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Spatial heterogeneity and gradients of organic matter resources (OMR) in a second – order alpine gravel stream (the Oberer Seebach, Lunz, Austria)

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Abstract: The nature of the zoobenthos, retained bedsediment organic matter resources (SOMR), epilithic organic matter resources (EOMR) and other related aspects are presented. A transverse discontinuity in the distribution of the various taxa is evident. A patch formation of Nematoda is conspicuous on Site 13 and animal abundances on this site differed significantly with those on Site 14 (Mann-Whitney U-test = 37.0, $P < 0.05$) and Site 16 (U-test = 31.5, $P < 0.05$). Animal abundances in the overflow area and the area influenced by the debris dam indicated a significant difference between these two biotopes ($F_{(1, 14)} = 7.760$, $P < 0.05$). Total organic carbon and total nitrogen of SOMR showed quantity gradients along the cross-profile transect.

The decay rate of the leaves of *ACER pseudoplatanus L.* approximated well to the classical negative exponential decay curve. 50% weight loss (WL_{50}) occurred after 22.7 days, the decay coefficient ($-k$) and longevity being 0.033 and about 132 days respectively. The overall C/N ratios ($\pm 95\%CL$) were 26.39 ± 3.60 (SOMR), 16.19 ± 8.34 (EOMR) and 33.16 ± 3.45 (LOMR residuals). EOMR was of the highest food quality. The overall "resource ratio signature" for EOMR : SOMR : LOMR is 1 : 1.6 : 2.0.

Introduction:

Organic matter resources (OMR) in the bedsediment of streams normally act as energy sources for aquatic biocoenosis. Of these organic matter resources, allochthonous organic matter resources have been over-emphasized in the last three decades as the most important source of energy for the stream biocoenosis in low-order streams (HYNES 1963, LEICHTFRIED 1985) whilst overlooking the potentially important role played by the epilithon (biofilm). OMR include the retained organic matter in the bedsediment (SOMR), epilithic organic matter (EOMR) and even faunal organic matter. These occur in mosaic patches (HORN & MACARTHUR 1972) which fluctuate in time. Indeed, environmental patchiness is recognised as pervasive and fundamental to the distribution of organisms (ELTON 1966). OMR also form multidirectional quantity and quality gradients. An OMR gradient is hereinafter defined as "a spatial and dynamic multidirectional inclination of an OMR continuum, emanating from a clearly defined space, time and amount and dictated by the prevailing abiotic and biotic conditions. It implies that it can occur longitudinally, vertically and laterally or in any other definable direction and distance. It entails OMR responses along clines of physical and biological environments".

Many food resources have spatially clumped (patchy) distribution in nature. The consumer is expected to encounter the food patches at random (LEWIS 1980) and after depleting the best patch the consumer should migrate to the next highest in value. They also move to

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occupy empty patches and/or niches. This tendency to occupy empty patches can be experimented by the use of litterbags and even artificial substrate baskets (MATHOOKO & MAVUTI 1992).

The rate at which leaf litter organic matter (LOMR) is fed upon depends on their palatability and this also influences their longevity. A carbon/nitrogen ratio of 17, or lower, apparently is required by most animals in order to obtain an adequate source of nitrogen (RUSSELL-HUNTER 1970). There is paucity of information on the distribution of fauna in relation to the qualities of EOMR, SOMR and LOMR along the cross-profile of the Oberer Seebach. This paper therefore aims to elucidate the existence/non-existence of OMR gradients and patches, the autochthonous and allochthonous OMR nutritive values and, LOMR patch (island) colonization and decomposition in order to bridge some of the hiati which exist in our knowledge on these important ecological aspects of aquatic ecosystems.

The Oberer Seebach and study site

The Oberer Seebach is a second-order (STRAHLER 1957) alpine gravel stream and drains a 20km² karstic catchment. It originates from Obersee, disappears underground after a short distance, reappears as limnocrenes in Mittersee and drains into Lunzer Untersee (600 m a. s. l.). Lunzer Untersee (47° 15'N 15° 04'E) is situated about 100 km beeline, SW of Vienna (Austria) in the northern limestone fringe of the eastern Alps.

The bedsediment (channel forming sediments, dominated by epigeic faunal elements) is mainly limestones (84%) intermixed with a few dolomites and sandstones (LEICHTFRIED 1988). It is a typical summer cold stream with temperatures below 12.0°C. The annual mean temperature of the surface water is always close to 7.0°C (BRETSCHKO & LEICHTFRIED 1988). The study transect was situated in the Oberer Seebach 63.6m upstream of the RITRODAT-LUNZ Experimental Area (Fig. 1).

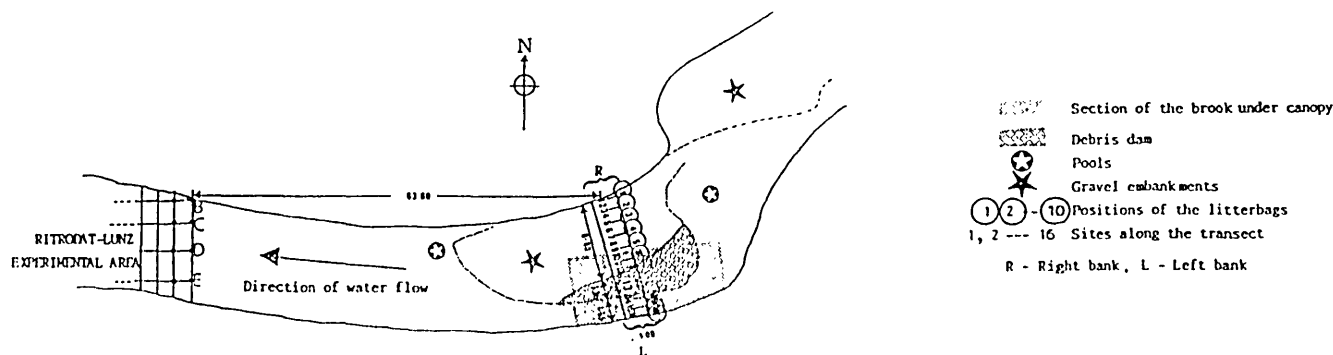


Figure 1: A sketch of the study site in the upstream of RITRODAT-LUNZ Experimental Area. (Not to scale; all units in metres)

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The transect was about 12.5m long and 1.0m wide, having a gravel embankment near the right bank and a debris dam towards the left bank. About 50% of it was shaded by a riparian vegetation canopy.

Materials and methods

FSI hemispheres (STATZNER & MÜLLER 1989), numbered 1 - 24, were used to determine the hydraulic stress. They provide a characterization of the water flow and turbulence conditions.

Sixteen samples for determinations of zoobenthic abundance, biomass and SOMR quality were collected about every one metre interval along a well delineated bedsediment cross-profile transect of the Oberer Seebach in July, 1991 using a modified Surber sampler with a working area of 0.0284m² (∅ 0.19m, mesh-size 80µm). 115 sediment materials (stones, pebbles, etc.) were also collected along the cross-profile to determine the quality of EOMR. The surficial 10 cm of the bedsediment were hand disturbed for about three minutes to collect the zoobenthos, SOMR and the stones and pebbles. The different zoobenthic taxa were sorted, identified, enumerated and separately oven-dried at 60°C for at least 24 hours and weighed to obtain the dry weight. Mann-Whitney U-test was used to test for differences between the sixteen samples. Green's coefficient of dispersion (GREEN 1966) was used to determine the existence of patchy distribution of the various taxa and ANOVA to test for differences between the zoobenthic distributional patterns in the overflown area and the area influenced by the debris dam.

The SOMR and EOMR were separately dried at 60°C for about 24 hours and then ground into a fine powder. Four fractions of about 10.0mg from each of the two organic resources were weighed. HC1 thinned 1:10 was added into two fractions of each of the two OMR to remove any inorganic carbon, filtered after one hour and the residue, together with the filter, put into a thin capsule and oven-dried at 60°C for further 24 hours. The dried organic matter was then burnt at 900°C in the LECO CHN-600 macroanalyser for total organic carbon (TOC) and total nitrogen (TON) determinations. The remaining two fractions from each OMR were analysed for total phosphorus (TOP).

The leaves of *ACER pseudoplatanus L.* were collected from the "dry store zone" to study the colonization, decomposition rates and longevity of the allochthonous LOMR. These leaves form the first leaf input into the brook as autumn approaches and also an early energy base for the bedsediment biocoenosis. The leaves were weighed into ten packs of about 15.0g and each pack put into a litterbag, mesh-size 0.5cm, mouth sewn and then put into a bigger bag of finer mesh (60µm). These litterbags were appropriately labelled LB1 - LB10 and placed serially across the transect with the mouths of the bigger bags facing upstream from August to September 1991. They were secured by tying them onto

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iron stakes and one litterbag randomly retrieved from the brook after every three days. Once retrieved, the residual leaf material was thoroughly rinsed of extraneous inorganic material and the invertebrates sieved using an 80 μ m mesh-size sieve, identified and enumerated. The animals and the leaf residuals were separately oven-dried at 60°C for at least 24 hours and then weighed to obtain the dry weight. The leaf residuals were ground into a fine powder. About 10.0mg of this powder were used for the determination of TOC, TON and TOP using the procedure described above. For comparison purposes, freshly plucked green leaves (FGL) and other freshly fallen leaves (FFL) collected from the "dry store zone" were analysed for TOC, TON and TOP. From the TOC and TON values, the C/N ratio, which is an indicator of food quality (HYNE 1978), was calculated. To calculate the decay coefficients (-k) of the leaves, the negative exponential decay model of HOWARD-WILLIAMS & DAVIES (1979) was used.

Results:

The cross-profile fauna was dominated by Chironomidae and Ephemeroptera (Fig. 2).

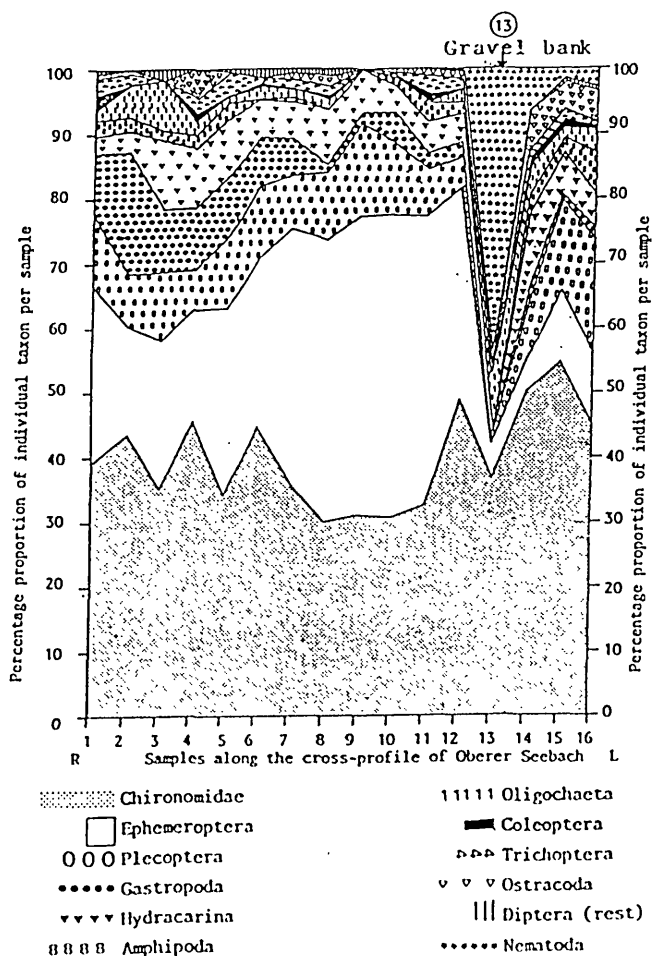


Figure 2: Percent variation of taxa along the cross-profile of the Oberer Seebach.

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This figure depicts the presence of a "depression" or a transverse discontinuity in the distribution of the various taxa. A patch formation of Nematoda is evident on Site 13 and animal abundances on this site indicated statistically significant differences between animal abundances on Site 14 (Mann-Whitney U-test = 37.0, $P < 0.05$) and on Site 16 (U-test = 31.5, $P < 0.05$). This emphasizes the role of emersion/immersion frequencies on animal distribution and abundance. Green's coefficient, as a measure of spatial heterogeneity, showed all taxa to have clumped (patchy) patterns of distribution along the cross-profile transect (Table 1).

| Taxa | Mean* \pm 95% CL | Green's coefficient of dispersion |
|----------------|---------------------|-----------------------------------|
| Plecoptera | 787.9 \pm 245.7 | 0.021 |
| Hydracarina | 471.0 \pm 126.1 | 0.016 |
| Chironomidae | 3163.1 \pm 783.1 | 0.013 |
| Diptera (rest) | 39.5 \pm 20.4 | 0.057 |
| Ephemeroptera | 2282.1 \pm 1052.1 | 0.047 |
| Oligochaeta | 173.9 \pm 78.0 | 0.044 |
| Amphipoda | 154.1 \pm 80.4 | 0.060 |
| Gastropoda | 380.8 \pm 160.5 | 0.039 |
| Coleoptera | 41.8 \pm 29.3 | 0.107 |
| Trichoptera | 112.3 \pm 45.1 | 0.035 |
| Ostracoda | 145.3 \pm 94.7 | 0.093 |
| Nematoda | 140.9 \pm 180.6 | 0.362 |

Table 1: Values for Green's coefficient of dispersion (* Mean number of animals per m^{-2} ; $n = 16$).

Analyses of variance on animal abundances in the overflowed area (Sites 1-9) and in the area influenced by the debris dam (10-16) indicated a significant difference between these two habitat zones ($F_{(1, 14)} = 7.760$, $P < 0.05$). Variations of animal abundances and biomass along the transect are indicated in Figure 3.

Figure 4 shows the variation of C/N ratio (SOMR), benthic animal abundances and hydraulic stress. The lowest C/N ratio (16.4) of the SOMR was on Site 11. TOC (SOMR) in the top 10cm was positively correlated with the sample sites ($r = 0.704$, $P < 0.01$) (Fig. 5a). A similar trend was indicated by TON (SOMR) ($r = 0.722$, $P < 0.01$) (Fig. 5b).

These elements showed quantity variations towards the left bank probably due to the accumulation of organic matter and debris from the riparian vegetation especially on Sites 14 - 16. TOP (SOMR) did not show the trend indicated by TOC (SOMR) and TON (SOMR).

The allochthonous LOMR have to be processed once they land on water and the conventional method of studying the processes is by the use of litterbags. The percent remaining dry weight (%RDW) of the leaves of *ACER pseudoplatanus L.* was decreasing with exposure time. Similarly, during the first three days of exposure, the decay

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rate was high and gradually decreased with exposure. The decay rate of the leaves approximates well to the negative exponential curve. To estimate the expected time when 50% of the leaves would disappear (WL_{50}), a cumulative curve of decay coefficients ($-k$)

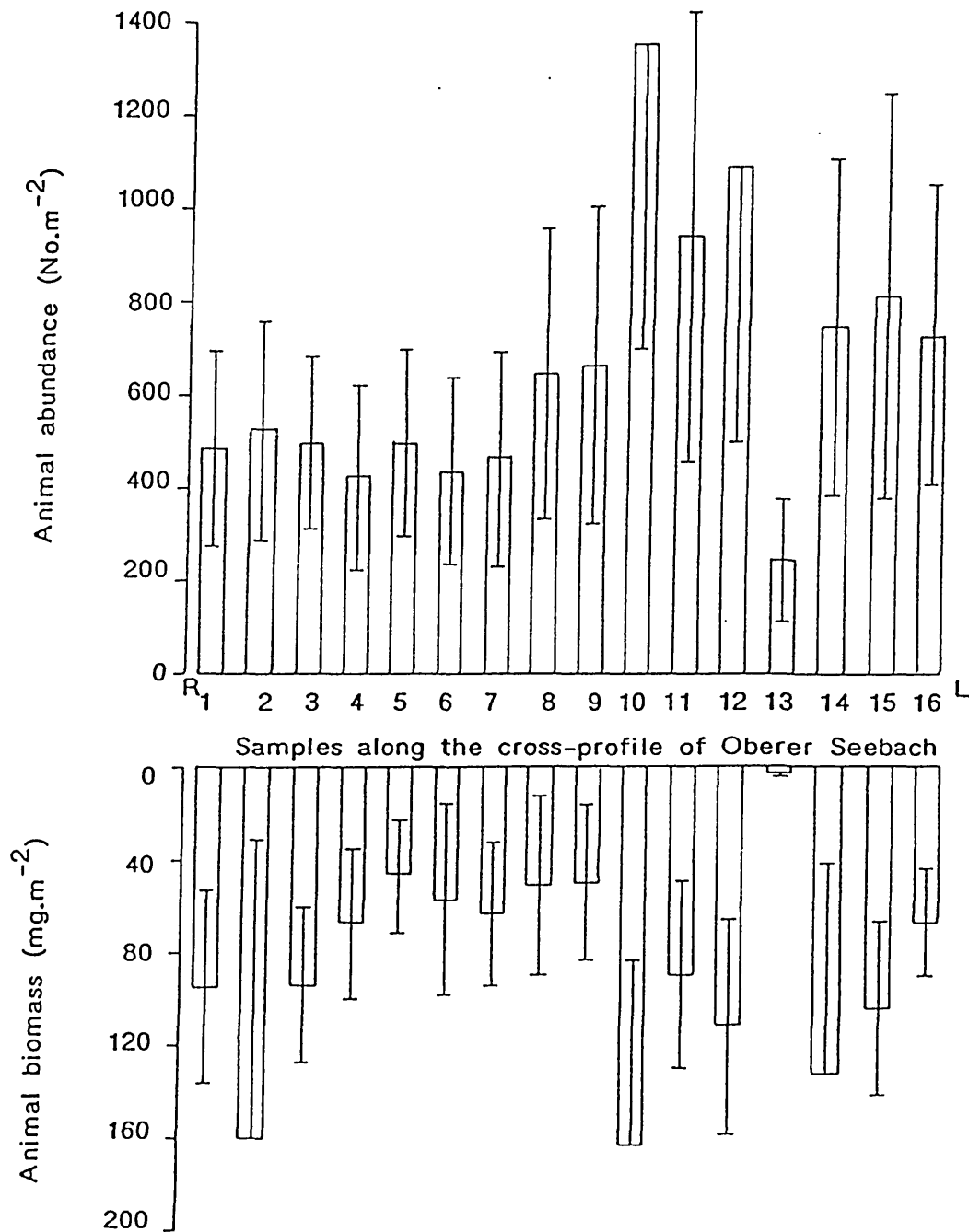


Figure 3: Variation of animal abundance and biomass along the cross-profile of the Oberer Seebach. Mean \pm S.E. ($n=12$), R = Right bank of the brook, L = Left bank of the brook.

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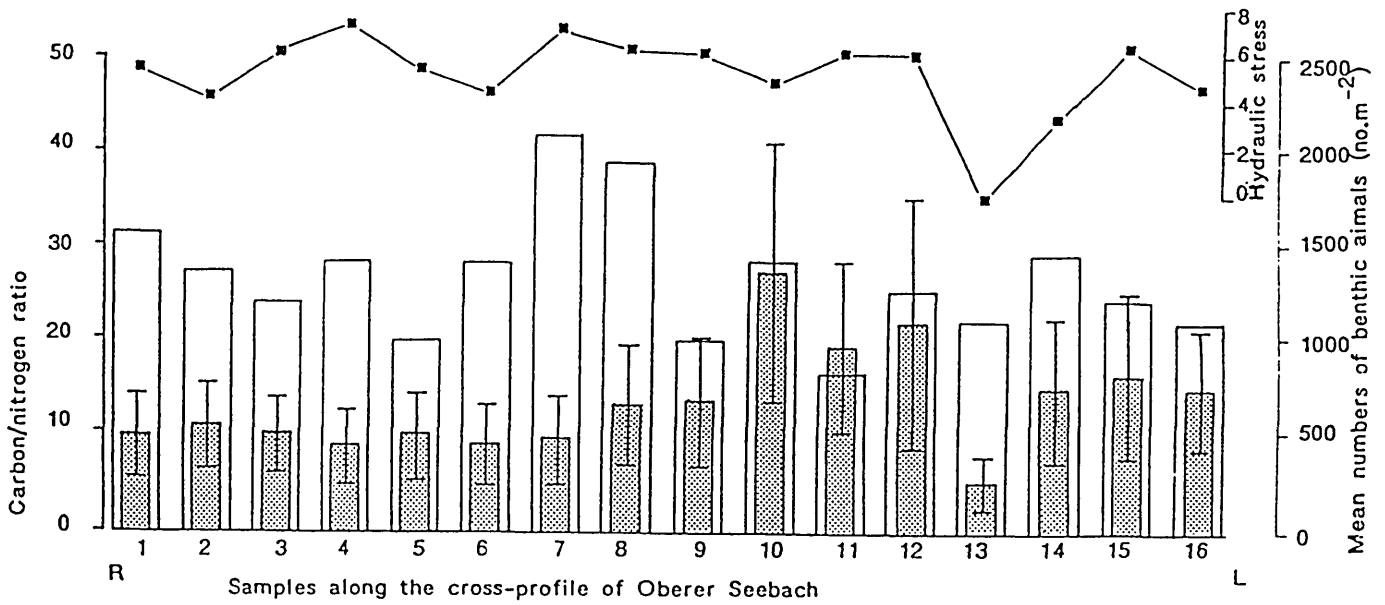
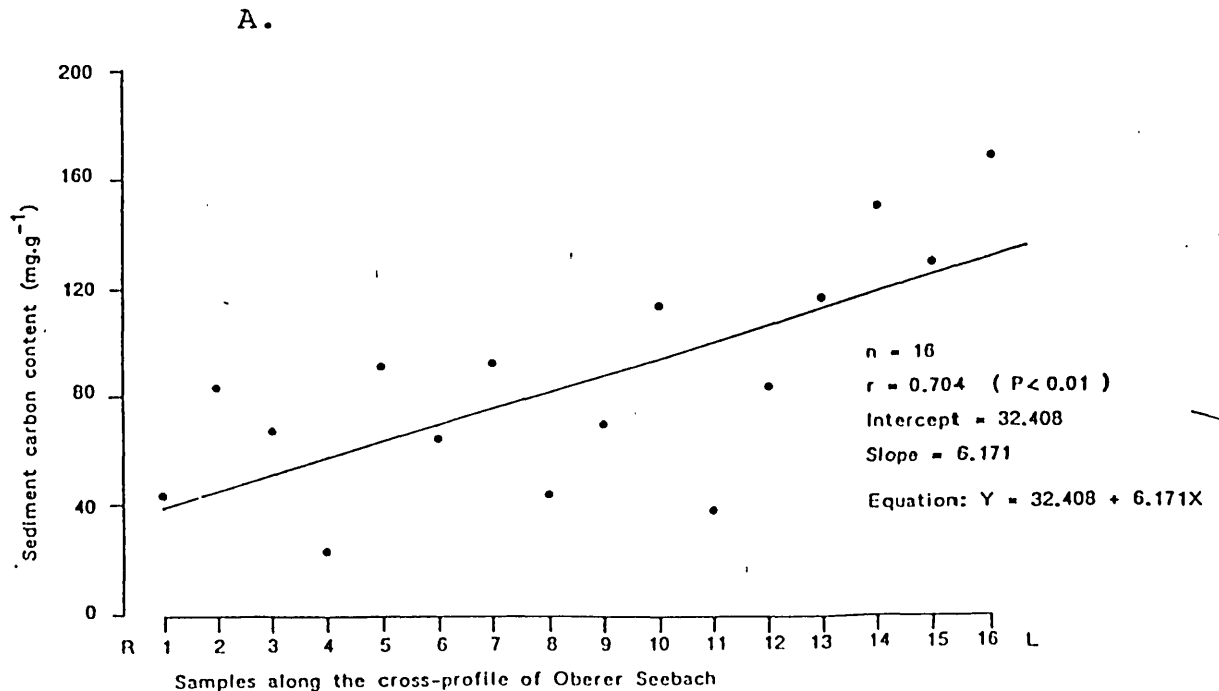


Figure 4: Variation of carbon/nitrogen (C/N) ratio, benthic animal abundance and hydraulic stress along the cross-profile of the Oberer Seebach. R = Right bank of the brook, L = Left bank of the brook.
 ■-■-■ Hydraulic stress (estimated using FSI Hemispheres) Checked bars - benthic animal abundance (Mean ± S.E, n = 12) Open bars - C/N ratio.

was plotted (Fig. 6). It reveals that WL_{50} would occur after 22.7 days. This agrees closely with the observed 21 days when 49.8% of the dry weight of the experimental leaves was



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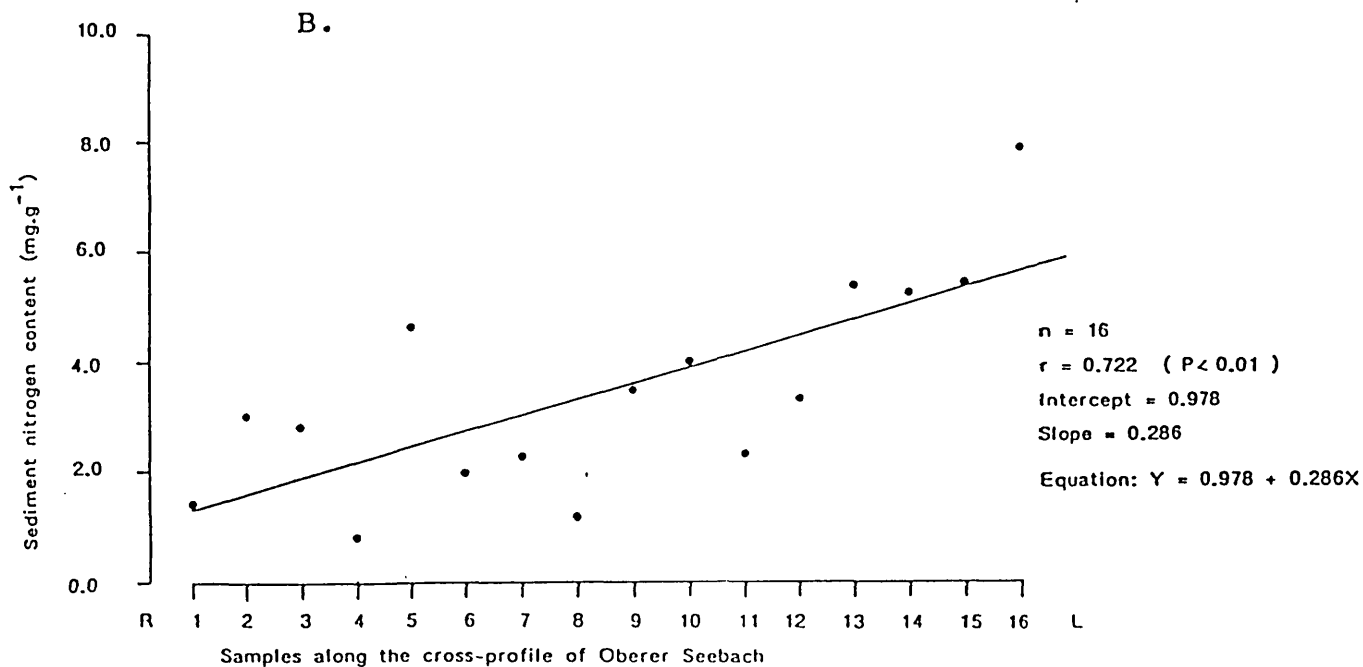


Figure 5: Relationship between sediment carbon (a) and nitrogen (b) contents and the sediment samples along the cross-profile of the Oberer Seebach. R = Right bank of the brook, L = Left bank of the brook.

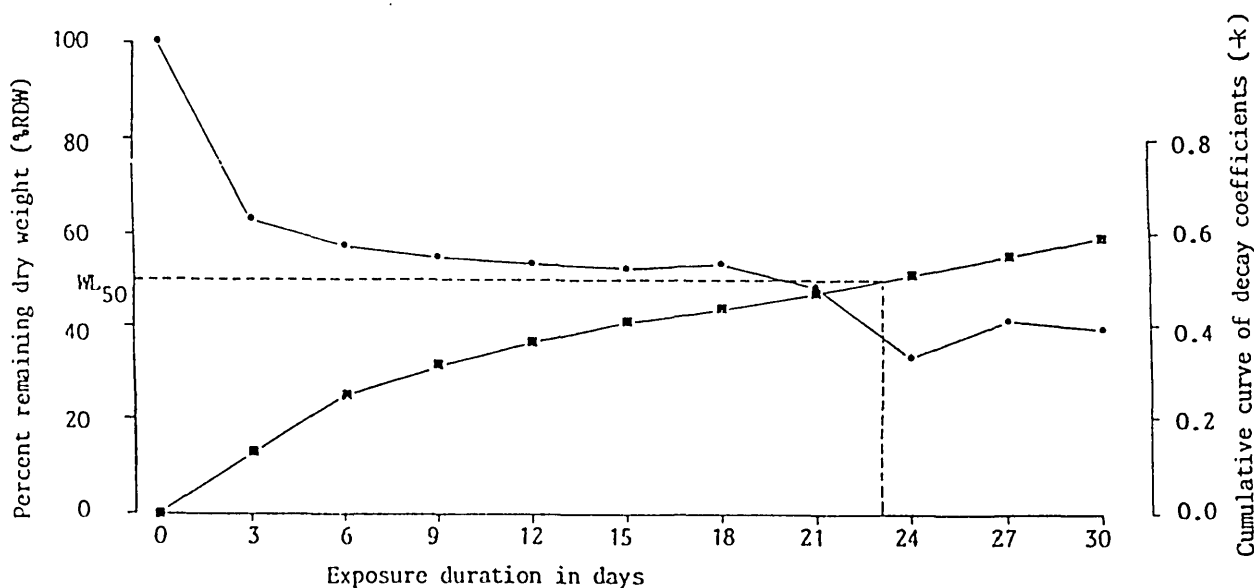


Figure 6: Percentage of remaining leaf dry weight in relation to the exposure duration and the cumulative curve of decay coefficients. WL₅₀ = Weight loss (50% of the leaf decomposed)

- Percent remaining leaf dry weight
- Cumulative curve of decay coefficients

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remaining (Table 2). The calculated $-k$ was 0.033 and WL_{75} , WL_{80} , WL_{99} , $WL_{99.9}$ were calculated assuming a monophasic decay rate. It was discerned that the leaves might have a longevity of 132 days (4.4 months) (see Table 3).

| Exposure duration (days) | Y_o (g) | Y_t (g) | % weight loss | $-k^*$ |
|--------------------------|-----------|-----------|---------------|--------|
| 3 | 15.06 | 9.51 | 36.85 | 0.153 |
| 6 | 15.03 | 8.61 | 42.71 | 0.093 |
| 9 | 15.02 | 8.27 | 44.94 | 0.067 |
| 12 | 15.02 | 8.11 | 46.01 | 0.052 |
| 15 | 15.03 | 8.04 | 46.51 | 0.042 |
| 18 | 15.00 | 8.15 | 45.67 | 0.034 |
| 21 | 15.01 | 7.48 | 50.17 | 0.033 |
| 24 | 15.00 | 5.10 | 66.00 | 0.045 |
| 27 | 15.07 | 6.05 | 59.85 | 0.034 |
| 30 | 15.09 | 5.96 | 60.50 | 0.031 |

Table 2: Weight loss and decay rates ($-k$) of the leaves of *ACER pseudoplanatus L.*

* Calculated using the negative exponential decay model (Howard-Williams & Davies, 1979)

$$Y_t = Y_o e^{-kt}$$

where Y_t = mass remaining at time t (days)
 Y_o = initial mass (g)
 k = decay coefficient (rate constant)

| Weight loss% (WL%) | %RDW | $-k$ | Duration (days) |
|--------------------|-------|-------|-----------------|
| * 50 | 49.83 | 0.033 | 21.0 |
| ** 50 | 50.00 | - | 22.7 |
| 75 | 25.00 | 0.033 | 42.0 |
| 80 | 20.00 | 0.033 | 48.8 |
| 90 | 10.00 | 0.033 | 69.8 |
| 99 | 1.00 | 0.033 | 130.3 |
| 99.9 | 0.10 | 0.033 | 131.5 |

Table 3: Leaf weight loss and the estimation of the longevity of the leaves of *ACER pseudoplanatus L.*

WL_{50} : * Experimental observation
 ** Obtained from the cumulative curve of decay coefficients
 %RDW: Percent remaining leaf dry weight

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An erratic increase in the decay rate ($-k = 0.045$) on the 24th day of exposure is observable (Fig. 7), about 1.4 times the preceding decay rate ($-k = 0.033$), a time when the animal biomass is also high, possibly due to the colonization of the leaf pack by high number of gammarids. The number of animals per gram of the remaining dry leaf weight increased with exposure time having a maximum value ($285.1 \text{ indiv.g}^{-1} \text{ RDW}$) on the 30th day of exposure. However, the animal biomass does not indicate a clearly defined trend

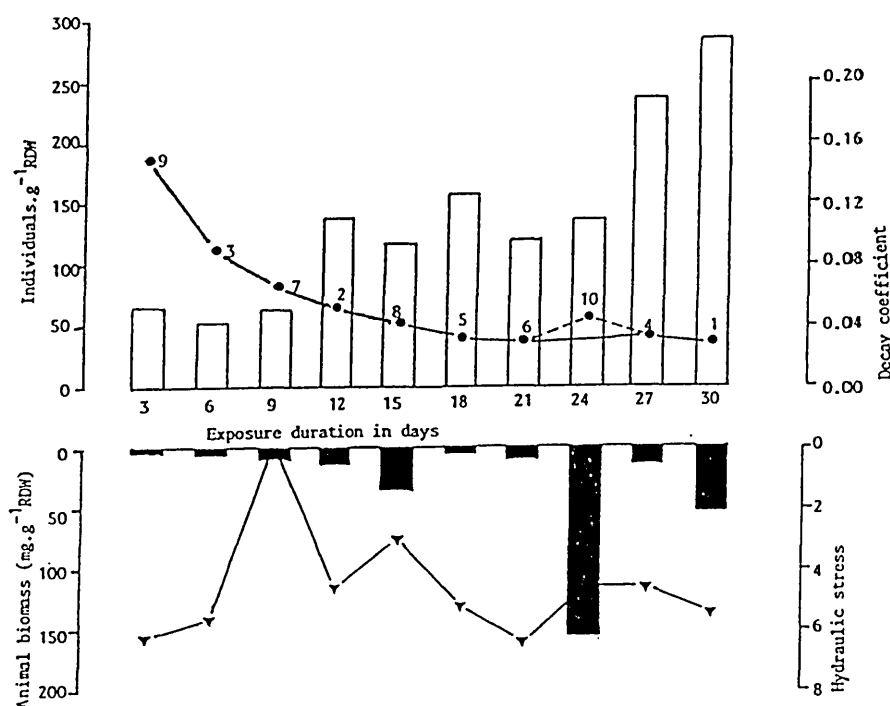


Figure 7: Leaf decay rates in relation to the animal abundance and biomass.

▲-▲-▲ Hydraulic stress (average FSI hemispheres) •-•-• Decay coefficients ($-k$)

Black bars - Animal biomass Open bars - Animal abundance

1-10 indicates number code of litterbag retrieved on that particular exposure duration, RDW - Remaining leaf dry weight

most possibly due to the zoobenthic size-class differences between successive sampling occasions.

Fresh green leaves (FGL) had higher TOP and TON than freshly fallen leaves (FFL). However, the results reveal that FFL had a slightly higher TOC probably as a result of some microbial colonization when the leaves were on the ground surface. The TOP (LOMR) showed a steady decrease with time. TOC (LOMR) also indicated the same trend although there seemed to be an initial increase when the leaves were exposed to the water current, biofilm formation being a plausible explanation. TON (LOMR) seemed to show two phases (Fig. 8).

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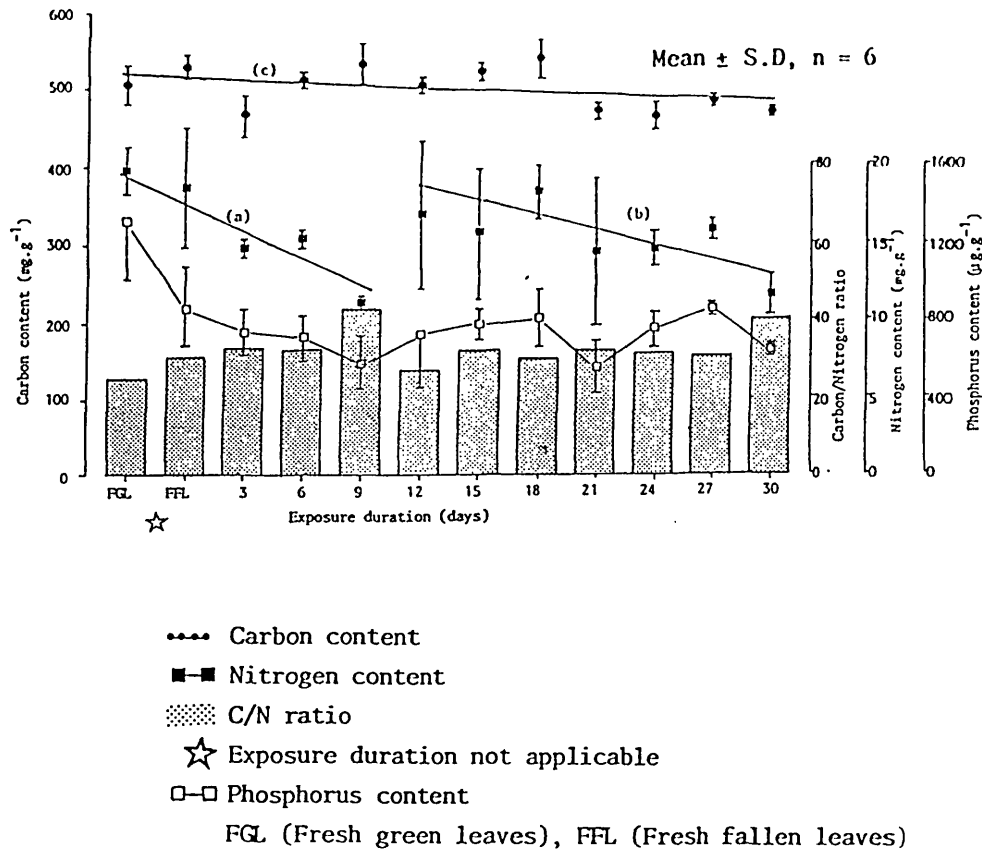


Figure 8: Variation of carbon content, nitrogen content, phosphorus content and C/N ratio in the leaves of *ACER pseudoplatanus* L. with exposure duration.

| | (a) | (b) | (c) |
|-----------|---------|---------|--------------|
| n | 5 | 7 | 12 |
| r | -0.837* | -0.812* | -0.458 (n.s) |
| Intercept | 17.847 | 22.018 | 514.921 |
| Slope | -0.585 | -0.304 | -1.268 |

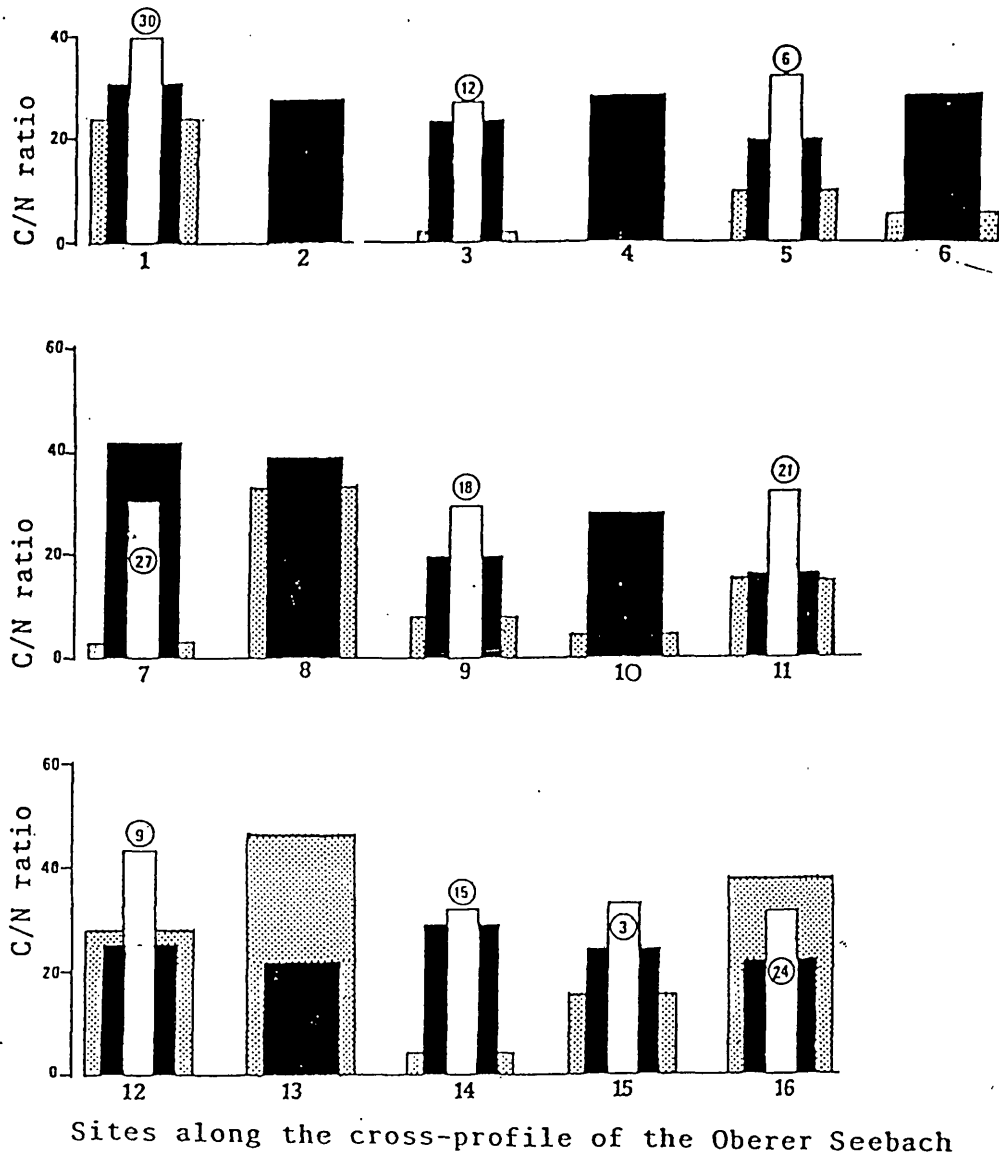
* P < 0.05

n.s - Not significant (P > 0.05)

The regression lines are fitted to show the unpredictable dynamism of the leaf nutritive status; the initial decline being as a result of leaching and a subsequent decline as a result of leaf utilization by the colonisers and the consequent reduced leaf quality as evidenced by the high C/N ratio on the 30th day. The C/N ratio (LOMR) ranged from 27.15 to 43.13. Leaching process seemed to take place up to the 9th day and this explains the increase in the C/N ratio (LOMR) up to this day after which the ratio declines shortly and subsequently oscillates around a steady level (31.90 ± 2.86, ±95% CL).

Figure 9 indicates the variations of SOMR, LOMR and EOMR C/N ratios along the cross-profile transect. The overall C/N ratios (± 95%CL) were 26.39 ± 3.60 for SOMR, 16.19 ± 8.34 for EOMR and 33.16 ± 3.15 for LOMR residuals. This indicates that EOMR is

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■ Sediment C/N ratio
 □ Leaf pack C/N ratio
 ▨ Epilithon C/N ratio

Figure 9: Variations of sediment, leaf pack and epilithon Carbon/Nitrogen ratios along the cross-profile of the Oberer Seebach:
 Encircled numbers indicate the exposure duration of the leaf pack:

of higher food quality than all the other OMR. EOMR : SOMR : LOMR ratios of the C/N ratios were calculated to indicate "resource ratio signatures" (Table 4). This gives an idea of the food quality options available to the aquatic biocoenosis. According to the "resource ratio signatures", the next food resource of high quality in the absence of EOMR would be SOMR. The overall "resource ratio signature" for EOMR : SOMR : LOMR is 1 : 1.6 : 2.0.

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| Sample Site | EOMR | SOMR | LOMR | Mean benthic animal abund. |
|-------------|------|--------|--------|----------------------------|
| 1 | 1 | : 1.3 | : 1.6 | 484.2 ± 208.7 |
| 2 | - | - | - | 525.3 ± 232.8 |
| 3 | 1 | : 15.4 | : 17.5 | 495.5 ± 186.8 |
| 4 | - | - | - | 428.5 ± 190.5 |
| 5 | 1 | : 3.3 | : 5.4 | 496.7 ± 199.5 |
| 6 | 1 | : 5.9 | - | 432.2 ± 206.1 |
| 7 | 1 | : 13.3 | : 9.6 | 463.5 ± 224.3 |
| 8 | 1 | : 1.2 | - | 643.6 ± 311.3 |
| 9 | 1 | : 3.2 | : 4.7 | 658.7 ± 341.6 |
| 10 | 1 | : 3.2 | - | 1346.9 ± 695.2 |
| 11 | 1 | : 1.1 | : 2.1 | 939.0 ± 472.5 |
| 12 | 1 | : 0.9 | : 1.7 | 1085.8 ± 587.6 |
| 13 | 1 | : 0.5 | - | 243.6 ± 129.0 |
| 14 | 1 | : 6.3 | : 7.1 | 748.3 ± 353.2 |
| 15 | 1 | : 1.7 | : 2.3 | 810.0 ± 427.0 |
| 16 | 1 | : 0.6 | : 0.8 | 727.7 ± 318.5 |

(Mean ± S.E, n = 12); Animal abundance (No. m⁻²)

Table 4: Resource ratio signatures for the Oberer Seebach based on the carbon/nitrogen ratios of epilithic organic matter resource (EOMR), sediment organic matter resource (SOMR) and leaf pack organic matter resource (LOMR) - (EOMR : SOMR : LOMR ratios), 29th July 1991.

Discussion:

According to models of foraging, a habitat patch will be used if feeding there yields a higher average rate of intake of food value, usually energy, than continuing the search with the expectation of encountering a richer patch of resources (PYKE et al. 1977). The existence of ephemeral archipelago of habitat patches in lotic ecosystems determines the distribution and density of stream biocoenosis. However, the response of biocoenosis to these patches will be not only to their richness but also to the biocoenoses' mobility.

Intermittent wetting and emersion of stream channel and distribution of the CPOM also influence the distribution of zoobenthos in stream biotopes. A transverse discontinuity existed in the distribution of animals in the Oberer Seebach as a result of the presence of a discontinuously flooded gravel bank. This possibly created an ecologically unstable environment for the animals, hence the low numbers encountered. Food is often assumed to be an important variable with patchy distribution (MORSE & FRITZ 1982). Clumped distribution of animals was evident in the present study perhaps due to the patchy distribution of organic matter food resources coupled with the existence of a discontinuously flooded area. Animal abundance was high in sites near the gravel bank due to the organic matter flocculent oozing out through the margins of the gravel bank. This organic matter ooze provides food to the animals hence their accumulation. It is also

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an area of low hydraulic regime reducing the danger of the animals being eroded away. Another factor is the retention of freshly fallen leaf materials which decay and release nutrients which are used as energy base by animals. This explains the high animal abundance in Sites 10, 11 and 12 which are adjacent to the gravel bank. The relatively low hydraulic regime and possibly low leaching rates might explain the relatively high food quality of the SOMR in Site 11. The presence of a debris dam in Site 14 and its corresponding high animal abundance than in Site 13 partially indicates that debris dam might be used as a refugium by the animals. A similar observation has also been made by KING et al. (1987).

The assertion that energy resource quantities as well as resource quality are distributed in discrete patches is verified when TOC (SOMR) and TON (SOMR) are considered. These showed significant accumulation gradients towards the left bank. The most plausible explanation is organic matter accumulation as the water recedes to the right bank, presence of debris dam and deposition of CPOM from the overhanging riparian vegetation. Because of the influence of physical instream structures and food quality of the SOMR, animal abundance showed a unimodal pattern, a distinct clumping towards the left bank, indicating a gradient in faunal distribution.

A common case of resource patchiness occurs when a habitat is divided into useable patches which are separated from one another by non-useable habitat (MERRIAM & FAHRIG 1985). Patches that are good for optimal foraging may accommodate a relatively large number of animals. In optimal patch utilization theory, the environment is assumed to consist of discrete patches with no resources between; hence the idea of using the leaf packets as organic matter "islands" or patches. The decrease of the weight of LOMR with increasing exposure agreed with the results of RICHARDSON (1990). Weight loss was high during the first three days, the period when leaching rate might have been high and this physical process might partially explain the initial high weight loss. Similar results have been noted elsewhere (e. g. KAUSHIK & HYNES 1971). The high weight loss on the 24th day of exposure could only be explained by the fact that this was the time when *Gammarus fossarum* increased in number in the leaf pack and possibly consumed part of the fraction in faster time. BERRIE (1976) reported similar observations. The longevity of the leaf material is important in connection with energy dynamics. Probably, the shorter the longevity the more useful the leaf would be as an energy source in the brook ecosystem. The estimated longevity of *A. pseudoplatanus* (4.4 months) might be attributed to several factors including leaf structure and resource level, faunal invasion/departure rates, distance of the leaves from potential colonisers and consumers and, the nature of the water system.

Leaf packs are fragile and ephemeral habitats and might be expected to have limited appeal to stream invertebrates (KING et al. 1987). However, invertebrates invade such

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habitats from the immediate bedsediment and/or from drift. The packs might have provided empty niches/patches, refugia or might have formed habitat islands of organic matter upon which the invertebrates could feed.

In the present investigation, it was found that the green leaves had higher TON than the freshly fallen leaves and those exposed to the water current. Along with the high TON content, MACARTHUR et al. (1986) found that green leaves contain higher amounts of TOP agreeing with the present results. The TOC in the fallen leaves was higher than that of the green leaves presumably due to some colonization by fungi/bacteria on the ground. The initial decrease in TON (LOMR) when the leaves were exposed to water current might have been due to leaching of the soluble proteins of the leaves. This can be understood as the first phase of the nitrogen content dynamics. After the leaching process, TON (LOMR) increased most probably as a result of biofilm formation. KAUSHIK and HYNES (1971) state that there is an increase in absolute density of nitrogen contents during decomposition due to fungi colonization. However, there was a second phase of TON (LOMR) decline seemingly as a result of the utilization of the leaves by the animals. TOC (LOMR) had an initial increase due to the formation of biofilm on the leaves. The initial increase in TOC (LOMR) emphasizes how the leaf packs act as "islands" of empty niches ready for colonization processes by the biofilm organisms.

C/N ratios tend to decrease during decomposition of plant material (PURIVETH 1980). The high ratio observed on the 9th day was an indication of the peak of leaching when the leaves became of reduced food quality. After this time, the quality improved possibly due to the colonization by biofilm. However, on the 30th day the C/N ratio (LOMR) was high due to the presence of leaf residuals of poor food quality after being leached and utilised by the animals. Conclusively, the decay of the leaves followed the classical negative exponential curve. The food quality of the leaves was generally poor hence partially explaining the long calculated longevity.

The epilithon of rivers and streams is a light and energy transducer (LOCK 1981). The TOC (EOMR) and TOP (EOMR) showed significant increases towards the left bank but this was not true for TON (EOMR). The increase of TOC (EOMR) might have been due to the combination of debris dam and gravel organic ooze which provided food to the biofilm components and presumably suitable biotic growth conditions provided by the ever overflowed condition of the brook. The C/N ratio (EOMR) showed a wide range and the brook's hydrographic regime and riparian vegetation shading might have been the contributing factors. However, when the C/N ratio (SOMR), C/N ratio (EOMR) and C/N ratio (LOMR) were compared, it was found that EOMR was of high quality and SOMR provided the second best alternative. This indicates that the leaves that fall on the bedsediment have to undergo physical, chemical and biological processes before their food quality becomes suitable to the stream biocoenosis. This was exemplified further when the

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"resource ratio signatures" were calculated. This was not surprising since epilithon is known to receive light energy, organic and inorganic energy and its polysaccharide matrix acts as a reserve energy source for the heterotrophic microorganisms (LOCK 1981). It acts as a "bank" of high quality organic matter and hence the relatively low C/N ratio in the present study. Overemphasizing the role of the high quality EOMR to explain the distribution of zoobenthos in the bedsediment is not presently warranted. But taking into consideration all the organic matter resources, it can be mentioned that the EOMR's role, whether acting singly or in combination with other organic matter resources, is of paramount importance in determining the overall bioenergetics of the Oberer Seebach brook.

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