RIVER RESEARCH AND APPLICATIONS

River Res. Applic. **23**: 21–33 (2007)

QUANTITY, CONTROLS AND FUNCTIONS OF LARGE WOODY DEBRIS IN MIDWESTERN USA STREAMS

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ABSTRACT

Large woody debris (LWD) can increase stream habitat heterogeneity by providing structure, altering flow patterns, enhancing sediment deposition, forming pools and retaining organic matter. In North America, the role of LWD has been studied extensively in streams of mature forests (e.g. Pacific Northwest), but few studies have assessed LWD in streams of younger forests (e.g. Midwestern USA). Our objectives were to: (1) quantify the volume and abundance of LWD in a set of Midwestern streams; (2) evaluate possible factors influencing LWD quantity; (3) identify the functional roles of LWD; and (4) compare LWD levels in the upper Midwest to those elsewhere in North America. In 2002 and 2003, we measured LWD and geomorphological variables in 15 low-gradient streams draining previously logged watersheds in the Upper Peninsula of Michigan. Mean (±SE) LWD volume ($0.77 \pm 0.12\,\mathrm{m}^3\,100\,\mathrm{m}^{-2}$) and abundance ($33 \pm 3$ pieces $100\,\mathrm{m}^{-1}$) were 71% and 10% lesser, respectively, than in streams of similar gradient elsewhere in North America. Channel shape (width:depth ratio) explained 30% of the variation in LWD volume (multiple stepwise regression, $P = 0.015$) while LWD length and length:channel width combined, explained 72% of the variation in LWD density (multiple stepwise regression, $P < 0.0001$). About 50% of the LWD either stored sediment or stabilized banks and 14% of the LWD formed pools, although pool density was not significantly related to LWD volume or density. LWD levels, overall, were low in upper Midwestern streams, but the relative importance of that LWD to ecosystem function may be magnified in these wood-poor systems. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS: large wood; forested streams; channel shape; geomorphic function; stream habitat

Received 16 June 2006; Accepted 20 June 2006

INTRODUCTION

At the watershed scale, streams are shaped by geology, water flow, material deposition, climate and landforms (Beschta and Platts, 1986; Rosgen, 1996). Locally, streams are shaped by bed and bank material, channel slope, hydrology and riparian vegetation (Rosgen, 1996). Riparian vegetation, such as trees, influence streams by providing shade, affecting the throughput of stream water, and contributing organic matter including large woody debris (LWD). LWD is often defined as wood pieces more than 10 cm in diameter and 1 m in length (Lamberti and Gregory, 1996; Gurnell *et al*., 2002), criteria that we will also adopt here. LWD enters streams because of natural events, such as wind, fire, disease, insects, floods, landslides and erosion (Harmon *et al*., 1986). Factors affecting LWD stability in stream channels include discharge, LWD size, bank stability, landslides, tree stand age, channel morphology and substrate size (Bilby and Ward, 1991; Martin and Benda, 2001). When LWD pieces are shorter than the channel width, the stream generally controls the distribution of wood. However, when LWD pieces are longer than the channel width, they may exert substantial control over the stream (Sullivan *et al*., 1987; Gurnell *et al*., 2002).

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Contract/grant sponsor: Challenge Cost Share Agreement; contract/grant number: 03-CS-11090700-012.
Contract/grant sponsor: Cooperative State Research, Education, and Extension Service, U.S. Department of Agriculture; contract/grant number: 2003-35101-12871.
Contract/grant sponsor: University of Notre Dame Environmental Research Center (Summer Graduate Fellowship).

LWD can affect channel heterogeneity by forming pools (Swanson *et al*., 1982; Wing and Skaugset, 2002; Triska, 1984), altering flow (Sullivan *et al*., 1987), changing substrate composition (Martin, 2001), or accumulating organic matter (Webster *et al*., 1994; Brookshire and Dwire, 2003). Such habitat heterogeneity depends upon LWD volume, abundance, spatial distribution, LWD size relative to channel size, orientation to flow, and channel gradient (Bilby and Likens, 1980; Bilby and Bisson, 1998). Amounts of LWD levels and their associated functions can vary within and among geographical regions (Martin, 2001). For example, LWD forms more pools in moderate-gradient streams than in low-gradient streams (Beechie and Sibley, 1997). In high-gradient streams, however, boulders rather than LWD form most pools (Martin, 2001). The levels and functions of LWD in streams can also be affected by regional differences in dominant vegetation and human influence (Martin, 2001). While many studies have assessed LWD within a region, few have compared LWD across regions to determine differences and potential controls (Harmon *et al*., 1986).

Our objectives in this study were to: (1) quantify the volume and abundance of LWD in low-gradient streams in the Upper Peninsula of Michigan; (2) evaluate possible factors influencing LWD abundance; (3) identify the functional roles of LWD in the study streams; and (4) compare LWD levels in the upper Midwest to LWD levels found elsewhere in North America. We predicted that in the heavily logged forests of the upper Midwest, stream LWD would be at low levels and would perform few of the ecological functions observed in streams of old-growth or mature forests (e.g. Harmon *et al.,* 1986).

METHODS

Study sites

During June–August of 2002 and 2003, 15 coolwater streams spanning the Ottawa National Forest (ONF), Michigan, were surveyed for LWD (Figure 1). These streams were chosen based upon similar geological land-type association (LTA), stream fish assemblage, stream size, surrounding forest age and accessibility (Table I). Trout species including brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), and rainbow trout (*Oncorhynchus mykiss*) inhabited all but three of the study streams. Stream bankfull width ranged from 2–12 m, and the study reach lengths were 15 times the bankfull width, or a minimum of 100 m. All streams drained watersheds that were logged at least once since 1804. One study reach was assessed per stream except for four streams, in which two reaches were assessed because of longitudinal heterogeneity in channel structure. For each reach, habitat assessments were done to calculate pool, riffle, and run habitat unit volume and area (modified from Hankin and Reeves, 1988). Sediment composition was also measured using a modified pebble count (Bain, 1999).

Quantification of LWD levels

All LWD pieces ($\geq$10 cm in diameter; $\geq$1 m in length) in the wetted and bankfull channels were directly counted and measured. Log calipers were used to measure diameter at the centre of each wood piece ($\pm$1 cm) and fibreglass tapes were used to measure length ($\pm$0.1 m). Volume (m^3) was calculated by assuming that the pieces were cylinders:

$$V = \pi r^2 L$$

where r is the radius of the wood piece (m) and L is the length (m).

Factors influencing LWD levels

Nine environmental variables were measured to determine their association with LWD volume and density in the stream channel: average bankfull channel width and depth, bankfull channel width:depth, water surface slope, average bank angle, average bank height, LWD length, LWD length:bankfull channel width, and the surrounding forest age. Channel width was measured at 1–3 points per habitat unit and depth was measured at three points across the channel where width was measured. Water surface slope was determined using a Lietz hand level and a stadia rod. Bank angle was measured from the water surface using a clinometer and metre-stick (Stevenson and Mills, 1999). Bank height was measured from the water surface to the top of the bank. Forest age, surrounding each

DOI: 10.1002/rra

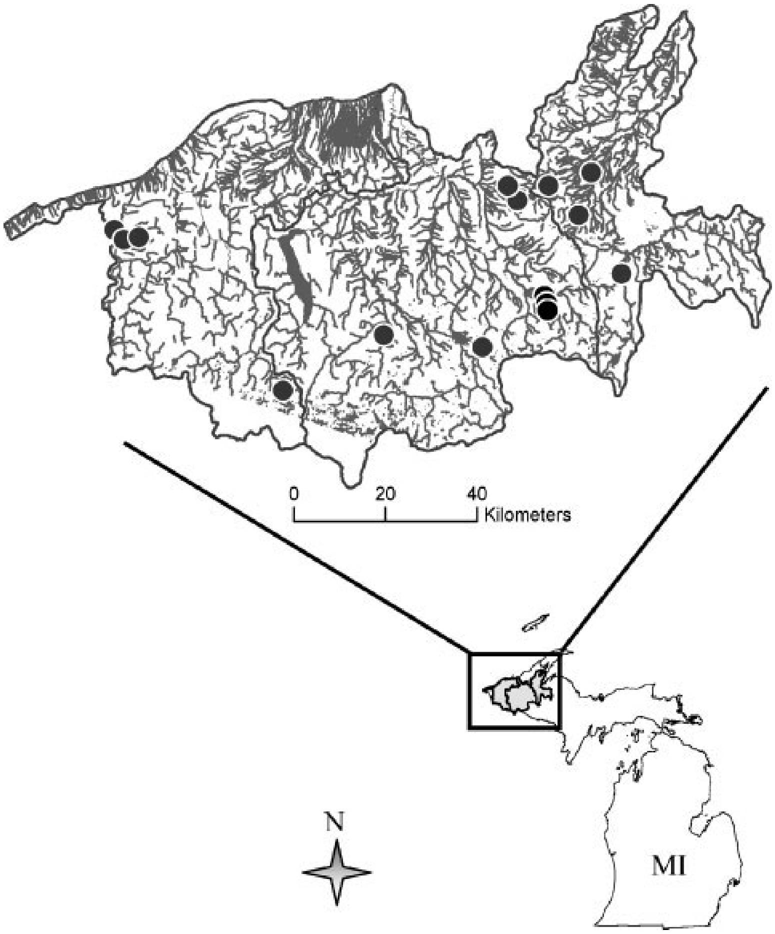

Figure 1. Location of 15 study streams within the Ottawa National Forest, Michigan

stream, was estimated by using GIS to locate the land area closest to the stream that had information on logging history (Ottawa National Forest database). Every 4 m along each stream reach, at 1–6 m from the active channel, a riparian tree diameter at breast height (DBH) was measured to estimate the average size of potentially recruitable logs into the stream channel. A dice was thrown to randomly select how far from the active channel the measured tree was.

Geomorphic functions of LWD

Within the wetted and bankfull channels during summer low-flow, LWD was surveyed visually to assign geomorphic functions to each piece (classification modified from Berg *et al*., 1998). Each LWD piece could have any, or a combination of, five functions: (1) forming pools and steps (LWD piece is upstream of pool/step and appears to help form it), (2) altering flow (LWD creates backwater or redirects flow), (3) stabilizing banks (LWD is part of a stream bank), (4) storing sediment (sediment is aggraded on upstream side of LWD), and (5) forming debris dams (LWD is key piece of debris pile). Individual rootwads and debris dams made solely of small wood were not included in this assessment.

Regional comparison of LWD levels

We used the literature to compare LWD volumes and abundances in our study streams to other North America streams (Appendix 1). To ensure comparability, only studies whose results were reported as, or could be calculated

DOI: 10.1002/rra

Table I. Characteristics of 19 study reaches in the Ottawa National Forest, Michigan

Stream	Year last logged	Watershed	Latitude	Longitude	Bankfull width (m)	Median substrate (D_{50})	Slope (%)	Surficial geology
East Branch Presque Isle	1936, 1940	Black-Presque Isle	46 16′ 35.4″	89 35′ 34.3″	9.4	gravel	1.3	Terminal moraine, coarse texture
Montowibo	1925	Black-Presque Isle	46 33′ 05.2″	90 00′ 31.7″	4.5	gravel	0.7	Ground moraine, coarse textured
Narrows	1910, 1915, 1926	Black-Presque Isle	46 33′ 40.5″	90 04′ 41.7″	5.9	gravel	0.9	Ground moraine, coarse textured
Reed	1910, 1925, 1935	Black-Presque Isle	46 34′ 17.0″	90 05′ 13.7″	4.0	gravel	1.0	Ground moraine, coarse textured
Jug	1937, 2001	Ontonagon	46 41′ 26.0″	88 58′ 09.6″	3.9	sand	0.8	Lake plains, coarse to medium textured
Leveque	1934, 1940	Ontonagon	46 40′ 04.7″	88 56′ 53.8″	4.3	gravel	0.8	Outwash plains, coarse textured
McGinty	1924, 1934, 1940	Ontonagon	46 21′ 19.7″	89 03′ 09.3″	5.0	sand	0.4	Terminal moraine, coarse texture
State (1)	1922, 1967	Ontonagon	46 24′ 49.1″	88 54′ 20.3″	2.3	gravel	2.4	Terminal moraine, coarse texture
State (2)	1918, 1924	Ontonagon	46 24′ 50.8″	88 54′ 26.7″	2.5	gravel	1.2	Terminal moraine, coarse texture
Shane (1)	1967	Ontonagon	46 27′ 51.8″	88 53′ 46.4″	2.7	sand	1.0	River valley and lake plain, coarse to fine texture
Shane (2)	1932, 1947	Ontonagon	46 27′ 49.3″	88 53′ 49.5″	2.9	sand	0.8	River valley and lake plain, coarse to fine texture
Two-mile (1)	1895, 1987	Ontonagon	46 23′ 10.2″	89 18′ 53.1″	12.0	cobble	0.6	Terminal moraine, coarse texture
Two-mile (2)	1930, 1938	Ontonagon	46 21′ 51.5″	89 19′ 52.6″	9.4	gravel	0.6	Terminal moraine, coarse texture
Walton (1)	1912	Ontonagon	46 26′ 44.8″	88 54′ 36.3″	1.9	sand	0.8	Recessional moraine, coarse textured
Walton (2)	1912, 1915	Ontonagon	46 26′ 46.8″	88 54′ 39.3″	2.6	sand	1.2	Recessional moraine, coarse textured
Perch	1804, 1840, 1870	Sturgeon	46 31′ 47.4″	88 39′ 07.8″	11.2	gravel	0.2	Ground moraine, fine textured
Silver	1880, 1885, 1890, 1912	Sturgeon	46 43′ 19.7″	88 44′ 02.8″	10.1	sand	0.3	Ground moraine, fine textured
Tradition	1820	Sturgeon	46 37′ 47.5″	88 47′ 37.2″	4.7	sand	1.2	Terminal moraine, fine textured
West branch Sturgeon tributary	1927	Sturgeon	46 41′ 38.9″	88 52′ 55.9″	4.5	sand	0.3	Terminal moraine, fine textured

DOI: 10.1002/rra

as, LWD volume per unit stream area ($m^3\,m^{-2}$) or LWD abundance per unit stream length (no. m^{-1}) were selected. These were the most common metrics reported in LWD studies, and therefore we also report our data in terms of these quantities. Results were categorized by climatic region and stream gradient. We also noted authors' definition of LWD, forest stand age, and the method of LWD assessment.

Statistical analyses

Stepwise multiple regression was used to determine which environmental variables, among those measured, explained the most variation in LWD volume and density (SAS 8.0, SAS Institute, Raleigh, NC, $\alpha = 0.05$). Simple linear regression was used to examine the statistical relationship between the number of pools and LWD volume or density. All data were first tested for conformance to normality and if violated, the following transformations were used: $\log_{10}$ transformation for average bankfull width, bankfull width:depth, and surrounding forest age; reciprocal transformation for bank height; square root transformation for LWD volume. Angle degrees were converted to radians.

RESULTS

Factors influencing LWD levels

In the 19 stream reaches, a total of 1024 LWD pieces were counted and measured within the bankfull channel. LWD piece length and volume were typically less than 4 m and 0.4 m^3, respectively. Average LWD (±SE) density in the wetted channel for each stream reach was 9.84 (±1.39) pieces 100 m^{-2} and volume was 0.89 (±0.15) m^3 100 m^{-2}. Average LWD piece diameter was 0.18 m and average riparian tree DBH was 0.12 m, suggesting that most trees were too young to contribute LWD in the channel. LWD volume was negatively related to bankfull channel width:depth, which explained 30% of the variation in LWD volume ($P = 0.015$; Figure 2). LWD density was positively related to LWD length:bankfull width and negatively related to average LWD length, which together explained 72% of the variation in LWD density ($P < 0.001$; Figure 3). All other variables (bankfull width, bankfull depth, water surface slope, bank angle, bank height, forest age) were not significantly ($P > 0.05$) related to LWD volume or density.

LWD functions

Across all streams during low flow, 27% of LWD pieces in the wetted channel stored sediment, 22% protected banks, 20% altered flow, 14% formed pools, and 9% were part of debris dams (Figure 4). In the smaller streams

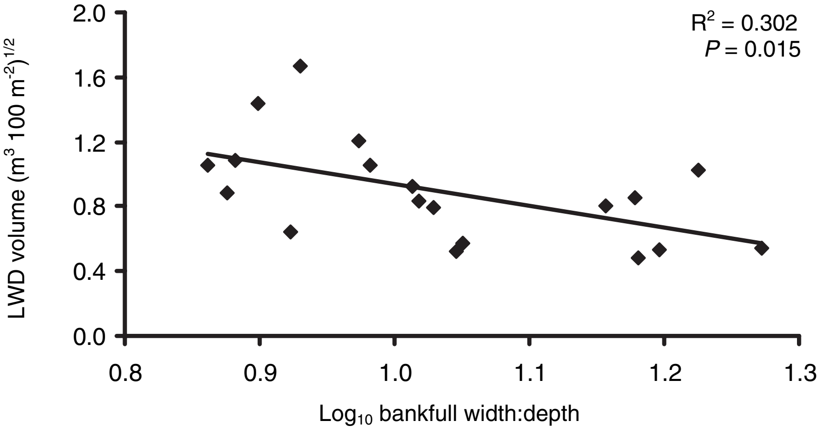

Figure 2. Relationship between LWD volume and channel width:depth in 19 stream reaches. [Stepwise multiple regression: square-root LWD volume = 2.29 − 1.35 ($\log_{10}$ width:depth)]

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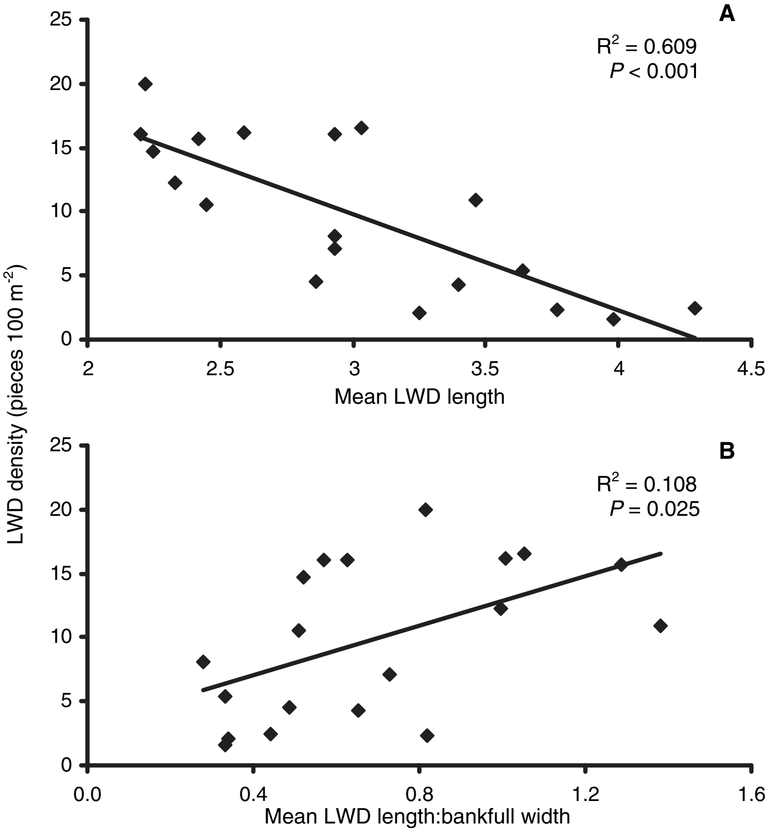

Figure 3. Relationships between (A) LWD abundance and length and (B) LWD density and piece length:bankfull width from 19 stream reaches. [Stepwise multiple regression: LWD density $= 25.3 + 6.3$ (LWD length:bankfull width)–6.6 (LWD length); $R^2 = 0.718$; $P < 0.001$]

($<$5 m wide), most wood pieces altered flow or stored sediment. In medium-sized (5–10 m wide) and large ($>$10 m) streams, most pieces stabilized banks or stored sediment. Debris dam formation was much more common in small and medium-sized streams than in large streams (Figure 4). Despite the fact that LWD formed pools in streams of all sizes, the frequency of pool habitats was not significantly related to the density ($P = 0.86$) or volume ($P = 0.89$) of LWD in the wetted channel.

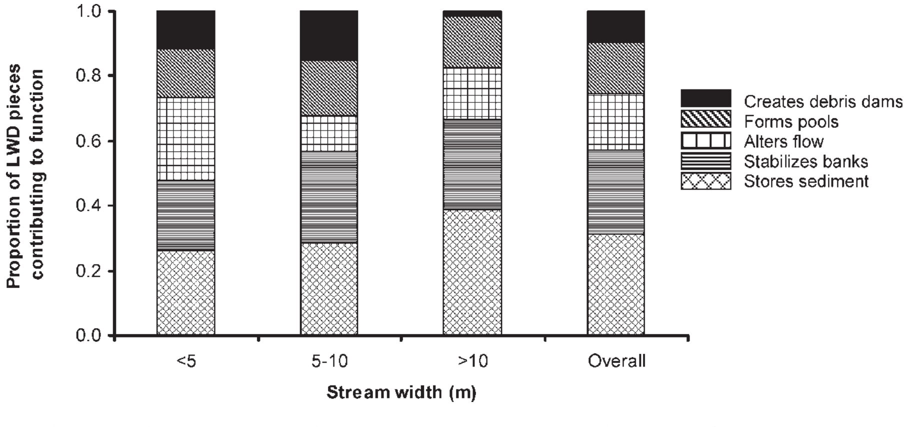

Figure 4. Geomorphic functions of 1024 LWD pieces found within the bankfull channel for small ($<$5 m, $n = 12$), medium (5–10 m, $n = 4$) and large ($>$10 m, $n = 3$) streams in the Ottawa National Forest, Michigan

DOI: 10.1002/rra

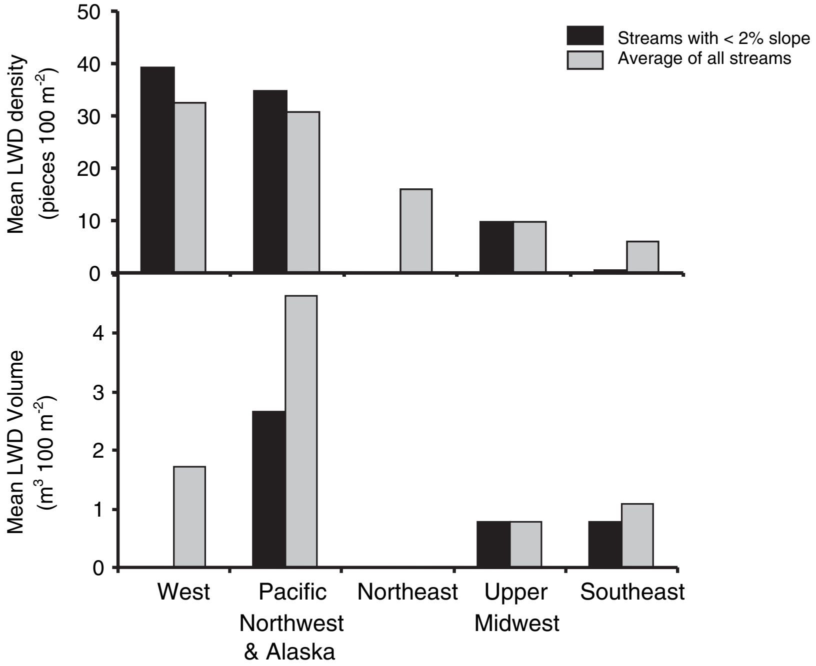

Figure 5. Comparison of LWD density and volume in streams of the upper Midwest (this study) with other regions of the US. Zero values indicate that data were not available

Regional comparisons of LWD levels

Mean densities of LWD in 200 streams from across North America ranged from 6.1–36.2 pieces $100\,m^{-1}$. LWD density in the Midwest (32.6 pieces $100\,m^{-1}$) was similar to other regions with similar gradient streams (33.2–39.3 pieces $100\,m^{-1}$) and was much higher than in Northeastern and Southeastern streams (16.1 and 0.4 pieces $100\,m^{-1}$, respectively; Figure 5a, Appendix 1). Average volumes of LWD for 191 North American streams ranged from 0.77–5.04 m^3 $100\,m^{-2}$. Mean LWD volume in upper Midwestern streams (0.77 m^3 $100\,m^{-2}$) was much lower than in streams with similar gradients elsewhere (1.64–3.68 m^3 $100\,m^{-2}$) except for Southeastern streams (also 0.77 m^3 $100\,m^{-2}$; Figure 5b, Appendix 1). If variation in LWD definitions and time since logging were considered, differences in LWD abundance may also have emerged, but we were unable to assess this for every study.

DISCUSSION

Factors influencing LWD levels in Midwestern streams

In our study streams, LWD volume was negatively associated with bankfull channel width:depth, which suggests that stream cross-sectional shape affected wood movement. As streams became narrower and deeper (i.e. more incised), more wood was found in the channel. As streams became wider and shallower, less LWD was found. Martin (2001) similarly noted that as low-gradient floodplain streams widened, wood amounts decreased. Furthermore, Jones and Smock (1991) noted that frequent floodplain interaction decreases particulate matter (e.g. small wood) movement in the stream channel, whereas less floodplain interaction increases particulate matter movement in the channel. Thus, in wider and shallower ONF streams, wood may be transported out of the channel (i.e. further downstream or onto the floodplain) by high flows. Therefore, channel morphology and likely stream flow may be important factors affecting LWD volumes in ONF stream channels.

LWD density was negatively related to mean length alone, suggesting that in these streams, short LWD pieces were abundant and that long pieces were scarce (i.e. pieces >4 m in length). Additionally, LWD density was

DOI: 10.1002/rra

positively related to the piece length:channel width ratio, suggesting that smaller pieces would be just as likely to be found as longer pieces in narrow streams such as these. The positive relationship between LWD density and LWD length:channel width suggests that channel width was important in determining the size of LWD retained. In wide streams, many LWD pieces were long (>4 m), whereas all sizes of LWD were present in smaller streams. Bilby and Bisson (1998) found that wider Northwest streams had less LWD, but our study revealed no significant relationship between stream width and LWD density. Perhaps because we had limited amounts of wood, or our range of stream sizes was relatively small, we were unable to detect a relationship between stream width and LWD density. However, our results are consistent with those of Gurnell *et al*. (2002) and Sullivan *et al*. (1987), who suggested that LWD abundance was determined primarily by LWD length:channel width.

Amounts of LWD in streams of the ONF were low, compared to other North American streams in older forests. Older forests contribute more in-stream LWD than do younger forests (Evans *et al*., 1993; Ralph *et al*., 1994). All ONF study sites were logged 30–180 years ago, and sometimes more than once during that interval, and thus were relatively young. After a disturbance (e.g. logging), LWD input to streams may take at least 40–60 years or longer to recover (Gregory *et al*., 1987). Ralph *et al*., (1994) found that streams in unlogged basins (old-growth) had more and larger LWD than did logged basins (second-growth). They also noted that increased logging intensity decreased the amount of LWD that interacted with the low-flow wetted channel. Therefore, past logging in the ONF may have reduced the natural input of LWD to streams, a legacy that is still expressed today.

Geomorphic functions of LWD

In streams of the ONF, LWD generally stored sediment, stabilized banks or altered flow. Geomorphic features altered by LWD depend on dominant substrate type (Berg *et al*., 1998), stream gradient (Beechie and Sibley, 1997; Hilderbrand *et al*., 1997; Young *et al*., 1999), and stream size (Bilby and Ward, 1989). Most ONF streams were dominated by sand and gravel, were low-gradient, and ranged in width from 2–12 m.

LWD was not statistically related to pool frequency in ONF streams, although 14% of all LWD formed pools. In ONF streams, pool formation by LWD may be more related to stream gradient and stream size, rather than by LWD redirecting flow and redistributing fine substrates (Beschta and Platts, 1986). Berg *et al*. (1998) found that LWD influence on pool formation was diminished in high-gradient streams because pool formation was highly influenced by cobbles and boulders. Beechie and Sibley (1997) reported that pool formation by LWD was less prominent in low-gradient streams than in moderate-gradient streams, likely due to differences in stream power. In contrast, pools were formed more frequently by LWD in low-gradient streams than in high-gradient streams where boulders formed most pool habitat (Hilderbrand *et al*., 1997; Martin, 2001). Therefore, the relative importance of LWD likely decreases in high-gradient streams dominated by boulders but increases in low-gradient streams dominated by small substrates, suggesting the LWD could assume added importance to pool formation in ONF streams as recruitment is enhanced in maturing forests.

Our results concur with other studies showing that the influence of LWD depended on stream size (Bilby and Ward, 1989; Gurnell *et al*., 2002). Gurnell *et al*. (2002) noted that in smaller streams, pieces of wood are typically larger in relation to channel size, and thus affected small streams more than large streams. In the ONF, LWD altered flows more often and formed more pools in small streams than in large streams. Also, in smaller ONF streams debris dams were more prevalent, which can alter flow and possibly organismal communities (Benke *et al*., 1985). LWD stored sediment across all stream sizes, which may also affect the types of organisms using those substrates (Hilderbrand *et al*., 1997).

Regional comparisons of LWD levels

Stream LWD volumes are thought to differ among regions because of differences in dominant forest composition (Harmon *et al*., 1986). Large coniferous trees, whose diameters can reach 5 m, grow in the coastal and montane forests of the Pacific Northwest and Alaska and contribute extremely large wood to streams (Harmon *et al*., 1986; Martin, 2001). Smaller coniferous and deciduous trees, whose diameters may reach only 1 m, grow in the ONF and contribute small wood to streams. For example, the largest wood piece that we measured was 67 cm in diameter and the largest riparian tree was 75 cm in diameter. Logging also strongly influences wood size in streams. Ralph *et al*.

DOI: 10.1002/rra

(1994) found that old-growth forests contributed large wood to stream channels, whereas managed forests contributed smaller wood to stream channels.

LWD abundance did not differ markedly among regions, although a range of definitions of LWD lower limits was found in the studies (0.05–0.30 m in diameter, 1–5 m in length). Wood exceeding 0.3 m in diameter was abundant in streams of the Pacific Northwest. When the minimum LWD size of 0.3 m was applied to our streams, LWD abundance declined dramatically. Only 10% of ONF LWD pieces exceeded 0.3 m in diameter, suggesting that LWD is small and sparse in ONF streams compared to the Pacific Northwest and other western states and may be comparable to amounts found in the Southeast. Differences in LWD abundance across regions may also be related to channel shape, stream width, substrate composition (Martin, 2001) and logging (Ralph *et al*., 1994). Therefore, in ONF streams, low wood volume and abundance is likely related to a combination of tree stand composition, channel morphology, logging history and forest management.

CONCLUSIONS

Little is known about LWD quantities and functions in streams of the upper Midwestern US even though LWD has been used to enhance trout habitat in Michigan streams since at least the 1920's (Hubbs *et al*., 1932). Our study suggests that LWD *abundance* in Midwestern streams is similar to low-gradient streams in other regions of North America, disregarding LWD size differences, but that LWD *volume* in the Midwest is very low by comparison. This disparity is a function of the overall small size of wood in Midwestern streams, even in relatively well managed national forests. Even at low volumes, LWD was often the only large substrate in these sandy Michigan streams and therefore represents an important ecological feature that increases habitat heterogeneity. In small streams of this region, LWD volume and density were influenced by channel morphology and LWD piece length:bankfull channel width. Because substantial regional differences in LWD volume and density were found, a need for regional perspectives on LWD in streams exists. Understanding regional and local stream characteristics will enable agencies to appropriately manage the level of LWD in streams and better use LWD for stream habitat enhancements in the future.

ACKNOWLEDGEMENTS

The authors thank the USDA-Forest Service, Ottawa National Forest, for support, especially Jerry Edde and John Pagel for field crew time, personnel, and equipment and Sean Dunlap for help in acquiring GIS information. The authors also thank Amy Shaw, Mike Habrat, Andy Borden, Brent Burish and Konrad Kulacki for field assistance. The authors express gratitude to Jennifer Tank, Dominic Chaloner, and Randy Bernot for editorial assistance and Ashley Moerke and Michelle Evans-White for statistical advice. Funding for this study was provided by a Challenge Cost Share Agreement (03-CS-11090700-012) between the University of Notre Dame and the USDA Forest Service, Ottawa National Forest. Additional support was provided by the Cooperative State Research, Education, and Extension Service, U.S. Department of Agriculture, under Agreement Number 2003-35101-12871, and from a Summer Graduate Fellowship to J. M. Miesbauer (now Cordova) from the University of Notre Dame Environmental Research Center.

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DOI: 10.1002/rra

Appendix 1. Mean, range (in parentheses), and sample size (n = #streams) of LWD abundance and volume, along with slope and channel width, in streams of different geographical regions of North America. N/A = data not available. Note: For use in Figure 5, LWD linear abundance was converted to area density using stream width.

Region	Slope	LWD abundance (pieces 100 m^{-1})	LWD volume (m^3 100 m^{-2})	Channel width (m)	Regional sources
East North Central	Overall	32.6 (9–64), $n = 22$	0.77 (0–3.12), $n = 93$	1.76–13.4	Miesbauer *et al.*, (this study)[a,b,c]
[Upper Midwest]	≥4%	N/A	N/A	N/A	Moerke and Lamberti
(MI, MN)	2–3.9%	N/A	N/A	N/A	(unpublished data)[c]
	<2%	32.6 (9–64), $n = 22$	0.77 (0–3.12), $n = 93$	1.76–13.4	Johnson *et al.* (2003)[b,d]
	unknown	N/A	N/A	N/A	
Alaska	Overall	25.1 (8–40.9), $n = 46$	4.27 (0.36–18.02), $n = 39$	2.1–23.8	Bryant (1983);[e,b]
	≥4%	N/A	6.86 (0.36–18.02), $n = 14$	3.3–7.3$^+$	Harmon *et al.* (1986)[a]
	2–3.9%	21.0 (8–40.3), $n = 31$	3.68 (2.41–5.78), $n = 9$	4.1–8$^+$	Martin and Benda (2001);[c]
	<2%	33.2 (21.6–40.9), $n = 15$	3.68 (1.34–6.96), $n = 11$	5–23.8$^+$	Martin (2001)[a,c]
	unknown	N/A	1.93 (0.55–3), $n = 5$	2.1–14.3	
West and	Overall	32.6 (5.2–91.2), $n = 12$	1.71 (0.03–5.2), $n = 19$	1.1–36.7	Harmon *et al.* (1986);[a]
West North Central	Overall	32.6 (5.2–91.2), $n = 12$	1.71 (0.03–5.2), $n = 19$	1.1–36.7	Berg *et al.* (1998)[b,c]
(CA, MT)	≥4%	22.6 (5.2–37.4), $n = 6$	1.43 (0.03–5.2), $n = 7$	1.1–14.4	Hauer *et al.* (1999)[b,c,f];
	2–3.9%	22.1 (11.2–32.6), $n = 6$	N/A	4–12.8	O'Connor Environmental
	<2%	39.3 (6–59.6), n = 8	N/A	3.9–36.7	Inc. (2000)[b,c]
	unknown	38.3 (7.6–91.2), $n = 12$	2.27, $n = 12$	7.5–29.8	
[Pacific] Northwest	Overall	36.2 (0.5–239), $n = 85$	5.04 (0.1–8.12), $n = 29$	1–165	House and Crispin (1990);[b,c]
(B.C., OR, WA)	≥4%	45.9 (12.3–239), $n = 13$	4.34 (2.4–8.12), $n = 3$	1–11.7	Reeves *et al.* (1993)
	2–3.9%	34.9 (9.9–104.1), $n = 16$	2.46 (1.7–3.8), $n = 9$	1–15.2	Beechie and Sibley (1997);[b,g]
	<2%	36.3 (0.5–131), $n = 56$	1.64 (0.1–6.6), $n = 17$	3.4–22.1	McHenry *et al.* (1998),[b,c]
	Unknown	12.8 (2.3–53), $n = 8$	N/A	20–165$^+$	Connolly and Hall (1999);[b,c]
					Young *et al.* (1999),[b,g]
					Hyatt and Naiman (2001);[b]
					Roni and Quinn (2001),[c]
					Wing and Skaugset (2002);
					Keim *et al.* (2002);[e,c]
					Gurnell *et al.* (2002)
Northeast and	Overall	16.1 (6–34), $n = 8$	N/A	1st–3rd	Thornton *et al.* (2000)[b]
Central (PA, WV)	≥4%	N/A	N/A	N/A	
	2–3.9%	N/A	N/A	N/A	
	<2%	N/A	N/A	N/A	
	unknown	16.1 (6–34), $n = 8$	N/A	1st–3rd	

DOI: 10.1002/rra

Southeast and Central (GA, NC, TN, VA)	Overall	6.1 (0.4–16.3), $n = 7$	1.09 (0.25–3), $n = 11$	3.6–33, 1st–3rd 3.4–6.5, 1st–3rd N/A 5–33 N/A	Wallace and Benke (1984);[d] Harmon *et al*. (1986)[a] Benke and Wallace (1990);[d] Hilderbrand *et al*. (1997)[a,b,c] Flebbe (1999)[a,b,c]
	≥4%	5.1 (2.9–6.9), $n = 4$	1.41 (0.4–3), $n = 7$		
	2–3.9%	N/A	N/A		
	<2%	0.4, $n = 1$	0.77 (0.25–2.35), $n = 4$		
	unknown	13.2 (10.1–16.3), $n = 2$	N/A		

[a] Old-growth forest.
[b] 2nd-growth forest.
[c] Straight LWD count.
[d] Line Intersect Method.
[e] Clear-cut forest.
[f] Unlogged forest.
[g] Other LWD method.
$^+$ = width not available for all streams.

DOI: 10.1002/rra