9

Watershed Clearcutting and Canopy Arthropods

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Introduction

The southern Appalachian forests are home to myriad species of insects, spiders, and other arthropods. There are more than 4,000 invertebrate species known in the Great Smoky Mountains National Park (Sharkey 2001), and easily a thousand insect species in the Coweeta basin alone. The forest environment, with its favorable microclimates and structural diversity, offers a large variety of niches, different host-plant species, and soil and litter habitats (figure 9.1). Of this vast assemblage of arthropod species, most are predators that keep prey populations at low abundances, and only a few insects ever reach population sizes that can cause any economic damage to the forest. When these occasional outbreaks do occur, they can be severe. The discipline of forest entomology has the goal of preventing timber loss to insects, and most of the knowledge of forest insects has been developed within the context of economic importance (Coulson and Witter 1984). The principal goal of insect ecology, in contrast, is to understand insect response to and influence on ecological processes (Schowalter 2011).

In the Coweeta basin, the notable death of trees has occurred due to the activities of the elm spanworm (*Ennomos subsignarius*) on hickories and oaks in 1954–1964 (Fedde 1964); the fall cankerworm (*Alsophila pometaria*) in 1972–1978, mostly on oaks (Swank et al. 1981); and the southern pine beetle (*Dendroctonus frontalis*) in 1986–1989 (Smith 1991; Kloeppel et al. 2003; Birt 2011). Other minor outbreaks have been documented, such as defoliation of oaks (*Quercus* spp.) by sawflies (*Periclista* spp.) in 1998–1999 (Reynolds et al. 2000). Southern pine beetle and sawfly outbreaks were associated with drought conditions.

A wood-boring beetle species was of special interest for the WS 7 clearcutting experiment. The locust borer (*Megacyllene robiniae*; figure 9.2) causes death of

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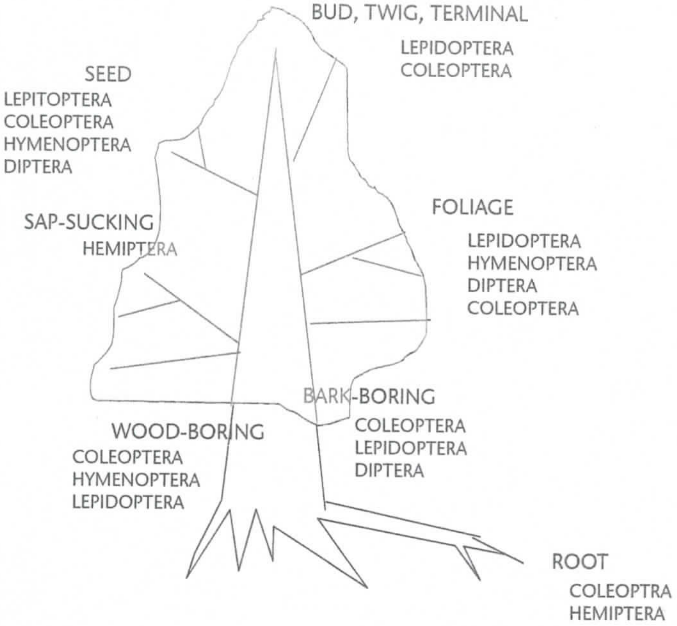

Figure 9.1 Categories of insect feeding relationships on forest trees. (Adapted from Franklin 1970)

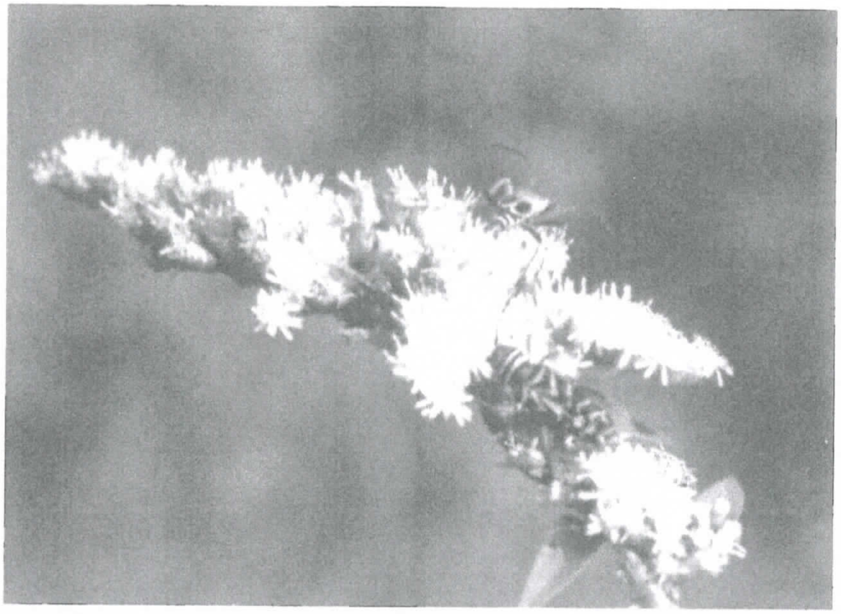

Figure 9.2 The locust borer, *Megacyllene robiniae.* (Photo by D. Crossley)

black locust (*Robinia psuedoacacia*) trees throughout the United States (Wollerman 1970). We anticipated the proliferation of black locust on WS 7 during the course of revegetation (see Boring et al., chapter 2, this volume), as earlier we had observed the death of stands of black locust on WS 6, following an outbreak of the locust borer. Nitrogen released from the dying trees appeared in the stream draining WS 6, and growth of tulip-poplar trees on that watershed was stimulated by nitrogen released from the dead and dying black locust trees (Boring 1982; Boring and Swank 1984). We expected that the locust borer would make its appearance in the form of an outbreak on WS 7 some 20–30 years following clearcutting.

Most of our research on canopy arthropods at Coweeta has been organized around the importance of insects in forest nutrient dynamics (Crossley et al. 1988), although defoliation by arthropods may reduce water uptake and thus improve tree survival during drought (Kolb et al. 1999). Arthropods and other animals may regulate nutrient cycling by influencing the rates of nutrient uptake by vegetation, return to the forest floor, and release during decomposition (figure 9.3). In research performed as a part of the International Biological Program and the Long-Term Ecological Research program of the National Science Foundation, we measured the biomass of canopy consumers and their nutrient content (Schowalter et al. 1981; Schowalter and Crossley 1983; Crossley et al. 1988). To evaluate the relative importance of the thousands of arthropod species, we arrayed them into functional groups according to their feeding type, trophic position in the food web, and life-history characteristics. For example, spiders and predaceous beetles were grouped together. Aphids and leafhoppers (sap-sucking insects) were analyzed separately from caterpillars (chewing insects). Functional groupings allowed us to compare canopy arthropod assemblages between tree species and across watersheds (Schowalter et al. 1981;

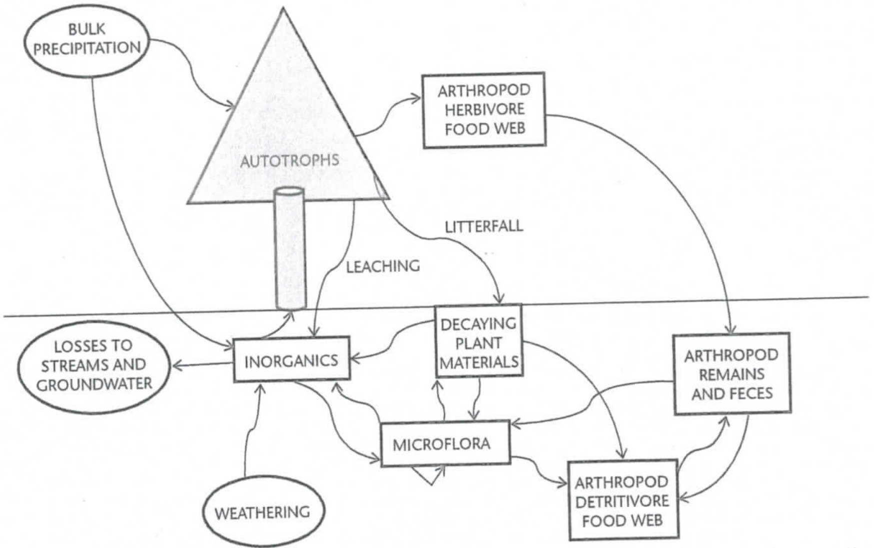

Figure 9.3 Simplified conceptual model of the influence of arthropods on nutrient cycling processes in forests. (Adapted from Seastedt and Crossley 1984)

Seastedt et al. 1983; Schowalter and Crossley 1983; Hargrove et al. 1984; Crossley et al. 1988; Schowalter and Crossley 1988; Risley and Crossley 1988; Risley and Crossley 1993; Reynolds and Crossley 1997).

The WS 7 clearcutting experiment posed some additional questions for studies of canopy arthropods. Given the expected shift in plant types (see Boring et al., chapter 2, this volume), how would the community of arthropods respond? Would the increase in herbaceous vegetation influence the community of insects on the tree vegetation? Would the regrowth foliage tissue be more tender, perhaps engendering outbreaks of defoliators? And, could we isolate those factors most responsible for the development of the insect community?

Methods for Sampling Canopy Arthropods

Modern research in forest canopies uses a variety of methods (Lowman 2004; Lowman et al. 2012), ranging from climbing techniques borrowed from mountain climbers (Schowalter 1995) to floating platforms and dirigibles (Hallé 1998). Large construction cranes have been erected in certain forests, allowing sampling of arthropods in the top of the canopy (Parker et al. 1992; Schowalter and Ganio 1998; Basset et al. 2003). Other forests have been fitted with extensive canopy walkway systems (Lowman and Bouricious 1995; Reynolds and Crossley 1995). These new approaches are allowing canopy access in unprecedented ways.

Canopy access on WS 7 was more limited. We simply used long-handled insect nets for access into lower canopies. For a few years, the low-regrowth vegetation on WS 7 could be sampled with ordinary insect nets. We fitted the insect net with a plastic bag that could be closed with a drawstring. The bag was slipped over a mass of leafy vegetation and quickly closed, capturing arthropods and the vegetation supporting them. A long pole pruner was then used to clip the branch. We expressed the density of arthropods as weight inhabiting the mass of vegetation captured in the net (table 9.1).

Table 9.1 Density of canopy arthropod functional groups on clearcut WS 7 and uncut control WS 2, means of five tree species (red maple, chestnut oak, dogwood, hickories, and tulip poplar).

	1975	1977		1978	
	WS 7 Precut	WS 2 Control	WS 7 1st year postcut	WS 2 Control	WS 7 2nd year postcut
Chewing herbivores	270.4 ±56.1	200.2 ±68.6	368.0 ±193.3	171.2 ±57.0	137.0 ± 62.0
Sucking herbivores	91.6 ±26.7	57.6 ±9.9	148.2 ±34.0	76.6 ±8.4	104.0 ±23.0
Omnivores	30.0 ±11.8	4.4 ±1.3	87.6 ±54.9	10.2 ±2.0	18.4 ±4.8
Predators	138.2 ±51.3	91.4 ±12.7	54.8 ±11.9	105.0 ±24.8	76.4 ±27.7
Totals	530.2	353.6	658.4	363.0	335.8

Note: Data are mg arthropods per kg foliage (± standard error).

The consumption of vegetation by chewing insects was estimated by measuring the holes in leaves—the leaf area missing. A digitizer and analyzer were constructed using an office copier and a small personal computer (Hargrove and Crossley 1988).

Results

Immediate Response of Canopy Arthropods to Clearcutting

The summer after WS 7 was clearcut, tree foliage returned on sprouts from stumps (see Boring et al., chapter 2, this volume). This leafy mass contained large numbers of arthropods, and their mass differed from that found before cutting or in the adjacent uncut control WS 2 (table 9.1). In comparison with WS 2, the clearcut had a greater mass of chewing herbivores, sucking herbivores, and omnivores. However, the mass of predators on the clearcut was lower. The chewing herbivores (caterpillars, beetles, crickets, leaf miners) exhibited nearly twice the mass found on WS 2. We had anticipated an increase in sucking herbivores (aphids, leafhoppers, and treehoppers) on succulent regrowth foliage. Aphids in particular increased in density on all tree species sampled, except for dogwood, the first year after cutting. The omnivores reported in table 9.1 were largely species of ants. Increases in ant density accompanied the increases in aphids (see also Crossley et al. 1988). Predators included a variety of spiders, predaceous beetles, lacewings, and wasps. By the second summer (1978) masses of chewing herbivores had declined to levels similar to those on WS 2, and masses of sucking herbivores and omnivores were only slightly elevated (table 9.1).

The data shown in table 9.1 are means for five tree species. The rather large standard errors attached to those means are due to large differences in attendant insects that were found among the tree species. For example, tulip-poplar foliage on WS 7 supported large masses of chewing insects (caterpillars and leaf-feeding beetles) and aphids, much in excess of those on WS 2. In contrast, chewing insects on dogwoods and hickories showed a smaller response (Schowalter et al. 1981).

The increases in arthropod density following cutting were not surprising. We anticipated that the regrowth foliage might be more palatable, and that opportunistic insects such as the aphids might increase in comparison with those on the control WS 2. The picture is less clear in view of the results of sampling WS 7 two years previous to the clearcut. Chewing herbivores, sucking herbivores, omnivores, and predators were all more abundant in precut WS 7 samples than on WS 2 in either of the postcut years (table 9.1). Unfortunately, no comparable samples are available from WS 2 in the precut year. Given the precut similarity of WS 2 and WS 7 in essential physical and vegetation characteristics, we would expect their precut arthropod communities to have been similar also. There is often a large year-to-year variation in insect abundance, and such annual variation may be a factor in the differences between 1975, 1977, and 1978. Furthermore, different personnel performed the sampling in 1975, and the discrepancies may reflect slight differences

Table 9.2 Density of canopy arthropods on clearcut WS 7 and uncut control WS 2, means of five tree species (red maple, chestnut oak, dogwood, hickories, and tulip poplar).

	1984		1985		1987	
	WS 2 Control	WS 7 Clearcut	WS 2 Control	WS 7 Clearcut	WS 2 Control	WS 7 Clearcut
Mean density	559.7	397.9	349.8	337.2	268.8	653.4
(Standard error)	(117.9)	(113.1)	(124.9)	(56.8)	(72.0)	(249.5)

Note: Data are mg arthropods per kg foliage (± standard error).
Source: Blanton (1989).

in sampling technique. In any case, the first postcut year (1977) had higher insect densities than the precut 1975 samples or concurrent samples from WS 2.

Further sampling of canopy arthropods in 1984–1987 was undertaken by Blanton (1989). She reported only total arthropod weight densities, not broken down into functional groups (table 9.2). During this period, a decade after the clearcut, there was no significant difference in arthropod mass density between WS 7 and WS 2. The years 1984 and 1985 were characterized by reduced rainfall in the Coweeta basin. Blanton noted that, during 1985, chewing herbivores decreased during this drought period and that sucking herbivores (aphids, membracids, psyllids) increased. Precipitation returned to more normal levels in 1987 and the proportion of chewing herbivores increased. Thus, the response of arthropod functional groups to a two-year drought resembled their response to clearcutting.

Black Locust: A Special Case

Black locust is an important tree species on successional watersheds because of its ability to fix atmospheric nitrogen in the rhizosphere. On WS 7, black locust was home to a large array of arthropod species. Large numbers of aphids (*Aphis craceivora*) and membracids (mostly *Vanduzea arquata*) were tended by colonies of ants (*Formica integra*) (Schowalter et al. 1981; Hargrove 1986; see figure 9.4). In the springtime the ants gathered in clusters at the tips of the tree branches, possibly feeding upon extrafloral nectaries. Chewing herbivores were well represented also, including geometrid caterpillars, the silver-spotted skipper (*Epargyrus clarus*) and numbers of flea beetles (*Derocrepis carinata*) (Hargrove 1986).

The density of arthropod functional groups measured on black locust was higher than the average density for arthropods on other tree species on WS 2 and WS 7 (table 9.3). Following clearcutting, densities of sucking herbivores increased dramatically over those measured during the precut year (1975) or on control WS 2. The omnivore category, largely ants, also increased markedly in the two postcut years. Blanton (1989) measured total arthropod density for black locust on WS 7 and found that density remained high in 1984 (1390 mg per kg foliage) and 1985 (1355 mg per kg), values similar to those reported in table 9.2 for the immediate postcut years.

Figure 9.4 Ants tending aphids. (Photo by T. Schowalter)

Table 9.3 Density of canopy arthropod functional groups on black locust foliage.

	1975	1977		1978	
	WS 7 Precut	WS 2 Control	WS 7 1st year postcut	WS 2 Control	WS 7 2nd year postcut
Chewing herbivores	956	414	851	359	251
	±200	±270	±331	±126	±70
Sucking herbivores	180	71	567	172	1486
	±30	±34	±264	±58	±561
Omnivores	7	25	149	64	227
	±4	±13	±62	±22	±75
Predators	164	57	77	96	48
	±72	±18	±36	±55	±17
Totals	1307	567	1644	691	2012

Note: Data are mg arthropods per kg foliage (± standard error).
Sources: 1975 data, Petursson (unpublished); 1977 and 1978 data, Schowalter et al. (1981).

Black locust foliage showed the effects of consumption by chewing herbivores. Hargrove (1983) estimated the amount of leaf area removed by reconstructing damaged leaflets and measuring the area with a digitizer (Hargrove and Crossley 1988), and showed that damage to black locust foliage accumulated during the summer (table 9.4). Leaf area missing due to insect feeding amounted to an average of 15% by September. Correspondingly, the numbers of undamaged leaflets declined during the summer. On the average, fewer than 10% of the leaflets showed no insect damage in September.

Table 9.4 Estimates* of leaf area consumed on black locust trees, WS 7, summer, 1980.

	Month			
	June	July	August	September
Mean leaf area consumed	4.8%	8.1%	13.2%	15.3%
(Range of values)	(2.8–6.2)	(4.8–11.4)	(8.1–16.1)	(7.3–24.7)
Percent of leaflets undamaged	50.8%	42.2%	15.3%	7.3%
(Standard error)	(6.88)	(6.61)	(3.26)	(2.58)

*Values represent means for six trees. Each tree sample consisted of 75 leaflets
Source: Adapted from Hargrove (1983)

Accumulation of damage in this manner is unusual for forest trees. Most measurements of holes in canopy leaves show that 3%–8% of leaf area is missing, and that area does not increase during the season (Risley 1987). Several factors may account for the lack of damage accumulation. In general, canopies have a burst of insect activity in May and June, and then little in midsummer, followed by another increase in herbivory in late August and September (Blanton 1989). For example, the most chewing consumption on chestnut oak occurred in June. Some tree species have an additional flush of leaves during the summer. Further, partially damaged leaves may abscise (Risley 1987). These considerations suggest that our estimates of herbivory on black locust may be low. But it appears from table 9.4 that little regrowth of foliage occurs on black locust and abscission of damaged leaflets would seem to be a minor factor.

To summarize, regrowth tree foliage one year after the clearcut had a greater mass of chewing herbivores, sucking herbivores, and omnivores, such as caterpillars, aphids, and ants, respectively, compared to the adjacent control watershed. Predators, such as spiders and predaceous beetles, decreased. Differences for black locust were especially marked, with greater densities seen especially for sucking herbivores and omnivores, particularly ants. Measurements of leaf area removed on black locust averaged 15% by September, a fairly high value. However, no obvious outbreaks of defoliators were observed.

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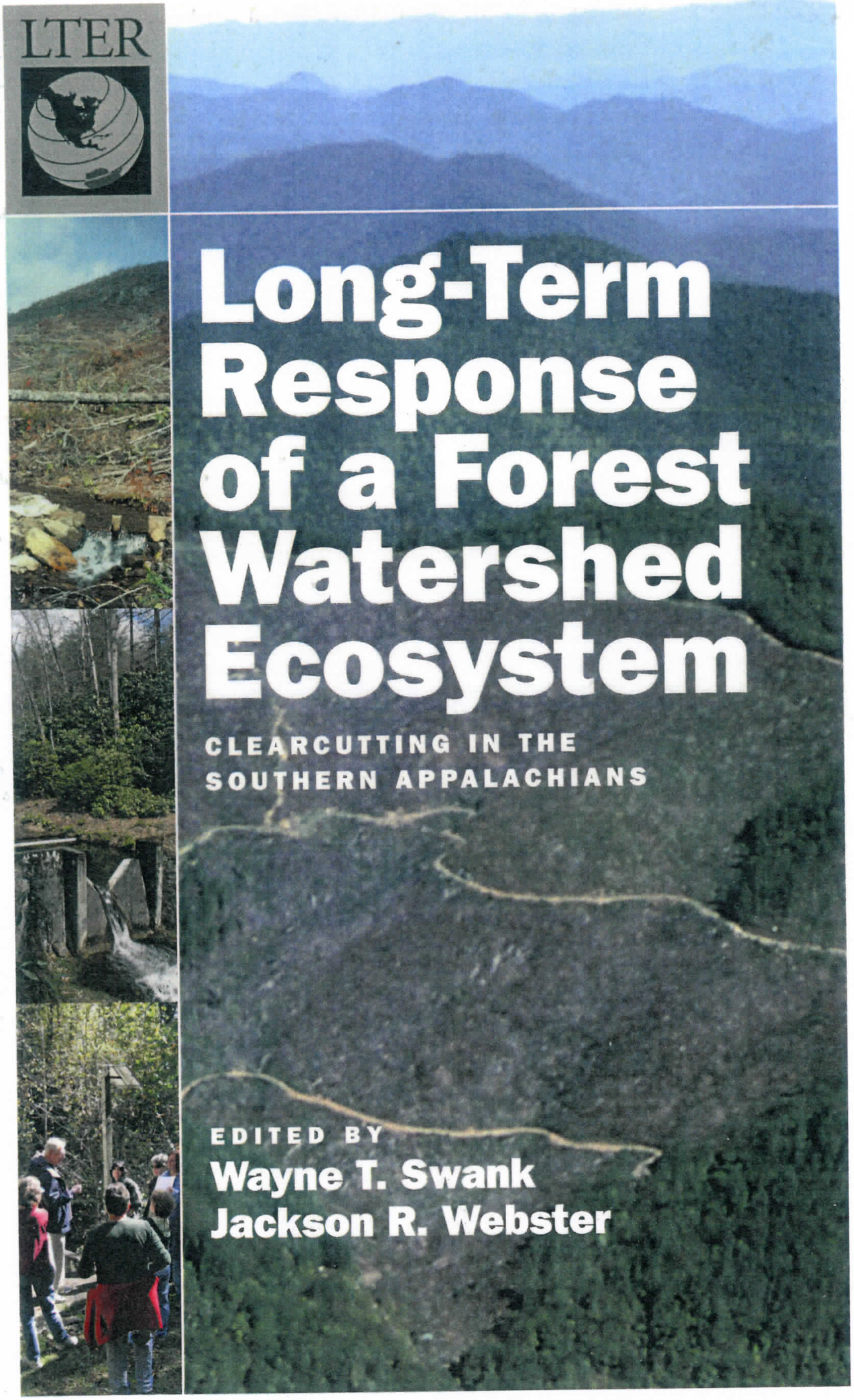

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Long-Term Response of a Forest Watershed Ecosystem

CLEARCUTTING IN THE SOUTHERN APPALACHIANS

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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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