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The significance of extracellular production and winter photosynthesis to estimates of primary production in a woodland stream community

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Abstract

Both winter photosynthesis and the release of extracellular DOC are commonly ignored in stream production studies. We examined these contributions in a second-order stream under a completely closed deciduous canopy. We estimate that in Sandy Run approximately 26% of the annual autochthonous particulate carbon is produced between December and March. Measured winter rates of photosynthesis were not significantly different than summertime rates. Contrary to implicit assumptions often made about stream primary productivity, winter production was as important as summer production. Highest rates of carbon assimilation, however, were measured in the spring and fall, and were significantly correlated with standing crops of stream algae as measured by chlorophyll concentration. The recovery of released DOC from stream algae indicated that this contribution was equivalent to 5% of the particulate contribution. Rates of DOC production were significantly correlated with rates of particulate production. We estimate that had winter photosynthesis and extracellular DOC production been ignored in Sandy Run, annual productivity would have been underestimated by about a third.

Introduction

The prevailing view of stream community energy budgets is based on an early paradigm that the stream community is primarily dependent on terrestrial allochthonous material for reduced carbon compounds and that autochthonous production within the stream is negligible (Hynes, 1963). Consequently, stream communities are considered to have a terrestrial carbon base. This paradigm was modified, however, by Minshall (1978) and Busch & Fisher (1981), who demonstrated the importance of autochthonous productivity in streams with a more favorable light environment due to limited riparian vegetation. Nevertheless, it remains widely accepted that allochthonous material is the overwhelming basis for community metabolism in low-order streams draining forested watersheds. Reasons given include the copious quantities of litter generated by forest canopies, the apparent small standing crop of algae attached to hard substrates, and the rapid attenuation of light by the forest canopy during a large part of the year that otherwise has the most favorable photoperiod. Empirical support for this paradigm includes a number of published studies, perhaps the most commonly cited being Fisher & Likens' (1973) examination of Bear Brook, NH, and Hornick et al.'s (1981) examination of Guys Run, VA, and two of its tributaries. In neither of these studies does autochthonous organic matter contribute more than 3% to the total energy budget of the stream community.

While there is no doubt that allochthonous loading greatly exceeds autochthonous production, much of this allochthonous material is exported unused. Leaves falling into streams may form packs behind obstructions in the stream channel, and while this material may be retained for some length of time, these leaf packs are continually dislodged and redistributed downstream with variations in stream discharge. Any processing that occurs only serves to reduce CPOM to FPOM and increase the transportability. Estimates of downstream export are highly variable between streams, between segments of the same stream, and between years, but export values in excess of 35% of loading for undisturbed streams are common and often approach 100% (Cummins et al., 1983; Dawson, 1980; Richardson, 1992; Webster, 1983; Webster et al. 1990). Such high export diminishes the local importance of allochthonous carbon.

These observations should generate renewed interest in stream primary productivity and underscore the importance of reliable techniques for its measurement. Much of what is known about primary productivity in streams comes from only a few studies. We suspect that these studies systematically underestimate autochthonous production for two reasons. First, most estimates of annual production are not based on year round measurements. Typically a few measurements made during summer are extrapolated to annual estimates (e.g. Fisher & Likens 1973; Rosenfeld & Roff, 1991). Less frequently, three season measurements are used (e.g. Hornick et al., 1981; Keithan & Lowe, 1985). Thus it is commonly assumed that winter productivity is insignificant even though in the absence of canopy cover the light environment may be better in winter months than in the summer.

Second, in none of these studies was the extracellular production of DOC by algae considered. Extracellular DOC is routinely measured in pelagic studies and has been shown to account for an appreciable percentage of the total primary production (Baines & Pace, 1991). There is convincing evidence that stream algae also produce appreciable quantities of dissolved organic matter (Kaplan & Bott, 1982) but this contribution has not been routinely measured, and only Fisher (1977) has adjusted measured primary productivity upward to account for an assumed extracellular DOC release of 10% of particulate production.

Recently, Aloi (1990) reviewed the literature on methods for measuring primary productivity in streams and made several recommendations which should lead to better estimates of autochthonous carbon production. To these recommendations we wish to add two more: that field programs not neglect measurements during the winter, and that when using the ^{14}C technique to measure primary productivity, extracellular production of dissolved organic carbon also be measured. We will show the potential significance of these considerations by presenting data generated on a second order forested stream segment.

Description of Study Area

This study was carried out on Sandy Run, East Mead Township, Crawford County, Pennsylvania (41° 36′ N, 80° 02′ W; USGS 7.5 minute series topographic — Cochranton quadrangle). Mean air temperature is 8.3° C, and annual precipitation is 1069 mm (U.S.D.A. 1979). Annual snowfall averages 235 cm. Sandy Run is a second-order stream draining approximately 9.3 km^2 of mixed farmland and second growth forest. Average annual discharge is about 4×10^6 m^3 yr. Total phosphorus concentration is approximately 15 - 20 μg/L and total nitrogen concentration is approximately 2.5 mg/l. Concentrations of both nutrients vary with season and discharge. Total channel length is approximately 5.9 km falling from 466 m ASL at its source to 370 m ASL at its confluence with Little Sugar Creek. The study segment is a 1700-m series of riffles and small pools; average channel width is 5.4 m (S.D. = 1.52, n = 25), although the stream does not fill the channel for much of the year. The stream bed is mostly cobble (74% of the sites examined), but a few locations have finer sand and silt, and about an equal number of sites are rocky. The study segment runs under a completely closed canopy dominated by sugar maple, hemlock, beech, cherry, and basswood. White and red pines from remnant plantations made important contributions to some plots. Soils are of the Holly, Cambridge, Chenango, and Frenchtown type, derived from glacial till or from materials weathered from glacial outwash.

Methods

We measured ^{14}C assimilation by algae attached to unglazed ceramic tile substrates measuring 3.8× 12.4 cm (1 1/2×4 7/8 in). Tiles were placed on the stream bottom across shallow riffles and anchored to steel rods with monofilament line. All tiles used for photosynthesis measurements were in place for at least 4 weeks. Pilot studies indicated that the algal community which developed on the tiles was not significantly different from the community on adjacent natural substrates. To measure ^{14}C assimilation, a single, colonized tile was placed in a clear 250-ml acrylic chamber. The chamber was filled with stream water, sealed, and attached to a field peristaltic pump. The chamber and contained tile were placed on the bottom of the stream channel. The pump recirculated stream water over the tile surface at about 1.9 l min^{-1}. An amount of ^{14}C-bicarbonate (0.8–1.0 μCi) was injected into the chamber through a septum, and the tile was incubated for 3–4 h. Meanwhile, we measured stream temperature, alkalinity and pH for the determination of total available natural inorganic carbon (Saunders et al., 1962). Light was continuously recorded with a Belfort Pyrheliograph. After the incubation the tile was recovered to estimate particulate production. In a subset of experiments an aliquot of the circulating water was retained for the estimation of labelled DOC.

In the laboratory, algae were removed from the tile by shaving with a glass slide and thoroughly brushing the tile surface with a stiff bristle brush and a gentle stream of water. Algae were collected, agitated to promote a uniform suspension, and triplicate aliquots were filtered through membrane filters for carbon assimilation measurements and through glass fiber filters for chlorophyll determination. Activity on the membrane filters was determined by liquid scintillation. Calculations to estimate mg carbon assimilated followed standard procedures (Vollenweider, 1974). Estimates of day rates (mg C fixed m^{-2} day^{-1}) were calculated by multiplying the rate of photosynthesis measured during the incubation by the ratio of total day light:incubation period light. Chlorophyll was determined by extracting in 90% acetone and using equations from Strickland & Parsons (1968).

The volume of the chamber water saved for the determination of extracellular production was acidified to pH 4.2 with H_2SO_4 and bubbled for 60 min with air (Schindler et al., 1972). The resulting sample was divided into two portions, one of which was filtered through a glass fiber filter. Aliquots of each of these portions were evaporated to dryness in scintillation vials, and activity measured by liquid scintillation. Activity given by the filtered water aliquots was taken to be a measure of extracellular DOC released by the algae. Any differences in activity between the unfiltered and filtered aliquots were assumed to be caused by suspended algae dislodged from the tile during incubation by browsing invertebrates, by natural sloughing, or by handling. This activity was generally quite low and in most experiments could be ignored, although in a few cases it was added to the particulate production activity.

Annual distribution of production

In all, we had 113 measurements of ^{14}C assimilation with concurrent measurements of chlorophyll, stream temperature and ambient light taken on 48 separate dates across all seasons of the year. Although up to three measurements were often taken simultaneously, and had identical stream water pH, alkalinity and temperature and sunlight, we considered them to be independent measurements since each tile varied in its own algal population as measured by chlorophyll concentration. We ran simple and step-down multiple linear regression analyses (Zar, 1974) to generate a model predicting particulate carbon assimilation using light, chlorophyll and temperature as independent variables based on the technique of Busch & Fisher (1981). The model with the greatest predictive power, based on the magnitude of r^2 was used to predict daily rates of photosynthesis based on measured (light) and/or interpolated (temperature, chlorophyll *a*) values of the appropriate independent variables.

Contribution of Algal DOC

Daily rates of DOC production were estimated in the same manner as were daily rates of particulate production. Extracellular DOC production was measured on a subset of 33 of the production experiments. Further, where multiple tiles were incubated simultaneously, the incubation chambers were connected in series (with a single recirculating pump) so it was not possible to separate the extracellular production by tile. Linking the tiles in series does not violate any assumptions of tracer methodology, but it does further reduce sample size since we expressed the measured labelled DOC as a function of the production and chlorophyll concentration of up to three tiles. Here again, we ran simple and step-down multiple linear regression analyses using light, chlorophyll, temperature and particulate production as independent variables to predict productivity in the form of DOC. Again, the model with the greatest predictive power was used to predict rates of DOC production to calculate the annual contribution.

Results

Stream temperature, light, chlorophyll and measured production for 113 experiments are given in Table 1. Stream temperature varied from 0 to 24°C as anticipated with season. As expected, we found appreciable attenuation of sunlight by the forest canopy during the summer months and measured the highest incident light in the months immediately prior to canopy closure. Once the canopy was fully leafed out, light incident on the steam channel was at an annual low, even lower than during the winter months. During this fully canopied period (approximately June through September) we measured only about 4% of open sunlight at the stream surface. There was also significant

Table 1. Measured parameters used to estimate annual productivity

Date	Temperature	Day light	Chlorophyll *a*	Particulate production	Extracellular production
Jan. 14	4.5	1.43	18.82	390.15	17.78
			34.01	1118.90	
			59.12	1520.26	
Jan. 30	0.2	3.20	0.62	6.19	
Feb. 01	0.5	6.33	12.16	68.55	12.41
			31.16	305.04	
Feb. 09	2.2	1.60	0.42	5.02	
Feb. 15	0.0	6.24	2.10	23.71	
Feb. 22	3.0	3.38	13.37	198.52	10.93
			29.49	176.85	
Mar. 08	2.0	9.60	3.65	36.20	
Mar. 13	2.3	6.60	15.02	162.91	
Mar. 19	4.0	4.27	181.73	76.63	
			64.62	167.26	
			153.91	219.32	
Mar. 20	6.0	13.52	86.43	580.15	
Mar. 26	5.3	5.04	27.19	441.97	
Mar. 28	9.5	14.00	59.30	673.17	
Apr. 03	6.5	16.30	129.42	306.00	
Apr. 04	9.5	14.20	165.56	1770.08	
Apr. 19	3.0	11.04	23.39	397.65	30.94
			42.37	343.94	
			101.49	773.73	
May. 04	7.0	9.46	165.21	1584.76	38.54
			203.11	1581.24	
			90.59	1471.77	
May 18	8.0	5.70	347.41	1003.23	146.96
			366.83	2306.31	
			361.68	2383.64	
May 27	9.5	3.64	553.13	1244.04	52.83
			522.26	1404.38	
			451.99	1364.30	
Jun. 03	13.0	1.32	25.83	418.40	21.86
			64.15	892.00	
			48.65	722.51	
Jun. 06	15.9	1.77	23.27	265.85	38.33
			17.70	245.13	
			17.24	269.88	
Jun. 13	17.0	2.28	10.84	136.70	28.78
			18.89	139.04	
Jun. 16	15.0	1.37	41.67	294.67	6.57
			63.04	354.64	
			49.88	313.37	
Jun. 18	22.5	1.40	62.10	319.23	38.01
			48.84	438.82	
			45.46	433.12	
Jun. 20	22.5	2.06	43.06	444.39	76.10
			48.39	452.65	
			28.29	322.01	

Table 1. (*Continued.*)

Date	Temperature	Day light	Chlorophyll *a*	Particulate production	Extracellular production
Jun. 25	21.0	1.03	25.38	383.07	35.75
			27.02	471.30	
			25.69	475.02	
Jun. 27	22.0	1.09	19.42	131.85	12.56
			18.55	177.21	
			48.91	270.09	
Jul. 02	20.0	0.96	36.19	89.12	13.07
			28.53	112.63	
			62.07	131.41	
Jul. 09	17.5	1.95	22.95	114.58	8.96
			45.99	197.52	
			49.62	195.48	
Jul. 11	20.0	1.75	83.09	510.74	105.05
			28.05	144.02	
			76.98	256.27	
Jul. 16	17.0	1.97	36.75	183.00	24.19
			21.56	132.25	
			30.78	169.33	
Jul. 18	23.0	1.89	39.04	587.49	46.51
			27.43	508.50	
			35.40	450.19	
Jul. 23	24.0	0.82	35.34	318.85	33.48
			30.70	205.50	
			18.47	155.02	
Jul. 25	20.0	1.50	47.66	111.30	21.96
			191.87	299.91	
			62.67	290.91	
Jul. 30	18.5	1.04	22.67	258.65	21.91
			38.38	555.80	
			33.62	449.88	
Aug. 01	19.0	1.71	44.10	376.85	23.33
			31.08	150.50	
			36.88	172.48	
Aug. 06	20.0	1.64	62.34	167.67	31.03
			36.30	142.66	
			37.74	180.27	
Aug. 08	18.5	0.63	39.86	211.80	15.88
			24.36	139.47	
			27.42	144.39	
Aug. 13	17.0	0.97	28.98	108.70	8.03
			30.77	109.28	
			19.91	65.41	
Aug. 23	18.0	1.07	14.65	61.24	3.15
			20.30	52.92	
			18.64	67.41	
Sep. 15	22.0	0.57	11.18	65.72	6.54
			15.74	80.12	
			14.49	50.67	

Continued on p. 92

Table 1. (*Continued.*)

Date	Temperature	Day light	Chlorophyll *a*	Particulate production	Extracellular production
Sep. 24	13.0	1.89	15.07	49.93	4.22
			38.10	101.89	
			40.00	96.87	
Oct. 27	15.0	2.12	110.09	1142.12	31.55
			72.79	1238.61	
			37.43	1081.81	
Nov. 02	11.3	2.40	16.04	295.98	
Nov. 11	5.1	2.38	48.76	72.28	
Nov. 15	4.8	3.89	74.98	298.63	
Nov. 23	8.0	1.35	35.75	301.71	11.90
			146.29	810.24	
			168.77	770.54	
Dec. 07	3.5	5.60	55.11	422.94	
Dec. 10	5.0	5.12	52.00	228.18	15.44
			37.56	293.91	
			50.39	650.39	

Temperature in degrees centigrade, day light in arbitrary units from planimetry of area under day light trace on pyrheliometer recorder, chlorophyll in mg.m^{-2}, and particulate and extracellular production in mgC.m^{-2}.d^{-1}.

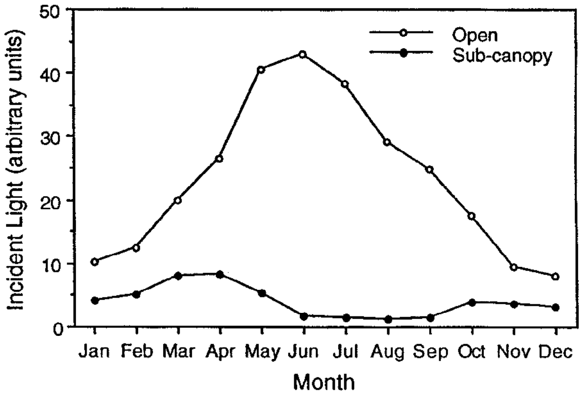

Figure 1. Average solar radiation received (arbitrary units from recorder) during each month at experimental site in Sandy Run. Open circles represent daily means from a station unaffected by canopy, and closed circles represent daily means from a station at stream side.

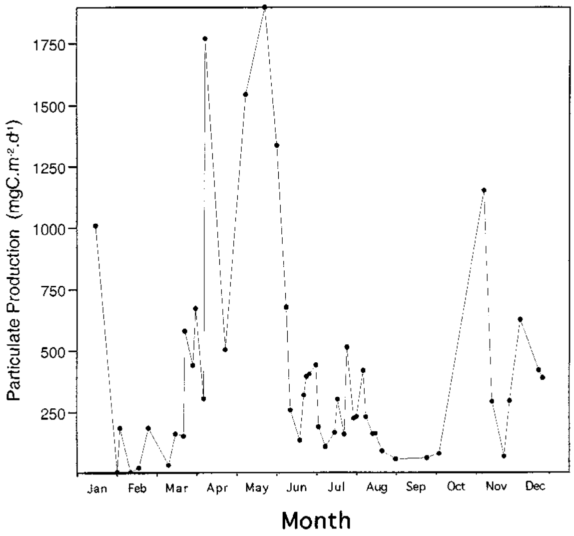

Figure 2. Mean daily particulate production (mgC m^{-2} day^{-1}) measured in Sandy Run.

reduction of sunlight during the winter when leafless branches and stems reduced measured sunlight to about 40% of open sun. Mean daily incident sunlight taken from our continuous measurements for each month in the open and at the stream surface are shown in Figure 1. The light environment in the stream was most favorable for autotrophic production from February to May, and least favorable during the summer. Compared to open sunlight, the light environment in the stream had lower variance.

Algal biomass measured as chlorophyll *a* varied from 0.4 to over 500 mg Chl m^{-2} . Highest concentrations were typically found in the spring before the canopy filled in, and again in the fall. Lowest concentrations were found in the summer, and sporad-

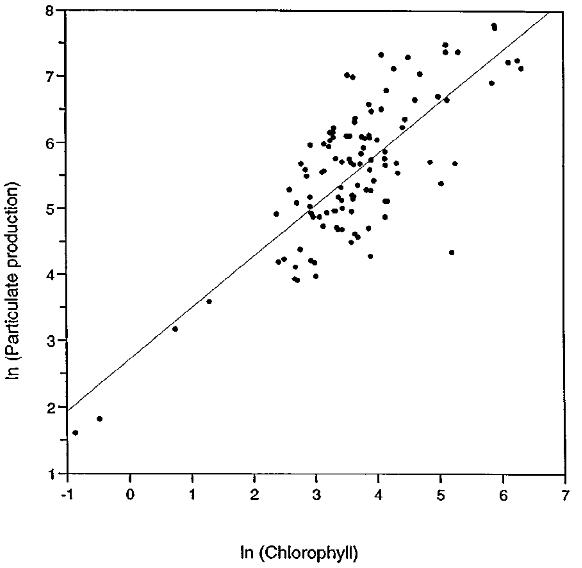

Figure 3. Relationship between ln (chlorophyll, mg m^{-2}) and ln (particulate production, (mgC m^{-2} day^{-1})). Regression equation: ln (particulate production) = 2.71 + 0.78 ln (chlorophyll). $r^2 = 0.60$, $p < 0.001$, $n = 113$.

ically in the winter due possibly to low temperatures and ice scour. Measured rates of particulate primary production varied from 2.3 to almost 2400 mgC m^{-2} d^{-1} (Figure 2). Highest measured rates were found in spring and in the fall.

Annual distribution of production

To illustrate the importance of winter photosynthesis our intention was to construct a model that would predict daily production rates from continuous measurements of light, and measured and interpolated values for temperature and chlorophyll (e.g., Busch & Fisher, 1981). Both ln (light) and ln (chlorophyll) were significantly correlated with ln (production) ($r = 0.29$, $p < 0.01$, and $r = 0.78$, $p < 0.001$, respectively). Ln (temperature), however, was not significantly correlated with ln (production). In a step-down multiple regression model, both ln (temperature) and ln (light) were eliminated, and the best predictor of ln (production) was

$$\ln \text{ (particulate production)} = 2.71 + 0.78 \ln \text{ (chlorophyll)} \quad r^2 = 0.60, p < 0.001, n = 113. \tag{1}$$

This relationship is shown in Figure 3.

Since this model does not make use of continuous light measurements, there was no advantage in using the model over simply estimating photosynthesis by interpolation between measured rates assuming monotonic increases or decreases. Using this latter approach, we predicted daily photosynthesis for 1 year. We estimate an annual autochthonous particulate photosynthetic contribution of 185 gC m^2. Highest predicted rates were found in May (month average, 1.6 gC m^{-2} day^{-1}) and the lowest in February, August and September (94–109 mgC m^{-2} day^{-1}). Daily rates were, in general, higher in the spring before canopy closure, and in the late fall after leaf abscission. Lowest rates were found in the winter and summer. We divided the year into four time periods. We defined winter (December–March) as that period of the year with short day length and low solar angle, but also with low attenuation through a leafless canopy. Summer (June–September) was a period with long day length, high solar angle, yet a completely closed canopy with high light attenuation. The remaining intervals (April–May, and October–November) were periods of increasing (decreasing) day length with increasing (decreasing) attenuation through the canopy. We found significant differences in measured particulate production during these intervals (ANOVA), but a multiple comparisons test indicates that there is no difference between winter and summer rates. These data are illustrated in Figure 4. About 26% of the estimated annual production occurred in the December to March interval. Only 13% of the estimated annual production occurred between June and September.

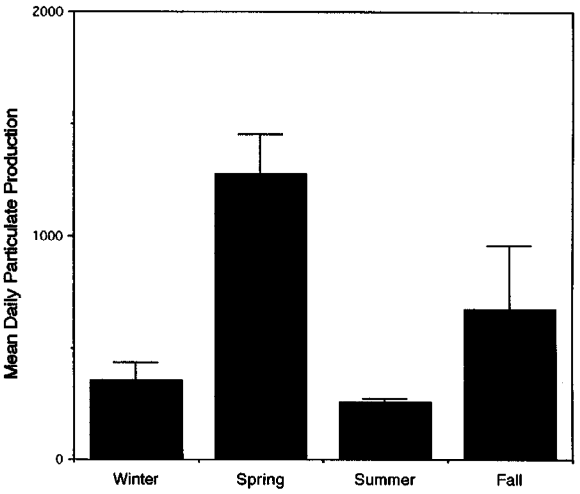

Figure 4. Means (± S.E.) for particulate production (mgC m^{-2} day^{-1}) measurements made during winter (Nov.–Mar.), spring (Apr.–May), summer (Jun.–Sep), and fall (Oct.–Nov.). Multiple comparisons test indicates: winter = summer < fall < spring.

Contribution of algal DOC

Calculated extracellular production of DOC for 33 experiments distributed across the year (Table 1) ranged from 3.15 to 146.96 mg C m^{-2} day^{-1} (1–35% of total autotrophic production). Ln (extracellular production) was strongly correlated with both ln (particulate production) and ln (chlorophyll) (r = 0.66, $p < 0.001$, and r = 0.50, $p < 0.01$, respectively), but not at all with either ln (light) or ln (temperature). Significant regression equations are:

$$\ln(\text{Extracellular DOC}) = -0.56 + 0.63 \ln (\text{Particulate production})\; r^2 = 0.43, n = 33, \quad (2)$$

$$\ln(\text{Extracellular DOC}) = 1.03 + 0.53 \ln (\text{Chlorophyll})\; r^2 = 0.25, n = 33. \quad (3)$$

The former relationship is shown in Figure 5.

To estimate the annual contribution of extracellular DOC to the carbon economy of the stream, we predicted DOC produced using Equation (2), and the monthly means of predicted particulate production . Predicted monthly averages ranged from 10 mgC m^{-2} day^{-1} in September to 59 mgC m^{-2} day^{-1} in May. The annual contribution is estimated to be 9.7 gC m^{-2} yr^{-1}, about 5% of the annual particulate production.

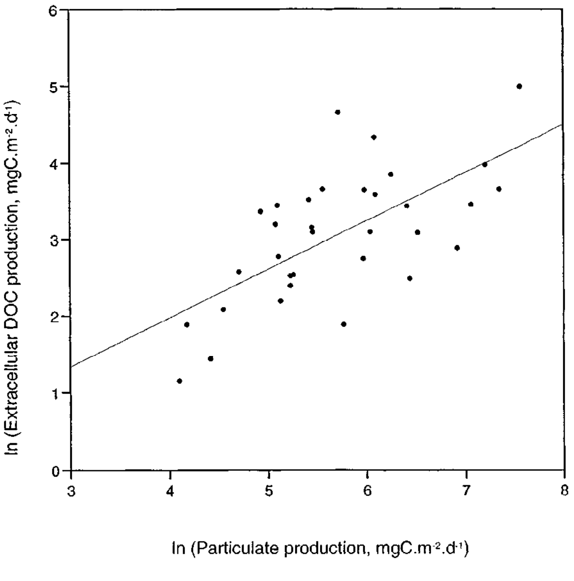

Figure 5. Relationship between ln (particulate production (mg C m^{-2} day^{-1})) and ln (extracellular DOC production (mg C m^{-2} day^{-1})). Regression equation: ln (extracellular DOC production) = –0.56 + 0.63 ln (particulate production). r^2 = 0.43, $p < 0.01$, n = 33.

Discussion

Sandy Run appears typical of low order forested streams in the Eastern Deciduous Forest Biome. The range of temperature, and the standing crops of algae are comparable to those reported for streams elsewhere (e.g. Hornick et al., 1981, Table 5; and Rosenfeld & Roff, 1991). In our empirical model (Eq. (1)) neither light nor temperature made any significant contribution to the prediction of particulate productivity. This observation is also common. In higher-order streams, light saturation probably explains a lack of correlation between light and productivity (Hill & Webster, 1982; Jasper & Bothwell, 1986). In low-order streams, productivity is more commonly correlated with chlorophyll *a* alone (Keithan & Lowe, 1985; Naiman & Sedell, 1980). It is possible that forested streams have relatively constant light environments (Figure 1), and that the primary cause of fluctuations in production is changes in algal biomass caused by periods of growth punctuated by burial or washout — both discharge related — or grazing. All of these causes are independent of light levels. As a result, it may not be possible to construct deterministic models of algal biomass given our inability to predict events causing variations in flow. The alternative is to measure biomass or productivity directly at frequent intervals.

Our data provide a compelling argument against the assumption that winter photosynthesis in inconsequential. Both our direct measurements of carbon assimilation, and interpolated monthly rates suggest that winter production is as important as summer production in the annual energy budget. High-standing crops of periphyton are common late in the fall and early winter, and available light is greater than at any time since before the canopy closed the previous spring. Further, if autochthonous carbon inputs are estimated from only a few measurements made in the summer, then the spring and fall periods of peak productivity are missed. Annual particulate production in Sandy Run is about 35% greater than our estimates would be had we measured particulate production from April through November and assumed minimal productivity during the winter months as is more common practice (Fisher & Likens, 1973; Hornick et al., 1981; Keithan & Lowe, 1985; Rosenfeld & Roff, 1991).

The measurement of extracellular dissolved organic matter is a common procedure in studies of planktonic photosynthesis, but does not seem to have been adopted for stream studies. Baines & Pace (1991) compiled data from a number of marine and limnetic studies and found that extracellular release ranged from <1 to 75% of particulate production in sample data, and from 3 to 40% when whole systems were considered. The production of extracellular DOC by plankton, then, is a significant component of total autotrophic production. Our results for Sandy Run indicate a similar sample range (1–35%) and a system average of 9% (standard error 1.2%). That extracellular DOC might be an important component of primary production in streams seems to have been considered only by Fisher (1977). While the contribution of extracellular DOC is included in productivity estimates using the oxygen technique, we could find no reference to its having been measured in any stream study using the ^{14}C technique. Combining the effects of winter particulate production, and year round production of extracellular DOC, the total autotrophic contribution to the carbon budget of Sandy Run is almost 41% greater than April to November measurements would indicate.

Could such an increase in our estimate of autochthonous carbon alter our perception of the carbon economy of low-order stream ecosystems? In many cases, even a doubling of estimates of autochthonous carbon production will not alter the conclusion that allochthonous carbon from litterfall, throughfall and groundwater is the larger contributor to stream carbon budgets (Webster & Meyer, 1997). In Sandy Run, however, annual litterfall and throughfall contribute 143 and 2.4 gC m^{-2} yr^{-1}, respectively (D. Weigel, C. Hasselback, unpublished data), so that autochthonous sources provide about 57% of the total carbon. Nonetheless, even in streams where the autochthonous carbon contribution is substantially less, any calculations of community efficiency, or projections of the size or activity of the next trophic level will be more reliable with more accurate assessment of autotrophic production. Further, there are numerous references indicating that fresh algal material may be of higher quality, is often preferred over allochthonous detritus (Anderson & Cummins, 1979; Mayer & Likens, 1982) and when dislodged is harvested with greater efficiency than allochthonous FPOC (Webster, 1983). It has also been well documented that algal extracellular DOC is readily and rapidly used by aquatic bacteria (Cole et al., 1982; Kaplan & Bott, 1985), whereas much of the DOC from throughfall and leaf leachate is more refractory, and is probably exported unused (Lock & Hynes, 1976). These observations suggest that the contribution of autochthonous carbon to stream energy budgets may be greater than simple mass comparisons would indicate.

We suspect that our results have general significance but we recognize that locations at higher elevations and latitudes may have more severe winter conditions with prolonged ice and snow covering low-order streams. Sandy Run has sufficient discharge that the riffle portions of the stream channel are open in all but the most severe winter periods. We do feel that by assuming winter periphyton production is insignificant, however, and by failing to consider extracellular production of DOC, the autochthonous contribution to the carbon budgets of many low order forested stream communities may have been seriously underestimated.

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