorphic posi-

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Abbreviations: ICP, inductively coupled plasma spectometry; WBW, Walker Branch Watershed.

tion are important in affecting soil properties with time (e.g., <20 yr).

MATERIALS AND METHODS

Site

Walker Branch Watershed is located on Chestnut Ridge within the Department of Energy's Oak Ridge Reservation near Oak Ridge, TN. The 97.5-ha watershed was established as a long-term ecological study area in 1967. The watershed is underlain by Knox group dolomite with several different formations occurring within the study area. The upland residual soils are developed from deep (up to 30 m) saprolite and saprolitic material, although areas of ancient and modern alluvium and colluvium of different ages also occur within the watershed boundary (Lietzke, 1994). Soils were originally mapped and representative pedons characterized with period procedures and concepts in 1967 (Peters et al., 1970). An intensive remapping and classification was accomplished in the early 1990s and published by Lietzke (1994). Major forest types were identified by Grigal and Goldstein (1971) and characterized predominately as upland hardwoods [oak (*Quercus* spp.), red maple (*Acer rubrum* L.), hickory (*Carya* spp.)] dominated by chestnut oak (*Q. prinus* L.) with some intermixing of pine [shortleaf pine (*Pinus echineta* Mill.) and Virginia pine (*P. virginiana* Mill.)] on ridges. Mesic coves and riparian zones are mainly yellow poplar (*Lirodendron tulipifera* L.) and American beech (*Fagus grandifolia* Ehrh.). The watershed is at ≈300 to 350 m elevation, has 14.5°C mean annual temperature, and receives ≈151 cm average annual precipitation of which 43–48% is estimated to undergo evapotranspiration (Henderson et al., 1978; Johnson et al., 1988).

In 1967, 298 vegetation inventory plots were established on the WBW per the protocol of Harris et al. (1973). Twenty-four of those plots were selected in 1972 to represent four major forest types (pine, yellow poplar, oak–hickory, and chestnut oak) for an intensive study of nutrient cycling. As part of that study, standing biomass, forest floor, and soils were sampled from four to six subplots at each location (Henderson and Harris, 1975; Henderson et al., 1978). Eight of those plots have served as the basis for assessing long-term changes in soil chemical properties and nutrient cycling (Johnson et al., 1988), and were resampled for this study.

The eight long-term soil study plots, although originally selected on the basis of cover type, represent different soil and geomorphic settings that are characteristic of the watershed locally, and more generally of the ridge and valley province of the Appalachians (Table 1). Three plots (Plots 179, 107, and 237) occur on soils formed in saprolite weathered from dolomite. They are characterized by a silt loam surface overlying a clay loam argillic horizon. The chert content is variable, ranging from 5 to 35%. Water infiltration is rapid, but perching may occur above the argillic. Two plots (Plots 98 and 281) represent the cove position that occurs near the base of the slope. The parent materials of the soils on these plots are derived from creep materials and underlying residuum. The soils are characterized by a thick, dark A horizon, tend to be moist, and are enriched by hydrologic inputs from up slope. Plot 26 is typified by saprolite weathered from dolomite, on the side slope of a doline. A doline is a collapse structure analogous to a sinkhole but without an open swallow hole. Plot 26 was originally selected to represent the pine-cover type, but because of mortality, the current vegetation is dominated by yellow poplar. Colluvial soils are typified by Plot 42. These soils are formed in deep colluvium derived from residual soils. The soils occur primarily in upper slope positions and may contain a restrictive fragic layer that can perch water. Chert content ranges from 15 to 50% by volume. Finally, soils that are formed in chert beds, 30 to 60% chert content by volume, are characterized by Plot 91. These soils occur in upper slope positions and tend to be dry due to the high coarse-fragment content.

Field and Laboratory

In spring 1993, the eight plots previously sampled in 1972 and 1982 were located by identifying the plot number on permanent aluminum corner stakes. The vegetation was remeasured and the soil resampled according to the sample

Table 1. Site characteristics of the eight long-term soil plots on Walker Branch Watershed, TN.

Plot	Soil/ geomorphic setting	Updated soil map unit†	Soil series	Soil classification	Slope position	Slope % /aspect	Current dominant vegetation	Original forest type‡
179	Saprolite	Dunmore-Chepultepec light surface phase	Fullerton cherty silt loam	Typic Paleudult; Clayey, Kaolinitic, Thermic	Upper slope near ridgetop	15/280	Chestnut oak, red maple	Chestnut oak
107	Saprolite	Dunmore-Chepultepec light surface phase	Fullerton cherty silt loam	Humic Paleudult: Clayey, Kaolinitic, Thermic	Secondary ridgetop	5.5/355	Black oak, hickory	Oak–hickory
237	Saprolite	Dunmore-Chepultepec light surface phase	Fullerton silt loam	Humic Paleudult: Clayey, Kaolinitic, Thermic	Midslope, slight depression	16/135	Chestnut oak, white oak	Chestnut oak
98	Cove	Fullerton-Longview clayey skeletal phase, Shack-Tassos Fragic Paleudults	Claiborne cherty silt loam	Humic Paleudult: Clayey, Kaolinitic, Thermic	Toe	10/130	Yellow-poplar, white oak	Yellow-poplar
281	Cove	Fullerton-Copperridge dark surface phase	Claiborne silt loam	Humic Paleudult: Clayey, Kaolinitic, Thermic	Toe	24/65	Yellow-poplar	Yellow-poplar
26	Doline-Saprolite	Dunmore-Chepultepec, light surface phase	Fullerton silt loam	Humic Paleudult: Clayey, Kaolinitic, Thermic	Mid Slope	5/260	Yellow-poplar	Pine
42	Collovium	Shack-Tassos Fragic Paleudults	Fullerton silt loam	Fragic Paleudults: Loamy-skeletal, Siliceous, Thermic	Ridgetop	13.5/160	Chestnut oak	Chestnut oak
91	Chert Bed	Bodine-Chapultepec	Bodine cherty silt loam	Typic Paleudults: Loamy-skeletal, Kaolinitic, Thermic	Secondary narrow ridgetop	12.5/110	Chestnut oak, hickory	Oak–hickory

† Updated soil classification from Lietzke (1994).
‡ Original classification by Grigal and Goldstein (1971).

procedures used previously. Using allometric equations established by Harris et al. (1973), change in tree biomass was calculated from measurements of diameter breast height on 0.0404-ha nested plots (Johnson and Van Hook, 1989). Vegetation nutrient contents were calculated from these mass data and nutrient concentrations obtained by destructive sampling on WBW (Henderson et al., 1978) and the Chestnut Ridge whole-tree harvest site (Johnson et al., 1982). More detailed descriptions of these procedures are found in the above publications.

Six 1-m^2 subplots within the 12-m^2 soil plot on each site were used for sampling. Subplots were randomly selected from the 12 by 12 m grid, excepting previously sampled subplots from the selection pool. Within each subplot, all wood of >2.5-cm diameter was collected. Wood of <2.5-cm diameter and the Oi and Oa horizons were sampled from a 0.25-m^2 ring located in the center of each subplot. Oi litter was defined as recognizable by species, while Oa was more highly decomposed forest floor (Oe material was included in the Oa sample). Using a 7.5-cm diameter bucket auger, soil cores were collected from the center of the subplot in 15-cm increments to a depth of 60 cm. The 60-cm depth was selected originally on the basis that most roots were present above that depth.

Twigs, bark, and leaves were separated from Oi and Oa samples before drying. Wood, woody litter, and O horizon samples were oven dried to constant weight at 100°C, while soil samples were dried at 60°C. Soil was separated from the coarse fragments with a 2-mm sieve. Forest floor samples were ground in a Tecator Cyclotec sample mill (Tecator, Herndon, VA). All soil and forest floor samples were stored in archival containers.

Samples collected in 1993 and archived samples from 1972 and 1982 were analyzed as follows. Soils were analyzed for pH using 1:1 soil solution in both water and 0.01 *M* $CaCl_2$. Carbon and N were determined using a Perkin Elmer 2400 CHN Analyzer (Perkin Elmer, Norwalk, CT). Exchangeable Ca^{2+}, Mg^{2+}, K^+, Na^+, and Al^{3+} were extracted with 1 *M* NH_4Cl and analyzed by inductively coupled plasma spectroscopy (ICP). Extractable P was obtained using dilute acid (0.5 *M* HCl) F (Olsen and Dean, 1965). Forest floor samples were analyzed for total N and C using a Perkin-Elmer 2400 CHN Analyzer (Perkin Elmer). Cation concentrations in the forest floor samples were obtained from an ICP scan following ashing and solubilization. All laboratory analyses included blanks, standards, and 10% duplication. Concentration data from mineral soils were converted to content using bulk density that had be adjusted for coarse fragment content from each soil horizon (Peters et al., 1970). Forest floor concentration data was converted to content using the actual mass of the sampled volume.

Design and Analytical Considerations

The principal factors affecting temporal assessment of soil data are season, sampling protocols, and laboratory methods. A previous study on the WBW (Johnson et al., 1988) documented significant seasonal fluctuations in soil chemical properties, hence the need to normalize season when assessing long-term trends. Since the sampling of the Walker Branch long-term soil assessment plots has taken place during the same month in each of the sampling years, seasonal variation should be minimized. Certainly there is some intraseasonal variation, but it is likely to be much smaller than the interseasonal variation that reflects larger shifts in temperature and moisture, especially in deeper soil horizons. Variation due to sampling was also minimized by using protocols that were identical to those used in the previous study (Johnson et al., 1988). Finally, variation in laboratory methods and techniques may cause significant variation in the analysis of a soil sample. To minimize this factor, samples from 1972 and 1982 were reanalyzed according to current methods. Accordingly, the temporal changes found in chemical soil properties should reflect responses to inherent ecosystem processes.

This study is based on plots that were originally selected as a subset of inventory plots to characterize selected forest types. Accordingly, replication was not a consideration in the original work. For purposes of this study, and the previously reported work from 1982, individual plots were considered as the experimental units. Analyses were conducted using a two-way analysis of variance (ANOVA) with year and plot as the treatment factors. Comparisons among years for individual plots was done using unpaired *t*-tests. Tests of significance were conducted at $P = 0.05$.

RESULTS

The 21-yr record for soils on the WBW includes samples collected from the A (0–15 cm) and B (45–60 cm) horizons. Results from these samples are presented first to assess change in soil chemical properties across the three measurement periods. Data for the entire 0- to 60-cm soil profile are available for the 1982 to 1993 period. Those results in conjunction with the biomass and forest floor data are presented to assess the ecosystem level changes during that 11-yr period.

Changes in Element Concentrations within the A and B Horizons

Surface and Subsurface Mineral Horizons

The concentration of Ca and Mg within the A horizon (0–15 cm) has been relatively stable during the 21-yr measurement period (Fig. 1). Some interdecade variation in base cation concentration is evident, but none of the surface mineral soil horizons exhibited either increasing or decreasing trends. Aluminum also did not exhibit significant changes. The content of cations within the A horizons does not appear to be strongly affected by soil type or physiographic position, although the cove soils (Plots 98 and 281) tended to have higher base cation content and lower Al than the other soils. In contrast, P concentrations were similar across soils, and most exhibited a reduction in P during the last 11-yr measurement period. The reduction in P was particularly pronounced on the saprolitic (Plots 107, 179, and 237) and the colluvial (Plot 42) soils, which experienced a 25 to 50% decline. Carbon and N tended to increase in the A horizon of all soils except for the saprolitic soils (Plots 107, 179, and 237), although the change was usually not statistically significant. The change in N relative to C was greater for the colluvium (Plot 42), chert (Plot 91), and doline (Plot 26) soils, resulting in a decrease in the C/N ratio. Conversely, the small change in N relative to C in the saprolitic soils resulted in an increase in C/N ratio. The cove soils (Plots 98 and 281) did not exhibit a change in C/N ratio.

The B soil (45–60 cm) has also exhibited changes in its chemical composition during the 21-yr measurement period (Fig. 2). Calcium and Mg exhibited a significant reduction in the first 10-yr period for all soils except

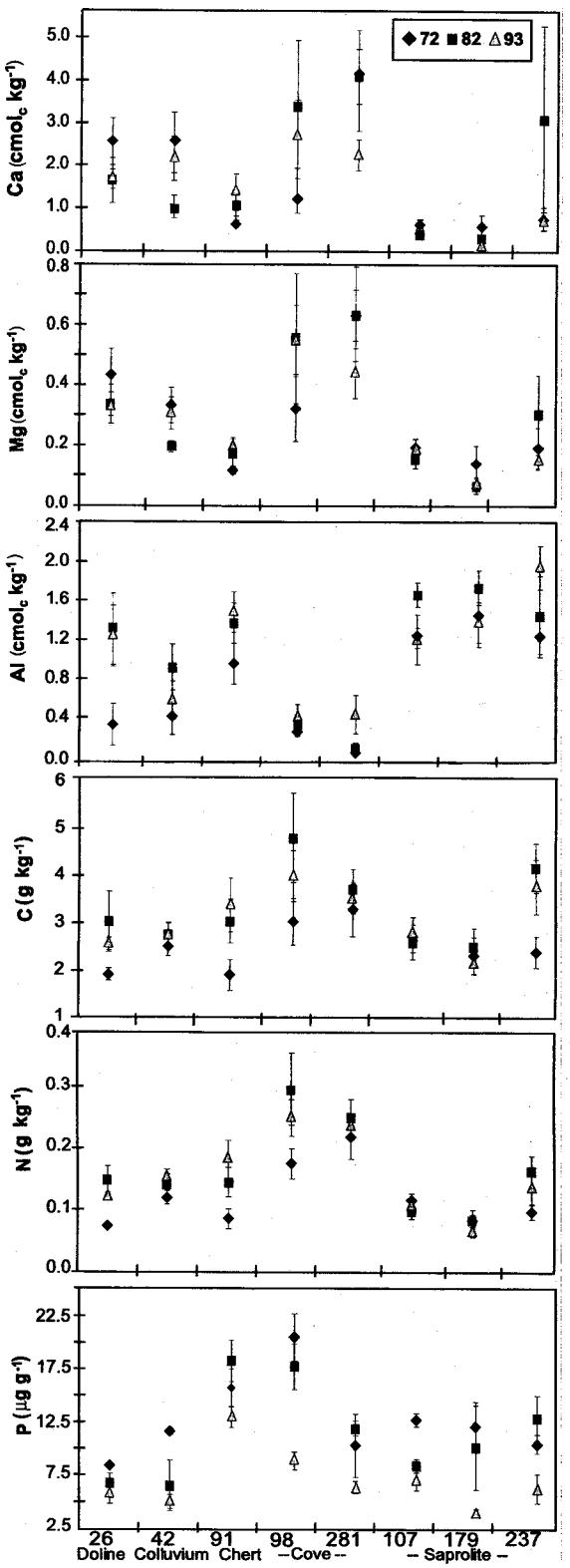

Fig. 1. Exchangeable Ca, Mg, Al, total C and N, and extractable P of soil from the A horizon (0–15 cm) in 1972, 1982, and 1993. Points represent means; extensions are the standard error. Note that the scales are different among the elements.

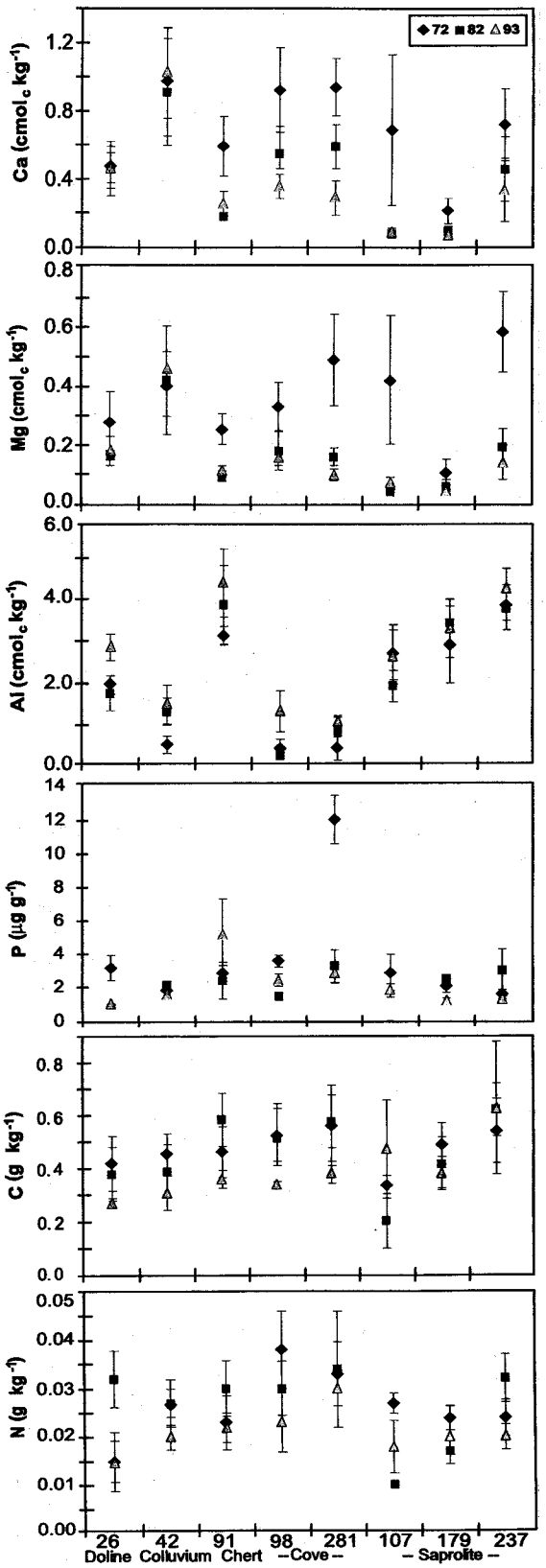

Fig. 2. Exchangeable Ca, Mg, Al, extractable P, and total C and N of soil from the B horizon (45–60 cm) in 1972, 1982, and 1993. Points represent means; extensions are the standard error. Note that the scales are different among the elements.

the deep colluvium (Plot 42) and doline (Plot 26). During the last 11-yr period, only the cove soils (Plots 98 and 281) exhibited a continued reduction in Ca. The influence of the doline on soil Ca and Mg concentrations was evident in Plot 26, which has shown consistent levels during the 21 yr. Similarly, the colluvial soil (Plot 42) has had constant Ca levels, presumably as a result of the high base status of the colluvium. Aluminum concentration in the B layer was greater than in the A layer. The concentration of Al in the B layer has been stable during the 21-yr measurement period for the saprolitic soils (Plots 107, 179, and 237), while the other soils showed increasing trends that were generally not statistically significant. Plots 26 (doline) and 42 (colluvium) continued to exhibit an increase in Al with no concomitant loss of cations. The cation loss in the B soil has not been accompanied by a decrease in pH except in the shallow colluvial soil (Plot 42). Phosphorus concentration in the B soil was relatively uniform across soil types and were low relative to the A layer. Phosphorus concentrations generally exhibited small reductions during the 21-yr period, although the changes are not significant (Fig. 2). Carbon concentrations in the B soil declined significantly in the cove soils (Plots 98 and 281) during the last measurement period. Other soils (Plots 26, 42, and 91) also exhibited reductions but differences were not statistically significant. Nitrogen concentrations also tended to be lower during the last measurement period, but the differences were not statistically significant. As a result of the corresponding changes in C and N, the C/N has remained consistent across measurement periods.

Forest Floor

Changes in forest floor nutrient pool size is a direct function of forest floor mass and nutrient concentration; those factors in turn are controlled by biomass production, organic matter decomposition, soil nutrient supply and nutrient retention. While periodic measurements of pool size does not allow an assessment of those causative factors, they do enable the assessment of the temporal changes and relationships with other soil and site variables. Litter (Oi) nutrient concentration is sensitive to soil supply and hence provides a more direct assessment of the interactions of long-term change in soil chemical properties and nutrient availability. Nitrogen concentrations declined in the Oi of the saprolitic (Plots 107, 179, and 237) and chert (Plot 91) soils (Fig. 3). Phosphorus concentration in the Oi followed the same pattern as the extractable P concentrations in the A soils, exhibiting significant reductions in the colluvial (Plot 42), chert (Plot 91), and the saprolitic (Plots 107, 179, and 237) soils for the entire measurement period. Similarly, Ca concentration in the Oi showed a significant reduction corresponding with the reduction in the B soil layer (45–60 cm) concentrations, excluding Plots 26 and 42. Magnesium concentration of the litter has increased, except for saprolitic soils (Plots 107, 179, and 237). The most pronounced increases in Mg concentration were on the colluvial soil (Plot 42) that has not experienced any change in mineral soil Mg or Ca.

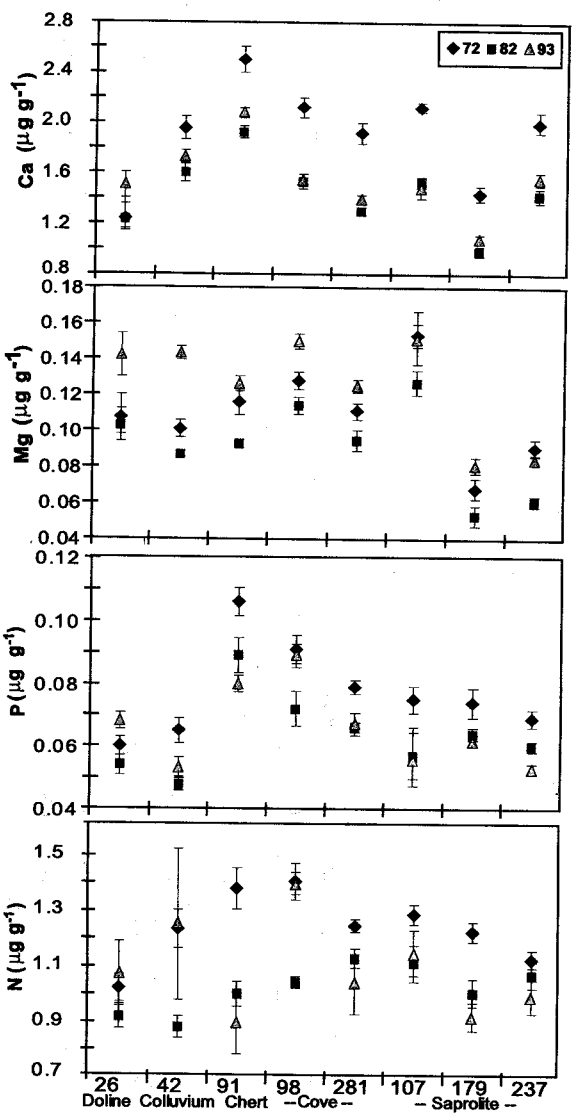

Fig. 3. Nutrient concentration within the Oi horizon for 1972, 1982, and 1993. Points represent means; extensions are the standard error. Note that the scales are different among the elements.

In contrast to the Oi horizon, nutrient concentration in the twig and Oa components of the forest floor did not show significant temporal changes and were relatively consistent among the three measurement periods. The forest floor mass (twigs, Oi, and Oa) showed a variable response among the plots, with most declining slightly during the last 11 yr (Table 2). Most of the change in forest floor mass is attributable to differences in Oi and twig components. Those components reflect recent (<5 yr) production and mortality. In contrast, the Oa reflects a more stable pool because it is partially decomposed and has a longer residence time. The cove soils (Plots 98 and 281) had the lowest forest floor mass. High moisture levels during the growing season in the coves promotes sustained decomposition; in contrast, the ridge soils (Plots 107, 179, and 237) exhibited periods of drought, thereby slowing organic matter decomposition. Otherwise, there was little discernible influence of cover type, parent material, and physiographic position on forest floor mass during the last 11 yr. Changes in forest floor

Table 2. Mean biomass, and C, N, P, Ca, Mg mass contained in the twig, Oi, and Oa components of the forest floor in 1972, 1982, and 1993.

	Plot 26			Plot 42			Plot 91			Plot 98			Plot 281			Plot 107			Plot 179			Plot 237		
	1972	1982	1993	1972	1982	1993	1972	1982	1993	1972	1982	1993	1972	1982	1993	1972	1982	1993	1972	1982	1993	1972	1982	1993
	kg ha^{-1}																							
	Biomass																							
Twigs	1 593	1326	1 683	4 760^{a}†	11 580^{b}	3 598^{a}	2 846	2 810	1233	1850^{a}	2 864^{a}	715^{b}	2490^{a}	2200	1008^{b}	1 220	2 742	1 466	1 206	3 020	1 265	1 856	4 928^{a}	1 135^{b}
Oi	10 950^{a}	7259^{b}	4 020^{c}	8 903^{a}	5 685^{b}	3 410^{c}	8 216^{a}	4 740^{b}	4296^{b}	6036^{a}	6 916^{a}	4296^{b}	7490^{a}	4964^{b}	2480^{c}	12 193^{a}	9 520^{a}	5 650^{b}	7 726^{a}	5 800^{a}	4 023^{b}	8 336^{a}	5 548	3 213^{b}
Oa	13 690	9772	14 131	17 956	15 940	14 516	23 463^{a}	11 115^{b}	9516^{b}	6000^{b}	10 792^{a}	3806^{b}	6446	9280	7980	22 790^{a}	32 876^{b}	20 470^{a}	30 203	36 830	24 706	17 123	21 600	21 246
	Carbon																							
Twigs	710	591	803	2 122^{a}	5 164^{b}	1 547^{a}	1 269^{a}	1 253	540^{b}	825^{a}	1 277^{a}	322^{b}	1110^{a}	981^{b}	414^{b}	544	1 223	605	538	1 346	571	828	2 197^{a}	513^{b}
Oi	4 839^{a}	3208^{b}	1 882^{c}	3 935^{a}	2 512^{b}	1 495^{c}	3 631^{a}	2 095^{b}	1875^{b}	2668^{a}	3 056^{a}	1271^{b}	3301^{a}	2194^{b}	1064^{c}	5 389^{a}	4 207^{a}	2 489^{b}	3 415^{a}	2 463^{a}	1 828^{b}	3 684^{a}	2 452	1 422^{b}
Oa	4 668	3332	4 931	6 123	5 435	4 907	8 001^{a}	3 790^{b}	3780^{b}	2046^{a}	3 680^{b}	1485^{a}	2198	3164	2588	7 771^{a}	11 210^{b}	6 541^{a}	10 299^{a}	12 559	6 959	5 839	7 365	6 449
	Nitrogen																							
Twigs	6	5	10	19^{a}	61^{b}	29	18	15	9	11^{a}	11^{a}	5^{b}	14^{a}	13	7^{b}	7	12	10	6	14	6	11	25^{a}	7^{b}
Oi	111^{a}	67^{b}	42^{c}	112^{a}	50^{b}	45^{b}	110^{a}	47^{b}	40^{b}	86^{a}	73^{a}	38^{b}	93^{a}	56^{b}	27^{c}	157^{a}	108^{b}	65^{c}	94^{a}	58^{b}	37^{c}	95^{a}	60	31^{b}
Oa	127	68^{a}	161^{b}	194	165	216	301^{a}	142^{b}	131^{b}	76	84	58	66	94	121	288	325	274	306	236	225	196	207	216
	Phosphorus																							
Twigs	0.3	0.3	0.5	1.3	3.1	0.6	1.5	1.3	0.7	0.7	0.8	0.3	0.8	0.8	0.4	0.3	0.7	0.5	0.4	0.9	0.4	0.6	1.7	0.3
Oi	6.5^{a}	3.9^{b}	2.7^{c}	5.8^{a}	2.6^{b}	1.8^{b}	8.7^{a}	4.3^{b}	3.4^{b}	5.6^{a}	4.9^{a}	2.4^{b}	5.9^{a}	3.2^{b}	1.7^{c}	9.3^{a}	5.6^{b}	3.1^{c}	5.7^{a}	3.7^{a}	2.5^{b}	5.9^{a}	3.3^{b}	1.7^{b}
Oa	7.1	4.3	7.7	11.1	9.0	7.8	23.4^{a}	11.3^{b}	8.5^{b}	5.0	7.2^{a}	2.9^{b}	4.2	5.0	5.1	17.1	19.9^{a}	13.9^{b}	17.7	16.4	11.8	11.8	12.6	11.9
	Calcium																							
Twigs	10	7	17	65^{a}	215^{b}	177	92^{a}	63^{a}	25^{b}	43^{a}	27^{a}	6^{b}	34^{a}	21	12^{b}	21	42	32	18^{a}	28^{a}	7^{b}	32	88	24
Oi	134^{a}	92^{b}	58^{c}	175^{a}	91^{b}	57^{b}	209^{a}	91^{b}	89^{b}	128^{a}	105^{a}	41^{b}	144^{a}	64^{b}	34^{c}	257^{a}	144^{b}	83^{c}	112^{a}	57^{b}	43^{c}	170^{a}	80^{b}	50^{b}
Oa	111^{a}	68^{b}	142^{a}	293	256	238	371^{a}	201^{b}	189^{b}	102	99	57	76	101	90	305^{a}	166^{b}	256^{a}	154^{a}	64^{b}	100	214	171	220
	Magnesium																							
Twigs	0.7	0.5	1.2	2.3^{a}	7.0^{b}	1.9^{a}	2.4	1.9	1.1	1.4^{a}	1.1^{a}	0.5^{b}	1.3^{a}	1.1	0.7^{b}	0.8^{a}	1.9^{b}	1.4	0.6	0.7	0.6	0.9	2.4^{a}	0.6^{b}
Oi	11.5^{a}	7.6^{b}	5.6^{b}	9.0^{a}	4.9^{b}	4.7^{b}	9.3^{a}	4.4^{b}	5.3^{b}	7.7^{a}	7.8^{a}	4.1^{b}	8.3^{a}	4.8^{b}	3.1^{b}	18.5^{a}	12.1^{b}	8.4^{c}	5.3	3.0	3.3	7.4^{a}	3.5^{b}	2.7^{b}
Oa	10.2^{a}	6.4^{b}	12.7^{a}	14.1	11.1	11.3	20.3^{a}	9.7^{b}	9.7^{b}	6.6	9.2	4.5	5.8	7.7	6.8	23.2	19.6	19.9	13.1	9.1	8.4	11.1	9.9	10.3

† Lower case letters indicate significant ($P < 0.05$) difference between years within plots for individual forest floor components.

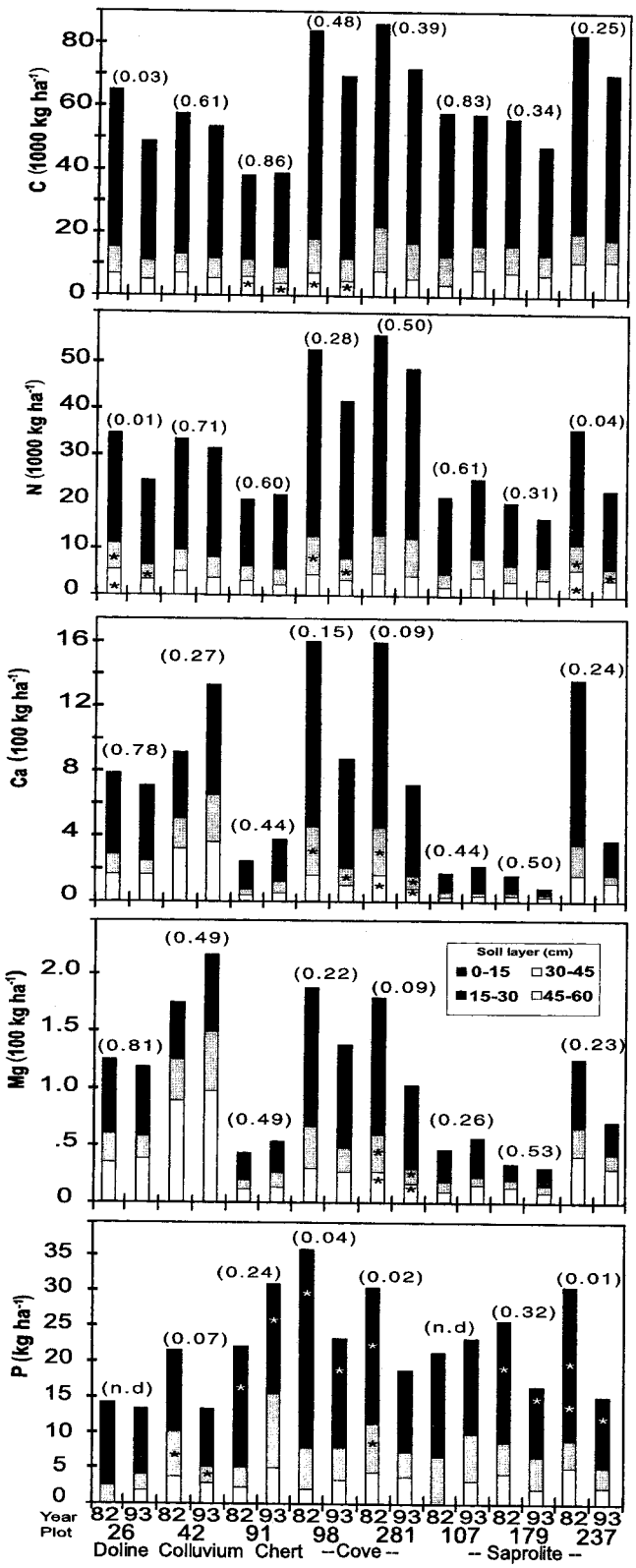

Fig. 4. Distribution of C, N, Ca, Mg, and P within the 0- to 60-cm soil depth in 1982 and 1993. The embedded asterisk indicates a significant difference (P = 0.05) between the years for the 15-cm soil increment; the P-value testing overall difference between years is given parenthetically above the bars for the plot. Note that the scales are different among the elements.

mass cause the total mass of C, N, P, Ca, and Mg to vary correspondingly (Table 2).

Whole Soil Changes (0–60 cm) during the Last 11 Years

In general, the whole soil (0–60 cm) results are consistent with observations made from the soil collected from the A and B horizons during the last 11 yr (Fig. 4). The decline in Ca was important among most of the soils, but it was particularly prominent for the cove soils (Plots 98 and 281), which exhibited a 52% reduction in Ca in the upper 45 cm. Plot 237 also exhibited a large reduction of Ca, while the other plots on saprolite (Plots 107 and 179) did not. The reduction in Ca appeared to be affected by the initial amounts. Plots 107 and 179 had low (<400 kg ha^{-1}) initial (1982) levels, as did Plot 91 (a chert soil); each subsequently showed little change during the 11-yr period. The only plot to show a significant increase in soil Ca in the upper 60 cm was the colluvial soil (Plot 42). The increase was particularly pronounced in the 0–15 and 30–45 cm depths. In each of the soils, the change in Ca and Mg was most evident in the upper 45 cm.

The reduction in P that was measured within in the A horizon was amplified when the 15- to 45-cm depth was considered. In each soil, except the chert (Plot 91), there was a consistent decline in P. For Plot 91, the increase in P was primarily within the upper 45 cm. The mean C content of the 0–60 cm zone within each of the soils declined during the last 11-yr measurement period (Fig. 4). However, only the change in Plot 26 was statistically significant. Among those soils, most of the reduction in C occurred within the 15- to 45-cm zone, although differences among individual sample layers were rarely significant. Nitrogen followed the same response as C except that the reduction in Plot 237 was significant. The loss of N from this plot corroborates the reduction in C, although the C analysis was more variable. Among all the soils, the cove (Plots 98 and 281) has the largest soil N pool.

Ecosystem Response

Carbon and nutrient pools for the forest floor and biomass of the eight plots in 1972, 1982, and 1993 are presented in Tables 2 and 3, respectively. The net increment by ecosystem component (soil to a depth of 60 cm, forest floor, and biomass) during the last 11 yr is presented in Fig. 5. Neither vegetation uptake nor biomass increment accounted for the reduction of Ca and Mg on cove soils (Plots 98 and 281) or Plot 237 of the saprolitic soils. In each of those soils, base cation loss was greater than accumulation in the vegetation or forest floor. The greatest positive increments in aboveground accumulation of Ca were on the saprolitic plots (Plots 107, 179, and 237). Plots 107 and 179, the ridge members in this group, had very low levels of extractable soil Ca, with the total pool significantly less than the net increment. The positive net increase in biomass Ca resulted in a net ecosystem gain for Ca on these plots. The colluvial site (Plot 42) was the only one to exhibit a net gain in Ca as a result of increases in extractable

Table 3. Mean amount of C, N, P, Ca, Mg contained in the tree biomass in 1972, 1982, and 1993.

Plot	Year	C	N	P	Ca	Mg
		kg ha^{-1}				
26						
	1972	73 715	333	31	615	77
	1982	86 531	391	33	672	86
	1993	87 197	394	33	671	84
42						
	1972	75 524	368	26	1453	53
	1982	84 852	411	29	1599	59
	1993	89 789	424	33	1721	70
91						
	1972	75 859	360	26	1396	80
	1982	84 998	405	29	1529	85
	1993	82 225	395	27	1393	64
98						
	1972	75 646	373	25	989	57
	1982	84 787	408	28	1121	70
	1993	108 159	433	29	1251	72
281						
	1972	87 393	413	31	710	84
	1982	102 458	480	36	826	97
	1993	109 487	509	38	804	101
107						
	1972	66 815	322	24	1453	76
	1982	87 305	417	31	1854	92
	1993	117 573	571	42	2522	115
179						
	1972	76 302	387	29	1098	56
	1982	88 864	451	33	1295	63
	1993	117 151	600	42	1746	78
237						
	1972	61 902	299	22	980	43
	1982	69 647	333	24	1136	48
	1993	83 521	400	27	1299	53

soil Ca. Sequestration in aboveground biomass did not appear to be a primary factor accounting for the decline in soil extractable P, except for Plot 107. As a result, five of the eight plots exhibited reductions in P during the last 11 yr.

Apparent net change in C within the plots is controlled by biomass increment and soils. Although all but one plot showed a net gain in biomass C during the last 11 yr, only three of the eight plots exhibited a net gain in C for the site (soil + vegetation). On the remaining plots (excluding Plot 91), soil C loss was a factor causing a net reduction in stored C within the site. However, due to inherent variability in the soil C measurements, the reductions are not statistically significant. Reductions in aboveground biomass caused the loss of C in Plot 91. Biomass increment (i.e., growth) was greatest on the saprolitic (Plots 107, 179, and 237) and cove (Plots 98 and 281) soils. Soil pools (to a depth of 60 cm) comprised ≈37% of the C storage in these forested ecosystems, with the aboveground biomass comprising the majority. We recognize that these estimates do not include root biomass and that the soil would contain a greater proportion of C if root biomass were included. Similarly, if a greater soil volume were included (e.g., >60 cm), the soil C pool would increase.

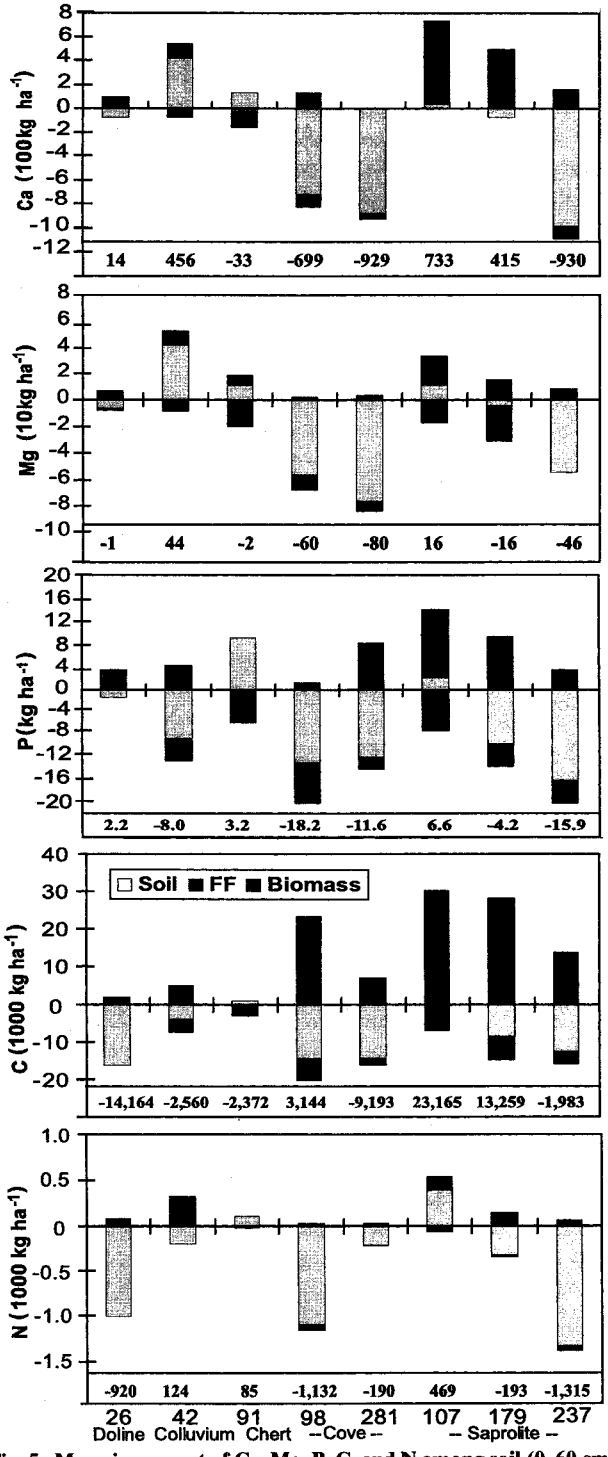

Fig. 5. Mean increment of Ca, Mg, P, C, and N among soil (0–60 cm), forest floor, and biomass between 1982 and 1993; the net total increment is presented below the bars. Note that the scales are different among the elements.

DISCUSSION

Changes Calcium and Magnesium

Vegetation uptake was identified as the primary cause of Ca loss on the WBW following the first 10-yr assessment period (Johnson and Todd, 1990). Uptake has also been reported to be a primary factor affecting Ca loss in Ultisols of the Appalachians (Knoepp and Swank, 1994), piedmont (Richter et al., 1994), and in young glaciated soils (Wilson and Grigal, 1995). However, in the 1982 to 1993 measurement period, uptake did not account for the Ca loss in five of the eight plots. On the saprolitic soils (Plots 107, 179, and 237), where Ca uptake was high, changes in soil Ca pools were insufficient to account for the change in biomass increment. In the case of Plots 107 and 179, soil decreases were less

than 20% of the biomass increment, thereby suggesting deep rooting as the mechanism for acquiring soil Ca. The residual soils are characterized by deep saprolite overlying dolomitic shelves and pinnacles (Lietzke, 1994). Presumably the roots on these plots have been exploiting some deeper source of Ca. Interestingly, these soils contained the lowest amounts of extractable Ca in the upper 60 cm, and the nutrient status of that zone would suggest Ca limitations to current and future growth. The high biomass increment and Ca sequestration on these two plots highlight the need to consider deeper soil depths. The implications of these findings for Plots 107 and 179 are inconsistent with reports on mixed oak stands where subsoil Ca was not considered to be an important source for trees (Wilson and Grigal, 1995). On each of the other plots, Ca uptake was either comparable to or lower than the respective soils increment. The only soil in the WBW to show a net increase in Ca in either period was the colluvial soil (Plot 42); this soil exhibited a small decline during the initial 10-yr period and a subsequent increase in the latest 11-yr period. The net change for the entire period was negligible for that plot.

Leaching is the primary mechanism attributed to reductions in soil Ca pools across a diverse set of Ultisols in the southeastern USA (Knoepp and Swank, 1994; Richter et al., 1994). Leaching was also attributed as the cause of Mg loss on the WBW following the first 10-yr assessment. Results from this study also suggest that leaching is an important cause of Ca loss. Sulfate is the primary anion associated with cation leaching in the southeastern USA (Johnson and Todd, 1990; Richter et al., 1994), although other anions and DOC may also be involved. While no leaching data were collected in this study, during the last 11-yr period the loss of soil Ca relative to fluxes into the forest floor or biomass was large for plots located in depressional settings (Plots 98, 237, and 281). Such low-lying topographic features function as a collection point for water, thereby increasing the potential for leaching. Leaching rates for Ca may range between 1 and 15 kg ha^{-1} yr^{-1} in southeastern Ultisols (Johnson and Todd, 1987; Richter et al., 1994). Accordingly, the losses measured in soils occurring in depressional positions greatly exceeded what would be expected. The only other site showing a net reduction in Ca was on the chert soil (Plot 91), and the cause was a reduction in biomass storage. Although the 45- to 60-cm depth layer showed a reduction in Ca, suggesting either leaching or uptake, the net soil increment (0–60 cm) was positive for plots representing the colluvium (Plot 42), chert (Plot 91), and one of the saprolitic soils (Plot 107). These data emphasize the need to consider adjacent soil layers within the primary rooting zone. The role of roots in Ca flux in these soils has not been considered, but it is likely to be an important factor. As previously noted, deep rooting is suspected as the mechanism for tapping deep subsoil sources of Ca. Correspondingly, retranslocation within the rooting zone may also be a means of affecting soil nutrient pools. Weathering is another mechanism for Ca release into the soil; however, the Ultisols on Walker Branch are highly weathered and weathering inputs are probably quite small (Johnson and Henderson, 1989).

There is little correspondence between the soil changes and the original forest types. Instead the soils on the ridge tops (Plots 91, 107, and 179) have lower levels than those in the mid-slope and depressional settings. The ridge soils are highly weathered, with no cation inputs other than atmospheric deposition. As a result, these soils showed little change during the last 11 yr. That response is expected to continue on those sites until the vegetation, with large Ca and Mg reserves, is recycled through the surface soil.

Acidification

Soil acidification usually occurs in agrading forests as a result of cation uptake and leaching losses (Binkley and Richter, 1987). Studying soil properties across 34 yr, covering conversion of an old field site to a loblolly pine (*P. taeda* L.) plantation, Markewitz et al. (1998) reported an increase in acidity that was primarily attributable to vegetation uptake, but that acid deposition was also an important factor, contributing an estimated 32% of the increased acidity. The Walker Branch soils did not show any consistent signs of acidification. The cove soils (Plots 98 and 281) did show a decline in pH and an increase in Al from the initial measurements in the B. The decline in pH is considered a result of cation leaching and Al release. Increased Al in the 45- to 60-cm B layer compared with the values from the initial measurements were also evident in Plots 26, 42, and 91, and has been attributed to the presence of polyhydroxy Al in the vermiculite clay of those soils (Johnson et al., 1988).

Phosphorus

Yanai (1992) developed a P budget for a northern hardwood forest where net P uptake by trees resulted in a net soil P decrease of 1.4 kg P ha^{-1} yr^{-1}. Reduction of P was primarily in the mineral soil, although the forest floor had a greater quantity of available P. The cumulative reductions measured in the upper 60 cm of soil on WBW during the last 11-yr period were within the range expected, assuming a net uptake of 1.4 kg P ha^{-1} yr^{-1}. However, P reductions in the soil and forest floor were not balanced by uptake in most of the stands on the WBW. Accordingly, there has been a net reduction in P representing a significant component of the extractable soil P. The reduction of soil P corresponded with those plots exhibiting changes in soil C. Yanai (1992) calculated that approximately one-third of the mineralizable soil P was in the organic fraction; accordingly, loss of that organic matter pool would further reduce potentially mineralizable P. Given that P leaching is minimal in these forest systems, the most probable explanation for the decline in soil extractable P is adsorption onto Fe and Al hydrous oxides. While we did not determine the fate of the P loss from the WBW plots, the net reduction in extractable soil P pools suggests the potential P limitations to forest growth in the future unless sources are available from deeper soil depths or

weathering. Correspondingly, the high proportion of the total ecosystem P contained in the biomass reflects the dependence of these forests on internal recycling of P.

Nitrogen

The first 10-yr assessment of soil changes on the WBW reported a small decline in soil N in the B horizons (Johnson et al., 1988). We also found a reduction in N across most soils, and the loss for some was great (900–1300 kg ha^{-1} yr^{-1}); however, despite the apparent large reductions, the reductions were not statistically significant except for Plots 26 and 237. For the other plots, within-plot variability was sufficiently large to preclude the detection of statistically significant differences. Few other studies have reported on the long-term changes of N in forest soils. Recently, a study on the Coweeta north and south reference watersheds also measured reductions in soil N during a 20-yr period (Knoepp and Swank, 1997). That study attributed the soil N loss to either leaching or transfers to soil pools below their 30-cm sampling depth. The reductions in soil N both in this study and the Coweeta study are contrary to many models that suggest a much more conservative soil N pool. For example, a model developed for Coweeta projected soil N losses of 4 kg ha^{-1} yr^{-1}, which is much less than the actual measured soil changes (Knoepp and Swank, 1997). The reductions in soil N at Coweeta were more pronounced on the north reference than the south watershed, suggesting to the authors that landscape position (e.g., precipitation, soil moisture, and particulate matter) had a significant effect on soil N pools. In the WBW, position did have a large affect on N pool size, with the highest pools in the cove (Plots 98 and 281) soils. However, changes in soil N were evident in soils with northeast (Plot 237) and southwest (Plot 26) exposures. Accordingly, the landscape position effect is not simple or direct.

Carbon

Soil C levels were expected to be constant or increasing given the undisturbed condition of the forest. The reduction in soil C, albeit quite variable for some soils, was unexpected. Lower C levels could suggest: (i) potentially important changes in the C balance of the site or active C pools (e.g., forest floor or soil organic matter), (ii) the importance of temporal variability in soil C pools, or (iii) a change toward a new equilibrium level. However, the overall differences noted among years for the 0- to 60-cm soil depth most likely reflects the variability and difficulty in detecting differences with relatively few samples for most sites. For those plots exhibiting relatively large reductions (Plots 26, 98, 281, 179, and 237), either a change in the organic matter inputs (e.g., production) or outputs (e.g., decomposition) are the primary mechanisms controlling soil C. Production levels did not correspond with changes in soil C pools, that is, sites exhibiting both high and low aboveground C sequestration rates exhibited loss of soil C. Carbon leaching is a small flux compared with CO_2 evolution (Johnson and Henderson, 1989); thus it is likely that decomposition is the primary factor affecting any reduction in soil C. Measurements from control stands on the southern reference watershed at Coweeta indicated declining soil C levels (Knoepp and Swank, 1997), but significant (>50%) interannual variation in soil C in A (0–10 cm) and B (10–30 cm) horizons effectively obscured definitive long-term trends or detection in net change in their 17-yr measurement period. The annual values exhibited a sinusoidal pattern, with peaks and troughs occurring within 3 to 5 yr in both horizons. Knoepp and Swank did measure a reduction in C in the A horizon in the northern reference forest during a 20-yr period, but due to the intraannual variability observed on the southern reference, they were uncertain about establishing a trend. Earlier work by Haines and Cleveland (1981) also reported significant seasonal variation in soil organic matter for several forest types. Testing a model on the development of soil C pools, Knoepp and Swank (1997) constructed a 70-yr chronosequence, originating with a clear-cut forest condition. They found that soil C pools would increase and then decline with time. A similar response was also reported by Snyder and Harter (1984) in northern hardwoods. However, other patterns have also been observed. Mattson and Smith (1993) reported that soil C pools did not change following cutting. In another study on the Oak Ridge Reservation adjacent to the WBW, Johnson and Todd (1998) reported net increases in soil C after 15 yr on sites that had been whole-tree and sawlog-only harvested, and the reference site for that study also exhibited a net soil C gain (11 Mg C ha^{-1}) in the upper 45 cm after 15 yr (1980–1995). That gain on a mixed oak site occurred on soils similar to those in this study. The differing response between these two sites on the Oak Ridge Reservation may be due to differences in slope, aspect, stand age, and development, as well as the sampling time and interval.

Other studies on long-term soil C changes have reported significant temporal changes that may be attributable to land management practices, vegetation type, temperature, precipitation, and soil physical and chemical properties. However, identifying the causative factor is often difficult because not all of the factors have been considered during the course of the study. While the role of temperature and soil moisture in regulating organic matter turnover in the short-term is well established (Olson, 1963), studies using long-term data have not attempted to consider the cumulative effect of the temperature and moisture factors on long-term soil C changes. Nor have studies of changes in soil C pools considered which organic matter fractions are contributing to the loss or change. Most organic matter fractionation schemes recognize labile and recalcitrant pools. The recalcitrant pools are considered to be "stable", with a turnover time typically measured in 100 to 1000 yr. Accordingly, the change in soil C measured in this study and others should reflect the change in the labile organic matter pool(s). If verified, seasonal and interannual variation in soil C pools would be expected as a result of changes in both biotic and abiotic factors that control organic matter turnover. Another limitation in

this study, and others assessing the effects of vegetation on soil C pools, is that belowground biomass production is not measured, thereby complicating the assessment of the sources of organic matter for the soil C pool. Other factors known to affect soil C pools include acidic precipitation, where competition for anion exchange sites between SO_4^- and DOC result in a reduction in soil C (Moore, 1997). However, mineralization, rather than leaching or changes in inputs, is probably the primary cause of reductions in soil C pools. Himes (1997) suggested that changes in soil C pools should induce changes in N and P pools corresponding with sequestration or mineralization. For most plots in this study, there was relative correspondence to the C/N (14:1) and C/P (70:1) ratios expected in soils when there was a reduction in soil C. On Plot 91, which exhibited a gain in soil C, there was great deviation from the reference norm, with a C/N gain of 7 and a C/P gain of 15.

This study and the relatively few other long-term studies on forest soil C pools demonstrate the variable and dynamic nature of the pools. As a result, there is danger in presuming whether mineralization or sequestration is occurring at any given point in time. It is well established that conversion of wildland soils to cultivation results in significant reductions in soil C pools (Mann et al., 1988). Similarly, reforestation of agricultural or disturbed sites is presumed to result in soil C gains. However, C pools in a mature forest soil must have some dynamic equilibrium range that is controlled by physical and chemical soil properties, biomass production and allocation, nutrients, and ambient conditions. The data from Walker Branch and Coweeta watersheds suggest that range may be quite large, and subject to both short- and long-term variation. Recognizing the dynamic nature of soil C pools in what appears to be a stable forest environment highlights the need for caution when assessing soil C sequestration potentials, modeling soil C fluxes, or assessing the role of soils in long-term C sequestration.

CONCLUSIONS AND PERSPECTIVES

Parent material, physiographic position, vegetation, time, and climate have long been recognized as factors affecting soil properties at any point in time. While this study cannot elucidate the effects of each of those factors, our results demonstrate the dynamic interactions that can occur during a relatively short period of time (21 yr) and the importance of considering spatial and temporal factors in any study that attempts to scale results to the watershed or landscape level. Soil parent material and physiographic setting are primary factors affecting nutrient status of the solum (<1 m depth). Leaching has been shown to be a primary factor affecting base cation loss, particularly in topographic positions that concentrate the flow of water or on upper slope positions that do not receive inputs from uphill sources. Also, the importance of the soil geomorphic setting is manifested in the different responses measured on the doline, colluvial, and chert soils. While the soil series may be the same or similar, the geomorphic setting is critical to understanding factors that may not be evident from the vegetation or near-surface soil properties.

A major finding after the first 10 yr of this study was the potential for cation depletion in these soils, particularly if vegetation were removed from the site (Johnson et al., 1988). That work prompted considerable interest and concern regarding the potential effects of whole-tree harvesting on sustainable nutrient supplies. As a result, numerous studies have been conducted confirming the potential for productivity decline as a result of nutrient removal in biomass. However, a major limitation of most of the forest soil assessments is that usually only the upper 50 to 100 cm of soil are considered. This practice is rationalized by the fact that the largest proportion of the roots is found near the surface. Interestingly, one of the important distinctions that forest soil scientists make about forest soils is that the trees are long lived and deep rooted, thereby affecting soil processes. While inferred, the effects of deep rooting on nutrient cycling have not been extensively studied. Our results suggest that deep rooting is a major factor controlling cation uptake in mature forests: although the upper 60 cm showed cation loss, productivity was sustained, apparently by deep soil pools. Similarly, cation cycling through deep rooting is presumably responsible for maintaining the cation balance on those sites not exhibiting cation loss. The capacity of deep soil supplies to satisfy present nutrient cycling demands has not been widely recognized. Both the role of rooting and deep soil pools need to be considered in future nutrient cycling studies.

The original nutrient cycling study was designed to consider differences among cover types within the WBW. As a result of natural stand development and succession, the cover types have changed during the past 21 yr, reflecting the ephemeral nature of forest types as the basis for identifying sites. Site classification systems that integrate soils, understory, and overstory have been used effectively to identify sites or ecosystem units that have similar functions. Our work reemphasizes the inadequacy of forest cover type as a common denominator for assessing nutrient cycling or other soil processes. Although, cover type and species distribution do tend to correspond with soils (Lietzke, 1994), reflecting both nutrient and moisture regimes.

Agrading forests are considered to be net C sinks, and mature forests are usually in equilibrium. Our results indicate that forests may be a net source of C when net aboveground productivity is low. Loss of soil C, the factor causing the net release of C from the ecosystem, is presumed to be primarily a result of decomposition. Temporal variability in soil C pools is known to be significant. Whether the results from three measurement points in this study during a 21-yr period represent a consistent trend is uncertain. Accordingly, considerably more work is needed to assess long-term soil C pools, organic matter fractions, and factors controlling organic matter dynamics in mineral soil horizons.

Originally, three soils and four cover types were recognized for this long-term study of nutrient cycling, suggesting a relatively simple system. The cumulative find-

ings for the 21-yr assessment period highlight the complexity of this upland landscape and the nuances in the interactions of vegetation, soils, and geomorphic position. These results further highlight the danger in extrapolating findings from one site or study to other sites or regions. Within the WBW, sites varied from a net source to a sink for cations, C, P, and N. Accordingly, any generalization derived form one particular site could be wrong for another site on the watershed. Unfortunately, we have not been able to directly determine the causes of changes in nutrient and C pools; that understanding would be useful in developing a more generalizable approach for thoroughly assessing long-term nutrient cycling. However, our consideration of the causative factors is well grounded in the literature and research on the WBW. Hence, this work should provide a basis for testing ideas and models regarding sustainable productivity and nutrient cycling.

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