

Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream

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Abstract

Estimates of carbon sources, as determined from ratios of stable isotopes, were used in conjunction with estimates of secondary production to determine the relative contribution of algal carbon to macroinvertebrate production across a gradient of elevation in a Rocky Mountain stream (North St. Vrain Creek, Colorado). The relative contribution of algal carbon to macroinvertebrate production was then compared to the relative availability of algal carbon. Although algal production accounted for less than 2–40% of the combined sources of organic matter to North St. Vrain Creek, the relative contribution of algal carbon to annual macroinvertebrate production ranged from approximately 40% at a subalpine site to nearly 80% at a more open site in the foothills. Thus, the proportional contribution of algal carbon to consumer production greatly exceeded the relative availability of algal carbon in North St. Vrain Creek. Despite the disproportionate importance of algal carbon to consumers, most macroinvertebrates in North St. Vrain Creek used some vascular plant carbon.

The abundance of terrestrial plant detritus in most shaded headwater streams has led ecologists to the conclusion that vascular plant detritus generally supports the growth of primary consumers in small, shaded streams. Although terrestrial plant detritus often is of lower nutritional value than other, less abundant food sources (e.g., algae), microbial colonization and processing increase its nutritional value (Cummins and Klug 1979). Algae are known to support most of the consumer production in some streams (e.g., desert streams; Minshall 1978), but it is generally accepted that consumers in small, canopied streams depend largely on terrestrial carbon.

Analyses of gut contents from macroinvertebrates often are consistent with the conclusion that vascular plant detritus is the main source of nutrition for primary consumers in shaded streams (e.g., Minshall 1967; Anderson and Sedell 1979; Hall et al. 2001). Also, recent work has shown that amorphous detritus, which usually is assumed to be derived from terrestrial plant material, can be an important component of gut contents of many stream consumers (Wallace et al. 1987; Benke and Jacobi 1994; Hall et al. 2001). Some analyses of gut contents, however, have suggested that algae

are nutritionally important, even when present in small amounts relative to vascular plant carbon (Koslucher and Minshall 1973; Minshall 1978; Mayer and Likens 1987).

Analysis of gut contents has been the primary method of tracing pathways of organic matter across trophic levels in streams and has been used successfully to study the complexity of trophic interactions among consumers (e.g., Benke et al. 2001), but this method is not ideally suited for estimation of the relative contribution of potential carbon sources to the growth of consumers. Because gut contents are not fully assimilated, analyses of gut contents can lead to overestimation of the importance of some food items (Rosenfeld and Mackay 1987). Also, identification of gut contents is not always possible, especially for detritivores.

Stable isotope ratios of carbon and nitrogen change predictably between diet and consumer (Peterson and Fry 1987; McCutchan 1999; McCutchan et al. unpubl. data) and have been used to study the use of potential food sources by consumers in several streams. Analysis of stable isotopes showed that algae were an important food source for consumers in the Kuparuk River, Alaska (Peterson et al. 1997) and in New Zealand streams (Rounick et al. 1982). In contrast, another study of stable isotopes showed that neither algae nor aquatic mosses were an important carbon source for consumers in the lower reaches of the Koroc River, Quebec (Bunn et al. 1989). For the Montmorency River, Quebec, Junger and Planas (1994) found that the contribution of algal carbon to consumers was greater at a fourth-order site than at a second-order site. Winterbourn et al. (1986) showed that consumers at shaded sites in two British streams were isotopically similar to terrestrial detritus, but many consumers at unshaded sites were isotopically similar to algae.

No published studies have partitioned production of an entire macroinvertebrate community according to its ultimate sources of organic matter. The goal of the work reported here is to determine, from stable isotope ratios and simultaneous estimates of consumer production, the relative contribution of algal carbon to the production of macroinvertebrates in a

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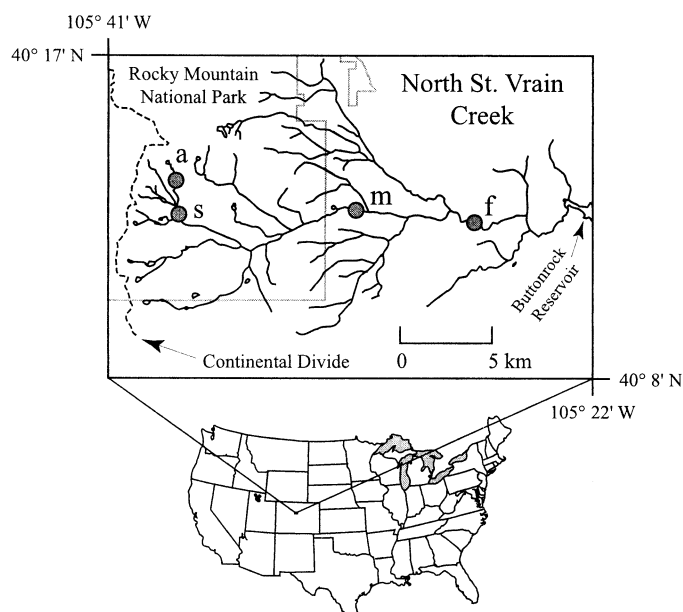


Fig. 1. Locations of sampling sites on North St. Vrain Creek (a = alpine site; s = subalpine site; m = montane site; f = foothills site).

Colorado mountain stream. The relative contribution of algal carbon to macroinvertebrate production is then compared to the relative availability of algal carbon; the purpose of the comparison is to test the null hypothesis that primary food resources in streams are used by consumers in proportion to their availability.

Methods

This study was conducted on North St. Vrain Creek, which is located in the Front Range of the Colorado Rockies; the four sampling locations vary in elevation and other features (Fig. 1; Table 1). Woody vegetation at the alpine site is sparse (Engelmann spruce, *Picea engelmannii*; willows, *Salix* sp.). The subalpine site, which is the most heavily canopied of the four, is dominated by subalpine fir (*Abies lasiocarpa*) and some Engelmann spruce. The montane site has blue spruce (*Picea pungens*), ponderosa pine (*Pinus ponderosa*), and Douglas fir (*Pseudotsuga menziesii*). The foothills site is dominated by blue spruce and alder (*Alnus tenuifolia*) along the stream edge; ponderosa pine and Douglas fir are found beyond the stream margin. The watershed for

North St. Vrain Creek has only a small human population and shows little human disturbance. Peak discharge typically occurs in June, following snowmelt, and discharge is lowest during winter. Discharge during snowmelt was much higher in 1995–1996 than in 1994–1995, particularly at the foothills site. Across all sites, dissolved oxygen remained near saturation and pH was circumneutral. The mean concentration of total dissolved phosphorus was similar across the highest three sites ($\sim 0.2 \mu\text{M}$) and was slightly higher at the foothills site ($0.3 \mu\text{M}$; McCutchan 1999). The mean concentration of dissolved inorganic nitrogen was less than $10 \mu\text{M}$ across all sites (McCutchan 1999).

Samples and field measurements were taken at each site as necessary to estimate (1) aquatic primary production, (2) litterfall, (3) macroinvertebrate production, and (4) stable isotope ratios for macroinvertebrates and their ultimate food sources. Sampling for estimates of aquatic primary production and macroinvertebrate production was monthly during summer and fall and was less frequent during spring and winter.

Aquatic primary production was estimated by the open-channel oxygen method (Odum 1956; Fellows et al. 2001; McCutchan et al. 2002). However, temporal resolution for these estimates was insufficient to provide reasonable annual estimates for all sites. For this reason, annual net primary production (NPP) was estimated from temperature and benthic chlorophyll *a* (Chl *a*) by use of the equation of Morin et al. (1999), based on the assumption that NPP is half of gross primary production. The dry mass of algae was assumed to be 50% carbon, and primary production under snow cover was assumed to be zero. For each site, benthic Chl *a* was estimated for each day of the year by linear interpolation from measured concentrations; on each sampling date, scrapings were taken from three or four stones collected from each of seven to ten transects (McCutchan 1999). A Monte Carlo approach, similar to that described in McCutchan et al. (1998), was used to estimate uncertainty in annual estimates of NPP; estimates of uncertainty incorporate uncertainty in the coefficients for the regression equation (Morin et al. 1999) and variation in chlorophyll concentration on each sampling date.

Direct litterfall (units of litterfall are $\text{gDM m}^{-2} \text{yr}^{-1}$) at canopied sites was predicted from watershed area (units are hectares [ha]) according to a relationship derived from published estimates of litterfall for temperate, canopied streams (Benfield 1997), as follows:

Table 1. Physical characteristics of the study sites. Discharge data are from USGS gage data or were estimated from watershed area and gage data for nearby streams.

	Alpine	Subalpine	Montane	Foothills
Mean elevation (m)	3,405	3,152	2,426	2,231
Watershed area (ha)	166	854	9,060	20,500
Mean annual discharge ($\text{m}^3 \text{s}^{-1}$)	0.05	0.15	1.50	2.38
Mean annual temperature ($^{\circ}\text{C}$)	2.6	3.0	4.1	4.8
Mean channel width (m)	2.8	4.3	10.6	11.0
Mean canopy cover (%)	1	39	28	29
Stream order	1	2	3	4

$$\begin{aligned} \log \text{ litterfall} &= 2.98 \pm 0.125 - 0.0542 \\ &\pm 0.00876(\log \text{ watershed area})^2; \\ R^2 &= 0.94 \end{aligned} \quad (1)$$

where units of watershed area are ha. Parameters for Eq. 1 are significantly different from zero ($p < 0.001$). Estimates of litterfall for uncanopied, temperate streams (Benfield 1997) were used to predict litterfall at the alpine site, as follows:

$$\log \text{ litterfall} = 1.48 \pm 0.92 \quad (2)$$

Quantitative samples for estimation of macroinvertebrate density and size frequency were collected at random X, Y coordinates with a modified Surber sampler (225- μm mesh, 0.14 m^2 or 0.25 m^2 area; typically seven to ten per date) and were preserved in 70% ethanol. Surber samples were divided into coarse (850- μm mesh) and fine (225- μm mesh) fractions, and a sample splitter similar to the one described by Waters (1969) was used to subsample the fine fraction. Macroinvertebrates were picked from samples under magnification and sorted to the lowest possible taxonomic division. For each sampling date, body length or width of preserved individuals was measured with an optical micrometer. Individual dry mass was estimated by use of exponential equations calibrated empirically (McCutchan 1999) or, in a few cases, taken from the literature (Winberg 1971; Smock 1980). Organisms used in the calibration of size-to-mass relationships were held overnight in filtered water for clearance of gut contents, measured with an optical micrometer, lyophilized, and weighed to the nearest μg .

For each site, macroinvertebrate production (MP) for each taxonomic group was estimated over the intervals between sampling dates. The instantaneous exponential form of the increment-summation method (Gillespie and Benke 1979) was used to estimate production of taxa that could be identified to species and followed over time as distinct cohorts. For taxa that could not be identified to species or could not be followed over time as distinct cohorts (e.g., Chironomidae), production was estimated by the instantaneous growth method (Gillespie and Benke 1979). Growth rates of non-cohort taxa were estimated with a multiple regression equation developed from growth rates of species in North St. Vrain Creek that could be followed as cohorts:

$$\begin{aligned} \log g &= -2.2 \pm 0.28 + 0.061 \pm 0.0034\bar{T} - 0.12 \\ &\pm 0.017 \log m; \quad R^2 = 0.42 \end{aligned} \quad (3)$$

where g is the instantaneous rate of growth, \bar{T} is average temperature in $^{\circ}\text{C}$, and m is mass in mg. All coefficients of Eq. 3 are significantly different from zero ($p < 0.0001$). Because no significant differences in growth rate were found among orders or families (Tukey-Kramer Honestly Significant Difference test), Eq. 3 was used for all taxa.

Plant material (living and dead) was collected from the riparian zone at each site. When sufficiently abundant, algal filaments or bryophytes were collected from the stream with forceps; samples were rinsed with water to remove fine particulate material and were picked clean under magnification. Epilithic material was scrubbed from the upper surfaces of cobbles and small boulders. Algal cells were isolated from

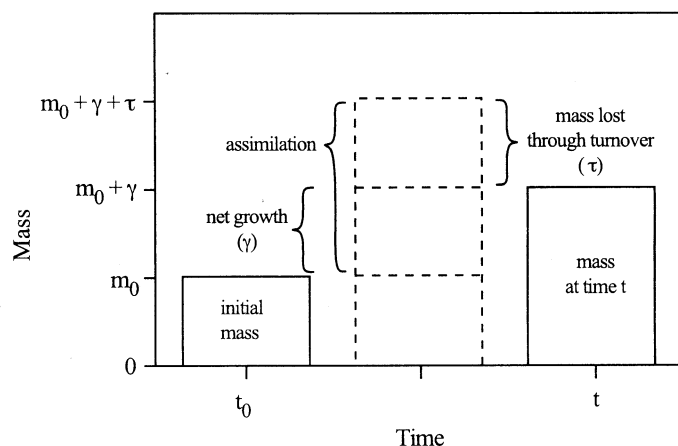


Fig. 2. Graphical representation of growth (γ) and turnover (τ) for a consumer. The parameter m_0 is the initial mass of the consumer and m_t ($m_0 + \gamma$) is the mass at time t . The sum of growth and turnover equals assimilation over the interval.

epilithon by centrifugation through colloidal silica and were collected on Whatman QM/A filters (Hamilton and Lewis 1992; Hamilton et al. 2001). All samples for isotope analysis were lyophilized and stored in a desiccator until analysis. Stable isotope ratios were measured on a Micromass Optima isotope-ratio mass spectrometer operated in conjunction with an elemental analyzer. Isotope ratios are reported here in standard δ notation ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$; units are ‰; Peterson and Fry 1987).

The mean individual mass of a consumer taxon at time t (m_t) is a function of initial mass (m_0), net growth over the interval ($\gamma = m_t - m_0$), and the mean loss of tissue through turnover (τ ; Fig. 2). The carbon isotope ratio of a consumer at time t ($\delta^{13}\text{C}_t$) can be approximated from the initial isotope ratio ($\delta^{13}\text{C}_0$), m_0 , γ , τ , the isotope ratio of the diet (i.e., that of ingested food, $\delta^{13}\text{C}_{\text{diet}}$), and the isotopic shift between diet and consumer ($\Delta\delta^{13}\text{C}$) as follows (McCutchan 1999; McCutchan and Lewis in press):

$$\delta^{13}\text{C}_t \approx \frac{\delta^{13}\text{C}_0 m_0 + (\gamma + \tau)(\delta^{13}\text{C}_{\text{Diet}} + \Delta\delta^{13}\text{C})}{m_0 + (\gamma + \tau)} \quad (4)$$

Over each interval of time, m_t was estimated from m_0 and g as follows:

$$m_t = m_0 e^{gt} \quad (5)$$

For species with identifiable cohorts, g was estimated from measurements of dry mass of consumers for each sampling date. For other taxa, g was estimated from temperature and dry mass (Eq. 3). For this study, τ was set equal to γ for aquatic insects (i.e., net production efficiency = 0.5) and three times γ for other macroinvertebrates (Humphreys 1979; Oertli 1993).

A model based on Eqs. 4 and 5 was used to estimate the proportional contribution of algal carbon ($k_{\text{algal carbon}}$) to the growth of each consumer taxon. The model predicts changes over time in isotope ratios of consumers from (1) temporal changes in isotope ratios of food sources, (2) estimates of growth and tissue turnover, and (3) the shift in isotope ratio between diet and consumer. For each interval between sam-

Table 2. Annual net primary production (NPP; mean \pm SD, estimated from benthic chl *a* and temperature), litterfall (mean \pm SD, predicted using relationships developed from Benfield 1997), and macroinvertebrate production (MP) at each sampling site; units of annual production and litterfall are gDM m⁻² yr⁻¹.

	Alpine		Subalpine		Montane		Foothills	
	1994–1995	1995–1996	1994–1995	1995–1996	1994–1995	1995–1996	1994–1995	1995–1996
NPP	23 \pm 14.3	5.2 \pm 2.8	24 \pm 14.1	4.6 \pm 2.6	37 \pm 20.7	24 \pm 13.0	82 \pm 48.9	36 \pm 19.9
Litterfall	53 \pm 83.4		345 \pm 119		148 \pm 66.6		105 \pm 52.8	
MP	5.78	4.73	4.71	3.33	8.11	6.34	12.1	10.1

pling dates, changes in isotope ratios of consumers and food sources (i.e., algae and terrestrial plants) and the mean individual mass of a given taxonomic group were predicted over short (daily) intervals of time. It was assumed that isotope ratios of sources changed linearly over time between adjacent sampling dates. $k_{\text{algal carbon}}$ was estimated by varying the estimate of the fraction of algae in assimilated organic matter to achieve the best fit between observed and predicted isotope ratios for each consumer taxon.

If $k_{\text{A nitrogen}}$, the relative contribution of nitrogen from one food source to the growth of a consumer, is known, trophic position can be estimated from $\delta^{15}\text{N}$ of a consumer and of its potential food sources. It is not possible, however, to solve simultaneously for $k_{\text{A nitrogen}}$ and trophic position. Therefore, estimations of trophic position were based on the assumption that $k_{\text{A nitrogen}} = k_{\text{A carbon}} \cdot \delta^{15}\text{N}_{\text{diet}}$, the $\delta^{15}\text{N}$ for assimilation of sources A ($\delta^{15}\text{N}_{\text{A}}$) and B ($\delta^{15}\text{N}_{\text{B}}$), was estimated by a simple two-source mixing model:

$$\delta^{15}\text{N}_{\text{diet}} = \delta^{15}\text{N}_{\text{B}} - k_{\text{A nitrogen}}(\delta^{15}\text{N}_{\text{B}} - \delta^{15}\text{N}_{\text{A}}) \quad (6)$$

If the trophic shift between diet and consumer differs between low-protein and high-protein diets (McCutchan 1999; Vander Zanden and Rasmussen 2001; McCutchan et al. unpubl. data), $\delta^{15}\text{N}$ for a consumer differs from that of the diet as follows:

$$\delta^{15}\text{N}_{\text{consumer}} = \delta^{15}\text{N}_{\text{diet}} + \Delta\delta^{15}\text{N}_{\text{low}} + (\lambda - 2)\Delta\delta^{15}\text{N}_{\text{high}} \quad (7)$$

where $\Delta\delta^{15}\text{N}_{\text{low}}$ is the trophic shift associated with primary consumption (i.e., diets low in protein), $\Delta\delta^{15}\text{N}_{\text{high}}$ is the trophic shift associated with the assimilation of animal material, and λ is trophic position; $\lambda = 2$ for a strict herbivores and, for trophic positions above 2, noninteger values of λ reflect feeding at more than one trophic level (as in Vander Zanden et al. 1997). Trophic position can be estimated by rearrangement of Eq. 7, as follows:

$$\lambda = \left(\frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{diet}} - \Delta\delta^{15}\text{N}_{\text{low}}}{\Delta\delta^{15}\text{N}_{\text{high}}} \right) + 2 \quad (8)$$

In the application of Eqs. 6 and 8 to the present study, mean isotope ratios of sources were used to estimate $k_{\text{algal nitrogen}}$ from $k_{\text{algal carbon}}$ where isotope ratios of sources did not vary significantly over the year. Where isotope ratios of sources did vary seasonally, they were interpolated between dates of measurement.

Preliminary estimates of $k_{\text{algal carbon}}$ were based on the assumption that the consumer was one trophic level above primary producers and that the trophic shift for carbon was 0.5‰ (McCutchan et al. unpubl. data). For each taxon, a

preliminary estimate of trophic position was calculated from Eqs. 6 and 8; $k_{\text{algal nitrogen}}$ was set equal to the preliminary estimate of $k_{\text{algal carbon}}$; trophic shift for nitrogen was set to 1.6‰ for the first trophic transfer and to 2.6‰ for subsequent transfers (McCutchan et al. unpubl. data). The estimate of trophic position (λ) then was used to recalculate $k_{\text{algal carbon}}$. Based on the second estimate of $k_{\text{algal carbon}}$, trophic level also was recalculated. Recalculations were necessary because $k_{\text{algal carbon}}$ affects estimates of trophic position when $\delta^{15}\text{N}$ differs between sources, but more than two iterations had little effect on final estimates.

For each taxonomic group, the amount of secondary production supported by algal carbon was estimated as the product of $k_{\text{algal carbon}}$ and production for each interval between sampling dates. Production supported by terrestrial carbon was estimated by difference. For each year of the study, macroinvertebrate production supported by algal carbon was summed across taxa for each site (to estimate the contribution of algal carbon to production by the entire community), as was macroinvertebrate production supported by terrestrial carbon.

Results

Production and litterfall—Estimates of annual NPP ranged from <10 gDM m⁻² yr⁻¹ at the alpine and subalpine sites in 1995–1996 to over 80 gDM m⁻² yr⁻¹ at the foothills site in 1994–1995 (Table 2). In each year of the study, estimates of annual NPP were similar for the alpine and subalpine sites and increased with watershed area below the subalpine site. For a given sampling location, NPP was 2–5 times as high in the first year of the study as in the second. Estimated annual litterfall was about 100–350 gDM m⁻² yr⁻¹ at the canopied sites and was about 50 gDM m⁻² yr⁻¹ at the alpine site (Table 2). Predicted litterfall for the subalpine site (345 gDM m⁻² yr⁻¹) was similar to measured rates of litterfall for a subalpine site near the University of Colorado Mountain Research Station (370 gDM m⁻² yr⁻¹; L. Scott-Denton unpubl. data).

Averaged across the two years, estimates of total macroinvertebrate production ranged from just over 4 gDM m⁻² yr⁻¹ at the subalpine site to over 10 gDM m⁻² yr⁻¹ at the foothills site and was higher in 1994–1995 than in 1995–1996 (paired *t*-test, $p < 0.01$; Table 2). The mean estimate of MP for the foothills site was higher than the mean for the alpine or subalpine sites (Tukey-Kramer HSD, $p < 0.05$) but did not differ significantly from MP at the montane site. Across the four sampling locations, macroinvertebrate production av-

Table 3. Secondary production for dominant macroinvertebrate taxa at each site (% of total; mean of both years ± SE). Taxa listed account for >80% of total production at each site.

Taxonomic group	Alpine	Subalpine	Montane	Foothills
Coleoptera: Elmidae	<0.1	0.7±0.49	7.3±0.24	4.8±0.92
Diptera: Chironomidae	26.2±3.87	31.4±1.27	12.4±0.81	9.6±1.55
Simuliidae	2.0±1.11	15.7±2.53	3.5±0.54	2.6±2.21
Ephemeroptera: <i>Baetis</i> sp.	2.8±1.81	9.3±1.53	11.4±1.06	10.5±3.1
<i>Cinygmula</i> sp.	10.6±5.73	2.9±0.44	1.7±0.13	0.4±0.18
<i>Drunella</i> sp.	0	3.6±0.41	7.1±2.49	10.1±0.92
<i>Epeorus</i> sp.	15.7±8.46	0.8±0.05	3.3±0.24	2.6±0.73
<i>Ephemerella</i> sp.	0	0	4.6±0.53	0.9±0.32
<i>Rithrogena</i> sp.	0	1.0±0.25	6.4±1.18	5.3±1.97
Plecoptera: Chloroperlidae	3.1±0.43	2.4±0.96	4.1±0.86	4.3±2.95
<i>Zapada</i> sp.	3.1±0.43	10.6±4.83	1.1±0.24	0.2±0.10
Trichoptera: <i>Arctopsyche grandis</i>	0	0	2.2±0.86	18.3±10.8
<i>Rhyacophila</i> sp.	22.9±3.46	7.4±0.05	13.2±5.26	4.0±0.52
Oligochaeta	6.5±0.69	3.4±1.15	4.8±0.30	3.7±0.15

eraged 37% (±9.9% SE) of aquatic NPP but only 5% (±1.0% SE) of the sum of NPP and litterfall (Table 2).

At each site, most of the annual macroinvertebrate production could be attributed to a small number of taxa (Table 3; Web Appendix 1 at http://www.aslo.org/lo/toc/vol_47/issue_3/0742a1.pdf). Chironomidae accounted for about 30% of total production at the alpine and subalpine sites and about 10% at the montane and foothills sites. *Baetis* accounted for about 10% of total production at the canopied sites but was less important at the alpine site. Heptageniidae and Ephemerellidae were important consumers at all sites except the subalpine site; *Cinygmula* and *Epeorus* accounted for nearly 30% of production at the alpine site and *Rithrogena* and *Drunella* were important at the montane and foothills sites. Other important taxa included Simuliidae (16% of total) and *Zapada* (11% of total) at the subalpine site and *Arctopsyche grandis* (18% of total) at the foothills site. In terms of production, *Rhyacophila* was an important predator (7–23% of total) at the upper three sites, but not at the foothills site (4% of total).

Together, scrapers and collector-gatherers accounted for 43–77% of macroinvertebrate production at each site (Table 4). Filtering collectors accounted for 11% of macroinvertebrate production at the subalpine site and 16% of production

at the foothills site. Shredders accounted for a higher fraction of production at the subalpine site (14% of total) than at other sites (≤6% of total). Predator production was similar (18–21% of total) across the alpine, subalpine, and montane sites but was somewhat higher (34% of total) at the foothills site.

Stable isotope ratios—At each site, the mean δ¹³C of algae was significantly higher than the mean δ¹³C of terrestrial plants (*t*-test, *p* < 0.001), as was mean δ¹⁵N (*t*-test, *p* < 0.05) except for the alpine site (Fig. 3). Isotope ratios of mosses and liverworts were similar to those of terrestrial plants. There were no significant seasonal trends in δ¹³C of terrestrial plants, but δ¹³C of algae at the montane and foothills sites and δ¹⁵N of algae at the montane site changed with season. The trend in δ¹³C of algae was similar for the montane and foothills sites; δ¹³C of algae increased abruptly during snowmelt, reached a maximum in late summer, and declined over the fall (Fig. 4). At the montane site, δ¹⁵N of algae was highest just before snowmelt and decreased over the summer.

Isotope ratios of consumers are shown for each site in Fig. 3. At each of the lower elevation sites, some consumers had

Table 4. Percentage of total macroinvertebrate production (MP) and mean (±SE) proportional contribution of algal carbon to production (*k*_{algal carbon}) by functional feeding groups at each site. Assignments of functional feeding groups are from Merritt and Cummins (1984) and Ward and Kondratieff (1992); for taxa belonging to multiple feeding groups, production was divided equally among groups.

Feeding group		Alpine	Subalpine	Montane	Foothills
Scraper	% of total MP	33	26	32	23
	<i>k</i> _{algal carbon}	0.64±0.11	0.30±0.12	0.68±0.18	0.73±0.27
Collector-gatherer	% of total MP	44	31	37	20
	<i>k</i> _{algal carbon}	0.59±0.13	0.34±0.22	0.60±0.21	0.69±0.27
Filtering collector	% of total MP	1	11	3	16
	<i>k</i> _{algal carbon}	0.13±0.07	0.12±0.03	0.75±0.18	0.71±0.24
Shredder	% of total MP	2	14	7	6
	<i>k</i> _{algal carbon}	0.42±0.08	0.31±0.17	0.52±0.27	0.57±0.29
Predator	% of total MP	19	18	21	34
	<i>k</i> _{algal carbon}	0.51±0.17	0.35±0.18	0.65±0.25	0.81±0.22

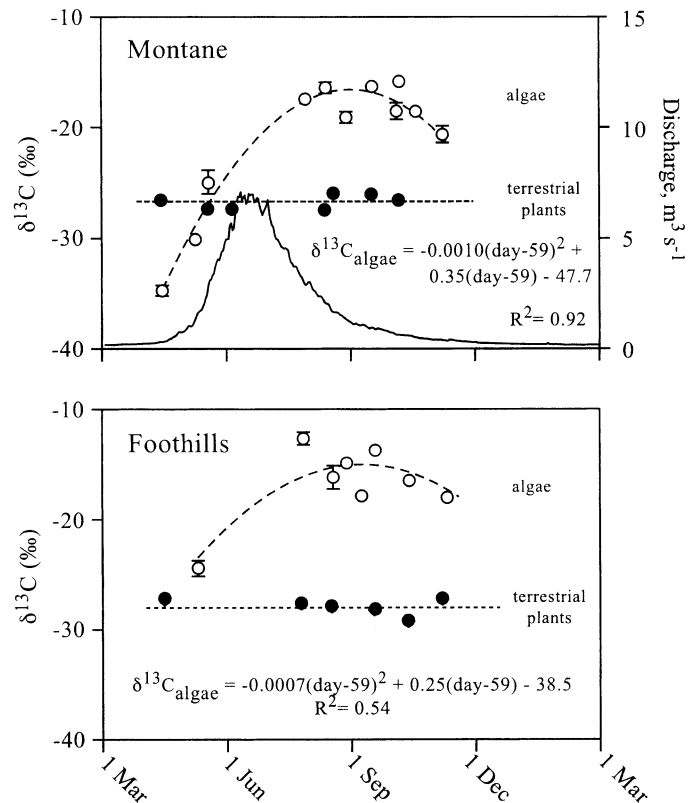
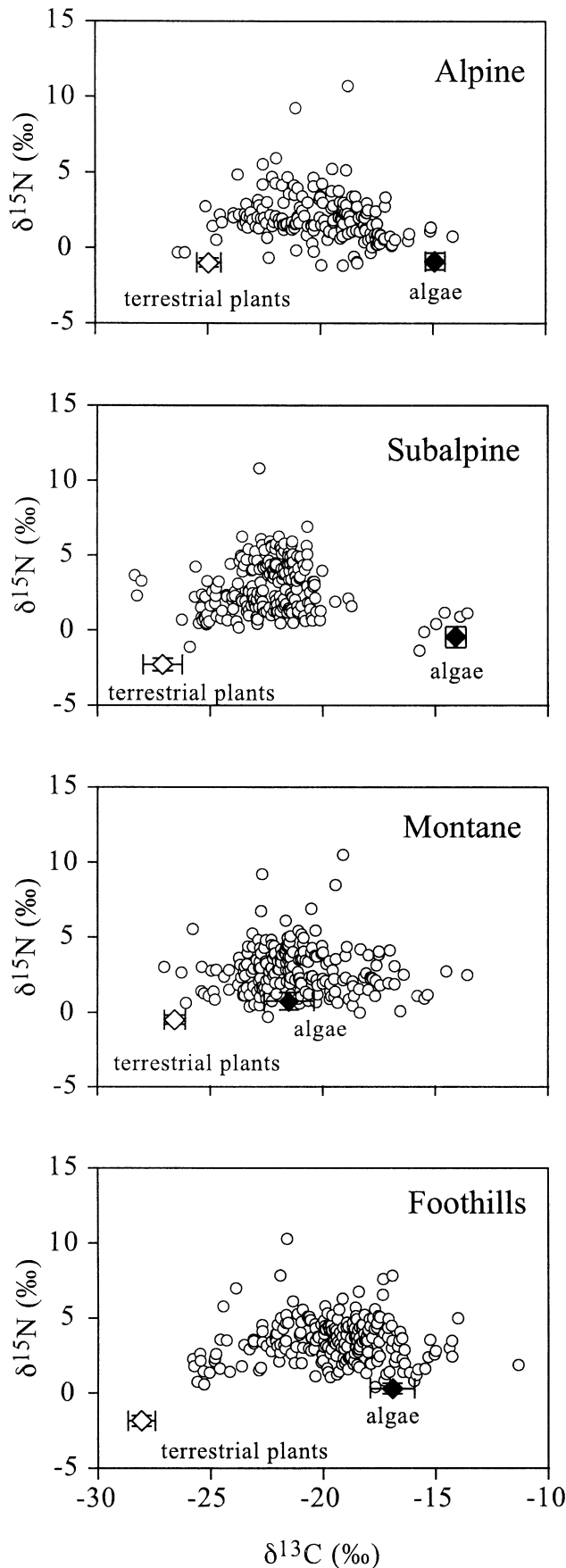


Fig. 4. The $\delta^{13}\text{C}$ of algae (mean \pm SE) and terrestrial plant material as a function of the day of the year at the montane and foothills sites. The regression equations were used to predict $\delta^{13}\text{C}$ of algae for days when no algae were collected. Mean daily discharge (solid line; from the U.S. Geological Survey) at the montane site is shown for reference.

higher $\delta^{13}\text{C}$ than the mean $\delta^{13}\text{C}$ of algae, but few consumers were more enriched than the most enriched algal samples. The $\delta^{15}\text{N}$ of consumers typically was 2–5‰ higher than that of primary producers, but some consumers were enriched in ^{15}N by more than 10‰ relative to primary food sources (i.e., algae and terrestrial plant material). Seasonal variation in isotope ratios of some taxa (e.g., Chironomidae at the montane site; Fig. 5) paralleled changes in isotope ratios of algae, but, for many consumers, isotopic changes lagged behind changes for algae (e.g., *Baetis bicaudatus* and Heptageniidae). Taxa with the most negative $\delta^{13}\text{C}$ values (i.e., near the ratio of terrestrial plants) generally showed little seasonal variation in $\delta^{13}\text{C}$ (e.g., Nemouridae; Fig. 5).

For some taxa, production-weighted means of $k_{\text{algal carbon}}$ were <0.15 (e.g., Simuliidae at the alpine and subalpine sites; Web Appendix 1) and, for shredders, means for estimates of $k_{\text{algal carbon}}$ ranged from 0.31 to 0.57 (Table 4). At

Fig. 3. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of algae (solid diamonds; mean \pm SE), terrestrial plants (open diamonds; mean \pm SE), and individual consumers (circles) at each sampling location. Means for sources reflect seasonal changes in isotope ratios; values for individual consumers represent single points in time.

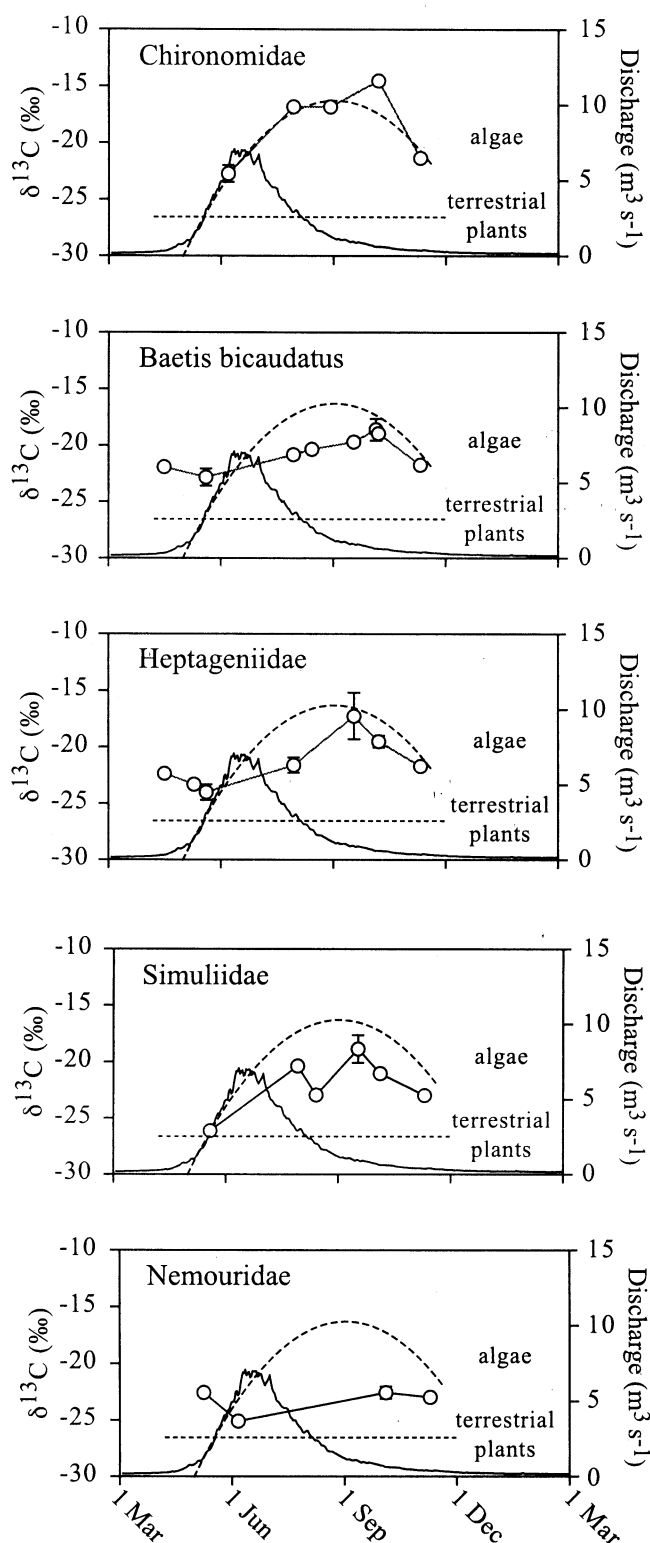


Fig. 5. Seasonal variation in $\delta^{13}\text{C}$ of selected taxa (circles; mean \pm SE) at the montane site. Mean daily discharge (solid line; from the U.S. Geological Survey) and $\delta^{13}\text{C}$ of algae and terrestrial plants (see Fig. 4; dashed lines) are shown for reference.

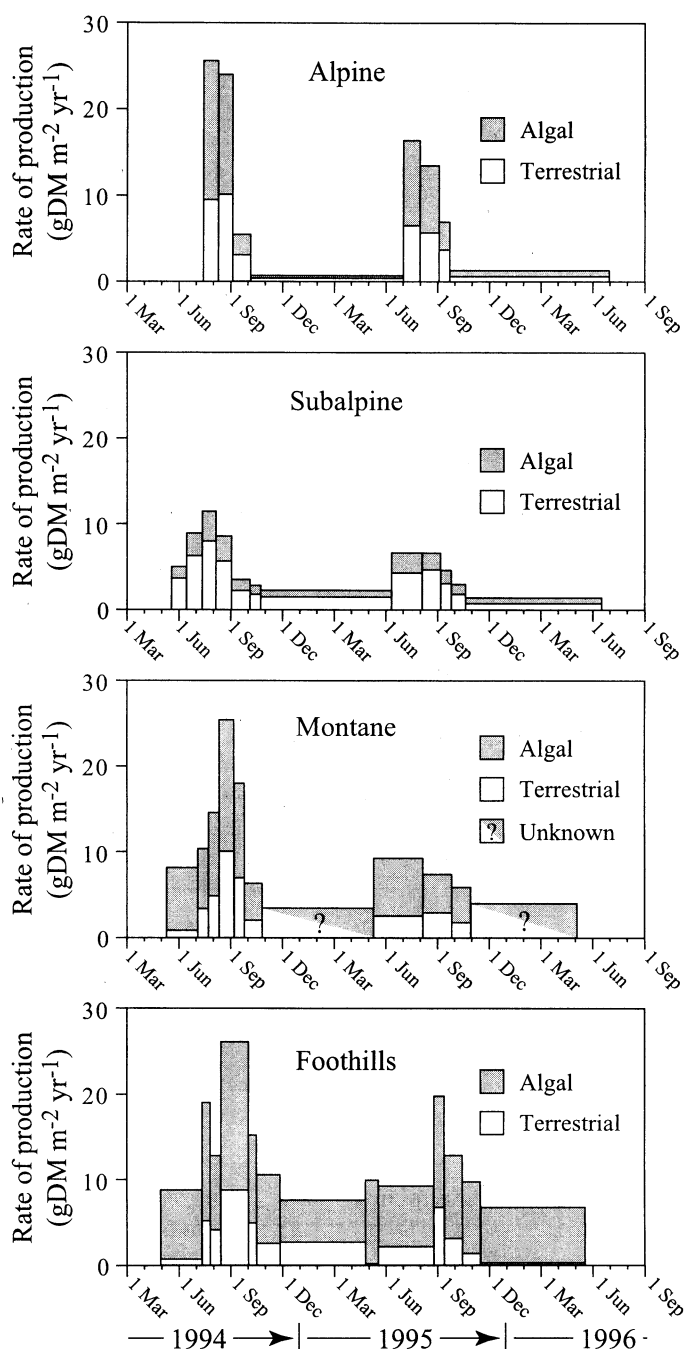


Fig. 6. Macroinvertebrate production supported by algal and terrestrial carbon at each site. Areas of bars represent production over intervals between sampling dates.

each study site, however, algal carbon supported a large proportion of macroinvertebrate production. The proportional contribution of algal carbon to macroinvertebrate production was highest at the foothills and alpine sites, but algae contributed substantially to consumer production even at the subalpine and montane sites, where canopy cover was high (Fig. 6). On an annual basis, the absolute contribution of terrestrial carbon to macroinvertebrate production (i.e., the amount of macroinvertebrate production supported by ter-

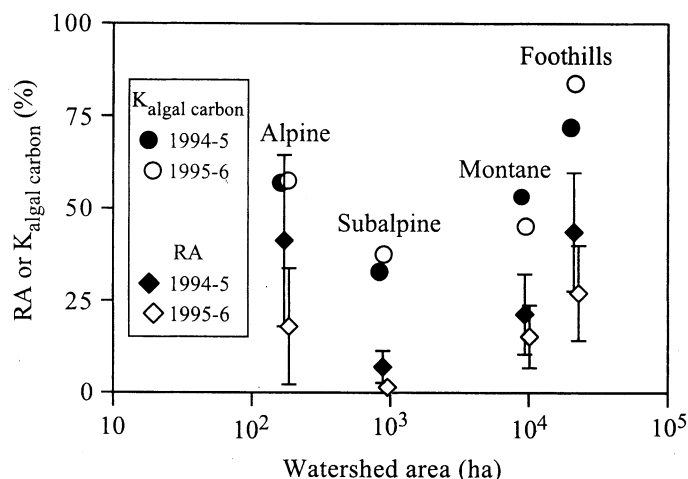


Fig. 7. Proportional contribution of algal carbon to total macroinvertebrate production ($k_{\text{algal carbon}}$ for the community or $K_{\text{algal carbon}}$) as a function of watershed area in 1994–1995 and 1995–1996. An index of the relative availability of aquatic primary production (RA, the ratio of NPP to the sum of NPP and litterfall; mean \pm SD) is shown for reference.

restrial carbon), averaged across all sites, was $2.5 (\pm 0.8 \text{ SD}) \text{ gDM m}^{-2} \text{ yr}^{-1}$ and did not differ significantly among sites (Tukey-Kramer HSD); the absolute contribution of algal carbon to consumer production averaged $3.8 (\pm 2.7) \text{ gDM m}^{-2} \text{ yr}^{-1}$ (Fig. 6). Algal carbon supported a similar amount of production across the higher elevation sites, but algae supported more production at the foothills site than at other sites (Tukey-Kramer HSD, $p < 0.05$).

The relative contribution of algal carbon to annual macroinvertebrate production ($k_{\text{algal carbon}}$ for the community or $K_{\text{algal carbon}}$) ranged from less than 40% at the subalpine site to nearly 80% at the foothills site (Fig. 7). Because inputs of dissolved organic matter and lateral inputs of litter often equal or exceed direct litterfall to streams (Webster and Meyer 1997), RA (the ratio of NPP to the sum of NPP and litterfall; Fig. 7) provides a minimum estimate of the relative availability of algal carbon. Thus, in North St. Vrain Creek, algal production accounted for less than 2–40% of the organic matter input across all sites, but the contribution of algal carbon to consumer production averaged six ($\pm 2.8 \text{ SE}$) times the relative availability of algal carbon.

Discussion

Macroinvertebrate production—Annual macroinvertebrate production in North St. Vrain Creek fell slightly below that for most streams of similar watershed area (Benke 1993; Grubaugh et al. 1997), possibly because of low temperatures relative to other streams (Table 1). Feeding and metabolic processes generally are reduced at low temperature (Hauer and Benke 1991). Ice cover interrupts the input of terrestrial detritus to the stream and also can limit aquatic primary production. Macroinvertebrate production was highest downstream where temperature was highest and was higher in the first year of the study when temperature was higher and discharge was lower. Across both years, macroinverte-

brate production was closely correlated with aquatic NPP ($r = 0.91$). Temperature or algal production may have limited macroinvertebrate production in St. Vrain Creek, but other factors probably played a role in the regulation of secondary production. For example, food quality can differ substantially between algae and terrestrial vascular plant material (Fuller and Mackay 1981) or among plant species (Cummins et al. 1973). Also, hydrologic differences (among sites and between years) may have affected the availability of algal and terrestrial sources of organic matter in a similar manner (e.g., high flow conditions may have reduced the availability of both algal and terrestrial sources of food).

Scrapers and collector-gatherers (mostly Chironomidae, Baetidae, Ephemerellidae, and Heptageniidae) accounted for much of the production at the upper three sites (Tables 3 and 4). Because of their high growth rates and high densities, Chironomidae and Baetidae often are among the most productive invertebrate taxa in small streams (Jackson and Fisher 1986; Wallace and Gurtz 1986; Gaines et al. 1992; Benke 1998). Shredders contributed little to total production in North St. Vrain Creek, even where canopy cover was high. Predators accounted for a large proportion of production at all sites. Although relative production by shredders was highest at the subalpine site and filtering collectors were important at the foothills site, downstream changes in the relative importance of functional feeding groups were small, contrary to the predictions of the River Continuum Concept (Vannote et al. 1980; Minshall et al. 1985).

Seasonal variation in isotope ratios of sources—Isotope ratios of algae were stable during summer months but changed during snowmelt at two sites. When $\delta^{13}\text{C}$ of available food sources changes seasonally, $\delta^{13}\text{C}$ of consumers may not reflect $\delta^{13}\text{C}$ of assimilated organic matter at the time of sampling. At the montane and foothills sites, changes in isotope ratios of many consumers dependent on algal carbon lagged behind changes in isotope ratios of algae (e.g., *Baetis bicaudatus* and Heptageniidae, Fig. 5). The lag was more pronounced for slowly growing taxa than for taxa with high growth rates (e.g., Chironomidae) and was more pronounced during winter when growth rates were low.

Estimates of the proportional contribution of food sources to consumers by use of standard mixing models depend on the assumption that consumers are in isotopic equilibrium with their food sources. Laboratory studies have shown that, when consumers are switched to a new diet, isotopic equilibrium usually is approached only after consumers have quadrupled in mass (Fry and Arnold 1982; Herzka and Holt 2000). Equations 3 and 5 predict that it would take nearly 5 months for a consumer of 10 mg to quadruple in mass at 5°C . Thus, during winter or at other times when growth rates of consumers are low relative to the time scale for changes in isotope ratios of food sources, assumptions implicit in standard two-source mixing models may not be met (McCutchan and Lewis in press; McCutchan et al. unpubl. data). The special measures taken in this study (i.e., density gradient centrifugation, frequent sampling of sources and consumers, and use of Eqs. 4 and 5) made it possible to estimate the proportional contribution of algal carbon to macroinver-

tebrate production over most of the year, even when isotope ratios of algae were changing.

Contribution of food sources to consumers—Although the extent of omnivory among stream consumers is widely appreciated, it has been hypothesized that algae are the dominant source of nutrition for scrapers whereas shredders and collectors are supported largely by carbon derived from terrestrial plants, and predators depend indirectly on both algal and terrestrial sources of carbon (Cummins and Klug 1979; Merritt and Cummins 1984). Stable isotope data indicate that few consumers in North St. Vrain Creek relied solely on algal or terrestrial carbon (Web Appendix 1). At the subalpine site, *Agraylea* (Hydroptilidae), a specialist on filamentous algae (Merritt and Cummins 1984), was the only taxon to obtain nearly all of its carbon from algae. *Bibiocephala grandis* (Blephariceridae), a scraper common at the montane site, also obtained nearly all of its carbon from algae. Nemouridae (mostly shredders) and Simuliidae (filtering collectors) at the subalpine site were largely dependent on terrestrial carbon. Most consumers, however, were omnivorous with respect to carbon sources, as shown by Mihuc (1997) for other streams.

Despite the absence of tree canopy at the alpine site, terrestrial plants supported the growth of many consumers there. Terrestrial carbon that enters the stream as detritus or as dissolved organic matter probably supports the growth of consumers at times when algae are not able to grow because of shading from snow cover (Wetzel 1995). Even though there was no tree canopy at the alpine site, some leaf litter from riparian herbs and willows reached the stream. Estimates of direct litterfall were higher at canopied sites than at the alpine site, but aquatic NPP at the alpine site was low (Table 2) and the nutritional quality of plant litter there may have been higher than at other sites. Terrestrial invertebrates, which derive their support from vascular plants, have high nutritional value and may have been an important source of organic matter for some consumers. Inputs of terrestrial invertebrates to streams vary seasonally but can be higher than the lowest estimates of aquatic NPP reported here (Wipfli 1997; Shepard and McCutchan unpubl. data). Terrestrial invertebrates can be an important trophic link between terrestrial plants and salmonids in some streams (Cada et al. 1994; Wipfli 1997), but their importance as a food source for macroinvertebrates in St. Vrain Creek is unknown.

Synthesis—Estimates of aquatic NPP and litterfall were necessary to test the assumption that food resources contribute to macroinvertebrate production in proportion to their availability. For some sites, low rates of aquatic photosynthesis and high reaeration rates led to low confidence in estimates of NPP based on the open-channel oxygen method (see McCutchan et al. 1998). For this reason and due to the remote locations of field sites, annual estimates of NPP were not possible with the open-channel method; instead, annual NPP was estimated from temperature and Chl *a*, based on the regression equation of Morin et al. (1999). Although estimates of primary production with the regression method are not as precise as estimates based on direct measurements, uncertainty with the regression method is much lower for

estimates of production integrated over time than for instantaneous estimates (Morin et al. 1999). Litterfall also was predicted by relationships developed from published estimates for a wide range of sites and uncertainty in predicted rates of litterfall was relatively large (Table 2). Also, some of the terrestrial plant material that enters a stream is retained only briefly before being exported downstream, where it collects in depositional areas. Thus, the rate at which terrestrial organic matter is supplied to consumers varies spatially and temporally and may differ from average rates of input. However, estimated litterfall, which is a conservative estimate of the input of terrestrial carbon to a stream, far exceeded aquatic NPP at the subalpine and montane sites in both years and at the foothills site in the second year of the study (Table 2).

During this study, algal production was not the dominant source of organic matter available to consumers, but algal carbon supported most of the consumer production in North St. Vrain Creek (Fig. 7). Nonetheless, algal production was adequate to support even more than the observed macroinvertebrate production. For the second trophic level, the maximum amount of production that can be supported by algal carbon is equal to the product of aquatic NPP (approximately $5\text{--}80\text{ gDM m}^{-2}\text{ yr}^{-1}$ for North St. Vrain Creek) and maximum net production efficiency for primary consumers (about 39%; Humphreys 1979). The maximum possible production for each higher trophic level is equal to the product of production by the previous level and net production efficiency for carnivores (about 56%; Humphreys 1979). The maximum secondary production that could have been supported by algae was 61% of NPP if there were two trophic levels above primary producers and 73% of NPP if there were three trophic levels above primary producers ($4\text{--}17\text{ gDM m}^{-2}\text{ yr}^{-1}$ at the alpine site; $26\text{--}60\text{ gDM m}^{-2}\text{ yr}^{-1}$ at the foothills site). The actual amount of macroinvertebrate production supported by algal carbon was much lower ($\sim 1\text{ gDM m}^{-2}\text{ yr}^{-1}$ at the subalpine site; $\sim 8\text{ gDM m}^{-2}\text{ yr}^{-1}$ at the foothills site). Thus, the contribution of algal carbon to macroinvertebrate production was well below its maximum potential, even though algal carbon contributed to macroinvertebrate production with greater efficiency than did terrestrial carbon.

Vannote et al. (1980) suggested that changes over a stream continuum in the composition of the consumer community result from changes in the physical environment and in the relative input of terrestrial organic matter to the stream. This assertion has become an important organizing principle in the study of stream ecosystems and provides a basis for understanding changes with stream size in community structure and ecosystem function. It often has been assumed from this assertion that the ultimate sources of organic matter in streams contribute to the growth of consumers in proportion to their availability. The assumption that sources of organic matter contribute to consumers in proportion to their availability does not apply, however, to North St. Vrain Creek. Although terrestrial plants are the dominant source of organic matter in this stream, algal carbon supports most of the macroinvertebrate production.

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