

Terrestrial litter inputs as determinants of food quality of organic matter in a forest stream

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Introduction

Inputs of leaf litter and other organic matter from the catchment exceed autochthonous production and provide an important food resource in most streams (WEBSTER & MEYER 1997, ANDERSON & SEDELL 1979). An experimental long-term exclusion of terrestrial litter inputs to a forested headwater stream (WALLACE et al. 1997) provided an opportunity to determine if the food quality of organic matter would be altered by the elimination of inputs of fresh litter. Secondary production of benthic invertebrates in mixed substrate habitats (cobble, pebble, and silt-sand) declined after litter was excluded from this stream (WALLACE et al. 1997), but it is not clear whether the reduction in secondary production was a consequence of reduction in organic matter quantity, quality, or both. We have reported on a decline in quantity of some organic matter fractions after litter exclusion (WALLACE et al. 1997, MEYER et al. 1998); here we use chironomid growth assays to investigate whether quality of organic matter also changed.

Methods

Terrestrial litter was excluded from the uppermost 170 m of a headwater stream (Catchment 55, C 55) at Coweeta Hydrologic Laboratory, North Carolina, USA, by suspending nets over and alongside the stream (WALLACE et al. 1997). Nets were installed in August 1993 and maintained for the 3-year study. Nets kept 95% of litter from entering the stream and did not alter the light regime (WALLACE et al. 1997).

Fine (FBOM) and coarse (CBOM) benthic organic matter was collected from the litter-excluded stream and from a nearby reference stream (Catchment 53, C 53). Both streams are similar in physical and chemical characteristics (MEYER et al. 1998). Four random samples of FBOM and CBOM were collected seasonally before (1 year) and during (3 years) litter exclusion. Starting in January 1994, samples of seston were also collected in each season using settling barrels (WALLACE et al. 1991). All samples

were frozen immediately after collection.

After thawing, CBOM samples were rinsed through a 1-mm sieve with deionized water, and all CBOM retained on the sieve (except wood >1 cm diameter) was ground in a blender for 1 min. Ground CBOM was rinsed through 1-mm and 45- μ m sieves, and material captured on the smaller sieve was used in growth assays. Preliminary assays indicated that leachate from ground CBOM was toxic to chironomids under static conditions. Hence CBOM samples received a 75% water change before larvae were introduced and again each day for the next 2 days. Thawed FBOM was swirled and decanted to remove sand and then used in growth assays. Seston was used as collected.

Subsamples of each type of organic matter were set aside for carbon/nitrogen (C/N) analysis (Carlo Erba Model NA 1500). C/N was determined on all seston samples used in the growth studies, on three seston samples collected from each stream before litter exclusion began, and on a subset of six CBOM and nine FBOM samples selected to represent a range of observed growth rates from each stream. CBOM samples for C/N analyses were collected after they had been ground and sieved but before the 2-day leaching described above.

The quality of CBOM, FBOM and seston from each stream was assessed by measuring the growth of larval *Chironomus tentans* (Diptera: Chironomidae) fed exclusively one type of organic matter for 1 week. *C. tentans* was selected for assays because it is a detritivore, is easily cultured in the laboratory (BATA-CATALAN & WHITE 1982), and is large enough to be handled in its final instars. Larval growth was measured on one seston sample and three to six subsamples of CBOM and FBOM from each season.

Groups of ten third-instar larvae (~0.1–0.2 mg ash-free dry mass (AFDM)) were grown at 21 °C in aerated culture dishes (0.36 L) containing 1–2 g AFDM of either CBOM, FBOM, seston, or culture medium (Tetramin and shredded paper towels) and 0.2 L dechlorinated tap water. To determine initial AFDM, larvae were weighed wet in groups of ten;

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five randomly selected groups were dried, ashed, and reweighed to determine AFDM/wet weight ratio. After 7 days, live larvae were counted, killed by freezing, dried, weighed, ashed, and reweighed. AFDM and % AFDM of remaining organic matter was also determined. Larval growth rate (day^{-1}) was calculated as $\ln(\text{final AFDM}/\text{initial AFDM})/7$ days (HURYN & WALLACE 1986). Growth rates were used only if mortality was $<40\%$ (95% of 308 growth experiments). If larvae lost weight during the experiment, their growth rate was recorded as zero.

Mean growth rates were calculated for each organic matter type on each date. Comparisons between types of organic matter and between streams were made using paired t-tests based on these mean growth rates. For some of the analyses, samples were grouped into periods before (August 1992–1993) and during (September 1993–1996) litter exclusion.

Results

Larval growth rate was not a function of % AFDM in the material fed to the larvae; % AFDM varied from 16% to 95%, but a regression of growth rate as a function of % AFDM explained little of the observed variation in growth rate ($r^2 < 0.02$). The C/N ratio also varied considerably among the samples (from 3 to 42), but was not related to chironomid growth rate when all size fractions were combined or when regressions for each size fraction were cal-

culated separately ($P > 0.1$).

In both streams and when all data were combined, larval growth rates were greater on FBOM than on CBOM ($P < 0.05$). Larval growth rates on FBOM and seston were not significantly different in either stream ($P > 0.05$), which reflects the fact that seston is derived from FBOM.

FBOM in the reference stream supported greater larval growth than FBOM from the litter-excluded stream both before and during litter exclusion (Fig. 1, $P < 0.05$). The mean difference in growth rates before litter exclusion was 0.036 day^{-1} , while it was 0.012 day^{-1} during litter exclusion; hence the similarity in growth on FBOM during litter exclusion was primarily a result of reduced growth on FBOM from the reference stream (Fig. 1). Percent AFDM in FBOM samples used in these experiments did not differ between streams (Table 1).

We conducted growth assays on seston only during litter exclusion and observed no differences in larval growth on seston from the two streams (Fig. 1, $P > 0.05$) even though % AFDM in seston used in the growth studies was greater ($P = 0.002$) in the reference stream (Table 1). C/N in seston did not differ in the two streams either before or after litter exclusion (Table 1).

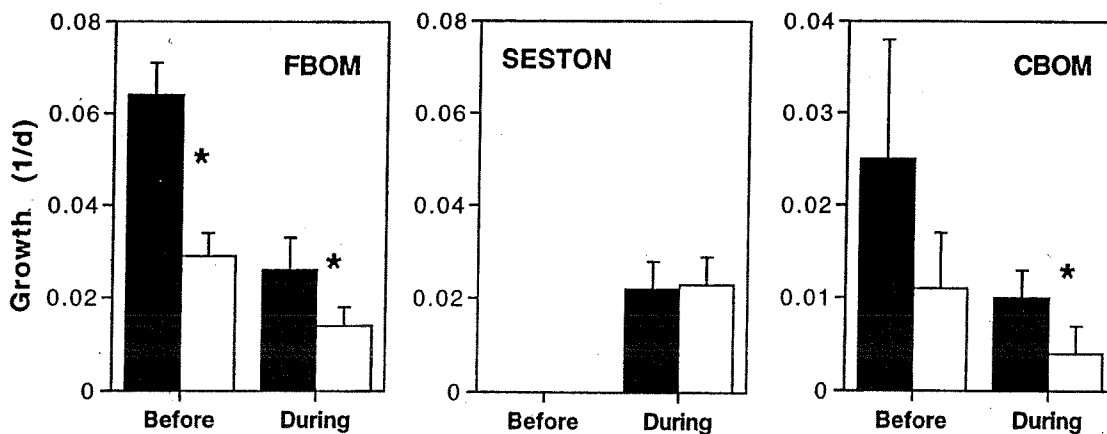


Fig. 1. Assessment of the food quality of FBOM, seston, and CBOM (note change of scale) from a reference (solid bars) and a litter-excluded (open bars) stream as measured by growth rates of *Chironomus tentans* fed exclusively on organic matter for 1 week. Values plotted are means \pm SE of growth rate measured on seasonal samples of organic matter collected for 1 year before installation of the litter exclusion net (Before) and three years during litter exclusion (During). Food quality of seston was assessed only during litter exclusion. Asterisks indicate values that are significantly different between streams (paired t-test, $P < 0.05$).

Table 1. Mean \pm SE values of % AFDM in FBOM, CBOM, and seston used in chironomid growth bioassays. The material was collected seasonally for 1 year before ($n = 4$, except no seston samples) and 3 years after ($n = 12$) installation of a net excluding terrestrial litter inputs from a stream (litter-excluded) and for the same periods from a reference stream. FBOM used in growth assays was separated from most of the inorganic particles, so these values do not reflect % AFDM of fine benthic particles in the stream. Mean \pm SE is also reported for carbon/nitrogen ratio (mg C/mg N) in three seston samples collected before net installation (September and November 1990 and January 1991) and nine samples collected after net installation (seasonal collections January 1994–January 1997). An asterisk indicates when mean values are significantly different between streams in a period (paired t-test, $P < 0.05$).

	Before net installation		After net installation	
	Reference	Litter-excluded	Reference	Litter-excluded
% AFDM				
FBOM	35.8 \pm 5.5	28.3 \pm 6.3	39.2 \pm 6.0	43.1 \pm 3.2
CBOM	89.1 \pm 1.6	90.5 \pm 0.8	87.7 \pm 0.5	86.3 \pm 1.6
Seston	no data	no data	46.8 \pm 1.7 *	33.2 \pm 2.5
Seston C/N	11.3 \pm 3.0	9.7 \pm 1.3	15.3 \pm 1.7	13.3 \pm 1.7

Differences in larval growth on CBOM from the two streams were not significant prior to litter exclusion. Although high variability in growth rates (Fig. 1) limits our ability to detect differences using a paired t-test, differences in growth rate before litter exclusion were also not detected with a non-parametric analysis (Wilcoxon signed rank test). In contrast, larval growth was significantly lower on CBOM from the treatment stream during litter exclusion (Fig. 1, $P < 0.002$, paired t-test and Wilcoxon signed rank test). During litter exclusion, growth rates on CBOM from the reference stream were consistently (92% of the dates) higher than growth rates on CBOM from the litter-excluded stream; prior to litter exclusion they were higher on only half of the dates. Hence we conclude that the food quality of CBOM decreased during litter exclusion.

Discussion

The standing stock of benthic organic matter declined during the period of litter exclusion (WALLACE et al. 1997, MEYER et al. 1998). Total CBOM in the litter-excluded stream declined from 64% of CBOM in the reference stream before treatment to 39% by the third year of exclusion. Leaf litter was virtually eliminated as a component of CBOM by the end of the second year of exclusion. FBOM in the litter-excluded stream showed a similar decline –

before net installation the standing crop of FBOM in the litter-excluded stream was 71% of that in the reference stream; FBOM in the litter-excluded stream was only 32% of FBOM in the reference stream by the third year of exclusion (MEYER et al. 1998).

Although exclusion of leaf litter from a stream for 3 years resulted in declines in quantity of benthic organic matter, results from chironomid bioassays suggest the quality of organic matter as a food resource for consumers changed only for CBOM (Fig. 1). Neither FBOM nor seston declined in quality as a result of treatment, and the apparent decline in food quality of CBOM is most likely a result of the increased proportion of woody material and the elimination of leaf litter from CBOM in the litter-excluded stream (WALLACE et al. 1997, MEYER et al. 1998). The year before litter exclusion, the fraction of CBOM as wood was similar in mixed substrate habitats of both streams (67% and 71% of the reference and treatment streams, respectively). By the third year of litter exclusion, wood represented 82% of CBOM in the litter-excluded stream and only 51% of CBOM in the reference stream.

The lack of change in quality of FBOM is an unexpected result. We anticipated that the highest quality FBOM would be derived from fresh leaf litter, and that as the supply of fresh leaf litter declined, FBOM would become more

refractory; yet we detected no decline despite 3 years of litter exclusion. This may be in part a result of an increase in microbial activity after litter exclusion, apparently in response to release from competition for nutrients with microbes decomposing leaves (TANK & WEBSTER 1998). In addition, soil organic matter continued to enter the stream from stream banks, and dissolved organic carbon (DOC) continued to be supplied from the watershed (MEYER et al. 1998). Benthic bacteria in the litter-excluded stream were more dependent on water-column DOC than on DOC leached from other sources (HALL & MEYER 1998). Although fewer bacterial exopolymers were present in the litter-excluded stream (HALL & MEYER 1998), the standing stock of chlorophyll was somewhat higher (J. L. MEYER unpublished data).

The growth assays examined the food quality of FBOM separated from most of the matrix of inorganic particles present on the stream bottom because they were designed to assess the quality of that organic matter. However, a benthic consumer feeds upon the mix of FBOM and inorganic particles in the stream. Because of the reduced amount of FBOM present after 3 years of litter exclusion, a consumer feeding on benthic fine particles would be getting more sediment and less organic matter with each mouthful ingested. This represents a lower quality food resource. Although larval growth rate did not vary with % AFDM in growth assays, an excess of organic matter was present in these experiments so that larval growth would not be limited by amount of food present. A similar surfeit of organic matter would not be encountered in the litter-excluded stream.

Secondary production of benthic invertebrates declined in mixed substrate habitats of the litter-excluded stream (WALLACE et al. 1997). Shredders, filterers, and gatherers are the primary functional feeding groups using the resources whose food quality was analyzed here, and the pattern of change in secondary production differs among these groups.

Prior to litter exclusion, annual secondary production of shredders in mixed substrate hab-

itats in the litter-excluded stream was 47% of that in the reference stream; by the third year of litter exclusion, shredder production in the litter-excluded stream had declined to only 18% of that in the reference stream (WALLACE et al. 1999). Shredder production in the litter-excluded stream during the third year of treatment was only 55% of its pre-treatment value (WALLACE et al. 1999). This decline in shredder secondary production appears to be a consequence of the absence of leaf litter in CBOM, which reduced CBOM quantity and food quality (Fig. 1) and reduced the availability of case-building material for two common shredders.

Little change in secondary production of filterers was observed in mixed substrate habitats of the litter-excluded stream, and there was no significant difference in secondary production on bedrock outcrop habitats, which are dominated by filter-feeders (WALLACE et al. 1997, 1999). This corresponds with a lack of change in either quantity or quality of seston over this period. Export of suspended organic matter was somewhat higher in the litter-excluded stream than in the reference stream during the first and second years of litter exclusion and only slightly lower during the third year (J. B. WALLACE and S. L. EGGERT unpublished data); the food quality of seston did not differ between the two streams (Fig. 1).

Gatherer production decreased during litter exclusion: prior to net installation annual gatherer secondary production in the litter-excluded stream was 52% of that in the reference stream and declined to 21% of reference stream production in the third year after installation; gatherer production in the third year of litter exclusion was only 46% of its pre-treatment value in the litter-excluded stream (WALLACE et al. 1999). The observed decline in gatherer production does not appear to be a result of changes in food quality (Fig. 1), but rather a result of declines in the amount of FBOM present. The standing crop of FBOM was 1,054 g AFDM m⁻² the year before litter exclusion and had declined to 521 g AFDM m⁻² by the third year of exclusion in the treatment stream, whereas FBOM standing stock in the reference stream changed only from 1,484 g

AFDM m^{-2} to 1,631 g AFDM m^{-2} over the same period (MEYER et al. 1998). Hence it appears that the observed decline in gatherer secondary production is a consequence of a reduction in the quantity of organic matter and not its quality.

Summary

We excluded terrestrial litter inputs to a southern Appalachian headwater stream for 3 years. In this stream and a nearby reference stream, the food quality of fine (FBOM) and coarse (CBOM) benthic organic matter and seston was assessed by measuring the growth rate of *Chironomus tentans*. Chironomid growth was not related to % AFDM or C/N ratio of the organic matter used in growth assays. Growth was least on CBOM and declined during litter exclusion. No significant changes in food quality of FBOM or seston were detected during the three years of litter exclusion. Therefore, observed decreases in secondary production of shredders with litter exclusion appear to be a response to reductions in both quantity and quality of CBOM; the lack of change in filterer production corresponds with little change in quality or quantity of seston; and decreases in gatherer production appear to be a response to decreases in the quantity rather than the quality of FBOM.

Acknowledgments

This research was supported by grants DEB 9207498 and DEB 9629268 from the National Science Foundation. We thank B. KEEBLEY, S. GREENE, and T. MADDOX for technical assistance and J. W. Jones Ecological Research Center for providing laboratory facilities for the larval growth assays.

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