

The contribution of the Coweeta Hydrologic Laboratory to developing an understanding of long-term (1934–2008) changes in managed and unmanaged forests

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ARTICLE INFO

Article history:

Received 17 November 2009
Received in revised form 11 March 2010
Accepted 16 March 2010
Available online 15 April 2010

Keywords:

Invasive species
Disturbance
Chestnut blight
Hemlock woolly adelgid
Ecosystem process

ABSTRACT

Long-term records from USDA Forest Service Experimental Forests and Ranges (EF&Rs) are exceptionally valuable scientific resources and common ground for research in natural resource management. Coweeta Hydrologic Laboratory, Southern Appalachian Mountains in western North Carolina, is one of 82 EF&Rs located throughout the United States and Puerto Rico. Since its establishment in 1934, the wealth and breadth of scientific knowledge gained from Coweeta Hydrologic Laboratory research has provided both public and private land managers information on forest land management and has added to the knowledge base of natural resource science.

We described the early watershed research at Coweeta and used long-term measurements and inventories (from 1934 to 2008) to: (1) explore the influences of large-scale disturbances and vegetation responses on ecosystem processes and (2) assess the long-term and short-term impacts of an exotic, invasive species on a southern Appalachian deciduous forest. We focused on changes in vegetation patterns influenced by natural and managed disturbances and then described the linkages between long-term vegetation measurements and water yield and quality responses. For natural disturbances, we used a network of over 900 permanent vegetation plots established in reference watersheds and unmanaged areas; first measured in 1934 and a subset re-measured in 1969–1972, 1988–1993, and 2003–2008. For the managed disturbances, clearcuts and species conversion experiments, vegetation was measured in permanent plots within treated watersheds before and after treatment.

By the time of the 1934 survey, the forest had only 10 years to recover from logging before chestnut blight (*Cryphonectria parasitica*) induced mortality of virtually all remaining *Castanea dentata* trees. With the loss of *C. dentata* as the dominant species, *Acer rubrum* and *Quercus montana* became the dominant species and *Liriodendron tulipifera* and *Tsuga canadensis* increased in coves and along riparian corridors. *T. canadensis* is currently threatened by another invasive species, hemlock woolly adelgid (HWA, *Adelges tsugae*), with 33% tree mortality between 2003 and 2008. Smaller-scale disturbances, such as drought and windthrow, have created canopy gaps and the disturbance agent, gap size, and species-specific demography (dispersal, survival, growth, and mortality) affected colonization and recruitment. In general, the composition of species recruiting into canopy gaps was a reflection of the vegetation already in place at the time of disturbance, because regeneration occurred primarily through saplings or sprouts. In managed forests, where gaps were much larger (9–59 ha), early successional species recruit and become established and the long-term vegetation patterns are different than in unmanaged forests. The vegetation data provide a description of changes in forest structure and composition through time and space, and they have been used to develop process-based models to scale-up to the catchment level. Long-term climatic, hydrologic, biogeochemical, and vegetation databases coupled with process-based ecohydrology and ecophysiology models are essential to understanding broader- and more complex environmental issues such as climate change, carbon cycling, atmospheric deposition, and water supply and quality.

Published by Elsevier B.V.

1. Introduction

The structure and function of southern Appalachian forests have been shaped by a combination of human and natural disturbances. Prior to 1842, the Cherokee Indians practiced semiannual burning, livestock grazing, and valley agriculture (DeVivo, 1991). Between

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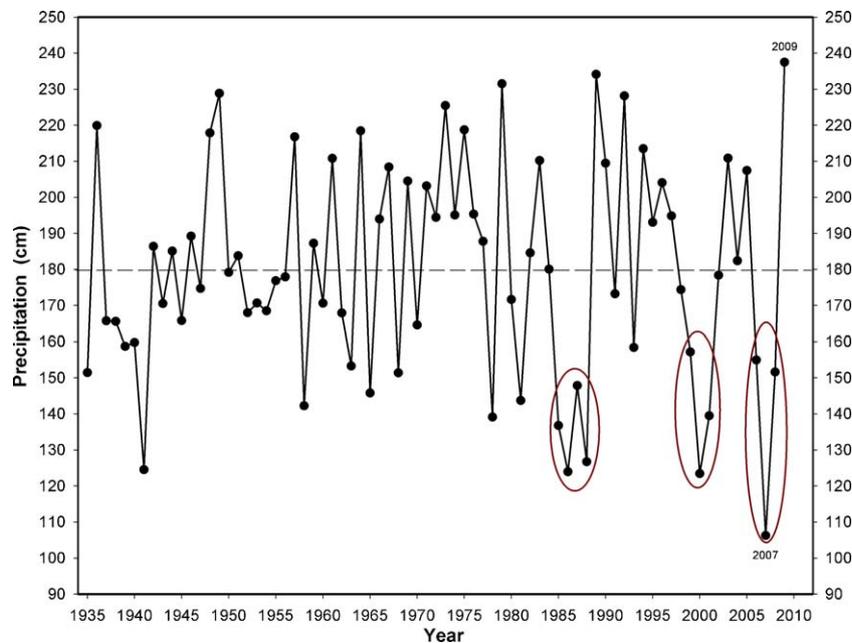


Fig. 1. Precipitation at Coweeta Climate Station 1 (low elevation, 655 m) from 1934 to 2009.

1842 and 1900, European settlers continued the practice of light semiannual burning and livestock grazing. Harvesting large trees from the late 1800s to the early 1900s was common across the region (Brose et al., 2001). *Castanea dentata* and *Quercus* spp. were harvested preferentially because they yielded valuable timber and *C. dentata* was a good source of tannic acid (Frothingham, 1924; Steer, 1948). Numerous large-scale, natural disturbance events have been recorded through the 20th and into the 21st century as well. For example, a summer drought in 1925 (based on Asheville, NC rainfall record, 1903–1929) resulted in early leaf senescence and mortality of small trees (Hursh and Haasis, 1931); succeeding droughts with more than one year of below average rainfall were recorded in years 1985–1988, 1999–2001 (Kloepfel et al., 2003; Riedel, 2006), and 2006–2008 (Fig. 1). Clinton et al. (1993) showed an increase in canopy gap formation from drought-induced *Quercus* mortality during the 1985–1988 drought. In addition, significant mortality of *Pinus rigida* L. occurred due to a combination of drought and subsequent attack by the southern pine beetle (SPB, *Dendroctonus frontalis* Zimmerman) (Smith, 1991). Several inland hurricanes have caused large blowdowns (Greenberg and McNab, 1998) and landslides (Hales et al., 2009), because coastal hurricanes can produce high winds and heavy rain as far as several hundred kilometers inland. The 1995 hurricane Opal produced an average wind speed of 39 km h⁻¹ sustained for an 8-h period with an associated 20 cm of rainfall within two days in the Coweeta Basin (Elliott et al., 2002b). In 2004, hurricanes Francis and Ivan resulted in heavy rainfall and subsequent landslides in the Coweeta Basin and across western North Carolina.

In addition to these human and natural disturbance regimes, the southern Appalachians have been impacted by non-native diseases and insects that have essentially eliminated individual species from the forest. The loss of tree species from North American forests has resulted in fundamental shifts in population and community dynamics of associated species (Elliott and Swank, 2008) and immediate and long-term changes in ecosystem dynamics (Ellison et al., 2005). For example, *C. dentata* (Marshall (Brookh.)) was a dominant tree species in forest communities of eastern North America, until it was virtually eliminated by chestnut blight (*Cryphonectria parasitica* (Murr.) Barr). Sprout dominated *C. dentata* contributes little to leaf area, wood production, or nut crops,

so that while it is still present in many forests, it is functionally insignificant.

Tsuga canadensis (L.) Carr., a species that increased following the loss of *C. dentata* (Elliott and Swank, 2008), is currently threatened by an invasive insect, hemlock woolly adelgid (HWA, *Adelges tsugae* Annand). *T. canadensis* occurs in ca. 1 × 10⁶ ha of eastern North American forests, from north Georgia to southern Canada and west to the central Lake States (McWilliams and Schmidt, 2000) and where it occurs it is considered a foundation species (Ellison et al., 2005). In the Northeast, it typically occurs along ridge tops, on steep slopes and in narrow valleys (Orwig et al., 2002). In the southern Appalachians, *T. canadensis* occurs primarily in riparian areas, along streams where it is often the only conifer and it plays a unique role as a riparian species. *T. canadensis* and *Tsuga caroliniana* Engelm., a species with extremely limited geographic range, are currently declining due to infestation by the HWA. Tree mortality can occur in as little as four years (McClure, 1987, 1991) after infestation, but sites in the Delaware Water Gap had experienced only 15% mortality of *T. canadensis* trees after eight years of infestation (Eschtruth et al., 2006).

The combination of a wide range of natural and human caused disturbances, long-term vegetation measurements, and corresponding water quantity and stream water chemistry measurements at Coweeta provides a unique opportunity to examine the linkages between vegetation structure and species composition, and ecosystem processes. In this paper, we describe the early watershed research and use long-term measurements and inventories (from 1934 to 2008) to: (1) explore the influences of large-scale disturbances and vegetation responses on ecosystem processes and (2) assess the long-term and short-term impacts of exotic, invasive species on a southern Appalachian deciduous forest.

2. Overview of Coweeta Hydrologic Laboratory

2.1. Site description

Coweeta Hydrologic Laboratory is a long-term research site of the USDA Forest Service, Southern Research Station. It is located in the Nantahala Mountain Range of western North Carolina, USA,

within the Blue Ridge Physiographic Province, near the southern end of the Appalachian Mountain chain (latitude 35°03'N, longitude 83°25'W). The 2185 ha laboratory consists of two adjacent, east-facing, bowl-shaped basins; Coweeta Basin and Dryman Fork Basin. The Coweeta Basin encompasses 1626 ha and is drained by Ball Creek and Shope Fork, two fourth-order streams. These streams join to form Coweeta Creek, which flows 7 km east to the Little Tennessee River. The Dryman Fork Basin, a 559 ha basin drained by Cold Spring Creek and Dryman Fork, was added to the laboratory in 1946. Elevations range from 675 to 1592 m. Slopes are steep ranging from 30% to over 100%. Soils are deep sandy loams and are underlain by folded schist and gneiss. Two soil orders are found within Coweeta, immature Inceptisols and older developed Ultisols (Thomas, 1996). The relief has a major influence on hydrologic, climatic, and vegetation characteristics. Streams flow throughout the year, fed by approximately 1800 mm of precipitation per year, most of which is rain. Mean annual temperature is 12.6°C and ranges from an average of 11.7°C in winter to 21.6°C in summer. Frequent rain, more than 130 storms distributed throughout the year, sustains high evapotranspiration rates and a humid climate (Swift et al., 1988). Vegetation is southern mixed deciduous forest. The principal overstory species are of the genera *Quercus*, *Carya*, and *Liriodendron*. There are scattered groups of *P. rigida* and *T. canadensis*. Evergreen shrubs (*Rhododendron* and *Kalmia*) combine with *Cornus*, *Robinia*, *Acer*, and *Betula* to form a dense understory cover (Day et al., 1988).

2.2. Establishment of Coweeta Hydrologic Laboratory

The Forest Service purchased the Coweeta basin in 1918, but rights to timber over 38 cm stump diameter were reserved for the J.A. Porter Logging Company. Logging began in 1919, and selective but heavy cutting continued until 1923. In 1923, the Forest Service took over administration of the basin. Charles Hursch was hired in 1926 at the Appalachian Forest Experiment Station (now Southern Research Station) to begin a research program on forest influences on streamflow and erosion. Hursch was the guiding influence behind the selection of Coweeta as a research site where his early studies addressed erosion control, stabilization of roadbanks, runoff as influenced by land use, accumulation of organic matter in soils, and water infiltration and percolation through soils (Douglass and Hoover, 1988).

Since its inception in 1934, the Coweeta Hydrologic Laboratory has served as a primary site for forest hydrological research in the USA. The classic small paired watershed studies (Fig. 2) have described rainfall – runoff relationships in managed and unmanaged forested watersheds and continue to provide a fundamental, typically empirical, understanding of the relationships among hydrologic inputs, vegetation, and hydrologic outputs (Swank and Crossley, 1988).

2.3. Installation of experimental paired-watersheds

The research program of the 1930s was directed toward instrumenting the basin with climate stations and weir gages. A network of 70 rain gages and 31 weirs were designed, calibrated, and installed on watersheds, and the period of watershed calibration began. In 1934–1935, watershed boundaries were surveyed, and vegetation plots were installed, permanently marked, inventoried and mapped as the baseline hydrology information accumulated to evaluate effects of forests on streamflow (Douglass and Hoover, 1988).

After five years of baseline data collection, the first watershed treatment was applied in 1939. During this experimental period, there were three general types of studies: (1) land use demonstrations, (2) forest cutting experiments, and (3) species conversion

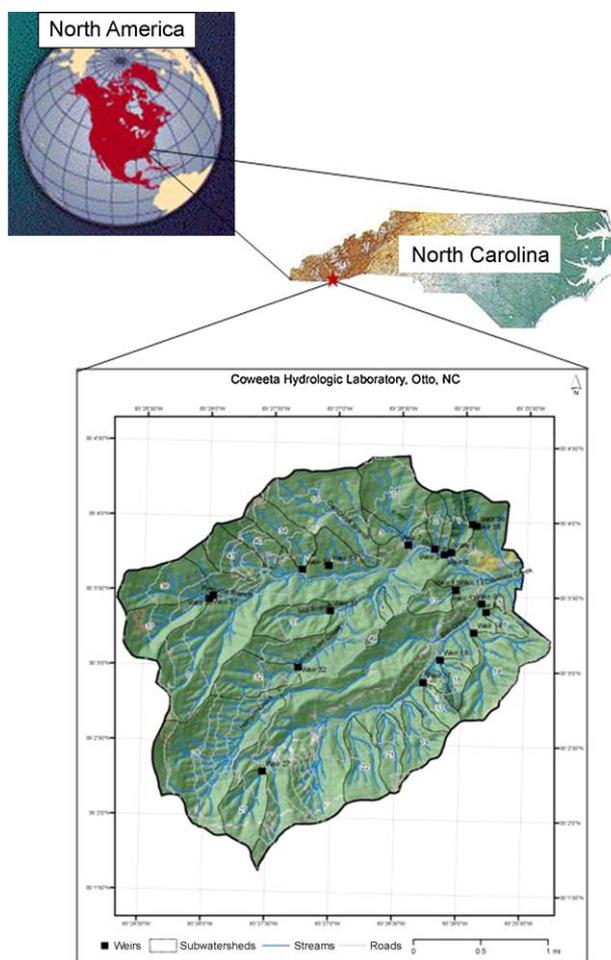


Fig. 2. Map of Coweeta Basin experimental watersheds, western North Carolina. Watershed numbers and boundaries are shown. Watersheds 1 and 17 are *Pinus strobus* plantations and their paired reference watersheds are WS2 and WS18. WS6 is the hardwood-to-grass experiment and WS14 is its paired reference. WS7 is a clearcut experiment and WS2 serves as its paired reference watershed.

studies (Swank and Crossley, 1988). The early land use demonstrations were designed to assess the effects of common prevailing land use practices. Land use demonstrations included mountain farming, grazing (Watershed 3, WS3), and abusive logging (WS10) (Fig. 2). The first experimental treatment was a clearcut in WS13, a low elevation, 16-ha catchment. Other forest cuttings included partial cutting (WS19, WS22, WS28, WS40 and WS41), a whole tree harvest (WS48), and a high elevation, clearcut (WS37). The objective of the forest cutting experiments was to assess the effect of various levels of cutting on quantity and timing of streamflow. The species conversion studies, hardwood-to-*Pinus strobus* L. (WS1 and WS17) and hardwood-to-grass (WS6), were designed to determine whether type of vegetation influences water yield (Douglass and Neary, 1980). The first 30 years of land use and hydrologic research provided the foundation for forest ecosystem studies at the watershed scale.

In the 1970s, while the hydrology research continued research expanded to include precipitation and stream water chemistry and nutrient transport, moving Coweeta into the area of water quality and biogeochemical cycling research. Coweeta now has a 40-year record of atmospheric deposition inputs and stream chemistry. To further assess ecosystem processes, WS7 was clearcut in 1977 as part of an interdisciplinary study of the physical, chemical, and biological effects on both terrestrial and aquatic components of the ecosystem (Swank and Caskey, 1982).

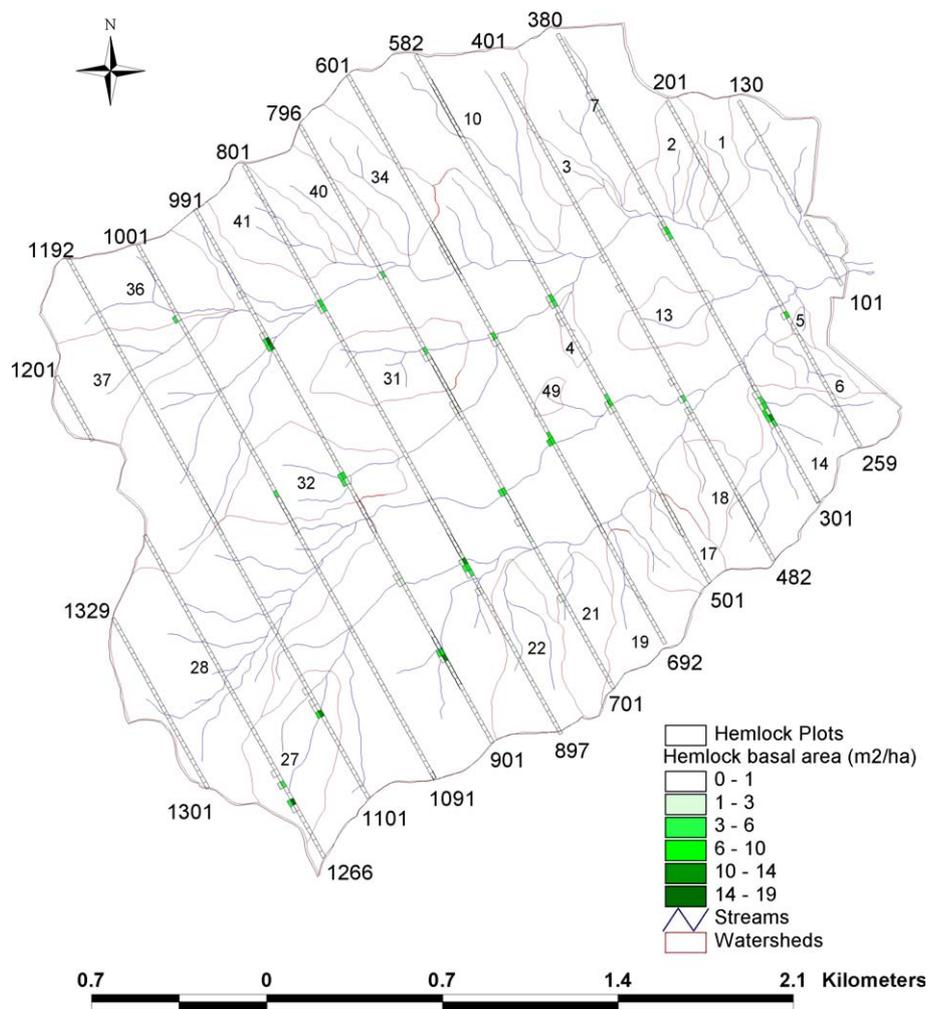


Fig. 3. Map of the Coweeta Basin permanent plot transects. Basal area of hemlock (*Tsuga canadensis*) measured in 1934–1935 and 1969–1973 is indicated with green shaded blocks. Plots measured in 1934–1935 with *T. canadensis* are offset to the southwest of actual plots. The numbers outside the perimeter indicate the plot number for the last plot on that transect line. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

2.4. Vegetation measurements (1934–1993)

The permanent vegetation plot (0.08 ha, 20 m × 40 m) network was established along 13 parallel, approximately north–south transects (330°) spanning the Coweeta Basin at 200 m intervals (Fig. 3). A total of 987 permanent plots were inventoried from 1934 to 1935 (hereafter 1934), 403 of the original permanent plots were re-inventoried from 1969 to 1973 (hereafter 1970s), and 297 permanent plots were re-inventoried from 1988 to 1993 (hereafter 1990s). Only plots located in unmanaged areas, without human disturbance since 1923 (Douglas and Hoover, 1988), were re-measured in the later inventories. In each inventory period, trees >1.37 m height and ≥2.5 cm dbh (diameter at 1.37 m height) were tallied by species in 2.5 cm diameter classes in each plot. Elliott and Swank (2008) used data from 281 permanent plots that were re-inventoried during all three periods (1934, 1970s, and 1990s) to describe changes in forest vegetation patterns of unmanaged forests over a 60-year period.

For the managed watersheds, clearcuts (WS7, WS13) and species conversion (WS1, WS6, and WS17), vegetation was measured in permanent plots within the treated watersheds before and after the treatments were applied. WS6, WS7, and WS13 were allowed to regenerate naturally with hardwoods after their final treatment; whereas, WS1 and WS17 have remained as pine plantations since 1958. In this paper, we will compare the long-term

vegetation changes on managed watersheds with the vegetation changes on the unmanaged, reference watersheds, specifically those that were clearcut (WS7, WS13) and cut + species conversion (WS6) (Elliott and Swank, 1994; Elliott et al., 1997, 1998).

2.5. Recent vegetation measurements (2003–2008)

In response to the discovery of Hemlock Woolly Adelgid in Macon County, NC in the early 2000s and first noticed on a few trees in the Coweeta Basin in 2003, we assessed the vegetation prior to *T. canadensis* decline (2003), and through canopy loss and mortality (2005–2008). We selected plots from the permanent plot network in unmanaged areas. All plots had a significant *Rhododendron maximum* L. component; and a comparable hardwood species mix with some variation in abundance of individual species.

In 2003, we identified 20 'Hemlock' plots, those that had greater than 30% basal area of hemlock at the last inventory in 1988–1993 (Fig. 3); and 10 adjacent 'Reference' plots. The Reference plots had similar terrain and species composition, but little to no hemlock. In 2005, we added plots to increase the number of samples and distribution of plots across the basin for a total of 30 Hemlock and 12 Reference plots. All *T. canadensis* trees were number tagged to follow HWA infestation, canopy loss, and mortality. For years 2003 to 2007, we measured vegetation composition; including overstory (woody stems ≥2.5 cm dbh), understory (woody stems <2.5 cm dbh,

>0.5 m height), and herbaceous layer (woody stems <0.5 m height and all herbaceous plants) cover. The overstory was measured in each 0.08 ha permanent plot; the understory was measured in a 5 m × 40 m subplot and the herbaceous layer was measured along a 40 m line-transect within the permanent plot. In 2008, we visited each tagged *T. canadensis* tree in all plots to assess crown loss and mortality.

3. Lessons from early long-term studies

The collaborative, interdisciplinary research program at Coweeta has produced a wealth of new knowledge in many areas of forest hydrology and ecosystem science – much too extensive to describe in this paper (over 1800 publications, <http://coweeta.uga.edu/publications>). Thus, we focus on changes in vegetation patterns influenced by natural (reference watersheds and unmanaged areas within Coweeta) and managed disturbances and then describe the linkages between long-term vegetation measurements and water yield and quality responses.

3.1. Vegetation patterns

In 1934, the Coweeta forest was recovering from logging activities that removed an average of 20% of the basal area from the Basin from 1919 to 1923 (Elliott and Swank, 2008). Douglass and Hoover (1988) estimated that more than 8 million board feet of timber was removed during this time period. Unfortunately, no species-specific information is available about the trees removed during the 1919–1923 harvesting period as cut stumps were not identified to species on the 1934 survey sheets. Most likely, *C. dentata* and *Quercus* species, the preferred commercial trees at that time (Ashe, 1911), were selectively cut from the forest. By the time of the 1934 survey, the forest had only 10 years to recover from logging before chestnut blight induced mortality of virtually all remaining *C. dentata* trees (Elliott and Swank, 2008). In addition to the large-scale, logging and *C. dentata* mortality early in Coweeta history, other smaller-scale disturbances, such as drought and windthrow, have occurred overtime and across the basin (Clinton et al., 1993) that

have influenced tree species recruitment and forest composition (Beckage et al., 2000).

Vegetation measurements have not only been collected over time on the permanent plots that span the basin, but also on some of the treated watersheds that were used for water yield experiments. Although permanent vegetation plots were first measured in 1934 and plots were added and measured in treated watersheds as early as 1948, these data were not utilized for ecological studies until much later. Nelson (1955) described the vegetation change over a 19-year period (1934–1953) for a high-elevation (990–1295 m) reference watershed (WS41); this paper was the first to describe species composition and quantify the loss of *C. dentata* in Coweeta. Day and Monk (1974) estimated aboveground biomass and species composition in WS18, a low-elevation (730–800 m) reference watershed. Later, Day and Monk (1977) quantified nutrient concentrations and nutrient pools for woody plants in WS18 and determined that individual species, within (e.g., deciduous trees) and among (e.g., deciduous vs. evergreen) growth forms, have different nutrient cycling strategies.

3.1.1. Unmanaged watersheds

In 1934, *C. dentata* was the dominant or co-dominant species (high frequency, density and basal area) across the Coweeta Basin; however, it was the most abundant at higher elevation (Elliott and Swank, 2008). Many small *C. dentata* stems were present in 1934 indicating successful recruitment following the earlier harvest and it also had more large stems than other species at that time. By the 1970s, only sprouting stems of *C. dentata* remained in the forest due to chestnut blight induced mortality. *Acer rubrum*, which is ubiquitous in the Coweeta basin, occurred in at least 95% of the plots in all inventories and increased in importance overtime (Fig. 4). Two of the oak species, *Quercus montana* and *Q. rubra*, increased in importance, while the other three oaks, *Q. coccinea*, *Q. alba*, and *Q. velutina*, decreased. *Liriodendron tulipifera*, a dominant species in moist, coves and concave slopes increased in importance; whereas, *Cornus florida* increased between 1934 and the 1970s, and then decreased from the 1970s to the 1990s (Fig. 4). This decline of *C. florida* was strongly influenced by dogwood anthrac-

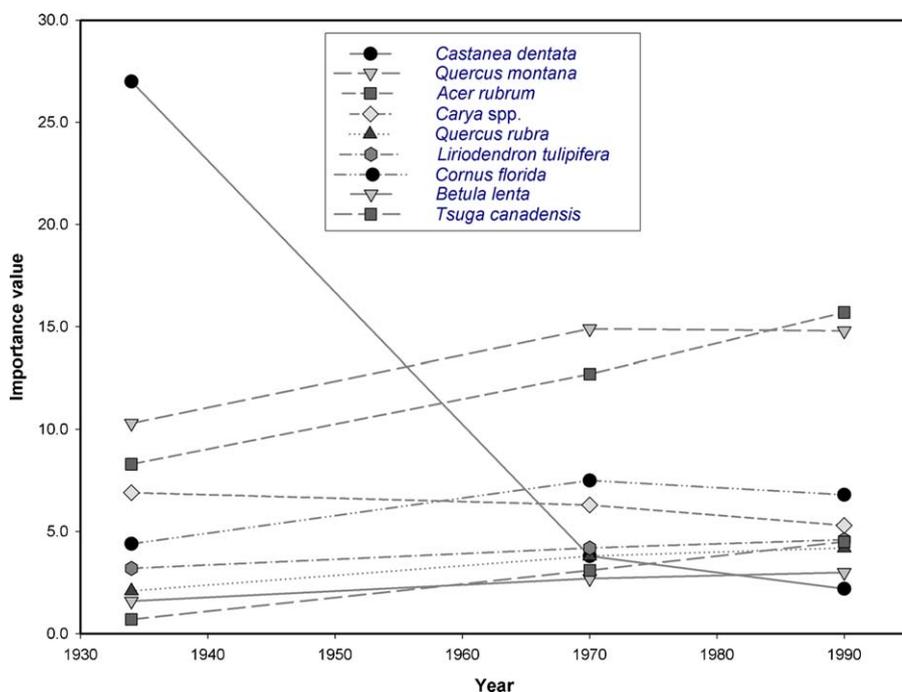


Fig. 4. Long-term changes in species composition for the unmanaged forest; measured in 1934–1935, 1969–1973, and 1988–1993 within Coweeta, western North Carolina. Importance value = (relative density + relative basal area)/2.

Table 1Rank abundance of dominant tree species for managed watersheds before and after treatment. Basal area ($\text{m}^2 \text{ha}^{-1}$) is in parentheses.

WS13 ^a			WS7 ^b		WS6 ^c		Reference ^d (55 years)	
1934	1962 23-years-old	1991 29-years-old	Before	1993 17-years-old	Before	1993 28-years-old	1934	1990s
<i>C. dentata</i> (8.4)	<i>Q. montana</i> (2.7)	<i>L. tulipifera</i> (9.8)	<i>Q. velutina</i> (5.2)	<i>L. tulipifera</i> (10.4)	<i>Q. montana</i> (4.2)	<i>Q. montana</i> (3.0)	<i>C. dentata</i> (10.1)	<i>Q. montana</i> (6.3)
<i>Q. montana</i> (3.0)	<i>Q. coccinea</i> (2.4)	<i>Q. montana</i> (5.1)	<i>L. tulipifera</i> (4.6)	<i>R. pseudoacacia</i> (5.1)	<i>Q. coccinea</i> (3.0)	<i>L. tulipifera</i> (2.8)	<i>Q. montana</i> (3.4)	<i>A. rubrum</i> (4.1)
<i>P. rigida</i> (3.0)	<i>L. tulipifera</i> (1.4)	<i>A. rubrum</i> (3.0)	<i>Carya</i> (4.2)	<i>C. florida</i> (3.0)	<i>A. rubrum</i> (1.8)	<i>A. rubrum</i> (2.8)	<i>Q. coccinea</i> (2.6)	<i>Q. coccinea</i> (2.6)
<i>Q. coccinea</i> (2.1)	<i>A. rubrum</i> (1.2)	<i>Q. coccinea</i> (2.0)	<i>Q. Montana</i> (3.1)	<i>A. rubrum</i> (2.0)	<i>R.</i> <i>pseudoacacia</i> ^e (0.2)	<i>T. canadensis</i> (2.6)	<i>Carya spp.</i> (1.6)	<i>Q. rubra</i> (2.4)
<i>L. tulipifera</i> (0.6)	<i>P. rigida</i> (1.12)	<i>P. rigida</i> (0.5)	<i>C. florida</i> (2.1)	<i>Q. montana</i> (0.5)	<i>L. tulipifera</i> (0.1)	<i>Q. coccinea</i> (2.1)	<i>A. rubrum</i> (1.5)	<i>L. tulipifera</i> (2.1)
<i>A. rubrum</i> (0.1)	<i>C. dentata</i> (0.01)	<i>C. dentata</i> (0.01)	<i>A. rubrum</i> (2.1)	<i>Q. velutina</i> (0.1)	<i>T. canadensis</i> (0.01)	<i>R.</i> <i>pseudoacacia</i> ^e (0.4)	<i>L. tulipifera</i> (0.7)	<i>T. canadensis</i> (1.2)
			<i>R. pseudoacacia</i> (0.5)	<i>Carya</i> (0.1)			<i>T. canadensis</i> (0.2)	<i>C. dentata</i> (0.2)

^a WS13 before the 1st cut, 23 years after the 1st cut and before the 2nd cut, and 29 years after the 2nd cut (Elliott and Swank, 1994).^b WS7 was measured in 1974 and clearcut in 1977 (Elliott et al., 1997).^c WS6 was measured in 1956 before the grass conversion treatments (Elliott et al., 1998).^d Permanent plot data (Elliott and Swank, 2008).^e *Robinia pseudoacacia* was the most abundant species in 1982 with a basal area of $7.8 \text{ m}^2 \text{ha}^{-1}$ (Elliott et al., 1998). By 1993, it had heavy mortality due to locust stem borer.

nose caused by *Discula destructiva* Redlin, a serious disease in these forests since 1985 (Anderson, 1991; Chellemi et al., 1992; Britton, 1993). *P. rigida*, a dominant species in the oak–pine community in the 1970s, declined in importance as a result of mortality induced by drought and SPB attack in the 1980s (Smith, 1991). Mortality of *Robinia pseudoacacia* L. was attributed to the locust borer (*Megacyllene robiniae*) (Elliott and Swank, 2008), which commonly infests young *R. pseudoacacia* in the southern Appalachians. The two most abundant understory taxa, *K. latifolia* and *R. maximum*, differed in their vegetation dynamics over time. *Kalmia latifolia* decreased in importance; all measures of its abundance were lower in the 1990s than the 1970s. In contrast, *R. maximum* increased in frequency and density (Elliott et al., 1999).

In 1992, canopy gaps were characterized across the Coweeta basin (Clinton et al., 1993). Two types of gap creation were defined, drought-induced (standing dead snags) and wind-induced (pit-and-mound formation). Clinton et al. (1993) accounted for other stressors or age related mortality and concluded that a large percentage of the gaps with standing dead snags were a result of the 1985–1988 drought. Based on the canopy gap descriptions (Clinton et al., 1993), small experimental gaps (314 m^2) were created in 1992 by girdling trees to simulate drought-induced mortality to evaluate tree demography. Gaps were created in areas with a dense *R. maximum* understory and areas without *R. maximum*. In general, seedling recruitment was minimal in these small gaps that close quickly by lateral ingrowth and no recruitment occurred under *R. maximum*. In gaps without *R. maximum*, only *A. rubrum* seedlings were successful, benefiting from abundant, well dispersed seed (Beckage et al., 2000).

Windthrow versus drought-created gaps have different consequences for tree recruitment because windthrow produces gaps that penetrate to the forest floor (i.e., pit and mound topography), causes breakage or mortality to surrounding trees, and creates larger canopy openings. In 2002, larger experimental gaps (ca. 1250 m^2) were created by pulling canopy trees with a winch until they were down to simulate windthrow (Dietze and Clark, 2008). In this case, recruitment from sprouts was found to constitute 26–87% of early gap regeneration and was the dominant pathway of regeneration for some species. Dietze and Clark (2008) found that tree species differed in their reliance on sprouting for regeneration; *A. rubrum*, *O. arboreum*, and *L. tulipifera* sprouted prolifically, while

Quercus spp. regeneration was dominated by saplings.

These long-term studies in unmanaged stands in the Coweeta basin have documented how the disturbance agent, gap size, and species-specific demography (dispersal, survival, growth, and mortality) affect colonization and recruitment. In general, the composition of species recruiting into canopy gaps is a reflection of the vegetation already in place at the time of disturbance, because regeneration occurs primarily through saplings or sprouts. Thus, for disturbances that create canopy gap openings, the forest condition before a disturbance strongly dictates future forest composition. In managed forests, where gaps were much larger (9–59 ha), early successional species recruited and became established and the long-term vegetation patterns were different than in unmanaged forests.

3.1.2. Managed watersheds

Hardwood forests in the Southern Appalachians regenerate quickly following disturbance because many tree species establish by both sexual and asexual reproduction and grow rapidly. Vegetation re-growth was relatively rapid following clearcutting watersheds (WS6, WS7, and WS13) in Coweeta Basin. For example, Boring et al. (1981) found that one year after clearcutting WS7, aboveground net primary productivity (NPP) was 1955 kg ha^{-1} , standing crop biomass was 1725 kg ha^{-1} , and LAI was $1.3 \text{ m}^2 \text{m}^{-2}$; 22% NPP, 1% biomass, and 26% LAI of the reference WS18 (Day and Monk, 1977). Eight years after cutting, leaf biomass and LAI were nearly equal to the amount estimated for the precut forest (Elliott et al., 2002a). Twenty years after cutting WS7, aboveground biomass (88 Mg ha^{-1}) was 57% of the precut forest (Elliott et al., 2002a).

Tree species differed in recruitment and growth rates, however, resulting in a change in forest composition after clearcutting. For example, *Quercus velutina*, *Q. coccinea*, *Q. alba*, and *Carya* spp. were much less abundant 20–30 years after clearcutting (Table 1) because their large seeds have limited dispersal distance, and their growth rates were slower than co-occurring species. Meanwhile, opportunistic species such as *L. tulipifera*, *R. pseudoacacia*, and *A. rubrum* were more abundant after clearcutting (Table 1; Elliott and Swank, 1994; Elliott et al., 1997, 1998). *L. tulipifera* and *R. pseudoacacia* attained early dominance because they sprout quickly and grow faster than other species. *A. rubrum*, a shade-tolerant species, reproduced prolifically after clearcutting; with

5000–9000 seedlings ha⁻¹ and 1800–6300 sprouts ha⁻¹ in WS7, depending on community type (Elliott et al., 1997). *L. tulipifera* and *A. rubrum* are both long-lived species; and once they attain a position in the canopy, they can remain in the forest for centuries; whereas, *R. pseudoacacia* is short-lived due to early mortality associated with locust stem borer (*M. robiniae*) (Boring and Swank, 1984). In the clearcut watersheds, *L. tulipifera* expanded its spatial distribution by recruitment and survival on dry, upper slopes. Even on drier sites, it has maintained its canopy position during drought conditions (Elliott and Swank, 1994). In contrast, *L. tulipifera* was restricted to moist coves and riparian areas in the reference watersheds (Elliott et al., 1999). *Rubus* spp. and *Vitis* spp. also recruited into clearcut watersheds and grew rapidly for one to two years after disturbance; thereafter, they were overtopped by hardwoods and substantially declined in abundance (Elliott et al., 1997, 1998).

3.2. Vegetation controls on water yield

Earlier syntheses have reported the results from catchment experiments (Douglass and Swank, 1975; Douglass and Neary, 1980), with the treatments being cutting alone or cutting + species conversion. In brief, the largest water yield increases occurred the first year after cutting when evapotranspiration (Et) was most reduced due to minimal leaf area index (LAI). As vegetation regrew, LAI and Et increased and streamflow declined logarithmically, until it returned to the pre-treatment level by five to six years after cutting (Swank et al., 2001). The first watershed-scale evidence that species composition influences streamflow was demonstrated in watersheds converted from hardwood to pine species (WS1 and WS17) (Swank and Miner, 1968). Swank and Douglass (1974) reported that water yield was reduced by 20% on WS17, the *P. strobus* watershed at 15-years-old, compared to a mature hardwood watershed. At that time, these findings were novel and had important implications for forest management and water conservation, as stated by the authors (Swank and Douglass, 1974, Science 185, p. 859) "It is clear that the quantity of streamflow can be substantially altered by changing the type of forest vegetation."

Knowledge gained from Coweeta's long-term hydrology research program has had broad application (for a recent review see: Jackson et al., 2004) and these small watershed studies have been invaluable for documenting catchment scale responses to changes in vegetation composition and structure. However, understanding the underlying response mechanisms required a more detailed, physiological, and species-specific based approach. As such, these early results stimulated further research to understand tree ecophysiology and watershed hydrology connections, and test process-based ecohydrology models. Ford et al. (2007) estimated evapotranspiration (Et) in WS17 through 2004 and 2005, the *P. strobus* watershed at 50-years-old. They scaled sap flux-based estimates of stand transpiration (Et) and surface area-based estimates of stand interception (Ei) to the watershed level and compared these with water balance estimates of evapotranspiration (E, precipitation minus runoff, P – Ro). Their estimates (Et + Ei) were only 7–14% lower than evapotranspiration estimated from P – Ro (Ford et al., 2007). Hwang et al. (2009) used a process-based ecohydrology model, RHESys (Band et al., 1993), and detailed measurements from reference WS18 to simulate NPP and Et along a topographic moisture gradient. They used species-specific ecophysiological parameters from numerous studies conducted within Coweeta (see Hwang et al., 2009) to parameterize RHESys. The spatial and temporal gradient of vegetation within a small catchment was estimated with fine-resolution satellite imagery, field measurements, and simulated vegetation growth patterns using different rooting and allocation strategies. Hwang et al. (2009) tested whether the simulated spatial pattern of vegetation corresponded to measured canopy patterns and an optimal state relative

to maximizing ecosystem productivity and water use efficiency at the catchment scale. Coweeta watersheds were an ideal location for adding this spatial complexity to process-based models because of the long-term vegetation and streamflow data required for model parameterization, calibration, and validation.

3.3. Vegetation controls on water chemistry

Long-term records on precipitation and stream chemistry for treated and reference watersheds have provided a basis for evaluating responses to forest management practices and natural disturbances of southern Appalachian forest ecosystems (Swank and Waide, 1988). Long-term measurements have shown that precipitation chemistry is dominated by H⁺ and SO₄²⁻ ions with a mean annual pH of 4.6. Streamwater chemistry of low-elevation watersheds is dominated by Na⁺ and HCO₃⁻; for high-elevation watersheds, SO₄²⁻ replaces HCO₃⁻. In addition, long-term trends of annual precipitation and stream chemistry have shown a significant decline in acidity (Fig. 5).

In general, reference watersheds are characterized as being highly conservative of nitrogen (N) with N deposition <9.0 kg ha⁻¹ year⁻¹ (675 m), and the stream water exports are below 0.25 kg ha⁻¹ year⁻¹. However, N deposition increases with elevation. Mean annual bulk deposition estimates for total N ranged from 9.4 kg ha⁻¹ year⁻¹ at low elevation (788 m) to 12.6 kg ha⁻¹ year⁻¹ at high elevation (1389 m); a 25% increase in N deposition across the gradient (Knoepp et al., 2008).

On treated watersheds where hardwood vegetation was clearcut (WS7, WS13, WS28, and WS37) and watersheds converted from hardwoods to pine (WS1 and WS17) or hardwoods to grass, changes in net nitrogen budgets are particularly noteworthy. Swank and Vose (1997) reported that mean stream NO₃⁻ concentrations 18–39 years after treatment ranged from 2 to 13 μmol L⁻¹, which substantially exceeded concentrations of reference streams (0.2–0.5 μmol L⁻¹). The highest NO₃⁻ concentrations (55 μmol L⁻¹) found in the basin occurred on WS6. It was converted from hardwoods to grass and fertilized and limed in 1959, treated with herbicide in 1966–1967, and subsequently reverted to successional vegetation. WS6 showed the most striking contrast to other disturbed ecosystems with a mean annual net loss of 4.0 kg N ha⁻¹ year⁻¹ for 29 years after the last treatment.

In both WS6 and WS7, the NO₃⁻ loss from the watersheds after the disturbance was partly due to changes in the structure (i.e., decline in density) and composition (i.e., presence of *R. pseudoacacia*) of the vegetation (Swank and Vose, 1997; Swank et al., 2001).

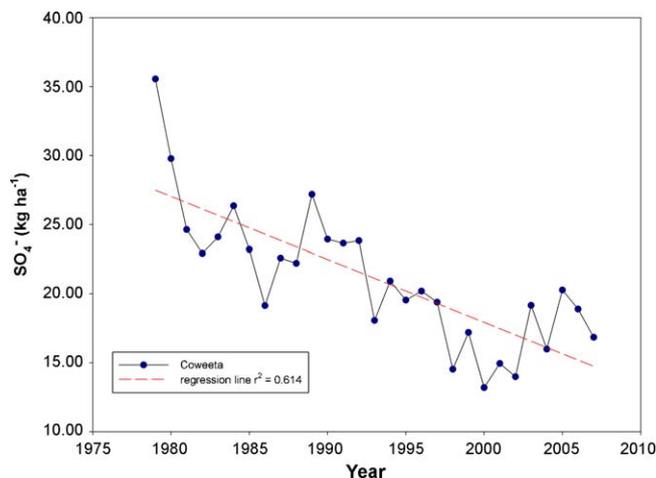


Fig. 5. Sulfate (SO₄²⁻) deposition collected at Coweeta Climate Station 1 (low elevation, 655 m) from 1978 to 2007.

Immediately after cutting, elevated NO_3^- leaching was attributed to reduced vegetation uptake and alteration of soil N transformation (Montagnini et al., 1986). With rapid re-growth of herbaceous and woody plants, stream NO_3^- declined, and then a second abrupt NO_3^- increase coincided with an infestation of the locust stem borer (*M. robiniae*) and subsequent mortality of *R. pseudoacacia* (Swank et al., 2001). Boring and Swank (1984) estimated that nitrogen fixation by *R. pseudoacacia* contributed $10 \text{ kg N ha}^{-1} \text{ year}^{-1}$ at the catchment scale, which is equivalent to the nitrogen contributed by atmospheric deposition.

3.4. Impacts of hemlock woolly adelgid (2003–2008)

Elliott and Swank (2008) reported that *T. canadensis* had increased in abundance and distribution in the Coweeta Basin between 1934 and the 1990s. The increase of *T. canadensis* coincided with the demise of *C. dentata*; and its increase was most notable near streams (low terrain) at low-to-mid elevations. With additional field measurements combined with GIS mapping methods, Narayanaraj et al. (2010) confirmed that *T. canadensis* is largely restricted to topographically concave, low-slope environments with a strong, negative exponential relationship with distance to stream. It was most abundant within 50 m of streams within Coweeta.

Concerns about the long-term effects of HWA on *T. canadensis* forest ecosystems have increased in recent years, as the rate of spread has accelerated through the southern Appalachians, causing nearly complete infestation of the host species and heavy mortality in some areas. In the Coweeta Basin, we found 100% HWA infestation with an average of 81% crown loss in less than three years (Fig. 6). In 2005, less than 1% of the *T. canadensis* trees were dead; by 2008, 33.1% of *T. canadensis* trees were dead (Fig. 7) and the remaining trees will most likely die within two years since crown loss was high (average of 88% crown loss in 2008, Fig. 6).

The loss of *T. canadensis* will substantially alter canopy composition, diversity, ecosystem structure, and ecosystem function in riparian areas of the southern Appalachians (Jenkins et al., 1999; Yorks et al., 2000; Eschtruth et al., 2006; Ford and Vose, 2007). Several studies of *T. canadensis*, particularly in the Northeast, have focused on detecting change in declining stands (Bonneau et al., 1999; Jenkins et al., 1999; Royle and Lathrop, 2002; Snyder et al., 2002; Stadler et al., 2006; Orwig et al., 2008). Similar to studies in

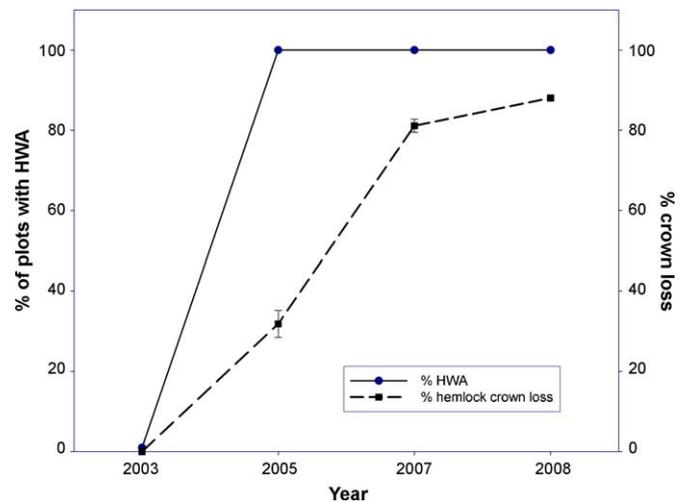


Fig. 6. Percentage of *Tsuga canadensis* trees infested with hemlock woolly adelgid (HWA) and percent crown loss in 2003, 2005, 2007, and 2008 within Coweeta, western North Carolina.

the Northeast (Foster and Zebryk, 1993; Orwig and Foster, 1998; Kizlinski et al., 2002), we found that HWA attacks hemlock trees of all ages and sizes (Fig. 7). Since infested trees seldom recover, HWA has the potential to remove *T. canadensis* from southern forests.

In the northeastern U.S., *T. canadensis* killed by the HWA are typically replaced by hardwoods, particularly *Betula* spp. (Orwig and Foster, 1998; Jenkins et al., 1999; Kizlinski et al., 2002). In the Coweeta Basin, we also found an increase in hardwoods (Table 2) as *T. canadensis* canopy declined, but *Acer* spp. and *Quercus* spp. were the dominant recruitment species. Herbaceous layer cover was much higher in Reference than Hemlock plots; no change in herbaceous layer cover has yet occurred in response to *T. canadensis* canopy decline and mortality. However, we also found high abundance of *R. maximum* in the Hemlock plots (Table 2). Post HWA successional patterns are likely to be influenced by co-occurring ericaceous shrubs (*R. maximum* and *K. latifolia*) which impact tree seedling recruitment and survival (Beckage et al., 2000) (Table 3).

Because *T. canadensis* is an important riparian species, effects of *T. canadensis* mortality on streams are of special concern. The loss of *T. canadensis* canopy cover due to HWA could substantially

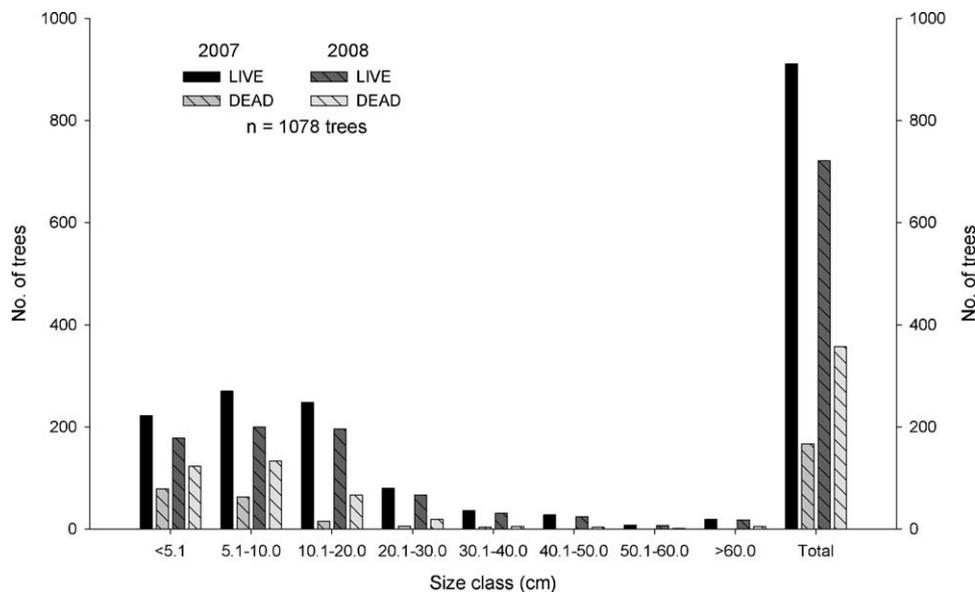


Fig. 7. Size class distribution of live and dead *Tsuga canadensis* trees in 2007 and 2008 within Coweeta, western North Carolina.

Table 2Overstory (stems ≥ 2.5 cm dbh) average density and basal area of hemlock (>20% basal area of hemlock) and reference (little to no hemlock present) plots.

	2005		2007	
	Hemlock	Reference	Hemlock	Reference
Density (stems ha ⁻¹)				
Total ^a	3199 (251)	3214 (719)	2708 (175)	3141 (444)
Deciduous ^b	587 (75.1)	724 (108.8)	642 (44.2)	671 (97.3)
Evergreen shrubs ^c	2265 (253)	2462 (748)	1753 (186)	2447 (483)
Tsuga ^d	347 (62.3)	26 (8.5)	313 (33.8)	22 (9.1)
Basal area (m ² ha ⁻¹)				
Total ^a	44.01 (1.80)	38.88 (3.02)	45.11 (1.16)	39.97 (2.68)
Deciduous ^b	26.51 (1.85)	30.16 (2.31)	30.59 (1.35)	30.32 (2.25)
Evergreen shrubs ^c	6.94 (0.91)	8.60 (2.24)	5.70 (0.70)	9.53 (1.67)
Tsuga ^d	10.55 (1.31)	0.12 (0.06)	8.75 (0.93)	0.12 (0.47)

Standard errors are in parentheses.

^a Total of all woody stems ≥ 2.5 cm dbh; hemlock ($n = 21$) and reference ($n = 12$) plots were measured in 2005 and 2007.^b Deciduous tree species only.^c Evergreen shrubs were *Rhododendron maximum* and *Kalmia latifolia* ≥ 2.5 cm dbh.^d Eastern hemlock (*Tsuga canadensis*).**Table 3**Understory (woody stems <2.5 cm dbh, ≥ 0.5 m height) density (stems ha⁻¹) in 2004 and 2007 in hemlock and reference plots.

	2004		2007	
	Hemlock	Reference	Hemlock	Reference
Woody not including <i>R. maximum</i>	1758 (486) a	8755 (4012) b	3354 (693) a	10368 (5490) b
Tree species	363 (86) a	1800 (720) b	1089 (308) b	1467 (542) b
<i>Acer</i> spp.	110 (23) a	608 (258) b	554 (237) b	900 (289) b
<i>Quercus</i> spp.	83 (33) a	750 (478) b	315 (138) b	270 (96) b
<i>R. maximum</i>	3264 (689) a	2667 (744) a	3308 (496) a	2854 (708) a

Standard errors are in parentheses. Values within rows followed by different letters are significantly different ($p \leq 0.05$) based on repeated measures analysis of variance (PROC MIXED, SAS 2002–2003).

affect stream environments (Ross et al., 2003). *T. canadensis* mortality will alter the hydrologic regime of streams because, unlike the hardwoods that will replace them, *T. canadensis* transpire at a low rate in the summer, continue to transpire through the winter and transpire heavily in the early spring, before deciduous trees leaf-out (Ford and Vose, 2007). Thus, the elimination of *T. canadensis* from watersheds will make streams more prone to summer droughts and spring floods.

In addition, *T. canadensis* loss may alter stream temperature, algal or aquatic plant production, and aquatic food chains (Ross et al., 2003; Lovett et al., 2006). In the southern Appalachians, *T. canadensis* co-occurs with deciduous broadleaved species, so a reduction in canopy cover may increase winter insulation reaching streams. However, potential impacts in near-stream areas might be attenuated by the co-occurrence of *R. maximum*, which is also abundant in these near-stream areas (Narayanaraj et al., 2010). *T. canadensis* provides especially dense year-round shade, maintaining cool summer temperatures in headwater streams (Snyder et al., 2002). Therefore, the ecological impacts of *T. canadensis* loss will be most pronounced in the riparian zones where *R. maximum* is less abundant or absent, and efforts at preservation and restoration should perhaps be concentrated in these riparian areas.

T. canadensis provides dense shade, and significant increases in light availability accompany *T. canadensis* mortality (Orwig and Foster, 1998; Jenkins et al., 1999; Kizilinski et al., 2002; Orwig et al., 2008). The shading and insulating character of *T. canadensis* stands produces cool, thermally stable microclimates and influences soil moisture such that *T. canadensis* death alters temperature and moisture regimes (Kizilinski et al., 2002; Snyder et al., 2002). *T. canadensis* litter maintains acidic soils, and *T. canadensis* mortality and replacement by hardwoods result in an increase in soil pH (Jenkins et al., 1999; Kizilinski et al., 2002) and nitrogen cycling (Kizilinski et al., 2002; Orwig et al., 2008). A recent study in Coweeta (Nuckolls et al., 2009) concluded that *T. canadensis* decline had a surprisingly rapid effect on carbon cycling.

While this section has focused on the short-term impacts of *T. canadensis* mortality, many of the impacts of HWA are likely to take decades or even centuries to manifest. For example, we expect substantial and pulsed increases in large wood in the stream and riparian areas as the dead *Tsuga* begin to fall. By contrast, we expect that nutrient cycling responses will be subtle and change gradually over time. In areas where *T. canadensis* will be replaced with species with higher quality litter, nutrient cycling rates should increase; whereas, in areas where *R. maximum* is abundant, we expect little or no change. The combination of existing long-term permanent plots and intensive short-term measurements has allowed us to quantify the spatial extent and initial impacts of hemlock mortality on ecosystem processes. The long-term permanent and new network of study plots provides an opportunity for tracking and quantifying longer-term responses.

4. Conclusions

Understanding how forest vegetation affects site water balance, nutrient cycling, and water quality requires detailed knowledge of forest structural and compositional changes. The long-term vegetation plots provide information that is needed to scale-up to the catchment level, as forest structure and composition changes with growth and development, and also as a result of management, disturbance, and climate change. With the long-term permanent vegetation plot data collected at Coweeta, we have documented changes in forest structure and species composition. Several large-scale and catastrophic disturbances have occurred over this 74-year period (1934–2008) resulting in a mosaic of species and age classes. The long-term vegetation data provide a description of changes in forest structure and composition through time and space. Further detailed measurements of plant demography (Clark and Ji, 1995; Clark et al., 1998) and ecophysiology are being developed to build predictive models of vegetation response to disturbance or climate change (Ibanez et al., 2009).

Much has been learned from the research on long-term responses to both natural and managed disturbances at Coweeta. The vegetation responses to disturbance are somewhat unique to the southern Appalachians due to the prehumid climate, prolific hardwood sprouting, an abundance of *R. pseudoacacia*, and invasive species. The observed changes in species composition have important long-term implications for ecosystem function (Elliott et al., 2002a). Linking long-term vegetation, streamflow, and biogeochemical cycling measurements clearly demonstrates that major changes in overstory and understory structure and composition affect site water use, organic matter quality and decomposition rates, carbon and nutrient cycling, and subsequently, stream water quantity and quality. Climatic, hydrologic and biogeochemical databases along with long-term measures of vegetation dynamics form a template that is essential to understanding broader- and more complex environmental issues such as climate change, carbon cycling, and atmospheric deposition as they relate to effects on water resources and the productivity and health of forests.

Acknowledgements

This research was primarily supported by USDA Forest Service and partially supported through grants from the National Science Foundation, Division of Environmental Biology to the University of Georgia for the LTER program #DEB-0823293. We also acknowledge the valuable contributions of Patsy Clinton, the late James Buchanan and other Forest Service staff, who provided field and logistical assistance throughout the conduct of this project.

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