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Small wood dynamics in a headwater stream

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Introduction

Wood influences a wide array of abiotic and biotic factors in streams (HARMON et al. 1986). Long-term estimates of export were combined with a litter exclusion study (WALLACE et al. 1997), and direct removal of all small wood ≤10-cm diameter to further reduce the link between a forested headwater catchment and its stream (WALLACE et al. 1999). This provided an excellent opportunity to address several aspects of wood dynamics in a small headwater stream. These include: (1) woody debris standing crop; (2) adequacy of non-destructive woody debris sampling versus complete removal of all woody debris ≤10 cm diameter; and (3) annual measurements of small woody debris input and losses.

Methods

Our study site is the stream draining Catchment 55 (C 55) at Coweeta Hydrologic Laboratory in western North Carolina, USA. Terrestrial vegetation on C 55 is mixed deciduous forest with a dense, evergreen *Rhododendron* understory along the riparian margin. Since August 1993, the entire stream has been covered by a gill net canopy in addition to a lateral movement fence on each bank to prevent litter from entering the stream from the surrounding forest (WALLACE et al. 1997).

Direct input of wood was measured with 0.25-m^2 traps (WALLACE et al. 1995) placed along or above the stream. Traps were placed inside (n = 16) and outside (n = 6) the net canopy. Lateral litter inputs were estimated using lateral movement traps (0.5 m long, WALLACE et al. 1995) placed inside (n = 16) and outside (n = 6) the lateral movement fence of C 55. Traps were emptied weekly during October and November and monthly during other periods. Woody litter input was measured for 4.4 years. All wood was dried, weighed, ashed (500 °C), and reweighed to obtain ash free dry mass (AFDM).

Export of coarse particulate organic matter (CPOM), including woody debris, has been measured continuously every 2 weeks since 1985. Export was measured with a large CPOM trap (4-mm mesh) that filters the entire stream flow at the base of the catchment (CUFFNEY & WALLACE 1988). AFDM of woody debris export was determined as described above for inputs. Stream flow is gauged continuously using "1 ft" H-flumes and both FW-1 and ISCO stage recorders.

Standing crop of wood in the wetted stream perimeter was assessed using three methods. First, wood was estimated from monthly benthic samples (n = 4) taken with a 400-cm^2 corer. Second, line intersect measurements (WALLACE & BENKE 1984) were made every 5 m (total n = 33) in which wood diameters were measured (to the nearest mm) for each piece of wood. Third, all wetted small wood (≤10 cm diameter) was removed by hand in 1996 following 3 years of litter exclusion. Additional hand removal of small wood was required on five dates between 1996 and early 1998 as previously buried wood was exposed following large storms. All wood removed from the stream was measured (length and diameter), wet-weighed, and a subsample of known volume was removed for wet-weight to dry-weight conversion and treated as above for AFDM conversions. The average specific gravity (0.356 g cm^{-3}) of these subsamples was applied to estimates of volume to convert line intersect volume to AFDM.

Breakdown rates of wood standing crop were based on data for wood breakdown rates of oak, *Quercus* spp., sticks in nearby Coweeta streams (WEBSTER et al. 1998). This study did not include sticks >4 cm in diameter; hence, we estimated breakdown rates (k) for larger diameters of wood by regressing k (day^{-1}) versus size class using an exponential function for the different sizes of oak sticks ($k = 0.000503 \times 10^{-0.0083x}$) where x = size class (diameter in mm). This size-specific k was multiplied by the volume of each piece of small wood measured in the line intersect method (n = 431) to obtain the amount of volume (representative of mass based on 0.356 g cm^{-3}) lost each day. Summing all of these individual losses gives an estimate of the total amount lost per day, which can be multiplied by 365 to get annual loss.

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Results

Direct input of woody litter from October 1993 through March 1998 (1,612 days) averaged 106.6 g AFDM m^{-2} $year^{-1}$ by estimates using litter traps (Table 1). During the same period lateral movement inputs of wood per linear meter (both sides) of stream averaged 71.8 g AFDM m^{-1} $year^{-1}$ (= 53.2 g AFDM m^{-2} $year^{-1}$) with total wood inputs averaging 160 g AFDM m^{-2} $year^{-1}$.

The standing crop of woody debris measured from monthly benthic samples averaged 437 g AFDM m^{-2} (range = 343–755, 48 samples $year^{-1}$, n = 6 years). On 27 August 1996, wetted wood standing crop measured by the line intersect technique was 2.8 kg AFDM m^{-2} of which 53% (1.47 kg) was ≤10 cm in diameter. On 31 August 1996, wetted surface small wood removed totaled 1.38 kg AFDM m^{-2} (total removed from stream = 316.35 kg). An additional 0.162 kg AFDM m^{-2} of previously buried wood was removed over a 492-day period following several large storms. Total wood ≤10 cm diameter removed from the wetted area of the stream was 1.542 kg AFDM m^{-2}, which was within 10% of that estimated using the line intersect estimate (Table 1).

Total wood export measured over the 13-year period was 79.4 kg AFDM. Annual export averaged 26.6 g AFDM m^{-2} $year^{-1}$ (range = 2.8–67.5, S.D. = 21.3). Wood export is "step-like" and illustrates the distinct effect of drought during the early years of the study (Fig. 1). With the exception of one large storm during the second year of the study (1986) there was little export of wood during the first 4 years. A strong positive relationship ($P < 0.001$) exists between maximum discharge during 2-week sampling intervals and wood export during the interval (Fig. 2).

As measured with line intersect methods, individual pieces of wood in the wetted stream area are strongly skewed toward smaller diameters with 98% of the pieces ≤10 cm diameter. The ≤10-cm wood represented 88% of the total surface area, but only 60% of the total volume of wood (Fig. 3). Mean breakdown rates of all wetted woody debris ≤10 cm diameter was calculated from the total estimated breakdown losses for each size class and averaged 0.00024 day^{-1} or 0.0876 $year^{-1}$.

An annual budget for small woody debris is given in Table 1. The standing crop of wetted small woody debris is about 9.6 × annual input. Small woody debris is apparently close to equilibrium with little net change over the annual cycle. Estimated turnover times using various

Table 1. Annual budget for small woody debris (≤10 cm diameter) for the stream draining Catchment 55. All values are expressed in g AFDM m^{-2} $year^{-1}$ based on a wetted stream area of 229.3 m^2 and stream length of 170 m. Estimated turnover times are in years.

A. Total input (107 direct + 53 lateral)	160
B_a. Wood standing crop (direct removal)[a]	1,542
B_b. Wood standing crop (line intersect method)[a]	1,469
C. Annual wood export	27
D_a. Wood breakdown (based on B_a above)[b]	135
D_b. Wood breakdown (based on B_b above)[b]	129
E_a. Net change $year^{-1}$ [(A)-(D_a+C)]	(–)2
E_b. Net change $year^{-1}$ [(A)-(D_b+C)]	5
Estimated turnover times	
1/k[b]	11.4 years
standing crop/input [(B_b/A) and (B_a/A)]	9.2–9.6 years
standing crop/breakdown + export [(B_b or B_a) /(D_a+C) or (D_b+C)]	9.1–9.9 years

[a]Does not include 1,327 g AFDM m^{-2} of wood >10 cm diameter
[b]Based on annual k of 0.0876

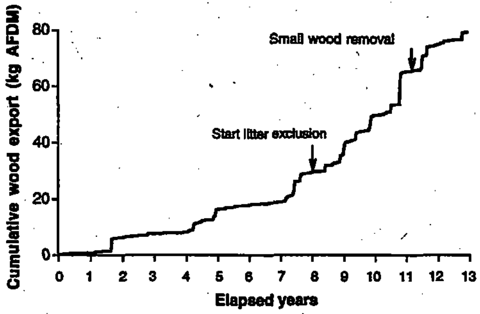

Fig. 1. Cumulative export of small woody debris from C 55 over a 13-year period (1985–1998). Note the "steps" in wood export, which are associated with storms.

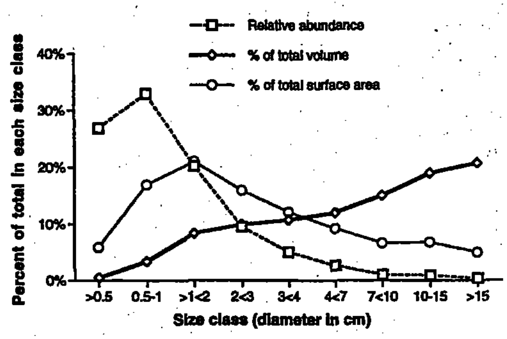

Fig. 3. Relative abundance, volume, and surface area of a woody debris standing crop in the stream by diameter size classes from line intersect measurements made at 5-m intervals.

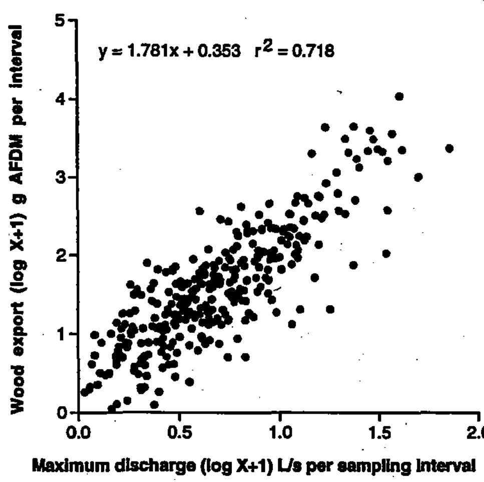

Fig. 2. Relationship between wood export and maximum discharge during each 2-week sampling interval between 1985 and1998.

methods range from 9.1 to 11.4 years (Table 1).

Discussion

Our value computed for small woody debris input (160 g AFDM m^{-2} $year^{-1}$) is remarkably close to that of 163 g AFDM m^{-2} $year^{-1}$ measured during 1985–1987 prior to canopy construction for this stream (Wallace et al. 1995). However, the standing crop of woody debris was greatly under-estimated using the 400-cm^2 coring device for benthic sampling. The latter device gave an estimate of only 437 g AFDM m^{-2}, which was ca. 30% of line intersect values (1,469 g AFDM m^{-2}). In contrast, the small wood standing crop estimated using the line intersect method was remarkably close to that obtained by manual removal of all small wood from the wetted perimeter (1,542 g AFDM m^{-2}). Thus, the line intersect method appears to be a good non-destructive sampling method for a small wood standing crop. During the coming year, we will assess the effectiveness of this method for large woody debris standing crop.

Our longest record is for wood export, which varied by as much as 24.1× between dry years (2.8 g exported m^{-2} $year^{-1}$) and years with large storms (67.5 g exported m^{-2} $year^{-1}$). Clearly, wood export is associated with periods of maximum discharge (Fig. 2). Although wood export increased during exclusion (Fig. 1), this increase is attributable to increases in storm flows because the slope of the relationship between maximum discharge and wood export did not change significantly between pretreatment and litter exclusion. Even following removal of small wood there was some export of wood as previously buried wood was transported during storm flows (Fig. 1).

There are no good estimates of breakdown rates for large (>4 cm diameter) wood in eastern USA streams. Breakdown of wood is much slower in freshwaters than in terrestrial systems (Harmon et al. 1986). We extended the equation of decay rate versus wood based on <4 cm diameter (Webster et al. 1999) to obtain estimates of larger size classes, i.e. >4 to ≤10 cm diameter. Since wood breakdown in freshwater habitats is primarily a surface area phenomenon (TRISKA & CROMACK 1980), our small wood breakdown rates may be too fast for >4 cm diameters. Several studies in terrestrial systems have measured hardwood decomposition slightly lower (ALBAN & PASTOR 1993, SCHOWALTER et al. 1998) or very similar to our values (ABBOTT & CROSSLEY 1982), which would also suggest that our decomposition rates were somewhat greater than what actually occur. This is a critical point for wetted wood for our study. For example, if our k value were reduced by only 25% less, then 31–36 g AFDM m^{-2} would be accumulating in the stream each year and the turnover time (1/k) would increase to 15.1 years.

We have not included any estimates of large woody debris, other than estimated standing crops, in our budget. Large woody debris represents less than 2% of the wood pieces found in the stream; however, it represents almost 40% of the total volume and hence a large, although refractory, mass of organic matter storage. The low abundance of large woody debris (>10 cm) in the stream is undoubtedly a legacy of extensive timber harvest throughout the lower portion of the Coweeta Basin between 1914 and 1919 (DOUGLASS & HOOVER 1988). However, with further maturity of the 2nd-generation forest, we would anticipate that inputs of large woody debris will accelerate during the coming decades. We have little knowledge of the input rates of large wood and even less about k values for large woody debris in freshwater. Since breakdown potentially is the largest part of wood loss (Table 1), data for aquatic breakdown rates of woody debris >4 cm diameter are badly needed.

Summary

We excluded terrestrial litter inputs including wood to a headwater stream in western North Carolina (USA) for 4 years. Following 3 years of exclusion, we removed all small wood (≤10 cm diameter), and obtained a whole stream assessment of wood. Weight of wood removed was only 1.1× greater than estimates with line-intercept techniques, but 3.6× higher than estimates obtained using a benthic corer. We constructed a mass balance for small wood based on estimates of wood input, storage, export and breakdown. Results of this budget indicate that small wood inputs and outputs are near equilibrium and turnover time for small wood is about a decade. However, much more information is needed on decomposition rates of woody debris in fresh waters to enhance our understanding of wood dynamics in streams.

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References

ABBOTT, D. T. & CROSSLEY, D. A., 1982: Woody litter decomposition following clear-cutting. – *Ecology* 63: 35–42.

ALBAN, D. H. & PASTOR, J., 1993: Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. – *Can. J. For. Res.* 23: 1744–1749.

CUFFNEY, T. F. & WALLACE, J. B., 1988. Particulate organic matter export from three headwater streams: discrete versus continuous measurements. – *Can. J. Fish. Aquat. Sci.* 45: 2010–2016.

DOUGLASS, J. E. & HOOVER, M. D., 1988. History of Coweeta. – In: SWANK, W. T. & CROSSLEY, D. A. (eds): *Forest Hydrology and Ecology at Coweeta*: 17–31. – Springer-Verlag, New York.

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. & CUMMINS, K. W., 1986: Ecology of coarse woody debris in temperate ecosystems. – *Adv. Ecol. Res.* 15: 133–302.

SCHOWALTER, T. D., ZHANG, Y. L. & SABIN, T. E., 1998: Decomposition and nutrient dynamics of oak *Quercus* spp. logs after five years of decomposition. – *Ecography* 21: 3–10.

TRISKA, F. J. &CROMACK, K., JR., 1980: The role of wood debris in forests and streams.– In: WARING, R. H. (ed.): *Forests: Fresh Perspectives from Ecosystem Analysis*: 171–190. – Oregon State University Press, Corvallis.

WALLACE, J. B. & BENKE, A. C., 1984: Quantification of wood habitat in subtropical Coastal Plain streams. – *Can. J. Fish. Aquat. Sci.* 41: 1643–1652.

WALLACE, J. B., EGGERT, S. L., MEYER, J. L. & WEBSTER, J. R., 1997: Multiple trophic levels of a forest stream linked to terrestrial litter inputs. – *Science* 277: 102–104.

WALLACE, J. B., WHILES, M. R., EGGERT, S. L., CUFFNEY, T. F., LUGTHART, G. W. & CHUNG, K., 1995: Long-term dynamics of coarse particulate organic matter in three Appalachian Mountain streams. – *J. N. Am. Benthol. Soc.* 14: 217–232.

WALLACE, J. B., EGGERT, S. L., MEYER, J. L. & WEBSTER, J. R.,

1999. Effects of resource limitation on a detrital-based ecosystem. – *Ecol. Monogr.* 69: 409–442.

WEBSTER, J. R., BENFIELD, E. F., EHRMAN, T. P., SCHAEFFER, M. A., TANK, J. L., HUTCHENS, J. J. & D'ANGELO, D. J., 1999: What happens to allochthonous material that falls into streams? – *Freshwat. Biol.* 41: 687–705.

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