Aboveground biomass and nutrient accumulation 20 years after clear-cutting a southern Appalachian watershed

Katherine J. Elliott, Lindsay R. Boring, and Wayne T. Swank

Abstract: In 1975, we initiated a long-term interdisciplinary study of forest watershed ecosystem response to clear-cutting and cable logging in watershed 7 at the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains of North Carolina. This paper describes ≈20 years of change in species composition, aboveground biomass, leaf area index (LAI), and nutrient pools in the 59-ha mixed hardwood forest of watershed 7 following commercial clear-cutting in winter 1977. We measured woody species in 24 permanently marked plots before cutting in 1974 and during subsequent years (1977–1997). By 1997 (≈20 years after cutting), aboveground biomass was 81.7, 96.9, and 85.4 $Mg \cdot ha^{-1}$ in the cove hardwood; mesic, mixed-oak; and dry, mixed-oak communities, respectively. Leaf biomass and LAI accumulated relatively faster than total aboveground biomass in all three communities. By 1984, only 7–8 years after cutting, leaf biomass and LAI were nearly equal to the amount estimated for the precut forest. In 1997, nitrogen accumulation was 36, 44, and 61% and phosphorus accumulation was 48, 66, and 59% in the cove-hardwoods; mesic, mixed-oak; and dry, mixed-oak communities of the corresponding precut communities, respectively. Potassium, calcium, and magnesium accumulations were less than either nitrogen or phosphorus accumulation.

Résumé : En 1975, nous avons initié un projet multidisciplinaire à long terme pour étudier la réaction de l'écosystème forestier d'un bassin-versant à une coupe à blanc et au débardage par câble. L'étude a été réalisée dans le bassin-versant 7 au Laboratoire hydrologique de Coweeta dans la partie sud des Appalaches, en Caroline du Nord. Cet article décrit les changements survenus sur une période de ≈20 ans dans la composition des espèces, la biomasse épigée, l'indice de surface foliaire (LAI) et les pools de nutriments dans une forêt feuillue mixte de 59 ha du bassin-versant 7, suite à une coupe à blanc commerciale à l'hiver 1977. Nous avons mesuré les espèces ligneuses dans 24 parcelles identifiées de façon permanente avant la coupe, en 1974, et au cours des années subséquentes (1977 à 1997). En 1997 (≈20 ans après la coupe), la biomasse épigée atteignait respectivement 81,7, 96,9 et 85,4 $Mg \cdot ha^{-1}$ dans les communautés riveraines et dans les communautés mésiques et xériques de chênes mélangés. La biomasse foliaire et la valeur de LAI ont augmenté un peu plus vite que la biomasse épigée totale dans les trois communautés. En 1984, seulement 7–8 ans après la coupe, la biomasse foliaire et la valeur de LAI étaient presque identiques aux valeurs obtenues avant la coupe. En 1997, l'accumulation d'azote atteignait respectivement 36, 44 et 61% et l'accumulation de phosphore, 48, 66 et 59% dans les communautés riveraines de feuillus et dans les communautés mésiques et xériques de chênes mélangés comparativement aux valeurs avant coupe dans les communautés correspondantes. Les accumulations de potassium, de calcium et de magnésium étaient inférieures à l'accumulation d'azote ou de phosphore.

[Traduit par la Rédaction]

Introduction

In forest ecosystems, post-disturbance biomass accumulation provides an index of carbon sequestration and the reestablishment of biological control over a variety of ecosystem processes, including those controlling water and nutrient cycles and losses (Swank et al. 2001). Thus, the rates and controls on biomass accumulation in aggrading secondary successional forests (sensu Bormann and Likens 1979; Oliver and Larson 1990) have implications when refining forest growth and nutrient cycling models (Mäkelä et al. 2000; Johnson et al. 2000). Numerous studies have shown that vegetative regrowth (i.e., biomass production) following disturbance is a function of climate (O'Neill and DeAngelis 1981; Pastor and Post 1986; Gholz et al. 1990; Mickler and Fox 1998), soil-nutrient status (McGuire et al. 1992; Kimmins 1996; Reich et al. 1997), disturbance size and intensity (Runkle 1985; Kimmins 1996), species composition prior to disturbance, and life history strategies of surviving and colonizing species (Peet and Christensen 1980; Canham and Marks 1985; Huston and Smith 1987).

Numerous experiments in the Coweeta Basin have focused on the resistance and resilience of southern Appalachian forests after large-scale disturbance (see Waide et al. 1988; Swank et al. 2001). In 1975, a long-term interdisciplinary study of forest watershed ecosystem response to clear-cutting and cable logging in watershed 7 (WS7) was initiated at the Coweeta Hydrologic Laboratory in the south-

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ern Appalachian mountains of North Carolina (Swank and Caskey 1982). Investigators found that clear-cutting in WS7 increased mean monthly temperatures by 8–11°C for the period May–October at the litter–soil boundary the first year after cutting. It also reduced forest floor litter moisture, increased soil moisture (Swank and Vose 1988), altered microarthropod activity in the litter (Seastedt and Crossley 1981; Seastedt et al. 1983*b*), and reduced first-year decomposition of woody litter, especially on xeric, south-facing slopes (Abbott and Crossley 1982). Other experiments on how clear-cutting affects vegetation dynamics have addressed the silvicultural and ecosystem aspects of early forest regeneration (Boring 1979; Boring et al. 1981, 1988; Parker and Swank 1982; Boring and Swank 1984; Leopold and Parker 1985; Leopold et al. 1985) and long-term changes in species composition and diversity (Elliott and Swank 1994*a*; Elliott et al. 1997, 1998). In a recent paper about WS7, Swank et al. (2001) described ≈20 years of change in water yield, the storm hydrograph, stream inorganic chemistry, and sediment yield. Our objective in this paper was to summarize ≈20 years of change in species composition, aboveground biomass, and nutrient accumulation in live vegetation for a 59-ha mixed-hardwood forest after commercial clear-cutting.

Material and methods

Study area

The study site, a 59-ha watershed (WS7), is located in the Coweeta Hydrologic Laboratory (35°04′30″N, 83°26′W) near Franklin, N.C. The Coweeta Basin is in the Nantahala Mountains, part of the Blue Ridge province in the southern Appalachians. WS7 has a south-facing aspect and ranges in elevation from 720 to 1065 m. Slopes range from 23 to 81%. Parent rocks of schist and gneiss have weathered to form deep soils with rock outcrops present on steep slopes at higher elevations (Hatcher 1974). At lower elevations, the dominant soil series is the Tusquitee, a member of the fine-loamy, mixed, mesic family of Humic Hapludults. Ridge and slope soils are dominated by the Chandler series, a member of the coarse-loamy, micaceous, mesic family of Typic Dystrochrepts (Thomas 1996). The mean annual temperature is 13°C; mean temperatures are 6.7°C in the dormant season and 18.5°C in the growing season. Mean annual precipitation is 183 cm (Swift et al. 1988).

Historically land use in the Coweeta Basin has included selective logging, woodland grazing, and burning. Before 1842, Cherokee Indians burned semiannually to improve forage for livestock. Between 1842 and 1900, European settlers also burned and grazed livestock in the basin. Between 1900 and 1923, logging operations occurred over the entire area, but cutting was heaviest on the lower slopes, valleys, and accessible coves. Since 1924, human activities have been restricted to experimental studies (see Douglass and Hoover (1988) for a complete description of the history of the Coweeta Basin). In a woodland grazing experiment on a portion of the watershed between 1941 and 1952, investigators assessed the impact of six head of cattle. Short-range effects primarily consisted of soil compaction and overgrazing in the cove area adjacent to the stream (Johnson 1952; Williams 1954).

Harvesting of WS7, begun in January 1977, was completed in June. Merchantable volume was tractor skidded on slopes less than 20% (about 9 ha); mobile cable-yarding system was used on the remaining area. A portion of the trees cut on ridgetops and xeric slopes were not cable logged because those areas had an inadequate volume of merchantable timber. All stems ≥2.5 cm diameter at breast height (DBH) were cut, and logging debris was left in place. No further site-preparation activities were conducted. This harvest technique reduced soil compaction and other structural disturbances of the forest floor and plant roots.

Sampling procedures

Before clear-cutting, we inventoried vegetation on 142 plots (20 × 40 m) systematically located in the watershed. Referring to previous studies (Williams 1954; Day et al. 1988), we identified three community types in WS7: (*i*) cove hardwoods at lower elevations and along ravines at intermediate elevations; (*ii*) mixed-oak hardwoods on mesic, southeast- and north-facing slopes at intermediate elevations; and (*iii*) mixed-oak hardwoods on dry to xeric southwest- and south-facing slopes at intermediate to upper elevations and ridgetops (previously described as hardwood-pine, but this community has only a minor component of pine). We classified plots into community types based on detrended correspondence analysis (DCA) (Gauch 1982) that used precut woody vegetation data from 1974 for 24 of the permanently marked plots (Elliott et al. 1997). The aerial coverage was approximately 15% for the cove hardwoods; 25% for the mesic, mixed oak; and 60% for the dry, mixed oak (Boring and Swank 1986). After clear-cutting in 1977, we sampled 18 of the 142 plots for regrowth: 8 in the cove hardwoods; 5 in the mesic, mixed-oak hardwoods; and 5 in the dry, mixed-oak hardwoods. In 1978, 5 plots from the 18 were dropped and 11 plots from the remaining 124 were added to total 24 permanently marked plots. We increased sample size in the mesic, mixed-oak and dry, mixed-oak communities to reflect their larger aerial coverage within the watershed. Seven plots represented the cove hardwoods; 7, the mesic, mixed-oak hardwoods; and 10, the dry, mixed-oak hardwoods. The 24 plots were remeasured in subsequent years (1979, 1984, 1993, and 1997) to observe changes in vegetation composition through succession.

Two quadrats (each 7 × 7 m) were located in opposite corners of each 0.08-ha plot. In 1977, we sampled hardwood sprouts in the 7 × 7 m quadrats and sampled seedlings in 3 × 3 m subplots; values were pooled for each pair. In years 1979 through 1997, woody species > 0.5 m height were sampled in 7 × 7 m quadrats. At the end of each growing season, we recorded densities by species and diameter class on each sample quadrat. Diameter classes were designated by 0.5-cm intervals up to a maximum of 3 cm in the first year (1977) and by 1.0-cm intervals up to a maximum of 8 cm for years 1979 and 1984. The diameter of different species was measured at 3 and 40 cm from ground level, depending on the species' potential growth rates. The 3-cm measurement gave the best fit for coupling biomass regression equations for slow-growing species; 40 cm was best for fast-growing species (Boring et al. 1981). In 1993, woody stems with a DBH ≥1.0 cm were measured to the nearest 0.1 cm at 1.37 m from ground level, and woody stems <1.0 cm DBH and >0.5 m height were measured at 3 cm

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Table 1. Allometric equations for aboveground biomass of woody species in watershed 7, data collected in 1988 and 1997 combined.

Species	n	Allometric equation	r^2	MSE	p	DBH (cm) Mean	DBH (cm) Range
Log_{10}(branch biomass)							
Acer rubrum	12	1.212 64 + 2.579 34 ($\log_{10}$ DBH)	0.91	0.016 78	0.0001	9.2	5.0–16.8
Cornus florida	10	1.578 44 + 2.522 67 ($\log_{10}$ DBH)	0.93	0.013 75	0.0001	4.8	2.3–8.1
Liriodendron tulipifera	16	0.719 55 + 2.704 44 ($\log_{10}$ DBH)	0.93	0.046 58	0.0001	12.6	3.1–31.0
Quercus prinus	13	0.465 97 + 3.305 05 ($\log_{10}$ DBH)	0.86	0.016 56	0.0001	12.6	9.2–17.5
Quercus rubra	12	0.209 48 + 3.701 07 ($\log_{10}$ DBH)	0.95	0.013 80	0.0001	8.0	5.1–15.0
Robinia pseudoacacia	23	1.076 82 + 2.532 62 ($\log_{10}$ DBH)	0.87	0.053 86	0.0001	13.5	4.2–30.6
All oaks	27	0.541 01 + 3.280 05 ($\log_{10}$ DBH)	0.94	0.017 58	0.0001	10.8	5.1–17.5
All tree species	43	1.582 38 + 2.113 19 ($\log_{10}$ DBH)	0.77	0.088 66	0.0001	9.7	2.3–31.0
Log_{10}(stem biomass)							
Acer rubrum	12	2.041 01 + 2.324 87 ($\log_{10}$ DBH)	0.97	0.003 92	0.0001		
Cornus florida	10	2.107 27 + 2.061 36 ($\log_{10}$ DBH)	0.86	0.019 86	0.0001		
Liriodendron tulipifera	16	1.902 72 + 2.337 25 ($\log_{10}$ DBH)	0.98	0.010 00	0.0001		
Quercus prinus	13	1.732 50 + 2.593 78 ($\log_{10}$ DBH)	0.93	0.004 99	0.0001		
Quercus rubra	12	2.007 03 + 2.350 49 ($\log_{10}$ DBH)	0.94	0.007 44	0.0001		
Robinia pseudoacacia	23	1.759 11 + 2.603 92 ($\log_{10}$ DBH)	0.98	0.008 75	0.0001		
All oaks	27	2.009 99 + 2.338 66 ($\log_{10}$ DBH)	0.96	0.005 77	0.0001		
All tree species	43	1.904 43 + 2.377 35 ($\log_{10}$ DBH)	0.96	0.017 54	0.0001		

Note: The allometric equation was as follows: dry mass (g) = $a + b$(DBH (cm)), where DBH is diameter at breast height (3.7 m above ground).

from ground level. In 1997, stems ≥5.0 cm DBH were measured at 1.37 m from ground level, and stems <5.0 cm DBH and >0.5 m height were measured to the nearest 0.1 cm at 3 cm from ground level.

Coupling regression analysis with sample plot measurements, we used standard dimension analysis techniques to estimate aboveground biomass and leaf area of woody species. To establish regression equations, we sampled individual young hardwoods (mostly of sprout origin) each August from years 1–3 at randomly chosen sample points within the study area (Boring et al. 1981). For year 8, hardwoods were sampled from adjacent sites in the Coweeta Basin (Boring and Swank 1986). We cut sample individuals at ground level or at the point of sprout origin on the stump. Diameters were measured at 3 and 40 cm from the base; the 3-cm measurement gave the best fit for slow-growing species, and 40 cm was best for the fast-growing species. All leaves were removed, bagged, dried at 70°C, and weighed. Stems and all branches were similarly dried and weighed (Boring and Swank 1986).

Specific leaf area (SLA; $cm^2 \cdot g^{-1}$) estimates were determined using leaf surface area/dry mass ratios measured on 20–40 leaves for each of 21 woody species in years 1977 (first growing season after cutting), 1979 (3 years after cutting), and 1984 (8 years after cutting). These ratios were established by subsampling leaves from several individuals of each species, measuring leaf area with a LI-COR portable leaf area meter (Lambda Instrument Co., Omaha, Nebr.), then drying and weighing the leaves. In 1993 (17 years after cutting) and 1997 (21 years after cutting), SLA was determined in the same manner as previous years using 10 of the dominant tree species. Leaf area index (LAI) was calculated as leaf biomass multiplied by SLA for each sample year.

After clear-cutting, all herbaceous vegetation was harvested in August each year (1977–1993) from one randomly placed 1.0-m^2 subplot within each quadrat. Vegetation was separated by species and oven-dried at 70°C to constant mass. All species identification followed nomenclature consistent with Radford et al. (1968).

Plant tissue samples were dried at 70°C and ground in a Wiley mill to pass through a 1-mm sieve. For years 1977 and 1979, phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) were analyzed on a Jarrell–Ash plasma emission spectrograph (Jones 1977; Fassel 1978) at the University of Georgia Institute of Ecology (Boring 1982). Total nitrogen (N) was determined on a Coleman Micro-Dumas nitrogen analyzer (Bremner 1965). In 1982 and 1997, plant tissue samples were analyzed for N with a Perkin-Elmer 20400 CHN elemental analyzer (Perkin Elmer Corp., Norwalk, Conn.), for P with a Perstorp Enviroflow 3500 ion chromatograph (Alpkem Corp., Wilsonville, Oreg.), and for cations (K, Mg, and Ca) with a Perkin-Elmer 300 atomic adsorption spectrophotometer (Perkin Elmer Corp., Norwalk, Conn.) at the Coweeta Hydrologic Laboratory using procedures outlined by Deal et al. (1996). The nutrient content of the plant biomass was determined by multiplying the nutrient tissue concentration for each species by aboveground biomass for the tissue.

Data analyses

To estimate aboveground biomass for years 1977 and 1979, we used allometric equations from Boring et al. (1981) for 1- to 3-year-old saplings. For 1984, we used allometric equations from Boring and Swank (1986) for 8-year-old saplings. For years 1993 and 1997, we used allometric equations from Martin et al. (1998) for leaf bio-

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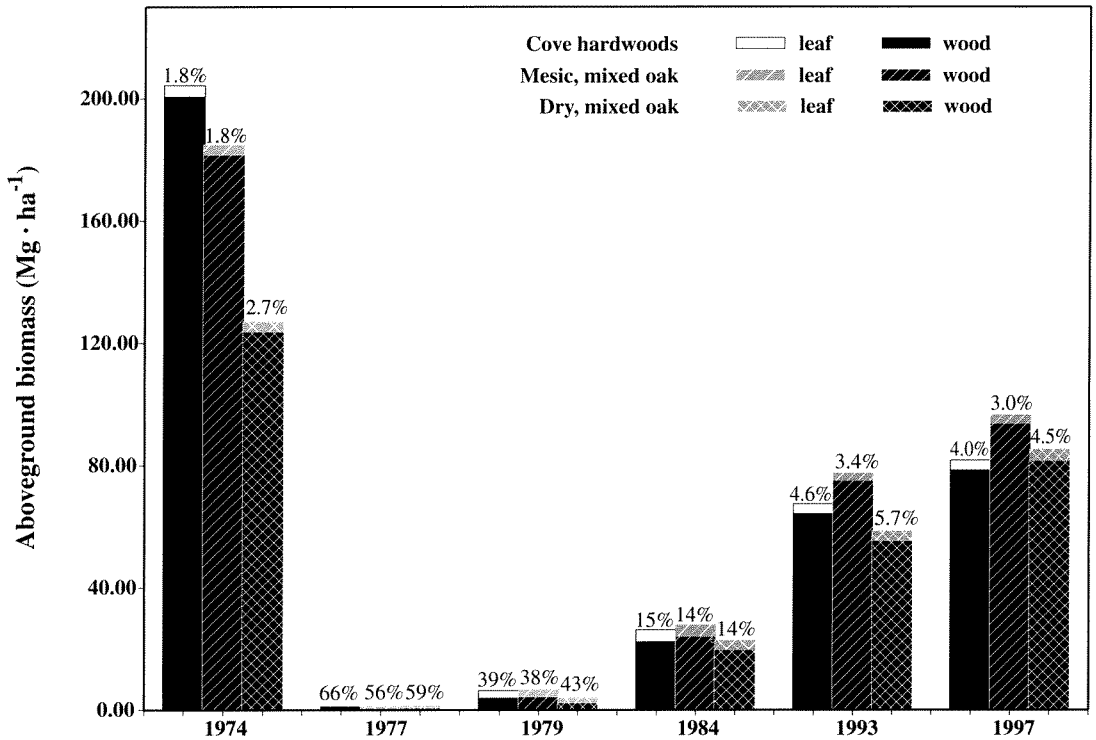
Fig. 1. Aboveground live biomass of woody species (≥1.0 cm diameter base of stem) and herbaceous layer species (herbaceous + woody species < 0.5 m height) for the three community types (cove hardwoods; mesic, mixed oak; and dry, mixed oak) before cutting (1974) and after cutting (1977, 1979, 1984, 1993, and 1997) for WS7, Coweeta Basin, western North Carolina. The herbaceous layer was not sampled in 1997. Values above bars are percent contribution of leaf tissue to total aboveground biomass.



mass. To validate the leaf biomass and LAI estimates for WS7, two litterfall traps were placed in each of the 7 × 7 m permanent plots; litter was collected every 2 months beginning the first week of October 1999, through April 2000 (cessation of leaf fall for the oaks, which retain their leaves longer than other deciduous hardwoods). Based on leaf fall collected in litter traps in 1999, mean LAI was 3.99 ± 0.173 (mean ± SE) for the cove hardwoods; 3.50 ± 0.178 for the mesic, mixed oak; and 4.24 ± 0.212 for the dry, mixed oak. LAI was also estimated by measuring light transmission within plots with the LI-COR LAI-2000 plant canopy analyzer (LI-COR 1992; Deblonde and Penner 1994). Based on measurements with the LAI-2000, mean LAI was 4.07 ± 0.277 for the cove-hardwood, 3.42 ± 0.110 for the mesic mixed-oak, and 3.72 ± 0.145 for the dry, mixed-oak communities. In 1997, based on leaf biomass equations from Martin et al. (1998), mean LAI was 3.57 for the cove-hardwood; 4.13 for the mesic, mixed-oak; and 4.23 for the dry, mixed-oak communities. Both the litter trap and the LAI-2000 methods suggested that allometric equations from Martin et al. (1998) provided reasonably good estimates for leaf biomass in WS7. In addition, no significant differences were detected between litterfall collections and allometric equations for any of the three communities: cove (paired t test; $t = 0.639$, $p = 0.535$); mesic, mixed oak (paired t test; $t = -0.537$, $p = 0.600$); and dry, mixed oak (paired t test; $t = -1.397$, $p = 0.181$).

To estimate branch and stem biomass for years 1993 and 1997, we developed allometric equations using a log–log transformation (PROC GLM; SAS Institute Inc. 1990). For this study, trees were harvested and destructively sampled (Table 1) using dimension analysis procedures outlined in Martin et al. (1998). Allometric equations for estimating branch and stem biomass are presented in Table 1. A general equation (i.e., Table 1, all trees) was applied to the minor species that were not destructively sampled for dimension analysis.

Results

Aboveground biomass and LAI

Before clear-cutting (1974), aboveground biomass was 204.3, 185.0, and 127.2 Mg·ha^{-1} in the cove-hardwood; mesic, mixed-oak; and dry, mixed-oak communities, respectively (Fig. 1). The first growing season after cutting, aboveground biomass was ≤1.6 Mg·ha^{-1} in each community, a small fraction of the precutting biomass. Herbaceous-layer species contributed 18, 8, and 14% to the aboveground biomass in the cove-hardwoods; mesic, mixed-oak; and dry, mixed-oak communities, respectively (Table 2). By the eighth year, biomass accumulation was 13 to 18% of the precut forest, depending on community type; and the herbaceous-layer species contributed only 1.0% to aboveground biomass in any community. By 1997 (≈20 years after cutting), aboveground biomass was 81.7, 96.9, and 85.4 Mg·ha^{-1} in the cove-hardwoods; mesic, mixed-oak; and dry, mixed-oak communities, respectively (Fig. 1). These values ranged from 40 to 67% of the precut forest, depending on community type.

Leaf biomass accumulated relatively faster than total wood biomass in all three communities (Fig. 2). In 1977, the first growing season after cutting, leaf biomass was

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Table 2. Aboveground biomass of woody species precut (1974) and 20 years after clear-cutting in each of the three community types of watershed 7, Coweeta Basin, western North Carolina.

	Total biomass (Mg·ha^{-1})					
	1974	1977	1979	1984	1993	1997
Cove hardwoods						
Carya spp.	55.395	0.007	0.049	0.929	0.586	2.730
Quercus rubra	39.545	0.086	0.622	2.089	5.744	7.045
Liriodendron tulipifera	25.638	0.060	0.364	2.773	16.643	26.302
Betula lenta	17.911	0.001	0.296	3.573	9.110	11.535
Tilia americana	14.827	0.002	—	0.081	0.496	0.964
Quercus prinus	12.415	0.002	0.035	0.266	0.586	0.493
Acer rubrum	9.994	0.127	0.897	2.792	4.838	5.457
Quercus alba	8.164	<0.001	—	0.005	0.002	—
Aesculus octandra	6.436	—	—	—	0.018	0.228
Fagus grandiflora	3.248	0.013	0.024	0.230	0.867	1.783
Rododendron maximum	2.811	0.001	0.006	0.450	2.797	2.970
Cornus florida	2.142	0.140	1.112	4.462	5.153	3.098
Quercus coccinea	2.079	0.005	—	0.008	0.095	0.021
Quercus velutina	1.449	0.003	—	0.148	0.137	1.387
Oxydendrum arboreum	1.016	0.012	0.104	0.265	2.144	1.005
Nyssa sylvatica	0.656	0.021	0.120	0.312	0.005	0.326
Hammamelis virginiana	0.338	0.032	0.335	1.663	2.345	3.175
Fraxinus americana	0.132	0.046	0.085	0.440	3.185	2.586
Tsuga canadensis	0.068	0.002	—	1.357	0.161	0.239
Kalmia latifolia	0.028	<0.001	0.001	0.056	0.238	0.165
Sassafras albidum	0.024	0.001	—	0.222	1.181	0.428
Robinia pseudoacacia	—	0.126	1.185	3.149	10.542	9.262
Amelanchier arborea	—	0.010	0.035	0.167	0.192	0.202
Vitis spp.	—	0.065	0.450	0.191	0.002	0.003
Herbs	—	0.351	0.841	0.376	0.106	—
Mesic, mixed oak						
Quercus prinus	44.236	0.059	0.227	1.355	7.557	12.624
Quercus velutina	43.025	0.001	—	0.007	0.297	0.723
Carya spp.	30.058	0.076	0.037	0.149	0.305	0.755
Liriodendron tulipifera	25.274	0.159	0.728	3.794	26.596	40.935
Acer rubrum	14.344	0.076	0.693	4.988	11.748	14.438
Cornus florida	6.316	0.239	1.176	4.832	6.691	6.390
Nyssa sylvatica	5.935	0.019	0.341	0.494	0.637	0.576
Quercus coccinea	3.802	0.014	0.099	0.627	0.298	0.546
Quercus rubra	3.549	0.106	0.212	0.528	2.072	3.399
Robinia pseudoacacia	3.452	0.272	2.323	7.644	17.590	10.117
Oxydendrum arboreum	3.355	0.003	0.067	0.413	0.989	2.557
Quercus alba	0.807	—	0.001	—	0.129	0.032
Kalmia latifolia	0.314	<0.001	0.001	0.046	0.175	0.075
Castanea dentate	0.223	0.038	0.089	1.638	0.088	0.016
Sassafras albidum	0.116	0.002	0.072	0.673	1.059	1.554
Amelanchier arborea	0.080	0.001	0.009	0.056	0.494	0.211
Fraxinus americana	0.058	0.002	0.010	0.087	0.163	0.394
Vitis spp.	—	0.001	0.001	0.083	0.001	0.002
Betula lenta	—	—	—	0.039	0.700	1.182
Herbs	—	0.185	0.574	0.294	0.031	—
Dry, mixed oak						
Quercus prinus	48.584	0.142	0.712	5.330	23.363	27.373
Quercus coccinea	36.590	0.005	0.498	3.003	7.152	14.365
Acer rubrum	11.203	0.099	0.465	2.754	6.897	12.278
Oxydendron arboreum	6.434	0.094	0.194	0.541	1.541	1.679
Quercus alba	4.507	—	0.042	0.298	0.620	2.358
Quercus velutina	4.456	—	0.005	0.033	0.069	0.158

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Table 2 (*concluded*).

	Total biomass (Mg·ha^{-1})					
	1974	1977	1979	1984	1993	1997
Kalmia latifolia	3.774	0.004	0.014	0.483	3.504	3.356
Carya spp.	2.699	0.011	0.034	0.849	1.005	1.666
Nyssa sylvatica	2.620	0.054	0.447	1.591	1.882	2.474
Robinia pseudoacacia	1.901	0.461	0.280	1.887	2.681	3.392
Cornus florida	1.775	0.086	0.213	0.994	1.400	2.050
Quercus rubra	0.887	0.021	0.050	0.296	0.666	3.340
Castanea dentata	0.727	0.104	0.272	2.088	2.010	0.919
Rhododendron maximum	0.306	—	0.001	0.148	1.059	1.422
Liriodendron tulipifera	0.302	0.006	0.058	0.547	3.563	6.175
Sassafras albidum	0.106	0.016	0.004	0.437	0.566	1.000
Amelanchier arborea	0.096	0.001	0.046	0.350	0.409	0.774
Castanea pumila	0.095	0.001	0.041	0.486	0.026	—
Pinus rigida	0.089	—	—	0.060	0.002	0.004
Symplocus tinctoria	—	—	0.085	0.374	0.137	0.444
Herbs	—	0.404	0.522	0.108	0.158	—

Note: All species with >0.02 Mg·ha^{-1} biomass in any year are included. Sample years begin in 1974 (before clear-cutting) through successional time (after clear-cutting in 1977 through 1997) for three communities in watershed 7, Coweeta Basin. In 1977 the number of sample plots was eight in the cove hardwoods; five in the mesic, mixed-oak hardwoods; and five in the dry, mixed-oak hardwoods. In 1974, 1979, 1984, 1993, and 1997, the number of sample plots was 7 in the cove-hardwoods, 7 in the mesic, mixed-oak hardwoods, and 10 in the dry, mixed-oak hardwoods. In 1974, 1993, and 1997 woody stems with a DBH of 1.0 cm or more were measured at 1.37 cm from the base, and stems with a DBH of less than 1.0 cm were measured at 3 cm from the base. In 1977, 1979, and 1984 all woody stems were measured at 3 and 40 cm from the base (Boring et al. 1981). Species nomenclature follows Radford et al. (1968).

≤1.0 Mg·ha^{-1} in each community, which constituted 56–66% of the total aboveground biomass (Fig. 1). Herbaceous-layer species contributed 15–33% to the total aboveground biomass and 22–45% to the total LAI in the first year. By 1984, only 8 years after cutting, leaf biomass and LAI were nearly equal to the amount estimated for the precut forest; leaf biomass in the dry, mixed-oak community was slightly less. Herbaceous-layer species contributed ≤1.0% to total aboveground biomass and between 2 and 6% to LAI in 1984 (Fig. 2). Between 1984 and 1993, a decline in leaf biomass and LAI was observed in two of the three communities; the exception was the dry, mixed-oak community (Fig. 2). By 1997, ≈20 years after cutting, leaf biomass constituted <5.0% of the total aboveground biomass in any of the three community types (Fig. 1). Leaf biomass increased substantially in the dry, mixed-oak communities and was higher than in either the cove hardwoods or mesic, mixed-oak hardwoods by 1997. For the dry, mixed-oak hardwoods, the increase in leaf biomass probably was due to the species-specific changes in leaf biomass between 1993 and 1997. While most species increased in leaf and total biomass over the 4-year period, a few species increased substantially (doubled) such as *Acer rubrum* and *Quercus coccinea* Muenchh. (Table 2). *Robinia pseudoacacia* L. and *Cornus florida* L., two species that had declined in the other two communities between 1993 and 1997, increased slightly in aboveground biomass between 1993 and 1997 in the dry, mixed-oak community (Table 2). In addition, *Kalmia latifolia* and *Rhododendron maximum* L., two evergreen understory species, contributed 1.2 Mg·ha^{-1} to leaf biomass and 0.75 m^2·m^{-2} to LAI by 1997.

In the precut cove hardwoods, five species accounted for 81% of the total aboveground biomass and ranked *Carya* spp. > *Quercus rubra* L. > *Liriodendron tulipifera* > *Betula lenta* L. > *Tilia americana* L. (Table 2). Eight years after cutting, the top five species accounted for 65% of the aboveground biomass and ranked *C. florida* > *B. lenta* > *R. pseudoacacia* > *A. rubrum* > *L. tulipifera*. Approximately 20 years after cutting, the top five species accounted for 73% of the total aboveground biomass and ranked *L. tulipifera* > *B. lenta* > *R. pseudoacacia* > *Q. rubra* > *A. rubrum*. *Carya* spp., which were dominant before cutting, constituted 27% of the biomass, but were a minor component after cutting where they occupied only 3.3% of the biomass by 1997. Oaks occupied 31% of the biomass before cutting and only 11% of the biomass 20 years later. *Robinia pseudoacacia* was not present in the precut inventory, yet was the most abundant species the first and second growing seasons, ranking second in 1984 and 1993 and third in 1997. Two species, *R. pseudoacacia* and *C. florida*, declined in biomass between 1993 and 1997. *Aesculus octandra*, an abundant species in the cove hardwoods before cutting, was only a minor component of the community after cutting.

In the precut mesic, mixed-oak community, five species accounted for 85% of the total aboveground biomass and ranked *Quercus prinus* L. > *Quercus velutina* Lam. > *Carya* spp. > *L. tulipifera* > *A. rubrum* (Table 2). Eight years after cutting, the five most abundant species accounted for 83% of the total biomass and ranked *R. pseudoacacia* > *A. rubrum* > *C. florida* > *L. tulipifera* > *Castanea dentata* (Marsh.) Borkh. Approximately 20 years after cutting, the five most abundant species accounted for 87% of the total aboveground biomass and ranked *L. tulipifera* > *A. rubrum* > *Q. prinus* > *R. pseudoacacia* > *C. florida*. *Carya* spp. and *Q. velutina*, abundant species before cutting, were minor species in this community through the 20-year period after

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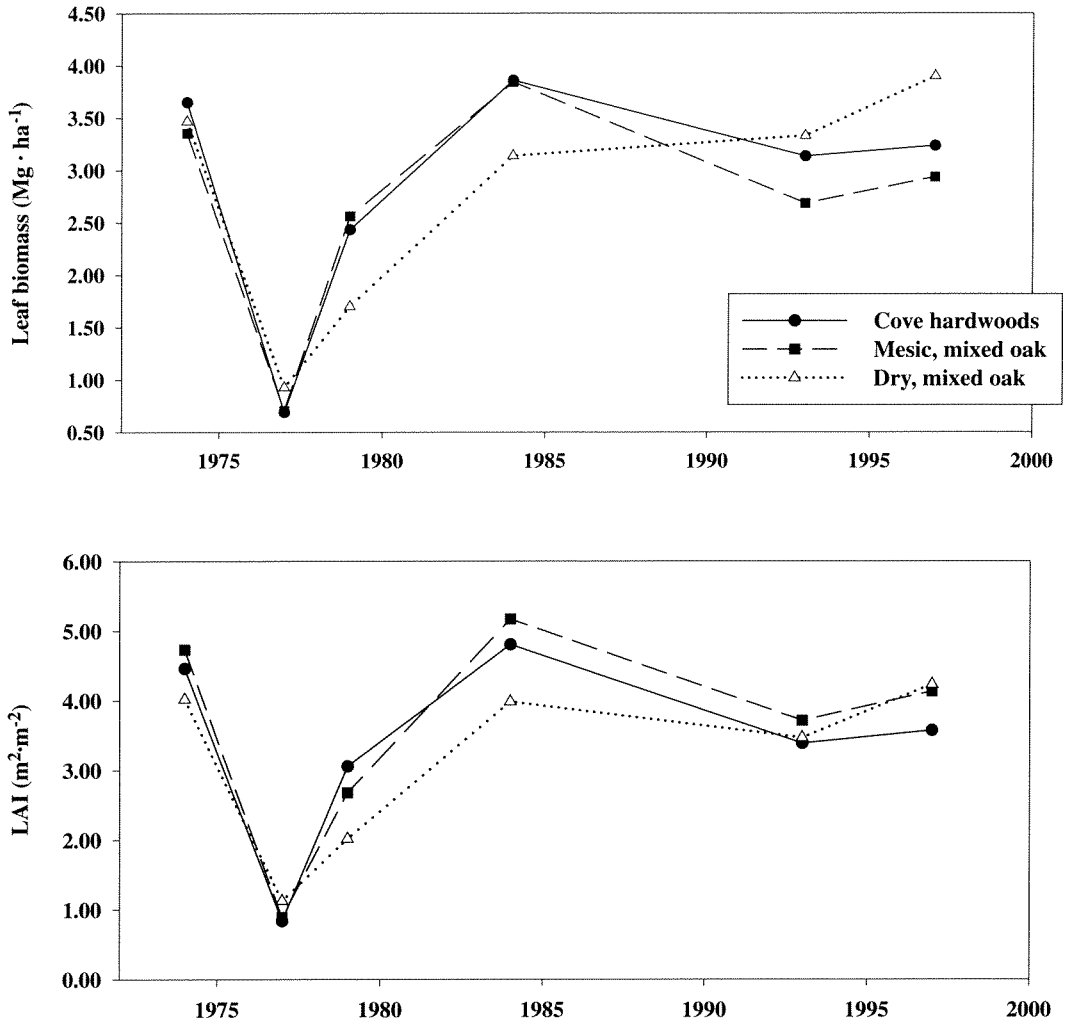
Fig. 2. Leaf biomass and leaf area index (LAI) for the three community types (cove hardwoods; mesic, mixed oak; and dry, mixed oak) before cutting (1974) and after cutting (1977, 1979, 1984, 1993, and 1997) for WS7, Coweeta Basin, western North Carolina.



cutting. In contrast, *L. tulipifera*, *A. rubrum*, and *Q. rubra* had achieved a comparable level of biomass in ≈20 years as they had before cutting. *Robinia pseudoacacia* had an almost threefold higher biomass after cutting than before, even though it declined in biomass between 1993 and 1997. Oaks, which accounted for 52% of the total aboveground biomass, occupied only 18% of the total aboveground biomass ≈20 years after cutting.

In the precut dry, mixed-oak community, the five most abundant species accounted for 84% of the total aboveground biomass and ranked *Q. prinus* > *Q. coccinea* > *A. rubrum* > *Oxydendrum aboreum* (L.) DC. > *Quercus alba* L. (Table 2). Eight years after cutting, the five most abundant species accounted for 66% of the total aboveground biomass and ranked *Q. prinus* > *Q. coccinea* > *A. rubrum* > *Castanea dentata* > *R. pseudoacacia*. Twenty years after cutting, the five most abundant species accounted for 74% of the total aboveground biomass and ranked *Q. prinus* > *Q. coccinea* > *A. rubrum* > *L. tulipifera* > *R. pseudoacacia*. Unlike the other two community types, the three dominant species in the dry, mixed-oak community before cutting retained their rank abundance after ≈20 years. *Kalmia latifolia* and *Rhododendron maximum* combined, evergreen understory species, were more abundant ≈20 years after than before cutting. In addition, *R. pseudoacacia* had twofold higher aboveground biomass ≈20 years after cutting.

In the dry, mixed-oak community, the two dominant species, *Q. prinus* and *Q. coccinea*, accumulated only 56 and 39% of their precut biomass in ≈20 years, respectively. In contrast, other species had the same or higher biomass ≈20 years after cutting than before. For example, biomass for *A. rubrum*, *K. latifolia*, and *Nyssa sylvatica* Marsh. was nearly the same before and ≈20 years after cutting. In contrast, *R. pseudoacacia*, *Q. rubra*, and *L. tulipifera* had substantially higher biomass ≈20 years after cutting than before.

Aboveground nutrient accumulation

Generally, leaf N and leaf K concentrations were increased significantly through succession (1982–1997), but no significant differences were detected for leaf P, Ca, or Mg between years (Tables 3 and 4). Significant differences were determined among species for all leaf nutrient concentrations (Table 3). *Cornus florida* had significantly higher leaf Ca concentration than the other species in both years. *Robinia pseudoacacia* had significantly higher leaf N concentration than the other species in both years. *Robinia*

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Table 3. Analysis of variance for leaf nutrient concentrations between years (1982 and 1997) and among the eight dominant tree species (*Acer rubrum*, *Betula lenta*, *Cornus florida*, *Liriodendron tulipifera*, *Quercus coccinea*, *Quercus prinus*, *Quercus rubra*, and *Robinia pseudoacacia*) within watershed 7, Coweeta Basin, western North Carolina.

Dependent variable	Source	df	MS	*F*	*P*
Nitrogen	Year	1	2.097 30	15.80	0.0001
	Species	7	3.627 05	27.32	0.0001
	Year × species	7	0.081 64	0.61	0.7424
	Error	97	0.132 76		
Phosphorus	Year	1	0.000 83	1.07	0.3041
	Species	7	0.006 22	7.99	0.0001
	Year × species	7	0.001 56	2.01	0.0614
	Error	97	0.000 78		
Potassium	Year	1	0.629 30	15.54	0.0002
	Species	7	0.736 82	18.19	0.0001
	Year × species	7	0.151 62	3.74	0.0012
	Error	97	0.040 51		
Calcium	Year	1	0.080 57	1.09	0.2998
	Species	7	2.361 64	31.85	0.0001
	Year × species	7	0.030 09	0.41	0.8967
	Error	97	0.074 16		
Magnesium	Year	1	0.001 75	0.39	0.5316
	Species	7	0.133 67	30.18	0.0001
	Year × species	7	0.016 68	3.77	0.0012
	Error	97	0.004 43		

Note: Mean squares are based on type III sums of squares.

pseudoacacia and *L. tulipifera* had higher K and P concentrations than the other species in both years (Tables 3 and 4). Concentration of nutrients in the other tissue types (i.e., branch, stem, and bark) followed the same pattern as leaf nutrient concentration (unpublished data).

In WS7, nutrient distribution and accumulation varied by community type (Fig. 3). Before cutting (1974), the dry, mixed-oak community had less nutrient mass than the other two community types for all five nutrients. By 1993, the mesic, mixed-oak community had the largest aboveground mass of P and Mg, and the dry, mixed-oak community had the smallest. The cove-hardwoods community had 27.9 kg P·ha^{-1} and 33.6 kg Mg·ha^{-1}; the mesic, mixed-oak community had 36.9 kg P·ha^{-1} and 36.8 kg Mg·ha^{-1}; and the dry, mixed-oak community had 16.8 kg P·ha^{-1} and 26.3 kg Mg·ha^{-1} (Fig. 3). The mesic, mixed-oak community had the highest P and Mg mass because of the large contribution of *L. tulipifera* to aboveground biomass (Table 2) and the high concentration of P and Mg in this species' leaf tissue (Table 4). Phosphorus mass was lower in the dry, mixed-oak community probably because of lower P concentration in *K. latifolia*, *Q. coccinea*, and *Q. prinus* (Table 4), the dominant species in this community (Table 3), combined with the lower aboveground biomass (Table 2) than the other two community types.

Before cutting (1974), estimated aboveground N mass ranged from 517.6 kg N·ha^{-1} in the cove-hardwoods community to 339.8 kg N·ha^{-1} in the dry, mixed-oak community (Fig. 3). In 1997 (≈20 years after cutting), nitrogen mass was 184.3 kg N·ha^{-1} (36% of the precut forest) in the cove-hardwoods; 210.1 kg N·ha^{-1} (44% of the precut forest) in the mesic, mixed-oak; and 208.8 kg N·ha^{-1} (61% of the precut forest) in the dry, mixed-oak community. Approximately 20 years after cutting, P accumulation in the cove-hardwood; mesic, mixed-oak; and dry, mixed-oak communities was 48, 66, and 59% of the corresponding precut (1974) communities, respectively. K accumulation in the cove-hardwood; mesic, mixed-oak; and dry, mixed-oak communities was 30, 42, and 59% of the precut (1974) communities, respectively. In 1997, Ca and Mg accumulations were less than either N or P accumulation. For example, Ca accumulation ranged from 31% of the precut forest in the cove hardwoods to 53% of the precut forest in the dry, mixed-oak community.

In the precut forest (1974), aboveground nutrient mass ranked Ca > N > K > Mg > P. Calcium mass was higher than any of the other nutrients because of the proportionately greater mass of wood to foliage tissue (Fig. 1) and the high concentration of Ca in wood tissue in the mature forest (1974). The first growing season after cutting (1977), aboveground nutrient mass ranked N > Ca ≈ K > Mg > P with high leaf:total ratios for all nutrients (Fig. 3). Later in succession, leaf:total nutrient ratios declined but were higher than leaf mass:total aboveground biomass ratios (Fig. 2). Leaf:total nutrient ratios differed because of changes in nutrient concentrations of specific tissue types (i.e., leaf, branch, stem) over time, differences among species in tissue nutrient concentrations, and shifts in leaf:total aboveground biomass ratios in each community. For example, the percentage of total aboveground N found in leaf tissue ranged from 15–20% in the precut forest, 76–83% in the first growing season, and fell to 35–38% ≈20 years after cutting depending on community type. By contrast, percentage of total aboveground Ca in leaf tissue ranged from 4.4 to 6.1% in the precut forest, 78–85% the first growing season after cutting, and then fell to 13–16% ≈20 years after cutting (Fig. 3).

One nitrogen-fixing species, *R. pseudoacacia*, contributed proportionately more to aboveground N (Table 5) than to total aboveground biomass because of its high concentration of nitrogen in plant tissue (Table 3). For example, in the mesic, mixed-oak community, *R. pseudoacacia* contributed 33% to total N versus 25% to total biomass in 1977, 42% to total N versus 28% to total biomass in 1984, 43% to total N versus 23% to total biomass in 1993, and 19% to total N versus 10% to total biomass in 1997 (Table 5). By contrast, in the same community, *L. tulipifera* contributed 12% to total N versus 15% to total biomass in 1977, 12% to total N versus 15% to total biomass in 1984, 29% to total N versus 34% to total biomass in 1993, and 34% to total N versus 42% to total biomass in 1997.

Discussion

Early successional recovery

Rapid regeneration of foliar biomass and LAI are important in the recovery of biotic control of ecological processes such as net primary productivity (NPP), evapotranspiration, and retention of nutrient and organic capital (Likens et al. 1977; Waring and Schlesinger 1985; Crowell and Freedman 1994; Bolstad et al. 2000; Swank et al. 2001). If regrowth is allowed to proceed, sprouting and rapid vegetative growth provide mechanisms for recovery in eastern deciduous for-

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Table 4. Leaf nutrient concentrations of eight dominant tree species (*Acer rubrum*, *Betula lenta*, *Cornus florida*, *Liriodendron tulipifera*, *Quercus coccinea*, *Quercus prinus*, *Quercus rubra*, and *Robinia pseudoacacia*) within watershed 7, Coweeta Basin, western North Carolina.

		Nutrient concentrations				
Species	Year	N (%)	P (%)	K (%)	Mg (%)	Ca (%)
Acer rubrum	1977*	2.03 (0.07)	0.20 (0.001)	0.76 (0.01)	0.24 (0.01)	1.17 (0.02)
	1982	1.57 (0.09)	0.14 (0.01)	0.60 (0.03)	0.27 (0.02)	1.01 (0.07)
	1997	1.95 (0.14)	0.14 (0.01)	0.84 (0.06)	0.34 (0.03)	1.15 (0.10)
Betula lenta	1977	ns	ns	ns	ns	ns
	1982	2.40 (0.21)	0.16 (0.01)	0.94 (0.06)	0.35 (0.02)	1.07 (0.12)
	1997	2.53 (0.08)	0.14 (0.01)	0.84 (0.04)	0.34 (0.04)	1.15 (0.12)
Cornus florida	1977	1.74 (0.02)	0.12 (0.004)	0.84 (0.04)	0.34 (0.04)	1.15 (0.12)
	1982	1.69 (0.04)	0.11 (0.002)	0.90 (0.05)	0.33 (0.02)	1.92 (0.08)
	1997	2.12 (0.29)	0.12 (0.02)	1.20 (0.10)	0.38 (0.08)	2.00 (0.20)
Liriodendron tulipifera	1977	2.92 (0.06)	0.22 (0.01)	1.12 (0.07)	0.58 (0.07)	2.61 (0.46)
	1982	2.47 (0.24)	0.14 (0.01)	0.95 (0.08)	0.51 (0.03)	1.51 (0.14)
	1997	2.90 (0.17)	0.18 (0.01)	1.53 (0.11)	0.42 (0.02)	1.44 (0.17)
Nyssa sylvatica	1977	2.06 (0.05)	0.17 (0.01)	1.14 (0.04)	0.75 (0.04)	0.98 (0.04)
	1982	1.68 (0.10)	0.09 (0.005)	0.79 (0.08)	0.27 (0.02)	1.41 (0.19)
	1997	2.57 (0.43)	0.15 (0.05)	1.33 (0.07)	0.37 (0.01)	0.71 (0.03)
Quercus coccinea	1977	2.43 (0.06)	0.17 (0.01)	1.52 (0.07)	0.26 (0.01)	0.98 (0.04)
	1982	2.04 (0.08)	0.11 (0.005)	0.70 (0.03)	0.14 (0.01)	0.52 (0.03)
	1997	2.03 (0.18)	0.11 (0.005)	0.56 (0.04)	0.11 (0.01)	0.36 (0.05)
Quercus prinus	1977	2.10 (0.01)	0.16 (0.003)	0.62 (0.02)	0.19 (0.01)	0.84 (0.02)
	1982	2.15 (0.09)	0.15 (0.01)	0.85 (0.08)	0.21 (0.02)	0.74 (0.07)
	1997	2.61 (0.13)	0.14 (0.01)	0.93 (0.03)	0.21 (0.01)	0.71 (0.04)
Quercus rubra	1977	1.82 (0.05)	0.16 (0.004)	0.65 (0.03)	0.28 (0.01)	1.67 (0.05)
	1982	2.22 (0.16)	0.15 (0.005)	0.88 (0.03)	0.26 (0.01)	0.80 (0.08)
	1997	2.41 (0.11)	0.13 (0.01)	1.00 (0.10)	0.22 (0.02)	0.73 (0.05)
Robinia pseudoacacia	1977	3.48 (0.05)	0.20 (0.002)	1.75 (0.04)	0.29 (0.01)	1.21 (0.04)
	1982	3.09 (0.08)	0.15 (0.005)	1.12 (0.06)	0.26 (0.02)	0.90 (0.07)
	1997	3.49 (0.15)	0.19 (0.01)	1.44 (0.11)	0.35 (0.02)	0.78 (0.11)
Kalmia latifolia†	1977	1.30 (0.13	0.11 (0.01)	0.96 (0.04)	0.37 (0.01)	1.35 (0.04)
	1982	1.15 (0.04)	0.06 (0.005)	0.48 (0.03)	0.21 (0.01)	0.83 (0.08)
Rhododendron maximum†	1977	1.24 (0.02)	0.12 (0.001)	1.10 (0.02)	0.31 (0.01)	1.16 (0.02)
	1982	0.93 (0.06)	0.06 (0.003)	0.51 (0.02)	0.22 (0.01)	1.18 (0.08)

Note: Values are means with SEs given in parentheses. ns, no sample.

*Nutrient concentrations for 1977 were taken from Boring (1979); no statistical tests could be conducted to compare nutrient concentrations for 1977 with years 1982 and 1997.

†These species were not used in statistical tests (Table 3) because no samples were collected for nutrient analyses in 1997.

ests. In WS7, leaf biomass and LAI recovered within 8 years after clear-cutting, similar to findings in other clear-cut successional forests at Coweeta (Swank and Helvey 1970; Swift and Swank 1981). This rapid recovery of LAI increased evapotranspiration, which reduced the extra water yield observed after clear-cutting; by the seventh year, annual streamflow had returned to pretreatment levels (Swank et al. 2001). In addition, the high rate of NPP and sequestration and storage of nutrients during early succession substantially moderated the loss of solutes from the watershed (Swank et al. 2001). By contrast, later in succession, the high rate of *R. pseudoacacia* mortality was associated with elevated losses of NO_3-N from the watershed (Swank et al. 2001). In the first 1–3 years following cutting, herbaceous-layer species including *Rubus* spp., *Panicum* spp., *Aster* spp., and *Solidago* spp. contributed significantly to accumulation of aboveground biomass, LAI, and nutrient capital (Boring et al. 1981; Boring 1982; Boring and Swank 1986). However, soon after cutting, woody species became increasingly abundant, and proportionately less biomass and nutrient capital were found in herbaceous-layer species. For example, by 1993, herbaceous-layer biomass contributed less than 0.1% to total aboveground biomass in any of the three community types (Elliott et al. 1997). These findings are consistent with other closed canopy forests in the southern Appalachians (Day and Monk 1974; Busing et al. 1993). Although our study showed that ground vegetation contributed considerably to aboveground biomass the first few years following disturbance, the contribution was proportionately less than found in northern forests (Crow et al. 1991; Reiners 1992; Crowell and Friedman 1994).

Previous papers (Elliott and Swank 1994*a*; Elliott et al. 1997, 1998) have described the species-specific changes following clear-cutting in three different watersheds in the Coweeta Basin. In brief, clear-cutting in the southern Appalachians favors shade-intolerant species such as *L. tulipifera* and *R. pseudoacacia*, and shade-tolerant understory species such as *Rhododendron maximum* and *K. latifolia*. In addi-

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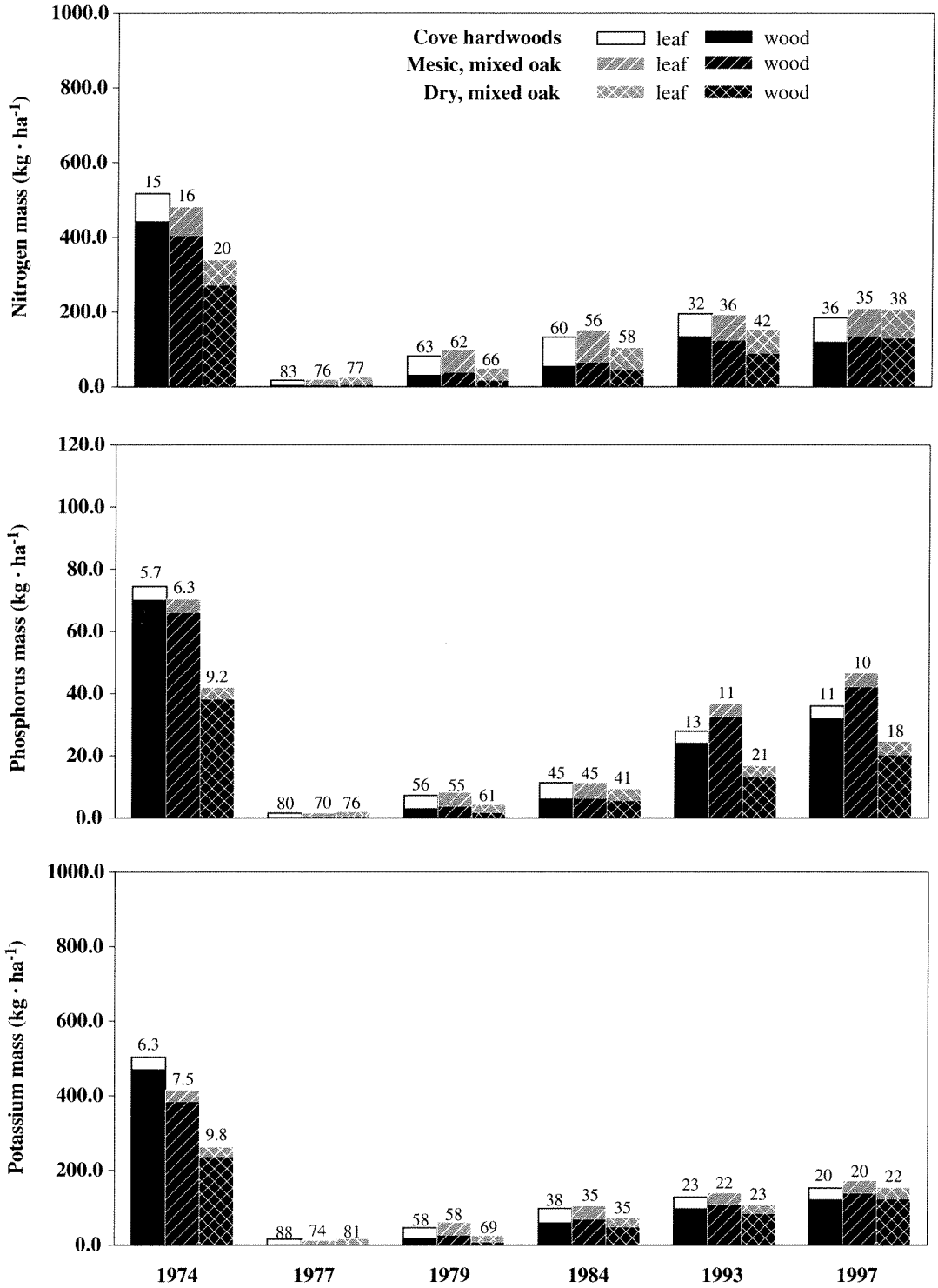
Fig. 3. Nitrogen, phosphorus, potassium, calcium, and magnesium capital for three community types (cove hardwoods; mesic, mixed oak; and dry, mixed oak) before cutting (1974) and after cutting (1977, 1979, 1984, 1993, and 1997) for WS7, Coweeta Basin, western North Carolina. Values above bars are percent contribution of leaf tissue to total aboveground nutrients.



tion, a substantial reduction in large-seeded and slower growing species, such as *Quercus*, *Carya*, *Tilia*, and *Aesculus*, have resulted from clear-cutting. These shifts in species composition had significant effects on biomass accumulation and, ultimately, aboveground nutrient accumulation. Although studies have shown an expansion in evergreen shrubs in the last several decades (Day and Monk 1974; Monk et al. 1985; Lipscomb and Nilsen 1990; Dobbs 1998) and reduced success of many *Quercus* species (Phillips and Murdy 1985; Van Lear 1991; Hedman and Van Lear 1995), clear-cutting appears to accelerate this phenomenon. In WS7, *L. tulipifera* and *R. pseudoacacia*, increased

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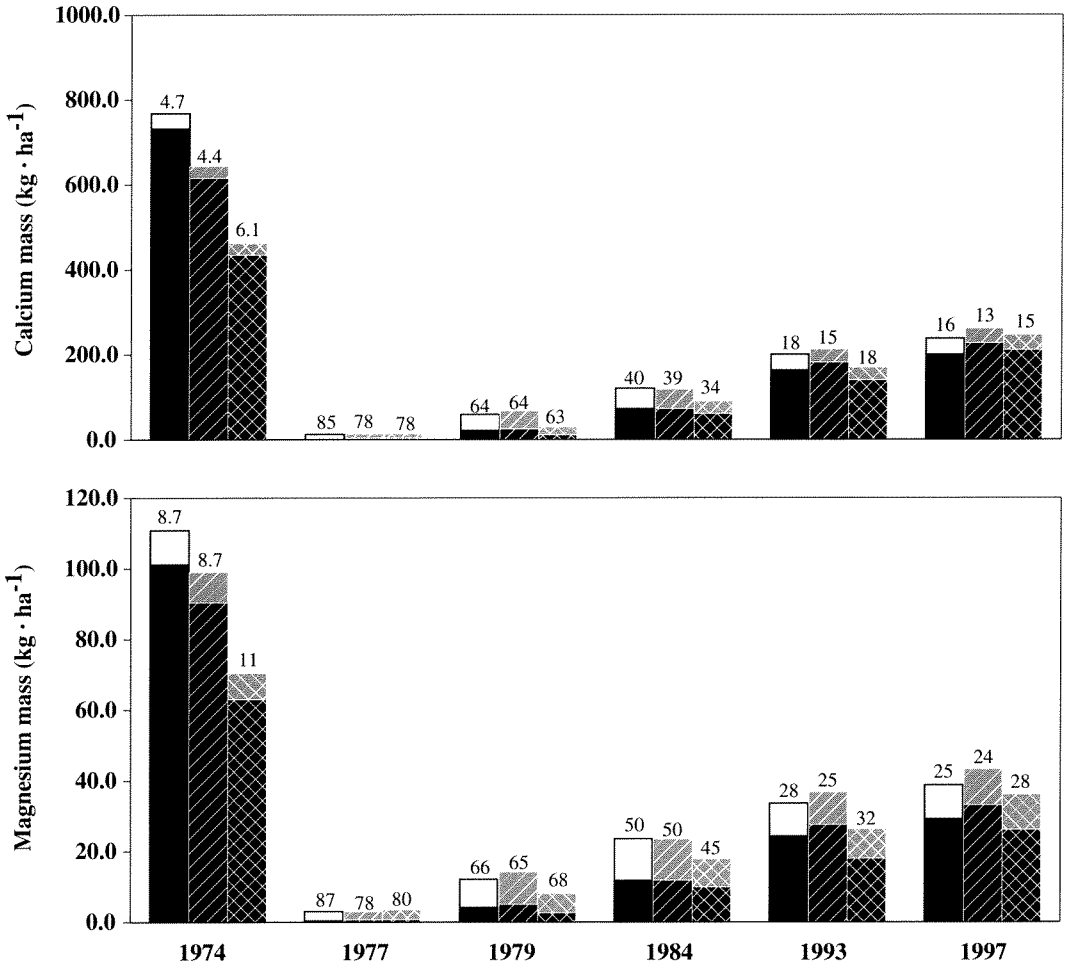
Fig. 3 (*concluded*).



in dominance in all three communities after cutting. *Robinia pseudoacacia* could be viewed as a traditional pioneer species that facilitates the growth of the next successional sere (Barnes et al. 1998), because it is short-lived, due to early mortality associated with locust stem borer (*Megacyllene robiniae* Forster) (Boring and Swank 1984), and fixes a substantial amount of nitrogen (Boring 1982; Boring and Swank 1984). In contrast, *L. tulipifera*, a shade-intolerant, fast-growing species, reaches the canopy quickly, yet is very long-lived (Buckner and McCracken 1978; Burns and Honkala 1990). Once established, even on drier sites, it maintains its canopy position even during drought conditions (Clinton et al. 1993; Elliott and Swank 1994*b*).

Diseases and insects were significant factors in the dynamics of vegetation recovery within community types on WS7. Mortality of *R. pseudoacacia* between ages 16 and 20 in the mesic, mixed-oak and cove-hardwood communities was due to the locust stem borer that commonly infects young *R. pseudoacacia* in the southern Appalachians (Boring and Swank 1984). The decline of dogwood from 1984 to 1997 was strongly influenced by dogwood anthracnose caused by *Discula destructiva* Redlin, a serious disease in southern Appalachian forests since about 1985. Studies at Coweeta have shown the climate is extremely conducive to disease development and a high incidence of disease and mortality occurs in the basin (Chellemi et al. 1992; Britton 1993). Additionally, the loss of *Castanea dentata* early in succession was due to the chestnut blight (*Endothia parasitica* (Murr.) P.) which has long been present at Coweeta (Woods and Shanks 1959; Day et al. 1988).

Spatial variability of LAI

In the mixed hardwoods forests within the Coweeta Basin, variation in annual net primary production (ANPP) and LAI have been attributed to an elevation gradient (with higher precipitation and lower temperatures at high elevations) and a topographic–terrain gradient (with higher temperatures and lower soil moisture on ridges) (Bolstad et al. 2001). This elevation gradient and terrain shape index also influences the species distributions (Elliott et al. 1999), and therefore affect the potential biomass and nutrient accumulation following a major disturbance such as clear-cutting.

Monk et al. (1970) estimated LAI of 4.0 $m^2 \cdot m^{-2}$ for a oak–hickory forest in the Georgia Piedmont (≈50-year-old forest). Our estimates for LAI of the precut (1974) forest of WS7 (≥70 years old) were slightly higher for a comparable forest type (i.e., mesic, mixed-oak) on a south-facing watershed, which received higher solar radiation (leading to higher temperatures). Monk et al. (1970) value for LAI was comparable to a young, mixed-deciduous forest in New England (DeLucia et al. 1998), but it was less than other reported LAI values within the Coweeta Basin. In another

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Table 5. Aboveground nitrogen mass of woody species precut (1974) and up to 20 years (1977–1997) after clear-cutting in each of the three community types of watershed 7, Coweeta Basin, western North Carolina.

	Total nitrogen mass (kg·ha^{-1})					
	1974	1977	1979	1984	1993	1997
Cove hardwoods						
Carya spp.	151.25	0.10	0.47	3.52	1.23	5.33
Quercus rubra	97.79	1.11	5.88	10.81	12.28	15.93
Liriodendron tulipifera	59.21	0.71	3.41	13.13	30.07	46.49
Betula lenta	36.49	0.01	2.90	17.63	12.93	16.34
Tilia americana	37.02	0.02	—	0.39	1.07	2.12
Quercus prinus	32.39	0.03	0.36	1.17	1.31	1.11
Acer rubrum	23.70	1.37	7.66	9.64	10.51	11.14
Quercus alba	21.57	0.01	—	0.03	0.02	—
Aesculus octandra	16.60	—	—	—	0.05	0.54
Fagus grandiflora	8.33	0.15	0.27	1.11	2.08	4.17
Rododendron maximum	11.56	0.01	0.06	2.40	9.41	14.17
Cornus florida	5.61	1.88	11.10	18.63	11.87	7.18
Quercus coccinea	4.84	0.07	—	0.05	0.15	0.05
Quercus velutina	3.50	0.04	—	0.80	0.21	2.48
Oxydendrum arboreum	3.09	0.13	0.88	1.09	5.42	2.58
Nyssa sylvatica	2.00	0.22	1.15	1.37	0.02	1.05
Hammamelis virginiana	1.09	0.41	3.34	7.91	5.92	7.86
Fraxinus americana	0.40	0.51	0.82	2.12	6.51	5.48
Tsuga canadensis	0.24	0.02	—	6.01	1.16	1.65
Kalmia latifolia	0.11	0.01	0.02	0.37	1.51	1.01
Sassafras albidum	0.08	0.01	—	1.06	2.57	0.93
Robinia pseudoacacia	—	2.04	16.64	23.49	41.70	35.79
Amelanchier arborea	—	0.11	0.33	0.74	0.50	0.51
Vitis spp.	—	0.01	0.01	1.70	0.02	0.03
Herbs	—	6.98	16.42	5.83	1.84	—
Mesic, mixed oak						
Quercus prinus	114.38	0.80	2.45	6.29	16.86	28.06
Quercus velutina	99.59	0.01	—	0.04	0.49	1.26
Carya spp.	83.47	0.90	0.40	0.66	0.65	1.56
Liriodendron tulipifera	61.12	1.84	6.90	17.68	47.28	71.62
Acer rubrum	33.18	0.81	6.39	17.24	24.96	29.64
Cornus florida	16.12	3.22	12.25	20.44	15.48	14.94
Nyssa sylvatica	18.85	0.20	3.36	2.21	2.05	1.78
Quercus coccinea	9.43	0.18	0.99	3.08	0.47	0.93
Quercus rubra	9.04	1.24	1.98	2.72	4.21	7.11
Robinia pseudoacacia	21.32	4.91	35.15	60.54	70.28	38.80
Oxydendrum arboreum	10.37	0.03	0.60	1.79	2.72	6.75
Quercus alba	2.59	—	0.02	—	0.42	0.14
Kalmia latifolia	1.20	<0.01	0.02	0.31	1.13	0.47
Castanea dentata	0.74	0.43	0.90	6.26	0.21	0.04
Sassafras albidum	0.34	0.03	0.80	3.23	2.45	3.50
Amelanchier arborea	0.26	0.01	0.10	0.25	0.11	0.51
Fraxinus americana	0.17	0.03	0.11	0.42	0.36	0.83
Vitis spp.	—	0.02	0.01	0.74	0.01	0.02
Betula lenta	—	—	—	0.20	0.99	1.67
Herbs	—	2.96	11.93	5.12	0.52	—
Dry, mixed oak						
Quercus prinus	126.21	1.97	7.51	23.72	52.08	60.99
Quercus coccinea	88.18	0.08	5.12	14.11	12.38	26.07
Acer rubrum	27.49	1.05	4.30	9.58	15.72	26.59
Oxydendron arboreum	20.19	0.90	1.72	2.28	4.29	4.55
Quercus alba	11.90	—	0.44	1.45	1.86	6.44
Quercus velutina	10.52	—	0.06	0.19	0.10	0.24

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Table 5 (*concluded*).

	Total nitrogen mass (kg·ha^{-1})					
	1974	1977	1979	1984	1993	1997
Kalmia latifolia	14.44	0.05	0.19	3.20	22.40	20.75
Carya spp.	7.80	0.13	0.38	3.37	2.11	3.48
Nyssa sylvatica	8.39	0.59	4.34	6.99	5.96	7.55
Robinia pseudoacacia	11.90	8.35	4.78	15.63	11.29	13.99
Cornus florida	4.58	1.21	2.26	4.35	3.17	4.69
Quercus rubra	2.32	0.29	0.49	1.49	1.36	7.70
Castanea dentata	2.37	1.14	2.79	8.24	4.52	2.30
Rhododendron maximum	1.34	—	0.01	0.80	5.33	6.68
Liriodendron tulipifera	0.76	0.07	0.59	2.56	6.42	10.86
Sassafras albidum	0.35	0.18	0.04	2.15	1.38	2.30
Amelanchier arborea	0.30	0.01	0.46	1.54	1.07	2.02
Castanea pumila	0.31	0.01	0.43	2.19	0.08	—
Pinus rigida	0.32	—	—	0.34	0.02	0.03
Symplocus tinctoria	—	—	1.03	1.97	0.45	1.25
Herbs	—	6.69	8.04	1.66	2.04	—

Note: The trees were harvested in 1977, and the sites were sampled thereafter.

undisturbed watershed, with evergreen species contributing up to 35% of the total standing crop of leaves (Monk and Day 1984), LAI was estimated at 6.2 m^2·m^{-2} (Monk and Day 1988). In mature (≥75-year-old) forests within the Coweeta Basin, Bolstad et al. (2001) reported a range in LAI from 2.7 to 8.2 m^2·m^{-2}, depending on elevation and terrain position (ridge, sideslope, or cove), with LAI decreasing as elevation increased (a function of lower temperatures) and as terrain position increased (ridges having the highest terrain shape index; a function of lower soil moisture (Helvey and Patric 1988; Yeakley et al. 1998)). For mature forests within 800–1000 m elevation (the elevation range of WS7), LAI ranged from 5.0 to 6.5 m^2·m^{-2} (Bolstad et al. 2001). However, we did not find a decrease in LAI from cove to ridge, primarily because of the abundance of *K. latifolia* and *Rhododendron maximum* that contributed substantially to total LAI in the dry, mixed-oak community located on upper slopes to ridges. Across communities, LAI in the ≈20-year-old forest of WS7 was already equal to the LAI in a 50-year-old forest reported by Monk et al. (1970) and within 65–80% of the ≥75-year-old mature forests at similar elevations reported by Bolstad et al. (2001).

Regional comparisons

Accumulation of aboveground biomass and nutrients in live vegetation was faster in the southern Appalachian hardwood forest than in northeastern hardwood forests. Reiners (1992) found that biomass accumulation was 52 Mg·ha^{-1} (38% of the total for a nearby, mature watershed) 20 years after clear-cutting a hardwood forest at Hubbard Brook, New Hampshire. Biomass accumulation was much higher (56–85%) in the southern Appalachian communities of WS7 than in the clear-cut watershed in Reiners' (1992) study. In addition, the aboveground pools of nutrients were almost twofold higher in WS7 than the northern hardwood forest at Hubbard Brook. However, in the Hubbard Brook study, experimental treatment differed from commercial clear-cutting in that timber was not removed and regrowth was suppressed with herbicides for the first 3 years following cutting. One of the effects of herbicide treatment may have been to decrease regeneration by sprouting, relatively important in northern hardwood forests (Martin and Hornbeck 1989; Reiners 1992). In a northern hardwood forest in Nova Scotia, Crowell and Freedman (1994) reported aboveground biomass of 17 Mg·ha^{-1} for woody species and nutrient standing stocks of 58 kg N·ha^{-1}, 14.5 kg P·ha^{-1}, 57 kg K·ha^{-1}, 64 kg Ca·ha^{-1}, and 14 kg Mg·ha^{-1} 8 years after clear-cutting; and aboveground biomass of 72 Mg·ha^{-1} and nutrient standing stocks of 160 kg N·ha^{-1}, 26 kg P·ha^{-1}, 102 kg K·ha^{-1}, 191 kg Ca·ha^{-1}, and 24 kg Mg·ha^{-1} 20 years after clear-cutting.

Several factors explain higher biomass and nutrient accumulation in the southern Appalachian hardwood forests, when compared with the northern hardwood forests of New England (Hornbeck et al. 1987; Reiner 1992; Crowell and Freedman 1994): the prehumid climate (higher temperature and precipitation), prolific sprouting ability of hardwoods (Kays and Canham 1992; Elliott et al. 1997), and abundance of *R. pseudoacacia*, a nitrogen-fixing species. Not only does *R. pseudoacacia* fix a substantial amount of N (estimated 30 kg N·ha^{-1} in young stands (Boring and Swank 1984)), it also accumulates large quantities of N in leaves, branches, stems, and roots (Boring and Swank 1984). In dense stands of *R. pseudoacacia*, Boring and Swank (1984) found much higher N standing stock in 17- and 38-year-old stands than we found in WS7. Monk and Day (1988) reported N standing stock of 563 kg N·ha^{-1} for a mature oak–hickory forest within the Coweeta Basin. The harvest method for WS7 was a commercial clearcut removing only merchantable sawlogs; thus, biomass and nutrient removals were only a fraction of total aboveground standing stocks before cutting (Mann et al. 1988). Only 43 Mg·ha^{-1} (≈26%) of the aboveground biomass and 13, 12, 13, and 22% of the N, P, K, and Ca, respectively, were actually removed from the watershed. Large quantities of coarse and fine woody debris (122 Mg·ha^{-1}) were delivered to the forest floor from logging and site preparation activities (Mattson et al. 1987). Thus, organic reserves released from the forest floor and decaying root

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systems from cut stumps were another major sources of nutrients for regrowth.

Southern Appalachian forests generally are more productive than other North American deciduous forests (Cannell 1982; Busing et al. 1993; Grier et al. 1989; Reich et al. 1997; Barnes et al. 1998; Waring et al. 1998); therefore, they have the potential to accumulate more aboveground biomass and nutrients following disturbance. For example, aboveground biomass estimates for cove-hardwood, old-growth forests (≈400 years old) in the Great Smoky Mountains of eastern Tennessee ranged from 326 to 384 $Mg \cdot ha^{-1}$ (Busing et al. 1993) with a corresponding ANPP of 6.3 to 8.6 $Mg \cdot ha^{-1} \cdot year^{-1}$. In young stands (42–63 years old), aboveground biomass ranged from 216 to 277 $Mg \cdot ha^{-1}$ with a corresponding ANPP of 11.7–13.1 $Mg \cdot ha^{-1} \cdot year^{-1}$ (Busing et al. 1993). By contrast, in the White Mountains of central New Hampshire, in the absence of logging, aboveground live biomass averaged 208 $Mg \cdot ha^{-1}$ (Martin and Bailey 1999). Crow et al. (1991) reported 151 $Mg \cdot ha^{-1}$ (<3% contributed by the understory) of aboveground live biomass in a 70-year-old maple–oak forest in northern Michigan, much less than what we found in cove hardwoods or mesic, mixed-oak communities of WS7 before cutting (≈50-year-old forest). Monk et al. (1970) estimated aboveground live biomass of 145 $Mg \cdot ha^{-1}$ for an oak–hickory forest in the Georgia Piedmont, and Day and Monk (1974) estimated aboveground live biomass of 140 $Mg \cdot ha^{-1}$ in a north-facing watershed in the Coweeta Basin (both ≈50-year-old forest; heavily logged between 1900 and 1923). Theirs were less than our estimates of aboveground live biomass in the precut (1974) forest (also ≈50 years old and heavily logged between 1900 and 1923) for either the cove hardwood or mesic, mixed-oak hardwood communities of WS7, a south-facing watershed. Within the Coweeta Basin, for mature stands (≥75 years old), Bolstad et al. (2001) reported a range of ANPP from least productive (5.2 $Mg \cdot ha^{-1} \cdot year^{-1}$) on ridges at high elevation to most productive (11.7 $Mg \cdot ha^{-1} \cdot year^{-1}$) in cove hardwoods. In a 50-year-old *L. tulipifera* stand in Tennessee, Cole and Rapp (1981) reported an aboveground biomass of 125 $Mg \cdot ha^{-1}$ and nutrient standing stocks of 305 kg $N \cdot ha^{-1}$, 47 kg $P \cdot ha^{-1}$, 173 kg $K \cdot ha^{-1}$, and 456 kg $Ca \cdot ha^{-1}$. In WS7, within only ≈20 years of cutting, aboveground biomass was 66–78% of that reported by Cole and Rapp (1981), depending on community type; nutrient standing stocks were 60–69% for N, 53–100% for P, 88–100% for K, and 52–57% for Ca.

In nearby mature (≈70-year-old), pine–hardwood stands in the southern Appalachians, Vose and Swank (1993) reported an estimated aboveground biomass between 92.2 and 183.8 $Mg \cdot ha^{-1}$. Although before cutting, the dry, mixed-oak community in WS7 was within this range of values, a larger component of oaks (our study; 93.3 $Mg \cdot ha^{-1}$ vs. Vose and Swank (1993); 32.1–88.9 $Mg \cdot ha^{-1}$), only a minor component of *Pinus rigida* Mill., and less *K. latifolia* (our study; 3.77 $Mg \cdot ha^{-1}$ versus Vose and Swank (1993); 12.6–29.7 $Mg \cdot ha^{-1}$) were present. However, with only ≈20 years of regrowth, biomass accumulation of *K. latifolia* was nearly equal to its precut value, and biomass of *Rhododendron maximum* was 4.6 times greater than before cutting in the dry, mixed-oak community. In addition, leaf biomass of these two evergreen species was 31% of total leaf biomass. Because these two species can retain foliage for up to 3 years, only 10–15% of their total leaf nutrient standing crop is lost annually through litterfall, and because sclerophyllous foliage decomposes slowly (Monk et al. 1985), the increased abundance of *K. latifolia* and *Rhododendron maximum* in WS7 could have long-term implications for ecosystem processes such as decomposition and nutrient cycling.

Implications for ecosystem structure and function

Southern Appalachian hardwood forests have a high relative resilience for recovery by rapid accumulation of biomass, NPP, LAI, and nutrient standing stocks (Boring et al. 1981). Early in succession, nutrient retention was related to rapid recovery of biogeochemical cycles associated with high rates of NPP and storage of nutrients in vegetation. In the first 1–3 years after cutting, herbaceous-layer species contributed substantially to accumulation of aboveground biomass, LAI, and nutrient capital. In addition, the increase in woody LAI by the third year after clear-cutting resulted in early canopy closure and a subsequent recovery of structural and functional forest processes. This rapid recovery of LAI increased evapotranspiration, which reduced the extra water yield observed immediately after clear-cutting; by the seventh year after cutting, annual streamflow had returned to pretreatment levels (Swank et al. 2001). The high rate of NPP and the sequestration and storage of nutrients during early succession substantially moderated the watershed's loss of solutes.

Later in succession, export of NO_3-N in streams increased above levels observed in the initial post-harvest period, a response indicative of significant changes in internal N-cycling processes (Swank et al. 2001). At that time, forest structure was partially dominated by the nitrogen-fixing early successional tree, *R. pseudoacacia*. However, forest composition was quickly changing because of competition and insect attacks by defoliators (Seastedt et al. 1983*a*) and stem borers upon the *R. pseudoacacia* (Boring and Swank 1984). The death of so many of these nitrogen-fixing trees resulted in elevated organic and inorganic nitrogen fluxes. Thus, later in succession, *R. pseudoacacia* mortality was associated with elevated losses of NO_3-N.

A prehumid climate, prolific hardwood sprouting, an abundance of *R. pseudoacacia* (a nitrogen-fixing species), and the observed changes in species composition have important implications for ecosystem function. Clear-cutting favored shade-intolerant, fast-growing species, such as *L. tulipifera* and *R. pseudoacacia*, subdominant *A. rubrum*, and shade-tolerant understory shrubs, such as *Rhododendron maximum* and *K. latifolia*. The abundance of large-seeded, slow-growing species, such as *Quercus* spp., *Carya* spp., and *T. americana*, declined after clear-cutting (Elliott et al. 1997). *Robinia pseudoacacia* and *L. tulipifera* lose their foliage in early fall, have high leaf-nutrient concentrations; and *L. tulipifera* and *A. rubrum* foliage decomposes quickly. *Quercus* spp. and *Carya* spp. lose their foliage in late fall through the winter, have lower leaf-nutrient concentrations, and their foliage decomposes slower than many of the other overstory species that replaced their dominance (Cromack et al. 1973; White et al. 1988). These reported shifts in overstory species composition would result in forest floor litter with higher nutrient concentrations,

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lower C/N ratios, and subsequently faster decomposition rates.

However, the dynamics of the increasingly dominant evergreen understory, *K. latifolia* and *Rhododendron maximum*, may be as important to future ecosystem functions as the changes in the overstory. They have also increased in abundance in the Coweeta Basin since the loss of *Castanea dentata* from the overstory, and clear-cutting on WS7 further increased their distribution, basal area, and density (Elliott 1997). In areas of the watershed where *K. latifolia* and *Rhododendron maximum* are abundant, the contribution of their ericaceous leaves to litterfall may reduce litter quality even with *L. tulipifera* and *R. pseudoacacia* in the overstory. *Kalmia latifolia* and *Rhododendron maximum* retain foliage for several years, have low leaf-nutrient concentrations, and the sclerophyllous leaves decompose slowly (White et al. 1988). The organic soils and root mats that these ericads form may potentially alter soil pH, decrease forest floor decomposition rates, shift soil nutrient availability, and alter overall soil quality (Knoepp et al. 2000). Because increased rates of litter decomposition accelerate nutrient cycling rates within an ecosystem, the composition and quality of litter have important implications in terms of nutrient loss and retention, soil nutrient availability, and soil quality (Knoepp et al. 2000). Less is known about how various deciduous species use water; and species differences in evapotranspiration would also have long-term effects on hydrologic cycles at the watershed scale (Swank et al. 2001). These major changes in overstory and understory composition affect forest structure, organic matter quality, and water use; consequently, vegetation dynamics may result in different watershed hydrologic and biogeochemical responses in the future.

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