TERRESTRIAL INVERTEBRATES AS A FOOD SOURCE FOR AQUATIC INVERTEBRATES IN SIX NEW ENGLAND HEADWATER STREAMS

MICHAEL A. SHEPARD
College of the Atlantic, Bar Harbor, ME 04609 USA

MENTOR SCIENTISTS: DRS. JAMES MCCUTCHAN[1] AND GENE E. LIKENS[2]
[1] Center for Limnology University of Colorado, Boulder, CO 80309 USA
[2]Institute of Ecosystem Studies, Millbrook, NY 12545 USA

Abstract. Most of the organic matter available to consumers in canopied headwater streams is derived from terrestrial leaf inputs, but in large streams, in-stream primary production can be the dominant source of organic matter. Recent studies have shown that algae play a disproportionately large role as a food source for consumers in headwater streams. Although terrestrial plant detritus may be more abundant, algae are higher in nitrogen and are more easily digestible than leaf litter. Terrestrial invertebrates also are high in nitrogen content and can be an important dietary component of fish in many streams, especially during summer months. Thus, terrestrial invertebrates may be an important food source for aquatic macroinvertebrates. To test this possibility, I estimated the input of terrestrial invertebrates to 6 headwater streams in Vermont and New Hampshire during the summer of 2001. Estimates of invertebrate input were then compared with estimates of litterfall and algal production. Input of terrestrial invertebrates averaged 6.7±12.69 gDM/m^2/y, compared to 13.7±5.64 gDM/m^2/y for aquatic net primary production and 300-700 for litterfall to the stream. Although terrestrial inputs to these streams were dominated by leaf material, terrestrial invertebrates may be an important source of food for invertebrates in New England streams.

INTRODUCTION

Budgets of organic matter for a wide range of streams (reviewed by Webster and Mayer (1997)) have traditionally focused on inputs of terrestrial leaf litter and, more recently, on in-stream primary production. In most small headwater streams in New England the majority of organic carbon available to aquatic insects (AI) is derived from terrestrial plant material (Likens 1972, Fisher and Likens 1973, Cummins 1974). This carbon enters streams in dissolved form and as particulate matter (i.e., leaf litter).

Due to its vast abundance, terrestrial carbon has long been considered the major trophic foundation for secondary production in small, forested, headwater streams (Cummins 1973, Fisher and Likens 1973). However, recent studies have revealed the importance of autochthonous (in-stream) algal production to AI as a food source, even in those streams with closed canopies. Although algal production is much lower in comparison to the input of allochthonous (out of stream) leaf litter, its quality as a food source makes it an important part of the benthic trophic structure (McCutchan 1999, Minshall 1978, Lamberti 1996).

Budgets of organic matter for streams have focused on terrestrial plant material and autochthonous primary production as the major sources of organic matter input into streams. Other sources of organic matter input (i.e. terrestrial invertebrates) generally make up only a small part of the organic matter balance in a stream, but may be important sources of nutrition for stream consumers. Support for this idea comes from research indicating the importance of insects floating on the surfaces of streams as a food source for fish (Cada et al 1987, Hunt 1975, Wipfli 1997) and the importance of animal material in the diets of many filter feeding AI (Fuller and MacKay 1981, Benke and Wallace 1980). Investigating levels of terrestrial insect input into forested headwater streams of New England and how it compares to the two established input types became the major focus of this study. Correlation between levels of TI input and other system components such as stream size, riparian forest age, and forest type were also examined in the study.

Although terrestrial insects have been ignored in many studies of organic matter in streams, some studies, such as Cadwallader et al. (1980), indicating the importance of overhanging vegetation for TI input, and Southwood (1961), showing that deciduous trees generally have more associated invertebrate species than do conifers, created expectations that smaller streams surrounded by younger deciduous forests would have higher levels of input than would larger streams with older coniferous forests. These expectations were enforced by the findings of Wipfli (1997) indicating that in southeastern Alaska younger alder forests have higher levels of input than do older ones.

The purpose of this study was to estimate the input of terrestrial invertebrates (TI) to 6 New England streams and determine the possibility of TI as a food source for AI. To assess the importance of TI as a source of food for AI, daily levels of input were recorded at each site. Algal samples were collected for primary production estimates and existent leaf litter data was obtained from past studies, namely Gosz et al. (1972). Riparian forest surveys and stream sizes were taken at each site to determine the influence of forest characteristics and stream size on TI and algal inputs. The null hypotheses were that TI input would be drastically lower than leaf litter input and somewhat lower than algal input.

Study Sites

This study was conducted on three streams in the Hubbard Brook Experimental Forest (HBEF) in the White Mountains of NH and three streams in the towns of Starksboro and Lincoln in the Green Mountains of VT. Streams ranged from first to third order. Each site consisted of a 30m stretch of stream broken into 6 sub-reaches of 5m. The Hubbard Brook site was 50m long and sub-reaches were 10m. All sites have experienced heavy logging within the past 100 years. All sites are located within New England and experience similar climatic conditions throughout the year including complete snow cover during the winter months. Study streams in VT ran across bedrock with high concentrations of calcium, through young deciduous forests, and normally experience complete snow cover in winter. Study streams in NH ran across bedrock with less calcium, through young coniferous forests, and normally experience complete snow cover as well. All study sites in VT are part of a single south-facing watershed, as are all NH sites. Brief descriptions of each site are included in table 1.

METHODS

Each stream was visited and sampled for TI and primary production levels twice during the month of July. Collection occurred at the VT sites 7/6/01-7/11/01 and 7/22/01-7/25/01; and at the NH sites 7/17/01-7/20/01 and 7/31/01-8/3/01. TI falling into streams were collected with square traps (2mm mesh; .25m^2). Trap frames floated on the stream surface with the mesh hanging below so that invertebrates interrupting surface tension were retained. Traps were anchored randomly within each grid at each site and were left in place for ~24 hours for each sampling date. Invertebrates were removed and preserved in 70% ethanol. Invertebrates were identified to order, measured for length to determine dry mass based on the equation of Rogers et al. (1976), and preserved in 95% EtOH for long-term storage. Any aquatic or emergent AI were also identified, measured, and stored for any possible future uses. Input rates for the vernal and autumnal months were considered to be half of that found during this study and zero during the winter months. Dry mass was assumed to be 50% organic carbon.

Primary production was estimated from temperature and benthic chlorophyll *a* by use of the equation of Morin et al. (1999). Chlorophyll *a* levels were obtained through removal of the algae covering a known area on each of 3 stones along a random transect within each grid. This was accomplished by placing a scintillation vial cap (of area 5.3cm^2) on the upper surface of each stone, scrubbing and rinsing off the algae surrounding it with a soft nylon brush, and collecting the remaining algae with a clean brush and clean stream water from the site of the transect. All samples from each transect were pooled and brought to a final volume of 150 ml with additional stream water. Samples of clean stream water were sampled for determination of suspended algae. Each transect and stream water sample was then filtered through a Whatman glass microfiber filter, which was immersed in 90% EtOH, sonicated to rupture cell walls, and boiled. Concentrations of chlorophyll *a*, corrected for phaophytin, were then measured by spectrophotometry. For each sampling date the amount of chlorophyll *a* suspended in the stream water samples was subtracted from the value found for each sample. Dry mass of algae was assumed to be 50% organic carbon. Primary production during vernal and autumnal months was assumed to be half that found in this study and zero under snow cover.

RESULTS

In VT input of TI across all sites averaged 32.32 mg Dry Mass (DM)/m^2/d; in NH the average input of TI across all sites of was 17.76 DM/m^2/d. See table 2 for by-site input data. Average daily TI input into streams across all sites and all sampling dates was 25.04 +/- 12.12 mg DM/m^2/d, within an order of magnitude of the inputs found in southern Alaska by Wipfli (1997). Year round TI input is estimated at 3.12 g DM/m^2/y. The total input in the younger more deciduous riparian forests of VT streams was 366 mg and in the older more coniferous forests of NH was 149.62 mg (figure 1). Unexpectedly the larger streams had greater amounts of TI input: first order streams had a total TI input of 126 mg, second order streams 193 mg, and third order 198 mg (figure 2).

Annual insect secondary production within streams is estimated at 3-5 g DM/m^2/y (personal communication McCutchan). Annual rates of leaf litter input are estimated to be 260 g DM/m^2/y (Gosz et al 1976).

Average net primary production (NPP) estimate for all sites was 15 +/- 1.4 mg DM/m^2/d. Annual NPP is estimated at 2.5 g DM/m^2/y. NPP estimates across stream orders parallels those expected based on the RCC; NPP was estimated at 48 g for all first order streams, 60 g for second order streams, and 72 g for third order streams. VT streams had a total NPP of 97 g and NH streams a total NPP of 83 g. See table 2.

DISCUSSION

Allochthonous leaf litter is the dominant source of organic carbon entering headwater streams in New England, followed by TI and in-stream primary production. The similarity of rates of input between TI and primary production allows for the possibility that they could reverse greater input roles depending on yearly conditions (snow pack, rainfall, cloud cover); while the rate of leaf litter input is an order of magnitude greater than either of these forms and is highly unlikely to ever decrease to the point that it should become a secondary source of organic carbon.

Despite its low availability, periphyton algae have been established as a food source for AI; its high nutritive value leads to higher rates of consumption per abundance than that found for leaf litter (McCutchan 1999, Lamberti 1996, Minshall 1978). TI, which is also of high nutritive content and modest abundance, could also be disproportionately utilized by AI as a food source. Establishment of TI as a definite AI food source has not been accomplished in this study. However, the established need for animal material in stages of some AI lifecycles (Fuller and MacKay 1981, Benke and Wallace 1980) provides substantiation of TI as a food source for AI. Observed herbivorous AI feeding on animal material in the absence of other food sources (personal communication Dr. James H. McCutchan) also adds validation to the concept of TI as an AI food source. These findings in combination with the levels of TI input found in this study create a strong possibility for TI to be utilized by some AI as a food source.

It is estimated that ½ of food consumed by AI is lost through respiration. If AI were to feed almost exclusively on TI and periphyton, up to ½-¾ of AI secondary production would be accounted for by these sources of organic carbon. However, TI input levels are not representative of TI availability to AI. Microbial action, fish, and amphibians reduce the levels of TI available to AI making TI unlikely to account for ½ of AI secondary production. Although highly improbable, such a high possible rate of TI based secondary production illustrates the availability and likely utilization of TI by AI.

The increase of TI input with stream size and the greater levels of input in VT than NH sites were unexpected results. The increase of TI input with each increase in stream order is in direct conflict with previous studies

(Cadwallader et al 1980) that indicate smaller streams with greater degrees of canopy cover should have higher levels of input; however, the correlation is strong and should not be ignored. Perhaps such data will provide new insight into TI input patterns in the future. Based on Southwood (1961) we contributed the differences between the states to the slightly younger and more deciduous forests of VT. We also believe that greater levels of calcium found in the bedrock of VT, (personal communication McCutchan, Morse) and the resultant effects on the vitality and fecundity of insects feeding on plants growing there, would have an impact on TI input levels.

It is important to note that this study was conducted over the course of the month of July 2001, a time of year when TI and primary production input rates are quite possibly at their height. Estimations of year round input rates are rough at best. However, use of such rough estimates across all fields compared provides a certain degree of accuracy in the comparison and allows conclusions to be drawn with some confidence.

The use of floating traps is a break from traditional sticky trap methods. Floating traps were chosen due to their greater perceived ability in capturing more precise levels of TI entering streams. We felt that the traditional sticky trap method would result in elevated input rates due to their propensity to ensnare all insects that near the water surface, while floating traps would capture only those that actually enter the stream; thus providing more accurate measurements of TI entering streams.

This study has not provided concrete evidence of utilization of TI by AI, but has shown that organic carbon is entering New England headwater streams in the form of TI in quantities sufficient to sustain a proportion of AI secondary production.

ACKNOWLEDGMENTS

Profound and sincere gratitude to James McCutchan, without his help this project would never have gotten off the ground. Thanks also to IES and the National Science Foundation's support of the REU program (Grant No. DBI-9988029) for this wonderful opportunity.

Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

LITERATURE CITED

Benke, A.C. and J.B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachain stream. Ecology 61:108-118.

Cada, G.F., J.M. Loar, and D.K. Cox. 1987. Food and feeding preferences of rainbow and brown trout in southern Appalachain streams. The Amer. Mid. Nat. 117:374

Cadwallader, P.L., A.K. Eden, and R.A. Hook. 1980. Role of streamside vegetation as a food source for *Galaxias olidus* Gunther (Pisces: Galaxidae). Aust. J. Mar. Freshwater Res. 31:257-262.

Cummins, K.W. 1974. Structure and function of stream ecosystems. Bioscience 24:631-641.

------------. 1973. Trophic relations of aquatic insects. Ann. Rev. Entomol. 18:183-206.

Fisher, S.G. and G.E. Likens. 1973. Energy flow in Bear Brook N.H.: an integrative approach to stream ecosystem metabolism. Ecol. Mono. 43:421-439.

Fuller, R.J. and R.J. MacKay. 1981. Effects of food quality on the growth of 3 *Hydropsyche* species (Trichoptera: Hydropsychidae). Can J. Zoo. 59:1133-1140.

Gosz, J.R., G.E. Likens, and F.H. Bormann. 1972. Nutrient content of litterfall on the Hubbard Brook experimental forest N.H. Ecology 53:769-784.

Hunt, R.L. 1975. Use of terrestrial invertebrates as food for salmonids. In A.D. Hasler (Ed.), Coupling of land and water systems. NY: Springer-Verlag.

Lamberti, G.A. 1996. The role of periphyton in benthic food webs. In R.J. Stevenson, M.L. Bothwell, and R.L. Lowe (Eds.), Algal ecology. (pp.533-572). San Diego, CA: Academic Press.

Likens, G.E. 1972. Eutrophication and aquatic ecosystems. In G.E. Likens (Ed.), Nutrients and eutrophication. Special Symposia Vol. 1. (pp.3-13). Amer. Soc. Lim. Ocean. Lawrence, KA: Allen Press.
McCutchan, J.H. 1999.Carbon sources for macroinvertebrates in St. Vrain Creek, Colorado. PhD dissertation, University of Colorado, Boulder, Colorado.
Minshall, G.W. 1978. Autotrophy in stream ecosystems. Bioscience 28:767-771.
Morin, A., W. Lamoureux, and J. Busnarda. 1999. Empirical models predicting primary productivity from chlorophyll *a* and water temperature for stream periphyton and lake and ocean phytoplankton. J. N. Amer. Benthol. Soc. 18:299-307.
Morse, S. 1999. Personal communication. College of the Atlantic, Bar Harbor, ME.
Rogers, L.E., W.T. Hinds, and R.L. Buschbom. 1976. A general weight vs. length relationship for insects. Ann. Entomol. Soc. Am. 69:387-389.
Southwood, T.R.E. 1961. The number of species of insect associated with various trees. J. Anim. Ecol. 30:1-8.
Webster, J.R. and J.L. Mayer (Eds.). 1997. Stream organic matter budgets. J. North Amer. Benthol. Soc. 16:3-161.
Wipfli, M.S. 1997. Terrestrial invertebrates as salmonids prey in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Can. J. Fish. Aquat. Sci. 54:1259-1269.

APPENDIX

TABLE 1. Brief site descriptions

Stream	**State**	**Order**	**Width**	**Canopy Cover**	**Riparian Vegetation**	**Age**
Simplicity	VT	1	2m	>75%	Deciduous	25 yrs
Baldwin	VT	2	5m	50%	Deciduous	75 yrs
New Haven	VT	3	15m	<10%	Deciduous	60 yrs
Falls	NH	1	3m	>75%	Coniferous	50 yrs
Beaver	NH	2	6m	50%	Coniferous	60 yrs
Hubbard	NH	3	12m	<10%	Coniferous	70 yrs

TABLE 2. TI input and primary production input data per site.

Site	Order	Average Daily TI Input (mg DM/ m^2/d)	Standard Deviation	Average NPP (mg)	Average Stadard Deviation
Simplicity	1	23.04	17.65	9.5	2.19
Baldwin	2	36.24	22.23	16.05	2.77
New Haven	3	37.68	14.1	22.8	1.56
Falls	1	5.04	1.02	14.5	2.11
Beaver	2	19.44	23.93	13.78	2.09
Hubbard	3	28.8	22.74	12.995	5.69

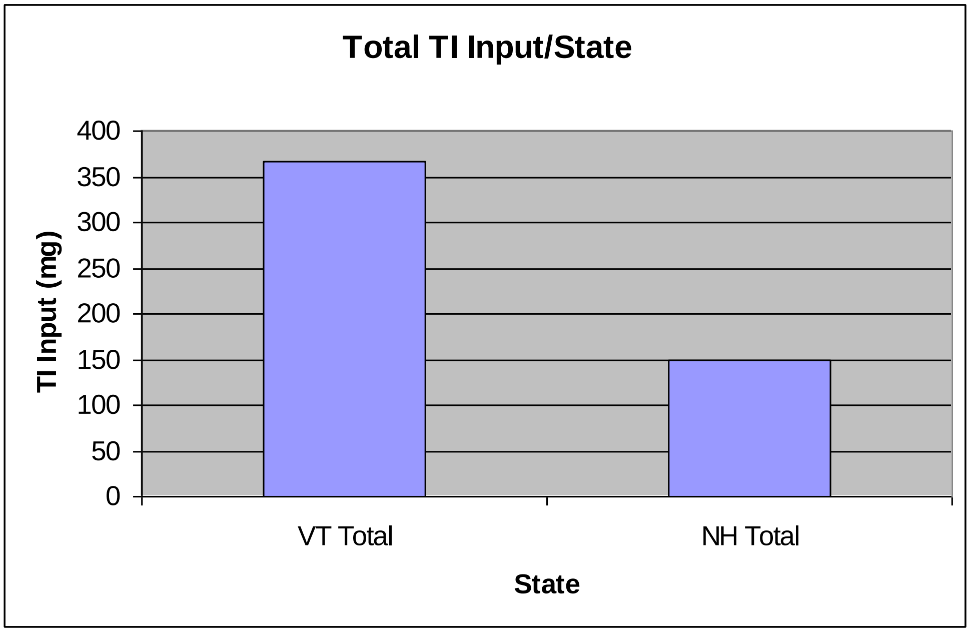

FIGURE 1. Total TI input in each state. The higher concentration of calcium in the bedrock in VT is believed to be an indirect causative agent of the higher rate of TI input there.

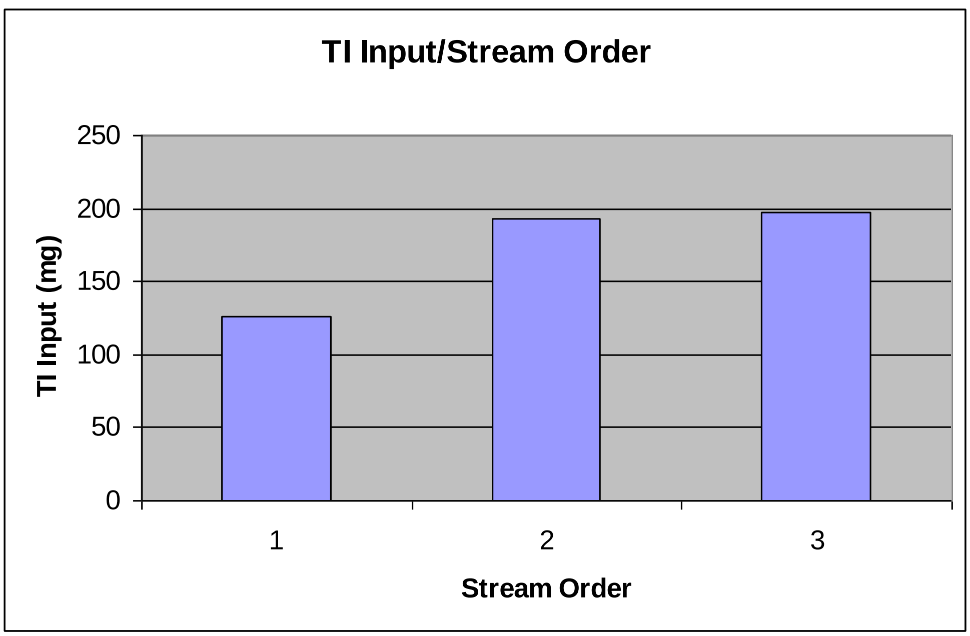

FIGURE 2. TI input levels across stream orders. Increases in TI input with stream order were unexpected