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Dynamics of wood recruitment in streams of the northeastern US

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ABSTRACT

Wood is an important component of forested stream ecosystems, and stream restoration efforts often incorporate large wood. In most cases, however, stream restoration projects are implemented without information regarding the amount of wood that historically occurred or the natural rates of wood recruitment. This study uses a space-for-time analysis to quantify large wood loading to 28 streams in the northeastern US with a range of in-stream and riparian forest characteristics. We document the current volume and frequency of occurrence of large wood in streams with riparian forests varying in their stage of stand development as well as stream size and gradient. Linear models relating stream wood characteristics to stream geomorphic and forest characteristics were compared using Akaike's Information Criterion (AIC) model selection. The AIC analysis indicated that the volume and frequency of large wood and wood accumulations (wood jams) in streams was most closely associated with the age of the dominant canopy trees in the riparian forest (best models: $\log_{10}$(large wood volume ($\mathrm{m}^3\ 100\ \mathrm{m}^{-1}$)) = (0.0036 × stand age) − 0.2281, $p < 0.001$, $r^2 = 0.80$; and large wood frequency (number per 100 m) = (0.1326 × stand age) + 7.3952, $p < 001$, $r^2 = 0.63$). Bankfull width was an important factor accounting for wood volume per unit area ($\mathrm{m}^3\ \mathrm{ha}^{-1}$) but not the volume of wood per length of stream ($100\ \mathrm{m}^{-1}$). The empirical models developed in this study were unsuccessful in predicting wood loading in other regions, most likely due to difference in forest characteristics and the legacy of forest disturbance. However, these models may be applicable in other streams in the northeastern US or in streams with comparable riparian forests, underlying geology, and disturbance regimes—factors that could alter long-term wood loading dynamics. Our results highlight the importance of understanding region-specific processes when planning stream restoration and stream management projects.

1. Introduction

Large wood and accumulations of large wood (wood jams) are widely recognized as important features in forested stream ecosystems. Large wood is important in stream pool formation (Montgomery et al., 1995), in sediment and organic matter retention (Bilby and Likens, 1980; Diez et al., 2000), and in creating fish and invertebrate habitat (Flebbe and Dolloff, 1995; Riley and Fausch, 1995; Wallace et al., 1995). Recent studies have also linked increased wood volume to greater nutrient cycling in headwater streams (Steinhart et al., 2000; Valett et al., 2002; Bernhardt et al., 2003; Warren et al., 2007). Given the importance of wood to stream ecosystems, the volume, abundance, characteristics, and function of wood in streams is of interest to both researchers and managers (Bisson et al., 2003; Bernhardt et al., 2005), and a number of studies have documented standing stocks and wood loading rates for streams in many regions of the country and the world (Richmond and Fausch, 1995; Meleason et al., 2005; Chen et al., 2006; Young et al., 2006). Few studies have evaluated the dynamics of wood in northeastern US stream ecosystems, leaving those engaged in stream research and management with little guidance regarding historic conditions and future changes in loading and abundance of large wood. In this study, we surveyed 28 streams across the northeastern US, and quantified wood, stream, and riparian forest metrics at each site. From these data we (1) evaluated stream wood dynamics in the northeastern US relative to other regions; (2) quantified temporal trends in wood loading to streams in mixed northern hardwood forests; (3) identified factors that best accounted for variability in the amount of wood in these study streams of mixed northern hardwood forests; and (4) developed empirical models to predict current and future wood loading in the northeastern US and other regions with comparable forest type, geologic conditions, and disturbance histories.

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Wood recruitment into streams occurs either as a result of individual tree mortality or as a consequence of fine to coarse scale disturbances affecting multiple trees in the riparian forest. Secondary forests that developed following clear-cutting or land abandonment (old-field succession) currently dominate much of the landscape in the northeastern US (Foster, 1992). In the absence of anthropogenic influences, natural disturbance regimes interact with successional processes in shaping forest structure (Lorimer, 1977; Bormann and Likens, 1979; Runkle, 1982; Frelich and Graumlich, 1994; Keeton et al., 2007). Within the northeastern US, forest development following a stand-replacing disturbance (natural or anthropogenic) begins with a single cohort of trees that persists as an even-aged stand for up to 150 years (Bormann and Likens, 1979). During this stage of stand development high tree densities and competition for resources (e.g. light, nutrients, and water) lead to high density-dependent tree mortality and thereby a high potential for wood input to streams (Franklin et al., 2002). Density-dependent mortality naturally thins stands of weaker, less competitive trees. These trees are often smaller in size, limiting their effectiveness in stream geomorphological functions, such as debris jam formation and bank stabilization. Wood function is likely to increase later in stand development as dominant canopy trees achieve diameters of 30 cm or more (Keeton et al., 2007).

Density independent factors, such as local disturbance events, have a stronger influence on stand structure in later stages of stand development (Frelich and Graumlich, 1994; Lorimer and White, 2003). Although mass wasting and fire have controlling effects on wood inputs in some regions (Chen et al., 2006; Young et al., 2006), these processes are uncommon found in northeastern US hardwood-conifer forests. High intensity, stand replacing disturbances are infrequent in inland north temperate hardwood forests across the upper mid-west and northeastern US. In coastal New England, stand-replacing wind events (e.g. hurricanes) occur relatively frequently, with a return interval of only about 100 years. However, in forests of inland New England and upstate New York, return intervals for hurricanes and comparable stand-replacing wind events are much longer (350 years or more; Boose et al., 2001). Average return intervals for stand replacing fires in this region often exceed 1000 years (Fahey and Reiners, 1981; McGee et al., 1999; Seymour et al., 2002; Lorimer and White, 2003). Frequent small-scale disturbance events dominate forest dynamics in old-growth hardwood forests in the northeastern US and upper mid-west, and these disturbances may ultimately be more important to long-term wood accumulation in both forests and streams (Frelich and Graumlich, 1994; Ziegler, 2002). Disease has also been highlighted as a factor that may be increasingly associated with coarse wood on forest floors in northern hardwood forests (McGee, 2000).

Wood export from streams occurs as a result of decay, physical abrasion/breakdown, and fluvial transport. In-stream wood experiences frequent drying and wetting that increases decay rates. As a rule, conifers generally decay more slowly than hardwoods in streams (Melillo et al., 1983; Bilby et al., 1999; Spanhoff and Meyer, 2004), but some hardwoods, such as oaks (*Quercus* spp.), also decay slowly. Species that decay more slowly will remain in the stream longer and will therefore have a longer term impact on standing stocks of large wood. Physical breakdown of wood is influenced by the species and the decay stage of the wood interacting with the energy of the stream and the presence of objects, such as bedload or ice that actively abrades wood. Wood mobility is strongly influenced by wood length relative to bankfull width (Lienkaemper and Swanson, 1987; Young, 1994; Gurnell et al., 2002; Warren and Kraft, 2008), particularly in the constrained stream channels common in the northeastern US. Large pieces of wood exceeding the width of the bankfull channel are more likely to remain stable and act as a trap for smaller pieces of wood, resulting in reduced large wood export. Similarly, mobility of large wood is reduced in small streams with narrow channels, and export via fluvial transport is more limited. We therefore expect stand age and stream size interaction to influence wood loading and accumulation in northeastern streams (Likens and Bilby, 1982).

We used a suite of commonly measured stream and riparian forest characteristics and assessed their relationship to stream large wood characteristics. Akaike's Information Criterion (AIC; Burnham and Anderson, 2004) model comparison techniques were used to test an a priori set of linear models for each response variable. The current study complements earlier research that focused more specifically on riparian zones in the Adirondack Mountains of New York alone and suggested the potential for a strong relationship between in-stream wood volume and stand age in those riparian forests (Keeton et al., 2007). The current study encompasses a broader regional scope and focuses on predicting the dynamics of in-stream wood for future management and research. We hypothesized that the age of dominant canopy trees in the riparian area and stream bankfull width together would be the factors most closely associated with the amount of large wood in streams and with the frequency and size of wood accumulations.

2. Study site

This study included a total of 28 streams surveyed in summer or early fall across northern New York and New Hampshire (Fig. 1). Riparian forests for all streams were classified as mixed northern hardwood forests, a forest community that includes both hardwoods and conifers. The dominant riparian trees included: white pine (*Pinus strobus*), red spruce (*Picea rubra*), eastern hemlock (*Tsuga canadensis*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), ash (*Fraxinus* spp.), and American beech (*Fagus grandifolia*). No large-scale forest disturbances were documented at any study sites during the study. Stream gradient ranged from ~1% to ~24% and mean bankfull widths ranged from 1.4 to 15.1 m (see Table 1 for a summary of stream characteristics at each site). The age of the dominant canopy trees in the riparian forest ranged from approximately 20 to 370 years (Table 1). The mean age of the dominant canopy trees was highly variable, especially in older uneven-aged stands (see below for stand age estimate methods and associated references).

This study was conducted in two mountain regions in the northeastern US. Eighteen streams were surveyed in the Adirondack Mountains region of New York from 2003 to 2006, and ten streams were surveyed in the White Mountain region of New Hampshire from 2004 to 2007. Most of the White Mountain sites were located in the Hubbard Brook Experimental Forest (HBEF) (Bormann and Likens, 1979; Likens and Bormann, 1995). Ten of the Adirondack streams were surveyed as part of an earlier study on forest–stream interactions (Keeton et al., 2007), and some of the data from that study were included here. The large wood censuses conducted for the current study were completed separately from estimates conducted by Keeton et al. (2007), but occurred along the same stream reaches (Warren et al., 2008). Stream survey data from four streams at HBEF (Watersheds 2, 3, 5, and 6) are reported in Warren et al. (2007), though riparian forest surveys at these sites were conducted for the current study alone and have not been reported elsewhere. All additional data (six sites in NY and six sites in NH) are unique to this study.

Logging and subsequent fires fueled by logging debris contributed to the substantial loss of primary forests in much of the Adirondack Mountain region of New York during the 1800s and early 1900s (McMartin, 1994). Yet a number of areas in the interior and western portions of the Adirondacks were unaffected by

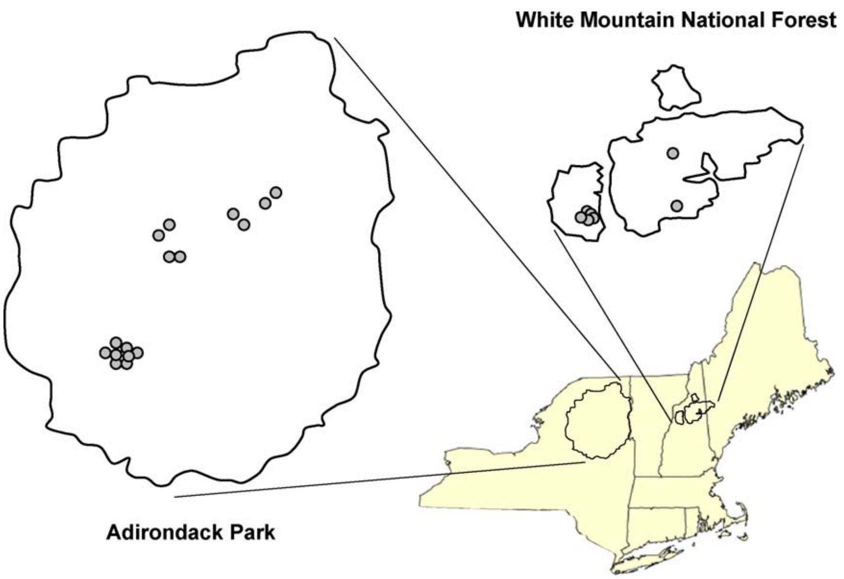

Fig. 1. Study sites across New York and New Hampshire. Grey dots indicate approximate locations of study streams.

logging or fire and currently contain some of the largest tracts of old-growth forests in the northeastern US (Leopold et al., 1988). Consequently, Adirondack old-growth forests have been used by many scientists to develop our understanding of old-growth conditions in the northern hardwood forests (McGee et al., 1999; Ziegler, 2002; Keeton et al., 2007).

The White Mountain region of New Hampshire is dominated by second-growth forests now between 70 and 150 years of age (Leak, 1991). Older forests are rare in this region, and restricted to isolated patches such as "The Bowl", an area of remnant old-growth in the central White Mountains with dominant canopy trees over 250 years of age (Leak, 1985; Martin and Bailey, 1999). Early records of forestry in the HBEF and surrounding forest indicate that the most recent logging occurred in the upper portions of HBEF watersheds prior to 1920 (Bormann and Likens, 1979; Peart et al., 1992). Although a number of the study streams in both regions have been impacted by logging or agriculture in the past, current activity on the streams is minimal, and as such anthropogenic wood removal was not considered to be a factor affecting our studies at these sites.

Table 1
Stream characteristics for the twenty-eight study streams from the White Mountains of New Hampshire and Adirondack Mountains of New York.

Stream	Stream gradient (%)	Mean bankfull (m)	Watershed area (ha)	Reach length (m)	Mean riparain basal area ($m^2\ ha^{-1}$)	%Conifer in riparain area	Dominant stand age (years)
White Mountain streams, NH							
HBEF W2	20	2.4	15.2	180	27.1	0.0	35
HBEF W3	21	4.0	42.4	310	32.5	1.4	86
HBEF W5	21	3.0	21.9	180	18.7	0.0	20
HBEF W6	24	2.9	13.2	246	29.5	1.5	86
HBEF W7	11	3.8	77.4	400	29.8	9.2	88
Trib b/t Can and Zig	18	1.4	1.9	200	33.5	2.8	88
Zig Zag—Mainstem	7	6.5	313.0	500	36.3	33.0	160
Hubbard Brk—Upper Mainstem	2	8.5	604.4	700	42.5	41.2	160
Hubbard BK—Lower Mainstem	3	15.1	2121.4	1200	34.8	14.5	88
The Bowl—Mainstem	5	3.7	28.0	300	38.3	5.7	223
Adirondack Mountain streams, NY							
Clear Lake (2)	8	2.5	27.2	120	41.7	29.0	315
LML Outlet—Oxbow	2	10.5	2430.3	500	25.5	34.0	109
Combs Brook	5	4.2	559.1	210	26.3	13.0	106
Witchhopple 1	3	6.6	452.7	200	33.7	34.0	254
Witchhopple 2	6	3.4	113.9	150	33.3	45.0	145
Canachaguala Brook	2	10.9	2317.7	250	26.4	55.0	94
Beth's Brook	1	3.7	177.7	150	22.6	18.0	81
East Lake Outlet	3	8.6	241.2	490	41.8	71.8	270
LML Outlet—below blockdam	2	7.3	1348.0	325	37.6	4.1	190
Ampersand—DuttonBrook	6	4.4	294.3	300	46.2	69.0	300
Ampersand—MellonberryBrook	4	4.7	315.1	350	40.6	69.0	280
Darby Brook	4	3.2	61.8	120	28.7	19.0	114
Otter Brook	1	5.0	583.2	230	34.8	32.0	132
Pico Creek	3	8.0	676.9	200	27.9	7.0	148
Clear Lake Outlet	3	8.0	300.7	190	41.1	36.0	370
Mature forests with Remant old growth (both systems)							
Elephant's Head (NH)	13	4.4	13.1	250	38.6	0.5	128
Constable Brook (NY)	2	6.0	420.1	150	31.8	61.0	144
Panther-trail trib (NY)	9	2.2	45.0	200	31.7	29.0	124

3. Methods

Surveyed stream reaches ranged from 120 to 1200 m in length and from 23 to >150 times the stream bankfull width, depending on the size of the stream. Whenever possible reaches were a minimum of 50 times the bankfull width (reaches were an average of 62 times the stream bankfull width; Table 1). Mean stream bankfull width was measured with five to fifteen evenly spaced bankfull width measurements along each reach. Reaches within a given stream were delineated beginning at geomorphic or landscape features (e.g. tributary confluences, lake outlets, or anthropogenic features such as trail crossings, bridges, or culverts). Reaches extended upstream or downstream from these starting points.

3.1. Riparian forest surveys

New riparian forest surveys were conducted at eighteen of the 28 sites. Riparian forests in the remaining ten streams were surveyed in association with Keeton et al. (2007) or in later comparable surveys by Keeton et al. (unpublished data, William S. Keeton, Rubenstein School of Environment and Natural Resources, University of Vermont). Data from those surveys included all relevant metrics for the current study. Riparian surveys consisted of a minimum of 5 randomly placed variable radius prism plots (2.3 metric basal area factor) within 75 m of either side of the streambed. Although trees 75 m from a stream edge are unlikely to contribute wood directly to the stream, all sample plots were taken within the broader riparian forest area and characterize the general forest condition in areas adjacent to the stream. Basal area and the relative abundance of species in the "dominant" canopy were estimated from these plots. At sites where forest age was unknown, and in which we could obtain permission to core trees, one core was taken from a dominant canopy tree at each plot to determine the mean age of the dominant canopy of the riparian forest following methods used in Keeton et al. (2007). All cores were mounted, sanded, and analyzed under a dissecting microscope. Mature forests containing scattered old-growth trees were classified as "mature with remnants". For these sites, the mean age of the canopy trees was estimated using only trees from the dominant, mature cohort, excluding remnant old-growth trees. These *mature with remnant* sites were not included in the regression analyses below because the two-aged structure of the dominant canopy did not conform to the age gradient we modeled. While this structural condition has not, until recently (see Keeton et al., 2007), been well described in northern hardwood systems, it may be more common than previously recognized due to partial, intermediate intensity disturbances (North and Keeton, 2008). For this reason, the three "mature-with-remnant" sites were included in our figures to evaluate how wood loading to streams in this riparian forest type differs from mature sites lacking remnant old-growth trees. For sites where we could not core trees, the age of the dominant canopy trees was determined using existing data from recent surveys, historical data on forest management, and/or historical data from earlier studies where trees were cored and aged (see Warren, 2008).

3.2. In-stream wood surveys

All large wood within the bankfull channel of each study reach was counted, and the approximate wood volume was estimated for each piece. Large wood was defined as dead wood greater than 10-cm diameter and 1-m length occurring within the bankfull stream channel. For each piece of large wood, we recorded: (1) the total estimated length of the piece >10-cm diameter, and (2) a single diameter measurement taken from a central point. Large wood

Table 2

Volume, mean size, and frequency of large wood, and the frequency and size of wood jams in study streams from White Mountains of New Hampshire and Adirondack Mountains of New York.

Stream	Wood volume (m^3 100 m^{-1})	Wood volume (m^3 ha^{-1})	Total #LW 100 m^{-1}	Mean LW diameter (m)	Mean LW length (m)	#Pieces >30 cm 100 m^{-1}	Proportion of wood in dams	Dams per 100 m	Mean dam size (m^3)
White Mountain streams, NH									
HBEF W2	0.72	29.2	9.4	0.19	2.3	2.2	0.41	2.8	0.57
HBEF W3	2.56	63.3	25.8	0.18	1.9	3.5	0.31	2.3	2.13
HBEF W5	0.40	13.4	7.2	0.20	1.7	0.6	0.31	1.1	0.92
HBEF W6	2.07	71.2	30.1	0.17	2.4	1.2	0.47	4.5	1.33
HBEF W7	1.18	31.5	25.3	0.16	1.9	0.8	0.44	3.3	1.19
Trib b/t Can and Zig	1.56	109.0	20.0	0.20	1.7	3.5	0.58	7.0	0.50
Zig Zag—Mainstem	2.54	39.0	20.6	0.19	2.6	2.6	0.63	1.8	3.00
Hubbard Brk—Upper Mainstem	2.27	21.6	19.9	0.18	2.9	2.3	0.42	0.7	10.83
Hubbard Brk—Lower Mainstem	0.83	5.5	5.8	0.17	3.8	0.7	0.24	0.4	3.48
The Bowl—Mainstem	2.44	65.8	30.0	0.17	2.3	2.3	0.40	3.0	1.37
Adirondack Mountain streams, NY									
Clear Lake (2)	5.83	236.9	43.3	0.21	2.1	8.3	0.35	0.8	0.35
LML Outlet—Oxbow	1.64	15.7	14.0	0.18	3.1	1.8	0.43	1.6	-
Combs Brook	1.55	37.3	17.6	0.21	2.0	3.8	0.03	1.0	0.46
Witchhopple 1	6.07	92.7	53.0	0.21	2.6	9.0	0.69	4.5	5.37
Witchhopple 2	0.67	19.5	10.7	0.15	2.3	0.7	0.25	2.0	0.70
Canachaguala Brook	0.98	9.0	7.6	0.19	3.6	0.8	0.00	0.4	7.50
Beth's Brook	1.19	32.0	24.7	0.14	2.6	0.7	0.19	1.3	0.35
East Lake Outlet	5.03	58.7	33.1	0.19	3.3	4.1	0.19	2.0	1.44
LML Outlet—below blockdam	3.68	50.1	35.4	0.17	2.7	2.2	0.38	3.7	2.02
Ampersand—DuttonBrook	6.01	137.2	44.0	0.21	2.4	7.7	0.33	3.3	1.88
Ampersand—MellonberryBrook	6.77	144.0	48.3	0.20	2.5	7.1	0.40	4.6	1.64
Darby Brook	2.19	67.4	33.3	0.19	1.8	5.8	0.50	1.7	0.51
Otter Brook	1.52	30.3	37.4	0.14	2.2	1.7	0.14	1.7	–
Pico Creek	3.12	39.2	47.5	0.17	2.2	1.5	0.53	6.0	2.04
Clear Lake Outlet	16.31	204.9	63.2	0.22	4.4	11.6	0.62	11.6	4.79
Mature forests with Remant old growth (both systems)									
Elephant's Head (NH)	5.54	127.21	48.8	0.22	2.3	9.2	0.60	2.8	8.04
Constable Brook (NY)	5.84	97.59	42.0	0.19	2.8	6.0	0.68	4.0	3.66
Panther-trail trib (NY)	3.34	150.05	16.5	0.24	3.2	5.0	0.15	0.5	0.19

length was estimated to the nearest 0.5 m using a 0.01 m delineated wading staff, and length estimates were verified using a field tape for the first 5 pieces in each stream. Similarly, wood diameter was estimated to the nearest 0.01 m and estimates were verified for the first 10 pieces in each stream. Diameter tapes were used on most large logs (>30 cm) where errors in the wading staff estimates were likely to have been greater. We used only the length of wood inside the bankfull channel for calculations of in-stream wood volume in order to isolate our measurements to functional wood (wood that is directly interacting with in-stream geomorphic and biological functions or processes). In this survey, wood volume for each individual piece was calculated using the formula of a cylinder, and total wood volume for each study reach was estimated by summing the total volume of wood within the bankfull channel. To allow comparison with other studies in both terrestrial and stream environments, we report both the volume of wood per linear 100 m of stream and the volume per hectare of streambed.

Wood jams – also commonly referred to as organic debris dams – were defined as accumulations of multiple pieces of coarse wood (dead wood between 0.5- and 1-cm diameter) against or around at least one key piece of large wood (Keeton et al., 2007). By our definition wood jams must also serve a “function” in the stream such as slowing or diverting water, retaining particulate organic matter (leaves and small pieces of wood), and/or retaining bedload or sediment. For wood jams that were not in the active channel and did not retain sediment or bedload at the time of our summer surveys, we estimated potential function based on a presumed bankfull flow event. Wood jams were counted and measured during the large wood surveys, and we recorded whether or not each piece was part of a wood jam. Size of the wood accumulation was approximated by estimating the length, width, and height of the structure (excluding impounded sediment) to the nearest 0.1 m. Wood accumulations without a key piece of LW that served a geomorphic function were not recorded. However, based on field observations, potentially functional wood accumulations lacking a key piece were rare or absent in these streams.

3.3. Wood jam characteristics

In analyzing wood jam characteristics, we first tested the relationship between wood jam frequency and size relative to stream bankfull width and stand age. Wood jams were expected to be larger in larger streams. We did not expect stand age to affect jam size once riparian forests approached maturity (>100 years for age of the dominant cohort) (Likens and Bilby, 1982; Bilby and Ward, 1989). We also quantified the proportion of all wood in a stream that occurred in wood jams. We expected the proportion of wood occurring in jams to increase with stream size (Gurnell et al., 2002). Data on jam size were unavailable for two streams, Little Moose Lake Outlet at Oxbow, and Otter Brook (Tables 1 and 2); with these two streams removed from the analysis, the distribution of bankfull widths for study streams was not normally distributed. Thus, bankfull width data were log transformed in all analyses relating wood jams to bankfull width.

3.4. Creating and selecting empirical models

We used Akaike’s Information Criterion (AIC, Burnham and Anderson, 2004) model comparison techniques to evaluate a series of linear models relating stream and riparian forest characteristics to each of the following response variables: large wood volume (m^3 100 m^{-1} and m^3 ha^{-1}), large wood frequency (number per 100 m), wood jam frequency (number per 100 m), and large log

Table 3
Top models for each of the stream wood metrics assessed in the AIC analyses.

Response variable factors in model	AIC_c weight	*p*-Value	r^2	Equation
LW volume (m^3) per 100 m of stream				
Stand age	0.461	<0.0001	0.80	$\log_{10}(\text{LWvol} \times 100\ \text{m}^{-1}) = (0.0036 \times \text{stand age}) - 0.2281$
Stand age + gradient	0.118	<0.0001	0.80	$\log_{10}(\text{LWvol} \times 100\ \text{m}^{-1}) = (0.0036 \times \text{stand age}) + (0.0322 \times \log_{10}(\text{gradient})) - 0.1922$
Stand age + watershed area	0.112	<0.0001	0.80	$\log_{10}(\text{LWvol} \times 100\ \text{m}^{-1}) = (0.0036 \times \text{stand age}) + (-0.0071 \times \ln(\text{watershed})) - 0.2141$
Stand age + bankfull	0.111	<0.0001	0.80	$\log_{10}(\text{LWvol} \times 100\ \text{m}^{-1}) = (0.0036 \times \text{stand age}) + (-0.0014 \times \text{bankfull}) - 0.2208$
LW volume (m^3) per hectare of streambed				
Stand age + bankfull	0.679	<0.0001	0.83	$\log_{10}(\text{LWvol} \times \text{ha}^{-1}) = (0.0033 \times \text{stand age}) + (-0.0717 \times \text{bankfull}) + 1.5358$
Bankfull + stand age + bankfull × stand age	0.232	<0.0001	0.84	$\log_{10}(\text{LWvol} \times \text{ha}^{-1}) = (0.0025 \times \text{stand age}) + (-0.0844 \times \text{bankfull}) + (0.0001 \times (\text{stand age} \times \text{bankfull})) + 1.6220$
Stand age + watershed area	0.060	<0.0001	0.79	$\log_{10}(\text{LWvol} \times \text{ha}^{-1}) = (0.0035 \times \text{stand age}) + (-0.2811 \times \ln(\text{watershed})) + 1.7209$
LW frequency (no. × 100 m^{-1})				
Stand age	0.315	<0.0001	0.63	$\text{LW freq} = (0.1326 \times \text{stand age}) + 7.3952$
Stand age + bankfull	0.244	<0.0001	0.66	$\text{LW freq} = (0.1355 \times \text{stand age}) + (-0.8730 \times \text{bankfull}) + 11.9058$
Bankfull + stand age + bankfull × stand age	0.135	<0.0001	0.69	$\text{LW freq} = (0.0782 \times \text{stand age}) + (-2{,}1243 \times \text{bankfull}) + (0.0105 \times (\text{bankfull} \times \text{stand age})) + 18.3606$
Large log (LW > 30 cm diameter) frequency (no. × 100 m^{-1})				
Stand age + bankfull	0.249	<0.0001	0.61	$\text{Large log freq} = (0.0033 \times \text{stand age}) + (-0.0290 \times \text{bankfull}) + 0.0190$
Stand age	0.199	<0.0001	0.55	$\text{Large log freq} = (0.0032 \times \text{stand age}) - 0.1309$
Stand age + lnwatershed	0.193	<0.0001	0.60	$\text{Large log freq} = (0.0034 \times \text{stand age}) + (-0.1114 \times \ln(\text{watershed})) + 0.0894$
Debris dam frequency (no. × 100 m^{-1})				
Watershed area + stand age + Watershed area × stand age	0.899	0.0002	0.61	$\log_{10}(\text{dam freq}) = (-0.0066 \times \text{stand age}) + (-0.6442 \times \ln(\text{watershed})) + (0.0039 \times (\text{stand age} \times \ln(\text{watershed}))) + 1.3800$
Bankfull + stand age + bankfull × stand age	0.085	0.0012	0.53	$\log_{10}(\text{dam freq}) = (-0.0025 \times \text{stand age}) + (-0.1336 \times \text{bankfull}) + (0.0007 \times (\text{bankfull} \times \text{stand age})) + 0.7959$
Gradient + stand age + gradient × stand age	0.004	0.0131	0.39	$\log_{10}(\text{dam freq}) = (-0.0062 \times \text{stand age}) + (0.9533 \times \log_{10}(\text{gradient})) + (10.0062 \times (\text{stand age} \times \log_{10}(\text{gradient}))) + 1.2173$

Models relate stream and riparian forest characteristics to each of five descriptors of wood in streams. The AIC weight, the *p*-value, the r^2 value and the equation for each of the top models are included for each stream wood metric.

(>30 cm) frequency (number per 100 m). The independent variables used in each set of models were as follows: (1) mean age of dominant canopy trees in the riparian area, (2) percent conifer in the riparian forest area, (3) mean riparian forest basal area, (4) mean bankfull width, (5) stream gradient, and (6) stream reach watershed area. All data sets were tested for normality and were log transformed when data were not normally distributed (assessed using an Anderson–Darling goodness-of-fit test, using $\alpha > 0.01$) (MINITAB® Release 14.20, 2005). The following data were log transformed: large wood volume per linear 100 m of stream, large wood volume per hectare of stream bed, watershed area (natural log transformed), gradient, and wood jam frequency.

Because the independent variables in linear models compared using AIC must be independent, we first constructed a correlation matrix for the six independent variables and ensured that correlated variables did not occur together in a single model. Within the limitations of the correlations, we established seventeen linear models for comparison using AIC model selection methods. These analyses excluded the three sites that lacked a clear estimate of stand age for the dominant riparian trees (mature forests with remnant old-growth), such that sample size (n) equaled 25 for all regressions unless otherwise noted. Low sample sizes necessitated the use of the corrected AIC value (AIC_c) for our analyses. The model with the lowest AIC_c value relative to other models in the set had the greatest support, and using the difference between this best model and subsequent models we calculated the AIC weight (w_i), a normalized likelihood, for each model (Burnham and Anderson, 2004). The AIC weight provides a measure of relative support for a given model (greater w_i indicates more support) and can be interpreted broadly as the probability that the model in question is actually the best model within the data set evaluated. In interpreting our analyses, we focused primarily on the model with the greatest w_i, but to allow for comparison of the top models we reported the top four models in each data set in Table 3. The AIC analysis ranks models and does not evaluate the significance of a model or provide parameter estimates. Regressions were run on the four best models in each analysis to estimate model parameters, determine significance, and quantify the variability explained by each model.

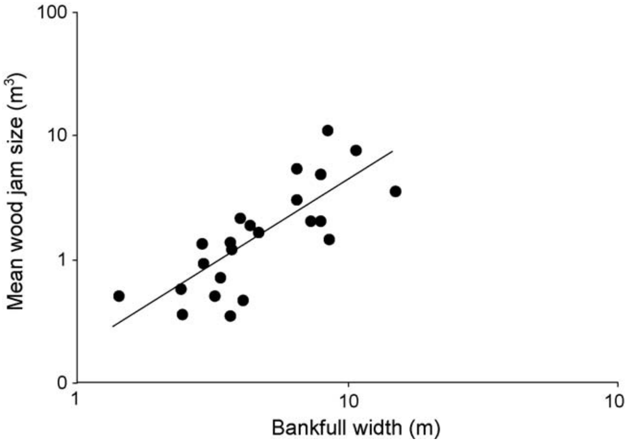

Fig. 2. Significant positive relationship between $\log_{10}$ of mean bankfull width and $\log_{10}$ of mean wood jam size ($p < 0.001$, $r^2 = 0.60$, $n = 23$).

4. Results

4.1. Large Wood characteristics

On an areal basis, large wood volume ranged from 5.5 to 236.9 $m^3\ ha^{-1}$ (Lower Mainstem of Hubbard Brook and Clear Lake 2, respectively Table 2) whereas the volume of large wood per

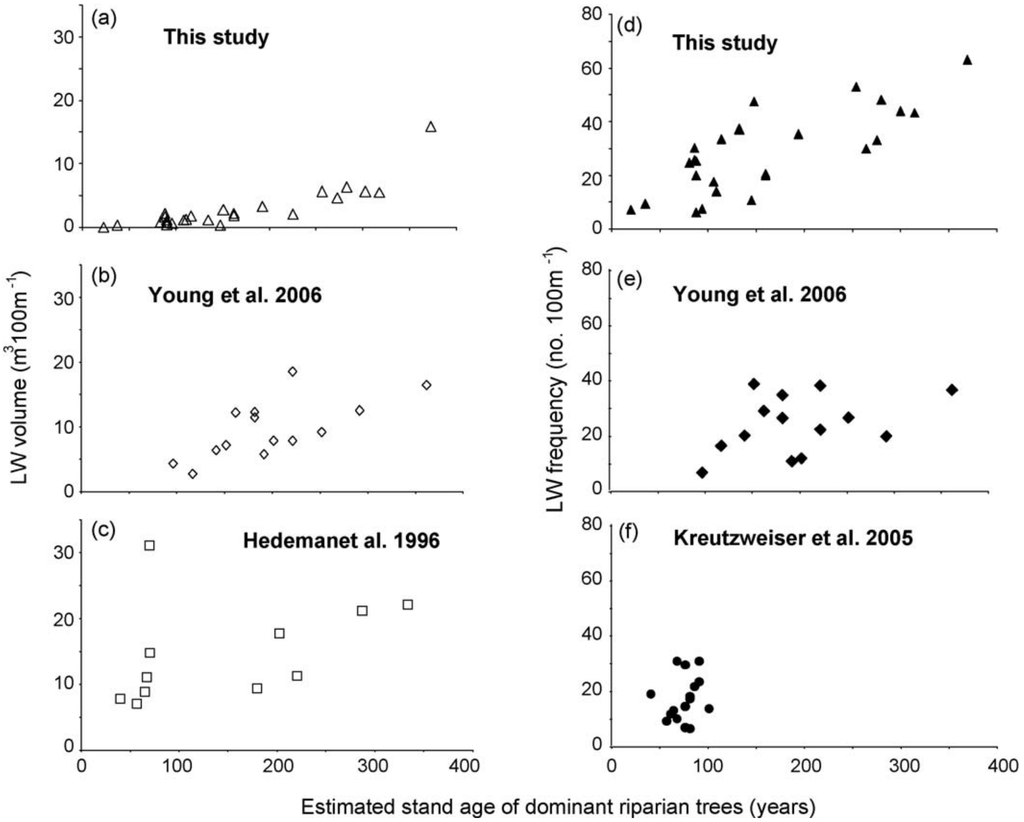

Fig. 3. Estimates of large wood volume and large wood frequency in streams relative to the age of the dominant riparian forest trees in our study as compared to three other studies: Young et al. (2006) in western Montana; Hedman et al. (1996) in the southern Appalachian Mountains; and Kreutzweiser et al. (2005) in the boreal forests of central Canada.

linear 100 m of stream ranged from 0.4 $m^3 \times 100\ m^{-1}$ (HBEF W5, youngest stand age) to 16.3 $m^3 \times 100\ m^{-1}$ (Clear Lake Outlet, oldest stand age; Table 2). The frequency of large wood (per linear 100 m) was greater in streams with older riparian forests (older mean stand age) than in those with younger riparian forests. Similarly, the frequency of large logs (>30 cm) was also greater in streams with older riparian forests.

4.2. Wood jam characteristics

All stream reaches contained at least one wood jam and several reaches contained more than 15 jams. Wood jam frequency ranged from 0.4 jams/100 m to 11.6 jams/100 m (Table 2). Although bankfull width was an important factor accounting for variability in wood jam frequency in a previous study (Warren et al., 2007), bankfull width alone was not significantly related to wood jam frequency in the current study ($n = 25$, $p = 0.07$, $r^2 = 0.13$). When stand age was included with bankfull width in a multiple regression analysis, the overall regression was significant ($p = 0.023$) and each of the metrics were significant ($p = 0.036$ and 0.038 for bankfull and stand age, respectively), however the regression explained only a small amount of variability in wood jam frequency ($r^2 = 0.29$). When the interaction of stand age with bankfull width was included in an AIC analysis, the explanatory power of the model increased ($r^2 = 0.53$), but this model was still not as predictive as the combination of watershed area and stand age (Table 3). Mean jam size was significantly related to the bankfull width ($n = 23$, $p < 0.001$, $r^2 = 0.60$; Fig. 2); however, the proportion of large wood pieces associated with wood jams was not significantly related to stream width ($n = 25$, $p = 0.51$).

4.3. Empirical models

The best model predicting the volume of wood per 100 m of stream included a single independent variable: age of the dominant riparian trees (Table 3). The mean age of dominant canopy riparian trees explained 80 percent of the variability in $\log_{10}$ transformed wood volume per 100 m ($n = 25$, $p < 0.001$, $r^2 = 0.80$; Fig. 3a). The three next-best models all included stand age with an additional independent variable – watershed area, gradient, or bankfull width – with little difference among these secondary models (Table 3).

Wood volume per hectare of streambed was best explained by the linear model including both dominant canopy stand age and bankfull width ($n = 25$, $p < 0.001$, $r^2 = 0.83$; Table 3). The model that combined basal area with bankfull width explained slightly more than 60% of the variability in wood volume per hectare in streams ($p < 0.001$, $r^2 = 0.65$). Stand age alone accounted for 60% of the variability in wood volume per hectare in our study streams ($n = 25$, $p < 0.001$, $r^2 = 0.60$; Fig. 4a). Large wood standing stocks in the "mature with remnants" sites was greater than would be expected given the age of dominant canopy trees alone, but less than was found in streams with entirely old-growth riparian forests (Fig. 4), suggesting that the remnant old-growth trees at these sites do lead to increased wood loading.

The frequency of large wood was also best explained by the model including stand age alone ($n = 25$, $p < 0.001$, $r^2 = 0.63$; Table 3, Fig. 4b), and all of the top models accounting for large wood frequency included stand age. A model including stand age and bankfull width together explained slightly more of the variation in large wood frequency ($r^2 = 0.66$; Table 3) but had a lower AIC weight. Two of the top four models included bankfull width, and one of the top models included watershed area (Table 3). Within the larger data set, models that included bankfull width (alone or in combination with other variables) had greater AIC weights than comparable models that included watershed area, though some of the differences in AIC weight were negligible. Bankfull width alone was not a significant predictor of large wood frequency ($n = 25$, $p = 0.62$, $r^2 = 0.01$).

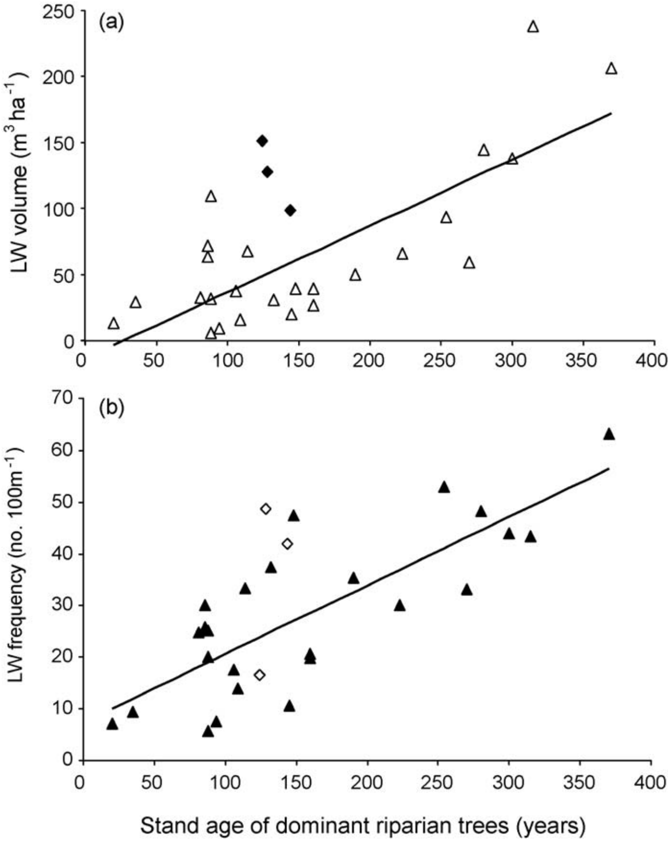

Fig. 4. Relationship between age of dominant canopy trees in the riparian forest and (a) the volume of large wood in associated streams (reported as cubic meters of wood per hectare of streambed; $p < 0.001$, $r^2 = 0.60$, $n = 25$) and (b) the frequency of large wood in associated streams (number per 100 m of stream; $p < 0.001$, $r^2 = 0.63$, $n = 25$). Diamonds (filled in (a) and open in (b)) represent sites with remnant old-growth trees present in a system dominated by a mature riparian forest.

The best overall model for predicting large log (large wood >30-cm diameter) frequency included both stand age and bankfull width ($n = 23$, $p < 0.001$, $r^2 = 0.61$), however, the AIC analysis indicated comparable support for the top two models (Table 3). Age of the dominant canopy (stand age) alone was the best single factor model ($p < 0.001$, $r^2 = 0.55$).

Wood jam frequency was best explained by a model including dominant canopy age, watershed area, and the interaction term between these factors ($n = 25$, $p = 0.001$, $r^2 = 0.61$; AIC weight = 0.90; Table 3). Stream bankfull width was not as strongly predictive as watershed area in the linear models evaluating wood jam frequency.

5. Discussion

Our results demonstrate that the volume of large wood in northern hardwood forest streams can be predicted from a few simple riparian forest and stream metrics. Age of the dominant riparian forest trees along with stream bankfull width were strong predictors of large wood volume and wood frequency in this region. These two metrics alone accounted for up to 83% of the variability in large wood volume and up to 66% of the variability in large wood frequency across streams. Overall, the volume of large wood in most northern hardwood forest streams is expected to increase as the age of dominant trees in the riparian forest increase over 100 years or more, well into the later stages of stand development.

5.1. Wood loading models

All of the top models relating riparian forest and stream characteristics to in-stream wood volume included the age of dominant riparian trees. Stream size was an important variable in predicting wood volume per hectare of streambed when included with stand age. However, stream size was less important in the models accounting for wood volume per linear 100 m of stream, at least for the range of stream sizes assessed in this study. This result indicates that the total amount of in-stream wood was comparable for a given dominant canopy age, independent of bankfull width, and implies either: (1) wood was transported downstream from its point of entry into the stream, but was retained in channel margins or in wood jams that were encompassed by our study reaches; or (2) wood input from upstream via fluvial transport was comparable to wood export from the reach via fluvial transport.

Old-growth forests generally have a greater total basal area (live and dead) (Tyrrell and Crow, 1994; Ziegler, 2002) and aboveground biomass (Keeton et al., 2007; Luyssaert et al., 2008) than younger forests. Disturbances that impact riparian trees and add wood to streams likely decrease riparian basal area, especially in older forests where a few large trees contribute disproportionately to stand basal area. A regression analysis of riparian forest basal area residuals versus stream large-wood volume residuals in older forests supported this expectation. We found no relationship between residuals in the younger forests but a clear negative trend in the older forests (riparian forest stand age >200 years; $n = 7$, $p = 0.05$). In streams with older riparian forests, stream reaches containing more large wood than expected for a given stand age (a positive wood volume residual) tended to have lower basal area than expected for that stand age (negative basal area residual). Conversely, lower than expected in-stream wood volumes corresponded to greater than expected riparian forest basal area in older forests.

It is important to recognize that a majority of the high intensity forest disturbance in the northeastern US during the past 200 years resulted from anthropogenic activities that removed large wood from both riparian forests and associated streams. Without abundant hold-over wood, wood accumulation in streams within young secondary forests start nearly ‘‘from scratch’’ and would not exhibit the ‘‘U’’-shaped temporal distribution in dead wood volume described in less disturbed locations where a pulse of wood volume is introduced into the system immediately following the disturbance, then decays, and then is rebuilt as the forest ages (terrestrial environment: Harmon et al., 1986, streams: Likens and Bilby, 1982; Valett et al., 2002). In systems with natural stand replacing events that do not lead to the physical removal of large wood or in systems where high mortality of slowly decaying tree species occur, hold-over wood is likely and a linear relationship between stand age and in-stream wood may be less apparent (Hedman et al., 1996).

Although natural stand replacing events are rare in the northeastern US (Seymour et al., 2002), intermediate, partial disturbance events are relatively common (Lorimer, 1977; Ziegler, 2002). In 1998, for example, an ice storm occurring across northern New York, northern New England and southern Quebec increased coarse wood recruitment to streams across the region (Kraft et al., 2002; Likens, 2004). Similarly, microbursts, isolated high wind events associated with thunderstorms, are regular intermediate-scale disturbance events in this region, with the potential to impact forest areas (Jenkins, 1995; Canham et al., 2001). Some of our study sites were within areas that were affected by the January 1998 ice storm and others were in the areas impacted by the microburst events. These disturbances likely increased the variability in our data. To the best of our knowledge, no such events occurred at any of the streams during our study.

Most mechanistic wood input models consider density-dependant mortality of individual trees during stand maturation to be a particularly important factor influencing wood loading. Gregory et al. (2003) indicated that most wood loading models from the Pacific Northwest maximize wood loading rates when the dominant stand reaches an age of 150–200 years and begin to switch from density-dependant to density-independent mechanisms for tree mortality. Although the rate of wood input may peak 150–200 years after disturbance, wood continues to accumulate beyond that point in time. Our results are consistent with projected increases in the standing stock of wood in Pacific Northwest streams for up to 300 years after stand replacement (Benda and Sias, 2003; Meleason et al., 2003), which is also consistent with previous observations reported by Keeton et al. (2007) for the Adirondack region.

Wood jam frequency was also related to the stage of stand development. Jam frequency was best explained by a model including both stand age and watershed area. Stream width was included as a factor among the top models but surprisingly, it was not included in the best model accounting for wood jam frequency. Similarly, stream gradient – a factor found to be important by Goebel et al. (2003) for streams in northern Michigan – received limited support (AIC weight of 0.04).

An increase in wood jam frequency with increasing stand age for streams with riparian forests 20 years of age or older is generally consistent with earlier work on a smaller number of streams at Hubbard Brook (Hedin et al., 1988; Warren et al., 2007). However, the oldest riparian forest evaluated by Warren et al. (2007) was only about 90 years old, and wood jam frequency as reported in Warren et al. (2007) reached a minimum when the riparian forest was approximately 20 years of age. This is the age of the youngest forest evaluated in the current study and is consistent with the expectation for a strong linear, rather than U-shaped, trend in wood loading over time in the current data set.

5.2. Relationships between large wood and stream size

Conclusions from studies of the relationship between stream size and the abundance of large wood in streams have been inconsistent. Some studies have found declines in the frequency and volume of large wood as stream size increases (Bilby and Ward, 1989; Bilby and Ward, 1991; Gomi et al., 2006), while other studies have found no relationship between stream size and large wood frequency (Beechie and Sibley, 1997; Gomi et al., 2001; Kreutzweiser et al., 2005; Young et al., 2006). Some have found increases in wood frequency as stream size increases (Robison and Beschta, 1990; Richmond and Fausch, 1995; Meleason et al., 2005). Stream width, one of two measures of stream size in this study, was not a strong factor accounting for the volume or frequency of wood per 100 m. This result contrasts with an observation from the Pacific Northwest, US that stream bankfull width was negatively related to large wood frequency (Bilby and Ward, 1991). These authors found that differences in riparian forest stand age led to differences in the slope of this relationship, similar to our observation of the importance of the interaction between stand age and stream size in accounting for large wood volume. Although the height of riparian trees likely exceeds bankfull width for most of these sites, the strong influence of stand age relative to bankfull width in regard to wood frequency suggests that, in these streams, the amount of wood present is more strongly affected by input from the riparian zone than output due to transport. For large logs, frequency was best explained by the model that included both bankfull width and stand age. Gurnell et al. (2002) noted that wood export is greater in larger streams, especially when stream bankfull width exceeds the height of riparian trees. Our inability to identify a strong relationship between in-stream wood volume ($100\ \mathrm{m}^{-1}$)

and bankfull width may have resulted from the fact that only three study streams had bankfull widths >10 m.

Early wood surveys in the Hubbard Brook Valley found that the frequency of debris dams declined as stream bankfull width increased (Bilby and Likens, 1980; Likens and Bilby, 1982), and we expected stream bankfull width to be a dominant feature influencing wood jam dynamics. Although wood jam size was related to stream bankfull width, wood jam frequency was not. This may be a result of sampling methodologies, as earlier studies in the Hubbard Brook Valley focused on channel spanning structures, while we evaluated all wood accumulations that contained a key piece of large wood and served a potential geomorphic function, but did not necessarily span the channel. We expected the proportion of large wood occurring in jams to increase as stream size increased due to greater wood transport in larger streams. However, we found no significant relationship between the proportion of wood occurring in wood jams and stream bankfull width. Although wood in the main channel may be more mobile, it also may be subject to deposition in a less organized fashion within channel margins and in association with irregularly occurring large boulders.

6. Conclusions

In the northeastern US, forest age is a strong predictor of large wood volume and frequency in streams. Using one or two parameters, forest age and stream bankfull width, we explained up to 80% of the variability in large wood volume in streams across two mountain regions in this area. The model results from this study support and expand upon our earlier work (Keeton et al., 2007) suggesting that the total volume and frequency of large wood and large logs in northeastern US streams will increase as riparian forests as this region continues to mature and progress toward later stages of stand development.

The linear models developed in this study provide the ability to estimate current and future wood loading to forested streams in this region from a few easily measured stream and riparian forest metrics. This information can be used by land managers to approximate the amount of large wood that is expected for a given stream, and then estimate the amount of wood needed to meet restoration goals, hence emulating natural conditions. This information may be particularly relevant in restoration efforts directed toward enhancing stream recovery from historical land-use practices in northern hardwood forest systems. Stream wood loads can be increased to mimic the abundance of structural features that would be found in a system with a riparian forest 50, 100 or 150 years later in stand development, depending on restoration goals and the stage of stand development in a stream's riparian forest. These empirical relationships also provide a capacity to predict future changes in wood volume within streams in landscapes where land use history is known or can be ascertained.

Models derived in this study are applicable to other forested streams in the northeastern US. However, broader application of the specific relationships described in this and other regional studies should be limited to systems with a comparable forest type, climate, forest disturbance regimes, land-use history, and underlying geological conditions. While the physical processes acting on wood itself are universal, differences in forest dynamics, wood recruitment rates and mechanisms, wood decay rates, and underlying geological conditions all act to create regionally specific standing stocks of large wood in streams. Results from one area cannot be applied universally across all stream ecosystems; stream restoration efforts that add wood should use local or regional wood volume and wood frequency estimates. Ultimately, restoration promoting the recovery of old-growth characteristics in streamside riparian forests may be the best way to enhance the natural frequency, volume and function of wood in streams.

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