In-stream large woody debris loading and riparian forest serai stage associations in the southern Appalachian Mountains

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Abstract: Large woody debris (LWD) is an important ecological component of mountain streams. However, the relation of LWD loading and riparian forest composition is poorly understood in the southern Appalachians. In this study, 500-m reaches of 11 riparian forest-stream systems representing a 300-year sere were inventoried and measured to obtain quantitative estimates and descriptions of in-stream LWD. Loading volumes ranged from 7.1 to 31.2 $m^3/100$ m of stream, or between 3.6 and 13.2 kg/m^2. LWD loadings were highly variable during midseral stages of plant community succession, primarily because of the wide range in loading of American chestnut (*Castanea dentata* (Marsh.) Borkh.). Loadings increased linearly in late-successional through old-growth systems over a 165-year interval. Eastern hemlock (*Tsuga canadensis* (L.) Carriere) and American chestnut were the most dominant carry-over LWD species in midsuccessional stream systems. Loading of eastern hemlock LWD increased from midsuccessional through old-growth stages as the species became dominant in the riparian forest. Without carry-over debris, LWD loadings would be extremely low in midsuccessional stream systems. American chestnut was a major component of LWD in midsuccessional stream systems, despite the fact that it has been unavailable for recruitment for decades.

Résume : Les gros debris ligneux (GDL) constituent des elements écologiques importants des cours d'eau de montagne. Cependant, la relation entre la charge en GDL et la composition de la foret riveraine est peu comprise dans les Appalaches méridionales. Dans la présente etude, des tron9ons de 500 m de 11 systemes cours d'eau–forêt riveraine, représentant une série evolutive de 300 ans, ont été inventories et mesures afin d'obtenir des estimations quantitatives et des descriptions de la charge en GDL dans les cours d'eau. Les volumes de la charge allaient de 7,1 a 31,2 $m^3/100$ m de cours d'eau, ou de 3,6 a 13,2 kg/m^{-2}. La charge en GDL a varié fortement pendant les stades intermediaires de la succession des communautés végétales, principalement en raison d'une grande amplitude de la charge due au chataignier d'Amerique *(Castanea dentata* (Marsh.) Borkh.). La charge a augmente de façon linéaire dans les stades tardifs de la succession des systemes des forêts agees durant un intervalle de 165 ans. Pendant les stades evolutifs intermediaires, les GDL des cours d'eau étaient dominés par des debris persistants de pruche du Canada *(Tsuga canadensis* (L.) Carriere) et de chataignier d'Amerique provenant de stades evolutifs avances antérieurs. La charge en GDL due a la pruche du Canada a augmente du stade évolutif intermédiaire au stade de foret agee, a mesure que cette espece devenait dominante dans la foret riveraine. Sans la presence de debris persistants, la charge en GDL serait extrëmement basse dans les systemes des cours d'eau du milieu de la succession. Le chataignier d'Amerique a été un element majeur des GDL dans les systemes du milieu de la succession, en dépit du fait qu'il n'était pas disponible pour le recrutement pendant des décennies.

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Introduction

Riparian zones are important ecotones that influence complex interactions between terrestrial and aquatic environments. The contribution of large woody debris (LWD) from riparian forests to streams exemplifies this complex link. LWD, i.e., bole, limb, root wad, or whole tree, is an important ecological and morphological component of low-order streams. Comprehensive reviews (Harmon et al. 1986; Maser et al. 1988) indicate that LWD can (1) control routing of sediment and water through channel systems; (2) dissipate stream energy; (3) define habitats; and (4) serve as a substrate for in-stream biological activity. In-stream LWD loading levels and distribution patterns are affected by the amount of carry-over debris, i.e., LWD present before disturbance and created by disturbance, the amount of LWD added by the regenerated stand, decay patterns of species composing each debris input category, and the transport power of streams (Maser et al. 1988). The relationship between in-stream LWD loading and riparian forest stand characteristics has received little study.

Triska and Cromack (1980) hypothesized that LWD loadings in Oregon streams increased linearly over time and perhaps reached a maximum level after 450-500 years of stand

Received March 15, 1995. Accepted March 26, 1996.

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Can. J. For. Res. **26:** 1218–1227 (1996). Printed in Canada / Imprimé au Canada

development. Spies et al. (1988) examined characteristics of terrestrial LWD in relation to stand age in Washington and Oregon and concluded that LWD loading curves were U-shaped over a 500-year period following major disturbance. Beyond 500 years, amounts of LWD declined to intermediate levels and steady-state loading conditions were achieved approximately 1000 years post-disturbance.

In the northeastern United States, Tritton (1980) examined a series of clear-cut northern hardwood forests and found that terrestrial LWD loading patterns were also U-shaped over the course of plant community succession. LWD loadings were highest 10 years after logging and in old forests, i.e., >100 years. The high mass of LWD in sites soon after logging was due to logging debris inputs. Lowest loadings occurred 40-57 years after logging.

In the southern Appalachians, studies of LWD loadings as a function of forest succession are uncommon. In the Great Smoky Mountains of Tennessee, Silsbee and Larson (1983) found that mean LWD volume in streams associated with old-growth forests was approximately four times greater than the volume found in streams draining watersheds logged 45-70 years previously. Webster and Swank (1985) hypothesized that LWD loadings in the southern Appalachians followed a U-shaped loading pattern over a 125-year post-disturbance interval. They reasoned that the highest levels would be found immediately after disturbance if logging residue were left in stream channels, followed by a sharp reduction around age 20 years and a gradual increase in standing stocks for the next 80–100 years.

Major disturbances in the southern Appalachians, e.g., chestnut blight (*Endothia parasitica)* and heavy logging early in this century, certainly affected LWD in-stream loadings. The loss of American chestnut (*Castanea dentata* (Marsh.) Borkh.) from riparian forests was especially critical because of its large size and resistance to decay.

The amount of LWD in southern Appalachian streams and the role of riparian forests in contributing LWD are poorly understood and represent a significant gap in knowledge regarding the functionality of forest ecosystems. We hypothesize that LWD changes as a function of riparian forest succession. The primary objective of this study was to quantify, characterize, and differentiate LWD in-stream loadings along a successional chronosequence following major disturbance and relate LWD loading dynamics to compositional and physical attributes of riparian forests.

Methods

This study was conducted in the Blue Ridge Mountain Physiographic Province of the southeastern United States, with the USDA Forest Service Coweeta Hydrologic Laboratory near Franklin, North Carolina, serving as the central location. Additional sites were located throughout the Wayah and Cheoah ranger districts of the Nantahala National Forest in North Carolina, the Andrew Pickens Ranger District of the Sumter National Forest in South Carolina, the Tallulah Ranger District of the Chattahoochee National Forest in Georgia, the City of Greenville Municipal Watershed in northwestern South Carolina, and private industrial forestland near the Nantahala National Forest.

Over 60 riparian-stream systems were field inspected before 11 were selected for study. Several watershed geomorphological features, including stream order, stream width, elevation, bank slope, stream gradient, and watershed area, guided the selection of study sites. Homogeneity of study sites was established via cluster analysis of mean bank slope, mean bankfull channel width, and mean stream gradient. Subsequent grouping of study sites into serai stages was based upon an analysis of riparian tree ages. Serai stage designations were verified by discriminant function analysis and regression analysis of overstory diameter distributions (Hedman 1992; Hedman and Van Lear 1995).

Sites were selected so that the stage of succession or time since major disturbance was the primary variant. Accordingly, riparian forests and associated stream systems were replicated and represented different points in time, i.e., midsuccessional, late successional, and old growth. Age of the riparian forest was determined by coring from 14 to 38 trees/site at breast height. In uneven-aged stands, the age of trees in the oldest cohort was used to characterize stand age (Hedman and Van Lear 1995).

Stream reaches approximately 500 m long were divided into 15 m long stations (sample plots) to facilitate data acquisition and mapping. Stations were installed along the thalweg of each stream. Stream gradient, bank slope, and bankfull channel width were measured at each station. All LWD located within an area delineated by the bankfull channel width plus an adjacent 1-m band was inventoried (Froehlich 1973; Swanson et al. 1982; Harmon et al. 1986). Individual pieces >10 cm diameter and >1.5 m long were located as to station and bank position; tagged; measured (length, diameter large and small ends); and identified to group (based on growth-ring anatomy), genus or species level, and decay class. LWD that met the minimum size requirement was scaled only if it was in contact with the stream, suspended above the stream (potential), or on the bank and within 1 m of the channel (effective) (Swanson et al. 1984). Portions of effective LWD that extended beyond the 1-m band were not included in volume-weight estimates. Importance value (relative density + relative volume/2 X 100) was calculated by species for each stream. The volume of each piece was calculated using the formula for the frustum of a paraboloid (Lienkaemper and Swanson 1987).

LWD identification was based on leaves and bark when present, branching patterns, and wood anatomical features. Hemlock (*Tsuga canadensis* (L.) Carrière) was usually distinguished from other coniferous species by bark texture, branching characteristics, and wood color. Tulip-tree *(Liriodendron tulipifera* L.), white basswood (*Tilia heterophylla* Vent.), yellow buckeye (*Aesculus octandra* Marsh.), maples *(Acer* spp.), birches (*Betula* spp.), and Fraser magnolia *(Magnolia fraseri* Walter) were sometimes difficult to identify in the field and were subsequently lumped into a diffuse-porous category. In some cases, wood was in an extremely advanced state of decay, which prevented positive identification. These samples were placed in either unknown or ring-porous categories, depending upon whether vessel patterns were discernable. Ring-porous species included oaks (*Quercus* spp.), chestnut *(Castanea dentata* (Marsh.) Borkh.), hickories (*Carya* spp.), black locust *(Robinia pseudoacacia* L.), and blackgum *(Nyssa sylvatica* Marsh.).

Estimates of LWD mass typically require sampling logs for density. However, specific gravity has rarely been measured in aquatic studies and a value of 500 kg/m^3 is often used. This value adequately represents the average specific gravity of undecayed wood for all species; however, it overestimates the density of coniferous wood by 20-40% and underestimates hardwood density by the same factor (Harmon et al. 1986). Therefore, the density of LWD is typically estimated by using a decay-class system (Lambert et al. 1980; Lang and Forman 1978), whereby LWD is sampled to obtain the mean density of each decay class (Harmon et al. 1986).

In this study, three LWD decay classes were utilized and determined by firmly pushing a 0.5 cm diameter metal surveyor's pin

Table 1. Characteristics of study streams and their watersheds.

Stream	Riparian forest age (years)[a]	Serai stage	Stream order	Basin area (ha)	Sample area elevation (m)	Mean width of bankfull channel (m)	Mean stream gradient (%)	Mean bank slope (%)	Basin aspect
Thompson River Tributary	40 (7)	Mid	1	98	899	5.5	4	25	SE
Dicks	57 (10)	Mid	2	393	1036	7.7	4	43	SE
Dryman-4	65 (9)	Mid	4	468	853	7.6	2	25	NE
Jones	67 (10)	Mid	2	547	883	8.9	4	19	NNE
Henson	69 (8)	Mid	3	217	884	9.2	10	42	NE
Dryman-3	70 (5)	Mid	3	159	899	4.8	6	27	NNE
Galloway	180 (10)	Late	2	185	472	6.4	9	39	S
Reed	203 (5)	Late	2	1068	640	9.5	4	46	SW
Harden	221 (9)	Late	1	97	701	5.0	8	32	SE
Indian Camp	287 (9)	Old growth	3	352	768	7.5	1	22	SSE
Little Santeetlah	334 (3)	Old growth	3	1106	774	10.9	4	22	ESE

[a] Coefficient of variation (%) is in parentheses.

Table 2. LWD loading measured in volume (m^3/100 m) and mass (kg/100 m and kg/m^2) for the 11 study steams.

Serai stage	Stream	Riparian forest age (years)	Volume (m^3/100 m)	Mass (kg/100 m)	Mass (kg/m^2)
Mid	Thompson River Tributary	40	8.0	3 040.4	5.5
	Dicks	57	7.1	2 791.8	3.6
	Dryman-4	65	8.9	3 430.1	4.5
	Jones	67	11.1	4 280.8	4.8
	Henson	69	31.2	12 116.0	13.2
	Dryman-3	70	14.9	5 640.9	11.8
Mean			13.3	5 131.8	6.3
SE			9.1	3 528.4	3.5
Late	Galloway	180	9.5	3 820.3	6.0
	Reed	203	17.8	7 450.4	7.8
	Harden	221	11.4	3 821.1	7.6
Mean			12.9	5 030.6	7.2
SE			4.4	2 095.6	1.0
Old growth	Indian Camp	287	21.2	8 300.1	11.1
	Little Santeetlah	334	22.3	8 629.0	7.9
Mean			21.7	8 464.5	9.5
SE			0.8	232.6	2.2

into LWD boles. Decay classes were defined as follows: slight (wood hard, penetration <0.5 cm); moderate (spongy wood, penetration between 0.5 cm to the center of the sample); and advanced (very soft wood, penetration through the bole) (Lang and Forman 1978; Lambert et al. 1980). Since decay rate may vary along an individual LWD bole, classification was determined by the decay state of >50% of the bole (Lambert et al. 1980).

Mean specific gravity was computed for each decay class. Ninety (90) wood samples (across three decay classes) comprising a variety of LWD species were oven-dried, weighed, dipped in melted paraffin, air dried, and placed in a graduated cylinder filled with water to estimate their volume (Barber and Van Lear 1984). Specific gravity equaled the core weight divided by the volume of water displaced. Individual LWD (piece) mass was equal to piece volume multiplied by the associated specific gravity value of that decay class, and then summed to give dry-weight estimates of LWD per stream.

Riparian forest structure and composition were determined by installing a series of square nested plots adjacent to stream sample areas (Hedman and Van Lear 1995). Vegetation data

Table 3. Mean frequency (Freq.), volume (m^3), importance value (IV), and mass (kg) of the five most important LWD species or species groups, ranked by importance value across serai stages and totaled for all streams.

Serai stage	Species or group	Freq./ 100 m	Freq. (%)	Volume/ 100 m (m^3)	Volume (%)	IV	Mass/ 100 m (kg)	Mass (%)
Mid	*Castanea dentata*	16.4	30.3	6.6	37.5	33.9	2 560.9	37.3
	Diffuse porous	14.1	32.0	2.5	20.5	26.3	910.8	19.5
	Tsuga canadensis	8.6	22.5	2.5	27.4	25.0	955.7	27.0
	Quercus spp.	3.0	6.3	1.1	9.0	7.7	471.9	10.3
	Robinia pseudoacacia	2.5	4.3	0.5	3.4	3.9	187.2	4.3
Late	*Tsuga canadensis*	9.8	23.0	6.0	45.3	34.1	2 457.0	38.0
	Diffuse porous	13.6	31.6	2.0	16.1	23.9	761.7	12.5
	Castanea dentata	7.7	17.6	2.9	21.3	19.5	974.3	19.6
	Quercus spp.	7.8	19.6	1.7	14.4	17.0	702.4	10.6
	Ring porous	1.3	2.8	0.1	1.0	1.9	55.8	1.0
Old growth	*Tsuga canadensis*	16.3	39.5	13.3	61.0	50.2	5 363.7	63.1
	Diffuse porous	11.2	25.0	2.8	13.0	19.0	1 056.5	12.4
	Castanea dentata	10.6	18.7	3.6	16.6	17.6	1 250.8	14.9
	Quercus spp.	5.8	9.1	1.6	7.6	8.4	651.1	7.8
	Robinia pseudoacacia	7.5	11.3	0.6	2.7	7.0	223.7	2.7
All streams[a]	*Castanea dentata*	728	28.4	280.0	34.5	31.5	104 985.0	33.4
	Tsuga canadensis	579	22.6	291.6	35.9	29.2	116 154.1	36.0
	Diffuse porous	738	28.7	132.7	16.3	22.5	49 108.9	16.0
	Quercus spp.	270	10.5	75.1	9.2	9.9	31 525.6	10.4
	Robinia pseudoacacia	118	4.6	16.3	2.0	3.3	7 654.4	2.5
	Carya spp.	35	1.4	4.9	0.6	1.0	1 711.9	0.5
	Ring porous	33	1.3	4.0	0.5	0.9	1 337.1	0.4
	Unknown	46	1.8	5.8	0.7	1.3	1 850.6	0.6
	Rhododendron maximum	16	1.6	0.4	0.1	0.4	189.7	0.1
	Fraxinus spp.	2	0.1	1.3	0.1	0.1	408.0	0.1
	Pinus spp.	1	0.0	0.0	0.0	0.0	12.2	0.0
	Kalmia latifolia	1	0.0	0.0	0.0	0.0	11.4	0.0
Total		2567	101.0	812.1	99.9	100.1	314 948.9	100.0

[a] Total frequency, volume, and mass across all 11 streams.

were summarized by canopy stratum for each plot. Relative density, basal area, and importance value (relative density + relative basal area/2 X 100) were measured and calculated for trees, tall shrubs, and saplings. Riparian forest vegetation data, i.e., species composition and physical dimensions, were compared with dimensional and compositional attributes of LWD.

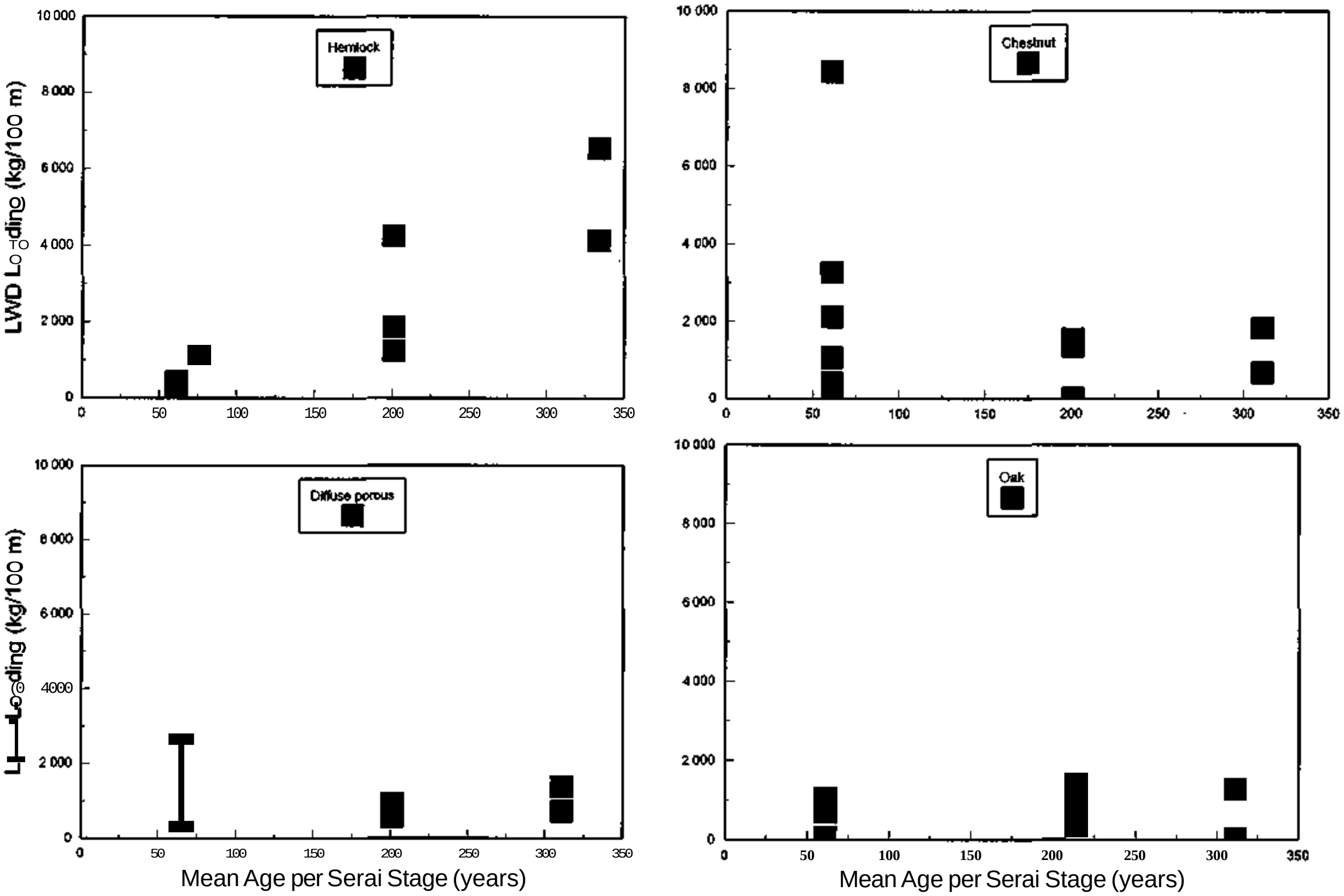
Descriptive statistics were computed for stream characteristics, riparian forest vegetation, and LWD. Relationships between LWD, riparian forest serai stage, and site and stream variables were explored via analysis of variance (ANOVA), mean separation, regression analysis using STATA (1990), cluster analysis, and discriminant function analysis using SAS (SAS Institute Inc. 1985).

Results and discussion

LWD loading levels

Ages of riparian forests ranged from 40 to 334 years, almost a 300-year sere (Table 1). Six of these systems were characterized as midseral stage, three as late serai stage, and two as old growth. Stream orders ranged from first through fourth, and basin area ranged from 97 to 1106 ha. Across all study streams, LWD loadings ranged from 7.1 to 31.2 m^3/100 m and 3.6 to 13.2 kg/m^2 (Table 2); volume and mass were highly correlated (r = 0.98) across serai stages. We found no trend between LWD volume (nrVlOO m) and bankfull channel width (p - 0.17, r^2 = 0.20). LWD loadings generally decrease with an increase in stream size (Harmon et al. 1986), and larger streams tend to have a smaller portion of their standing stock of organic matter in organic debris dams (Bilby and Likens 1980), suggesting that they have a higher capability of flushing LWD downstream and onto floodplains. High loading (mass = 13.2 kg/m^2) in Henson Creek was particularly impressive considering it was a relatively wide stream (bankfull width - 9.2 m). Although we found no relationship between stream width and LWD loadings in our topographically constrained streams, Nakamura and Swanson (1994) found that wood loading in low-gradient channels increased with channel width and sinuousity.

Fig. 1. LWD loading mass (kg/100 m) contributed by dominant LWD species groups across serai stages for 11 study streams.



Loadings were highly variable, especially in streams associated with midsuccessional riparian forests (Table 2). No significant differences (ANOVA) in loadings among serai stages were found across the entire 300-year sere (p = 0.70). Apparently, the high variability in loading for streams draining midseral riparian stands masked any potential loading trends when all three serai stages were considered. However, when loadings were analyzed by species or species groups (see next section), patterns of loading over time became clearer.

We found that LWD volume (m^3/100 m: p = 0.07; r^2 = 0.71) and mass (kg/m^2: p - 0.18, r^2 = 0.82) increased linearly in streams associated with late-successional through old-growth riparian forests, a time period of 165 years. This increase in loading, suggests that in-stream loadings build and stabilize in later stages of succession. Stabilized or less variable LWD loadings provide a relative permanency of conditions that are important to aquatic organisms that depend upon LWD for cover and food (Bilby and Likens 1980).

The period between 70 and 180 years post-disturbance represents a large temporal gap in our database. None of the 60 streams inspected had significant reaches (≥500 m) within this age group. During this interval, i.e., when midseral conditions grade into late serai, the extant riparian forest is the primary contributor of LWD. Consequently, in-stream LWD standing stocks are thought to be low in the early part of this phase (70-180 years) because the surrounding forest is young, mortality rates are relatively low, and corresponding decay rates are relatively rapid (Webster and Swank 1985; Harmon et al. 1986; Spies et al. 1988). Hedman and Van Lear (1995) showed that midsuccessional riparian forests in this study were even aged, while late-successional and old-growth forests had an uneven-aged structure. Diameter distribution patterns suggested a low mortality rate when forests are dominated by moderate-sized trees and a high mortality rate for large-diameter trees in these older stands.

LWD contributions from the current riparian forest are minimal during the midsuccessional stage and apparently begin to increase from overstory mortality approximately 100-150 years post-disturbance. High loading variability in midseral stages is attributable, in part, to differences in stand disturbance histories and the time since stand replacement disturbances occurred (Harmon et al. 1986; Spies et al. 1988). However, logging history alone does not explain why LWD loadings at Henson Creek and Dryman Fork-3 were much higher than those at streams of similar age and stand history in the midsuccessional sere. Differences in loadings within and among serai stages are also influenced by the composition and successional stage of riparian vegetation.

Table 4. Frequency (Freq.) basal area, and importance value (IV) of the most important overstory trees in riparian zones of study streams.

Serai stage	Genus or species	Freq. (%)	Basal area (%)	IV
Mid	*Liriodendron tulipifera*	23.1	31.3	25.5
	Betula lenta	23.0	17.4	20.2
	Tilia heterophylla	6.8	12.5	9.7
	Tsuga canadensis	7.3	6.6	6.9
	Betula alleghaniensis	7.2	4.9	6.0
	Acer saccharum	4.5	4.4	4.5
	Aesculus octandra	4.4	2.9	3.6
	Magnolia fraseri	5.4	1.9	4.7
	Carya spp.	2.9	2.2	2.5
	Acer rubrum	4.7	3.1	3.9
	Quercus rubra	2.1	4.6	3.3
	Quercus alba	0.8	2.9	1.8
	Robinia pseudoacacia	0.3	1.0	0.7
Total		92.5	95.7	93.3
Late	*Tsuga canadensis*	28.1	27.1	27.6
	Quercus alba	10.6	15.2	12.9
	Rhododendron maximum	17.3	3.6	10.5
	Pinus strobus	4.9	14.2	9.6
	Liriodendron tulipifera	4.2	13.3	8.8
	Acer rubrum	7.5	5.0	6.2
	Carya spp.	5.7	5.5	5.6
	Oxydendrum arboreum	6.1	3.1	4.6
	Quercus rubra	1.8	2.3	2.1
Total		86.2	89.3	87.9
Old growth	*Tsuga canadensis*	31.7	46.2	39.0
	Pinus strobus	3.5	13.6	8.5
	Rhododendron maximum	12.9	2.2	7.5
	Betula lenta	8.1	4.4	6.2
	Liriodendron tulipifera	2.8	8.2	5.5
	Quercus alba	3.8	5.3	4.6
	Oxydendrum arboreum	5.7	2.7	4.2
	Kalmia latifolia	7.4	0.7	4.1
	Acer saccharinum	5.0	2.0	3.5
	Betula alleghaniensis	4.3	2.4	3.4
	Platanus occidentalis	0.6	4.7	2.7
Total		85.8	92.4	89.2

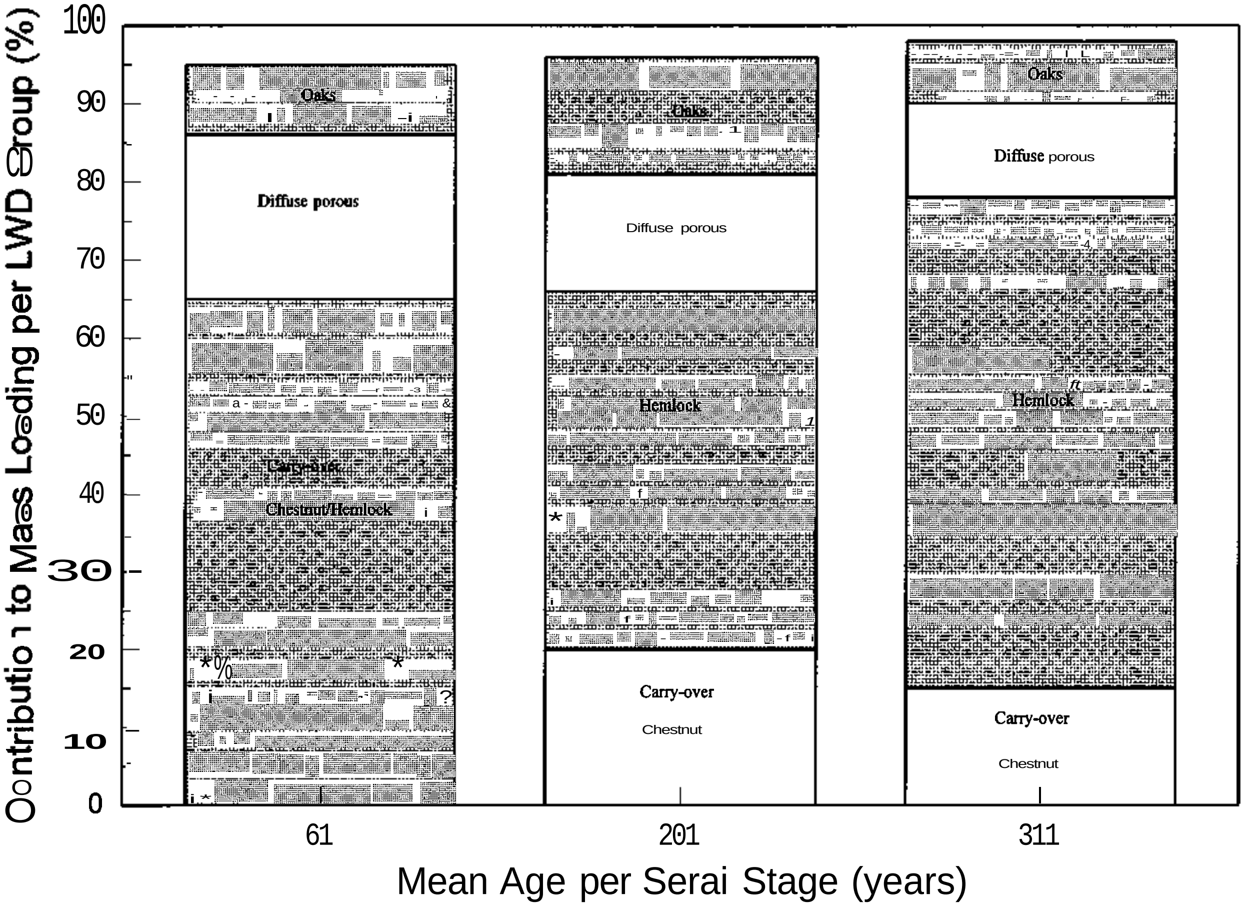
Note: The data are grouped by serai stage and ranked by importance value.

LWD loading by dominant species groups

The majority of LWD (68%) was identified to genus or species level, and less than 2% was placed in an "unknown" category. Across all streams, chestnut (importance value (IV) = 32), hemlock (IV = 29), diffuse-porous species (IV = 23), and oaks (IV = 10) dominated standing stocks (Table 3). These four species groups also accounted for 96% of LWD by mass across all streams. Chestnut (IV = 34), diffuse-porous (IV = 26), and hemlock (IV = 25) dominated midsuccessional stream systems. Hemlock (IV = 34), diffuse-porous (IV = 24), chestnut (IV = 20), and oaks (IV = 17) were the most important species found in late-successional streams. LWD in old-growth streams was primarily composed of hemlock (IV = 50), diffuse-porous (IV = 19), and chestnut (IV = 18).

LWD dominance (kg/100 m) changed across serai stage and time (Fig. 1). Hemlock mass increased from midsuccessional through old-growth stages (*p* = 0.00). A positive linear trend also existed across time ($p = 0.00$, $r^2 = 0.69$). Diffuse-porous, oaks, and chestnut loadings were not significantly different (ANOVA) among serai stages, and loading patterns were adequately described by lines with zero slope. Chestnut loading varied widely in midsuccessional stages. This variability suggests either that

Fig. 2. Percent contributions (kg) of dominant LWD, including carry-over debris across serai stages.



riparian forest composition varied widely in its proportion of chestnut or, more likely, that chestnut was harvested from some riparian forests following the blight.

Even though hemlock loading increased significantly across serai stages, significant loading increases of all species across the whole 300-year sere were only detected during late-serai through old-growth stages. Hemlock is a long-lived, decay-resistant, shade-tolerant species that contributes heavily to LWD loading and riparian forest composition in southern Appalachian cove forests during late-serai and old-growth stages of succession (180-334 years).

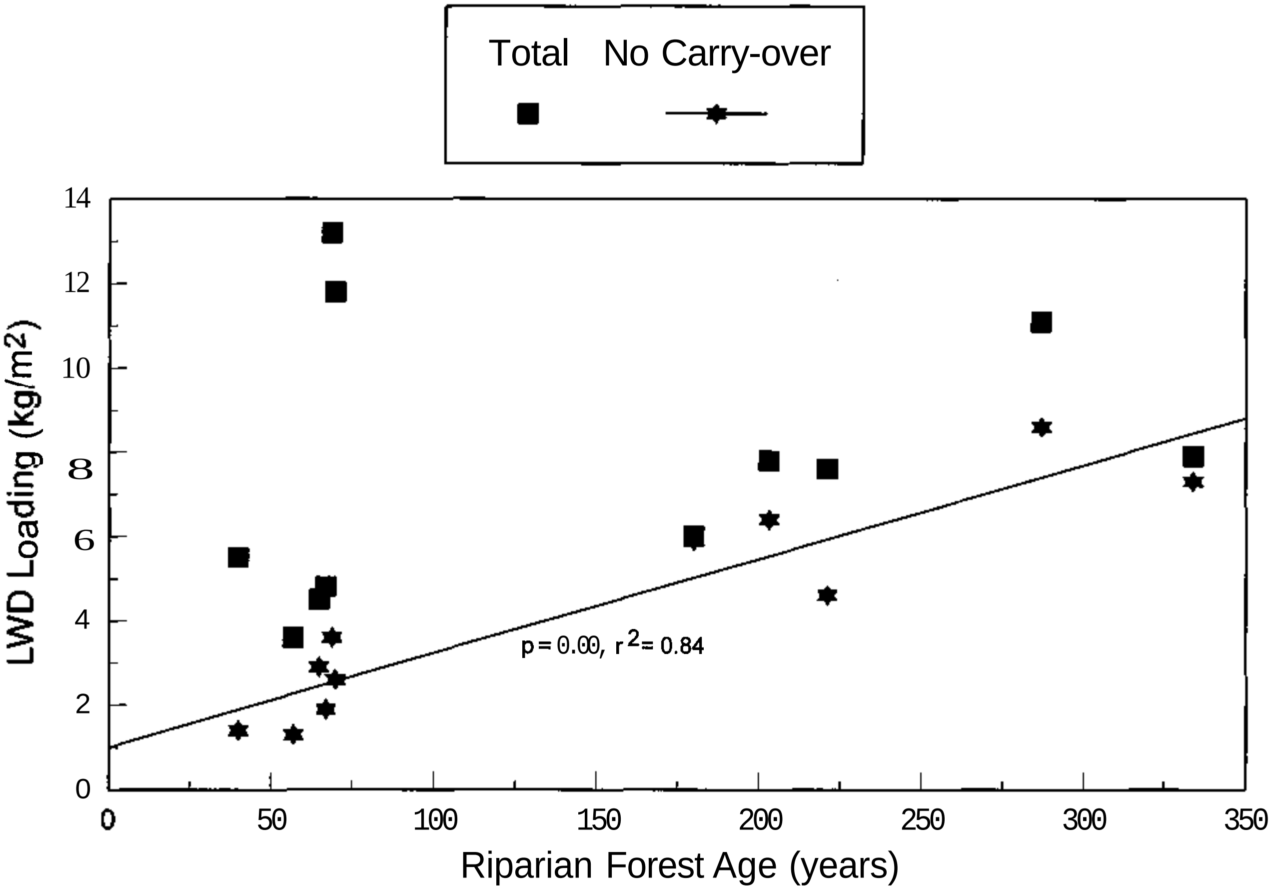
Interrelationships of riparian forest composition and LWD loading

The 11 stream systems in this study drained riparian forests that represented conditions and ages ranging from 40 through 334 years post stand-level disturbances. Riparian forests were representative of the mixed mesophytic deciduous forest, eastern hemlock forest, and transitions between these types (Hedman and Van Lear 1995). Midsuccessional southern Appalachian riparian forests are dominated by diffuse-porous species. Accordingly, diffuse-porous species would be expected to dominate LWD loadings in streams associated with this 40- to 70-year period. However, this was not the case.

Decay-resistant, carry-over debris (hemlock and chestnut) dominated elevated loadings in some 40- to 70-year streams (Table 2), yet both species were almost absent from the extant riparian forest (Table 4). Chestnut was characterized as carry-over debris based upon compositional disparities between the riparian forest and the LWD pool and upon the timing (60-80 years ago) and dynamics (specific and acute) of the chestnut blight. All chestnuts would have entered streams before and (or) during this interval by either natural means or logging. No new chestnut LWD has been added since the last stand-generating disturbance. Hemlock LWD was also considered carry-over debris based on its relative absence (relative frequency - 7.2%) from midseral riparian forests, i.e., compositional disparities. Carry-over debris was important to loadings in the Cascade Range of Washington and Oregon, where in 60- to 80-year-old stands, carry-over debris accounted for approximately 76% of all LWD and 39% in stands 120-160 years old (Spies et al. 1988).

Most hemlock LWD in 180- to 334-year streams was probably generated by the extant riparian forest, where the importance value of hemlock increased significantly across serai stages (*p* = 0.04) and through time (*p* = 0.00, r^2 = 0.63). Although hemlock is highly resistant to decay, an individual piece of debris would likely be lost through decomposition and (or) downstream transport by late serai stages of riparian forest succession. Therefore, hemlock LWD in 180- to 334-year study streams was considered the result of small-scale, within-stand (not stand-replacing)

Fig. 3. Relationship of total LWD mass, with and without carry-over debris (hemlock and chestnut), and riparian forest age.



mortality. This reasoning was utilized by Spies et al. (1988), who postulated that Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii)* LWD would disappear 250 years postdisturbance. Since Douglas-fir attains much greater mass than hemlock and the southern Appalachians have warmer climates and more equitable moisture regimes than the Pacific Northwest (Muller and Liu 1991), it is reasonable to conclude that most carry-over hemlock would disappear in less than 200 years.

Compositional disparities between present-day riparian forests and LWD illustrate the importance of carry-over debris and the fact that midseral stands are capable of producing little, if any, LWD. The conspicuous presence of carry-over debris in certain streams is further evidenced by the lack of relationships between LWD volume and basal area of current riparian overstory trees (p = 0.39, r^2 - 0.02), and LWD mean diameter and riparian tree mean diameter (p - 0.16, r^2 = 0.21). Conversely, when chestnut and hemlock carry-over debris was subtracted from LWD standing stocks, the LWD volume - overstory basal area relationship improved (p = 0.09, r^2 = 0.29). The relationship between LWD mean diameter and tree mean DBH was still not significant (p = 0.96, r^2 = 0.00). .

The lack of significant relationships between physical attributes of riparian forest and LWD components indicates that in these younger stream systems (40-70 years post-disturbance), LWD is primarily the result of previous stand-generating disturbances and not mortality of trees occupying the present riparian forest. Carry-over debris is eventually lost from stream systems (Fig. 2), and in the Southern Appalachians, hemlock eventually replaces it as the primary source of new LWD. Chestnut, of course, is no longer available for recruitment. During this transition, loading levels may be low if decomposition and downstream transport exceed riparian forest inputs. As riparian forest succession proceeds from late seral through old growth, the importance of hemlock as a contributor of LWD increases and consequently, loading levels gradually increase.

LWD loadings did not differ significantly among seral stages, partly because of the high levels of carry-over debris in some study streams. Had carry-over debris not been dominated by large, decay-resistant species (hemlock and chestnut) with long in-stream residence times, it is likely that loadings in streams associated with midsuccessional riparian forests would have been much lower. This supposition is supported by the fact that the mean diameter of carry-over chestnut (p - 0.00) and hemlock (p = 0.04) were both greater than that of the rest of the LWD population. In fact, highly significant differences in loading (mass and volume) across seral stages (p = 0.00) and a highly significant trend over time (p = 0.00,