

W.T. Swank and D.A. Crossley Jr.

**Ecological Studies, Vol. 66:**

**Forest Hydrology and Ecology at Coweeta**

---

© 1988 Springer-Verlag New York, Inc.

Printed in the United States of America



Springer-Verlag  
New York Berlin Heidelberg  
London Paris Tokyo

---

## 12. Dynamics of Early Successional Forest Structure and Processes in the Coweeta Basin

L.R. Boring, W.T. Swank, and C.D. Monk

Clearcutting is a prevalent silvicultural practice used to regenerate mixed hardwood forests in the southern Appalachians and to improve stands degraded by prior selection-cutting practices. Its widespread application is due in part to the economy of harvesting, but primarily due to its potential for regenerating economically desirable species (Smith 1962; McGee and Hooper 1970).

Research on the effects of clearcutting in the southern Appalachians has addressed silvicultural aspects of early forest regeneration (McGee and Hooper 1970, Trimble 1973) and subsequent hydrologic responses (Swank and Helvey 1970; Swank and Swank 1981), but major gaps still exist in our knowledge about regeneration in southern Appalachian forests. These gaps include understanding how initial patterns of species establishment affect stand composition in later years and how regeneration trends vary with different sites and forest communities.

Perhaps more importantly, there is a need to couple early successional changes in forest structure with associated changes in nutrient cycling processes. Biogeochemical studies subsequent to forest cutting have indicated basic changes in forest processes and nutrient uptake by vegetation (Marks and Bormann 1972; Swank and Douglass 1977; Bormann and Likens 1979). Johnson and Swank (1973) hypothesized that after clearcutting southern Appalachian forests, vegetation rapidly accumulates biomass, recovers nutrient uptake quickly, and consequently conserves nutrients that could otherwise be leached from the soil. Some of these mechanisms were shown to be important in reducing nutrient losses in early successional northern hardwood forests, although nutrient loss by soil leaching (especially  $\text{NO}_3\text{-N}$ ) was observed immediately after cutting.

---

following forest removal (Marks and Bormann 1972; Marks 1974). However, Coweeta nutrient losses of early successional forests are relatively conservative and it was hypothesized that the recovery of nutrient uptake rates are relatively rapid (Johnson and Swank 1973; Swank and Douglass 1977). Changes in decomposition rates and forest floor processes were also hypothesized to result in nutrient conservation (Seastedt and Crossley 1981; Abbott and Crossley 1982).

A hardwood forested watershed at Coweeta was clearcut as part of an interdisciplinary study of the physical, chemical, and biological effects on both terrestrial and aquatic components of the ecosystem. Our specific objectives addressed here were (1) to examine differences in forest regeneration trends among former cove, chestnut oak, and xeric scarlet oak–pine sites on the clearcut watershed; (2) to compare species composition, leaf area index (LAI), biomass, net primary production (NPP), nutrient uptake and nutrient accretion over the first 3 years of regeneration with values from an adjacent, uneven-aged, mixed hardwood forest; and (3) to relate regeneration and forest structure to fundamental ecosystem processes of nutrient uptake, immobilization, and transfers.

## Materials and Methods

### Study Areas

Watershed 7 (WS 7) was the primary site for this study. On the basis of an earlier study (Williams 1954), the watershed was stratified into four plant communities, similar to those identified in recent studies of vegetation classification in the Coweeta Basin (Chapter 10). Based upon these previous studies and the delayed completion of preparation on xeric sites, three sampling strata were identified: (1) a cove hardwood community found at lower elevations and along ravines at intermediate elevations; (2) a chestnut oak community on mesic southeast- and north-facing slopes at intermediate elevations; and (3) a scarlet oak–pine community on xeric southwest and south-facing slopes at intermediate to upper elevations and ridgetops, which combines the two vegetation types from the previous studies.

Timber cutting and yarding with a mobile cable system began in January 1977 and was completed the following June. Tractor skidding was used on about 9 ha where slopes were less than 20%, and the remainder was yarded with a mobile cable system. Most of the ridgetops and xeric slopes were cut for the purpose of the experiment and were not logged due to an insufficient volume of marketable timber. The site preparation treatment, completed in October 1977, consisted of clear-felling all remaining stems >2.5 cm dbh. This treatment was completed on the xeric half of the watershed 6 months later than on the mesic half, thus introducing an age difference in hardwood regeneration between the two halves of the watershed.

Comparative data for net primary production (NPP) and element standing crop from an uneven-aged hardwood forest were taken from WS 18 (Day and Monk 1977) because these measurements were not made on WS 7 prior to clearcutting. Detailed NPP information is available for WS 18, a 12.5 ha watershed which primarily differs from WS 7 in having a northern aspect. Although species dominance varies among

---

oaks on these two watersheds, there were no major differences in the overall tree species composition, basal area (25.6 vs. 25.3 m<sup>2</sup> ha<sup>-1</sup>), density (3044 vs. 3058 stem >2.5 cm dbh), and aboveground biomass (139 vs. 130 t ha<sup>-1</sup>) (Boring 1979).

### Forest Composition and Production

Standard dimension analysis techniques were used to estimate biomass, NPP, and of woody species (Whittaker and Woodwell 1968; Whittaker et al. 1974; Phillip Saucier 1979). Individual young hardwoods (mostly of sprout origin) were sampled each August from 1977 to 1979 from randomly chosen sample points within the area to establish regression equations (Table 12.1). Sampled individuals were cut ground or at the point of sprout origin on the stump. Diameters were measured at 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, oven-dried to a constant weight at 70°C, and weighed. Stems and all branches were similarly dried and weighed. Wood weights included all aboveground woody components.

An untransformed linear equation using diameter and basal area as independent variables and a logarithmic transformed equation using log<sub>10</sub> diameter were compared relative goodness of fit using *r*<sup>2</sup> and Furnival's index of fit. Log<sub>10</sub> regression equations based upon pooled 1 to 3-year-old stem diameters provided the best fits and were selected to predict leaf and wood biomass for eleven species (Table 12.1). Bias from logarithmic transformation was corrected using a base 10 modified Baskerville equation (Baskerville 1972).

Prior to clearcutting, the vegetation was inventoried from 142 0.08 ha plots systematically located over WS 7. Following clearcutting, thirteen of the original plots were randomly selected among mesic sites and sampled for regrowth, including five plots in the cove and eight chestnut oak plots (Figure 12.1). In 1978, eleven additional plots were also randomly selected in the xeric scarlet oak-pine area. Two quadrats were located in opposite corners of each 0.08 ha plot. Hardwood sprouts and seedlings were sampled in each quadrat with subplots of 7 × 7 m and 3 × 3 m, respectively, and were pooled for each pair (Shimwell 1971).

Herbaceous vegetation was destructively sampled in August of each year from randomly placed 1 m<sup>2</sup> subplot within each quadrat, separated by species, or grouped by species, and oven-dried to constant weight at 70°C. Total herb NPP was estimated by equating it with August standing crop biomass, since a study in the first year showed that most species attained peak biomass at that time (Boring et al. 1981).

LAI estimates were determined from leaf surface area to dry weight ratios measured on at least 20 leaves for each of 21 woody species (including *Rubus* spp.) in both 1977 and 1979. 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 Company, Omaha, Nebraska), and then drying and weighing the leaves. For herbs, whole plant biomass to leaf surface area ratios were determined for three dominant composite species and a miscellaneous category.

At the end of the growing season, sprout and seedling densities were recorded separately by species and diameter class on each 7 m × 7 m sample plot. For the following year, diameter classes were designated by 0.5 increments up to a maximum of 3 cm.

Table 12.1. Sample Sizes, Diameter Ranges, Regression Equations and Correction Factors (K) for Estimating Leaf and Wood Biomass of 1 to 3 Year-Old Hardwood Sprouts (Y = Dry Weight Biomass (g) and X = Diameter (mm))

Species	n	Range (mm)	Leaf Biomass	K <sup>a</sup>	r <sup>2</sup>	Wood Biomass	K <sup>a</sup>	r <sup>2</sup>
Group A (Diameter at 40 cm)								
<i>Acer rubrum</i>	26	3-57	$\log_{10}Y = -0.565 + 2.083 \log_{10}X$	1.036	0.98	$\log_{10}Y = -0.990 + 2.605 \log_{10}X$	1.031	0.99
<i>Castanea dentata</i>	16	3-27	$\log_{10}Y = -0.329 + 1.799 \log_{10}X$	1.095	0.91	$\log_{10}Y = -1.022 + 2.527 \log_{10}X$	1.090	0.96
<i>Liriodendron tulipifera</i>	25	5-77	$\log_{10}Y = -0.759 + 2.140 \log_{10}X$	1.070	0.96	$\log_{10}Y = -1.444 + 2.799 \log_{10}X$	1.082	0.97
<i>Quercus prinus</i>	20	5-42	$\log_{10}Y = -0.267 + 1.871 \log_{10}X$	1.076	0.93	$\log_{10}Y = -0.688 + 2.476 \log_{10}X$	1.091	0.97
<i>Quercus rubra</i>	14	5-33	$\log_{10}Y = -0.267 + 1.871 \log_{10}X$	1.076	0.93	$\log_{10}Y = -0.688 + 2.476 \log_{10}X$	1.091	0.97
<i>Robinia pseudo-acacia</i>	19	3-76	$\log_{10}Y = -0.308 + 1.968 \log_{10}X$	1.069	0.97	$\log_{10}Y = -0.922 + 2.636 \log_{10}X$	1.032	0.99
Group B (Diameter at 3 cm)								
<i>Carya ovalis, C. tomentosa</i>	18	6-36	$\log_{10}Y = -0.844 + 2.212 \log_{10}X$	1.121	0.89	$\log_{10}Y = -2.479 + 3.487 \log_{10}X$	1.197	0.92
<i>Cornus florida</i>	26	3-36	$\log_{10}Y = -0.796 + 2.168 \log_{10}X$	1.052	0.97	$\log_{10}Y = -1.317 + 2.758 \log_{10}X$	1.046	0.98
<i>Kalmia latifolia</i>	24	2-12	$\log_{10}Y = -0.556 + 1.814 \log_{10}X$	1.080	0.89	$\log_{10}Y = -0.803 + 2.162 \log_{10}X$	1.048	0.95
<i>Nyssa sylvatica</i>	20	4-41	$\log_{10}Y = -0.741 + 2.087 \log_{10}X$	1.071	0.96	$\log_{10}Y = -1.666 + 2.972 \log_{10}X$	1.055	0.98
<i>Oxydendrum arboreum</i>	20	3-40	$\log_{10}Y = -0.732 + 2.054 \log_{10}X$	1.070	0.96	$\log_{10}Y = -1.285 + 2.694 \log_{10}X$	1.064	0.98
<i>Rhododendron maximum</i>	20	4-18	$\log_{10}Y = -1.176 + 2.555 \log_{10}X$	1.115	0.87	$\log_{10}Y = -2.027 + 3.218 \log_{10}X$	1.121	0.94

<sup>a</sup> Correction factor using the base 10 modified Baskerville correction (Baskerville 1972) where:  $K = \text{antilog} [(S^2/2)\log_e 10]$ , and  $Y(\text{corrected}) = [\text{antilog}(a+b \log_{10}X)]K$ .

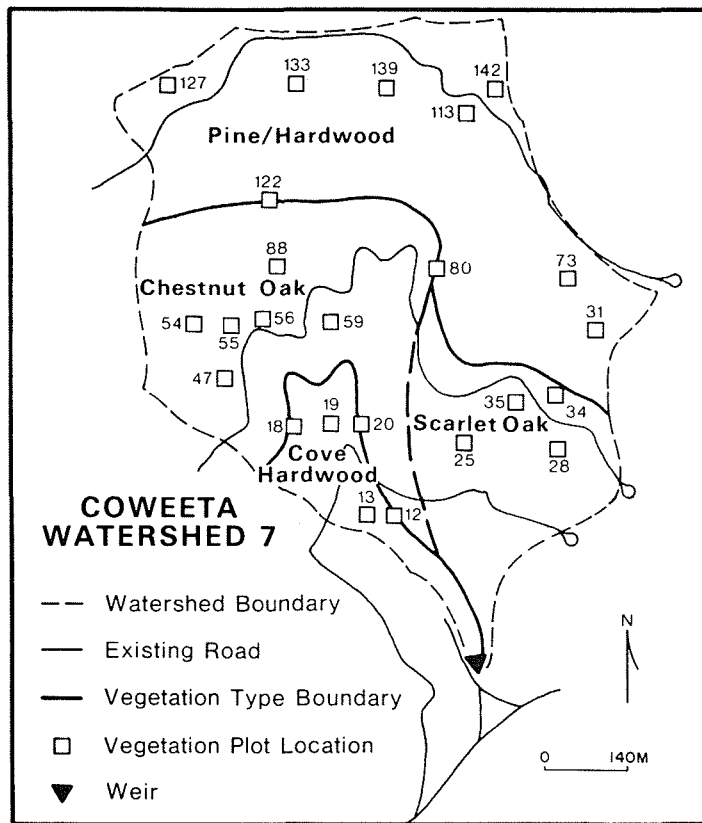


Figure 12.1. Map of Coweeta WS 7, vegetation types, and the vegetation plot location

the second and third years, classes were in 1 cm increments up to 8 cm. Aboveground leaf, wood and total biomass ( $\text{kg ha}^{-1}$ ) were determined for each species by multiplying the stem densities for each size class by midpoint biomass values estimated by regression analysis. Summation of the wood and leaf biomass from each size class yields total biomass per species for each plot. LAI was determined by multiplying the area/dry weight ratios times leaf biomass for each species.

For watershed estimates of biomass and leaf area, values for each species were calculated by multiplying its mean biomass or leaf area in a forest type by the relative area of that vegetation type: (1) equating first-year biomass with NPP; and (2) for second and third years, subtracting the previous year's woody biomass and evergreen leaf biomass from total biomass.

#### Element Concentrations and Standing Stocks

Element analyses for N, P, K, Ca, and Mg were conducted on wood and leaf tissue of all dominant hardwood sprout, seedling, herb, and vine species for 1977 to 1979. A total of 6 to 12 individuals per species were sampled, oven-dried and ground in a V

mill through a 425  $\mu$  mesh screen. Three to six replicate 0.5 g tissue samples for species were ashed at 400°C for 4 hr, digested in 10 ml of 20% HNO<sub>3</sub>, and analyzed for P, K, Ca, and Mg on a Jarrell-Ash plasma emission spectrograph (Jones 1977; Felt 1978). Total N content was determined on a Coleman Micro-Dumas nitrogen analyzer (Bremner 1965). Orchard leaf standards (United States National Bureau of Standards) were utilized for quality control. All element data, expressed as mg kg<sup>-1</sup>, were tested for significant differences in mean concentrations by SAS General Linear Models procedures and ranked by Duncan's multiple range test (Sokal and Rohlf 1969; Helwig and Council 1979).

## Results and Discussion

### Species Regeneration Patterns

Prior to clearcutting, the highest biomass (166 t ha<sup>-1</sup>) was in the cove hardwood community, followed by the scarlet oak-pine (133 g ha<sup>-1</sup>) and chestnut oak (119 t ha<sup>-1</sup>) communities (Table 12.2). These results are not surprising, since the site quality of the forest was highest and the scarlet oak-pine sites had the least logging activity in the past. However, these biomass figures represent stands which have a complex disturbance history, to include high-grade logging and high mortality of American chestnut (*Castanea dentata*) (Chapter 11). Old growth cove and chestnut oak forests on similar sites in the Great Smoky Mountains may exceed 400 t ha<sup>-1</sup> (Whittaker 1966).

Although northern red oak (*Quercus rubra*) and hickories (*Carya* spp.) comprised 36% of the cove forest biomass before clearcutting, in the second year after cutting decreased to 12% of the woody species biomass, while yellow-poplar (*Liriodendron tulipifera*) continued to comprise 18% (Table 12.2). Red maple (*Acer rubrum*), flowering dogwood (*Cornus florida*), and yellow-poplar dominated the regeneration although vine and herbaceous biomass comprised 47% of the total community biomass. Most of the oaks and hickories in the cove likely originated from seedlings that were established prior to clearcutting (Sander 1972; Trimble 1973). The number of yellow-poplars were predominantly seedlings (18,444 ha<sup>-1</sup>) that germinated following clearcutting (Table 12.3). Although silver-leaf grape (*Vitis aestivalis* var. *argentea*) sprouts were faster growing than seedlings, the latter were more numerous, with 2 ha<sup>-1</sup> vs. 16,222 ha<sup>-1</sup>.

Prior to clearcutting, oaks and hickories composed 60% of the biomass in the chestnut oak (*Q. prinus*) community, followed by red maple and yellow-poplar (22%) (Table 12.2). Following clearcutting, black locust (*Robinia pseudo-acacia*), flowering dogwood, yellow-poplar, and red maple comprised 57% of the woody regeneration, while oaks and hickories reduced to 15%. Although their biomass was relatively low, mountain laurel (*Kalmia latifolia*) sprouts and grape seedlings were present (Table 12.3). Herbaceous vegetation and blackberries (*Rubus* spp.) comprised 29% of total biomass.

Except for yellow-poplar and silver-leaf grape, the dominant woody species regenerated primarily from stump or root sprouts. The scarlet oak-pine (*Q. coccinea/P. rigida*) community was dominated by chestnut oak, scarlet oak, black oak (*Q. velutina*)

---

Table 12.2. Aboveground Biomass for Woody Species Before and 2 Years (2.5 Years for Scarlet Oak-Pine) After Clearcutting on Former Cove Hardwood, Chestnut Oak, and Scarlet Oak-Pine Sites on WS 7

Species	Cove Hardwood				Chestnut Oak				Scarlet Oak-Pine			
	Postcut		Precut		Postcut		Precut		Postcut		Precut	
	t ha <sup>-1</sup> Biomass	% Biomass	% Biomass	t ha <sup>-1</sup> Biomass	t ha <sup>-1</sup> Biomass	% Biomass	% Biomass	t ha <sup>-1</sup> Biomass	t ha <sup>-1</sup> Biomass	% Biomass	% Biomass	t ha <sup>-1</sup> Biomass
<i>Acer rubrum</i>	0.6	27	3	4.3	0.2	6	10	11.7	0.7	18	6	8.4
<i>Betula lenta</i>	<0.1	<1	9	14.2	<0.1	1	1	0.6	0	0	<1	<0.1
<i>Carya</i> spp.	<0.1	1	16	26.6	<0.1	1	16	18.9	<0.1	1	4	5.2
<i>Castanea</i> <i>dentata</i>	0	0	0	0	0.1	2	<1	0.5	0.2	5	1	1.2
<i>Cornus</i> <i>florida</i>	0.3	14	2	3.1	0.8	21	6	6.5	0.1	3	2	2.7
<i>Kalmia</i> <i>latifolia</i>	0	0	<1	0.2	0.3	8	2	2.5	0.8	20	11	15.2
<i>Liriodendron</i> <i>tulipifera</i>	0.4	18	18	29.4	0.3	7	12	13.6	<0.1	1	3	4.0
<i>Nyssa</i> <i>sylvatica</i>	<0.1	1	<1	0.9	0.2	5	2	2.6	0.2	6	4	4.9
<i>Pinus rigida</i>	0	0	0	0	0	0	<1	0.4	0	0	3	3.4
<i>Quercus alba</i>	0	0	6	10.0	0	0	<1	0.3	<0.1	1	5	6.3
<i>Quercus</i> <i>coccinea</i>	0	0	1	1.4	<0.1	1	9	10.5	0.5	13	15	20.2
<i>Quercus</i> <i>prinus</i>	0	0	2	3.9	0.3	8	22	26.6	0.4	10	26	35.1
<i>Quercus rubra</i>	0.2	11	20	34.0	0.2	5	4	5.1	<0.1	2	<1	0.6
<i>Quercus</i> <i>velutina</i>	<0.1	<1	<1	0.1	<0.1	<1	9	10.8	<0.1	<1	12	15.6

(Continued)



Table 12.2. (Continued)

Species	Cove Hardwood				Chestnut Oak				Scarlet Oak-Pine			
	Postcut		Precut		Postcut		Precut		Postcut		Precut	
	t ha <sup>-1</sup> Biomass	% Biomass	% Biomass	t ha <sup>-1</sup> Biomass	t ha <sup>-1</sup> Biomass	% Biomass	% Biomass	t ha <sup>-1</sup> Biomass	t ha <sup>-1</sup> Biomass	% Biomass	% Biomass	t ha <sup>-1</sup> Biomass
<i>Rhododendron maximum</i>	0.1	4	3	5.3	<0.1	1	2	2.5	<0.1	1	<1	0.4
<i>Robinia pseudoacacia</i>	<0.1	1	0	0	0.9	23	1	0.8	0.4	10	2	2.9
<i>Vitis aestivalis</i>	0.2	8	—	—	0.2	6	—	—	<0.1	1	—	—
Others	0.3	15	20	32.7	0.2	5	4	5.2	0.3	8	6	7.6
Total for woody species	2.1	100	100	166.1	3.7	100	100	119.1	3.8	100	100	133.8

<sup>a</sup> Postclearcutting data include all stems, and precut data include all stems  $\geq 2.5$  cm dbh.

Table 12.3. Stem Density by Species Before and 2 Years After Clearcutting on Former Cove Hardwood, Chestnut Oak, and Scarlet Oak-Pine Sites on WS 7<sup>a</sup>

Species	Cove Hardwood				Chestnut Oak				Scarlet Oak-Pine			
	Postcut			Precut	Postcut			Precut	Postcut			Precut
	Sprouts/ ha	Sdgs/ ha	% Density	% Density	Sprouts/ ha	Sdgs/ ha	% Density	% Density	Sprouts/ ha	Sdgs/ ha	% Density	% Density
<i>Acer rubrum</i>	2,876	6,222	12	6	3,172	4,861	7	7	6,956	5,389	13	6
<i>Betula lenta</i>	816	3,000	5	4	765	628	1	<1	0	0	0	<1
<i>Carya</i> spp.	306	1,222	2	4	1,010	278	1	7	1,285	356	2	3
<i>Castanea</i> <i>dentata</i>	0	0	0	0	1,112	0	1	3	1,938	0	2	4
<i>Cornus</i> <i>florida</i>	7,589	111	10	14	17,901	350	16	16	3,029	0	3	4
<i>Kalmia</i> <i>latifolia</i>	0	0	0	2	13,903	139	13	17	40,555	0	42	56
<i>Liriodendron</i> <i>tulipifera</i>	510	18,444	24	5	1,836	6,739	8	6	176	1,211	1	1
<i>Nyssa</i> <i>sylvatica</i>	408	222	<1	1	5,314	767	6	5	5,773	250	6	4
<i>Pinus rigida</i>	0	0	0	0	0	0	0	<1	0	0	0	1
<i>Quercus alba</i>	0	0	0	1	0	0	0	<1	571	406	1	1
<i>Quercus</i> <i>coccinea</i>	0	0	0	<1	316	1,600	2	2	2,009	3,839	6	2
<i>Quercus</i> <i>prinus</i>	0	0	0	2	3,121	417	3	7	3,121	606	4	5

(Continued)

Table 12.3. (Continued)

Species	Cove Hardwood				Chestnut Oak				Scarlet Oak-Pine			
	Postcut			Precut	Postcut			Precut	Postcut			Precut
	Sprouts/ ha	Sdgs/ ha	% Density	% Density	Sprouts/ ha	Sdgs/ ha	% Density	% Density	Sprouts/ ha	Sdgs/ ha	% Density	% Density
<i>Quercus rubra</i>	1,142	1,444	3	1	979	1,389	2	1	120	656	1	<1
<i>Quercus velutina</i>	0	889	1	<1	13	211	<1	2	65	556	<1	1
<i>Rhododendron maximum</i>	4,488	0	6	46	2,499	139	2	19	1,867	0	2	2
<i>Robinia pseudoacacia</i>	408	444	1	0	2,122	1,322	3	<1	1,275	200	2	1
<i>Vitis aestivalis</i>	2,244	16,222	23	—	2,387	28,000	27	—	1,234	1,417	3	—
Others	7,610	2,832	13	13	4,764	3,412	7	10	9,723	1,967	12	9
Totals	28,397	51,052	100	100	61,214	50,252	100	100	79,697	16,853	100	100

<sup>a</sup>Postcut data include all woody stems, and precut data include all stems  $\geq 2.5$  cm dbh. The % density of postcut stems includes both seedlings and sprouts.

and mountain laurel, which comprised 64% of the biomass prior to clearcutting (Table 12.2). Afterwards, mountain laurel and red maple were dominant (38%), followed by black locust (10%), American chestnut, chestnut oak, and scarlet oak (28%).

In the third year following clearcutting, there was little difference in herbaceous biomass between cove and chestnut oak sites, but both were higher than the scarlet oak–pine sites (Figure 12.2). Blackberries were dominant, ranging from 2026 kg on cove sites to 83 kg ha<sup>-1</sup> on scarlet oak sites. This range in herbaceous biomass can be attributed to the desiccating conditions in the upper forest floor along the south-facing slopes and ridges.

The density of seedlings decreased along the gradient from cove to chestnut oak to scarlet oak–pine communities (Table 12.3). This trend was likely due to lack of prunegules, as well as to high mortality resulting from the xeric forest floor microclimate along the south-facing slopes and ridges. High numbers of silver-leaf grape and yellow poplar seedlings germinated on the rich, moist cove sites (up to 16,222 and 18,000 seedlings ha<sup>-1</sup>, respectively). The scarlet oak–pine sites were occupied only by 1417 and 1417 seedlings ha<sup>-1</sup> of the two species.

Woody sprout densities increased from cove to chestnut oak to scarlet oak–pine communities, an inverse trend observed for seedling density (Table 12.3). Large red

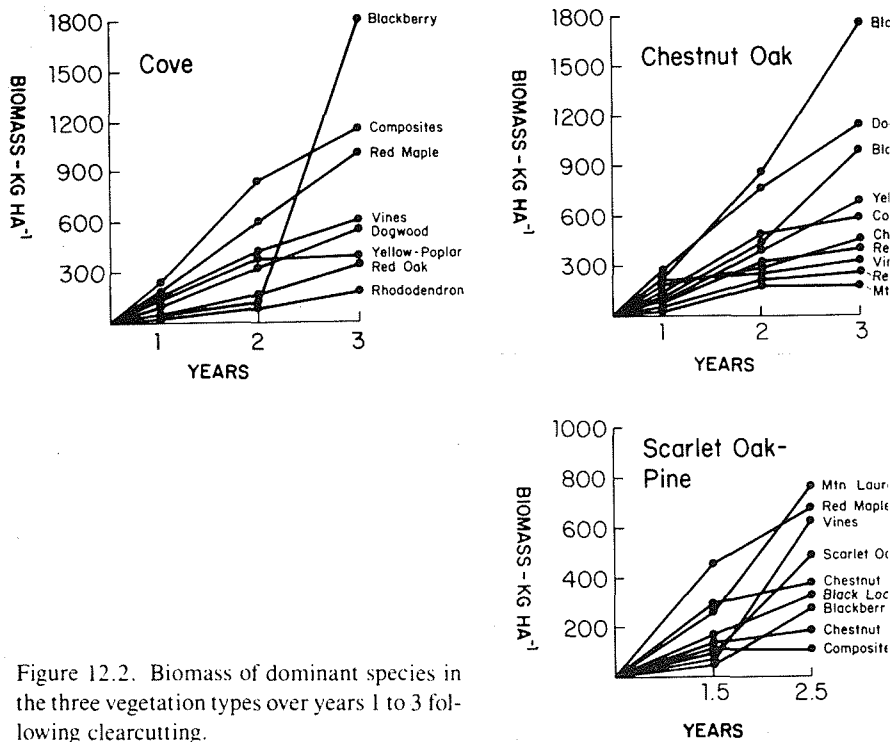


Figure 12.2. Biomass of dominant species in the three vegetation types over years 1 to 3 following clearcutting.

and hickories in the cove plots had poor sprouting capabilities (Sander 1972; Jackson 1975; McGee 1978), and sprout biomass was relatively low. The chestnut and scarlet oak-pine sites were occupied by species with superior sprouting abilities such as black locust, flowering dogwood, red maple, mountain laurel, and black gum (*Nyssa sylvatica*). The scarlet oak-pine community lacks the rapid growth that characterizes cove and chestnut oak communities with tall, dense stands of black locust, yellow-poplar, chestnut oak, and dogwood. However, the scarlet oak-pine community had a higher density of small diameter individuals, including mountain laurel, red maple, oak, blackgum, and American chestnut. American chestnut retained its ability to sprout vigorously, despite the introduction of chestnut blight in mid 1920s.

This 3-year study may be placed in a longer-term perspective by comparing to a nearby stand on WS 13, which was sampled at 9, 13, and 23 years following clearcutting (Swift and Swank 1981, Figure 12.3). Generally, the relative basal areas show early dominance of oak, red maple, black locust, and American chestnut. After 23 years, the oaks and red maple maintain dominance, but black locust and chestnut drop in significance. Yellow-poplar and flowering dogwood increase their dominance. There was a 73% recovery of basal area in 23 years following first clearcut and an 80% recovery in 21 years following a second cutting (Leopold and Parker 1985). In a related study, Parker and Swank (1982) found that regeneration response varied by species and physiographic position. After two clearcut treatments on WS 13 they found no overall change in the number of species present but rather an increased density of a few species; notably yellow-poplar, red maple, and chestnut oak. The other remaining species, except various oaks, declined in number.

Following clearcutting, the successional sequences (Figures 12.2 and 12.3) show black locust quickly sprouts, grows faster than other species, and attains e

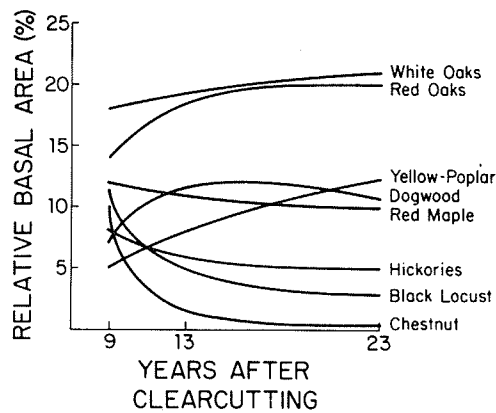


Figure 12.3. Relative basal area of dominant species on WS 13 from 9–23 years following clearcutting. (Data from Swift and Swank 1981.)

dominance. Similar establishment patterns have been documented throughout southern Appalachian region (Beck and McGee 1974; McGee and Hooper 1974). However, the dense stands eventually decrease in vigor, suffer high mortality concurrent with locust stem borer attack (*Megacyllene robiniae*), and decline, leaving enriched soil and organic matter for exploitation by other species (Craighead 1974; Boring and Swank 1984a).

Early thinning changes the structure of the coppice forest as codominant and dominant individuals fill gaps left by shorter-lived early dominants such as black locust and American chestnut. The relatively understory-tolerant oaks, hickories, and oaks species (*A. rubrum*, *Oxydendrum arboreum*) in the stand should eventually increase relative density and biomass. It is well documented that yellow-poplar increase density and basal area following clearcutting due to prolific seedling establishment and sprouting ability (Smith 1963; Trimble 1973; Beck and Della-Bianca 1981). This is clearly the pattern on WS 7 and WS 13 (Parker and Swank 1982). The species is long-lived and could conceivably occupy these sites for several hundred years (Buckner and McCracken 1978), or certainly until the end of the next harvest rotation. Yellow-poplar eventually attains a massive size (Lorimer 1980), and young stands in eastern Tennessee have been documented to have very high productivity, approximating  $12.0 \text{ t yr}^{-1}$  of NPP (Sollins 1972).

### Recovery of NPP and LAI

The recovery of aboveground NPP was rapid (Figure 12.4). The third year mesic site NPP was  $5.4 \text{ t ha}^{-1} \text{ yr}^{-1}$ , or 62% of the NPP estimated for the uneven-aged mixed hardwood forest on WS 18 (Day and Monk 1977a). After clearcutting, NPP on mesic sites was greater than on xeric sites, due to rapid sprout growth and abundance of herbaceous vegetation. The xeric site NPP was  $3.0 \text{ t ha}^{-1}$ , or 36% of the value for the older, uneven-aged forest on WS 18; although sprout density was high, the dominant species was mountain laurel, which is relatively slow growing. However, before logging it is likely that the NPP on these mesic sites was high and xeric site NPP was lower than the weighted watershed mean for WS 18. Although the NPP appears to recover quickly, it may not represent an actual "recovery" NPP. The root systems of the rapidly growing sprouts were intact to function for water and nutrient uptake, as well as to provide stored photosynthates and essential elements.

LAI comparisons with other sites in the Coweeta Basin show a rapid recovery; both the mesic and xeric sites (Figure 12.4). Including herbaceous leaf area, LAI in the third year was  $4.2 \text{ m}^2 \text{ m}^{-2}$ , or 68% of the estimate for a mature mixed hardwood forest on WS 18 (LAI =  $6.2 \text{ m}^2 \text{ m}^{-2}$ ; Chapter 10). The LAI on xeric sites was 48% of mature forest in 2.5 years. Although there was a rapid recovery of LAI, it does not necessarily follow that evapotranspiration will return rapidly to pretreatment levels. Other Coweeta research on WS 13 has shown increases in streamflow for 23 years following clearcutting (Swank and Helvey 1970). There are likely different rates of evapotranspiration for early successional woody species and herbs in comparison to uneven-aged mixed hardwoods which dominate mature watersheds.

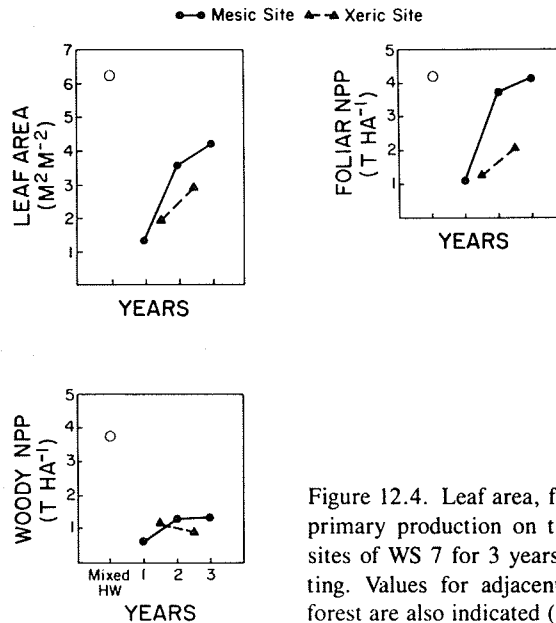


Figure 12.4. Leaf area, foliar and woody primary production on the mesic and xeric sites of WS 7 for 3 years following clearing. Values for adjacent mature hardwood forest are also indicated (°).

The patterns of early regeneration in southern Appalachian hardwood forests differ somewhat from those observed following clearcutting of northern hardwood Pacific northwest coniferous forests (Marks 1974; Bicknell 1979; Gholz et al. 1985). The prolific hardwood sprout, herb, and vine growth shown in this 3-year study results in more rapid biomass accretion (4.3 to 8.4 t ha<sup>-1</sup>) than reported elsewhere. Pacific northwest coniferous forests at the H.J. Andrews Forest have profuse herbaceous regrowth, but Douglas fir seedling establishment and early growth are slow, resulting in aboveground biomass of only 2.6 t ha<sup>-1</sup> in the third year (Gholz et al. 1985). Sprouting was less important and regeneration was slower for the first three years in the Hubbard Brook northern hardwood stands. A mixed northern hardwood stand 3 years after clearcutting had a comparative biomass of 4.7 t ha<sup>-1</sup> (Bicknell 1979). By 4 years, however, cherry (*Prunus pennsylvanica*) was well established from dormant seeds in the forest floor, resulting in increased accretion rates of biomass and nutrients, especially in dense pin cherry stands (Marks 1974). Although southern Appalachian mesic hardwood forests at Coweeta initiate regrowth and accumulate nutrients more rapidly, regrowth rates in the intermediate-aged northern hardwood stands at Hubbard Brook may later minimize these early differences in vegetation processes (Marks and Boring 1972).

### Nutrient Accumulation and Cycling

In the clearcut watershed, significantly ( $p < .05$ ) higher concentrations of N and P were found in leaves of early successional woody species in comparison to other woody species.

species. These species included black locust (high N, P, and K), yellow-poplar (high P, Ca and Mg), and silver-leaf grape (high N and P). Comparisons among growth forms (herbs, vines, woody species) revealed several trends which were highly significant ( $p < .05$ ): higher leaf K in herbs, and higher leaf Ca and P in sprouts. Most differences among species were significant in all 3 years, although the first year leaf and stem concentrations were greater than the second or third year for most species.

As a result of the high element concentrations in early successional woody species and herbs, as well as their rapid growth rates, there was a relatively large quantity of nutrients immobilized in the aboveground biomass by the third year in comparison to the control mixed hardwood forest (Table 12.4). Quantities of N, P, K, Ca, and Mg on the mesic sites were 27, 13, 36, 10, and 31% of the control forest, respectively. Estimates for the xeric sites after 2.5 years were 16, 10, 20, 5, and 17%. The relative amounts of nutrients contained within the foliar fraction is very high. Sprout leaves of herbs comprise 70 to 78% of the total standing stocks of all elements on mesic sites, 62 to 67% of all elements on xeric sites. Although large quantities of nutrients are immobilized each growing season, there is a proportionately large amount in the biomass, resulting in an autumnal flux back to the forest floor as litterfall and leachate (White 1986). These values, along with an estimate of retranslocation, are not currently available for comparison in these stands, but this flux likely comprises the majority of the nutrients in the foliar standing stocks. There is a need to understand more fully the transfer and turnover of nutrients in early successional stands.

Annual aboveground NPP on the 3-year-old mesic sites contained a large amount of nutrients relative to the mature, uneven-aged mixed hardwood forest (Figure 12.5). The N, P, K, Ca, and Mg were 93, 57, 141, 91, and 105% of the values for the mature forest. The xeric sites after 2.5 years were estimated to contain approximately half the nutrients contained on the mesic sites. The species responsible for most of the NPP had high ratios of leaf/stem production and high tissue concentrations relative to dominant later-successional species in the uneven-aged hardwood forest. This is especially true for herbaceous and vine regrowth, but is also representative of the fast-growing black locust, yellow-poplar, and other woody opportunistic species.

The early recovery of nutrients in NPP is likely a result of the ability of early successional species to quickly respond to forest floor nutrient availability following clearcutting. Sprouting hardwoods have extensive residual root systems to facilitate water and nutrient uptake. Also, studies of root uptake kinetics (Haines 1986) have shown that certain early successional southern Appalachian plant species have the physiological potential to extract nutrients more rapidly from solution than can later successional species.

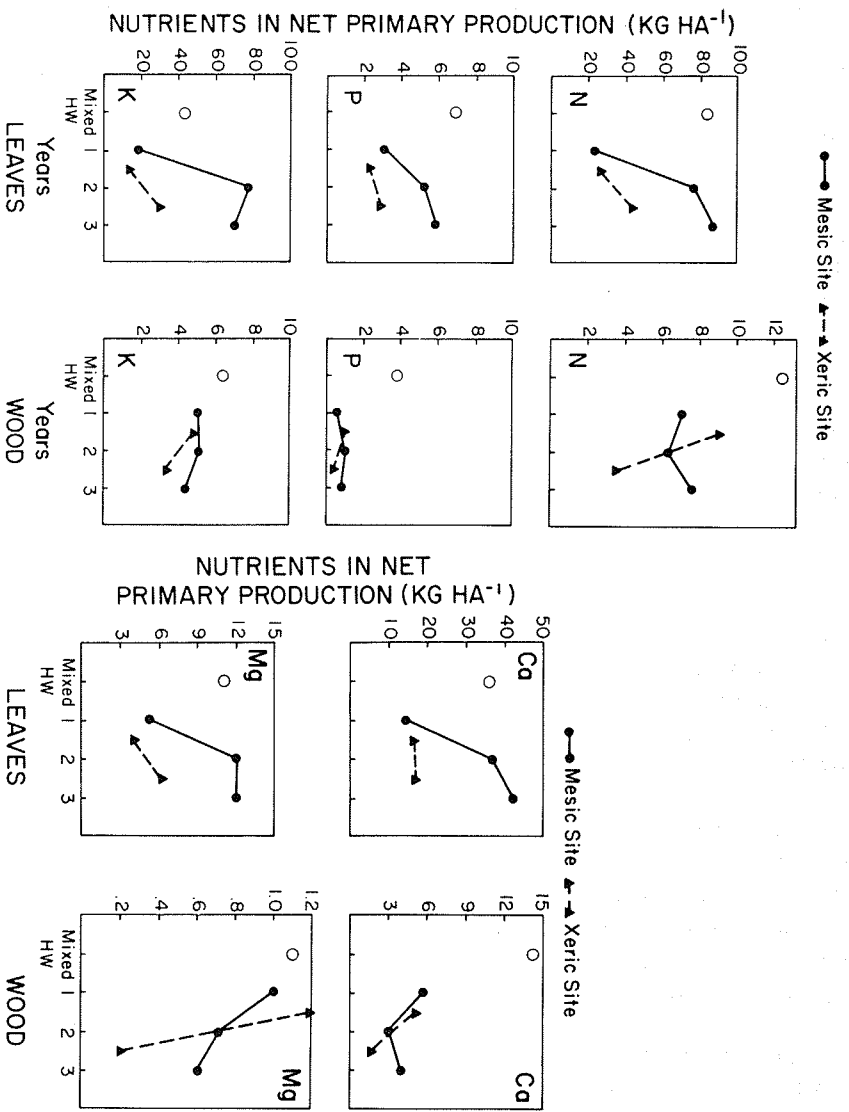
Although decomposition was initially slowed by the hot and dry forest floor microclimate which followed clearcutting (Abbott and Crossley 1982; Seastedt and Crossley 1981), there was nutrient enrichment of throughfall as water passed through the woody logging residue (W.T. Swank, unpublished data). In the third year (Figure 12.5), the decrease in the rate of biomass nutrient accretion on mesic sites may have been attributable to depletion of readily leachable nutrients from this source, or to increased internal conservation of nutrients within individuals. A corollary hypothesis is that the aboveground standing stocks of nutrients may have originated from the in-



Table 12.4. Nutrient standing crops (kg ha<sup>-1</sup>) in aboveground biomass from mesic (cove chestnut oak) and xeric (scarlet oak and pine hardwood) sites on WS 7 following clearcutti

Element	Growth Form	Mesic Sites			Xeric Sites		WS 18
		Years			Years		Uneven-a
		1	2	3	1.5	2.5	
N (kg ha <sup>-1</sup> )	Sprouts						
	Leaf	12	31	45	18	36	95
	Stem	5	9	17	8	10	310
	Seedlings	1	9	8	2	8	—
	Vines	3	8	3	2	3	—
	Herbs	8	31	35	5	6	—
	Total	29	88	108	35	63	405 <sup>a</sup>
P (kg ha <sup>-1</sup> )	Sprouts						
	Leaf	0.5	2	3	2	3	8 <sup>c</sup>
	Stem	0.5	1	1	1	1	52 <sup>b</sup>
	Seedlings	<1	1	1	<1	1	—
	Vines	<1	0	<1	<1	<1	—
	Herbs	1	3	3	<1	<1	—
	Total	3	7	8	3	6	60
K (kg ha <sup>-1</sup> )	Sprouts						
	Leaf	5	18	26	9	22	47
	Stem	4	6	10	4	7	183
	Seedlings	1	6	5	1	5	—
	Vines	2	7	3	1	3	—
	Herbs	13	49	38	6	8	—
	Total	25	86	82	21	45	230 <sup>c</sup>
Ca (kg ha <sup>-1</sup> )	Sprouts						
	Leaf	8	13	17	12	15	47
	Stem	4	5	9	5	6	504
	Seedlings	1	4	4	1	3	—
	Vines	3	7	3	1	2	—
	Herbs	4	16	21	2	3	—
	Total	20	45	54	21	29	551 <sup>c</sup>
Mg (kg ha <sup>-1</sup> )	Sprouts						
	Leaf	2	3	5	3	4	13
	Stem	1	1	2	1	1	35
	Seedlings	<1	1	1	<1	1	—
	Vines	<1	2	1	<1	1	—
	Herbs	2	7	6	1	1	—
	Total	6	14	15	5	8	48

<sup>a</sup>From Mitchell, Waide and Todd 1975.<sup>b</sup>From Duvigneaud and Denayer-DeSmet 1969.<sup>c</sup>From Day and Monk 1977b.<sup>d</sup>Comparative estimates from WS 18 average all sites on the control watershed.



roots of sprouting hardwoods in conjunction with stored photosynthate. The third may represent the point at which hardwood sprout reserves were tapering off uptake was the sole source of nutrients. For a few years, a large percentage of the nutrients concentrated by early successional woody species may be retranslocated internally recycled to maintain growth beyond the initial period of high nutrient availability (Ryan and Bormann 1982). Other potential factors affecting the decreased accretion rates in the third year include annual variations in NPP due to climate, and mortality resulting from competition.

Black locust symbiotically fixes at least  $30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (Boring and Swank 1984a) and accumulates large quantities of N in its biomass (Boring and Swank 1984a), and maintains elevated concentrations of other nutrients in both leaves and wood (Boring and Swank 1981). The biomass of this short-lived species may be regarded as a nutrient storage sink for an intermediate span of time, approximating the life of the stand (15 to 20 years). In plantation studies, elevated soil N from black locust has been shown to accelerate the growth of associated vegetation over the long-term (Chapman 1981). The high annual transfers of N in litterfall, throughfall, and root turnover are apparently the source of elevated  $\text{NO}_3\text{-N}$  in soil underneath black locust stands (Boring and Swank 1984a); intuitively, the transfer and availability of N should be maximal at the time of stand senescence. Of additional importance, the N ultimately transferred to the soil at stand senescence may potentially alter C/N ratios and affect decomposition and availability of other macronutrients.

### Vegetation Influences

Other investigators at Coweeta have found that clearcutting results in first-year forest floor temperatures up to  $47^\circ\text{C}$ , severe wetting and drying cycles in forest floor surface horizons, alteration of microarthropod activity in litter (Seastedt and Crossley 1982) and slow first-year decomposition of woody litter, especially on xeric sites (Abbott and Crossley 1982). The return of a high LAI by the third year results in shading, amelioration of the harsh forest floor microclimate, and dampening of environmental effects on forest floor biota and their processes. With early canopy closure, there should be a concomitant increase in the decomposition rates of woody and leaf litter. By the sixth year following clearcutting, there is a large cumulative amount of decomposition in leaf and woody litter, with decreases in wood density of some species exceeding 50% (Matlack 1986). Woody debris can act as a nutrient sink at least during early phases of decomposition (Abbott and Crossley 1982), and the gradual reduction of this material (as well as dead roots) to humus should partially account for observed soil organic matter (0 to 15 cm depth) increases during the first few years following clearcutting (Chapter 10). The increase in soil organic matter increases storage pools of N and P in the soil, likely through increases in the exchange capacity and the amount of exchangeable nutrients that may be immobilized.

In summary, the effects of early successional forest vegetation upon ecosystem nutrient cycling processes in the southern Appalachians may be grouped into two major categories: (1) direct seasonal immobilization of nutrients in biomass, and (2) hypothesized high annual throughfall and litterfall nutrient transfers to the forest floor.

---

as a result of accelerated nutrient uptake and concentration; (2) enrichment through symbiotic N fixation, immobilization, and eventual transfer of N to the floor with potential influence upon the rates of availability of other nutrients; an early shading and the recovery of forest floor temperature and moisture conditions resulting in the rapid recovery of biological activities which control decomposition, mineralization, and the potential mobility of nutrients.

---