

Changes in Vegetation Structure and Diversity After Grass-to-Forest Succession in a Southern Appalachian Watershed

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ABSTRACT.—To document how species richness and diversity (H') recover from severe large-scale disturbance, we report temporal patterns of species composition and diversity following grass-to-forest succession from a long-term experiment in the Coweeta Basin, western North Carolina. The original experiment—clear-cutting, 5 yr of grass cover followed by a herbicide treatment, and abandonment in a Southern Appalachian mixed deciduous forest—represents the most severe human disturbance in the Coweeta Basin. For several years after cessation of management, *Robinia pseudoacacia* quickly sprouted from roots and exceeded the growth rates of other species. *Liriodendron tulipifera* increased in density and basal area because of its prolific seedling establishment and rapid growth rate. Regeneration of large seeded species was mixed—sparse for *Quercus rubra* and *Q. coccinea* and nonexistent for *Q. prinus* and *Q. velutina*. In the overstory, density-based H' increased from 1958, before grass conversion, to 15 yr and 28 yr following disturbance. In contrast, basal area-based H' had significantly declined at 15 yr, then increased at 28 yr. The initial decline in basal area-based H' was attributed to a decline in evenness of species distribution (J') rather than to a change in species richness. The severe disturbance increased the abundance of early successional woody species and of herbaceous genera that tolerate open habitats, such as *Eriochitites*, *Phytolacca*, and *Erigeron*. Shade-tolerant understory ferns and herbs such as *Polystichum acrostichoides*, *Dennstaedtia punctilobula*, *Galium latifolium* and *Viola cucullata* gradually became more abundant. The 28-yr-old forest of WS6 had much lower species richness than the adjacent reference watersheds, but more than threefold higher density.

INTRODUCTION

Disturbance and subsequent successional development are the keys to understanding the regulation of biological diversity on ecological time scales (Petraitis *et al.*, 1989; Huston 1994). As Peet (1981) and others (*see* Pickett and White, 1985, for review) have shown, unique events in the development of forest stands, particularly at the onset, can produce effects that last for decades. The rate of recovery from a disturbance depends in large part on the characteristics of the disturbance. If the disturbance is severe (such as long-term agriculture that eliminates saplings and the seed pool) and is conducted over a large area (which diminishes seed rain potential) the result can be a very protracted recovery time (Runkle, 1985). In addition, differences in species life histories (such as dispersal rate, growth rates, mode of reproduction, lifespan and growth form) may be responsible for many of the successional patterns observed in forest development (Grime, 1979; Pickett 1982; Busing and Clebsch, 1983; Keefer, 1983; Leps, 1987). Individuals growing after disturbance can be present at the time of disturbance as suppressed seedlings and saplings.

as seeds buried in the soil or as seeds newly dispersed into the area. The interaction of life histories and assimilative capabilities of species with the size, frequency and persistence of disturbance will determine community recovery and overall diversity pattern (Pickett and White, 1985; Roberts and Gilliam, 1995).

Previous studies in forest ecosystems have found conflicting patterns of diversity (*see* Halpern and Spies, 1995; Meier *et al.*, 1995; and Roberts and Gilliam, 1995 for reviews). Plant diversity may decrease in late succession, as the largest and most shade-tolerant functional types dominate, as their high leaf area reduces light availability, and as shade-intolerant functional types become suppressed (Huston, 1994). Therefore, different strata of vegetation can have very different patterns of diversity over the course of succession—an important consideration in the temperate forests of the eastern United States, where natural disturbance and past land use practices led to a preponderance of secondary forests (Marquis and Johnson, 1989).

Numerous experiments in the Coweeta Basin demonstrate the resilience of Southern Appalachian forests after large-scale disturbance; these experiments evaluated the structural and functional aspects of ecosystem recovery by measuring streamflow, stream nutrient concentrations, nutrient export, leaf area and biomass, tree density and basal area (Waide, 1988). Other experiments on the effects of clear-cutting in the Southern Appalachians addressed the silvicultural and ecosystem aspects of early forest regeneration (McGee and Hooper, 1970, 1975; Trimble, 1973; Leopold and Parker, 1985; Leopold *et al.*, 1985; Boring *et al.*, 1988). In this study, we report successional changes in species composition and plant diversity in a Southern Appalachian mixed-deciduous forest after a severe disturbance regime. The study site was a watershed that had been subjected to clear-cutting, 5 yr of grass cover, 2 yr of herbiciding and regrowth of woody species for 28 yr. Although this set of disturbances was the most severe in the Coweeta Basin since research began there in 1934, this disturbance regime is similar to abandoned agriculture and pastures that are common throughout much of the Southern Appalachians. Although the grass was not cut or grazed, the lime and fertilizer amendments with attendant high productivity and nutrient uptake by fescue make these practices similar to agricultural practices. The original objective was to test the effects of different vegetation types on evapotranspiration and on the quantity and timing of streamflow (Hibbert, 1969; Swank *et al.*, 1988; Burt and Swank, 1992). The objective of this new study was to document how community structure, and plant species richness and diversity recover from severe and large scale disturbance.

METHODS

Study area.—Watershed 6 (WS6), is a 9.0 ha NW-facing catchment located in the Coweeta Basin, southwestern North Carolina, Lat 35°03'N, Long 83°25'W. Elevation ranges from 700 to 900 m, mean slope is 50% and mean annual precipitation is ca. 1800 mm. Mean annual temperature is 12.6 C and average temperature ranges from 6.7 C in the dormant season to 18.5 C in the growing season (Swift *et al.*, 1988). Parent rocks of schist and gneiss have weathered to form deep soils (Hatcher, 1988). Three soil types occur across the watershed. Along the riparian corridor and where slopes are 30–90% at higher elevations the soil type is the Trimont gravelly loam, a fine-loamy, mixed mesic Humic Hapludults; where slopes are 8–50% at lower elevations the soil type is Saunook gravelly loam, stony, a fine-loamy, mixed, mesic Humic Hapludults. The dominant ridge soils are Evard-Cowee gravelly loam, a fine-loamy, oxidic/mixed, mesic Typic Hapludults.

History of disturbance.—Before 1842, the Coweeta Basin was occupied by the Cherokee Indians who practiced semiannual burning to control understory shrubs and weeds and to expose nuts and other mast in the autumn for wildlife (Douglass and Hoover, 1988). Be-

tween 1842 and 1900, European settlers continued the practice of light semiannual burnin and grazing. A small sawmill operated near WS6 in 1912, and the stand was heavily culle until 1923 (Douglass and Hoover, 1988). In the early 1920s chestnut blight [*Endothia pa asitica* (Murr.) P.] was first noted in the Coweeta Basin. About 30% of the basal area in th watershed was in *Castanea dentata* trees most of which were infected with the chestnu blight fungus by 1930 (Woods and Shanks, 1959).

In 1941, all woody vegetation was cut in a 5-m width corridor (1.06-ha area) above th stream to determine how riparian vegetation affects streamflow (Dunford and Fletche 1947; Hursh, 1951). By 1958, 17 yr later, this 1.06-ha area had 6501 stems ha⁻¹ but bas: area was only 4.32 m² ha⁻¹. In contrast, the portion of the watershed that was not cut i 1941 (remaining 8.0-ha area) had an average density of 5735 stems ha⁻¹ and average bas: area of 20.21 m² ha⁻¹ in 1958. Because the riparian corridor had been cut before the gra conversion experiment, it was not included in further vegetation analyses.

In 1958, the entire watershed was clear-cut, merchantable timber was removed, and th residue was piled and burned. In 1959, surface soil was scarified and planted to Kentuck 31 fescue grass (*Festuca octiflora* Walter). In 1960, the watershed was treated with a on: time application of 1100 kg ha⁻¹ lime, 110 kg ha⁻¹ 30-10-0 NPK and 18.4 kg ha⁻¹ granul: 60% potash. Between 1960 and 1965, *Kalmia latifolia*, *Rhododendron maximum*, and othe hardwood sprouts were suppressed with spot applications of 2,4-D[(2,4-dichlorophenoxy acetic acid] to maintain the watershed in grass cover (Hibbert, 1969). In 1965, the wate shed was fertilized again. In 1967, the grass was herbicided with atrazine [2-chloro-(4-eth lamino)-6-9-isopropylamino)-S-trizine], paraquat [1,1-dimethyl-4,4-bipyridinium ion (d chloride salt)], and 2,4-D[(2,4-dichlorophenoxy) acetic acid] (Douglass *et al.*, 1969), an then left undisturbed. The objectives of the conversion were to compare water use of gra versus hardwoods (Hibbert, 1969; Swank *et al.*, 1988) and to determine how conversion t grass affects discharge characteristics (Burt and Swank, 1992).

Overstory sampling.—In 1958, a pretreatment strip inventory sampled 25% of the are with 10-m width strips approximately 40-m apart extending along a N 35°E transect fro: the ridge-top to the stream channel. This sampling method resulted in a total of 27 unequ: sized plots (ranging from 0.02 to 0.14 ha), excluding the riparian corridor. All woody sten ≥2.54 cm dbh were measured by species and separated into 2.54-cm diam classes. Media values multiplied by number of individuals per diameter class were used to calculate bas area.

In 1982, 26 0.02-ha plots were permanently marked continuously along five transects o a N 45°E compass bearing from ridge-top to near stream, excluding the riparian corrido and woody stems, ≥2.54 cm dbh, were measured and tagged. In 1995, diameters of a woody stems, ≥2.54 cm dbh, were remeasured to the nearest 0.1 cm in the 26 plots.

Two adjacent 70-yr-old forests (WS14 and WS18) undisturbed since 1923, were selecte as references for the developing forest conditions of the 1-yr-old field in 1968, 15-yr-ol forest in 1982, and 28-yr-old forest in 1995 of WS6. These adjacent forests were sample: in 1993 with 13, 0.08-ha permanent sample plots with similar aspect and elevation as WS6.

Understory sampling.—Regeneration was quantified by measuring diameter at stem bas: for all woody stems <2.54 cm dbh and >1.0 m height in two 3 × 5-m plots at opposi: corners of each 0.02-ha plot. Ground flora was sampled in each of the summer mont: (June through September) of 1968. All aboveground live vegetation was clipped from 2 randomly located 1.0-m² plots in WS6. Samples were separated by species, dried at 105 for >24 h, and weighed. Since samples collected in early September showed peak bioma: for the season, we used the data collected in this sample month to compare with data fro: following years.

In mid-to-late August of 1982 and 1995, all herbaceous species and woody vegetation ≤ 1.0 m height were clipped in two randomly located 1.0-m² subplots within each permanent 0.02-ha plot in WS6. In 1993, two 4.0-m² subplots within each 0.08-ha permanent plot were sampled for plant density by species in the reference plots (WS14 and WS18) (Sankovski, 1994). Plant species nomenclature follows Radford *et al.*, 1968.

Data analyses.—We used several indices—species richness, Shannon-Weiner's index of diversity (H') and Pielou's (1966) evenness index (J')—to evaluate the change in diversity during succession on WS6 and the current condition of WS6 in comparison with the 70-yr-old reference forests. Shannon-Weiner's index is a simple quantitative expression that incorporates both species richness and the evenness of species abundance. Because H' alone fails to show the degree that each factor contributes to diversity, we calculated a separate measure of species evenness (J'). Species diversity was calculated as: $H' = -\sum p_i \ln p_i$, where p_i = proportion of total abundance of species i , with abundance of woody species = stem density (stems ha⁻¹) or basal area (m² ha⁻¹); and abundance of herbaceous species = density (plants m⁻²) or biomass (g m⁻²). Species evenness was calculated as: $J' = H'/H'_{\max}$, where H'_{\max} = maximum level of diversity possible within a given community = $\ln(S)$. We used pairwise t-tests (Magurran, 1988) to examine the differences in H' between WS6 for sampling years 1958, 1982 and 1995 and the reference plots sampled in 1993.

RESULTS

Overstory.—Before conversion to grass in 1958, *Kalmia latifolia*, *Rhododendron maximum*, and *Quercus prinus* were the three most abundant woody species in WS6; when combined, they occupied 53.0% of the IV and 31.3% of the basal area (Table 1). Their high density gave *K. latifolia* and *R. maximum* the highest IVs; in contrast, their basal areas were low. The most abundant species in 1958, based only on basal area, were *Q. prinus*, *Q. coccinea*, *Acer rubrum*, *Carya* spp. and *Pinus rigida*. *Quercus* species (*prinus*, *coccinea*, *rubra*, *alba*, *velutina*) occupied 28.4% of the IV and 49.2% of the basal area. In 1982, 15 yr after cessation of management, *Q. prinus* and *P. rigida* were minor species, and *Quercus* species abundance had declined dramatically to 1.3% of the IV and 1.0% of the basal area (Table 1). In 1995, *Quercus* species were 1.2% of the IV and 1.5% of the basal area. Although *Q. coccinea* ranked fourth in basal area (15.0% of total basal area) before conversion to grass, by 1982 it had disappeared from the overstory; whereas, *Robinia pseudoacacia* and *Liriodendron tulipifera* combined accounted for 71.6% of the IV and 83.9% of the basal area. By 1995 (28-yr-old forest), these two species accounted for 50.8% of the IV and 73.7% of the basal area. In 1958, *Liriodendron tulipifera* accounted for <0.5% of the IV, but by 1982 (15 yr after cessation of management) its IV and frequency of occurrence was much higher. *Acer rubrum* increased in IV from 1982 to 1995; in 1995, its density was twofold higher and basal area was sixfold higher and it had exceeded the preconversion level of density and basal area.

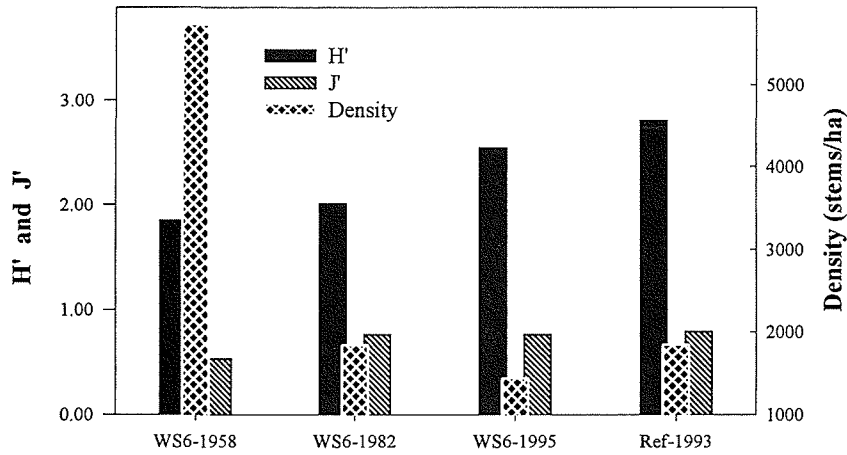
From 1982 to 1995 in WS6, average mortality for all tree stems was 35.3% and average ingrowth was 33.6%. *Robinia pseudoacacia* average mortality was 72.7% with no ingrowth over the 13-yr period, *Liriodendron tulipifera* had 15.3% mortality and 19% ingrowth, and *Acer rubrum* had 17% mortality and 54.7% ingrowth (via recruitment into additional plots).

In the reference forests, *Quercus* species constituted 19.8% of the IV and 29.5% of the basal area. *Quercus prinus* had the highest relative basal area and ranked third in IV value in the reference plots (Table 1), compared to <1.0% of the basal area and a ranking of 14 in IV for WS6. *Quercus coccinea* had disappeared from the overstory of WS6, yet it accounted for 7.3% of the basal area and was ranked eighth in IV in the reference plots. In the reference plots, *Kalmia latifolia* was the most important species with high relative density

TABLE 1.—Distribution of dominant woody species (≥ 2.5 cm dbh) for WS6 in 1958, before the grass conversion experiment; in 1982, 15-yr-old forest; in 1995, 28-yr-old forest; and the reference watershed plots (WS14 and WS18; 70-yr-old forest). Values in columns are percent frequency (Freq = proportion of total number of plots), density (stems ha^{-1}), basal area (BA; $\text{m}^2 \text{ha}^{-1}$), and importance value [IV = (relative density + relative basal area)/2]. Species are ranked by IV in 1958

| Species | WS6—1958 | | | | WS6—1982 | | | | WS6—1995 | | | | Reference watersheds—1993 | | | |
|--------------------------------|----------|---------|------|------|----------|---------|------|------|----------|---------|------|------|---------------------------|---------|------|------|
| | Freq (%) | Density | BA | IV | Freq (%) | Density | BA | IV | Freq (%) | Density | BA | IV | Freq (%) | Density | BA | IV |
| <i>Kalmia latifolia</i> | 92 | 2489 | 1.3 | 24.8 | 4 | 2 | 0.1 | 0.1 | 23 | 123 | 0.1 | 4.6 | 38 | 463 | 1.0 | 14.2 |
| <i>Rhododendron maximum</i> | 89 | 1620 | 0.8 | 16.2 | 15 | 29 | 0.02 | 0.8 | 31 | 162 | 0.2 | 6.0 | 85 | 118 | 0.5 | 4.2 |
| <i>Quercus prinus</i> | 81 | 175 | 4.2 | 12.0 | 19 | 14 | 0.1 | 0.7 | 12 | 8 | 0.2 | 0.8 | 85 | 92 | 3.0 | 7.7 |
| <i>Quercus coccinea</i> | 89 | 119 | 3.0 | 8.5 | — | — | — | — | — | — | — | — | 69 | 36 | 2.1 | 4.6 |
| <i>Acer rubrum</i> | 96 | 245 | 1.8 | 6.5 | 73 | 112 | 0.3 | 4.1 | 92 | 219 | 1.6 | 11.1 | 100 | 251 | 2.8 | 11.7 |
| <i>Carya</i> spp. | 89 | 227 | 1.7 | 6.2 | 27 | 38 | 0.1 | 1.6 | 31 | 29 | 0.3 | 1.6 | 77 | 82 | 1.5 | 4.9 |
| <i>Pinus rigida</i> | 26 | 18 | 1.6 | 4.0 | 8 | 10 | 0.1 | 0.7 | 4 | 2 | 0.02 | 0.1 | 38 | 29 | 1.8 | 3.9 |
| <i>Quercus velutina</i> | 70 | 44 | 1.2 | 3.4 | 4 | 7 | 0.01 | 0.3 | 4 | 4 | 0.02 | 0.2 | 46 | 21 | 1.2 | 2.6 |
| <i>Quercus alba</i> | 56 | 77 | 1.1 | 3.3 | 4 | 8 | 0.04 | 0.4 | 4 | 8 | 0.1 | 0.5 | 38 | 25 | 0.8 | 2.1 |
| <i>Cornus florida</i> | 85 | 183 | 0.6 | 2.8 | 38 | 40 | 0.1 | 1.4 | 42 | 56 | 0.3 | 2.6 | 62 | 80 | 0.5 | 3.0 |
| <i>Nyssa sylvatica</i> | 92 | 85 | 0.6 | 3.1 | — | — | — | — | — | — | — | — | 77 | 53 | 0.7 | 2.7 |
| <i>Oxydendrum arboreum</i> | 92 | 94 | 0.9 | 3.0 | 50 | 56 | 0.1 | 2.0 | 50 | 54 | 0.3 | 2.6 | 85 | 86 | 1.7 | 5.2 |
| <i>Robinia pseudoacacia</i> | 56 | 18 | 0.2 | 0.6 | 96 | 919 | 7.8 | 57.7 | 92 | 225 | 7.9 | 25.7 | 38 | 16 | 0.4 | 1.1 |
| <i>Liriodendron tulipifera</i> | 44 | 24 | 0.1 | 0.4 | 88 | 173 | 2.2 | 13.9 | 88 | 177 | 8.4 | 25.1 | 62 | 66 | 2.8 | 6.6 |
| <i>Betula lenta</i> | 37 | 13 | 0.04 | 0.2 | 27 | 112 | 0.3 | 4.1 | 35 | 65 | 1.1 | 4.7 | 31 | 37 | 1.0 | 2.7 |
| <i>Tsuga canadensis</i> | 4 | 7 | 0.01 | 0.1 | — | — | — | — | — | — | — | — | 46 | 59 | 2.6 | 6.0 |
| <i>Quercus rubra</i> | 33 | 20 | 0.4 | 0.9 | 15 | 10 | 0.02 | 0.4 | 8 | 3 | 0.01 | 0.1 | 46 | 12 | 0.1 | 2.8 |
| Total | | 5735 | 20.2 | | | 1838 | 11.9 | | | 1436 | 21.0 | | | 1843 | 29.0 | |
| Species richness | | 33 | | | | 27 | | | | 28 | | | | 34 | | |

a) Density-based diversity (H') and evenness (J')



b) Basal area-based diversity (H') and evenness (J')

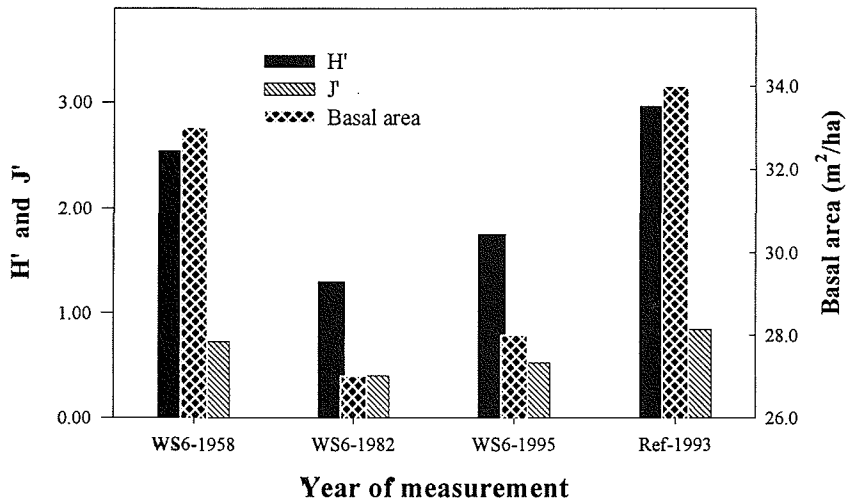


FIG. 1.—Average density, average basal area, diversity (H') and evenness (J') for overstory species for WS6 in 1958, before the grass conversion experiment; in 1982, 15-yr-old forest; in 1995, 28-yr-old forest; and the reference watersheds, 70-yr-old-forest. (a) density-based H' and J' , and average density; (b) basal area-based H' and J' , and average basal area

producing a high IV (Table 1). In contrast, in WS6, 28 yr after the cessation of management, *K. latifolia* was ranked 13th based on relative basal area, and it tied for the 15th position with four other species based on frequency (Table 1).

The reference plots had significantly higher density-based H' and basal area-based H' than WS6 in any year (Fig. 1a and Table 2). However, density-based J' was comparable

TABLE 2.—T-statistics for differences among sample years and reference watershed plots for overstorey species density-based and basal area-based diversity

| Comparison | Based on | H' values | t-value | df | P-value |
|--------------------|------------|-----------|---------|----|---------|
| 1958 vs. 1982 | Density | 1.85–2.01 | –4.107 | 43 | <0.0001 |
| | Basal area | 2.54–1.30 | 3.267 | 27 | <0.005 |
| 1958 vs. 1995 | Density | 1.85–2.54 | –22.180 | 55 | <0.0001 |
| | Basal area | 2.54–1.75 | 2.981 | 28 | <0.01 |
| 1982 vs. 1995 | Density | 2.01–2.54 | –12.550 | 49 | <0.0001 |
| | Basal area | 1.30–1.75 | –0.967 | 24 | ns |
| 1995 vs. Reference | Density | 2.54–2.80 | –7.140 | 62 | <0.0001 |
| | Basal area | 1.75–2.96 | –4.537 | 28 | <0.0001 |

among time periods (Fig. 1a). In WS6, density-based H' was significantly higher in 1995 than in 1958. However, basal area-based H' significantly declined from 1958 to 1982, and then significantly increased in 1995 (Fig. 1b and Table 2).

Understorey.—In 1995, increased regeneration was limited to only a few tree species in the understorey of WS6. The most abundant saplings were *Acer rubrum* and *Symplocos tinctoria*. *Liriodendron tulipifera* and *Quercus* spp. saplings were rare. *Pyrularia pubera* and *Kalmia latifolia* were the most abundant shrubs in the >1.0 m height stratum. In the ground floor plots (≤1.0 m height), the average number of shrubs was 21,340 stems ha⁻¹, and the average number of trees was 11,150 seedlings ha⁻¹. The most abundant shrubs were *Rubus alleghaniensis* with 11,530 stems ha⁻¹ and *Gaylussacia ursina* with 8080 stems ha⁻¹. *Acer rubrum* was the most abundant tree species with 5000 seedlings ha⁻¹; *L. tulipifera* and *Prunus serotina* each had 960 seedlings ha⁻¹, and *Quercus rubra* and *Quercus coccinea* combined had 960 seedlings ha⁻¹.

The ground flora subplots of the reference plots had 68,540 stems ha⁻¹ of shrubs and 16,680 seedlings ha⁻¹ of trees. *Gaylussacia ursina* was the most abundant shrub with 59,700 stems ha⁻¹. The most abundant tree seedlings were *Acer rubrum*, *Quercus rubra*, and *Liriodendron tulipifera* with 8880, 3030 and 1120 seedlings ha⁻¹, respectively. All the *Quercus* species combined (*rubra*, *prinus*, *velutina* and *coccinea*) had 4150 seedlings ha⁻¹, fourfold higher than the 28-yr-old forest of WS6.

In the 1982 ground flora inventory, not all plants were identified to species—a category designated as “others” contained 1.02% of the total biomass, and plants of *Solidago*, *Lupinus*, *patorium* and *Aster* were not identified to species. Thus, the low number of species present in 1982 may be attributed to the lumping of rare species rather than to a true decline (Table 3).

In 1968, WS6 had only 23 species with four (*Erechtites hieracifolia*, *Phytolacca americana*, *Equisetum arvense* and *Fescue octiflora*) accounting for 92.3% of the biomass. Of these, only *F. octiflora* remained in 1982, but it had decreased in frequency and relative biomass (Table 3), and by 1995, it was lower in biomass. *Erechtites hieracifolia* and *Erigeron canadensis* reappeared as minor species in 1995 with only 0.20% of the biomass. Based on relative biomass the ranking of ground flora species in 1995 was *Eupatorium* spp., *Polystichum acrostichoides* and *Smilax* spp. (Table 3). Other species that occurred frequently in relatively high biomass in 1995, but were not identified in 1968, were *Rubus alleghaniensis*, *Dennstaedtia punctilobula* and *Clematis virginiana*.

Unlike WS6, in the reference plots, *Gaylussacia ursina*, *Acer rubrum*, *Galax aphylla* and *Thelypteris noveboracensis* were the four most abundant species based on relative dens-

TABLE 3.—Distribution of dominant ground flora species (woody species ≤ 1.0 m height and all herbaceous species) for a disturbed watershed (WS6), Coweeta Basin in 1968 (1-year-old field), 1982 (15-year-old forest), and 1995 (28-year-old forest). Values in columns are percent frequency (proportion of total number of plots), biomass (g m^{-2}), and relative biomass. Species are ranked by relative biomass in 1968

| Species | 1968 | | | 1982 | | | 1995 | | |
|-----------------------------------|-------------------------------------|---------|---------------------|-------------------------------------|---------|---------------------|-------------------------------------|---------|---------------------|
| | Per- cent fre- quen- cy | Biomass | Relative biomass | Per- cent fre- quen- cy | Biomass | Relative biomass | Per- cent fre- quen- cy | Biomass | Relative biomass |
| <i>Erechtites hieracifolia</i> | 100 | 181.96 | 37.1 | — | — | — | 8 | 0.09 | 0.2 |
| <i>Phytolacca americana</i> | 10 | 138.57 | 28.3 | — | — | — | — | — | — |
| <i>Equisetum arvense</i> | 64 | 90.30 | 18.4 | — | — | — | — | — | — |
| <i>Festuca octiflora</i> | 54 | 14.51 | 8.5 | 27 | 2.74 | 1.0 | 35 | 0.51 | 1.1 |
| <i>Robinia pseudoacacia</i> | 4 | 8.24 | 1.7 | — | — | — | 8 | <0.01 | <0.1 |
| <i>Smilax rotundifolia</i> | 45 | 3.40 | 0.7 | 32 | 105.39 | 39.2 | 81 | 7.01 | 14.7 |
| <i>Solidago</i> spp. | 4 | 0.03 | <0.1 | 23 | 8.70 | 3.2 | 19 | 0.05 | 0.1 |
| <i>Eupatorium</i> sp. | 4 | 0.02 | <0.1 | 41 | 5.48 | 2.0 | 100 | 17.38 | 36.5 |
| <i>Rubus alleghaniensis</i> | — | — | — | 77 | 116.98 | 43.5 | 77 | 3.41 | 7.2 |
| <i>Polystichum acrostichoides</i> | 4 | 0.21 | <0.1 | 54 | 13.95 | 5.2 | 77 | 10.99 | 23.1 |
| <i>Clematis virginiana</i> | — | — | — | 32 | 4.90 | 1.8 | 46 | 1.15 | 2.4 |
| <i>Dennstaedtia punctilobula</i> | — | — | — | — | — | — | 46 | 1.46 | 3.1 |
| Total | | 490.20 | 97.1% | | 196.80 | 97.9% | | 47.60 | 91.2% |

(Table 4). In WS6, *Eupatorium* spp. occurred in all 26 sample plots, and *Polystichum acrostichoides* and *Rubus alleghaniensis* occurred in 20 of the plots. Taxa that were similar between the reference watersheds and WS6 were *Dioscorea villosa*, *Arisaema triphyllum*, *T. noveboracensis*, *Dennstaedtia punctilobula*, *Houstonia purpurea*, *Smilacina racemosa* and *Galium latifolia*. WS6 had fewer species than the reference plots but average density was 3.6 times greater (Table 4).

DISCUSSION

Distribution of woody species.—The canopy of the 28-yr-old WS6 forest differed from that of the reference watersheds. Species richness was slightly lower, and basal area-based H' was significantly lower. We attributed the initial decline in basal area-based H' to the evenness of species distribution (J')—which declined from 1958 to 1982, and the subsequent increase to the corresponding increase in J' . Thus, the changes in overstory diversity among years was driven by changes in dominance rather than changes in the number of overstory species. The reference forests had a large component of *Quercus* species and *Tsuga canadensis* along with *Liriodendron tulipifera*. In WS6, *Quercus* species were a minor component, *T. canadensis* was absent, and *Robinia pseudoacacia* and *L. tulipifera* were the dominant species in the first 28 yr of succession. Clebsch and Busing (1989) found that *R. pseudoacacia* and *L. tulipifera* dominated a 15-yr-old cove forest after abandonment from agriculture, but that *R. pseudoacacia* disappeared by the 42nd yr of development. Clebsch and Busing (1989) also compared an old-growth stand to an adjacent abandoned agricultural field that was dominated by *L. tulipifera* at age 48. They found that species richness peaked during mid-succession (≈ 50 yr). Density-based H' was highest in the 48-yr-old stand, whereas biomass-

TABLE 4.—Distribution of dominant ground flora species (woody species ≤ 1.0 m height and herbaceous species) for reference watersheds (WS14 and WS18, 70-yr-old forest, with similar aspect and elevation as WS6) sampled in 1993 and WS6 sampled in 1995 (28-yr-old forest). Values in column are percent frequency (proportion of total number of plots), density (plants m^{-2}), and relative density. Species are ranked by relative density of reference watersheds

| Species | Reference watersheds—1993 | | | WS6—1995 | | |
|-----------------------------------|---------------------------|---------|------------------|-------------------|---------|------------------|
| | Percent frequency | Density | Relative density | Percent frequency | Density | Relative density |
| <i>Gaylussacia ursina</i> | 38 | 6.0 | 36.9 | 12 | 0.8 | 1.4 |
| <i>Acer rubrum</i> | 50 | 0.9 | 5.5 | 32 | 0.5 | 0.5 |
| <i>Smilax</i> spp. | 58 | 0.9 | 5.4 | 62 | 2.5 | 4.3 |
| <i>Galax aphylla</i> | 38 | 0.8 | 5.1 | 3 | 0.1 | <0.1 |
| <i>Thelypteris noveboracensis</i> | 15 | 0.7 | 4.2 | 3 | 0.4 | 0.7 |
| <i>Vaccinium vacillans</i> | 23 | 0.5 | 3.1 | — | — | — |
| <i>Houstonia purpurea</i> | 15 | 0.5 | 2.8 | 15 | 0.2 | 0.4 |
| <i>Dennstaedtia punctilobula</i> | 4 | 0.4 | 2.2 | 35 | 3.1 | 5.4 |
| <i>Parnassia asarifolia</i> | 4 | 0.3 | 2.1 | — | — | — |
| <i>Desmodium nudiflorum</i> | 12 | 0.3 | 1.8 | 29 | 1.6 | 2.7 |
| <i>Viola</i> spp. | 42 | 0.3 | 1.7 | 35 | 2.8 | 4.8 |
| <i>Panicum</i> spp. | 12 | 0.3 | 1.6 | 41 | 2.2 | 3.8 |
| <i>Polystichum acrostichoides</i> | 35 | 0.2 | 1.1 | 59 | 15.4 | 26.4 |
| <i>Eupatorium rugosum</i> | 12 | 0.1 | 0.4 | 76 | 15.8 | 27.1 |
| <i>Lonicera japonica</i> | — | — | — | 32 | 1.7 | 3.0 |
| <i>Fescue octiflora</i> | — | — | — | 18 | 1.6 | 2.7 |
| Total density | | 16.2 | 84.1% | | 58.2 | 90.6% |
| Species richness | | 81 | | | 63 | |

based H' was highest in the old-growth stand. In our study, *R. pseudoacacia* declined abundance from 1982 to 1995, but was still the dominant species 28 yr after cessation management; whereas, *L. tulipifera* increased in abundance.

Using data from the Coweeta Basin, we compared the results from WS6 with two watersheds that had different patterns of cutting and succession: a treated S-facing watershed which had a single clear-cut harvest followed by 17 yr of succession (Elliott *et al.*, 1997) and an NE-facing watershed, which had two clear-cuts separated by 23 yr of unimpeded growth (Elliott and Swank, 1994). In the 17-yr-old once-clear-cut forest, relative basal area of *Robinia pseudoacacia* was 9.5% for cove-hardwoods, 21.3% for mixed-oak hardwoods, and 3.4% for hardwood-pine communities (Elliott *et al.*, 1997). In WS6, relative basal area of *R. pseudoacacia* was 65.4% for the 15-yr-old forest and 25.7% for the 28-yr-old forest. In addition, *Acer rubrum*, a ubiquitous component of Southern Appalachian forests that was abundant in WS6 before conversion to grass, regained its position in the canopy after cessation of management, and remained important in the 28-yr-old forest. In the once-clear-cut watershed, basal area-based H' ranged from 1.76 to 2.57 depending on community type after 17 yr of forest development, whereas in WS6 basal area-based H' was 1.30 after 15 yr and only 1.75 after 28 yr of forest development. The twice-clear-cut watershed had higher diversity than WS6. Basal area-based H' ranged from 2.31 to 2.61 in the 8 to 23 yr following the first clear-cut, and from 2.55 to 2.06 in the 7 to 29 yr following the second clear-cut (Elliott and Swank, 1994).

The recovery of WS6 following large-scale, severe disturbance, results partly from the li

history traits of the species that colonized the watershed. A major difference between WS6 and the other nearby clear-cut watersheds in the Coweeta Basin is in the species mechanisms for sexual and vegetative reproduction. Both the once- and twice-clear-cut watersheds were allowed to regrow immediately after clear-cutting, making sprouting from cut stumps the primary mode of reproduction. However, in WS6 vegetative reproduction was only apparent for *Robinia pseudoacacia*. To keep the watershed in grass cover for 5 yr, stump sprouting was eliminated, and woody species were spot-herbicided. Following cessation of management, regeneration could only come from seeds that had survived in the soil for many years, from small, wind-dispersed seeds such as the winged-samaras of *Liriodendron tulipifera* and *Acer rubrum*, or species that could sprout from extensive, persistent root systems (for species like *R. pseudoacacia*). Large seeded species such as *Quercus rubra* and *Q. coccinea* were regenerating, but were in low numbers; and some species, including *Q. prinus* and *Q. velutina* had disappeared from the understory.

Following cessation of management, *Robinia pseudoacacia* quickly sprouted from roots to outperform other species for several years, similar to patterns that have been documented throughout the Southern Appalachians (Beck and McGee, 1974; McGee and Hooper, 1970, 1975; Clebsch and Busing, 1989). The dense stands eventually decrease in vigor, succumb to locust stem borers (*Megacyllene robiniae*), and decline (Hoffard and Anderson, 1982) leaving N-enriched soil and organic matter for exploitation by other species (Boring and Swank, 1984a). *Robinia pseudoacacia* is a dominant Southern Appalachian successional tree that symbiotically fixes N, grows rapidly and has a relatively short lifespan (Boring and Swank, 1984b). Although *R. pseudoacacia* regenerated quickly following cessation of management, it began to experience heavy stem borer mortality in 1979; by 1982, 21% of the *R. pseudoacacia* trees were dead, 18% were severely injured, and many of the remaining trees showed evidence of canopy decline. Since 1982, there has been no ingrowth and it is not found in the shrub stratum.

Liriodendron tulipifera increases in density following clear-cutting due to its prolific seedling establishment (Trimble, 1973). It is a rapidly growing, shade-intolerant, early successional species often found in pure stands on abandoned fields. Yet the species is long-lived, can achieve diameters in excess of 2 m, and can occupy sites for hundreds of years (Buckner and McCracken, 1978). Apsley (1987) demonstrated that *Robinia pseudoacacia* enhanced the growth of *L. tulipifera* in a 10-yr-old stand in the Coweeta Basin, presumably by substantially increasing nitrogen availability (Boring and Swank, 1984a). Other researchers report a large pulse in *R. pseudoacacia* mortality approximately 10–20 yr following clear-cutting (Della-Bianca, 1983; Leopold *et al.*, 1985; Elliott *et al.*, 1997). For these reasons, we predict that *L. tulipifera* will maintain its canopy dominance in WS6, whereas *R. pseudoacacia* will continue to decline in the absence of any further large-scale disturbance.

Understory.—Because of its heterogeneity of resources, the understory is typically the most diverse stratum in mature eastern deciduous forests (Huebner *et al.*, 1995). Richness of the ground flora was much higher in the 28-yr-old forest than the 1-yr-old field of WS6. Much of this richness came from woody species colonizing the watershed. There were only four woody species in the sample plots in 1968 and five in 1982; however, that number had increased to 22 (nine shrubs, 13 trees) by 1995.

Recovery rates of woody species richness and cover were much faster in WS6 than in other studies of old-field abandonment (Myster and Pickett, 1990; Myster and Pickett, 1994; Inouye and Tilman, 1995), yet slower than in experimental clear-cut watersheds (Boring *et al.*, 1981; Reiners, 1992). Inouye and Tilman (1995) found that species richness increases with field age and soil nitrogen, but woody species contributed <15% cover even in the oldest fields (56-yr-old). In our study, woody species contributed <3.0% to the total above-

ground biomass in the 1st yr after cessation of management, 67.8% by the 3rd yr, and >99.0% in 1982 and 1995. In 1995 (28-yr since cessation of management), woody species contributed 6.6% of the density, 10.5% of the cover, and 15.6% of the biomass in the ground flora stratum alone. The rate of woody species recovery following disturbance depends largely on the previous land use practices, such as the number of years under agricultural practice and the extent of nutrient amendments. In WS6, the grass cover remained for 5 yr, there was no grass utilization, and the site received large additions of lime and fertilizer. Nevertheless, woody species recovery was slower than that of a clear-cut and herbicide northern hardwood forest at Hubbard Brook (Reiners, 1992), where woody species contributed 53.6% of the aboveground biomass in the 1st yr following recovery and 86.7% by the 3rd yr. Although there are differences in climate, soils and vegetation composition between the Hubbard Brook watershed and Coweeta Basin's WS6, a major factor influencing the rate of recovery of woody species in WS6 was the impact of planting, herbicide use of woody species and maintaining grass cover for 5 yr.

Diversity may remain low even decades after logging because herbaceous plants of late successional or mature forests colonize slowly, with some species needing a decade or more from seed to first flowering (Bierzychudek, 1982). In WS6, clear-cutting, 5 yr of grass cover followed by herbiciding, increased the abundance of genera—such as *Erechtites*, *Phytolacca* and *Erigeron*, as well as early successional woody species—that tolerate open habitats. In contrast, shade-tolerant understory ferns and herbs such as *Polystichum acrostichoides*, *Desmodium punctilobula*, *Galium latifolium* and *Viola cucullata* have only become more abundant as the forest matured.

Large-scale, severe disturbance decreased plant diversity and dramatically altered community structure in a small Southern Appalachian watershed. Although recovery of woody species richness and cover was faster than in other studies following old-field abandonment, it was slower than in experimental clear-cut watersheds. Twenty-eight yr since cessation of management, overstory diversity has begun to increase and shade-tolerant ferns and herbs are becoming more abundant. To address long-term effects, we need to know how species responses vary with changes in stand development, life-history characteristics, and disturbance severity and spatial scale. Comparative studies in different ecosystem types would provide insights into the relative importance of processes that influence diversity. These studies would help clarify the patterns and mechanisms that different ecosystems have in common as well as those that are unique.

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LITERATURE CITED

- APSEY, D. K. 1987. Growth interactions and comparative water relations of *Liriodendron tulipifera* and *Robinia pseudoacacia* L. M.Sc. Thesis, University of Georgia, Athens. 83 p.
- BECK, D. A. AND C. E. MCGEE. 1974. Locust sprouts reduce growth of yellow-poplar seedlings. *U.S. Serv. Res. Note SE-201*. 6 p.
- BIERZYCHUDEK, P. 1982. Life histories and demography of shade-tolerant temperate forest herbivores. *New Phytol.*, **90**:757–776.
- BORING, L. R., C. D. MONK AND W. T. SWANK. 1981. Early regeneration of a clear-cut South Appalachian forest. *Ecology*, **62**:1244–1253.
- AND W. T. SWANK. 1984a. The role of black locust (*Robinia pseudoacacia*) in forest succession. *J. Ecol.*, **72**:749–766.
-

- AND ———. 1984b. Symbiotic nitrogen fixation in regenerating black locust (*Robinia pseudoacacia* L.) stands. *For. Sci.*, **30**:528–537.
- , ——— AND C. D. MONK. 1988. Dynamics of early successional forest structure and processes in the Coweeta Basin, p. 161–179. *In*: W. T. Swank and D. A. Crossley, Jr. (eds.). *Forest hydrology and ecology at Coweeta*. Ecological Studies 66, Springer-Verlag, New York.
- BUCKNER, E. AND W. MCCracken. 1978. Yellow poplar: a component of climax forests. *J. For.*, **76**:421–423.
- BURT, T. P. AND W. T. SWANK. 1992. Flow frequency responses to hardwood-to-grass conversion and subsequent succession. *Hydrol. Proc.*, **6**:179–188.
- BUSING, R. T. AND E. E. C. CLEBSCH. 1983. Species composition and species richness in first-year old fields: responses to season of soil disturbance. *Bull. Torr. Bot. Club*, **110**:304–310.
- CLEBSCH, E. E. C. AND R. T. BUSING. 1989. Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. *Ecology*, **70**:728–735.
- DELLA-BIANCA, L. 1983. Sixty years of development in a southern Appalachian cove hardwood stand. *For. Ecol. Manage.*, **5**:229–241.
- DOUGLASS, J. E., D. R. COCHRANE, G. W. BAILEY, J. I. TEASLEY AND D. W. HILL. 1969. Low herbicide concentration found in streamflow after a grass cover is killed. *U.S. For. Serv. Res. Note SE-108*. 3 p.
- AND M. D. HOOVER. 1988. History of Coweeta, p. 17–34. *In*: W. T. Swank and D. A. Crossley, Jr. (eds.). *Forest hydrology and ecology of Coweeta*, Ecological Studies 66, Springer-Verlag, New York.
- DUNFORD, E. G. AND P. W. FLETCHER. 1947. Effect of removal of stream-bank vegetation upon water yield. *Trans. Am. Geophys. Union*, **28**:105–110.
- ELLIOTT, K. J., L. R. BORING, W. T. SWANK AND B. L. HAINES. 1997. Successional changes in plant species diversity and composition after clearcutting a Southern Appalachian watershed. *For. Ecol. Manage.*, **92**:67–85.
- AND W. T. SWANK. 1994. Changes in tree species diversity after successive clearcuts in the southern Appalachians. *Vegetatio*, **115**:11–18.
- GRIME, J. P. 1979. *Plant strategies and vegetation processes*. John Wiley & Sons, New York. 222 p.
- HALPERN, C. B. AND T. A. SPIES. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecol. Appl.*, **5**:913–934.
- HATCHER, R. D., JR. 1988. Bedrock geology and regional geologic setting of Coweeta Hydrologic Laboratory in the eastern Blue Ridge, p. 81–92. *In*: W. T. Swank and D. A. Crossley, Jr. (eds.). *Forest hydrology and ecology of Coweeta*, Ecological Studies 66. Springer-Verlag, New York.
- HIBBERT, A. R. 1969. Water yield changes after converting a forested catchment to grass. *Water Resour. Res.*, **5**:634–640.
- HOFFARD, W. H. AND R. L. ANDERSON. 1982. A guide to common insects, diseases, and other problems of black locust. *U.S. For. Serv. For. Rep. SA-FR*. 19 p.
- HUEBNER, C. D., J. C. RANDOLPH AND G. R. PARKER. 1995. Environmental factors affecting understory diversity in second-growth deciduous forests. *Am. Midl. Nat.*, **134**:155–165.
- HURSH, C. R. 1951. Research in forest-streamflow relations. *UNASYLVA*, **5**:2–9.
- HUSTON, M. A. 1994. *Biological diversity: the coexistence of species on changing landscapes*, Cambridge University Press, Cambridge, UK. 681 p.
- HURLBERT, S. H. 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology*, **52**:577–586.
- INOUE, R. S. AND D. TILMAN. 1995. Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. *Ecology*, **76**:1872–1887.
- KEEVER, C. 1983. A retrospective view of old-field succession after 35 years. *Am. Midl. Nat.*, **110**:397–404.
- LEOPOLD, D. J. AND G. R. PARKER. 1985. Vegetation patterns on a southern Appalachian watershed after successive clearcuts. *Castanea*, **50**:164–186.
- , ——— AND W. T. SWANK. 1985. Forest development after successive clearcuts in the Southern Appalachians. *For. Ecol. Manage.*, **13**:83–120.
-

- LEPS, J. 1987. Vegetation dynamics in early oldfield succession: a quantitative approach. *Vegetatio*, 95:95–102.
- MAGURRAN, A. E. 1988. Ecological diversity and its measurement, Princeton University Press, Princeton N.J. 179 p.
- MARQUIS, D. A. AND R. L. JOHNSON. 1989. Silviculture of eastern hardwoods. The scientific basis for silvicultural and management decisions in the national forest system, compiled by R.M. Bur: p. 9–17. *U.S. For. Serv. Gen. Tech. Rep. WO-55*.
- MCGEE, C. E. AND R. M. HOOPER. 1970. Regeneration after clearcutting in the southern Appalachia *U.S. For. Serv. Res. Note SE-70*. 12 p.
- AND ———. 1975. Regeneration trends ten years after clearcutting of an Appalachian hardwood stand. *U.S. For. Serv. Res. Note SE-227*. 3 p.
- MEIER, A. J., S. P. BRATTON AND D. C. DUFFY. 1995. Possible ecological mechanisms for loss of vernal herb diversity in logged Eastern deciduous forests. *Ecol. Appl.*, 5:935–946.
- MYSTER, R. W. AND S. T. A. PICKETT. 1990. Initial conditions, history and successional pathways on contrasting old fields. *Am. Midl. Nat.*, 124:231–238.
- AND ———. 1994. A comparison of rate of succession over 18 years in 10 contrasting old fields. *Ecology*, 75:387–392.
- PATIL, G. P. AND C. TAILLIE. 1979. An overview of diversity, p. 3–27. *In*: J. F. Grassle, G. P. Patil, J. Smith and C. Taillie (eds.). Ecological diversity in theory and practice, International Cooperative Publishing House, Fairland, Md.
- AND ———. 1982. Diversity as a concept and its measurement. *J. Am. Statist. Assoc.*, 77:545–567.
- PEET, R. K. 1981. Changes in biomass and production during secondary forest succession, p. 324–335. *In*: D. C. West, H. H. Shugart and B. D. Botkin (eds.). Forest succession: concepts and application. Springer-Verlag, Berlin and New York.
- PETRAITIS, P. S., R. E. LATHAM AND R. A. NIESENBAUM. 1989. The maintenance of species diversity through disturbance. *Quart. Rev. Biol.*, 64:393–418.
- PICKETT, S. T. A. 1982. Population patterns through twenty years of oldfield succession. *Bot. Rev.*, 49:335–371.
- PICKETT, S. T. A. AND P. S. WHITE. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Inc., Orlando, Fla. 472 p.
- PIELOU, E. C. 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.*, 13:131–144.
- RADFORD, A. E., H. E. AHLES AND C. R. BELL. 1968. Manual of the vascular flora of the Carolinian region. University of North Carolina Press, Chapel Hill. 1183 p.
- REINERS, W. A. 1992. Twenty years of ecosystem reorganization following experimental deforestation and regrowth suppression. *Ecol. Monogr.*, 62:503–523.
- ROBERTS, M. R. AND F. S. GILLIAM. 1995. Patterns and mechanisms of plant diversity in forest ecosystems: implications for forest management. *Ecol. Appl.*, 5:969–977.
- RUNKLE, J. R. 1985. Disturbance regimes in temperate forests, p. 17–34. *In*: S. T. A. Pickett and P. S. White (eds.). The ecology of natural disturbance and patch dynamics, Academic Press, In Orlando, Fla.
- SANKOVSKI, A. G. 1994. Diversity and structure of Southern Appalachian and southwestern Caucasian forests with respect to historical events and present environment. Ph.D. Thesis, University of Georgia, Athens. 212 p.
- SWANK, W. T., L. W. SWIFT JR. AND J. E. DOUGLASS. 1988. Streamflow changes associated with forest cutting, species conversions, and natural disturbances, p. 297–312. *In*: W. T. Swank and D. A. Crossley, Jr. (eds.). Forest hydrology and ecology at Coweeta, Ecological Studies 66, Springer-Verlag, New York.
- SWIFT, L. W., JR., G. B. CUNNINGHAM AND J. E. DOUGLASS. 1988. Climatology and hydrology, p. 35–52. *In*: W. T. Swank and D. A. Crossley, Jr. (eds.). Forest hydrology and ecology at Coweeta, Ecological Studies 66, Springer-Verlag, New York.
-

- TRIMBLE, G. R. 1973. The regeneration of central Appalachian hardwoods, with emphasis on the effects of site quality and harvesting practice. *U.S. For. Serv. Res. Note SE-282*. 14 p.
- WAIDE, J. B. 1988. Forest ecosystem stability: revision of the resistance-resilience model in relation to observable macroscopic properties of ecosystems, p. 383-405. *In*: W. T. Swank and D. A. Crossley, Jr. (eds.). *Forest hydrology and ecology at Coweeta*, Ecological Studies 66, Springer-Verlag, New York.
- WOODS, F. W. AND R. E. SHANKS. 1959. Natural replacement of chestnut by other species. *Ecology*, **40**: 349-361.

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