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Nutritional value of lotic insect feces¹ compared with allochthonous materials¹

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With 2 figures, 2 tables and an appendix in the text

Abstract

Proximate composition, carbon, nitrogen, ash, and caloric content was determined for feces of some aquatic insect species, allochthonous leaf litter, and epibenthic detritus from a small, Rocky Mountain stream. Feces averaged 12% AFDW protein compared to 8% AFDW for leaves and 13% AFDW for epibenthic detritus. Organic matter for feces was ca. 75%; leaves varied from 76—92% and other detritus was 66% organic. KRUSKAL-WALLIS tests revealed no significant differences within feces for any parameter, nor between materials for caloric content. However, leaf species were different at the 5% level as were comparisons between materials. Fecal material was obtained from laboratory cultures of *Ephemeraella inermis*, *E. grandis*, *Pteronarcys californica*, and *Tribula* sp. and characterized morphologically. Unlike amphipods and isopods, these insects did not produce distinct "pellets" except for an occasional *Ephemeraella*; most fecal material consisted of particles ca. 1 μ m diameter in a mucus-like matrix. Small fragments of undigested leaves and wood were also observed. Comparisons of feces, leaves, and epibenthic detritus by most standards of food quality indicate that the former have the potential of being a high quality food resource and comparative proximate composition may be a useful intrinsic index of food quality.

Introduction

The input of coarse particulate organic matter and its subsequent transformations are important aspects of stream ecosystem dynamics (CUMMINS 1974; ANDERSON & SEDELL 1979; VANNOTE et al. 1980). Through physical and biological degradation the particles gradually are reduced in size and their contents extracted.

Animals play an important role in the comminution of organic matter in streams (IVERSEN 1973; SHORT & MASLIN 1977) and their feces could provide an important food base for fine-particle feeders in the community

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(GRAVUS & ANDERSON 1979). Since all active benthic insects ingest more food than they assimilate it is reasonable to expect that their feces will retain sufficient nutritional value to be used as a food resource either by themselves or by other detritivores locally or further downstream.

Nutritional value, or food quality (rather than quantity), may affect selection of a specific food by a particular individual or species, growth rates, survival rates, and pupation or emergence (KOSTALOS 1971; COLBO & PORTER 1979; WARD & CUMMINS 1979).

Our overall goal is to elucidate the significance of insect feces in lotic community processing by investigating some of the more important parameters. This paper considers the morphological description of feces from several lotic insects and the comparison of intrinsic food quality parameters of those feces with allochthonous leaves and epibenthic detritus. Data on coprophagy and the overall role of feces in lotic community processes will be published separately.

Methods and materials

All samples were collected from 2 riffles in Mink Creek, Bannock County, Idaho, adjacent to sites used by MINSHALL & MINSHALL (1977) and RABENI & MINSHALL (1977). The riparian vegetation is thick shrubs of willow (*Salix exigna*), dogwood (*Cornus stolonifera*), hawthorn (*Crataegus douglasii*), chokecherry (*Prunus virginiana*), rose (*Rosa woodii*), and birch (*Betula occidentalis*). The first three were the only identifiable leaves found within the two riffles. Leaf material was hand picked from the bottom and from overhanging branches trailing in the water, placed in bottles with a small amount of stream water, and returned to the laboratory where they were rinsed clean of all debris, sorted (all unidentifiable fragments were called "mixed"), and dried to constant weight; this protocol was also used for fecal and detrital samples.

Benthic invertebrates were collected using a dip-net, sorted in the field, and transported live to the laboratory in containers filled with stream water. During the summer, battery-powered aerators were used to keep the water oxygenated while being transported. In winter, snow was added to the samples to retard the rate of temperature rise; this reduced thermal shock as the insects acclimated to the temperature of the room in which they were maintained (ca. 11 °C). Separate, aerated culture dishes were maintained for each of the two genera of major interest: *Pteronarcys californica* (Plecoptera: Pteronarcyidae) and *Ephemera intermis* and *E. grandis* (Ephemeroptera: Ephemerellidae). A third culture of mixed species (*Baetis intermedius*, *Cinygmula tinnis*, *Nemoura* sp., *Hydropsyche* spp., and *Trifida* sp.) also was maintained.

Fecal material was collected approximately once a week from the culture dishes by pouring the contents through a series of 5 sieves ranging in mesh size from 1 mm to 53 μ m. The collected water was diluted with distilled water and returned to the culture dishes along with the insects, leaf fragments, and detritus larger than 250 μ m. Evaporated water was replaced with distilled as required. The material retained by the 106 and 53 μ m screens was dried to constant weight, pulverized with a mortar and pestle, and stored in stoppered vials prior

to chemical analysis and calorimetry. Separate (untreated) samples of fecal material were examined using a stereomicroscope at 30X; random samples of different sized particles were measured with a calibrated ocular scale.

Ash content of the various materials was determined by incineration at 425 °C for 6 h in a muffle furnace. The residue was then held at 60 °C for 24 h, cooled in a desiccator, and weighed to the nearest 0.1 mg. Aliquots of the dried materials were mixed with 0.1 N NaOH with a mortar and pestle, total protein extracted with Biuret's reagent, and concentration of protein (per mg sample) read at 520 nm on a Beckman DB-G spectrophotometer (BRADSHAW 1966). A standard curve was constructed using bovine serum albumin (BSA) (3 replicates at each concentration of 0.2, 0.4, 0.6, 0.8, and 1.0 mg/ml); the coefficient of determination (r^2) for the regression was 0.99. Because the samples colored the Biuret reagent, it was necessary to add 1.0 mg activated charcoal per mg sample then centrifuge the sample at 2,000 rpm for 4 min before reading the concentration. Nitrogen content of a mixed feces sample, determined by micro-Kjeldahl analysis, was compared with the Biuret protein extraction using the relationship: %N = % protein/6.25 (MACIOLEK 1962; PAINE 1971; McMANON et al. 1974) and a correction factor established for the protein values.

Carbon content of 10 replicates of each sample type was done by dichromate oxidation (MACIOLEK 1962). Accuracy of the assays was determined two ways: by oxidizing a series of ammonium tartrate standards and comparing the calculated organic content with the known amount used; and by comparing calculated organic content of the sample materials with the values determined by ashing. Accuracy of the oxidations was 98.5%. Lipid content was calculated using the equation: %L = $1100(O.E. - 1.2)m(0.3(\%C.P.)/1.5)$, where O.E. is the oxygen equivalent and C.P. is crude protein (MACIOLEK 1962). Percentage of carbohydrate was then calculated by difference. Energy content was determined by micro-bomb calorimetry (using a Gentry instrument) with 4 to 5 replicates per sample type. All values are expressed on an ash-free dry weight (AFDW) basis.

Before comparing the mean values of the chemical parameters for each type of material, DUKETT's test for homoscedasticity of variances was performed on all data; because some data sets had heterogeneous variances (precluding the use of Analysis of Variance) the KRUSKAL-WALLIS test was used (SOKAL & ROHLF 1969).

Results

Morphological Description of Feces

Microscopic examination of fecal material (from *Ephemera intermis*, *E. grandis*, *Pteronarcys californica*, and *Trifida* sp.) showed that very few distinct "pellets" were produced; the majority of the material was amorphous and covered with a mucus-like substance. Only *Ephemera intermis* and *grandis* sometimes produced cohesive, peritrophic membrane-covered pellets. Because other authors (e.g., RICHARDS & RICHARDS 1977) have reported that herbivore/detritivore consumers should produce peritrophic membranes to protect the mid and hind guts from abrasion by rough food particles, direct examination of the gut was done to determine if the sample of species from Mink Creek produced peritrophic

membranes which disintegrated rapidly upon defecation. Entire guts of approximately 20 individuals each of *Pteronarcys callifornica*, *Ephemera inermis*, *E. grandis*, and *Tipula* sp. were removed intact by microdissection. No evidence of peritrophic membranes was visible through the gut wall; only individual fragments of leaves and loose aggregates of amorphous fecal material could be seen. When the mid and hind guts were carefully opened the contents floated out separately with no indication that they had been contained within a membrane.

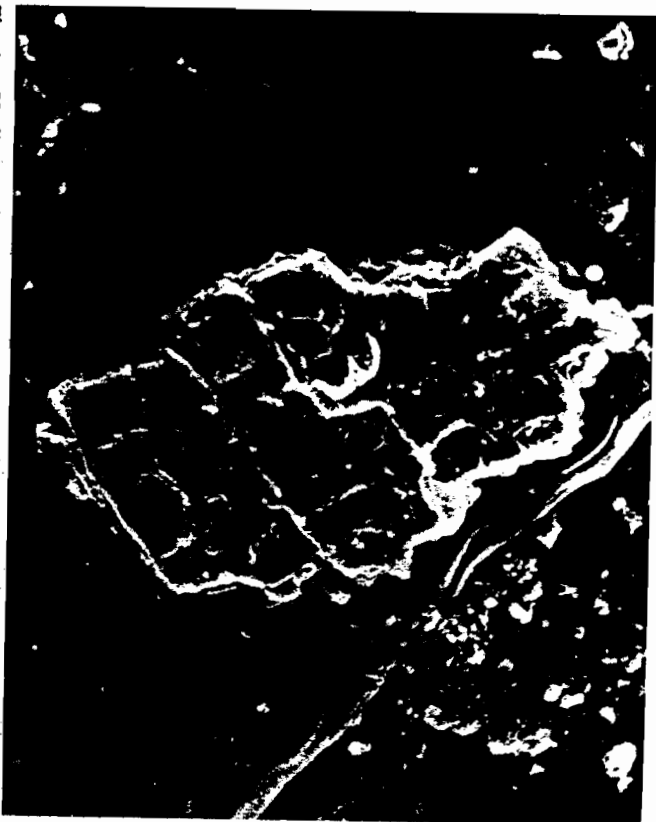


Fig. 1 a. Undigested leaf fragment in feces from mixed cultures. "Waffle" appearance due to drying of specimen. Magnification 280X.

Feces from all species examined (both directly and by filtration of the culture water) fall into three distinct types. The predominant form was amorphous, loosely aggregated particles of ca. 1 μ m diameter in a clear, mucus-like matrix. These ultrafine particles were uniform in size and light brown in color. This type comprised about 80% of the *Ephemera* and mixed feces and about 99% of the *Pteronarcys* feces. The next most common form were small, flat fragments (100–250 μ m/side) which appeared to be pieces of undigested leaf or wood (Fig. 1). These fragments were dark brown to black in color and had rough surfaces and edges. These

constituted about 1% of the *Pteronarcys* feces and 5–10% of the *Ephemera* and mixed feces. Distinct spherical (150–200 μ m diameter) and elliptical (150–500 μ m long) pellets were observed only in the *Ephemera* and mixed samples; about 10–15% of the former and about 10% of the latter (Fig. 2). These pellets appeared to be covered with a membrane, ranged in color from light brown to black, and were very soft and easily disrupted with a probe. When produced, fecal pellets appear to maintain their physical integrity only when produced on a grid or filter paper; in water they rapidly disintegrate (D. Funk, Stroud Water Resources Center, personal communication).



Fig. 1 b. Undigested leaf or woody tissue common in fecal samples. Magnification 288X.

Chemical Composition of Allochthonous Material

Leaf material from the stream had a wide range of values for most parameters measured (Table 1). Ash content ranged from 8.4% (*Salix*) to 24.0% (mixed species), carbon ranged from 34.6% to 42.4%, and nitrogen varied between 0.7% and 1.7%. Carbon:nitrogen ratios were calculated from mean values; the mixed leaves being lowest at 21:1 and *Corylus* the highest at 57:1. Proximate composition of the leaves was

Table 1. Mean percent AFDW \pm standard error for all chemical parameters measured or calculated. Caloric values are per mg AFDW. N = 10 for C, N, and proximate composition; N = 5 for ash and leaf calories; N = 4 for fecal and detrital calories.

Material	C:N	Carbon	Nitrogen	Protein	Lipid	Carbo- hydrate	Ash	Calories
A. Leaves								
<i>Cornus stolonifera</i>	57 \pm 28.6	40 \pm 0.4	0.7 \pm 0.1	5 \pm 0.7	10 \pm 0.3	85 \pm 0.5	17.2 \pm 0.18	4.2 \pm 0.03
<i>Salix exigua</i>	28 \pm 4.0	42 \pm 0.6	1.5 \pm 0.1	9 \pm 0.8	6 \pm 0.2	85 \pm 0.8	8.4 \pm 0.32	4.2 \pm 0.08
<i>Crataegus douglasii</i>	26 \pm 1.4	36 \pm 0.7	1.4 \pm 0.05	9 \pm 0.3	8 \pm 0.3	83 \pm 0.2	22.8 \pm 0.66	4.0 \pm 0.12
mixed	21 \pm 2.1	35 \pm 0.4	1.7 \pm 0.1	10 \pm 0.6	5 \pm 0.1	85 \pm 0.6	24.0 \pm 0.94	4.0 \pm 0.11
B. Epibenthic detritus								
	23 \pm 2.6	50 \pm 2.9	2.2 \pm 0.1	13 \pm 0.8	60 \pm 0.9	27 \pm 0.6	34.0 \pm 3.3	4.4 \pm 0.18
C. Feces								
<i>Ephemera inermis</i>	29 \pm 4.0	54 \pm 4.0	1.9 \pm 0.1	12 \pm 0.9	33 \pm 1.0	55 \pm 1.6	25.6 \pm 0.62	5.2 \pm 0.23
<i>Pteronarcys californica</i>	21 \pm 4.7	46 \pm 3.8	2.2 \pm 0.2	13 \pm 1.6	35 \pm 1.8	52 \pm 1.4	25.3 \pm 0.91	4.9 \pm 0.36
mixed	25 \pm 3.2	45 \pm 1.0	1.8 \pm 0.1	11 \pm 0.9	33 \pm 0.5	56 \pm 1.0	25.1 \pm 1.0	3.4 \pm 0.31

significantly different between types. Carbohydrates were the predominant compounds and lipids represented only a small percentage of the total. There was more than a two-fold difference in the amount of protein in *Cornus* and in the mixed leaves. Energy content (4.0—4.2 cal/mg AFDW) was fairly uniform and was slightly lower than expected when compared to published values (CUMMINS & WYSCHEK 1971).



Fig. 2a. Fecal pellets from *Ephemera* spp. Fresh pellets appeared covered with a shiny membrane when viewed at low magnification (30 \times) with a light microscope; no membrane is visible with the SEM (495 \times). Pellets would appear to retain integrity only by compaction. Note diatom at top (left of center). White line = 50 μ m.

Chemical Composition of Detritus

Epibenthic detritus collected from erosional areas was almost 34% ash (for the 53—250 μ m size class examined). The C:N ratio was 23:1. A little more than 13% of the composition was proteins and the percentage of lipids (60%) was very high; carbohydrates were correspondingly low. The heterogeneous origins of this fine detritus was reflected in the high variances of the replicates, or large standard errors of the means. This variance may explain the relatively low caloric content (4.4 cal/mg AFDW) associated with the amount of lipid.



Fig. 2 b. Elliptical fecal pellet from *Ephemerella* spp. (352X). Small fragments have broken off during preparation. These, too, appeared shiny when viewed at low magnification (30X) with a light microscope. White line = 50 μ m.

Chemical Composition of Feces

Fecal samples were more uniform in their chemical constituents than were the leaf materials (Table 1). Ash values, for example, ranged from 25.1% (mixed samples) to 25.6% (*Ephemerella*). Carbon content extended over a range of 7.6% while nitrogen values ranged 0.4%; C:N ratios were correspondingly close and ranged from 21:1 to 29:1. The proximate composition was quite uniform but the higher percentage of protein for *Pteronarcyx* compared with the other organisms resulted in a significant difference for this parameter; all other parameters were not significantly different at the $P = 0.05$ level. All fecal samples were high in lipids (about 33%) and low in carbohydrates. Fecal materials had high caloric contents (averaging 4.5 cal/mg AFDW) covering a range from 3.4 to 5.2 cal/mg AFDW.

Comparison of mixed leaves, detritus, and mixed feces resulted in differences significant at the $P = 0.05$ level for all parameters except energy content (Table 2). Only the composite ("mixed") leaves and feces were compared for two reasons: first, there were no statistical differences within the composition of the feces examined; and second, the intent of this

research is to compare nutritive values for the different types of food resources as groups rather than by genus or species. Leaves and feces had very similar ash contents but were lower than the epibenthic detritus. For all other measured parameters no distinct associations emerged. In particular, the proximate composition of the materials showed no definite similarities; for example, leaf and fecal proteins differed by about 1%

Table 2. Summary of results of single factor Kruskal-Wallis non-parametric analysis of variance within leaf species, within feces of different species of benthic insects, and between leaves, feces, and epibenthic detritus. * = significant at $P = 0.05$ level; n. s. = not significant.

Parameter	Leaves	Feces	Between
Carbon	*	n. s.	*
Nitrogen	*	n. s.	*
Protein	*	*	*
Lipid	*	n. s.	*
Carbohydrate	*	n. s.	*
Ash	*	n. s.	*
Calories	n. s.	n. s.	n. s.

from each other and by about 3% from detrital protein while the lipid content difference was about 29% between leaves and feces and about 27% between feces and detritus (Table 1).

Discussion

Published reports on the composition of organic materials in freshwater ecosystems and their watersheds reveals that much more attention has been given to the inorganic nutrients than to the organic components (Appendix 1). The percentage of nitrogen is the only parameter reported by all authors; it varies from 0.57% to 2.8% of dry weight in terrestrial litter and from 0.04% to about 10% in aquatic systems. In general, the nitrogen content of benthic invertebrates is higher than of the flora. One of the most striking features is the large range of values encountered for almost all compounds; for example, percent carbon ranges from 4.50 in oak litter to 60.98 in Douglas fir and C:N values have been reported from about 15:1 for red alder leaves to greater than 1300:1 for Douglas fir wood.

The rationale for using C:N ratios as indicators of food quality is that carbon is a component of all organic materials while nitrogen is present only in proteins. Therefore, low C:N ratios reflect more protein available for consumption. RUSSELL-HUNTER (1970) reports that for all animals (except ruminants) for which data are available, the minimum amount of protein required in the diet to maintain health is about 16.5% of dry

weight; this value is equivalent to a C : N ratio of about 17 : 1. This correlation (between protein and C : N ratios) exists in the present study where the highest C : N ratio is associated with the lowest percentage of protein (Сотник, Table 1). If C : N ratios can be accepted as indices of food quality then fecal material and epibenthic detritus in Mink Creek are as good a food resource as the leaves because the C : N ratios of the first two fall on the lower end of the range of the latter (Table 1).

The quality of the food may also be a function of both conditioning time and particle size. KAUSNIK & HYNES (1971) found that smaller sized particles are conditioned more rapidly than larger particles, and all detritus contains more nitrogen as it becomes conditioned so that C : N ratios decrease with time. FENCHEL (1973) found that colonization of fecal pellets by bacteria also resulted in decreased C : N ratios. МСМАНОВ et al. (1974) estimated (for aufwuchs) a critical level of protein above which the food quality (in terms of supporting consumer growth and reproduction) is more dependent upon proximate composition than on biomass. If this "minimum protein level" concept is valid then all materials in Mink Creek represent high quality foods.

The difficulty in interpreting proximate composition data is that there is neither an indication of how accessible these compounds are to consumers nor any solid data on the nutritional requirements of the consumers. Despite this lack of knowledge, trends emerge which indicate the processing patterns of the benthic insects. Dogwood is very abundant in the stream just after abscission but disappears as a recognizable entity by mid-December. This leaf species is the lowest in protein of those examined but has the highest percentage of lipids. It is possible that its rapid disappearance is due to the consumer's need for a large amount of lipid for the winter months, a situation observed by ОТТО (1974) in his study of *Potamophylax cingulatus*. Further evidence that this may occur in Mink Creek is found in the proximate composition of the mixed leaves which are present (in low abundance) in the late spring and early summer and contain very little lipid (< 1%).

Fecal material is quite different from leaves available in the stream because of its low percentage of carbohydrates. This may reflect the relative refractory nature of the different compounds (proteins vs. carbohydrates) or may indicate that regardless of the type of leaf consumed and the reason for choosing it, a large proportion of the available carbohydrates are assimilated. BROWN (1961) and MCCULLOUGH et al. (1979) reported that detritus-eating mayflies have a low gut retention time so that only the more labile components of their food may be assimilated; our investigation supports this contention because, of the three types of potential food resources analyzed, epibenthic detritus has the least amount of

carbohydrates per unit weight. The gut microflora, and bacteria and fungi in the substrate, can use these compounds for their own metabolism and perhaps make the refractory ones more easily assimilable by other detritivores.

Fecal material itself is sufficiently nutritious to maintain aquatic macroinvertebrates and may even be necessary to enhance survival of juveniles (HYNES 1954). HYNES (1970) cites several studies of coprophagy among lotic macroinvertebrates and more recent works (УНИТЛАНС 1974; НАКРАВЕ 1976; ТЕНОРЕ et al. 1979) indicate that estuarine invertebrates also use feces for food. Among lotic insects, it recently has been shown that growth rates of *Paratendipes albimanus* are associated with the type of food consumed; *Tijula* feces produced rates intermediate to conditioned leaves and epibenthic detritus (WARD & СУМИНС 1979). This preference is ascribed to a difference in food quality as measured by microbial densities (ATP and respiration values) but no data are given on the proximate composition of the different food resources.

Within any particular lotic ecosystem, food resource availability is a function of habitat heterogeneity and varies both seasonally and spatially. This is well documented for CPOM (such as leaves) but is not yet fully determined for FPOM such as feces. WIGGINS & МАСКАУ (1978), in a study of distribution of Nearctic trichopteran filter feeders in the families Philopotamidae, Polycentropodidae, and Hydroptychidae, suggest that the distributions observed in the Eastern United States compared with those in the Western states are due to quantitative or qualitative differences in the FPOM resources, and FPOM used by the latter two families most likely originates in the feeding activity and fecal production of shredders. The importance of geographic variability of FPOM quality is evident by the number of studies and reviews (e.g., ANDERSON & SEBEL 1979) in the recent literature. Because of the paucity of data on different types of FPOM, we are initiating studies of the spatial and temporal differences in proximate composition of fecal material and other fine detritus as it relates to food quality for benthic macroinvertebrate consumers.

There is still very little definitive information on what would constitute a good index of food quality and the role it plays in lotic structure and function. We suggest that proximate composition may be the most fruitful approach because it reflects more than both carbon: nitrogen ratios and biological conditioning associated with the different materials. Lipid content, for example, may be important in the selection of a food resource by a detritivore during specific stages of its life cycle. Both ОТТО (1974) and БЕАТТИЕ (1978) demonstrated variable lipid content in aquatic larvae as they developed. For insects in general, the review by DOWNER & МАТТЮНС (1976) shows that lipid availability is crucial in embryogenesis,

larval development, metamorphosis, adult flight, and diapause; this may necessitate a change in diet.

In lotic ecosystems, food quality may surpass the direct effects of temperature on controlling growth rates of nymphal or larval insects (ANDERSON & CUMMINS 1979; CUMMINS & KLUG 1980). Because food quality is affected by spatial and temporal change, both life history and distributional phenomena are reflections of the food available. If proximate composition proves to be an accurate, unbiased index of all the environmental parameters affecting food quality then it will permit inter-biome comparisons of community and ecosystem processes and allow the formation of testable generalizations concerning lotic processes.

Zusammenfassung

Der annähernde Gehalt an Kohlenstoff, Stickstoff und Asche sowie der kalorische Wert wurden von Faeces einiger aquatischer Insektenarten sowie von allochthonem Laub und epibenthischem Detritus eines kleinen Baches der Rocky Mountains bestimmt. Die Faeces enthielten durchschnittlich 12% Protein in der anschließenden Trockensubstanz, die Blätter 8% und der epibenthische Detritus 13%. Die entsprechenden Werte für organische Substanz betragen 75% bzw. 76–92% bzw. 66%. Der Kruskal-Wallis-Test ergab keine eindeutigen Unterschiede zwischen den Faecesarten weder für irgendeinen der Parameter noch hinsichtlich der Kalorienwerte. Jedoch unterschieden sich die Blattarten auf dem 50%-Niveau. Das Faeces-Material wurde von Laboratoriumskulturen von *Ephemera inermis*, *E. grandis*, *Pteronarcy's californica* und *Tipula* sp. gewonnen und morphologisch charakterisiert (vgl. Fotoabbildungen). Zum Unterschied von Amphipoden und Isopoden bildeten diese Insekten keine bestimmten "pellets" (Faeces-Kügelchen), ausgenommen einmal bei *Ephemera*. Der größte Teil des Faecesmaterials bestand aus Partikeln von ca. 1 µm Durchmesser in schleimiger Matrix. Auch wurden kleine Überreste von unverdaulichen Blättern und Holzstückchen beobachtet. Die Faeces haben offenbar einen größeren Nahrungswert als die Blätter und epibenthische Detritus. Eine vergleichende Beurteilung der annähernden Zusammensetzung dieser Teillehen wird als ein nützlicher Index der Nahrungsqualität angesehen.

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Appendix I. Representative values of carbon, nitrogen, ash, and proximate compounds for various species of plants, animals, and some organic detritus. Aquatic/terrestrial refers to the system studied, not the origin of the material. Results (*) reported on ash-free dry weight basis; all others are on dry weight basis.

Material	Location	% N	% C	C:N	% Ash	% Protein	% Carbohydrates	% Lipid	Reference
A. Terrestrial									
<i>Acer saccharinum</i> (Sugar maple) (leaves)	New Hampshire	0.57—1.56				3.56—9.75			10
<i>Picea abies</i> (Norway spruce)	Sweden	0.7			9.0	(4.81)*			18
<i>Fagus silvatica</i> (beech)	Sweden	0.7			6.8	(4.69)*			19
<i>Quercus petraea</i> (oak)	England	0.77—1.79	4.50—49.4	6.8—32.3		4.81—11.19			3
<i>Populus tremuloides</i> (Quaking aspen) (leaves)	Alberta, Canada	0.8—2.6	43.6—47.4	21.3—63.8		5.00—16.25			7
<i>Betula</i> sp. (birch) (leaves)	New Hampshire	0.82—1.69				5.13—10.56			10
<i>Betula lutea</i> (yellow birch) (leaves)	New Hampshire	0.85—2.31				5.31—14.44			10
<i>Betula</i> sp. (branches)	New Hampshire	0.86—0.98				5.38—6.13			10
<i>Pinus nigra</i> (black pine)	England	0.87	60.58	81.5	2.82	5.60*			21
<i>Betula verrucosa</i> (birch)	Sweden	0.87			4.6	6.13*			17
<i>Acer saccharinum</i> (sugar maple) (branches)	New Hampshire	0.88—0.96				5.50—6.00			10
<i>Populus tremuloides</i> (quaking aspen) (twigs)	Alberta, Canada	0.9—4.2	44.2—48.2	13.4—57.5		5.63—26.25			7
<i>Betula lutea</i> (yellow birch) (branches)	New Hampshire	0.94—1.08				5.88—6.75			10
<i>Populus</i> sp. (yellow poplar)	North Carolina	0.94				5.88			6
<i>Quercus alba</i> (white oak)	North Carolina	0.96				6.00			6

Material	Location	%N	%C	C:N	% Ash	% Protein	% Carbo- hydrates	% Lipid	Refer- ence
<i>Acer</i> sp. (maple)	North Carolina	0.96				6.00			6
miscellaneous litter	North Carolina	0.99				6.19			6
<i>Quercus coccinea</i> (scarlet oak)	North Carolina	1.01				6.31			6
<i>Pseudotsuga toxifolia</i> (douglas fir)	England	1.02	60.98	70.0	5.10	6.72*			21
<i>Quercus Muehlenbergii</i> (chestnut oak)	North Carolina	1.03				6.44			6
<i>Quercus borealis</i> (northern red oak)	North Carolina	1.03				6.44			6
<i>Quercus nigra</i> (black oak)	North Carolina	1.08				6.75			6
<i>Fraxinus excelsior</i> (ash)	Sweden	1.1			7.5	7.43			16
<i>Fagus silvatica</i> (beech)	England	1.19 - 1.77				7.44 - 11.06			13
<i>Larix leptolepis</i> (larch)	England	1.24	57.16	53.9	4.08	8.08			21
<i>Carya</i> sp. (hickory)	North Carolina	1.30				8.13			6
<i>Corylus avellana</i> (hazel)	England	1.39 - 2.34	47.3 - 49.7	24.8 - 39.8		8.69 - 14.63			3
<i>Betula lenta</i> (sweet birch)	North Carolina	1.41				8.81			6
<i>Fraxinus</i> sp. (ash)	North Carolina	1.43				8.49			6
<i>Betula alba</i> (white birch)	England	1.44	55.34	45.0	6.11	9.59*			21
<i>Fraxinus excelsior</i> (ash)	England	1.50 - 2.79	41.7 - 51.2	21.9 - 32.5		9.38 - 17.06			3
<i>Oxydendrum arboreum</i> (sourwood)	North Carolina	1.53				9.56			6
<i>Alnus glutinosa</i> (black alder)	England	1.62 - 3.78	49.8 - 52.5	16.2 - 36.0		10.13 - 23.63			31
<i>Cornus</i> sp. (dogwood)	North Carolina	1.62				10.13			6

Material	Location	%N	%C	C:N	% Ash	% Protein	% Carbo- hydrates	% Lipid	Refer- ence
<i>Prunus serotina</i> (black cherry)	North Carolina	1.85				11.56			6
<i>Robinia Pseudo-Acacia</i> (black locust)	North Carolina	2.20				13.75			6
<i>Alnus incana</i> (white alder)	England	2.65	51.87	22.9	7.97	18.00*			21
<i>Alnus glutinosa</i> (black alder)	Sweden	2.8			5.3	17.50			19
B. Aquatic									
<i>Pseudotsuga</i> sp. (douglas fir) (wood)	Oregon	0.04 - 0.20	40.2 - 45.9	235 - 1.343		0.25 - 1.25			1
<i>Pseudotsuga menziesii</i> (douglas fir)	Oregon	0.15 - 1.1	32.0 - 42.3	45 - 250	1.9	0.96* - 7.01*			25
<i>Tsuga heterophylla</i> (western hemlock)	Oregon	0.15 - 1.1		45 - 250	1.9	0.96* - 7.01*			25
<i>Nothofagus solandri</i> (mountain beech)	New Zealand	0.16 - 0.96	41 - 46	90.9	4.5 - 12.7	1.0 - 6.0			8
pine needle	Mississippi	0.18 - 0.53	45.5 - 49.4	158.8	2.5 - 3.8	1.15* - 3.44*			22
woody twigs	Mississippi	0.23 - 0.44	47.7 - 49.2	171.8	1.2 - 2.9	0.22* - 0.43*			22
<i>Acer macrophyllum</i>	Oregon	0.4 - 1.5	25.6 - 46.2	20 - 135	1.6	0.39* - 1.46*			25
<i>Ulmus rubra</i> (red elm)	Kentucky	0.41* - 0.73				2.58 - 4.54*	2.16 - 6.55*	1.3 - 3.5*	14
<i>Acer circinatum</i> (vine maple)	Oregon	0.45 - 1.5	38.5 - 40.4	30 - 105	2.9	2.90* - 9.65*			25
deciduous leaf	Mississippi	0.45 - 0.51	45.1 - 46.2	106 - 117	3.4 - 7.0	2.91* - 3.43*			22
<i>Typha latifolia</i> (common cat-tail)	South Carolina	0.51 - 1.68			7.5	3.2 - 10.5			4, 5
<i>Pseudotsuga</i> sp. (douglas fir) (leaves)	Oregon	0.51	42.3	97		3.19			1
<i>Acer circinatum</i> (vine maple)	Oregon	0.56	36.8	77		3.50			1
<i>Platanus occidentalis</i> (sycamore)	Kentucky	0.67* - 1.14				4.2 - 7.1*	1.3 - 7.26*	4.0 - 7.0*	11

Material	Location	%N	%C	C:N	% Ash	% Protein	% Carbo- hydrates	% Lipid	Refer- ence
<i>Fagus sylvaticus</i> (beech)	Denmark	0.69 - 1.45				4.31 - 9.06			16
<i>Cornus</i> sp. (dogwood)	Idaho	0.70*	39.6*	56.6*	17.15	4.4*	85.1*	10.5*	27
<i>Quercus alba</i> (white oak)	Michigan	0.71				4.44		4.90	24
<i>Acer macrophyllum</i> (bigleaf maple) (leaves)	Oregon	0.74	39.2	62		4.63			1
mosses	Oregon	0.8 - 1.2				5.00 - 7.50			1
<i>Fagus</i> sp. (beech)	Kentucky	1.05* - 1.44				6.55 - 9.0*	2.0 - 6.0*	2.1 - 8.1*	14
<i>Alnus rubra</i> (red alder)	Oregon	1.2 - 2.9	15.4 - 99.2	15 - 40	1.0	8.33 - 20.14*			12
<i>Fagus</i> (beech)	Denmark	1.22*			8.1	7.63*			12
<i>Picea</i> (spruce)	Denmark	1.36*			8.0	8.50*			12
<i>Crataegus</i> sp. (hawthorn)	Idaho	1.38*	35.2*	26.2	22.81	8.6*	83.8*	7.6*	27
<i>Myriophyllum exalbescens</i> (water milfoil)	Wisconsin	1.48				9.25			15
<i>Carya glabra</i> (pignut hickory)	Michigan	1.48				9.25		5.22	24
<i>Alnus glutinosa</i> (black alder)	Sweden	1.49	51.05	40.1	4.84	9.32			20
<i>Salix</i> sp. (willow)	Idaho	1.49	42.4*	28.5	8.39	9.3*	84.6*	6.1*	27
mixed leaves (unidentifiable)	Idaho	1.66	34.6*	20.8*	24.00	10.4*	85.0*	4.6*	27
<i>Hydrotrida carolinensis</i>	South Carolina	1.68				10.5			4, 5
<i>Brasenia schreberi</i> (water shield)	South Carolina	1.74			7.6	10.9			4, 5
<i>Utricularia inflata</i> (inflated bladderwort)	South Carolina	1.82			14.0	11.4			4, 5
<i>Fagus sylvatica</i> (beech)	Sweden	1.89	47.00	29.1	10.09	11.80			20
<i>Quercus</i> (oak)	Denmark	1.93*			10.2	12.06*			12
<i>Nelumbo lutea</i> (yellow nelumbo)	South Carolina	1.94			8.8	12.1			4, 5
<i>Alnus rubra</i> (red alder) (leaves)	Oregon	2.03	39.9	23		12.69			1

Material	Location	% N	% C	C:N	% Ash	% Protein	% Carbo- hydrates	% Lipid	Refer- ence
<i>Myriophyllum heterophyllum</i> (diverse-leaved water milfoil)	South Carolina	2.16			12.2	13.5			4, 5
<i>Eleocharis acicularis</i> (needle-shaped sedge)	South Carolina	2.26			11.2	14.1			4, 5
<i>Najas guadalupensis</i> (magnus naiad)	South Carolina	2.30			12.8	14.4			4, 5
<i>Nymphaea odorata</i> (fragrant water-lily)	South Carolina	2.34			8.1	14.6			4, 5
<i>Myriophyllum exalbescens</i> (water milfoil)	Wisconsin	2.63			11.6	16.44			9
<i>Ceratophyllum demersum</i> (submerged hornwort)	South Carolina	2.74			14.9	17.1			4, 5
<i>Myriophyllum exalbescens</i> (water milfoil)	New Jersey	2.81				12.6			23
<i>Nuphar advena</i> (yellow pond-lily)	South Carolina	3.46			10.6	21.6			26
<i>Alnus</i> sp. (alder)	Denmark	4.16* - 4.82			13.7	26.0 - 30.1			12
algae	Oregon	6 - 10				37.5 - 62.5			1
net phytoplankton	Netherlands	6.36* - 11.26	47.55* - 51.16	5.3 - 8.8	4.17 - 18.54	13.06 - 37.13*			11
<i>Sericostoma personatum</i> (Trichoptera) (larvae)	Denmark	7.70* - 8.30			6.8	48.13* - 51.88*			12
<i>Pentapedilum uncinatum</i> (Diptera: Chironomidae)	Netherlands	8.80 - 11.36				55 - 71	20 - 31	6 - 14	2
Chironomid larvae	Wisconsin				3.1 - 6.3				26
<i>Potamophylax cingulatus</i> (Trichoptera)	Sweden							4.3 - 9.1	20
Sediments (Lake Mendota)	Wisconsin	0.104	0.94	14.1 - 28.3		0.65			15

Appendix I. cont.

Material	Location	%N	%C	C:N	% Ash	% Protein	% Carbo- hydrates	% Lipid	Refer- ence
<i>P. cingulatus</i> feces	Sweden	1.24-1.53	44.02-45.96	35.2-41.5	7.30-11.99	7.74-9.55			20
<i>S. personatum</i> (cases)	Denmark	1.57-14.80			89.4	9.81-9.25			12
insect feces (mixed)	Idaho	1.82	45.4*	25.0*	25.10	11.4*	55.5*	33.1*	27
stream detritus	Idaho	2.15*	49.6*	23.1*	33.4*	13.4*	26.6*	60.0*	27
Total Seston		5.10*-7.88	39.60*-44.65	6.6-9.1	18.39-49.59	31.88-49.25*			11

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Buchbesprechungen

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SCHWOBEBEL

Decheniana — Verhandlungen des Naturhistorischen Vereins der Rheinlande und Westfalens (Schriftleiter H. BICK), Beihefte 23, NORBERT CASPERS: Die Emergenz eines kleinen Waldbaches bei Bonn. 175 Seiten, 1980. — Selbstverlag des Vereins, Bonn. Preis DM 20,—.

Mit der Schlitzer Glashauss-Methode wurde im Annaberger Bach bei Bonn die Zusammensetzung und Menge der Insektenemergenz von April 1976 bis Ende 1977 ermittelt. Durch die Lage des Gewächshauses wurden sowohl limnische als auch semiaquatische Flächen erfaßt. Der Bach wird charakterisiert als Waldbach mit geringer Photoassimilation und hohem Falllaub- und Detritusimport; es überwiegen die Kenn- und Begleitarten der Quellregion und des Quellbaches, was allerdings ganz im Gegensatz zu den thermischen Verhältnissen steht. Die Emergenz der Ephemeroptera, Plecoptera, Coleoptera, Planipennia, Trichoptera und besonders differenziert der Diptera wird nach Abundanz und Biomasse aufgelistet und diskutiert sowie mit den Daten aus dem Breitenbach, dem Rohrwiesenbach und dem afrikanischen Kalengo verglichen. Eine Fehlerdiskussion schließt