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Successional Forest Dynamics
30 Years Following Clearcutting

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Introduction

For the past several decades, clearcuts on experimental watersheds have provided an opportunity to examine how these large-scale forest disturbances influence various ecosystem processes, including stream hydrology (Swank and Helvey 1970; Likens et al. 1977; Swift 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; Bormann and Likens 1979; Swank and Caskey 1982; 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; Leopold et al. 1985; Leopold and Parker 1985; Hornbeck et al. 1987; Boring et al. 1988; Reiners 1992; Gove et al. 1992; Elliott and Swank 1994a; Elliott et al. 1997; Elliott et al. 1998). For the investigation of vegetation diversity and successional patterns in the WS 7 clearcut in the Coweeta basin, inventories were conducted 1, 3, 8, 17, 20, and 30 years after disturbance (Boring 1979; Boring et al. 1981, 1988; Boring and Swank 1986; Elliott et al. 1997; Elliott et al. 2002; see table 2.1). Other, related, nitrogen cycling and productivity studies were conducted in early successional black locust (*Robinia pseudoacacia*) stands on both WS 7 (Boring and Swank 1984) and the old-field successional WS 6 (White et al. 1988; Montagnini et al. 1989; Elliott et al. 1998). These Coweeta studies collectively examined the role of dominant early successional species in forest recovery and ecosystem processes and addressed impacts of disturbance on longer-term species composition and diversity.

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Table 2.1 Average abundance (for overstory, based on basal area in m²/ha; for ground flora, based on number of plants/m² in 1952 and biomass in g/m² in all other years) and diversity (H′, Shannon index) of woody species (≥ 0.5 m height) and herbaceous + woody (< 0.5 m height) ground flora species for three community types in WS 7, Coweeta basin.

Overstory species	Year	F	G	S	Abundance	H'
Cove hardwoods	1974	12	13	14	23.7	2.52
	1977	20	23	28	4.6	2.64
	1979	20	24	32	7.9	2.73
	1984	23	29	36	13.7	2.75
	1993	21	27	36	24.8	2.57
	2008	17	23	28	35.6	2.18
Mesic, mixed-oak	1974	16	21	26	24.9	2.13
	1977	14	17	20	5.3	2.13
	1979	11	14	19	7.3	2.22
	1984	15	18	22	9.2	2.47
	1993	13	14	22	23.8	1.76
	2008	12	20	26	37.7	2.86
Dry, mixed-oak	1974	13	16	19	27.5	2.28
	1977	13	15	19	6.0	2.41
	1979	15	19	25	9.2	2.37
	1984	20	24	30	16.3	2.49
	1993	19	25	36	20.5	2.35
	2008	13	22	30	32.2	2.33
Ground flora species						
Cove hardwoods	1952	12	17	27	16.5	2.52
	1977	12	17	19	33.3	2.49
	1979	12	20	22	97.8	2.19
	1984	16	19	21	37.6	1.85
	1993	14	19	20	8.0	0.82
	2008	23	30	32	15.3	2.73
Mesic, mixed-oak	1952	23	39	49	11.4	3.14
	1977	7	9	10	20.3	1.55
	1979	12	17	18	84.9	2.04
	1984	8	12	13	20.8	1.73
	1993	12	16	16	2.1	1.32
	2008	23	35	41	71.8	2.02
Dry, mixed-oak	1952	18	42	45	13.2	2.40
	1977	10	15	16	43.0	1.99
	1979	12	22	25	46.9	2.28
	1984	16	21	24	17.5	1.65
	1993	16	25	27	3.7	1.90
	2008	16	23	26	28.1	1.91

Note: F, total number of families; G, total number of genera; and S, total number of species present in each community.
Sources: Elliott et al. 1997; Elliott, unpublished.

was its scope and time frame expanded, through continued funding by the NSF's Long-Term Ecological Research Program and the USDA Forest Service's research on biological diversity. Public debate and opposition to clearcutting in the 1980s and 1990s necessitated that more emphasis be placed upon questions related to the impact of forest harvesting on plant species diversity. Fortuitously, the vegetation data sets for the original study had detailed species-level measurements for herbaceous groundcover, shrubs, and trees, and additional studies had also been conducted on the watershed throughout the long-term history of Coweeta. Those early measurements and later finer-resolution sampling at the species and community scales provided additional insights into the whole ecosystem response to clearcutting and improved our fundamental understanding of how early successional vegetation dynamics influence the longer-term recovery of southern Appalachian forests.

We also understand that prior to experimental clearcutting, the forest ecosystem on WS 7 (figure 2.1) was in a highly dynamic state of change and recovery from both climatic and earlier human influences. To keep the subsequent research in perspective, we therefore suggest that regional climatic disturbances and past land-use history be considered in the baseline characterization of the forest ecosystem.

Past human influences included Native American burning and valley agriculture, followed by settlement-period woodland burning and grazing by cattle and hogs. Later, private and federal ownership included intensive early logging practices and total fire suppression (figure 2.2). In the 1930s chestnut blight (*Endothia parasitica*) greatly altered the forest structure because of the removal of the American chestnut (*Castanea dentata*), the most dominant single species of canopy tree at that time (Day and Monk 1974; Elliott and Swank 2008).

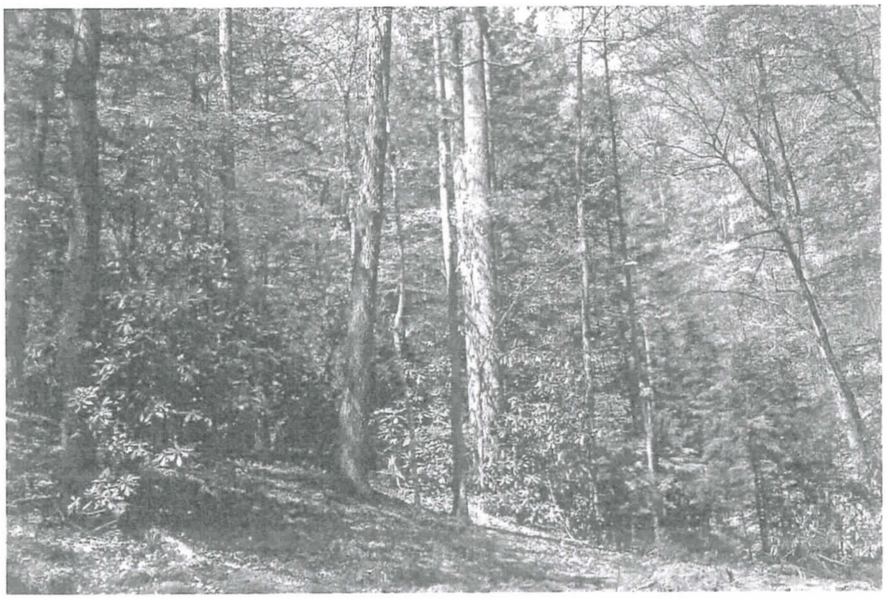

Figure 2.1 Mature, mixed-hardwood forest on WS 7, April 1976. (USDA Forest Service photo)

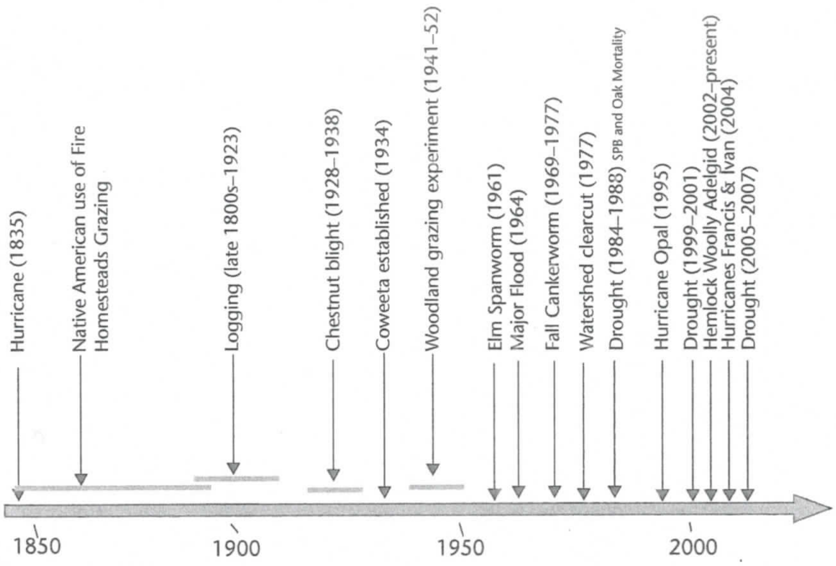

Figure 2.2 Timeline for major disturbances in the Coweeta basin.

Between 1900 and 1923, logging operations occurred over the entire basin, but the 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). A woodland grazing experiment occurred on WS 7 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 riparian area adjacent to the stream (Johnson 1952; Williams 1954).

The individual vegetation and ecosystem research projects on WS 7 have been extensively reported in the literature during the past 30 years. The objective of this chapter is to synthesize the long-term results on successional vegetation dynamics, including species composition, species diversity, biomass and nutrient content, functional roles of key dominant species, and to integrate related short-term studies.

Dynamics of Plant Species Composition and Diversity

Previous papers (Elliott and Swank 1994a; Elliott et al. 1997; Elliott et al. 1998) have described the species-specific changes following clearcutting in three different watersheds in the Coweeta basin. Initially, clearcutting in the southern Appalachians favors shade-intolerant woody species such as *Liriodendron tulipifera* and *R. pseudoacacia*, accompanied by numerous early-successional groundcover species and vines (Boring at al. 1981). After 10–15 years, the shade-tolerant evergreen species *Rhododendron maximum* and *Kalmia latifolia* developed strong dominance in the understory. A substantial reduction in large-seeded and slower-growing species, such as *Quercus* spp., *Carya* spp., *Tilia americana,* and *Aesculus flava,* has resulted from clearcutting, competitive exclusion, and lack of the time and conditions necessary for seed dispersal. These shifts in species composition had significant effects on biomass accumulation and, ultimately, aboveground nutrient accumulation. Although studies have shown a general expansion in evergreen shrubs in the last century (Day and Monk 1974; Monk et al. 1985; Lipscomb and Nilsen 1990; Dobbs 1998; Dobbs and Parker 2004; Elliott and Vose 2012) and a reduced importance of *Quercus* species (Phillips and Murdy 1985; Van Lear 1991; Hedman and Van Lear 1995), with the exception of *Q. prinus* and *Q. coccinea* (Elliott and Swank 2008), clearcutting appears to accelerate this phenomenon.

In WS 7, *L. tulipifera* and *R. pseudoacacia* increased in dominance in all three plant communities after cutting. *Robinia pseudoacacia* could be viewed as a traditional pioneer species that facilitates the growth of the next successional sere (Barnes et al. 1998) because it is short-lived due to early mortality associated with the locust stem borer (*Megacyllene robiniae*) and numerous defoliating insects (Boring and Swank 1984). As a legume, it fixes a substantial amount of nitrogen during its 15 –20 years of site dominance (Boring 1982; Boring and Swank 1984). In contrast, *L. tulipifera,* a shade-intolerant, fast-growing species, reaches the canopy quickly yet is very long-lived (Buckner and McCracken 1978; Burns and Honkala 1990). Once established, even on drier sites, it maintains its canopy position even during drought conditions (Clinton et al. 1993; Elliott and Swank 1994b).

The decline of dogwood (*Cornus florida*) from 1984 to 1997 was strongly influenced by dogwood anthracnose (*Discula destructiva*), a serious disease in southern Appalachian forests since about 1985. Although *C. florida* initially increased in relative dominance, 17 years after cutting (1993), it began a decline that is probably attributable to disease (Elliott et al. 1997). Dogwood anthracnose average incidence of *C. florida* infection was 87% for 1990 in the Coweeta basin (Chellemi et al. 1992; Britton 1993). Also, the loss of initially abundant *C. dentata* sprouts early in succession was due to the chestnut blight that has long been present at Coweeta (Day et al. 1988; Elliott and Swank 2008).

Woody Species Responses

The response of plant communities to clearcutting varied within the watershed. Woody-species richness increased in the cove-hardwood and dry, mixed-oak communities immediately after clearcutting and through 30 years of succession, but remained relatively constant in the mesic, mixed-oak community (table 2.1). In all three communities, there was a trend toward increased diversity (Shannon diversity index, H') in the first 8 years after clearcutting, but none of these differences among years were significant (Elliott et al. 1997). Only in the mesic, mixed-oak community was there a significant decline in diversity, between 1984 and 1993, and then diversity increased again by 2008 (table 2.1). In addition, the number of genera and families also increased in the cove hardwoods and dry, mixed-oak (table 2.1). *Liriodendron tulipifera* increased in dominance in all three communities after clearcutting. *Rhododendron maximum* increased in the cove hardwoods;

R. pseudoacacia increased in the cove hardwoods and mesic, mixed-oak; and *K. latifolia* and *Acer rubrum* increased in the dry, mixed-oak. *Carya* spp. and *Quercus rubra* declined in dominance in the cove hardwoods; *Quercus velutina* and *Carya* spp. declined in the mesic, mixed-oak; and *Pinus rigida* and *Q. velutina* declined in the dry, mixed-oak. In contrast, *R. pseudoacacia* continued to increase in early stages. *Quercus rubra* also decreased in cove-hardwood plots, and *A. rubrum*, important 2 years after cutting, had returned to its precut importance in the community (figure 2.3).

These trends in diversity are similar to those found in other southern Appalachian hardwood forests (Beck and Hooper 1986; Phillips and Shure 1990; Elliott and

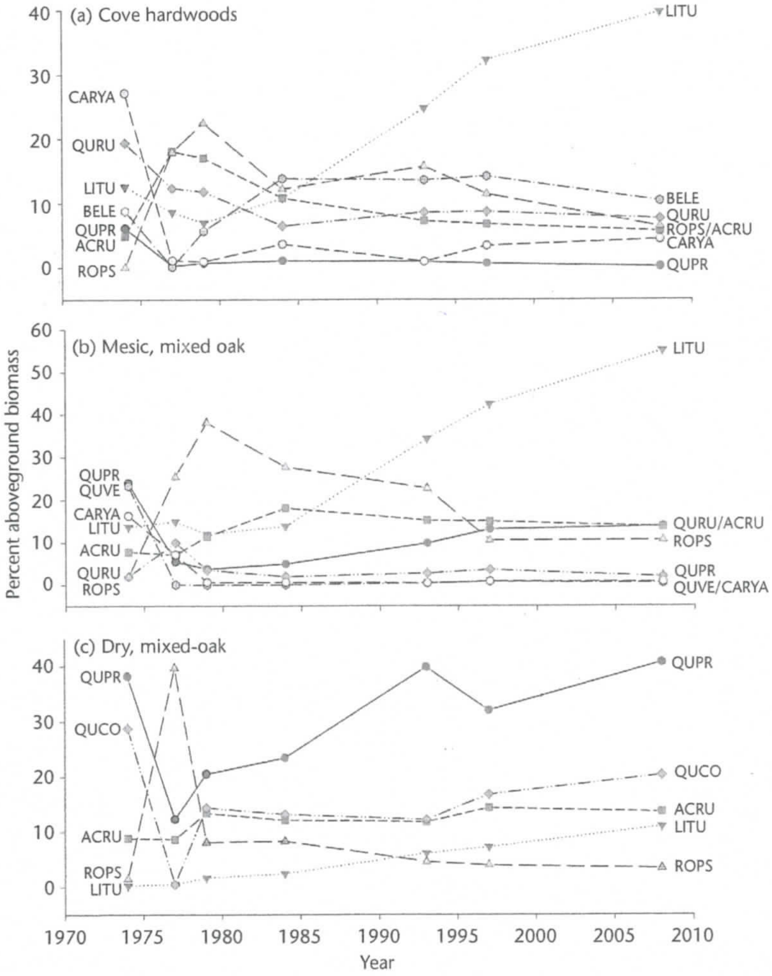

Figure 2.3 Percent aboveground biomass for the three community types in WS 7 through time. Species codes are ACRU, *Acer rubrum*; BELE, *Betula lenta*; CARYA, *Carya* spp.; LITU, *Liriodendron tulipifera*; QUCO, *Quercus coccinea*; QUPR, *Quercus prinus*; QURU, *Quercus rubra*; QUVE, *Quercus velutina*; ROPS, *Robinia pseudoacacia*.

Swank 1994a; Shure et al. 2006) but are somewhat different than those found in northeastern deciduous forests (Gove et al. 1992; Reiners 1992; Wang and Nyland 1993). For example, in the northeast, Gove et al. (1992) showed a decline in tree diversity 10 years after clearcutting, while Reiners (1992) found a gradual decline in diversity and an increase in richness after clearcutting and applying herbicide. In the southern Appalachians, others have found that species composition changed after clearcutting of the mixed-hardwood sites (Beck and Hooper 1986; Phillips and Shure 1990; Elliott and Swank 1994a; Elliott et al. 1998; Shure et al. 2006). These studies also reported that species such as *L. tulipifera*, *R. pseudoacacia*, *C. florida*, and *A. rubrum* increased in dominance after clearcutting; whereas, *Q. rubra*, *Q. velutina*, and *Carya* spp. declined in relative abundance.

Because many species reproduce or sprout and grow rapidly, hardwood forests in the southern Appalachians quickly revegetate and accumulate biomass after disturbance (figure 2.4). Even though revegetation was relatively rapid in WS 7, the successional composition of the forest dramatically changed. For example, *Carya* spp., the leading dominants in the cove-hardwoods community and the third leading dominants in the mesic, mixed-oak community before harvest, comprised less than 3% of the total aboveground live biomass in these communities in 2008 (figure 2.2). Mid- and later successional 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*, though a shade tolerant species, produced a high number of seedlings in the first few years after cutting in all community types (Elliott et al. 1997). In addition, *A. rubrum* was one of the most prolific sprouting species. Its

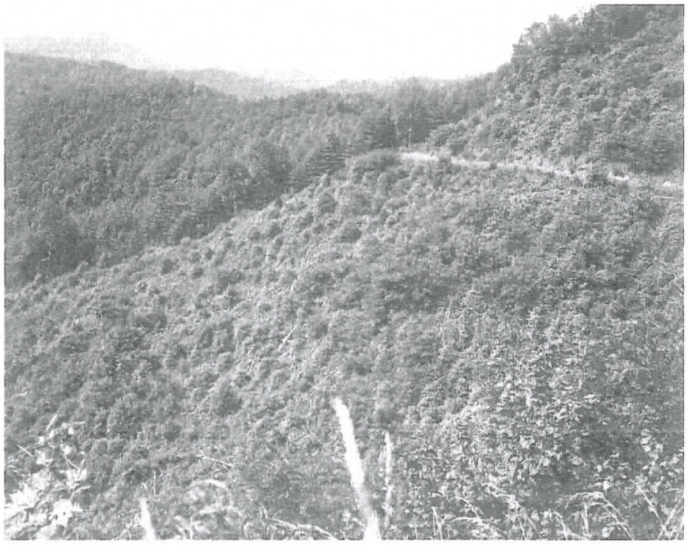

Figure 2.4 Regrowth vegetation on WS 7 in June 1979, two growing seasons after harvest. (USDA Forest Service photo)

establishment by both sexual and asexual reproduction contributes to its successful regeneration following disturbance.

The revegetation process on WS 7 was similar to that of other eastern hardwood forests, where sprouts, root suckers, and early successional herbs and vines dominate vegetation after clearcutting (Brown 1974; Ross et al. 1986; Phillips and Shure 1990; Crow et al. 1991; White 1991). In the first year after clearcutting, seedling reproduction and sprout reproduction were about equal, except in the dry, mixed-oak, where sprout reproduction was higher (Boring et al. 1981; Elliott et al. 1997). By 1979, the proportion of stems originating from sprouts increased in all communities. In the dry, mixed-oak community, the high percentage of stems originating from sprouts (81%) probably occurred because seed propagules were scarce and because the xeric forest floor microclimate along the southwest facing slopes and ridges (Swank and Vose 1988) produced a high seedling-mortality rate.

Early and copious production of light, wind-dispersed seeds is generally correlated with the ability to respond to large disturbances (Canham and Marks 1985). Two species that reproduced primarily by seed, *L. tulipifera* and *Q. velutina*, in the cove-hardwoods and mesic, mixed-oak communities provide a striking contrast (figure 2.2). *Q. velutina*, a leading dominant in the mesic, mixed-oak before clearcutting, reproduced only from seed germination or advance seedling growth. *Q. velutina* seedlings totaled 300–700 seedlings/ha, with many present before harvesting (Elliott et al. 1997). 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). 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.

In contrast, *L. tulipifera*, a copious seed producer, established successfully in the cove-hardwood and mesic, mixed-oak communities after clearcutting with 8,000–10,000 seedlings/ha produced during the first year after cutting. In 2008, it was the leading dominant species contributing 55% and 40% to the total aboveground live biomass in the cove hardwoods and mesic, mixed-oak, respectively (figure 2.3). A combination of factors, including prolific seed production, extended seed viability in the forest floor, survival of new germinants, relatively fast growth, tolerance of the codominant *R. pseudoacacia,* and some stump sprouting are responsible for this success. By 1993, *R. pseudoacacia* declined, but its fixed nitrogen apparently enhanced *L. tulipifera* growth in contrast to other site competitors (Apsley 1987).

Ground Flora Responses

Ground flora was in a transitional state between early and late successional species 17 years after clearcutting (Elliott et al. 1997). Early successional *Aster*, *Solidago*, and *Eupatorium* species declined in abundance because woody species grew rapidly and the canopy closed within 3 to 6 years. Late successional herbaceous species had not become abundantly established, which caused a significant decline in ground flora diversity in the cove hardwoods and mesic, mixed-oak. Total number of plant species present (woody + ground flora) increased in all three communities during the first 3 years after cutting. Then, total species remained relatively constant in the cove hardwoods and mesic, mixed-oak from 1979 to 1993; however, total species continued to increase through 1993 in the dry, mixed oak. Thirty years after cutting (2008), total species had reached the precut forest condition in the cove-hardwoods and mesic, mixed-oak communities, yet the dry, mixed-oak community remained lower than the precut forest (table 2.1).

In general, ground flora diversity (H') declined from 1977 to 1993 in the cove hardwoods and mesic, mixed-oak communities but did not decrease significantly in the more open-structured dry, mixed-oak (table 2.1). In every community on the watershed, more species were present before than in the years after clearcutting until 2008 (table 2.1). 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 through year 9. Similarly, in a chronosequence study of diversity trends following clearcutting (6 stands ranging from 1 to 26 years old) in Allegheny hardwoods, Yorks and Dabydeen (1999) found no significant differences between diversity indices and stand age, but they did show a trend in higher herbaceous diversity in recent clearcuts (4 years old) than control sites (> 75 years old). In addition, Gilliam et al. (1995) and Gilliam (2002) compared two 20-year-old clearcut forests and two mature forests (> 70 years old) in the Allegheny Mountains of West Virginia. They reported no significant differences between young (20-year-old clearcut) forests and mature forests in ground flora diversity. In northern Wisconsin, Brosofske et al. (2001) also found no differences in diversity (H') between young (10–15 years old) and mature northern hardwood forests, but they did find higher richness and diversity in clearcut (4–8 years old) forests compared to the young and mature forests. In WS 7, it was 30 years after clearcutting when species richness and diversity of the cove hardwoods exceeded and the mesic, mixed oak reached the precut forest condition (table 2.1).

In WS 7, the abundance (i.e., g biomass/m^2) of ground flora was also lower in 1993 compared to 1984; 79% less in the cove hardwoods; 90% less in the mesic, mixed-oak; and 79% less in the dry, mixed oak. With the growth of overstory trees and canopy closure, the number of early successional, shade-intolerant genera, such as *Erechtites*, *Solidago*, *Eupatorium*, *Panicum*, *Rubus,* and *Aster* had declined. Late successional, shade-tolerant species such as *Viola*, *Galium*, *Sanguinaria*, *Uvularia*, *Veratrum,* and ferns had not become well established in the watershed. WS 7 was still in a transition state between early and late successional species abundance. After 30 years (2008), biomass of ground flora increased substantially because late successional species were again abundant. For example, in the mesic, mixed-oak, two species contributed 63% to the total ground flora biomass, *Polystichum acrostichoides* and *Solidago curtissii*, a common forest herb. Other spring ephemerals may have recovered over time, however, the timing of measurements prevented examining the response of these species, such as *Trillium*, *Anemone*, and *Claytonia*. Because spring ephemerals respond to changes in temperature and light (Collins et al. 1985), clearcutting may have reduced these species via heat stress or triggered changes in seasonal phenology, growth, and reproductive potential in the earlier years after cutting.

After 30 years of recovery, ground flora species diversity and richness in WS 7 was similar to a nearby 30-year-old clearcut watershed (WS 13) with the same community types (Elliott and Swank 1994a). Time since disturbance seems to be an overriding factor even though there are other differences between these two watersheds including: the larger spatial scale of disturbance in WS 7 (59 ha cut in WS 7 vs. 16 ha cut in WS 13); southwest-facing aspect of WS 7, which receives higher solar radiation than the east-facing aspect of WS 13.

Changes in Forest Species Composition

Clearcutting favors shade-intolerant woody pioneering species, such as *L. tulipifera* and *R. pseudoacacia*, and shade-tolerant woody understory species, such as *R. maximum* and *K. latifolia*. There are strong positive responses to clearcutting by these two markedly different groups of plants. This strongly indicates that retention of formerly dominant and ecologically critical mid- and later successional overstory species (especially *Quercus* and *Carya*) is questionable. Their regeneration with successional development is dependent upon past ecological conditions, which included a relatively open understory light environment without evergreen shrub dominance and periodic presence of fire (Tainter et al. 1984; Van Lear 1991).

Both anthropogenic (e.g., chestnut blight, fire exclusion, and cattle grazing) and natural disturbances (e.g., drought) shaped forest composition in WS 7 before clearcutting. The composition of southern Appalachian forests has been significantly altered by the loss of *C. dentata* (Woods and Shanks 1959; Arends 1981; Day et al. 1988; Busing 1989). Chestnut blight was a major impact in the Coweeta basin, because *C. dentata* made up an estimated 35%–40% of the basal area of some forest stands (Day et al. 1988). Canopy openings due to *C. dentata* mortality in the late 1930s has favored the expansion of *Rhododendron* (Day and Monk 1974; Monk et al. 1985; Elliott and Vose 2012); and fire suppression has likely favored the expansion of *Kalmia latifolia* on upper slopes and ridges (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 stratum (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-hardwood community of WS 7 during a 12-year period (1940–1952) of heavy grazing; however, the mesic, mixed-oak and dry, mixed-oak 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 United States (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).

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 the 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.

It should be stressed that the disturbance legacies of the southern Appalachians are not simply cumulative but are probably synergistic. Fire suppression coupled with both early-century exploitive logging and chestnut blight impacts have resulted in great expansion in the distribution and increased importance of fire-intolerant, thin-barked opportunistic species including *A. rubrum*, *L. tulipifera*, *K. latifolia,* and *R. maximum*. Fire suppression in isolation of drastic canopy disturbance likely would not have changed forest composition so rapidly. Furthermore, structural disturbances with continued low intensity burning would have likely favored regeneration of more *Quercus*, *Carya,* and *Pinus* species, all moderately fire-tolerant.

Before clearcutting, many of the opportunistic species were well poised to respond aggressively to this disturbance. Because of the series of preceding forest structural disturbances, they had already increased in importance, as documented with *L. tulipifera* on the clearcuts WS 13 and WS 6 (Elliott and Swank 1994a; Elliott et al. 1998), and by the other species responses to clearcutting on WS 7 (Elliott et al. 1997). Their life-history characteristics and physiological adaptations made them highly adaptable to take advantage of these disturbance-compounded forest conditions.

Dynamics of Forest Biomass, Leaf Area, and Nutrient Accumulation

Early Successional Recovery

Rapid regeneration of foliar biomass and leaf area index (LAI) are important in the recovery of biotic control of ecological processes such as net primary production (NPP), evapotranspiration, and retention of nutrient and organic capital (Waring and Schlesinger 1985; Mann et al. 1988; Crowell and Freedman 1994; Bolstad et al. 2001; Swank et al. 2001). Sprouting and rapid vegetative growth provide mechanisms for rapid recovery in eastern deciduous forests. In WS 7, leaf biomass and LAI recovered within 8 years after clearcutting (figure 2.5), similar to findings in other clearcut successional forests at Coweeta (Swank and Helvey 1970; Swift and Swank 1981). This rapid recovery of LAI increased evapotranspiration, which reduced the extra water yield observed after clearcutting; by the seventh year, annual streamflow had returned to pretreatment levels (Swank et al. 2001). In addition, the high rate of NPP and sequestration and storage of nutrients during early succession substantially moderated the loss of solutes from the watershed (Swank et al. 2001). At age 30 years, the aboveground biomass on WS 7 had exceeded the precut biomass (table 2.2). Similarly, the accumulations of nutrients aboveground showed major recovery in two decades ranging from 57% to 83% for P and 35% to 50% for Mg, depending on community type. Substantial spatial variability in nutrient accumulation was present across the three communities, reflecting soils and species nutrient requirements.

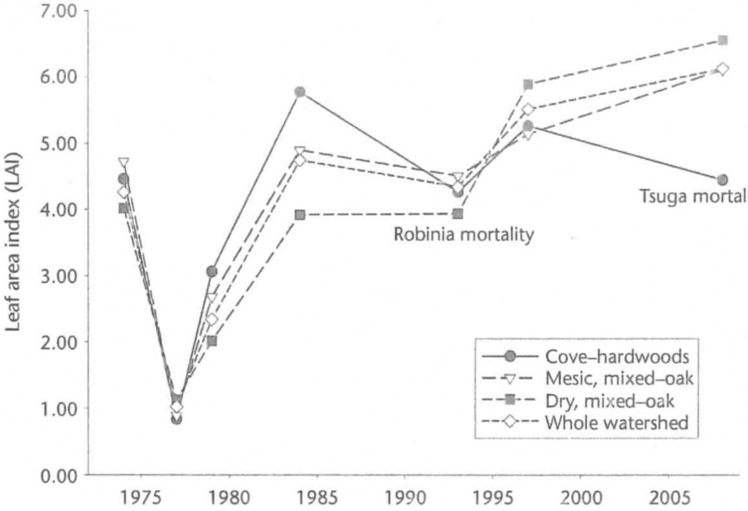

Figure 2.5 Leaf area index (m^2/m^2) for the cove hardwoods (closed circles), mesic, mixed-oak (*open triangle*), and the dry, mixed-oak (*closed square*) communities in WS 7 and the whole watershed (*open diamond*).

In the first 1–3 years following cutting, herbaceous-layer species including *Rubus*, *Panicum*, *Aster*, and *Solidago* spp. contributed significantly to accumulation of aboveground biomass, LAI, and nutrient capital (Boring et al. 1981; Boring 1982; Boring and Swank 1986). However, soon after cutting, woody species became increasingly abundant, and proportionately less biomass and nutrient capital were found in herbaceous-layer species (figure 2.6). For example, by 1993, herbaceous-layer biomass contributed less than 0.1% to total aboveground biomass in any of the three community types (Elliott et al. 1997). These findings are consistent with other closed canopy forests in the southern Appalachians (Day and Monk 1974; Busing et al. 1993). Although the ground vegetation contributed considerably to aboveground biomass the first few years following disturbance in WS 7 (Elliott et al. 2002), the contribution was proportionately less than found in northern forests (Crow et al. 1991; Reiners 1992; Crowell and Freedman 1994).

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 WS 7 increased mean monthly temperatures at the litter/soil boundary for the period May–October by 8°C to 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. 1983a), 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 on forest floor biota and their processes. Although seedlings and ground

Table 2.2 Aboveground biomass, leaf biomass, and aboveground nutrient mass in three community types and weighted watershed values before cutting (1974) and after cutting (1977–2008).

	Year	Aboveground	Leaf mass	Nitrogen	Phosphorus (kg/ha)	Potassium	Calcium	Magnesium
Cove Hardwoods	1974	204,330	3650	516.9	74.4	503.3	768.0	110.8
	1977	1,054	691	9.0	0.6	5.3	12.8	3.0
	1979	6,299	2434	55.4	4.1	31.9	59.1	12.1
	1984	26,263	3964	133.7	12.6	97.6	120.5	23.5
	1993	67,454	3135	203.2	30.8	166.6	200.4	33.6
	1997	81,692	3236	251.9	42.7	223.2	237.8	38.8
	2008	183,159	4669	—	—	—	—	—
Mesic, mixed-oak	1974	184,973	3354	482.3	70.5	415.6	643.9	99.0
	1977	1,255	705	14.7	1.0	8.5	14.1	3.0
	1979	6,779	2562	72.5	4.7	40.0	67.8	14.2
	1984	27,896	3883	150.8	13.6	108.8	118.0	23.4
	1993	77,720	2684	262.2	42.1	207.7	212.1	36.8
	1997	96,617	2936	318.0	58.6	290.6	260.4	43.2
	2008	212,835	4239	—	—	—	—	—
Dry, mixed-oak	1974	127,196	3467	339.8	42.0	262.7	462.3	70.4
	1977	1,562	928	16.7	1.1	8.8	14.2	3.5
	1979	3,987	1701	37.0	2.8	21.7	30.0	8.1
	1984	22,851	3163	114.4	10.9	79.2	90.7	17.8
	1993	58,705	3332	143.5	17.1	105.1	169.4	26.3
	1997	85,429	3900	216.7	27.4	163.9	245.4	36.0
	2008	152,449	5169	—	—	—	—	—
Watershed	1974	153,203	3466	401.7	53.9	336.9	553.6	83.6
	1977	1,406	835	15.1	1.0	8.1	13.9	3.2
	1979	5,034	2022	48.6	3.4	27.8	43.9	10.2
	1984	24,627	3462	126.4	11.9	89.3	102.0	20.0
	1993	64,763	3140	182.2	25.4	140.0	184.7	30.0
	1997	87,661	3559	247.3	37.4	204.4	248.0	38.3
	2008	172,152	4861	—	—	—	—	—

Note: Plant tissue for nutrient analysis was not collected in 2008.

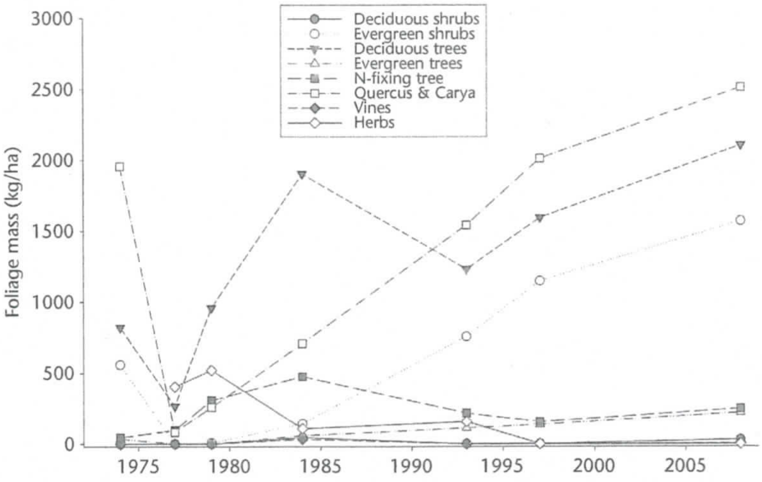

Figure 2.6 Leaf biomass of different growth forms for the whole WS 7.

flora may have been impacted by high mortality immediately after clearcutting, canopy closure within three years enabled a subsequent rapid recovery of structural and functional forest processes.

Spatial Variability of LAI

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

Our estimates for LAI of the precut (1974) forest of WS 7 (70+ years old) were slightly higher than for a comparable forest type (i.e., mesic, mixed-oak) on a south-facing watershed (Monk et al. 1970), which received higher solar radiation (leading to higher temperatures). Monk et al.'s (1970) value for LAI was similar to that of a young, mixed-deciduous forest in New England (Delucia et al. 1998), but it was less than other reported LAI values within the Coweeta basin. In another undisturbed watershed, where evergreen species contributed up to 35% of the total standing crop of leaves (Monk and Day 1984), LAI was estimated at 6.2 m^2/m^2 (Monk and Day 1988). In mature (75+ year old) forests within the Coweeta basin, Bolstad et al. (2001) reported a range in LAI from 2.7 to 8.2 m^2/m^2, depending on elevation and terrain position (ridge, sideslope, or cove), with LAI decreasing as elevation increased (a function of lower temperatures) and as terrain position increased (ridges having the highest terrain shape index; a function of lower soil moisture (Helvey and Patric 1988; Yeakley et al.

1998). For mature forests within 800–1000 m elevation (the elevation range of WS 7), LAI ranged from 5.0 to 6.5 m^2/m^2 (Bolstad et al. 2001). However, we did not find a decrease in LAI from cove to ridge, primarily due to the abundance of *K. latifolia* and *R. maximum* that contributed substantially to total LAI in the dry, mixed-oak community located on upper slopes to ridges. Across communities, LAI in the 30-year-old forest of WS 7 was already greater than the LAI in a 50-year-old forest reported by Monk et al. (1970) and nearly as high as the 75+-year-old mature forests at similar elevations reported by Bolstad et al. (2001).

Ecosystem Influences of N_2 fixation

Later in succession (10–15 years), though forest structure was still partially dominated by the N_2-fixing tree *R. pseudoacacia*, WS 7 NO_3-N export increased above previously observed levels, indicative of significant changes in ecosystem N-cycling (Swank et al. 2001). Forest composition was changing because of intense stand competition and insect attacks by defoliators and stem borers upon *R. pseudoacacia* (Boring and Swank 1984; Apsley 1987). The death and defoliation of so many of these trees resulted in elevated organic and inorganic nitrogen flux.

The successional *R. pseudoacacia* stands were estimated to have fixed 30–75 kg N ha^{-1} yr^{-1}. Related N-cycling studies of senescent, defoliated stands of *R. pseudoacacia* in an old-field successional forest documented: (a) high leaf litter N transfers (60 vs. 21 kg N $ha^{-1}yr^{-1}$ for similar pine hardwoods) with moderate decomposition rates (White 1986; White et al. 1988); (b) high root litter transfers, high substrate quality and decomposition rates (Grimm 1988); (c) elevated growing season N deposition (> 30 vs. 8 kg N ha^{-1} yr^{-1} for pine hardwoods) via insect frass and fine particulates associated with canopy defoliation (Boring et al. 1987; Seastedt et al. 1993b); (d) elevated net throughfall flux of organic N and NH_4-N (8 vs. < 1 kg N ha^{-1} yr^{-1} for pine hardwoods; Boring et al. 1987); and (e) elevated soil net mineralization and nitrification rates (Montagnini et al. 1986; Montagnini et al. 1989). This N_2-fixing species plays a significant role in the regeneration phase of southern Appalachian forests following disturbance. Thus, *R. pseudoacacia*'s influence is great in early sequestration of nutrients, moderation of microclimatic, elevation of N inputs, availability, and flux, and its legacy of residual N to the later successional forest.

Regional Comparisons

Accumulation of aboveground biomass and nutrients in live vegetation was faster in the southern Appalachian hardwood forest on WS 7 than in northeastern hardwood forests. Reiners (1992) found that biomass accumulation was 52 Mg/ha (38% of the total for a nearby, mature watershed) 20 years after clearcutting a hardwood forest at Hubbard Brook, New Hampshire. In WS 7, biomass accumulation was much higher (56%–85%) than in the clearcut watershed in Reiners's (1992) study. In addition, the aboveground pools of nutrients were almost twofold higher in WS 7 than in the northern hardwood forest at Hubbard Brook. However, in the Hubbard Brook study, the experimental treatment differed from commercial clearcutting in that timber was not removed and regrowth was suppressed with herbicides for the first 3 years following cutting. One of the effects of herbicide treatment may have been to decrease regeneration by sprouting, which is relatively important in northern hardwood forests (Martin and Hornbeck 1989; Reiners 1992). In a northern hardwood forest in Nova Scotia, Crowell and Freedman (1994) reported lower aboveground biomass and nutrient stocks for woody species 8 and 20 years after clearcutting than those reported for WS 7 (Elliott et al. 2002).

Several factors explain higher biomass and nutrient accumulation in the southern Appalachian hardwood forests, when compared to the northern hardwood forests of New England (Reiners 1992; Crowell and Freedman 1994): the pre-humid climate (higher temperature and precipitation), prolific sprouting ability of hardwoods (Kays and Canham 1992; Elliott et al. 1997), and abundance of the N-fixing *R. pseudoacacia*. Not only does *R. pseudoacacia* fix a substantial amount of N in young stands (Boring and Swank 1984), it also accumulates large quantities of N in leaves, branches, stems, and roots and facilitates growth of associated woody species (Apsley 1987). Much higher-N standing stocks were measured in 17- and 38-year-old dense stands of *R. pseudoacacia* (Boring and Swank 1984) than found in mixed hardwood stands on WS 7.

Southern Appalachian forests have the potential to accumulate more aboveground biomass and nutrients in all steps of succession than do most North American deciduous forests (O'Neill and DeAngelis 1981; Cannell 1982; Grier et al. 1989; Busing et al. 1993; Reich et al. 1997; Barnes et al. 1998; Waring et al. 1998). For example, in the Great Smoky Mountains of eastern Tennessee, aboveground biomass estimates for cove-hardwood, old-growth forests (≈ 400 year old) was > 300 Mg/ha (table 2.3) with a corresponding ANPP of 6.3 to 8.6 Mg ha^{-1} yr^{-1}. In young stands (42–63 years old), aboveground biomass ranged from 216 to 277 Mg/ha with a corresponding ANPP of 11.7–13.1 Mg ha^{-1} yr^{-1} (table 2.3). By contrast, a northern hardwood forest in central New Hampshire, in the absence of logging (Martin and Bailey 1999) and a 70-year-old maple-oak forest in northern Michigan (Crow et al. 1991) (table 2.3) had less aboveground biomass than what we found in cove-hardwoods or mesic, mixed-oak communities of WS 7 before clearcutting (≈60 year old forest) (table 2.3). Monk et al. (1970) estimated aboveground live biomass of 145 Mg/ha for an oak-hickory forest in the Georgia piedmont, and Day and Monk (1974) estimated aboveground live biomass of 140 Mg/ha in a north-facing watershed in the Coweeta basin (heavily logged between 1900 and 1923). Theirs were less than our estimates of aboveground live biomass in the precut (1974) forest (also heavily logged between 1900 and 1923) for either the cove-hardwood or mesic, mixed-oak communities of WS 7, a south-facing watershed. Within the Coweeta basin, for mature stands (75+ year old), Bolstad et al. (2001) reported a range of ANPP from least productive (5.2 Mg ha^{-1} yr^{-1}) on ridges at high elevation to most productive (11.7 Mg ha^{-1} yr^{-1}) in cove hardwoods. In a 50-year-old *L. tulipifera* stand in Tennessee, Cole and Rapp (1981) reported an aboveground biomass of 125 Mg/ha and nutrient standing stocks of 305 kg N ha^{-1}, 47 kg P ha^{-1}, 173 kg K

Table 2.3 Aboveground biomass of eastern North American deciduous forests.

Location	Forest type	Forest age (years)	Above-ground biomass (Mg/ha)	Citation
Great Smoky Mountains, TN	Cove-hardwood	~400	326–384	Busing et al. 1993
Great Smoky Mountains, TN	Cove-hardwood	42–63	216–277	Busing et al. 1993
White Mountains, NH	Northern hardwood	100	208	Martin and Bailey 1999
Hubbard Brook, NH	Northern hardwood	20	152	Reiners 1992
Hubbard Brook, NH	Northern hardwood	~70	400	Reiners 1992
Northern, MI	Maple-oak	70	151	Crow et al. 1991
Eastern, USA	Hardwoods	< 100	159	Brown et al. 1999
Piedmont, GA	Oak-hickory	50	145	Monk et al. 1970
Southern Appalachians, NC	Pine-hardwood	70	92–184	Vose and Swank 1993
Southern Appalachians, NC	Mixed deciduous	50	140	Day and Monk 1974
Southern Appalachians, TN	*L. tulipifera*	50	125	Cole and Rapp 1981
Mid-Atlantic region	Oak-hickory	< 100	199	Jenkins et al. 2001
Mid-Atlantic region	Maple-beech-birch	< 100	207	Jenkins et al. 2001
Mid-Atlantic region	Oak-pine	< 100	162	Jenkins et al. 2001
White Mountains, NH	Northern hardwood	~80–120	192	Goodale and Aber 2001
White Mountains, NH	Northern hardwood	>150	261	Goodale and Aber 2001
Northern WI	Aspen-maple-birch	~80	92–118	Crow 1978
South-central CN	Oak-hickory-maple	80	166–185	Tritton et al. 1987

Note: Mid-Atlantic included 7 states; NY, PN, NJ, MD, DL, WV, VA and aboveground tree biomass was estimated from FIA data.

ha^{-1}, and 456 kg Ca ha^{-1}. In WS 7, within only ≈20 years of cutting, aboveground biomass was 66%–78% of that reported by Cole and Rapp (1981), depending on community type; nutrient standing stocks were 60%–69% for N, 53%–100% for P, 88%–100% for K, and 52%–57% for Ca.

In nearby mature (≈70 years old), pine-hardwood stands in the southern Appalachians, Vose and Swank (1993) reported a range in aboveground biomass (table 2.3). Although before cutting, the dry, mixed-oak community in WS 7 was within this range of values (table 2.2), it had a larger component of oaks (93.3 Mg/ha), only a minor component of *P. rigida*, and less *K. latifolia* (3.77 Mg/ha). However, with only ≈20 years of regrowth, biomass accumulation of *K. latifolia* was nearly equal to its precut value, and biomass of *R. maximum* was 4.6 times greater than before cutting in the dry, mixed-oak community. In addition, leaf biomass of these two evergreen species was 31% of total leaf biomass. Because these two species can retain foliage for up to 3 years, only 10%–15% of their total leaf nutrient standing crop is lost annually through litterfall, and because sclerophyllous foliage decomposes slowly (Monk et al. 1985), the increased abundance of *K.*

latifolia and *R. maximum* in WS 7 could have long-term implications for ecosystem processes such as decomposition and nutrient cycling.

Long-Term Ecosystem Implications

The exceptionally high species diversity and ecosystem complexity of southern Appalachian forests should be considered when assessing changes in the structure and function of the forest after clearcutting. The high plant-species richness, diverse functional groups, interactions among species, and the variety of life histories result in their diverse light-, water-, carbon-, and nutrient-use strategies. This is reflected in their requirements for unique successional niches. Recent debates have raged in the ecological community about the potential relationships between species richness and the stability of ecosystem function.

A pre-humid climate, prolific hardwood sprouting, an abundance of *R. pseudoacacia,* and the observed changes in species composition have important long-term implications for ecosystem function (Elliott et al. 2002). Clearcutting favored shade-intolerant, fast-growing species, such as *L. tulipifera* and *R. pseudoacacia*; subdominant *A. rubrum*; and shade-tolerant understory shrubs, such as *Rhododendron maximum* and *K. latifolia*. The abundance of large-seeded, slow-growing species, such as *Quercus* spp. and *Carya* spp. declined after clearcutting (Elliott et al. 1997). *Robinia pseudoacacia* and *L. tulipifera* lose their foliage in early fall and have high leaf-nutrient concentrations; *L. tulipifera* and *A. rubrum* foliage decomposes quickly. *Quercus* spp. and *Carya* spp. lose their foliage in late fall through the winter and have lower leaf-nutrient concentrations; and their foliage decomposes slower than many of the other overstory species that replaced their dominance (Cromack 1973; White et al. 1988). These reported shifts in overstory species composition could result in forest floor litter with higher nutrient concentrations, lower C/N ratios, and subsequently faster decomposition rates.

However, the dynamics of the increasingly dominant evergreen understory *K. latifolia* and *R. maximum* may be as important to future ecosystem functions as the changes in the overstory (Elliott et al. 2002). Both species have also increased in abundance in the Coweeta basin since the loss of *C. dentata* from the overstory, and clearcutting on WS 7 further increased their distribution, basal area, and density (Elliott et al. 1997). In areas of the watershed where *K. latifolia* and *R. maximum* are abundant, the contribution of their ericaceous leaves to litterfall may reduce litter quality, even with *L. tulipifera* and *R. pseudoacacia* in the overstory. *Kalmia latifolia* and *R. maximum* retain foliage for several years and have low leaf-nutrient concentrations, and the scherophyllous leaves decompose slowly (White 1986; White et al. 1988). The organic soils and root mats that these ericads form may potentially alter soil pH and decrease forest floor decomposition rates (Knoepp et al. 2000). Because decreased rates of litter decomposition would slow nutrient cycling rates within an ecosystem, the composition and quality of litter have important implications in terms of nutrient loss and retention, soil nutrient availability, and soil quality (Knoepp et al. 2000). Species differences in evapotranspiration would also have long-term effects on hydrologic cycles at the watershed scale

(Swank et al. 2001). These major changes in overstory and understory composition affect forest structure, organic matter quality, and water use; consequently, these vegetation dynamics could result in different watershed hydrologic and biogeochemical responses in the future.

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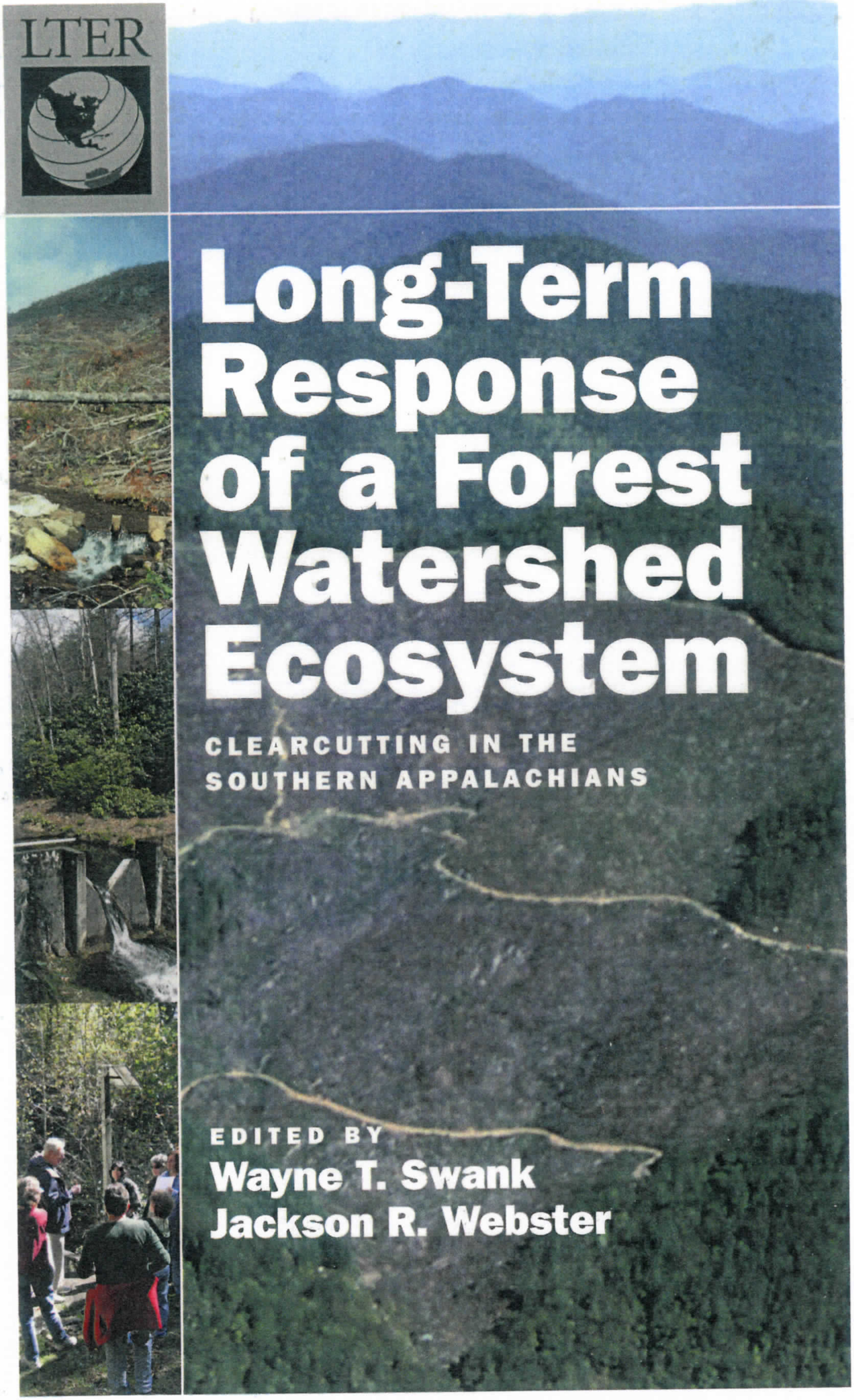

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Long-Term Response of a Forest Watershed Ecosystem

CLEARCUTTING IN THE SOUTHERN APPALACHIANS

EDITED BY

Wayne T. Swank

Jackson R. Webster

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Our North American forests are no longer the wild areas of past centuries; they are an economic and ecological resource undergoing changes from both natural and management disturbances. A watershed-scale and long-term perspective of forest ecosystem responses is requisite to understanding and predicting cause and effect relationships. This book synthesizes interdisciplinary studies conducted over thirty years, to evaluate responses of a clear-cut, cable-logged watershed at the Coweeta Hydrologic Laboratory in the Nantahala Mountain Range of western North Carolina. This research was the result of collaboration among Forest Service and university researchers on the most studied watershed in the Lab's 78-year history. During the experiment, a variety of natural disturbances occurred: two record floods, two record droughts, a major hurricane, a blizzard of the century, major forest diseases, and insect infestations. These disturbances provided a unique opportunity to study how they altered the recovery of the forest ecosystem. This book also shows that some long-term forest trends cannot be forecast from short-term findings, which could lead to incorrect conclusions of cause and effect relationships and natural resource management decisions.

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