

Successional changes in plant species diversity and composition after clearcutting a Southern Appalachian watershed

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Abstract

Watershed 7, a southwest-facing watershed in the Coweeta Basin, western North Carolina, USA, was clearcut in 1977. Twenty-four permanent plots were inventoried in 1974 before cutting and in 1977, 1979, 1984, and 1993 after clearcutting. This study evaluates changes in species diversity during early succession after clearcutting and differences in overstory tree and ground flora response to disturbance by clearcutting and their interaction with previous disturbances and subsequent stand development. To quantify species diversity, we computed Shannon–Weaver's index of diversity (H') and Pielou's evenness index (J'). Woody species diversity remained relatively stable; however, woody species richness increased in the cove-hardwoods and hardwood-pines, but remained relatively constant in the mixed-oak hardwoods. Although revegetation was rapid, forest composition has changed through succession. Opportunistic species, such as *Liriodendron tulipifera*, *Robinia pseudoacacia*, and *Acer rubrum*, increased in abundance, whereas *Quercus velutina*, *Carya* spp., and *Q. rubra* decreased. Ground flora diversity declined in the cove-hardwoods and mixed-oak hardwoods communities, but the decrease in the hardwood-pines was not significant. The abundance (g biomass m^{-2}) of ground flora was much lower in 1993 than in 1984; 79% less in the cove-hardwoods, 90% less in the mixed-oak hardwoods, and 79% less in the hardwood-pines. Watershed 7 is apparently in a transition state between early and late successional species abundance. Early successional, shade-intolerant species, such as *Erechtites*, *Solidago*, *Eupatorium*, *Panicum*, and *Aster*, have declined, whereas late successional, shade-tolerant species, such as *Viola*, *Galium*, *Sanguinaria*, *Uvularia*, and *Veratrum* are not yet well established.

Keywords: Stand dynamics; Herbaceous and woody flora; Disturbance

1. Introduction

Maintenance of species diversity has become an important topic in forest management studies (Norse

et al., 1986; Hunter, 1990; Burton et al., 1992), with special emphasis on understanding the role of various species in the recovery of forest structure and processes (Boring et al., 1981; Schoonmaker and McKee, 1988; McMinn, 1991; Huston, 1994). The effects of human-induced disturbances in forested ecosystems on forest regeneration, structure, produc-

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tivity, and diversity vary with frequency, intensity, and scale of disturbance (Runkle, 1985; Petraitis et al., 1989; Huston, 1994). Although no single generalization prevails for describing changes in species richness and diversity through succession, eastern forest systems tend to increase in both measures after forest harvesting then decline as forests mature (Bicknell, 1979; Hibbs, 1983; Reiners, 1992; Roberts, 1992; Wang and Nyland, 1993).

Huston and Smith (1987) described succession as a sequential change in the relative abundances of the dominant species in a community. During early succession, physiological characteristics, such as stress tolerance, rapid growth rate, or high nutrient acquisition, may influence species abundance. Later in succession, size and shade tolerance may emerge as the physiological characteristics that affect species abundance. Species are also capable of changing their competitive ability when conditions change, but they are unable to adapt to all successional stages or environmental conditions (Huston and Smith, 1987). This description implies that certain species or groups of species will lose dominance unless a disturbance or environmental change interferes. Thus, some successional stages may have more species, as well as different sets of species, than others (Hunter, 1990). However, forests are always changing owing to natural disturbances, such as wind, fire, drought, or single or multiple tree mortality, that may create canopy gaps with earlier stages of succession. Therefore, competitive equilibrium or steady state rarely occurs (Huston, 1979).

Many generalizations for successional change have been inferred from analysis of chronosequences of stands representing different ages (Peet and Loucks, 1977; Finegan, 1984; Roberts and Christensen, 1988). However, variation among forest stands along a chronosequence can arise from interacting sources including historical factors (e.g. disturbance, variations in seed rain), site environment (e.g. climate, slope, aspect, and soil variables), and autogenic successional change. The most direct and unambiguous method of documenting succession involves measuring changes in a single site through time. Because the time scale is long, few studies have used this approach (e.g. Peet and Christensen, 1980; Hibbs, 1983; Hartnett and Krofta, 1989; Reiners, 1992; Fain et al., 1994).

For the past several decades, experimental clearcuts have provided an opportunity to examine how these large-scale forest disturbances influence various processes, such as stream hydrology (Swank and Helvey, 1970; Likens et al., 1977; Swank et al., 1988), soil erosion (Hewlett, 1979; Van Lear et al., 1985), nutrient cycling (Johnson and Swank, 1973; Bormann et al., 1974, Bormann et al., 1977; Likens et al., 1977; Gholz et al., 1985; Boring et al., 1988; Waide et al., 1988; Reiners, 1992), and vegetation diversity and successional patterns (Parker and Swank, 1982; Gholz et al., 1985; Hornbeck et al., 1987; Boring et al., 1988; Reiners, 1992; Gove et al., 1992; Elliott and Swank, 1994a). In a regeneration project conducted in a clearcut watershed in the Coweeta Basin, southwestern North Carolina, studies were conducted 1, 3, and 8 years after disturbance (Boring, 1979; Boring et al., 1981, Boring et al., 1988; Boring and Swank, 1986). These studies examined the role of dominant early successional species in forest recovery and ecosystem processes, but did not address longer-term species patterns, diversity, and richness. In this study, we analyze successional patterns in composition and diversity of herbaceous and woody species in the same clearcut watershed to age 17 years. Our objectives were to describe changes in species diversity during early succession after clearcutting, and evaluate differences in overstory and ground flora vegetation response to disturbance by clearcutting.

2. Methods

2.1. Site description

The study site, a 59 ha watershed (WS7), is located in the Coweeta Hydrologic Laboratory (35°04'30"N, 83°26'W) near Franklin, NC. The Coweeta Basin is in the Nantahala Mountains—part of the Blue Ridge province in the Southern Appalachians. Watershed 7 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 high 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. The 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, and average 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).

The land-use history in the Coweeta Basin includes selective logging, woodland grazing, and burning. Before 1842, Cherokees burned semi-annually to improve forage for livestock. Between 1842 and 1900, European settlers moving into the area also burned and grazed the basin. A few hectares in WS7 were probably cultivated around 1901. Be-

tween 1900 and 1923, logging operations occurred over the entire basin, but cutting was heaviest on the lower slopes, valleys, and accessible coves. Since 1924, human disturbances 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 in WS7 between 1941 and 1952, six head of cattle were used to assess the impact of woodland grazing on a portion of the watershed. Short-range effects were limited primarily to soil compaction and overgrazing in the cove area adjacent to the stream (Johnson, 1952; Williams, 1954).

Watershed 7 was clearcut in 1977 as part of an interdisciplinary study of the physical, chemical, and biological effects on both terrestrial and aquatic

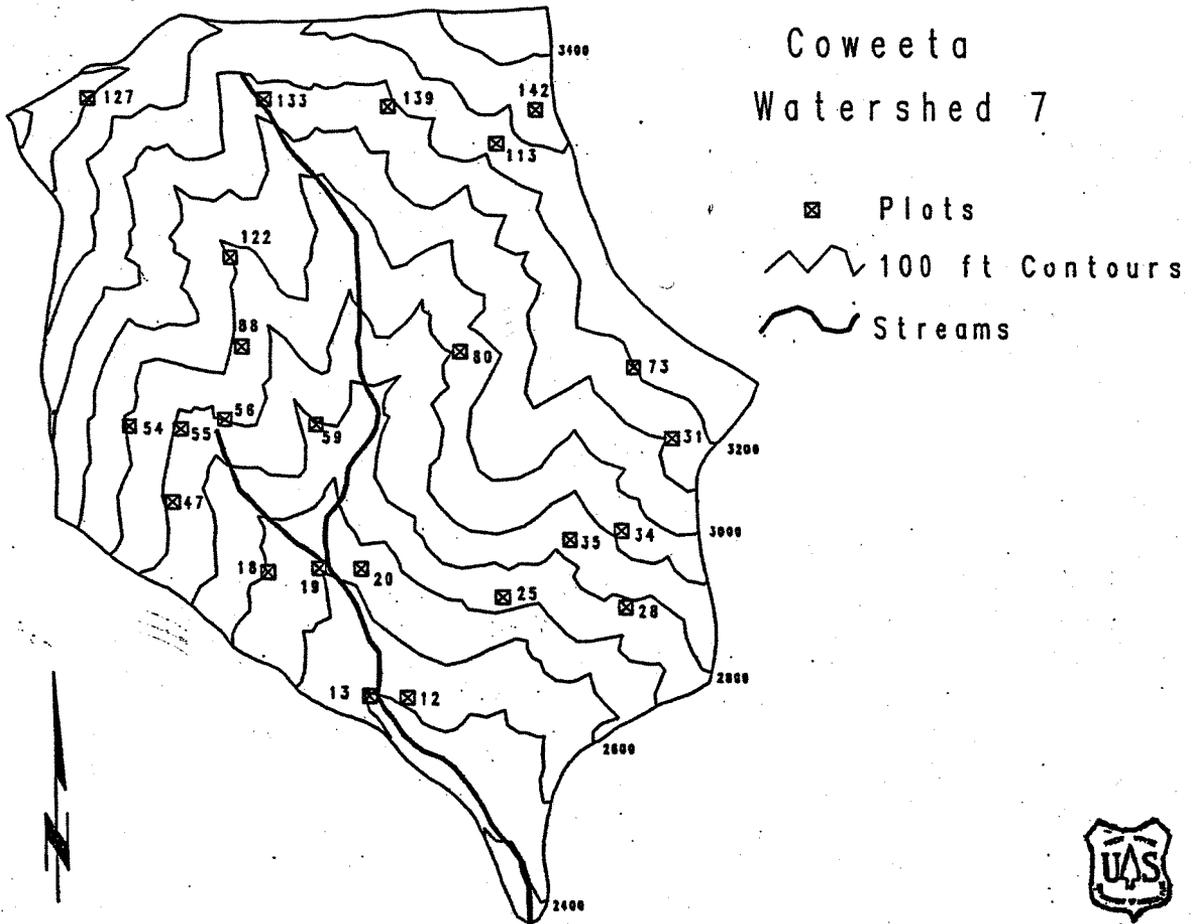


Fig. 1. Topographic map of plot locations including streams in Watershed 7, Coweeta Basin, western North Carolina, USA.

components of the ecosystem (Swank and Caskey, 1982). Harvesting, begun in January 1977, was completed in June. Tractor skidding was used on slopes less than 20% (about 9 ha), and yarding with a mobile cable system on the remaining area. In the cutting operation, marketable timber was removed by cable logging. Most of the ridgetops and xeric slopes were cut, but were not cable logged because the volume of marketable timber was insufficient. All stems of 2.5 cm or more dbh (diameter at breast height) were cut and logging debris was left in place with no further site preparation. This harvest technique minimizes soil compaction and other structural disturbances of the forest floor and plant roots.

2.2. Sampling procedures

Before clearcutting, vegetation was inventoried from 142 plots of 20 m × 40 m systematically located over WS7. Based on previous studies (Williams, 1954; Day et al., 1988), three community types were identified in WS7: (1) cove-hardwoods found at lower elevations and along ravines at intermediate elevations; (2) mixed-oak hardwoods on mesic southeast-facing and north-facing slopes at intermediate elevations; (3) hardwood-pines on xeric southwest- and south-facing slopes at intermediate to upper elevations and ridgetops. Plots were classified into community types based on detrended correspondence analysis (DCA) (Gauch, 1982) that used pre-cut wood vegetation data from 1974 for 24 permanently marked plots. The cove-hardwoods community had high numbers of *Rhododendron maximum*, *Hamelis virginiana*, *Liriodendron tulipifera* and *Betula lenta*, with some mesic species such as *Tilia heterophylla* and *Aesculus octandra*. The mixed-oak hardwoods community had high numbers of diverse oak species, *Liriodendron tulipifera*, *Cornus florida* and no or low densities of understory ericaceous shrubs, such as *Rhododendron maximum* or *Kalmia latifolia*. The hardwood-pines community had high numbers of *Quercus prinus*, *Q. coccinea* and *K. latifolia*, and scattered *Pinus rigida* and *Prunus serotina* (Fig. 1).

After cutting in 1977, 18 of the 142 plots were sampled for regrowth: eight in the cove-hardwoods, five in the mixed-oak hardwoods, and five in the hardwood-pines. In 1978, five plots from the 18

were dropped and 11 plots from the remaining 124 were added to total 24 permanently marked plots. Sample sizes were increased to reflect relative areal coverage of each community within the watershed. Seven plots represented the cove-hardwoods, five the mixed-oak hardwoods, and 12 the xeric hardwood-pines (Fig. 2). The 24 plots were remeasured in subsequent years (1979, 1984 and 1993) to observe the changes in vegetation composition through succession.

Two quadrats were located in opposite corners of each 0.08 ha plot. Hardwood sprouts were sampled in 7 m × 7 m subplots and seedlings were sampled in 3 m × 3 m subplots; values were pooled for each pair. To understand the mode of reproduction, each woody stem was classified into one of two categories: sprout, if it originated from a previously established stump or root system; seedling, if it originated from seed since clearcutting or was a single stem from advance regeneration. This differentiation may overestimate seed origin reproduction, particularly because root sprouts are difficult to distinguish from seed origin without partial exposure of the root systems and because many established small root systems may send up single sprouts. *Robinia pseudoacacia* sprouts were distinguished by their attachment to lateral roots.

At the end of each growing season, densities of sprouts and seedlings were recorded separately 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. Different species were 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 of 1.0 cm or more were measured to the nearest 0.1 cm at 1.37 m from ground level. Stems with less than 1.0 cm dbh were measured to the nearest 0.1 cm at 3 and 40 cm from ground level.

Mid-point values of each diameter class multiplied by the number of stems in that class were used to calculate basal area for years 1977–1984. Basal area of saplings estimated from diameters at 3 cm

from the base would overestimate basal area. Because sapling basal areas (years 1977, 1979, and 1984) were estimated entirely from diameters measured at 3 and 40 cm from the base, the values were exaggerated compared with tree basal areas of stems of more than 1 cm dbh measured at conventional breast height (1.37 m).

After clearcutting, all herbaceous vegetation was harvested in August each year (1977–1993) from one randomly placed 1.0 m² subplot within each quadrat. Vegetation was separated by species and oven-dried to constant weight at 70°C. All species identification followed nomenclature consistent with Radford et al. (1968).

A woodland grazing experiment conducted from 1941 to 1952 (Williams, 1954) furnished the only

data available on herbaceous species presence and abundance in WS7 before clearcutting. Williams also provided insights into the impact of traditional land-use activity on species diversity. Data collected in 1952 from 17 ungrazed, fenced plots containing two 4.04 m² subplots provided information on understory plants 30 years after recovery from the selective logging that occurred from 1900 to 1923 and before the large-scale clearcutting in 1977. This data allowed a qualitative comparison of herbaceous species presence and abundance before and after clearcutting.

2.3. Data analysis

To evaluate species diversity, Shannon–Weaver's index of diversity (H') (Shannon and Weaver, 1949)

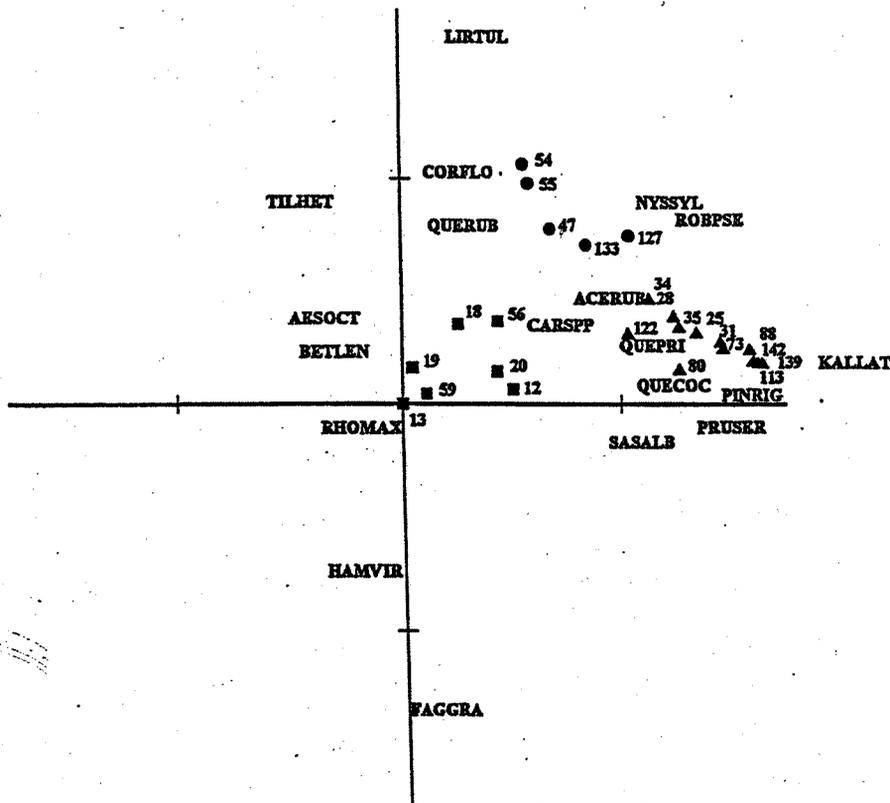


Fig. 2. Detrended correspondence analysis of the 24 permanent plots along the first two ordination axes with location of species along ordinations. ■, Cove-hardwoods; ●, mixed-oak hardwoods; ▲, hardwood-pines. Species codes: LIRTUL, *Liriodendron tulipifera*; ACERUB, *Acer rubrum*; KALLAT, *Kalmia latifolia*; RHOMAX, *Rhododendron maximum*; QUECOC, *Quercus coccinea*; QUEPRI, *Quercus prinus*; QUERUB, *Quercus rubra*; CORFLO, *Cornus florida*; AESOCT, *Aesculus octandra*; HAMVIR, *Hamamelis virginiana*; BETLEN, *Betula lenta*; FAGGRA, *Fagus grandifolia*; NYSSYL, *Nyssa sylvatica*; ROBPSE, *Robinia pseudoacacia*; CARSP, *Carya* spp.; TILHET, *Tilia heterophylla*; PINRIG, *Pinus rigida*; PRUSER, *Prunus serotina*.

and Pielou's evenness index (J') (Pielou, 1966) were computed. Shannon–Weaver's index is a simple quantitative expression that incorporates both species richness and the evenness of species abundance. Because the calculated value of H' alone does not show the degree to which each factor contributes to diversity, a separate measure of evenness (J') was calculated. Diversity was calculated on the basis of stem basal area per hectare for woody species and biomass per square meter for herbaceous species: $H' = -\sum p_i \ln p_i$, where p_i is the proportion of total basal area of species i . Species evenness was calculated as $J' = H'/H'_{\max}$, where H'_{\max} is the maximum level of diversity possible within a given population, which equals $\ln(\text{number of species})$. We used pairwise t -tests (Magurran, 1988) to examine the differences in diversity between sampling years from 1974 to 1993. No statistical tests were performed for 1952 because ground flora measurements were based on density rather than biomass.

3. Results

3.1. Changes in woody species

In each community, more than 15 tree species regenerated after clearcutting. Shade-tolerant species were *Acer rubrum*, *Nyssa sylvatica*, *Fagus grandifolia*, *Cornus florida*, *Tsuga canadensis*, *Oxydendrum arboreum*, *Amelanchier arborea*, and *Hamamelis virginiana*. Species with intermediate shade tolerance included *Carya* spp., *Fraxinus americana*, *Quercus prinus*, *Q. rubra*, and *Q. velutina*. Shade-intolerant species included *Liriodendron tulipifera*, *Betula lenta*, *Robinia pseudoacacia*, and *Q. coccinea* (Burns and Honkala, 1990). Species regenerating infrequently were *Tilia heterophylla*, *Diospyros virginiana*, *Sassafras albidum*, *Symplocos tinctoria*, *Prunus serotina*, and *A. pensylvanicum*.

In 1974, *Carya* spp., *Q. rubra*, and *L. tulipifera* were the three most abundant tree species in the cove-hardwoods community (Table 1). After clearcutting in 1977, *C. florida*, *A. rubrum*, and *L. tulipifera* became the most dominant tree species. The woody vine, *Vitis* spp., was more dominant than *L. tulipifera*. By 1984, *Vitis* spp. began to lose its dominant position in the community, and *R. maxi-*

mum became the most abundant species. By 1993, *L. tulipifera* was the leading dominant species at 22% of the total basal area.

In the mixed-oak hardwoods community before cutting, *Q. velutina*, *L. tulipifera*, and *Carya* spp. were the most abundant species, occupying 56% of the total basal area. After cutting in 1977, *C. florida*, *Vitis* spp., and *L. tulipifera* made up 64% of the basal area. *C. florida* remained the leading dominant to 1984. *L. tulipifera* regained its dominance by 1993 with 44% of the total basal area, and *R. pseudoacacia* became increasingly more important in the community. *Q. velutina* did not regain its dominant position and made up less than 1% of the total basal area from 1977 through 1993.

In the hardwood-pines community before cutting, *Q. prinus*, *K. latifolia*, and *Q. coccinea* were the three most abundant species with 63% of the basal area. *Vitis* spp. became important after disturbance but declined rapidly. *K. latifolia* remained dominant after cutting and increased in importance through succession. *A. rubrum* increased in importance 2 years after cutting and remained dominant to 1993 (Table 1). *C. florida* and *R. pseudoacacia* were more abundant immediately after clearcutting, but began to decline by 1979. With 60% of the total basal area, *K. latifolia*, *Q. prinus*, and *A. rubrum* were the leading dominants in 1993.

Some woody species were present after clearcutting, but not recorded in the overstory woody measurements before clearcutting. Most of these species were shrubs and vines. Because only stems with dbh of 2.5 cm or more were recorded in 1974, small stemmed shrubs and vines, such as *C. florida*, *E. americanus*, *P. pubera*, and *Vitis* spp., were probably not recorded because they were small, not absent.

In 1974, stem density in the hardwood-pines community was more than two times greater than in the other two communities (Table 2). This higher density was attributed primarily to *K. latifolia*, which grows on the upper slopes and ridges of the watershed. *K. latifolia* contributed 62% of the density and 19% of the basal area in the hardwood-pines (Table 1). Without *K. latifolia*, stem density in the hardwood-pines community would have been 1523 stems, and basal area $22.25 \text{ m}^2 \text{ ha}^{-1}$, which would have been lower than the other two communities.

Density increased substantially in all communities following harvest, with 24–46 times more stems per hectare in 1977 than in the pre-cut forest. By 1993, densities were still 6–9 times greater than in the pre-cut forest. The 17-year-old forest (1993) of WS7

Table 1

Leading dominant woody species (more than 2% of basal area in any year) ordered by sequence of maximum percentage contribution to basal area in 1974

| Species | Year | | | | |
|-----------------------------------|-------------|-------------|-------------|-------------|-------------|
| | Pre-cut | | Post-cut | | |
| | 1974 | 1977 | 1979 | 1984 | 1993 |
| Cove-hardwoods | | | | | |
| <i>Carya</i> spp. | 18.0 | 1.4 | 1.2 | 1.9 | 0.9 |
| <i>Quercus rubra</i> | 15.1 | 6.2 | 4.9 | 4.0 | 5.7 |
| <i>Liriodendron tulipifera</i> | 12.0 | 10.7 | 11.1 | 6.4 | 21.6 |
| <i>Betula lenta</i> | 7.8 | 0.2 | 5.0 | 7.5 | 12.0 |
| <i>Rhododendron maximum</i> | 7.8 | 6.6 | 9.4 | 20.9 | 11.2 |
| <i>Tilia heterophylla</i> | 6.8 | 0.3 | 0.8 | 0.3 | 0.6 |
| <i>Quercus prinus</i> | 6.3 | 0.2 | 0.4 | 0.3 | 0.7 |
| <i>Acer rubrum</i> | 6.0 | 14.9 | 11.7 | 9.8 | 5.7 |
| <i>Quercus alba</i> | 5.0 | 0.1 | 0.1 | 0.4 | 0.01 |
| <i>Aesculus octandra</i> | 3.8 | 0.0 | 0.1 | 0.0 | 0.04 |
| <i>Cornus florida</i> | 2.8 | 18.4 | 15.1 | 11.5 | 6.6 |
| <i>Tsuga canadensis</i> | 2.3 | 2.2 | 1.5 | 2.3 | 7.5 |
| <i>Fagus grandifolia</i> | 1.9 | 2.4 | 1.7 | 1.0 | 1.4 |
| <i>Vitis</i> spp. | 0.0 | 12.0 | 12.4 | 6.1 | 1.1 |
| <i>Hamamelis virginiana</i> | 0.4 | 3.7 | 5.8 | 6.6 | 3.9 |
| <i>Fraxinus americana</i> | 0.2 | 3.5 | 2.2 | 1.5 | 3.8 |
| <i>Kalmia latifolia</i> | 0.2 | 5.1 | 4.1 | 4.6 | 1.5 |
| <i>Amelanchier arborea</i> | 0.0 | 2.3 | 1.6 | 1.0 | 0.3 |
| <i>Nyssa sylvatica</i> | 0.6 | 2.2 | 2.5 | 1.3 | 0.02 |
| <i>Robinia pseudoacacia</i> | 0.0 | 1.8 | 3.2 | 1.5 | 9.5 |
| <i>Oxydendrum arboreum</i> | 0.9 | 1.7 | 1.3 | 0.1 | 2.7 |
| Total | 97.9 | 95.9 | 96.1 | 89.0 | 96.8 |
| Mixed-oak hardwoods | | | | | |
| <i>Quercus velutina</i> | 20.9 | 0.1 | 0.3 | 0.5 | 0.6 |
| <i>Liriodendron tulipifera</i> | 18.5 | 14.7 | 13.1 | 7.1 | 43.7 |
| <i>Carya</i> spp. | 16.7 | 6.2 | 1.2 | 1.4 | 0.5 |
| <i>Quercus prinus</i> | 12.5 | 3.5 | 1.0 | 2.3 | 2.1 |
| <i>Acer rubrum</i> | 8.3 | 6.3 | 4.3 | 8.8 | 8.2 |
| <i>Cornus florida</i> | 8.3 | 27.2 | 29.8 | 31.8 | 12.5 |
| <i>Nyssa sylvatica</i> | 5.7 | 2.4 | 13.1 | 4.1 | 1.2 |
| <i>Oxydendrum arboreum</i> | 3.5 | 0.4 | 1.5 | 2.0 | 1.3 |
| <i>Quercus rubra</i> | 2.4 | 5.1 | 3.2 | 3.1 | 3.6 |
| <i>Robinia pseudoacacia</i> | 1.9 | 6.4 | 9.5 | 10.1 | 21.3 |
| <i>Vitis</i> spp. | 0.0 | 21.9 | 11.0 | 6.0 | 1.0 |
| <i>Castanea dentata</i> | 0.6 | 3.3 | 0.6 | 2.8 | 0.0 |
| <i>Kalmia latifolia</i> | 0.0 | 0.0 | 1.9 | 3.9 | 0.2 |
| <i>Sassafras albidum</i> | 0.0 | 0.6 | 6.2 | 6.0 | 1.3 |
| <i>Rhododendron calendulaceum</i> | 0.04 | 0.0 | 1.3 | 3.2 | 0.1 |
| Total | 99.3 | 98.1 | 98.0 | 93.1 | 97.6 |

Table 1 (continued)

| Species | Year | | | | |
|--------------------------------|-------------|-------------|-------------|-------------|-------------|
| | Pre-cut | | Post-cut | | |
| | 1974 | 1977 | 1979 | 1984 | 1993 |
| Hardwood-pines | | | | | |
| <i>Quercus prinus</i> | 26.0 | 6.0 | 6.4 | 5.6 | 22.2 |
| <i>Kalmia latifolia</i> | 18.8 | 20.5 | 37.1 | 34.7 | 23.3 |
| <i>Quercus coccinea</i> | 18.0 | 0.9 | 5.7 | 4.8 | 8.0 |
| <i>Acer rubrum</i> | 6.8 | 6.9 | 12.9 | 11.7 | 14.2 |
| <i>Oxydendrum arboreum</i> | 5.5 | 5.9 | 2.5 | 1.0 | 2.5 |
| <i>Quercus velutina</i> | 4.1 | 0.0 | 0.3 | 0.2 | 0.2 |
| <i>Nyssa sylvatica</i> | 3.2 | 5.0 | 5.9 | 4.8 | 2.6 |
| <i>Carya</i> spp. | 2.7 | 1.2 | 1.7 | 1.4 | 1.6 |
| <i>Quercus alba</i> | 2.6 | 0.0 | 0.6 | 0.4 | 0.7 |
| <i>Cornus florida</i> | 2.6 | 9.9 | 4.0 | 5.1 | 1.7 |
| <i>Pinus rigida</i> | 2.2 | 0.0 | 0.0 | 0.02 | 0.1 |
| <i>Robinia pseudoacacia</i> | 1.8 | 8.0 | 2.2 | 2.3 | 3.4 |
| <i>Liriodendron tulipifera</i> | 1.8 | 1.1 | 1.2 | 1.77 | 6.2 |
| <i>Castanea dentata</i> | 1.0 | 5.6 | 3.6 | 3.3 | 2.8 |
| <i>Vitis</i> spp. | 0.0 | 21.0 | 3.9 | 2.5 | 0.2 |
| <i>Quercus rubra</i> | 0.7 | 2.4 | 0.1 | 0.6 | 0.88 |
| <i>Symplocos tinctoria</i> | 0.0 | 1.6 | 2.1 | 2.2 | 0.3 |
| <i>Sassafras albidum</i> | 0.2 | 1.5 | 2.2 | 2.0 | 1.4 |
| <i>Rhododendron maximum</i> | 0.8 | 0.0 | 1.8 | 6.3 | 4.8 |
| <i>Pyrularia pubera</i> | 0.0 | 0.0 | 0.7 | 3.1 | 0.1 |
| Total | 98.8 | 97.5 | 94.9 | 95.7 | 97.1 |

Sample years begin in 1974 (before clearcutting) through successional time (after clearcutting in 1977) for three communities in WS7, Coweeta Basin. In 1977, number of sample plots was eight in the cove-hardwoods, five in the mixed-oak hardwoods, and five in the hardwood-pines. In 1974, 1979, 1984, and 1993, number of sample plots was seven in the cove-hardwoods community, five in the mixed-oak hardwoods, and 12 in the hardwood-pines. In 1974 and 1993, 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 and 40 cm from the base (Boring et al., 1981). 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).

is still aggrading, with most woody stems in smaller size classes (Fig. 3). In the cove-hardwoods, 58% of the density and 12% of the basal area were from stems of less than 2.5 cm dbh; in the mixed-oak hardwoods, 35% of the density and 3% of the basal area were from stems of less than 2.5 cm dbh; in the hardwood-pines, 89% of the density and 33% of the basal area were from stems of less than 2.5 cm dbh. Densities of stems with dbh greater than 5.0 cm were 2609 ha⁻¹, 2405 ha⁻¹, and 1811 ha⁻¹, occupying 18.24 m² ha⁻¹, 19.57 m² ha⁻¹, and 11.47 m² ha⁻¹

basal area in the cove-hardwoods, mixed-oak hardwoods, and hardwood-pines, respectively.

Although the number of woody species present increased in the cove-hardwoods and hardwood-pines communities after clearcutting, differences in diversity were not significant (H' ; $P \leq 0.10$, based on pairwise t -statistics) among years. In the mixed-oak hardwoods, the number of species decreased immediately after clearcutting (Table 2), but the difference in H' was not significant. However, a significant decline in H' (based on a pairwise t -statistic; Magurran (1988) ($t_{df=23}$, $P \leq 0.05 = 2.059$)) did occur in the mixed-oak hardwoods community from 1984 to 1993. This decline was attributed primarily to the increased dominance of two species, *L. tulipifera* and *R. pseudoacacia*, which occupied 65% of the total basal area in 1993, and the reduced basal area of *Q. prinus*.

3.2. Origin of woody species reproduction

In the cove-hardwoods, 58% of stems originated from seedlings in 1977; however, by 1979 seedling

and sprout reproduction were about equal, probably a result of heavy mortality of seedlings. In the mixed-oak hardwoods, seedling and sprout reproduction were about equal in 1977, but by 1979 sprouts accounted for 69% of the reproduction. In the hardwood-pines type, sprout reproduction was higher than seedling reproduction, with 64% and 82% of the stems originating from sprouts in 1977 and 1979, respectively.

Community type often affected a species' primary mode of reproduction. Species that regenerated primarily by sprouting in all three communities were *Castanea dentata*, *C. florida*, *N. sylvatica*, *O. arboreum*, and *R. pseudoacacia*. *Carya* spp. and *Q. prinus* regenerated primarily by sprouting in the mixed-oak hardwoods and hardwood-pines types. *Rhododendron maximum* and *K. latifolia* regenerated almost entirely by sprouting in the cove-hardwoods and hardwood-pines. *A. rubrum* regenerated primarily by seed germination in the cove-hardwoods, seedling and sprout reproduction were about equal in the mixed-oak hardwoods, and the dominant mode of regeneration in the hardwood-

Table 2

Average density, basal area, diversity (H' ; based on basal area) and evenness (J') of woody species for three communities in WS7, Coweeta Basin, for sample years 1974, 1977, 1979, 1984, and 1993

| Community | Year | F | G | S | Density (stems ha ⁻¹) | Basal area (m ² ha ⁻¹) | H' | Variance of H' | CI of H' | J' |
|---------------------|-------------------|----|----|----|--------------------------------------|--|------|---------------------|---------------|-------|
| Cove-hardwoods | 1974 ^a | 12 | 13 | 14 | 1566 | 23.67 | 2.52 | 0.017 | ±0.056 | 0.804 |
| | 1977 | 20 | 23 | 28 | 72507 | 4.57 | 2.64 | 0.134 | ±0.138 | 0.784 |
| | 1979 | 20 | 24 | 32 | 65979 | 7.91 | 2.73 | 0.017 | ±0.046 | 0.781 |
| | 1984 | 23 | 29 | 36 | 70294 | 13.68 | 2.75 | 0.032 | ±0.055 | 0.756 |
| | 1993 | 21 | 27 | 36 | 13267 | 24.85 | 2.57 | 0.022 | ±0.050 | 0.717 |
| Mixed-oak hardwoods | 1974 ^a | 16 | 21 | 26 | 1762 | 24.87 | 2.13 | 0.015 | ±0.063 | 0.752 |
| | 1977 | 14 | 17 | 20 | 76236 | 5.26 | 2.12 | 0.017 | ±0.067 | 0.748 |
| | 1979 | 11 | 14 | 19 | 55685 | 7.34 | 2.22 | 0.044 | ±0.098 | 0.741 |
| | 1984 | 15 | 18 | 22 | 43593 | 9.21 | 2.47 | 0.058 | ±0.101 | 0.777 |
| | 1993 | 13 | 14 | 22 | 9993 | 23.78 | 1.76 | 0.050 | ±0.099 | 0.569 |
| Hardwood-pines | 1974 ^a | 13 | 16 | 19 | 3970 | 27.47 | 2.28 | 0.035 | ±0.077 | 0.708 |
| | 1977 | 13 | 15 | 19 | 93416 | 6.05 | 2.41 | 0.161 | ±0.030 | 0.804 |
| | 1979 | 15 | 19 | 25 | 93551 | 9.23 | 2.37 | 0.099 | ±0.127 | 0.727 |
| | 1984 | 20 | 24 | 30 | 98189 | 16.33 | 2.49 | 0.066 | ±0.091 | 0.718 |
| | 1993 | 19 | 25 | 36 | 35573 | 20.50 | 2.35 | 0.038 | ±0.062 | 0.637 |

In 1977, 1979, and 1984, basal area was calculated from diameter measurements at 3 or 40 cm above ground line depending on species' potential growth rates (Boring et al., 1981). In 1993, diameters of trees with dbh of 1.0 cm or more were measured at 1.37 m above ground line and samplings with dbh of less than 1.0 cm were measured as in 1977, 1979, and 1984.

F, Total number of families present in each community; G, total number of genera in each community; S, total number of species present in each community.

^a Sampling in 1974 included woody species with dbh of 2.5 cm or more; diameter was measured at 1.37 m above ground line.

pinus was sprouting. *A. arborea*, *Q. coccinea*, and *L. tulipifera* regenerated primarily from seed in all three communities. *B. lenta*, absent in the mixed-oak

hardwoods and hardwood-pines communities, regenerated predominantly from seed in the cove-hardwoods. *Q. velutina*, a dominant species in the

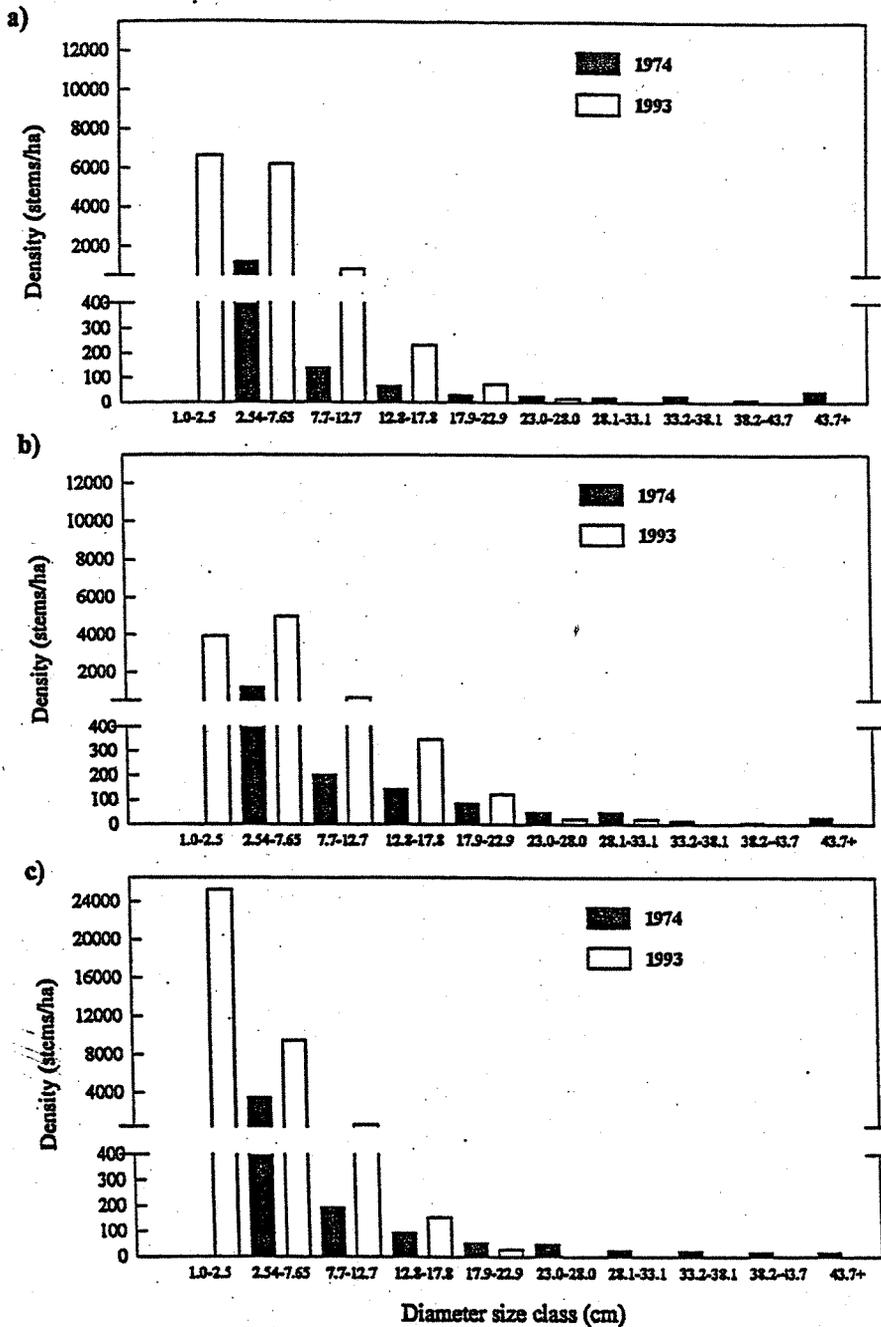


Fig. 3. Size class distributions of stems (1.0 cm or more dbh) in three communities in Watershed 7, Coweeta Basin for years 1974 and 1993: (a) cove-hardwoods; (b) mixed-oak hardwoods; (c) hardwood-pines. Diameters were measured at 1.37 m above ground line.

Table 3

Leading dominant ground flora species (2% or more of total biomass in any year) ordered by sequence of maximum percentage contribution to biomass through successional time, after clearcutting in 1977, for three communities in WS7, Coweeta Basin

| Species | Density | Biomass (%) | | | |
|---|---------|-------------|------|------|------|
| | 1952 | 1977 | 1979 | 1984 | 1993 |
| Cove-hardwoods | | | | | |
| <i>Parthenocissus quinquefolia</i> | 12.4 | 19.2 | 3.4 | 0.2 | 0.3 |
| <i>Asters (divaricatus, acuminatus, and undulatus)</i> | 4.1 | 11.8 | 8.3 | 5.6 | 0.8 |
| <i>Viola cucullata</i> | 22.5 | 11.3 | 0.1 | 2.4 | 0.3 |
| <i>Erechtitis hieracifolia</i> | 0.0 | 7.7 | 0.2 | 0.0 | 0.0 |
| <i>Solidago</i> spp. (mostly <i>odora</i> and <i>curtisii</i>) | 1.9 | 7.2 | 11.1 | 6.8 | 1.6 |
| <i>Panicum</i> spp. | 1.1 | 6.5 | 19.0 | 0.0 | 0.0 |
| <i>Acalypha rhomboidea</i> | 0.0 | 4.4 | 0.0 | 0.0 | 0.0 |
| <i>Smilax rotundifolia</i> | 3.4 | 3.5 | 2.1 | 19.2 | 78.4 |
| <i>Potentilla canadensis</i> | 3.0 | 3.2 | 6.2 | 0.9 | 0.0 |
| <i>Eupatorium rugosum</i> | 0.0 | 3.0 | 1.6 | 0.0 | 0.0 |
| <i>Botrychium virginianum</i> | 0.7 | 2.2 | 4.7 | 0.7 | 0.0 |
| <i>Polystichum acrostichoides</i> | 0.0 | 2.0 | 0.0 | 3.4 | 14.6 |
| <i>Tiarella cordifolia</i> | 0.0 | 1.7 | 1.8 | 0.0 | 0.0 |
| <i>Rubus</i> spp. (mostly <i>alleghehiensis</i>) | 0.0 | 0.8 | 30.0 | 46.6 | 0.1 |
| <i>Houstonia purpurea</i> | 0.7 | 0.0 | 7.7 | 0.5 | 0.0 |
| <i>Desmodium nudiflorum</i> | 18.0 | 0.0 | 0.2 | 1.6 | 0.0 |
| <i>Monarda clinopodia</i> | 3.4 | 0.0 | 0.2 | 0.0 | 0.01 |
| <i>Cimicifuga racemosa</i> | 0.7 | 0.0 | 0.0 | 3.2 | 0.0 |
| <i>Poa</i> spp. | 0.0 | 0.0 | 0.0 | 3.1 | 0.0 |
| <i>Galium circaeans</i> | 13.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Sanguinaria canadensis</i> | 5.2 | 0.0 | 0.0 | 0.0 | 0.04 |
| Unidentifiable | 1.1 | 13.4 | 1.5 | 3.6 | 0.04 |
| Total | 91.3 | 97.9 | 97.9 | 97.8 | 96.5 |
| Mixed-oak hardwoods | | | | | |
| <i>Solidago</i> spp. (mostly <i>odora</i> and <i>curtisii</i>) | 1.2 | 54.0 | 4.6 | 6.4 | 8.5 |
| <i>Eupatorium rugosum</i> | 0.0 | 15.7 | 6.7 | 2.9 | 10.3 |
| <i>Viola cucullata</i> | 2.9 | 6.7 | 0.0 | 0.0 | 2.9 |
| <i>Asters (divaricatus, undulatus, and acuminatus)</i> | 1.2 | 4.7 | 6.5 | 4.2 | 1.7 |
| <i>Galium latifolium</i> | 0.0 | 4.7 | 0.0 | 0.0 | 0.0 |
| <i>Botrychium virginianum</i> | 0.0 | 4.1 | 0.4 | 0.1 | 0.0 |
| <i>Potentilla canadensis</i> | 2.3 | 0.0 | 0.3 | 0.0 | 0.0 |
| <i>Panicum</i> spp. | 4.4 | 0.0 | 8.2 | 0.0 | 0.0 |
| <i>Rubus</i> spp. (mostly <i>alleghehiensis</i>) | 0.0 | 0.0 | 30.4 | 37.1 | 0.0 |
| <i>Clematis virginiana</i> | 0.0 | 0.0 | 27.4 | 0.0 | 0.0 |
| <i>Monarda clinopodia</i> | 0.0 | 0.0 | 4.9 | 0.0 | 0.0 |
| <i>Parthenocissus quinquefolia</i> | 0.0 | 0.0 | 4.3 | 5.4 | 65.1 |
| <i>Desmodium nudiflorum</i> | 2.0 | 0.0 | 1.1 | 0.2 | 0.0 |
| <i>Cimicifuga racemosa</i> | 0.0 | 0.0 | 0.6 | 11.5 | 0.0 |
| <i>Vaccinium vacillans</i> | 20.2 | 0.0 | 0.3 | 0.0 | 0.0 |
| <i>Polystichum acrostichoides</i> | 0.0 | 0.0 | 0.0 | 28.3 | 0.0 |
| <i>Smilax glauca</i> | 8.3 | 0.0 | 0.0 | 1.1 | 6.6 |
| <i>Epigaea repens</i> | 8.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Chimaphila maculata</i> | 3.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Houstonia purpurea</i> | 2.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Prenanthes</i> spp. | 6.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Ruellia ciliosa</i> | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Uvularia pudica</i> | 2.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Vaccinium stamineum</i> | 10.0 | 0.0 | 0.0 | 0.0 | 0.0 |

Table 3 (continued)

| Species | Density | Biomass (%) | | | |
|--|---------|-------------|------|------|------|
| | 1952 | 1977 | 1979 | 1984 | 1993 |
| <i>Veratrum parviflorum</i> | 2.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| Unidentifiable | 0.6 | 7.0 | 0.9 | 0.6 | 0.3 |
| Total | 79.6 | 96.9 | 96.6 | 96.9 | 95.4 |
| Hardwood-pines | | | | | |
| <i>Solidago</i> spp. (mostly <i>odora</i> and <i>curtisii</i>) | 1.3 | 41.1 | 0.04 | 0.9 | 0.6 |
| <i>Parthenocissus quinquefolia</i> | 0.0 | 16.2 | 0.0 | 0.05 | 0.0 |
| <i>Smilax rotundifolia</i> | 0.1 | 9.2 | 19.6 | 49.8 | 33.5 |
| <i>Eupatorium rugosum</i> | 0.2 | 7.8 | 0.04 | 0.0 | 0.8 |
| <i>Vaccinium vacillans</i> | 33.2 | 3.7 | 13.9 | 0.0 | 22.7 |
| Asters (<i>divaricatus</i> , <i>undulatus</i> , and <i>acuminatus</i>) | 0.4 | 2.8 | 0.4 | 0.2 | 0.0 |
| <i>Panicum</i> spp. | 2.0 | 2.6 | 23.0 | 0.5 | 0.1 |
| <i>Potentilla canadensis</i> | 0.7 | 2.5 | 4.6 | 0.0 | 0.1 |
| <i>Viola cucullata</i> | 0.7 | 2.2 | 0.3 | 0.66 | 13.1 |
| <i>Rubus</i> spp. (mostly <i>allegheniensis</i>) | 0.1 | 0.8 | 13.4 | 23.4 | 4.6 |
| <i>Helianthus microcephalus</i> | 0.0 | 0.0 | 6.6 | 0.0 | 0.5 |
| <i>Epigaea repens</i> | 6.0 | 0.0 | 3.0 | 1.6 | 0.4 |
| <i>Galax aphylla</i> | 19.0 | 0.0 | 2.2 | 6.5 | 14.8 |
| <i>Coreopsis major</i> | 0.0 | 0.0 | 2.2 | 0.2 | 0.0 |
| <i>Smilax glauca</i> | 12.1 | 0.0 | 0.4 | 0.6 | 1.3 |
| <i>Pteridium aquilinum</i> | 0.2 | 0.0 | 0.0 | 7.3 | 0.0 |
| <i>Chimaphila maculata</i> | 4.3 | 0.0 | 0.0 | 0.0 | 0.1 |
| Unidentifiable | 0.9 | 6.8 | 2.4 | 2.8 | 0.01 |
| Total | 81.3 | 95.7 | 96.1 | 94.1 | 96.3 |

In 1952 (before clearcutting), dominant species were based on 2% or more of total density. In 1952, number of sample quadrats was four for the cove-hardwoods community, 14 for the mixed-oak hardwoods, and 16 for the hardwood-pines, with a sample area of 4.0 m² per quadrat. In 1977, number of sample quadrats was eight in the cove-hardwoods, five in the mixed-oak hardwoods, and five in the hardwood-pines, with a sample area of two (1.0 m²) quadrats. In 1979, 1984, and 1993, number of sample quadrats was seven for the cove-hardwoods community, five for the mixed-oak hardwoods, and 12 for the hardwood-pines, with a sample of two (1.0 m²) quadrats. Species nomenclature follows Radford et al. (1968).

mixed-oak hardwoods community before cutting, reproduced only by seed germination.

3.3. Changes in woody + herbaceous ground flora

In 1952, the three most abundant herbaceous taxa were *Viola cucullata*, *Desmodium nudiflorum*, and *Galium circaezans* in the cove-hardwoods. After cutting in 1977, *Parthenocissus quinquefolia*, *V. cucullata*, and species within the Asteraceae family were the most abundant. In the mixed-oak hardwoods, *Vaccinium* spp. (*vacillans* and *stamineum*), *Smilax glauca*, and *Epigaea repens* were the most abundant species in 1952. One year after clearcutting, *Solidago* spp., *Eupatorium rugosum*, *V. cucullata*, and *Aster* spp. were the most dominant. In the hardwood-pines, *Vaccinium* spp., *Galax aphylla*, and *S.*

glauca made up 64% of the density in 1952. In 1977, *Solidago* spp., *P. quinquefolia*, *S. rotundifolia*, and *E. rugosum* were the most abundant species and accounted for 74% of the total biomass. *G. aphylla* began to recover by 1993 in the hardwood-pines community (Table 3). In 1979 and 1984, *Rubus* spp. was the most abundant species in all three communities. However, by 1993, it had declined to less than 1.0% of the total ground flora biomass in the cove-hardwoods, 0% in the mixed-oak hardwoods, and 5% in the hardwood-pines, and *P. quinquefolia* dominated in the mixed-oak hardwoods.

Changes in ground flora through succession were attributed to species that established or disappeared after disturbance or species that were short-lived or transitory. Species established after clearcutting included *Polystichum acrostichoides* in the cove-

hardwoods, and *E. rugosum* and *P. quinquefolia* in the mixed-oak hardwoods. Short-lived or transitory species included *Erechtites hieracifolia*, *Acalypha rhomboidea*, *E. rugosum*, *Tiarella cordifolia*, and *Rubus* spp. in the cove-hardwoods; *Botrychium virginiana*, *G. latifolia*, *Rubus* spp., *Clematis virginiana*, *Monarda clinopodia*, *Cimicifuga racemosa*, and *P. acrostichoides* in the mixed-oak; *P. quinquefolia*, *Helianthus microcephalus*, and *Coreopsis major* in the hardwood-pines (Table 3).

Less common species in 1952 not found after clearcutting included *Agrimonia parviflora*, *Aristolochia macrophylla*, *Triphora trianthophora*, and *Veratrum parviflorum* in the cove-hardwoods; *Angelica venenosa*, *Clintonia umbellata*, *Erigeron pulchellus*, *Lilium michauxii*, *Linum striatum*, *Lyonia ligustrina*, *Persicaria hydropiperoides*, *Phryma leptostachy*, *Pilea pumila*, *T. cordifolia*, and *T. trianthophora* in the mixed-oak hardwoods; *Campanula divaricata*, *Erythronium americanum*, *Habenaria ciliaris*, *Menziesia pilosa*, *Polygonatum biflorum*, *Smilacina racemosa*, and *Trillium* spp. in the hardwood-pines.

Ground flora biomass peaked in 1979 in each community type then declined substantially by 1993. Currently, ground flora biomass in the cove-hardwoods, mixed-oak hardwoods, and hardwood-

pines is only 8.0%, 2.0%, and 8.0%, respectively, of the peak biomass in 1979 (Table 4).

In contrast to the pattern for woody species, many more ground flora species were present in all communities in 1952 than in the years after clearcutting (Table 4). In addition to the species level changes within communities, family distributions (including woody species) have also changed since clearcutting (Tables 2 and 4). In the cove-hardwoods, the number of families present increased from 24 in 1952 to 29 in 1977 and 1979, and to more than 30 in following years. However, in the mixed-oak hardwoods, there were many more families represented before clearcutting; 39 families were present in 1952, reduced to only 21 families in 1977, then increased to 22 by 1993. In the hardwood-pines, 31 families were present in 1952 compared with only 22 families immediately after cutting, which then increased to 34 families by 1984 (Tables 2 and 4). Although most families were represented by only one or two genera, families that were well represented by several genera were the Asteraceae, Ericaceae, Rosaceae, Fabaceae, and Liliaceae. For example, in the hardwood-pines, 11 genera were found within the Liliaceae family in 1952. After clearcutting in 1977, only *Smilax* remained, in 1979 *Lilium* was found, and in 1984 *Medeola* and *Uvularia* were sampled. Families that

Table 4

Average abundance (number of plants m^{-2} in 1952; g mass m^{-2} in all other years), diversity (H' , Shannon–Weaver's index), and evenness (J' , Pielou's index) of ground flora species for three community types in WS7, Coweeta Basin

| Community | Year | F | G | S | Abundance (m^{-2}) | H' | Variance of H' | CI of H' | J' |
|---------------------|-------------------|----|----|----|------------------------|------|------------------|------------|-------|
| Cove-hardwoods | 1952 ^a | 12 | 17 | 27 | 16.5 | 2.52 | 0.054 | ±0.092 | 0.765 |
| | 1977 | 12 | 17 | 19 | 33.3 | 2.49 | 0.014 | ±0.057 | 0.846 |
| | 1979 | 12 | 20 | 22 | 97.8 | 2.19 | 0.010 | ±0.043 | 0.689 |
| | 1984 | 16 | 19 | 21 | 37.6 | 1.85 | 0.040 | ±0.092 | 0.608 |
| | 1993 | 14 | 19 | 20 | 8.0 | 0.82 | 0.137 | ±0.174 | 0.274 |
| Mixed-oak hardwoods | 1952 ^a | 23 | 39 | 49 | 11.4 | 3.14 | 0.038 | ±0.055 | 0.807 |
| | 1977 | 7 | 9 | 10 | 20.3 | 1.55 | 0.057 | ±0.168 | 0.673 |
| | 1979 | 12 | 17 | 18 | 84.9 | 2.04 | 0.013 | ±0.056 | 0.706 |
| | 1984 | 8 | 12 | 13 | 20.8 | 1.73 | 0.040 | ±0.116 | 0.674 |
| | 1993 | 12 | 16 | 16 | 2.1 | 1.32 | 0.008 | ±0.047 | 0.476 |
| Hardwood-pines | 1952 ^a | 18 | 42 | 45 | 13.2 | 2.40 | 0.107 | ±0.099 | 0.630 |
| | 1977 | 10 | 15 | 16 | 43.0 | 1.99 | 0.028 | ±0.089 | 0.718 |
| | 1979 | 12 | 22 | 25 | 46.9 | 2.28 | 0.018 | ±0.056 | 0.708 |
| | 1984 | 16 | 21 | 24 | 17.5 | 1.65 | 0.085 | ±0.125 | 0.519 |
| | 1993 | 16 | 25 | 27 | 3.7 | 1.90 | 0.141 | ±0.152 | 0.576 |

F, Total number of families present in each community; G, total number of genera present in each community; S, total number of species present in each community.

Table 5

T-Statistics for ground flora species diversity (H') for pairwise comparisons among years within each community in WS7, Coweeta Basin

| Community | Comparison | t value | df | P value |
|---------------------|---------------|---------|----|---------|
| Cove-hardwoods | 1977 vs. 1979 | 1.905 | 84 | 0.10 |
| | 1977 vs. 1984 | 2.744 | 61 | 0.01 |
| | 1977 vs. 1993 | 4.293 | 10 | 0.002 |
| | 1979 vs. 1984 | 1.525 | 58 | ns |
| | 1979 vs. 1993 | 3.575 | 9 | 0.01 |
| Mixed-oak hardwoods | 1984 vs. 1993 | 2.448 | 13 | 0.05 |
| | 1977 vs. 1979 | 2.872 | 30 | 0.01 |
| | 1977 vs. 1984 | -0.578 | 40 | ns |
| | 1977 vs. 1993 | 0.902 | 22 | ns |
| | 1979 vs. 1984 | 1.337 | 35 | ns |
| Hardwood-pines | 1979 vs. 1993 | 5.006 | 14 | 0.0001 |
| | 1984 vs. 1993 | 1.860 | 22 | 0.10 |
| | 1977 vs. 1979 | -1.352 | 84 | ns |
| | 1977 vs. 1984 | 1.011 | 30 | ns |
| | 1977 vs. 1993 | 0.219 | 5 | ns |
| | 1979 vs. 1984 | 1.934 | 25 | 0.10 |
| | 1979 vs. 1993 | 0.933 | 5 | ns |
| | 1984 vs. 1993 | 0.527 | 9 | ns |

T-Statistics and calculations for requisite degrees of freedom follow Magurran (1988); ns, not significant.

were shared by woody and ground flora species were the Ericaceae, Fabaceae, and Rosaceae.

In the cove-hardwoods community, H' was significantly higher in 1977 than in all subsequent years. The difference in H' between 1979 and 1984 was not significant. Diversity declined significantly in 1993 (Tables 4 and 5). Two species (*S. rotundifolia* and *P. acrostichoides*) representing 93% of the total biomass accounted for the low J' in 1993 (Table 4). In the mixed-oak hardwoods community, H' increased significantly from 1977 to 1979, began to decline in 1984, and was significantly lower by 1993. H' in 1993 was significantly lower than in 1979 or 1984 (Tables 4 and 5). Differences in H' were not significant between 1977 and 1984 or 1993. In the hardwood-pines, the difference in H' was significant between 1979 and 1984, but differences were not significant between other years (Table 5). Although no statistical tests were performed between 1952 and post-clearcut years because abundance measures differed, H' based on density was higher in 1952 in the mixed-oak hardwoods and hardwood-pines communities than H' based on biomass in the years after clearcutting.

4. Discussion

4.1. Woody species' responses

The diversity of woody species was relatively stable in WS7; however, tree species richness increased through succession. This trend in diversity, similar to that found in other eastern hardwood forests (Reiners, 1992; Wang and Nyland, 1993), was also found after clearcutting in a nearby watershed within the Coweeta Basin (Elliott and Swank, 1994a). These successional changes are somewhat different from those found in northeastern deciduous forests. For example, Gove et al. (1992) showed a decline in tree diversity 10 years after clearcutting whereas Reiners (1992) found a gradual decline in diversity and an increase in richness after clearcutting and herbiciding. Two years after clearcutting, Reiners' data (Reiners, 1992) suggested a trend in secondary succession with a mixed component of 'relay floristics' and 'initial composition'. Although most species in his undistributed reference forest eventually regenerated in the clearcutting site, most woody biomass in the latter was produced by two species uncommon in the former forest (*P. pensylvanica* and *B. papyrifera*). Phillips and Shure (1990) found that species composition changed after clearcutting small (2.0 ha size patch) mesic, mixed-hardwood sites in the Southern Appalachians. In their study, *L. tulipifera* remained dominant 2 years after cutting whereas *Q. rubra* and *Carya* spp. declined in relative biomass, and *R. pseudoacacia*, *C. florida*, and *A. rubrum* increased. Beck and Hooper (1986) found that clearcutting a mixed-hardwood forest dominated mostly by oak resulted in a 20-year-old stand dominated by *L. tulipifera*, *R. pseudoacacia*, and *A. rubrum*. In our study, *C. florida* and *R. pseudoacacia* also increased in relative dominance. However, 17 years after cutting (1993), *C. florida* began to decline in dominance. The substantial decline in *C. florida* from 1984 to 1993 was probably attributed to disease. Dogwood anthracnose, caused by *Discula destructiva* Redlin., had an average incidence of infection of 87% in *C. florida* for 1990 in the Coweeta Basin (Chellemi et al., 1992). In contrast, *R. pseudoacacia* continued to increase. *Q. rubra* also decreased in our cove-hardwood plots and *A. rubrum*, important 2 years

after cutting, had returned to pre-cut levels in the community.

Hardwood forests in the Southern Appalachians revegetate quickly after disturbance because many species reproduce and grow rapidly. Although revegetation was relatively rapid in WS7, the composition of the forest changed. For example, *Carya* spp., the leading dominant in the cove-hardwoods community before harvest, currently makes up less than 1% of the total basal area in these communities. Species such as *Carya* spp. will probably not become a significant component of the stand for many decades because they disperse seed and grow slowly. Meanwhile, opportunistic species such as *L. tulipifera*, *R. pseudoacacia*, and *A. rubrum* have increased. Because *L. tulipifera* and *R. pseudoacacia* sprout quickly and grow faster than other species, they attain early dominance. *Acer rubrum*, although a shade-tolerant species, produced 5000–9000 seedlings ha⁻¹ the first year after cutting in the cove-hardwoods and mixed-oak hardwoods, and over 5000 seedlings ha⁻¹ in the hardwood-pines 2 years after cutting. *Acer rubrum* was also one of the most prolific sprouting species, with 1800–6300 sprouts ha⁻¹, depending on community type. Its ability to establish by both sexual and asexual reproduction may explain its successful regeneration following disturbance.

Sprouts play a major role in the revegetation process of these hardwood forests. The revegetation process on WS7 was similar to that in other eastern hardwood forests, where sprouts and suckers dominate vegetation after clearcutting (Ross et al., 1986; Phillips and Shure, 1990; White, 1991; Crow et al., 1991; Brown, 1994). In the first year after clearcutting, seedling and sprout reproduction was about equal, except in the hardwood-pines where sprout reproduction was higher. By 1979, the proportion of stems originating from sprouts increased in all communities. In the hardwood-pines, the high percentage of stems originating from sprouts (81%) probably occurred because seed propagules were scarce and the xeric forest floor microclimate along the southwest-facing slopes and ridges (Swank and Vose, 1988) produced a high mortality rate of seedlings.

In Southern Appalachian forests, mode of reproduction alone does not guarantee success. Comparing two species that reproduced primarily by seed, *L.*

tulipifera and *Q. velutina*, in the cove-hardwoods and mixed-oak hardwoods communities provides a striking contrast. *Q. velutina*, a leading dominant in the mixed-oak hardwoods before clearcutting, reproduced only from seed germination or advance seedling growth. Although stumps of *Q. velutina* sprout less frequently than *Q. rubra*, *Q. prinus*, and *Q. coccinea*, the majority of the reproduction after harvest is usually from stump sprouting (Burns and Honkala, 1990). Because seedlings established after harvest grow too slowly to compete with sprouts of other tree species and other vegetation, they usually die after a few years (Burns and Honkala, 1990). In our study, the low basal area for this species after disturbance may be the result of a combination of factors, including low dispersal of seed in the large opening, low survival of seedlings, slow growth of seedlings, and lack of sprouting. Before cutting, 30% of the *Q. velutina* stems were of greater than 23 cm dbh, which probably limited sprouting; likewise, the high percentage (53%) of *Q. velutina* stems of less than 5 cm dbh also limited sprouting. Stump sprouting from large stumps of old trees is less than from small stumps of young trees (Kays et al., 1988; Kays and Canham, 1992).

In contrast, *L. tulipifera* established successfully in both the cove-hardwoods and mixed-oak hardwoods communities after clearcutting. In 1993, it was the leading dominant species, occupying 22% and 44% of the total basal area in the cove-hardwoods and mixed-oak hardwoods types, respectively. A combination of factors, including prolific seed production, extended seed viability in the forest floor, survival of new germinants, relatively fast growth, and some stump sprouting, are responsible for this success. *L. tulipifera* was a copious seeder, with 8000–10 000 seedlings ha⁻¹ produced during the first year after cutting, whereas *Q. velutina* seedlings totaled 300–700 seedlings ha⁻¹, with many present before harvesting.

Early and copious production of light, wind-dispersed seeds is generally correlated with the ability to respond to large disturbances (Canham and Marks, 1985). Small-seeded and less shade-tolerant species such as *L. tulipifera* and *B. lenta* exhibit minimal delay between dispersal and germination and often release seeds from autumn until spring (Canham and Marks, 1985). However, *B. lenta* seedling produc-

tion was low in the cove-hardwoods until 2 years after clearcutting, when the species produced 2774 seedlings ha⁻¹.

The stem exclusion stage of stand development (Oliver and Larson, 1990) was most dramatic during the 9 year period between 1984 and 1993. Although WS7 is a young forest with most stems in small size classes, the stem exclusion stage has begun, as indicated by the decrease in stem density by 81%, 77%, and 64% for the cove-hardwoods, mixed-oak hardwoods, and hardwood-pines, respectively. Density of stems of 5.0 cm or more is less than in a nearby 30-year-old clearcut watershed, whereas basal area of stems with dbh of 5.0 cm or more is much higher than values reported for this same watershed (Elliott and Swank, 1994a).

4.2. Ground flora responses

In general, ground flora diversity declined from 1977 to 1993 in the cove-hardwoods and mixed-oak hardwoods communities, but did not decrease significantly in hardwood-pines. In every community, more species were present in 1952 than in the years after clearcutting. This pattern parallels results reported by Gove et al. (1992), where diversity of all plant species (overstory and ground flora combined) decreased 10 years after clearcutting in New Hampshire. Nixon and Brooks (1991) found that herbaceous species diversity peaked in Year 3 after clearcutting a deciduous forest in east Texas then subsided to Year 9.

The abundance (i.e. g biomass m⁻²) of ground flora was also lower in 1993 compared with 1984: 79% less in the cove-hardwoods, 90% less in the mixed-oak hardwoods, and 79% less in the hardwood-pines. With growth of overstory trees and canopy closure, the number of early successional, shade-intolerant species, such as *Erechtites*, *Solidago*, *Eupatorium*, *Panicum*, and *Aster*, has declined. Late successional, shade-tolerant species, such as *Viola*, *Galium*, *Sanguinaria*, *Uvularia*, and *Vernonia*, are not well established in the watershed, even though they are common in other areas within the Coweeta Basin. Watershed 7 is apparently in a transition state between early and late successional species abundance. The timing of measurements pre-

vented examining the response of spring ephemerals, such as *Trillium*, *Anemone*, and *Claytonia*, after clearcutting. Because spring ephemerals respond to changes in temperature and light (Collins et al., 1985), clearcutting may have triggered changes in seasonal phenology, growth, and reproductive potential of these species.

Total numbers of species in each community were lower after clearcutting in 1977 than in 1952. However, to quantitatively compare species richness and diversity in 1952 with years after harvest is difficult because data on ground flora immediately before 1977 are lacking, and plot sizes and locations differ. The 25 years of succession between 1952 and 1977, and cumulative effects of land-use history (i.e. grazing and fire suppression), prevent interpretation of the effects of clearcutting alone.

Ground flora species diversity and richness in WS7 were lower in the cove-hardwoods and mixed-oak hardwoods and higher in the hardwood-pines when compared with a nearby 30-year-old clearcut watershed (WS13) with the same community types (K.J. Elliott, personal observation, 1991). The lower ground flora H' in two of the community types in WS7 may be the result of several factors, including (1) the larger spatial scale of disturbance in WS7 (57 ha cut in WS7 vs. 16 ha cut in WS13); (2) southwest-facing aspect of WS7, which receives higher solar radiation than the east-facing aspect of WS13; (3) total tree removal in WS7 whereas trees were cut and left in place in WS13.

4.3. Influences of complex disturbances

Large forest openings significantly change the forest floor microclimate for all residual biota, including woody seedlings and late successional herbaceous species (Phillips and Shure, 1990). Other investigators at Coweeta have found that clearcutting on WS7 increased mean monthly temperatures at the litter-soil boundary for the period May–October by 8–11°C the first year after cutting, 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), and reduced first-year decomposition of woody litter, especially on xeric south-facing slopes

(Abbott and Crossley, 1982). The increase in woody leaf area index by the third year after clearcutting resulted in forest floor shading, amelioration of the altered forest floor-microclimate, and dampening of environmental effects of forest floor biota and their processes. Although seedling and ground flora may have been affected by high mortality immediately after clearcutting, canopy closure within 3 years allowed a subsequent rapid recovery of structural and functional forest processes.

Both anthropogenic (e.g. chestnut blight, fire exclusion, and cattle grazing) and natural disturbances (e.g. drought) shaped forest composition in WS7 before clearcutting. The composition of Southern Appalachian forests has been significantly altered by the loss of American chestnut (*C. dentata*) (Woods and Shanks, 1959; Arends, 1981; Day et al., 1988; Busing, 1989). Chestnut blight had a major impact in the Coweeta Basin, because chestnut made up an estimated 35–40% of the basal area of some forest stands (Day et al., 1988). Fire exclusion in the Southern Appalachians has favored the expansion of evergreen shrubs (Day and Monk, 1974; Monk et al., 1985; Lipscomb and Nilson, 1990) and has reduced regeneration success of many *Quercus* species (Phillips and Murdy, 1985; Van Lear, 1991). *Rhododendron* often dominates understory canopy layers in riparian stands, and adversely affects development and richness of herbaceous and understory strata (Baker, 1994; Hedman and Van Lear, 1995). Heavy cattle grazing can also have a dramatic effect on species richness and diversity. For example, Williams (1954) found a loss of 31 species in the cove-hardwoods community of WS7 during a 12 year period (1940–1952) of heavy grazing; however, the mixed-oak and hardwood-pines types showed little to no loss of species on slopes and ridges, where cattle were less likely to travel. In addition, severe droughts have caused substantial tree mortality in the Southern USA (Hursh and Haasis, 1931; Tainter et al., 1984; Stringer et al., 1989; Starkey et al., 1989; Smith, 1991; Clinton et al., 1993; Elliott and Swank, 1994b). The combined impacts of these sequential and simultaneous disturbances on plant diversity before clearcutting in 1977 would be impossible to sort out, yet their cumulative effects are probably notable.

5. Conclusion

The response of plant communities to clearcutting varied in a Southern Appalachian watershed. Woody species richness increased in the cove-hardwoods and hardwood-pines immediately after clearcutting and through 17 years of succession but remained relatively constant in the mixed-oak hardwoods community. Woody species diversity decreased in the mixed-oak hardwoods but remained relatively constant in the cove-hardwood and hardwood-pines communities. *L. tulipifera* increased in dominance in all three communities. In addition, *R. maximum* increased in the cove-hardwoods, *R. pseudoacacia* increased in the mixed-oak hardwoods, and *K. latifolia* and *A. rubrum* increased in the hardwood-pines. *Carya* spp. declined in dominance after clearcutting in the cove-hardwoods, *Q. velutina* and *Carya* spp. declined in the mixed-oak hardwoods, and *Q. coccinea* and *Q. velutina* declined in the hardwood-pines.

Ground flora was in a transitional state between early and late successional species, 17 years after clearcutting. Early successional *Aster*, *Solidago*, and *Eupatorium* species have declined in abundance because woody species have grown rapidly and the canopy has closed. Late successional species have not become abundantly established, which has caused a significant decline in ground flora diversity in the cove-hardwoods and mixed-oak hardwoods. Total number of plant species present (woody + ground flora) increased in all three communities during the first 3 years after cutting. Total species remained relatively constant in the cove-hardwoods and mixed-oak hardwoods from 1979 to 1993; however, total species continued to increase to 1993 in the hardwood-pines.

Clearcutting favors shade-intolerant pioneering species, such as *L. tulipifera* and *R. pseudoacacia*, and shade-tolerant understory species such as *R. maximum* and *K. latifolia*. The positive responses to clearcutting by these two markedly different groups of plants strongly indicates that retention of species of *Quercus* and other hard-mast producing species that have critical ecosystem functions will require additional management measures.

In addition to the altered microclimatic influences

of clearcutting, past disturbances such as selective logging, chestnut blight, fire suppression, and woodland grazing have also shaped the current conditions in WS7. Although separating the cumulative effects on vegetation dynamics is difficult, this complex of disturbances is typical of conditions throughout much of the Southern Appalachians. The cumulative vegetation responses to clearcutting and other disturbances found here are indicative of regional responses of forests since the early twentieth century. Other influences of regional atmospheric pollution and climate change may also have an undefined influence on species richness and community composition.

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References

- Abbott, D.T. and Crossley, Jr., D.A., 1982. Woody litter decomposition following clearcutting. *Ecology*, 63: 35–42.
- Arends, E., 1981. Vegetation patterns a half century following the chestnut blight in the Great Smoky Mountains National Park. M.S. Thesis, University of Tennessee, Knoxville.
- Baker, T.T., 1994. The influence of *Rhododendron maximum* on species richness in the riparian zone of Wine Spring Creek. M.S. Thesis, Clemson University, Clemson, SC.
- Beck, D.E. and Hooper, R.M., 1986. Development of a Southern Appalachian hardwood stand after clearcutting. *S. J. Appl. For.*, 10: 168–172.
- Bicknell, S.E.H., 1979. Pattern and process of plant succession in a revegetating northern hardwood ecosystem. Ph.D. Dissertation, Yale University, New Haven, CT.
- Boring, L.R., 1979. Early forest regeneration and nutrient conservation on a clearcut Southern Appalachian watershed. M.S. Thesis, University of Georgia, Athens.
- Boring, L.R. and Swank, W.T., 1986. Hardwood biomass and net primary production following clearcutting in the Coweeta Basin. In: R.T. Brooks, Jr. (Editor), Proc. 1986 Southern Forest Biomass Workshop, 16–19 June 1986, Knoxville, TN. Tennessee Valley Authority, Norris, pp. 43–50.
- Boring, L.R., Monk, C.D. and Swank, W.T., 1981. Early regeneration of a clear-cut Southern Appalachian forest. *Ecology*, 62: 1244–1253.
- Boring, L.R., Swank, W.T. and Monk, C.D., 1988. Dynamics of early successional forest structure and processes in the Coweeta Basin. In: W.T. Swank and D.A. Crossley, Jr. (Editors), *Forest Hydrology and Ecology at Coweeta*, Ecological Studies 66. Springer, New York, pp. 161–180.
- Bormann, F.H., Likens, G.E., Siccama, T.G., Pierce, R.S. and Eaton, J.S., 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. *Ecol. Monogr.*, 44: 255–277.
- Bormann, F.H., Likens, G.E. and Melillo, J.M., 1977. Nitrogen budget for an aggrading northern hardwood forest ecosystem. *Science*, 196: 981–983.
- Brown, D., 1994. The development of woody vegetation in the first 6 years following clearcutting of a hardwood forest for a utility right-of-way. *For. Ecol. Manage.*, 65: 171–181.
- Burns, R.M. and Honkala, B.H., 1990. *Silvics of North America*, Vol. 2, Hardwoods. USDA For. Serv. Handb. 654, Washington, DC, 877 pp.
- Burton, P.J., Balisky, A.C., Coward, L.P., Cumming, S.G. and Kneeshaw, D.D., 1992. The value of managing for biodiversity. *For. Chron.*, 68: 225–237.
- Busing, R.T., 1989. A half century of change in a Great Smoky Mountains cove forest. *Bull. Torrey Bot. Club*, 116: 283–288.
- Canham, C.D. and Marks, P.L., 1985. The response of woody plants to disturbance: patterns of establishment and growth. In: S.T.A. Pickett and P.S. White (Editors), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York, pp. 197–216.
- Chellemi, D.O., Britton, K.O. and Swank, W.T., 1992. Influence of site factors on Dogwood Anthracnose in the Nantahala Mountain Range of western North Carolina. *Plant Dis.*, 76: 915–918.
- Clinton, B.D., Boring, L.R. and Swank, W.T., 1993. Characteristics of drought-induced canopy gaps in oak forests of the Coweeta Basin. *Ecology*, 74: 1551–1558.
- Collins, B.S., Dunne, K.P. and Pickett, S.T.A., 1985. Response of forest herbs to canopy gaps. In: S.T.A. Pickett and P.S. White (Editors), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York, pp. 217–234.
- Crow, T.R., Mroz, G.D. and Gale, M.R., 1991. Regrowth and nutrient accumulations following whole-tree harvesting of a maple-oak forest. *Can. J. For. Res.*, 21: 1305–1315.
- Day, F.P. and Monk, C.D., 1974. Vegetation patterns on a Southern Appalachian watershed. *Ecology*, 55: 1064–1074.
- Day, F.P., Phillips, D.L. and Monk, C.D., 1988. Forest communities and patterns. In: W.T. Swank and D.A. Crossley, Jr. (Editors), *Forest Hydrology and Ecology at Coweeta*, Ecological Studies 66. Springer, New York, pp. 141–150.
- Douglass, J.E. and Hoover, M.D., 1988. History of Coweeta. In: W.T. Swank and D.A. Crossley, Jr. (Editors), *Forest Hydrology and Ecology at Coweeta*, Ecological Studies 66. Springer, New York, pp. 17–34.
- Elliott, K.J. and Swank, W.T., 1994a. Changes in tree species diversity after successive clearcuts in the Southern Appalachians. *Vegetatio*, 115: 11–18.

- Elliott, K.J. and Swank, W.T., 1994b. Impacts of drought on tree mortality and growth in a mixed hardwood forest. *J. Veg. Sci.*, 5: 229–236.
- Fain, J.J., Volk, T.A. and Fahey, T.J., 1994. Fifty years of change in an upland forest in south-central New York: general patterns. *Bull. Torrey Bot. Club*, 121: 130–139.
- Finegan, B., 1984. Forest succession. *Nature*, 312: 109–114.
- Gauch, Jr., H.G., 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge, 298 pp.
- Gholz, H.L., Hawk, G.M., Campbell, A. and Cromack, K., 1985. Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon. *Can. J. For. Res.*, 18: 1427–1436.
- Gove, J.H., Martin, C.W., Patil, G.P., Solomon, D.S. and Hornbeck, J.W., 1992. Plant species diversity on even-aged harvests at the Hubbard Brook Experimental Forest: 10-year results. *Can. J. For. Res.*, 22: 1800–1806.
- Hartnett, D.C. and Krofta, D.M., 1989. Fifty-five years of post-fire succession in a southern mixed hardwood forest. *Bull. Torrey Bot. Club*, 116: 107–113.
- Hatcher, R.D., 1974. *An Introduction to the Blue Ridge Tectonic History of North-east Georgia*, Guidebook 13-A. Georgia Geological Survey, Georgia Department of Natural Resources, Atlanta.
- Hedman, C.W. and van Lear, D.H., 1995. Vegetative structure and composition of Southern Appalachian riparian forests. *Bull. Torrey Bot. Club*, 122: 134–144.
- Hewlett, J.D., 1979. Forest water quality: an experiment in harvesting and regenerating Piedmont forests. *Ga. For. Res. Pap.*
- Hibbs, D.E., 1983. Forty years of forest succession in central New England. *Ecology*, 64: 1394–1401.
- Hornbeck, J.W., Martin, C.W., Pierce, R.S., Bormann, F.H., Likens, G.E. and Eaton, J.S., 1987. The northern hardwood forest ecosystem: ten years of recovery from clear-cutting. *US For. Serv. Northeast. For. Exp. Stn. Res. Pap. NE-RP-596*.
- Hunter, Jr., M.L., 1990. *Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity*. Prentice-Hall, Englewood Cliffs, NJ, 370 pp.
- Hursh, C.R. and Haasis, F.W., 1931. Effects of 1925 summer drought on Southern Appalachian hardwoods. *Ecology*, 12: 380–386.
- Huston, M.A., 1979. A general hypothesis of species diversity. *Am. Nat.*, 113: 80–101.
- Huston, M.A., 1994. *Biological Diversity. The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge, 681 pp.
- Huston, M.A. and Smith, T.M., 1987. Plant succession: life history and competition. *Am. Nat.*, 130: 168–198.
- Johnson, E.A., 1952. Effect of farm woodland grazing on watershed values in the Southeast. *J. For.*, 50: 109–113.
- Johnson, P.L. and Swank, W.T., 1973. Studies of cation budgets in the Appalachians of four experimental watersheds with contrasting vegetation. *Ecology*, 54: 70–80.
- Kays, J.S. and Canham, C.D., 1992. Effects of time and frequency of cutting on hardwood root reserves and sprout growth. *For. Sci.*, 37: 524–539.
- Kays, J.S., Smith, D.W., Zedaker, S.M. and Kreh, R.E., 1988. Factors affecting natural regeneration of Piedmont hardwoods. *S. J. Appl. For.*, 12: 98–102.
- Likens, G.E., Bormann, F.H., Pierce, R.S., Eaton, J.S. and Johnson, N.M., 1977. *Biogeochemistry of a Forested Ecosystem*. Springer, New York, 146 pp.
- Lipscomb, M.V. and Nilsen, E.T., 1990. Environmental and physiological factors influencing the natural distribution of evergreen and deciduous ericaceous shrubs on northeast and southwest slopes of the S. Appalachian Mountains. I. Irradiance tolerance. *Am. J. Bot.*, 77: 108–115.
- Magurran, A.E., 1988. *Ecological Diversity and its Measure*. Princeton University Press, Princeton, NJ, 179 pp.
- McMinn, J.W., 1991. *Biological diversity research: an analysis*. US For. Serv. Southeast. For. Exp. Stn. Gen. Tech. Rep. SE-71.
- Monk, C.D., McGinty, D.T. and Day, F.P., 1985. The ecological importance of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forest of the Southern Appalachians. *Bull. Torrey Bot. Club*, 112: 193–197.
- Nixon, E.S. and Brooks, A.R., 1991. Species diversity following clearcutting in eastern Texas. *Tex. J. Sci.*, 43: 399–403.
- Norse, E.A., Rosenbaum, K.L., Wilcove, D.S., Wilcox, B.A., Roome, W.H., Johnston, D.W. and Stout, M.L., 1986. *Conserving Biological Diversity in Our National Forests*. Wilderness Society, Washington, DC.
- Oliver, C.D. and Larson, B.C., 1990. *Forest Stand Dynamics*. McGraw-Hill, New York, 467 pp.
- Parker, G.R. and Swank, W.T., 1982. Tree species response to clear-cutting a Southern Appalachian watershed. *Am. Midl. Nat.*, 108: 304–310.
- Peet, R.K. and Christensen, N.L., 1980. Succession: a population process. *Vegetatio*, 43: 131–140.
- Peet, R.K. and Loucks, O.L., 1977. A gradient analysis of southern Wisconsin forests. *Ecology*, 58: 486–499.
- Petráitís, P.S., Latham, R.E. and Niesenbaum, R.A., 1989. The maintenance of species diversity by disturbance. *Q. Rev. Biol.*, 64: 393–418.
- Phillips, D.L. and Murdy, W.H., 1985. Effects of rhododendron (*Rhododendron maximum* L.) on regeneration of Southern Appalachian hardwoods. *For. Sci.*, 31: 226–233.
- Phillips, D.L. and Shure, D.J., 1990. Patch-size effects on early succession in Southern Appalachian forests. *Ecology*, 71: 204–212.
- Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.*, 13: 131–144.
- Radford, A.E., Ahles, H.E. and Bell, C.R., 1968. *Manual of the Vascular Flora of the Carolinas*. University of North Carolina Press, Chapel Hill, 1183 pp.
- Reiners, W.A., 1992. Twenty years of ecosystem reorganization following experimental deforestation and regrowth suppression. *Ecol. Monogr.*, 62: 503–523.
- Roberts, M.R., 1992. Stand development and overstory-understory interactions in an aspen-northern hardwoods stand. *For. Ecol. Manage.*, 54: 157–174.
- Roberts, M.R. and Christensen, N.L., 1988. Vegetation variation among mesic successional forest stands in northern lower Michigan. *Can. J. Bot.*, 66: 1080–1090.

- Ross, M.S., Sharik, T.L. and Smith, D.W., 1986. Oak regeneration after clear felling in southwest Virginia. *For. Sci.*, 32: 157–169.
- Runkle, J.R., 1985. Disturbance regimes in temperate forests. In: S.T.A. Pickett and P.S. White (Editors), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York, pp. 17–34.
- Schoonmaker, P. and McKee, A., 1988. Species composition and diversity during secondary succession of coniferous forests in the Western Cascade Mountains of Oregon. *For. Sci.*, 34: 960–979.
- Seastedt, T.R. and Crossley, Jr., D.A., 1981. Microarthropod response following cable logging and clearcutting in the Southern Appalachians. *Ecology*, 62: 126–135.
- Seastedt, T.R., Crossley, Jr., D.A., Meentemeyer, V. and Waide, J.B., 1983. A two-year study of leaf litter decomposition as related to macroclimatic factors and microarthropod abundance in the Southern Appalachians. *Holarct. Ecol.*, 6: 11–16.
- Shannon, C.E. and Weaver, W., 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- Smith, R.N., 1991. Species composition, stand structure, and woody detrital dynamics associated with pine mortality in the Southern Appalachians. M.S. Thesis, University of Georgia, Athens.
- Starkey, D.A., Oak, S.W., Ryan, G.W., Tainter, F.H., Redmond, C. and Brown, H.D., 1989. Evaluation of oak decline area in the South. *Forest Protection Rep. R8-TR 17*, USDA, For. Serv., Washington, DC.
- Stringer, J.W., Kimmerer, T.W., Overstreet, J.C. and Dunn, J.P., 1989. Oak mortality in eastern Kentucky. *S. J. Appl. For.*, 13: 86–91.
- Swank, W.T. and Caskey, W.H., 1982. Nitrate depletion in a second-order mountain stream. *J. Environ. Qual.*, 11: 581–584.
- Swank, W.T. and Helvey, J.D., 1970. Reduction of streamflow increases following regrowth of clearcut hardwood forests. In: D.L. Correll (Editor), *Watershed Research in North America*. Chesapeake Bay Center for Environmental Studies, Edgewater, MD, pp. 345–364.
- Swank, W.T. and Vose, J.M., 1988. Effects of cutting practices on microenvironment in relation to hardwood regeneration. In: H.C. Clay, A.W. Perkey and W.E. Kidd, Jr. (Editors), *Guidelines for Regenerating Appalachian Hardwood Stands: Proc. Workshop*, Morgantown, WV, 24–26 May 1988. Society of American Foresters Publication 88-03, West Virginia University Books, Morgantown, pp. 71–88.
- Swank, W.T., Swift, Jr., L.W. and Douglass, J.E., 1988. Streamflow changes associated with forest cutting, species conversions, and natural disturbances. In: W.T. Swank and D.A. Crossley, Jr. (Editors), *Forest Hydrology and Ecology at Coweeta*, Ecological Studies 66. Springer, New York, pp. 297–312.
- Swift, Jr., L.W., Cunningham, G.B. and Douglass, J.E., 1988. Climatology and hydrology. In: W.T. Swank and D.A. Crossley, Jr. (Editors), *Forest Hydrology and Ecology at Coweeta*, Ecological Studies 66. Springer, New York, pp. 35–56.
- Tainter, F.H., Fraedrich, S.W. and Benson, D.M., 1984. The effect of climate on growth, decline, and death of northern red oaks in the western North Carolina Nantahala mountains. *Castanea*, 49: 127–137.
- Thomas, D.J., 1996. *Soil Survey of Macon County, North Carolina*. USDA Natural Resources Conservation Service, Washington, DC, 322 pp.
- Van Lear, D.H., 1991. Fire and oak regeneration in the Southern Appalachians. *US For. Serv. Southeast. For. Exp. Sta. Gen. Tech. Rep.*, SE-69: 15–21.
- Van Lear, D.H., Douglass, J.E., Cox, S.K. and Augspurger, M.K., 1985. Sediment and nutrient export in runoff from burned and harvested pine watersheds in the South Carolina piedmont. *J. Environ. Qual.*, 14: 169–174.
- Waide, J.B., Caskey, W.H., Todd, R.L. and Boring, L.R., 1988. Changes in soil nitrogen pools and transformations following forest clearcutting. In: W.T. Swank and D.A. Crossley, Jr. (Editors), *Forest Hydrology and Ecology at Coweeta*, Ecological Studies 66. Springer, New York, pp. 221–232.
- Wang, Z. and Nyland, R.D., 1993. Tree species richness increased by clearcutting of northern hardwoods in central New York. *For. Ecol. Manage.*, 57: 71–84.
- White, A.S., 1991. The importance of different forms of regeneration to secondary succession in a Maine hardwood forest. *Bull. Torrey Bot. Club*, 118: 303–311.
- Williams, J.G., 1954. A study of the effect of grazing upon changes in vegetation on a watershed in the Southern Appalachian mountains. M.S. Thesis, Michigan State College of Agriculture and Applied Science, East Lansing.
- Woods, F.W. and Shanks, R.E., 1959. Natural replacement of chestnut by other species. *Ecology*, 40: 349–361.