Composition and Structure of Hemlock-Dominated Riparian Forests of the Northern Allegheny Plateau: A Baseline Assessment

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Abstract

We assessed the species composition and structure of three riparian forest stands of differing ages (old-growth, late-successional, mid-successional), dominated by eastern hemlock (*Tsuga canadensis* Carr.), in the Allegheny National Forest of northwestern Pennsylvania. Our objectives were to: 1) quantify structural and compositional attributes of hemlock-dominated riparian forests along a successional chronosequence; 2) describe in-stream coarse woody debris (CWD; logs $\geq$ 10 cm basal diameter and $\geq$ 1 m in length) loadings along this chronosequence; and 3) establish a benchmark series of permanent plots and transects with which future changes in forest composition and structure, and in-stream CWD loadings, could be monitored. Eastern hemlock, yellow birch (*Betula alleghaniensis* Britt.) and American beech (*Fagus grandifolia* Ehrh.) dominated the large (stems $\geq$ 10.0 cm dbh) and small (stems $\geq$ 2.5 cm dbh but < 10.0 cm dbh) tree strata at each site. However, structural data suggested that only American beech was successfully regenerating. Species richness of summer and spring herbs was greater for the mid-successional site than for either the late-successional or old-growth sites, due in large part to the greater habitat heterogeneity provided by small wetland inclusions, and lower canopy cover, at the younger site. In-stream CWD loading varied among sites and increased with riparian forest age. CWD loading at the old-growth site, similar to CWD loading recorded for old-growth hemlock-dominated riparian forest-stream systems in the southern Appalachian Mountains, was more than twice that recorded at the late-successional site and over three times that at the mid-successional site. Remeasurement of permanent vegetation plots and CWD transects at periodic intervals will provide useful information on the dynamics of hemlock-dominated riparian forest-stream systems that can be used in the development of adaptive management plans.

Introduction

Forests dominated by eastern hemlock (*Tsuga canadensis* Carr.) were an important component of presettlement landscapes of the nonglaciated Allegheny Plateau of northwestern Pennsylvania. Most common in mesic coves and stream valleys (Whitney 1990, Abrams and Ruffner 1995), hemlock-dominated forests of the region were heavily exploited for lumber and bark during the late 1800s and early 1900s, greatly diminishing their abundance (Whitney 1990, Abrams and Ruffner 1995). After harvest, many hemlock stands, particularly on upland sites, were converted to stands of early successional Allegheny hardwoods (dominated primarily by black cherry, *Prunus serotina* Ehrh., and red maple, *Acer rubrum* L.) (Whitney 1990). Today, silvicultural practices that perpetuate dominance of valuable hardwoods, and intense browsing by white-tailed deer (*Odocoileus virginianus* Zimmerman), continue to limit the development of late-successional, hemlock-dominated forests in much of the region (Hough 1965, Whitney 1984, 1990, Rooney and Dress 1997).

In contrast to upland sites, eastern hemlock has remained an important overstory species in many headwater riparian forests of the northern Allegheny Plateau. Riparian forests of the region have only recently received focused scientific attention (e.g., Williams and Moriarity 1997) and little is known of the ecological importance of eastern hemlock to the structure and function of stream-riparian systems. In the southern Appalachian Mountains, eastern hemlock is a major source of coarse woody debris to stream systems, especially those that are flanked by old-growth forest (Hedman et al. 1996). By input of persistent wood that accumulates through successional time (Hedman et al. 1996), eastern hemlock may greatly influence aquatic biodiversity (Terrick 1996). In addition, light attenuation by dense hemlock overstory, in conjunction with allelopathy, can regulate the diversity and abundance of ground-layer vegetation in riparian zones (Daubenmire 1930, Ward and McCormick 1982, Williams and Moriarity 1998). Thus, by influencing pattern and process in both aquatic and terrestrial ecosystems, eastern hemlock may be a keystone species (e.g., Mills et al. 1993) in riparian forests and streams.

The goal of this study was to provide baseline ecological information on hemlock-dominated riparian forests of the northern Allegheny Plateau. Our specific objectives were to: 1) quantify structural and compositional attributes of hemlock-dominated riparian forests along a successional chronosequence; 2) describe in-stream coarse woody debris (CWD) loadings along this chronosequence; and 3) establish a benchmark series of permanent plots and transects with which future changes in forest composition and structure, and in-stream CWD loadings, could be monitored. The last objective was of particular interest because of potential invasion of the region by the introduced hemlock woolly adelgid (*Adelges tsugae* Annand) (Homoptera: Adelgidae), and the compositional and structural changes that may occur in riparian forests and streams as a result of extensive adelgid-induced mortality of eastern hemlock (e.g., Orwig and Foster 1998).

Materials and Methods

Study area and sites

This study was conducted in the Allegheny National Forest (ANF) (41° 45' N, 79° 00' W) located in the nonglaciated Allegheny Plateau Physiographic Province of northwestern

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Table 1.—Characteristics of the three study streams in northwestern Pennsylvania and their riparian vegetation. Values in parentheses under basal area and tree density are percentages of each category comprised by *Tsuga canadensis*. Canopy cover and ground cover values are means ± 1 SE. Means bearing the same letter do not differ significantly (one-way ANOVA followed by Tukey test; $P = 0.0001$ for canopy cover; $P = 0.039$ for ground cover).

Site	Seral Stage	Watershed aspect	Stream order	Basal area[1] (m^2/ha)	Tree density[1] (stems/ha)	Canopy cover (%)	Ground cover (%)
East Fork Run	Old-growth	NE-SW	3rd	61.1 (79.5)	499.5 (73.3)	91.8 ± 0.5a	13.4 ± 4.0a
Coon Run	Late	N-SE	2nd	50.4 (84.4)	330.0 (69.7)	93.6 ± 0.5a	12.0 ± 3.7a
Waid Run	Mid	W-SE	2nd	43.1 (58.3)	400.0 (67.5)	89.2 ± 0.5b	24.3 ± 2.6b

[1]Stems ≥ 10.0 cm dbh

Pennsylvania. The ANF lies in a transition zone between the hemlock-white pine-northern hardwood forest of Braun (1950) and the more southerly Appalachian oak forest of Kuchler (1964). The landscape is typified by relatively flat to gently rolling plateaus dissected by deep, dendritic, u- or v-shaped stream valleys (Hough and Forbes 1943). Plateau elevations range from 400 to 600 m above sea level; stream valley floors generally range from 300 to 400 m in elevation (Cerutti 1985, Kopas 1985, Whitney 1990). Summers are cool with an average temperature of 18.9°C (Whitney 1990). Precipitation is distributed fairly evenly throughout the year and averages between 100 and 110 cm (Cerutti 1985, Kopas 1985). Sandstones and shales of Pennsylvanian age are the dominant parent material from which soils of the region are derived (Whitney 1990).

Three hemlock-dominated riparian forest stands, each of a different age, were studied (Table 1). East Fork Run, located within the Tionesta Research Natural Area, is an old-growth (overstory age ≥ 300 years) site; Coon Run is a late-successional (overstory age ≥ 150 years) site that may have been selectively logged; and Waid Run is a mid-successional (overstory age = 60-80 years) site. The East Fork Run and Waid Run sites are located on relatively level, undulating floodplains dominated by alluvial soils; the Coon Run site is located near the streamside base of a steep hillslope dominated by colluvial soil (Table 2).

Field sampling

Vegetation was sampled in ten permanently marked 10 X 10 m plots at each site. Plot arrangement differed among sites. At East Fork Run and Waid Run, five generally contiguous plots were placed on opposite sides of the stream; at Coon Run, all ten plots were positioned more or less contiguously on the northeastern side of the stream valley because of the predominance of eastern hemlock at this aspect. All trees ≥ 2.5 cm dbh were identified and measured within each 100 m^2 plot; each tree tallied was marked by a numbered aluminum tag at its base. Saplings (stems < 2.5 cm dbh but > 1 m tall) were identified and counted in each 100 m^2 plot. Woody plant seedlings (stems ≤ 1 m tall) were identified and counted, and percent cover by species of herbaceous vascular plants was estimated, in two 1 m^2 plots located randomly in each 100 m^2 plot. Woody plant and summer herbaceous layer vegetation data were collected during mid-August 1993 at Coon Run, late-June 1995 at East Fork Run, and mid-July 1996 at Waid Run. At each site, all 100 m^2 plots were surveyed for vernal herbs (presence/absence) in the spring (late April to mid-May) following respective summer sample years.

Soil and physical site characteristics were recorded within each 100 m^2 plot. Depth and texture of soil horizons were determined from profiles taken with a soil auger. Plot aspect and slope were measured with compass and clinometer. Plot position on the landform (floodplain, slope), landform shape (concave, convex, linear) and percent rock cover were estimated visually. Plot elevation was determined from topographic maps. The latitude and longitude of each plot was determined with a hand-held global positioning system. A spherical densiometer (Lemmon 1956) was used to estimate percent canopy cover at the center of each plot.

In-stream CWD (logs ≥ 10 cm basal diameter and ≥ 1 m in length) was sampled at each study site by a line-intercept method (Martin 1976) using two contiguous 50 m transects centered within each stream. Each log crossing a transect was identified, and its total length and upper and lower diameter were measured. Logs that could not be readily identified in the field were tallied as unknown. Transect ends were marked with iron rebar to allow subsequent remeasurements.

Data analysis

Density (number of stems/m^2 or ha), basal area (m^2/ha) or cover, frequency (percent occurrence across plots), and importance were used to describe the vegetation of each site (Kent and Coker 1994). Trees were divided into two structural classes for analysis: small (stems ≥ 2.5 cm dbh but < 10 cm dbh) and large (stems ≥ 10.0 cm dbh) trees. The importance value (IV; 0 to 100%) for small and large trees was calculated as relative density + relative basal area + relative frequency/3 (Curtis and McIntosh 1951). The IV for saplings and seedlings was calculated as relative density + relative frequency/2. The IV for herbaceous layer plants (all vascular plants, except for tree seedlings, ≤ 1 m tall) was calculated as relative cover + relative frequency/2. To assess the regeneration status of eastern hemlock and other canopy potential tree species, stem density (number/ha) was summed within sites by structural class (i.e., seedling, sapling, small tree, and large tree). Nomenclature follows Gleason and Cronquist (1991).

Table 2.—Mean (± 1 SE) soil and site characteristics for the three riparian study sites in northwestern Pennsylvania. Means followed by the same letter do not differ significantly (Tukey test, P ≤ 0.05).

Soil/site characteristic	East Fork Run	Coon Run	Waid Run	*P*-value
Elevation (m)	467.6 ± 1.4a	561.5 ± 0.7b	369.0 ± 0.0c	0.0001
Aspect (°N of S)	298.4 ± 14.8a	73.8 ± 7.8b	244.5 ± 6.0c	0.0001
% Slope	10.6 ± 2.8a	72.6 ± 5.8b	3.4 ± 0.6a	0.0001
Plot position	Streamside	Lower slope	Streamside	—
Landform shape	Undulating	Linear/concave	Undulating	—
% Rock cover	20.8 ± 10.5	14.8 ± 3.6	5.2 ± 3.0	0.085
Predominant soil series	Philo-Pope	Buchanan	Ernest	—
Depth of litter layer (cm)	1.7 ± 0.2a	3.7 ± 0.5b	2.3 ± 0.3a	0.011
Depth of humus layer (cm)	3.4 ± 0.3a	1.5 ± 0.2b	2.3 ± 0.3a	0.004
Depth of A horizon (cm)	11.9 ± 2.5a	4.5 ± 0.5b	6.0 ± 1.7a	0.025
Texture of A horizon	Silt loam	Stony silt loam	Silt loam	—
Depth of B horizon (cm)	46.3 ± 7.7a	25.5 ± 3.8b	14.5 ± 2.3c	0.0001
Texture of B horizon	Silt loam	Stony silt loam	Silt loam	—
Total soil depth	63.4 ± 9.4a	34.9 ± 3.6b	20.0 ± 3.4c	0.0001

Table 3.—Importance values (relative frequency + relative density + relative basal area/3) for large (stems ≥ 10.0 cm dbh) and small (stems ≥ 2.5 cm dbh but < 10.0 cm dbh) trees at the three riparian study sites in northwestern Pennsylvania. Nomenclature follows Gleason and Cronquist (1991).

	East Fork Run		Coon Run		Waid Run	
Species	Large Tree	Small tree	Large Tree	Small tree	Large Tree	Small tree
Tsuga canadensis Carr.	86.6	58.1	71.0	—	59.6	62.1
Betula alleghaniensis Britt.	18.5	16.1	4.1	—	18.7	12.5
Fagus grandifolia Ehrh.	7.3	15.0	10.5	81.7	3.1	25.5
Acer saccharum Marsh.	2.9	—	10.5	—	—	—
Acer rubrum L.	—	—	4.1	—	3.8	—
Pinus strobus L.	—	—	—	—	14.8	—
Amelanchier arborea (Michx. f.) Fern.	2.7	5.6	—	—	—	—
Hamamelis virginiana L.	—	5.1	—	10.1	—	—
Acer pensylvanicum L.	—	—	—	8.2	—	—

Log diameter measurements were converted to total volume using the equation for the right frustrum of a parabaloid (Lienkamper and Swanson 1987). Log volume (m^3) by site and species was calculated by summing values obtained from the two 50 m transects and expressing them on a 100 m basis. Log frequency (percent occurrence on transects) and percent log volume were used to construct importance values (IV = % frequency + % volume/2) for each species.

One-way analysis of variance (P ≤ 0.05) was used to examine differences in selected soil, site and vegetation characteristics across community types. When ANOVAs were significant, the Tukey multiple range test was used to separate means. Data were transformed [cos(45 - aspect) + 1 for aspect data; arcsin transformation for percentage data; log(x + 0.5) for other continuous data] prior to analysis to stabilize variances (Beers et al. 1966, Zar 1996) and back-transformed for tabular presentation. Box plots were used to graphically compare variation in in-stream CWD length and basal diameter across sites. Statistical analyses were done using SYSTAT version 7.0 (Wilkinson 1997).

Results

Soil and site characteristics

Eight of 9 quantitative soil and site characteristics varied significantly across study sites (Table 2). Most soil and site factors varied as a result of topography or location in the landscape and not because of differences in stand age (e.g., elevation, aspect, slope). Total soil depth ($F_{2,28}$ = 14.47, $P <$ 0.0001) and depth of the soil B horizon ($F_{2,28}$ = 10.84, $P <$ 0.0001) increased significantly with increasing forest age.

Vegetation

Seven species occurred in the large tree stratum across study sites (Table 3). Eastern hemlock was dominant across

Table 4.—Importance values (relative frequency + relative density/2) for woody plant seedlings (stems ≤ 1 m tall) at the three riparian study sites in northwestern Pennsylvania. tr = trace (importance value < 1.0). Nomenclature follows Gleason and Cronquist (1991).

Species	East Fork Run	Coon Run	Waid Run
Tsuga canadensis Carr.	84.1	48.3	—
Betula alleghaniensis Britt.	13.1	16.8	51.1
Fagus grandifolia Ehrh.	tr	6.2	16.3
Acer saccharum L.	—	1.2	17.4
Prunus serotina Ehrh.	tr	3.5	1.5
Acer pensylvanicum L.	tr	11.5	—
Acer rubrum L.	tr	10.0	—
Magnolia acuminata (L.) L.	—	2.2	1.5
Fraxinus americana L.	—	—	12.5
Viburnum alnifolium Marsh.	—	tr	—
Amelanchier arborea (Michx. f.) Fern.	tr	—	—
Hamamelis virginiana L.	tr	—	—

sites with yellow birch (*Betula alleghaniensis* Britt.) and American beech (*Fagus grandifolia* Ehrh.) as important secondary species (Table 3). Large tree density ranged from 330 stems/ha to 499 stems/ha and was greatest at East Fork Run and lowest at Waid Run. Large tree basal area ranged from 43.1 to 61.1 m^2/ha was greatest at East Fork Run and lowest at Waid Run (Table 1). Six species occurred in the small tree stratum across sites with eastern hemlock dominant at East Fork Run and Waid Run; eastern hemlock was absent as a small tree at Coon Run (Table 3). American beech dominated the small tree stratum at Coon Run and, along with yellow birch, was an important secondary small tree species at East Fork Run and Waid Run. Canopy cover differed significantly among sites ($F_{2,28}$ = 18.26, $P < 0.0001$) and was lowest at Waid Run and greatest at East Fork Run and Coon Run (Table 1).

Twelve species were recorded from the woody plant seedling stratum across study sites (Table 4). Eastern hemlock was the dominant seedling species at East Fork Run and Coon Run but was absent at Waid Run where yellow birch was dominant. Overall species richness of woody plant seedlings, summed by site, was similar between Coon Run (S = 9) and East Fork Run (S = 8) but was lowest at Waid Run (S = 6). On a per plot basis, species richness of woody plant seedlings differed significantly among sites ($F_{2,58}$ = 29.81, P < 0.0001); woody plant seedling richness was greatest at Coon Run (mean = 4.9 ± 0.2 SE species/m^2) followed by East Fork Run (mean = 3.7 ± 0.3 SE species/m^2) and Waid Run (mean = 2.2 ± 0.2 SE species/m^2). The sapling layer was the most species-poor vegetational stratum across sites and consisted only of root sprouts of American beech (IV = 100 at each site).

The summer herbaceous layer was generally the most species-rich of all vegetational strata with 28 species recorded across sites (Table 5). Two species, common wood sorrel (*Oxalis acetosella* L.) and wood fern [*Dryopteris intermedia* (Muhl.) A. Gray] strongly dominated the herbaceous layer at East Fork Run and Coon Run; wood fern was dominant, and common wood sorrel absent, at Waid Run. Other moderately important (IV > 5.0) herbaceous species at one or more sites included Canada mayflower (*Maianthemum canadense* Desf.), sweet white violet (*Viola blanda* Willd.), Indian cucumber-root (*Medeola virginiana* L.), New York fern [*Thelypteris noveboracensis* (L.) Nieuwl.], round-leaved violet (*Viola rotundifolia* Michx.), and partridgeberry (*Mitchella repens* L.). Summed by site, Waid Run (S = 24) had the highest overall species richness followed by Coon Run (S = 11) and East Fork Run (S = 5). On a per plot basis, species richness of summer herbs differed significantly among sites ($F_{2,58}$ = 28.74, P < 0.0001. Summer herb species richness was greatest at Waid Run (mean = 5.1 ± 0.4 SE species/m^2) and lowest at Coon Run (mean = 2.7 ± 0.2 SE species/m^2) and East Fork Run (mean = 2.1 ± 0.2 SE species/m^2). Six species of vernal herbs were tallied across sites with 5 species occurring at Waid Run, 2 species at East Fork Run and 1 species at Coon Run (Table 6). Except for toothwort [*Cardamine diphylla* (Michx.) A. Wood] at Waid Run, vernal herbs were infrequently encountered across sites. Total ground-layer cover (including summer herbs and woody plant seedlings) varied significantly among sites ($F_{2,28}$ = 4.28, P = 0.039) and was greatest at Waid Run (Table 1).

The distribution of structural data for eastern hemlock and yellow birch was generally bimodal across sites with peaks in the seedling and large tree classes and troughs in the sapling and small tree classes (Table 7). Seedlings of eastern hemlock were not recorded from plots at Waid Run. The structural distribution for American beech approached an inverse-J shaped curve.

In-stream CWD

Three species, eastern hemlock, yellow birch and American beech, were the most important contributors to in-stream CWD across sites (Table 8). Only 14% of logs across sites (n = 7) could not be readily identified to species. Logs of eastern hemlock were generally the most numerically

Table 5.—Importance values (relative frequency + relative cover/2) for summer herbaceous plants at the three riparian study sites in northwestern Pennsylvania. Nomenclature follows Gleason and Cronquist (1991).

Species	East Fork Run	Coon Run	Waid Run
Oxalis acetosella L.	55.9	54.8	—
Dryopteris intermedia (Muhl.) A. Gray	27.8	21.3	41.1
Thelypteris noveboracensis (L.) Nieuwl.	7.0	1.1	—
Medeola virginiana L.	5.4	7.6	—
Maianthemum canadense Desf.	4.0	1.1	9.9
Dennstaedtia punctilobula (Michx.) Moore	—	4.6	1.7
Asplenium montanum Willd.	—	3.6	1.2
Viola blanda Willd.	—	2.4	8.7
Viola rotundifolia Michx.	—	1.2	2.6
Mitchella repens L.	—	—	6.2
Impatiens capensis Meerb.	—	—	5.3
Arisaema triphyllum (L.) Schott.	—	—	3.6
Pilea pumila (L.) A. Gray	—	—	3.4
Galium L. spp.	—	—	2.7
Tiarella cordifolia L.	—	—	2.3
Viola sororia Willd.	—	—	2.3
Hydrocotyle americana L.	—	—	1.8
Trientalis borealis Raf.	—	—	1.8
Adiantum pedatum L.	—	1.7	—
Symplocarpus foetidus (L.) Nutt.	—	—	1.7
Disporum lanuginosum (Michx.) Nichol.	—	1.1	—
Other[1]	—	—	4.2

[1]Includes: *Cardamine diphylla* (Michx.) A. Wood, *Carex* L. sp., *Circaea alpina* L., *Geranium maculatum* L., *Lilium canadense* L., *Prenanthes alba* L., *Streptopus roseus* Michx.

Table 6.—Frequency (%) of spring ephemeral herbs in 100 m² plots (n = 10 plots/site) at the three riparian study sites in northwestern Pennsylvania. Nomenclature follows Gleason and Cronquist (1991).

Species	East Fork Run	Coon Run	Waid Run
Trillium erectum L.	—	30	10
Trillium undulatum Willd.	10	—	10
Cardamine diphylla (Michx.) A. Wood	—	—	60
Panax trifolius L.	—	—	20
Podophyllum peltatum L.	—	—	20
Anemone quinquefolia L.	10	—	—

common of CWD species recorded on stream transects and generally comprised the largest volume. In-stream CWD loadings [log volume (m^3)/100 m of stream] varied among sites and increased with riparian forest age. CWD loading at East Fork Run was more than twice that recorded at Coon Run and over three times that recorded at Waid Run (Table 7). Basal diameter (Fig. 1) and length (Fig. 2) of in-stream logs at East Fork Run and Coon Run were strongly skewed toward larger sizes. In contrast, the distributions of basal diameter and length of in-stream-logs at Waid Run showed considerably less variation than logs tallied at East Fork Run and Coon Run, and were generally skewed toward smaller sizes.

Discussion

We observed no major differences in vegetational composition across our riparian study sites that could be clearly attributed to forest age. Composition of arboreal strata (i.e., large trees, small trees, seedlings, saplings) did not differ markedly across sites and was similar to that documented in other studies of regional hemlock forests (Hough 1936, Hough and Forbes 1943). Likewise, summer herbs such as wood fern, common wood sorrel, and Canada mayflower, widespread in hemlock-dominated forests (Rogers 1980), were generally dominant across our study sites, and spring herbs, typically of low importance in hemlock stands (Beatty 1984), were uncommon.

Table 7.—Regeneration of dominant canopy potential tree species across the three riparian study sites. Seedlings = stems ≤ 1 m tall; saplings = stems < 2.5 cm dbh but > 1 m tall; small trees = stems ≥ 2.5 cm dbh but < 10.0 cm dbh; large trees = stems ≥ 10.0 cm dbh.

		No. stems/ha			
Site	Species	Seedlings	Saplings	Small trees	Large trees
East Fork Run	*Tsuga canadensis*	417,200	0	133	337
	Betula alleghaniensis	64,500	0	33	78
	Fagus grandifolia	2,600	555	33	33
Coon Run	*Tsuga canadensis*	1,040,500	0	0	230
	Betula alleghaniensis	190,700	0	0	10
	Fagus grandifolia	15,700	500	120	30
Waid Run	*Tsuga canadensis*	0	0	90	270
	Betula alleghaniensis	50,500	0	10	80
	Fagus grandifolia	9,500	2,170	120	30

Table 8.—Frequency, volume and importance value (IV = % frequency + % volume/2) of logs recorded from the three stream-riparian study sites in northwestern Pennsylvania. Values are per 100 m of stream.

Site	Species	*n*	Frequency (%)	Volume (m^3)	Volume (%)	IV
East Fork Run	*Tsuga canadensis*	11	52.4	22.11	82.1	67.3
	Betula alleghaniensis	4	19.1	2.57	9.6	14.4
	Unknown	4	19.1	0.28	1.0	10.1
	Fagus grandifolia	2	9.5	1.96	7.3	8.4
	Overall	21	—	26.92	—	—
Coon Run	*Fagus grandifolia*	9	52.9	3.33	29.1	41.0
	Tsuga canadensis	4	23.5	4.86	42.4	33.0
	Acer saccharum	1	5.9	1.96	17.1	11.5
	Betula alleghaniensis	1	5.9	1.11	9.7	7.8
	Unknown	2	11.8	0.18	1.6	6.7
	Overall	17	—	11.44	—	—
Waid Run	*Tsuga canadensis*	7	58.3	3.71	46.6	52.5
	Betula alleghaniensis	3	25.0	1.60	20.1	22.6
	Fagus grandifolia	1	8.3	2.53	31.8	20.1
	Unknown	1	8.3	0.12	1.5	4.9
	Overall	12	—	7.96	—	—

Rooney and Dress (1997) found that species richness of tree seedlings and herbs differed significantly between old-growth and second-growth hemlock-hardwood forests in northwestern Pennsylvania. Similarly, we found significantly higher species richness of woody plant seedlings at the 1 m^2 scale at our old-growth and late-successional study sites compared to the mid-successional site. However, species richness of summer herbs did not follow this trend and was significantly greater at Waid Run, the mid-successional site. In fact, overall species richness at Waid Run was over twice that recorded at Coon Run, the late-successional site, and nearly five times that recorded at East Fork Run, the old-growth site. The elevated species richness at Waid Run was probably due in large part to the greater habitat heterogeneity provided by small wetland inclusions, primarily seeps, that occurred at this site, and significantly lower canopy cover due to uprooting of shallow-rooted hemlock and white pine in the comparatively thin soil. Several herbs recorded exclusively at Waid Run are facultative wetland species [e.g., *Impatiens capensis* Meerb. (jewel-weed); *Arisaema triphyllum* (L.) Schott.(jack-in-the-pulpit); *Pilea pumila* (L.) A. Gray (clearweed); *Hydrocotyle americana* L. (marsh-pennywort); *Symplocarpus foetidus* (L.) Nutt. (skunk-cabbage); *Circaea alpina* L. (dwarf enchanter's nightshade)] that are uncommon on sites that lack saturated soils such as the East Fork Run and Coon Run study sites. Also, low canopy cover provides light conditions that allow the coexistence of a wide variety of shade-intolerant and

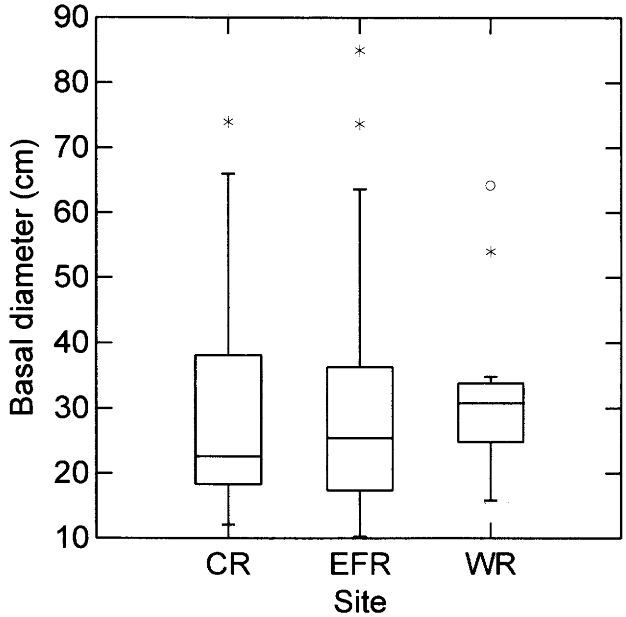

Figure 1.—Box plot diagrams depicting the distribution of basal diameters (cm) for in-stream logs sampled at the three riparian forest-stream study sites in northwestern Pennsylvania. CR = Coon Run; EFR = East Fork Run; WR = Waid Run. The horizontal line through each box depicts the median, the box depicts the central 50th percentile of data, and the vertical lines depict the 95th percentile of data. Asterisks represent outliers, and open circles represent extreme outliers, beyond the 95th percentile range.

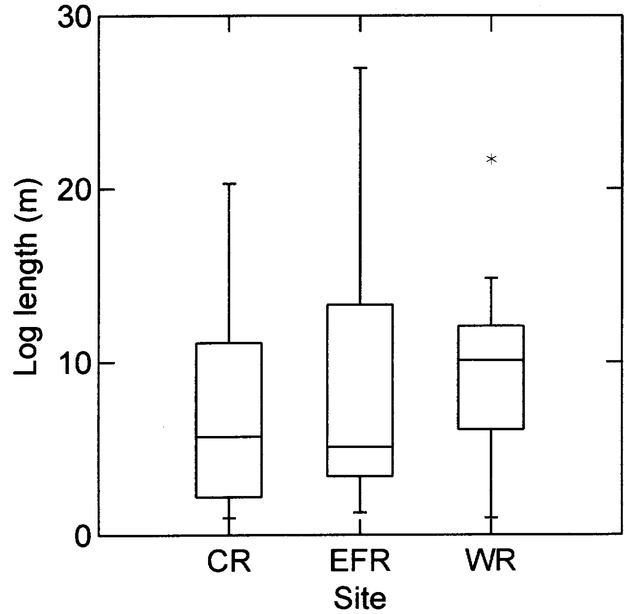

Figure 2.—Box plot diagrams depicting the distribution of lengths (m) for in-stream logs sampled at the three riparian forest-stream study sites in northwestern Pennsylvania. CR = Coon Run; EFR = East Fork Run; WR = Waid Run. The horizontal line through each box depicts the median, the box depicts the central 50th percentile of data, and the vertical lines depict the 95th percentile of data. Asterisks represent outliers beyond the 95th percentile range.

shade-tolerant riparian herb species (Williams et al. 1999). Thus, when comparing plant species richness in a hemlock-dominated riparian forest chronosequence, it may be necessary to first assess the potential confounding influence of within-site habitat heterogeneity on richness measures.

We noted a gap in the sapling and/or small tree structural classes for eastern hemlock and yellow birch across study sites. American beech, in contrast, was well-represented in all structural classes. Hough (1936) and Hough and Forbes (1943) observed very similar patterns in structural classes for these three species in old-growth forests on the northern Allegheny Plateau. They attributed the bimodal distribution of eastern hemlock in particular to episodic recruitment patterned by yearly variation in seed crops and favorable conditions for seed germination and seedling establishment. Since the 1940s, however, white-tailed deer populations have increased dramatically on the Allegheny Plateau and heavy browsing has strongly influenced forest pattern and process (Tilghman 1989). Thus, it is possible that gaps in the smaller size classes of eastern hemlock and yellow birch are due in part to deer browsing in conjunction with seed rain and seed bed conditions. In contrast, seedlings and saplings of American beech are relatively unpalatable to deer; as a result, this species is one of the few to regenerate at high deer densities on the Allegheny Plateau (Whitney 1984). Periodic monitoring of tree regeneration and browse damage, in conjunction with monitoring of deer density and activity, will be necessary to determine the long-term impact of deer browsing on tree and herb populations at our study sites (e.g., Mosbacher 1999, Williams et al. 2000).

Other than large tree basal area and density, in-stream CWD loading was the only structural characteristic that clearly increased with riparian forest age. The in-stream CWD loading that we measured at East Fork Run is similar to values recorded by Hedman et al. (1996) in old-growth hemlock forest-stream systems in the southern Appalachian Mountains. We recorded a total volume of 26.92 m^3/100 of stream at East Fork Run; Hedman et al. (1996) recorded an average volume of 21.9 m^3/100 m of stream in old-growth forest. The in-stream CWD loading that we recorded at Coon Run (11.44 m^3/100 m of stream) also compares favorably with the mean late-successional in-stream loading observed by Hedman et al. (1996) (12.7 m^3/100 m of stream). However, mean in-stream CWD loading for mid-successional sites in the southern Appalachians (13.2 m^3/100 m of stream) is nearly twice that recorded at Waid Run (7.96 m^3/100 m of stream). Hedman et al. (1996) found that carry-over CWD from previous stands contributed significantly to in-stream CWD loading at mid-successional sites in the southern Appalachians. It is unknown how carry-over CWD may influence loadings in streams that drain mid-successional forests of the northern Allegheny Plateau. However, the past practice of using streams to transport logs, aided by large volumes of water released from splash dams in the spring, may have ensured that little CWD remained in streams after their valleys were logged. Instream logs may have been washed downstream when splash dams were opened or they may have been intentionally removed to minimize log jams, diminishing CWD carry-over potential.

Past studies of hemlock-dominated forests of the northern Allegheny Plateau have primarily emphasized descriptions of soil and site factors that affect tree growth and distribution (Hough 1942, 1943, Aguilar and Arnold 1985) or considered potential silvicultural options from stand-level studies (Hough and Forbes 1943). Little direct emphasis was placed on assessment of other forest elements such as downed word or herbaceous plant diversity in hemlock forests of the region (but see Hough 1936, 1965, Rooney and Dress 1997). Our study was designed to provide baseline data on key structural and compositional attributes of hemlock-dominated riparian forest-stream systems with the ultimate goal of monitoring long-term change. Hough's (1965) classic study of compositional shifts in forest understory, induced by heavy deer browsing, clearly illustrates the value of long-term monitoring in detecting subtle ecological change in regional forests. Similarly, we expect that remeasurement of our plots and transects in the coming years will yield information useful for understanding the dynamics of hemlock-dominated riparian forest-stream systems, and to assess their response to both natural and anthropogenic perturbations, such as invasion of the hemlock woolly adelgid. Adaptive management plans for hemlock-dominated riparian forests of the Allegheny Plateau should include a long-term monitoring component, using selected structural and compositional attributes (e.g., Noss 1999), to ensure that current scientific knowledge drives timely, informed management decisions.

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