

Long-term dynamics of large woody debris in a managed boreal forest stream

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Abstract

Little is known about how past forest management in Sweden influenced the quantity and quality of large woody debris (LWD) in streams. The present study provides information of the long-term dynamics of LWD in a reach of a boreal stream intersecting a managed forest. Dendrochronological methods were used to reconstruct mortality years of the pieces of LWD and the general history of fire and cuttings of the surrounding riparian forest. Today, spruce dominates among the living trees, whereas the LWD is dominated by birch in the forest and by pine in the stream. Fire frequency prior to active fire suppression was similar to values reported from boreal forests. Pine trees were more abundant in the riparian forest before selective logging operations and active fire suppression began in the 1800s. Many of the pieces of LWD found in the stream today died more than 200 years ago and derived from a cohort of pines that generated in the early 1600s. Pine LWD in stream channels is highly resistant to decomposition and can reside for more than 300 years. A substantial amount of the LWD found today in managed forest streams in boreal Sweden most likely derives from the time before extensive human influence and is likely to decrease further in the future. Management of riparian forests to ascertain future supply of long-lived LWD in streams should target to increase the proportion of pine trees.

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1. Introduction

Large woody debris (LWD) is an important component of aquatic ecosystems in forested areas (Harmon et al., 1986; Bisson et al., 1987; Bilby and Bisson, 1998). In rivers and streams, it creates physical

obstructions that alter flow and create habitat for aquatic organisms (Maser and Sedell, 1994; Richmond and Fausch, 1995; Bilby and Bisson, 1998). LWD in streams affects the abundance and geometry of pools (Robison and Beschta, 1990b; Beechie and Sibley, 1997) and the retention of organic and inorganic matter (Bilby and Likens, 1980; Bilby, 1981; Ehrman and Lamberti, 1992). The abundance and temporal variation of LWD in a stream reach are

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determined by rates of recruitment and depletion, which, in turn, are influenced by riparian forest characteristics, stream size, hydrologic conditions, topography, and substrate (Naiman et al., 2002).

Most rivers and streams in the boreal forest of Sweden have undergone extensive human-induced changes over the last 200 years. Clearing and excavation to facilitate timber floating, and excavation to improve drainage and increase tree growth have degraded many aquatic environments. In addition, fire suppression, altered densities of herbivore populations, and timber harvesting in upland and riparian areas have affected the linkages between aquatic and terrestrial environments. Swedish forests have been converted to even-aged stands with few large old trees, and the amount of woody debris has generally decreased to about one-tenth of its pristine values (Linder and Östlund, 1998; Fridman and Walheim, 2000; Siitonen, 2001). This alteration has reduced the abundance of many forest-dwelling species, and management strategies have been developed in an attempt to mimic more natural conditions, such as the retention of high stumps, large trees, and the maintenance of buffer strips along margins of wetlands, lakes and streams (e.g. Macdonald et al., 2004).

North American studies have demonstrated that logging in riparian areas has reduced LWD recruitment in many streams (Andrus et al., 1988; Murphy and Koski, 1989) and LWD frequency and volume (Bilby and Ward, 1991). In some studies, the difference is minor but in general, unmanaged forest streams have larger-sized LWD (Ralph et al., 1994). Little is known about how past forest management in Sweden influenced the quantity and quality of LWD in streams and its effects on the aquatic environment. Dahlström and Nilsson (2004) demonstrated that woody debris plays an important role for the morphology of small forest streams, and that streams in old-growth forests with minor impacts from forestry contained twice as many pieces and four times the volume of woody debris when compared to mature managed forests. An important objective for forest managers is to maintain the essential functions of LWD in aquatic environments, which may be achieved by mimicking the natural composition and dynamics of the riparian forest. Maintaining forested buffer strips along streams may be a useful way to guarantee future supply of LWD to the aquatic environment.

However, present-day riparian forests are more or less transformed by human activities and may not be able to maintain sufficient amounts of LWD in streams.

In this paper, we use dendrochronological methods to evaluate how riparian forest history has influenced the temporal variation in amount and type of LWD in a stream reach with a forest history that represents many boreal forest streams in Sweden. We specifically address two hypotheses: (1) the species composition of stream LWD is proportional to that in the riparian forest and (2) the density of LWD in the stream is equal to that on the forest floor. We also explore whether the age of LWD in the stream is similar to that on the forest floor and discuss management of riparian forests to ascertain future supply and amounts of LWD in streams.

2. Material and methods

2.1. The study area

The studied stream reach is situated at 63°20' N, 15°41' E in the boreal forest landscape in central Sweden. The Öravatt Stream (local name Öravattsbäcken) has its outlet in the Ammer River (local name Ammerån), a tributary to the Indal River (local name Indalsälven), approximately 140 km from the coast of the Gulf of Bothnia. The stream reach is located 1 km from the Ammer River and 5 km from the nearest village Öravattnet (Fig. 1). The studied section has never been cleaned of rocks, excavated, or used for timber floating. The drainage area is 16.4 km² with an

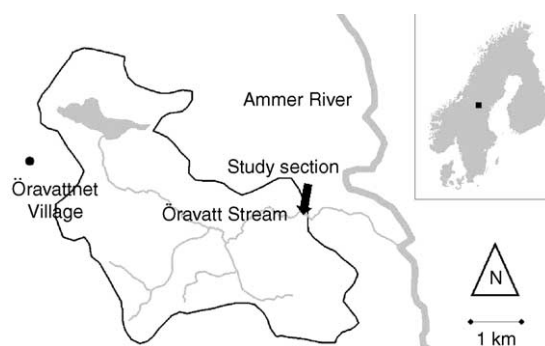


Fig. 1. Location of the Öravatt Stream in central Sweden (see inset), the study section (arrow), and the drainage area upstream the study section (solid line).

elevation ranging from 265 to 435 m a.s.l., and consists of managed forest in different successional stages, as well as lakes (3.3%) and mires (9.7%). The region is topographically moderately broken, and the bedrock that underlies the study section consists of Precambrian granite (Gorbatshev, 1997–1998) and is covered by a sandy glacial till from the latest glaciation that ended approximately 9000 years ago (Lundqvist, 1969). The stream surroundings are mostly flat, and hillslope processes are extremely rare due to the small stream size, moderate slopes and coarse substrate. The stream intersects a 500-m wide, treeless mire ending ca. 100 m upstream, the start of the studied stream reach. Mean annual precipitation is 600 mm/year and mean January and July temperatures are -10 and 14 °C, respectively (Raab and Vedin, 1995). Snowmelt in spring causes an annual flow peak, but flooding may also occur after heavy rains in summer and autumn. The forest vegetation is dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) with various proportions of deciduous trees, mainly birch (*Betula* spp.), gray alder (*Alnus incana*), and aspen (*Populus tremula*).

2.2. General forest history of the region

Fire was a major disturbance factor in the boreal forests of Sweden before the era of commercial logging when fire suppression started (at around 1880) (Esseen et al., 1997). Fires typically killed spruce, deciduous trees and small pines. Larger pine trees often survived and could become >400 years old and >30 m high (cf. Linder et al., 1997; Andersson and Östlund, 2004). Average fire intervals at a particular point are reported to be around 50–100 years, but show great variability depending on forest type (Zackrisson, 1977; Engelmark, 1984) and isolation by larger fire barriers (Engelmark, 1987; Niklasson and Granström, 2000). Prior to the 1800s, most forests in the area were unexploited by humans and the utilization was mainly limited to grazing by domestic animals and local use of wood for construction and fires (Esseen et al., 1997). During the 1800s, selective logging of large, high-quality pine trees began. This produced huge amounts of large-sized logging residuals (Östlund, 1993). Later, smaller trees of pine and from around 1900, also spruce were utilized. Clear-cutting forestry practices were introduced in the mid-1900s.

Öravattnet village was established in 1758 and the inhabitants floated timber in the Ammer River before 1802 (Östlund, 1993). However, larger-scale cuttings along this section of the Ammer River valley started around 1820 (Östlund, 1993). The Ammer River has probably been used for timber transport from the late 1700s until timber floating ended in 1967.

European beaver (*Castor fiber*) is a major ecosystem engineer that alters geomorphology and forest composition along streams. Beaver were extirpated from Sweden in the 1870s, mainly due to over-hunting. The population decline had started much earlier, and in the early 1800s only a few known populations occurred in eastern Jämtland, among them one in the Öravatt Stream. Beaver were reintroduced in Sweden from 1922 and onwards. The closest location where populations were successfully introduced is approximately 40 km north of the Öravatt Stream (Hartman, 1994). The first 'new' beavers were observed in the Ammer River in the 1950s and the first known beaver colony in the Öravatt Stream appeared in the early 1970s after approximately 170 years of absence.

2.3. Stream wood sampling and measurements

Fieldwork was undertaken during base flow conditions in autumn 2000. A 400-m long stream reach not affected by timber floating or stream cleaning and surrounded by mature forest was selected. All pieces of woody debris with a diameter exceeding 10 cm, situated in or above the bankfull stream channel, were included in the survey. The species was identified, and the length and diameter at both ends were measured. Wood volume was calculated assuming the shape of a truncated cone. The orientation and position of the LWD, and whether the pieces belonged to an accumulation of debris were recorded, as was the decay class, following the five-class system of Robison and Beschta (1990a). The trunk form was divided into three classes, straight, bent, and strongly bent. The fractured ends of each piece were divided in root wad, cut by beaver, cut by saw or axe, broken, eroded, and hidden. Wood disks were collected from every coniferous piece of LWD. Only a few pieces of deciduous wood were sampled for dating not only because of the bad quality of the pieces, but also because of the difficulties of correct

dating (Schweingruber, 1996). The disks were cut by handsaw through the most intact section, and sometimes multiple samples were collected. The samples were labeled and taped to preserve the disks during transport and preparation. The possibility of finding the original outermost ring was visually estimated both in the field and laboratory in the following classes.

- (1) Highly possible: samples with intact bark or traces of bark.
- (2) Possible: pieces with relatively fresh wood with a large smooth surface and sometimes with small intact twigs.
- (3) Uncertain: pieces without a large smooth surface on the most intact section.
- (4) Impossible: Extensively rotten, not possible to have good wood samples or find the outermost ring.

Identification of species on collected wood samples was microscopically verified by wood anatomy in laboratory (Schweingruber, 1978).

2.4. Forest structure, composition, and history

The riparian forest was examined by using strip transects located perpendicular to the stream. The transects were 10 m wide and 30 m long and placed on both sides of the stream channel at 50, 110, 230 and 300 m downstream from the starting point of the studied stream section, covering an area of totally 0.24 ha. All living trees, snags, stumps, and logs with a diameter >10 cm were measured in transects. Snags were defined as specimens reaching >1.3 m above ground. For every snag, log, and stump, diameter, decay class, and species were recorded. Wood volumes for logs were calculated assuming the shape of a truncated cone, whereas volumes for trees and snags were calculated for the sections above and below breast height, respectively. Tree heights for all species were obtained from a length-to-diameter relationship of 20 spruce trees measured in the riparian forest. To access stand age and date events of fires and logging ca. 25 wood samples from stumps and logs were collected, and 12 dominant living trees were cored at the root neck within the 30–50 m wide mesic surroundings of the stream reach.

2.5. Cross dating

Cross dating was performed to determine the year of the outermost ring of the wood samples. The wood samples were stored to dry slowly and homogeneously before preparation with scalpel. One–four radii were measured on each wood disk and were synchronized with each other using the CATRAS statistical program package (Aniol, 1983). Dating was made using COFECHA (Holmes, 1997) towards two existing chronologies in the area (K. Jönsson, unpublished observations) and the cored, living trees. The unpublished chronologies have been verified towards a pine chronology spanning 1107–1978 A.D., downloaded from the International Tree-Ring Data Bank (ITRDB) submitted by F.H. Schweingruber. In addition to the electronic dating, wood cross-sections were visually compared using pointer years and ring-width plots. Wooden disks from a total of 123 conifer pieces of LWD were collected in the studied stream reach. Thirty-nine of these and most of the deciduous samples lacked the outermost ring, or were too rotten to allow tree-ring measurement. Of the remaining 84 conifer samples, seven contained less than 30 rings and were omitted, 65 (35 pine and 30 spruce samples) were dated with confidence, and 11 were undated. Only two birch samples were adequately dated. Only the dated samples were included in further temporal analyses.

3. Results

3.1. Stream characteristics and amounts of LWD

The average bankfull width of the stream reach was 3.2 m with low sinuosity, and the overall channel gradient was 5% with no abrupt changes along the reach. Boulders covered approximately 50% of the stream channel bottom, and there were no signs of lateral channel movement except for local erosion in a thin sandy peat layer on the channel edges. The wood volume recorded in the bankfull channel was dominated by pine (Table 1). The average diameter of the basal end was 15 cm with maximum values for birch, spruce and pine of 27, 36, and 34 cm, respectively. Average length was 2.6 m with 6% of pieces over 5 m. Most pieces had ends that were eroded or broken, and a few had buried ends. Beaver-cut pieces

Table 1

Characteristics of large woody debris in the stream channel, and of trees, snags, logs and stumps in the riparian forest of the Öravatt Stream, central Sweden

	Species				
	Gray alder	Birch	Norway spruce	Scots pine	All
Large woody debris					
No of pieces/100 m	2	21	12	19	53
Volume (m ³ /ha)	2	21	13	28	65
Mean diameter at basal end (cm)	14	14	15	17	15
Mean length (m)	3.8	3.0	2.3	2.2	2.6
Living trees					
>10 cm at base (no./ha)	37	338	1200	117	1692
>10 cm at breast height (no./ha)	0	213	808	117	1138
Basal area (m ² /ha)	0	5	17	4	27
Volume (m ³ /ha)	1	35	130	41	209
Snags					
>10 cm at base (no./ha)	17	129	42	8	196
Basal area (m ² /ha)	0.2	1.8	0.40	0.10	2.5
Volume (m ³ /ha)	1.0	8.0	2.2	0.4	11.7
Logs					
No./ha	12	212	13	25	262
Volume (m ³ /ha)	0.6	10.7	2.1	3.1	16.6
Stumps					
Broken (no./ha)	0	29	17	4	50
Cut (no./ha)	0	17	117	67	201
Beaver cut (no./ha)	0	17	0	0	17

accounted for 2.3% of all pieces (6% of the birch pieces), 17% had an attached root wad, and 13% were cut by axe or saw. Twelve debris dams occurred along the studied stream reach, and 39% of the wood pieces were associated with those dams.

3.2. Age structure and recruitment

The two dated birch samples had inner rings from 1903 and 1908, and died in 1980 and 1994, respectively. In the further analyses, only dated LWD from conifers was included. Inner and outer rings of dated samples of pine and spruce are shown in Fig. 2 and cumulative volumes are shown in Fig. 3. Dated LWD of pine represents 46% by number and 64% by volume of the total amount of pine LWD. Similar figures for spruce LWD are 64 and 62%. Eleven percent of the LWD pieces from spruce (dated and undated), representing 7.6% of the wood volume of spruce, were relatively fresh (decay classes 1 and 2) indicating that they probably had been recruited later than the youngest dated spruce piece, which had an

outer ring from 1968 and belonged to decay class 3. No LWD of pine was assigned to decay classes 1 or 2. The basal-end diameter and volume of LWD pieces showed a weak but significant increase with increasing

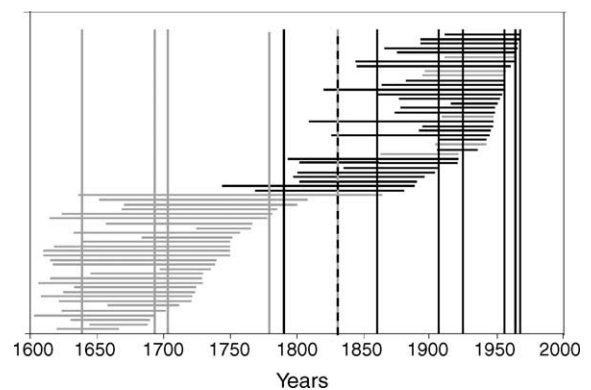


Fig. 2. Temporal input of dated conifer LWD ($n = 65$) at the study site of the Öravatt Stream. The length of each horizontal bar corresponds to the dated years in the wood sample. The trees are shown sorted according to their last dated year. Vertical lines show events of dated fires (gray) and logging (black). Horizontal bars show Scots pine ($n = 35$; gray) and Norway spruce ($n = 30$; black).

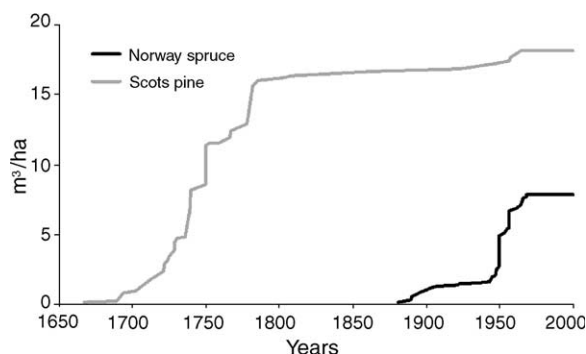


Fig. 3. Cumulative volume of dated conifer LWD separated in Scots pine and Norway spruce.

time since death (Spearman's rank correlation, $r = 0.29$, $P = 0.025$, and $r = 0.25$, $P = 0.042$) while the length of LWD pieces showed no pattern ($P > 0.05$). Dated members of debris dams ($n = 30$) were older than other pieces ($n = 35$), but the difference was not statistically significant (median age = 206 versus 78 years, Mann–Whitney U -test, $P = 0.079$).

3.3. Characteristics of the riparian forest

The riparian forest covered a 30–50 m wide, flat zone along the studied stream reach and consisted of a mesic and partly moist mature forest dominated by spruce. By volume, pine was the second-most abundant tree species. However, only a few saplings of pine occurred in the riparian zone, and no pine tree >1.3 m in height was found with a basal end diameter <10 cm. Birch was the most abundant deciduous tree species (Table 1). The understory consisted of *Vaccinium* spp. and mosses with small patches of more species-rich vegetation. The dry surrounding upland forest was dominated by Scots pine with scattered, small spruce trees and an understory of lichens. Dominant trees in the riparian forest were between 100 and 160 years old. Trees >30 cm at breast height were sparse (27/ha). One hundred and seventy-eight trees per hectare were >20 cm in diameter at breast height. Snag and log volumes were dominated by birch. Nearly all logs were in intermediate or late stages of decay, and many were overgrown by bryophytes. No traces of more recent human forest activities were observed in the riparian zone. Cut stumps of conifers of different sizes were abundant (Table 1). Cut stumps of spruce were most

numerous, followed by pine. Birch stumps were also present, of which 17 stems/ha were cut by beaver. Scattered, larger pine stumps cut by axe (21/ha) indicated forest operations prior to the introduction of the saw in the 1880s (Östlund and Linderson, 1995).

3.4. Dated cuttings and fires

Because most of the cut stumps in the riparian forest had a decayed outer layer, it was not possible to determine the original outermost ring. The dendro-chronological analyses of cut stumps of better quality revealed cuttings of trees that died in 1790, 1831, 1860, 1907, 1925, 1956, 1964, and 1968 (note that especially pine trees can die and remain standing during several decades, implying that cutting is not necessarily the cause of death). Other cutting operations may have passed undetected due to limited availability of suitable samples. Furthermore, the extent of cutting is also difficult to estimate. However, the cuttings in 1956 seem to have included many large as well as small stems. Seven wood samples from the riparian zone contained fire scars, three on stumps standing on the southern side and four on the northern side of the stream. The earliest dated fire occurred in 1367 and was registered on a broken pine snag, 1.8 m in height, standing on the southern side of the stream. This pine germinated around 1280 and died in the late 1500s. A cohort of pines found on both sides of the stream originated from the very late 1590s, probably having become established after a fire. The next fires dated in the samples occurred on the northern side of the stream in 1639 and 1693. In 1703, fire scars were found on the southern side of the stream, and in 1780 fires were registered on both sides. A fire in 1831 on the northern side of the stream was the latest one in the riparian forest at the studied stream reach. The summers in 1703 and 1831 were both warm in northern Sweden and this could have facilitated fires (Briffa et al., 1990).

4. Discussion

4.1. Stream characteristics, amounts, and origin of LWD

Many characteristics of the studied stream reach are also typical for other small boreal forest streams in

Sweden. They often drain through morainic deposits; they have a coarse channel substrate, intermediate gradient, low sinuosity, and are surrounded by a managed spruce-dominated forest. The amounts of LWD found in the studied stream reach were lower than most values reported from old-growth conditions, but exceeded volumes typically found in other managed forest streams (cf. Dahlström and Nilsson, 2004). The average length of LWD pieces found in the channel was nearly equal to the width of the bankfull channel. Together with the coarse channel substrate that anchored many pieces, and the presence of channel-spanning accumulations of debris, this suggests little mobility of wood pieces and consequently that most pieces originated from the adjacent riparian forest. The treeless mire (i.e., the mire did not provide tree habitat) upstream the studied supports this conclusion. Visual observations of the studied stream reach before and after a major flood in the summer of 2000 confirm that all debris jams remained in place. The flood resulted from two weeks of precipitation in July that was record intensive according to 100 years of measurements (SMHI, 2000).

4.2. History of cuttings and fire

The history of the studied riparian forest is consistent with that of other forests in the area (Östlund and Linderson, 1995) and of other boreal forests in Sweden (Östlund et al., 1997), i.e., absence of fires after introduction of fire suppression and various forest management operations since the 19th century. Signs of characteristic fire reactions, and in some cases fire scars, were seen in the tree rings of the sampled LWD from the channel. The observed fire responses coincide with the pattern seen in fire scars in stumps of the riparian forest. Consequently, some samples had signs of fires occurring on the northern side of the stream and others of fires occurring on the southern side of the stream. This shows that prior to active fire suppression, frequent fires affected the riparian forest. Furthermore, the stream but not the riparian forest has occasionally been a barrier to fire, at least at the reach scale.

The oldest cut stump derived from a tree that died in 1790; however, this does not necessarily mean that logging was performed at that time because dead standing pines of good quality were also cut. The same

might be true for the trees that died in 1831, the year with the last fire in the riparian forest. High-quality pine trees were the major targets in the first cuttings and fire-damaged trees were considered less suitable (Östlund, 1993). Less frequent fires and a higher productivity in the riparian zone may well have resulted in trees of better quality than on the drier sites. This, in combination with the short distance from the Ammer River, probably contributed to the early start of logging activities along the studied stream reach. One important difference from most North American studies about the influence of forestry on LWD amounts in streams is that forestry operations have been made repeatedly during a long time.

4.3. Dynamics of in-channel LWD

The flat surroundings and small stream size with coarse bed material and no lateral channel movement imply that bank erosion is a limited process for LWD recruitment. Other studies have shown that LWD recruitment from bank erosion is limited in smaller, steeper channels (Murphy and Koski, 1989) and in coarse substrate (Bilby and Wasserman, 1989). Although not measured, no tendency for trees to lean or fall towards the channel was observed. Trees growing on the channel edges are exceptions, but these trees are typically small with bent trunks and asymmetric root wads, and contribute only to 9% of the wood volume found in the channel. Thus, input processes to the stream are mainly controlled by factors that also control the input of wood to the forest floor. Despite similar input processes, the amounts of LWD found in the stream were considerably higher than the amounts found in the riparian forest. The results suggest that differences in depletion rates of woody debris between the stream channel and riparian forest are the main reason for the observed pattern (cf. Harmon et al., 1986; Guyette et al., 2002).

4.4. Species composition and residence time of LWD

The proportions of tree species found as LWD in the stream differed notably from the proportions found among living trees, but also among snags and logs in the riparian forest (Table 1). This can either be explained by different decomposition rates among species, differences in mortality among species,

changes in the species composition over time, or various combinations of these. Judging from stumps and the age distribution of the woody debris, pine trees seem to have been more abundant previously. The combination of logging of primarily pine trees and the absence of fires after 1831 has probably favored spruce, which is a late successional species. At present, pine regeneration is sparse according to the limited number of saplings found in the riparian forest. This pattern has also been observed in other areas with an altered fire regime (Linder et al., 1997; Linder, 1998). Decomposition rates differ among species. Hyatt and Naiman (2001) found more living hardwoods than conifers in the riparian zone, and a reverse pattern in the Queets River channel, indicating that the decomposition of hardwood species is faster than that of conifer species in the aquatic environment. Similar findings have also been made both in the aquatic and terrestrial environment in other studies (Harmon et al., 1986, 2000; Tarasov and Birdsey, 2001). The present species composition, the mesic surroundings of the stream, which is a habitat favored by spruce, the presence of old pine stumps, and the ages of pine LWD indicate that both spruce and pine have probably been inhabitants of the riparian zone for several centuries. The oldest piece of pine LWD originated from the late 1600s, while the oldest spruce pieces were a little more than 100 years old, possibly suggesting that pinewood remains in the channel nearly three times as long as spruce wood does. The limited data on deciduous trees indicate a rapid decomposition. Differences in decomposition rates are also influenced by the sizes of LWD. Biological breakdown of pieces is most active on the surface of LWD (Harmon et al., 1986). Larger pieces have a lower surface area to volume ratio than small pieces and decompose more slowly (Bisson et al., 1987). The size also affects the stability of LWD in the stream channel, such that larger, resident pieces experience less physical abrasion. The sizes of LWD in our study reach have probably changed over time, thus further complicating the interpretation of the temporal variation in wood input. Small-sized older wood may have disappeared faster than larger pieces. Moreover, the year when the tree died and when its wood was added to the channel may not be the same (cf. Linder, 1998; Storaunet and Rolstad, 2002). This is clearly illustrated by the still-standing pine snag in our study site that died in the late 1500s.

It is not possible to calculate any meaningful mean residence time for the LWD pieces in the present study because of changes in input rate, species composition, and piece size. This would require a steady-state situation. Other studies have demonstrated that key pieces of LWD can reside in streams for centuries (Swanson et al., 1976; Murphy and Koski, 1989). Lienkaemper and Swanson (1987) found mean residence times of 12–83 years for LWD in first- to fifth-order streams. Hyatt and Naiman (2001) found a mean residence time of 30 years for key pieces of LWD > 60 cm in diameter in the Queets River, Washington, but downstream transport is an important removal process in that system. The oldest piece in their study was dated by ^{14}C to 658 A.D. That LWD piece was probably buried and released from sediment during a flood. Burial and release from sediment have also been reported for other extremely old pieces found in rivers and streams (Becker et al., 1991; Nanson et al., 1995). The coarse sediment in our study reach prevents pieces > 10 cm in diameter from being buried in sediment.

Although only marginally significant, the finding that LWD in debris dams was older than other pieces of LWD can either be interpreted as it takes some time for LWD to settle in debris dams, or that LWD in debris dams decomposes more slowly due to limited mobility. If the latter is true, large amounts of LWD resulting in more frequent debris dams may have a positive feedback on the amount of LWD in the stream by retarded physical abrasion. There may be a threshold in the amount of LWD below which the formation of debris dams is limited and LWD breakdown is elevated. Dahlström and Nilsson (2004) found that formation of debris dams at the reach scale in streams with bankfull widths up to 3.1 m requires a LWD loading of approximately 1000 pieces/ha. The size limit for LWD in that study was 5 cm in diameter and 0.5 m in length.

4.5. Temporal patterns of LWD recruitment and relation to management

Pulses of germination and mortality often characterize natural forest stands (Esseen et al., 1997). Although exact dating was not possible for some old wood pieces, the overall pattern remains the same; the cohort of pine that germinated in the very late 1590s

and early 1600s resulted in elevated input of woody debris, probably as a result of competition and self-thinning of the stand in the 1700s and early 1800s. Later in the 1800s, the input of pieces of pinewood stopped according to the dated pieces. The rate of individual tree mortality often decreases with stand age, but the decreased input coincided with the early cuttings of pine trees. However, there were no signs of an increased input of logging residues to the stream. Loggers probably tried to avoid felling trees over the stony stream channel. However, some dates of forest activities during the 1900s correspond with increased inputs of LWD to the stream. Such wood represents logging residue and in 1956 also results from forest thinning. The general trend is, however, a decreasing input over time with mostly old wood pieces in the stream. Our data show a reverse pattern from what is found in rivers and streams unaffected by forestry (Guyette and Cole, 1999; Hyatt and Naiman, 2001; Martin and Benda, 2001). Notable is the limited input of conifer LWD after the latest forest operations in 1968. This can probably be attributed to more extensive forestry operations in the mid 1900s. Timber harvesting in riparian areas not only removes wood that potentially could reach the channel, but also increases survival of remaining trees by reduced competition and self-thinning, thereby further reducing wood input to streams. The analyses of woody debris, living trees, and stumps show that trees over approximately 30 years in age that can produce LWD have been present in the riparian zone at least from 1630 and onwards. Combined with the slow decomposition rate of pinewood, this suggests that there are limited variations in the amounts of woody debris at the reach scale under pristine conditions. Total absence of larger trees along stream channels, as is the case in clear-cut areas, provides a situation that differs strongly from the natural one.

4.6. Influence of beaver

Locally along streams, beaver can have a substantial effect on wood amounts. Beaver prefer tranquil reaches with fine substrate to build dams and huts (Hartman, 1996), but they use larger areas for feeding, and thus, also cut deciduous trees along turbulent reaches. However, the influence in such reaches is generally limited and according to the low

proportion of beaver cut pieces and stumps, this holds true also in our studied stream reach.

5. Conclusions

The present study provides important, previously not documented information about the long-term dynamics of LWD in boreal forest streams. It shows that the proportions of wood of different species differed between the stream channel and the riparian forest, and that the stream had more wood and older wood than the surrounding riparian forest. This demonstrates that (at least pine) wood is better preserved in water than on the ground, but also indicates a change in riparian management with time. Similar to the studied stream, numerous riparian forests along small boreal streams have been transformed by selective logging and fire suppression, producing a forest that may lack the capacity to sustain adequate amounts of LWD in streams. Much of the pine LWD found in managed forest streams today most likely derives from the time before extensive human influence and is likely to decrease further in the future. A potentially alarming finding is the suggested threshold below which breakdown rates of LWD should be faster. Management recommendations that suggest cutting of conifer species to favor and increase the content of broad-leaved trees in riparian zones (Tostebj, 1995; de Jong et al., 1999) may worsen this situation. Buffer strips along streams have multiple functions that include temperature control by shading, erosion control by roots, and input of allochthonous energy to the stream ecosystem. If only the long-term supply and abundance of wood are considered, management should target an increase in the proportion of pine trees that can provide long-lived woody debris that increases LWD abundance in streams and dampens temporal variations in wood supply.

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