The dynamics of coarse woody debris in boreal Swedish forests are similar between stream channels and adjacent riparian forests

Niklas Dahlström and Christer Nilsson

Abstract: Although numerous studies have focused on the dynamics of coarse woody debris (CWD) in boreal Fennoscandian forests, information on CWD in streams remains limited. To achieve a better understanding of CWD dynamics in streams we compared amounts and characteristics of CWD between streams and adjacent riparian forests in old-growth and managed forest sites, respectively. We also identified distances to the sources of CWD and evaluated these in relation to the lateral zonation of riparian trees. CWD volumes found in the stream channels were related to, but exceeded, the volumes found in the adjacent forest. In-channel volumes separated by species were better correlated with terrestrial volumes of CWD than with volumes of living trees. Tree species appeared to be zoned across the riparian zone, with slightly higher abundances of deciduous trees and lower abundances of Scots pine trees close to the stream. Similar to upland forests, riparian forests were dominated by coniferous tree species, mainly Norway spruce (*Picea abies* (L.) Karst.). These findings suggest large similarities in CWD input between streams and riparian forests and substantially slower decomposition rates in stream channels compared with those in riparian forest. The results provide an improved basis for creating reliable models of CWD supply and maintenance in streams based on knowledge of forest development and CWD dynamics in the terrestrial environment. Site productivity could potentially be used to predict CWD volumes in stream channels under pristine conditions.

Résumé : Bien que plusieurs études aient mis l'accent sur la dynamique des débris ligneux grossiers (DLG) dans les forêts boréales de la Fennoscandie, l'information sur les DLG dans les cours d'eau demeure limitée. Pour avoir une meilleure compréhension de la dynamique des DLG dans les cours d'eau, les auteurs ont comparé la quantité et les caractéristiques des DLG entre les cours d'eau et les forêts ripariennes adjacentes dans une forêt ancienne et une forêt aménagée. Ils ont identifié la distance des sources de DLG qu'ils ont évaluée en relation avec la zonation latérale des arbres riverains. Le volume de DLG retrouvés dans le lit des cours d'eau était relié au volume de DLG retrouvés dans la forêt adjacente mais il était plus important. Le volume de DLG de chaque espèce présente dans les cours d'eau était davantage corrélé avec le volume de DLG terrestre qu'avec le volume des arbres vivants. Il semblait y avoir une zonation des espèces d'arbre dans la zone riparienne avec une abondance légèrement plus élevée de feuillus et moins élevée de pin sylvestre près du cours d'eau. Comme les forêts des terres hautes, les forêts ripariennes étaient dominées par des conifères, surtout l'épicéa commun (*Picea abies* (L.) Karst.). Ces résultats indiquent qu'il y a une grande similitude entre les cours d'eau et les forêts ripariennes dans l'apport de DLG et un taux de décomposition substantiellement plus faible dans le lit des cours d'eau que dans la forêt riparienne. Les résultats fournissent une meilleure base pour créer des modèles fiables de l'apport et du maintien des DLG dans les cours d'eau sur la base de connaissances sur le développement de la forêt et de la dynamique des DLG dans l'environnement terrestre. La productivité du site pourrait probablement être utilisée pour prédire le volume de DLG dans le lit des cours d'eau dans des conditions naturelles non perturbées.

[Traduit par la Rédaction]

Introduction

An important challenge for forest managers is to restore and sustain the ecological functions of coarse woody debris (CWD) in terrestrial and aquatic environments. Attaining this goal requires thorough knowledge of CWD dynamics. In terrestrial ecosystems of boreal Fennoscandia, CWD is important for the conservation of many threatened species as well as for biodiversity maintenance in general (Samuelsson et al. 1994; Siitonen 2001). Therefore, an increasing body of ecological studies has focused on CWD, including its spatial and temporal variations (Jonsson and Dynesius 1993; Jonsson 2000), input processes (Esseen 1994), decomposition rates (Krankina and Harmon 1995; Naesett 1999; Jonsson 2000; Kruys et al. 2002), and the assessment of pristine conditions (review in Fridman and Wahlheim 2000; Siitonen 2001). Several recently developed models allow predictions of the quality and amounts of terrestrial CWD

Received 4 July 2005. Accepted 11 January 2006. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 13 April 2006.

N. Dahlström.[1,2] Department of Natural Science, Mid Sweden University, SE-851 70 Sundsvall, Sweden.
C. Nilsson. Landscape Ecology Group, Department of Ecology and Environmental Science, Uminova Science Park, Umeå University, SE-901 87 Umeå, Sweden.

[1]Corresponding author (e-mail: niklas.dahlstrom@y.lst.se).
[2]Present address: The County Administration of Västernorrland, SE-871 86 Härnösand, Sweden.

 doi:10.1139/X06-015

under different forest management conditions (Ranius et al. 2003; Ranius and Kindvall 2004).

Riparian forests serve a vital role in stream ecosystems by controlling many environmental factors and providing energy and nutrients (Vannote et al. 1980; Gregory et al. 1991; Naiman and Bilby 1998). In many areas, CWD from stream margins strongly influences channel morphology (Harmon et al. 1986; Bisson et al. 1987; Naiman et al. 2002), habitat diversity (Harmon et al. 1986), and the retention of organic matter (Bilby and Likens 1980; Ehrman and Lamberti 1992; Raikow et al. 1995). Regardless of the ecological effects of CWD and the attention it has received from researchers and managers in many regions of the world, Fennoscandian data on its functions, amounts, dynamics, quality in streams, and how it is affected by forestry are almost absent. Furthermore, base-line data reflecting pristine conditions are scarce. Despite extensive research in other regions, understanding of the CWD dynamics in streams remains limited, especially concerning supply and decomposition rates (Naiman et al. 2002).

Studies on CWD in streams often include general information about stream channel management (Shields and Smith 1992; Piégay and Gurnell 1997; Gurnell and Sweet 1998) and the surrounding riparian vegetation. These include forest type (Harmon et al. 1986; Bilby and Bisson 1998), forest age (Hedman et al. 1996; Rot et al. 2000), forest management (Bilby and Ward 1989, Dahlström and Nilsson 2004), and the occurrence of major disturbance events, such as slope processes (Gomi et al. 2003; May and Gresswell 2003), volcanic eruptions (Lisle 1995), flooding (Palik et al. 1998), and fire (Young 1994; Zelt and Wohl 2004). Surprisingly few studies have compared CWD quantities between riparian forests and stream channels (but see Bilby and Wasserman 1989; Rot et al. 2000; Acker et al. 2003). Evaluations of riparian–aquatic relationships could provide valuable information about the processes involved in CWD dynamics and identify relationships between the terrestrial and aquatic environments. Prediction of CWD amounts in streams under different management scenarios can potentially be based on the development of the adjacent forest (cf. Van Sickle and Gregory 1990; Acker et al. 2003) and the reasonably well-known CWD dynamics of upland forests. Successful attempts to develop such models have been made in North America (Beechie et al. 2000; Welty et al. 2002).

Vegetation along rivers and large streams in boreal Fennoscandia is often laterally zoned, and factors responsible for this pattern are typically attributed to gradients in light, nutrients, moisture, and disturbance (such as ice damage, flooding, and fire) from the channel to the forest (Gregory et al. 1991). However, the processes involved in the maintenance of this zonation are less evident along smaller streams, which instead are more similar to upland forests (Naiman et al. 1993). Dahlström et al. (2005) suggested that the input of CWD in a reach of a boreal forest stream, draining through a coarse morainic deposit, was primarily controlled by the same mechanisms as those operating in terrestrial environments. They also posited that the greater amounts of CWD found in the stream reach compared to that in the riparian forest floor were primarily a result of slower decomposition in the stream channel. In this study we compared CWD amounts and characteristics in streams and adjacent riparian old-growth and managed forests to gain a better understanding of similarities and dissimilarities in CWD dynamics. Furthermore, we explored the zonation of riparian forest stands along near-natural headwater streams and identified distances to the sources of in-channel CWD.

Based on the results by Dahlström et al. (2005) we hypothesized that the amount of CWD found in stream channels would exceed, but be related to, the amount of CWD found on the adjacent riparian forest floor. We also hypothesized that differences in CWD amounts between old-growth and managed forests would be larger for riparian zones than for stream channels because wood decomposes slower in water. We thus posit that streams have a better "ecological memory", that is, prelogging conditions are encoded in their current structure.

Material and methods

Study area

The studied stream reaches and adjacent riparian forests were located in central Sweden, in the middle and northern boreal zones (Ahti et al. 1968), between 63°00′–65°70′N and 15°60′–19°00′E, in four provinces (southern Norrbotten, central Västerbotten, eastern Jämtland, and northern Västerbotten). Dominant tree species in this region are Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.). The bedrock is dominated by Precambrian granites and gneisses, and forested areas are mainly underlain by coarse till (Fredén 1994). The mean annual temperature is about 2 °C, and mean annual precipitation ranges from 600 to 800 mm (Raab and Vedin 1995). Streams experience high discharges in spring during snowmelt and occasionally after heavy rains in summer and autumn.

The stream reaches all drain through morainic deposits with smooth surfaces that are gently sloping towards the stream channels. Typical stream valleys and floodplains are not developed, but stream channels are incised in the underlying substrate. Occasionally, patches of sorted sediment occur along stream margins. The channels are all dominated by boulder- and cobble-sized material. The mean bank-full widths of the studied stream reaches ranged between 0.7 and 5.1 m, with high to intermediate channel gradients and low sinuosity (i.e., <1.3; Table 1). The altitude of the studied reaches ranged between 260 and 510 m.

Average fire intervals in the boreal forest of Sweden were typically 50–100 years before fire suppression started in the late 1800s (Esseen et al. 1997). The "timber frontier" moved across the landscape during the 1800s and large pine trees of good quality were selectively cut. Later, smaller trees of both Scots pine and Norway spruce were utilized. Clear-cutting forestry started in the mid 1900s (Östlund 1993).

Site selection

A large number of stream reaches situated in old-growth forest reserves were visited in the field. Thirteen of those were surrounded by productive forests and had no visible traces of human activities except for a few old, cut stumps. The reaches were all single-channelled and homogeneous with regard to channel gradient, forest composition, and valley profile. For comparison, 11 stream reaches intersecting

Table 1. Site characteristics for the two types of stands.

Site variable	Old-growth (n = 13)	Managed (n = 11)	P value[a]
Elevation (m a.s.l.)	376 (84)	341 (56)	>0.05
Channel characteristic			
Bank-full width (m)	2.4 (1.1)	2.0 (0.9)	>0.05
Gradient (%)	5.2 (2.7)	5.9 (3.5)	>0.05
CWD frequency (no./100 m)	64.1 (21.9)	37.4 (21.0)	0.01
CWD in-channel (m^3/ha)	91.2 (51.0)	26.2 (15.3)	<0.001
Deciduous (m^3/ha)	11.9 (15.2)	9.5 (9.6)	>0.05
Scots pine (m^3/ha)	17.6 (22.1)	7.4 (8.7)	>0.05
Norway spruce (m^3/ha)	61.7 (51.0)	9.2 (10.7)	<0.001
Forest characteristic			
Basal area (m^2/ha)	27.7 (5.6)	27.5 (4.9)	>0.05
Cut stumps (no./ha)	72 (80.9)	357 (232)	<0.001
Living stems (no./ha)	1332 (597)	1765 (578)	>0.05
Living trees (m^3/ha)	278.1 (80.4)	258.4 (116.8)	>0.05
Deciduous (m^3/ha)	29.3 (31.6)	19.3 (13.4)	>0.05
Scots pine (m^3/ha)	53.2 (51.0)	35.5 (55.5)	>0.05
Norway spruce (m^3/ha)	195.6 (79.5)	203.7 (97.6)	>0.05
Logs (m^3/ha)	35.5 (16.5)	16.8 (11.3)	0.004
Deciduous (m^3/ha)	4.9 (5.7)	4.5 (5.5)	>0.05
Scots pine (m^3/ha)	5.6 (8.6)	3.4 (6.0)	>0.05
Norway spruce (m^3/ha)	24.6 (16.3)	8.9 (11.5)	0.009
Snags (m^3/ha)	32.3 (15.9)	10.3 (10.8)	0.001
Deciduous (m^3/ha)	5.2 (4.6)	1.7 (2.5)	>0.05
Scots pine (m^3/ha)	5.4 (9.8)	1.2 (1.6)	>0.05
Norway spruce (m^3/ha)	21.8 (14.2)	7.3 (10.7)	<0.001

Note: Data are mean values (with standard deviation in parentheses). CWD, coarse woody debris.
[a]Significance level of Mann–Whitney U test.

mature forests with evidence of forest management (i.e., abundant cut stumps) were selected in the same region based on the same criteria. These streams were reasonably similar in width, elevation, gradient, forest type, and understorey vegetation (dominated by *Vaccinium* spp. and bryophytes).

Field surveys

The stream reaches situated in old-growth forests ranged between 60 and 181 m in length, and streams intersecting managed forest between 32 and 189 m. Average bank-full channel width was measured every 2–3 m, the gradient was quantified by using a level and rod, and sinuosity was determined by dividing channel length by the straight line distance between the reach endpoints. All pieces of CWD fulfilling a minimum criterion of a basal end diameter >5 cm and a length >0.5 m were measured if any part was situated within or was suspended above the bank-full stream channel. Measurements included lengths and end diameters inside and outside the stream channel, trunk shape (straight, bent, and strongly bent), species, and whether the piece was embedded in a debris dam. The degree of decay was noted for each piece according to the five-grade classification system by Robison and Beschta (1990*a*), with class 1 being least decayed and class 5 most decayed. The degree of wood softening was the major criterion for classifying the decay of logs, snags, and in-channel CWD (Robison and Beschta 1990*a*).

Measurements of the riparian forest were made using four 10 m wide × 30 m long transects located perpendicularly to each stream reach. The transect length represents the maximum source distance for which CWD can enter streams with regard to the maximum tree height (ca. 30 m). The transects were located on both sides of the stream channel at one-third and two-thirds of the reach length. All living trees, snags (standing dead trees), stumps, and logs that originated in the transects and had a basal end diameter >5 cm were recorded. For each tree, snag, stump, and log, distance to channel edge, species, and diameters at base and breast height (DBH) were measured. For snags, stumps, and logs, the fracture end, length, and decay class were noted.

Statistical analyses

Volumes of CWD in the riparian forest and in the stream channels were calculated assuming the shape of truncated cones, whereas volumes for trees and snags were calculated from functions provided by Näslund (1947). Species-specific volume functions for northern Sweden were used for Scots pine and Norway spruce, but for all deciduous trees functions for birch (*Betula* spp.) were used. Tree heights for all species were derived from a length to diameter relationship of approximately 20 Norway spruce trees measured in each of the riparian forests. If a minimum diameter of CWD is set (5 cm in this study), the tree height that exceeds the minimum criterion is called effective height. In this study this was set to the tree height minus 2 m. If the effective tree height exceeds the distance to channel edge, the probability for a tree falling in a random direction to enter the stream channel is a function of tree height and distance from channel edge. Taller trees and trees closer to the channel have a greater probability to enter the stream channel (McDade et al. 1990; Robison and Beschta 1990*b*; Van Sickle and Gregory 1990). The probability of entry can be described as

$$[1] \qquad \text{Probability of entry} = \frac{\cos^{-1}(x/h)}{180°}$$

where h is effective tree height and x is distance to channel edge (Robison and Beschta 1990*b*).

Trends in DBH with distance to channel edge were tested by using linear regressions on $\log_{10}$-transformed data. Zonation of riparian trees and CWD was examined by dividing the pooled transects of each reach in five equally long (6 m) sections. Values for the five sections at each reach were standardized by subtracting the mean and dividing by the standard deviation. The values from all old-growth reaches were then analysed using linear regression to identify trends with distance to channel edge in basal area, density of trees, and volumes of snags and logs. The tree species data were divided into deciduous species, Norway spruce, and Scots pine.

Relationships were tested using simple and multiple regressions, and interactions were tested with an indicator variable, MA (old-growth, 0; managed, 1). To improve normality, proportional data were arcsine square root transformed prior to analysis. Comparisons between CWD characteristics in stream channels and in the riparian forest in the old-growth sites were made using pooled data.

Results

Characteristics of wood in streams

In the old-growth streams, 59.3% of the CWD pieces had basal end diameters >10 cm and average piece length of 2.9 m, with 6.5% of pieces >10 m. In the managed forest streams, 40.7% of the CWD pieces had basal end diameters >10 cm and average pieces length of 2.1 m, with 1.9% of pieces >10 m. The frequency and bank-full volume of CWD did not correlate with bank-full channel width ($P > 0.05$).

Characteristics of riparian forests

The old-growth riparian forests all had multilayered tree canopies. Along all but one old-growth and one managed reach, Norway spruce was the dominant tree species, representing 38.6%–94.6% (old-growth) and 39.7%–95.2% (managed) of the total basal area. Scots pine was the second most abundant tree species, representing on average 16% of the basal area (range 0%–49.2%) in the old-growth forests and 13.5% (range 0%–51.9%) in the managed forests. Basal area of birch (*Betula* spp.) averaged 8.7% (range 0.8%–26%) in the old-growth forests and 9.4% (range 1.8%–17.4%) in the managed forest. Cut stumps in the old-growth forests were mainly from Scots pine trees. These were cut by axe, covered by bryophytes, and sometimes extensively rotten, indicating that they were old and most likely originating from the early logging of large Scots pine trees in the 1800s. In the managed riparian forest, 67.4% of the cut stumps originated from Norway spruce trees, 31.7% from Scots pine, and 0.9% from deciduous species. Fire scars and charred stumps, indicating ancient fires, were found along 8 of the 13 stream reaches in the old-growth forests and along 8 of the 11 stream reaches intersecting managed forests. Very few large fires have occurred in the boreal zone of Sweden since fire-suppression started in the early 1900s.

In the old-growth forests, the average length of terrestrial logs was 5.1 m, 11.8% were longer than 10 m, and 81.7% had basal end diameters >10 cm. In the managed forests, the average log was 3.9 m long, and 9.4% were longer than 10 m. The proportion of CWD (snags and logs) of the total amount of wood (living and dead) in the old-growth forest averaged 20.3% (range 7.3%–35.5%). In the managed forests the average value was 10.2% (range 2.8%–23.0%). In the old-growth forests this proportion decreased as the number of cut stumps increased (Spearman's rank correlation: $r = -0.74$, $P < 0.01$), but it was not related to the number of cut stumps in the managed forests.

Comparison of CWD and tree species composition between managed and old-growth sites

The total volumes of living trees and proportions among species were similar in the old-growth and managed forests (Table 1), but more CWD was found in old-growth than in managed forest sites when comparing volumes of snags, logs, and in-channel CWD (Table 1). In general, Norway spruce dominated the volume of living trees and CWD, but in the managed forest streams deciduous species dominated the in-channel CWD. While analysing the differences in CWD volume for individual tree species (Norway spruce, Scots pine, and deciduous trees) in the stream channel and in the riparian forest, we found that only Norway spruce had significantly lower volumes of CWD as snags, logs, and in-channel CWD in the managed compared to the old-growth forest sites. Separated into Scots pine, Norway spruce, and deciduous species, the volumes of in-channel CWD were better correlated with the volumes of riparian CWD than with the volumes of living trees (Table 2). In general, deciduous species dominated in earlier decay classes and Scots pine in later decay classes among the in-channel CWD, but the patterns were stronger in the managed forest streams (Fig. 1), where conifer species were scarce in early decay classes but dominated in late decay classes. A similar pattern among decay classes was also found among logs in the riparian forest floor (Fig. 1).

Larger volumes of CWD were found in the stream channels than in the riparian forest (Table 1). This applied to reaches both in old-growth ($P < 0.001$) and in managed ($P = 0.036$) forest sites. On average, the CWD volume in the managed forest stream channels was 27.8% of that in the old-growth forest streams, and the same figure for terrestrial volumes of CWD (snags plus logs) was 39.8% (41.7% for logs and 31.8% for snags). The volumes of CWD in the stream channel were related to the volumes of CWD as logs in the riparian forest (Table 3). The relationship was different for the old-growth and managed forest sites, and the interaction term was included in a multiple regression model explaining CWD volumes in stream channels. Managed forests showed less of an increase in CWD volume in the stream channel with increasing CWD volumes on the riparian forest floor. No other variable explained any significant

Table 2. Spearman's rank correlations between coarse woody debris (CWD) volumes in stream channels and riparian forests and between CWD within stream channels and living trees in the riparian forests.

Volume of in-channel CWD	Riparian CWD	Living trees
Old-growth		
Deciduous	0.84**	0.52
Scots pine	0.64*	0.73*
Norway spruce	0.67*	0.30
Managed		
Deciduous	0.92**	0.72*
Scots pine	0.89**	0.41
Norway spruce	0.91**	0.47

Note: Correlations are separated into Scots pine, Norway spruce, and deciduous species and in old-growth and managed forest sites. *, $P < 0.05$; **, $P < 0.01$.

degree of variation (Table 3). Also the density of living trees >5 cm in basal end diameter in the riparian forest was related to the frequency of CWD in the stream channels of the old-growth sites. The interaction term was included, and the managed forest sites showed little increase with increasing number of riparian trees (Table 3).

CWD characteristics in the old-growth forests and intersecting streams

The average length of CWD pieces in the stream channel decreased with increasing stage of decay, whereas riparian CWD as logs showed less alteration with increasing decay (Fig. 2*a*). The average diameters of CWD pieces in the stream channel did not vary with decay, but the average diameter of riparian logs increased with increasing decay (Fig. 2*b*). Almost no bent logs were found in the old-growth riparian forest, but 11.7% of the volume of CWD in the stream channel had bent trunks (14.3% of the volume of Norway spruce, 28.6% of deciduous trees, and 2.5% of Scots pine). The proportion of bent trunks in the channel increased with channel width but showed no correlation with other variables ($r = 0.65$, $P < 0.01$). By volume, 29.8% of riparian logs had an intact root wad, with no difference among species. The same figure for CWD in the channel was 36.9%.

The average tree height exceeded the average length of riparian CWD (logs), and length of riparian logs exceeded that of CWD in the channel (ANOVA on $\log_{10}$-transformed data: $P < 0.01$). Mean basal end diameters of in-channel CWD (average 13.0 cm) were significantly less than for riparian snags (15.4 cm), logs (14.9 cm), and trees (17.8 cm), and riparian trees had significantly larger basal end diameters than logs and snags ($P < 0.01$, ANOVA on $\log_{10}$-transformed data). Mean basal end diameter of in-channel CWD in decay class 1 was 16.3 cm. Of the in-channel CWD in decay class 1, 73% had an intact top section, and the same figure for logs on the riparian forest floor was 68%. These proportions decreased with increasing decay class. The proportion of the volume of in-channel CWD in decay class 5 decreased with increasing channel width ($r = -0.86$, $P < 0.001$).

Zonation of riparian trees

The DBH for all tree species together did not show any significant trend with distance to channel edge ($P > 0.05$, $\log_{10}$-transformed data). Divided into deciduous species, Scots pine, and Norway spruce, the DBH of deciduous trees and Norway spruce, respectively, increased with distance ($P < 0.05$), but the degree of explanation was too low (< 3%) to be ecologically meaningful. There was no correlation between the total basal area of all trees and distance to channel edge, but the total basal area of Scots pine increased with distance to channel edge ($R^2 = 30.5$, $P < 0.01$). No trend was found in stem density for all trees, but deciduous tree density decreased with distance to channel edge ($R^2 = 9.3\%$, $P < 0.05$). Neither the volume, nor the density of riparian logs and snags showed any relation to distance from channel edge.

Source distances of CWD

The average line in Fig. 3 of the source distances calculated for the 13 old-growth forest streams shows that, assuming random tree fall, 99.5% originate from within 20 m of riparian forest closest to the channel, ca. 80% from the bordering 10 m, and more than half from the bordering 5 m (Fig. 3). The source distances for the 11 reaches situated in managed forests showed a similar pattern. The intercept of the lines indicates that approximately 10% of the in-channel CWD originates from trees growing on the channel edge.

Discussion

Comparisons of wood volumes

The volumes of CWD in the stream channels were related to CWD volumes found on the forest floor. This result was expected based on the assumption that similar input mechanisms would be operative in streams of similar sizes and characteristics. The generally stronger correlations among the species-specific volumes of CWD in stream channels and the riparian forest than among volumes of CWD in channels and volumes of living trees also support this hypothesis. The volume of CWD found in the stream channels exceeded the volume found in the adjacent riparian forest. This result was also expected based on Dahlström et al. (2005), who found slow decomposition rates of conifers, especially Scots pine, in stream channels. Several other studies have found slow decomposition rates of CWD in streams (Lienkaemper and Swanson 1987; Murphy and Koski 1989; Hyatt and Naiman 2001) and reported lower decay rates and longer residence times than those reported from studies on wood in terrestrial habitats (Harmon et al. 1986, 2000; Tarasov and Birdsey 2001). Although breakdown of CWD in the channel is attributed to both physical and biological decay, the decay on the forest floor, which is generally restricted to biological processes, seems faster.

Other mechanisms could also generate a pattern with higher volumes of CWD found in stream channels than on the riparian forest floor, for instance, a tendency for trees to fall towards the channel. CWD with bent trunks may represent trees that have been growing on the channel edge. Ac-

Fig. 1. Proportions of pine, spruce, and deciduous species coarse woody debris within five decay classes in stream channels intersecting old growth (C-OG) and managed (C-M) forests and on old-growth (F-OG) and managed (F-M) forest floor.

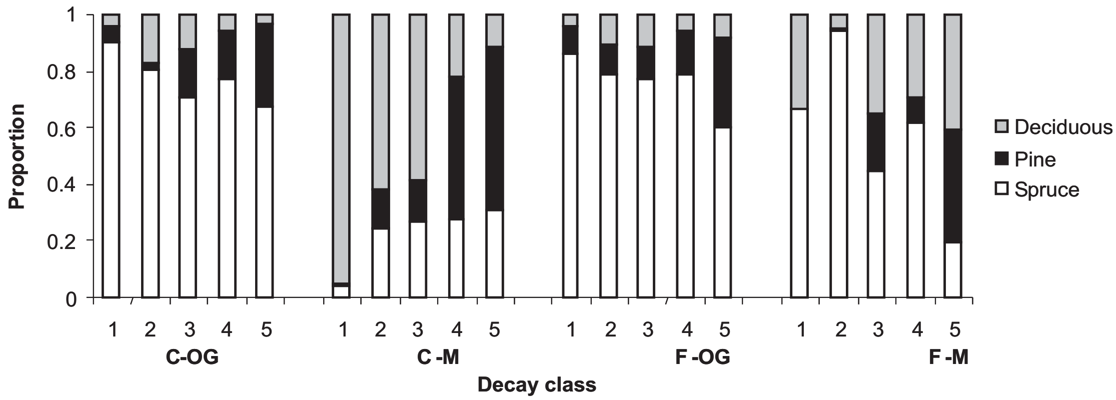


Table 3. Regression equations including the riparian forest variables coarse woody debris (CWD) (m^3/ha) as logs and density of living trees >5 cm in basal end diameter (no./ha) and an indicator variable (MA) for difference between old growth (MA = 0), and managed forest (MA = 1), describing the variability in the stream channel's volume and frequency of woody debris.

Dependent variable	Regression equation	R^2	*P* value
CWD volume in channel (m^3/ha)	16.7 + 2.08 CWD – 1.46 CWD × MA	65.5	<0.001
Frequency of CWD in channel (no./100 m)	33.2 + 0.0236 living stems – 0.0215 living stems × MA	48.4	<0.001

Fig. 2. Comparison of average length (*a*) and mean diameter (*b*) of coarse woody debris (CWD) in five decay classes in the stream channel (□) and downed CWD in the riparian forest (■) in the old-growth sites. Bars represent standard deviation.

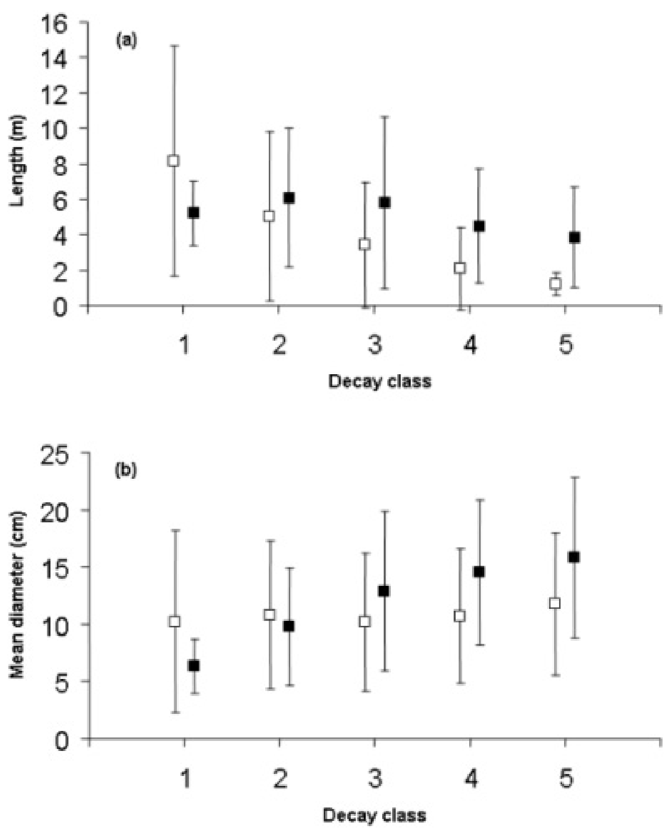
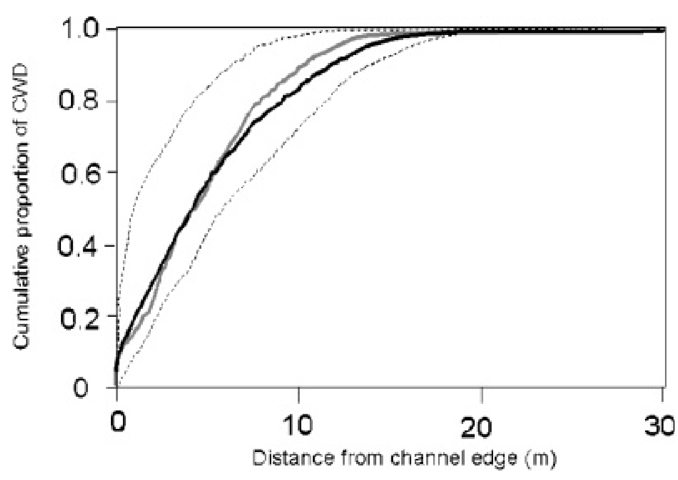


Fig. 3. Cumulative proportion of coarse woody debris (CWD) delivered to the stream channel as a function of distance from channel edge. The black line shows the average for old-growth sites, and the grey line the same for managed sites. The area between the two broken lines delineates the range of old-growth sites.



cording to source distances that would be generated from purely random tree fall, approximately 10% of the wood that enters channels derives from trees growing on the channel edge, which is a similar proportion to that found in the stream channels. However, not all trees growing on the channel edge have bent trunks. Even trees with relatively straight trunks may have asymmetrical crowns, possibly caused by better light availability over the channel, which may make it more likely for them to fall towards the channel. Along small streams with coarse substrates and flat surroundings, this effect is unlikely to be important, and the possibly higher probability for some trees to fall towards the channel cannot alone explain the more than twofold volume of CWD found in the stream channels compared to that on the riparian forest floor. Also, no trends were observed of increased amounts of CWD as logs or snags towards the channel. Another possible reason for the higher volumes of CWD in stream channels is that CWD may have burnt on the forest floor (Siitonen 2001), but not in the stream channel, thus resulting in lowered volumes in the riparian forest. However, the difference in wood volumes between the terrestrial and aquatic environments was equally strong for the reaches that lacked traces of fires.

When comparing CWD volumes between managed and old-growth sites, the difference on the forest floor was of the same magnitude as the one in stream channels. This finding is unexpected. On average, the managed riparian forest in this study contained 39.8% of the CWD volume found in the old-growth forest, which is a smaller difference than in many other similar comparisons. Volumes of CWD in managed forests are reported to be typically less than 30% and often closer to 10% of the volumes in unmanaged forests (Linder and Östlund 1998; Fridman and Walheim 2000; Siitonen 2001). The volumes of CWD found in the old-growth riparian forest (mean 67.8 m^3/ha) and their proportion relative to the living and dead volumes (mean 20.3%) represent typical values reported from other old-growth forests in boreal Fennoscandia (Siitonen 2001). However, the CWD volumes found in the managed forest (27.0 m^3/ha) are slightly higher than average values reported from managed forests in central and northern Sweden, which contain approximately 6–10 m^3/ha, and managed mature forests approximately 10–15 m^3/ha (Fridman and Walheim 2000). The explanation for the observed pattern is most likely to be found in the history of the managed forests. They are all mature and have been targeted for repeated selective cuttings of various frequencies and intensities. The absence of recently cut stumps, the presence of large trees, and the basal area and standing volume of living trees similar to that in the old-growth forests suggest that extensive recent cuttings are lacking. Historically, coniferous trees were the only commercial tree species, and except for local use as firewood near villages and potash production between ca. 1800 and 1860 (Östlund et al. 1998), cutting of deciduous trees was limited before introduction of clear-cutting forestry in the 1950s. Analyses of cut stumps in the managed forests show that only a minor proportion consisted of deciduous species. Accordingly, the managed forests have escaped cuttings for at least 50 years, and the earlier cuttings targeted coniferous trees, although rapid decay of deciduous stumps may mask earlier cuttings.

Initially, timber harvesting may add large amounts of smaller sized CWD as logging residue to the forest and stream channels (Lisle 1986; Hedman et al. 1996). However, after harvesting the input of CWD decreases due to fewer trees and reduced stem suppression, the CWD volumes decline, and increases do not occur until the forest stand starts to produce new CWD. If the CWD volumes and frequencies of debris dams in the channel reaches become critically low, the remaining small-sized CWD in the channels probably becomes sensitive to flushing, and CWD amounts in channels may decrease further. Most likely, in the managed forest and streams, CWD of mainly deciduous trees has started to accumulate recently (from low values), and the elevated volumes in stream channels as compared to riparian forest floors that would have been generated by lower decomposition rates in the stream channel have not yet developed. Selective cutting of mainly coniferous trees has probably favoured remaining and early succession of deciduous trees, and today dieback of mainly deciduous trees has generated volumes of deciduous CWD in the streams equal to the volumes found in the old-growth sites. As mentioned, among species, only Norway spruce CWD was significantly lower in the managed forest and intersecting streams than in the old-growth sites. Dahlström et al. (2005) suggested that in stream channels birch decays more rapidly than Norway spruce, and Norway spruce more rapidly than Scots pine. This sequence of increasing decay rates is consistent with studies on terrestrial logs of the same species (Harmon et al. 2000; Tarasov and Birdsey 2001). These findings are in agreement with the suggestion that the amount of deciduous CWD found in the managed forest and streams is a result of more recent dieback and that Scots pine is predominantly a remnant from leftover debris and the time before the first cuttings (cf. Dahlström et al. 2005). Norway spruce, which was the most abundant living tree, has not yet started to accumulate as debris in the stream channels, and much of the ancient Norway spruce wood has decayed. Also the proportion of CWD in channels among species, separated into decay classes, corresponds to this finding. Wood from deciduous species was on average less decomposed in the managed forest sites than in the old-growth forest, whereas Scots pine wood was more decomposed.

CWD in the old-growth forests and intersecting streams

Despite the relationships between stream channels and the adjacent riparian forest in the proportions of tree species and wood volumes, significant differences exist in CWD characteristics that are attributed to differences in CWD dynamics in the riparian zone and in the stream channel. Both the average tree heights and the majority of the in-channel CWD exceed channel width, resulting in low transport capacities and lower physical abrasion than in larger streams (Swanson et al. 1984). The lower proportions of wood in decay class 5, and increased proportions of bent trunks in wider streams, suggest that physical abrasion may be more important in streams with higher abilities to move pieces and that channel stability decreases with increasing channel widths. However, we found no significant negative trends in in-channel CWD volumes or frequencies with increasing channel widths.

The average length of CWD found in streams was significantly less than the height of trees in the riparian forest, similar to the result found by Bilby and Ward (1989). They concluded that trees typically become fragmented when they fall. Lienkaemper and Swanson (1987) also found that tree trunks split and contributed multiple pieces of CWD to the stream channel. In our study, trees were significantly longer than logs in the riparian zone, and logs there were significantly longer than in-channel CWD. However, according to the high proportion of intact top sections of in-channel

CWD and logs in decay class 1, the majority of trees that fell directly or within a few years after mortality did not break into multiple pieces when they fell. The differences between studies are probably attributed to the much larger tree sizes in the North American studies, where a tree fall exposes the wood to a much stronger force. The high proportion of snags compared to that of downed CWD suggests that many trees do not fall when they die, but remain standing as snags and reach higher decay classes before they eventually fall. The wood is more fragile in higher decay classes, and falling snags probably generate multiple pieces more frequently than trees that fall and die. A comparison of length distributions of aquatic and terrestrial CWD separated into decay classes shows that in-channel CWD in decay class 1 is generally longer than logs in decay class 1. This is explained by the higher probability of longer pieces to reach the channel. In later decay stages CWD pieces in streams are broken by stream flow but the average diameters remain, whereas logs retain their length. Also, in small streams where the average tree heights exceed channel widths, many fallen trees bridge the channel for a number of years before breaking.

Riparian trees and sources of in-channel CWD

The zonation of trees within 30 m from the channel edge shows the same pattern as along larger watercourses with a higher proportion of deciduous trees and a lower proportion of Scots pine close to the channel. As expected, however, the old-growth riparian forests are, as for upland forests, dominated by coniferous trees and only show minor changes with distance to channel edge. Our results suggest that the recommendations of foresters to create a zone dominated by deciduous trees along streams (Tosteby 1995; de Jong et al. 1999) are not ideal for mimicking natural species composition along small streams intersecting old-growth boreal forest.

In many regions, headwater streams are typically deeply incised, and their channels are confined by steep hill slopes. In such channels, processes attributed to mass wasting can be of significant importance for CWD input (Keller and Swansson 1979; Bilby and Bisson 1998). In larger watercourses with extensive alluvial floodplains and migrating channels, bank cutting is an important input mechanism of CWD (Murphy and Koski 1989). The streams in the present study, and many streams over large areas of the forested boreal Fennoscandia, drain through morainic deposits originating from crystalline rocks. As such, they lack deeply incised stream valleys, and slope processes and bank cutting are rare. In the studied streams, few processes are able to transport CWD to the stream channels further than a tree height. Thus, the source area for CWD consists of a narrow zone along the streams, and the vast majority of all wood that can enter the channel is found within the closest 15 m zone. Similar results have been found in other areas where recruitment is dominated by random tree fall (Murphy and Koski 1989; McDade et al. 1990; Van Sickle and Gregory 1990). Possibly, trees growing on or near the channel edge have a higher probability than a random outcome to fall towards the channel. This is caused by bank cutting, asymmetric root wads, trunks, or crowns. In such cases, the source distances of CWD are even shorter.

Modelling possibilities of in-channel CWD

This study provides support for the idea that CWD input to small stream channels and to the adjacent riparian forest mainly results from similar mechanisms. This finding increases the possibility to create reliable models of CWD supply and amounts based on knowledge of forest development and CWD dynamics in the terrestrial environment. The volume of CWD in a forest without timber harvest primarily depends on site productivity, decomposition rate, and disturbance affecting CWD input rates and stand succession (Harmon et al. 1986). Volumes of CWD in stream channels should be affected by the same processes. Assuming small differences among sites in decay rates and disturbance, differences in CWD volumes among stands will be determined by site productivity. Based on data (Linder et al. 1997) from plots dominated by Norway spruce, Ranius et al. (2004) reported that the volume of living trees equals the site productivity times 70. Our data correspond with this relationship if based on site productivity calculated from average tree heights of dominant trees (Hägglund and Lundmark 1981). The proportion of dead wood to the total volume of dead and living trees averaged 20.3% for the old-growth riparian forests. Siitonen (2001) reviewed the proportion of CWD to the total amount of wood (living and dead) and reported values of 18%–40% with a mean of 28% in stands dominated by Norway spruce and approximately the same figures from stands dominated by Scots pine (18%–37% with a mean of 25%). Nilsson et al. (2002) concluded that in old-growth forests, about 30% of the basal area and volume of CWD are standing. If applicable to riparian areas of small forest streams, this means that site productivity can be directly transformed to CWD loading, and based on the relationship between CWD volumes on the riparian forest floor and streams, site productivity could potentially be used to estimate volumes of CWD in headwater streams under pristine conditions.

In conclusion, small streams represent a large fraction of the total length of drainage networks, and their adjacent riparian forests constitute much of the area that may be targeted for future management to maintain the multiple functions of riparian zones. The type of management carried out in riparian forests will be fundamental for the future forest development and recruitment of CWD to streams. For example, by leaving a larger proportion of Scots pine trees in the riparian forest, the mass of wood in the stream will eventually increase. Most of the examined old-growth forests have to some extent been affected by previous harvesting and do not represent purely pristine conditions, mainly because of the present lack of forest fires. The fact that the proportion of CWD in the riparian forest decreased with increasing number of cut stumps suggests that even a small influence of earlier cuttings of relatively few, predominantly large Scots pine trees affects current volumes of CWD. However, the degree of cutting was not observed in reduced volumes of CWD found in the stream channels of the old-growth forests. Charred old stumps were present along several streams, suggesting that fires previously affected the riparian forest. Detailed knowledge about the forest history is needed to evaluate how current wood amounts found in streams have been affected by different types of natural and human disturbances.

Acknowledgments

We thank Daniel Holmqvist and Hans Wallin for fieldwork assistance and Shawn Fraver for comments on the manuscript. The study was supported by the Ebba and Sven Schwartz' Foundation and was carried out when N. Dahlström was a Ph.D. student at Mid Sweden University, Sundsvall, Sweden. We thank two anonymous reviewers for valuable comments on the manuscript.

References

Acker, S.A., Gregory, S.V., Lienkaemper, G., McKee, W.A., Swanson, F.J., and Miller, S.D. 2003. Composition, complexity, and tree mortality in riparian forests in the central Western Cascades of Oregon. For. Ecol. Manage. **173**: 293–308.

Ahti, T., Hämet-Ahti, L., and Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. Ann. Bot. Fenn. **5**: 169–211.

Beechie, T.J., Pess, G., Kennard, P., Bilby, R.E., and Bolton, S. 2000. Modeling recovery rates and pathways for woody debris recruitment in northwestern Washington streams. N. Am. J. Fish. Manage. **20**: 436–452.

Bilby, R.E., and Bisson, P.A. 1998. Function and distribution of large woody debris. *In* River ecology and management. *Edited by* R.J. Naiman and R.E. Bilby. Springer-Verlag, New York, New York. pp. 324–346.

Bilby, R.E., and Likens, G.E. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology, **61**: 1107–1113.

Bilby, R.E., and Ward, J.W. 1989. Changes in characteristics and function of woody debris with increasing size of streams in western Washington. Trans. Am. Fish. Soc. **118**: 368–378.

Bilby, R.E., and Wasserman, L.J. 1989. Forest practices and riparian management in Washington State: data based regulation development. *In* Practical approaches to riparian resource management. *Edited by* R.E. Gresswell, B.A. Barton, and J.L. Kershner. USDI Bureau of Land Management, Billings, Montana. pp. 87–94.

Bisson, P.A., Bilby, R.E., Bryant, M.D., Dollof, C.A., Grette, G.B., House, R.A., Murphy, M.L., Koski, K.V., and Sedell, J.R. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. *In* Streamside management: forestry and fishery interactions. *Edited by* E.O. Salo and T.W. Cundy. University of Washington, Seattle, Wash. pp. 143–190.

Dahlström, N., and Nilsson, C. 2004. Influence of woody debris on channel structure in old growth and managed forest streams in central Sweden. Environ. Manage. **33**: 376–384.

Dahlström, N., Jönsson, K., and Nilsson, C. 2005. Long-term dynamics of large woody debris in a managed boreal forest stream. For. Ecol. Manage. **210**: 363–373.

de Jong, J., Larsson-Stern, M., and Liedholm, H. 1999. Greener forests. National Board of Forestry, Jönköping, Sweden.

Ehrman, T.P., and Lamberti, G.A. 1992. Hydraulic and particulate matter retention in a 3rd order Indiana stream. J. N. Am. Benthol. Soc. **11**: 341–349.

Esseen, P.-A. 1994. Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. Biol. Conserv. **68**: 19–28.

Esseen, P.-A., Ehnström, B., Ericson, L., and Sjöberg, K. 1997. Boreal forest. Ecol. Bull. **46**: 16–47.

Fredén, C. (*Editor*). 1994. Geology. The national atlas of Sweden. SNA Publishing, Stockholm.

Fridman, J., and Walheim, M. 2000. Amount, structure and dynamics of dead wood on managed forestland in Sweden. For. Ecol. Manage. **131**: 23–26.

Gomi, T., Roy, C., Sidle, R.C., Woodsmith, R.D., and Bryant, M.D. 2003. Characteristics of channel steps and reach morphology in headwater streams, southeast Alaska. Geomorphology. **51**: 225–242.

Gregory, S.V., Swanson, F.J., McKee, W.A., and Cummins, K.W. 1991. An ecosystem perspective of riparian zones. Bioscience, **41**: 540–551.

Gurnell, A.M., and Sweet, R. 1998. The distribution of large woody debris accumulations and pools in relation to woodland stream management in a small, low-gradient stream. Earth Surf. Process. Landf. **23**: 1101–1121.

Hägglund, B., and Lundmark, J.-E. 1981. Handledning i bonitering med Skogshögskolans boniteringssystem. I–III. Skogsstyrelsen, Jönköping, Sweden. [In Swedish.]

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. **15**: 133–302.

Harmon, M.E., Krankina, O.N., and Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Can. J. For. Res. **30**: 76–84.

Hedman, C.W., Van Lear, D.H., and Swank,W.T. 1996. In-stream large woody debris loading and riparian forest seral stage associations in the southern Appalachian mountains. Can. J. For. Res. **26**: 1218–1227.

Hyatt, T.L., and Naiman, R.J. 2001. The residence time of large woody debris in the Queets river, Washington, USA. Ecol. Appl. **11**: 191–202.

Jonsson, B.G. 2000. Availability of coarse woody debris in a boreal old-growth *Picea abiea* forest. J. Veg. Sci. **11**: 51–56.

Jonsson, B.G., and Dynesius, M. 1993. Uprooting in boreal spruce forests: long-term variation in disturbance rate. Can. J. For. Res. **23**: 2383–2388.

Keller, E.A, and Swanson, F.J. 1979. Effects of large organic material on channel form and fluvial processes. Earth Surf. Proc. **4**: 361–380.

Krankina, O.N., and Harmon, M.E. 1995. Dynamics of dead wood carbon pool in northwestern Russian boreal forests. Water Air Soil Poll. **82**: 227–238.

Kruys, N., Jonsson, B.G., and Ståhl, G. 2002. A stage-based matrix model for the decay class dynamics of woody debris. Ecol. Appl. **12**: 773–781.

Lienkaemper, G.W., and Swanson, F.J. 1987. Dynamics of large woody debris in streams in old-growth Douglas-fir forests. Can. J. For. Res. **17**: 150–156.

Linder, P., and Östlund, L. 1998. Structural changes in three midboreal Swedish forest landscapes, 1885–1996. Biol. Conserv. **85**: 9–19.

Linder, P., Elfving, B., and Zackrisson, O. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. For. Ecol. Manage. **98**: 17–33.

Lisle, T.E. 1986. Effects of woody debris on anadromous salmonid habitat, Prince of Wales Island, Alaska. N. Am. J. Fish. Manage. **6**: 538–550.

Lisle, T.E. 1995. Effects of coarse woody debris and its removal on a channel affected by the 1980 eruption of Mount St. Helens, Washington. Water Resour. Res. **31**: 1797–1808.

May, C.L., and Gresswell, R.E. 2003. Large wood recruitment and redistribution in headwater streams in the southern Oregon Coast Range, U.S.A. Can. J. For. Res. **33**: 1352–1362.

McDade, M.H., Swanson, F.J., McKee, W.A., Franklin, J.F., and Van Sickle, J. 1990. Source distances for coarse woody debris entering small streams in western Oregon and Washington. Can. J. For. Res. **20**: 326–330.

Murphy, M.L., and Koski, K.V. 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. N. Am. J. Fish. Manage. **9**: 427–436.

Naiman, R.J., and Bilby, P.A. 1998. River ecology and management. Springer-Verlag, New York, New York.

Naiman, R.J., Décamps, H., and Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecol. Appl. **3**: 209–212.

Naiman, R.J., Balian, E.V., Bartz, K.K., Bilby, R.E., and Latterell, J.J. 2002. Dead wood dynamics in stream ecosystems. *In* Proceedings of the symposium on the ecology and management of dead wood in Western Forests. *Edited by* P.J. Shea, W.F. Laudenslayer, Jr., B. Valentine, C.P. Weatherspoon, and T.E. Lisle. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181. pp. 23–48.

Näslund, M. 1947. Funktioner och tabeller för kubering av stående träd. Medd. Stat. Skogsforskningsinst. **36**. [In Swedish.]

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G., and Ranius, T. 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. For. Ecol. Manage. **161**: 189–204.

Östlund, L. 1993. Exploitation and structural changes in the north Swedish boreal forest 1800–1992. Ph.D. dissertation, Swedish University of Agricultural Sciences, Umeå, Sweden.

Östlund, L., Zackrisson, O., and Strotz, H. 1998. Potash production in northern Sweden: history and ecological effects of pre-industrial forest exploitation. Environ. Hist. **4**: 345–358.

Palik, B., Golladay, S.W., Goebel, P.C., and Taylor, B.W. 1998. Geomorphic variation in riparian tree mortality and stream coarse woody debris recruitment from record flooding in a coastal plain stream. Ecoscience, **5**: 551–560.

Piégay, H., and Gurnell, A.M. 1997. Large woody debris and river geomorphological pattern: examples from S.E. France and S. England. Geomorphology, **19**: 99–116.

Raab, B., and Vedin, H. 1995. National atlas of Sweden. Vol. 14. Climate, lakes and rivers. Almqvist & Wiksell, Stockholm.

Raikow, D.F., Grubbs, S.A., and Cummins, K.W. 1995. Debris dam dynamics and coarse particulate organic matter retention in an Appalachian mountain stream. J. N. Am. Benthol. Soc. **14**: 535–546.

Ranius, T., and Kindvall, O. 2004. Modelling the amount of coarse woody debris produced by the new biodiversity-oriented silvicultural practices in Sweden. Biol. Conserv. **119**: 51–59.

Ranius, T., Kindvall, O., Kruys, N., and Jonsson, B.G. 2003. Modelling dead wood in Norway spruce stands subject to different management regimes. For. Ecol. Manage. **182**: 13–29.

Ranius, T., Jonsson, B.G., and Kruys, N. 2004. Modeling dead wood in Fennoscandian old-growth forests dominated by Norway spruce. Can. J. For. Res. **34**: 1025–1034.

Robison, E.G., and Beschta, R.L. 1990*a*. Characteristics of coarse woody debris for several coastal streams of southeast Alaska, USA. Can. J. Fish. Aquat. Sci. **47**: 1684–1693.

Robison, G.E., and Beschta, R.L. 1990*b*. Identifying trees in riparian areas that can provide coarse woody debris to streams. For. Sci. **36**: 790–801.

Rot, B.W., Naiman, R.J., and Bilby, R.E. 2000. Stream channel configuration, landform, and riparian forest structure in the Cascade Mountains, Washington. Can. J. Fish. Aquat. Sci. **57**: 699–707.

Samuelsson, J., Gustafsson, L., and Ingelög, T. 1994. Dying and dead trees: a review of their importance for biodiversity. Swedish Threatened Species Unit, Uppsala, Sweden.

Shields, F.D., Jr., and Smith, R.H. 1992. Effects of large woody debris removal on physical characteristics of a sand-bed river. Aquat. Conserv.-Mar. Freshw. Ecosyst. **2**: 145–163.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. **49**: 11–41.

Swanson, F.J., Bryant, M.D., Lienkaemper, G.W., and Sedell, J.R. 1984. Organic debris in small streams, Prince of Wales Island, southeast Alaska. USDA For. Serv. Gen. Tech. Rep. PNW-166.

Tarasov, M.E., and Birdsey, R.A. 2001. Decay rate and potential storage of coarse woody debris in Leningrad Region. Ecol. Bull. **49**: 137–147.

Tosteby, A. 1995. Vattenvård i AssiDomän Skog och Trä. Skog och Forskning, **4**: 60–65. [In Swedish.]

Vannote, R.L., Minshall, G.W., Cummings, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37**: 120–137.

Van Sickle, J., and Gregory, S.V. 1990. Modeling inputs of large woody debris to streams from falling trees. Can. J. For. Res. **20**: 1593–1601.

Welty, J.J., Beechie, T., Sullivan, K., Hyink, D.M., Bilby, R.E., Andrus, C., and Pess, G. 2002. Riparian aquatic interaction simulator (RAIS): a model of riparian forest dynamics for the generation of large woody debris and shade. For. Ecol. Manage. **162**: 299–318.

Young, M.K. 1994. Movement and characteristics of stream-borne coarse woody debris in adjacent burned and undisturbed watersheds in Wyoming. Can. J. For. Res. **24**: 1933–1938.

Zelt, R.B., and Wohl, E. 2004. Channel and woody debris characteristics in adjacent burned and unburned watersheds a decade after wildfire, Park County, Wyoming Geomorphology, **57**: 217–233.