Oecologia (Berl.) 21, 131—139 (1975)

Energy Flow and Organic Matter Decomposition in an Abandoned Beaver Pond Ecosystem

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Received June 14, 1975

Summary. A beaver pond can be considered an open ecosystem with a number of energy inputs and outputs. The net difference between input and output represents the accumulation of energy within the system. During 1973 input-output parameters were measured independently for one spring fed pond (surface area 736 m^2) in the Kananaskis Valley, Alberta, Canada. The yearly energy budged indicated that allochthonous energy inputs into the pond were much greater than autochthonous inputs. Of the total yearly energy input 18% was exported, 26% was respired and 56% accumulated in the sediments. This percentage utilization for respiration was low when compared with similar data from the literature for five aquatic ecosystems elsewhere. However the actual annual mean sediment respiration rate of 8.4 ml m^{-2} hr^{-1} compared favourably with the figure of 6.1 ml m^{-2} hr^{-1} predicted from Hargrave's 1969 respiration equation for benthic communities. This situation suggests that the allochthonous input, while dominant, is highly refractive and rapidly becomes locked up in the sediments. The high photosynthesis-respiration ratio of 0.81 together with the results of earlier litter bag experiments (Hodkinson, 1975) support this conclusion. Thus the beaver pond is a highly accretive heterotrophic ecosystem.

Introduction

Previous papers have examined the rate of organic matter breakdown in an abandoned beaver pond ecosystem and the role of the benthic insect communities in this process (Hodkinson, 1975a, b). This paper is an attempt to produce a balance sheet which illustrates, on a gross scale, energy dynamics within the pond system.

One can consider a pond to be an open ecosystem with a number of energy inputs and outputs. Energy inputs include drift of particulate and dissolved organic matter in input streams, litter fall, marginal vegetation, pushed into the pond by snow, photosynthesis, and surface runoff. Energy outputs include drift of particulate and dissolved organic matter in the output streams, and respiration. The net difference between energy input and output represents the accumulation of organic matter in the sediments. This overall energy budget is summarised in Fig. 1. During 1973 an attempt was made to measure independently each of these parameters for one pond over a one year period.

Study Area

This study was made on a series of abandoned beaver ponds in the Kananaskis Valley, Alberta, Canada (51° 2′N, 115° 2′W), previously described in detail by Pritchard and Hall (1971). All data presented in this paper relate to the Middle Pond.

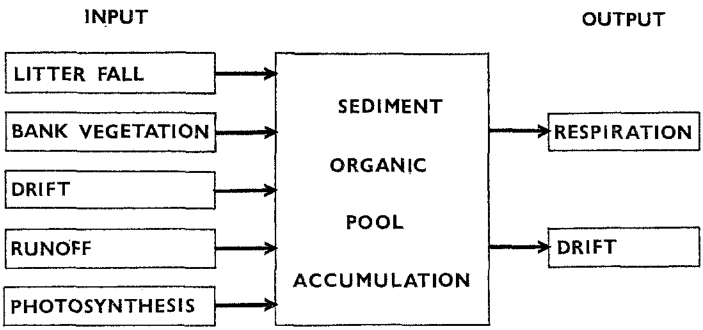

Fig. 1. Energy budget model for the Middle Pond showing major input and output parameters

Certain important features of the pond system are worth re-emphasising. The pond system is spring fed and consequently the throughput of water, and hence the water level, remains constant throughout the year. Furthermore the pond system lies in a discrete basin and surface runoff into the system is minimal. Water enters the Middle Pond via two feeder streams and leaves via a single well-defined breach in the old beaver dam. The Middle Pond (area = 736 m^2) is thus an ideal system in which inputs and outputs can be monitored comparatively easily.

The dominant vegetation around the margin of the Middle Pond is *Juncus tracyi* Rydberg and *Deschampsia cespitosa* (L.) Beav. *Salix* spp. grow profusely along the old beaver dam. The streams entering the pond pass through *Picea glauca* (Moench) Voss forest and thus much of the organic drift into the pond is of coniferous origin. Because of its position in a hollow, the Middle Pond receives substantial amounts of wind-blown litter from the surrounding area.

Methods

1. Litter Input. Aerial litter input was measured using 21 circular litter traps of 0.17 m^2 surface area, arranged on a stratified random grid over the surface of the pond. Trial sampling during the previous year had indicated that litter input was highest, as expected, around the pond margin. Therefore, for sampling purposes, the pond was divided into 3 areas:

1. a 5 m strip adjoining the dam,
2. a 5 m strip around the rest of the margin, and
3. a central area.

Litter traps were emptied at approximately fortnightly intervals and the litter from each was sorted into nine components, dried at 105° C for 24 hrs, and weighed. The nine components were: *Salix* sp. leaves, *Pinus contorta* Louden needles, *Picea glauca* needles, bark, *Pinus contorta* male strobili, twigs, bud scales, other herbaceous litter, and miscellaneous. Input of each litter component was then expressed in energy units per square metre using the appropriate energy equivalent (Table 1) and the data for each trap were summed for the whole year.

2. Bank Vegetation. At the beginning of each winter a certain amount of vegetation was pushed into the pond by the first heavy snowfall. The amount of such vegetation was measured by a harvest method, along twenty randomly selected linear metre lengths of bank. Marginal vegetation was densest along the dam and the sampling procedure was stratified accordingly.

Samples were sorted into species (*Juncus tracyi*, *Deschampsia cespitosa* and other), dried at 105° C for 24 hrs and weighed. A certain weight loss due to leaching in the water would be expected but this was small (Hodkinson, 1975a) and has been ignored.

Table 1. Energy content of organic inputs

Material	n	Energy content ($Kj\ g^{-1}$)	S.E.
Juncus tracyi	3	18.046	0.205
Pinus contorta needles	3	20.829	0.092
Picea glauca needles	3	20.398	0.067
Salix	3	19.954	0.109
Bark	5	19.871	0.117
Twigs	2	20.294	0.121
Deschampsia cespitosa	4	17.443	0.126
Pinus male strobili	2	20.235	0.435
Other herbaceous	3	20.180	0.201
Drift Input 1	9	11.674	0.075
Drift Input 2	8	13.002	0.105
Drift Output 1	7	12.999	0.113

3. Organic Drift. Drift input of particulate organic matter was measured for the two input and one output streams using drift nets of 30 cm width and 210 μ mesh size. These nets were calibrated against both depth and current velocity. Trial studies showed that the efficiency of these nets declined, due to clogging, after 2 days and therefore drift was sampled over 1 day periods. The narrow range of drift estimates obtained on different dates reflected the constant throughput of water and there was no significant correlation between drift and rainfall. Particulate drift was sampled on 24 occasions during 1973. An estimate of the yearly total for each stream was obtained by plotting the amount of drift collected against date and integrating the area under the curve (Fig. 2).

A mesh size of 210 μ does not catch all the particulate organic matter. Therefore samples of water which had passed through the drift net were analysed on six occasions for particulate and dissolved organic carbon. Even though seasonal differences were apparent it was not possible to demonstrate differences between the input and output streams. A similar situation was observed by Fisher and Likens (1973) in Bear Brook, New Hampshire. Wetzel and Manny (1972) showed that the T_{50} for the decomposition of refractive dissolved organic compounds leached from leaves was 80 days. As the retention time of input water in the pond was much less than one day, and as most of the pond organic matter (*i.e.* drift) was preleached before deposition, it is not surprising that differences were not measurable. Thus for the sake of this paper it must be concluded that the two are equal and can therefore be ignored. This may, however, have led to quite large errors as non-measurable differences can be greatly magnified when one considers the total volume of water passing through the system in 1 year. However one might expect the pond to act a settling tank for small particulate organic matter and the rate of input should be greater than the rate of output. The overall effect should therefore be to understimate rather than overestimate the total net input of at least the particulate organic drift.

4. Energy Content of Material. The energy content of all organic inputs and outputs was determined using a Parr bomb calorimeter.

5. Surface Runoff. No attempt was made to measure organic input in surface runoff since it was assumed to be negligible.

6. Respiration and Photosynthesis. Respiration and photosynthesis were estimated in situ using a modification of the light and dark bottle technique. Sediment respiration was measured using 45 cm long, black glass cylinders of 51.25 cm^2 cross sectional area which were pushed into the sediment, sealed, and left for 24 hrs. Each whole cylinder with sediment core and water column intact was then removed from the pond and the enclosed water column stirred gently using an integral stirrer. Oxygen concentration in replicate samples from the water column (a check on adequacy of stirring) was then measured using Carpenter's modification of the Winkler technique. The difference between the mean of these values and the original

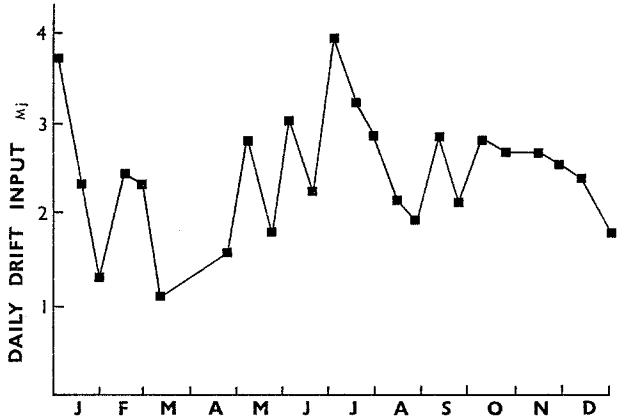

Fig. 2. Organic particulate drift estimates for input stream 2 during 1973

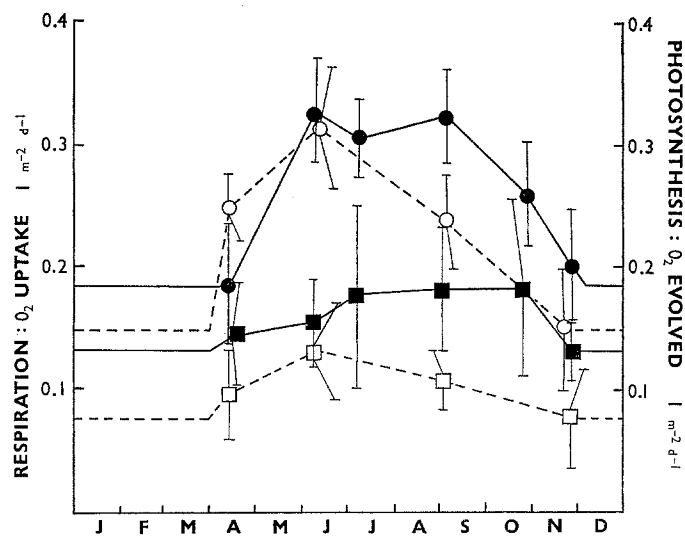

Fig. 3. Respiration and photosynthesis data for the Middle Pond during 1973: •——• respiration area B, ▪——▪ respiration area C+D, o---o photosynthesis area B, □---□ photosynthesis area C+D

oxygen concentration of the water was used to estimate respiration. Photosynthesis was measured in a similar manner, as the difference between net respiration in a black cylinder and in a clear glass cylinder.

In certain deeper areas of the pond the respiration chambers were insufficiently long to enclose an entire vertical column of pond water plus sediment. However trial studies showed that respiration and photosynthesis in the water itself was negligible when compared with photosynthesis and respiration of the sediments, *i.e.* epipelic algae were the dominant producers Thus the errors involved in disregarding a certain volume of the water column were minimal.

For the purpose of measuring respiration and photosynthesis the pond was divided into two areas: first the area where drift deposition of coniferous material occurred and second the area relatively unaffected by such deposition. These correspond to areas B and C+D

Table 2. Drift, bank vegetation and litter input data for the middle pond during 1973. Error terms are 95% confidence intervals

Drift

Stream	Total yearly drift (*Mj*)
Input 1	1972
Input 2	870
Output 1	741

Bank vegetation

Location	% Composition			Yearly input g per m length of bank	Total yearly input (*Kj*)
	J. tracyi	*D. cespitosa*	other		
Dam	51.0	46.6	2.4	53.1 ± 20.0	49954
Remainder of bank	69.4	30.6	0.0	13.3 ± 6.6	28604
				Total	78558

Litter input

% Composition	Area		
	1	2	3
Salix leaves	74.2	6.5	6.5
Pinus contorta needles	5.5	5.7	45.1
Picea glauca needles	5.1	11.2	22.3
Bark	3.1	40.4	13.4
P. contorta ♂ strobili	1.6	4.9	8.3
Twigs	7.9	21.9	0.4
Bud scales	0.5	6.1	2.3
Other herbaceous	1.2	1.2	0.5
Miscellaneous	0.9	1.8	1.0
Yearly input (Kj m^{-2})	561 ± 190	331 ± 135	74 ± 19
Total yearly input (*Kj*)	131068	101508	14436
Total	input (*Mj*) = 247		

described by Hodkinson (1975b). Respiration was measured in each of these areas on six occasions during 1973, but photosynthesis was measured on only four occasions. No measurements were made during the periods January-March, and December as the pond was covered by a thick layer of ice.

Total yearly respiration and photosynthesis were estimated by expressing each on a square metre basis, plotting against time, and integrating the area under the curve (Fig. 3). The lowest yearly estimates were extrapolated to cover the winter period for which no data were available. Equivalents of 19.67 j ml^{-1} and 20.97 j ml^{-1} were then used to convert respiration and photosynthesis, measured as volumes of oxygen into energy units. All data were then expressed on a total pond area basis.

Table 3. Respiration and photosynthesis data for the middle pond during 1973

Area	Respiration $Kj\ m^{-2}\ y^{-1}$	Photo-synthesis $Kj\ m^{-2}\ y^{-1}$	Total respiration (Mj)	Total photo-synthesis (Mj)	$\frac{P}{R}$
B	1097	731	386	257	0.67
C+D	1776	1594	682	612	0.90
Total			1068	869	

Table 4. Estimated total energy flux through the Middle Pond (736 m^2 surface area) during 1973 and calculated ratios of input-output parameters

Input (Mj)		Output (Mj)	
Drift	2842	Drift	741
Litter fall	247	Respiration	1068
Marginal vegetation	79		
Photosynthesis	870		
Total	4038		1809

Total net input, sediment accumulation (input—output)	= 2229 Mj
Total gross input (input—drift output)	= 3297 Mj
Photosynthesis/gross input (%)	= 26
Respiration/gross input (%)	= 32
Photosynthesis/respiration (%)	= 81

Results

Energy content values for organic inputs and outputs are given in Table 1, Drift data, bank vegetation input data and litter input data are summarised in Table 2 and respiration and photosynthesis data are summarised in Table 3. An energy balance sheet for the pond system is presented in Table 4, together with certain ratios of input/output parameters. Results have been expressed primarily on a whole pond basis as the different sampling stratification systems used for the estimation of different parameters do not readily permit meaningful comparison between sub-areas of the pond.

The low respiration-gross input ratio of 32% (Table 4) shows that organic matter was entering the pond at a much greater rate than it was being broken down, and was therefore rapidly accumulating in the sediments. Furthermore the photosynthesis-gross input ratio (Table 4) was similarly low (26%) indicating that energy fixed within the pond contributed little to the total energy input, and that drift input of particulate organic matter provided the main energy input contribution to the system. This suggests that the pond system was predominately heterotrophic. However the photosynthesis-respiration ratio of 81% (Table 4) is approaching unity, a situation one might not expect in such a heterotrophic system. This probably indicates that the bulk of the allochthonous organic matter entering the pond rapidly becomes locked up in the sediments and is only decomposed very slowly. The very slow breakdown rates of the more refractory types of litter suggest that this is probably the case. (Hodkinson, 1975a). This view is also supported by the fact that the sediment respiration rate in the area of drift deposition of coniferous material (B) is approximately half that in the area not markedly affected by deposition (C+D) (Table 3).

Discussion

The ratio of total community photosynthesis (P) to total community respiration (R) has been widely used to classify communities into autotrophic or heterotrophic types. This classification system works well for most closed terrestrial and aquatic ecosystems but does not adequately describe many aquatic 'ecosystems', which are open and dependent on imported organic matter as an energy source. Odum (1956) first recognised the importance of using energy import (I) and energy export (E) terms to qualify the above ratio and his ideas have subsequently been extended by Fisher and Likens (1973) who described the ecosystem in terms of the energy balance equation

$$I + P = R + E + \Delta S,$$

where ΔS is the change in standing crop of 'energy' within the system. For a steady state ecosystem $\Delta S = 0$: where ΔS is positive the ecosystem is accretive but where ΔS is negative the ecosystem is remissive. Thus using the Fisher and Likens classification the Kananaskis pond, with a P/R ratio < 1 and a $\Delta S > 0$, would be considered a highly accretive heterotrophic ecosystem.

In such a system the quality of input greatly effects the degree of heterotrophy, as measured by the P/R ratio. In the Middle Pond the major energy input is refractive coniferous material which is relatively unavailable for respiration. Community respiration is low in relation to total energy input and is largely balanced by photosynthesis. Thus the P/R ratio remains high and the system remains aerobic. However if the energy input was more biologically labile then community respiration would rise, the P/R ratio would fall and the system would tend to become oxygen deficient. Thus a high rate of accretion may prevent stagnation within a system dominated by allochthonous energy input. Sedell *et al.* (1974) have suggested that in heterotrophic streams detrital input is analogous to gross primary production in terrestrial ecosystems and similarly detritus respiration is analogous to autotrophic respiration. Thus ecosystem maintenance efficiency in such ecosystems can be defined as the ratio of detritus respiration to detritus input. Table 5 compares maintenance efficiency in 6 aquatic ecosystems; in each case input is defined as the sum of autochthonous and allochthonous particulate 'energy' input and respiration is defined as the sum of heterotroph and autotroph respiration. In Bear Brook, WS 10 Cascades, Cone Spring and Silver Springs at least 57% of the total energy input was respired. Of that remaining, a large proportion was exported and little or no energy accumulated within the system. In contrast the Kananaskis beaver pond was a more closed system and only 18% of the energy input was exported. However just 26% of the energy input was respired and energy accumulated rapidly. Root Spring had a similarly low level of export but a much higher R/I ratio and thus a lower rate of sediment

Table 5. Yearly mean ecosystem maintenance efficiencies for different aquatic ecosystems. Data from Odum (1957), Teal (1957), Tilly (1968), Fisher and Likens (1973), and Sedell *et al.* (1974). Tilly's energy budget does not balance and the R/I figures represent the probable range in which the true value lies

System	R/I %	E/I %	$\Delta S/I$ %
Bear Brook	63	37	0
WS 10, Cascades	59	23	17
Cone Spring	57–81	43	0
Root Spring	71	0	28
Silver Springs	92	12	0
Kananaskis Pond	26	18	56

accumulation. Therefore on a comparative scale the degree of input utilization within the Kananaskis Pond was extremely low. However, Hargrave (1969) showed that benthic communities, from a wide variety of aquatic habitats, have similar rates of oxygen uptake when corrected for temperature differences. Applying his equation $\log_e(y) = 1.74\log_e(x) - 1.30$ (y = sediment O_2 consumption ml m^{-2} hr^{-1} and x = temperature °C), to the mean annual pond sediment temperature of 6°C one obtains a respiration rate of 6.1 ml m^{-2} hr^{-1}. This is slightly less than the actual value of 8.4 ml m^{-2} hr^{-1} measured for the pond. Thus the community respiration rate for the pond is not particularly low and this suggests that the system is, to a certain extent, swamped by inordinately large amounts of refractive allochthonous input.

Hodkinson (1975a), using a litter bag technique, recorded yearly decay coefficients (k values of Olson) of 0.12 to 0.98 for a range of litter types within the Middle Pond. By assuming that the total net input of energy per annum represents a starting value (W_o) and the sediment accumulation represents a final value (W_t) in the negative exponential decay equation $W_t = W_o\, e^{-kt}$, an approximate integrated estimate of k can be calculated for all litter types in the pond over a 1 year period. The k value of 0.39 thus obtained lies within the above range, although towards the lower end. This again emphasises the predominance of the more refractory types of litter input.

Acknowledgements. I thank Dr. J. B. Cragg for his constructive criticism during the course of the project, and Messrs. John Bogner, Colin James and John Corbin for technical assistance. The experimental part of the work was financed by a National Research Council of Canada grant to the Environmental Sciences Centre.

References

Fisher, S. G., Likens, G. E.: Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. Ecol. Monogr. **43**, 421–439 (1973)

Hargrave, B. T.: Similarity of oxygen uptake by benthic communities. Limnol. Oceanogr. **14**, 801–805 (1969)

Hodkinson, I. D.: Dry weight loss and chemical changes in vascular plant litter of terrestrial origin occurring in a beaver pond ecosystem. J. Ecol. **63**, 131–142 (1975a)

Hodkinson, I. D.: A community analysis of the benthic insect fauna of an abandoned beaver pond. J. Anim. Ecol. **44**, 535–553 (1975b)

Odum, H. T.: Primary production in flowing water. Limnol. Oceanogr. **1**, 102–117 (1956)

Odum, H. T.: Trophic structure and productivity of Silver Springs, Florida. Ecol. Monogr. **27**, 55–112 (1957)

Pritchard, G., Hall, H. A.: An introduction to the biology of craneflies in a series of abandoned beaver ponds, with an account of the life cycle of *Tipula sacra* Alexander (Diptera: Tipulidae). Canad. J. Zool. **49**, 467–482 (1971)

Sedell, J. R., Triska, F. J., Hall, J. D., Anderson, N. H., Lyford, J. H.: Sources and fates of organic inputs in coniferous forest streams. Integrated research in the Coniferous Forest Biome. Proceedings AIBS Symposium on Coniferous Forest Ecosystems. Conif. For. Biome. Bull. **5**, 57–69 (1974)

Teal, J. M.: Community metabolism in a temperate cold spring. Ecol. Monogr. **27**, 283–302 (1957)

Tilly, L. J.: The structure and dynamics of Cone Spring. Ecol. Monogr. **38**, 169–197 (1968)

Wetzel, R. G., Manny, B. A.: Decomposition of dissolved organic carbon and nitrogen compounds from leaves in an experimental hard-water stream. Limnol. Oceanogr. **17**, 927–931 (1972)

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