

- world's freshwaters. *Limnology and Oceanography* 23:478-486.
- SHEATH, R. G., J. M. BURKHOLDER, J. H. HAMBROOK, A. M. HOGELAND, E. HOY, M. E. KANE, M. O. MORISON, A. D. STEINMAN, AND K. L. VAN ALSTYNE. 1986. Characteristics of softwater streams in Rhode Island. III. Distribution of macrophytic vegetation in a small drainage basin. *Hydrobiologia* 140:183-191.
- STEINMAN, A. D. 1992. Does an increase in irradiance influence periphyton in a heavily-grazed woodland stream? *Oecologia* 91:163-170.
- STEINMAN, A. D. 1996. Effects of grazers on freshwater benthic algae. Pages 341-373 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego, California.
- STEVENSON, R. J. 1990. Benthic algal community dynamics in a stream during and after a spate. *Journal of the North American Benthological Society* 9:277-308.
- VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- WEBSTER, J. R., AND R. L. MEYER. 1997. Stream organic matter budgets—introduction. Pages 5-13 in J. R. Webster and J. L. Meyer (editors). *Stream organic matter budgets*. *Journal of the North American Benthological Society* 16:3-161.

Comparison of litterfall input to streams

E. F. BENFIELD

*Department of Biology,
Virginia Polytechnic Institute and State University,
Blacksburg, Virginia 24061 USA*

Allochthonous organic matter is an important source of energy for many streams and the major energy source for woodland streams or streams with well developed riparian corridors of vegetation (e.g., Cummins et al. 1983). Litterfall may be defined as allochthonous material entering streams from riparian vegetation. It may include leaves and leaf fragments, floral parts, bark, wood (branches and twigs), cones and nuts, fruits, and other plant parts (Bray and Gorham 1964). Litter may reach streams by direct fall or lateral movement (blowing or sliding down the stream banks). The relative amounts of material reaching streams by these 2 routes

vary considerably. Lateral movement may vary with wind patterns, aspect, bank slope, and other site-specific factors (Wallace et al. 1992). For example, lateral movement accounted for about 24% of total litter input to 4 southern Appalachian streams (Webster et al. 1995), about 66% in a Douglas fir-hemlock forest stream in the western US (Sedell et al. 1982), but only about 10% in a eucalyptus forest stream in Australia (Campbell et al. 1992). The composition of litterfall varies with vegetation type and location. As a general average, non-leaf litterfall for forests around the world is about 30% (Bray and Gorham 1964) but may be up to 70% in some forests in southeastern Australia (Blackburn and Petr 1979, Briggs and Maher 1983).

In temperate deciduous forests, the bulk of litterfall occurs in autumn but material may continue entering streams by lateral movement over the remainder of the year. Needle-fall from coniferous evergreen trees varies considerably with species and location and may range from distinctly seasonal to irregular throughout the year (Bray and Gorham 1964). Litterfall from tropical wet forest trees and shrubs is usually non-synchronous and leaves enter streams relatively evenly over the entire year (Stout 1980).

In streams with broadly developed valleys or in lowland systems, litter may be entrained from the floodplain as streams rise during periods of increasing discharge (Cuffney 1988). Conversely, litter may be deposited on the floodplain as streams retreat during falling hydrographs (Post and de la Cruz 1977, Shure and Gottschalk 1985). Floodplain entrainment/deposition cycles of litter during changing hydrographs may also occur in smaller, montane streams (Wallace et al. 1992) and tundra streams (Peterson et al. 1986). Thus floodplain areas may be sources or sinks for litterfall depending on hydrodynamics, topography, sediment loads, and other factors (Cuffney 1988). In some floodplain systems, litterfall may be largely processed on the floodplain and the resulting particles entrained by streams during high flows (Smock 1990).

The objectives of this chapter are to summarize data on direct fall and lateral movement of litter to streams that were included in the earlier site-description chapters, and to analyze whether patterns of direct litterfall to these streams might be explained on the basis of local or spe-

TABLE 1. Order, latitude, and litter inputs for the 33 streams analyzed. NI = No information.

Stream	Order	Latitude (degrees)	Litterfall ($\text{g}^{-2} \text{y}^{-1}$)	Lateral movement ($\text{g}^{-2} \text{y}^{-1}$)	Total litter input ($\text{g}^{-2} \text{y}^{-1}$)	Cover type
Satellite Br, North Carolina	1	35	492	137	629	Mixed deciduous forest
Walker Br, Tennessee	1	36	459	106	565	Mixed deciduous forest
Buzzards Br, Virginia	1	37	528	NI	528	Mixed deciduous forest
August Cr, Michigan	1	42	448	NI	448	Mixed deciduous forest
WS10-1973, Oregon	1	45	537	667	1204	Coniferous forest
WS10-1974, Oregon	1	45	567	1111	2789	Coniferous forest
Devil's Club Cr, Oregon	1	45	736	NI	736	Coniferous forest
Rattlesnake Sp, Washington	1	47	242	NI	242	Shrub cover
First Choice Cr, Quebec	1	50	417	344	761	Mixed deciduous forest
Breitenbach, Germany	1	51	700	NI	700	Mixed deciduous forest
Caribou Cr 2, Alaska	1	65	37	NI	37	Mixed deciduous forest
Caribou Cr 3, Alaska	1	65	37	NI	37	Mixed deciduous forest
Canada St, Antarctica	1	78	0	0	0	Open
Hugh White Cr, North Carolina	2	35	506	71	577	Mixed deciduous forest
Deep Cr, Idaho	2	43	3	NI	3	Shrub/grass cover
Bear Brook, New Hampshire	2	44	594	NI	594	Mixed deciduous forest
Beaver Cr, Quebec	2	50	217	56	273	Mixed deciduous forest
Monument Cr, Alaska	2	65	62	19	81	Mixed deciduous forest
Creeping Swamp, North Carolina	3	35	696	NI	696	Mixed deciduous forest
Kings Cr (prairie), Kansas	3	39	100	18	118	Shrub/grass cover
White Clay Cr, Pennsylvania	3	40	313	NI	313	Mixed deciduous forest
Mack Cr, Oregon	3	45	730	NI	730	Coniferous forest
Keppel Cr, Australia	4	37	677	68	745	Mixed deciduous forest
Fort R, Massachusetts	4	42	384	NI	384	Mixed deciduous forest
Kuparuk R, Alaska	4	70	0	500	500	Shrub/sedge cover
Sycamore Cr, Arizona	5	33	17	3	20	Shrub cover
Kings Cr (forest), Kansas	5	39	357	369	726	Mixed deciduous forest
Lookout Cr, Oregon	5	45	730	NI	730	Coniferous forest
Muskkrat R, Quebec	5	50	30	11	41	Mixed deciduous forest
Ogeechee R, Georgia	6	32	843	3520	4363	Mixed deciduous forest
Matamek R, Quebec	6	50	16	3	19	Mixed deciduous forest
McKenzie R, Oregon	7	45	218	NI	218	Coniferous forest
Moisie R, Quebec	9	50	2	1	3	Mixed deciduous forest

cial topography, latitude, stream order, and riparian vegetation.

Methods

Litterfall data used in this analysis were drawn from 33 sites. Only 18 of the 33 sites had lateral movement data so the quantitative analyses were limited to direct litterfall. Linear regression was performed on direct litterfall versus stream order, latitude, and annual precipitation. Differences in litterfall among groups of vegetation cover types were tested with ANOVA followed by the LS means procedure.

Results

The present data set includes information from 33 sites ranging in latitude from 78°S to 70°N, but most of the sites are between 32° and 65°N on the North American continent (Table 1). Direct litterfall varied over a broad range from 0.0 $\text{g m}^{-2} \text{y}^{-1}$ in Canada Stream (Antarctica) and the Kuparuk River (Alaska), to 843 $\text{g m}^{-2} \text{y}^{-1}$ in the Ogeechee River (Georgia) (Table 1). Lateral movement values were available for only 18 sites and ranged from a high of 3520 $\text{g m}^{-2} \text{yr}^{-1}$ in the Ogeechee River to 3 $\text{g m}^{-2} \text{y}^{-1}$ or less in Sycamore Creek (Arizona) and the Matamek and

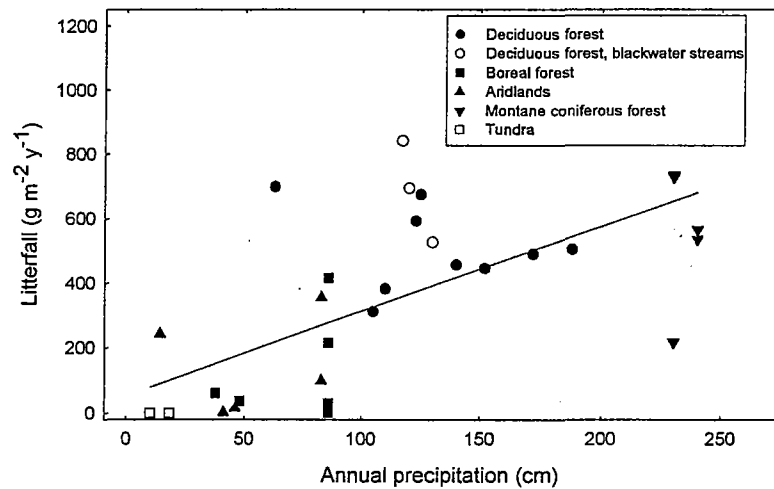


FIG. 1. Linear regression of litterfall vs. stream order ($p = 0.29$, $r^2 = 0.04$, $n = 33$).

Moisie rivers (Quebec). In the deciduous forest sites of the eastern US, lateral movement was generally less than or equal to 30% of direct litterfall. However, lateral movement in the Ogeechee River was >4 times direct litterfall but much of the lateral movement was actually litterfall on an extensive lowland floodplain that was periodically inundated. Lateral movement in the Kuparuk River was limited to erosion of peat from the stream banks and tundra plant litter entrained and deposited by floods. The stream draining Watershed 10 at the Andrews Forest (Oregon) had lateral movement about double direct litterfall in 2 successive years. Steep slopes in the watershed promoted litter from up-slope sliding down into the stream, accounting for the high input of lateral movement material. A reach of Kings Creek (Konza Prairie, Kansas) passing through gallery forest had slightly higher lateral movement than direct litterfall but another reach passing through prairie had a lateral input of about 18% of total. Total litter input, i.e., litterfall plus lateral movement, ranged from $0.0 \text{ g m}^{-2} \text{ y}^{-1}$ (Canada Stream) to $4363 \text{ g m}^{-2} \text{ y}^{-1}$ in the Ogeechee River.

Stream order in the data set ranged between 1st and 9th order: 13 of the direct litterfall values were from 1st-, and 5 were from 2nd-order streams (Table 1). There were 4 or fewer measurements from other orders. Interestingly, the 2 highest values for total litterfall were at nearly opposite ends of the spectrum in terms of stream order, location, and vegetation type. The

highest value was measured in a 6th-order, southeastern floodplain stream draining a mixed deciduous forest (Ogeechee River). The second highest value was measured in a 1st-order mountain stream (Watershed 10, 1974 data) draining a western coniferous forest. Both sites have special attributes, as discussed above, that account for the patterns of exceptionally high lateral movement input. Highest values for direct litterfall were from the Ogeechee River and a 1st-order stream in coniferous forest of western USA (Devil's Club Creek). The general trend that might be expected of litterfall decreasing with increasing stream order (e.g., Connors and Naiman 1984) was not observed here, i.e., there was no significant relationship between litterfall and stream order (Fig. 1). The data set demonstrates that there was significant variation in the quantity and types of litter input to streams of similar order but draining different kinds of terrestrial systems at different latitudes.

Numerous vegetation types are represented in the data set, but I lumped them into 3 general site types to look for general patterns in litterfall. The most frequently encountered type (20 of the 33 sites) is what I designated as "mixed deciduous"; however, this is a very heterogeneous grouping of sites. For example, Satellite Branch and Hugh White Creek (North Carolina) drain an oak-hickory-yellow poplar association, Keppel Creek (Australia) drains a eucalyptus forest, First Choice Creek (Quebec) drains a largely coniferous forest but the bulk of litter

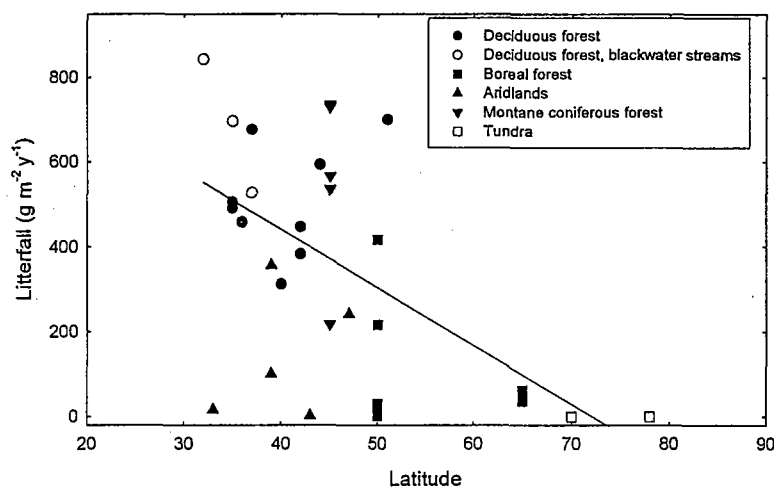


FIG. 2. Linear regression of litterfall vs. latitude ($p < 0.001$, $r^2 = 0.30$, $n = 33$).

input is a mixture of leaves and needles, and Monument Creek (Alaska) receives a mixture of alder, birch, and willow. Within the mixed deciduous sites, litterfall ranged from $2 \text{ g m}^{-2}\text{y}^{-1}$ in the 9th order Moisie River to $843 \text{ g m}^{-2}\text{y}^{-1}$ in the 6th order Ogeechee River. As in the case for the whole data set, there was no consistent relationship between stream order and litterfall among the streams draining mixed deciduous forests.

The 2nd-most-frequent site type was coniferous forest (6 of the 33 sites), all of which were in the Oregon Cascade Mountains. Litterfall ranged from $218 \text{ g m}^{-2}\text{y}^{-1}$ in the 7th order

McKenzie River to $730 \text{ g m}^{-2}\text{y}^{-1}$ in Devil's Club Creek (1st order). A 3rd- and 5th-order stream in the area each had litterfall of $730 \text{ g m}^{-2}\text{y}^{-1}$. The remaining sites ("other") are hot/arid or cold/arid sites that drain vegetation types composed of shrubs, grasses, sedges, or some mixture. The Antarctic site has no vegetation. There was no significant difference between mean litterfall in streams draining mixed deciduous and coniferous sites, but both were significantly different from the "other" sites (ANOVA, LS means procedure, $p < 0.01$).

The great diversity of vegetation, latitude, and stream order incorporated in this data set seems

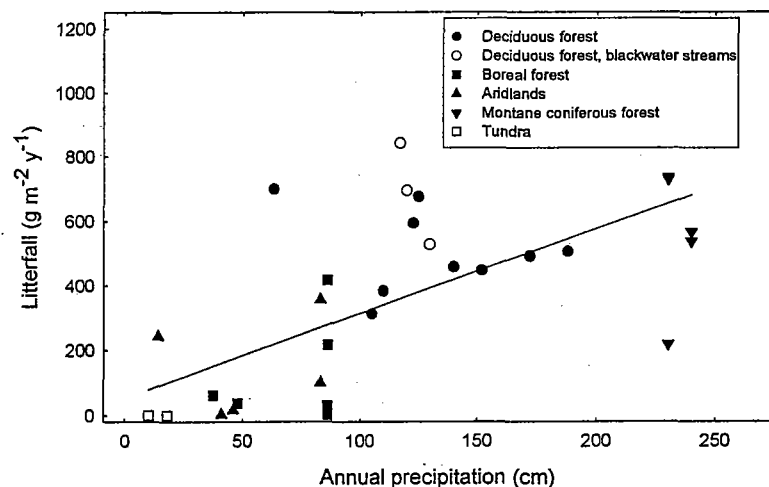


FIG. 3. Linear regression of litterfall vs. annual precipitation ($p < 0.001$, $r^2 = 0.44$, $n = 33$).

to preclude generalizations about litterfall patterns. There do appear to be significant relationships between litterfall and latitude (Fig. 2) and between litterfall and annual precipitation (Fig. 3). However, most of the streams at latitudes higher than 50° had very low or no litterfall input; exceptions are Beaver Creek and First Choice Creek (Quebec) and Breitenbach (Germany). Clearly, vegetation type (forested versus non-forested) is the critical determinant for litterfall at most of the sites. Stream order does not appear to be important when the entire data set is considered perhaps because the sites are scattered and bear little relationship to each other. However, there does appear to be a relationship between stream order and litterfall in Quebec where the sites, although not all in the same catchment, have been considered as a stream-order continuum (Connors and Naiman 1984), i.e., litterfall is highest in the 1st-order stream and gradually diminishes to a low in the 9th-order stream.

Literature Cited

- BLACKBURN, W. M., AND T. PETR. 1979. Forest litter decomposition and benthos in a mountain stream in Victoria, Australia. *Archiv für Hydrobiologie* 86:453-498.
- BRAY, J. R., AND E. GORHAM. 1964. Litter production in forests of the world. *Advances in Ecological Research* 2:101-157.
- BRIGGS, S. V., AND M. T. MAHER. 1983. Litter fall and leaf decomposition in a river red gum (*Eucalyptus camaldulensis*) swamp. *Australian Journal of Botany* 13:307-316.
- CAMPBELL, I. C., K. R. JAMES, B. T. HART, AND A. DEV-
EREAUX. 1992. Allochthonous coarse particulate organic material in forest and pasture reaches of two south-eastern Australian streams. I. Litter accession. *Freshwater Biology* 27:341-352.
- CONNORS, M. E., AND R. J. NAIMAN. 1984. Particulate allochthonous inputs: relationship with stream size in an undisturbed watershed. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1473-1484.
- CUFFNEY, T. F. 1988. Input, movement and exchange of organic matter within a sub-tropical coastal blackwater river-flood plain system. *Freshwater Biology* 19:305-320.
- CUMMINS, K. W., J. R. SEDELL, F. J. SWANSON, G. W. MINSHALL, S. G. FISHER, C. E. CUSHING, R. C. PETERSEN, AND R. L. VANNOTE. 1983. Organic matter budgets for stream ecosystems: problems in their evaluation. Pages 299-353 in J. R. Barnes and G. W. Minshall (editors). *Stream ecology*. Plenum Press, New York.
- PETERSON, B. J., J. E. HOBBIE, AND T. L. CORLISS. 1986. Carbon flow in a tundra stream ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1259-1270.
- POST, H. A., AND A. DE LA CRUZ. 1977. Litterfall, litter decomposition, and flux of particulate organic material in a coastal plain stream. *Hydrobiologia* 55:201-207.
- SEDELL, J. R., F. J. TRISKA, AND S. V. GREGORY. 1982. Coniferous forest streams. Pages 292-332 in R. L. Edmonds (editor). *Analysis of coniferous forest ecosystems in the western United States*. Hutchinson Ross Publishing Co., Stroudsburg, Pennsylvania.
- SHURE, D. J., AND M. R. GOTTSCHALK. 1985. Litter-fall patterns within a flood plain forest. *American Midland Naturalist* 114:98-111.
- SMOCK, L. A. 1990. Spatial and temporal variation in organic matter storage in low-gradient headwater streams. *Archiv für Hydrobiologie* 118:169-184.
- STOUT, J. 1980. Leaf decomposition rates in Costa Rican lowland tropical rain forest streams. *Biotropica* 12:264-272.
- WALLACE, J. B., J. R. WEBSTER, AND R. L. LOWE. 1992. High-gradient streams of the Appalachians. Pages 133-191 in C. T. Hackney, S. M. Adams, and W. A. Martin (editors). *Biodiversity of southeastern United States aquatic communities*. John Wiley & Sons, New York.
- WEBSTER, J. R., J. B. WALLACE, AND E. F. BENFIELD. 1995. Organic processes in streams of the eastern United States. Pages 117-187 in C. E. Cushing, G. W. Minshall, and K. W. Cummins (editors). *River and stream ecosystems*. Elsevier, Amsterdam.