THE EFFECT OF ENVIRONMENTAL PATCHINESS ON THE BREAKDOWN OF LEAF LITTER IN A WOODLAND STREAM

Dissertation for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
SETH ROBERT REICE
1973

This is to certify that the

thesis entitled

THE EFFECT OF ENVIRONMENTAL
PATCHINESS ON THE BREAKDOWN OF
LEAF LITTER IN A WOODLAND STREAM

presented by

SETH ROBERT REICE

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Zoology

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Date July 1973

O-7639

ABSTRACT

THE EFFECT OF ENVIRONMENTAL PATCHINESS ON THE BREAKDOWN OF LEAF LITTER IN A WOODLAND STREAM

By

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The breakdown of allochthonous leaf litter in woodland streams is a community level process. The object of this study is to test if this process is patchily distributed in space. Two types of environmental patches were tested: the type of bottom sediments and the size of the leaf pack.

Four sediments, aligned along a series of environmental gradients, were studied: rock, gravel, sand and silt. Five pack sizes were studied: 1, 5, 10, 20 and 40 g. Preweighed packs of white ash (Fraxinus americana) leaflets were tied to bricks and set on the sediments. These were destructively sampled weekly for six weeks, and the dry weight remaining was determined. This design was followed in each of the four seasons to test the seasonal variability in leaf litter breakdown.

The data were handled as percent weight lost. Analysis of variance and comparison of means show that in all seasons sediment and pack size effects are highly significant ($p < .001$). Leaf packs of all sizes were broken down least in the silt than on the other sediments in all seasons. The sediment patterns are consistent with the community level effects of physical heterogeneity and stability. The pack size effects were highly variable from season to season. However, the degree of breakdown separated the leaf packs into different groups in every season, with one or another size displaying major differences from the others. The seasonal patterns in breakdown reflect the temperature dependent nature of this process, showing the amount of breakdown increasing with increasing temperature.

This study shows that the community level process of leaf litter breakdown in streams is patchily distributed in space. This suggests a meaningful level of organization between the population and the community, namely, the patch-specific component community.

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1973

ACKNOWLEDGMENTS

I would like to recognize the constant help and encouragement of my wife, Teme. Dr. William E. Cooper provided invaluable advice and criticism. My guidance committee, G. A. Coulman, K. W. Cummins, D. J. Hall, and S. N. Stephenson all offered valuable suggestions. Ms. Bodil Burke and Ms. Betty Kronemeyer provided important technical assistance. This work was supported by NSF Grant GI-20.

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CHAPTER I

INTRODUCTION

The study of ecological communities has grown considerably in recent years. In this perspective, it is possible to think of processes occurring at the community level. A community level process is one which involves the actions and interactions of several populations. Such community level processes are comparable to events at the population level. As individual feeding rates are studied at the population level, so total decomposition rates can be analyzed at the community level. As single species growth rates are studied at the population level, so total productivity can be assessed at the community level. The purpose of this study is to examine one community level process and attempt to characterize how it is effected by different environmental gradients, both spatial and temporal.

As an initial step it is necessary to present a working definition of a community. In this work a community is considered to be all of the biological populations in an area. However the boundaries of that area are defined, the community is all of the animals, plants and microbes contained within it. In this sense, the community is "the living part of the ecosystem" [Odum (1971)]. This is in contrast to workers who regard a few populations at one trophic level as a community. While it is sometimes convenient to refer to such a trophic categorization as a community (i.e. the plant community) this tends to confuse the community concept. Until a consensus is reached, each worker in community ecology must define his usage of the term "community."

For an overview of community ecology a useful distinction is between static and dynamic studies. The static studies, usually descriptive, tend to present a snapshot view of the community, giving a species list and perhaps one of the diversity indices. The dynamic studies concentrate on community level processes such as productivity, respiration, community metabolism and energy flow. Most of these tend to aggregate very diverse systems into a single, homogenized perspective. Examples of this are Odum (1957) and Teal (1962).

However, some studies have sought to dissect the community into smaller coherent parts on a geographical basis. Environmental patches are recognized. This is the concept set forth by Root (1973) on component versus compound communities. His idea, which is central to this work, is briefly as follows: communities can be regarded as compound units composed of discrete component parts, and their interactions. In this view, a component community is a set of populations which have coevolved to live in a particular habitat as, for instance, a tree hole or bog mat. The compound community describes a larger scale system embracing many of these component communities. In its essence, this point of view stresses the hierarchical nature of ecological communities.

The heterogeneous distribution of associations of animals and plants has been shown in a variety of systems. It is consistent with this overview, that the rates of community dynamic processes should be heterogeneously distributed as well. Given the tremendous complexity of information available on ecological communities, it is necessary to search for some unifying or simplifying factors to enable ecologists to structure their thinking. One likely starting point is to examine the community level effects of heterogeneity to elucidate the possibility that the pattern of environmental gradients in space may be logically reflected in gradients of processes.

The concept of spatial heterogeneity or environmental patchiness has been diversely explored. MacArthur and Levins (1964) introduced the concept of fine-grained versus coarse-grained environments. The role of this in competition is stressed by MacArthur and Wilson (1967). Levins (1968) applied the concept to the evolutionary and adaptive strategies of populations. Grain size enters into predator-prey studies [MacArthur and Pianka (1966)] ,in the concept of the refuge. A more complex environment offers more refuges for prey than a simple environment [Gause (1934); Gause et al. (1936);Huffaker (1958); and Salt (1967)]. An extrapolation of this idea is seen in species diversity studies. Pianka (1966) states it clearly: "The more heterogeneous and complex the physical environment becomes, the more complex and diverse the plant and animal communities supported by that environment." Support and elaboration is presented by Kohn (1959, 1967, 1968) and Smith (1971).

Plant ecologists have recognized patchily distributed plant associations. This gave rise to the Zurich-Montpellier school of phytosociology, which regards communities as discrete integrated units with clear, sharp boundaries [Clements (1905, 1916); Braun-Blanquet (1932); and Daubenmire (1966)]. However, even discrete patches are generally aligned on some sort of gradient. These gradients can be biotic or environmental. The relationship between the latter gradients and patchiness is reflected in the dominant theme of modern plant community ecology, the continuum concept [Gleason (1926); Langford and Buell (1969); Whittaker (1967)]. In this view communities are not the discrete units of the Montpellier school, but rather are organized as a continuum, with one association blending gradually into another. The continuum is viewed as being arrayed along an environmental gradient such as soil type, moisture or elevation. For a comprehensive review, see McIntosh (1967).

However, some workers, notably Whittaker (1966) and McNaughton (1968) have gone one step further. These scientists have studied the problems of variability in such community parameters as productivity and respiration along the environmental gradient. With this sort of analysis, insight is gained into the responses of the community to different levels of environmental variables. If these relationships are quantified and modeled it should be possible to predict the relative magnitudes of important rates of community level processes on the basis of simple environmental measurements. Gradient analysis is an important simplifying and ordering concept in community ecology. The perspective it offers is that community dynamics may well be ordered along easily measured environmental gradients.

Another important concept which may serve as a simplifying assumption in community ecology is the role of particle size. Several workers, notably Ivlev (1961), Brooks and Dodson (1965), Cooper (1965), Galbraith (1967), Brooks (1968) and Hall et al. (1970), have demonstrated the size specific nature of predation by fish. Hall et al. (1970) have shown the effects of this size selective feeding. In their experimental pond study they noted that the great complexity of prey species distributions and population dynamics reduced to simplicity when the various species were considered as food particles of different size classes. Size selective feeding had resulted in a reorganized community structure in the ponds with fish present, in comparison to the no-fish ponds. The possibility of other size-specific interactions working to structure community dynamics surely exists. While many workers have examined the role of size as it refers to single individuals and search image (see above), it is possible that size selectivity also operates in the choice of an environmental patch. This idea is raised by MacArthur and Wilson (1967). The organism is seen as selecting an area which will maximize his food gathering potential, while minimizing the risk of exposure to predators and competitors. Patch specific population dynamics in predator-prey relations are explored by MacArthur and Pianka (1966). The idea of organisms selecting environmental patches suggests the possibility of patch-specific dynamics. This is supported by the findings of Root (1973) who showed considerable variation in population and community parameters based on the size and arrangement of stands of collard plants (*Brassica oleracea*). Thus, a patch of particular environmental characteristics may well be a component community in the larger overall community. This is saying that there is a level of organization between populations and large compound communities. This level is the patch specific component community. The landscape of a compound community is seen as a mosaic of patches, each with unique properties, predictable from the characteristics of the local environment. This perspective is the foundation of this work.

The breakdown of organic detritus in a temperate zone woodland stream is a community level process. Excellent work on this subject is presented in Cummins (1973), Cummins et al. (1973), Kaushik and Hynes (1971), Boling et al. (1973a) and Boling et al. (1973b). To make this point let us briefly trace the events following the input of some allochthonous organic matter to a stream. Consider leaves falling into the water. These are leached of most of their nitrogenous material within a 24-hour period. Bacteria and fungi attack the leaf surfaces and colonize the leaf [Triska (1970)]. The microbially conditioned leaf is now a good source of protein for large detritivores [Kaushik and Hynes (1971)]. These animals, mostly aquatic insect larvae and some crustaceans, feed on the leaves, either shredding them or gleaning the bacteria and fungi. The mechanical action of their feeding breaks the leaf into smaller particles or converts it to feces. These new particles are the food sources for fine particle feeding detritivores. The process is iterative, resulting in the breakdown of the detritus, with conversion to animal biomass and subsequent mineralization [Boling et al. (1973b)]. Although this has been outlined for leaf litter, it is the basic pattern followed by all large particle detritus, regardless of origin. This sequence of events, or detritus processing, is clearly a community level process, for it involves many species populations from many phyla, operating across trophic levels.

The importance of allochthonous organic matter to the energy budget of temperate zone woodland streams has been made abundantly clear in recent years [Nelson and Scott (1962); Minshall (1967, 1968); Vannote (1970); Fisher (1971); Hall (1971); Kaushik and Hynes (1971); Fisher and Likens (1972); Cummins (1972, 1973); Cummins et al. (1972, 1973)]. These works all support the concept that allochthonous organic matter is the predominant source of energy to the stream community. Minshall (1967) stated that "the most important food [in the stream] was allochthonous leaf materials." Vannote (1970) stated, "In a woodland stream, the allochthonous detritus input may support up to two-thirds of the annual energy requirements of primary consumer organisms." Fisher (1971) points out that over 99 percent of the annual input of energy to Bear Brook is allochthonous. Leaf litter alone accounted for 29 percent of the annual input of energy.

In this context, it is clear that an understanding of the dynamics of the allochthonous inputs is an essential step in understanding the dynamics of the woodland stream ecosystem. The above authors have demonstrated that a woodland stream is a heterotrophic system, deriving the bulk of its energy from the surrounding forest.

The forest contributes energy to the stream, while the stream serves as a sink for forest nutrients and transports them downstream. A major link between the two systems is the input of energy to the stream through leaf fall. This study has focused on that link. Answers to the questions about temporal and spatial patterns in the breakdown of leaf litter can only add to the understanding of how the stream community responds to the input of terrestrial organic matter.

The bottom sediments of a stream are patchy. It is the usual case to encounter silt beds, gravel beds, sand banks and rocky zones. This is seen in the common riffle-pool-riffle-pool arrangement of streams [Hynes (1970)]. The patches are often distinct. The stream bottom is a mosaic of different sediments. One characteristic of these sediments is that they are arrayed along a gradient of particle size, from the fine-grained silt, through sand, gravel and on to large rocks and boulders.

Many stream ecologists have noted and analyzed the causes and potential effects of these marked distributions. Hynes (1970) has reported the relationship between stream current velocity and sediment type. In fast flowing waters the scouring effect of the water leaves many large particle size sediments such as rock, cobbles and pebbles. In slower flowing waters, suspended fine particles are deposited, resulting in bottom types such as sand and silt. This is the "erosion-deposition" concept as set forth by Moon (1939). The gradient of particle size of sediments is a manifestation of the current regime.

As the particle size of the sediments increases the physical complexity also increases. A siltbed is a nearly uniform substrate in two dimensions with variation being restricted to the vertical depth into the silt. Consider by contrast the tremendous three-dimensional variability inherent in the different surfaces and interstices of a loose accumulation of large rocks, as in a riffle. The niche diversity should increase as the maximum particle size of the sediments increase. Similarly a diverse patch of sediment, say scattered rocks on a bed of sand, should have a greater habitat diversity than a pure sand patch. MacArthur and MacArthur (1961) have shown that habitat (niche) diversity and species diversity are correlated.

It follows, then, that larger numbers of species and individuals should be associated with more complex sediments than simple ones. This is precisely what Percival and Whitehead reported in their classical study (1929) on the fauna associated with different stream beds. In a single stream a 128 fold increase in numbers of individuals from simple to complex sediments was observed. In addition, the percentage breakdown of the principle animal groups varied tremendously. Similar, but less spectacular results are cited by Sprules (1947). Mackay and Kalff (1969) noted that the number of species increases with the heterogeneity of the substrate. Carpenter (1927) proposed a classification scheme for stream fauna based on sediment associations. The lithophilous association lives on rock; the limnophilous group lives in or on mud or gravel; while the phylophylous group lives on plants, etc. She found it necessary to subdivide the lithophilous group into three classes based on where on the rock they live (i.e., on it, under it, or behind it). This is only a coarse view of the niche differentiation possible in rocky sediments. Another such breakdown of the fauna is presented by Hora (1930), while a modern example of this is presented by Thorup (1966). Hynes (1970) gives an extensive review of the substratum preferences of stream invertebrates, discussing the patterns in species diversity and biomass. He summarizes as follows: "In general it can be stated that the larger the stones, and hence the more complex the substratum, the more diverse is the invertebrate fauna. Sand is a relatively poor habitat with few specimens of few species, apart from its microfauna, but silty sand is richer, and muddy substrata may be very rich in biomass, although not in variety of species." The literature on this subject may be best found in Cummins (1966), Cummins and Lauff (1969) and Chapter XI of Hynes's (1970) book.

A factor involved in the distributional patterns of macro-invertebrates in streams is the stability or permanence of the sediments [Hynes (1941); Moon (1939)]. Greater physical stability is expected to support a larger, more diverse fauna. Maitland (1964) writes, "The fauna of stones is richer and much more varied than that of sand, though both substrates appear to be unstable and may be drastically affected by spates." Maitland then compared five studies from around the world where stream beds of sand and rock had been contrasted. In every case the total biomass was greater in the stony substratum. O'Connell and Campbell (1953) assert that the bottom fauna of riffles is twice as productive as that of pools (which are usually sandy or silty). Hynes (1970) says that, in general, the fauna of clean stony runs is richer than that of silty reaches and pools both in number of species and in their total biomass." The correlation of physical heterogeneity and physical stability in stream sediments is so great that it is difficult to distinguish their effects. It should be noted that the terms stability and heterogeneity as used throughout this work pertain to the physical properties of the environment and not to the biota.

A laboratory experiment by Cummins (1969) showed that the observable substrate preferences by stream macrobenthos species is not accidental. In these experiments about half the species tested actively selected microhabitats on the basis of particle size of the sediments. Similar substrate selection was demonstrated by Mackay (1972) for three species of *Pychnopsyche*.

All these data point out that clear differences in species composition, population sizes, and total biomass of the stream macrobenthos are found in association with sediment patches of different particle sizes. This points out that the benthic community, i.e., all the populations present in a restricted region of the stream bed, changes with differences in the particle size composition of the sediments. It follows that if the benthic community differs, then the nature or magnitude of community level processes should differ as well. One such process is the breakdown of leaf litter.

Variation in leaf litter processing was the subject of these experiments. These experiments tested two questions in this area: 1) Is the amount of processing of leaf litter patchily distributed in space? and 2) If it is, is the distribution consistent with the hypotheses concerning physical stability and diversity of sediments?

Patchiness enters this work in another form. When leaves fall into streams they aggregate into clumps and clusters against various obstacles (branches, boulders, etc.). These aggregations, or leaf packs, occur in a wide range of sizes, from a few to hundreds of leaves. Each leaf pack can be considered a patch of resources from the perspective of a free-ranging detritivore. As the detritus feeders search for places to live and feed one can hypothesize that the size of the resource patches which they encounter will affect their choice. Alternatively, the conditions in the patch may produce different mortality rates. Whether through differential selection or mortality, the effect of patchiness would be reflected in the differing amounts of breakdown per unit time in patches of different sizes. If such evidence is forthcoming, it indicates the possibility that leaf litter breakdown may be organized on the basis of patch size specific interactions. To test this hypothesis leaf packs of different sizes were distributed among the different sediment patches, and sampled for weight loss through time.

Subsidiary questions to be tested included the following: 1) Is the distribution of the process of leaf litter breakdown in streams a seasonal one, and 2) if it is, are the differences in breakdown among sediment and leaf pack size patches consistent? These questions arise because detritus processing in streams appears, superficially, to be dominated by autumn leaf fall. It is important to know, from considerations of the current degree of organic loading via certain forms of pollution, whether the stream community can process large particulate organic matter year round

This work was an attempt to determine if the community level process of leaf-litter decomposition in woodland streams is heterogeneously distributed in association with two types of environmental patches. One is the particle size of the inorganic sediments, i.e., silt beds versus gravel beds. The other is the size of the pack of leaves being decomposed. The work also examined how a community level process varies through the seasons.

CHAPTER II

EXPERIMENTAL DESIGN

Study Site

The study was carried out in Augusta Creek, in Kalamazoo County, in Southcentral Lower Michigan. The experiments were conducted in a stretch of the stream which flows through the Kellogg Forest, an experimental facility of Michigan State University.

Four discrete sampling sites were chosen. Each site encompassed a sediment type along a sediment particle size gradient. The classification of particle size will be by the Phi scale [after Cummins (1962)], a modification of the Wentworth classification. Note that phi is the negative log to the base 2 of the particle size in millimeters. The four sites were:

1. Rock - actually a mix of boulders (phi = -8) separated by sand (phi = 1,2).

2. Gravel - includes small cobbles (phi = -6), pebbles (phi = -4, -5) and gravel (phi = -3).

3. Sand - coarse (phi = 1) and medium (phi = 2).

4. Silt - (phi = 5,6,7,8).

Each of the sites is easily distinguishable from the other sites. The rock and gravel sites incorporate a wide range of particle sizes.

Additional physical complexity arises from the positioning of individual particles. Sites 3 and 4 are relatively homogeneous within their boundaries.

Natural sediments found in Augusta Creek were used. This preempted the need for maintenance of artificial substrates. Therefore, the study was conducted in the presence of the established biotic community on those substrates. Each site was a minimum of four m^2 in a rectangular shape.

Sampling Method

The goal of this study was to monitor the rate of breakdown of leaf packs in the benthic zone of a temperate woodland stream. The leaves must be placed in the stream in a way which closely resemble the natural placement of leaf litter in the stream. After the leaves fall into the stream, they sink to the bottom or get caught on an obstacle. These obstacles include rocks, sunken logs, etc. At such a point the leaves begin to pile up, forming a leaf pack.

The problem, then, was to devise a method which allowed the experimenter to (1) place leaf packs in the stream, (2) affix them to the bottom, (3) be able to remove them at a later date, and (4) keep them exposed to both physical and biotic factors at all times. The first three conditions were met by the mesh bag approach. In this method, the material under study is enclosed in a nylon mesh bag. This approach severely limits the natural access by the macroscopic benthic fauna and constrains the physical flow of water. Any accrual of debris could clog the mesh, limiting the flow of water and nutrients. With this method the primary effect observed could well be the effect of the container.

To avoid these exclosure effects a sampler devised by Dr. Kenneth Cummins was employed (Petersen and Cummins, 1973). The method is based on the way leaf packs form in nature. A preweighed pack of leaves is attached to a brick with nylon monofilament. The brick is placed in the stream with the leaves on the upstream surface. This artificial construction mirrors the natural case. A limitation is that natural leaf packs probably break up and reform. Therefore, the man-made pack is unnaturally stable.

Once the leaves were pre-weighed (after oven drying at 40°C), the leaves were moistened in water until they were flexible and pliant. This took about fifteen minutes in warm water. Then the leaves were stacked up and stapled together with a Buttoneer (Dennison, Inc.) which inserts a nylon I-bar. Then the whole bundle is laced together with 6 lb.-test nylon monofilament. Using this monofilament, the leaf pack was tied to a brick. This simple arrangement will hold the leaves in place in the stream. The brick acts like the obstruction which snags the leaves in nature.

White ash leaves (Fraxinus americana) were used throughout. The leaves were preweighed to amounts of one, five, ten, twenty and forty grams. These weights were chosen for the following reasons. Forty grams is about as large as leaf packs can get, while still remaining stable. It was hoped, therefore, that this size pack would bracket the upper end of the range of size of naturally occurring leaf packs. One gram, similarly, is the approximate lower end of the range, since a single large ash leaf will sometimes weigh one gram. Much data had been gathered by Petersen and Cummins (1973) on leaf packs of the ten-gram size using various species of leaves. Therefore, for maximum comparability, ten grams was chosen as the middle weight. Twenty and five grams were selected as the other interemediate weights falling between ten grams and the extreme sizes, and providing for ease of comparison.

The choice of white ash leaves (Fraxinus americana) was initially biased by the supply of leaves on hand. However, it proved to be fortuitous. Research completed after the onset of these experiments showed ash leaves to be processed in the stream faster than any other species of leaves. The idea was to use a leaf species that is processed quickly by the stream organisms in order to achieve the clearest possible results in the shortest amount of time. Using ash leaves, processing is so rapid that a six-week sampling schedule shows marked deterioration and weight loss. On the other end of the spectrum, oak, which is processed slowly, would show only a slight weight loss. The technique involved is destructive replicate sampling, starting with the total leaf input and removing 1/6 of the leaves weekly.

For each season 360 leafpacks (6 weeks x 5 pack sizes x 4 sites x 3 replicates) were required. The forty gram packs were tied separately, one to a brick. The other sizes were small enough to be tied two to a brick. In order to avoid any consistent neighbor bias, 24 bricks each of the six combinations of leaf packs listed below were constructed and tagged with colored markers:

20-10
20-5
20-1
10-5
10-1
5-1

In addition, 72 forty gram packs were constructed. A single day's sample from one site then, consisted of nine bricks: one each of the six combinations listed above plus three bricks with forty gram packs.

The bricks were placed in the stream in the following way. All packs were oriented upstream. The distance between packs on a single brick was quite similar to the distance between packs on adjacent bricks. Thus, by varying the order of placement of bricks in the stream (i.e., placing one size next to another at random), a close approximation to a truly random assortment is achieved. Each sediment type required 90 leaf packs per season on 54 bricks. Hence, the bricks were arrayed in six rows of nine bricks each. The nine bricks in a given row included the full assortment necessary for a sample on any given day (i.e., three replicate packs of each of five sizes. The rows were perpendicular to the direction of the current. The rows were between 15 and 30 cm. apart. Entire rows were sampled at a time. The most upstream rows were taken on each day. In more narrow sites the rows alternated between five and four bricks, with two adjacent rows composing the sample. It is likely that there is a bias in these data due to the presence of the bricks. The brick effect may be more important in the silt than in the rocky sediments, since the difference between the brick and sediment morphologies are greater. This would tend to make the sediment differences harder to detect. The bias is against finding significant differences.

Sampling proceeded as follows. The bricks were lifted from the streambed and placed in a styrofoam cooler with a wooden reinforced bottom. This box was floated to shore. All animals retained in the box were collected. The bricks with leaf packs still attached were transferred to a carrying box and transported to the laboratory. There the lines holding the leaf packs to the bricks were cut. The leaf packs were disassembled and thoroughly rinsed in cold water into a screen to remove any sediments or clinging organisms. Organisms thus removed were collected. The organisms were sorted by eye, primarily to provide a check against the appearance of unusual species. The leaves were blotted on paper towels and then spread in a thin layer on a dry paper towel. The leaves were dried in incubators for 48 hours at 50°C. Then they were removed from the towels and weighed on a Metler balance. These actual dry weights remaining were converted into percent weight lost, as follows.

$$\%\ \text{weight lost} = \frac{\text{initial dry weight (g)} - \text{dry weight remaining (g)}}{\text{initial dry weight (g)}} \times 100$$

This form allows comparison of the dynamics of the different pack sizes. The use of percent loss data avoids distortions based on initial weight. For instance, if a one gram pack and a 40 gram pack each lose one gram, the one gram pack has lost 100 percent of its initial weight while the 40 gram pack has only lost 2.5 percent. So, on a 40 gram starting basis, 40 one gram packs would have been completely destroyed, while one 40 gram pack would still lose only 2.5 percent of its initial weight. All calculations and analyses of variance were performed on these percent loss data.

The data, although presented in terms of percent loss, can also be viewed as a rate of loss or breakdown by dividing by the number of days of exposure in the stream. However, this conversion implies a constant weight loss rate, which was not justified by these data. Therefore, the data will appear as percent weight lost per period of exposure.

These procedures were followed in four seasonal, replicated experiments. The first, the summer experiment, was initiated on June 27, 1972 and ran until August 8, 1972. The second, the autumn experiment, ran from October 17, 1972 until November 28. The winter experiment spanned the period January 15, 1973 until February 28. The spring study began on

April 2, 1973 and was concluded on May 14, 1973. These four periods, one in the midst of each of the four seasons, are then compared to each other. Each seasonal experiment is a replicate of the others with only seasonal variation in physical and biological factors changing.

Velocity Study

A small-scale experiment was designed to test whether water velocity per se, in the absence of biological activity, could be responsible for the observed differences between sediment treatments. Two flow treatments were used, fast and standing water.

For the former, a recirculating channel was built of galvanized aluminum sheeting. It was rectangular, four feet long, 8.25 inches wide and 4.5 inches deep. It was built up to six inches deep at the inflow end. The water entered through a hose, was dispersed by a baffle and flowed to another baffle at the downstream, which served to maintain the water level. The water flowed out through a spout into a catchment tank and was pumped back into the channel. Twenty-one vertical barriers (2 1/2 inches wide, four inches tall) were placed in the channel to support leaf packs. The channel maintained a turbulent flow rate of four cm/sec.

The standing water treatment was simply a 20-gallon aquarium. In each treatment the water was treated with $CuSO_4 \cdot 5H_2O$ (2.66×10^{-4} molar solution) to inhibit bacterial and fungal growth.

Nine leaf packs each of the one gram and ten gram sizes were placed in each apparatus. Leaf packs in the flow channel were attached to the barriers so that the broad surface of the pack was perpendicular to the current. In the aquarium leaf packs just settled to the bottom. At two week intervals, three replicate packs of each of the two pack sizes were sampled, dried, weighed and analyzed like the field samples.

Statistical Design

The statistical experimental design employed was a three-way analysis of variance in a completely randomized factorial design. The analysis was performed on the percent weight loss data. Teaves were assigned to leaf packs at random. Leaf packs were assigned to sediments, dates and replicates at random so the assumption of randomization is met. The design, nomenclature and computational procedures are drawn from Kirk (1969). The design is referred to as CRF-pqr, i.e., it is a completely randomized factorial design with three treatments. The procedures used are analogous to those found in Cochran and Cox (1950).

There are three treatments: sediment type, time and pack size. Let these be represented by the letters A, B, and C, respectively. Let S denote the number of samples. The nomenclature employed follows.

Factor	Symbol	Levels
Sediment type	A	p levels of a_i, where p = 4
Time	B	q levels of b_j, where q = 6
Pack Size	C	r levels of e_k, where r = 5
Replicate Samples	S	n levels of s_m, where n = 3.

The total number of samples is N.

The linear model underlying the design is:

$$X_{ijkm} = \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk} + E_{m(ijk)}$$

where:

μ = grand mean of all treatment populations

α_i = effect of treatment i of factor A

β_j = effect of treatment j of factor B

γ_k = effect of treatment k of factor C

$\alpha\beta_{ij}$ = effect of the interaction of factors A and B

$\alpha\gamma_{ik}$ = effect of the interaction of factors A and C

$\beta\gamma_{jk}$ = effect of the interaction of factors B and C

$\alpha\beta\gamma_{ijk}$ = effect of the interaction of factors A, B and C

$E_{m(ijk)}$ = experimental error

The total number of treatment combinations is pqr = (4)(6)(5) = 120. The total number of samples N = pqrn = (4)(6)(5)(3) = 360. The analysis of variance table format is given in Table I [after Kirk (1969)]. Expected mean squares can be found in that work. Note the large number of degrees of freedom of error (240) available for testing purposes. This is a virtue of the CRF-pqr design, when one uses many levels of each treatment. It allows for distinguishing differences with fine resolution while using a reduced degree of replication. This tradeoff of lower replication for more treatment levels proved advantageous. It increases the information gained per sample. The identical format is used for the velocity study with p = 2, q = 3, r = 2, and n = 3. N then equals 36 samples.

Hypotheses designed to be tested include the following

<u>Main Effects and Interaction Effects</u>

$H_o: \sigma^2_A = 0$	$H_o: \sigma^2_{AB} = 0$
$H_1: \sigma^2_A \neq 0$	$H_1: \sigma^2_{AB} \neq 0$
$H_o: \sigma^2_B = 0$	$H_o: \sigma^2_{AC} = 0$
$H_1; \sigma^2_B \neq 0$	$H_1: \sigma^2_{AC} \neq 0$
$H_o: \sigma^2_C = 0$	$H_o: \sigma^2_{BC} = 0$
$H_1: \sigma^2_C \neq 0$	$H_1: \sigma^2_{BC} \neq 0$
$H_o: \sigma^2_{ABC} = 0$	
$H_1: \sigma^2_{ABC} \neq 0$	

In addition, multiple comparisons of means will be made to further partition main effects. A priori comparisons between rock and gravel versus sand and silt, and within each couplet will be made via orthogonal contrasts (after Sokal and Rohlf, 1969). A posteriori tests will be made with Tukey's HSD (Honest Significant Difference) procedure [Steel and Torrie (1960)]. Such a test compares every treatment mean with every other treatment mean. It is used to pinpoint the location of the significant differences between levels of a given treatment. This test is recommended by Gill (1973) over Duncans New Multiple Range Test, which has an uncontrolled Type I error rate.

In comparing the experiments conducted in the different seasons, all effects may be tested by the orthogonal contrasts method. Between four seasons, three degrees of freedom are available, so three (one degree of freedom) hypotheses may be tested. The three chosen are:

1. Fall and Winter vs. Summer and Spring
2. Fall vs. Winter
3. Summer vs. Spring.

This is an orthogonal set of questions which will dissect any seasonal effects. It will be applied to all nine factors tested (five different pack sizes and four sediments).

In summary, these tests have been built into the structure of this experimental design. The statement of the above a priori hypotheses allows the utilization of the statistical tests which provide increased power and precision over any a posteriori tests available [Gill (1973)]. This is one advantage of employing experimental design procedures with clearly formulated questions prior to conducting experiments.

TABLE I

ANALYSIS OF VARIANCE TABLE
(CRF-pqr Design)

Source	Degrees of Freedom	F-Testing
1. A (Sediments)	p-1 = 3	[1/8]
2. B (Time)	q-1 = 5	[2/8]
3. C (Pack Size)	r-1 = 4	[3/8]
4. AB	(p-1)(q-1) = 15	[4/8]
5. AC	(p-1)(r-1) = 12	[5/8]
6. BC	(q-1)(r-1) = 20	[6/8]
7. ABC	(p-1)(q-1)(r-1) = 60	[7/8]
8. Within Cell	prq(n-1) = 240	
Total	npqr-1 = 359	

CHAPTER III

DATA ANALYSIS

Summer 1972 (June 27-Aug. 8)

The data are presented graphically in Figs. 1 and 2. The analysis of variance is given in Table II. Note that all main affects and two-way interactions are significant at the .001 level. Further breakdown of the data is presented in Tables VII and VIII. It should be noted that the standard error for each cell mean was less than 10 percent of the mean in almost every case. Therefore, error bars have been left out of the figures for the sake of clarity. Instead, a summary statistic, the mean cell standard error is included.

Sediments: The effect of the sediments on the weight loss from the leaf packs was marked (Fig. 1). The weight loss from the complex sediments (rock and gravel) was significantly greater than that from the simple sediments (sand and silt) (Table VII). However, rocky and gravel sediments were indistinguishable in their effects on leaf litter breakdown. This is in contrast to the simple sediments where sand effected much greater loss than the silt. Note that these effects occur across all pack sizes (Fig. 2). The effects become more pronounced through time. The final order of percent loss is always: rock or gravel with most loss, then sand, then silt.

TABLE II

Summer '72

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	$P(F_{i,j})$
A (Sediment)	5353.8802	3	1784.6267	25.06	.001
B (Time)	90702.1402	5	18140.4280	254.76	.001
C (Pack Size)	28647.2626	4	7161.8157	100.58	.001
AB	10633.4028	15	708.8935	9.96	.001
AC	2517.7846	12	209.8154	2.95	.001
BC	8012.0703	20	400.6035	5.63	.001
ABC	5445.1703	60	90.7528	1.27	ns
W. CELL	17089.6756	240	71.2070		
TOTAL	168401.3866	359	469.0846		

Figure 1. Summer data. Time trend of percent loss, pack sizes within sediments. Cell standard errors, $\overline{X} \pm s = 3.83 \pm 3.04$.

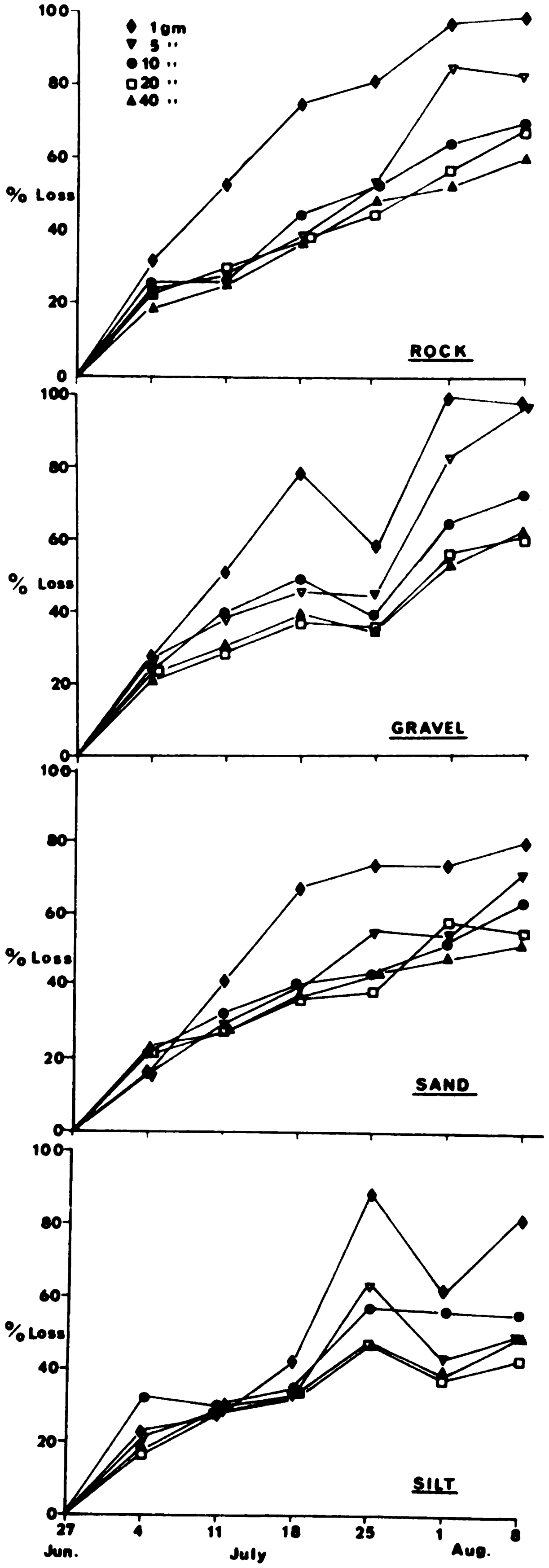
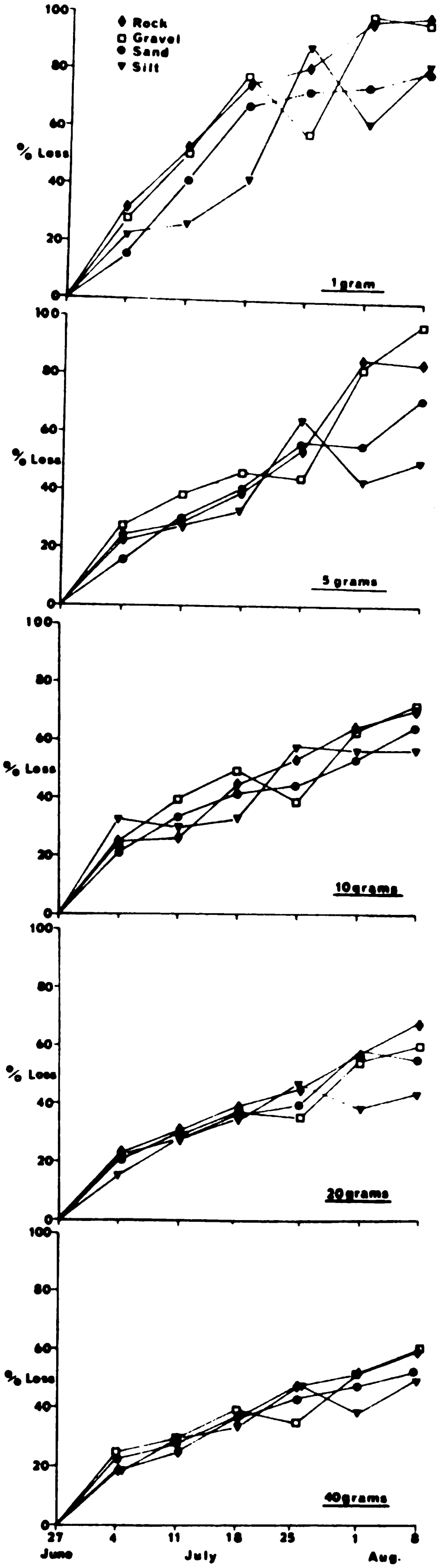

♦ 1gm
▼ 5 ''
● 10 ''
□ 20 ''
▲ 40 ''
% Loss
100
80
60
40
20
0
ROCK
GRAVEL
SAND
SILT
27
Jun.
4
11
July
18
25
1
Aug.
8

Figure 2. Summer data. Time trend of percent loss, sediments within pack sizes. Cell standard errors, $\overline{X} \pm s = 3.83 \pm 3.04$.


♦ Rock
□ Gravel
● Sand
▼ Silt
% Loss
0
20
40
60
80
100
1gram
5 grams
10grams
20grams
40grams
27
June
4
11
18
25
July
1
8
Aug.

Pack Size: The effect of pack size on the weight loss from the leaf packs was highly significant. The percent weight loss was inversely related to the size of the pack (Fig. 3). The most loss (percent) was associated with the one gram leaf pack and the least percent loss was from the largest leaf packs (40 grams). With minor deviations, this effect is seen across all sediments. What is also clear (Table VIII is that the losses from the one gram packs are significant different from all other sizes. The five and ten gram packs have statistically indistinguishable percentage weight losses. The same is true for the largest sizes, the 20 and 40 gram leaf packs, which, while they are similar, are different from all other sizes.

Time: With minor deviations (Figs. 1 and 2) the main effect of time is consistent throughout the season. The longer the leaf packs remain in the stream, the greater the weight loss. This trend is clear across all pack sizes and sediments. There is a change in the slope of the percent loss curves after the first week in all pack sizes but one gram (Fig. 2).

Interactions: All two-way interactions are highly significant (Table II). Simply put, the main effects of sediments (A) and pack size (C) become more exaggerated with increasing exposure to the stream community. This causes the resultant increasing divergence of the slopes of the lines in Figs. 1 and 2. This spreading out accounts for much of the observed interaction. However, there are particular weeks where the slopes altered significantly. This phenomenon contributes to the AB and BC interactions.

The AC or sediment-pack size interaction reflects the strong main effects in that, for example, the difference between one gram leaf pack and a 40 gram leaf pack is greater in the rocky habitat than in the silt-bed. The three-way interaction is non-significant.

Fall 1972 (Oct. 17-Nov. 28)

The data are summarized in Figs. 3 and 4. The analysis of variance is given in Table III. Subanalyses are given in Tables VII and VIII. The percent losses across all treatments is much reduced when compared to the summer. In the summer the range of losses was from 16 to 100 percent. In the fall, the range is depressed to from five to 43 percent. It should be noted, however, that the significance of main effects and two-way interactions follows the same pattern as the summer data. This is in spite of the general reduction in the weight loss.

Sediments: The weight loss data parallels the summer observations. Again the complex sediments manifest significantly greater losses across all pack sizes than do the simple sediments. Rock and gravel were not significantly different from each other while sand and silt were. The similarity of the percent loss data from summer and fall in response to sediments is apparent from Table VII.

Pack Size: The main effect of size of leaf pack is very significant ($P < .001$). However, a major difference from the summer data has appeared. The one gram size, which was broken down fastest and most completely in the summer, displays the least loss of weight on a percentage basis in the sutumn. All other pack sizes are broken down to the same relative degree. The five gram and ten gram sizes are still broken down more than the 20 and 40 gram leaf packs, and these groupings still persist (see Table VIII).

TABLE III

Fall '72

ANALYSIS OF VARIANCE TABLE

Source	SS	DF	MS	F	$P(F_{i,j})$
A (Sediment)	759.5961	3	253.1987	12.98	<.001
B (Time)	10207.8040	5	2041.5608	104.65	<.001
C (Pack Size)	4406.5341	4	1101.6335	56.47	<.001
AB	825.1472	15	55.0098	2.82	<.001
AC	406.9568	12	33.9131	1.74	<.05
BC	1719.9936	20	85.9997	4.41	<.001
ABC	662.6149	60	11.0436	.57	ns
W.CELL	4682.0196	240	19.5084		
TOTAL	23670.6662	359	65.9350		

Figure 3. Fall data. Time trend of percent loss, pack sizes within sediments. Cell standard errors, $\overline{X} \pm s = 1.96 \pm 1.63$.

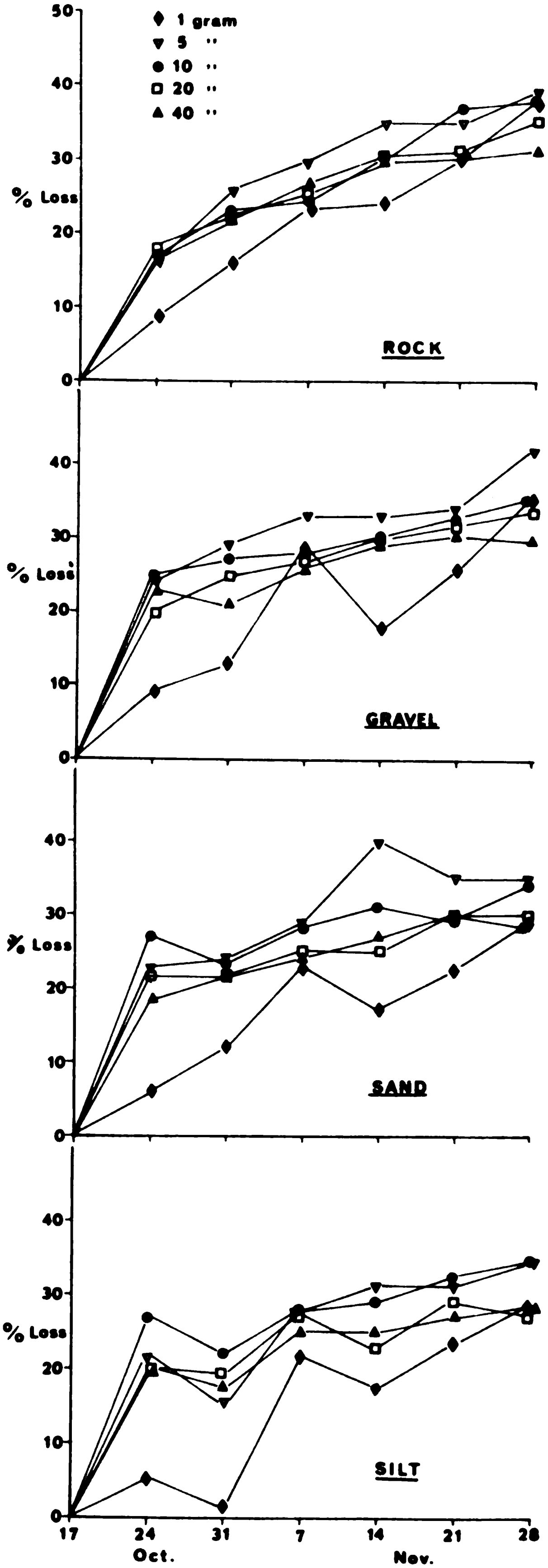
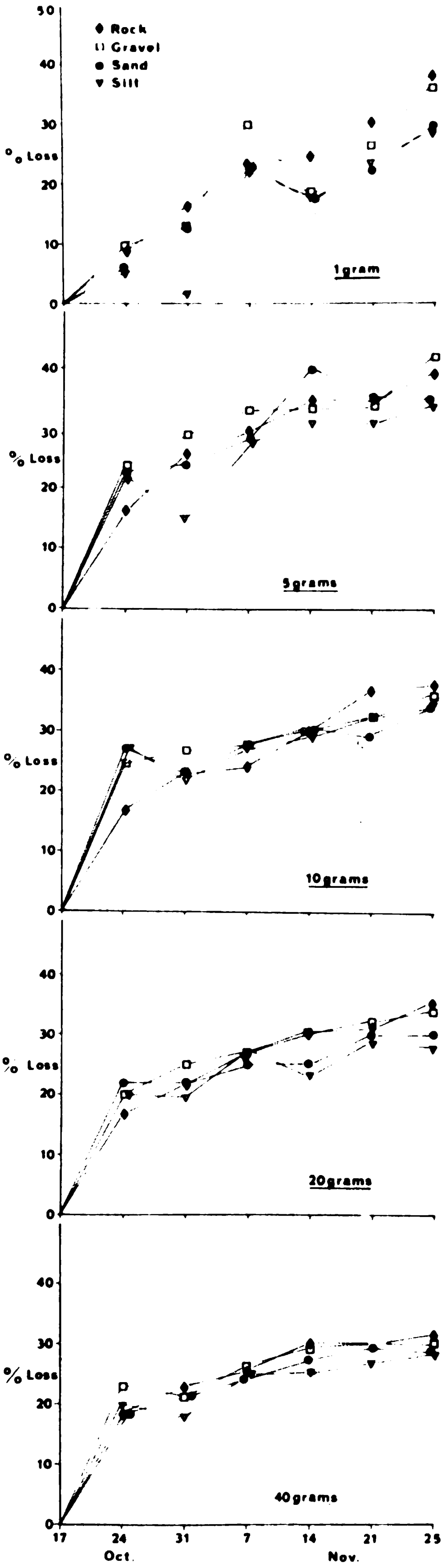

♦ 1 gram
▼ 5 ''
● 10 ''
□ 20 ''
▲ 40 ''
50
40
30
20
10
0
% Loss
ROCK
GRAVEL
SAND
SILT
17
24
31
7
14
21
28
Oct.
Nov.

Figure 4. Fall data. Time trend of percent loss, sediments within pack sizes. Cell standard errors, $\overline{X} \pm s = 1.96 \pm 1.63$.



◆ Rock
□ Gravel
● Sand
▼ Silt
50
40
30
20
10
0
% Loss
1gram
5grams
10grams
20grams
40grams
17
24
31
7
14
21
25
Oct.
Nov.

Time: The strong main effect of time is that more weight is lost as time in the stream increases. This is, with minor variations, the same phenomenon as in the summer and can be seen in Figs. 3 and 4. The slope of these percent loss curves drops dramatically after the first week in nearly every case. The curves are effectively broken into two portions.

Interactions: As in the summer, all the two-way interactions are significant while the three-way interaction is not. During the autumn the AC interaction (sediment-pack size) is considerably weaker in comparison to the time interactions.

Winter 1973 (Jan. 15 to Feb. 26)

The data are presented graphically in Figs. 5 and 6. The analysis of variance is given in Table IV. All main effects and most interaction terms are significant at the .001 level. The AC interaction is significant at the .01 level.

Sediments: As in previous seasons, the sediment effect was dramatic. However, the significance of the orthogonal contrasts must be tempered by an awareness that the mean weight loss of sand was intermediate to those of rock and gravel. Therefore, sand, while being significantly different from silt, is actually quite similar to rock and gravel (see Table VII).

Pack Size: According to Tukey's HSD (Table VIII) the five gram pack has significantly greater percent loss than all other sizes, which are essentially the same. This was a major change from previous seasons, although the five gram packs were processed greatly in the fall, too.

TABLE IV

Winter '73

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	$P(F_{i,j})$
A (Sediment)	1248.2423	3	416.0808	26.62	<.001
B (Time)	4404.9726	5	880.9945	56.37	<.001
C (Pack Size)	7899.8558	4	1974.9639	127.37	<.001
AB	772.4843	15	51.4996	3.30	<.001
AC	469.9089	12	39.1591	2.51	<.01
BC	739.5265	20	36.9763	2.37	<.001
ABC	1841.7622	60	30.6960	1.96	<.001
W.CELL	3750.9300	240	15.6289		
TOTAL	21127.6827	359	58.8515		

Figure 5. Winter data. Time trend of percent loss, pack sizes within sediments. Cell standard errors, $\overline{X} \pm s = 1.67 \pm 1.55$.

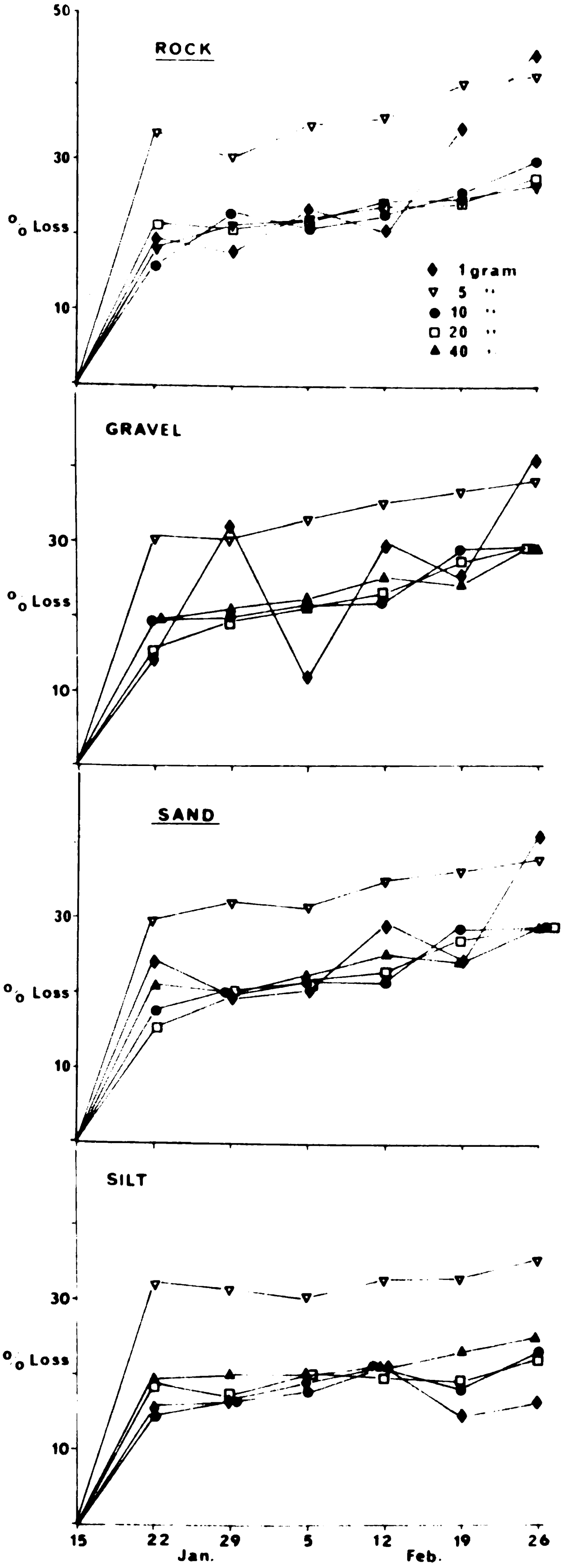
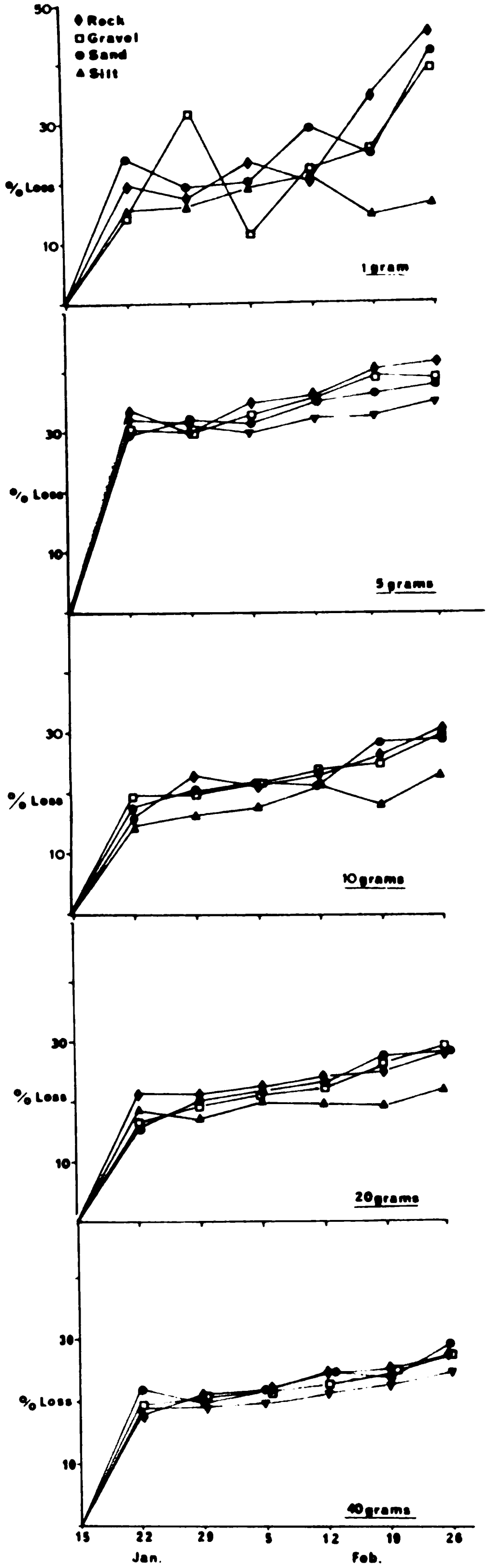

ROCK
50
30
10
% Loss
♦ 1 gram
▽ 5 ״
● 10 ״
□ 20 ״
▲ 40 ״
GRAVEL
30
10
% Loss
SAND
30
10
% Loss
SILT
30
10
% Loss
15
22
29
5
12
19
26
Jan.
Feb.

Figure 6. Winter data. Time trend of percent loss, sediments within pack sizes. Cell standard errors, $\overline{X} \pm s = 1.67 \pm 1.55$.


♦ Rock
□ Gravel
● Sand
▲ Silt
50
30
% Loss
10
1 gram
30
% Loss
10
5 grams
30
% Loss
10
10 grams
30
% Loss
10
20 grams
30
% Loss
10
40 grams
15
22
29
5
12
19
26
Jan.
Feb.

Time: The effects in winter are similar to those of previous seasons. As time goes on, more weight is lost across all sediments and packksizes. The break in the slope of the curves noted in previous sections occurs more sharply in winter. The slope of the losses in the first week are steep, but are nearly horizontal thereafter.

Interactions: Most interpretations follow the analysis of summer and fall. One notable feature, however, is that in all sediments, in the first week, about 30 or more percent of the five gram pack is lost. This extraordinary feature strengthens the BC (pack size-time interaction), as does the sudden late season decay of the one gram pack. The latter does not take place in the silt bed. This feature affects the AC (sediment-pack size) interaction, which is slightly weaker than the other interaction terms. The three-way interaction is significant.

Spring 1973 (April 2-May 14)

The data are presented graphically in Figs. 7 and 8, while ANOVA is given in Table V. All main effects and two-way interactions are significant at the .001 level, while the ABC interaction is significant at the .05 level.

Sediments: The sediment effect was great and in the same pattern as in previous seasons. Sand has the greatest degree of processing, exceeding slightly that of rock and gravel. The orthogonal contrasts repeat the earlier patterns (Table VII).

Pack Size: Using Tukey's HSD procedure the magnitudes of breakdown were compared (Table VIII). The one gram packs had greater and significantly different mean percent loss than all other pack sizes. Ten, five and 20 gram packs followed in degree of breakdown, being statistically equivalent. The 40 gram pack size was similar to the 20 gram size,

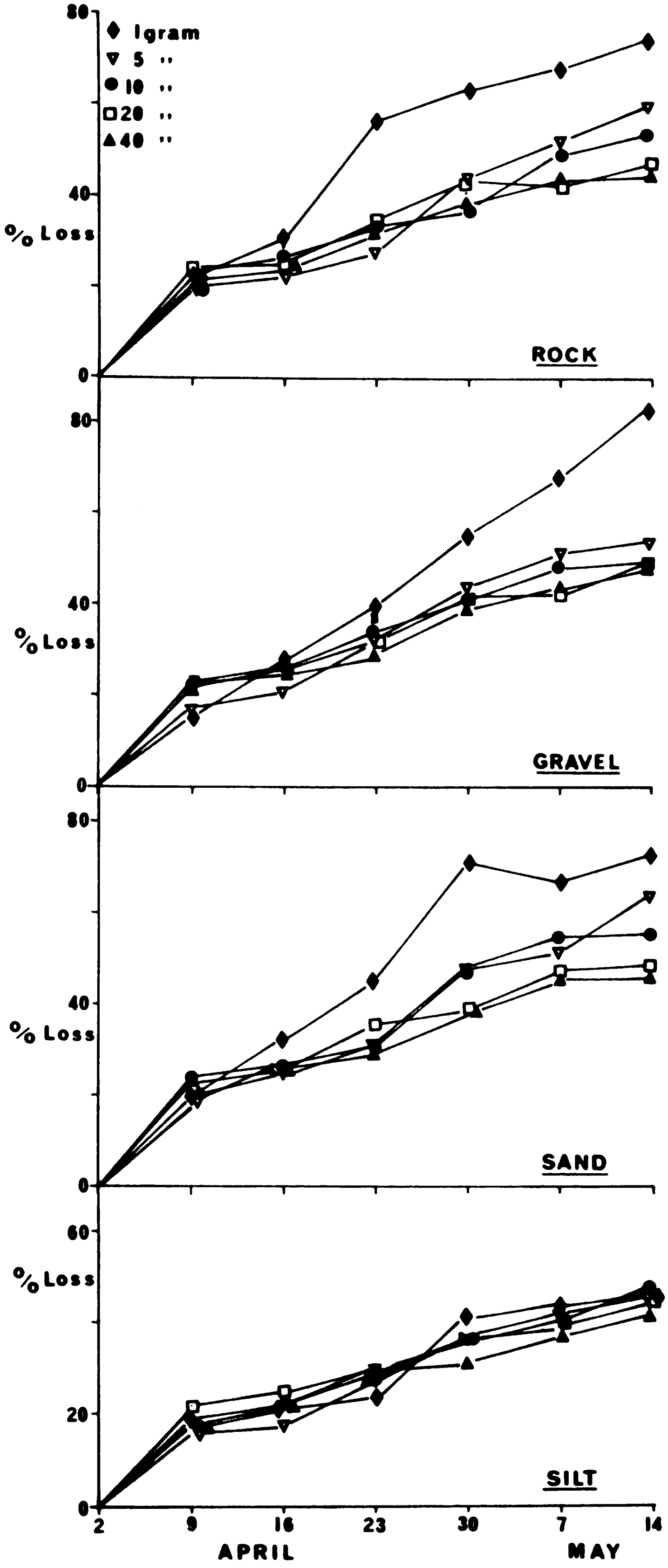
TABLE V

Spring '73

ANALYSIS OF VARIANCE TABLE

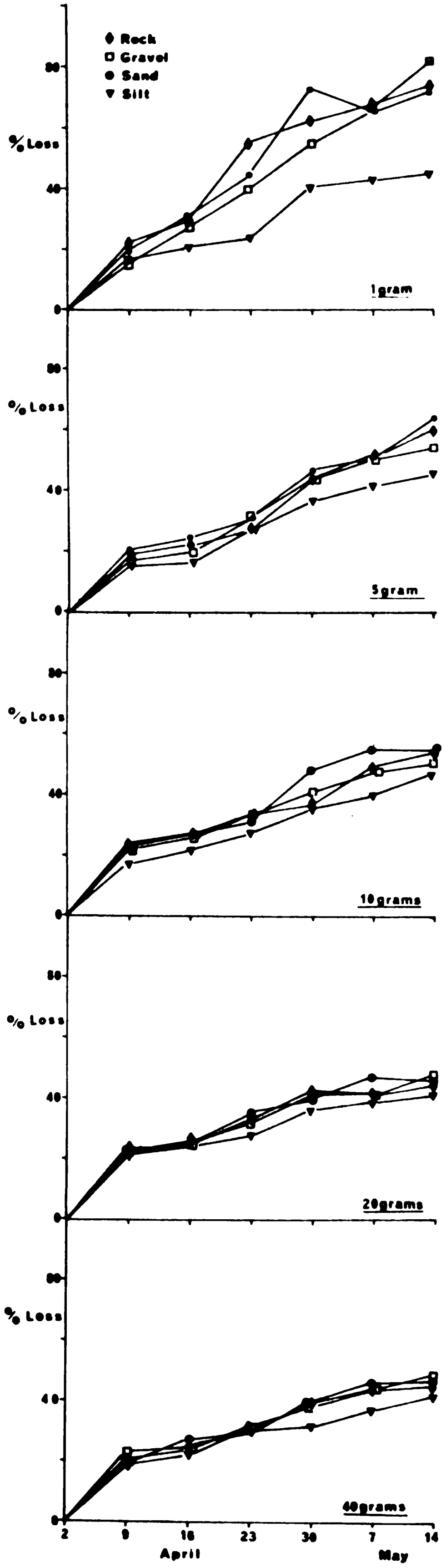
Source	SS	DF	MS	F	$P(F_{i,j})$
A (Sediment)	4293.3788	3	1431.1263	62.25	<.001
B (Time)	55229.5227	5	11045.9045	480.49	<.001
C (Pack Size)	7146.6758	4	1786.6690	77.72	<.001
AB	1005.8831	15	67.0589	2.92	<.001
AC	2233.0396	12	186.0866	8.09	<.001
BC	4855.4270	20	242.7714	10.56	<.001
ABC	2238.1401	60	37.3023	1.62	.05
W.CELL	5517.3154	240	22.9888		
TOTAL	82519.3825	359	229.8590		

Figure 7. Spring data. Time trend of percent loss, pack sizes within sediments. Cell standard errors, $\overline{X} \pm s = 1.94 \pm 1.98$.



◆ Igram
▽ 5 ''
● 10 ''
□ 20 ''
▲ 40 ''
% Loss
80
40
0
ROCK
GRAVEL
SAND
SILT
60
20
2
9
16
23
30
7
14
APRIL
MAY

Figure 8. Spring data. Time trend of percent loss, sediments within pack sizes. Cell standard errors, $\overline{X} \pm s = 1.94 \pm 1.98$.


♦ Rock
□ Gravel
● Sand
▼ Silt
% Loss
80
40
0
1gram
5gram
10grams
20grams
40grams
2
9
16
23
30
7
14
April
May

but different from all others. This ordering and degree was similar in form to the summer data.

Time: Again, the pattern is one of increasing weight loss through time, across all sediments and pack sizes. The sharp break in the slopes of Figs. 7 and 8 is again noticeable after the first week.

Interactions: All interaction effects are significant, although the ABC interaction is just barely so. There are no major differences from the general patterns of the other seasons in the two-way interactions.

Velocity Study

The analysis of variance is shown in Table VI. From this, it is noteworthy that neither velocity or pack size main affects are significant, although their interaction is just barely significant at the .05 level. The only high significance is the time treatment, showing significant weight loss in both velcoity treatments through time. The primary cause of this is the effect of the initial leaching. Subsequent weight losses were minor.

Seasonal Effects

The major seasonal effects are presented in Tables VII and VIII. Two figures give summaries of the seasonal trends. In Fig. 9 the mean percent losses for each of the five pack sizes (across all sediments) are presented for the four seasons. Similarly, in Fig. 10 the mean percent losses for the four sediments, averaged for all pack sizes, are presented for each season. More detailed graphs, i.e., splitting out each sediment at each pack size and vice versa presents largely redundant information. In each season the array is as shown, with minor variations: the trends and patterns of Figs. 9 and 10 persist.

So
A (Ve
B (Ti
C (Pa
AB
AC
BC
ABC
W. Ce
Total

TABLE VI

VELOCITY STUDY

ANALYSIS OF VARIANCE TABLE

Source	SS	DF	MS	F	$P(F_{i},j)$
A (Velocity)	0.9344	1	0.9344	.06	ns
B (Time)	584.9089	2	292.4544	20.09	$< .001$
C (Pack Size)	28.8011	1	28.8011	1.98	ns
AB	25.3089	2	12.6544	0.87	ns
AC	86.4900	1	86.4900	5.94	.05
BC	29.1822	2	14.5911	1.00	ns
ABC	28.0267	2	14.0133	0.96	ns
W. Cell	349.3867	24	14.5578		
Total	1133.0389	35	32.3725		

Figure 9. Seasonal mean percent losses for each pack size.

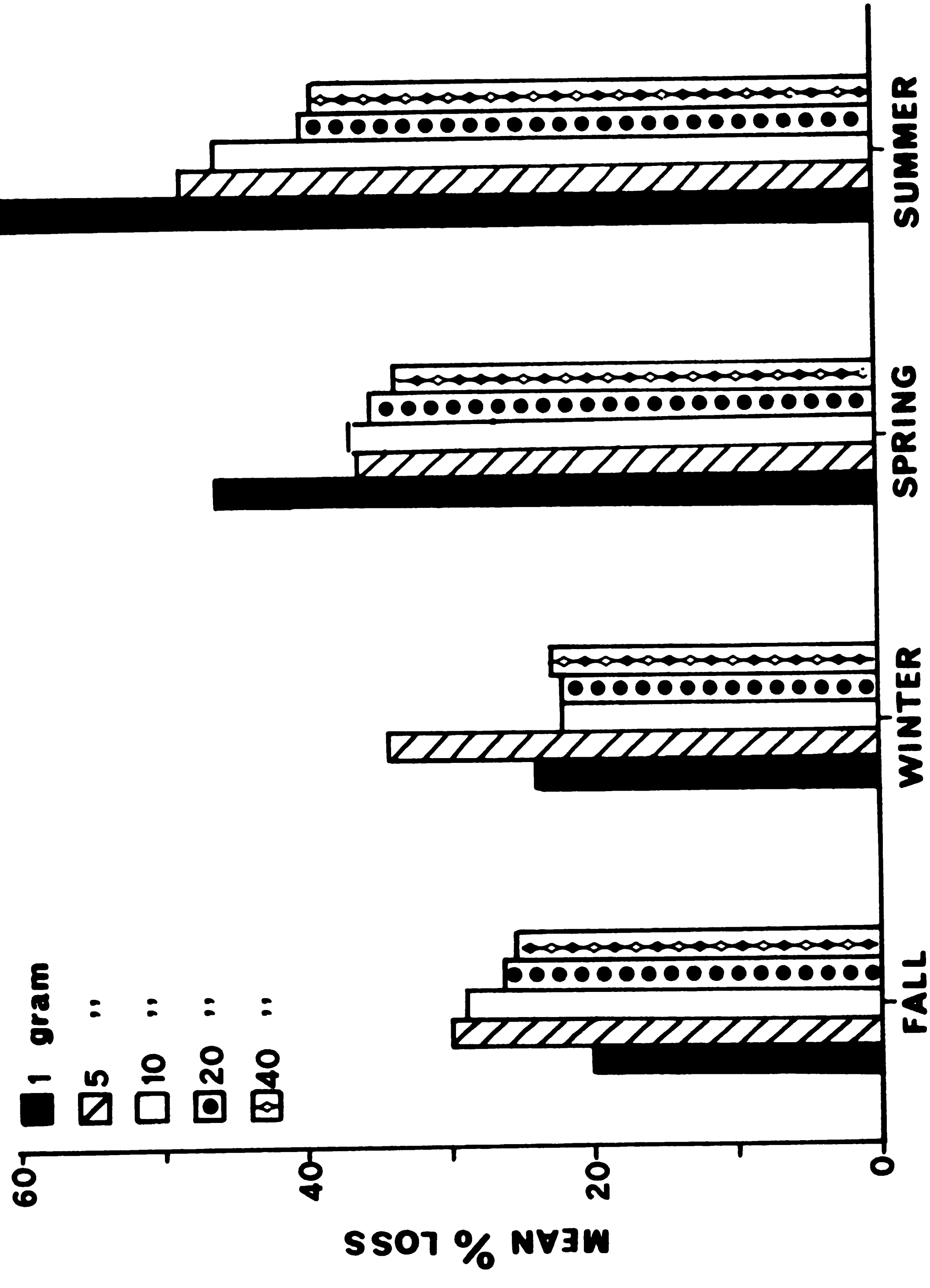

MEAN % LOSS
60
40
20
0
FALL
WINTER
SPRING
SUMMER
1 gram
5 "
10 "
20 "
40 "

Figure 10. Seasonal mean percent losses for each sediment type.

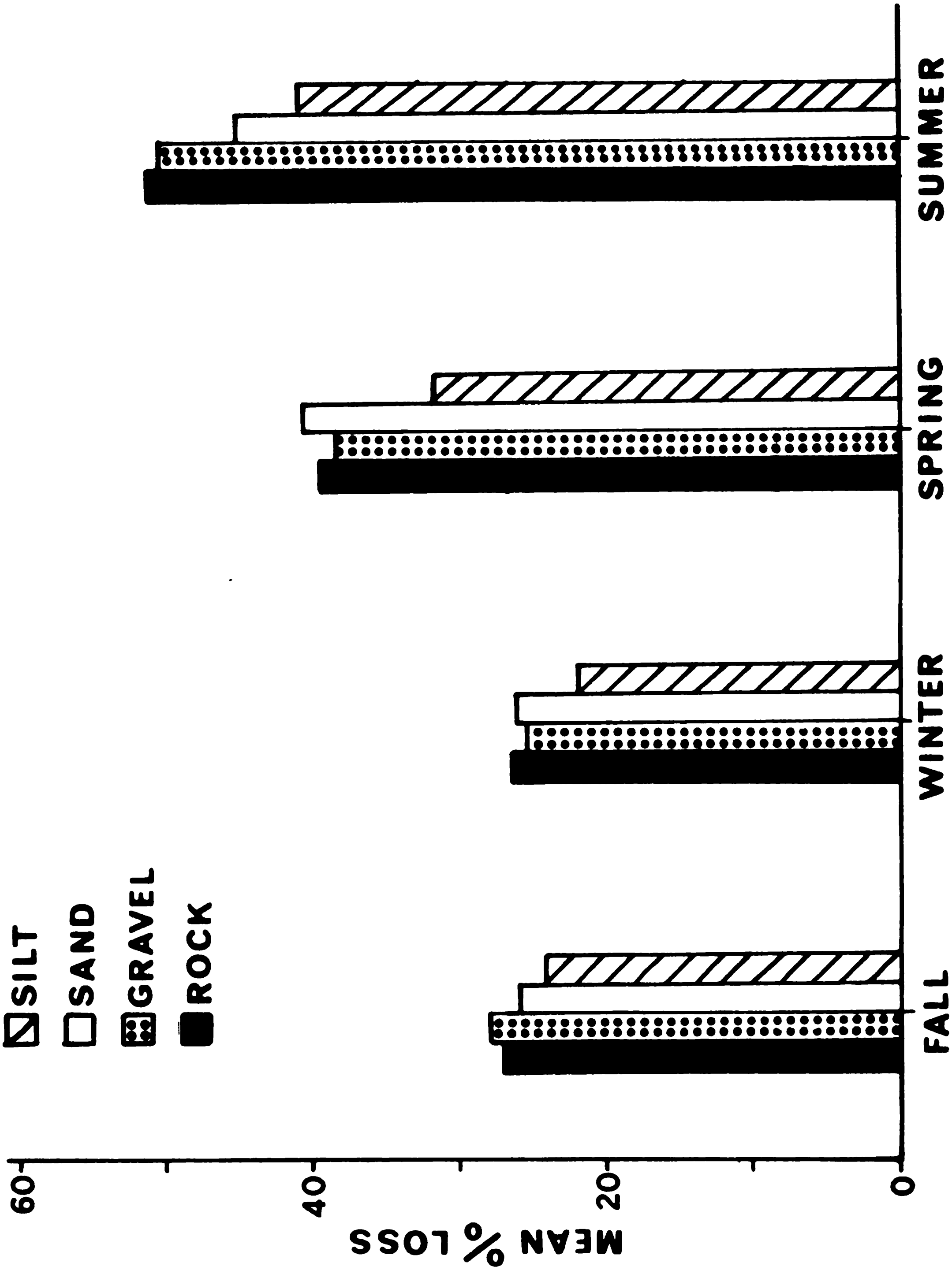

SILT
SAND
GRAVEL
ROCK
MEAN % LOSS
0
20
40
60
FALL
WINTER
SPRING
SUMMER

TABLE VII

SEDIMENT DIFFERENCES

Single Degree of Freedom F-Tests (Orthogonal Contrasts)

Contrast	SS=MS	F	$P(F_{1,240})$
Summer Data			
(Rock and gravel) vs. (sand and silt)	4865.1930	63.32	<.001
Rock vs. gravel	28.760	0.40	ns
Sand vs. silt	459.7268	6.46	<.0125
Fall Data			
(Rock and gravel) vs. (sand and silt)	592.9641	30.40	<.001
Rock vs. gravel	31.6051	1.62	ns
Sand vs. silt	135.0267	6.92	<.005
Winter Data			
(Rock and gravel) vs. (sand and silt)	416.4013	26.64	<.001
Rock vs. gravel	57.6584	3.69	ns
Sand vs. silt	774.1827	49.54	<.001
Spring Data			
(Rock and gravel) vs. (sand and silt)	715.5045	31.12	<.001
Rock vs. gravel	57.122	2.49	ns
Sand vs. silt	3520.752	153.15	<.001

TABLE VIII

PACK SIZE DIFFERENCES

Multiple Comparisons of Means
(Tukey's HSD Procedure)

Summer Data

Pack Size (gm.)	1	5	10	20	40
$\bar{X}_i$ (% loss)*	63.310	48.332	45.653	39.597	39.006

Fall Data

Pack Size (gm.)	5	10	20	40	1
$\bar{X}_i$ (% loss)	30.236	29.005	26.388	25.484	20.181

Winter Data

Pack Size (gm.)	5	1	40	10	20
$\bar{X}_i$ (% loss)	34.253	23.778	22.842	22.050	21.958

Spring Data

Pack Size (gm.)	1	10	5	20	40
$\bar{X}_i$ (% loss)	46.222	36.663	36.278	35.352	33.456

*Means not underlined by the same line are significantly different at the P = .01 level.

TABLE IX

ORTHOGONAL CONTRASTS FOR SEASONS

		(Fall & Winter) vs. (Spring & Summer)	Fall vs. Winter	Spring vs. Summer
1 gram	SS	62,486.390	372.672	8,706.964
	F	1,932.572***	11.526***	269.290***
5 grams	SS	5,829.810	464.648	4,184.725
	F	180.305***	14.371***	129.426***
10 grams	SS	14,000.444	1,413.441	2,351.774
	F	433.008***	43.715***	73.417***
20 grams	SS	10,191.152	565.339	518.892
	F	315.194***	32.333***	16.048***
40 grams	SS	8,387.965	201.084	886.974
	F	259.424***	6.219*	27.432***
Rock	SS	31,013.854	11.974	6,219.629
	F	959.201***	0.370 ns	192.362***
Gravel	SS	28,346.839	278.072	6,570.675
	F	876.715***	8.600**	203.219***
Sand	SS	25,914.514	0.678	936.980
	F	801.488***	0.021 ns	28.979***
Silt	SS	17,358.000	236.557	4,692.271
	F	536.851***	7.316*	145.123***

*** $P(F_{1,240}) < .001$

** $P(F_{1,240}) < .01$

* $P(F_{1,240}) < .05$

Pack Size: In Fig. 9 the predominant trend is for a modest degree of breakdown in the fall, less breakdown in winter, more in the spring and the most in the summer. The statistical evidence for this is presented below (see Planned Comparisons). While this trend occurs in general terms, particular details should be noted. These are as follows:

1. The relative magnitudes of the one and five gram pack means show more and greater fluctuations than the other sizes. This is clear from Table VIII. Note the preeminance of the one gram packs in spring and summer, and the five gram pack in fall and winter.

2. There is a wide spread among all the means in the summer.

3. There is clear differentiation of at least one particular size in each season.

Sediments: In Fig. 10 the overall seasonal trend is the same as in Fig. 9. Within this trend, particular sediment patterns can be discerned.

1. Silt has the least breakdown in all four seasons.

2. In fall, winter and spring, rock, gravel and sand mean are closely bunched and clearly distinguishable as a group from the mean of the silt.

3. There is a wider spread of sediment means in the summer, with sand clearly intermediate between silt and the pairing of rock and gravel.

Planned Comparisons

As mentioned in the design section a series of planned comparisons were made using orthogonal contrasts (single degree of freedom F-tests). The pairing was based, a priori, on the usual seasonal availability of terrestrially produced organic detritus. Therefore fall and winter were tested against spring and summer. This also splits the seasons by average temperature. Contrasts were made within each pairing as well. The sums of squares for each contrast (equal to the mean square in a single degree of freedom test), the F-ratio and level of significance of that ratio are found in Table IX. All contrasts are significant at the .001 level except the fall-winter contrast for sediments and the 40-gram pack size. Rock and sand means, contrasted for all and winter, were not significantly different.

It must be noted that the mean square errors for the four seasons were not homogeneous. The mean square error for the summer data was more than triple that of each of the other seasons (see Tables I-IV). The average of the four error terms was used in calculating the contrasts of Table 7. This biases the contrasts by making the error term of each contrast larger than it would have been, had the mean square error of the summer experiment been smaller. This results in smaller sums of squares for each contrast. Consequently the direction of the bias is to reduce the F-ratios somewhat. Hence, significance is harder to demonstrate. The degree of significance of the 40, silt and gravel contrasts for fall versus winter might have been higher. However, the non-significant contrasts would remain non-significant. Note that all four seasonal means square errors are valid estimates. The problem discussed here is a statistical bias due to the non-homogeneity of the errors. It does not reflect on the relative accuracy of any one estimate.

CHAPTER IV

DISCUSSION

A Framework for Community Level Investigations

In any biological study, the hierarchical organization of biological systems is one of the implicit assumptions. Embedded in the accepted framework is an important notion. That is that a behavior at a given level of organization is related to the levels above and below it. The constraints on the behavior are, in general, imposed from the levels above. The mechanisms determining the behavior operate at lower levels of organization.

When a community level behavior or process is being studied the constraints will come from the level above, namely the physical environment. The mechanisms will arise from levels below, i.e., the population level interactions such as predation and competition. Paine's (1966) work on the organizing effects of removing the starfish predator from the marine intertidal system is a good example of a study which focused on manipulating the mechanism (i.e., predation) and studying the community behavior. Similarly, Hall et al. (1970) manipulated fish and insect predation to study the effects on pond communities. By contrast, in this study, the relationship between the constraints, i.e., patches in the physical environment, and the behavior, i.e., leaf litter breakdown, were investigated.

Sediment Effects

A major finding of this study is that the community level process of leaf litter breakdown is heterogeneously distributed in alignment with patches of different bottom sediments in streams. There are several statistically important effects of sediments. Clearly, the effect of sediments is highly significant in all seasons (see Fig. 10 and Table VII). The breakdown on rocky and gravel sediments is not significantly different from each other. Silt always has less breakdown than the other sediments. Sandy sediments have the most variable relative breakdown. Sometimes it is more similar to rock and gravel (in winter and spring) and sometimes is intermediate between the rock-gravel combination and silt (in summer and fall). The essential point is that the community level process of leaf litter decomposition is patchily distributed in space, along a gradient of sediment types. These sediment patches are actually arrayed along several environmental gradients simultaneously. These are the gradients of sediment particle size, heterogeneity of particle size, stability of sediments and stream current velocity. A detailed discussion on the physical relations between these factors can be found in Leopold et al. (1964).

In these experiments, the direct effects of velocity appear to be minimal. The bricks to which the leaf packs were tied were set down on the bottom of the stream. At this depth the leaf packs were either within the boundary layer at the sediment-water interface (where current velocity = 0) or just into the flow where velocities are quire slow (for a succinct discussion of current velocity-depth relations in streams see Hynes (1970)). In the experimental flow channel velocity of 4 cm/sec. was maintained.

This approximates the velocity at the stream bottom in the rock and gravel sediments. No significant differences were found when comparing the breakdown of leaf packs in the flow channel to the breakdown in a standing water system (Table VII). This experiment was conducted with biological activity surpressed by $CuSO_4 \cdot 5H_2O$. The conclusion reached is that velocity per se does not directly account for the differences of breakdown found among sediments in the natural stream. That is not to say that velocity has no effect at all. Indirect effects, such as the structuring of different biological communities, different oxygen regimes, or carrying away leaf fragments sluffed from leaf surfaces following microbial activities are surely important. However, in such cases the role of velocity is secondary to the direct activities of the different communities inhabiting the different sediments. Another significant aspect of the velocity question is the role of current in sediment transport. Sediment laden waters can have a major abrasive effect on leaf litter. This relationship deserves further investigation. The laboratory studies presented here do not broach this issue. The fixed, stable nature of the experimental leaf packs also minimizes the effect of velocity.

It is interesting to note that the breakdown of leaf litter was consistently and significantly less in silt than in all other sediments. This trend holds true during all seasons. The silt bed has the finest particle size of sediments, the least within patch heterogeneity and the least sediment stability. The silt bed is relatively homogeneous in the horizontal plane. Variation in the silt bed is only apparent with regard to the depth of the layer of silt. The vertical dimension may show variation in oxygen, pH or other environmental variables. This reduced heterogeneity can be expected to result in diminished species diversity, and a community of reduced complexity compared to a more heterogeneous site. In addition, the inherent instability of the silt tends to further reduce the potential of the site for developing a complexccommunity when compared with the other three. The vaguaries of the environment in a silt bed make it a difficult place for aerobic organisms to live. Anaerobic conditions may play an important role in reducing the amount of breakdown in the silt bed. It was a common occurrence for the samples in this study to be completely buried in the silt after a period of high water. This sort of occurrence brings home the meaning of Moon's (1939) categorizing silt as a depositional substrate.

The rock and gravel sediments have consistently similar amounts of breakdown of leaf litter. There are no significant differences between these sediments in any season. From Fig. 10, it is apparent that the degree of breakdown in the sand sediment patch is also quite similar in the winter and spring, and to a lesser extent in the fall. In summer, sand has considerably less breakdown than the other two. Rock and gravel are the two most heterogeneous substrates. Both have considerable variation in three dimensions. Sand has intermediate heterogeneity between silt and the other two sediments. Adequate quantification of the degree of heterogeneity of a sediment patch awaits future research. When this is understood then different microhabitats can be more meaningfully defined. These steps are necessary to study the relations between physical structure and community function. When subjectively ranking relative stability of the sediments, gravel is greatest, followed by rock and sand and, of course, silt. As noted in the design section, the rocky sediments consisted of large boulders surrounded by sand. It is the sand part of the rocky site which contributes to the lower stability ranking of the site. In both rocky and sandy sediments bricks were partially covered by sand (to a greater degree in the pure sand substrate). It appears that the heterogeneity and stability factors, both of which should influence the structure and function of the community, are confounded in these sediments. However, in the summer, the heterogeneity gradient of 1) rock and gravel, 2) sand and 3) silt is apparent in the ranking of the degree of breakdown (Fig. 10). In the summer, the relative stability could be less important, since the system is not subject to the floods and high waters which were common in the other seasons (an unseasonable thaw in late December caused a "spring flood" in the winter, too). Consequently, the environmental stability effect would be minimized in the summer, allowing the effect of the heterogeneity gradient to manifest itself.

Although species diversity was not measured, it may be related to the different community responses observed. Mackay and Kalff (1969) have suggested that species diversity in stream sediments is proportional to the relative heterogeneity and stability of the sediments. The theory of species diversity asserts that diversity increases with greater environmental stability and heterogeneity [MacArthur and Levins (1964); Pianka (1966a); Sanders (1968, 1969); Slobodkin and Sanders (1969)]. In this work, the least breakdown of leaf detritus was found in the silt bed. In the animal collections made in the process of sampling leaf packs, there appeared (qualitatively) to be less biomass and lower species diversity in the silt than in the other sediments. While it may be appealing to assert that the conditions which produce higher species diversity also produce greater rates of community level processes, definite proof of that hypothesis is still pending. A possible relationship between increasing species diversity and increasing the number of pathways (functional diversity) for a given process, with subsequent increased efficiency is a potential connection between processing and diversity.

Species diversity is not the only variable which may differ from one sediment patch to another. As suggested above, the relative oxygen conditions probably vary as well. Silt has a greater tendency to anaerobiasis than the other sediments. Possibly the differences in current at the four sites also affect the available oxygen. Such differences could have highly significant effects on the degree of breakdown of leaf litter. Another related factor is the different potential for microbial colonization at the different sites. While one dimension of that issue is the available microbial diversity, it may also be related to the oxygen regime, current patterns, or a variety of other factors. The main point is that many different mechanisms at the community and population levels may be responsible for the highly significant sediment differences in leaf litter breakdown reported here.

Pack Size Effects

The size of a leaf pack has a highly significant effect on the extent to which it will be broken down.

It must be noted that the presentation of the data as percent of initial weight lost, while of considerable use for comparing losses across pack sizes, does contain an inescapable distortion. The percent loss does not accurately reflect the actual weight lost in grams. For instance, a 50 percent loss from a one gram pack is equivalent in weight to a 1.25

percent loss from a 40 gram pack. Both have lost 0.5 grams. Equivalent percent losses from different pack sizes obscure the reality that more actual biomass has been lost from the larger pack size. Therefore, when seasonal mean percent losses are compared (Fig. 9, Table 6), it should be remembered that the actual weight lost was always in rough proportion to the initial weight. The most weight actually lost was from the 40 gram packs, and the least from the one gram packs.

This difference is not surprising since it is known that leaching removes a fairly constant percentage of leaf weight through direct physical factors [Nykvist (1959a)]. Since, in ash leaves this takes place in only about 24 hours, the leaching effect is detected in the first sample, i.e., after one week. The steep initial slope of the loss curves in all pack sizes in all seasons as seen in Figs. 2, 4, 6 and 8 is due primarily to this factor. Although the time course of the leaching process is likely to vary from pack size to pack size, it is reasonable to assume that all of the leaching has taken place by the end of the first week of exposure to the stream. After this time the percent loss lines (for each pack size) take on less steep slopes. However, the week-to-week fluctuations can be quite extreme, particularly in the smaller leaf packs. These data are inconsistent with the assumption of a single, constant loss rate for a particular type of leaf litter [for example, see Petersen and Cummins (1973)]. These data indicate that there are at least two parts to the breakdown curve, one slope for leaching and one for decomposition. While the decomposition part might approximate a constant slope in controlled conditions and in the absence of macroscopic detritivores, in the natural stream there are wide and unpredictable fluctuations. These fluctuations raise many interesting mechanistic questions which this study was not designed to answer.

In each season different size leaf packs are outstandingly deviant from the general pattern. In the fall, the one gram size is broken down least. In the fall and winter, the five gram size is broken down least. In the fall and winter, the five gram size is broken down most. In the spring and summer, the one gram size has the greatest breakdown by far. It is common for groupings to occur among the other sizes as well. These are shown, with the significant differences in Table VIII. In all seasons, the 20 and 40 gram pack sizes are treated similarly. That is the case for the five and ten gram sizes in all but the winter set. It is only in the winter that the one gram pack size is not significantly different from the other sizes.

The summer results are the only ones which seem easy to explain. The degree of breakdown increased as the pack size declined. The relative magnitudes of the mean breakdown for each pack size were in rough proportion to a surface area to volume ratio (i.e., the initial outer area/total initial volume. After the leaf pack is colonized and eaten the surface-to-volume ratio becomes highly variable since each insect bite opens up new surfaces.) The initial surface area-to-volume ratio is highest for the one gram packs and decreases with increasing pack size to the low for the 40 gram packs. That would be a reasonable determinant of a physical or even a predominantly microbial process. However, the other data sets do not support such an orderly hypothesis. In the fall, where the relative rankings of the four largest leaf packs were unchanged, the one gram packs have the least breakdown. This pattern is consistent across all four substrates (see Figs. 3 and 4). The one gram size is still significantly different from the others, as in summer, but in the opposite direction. The summer data suggest that a fairly simple physical factor governs the community response to pack size. The unexpected results of the fall suggest a more complex sort of discrimination or selection. Is there an active selection for the one gram packs in the summer, and then an equally active selection against them in the fall? It should be noted that it is impossible to distinguish two equally plausible explanations for these results. One cannot separate the effects of pack size selective feeding from differential mortality in different size leaf packs. However, whatever the actual mechanism is, the size of the leaf pack is an important factor in leaf litter breakdown in streams.

In the winter and spring four of the five sizes are treated very much alike, with one size being processed considerably more. The highest percentage breakdown occurred in the five gram packs in the winter, and in the one gram packs in the spring. Again, these patterns hold across all sediments (see Figs. 5 and 7).

The basic finding is that in every season, there has been a pack size specific response by the stream community in the complex community level process of leaf litter breakdown. In the lab experiments with microbes surpressed and at room temperature (Table VI), no such differentiation occurred. One and ten gram packs were not significantly different from each other. In the field, at comparable temperature (i.e., in summer) these sizes were processed differently. The implication is that pack size effects are not the result of purely physical processes alone but rather result from different degrees of biological activity in the different pack sizes which are mediated by physical factors. That means that the biological community in a given area responds differently to different sizes of the same material. The significant interaction between sediments and pack sizes in all seasons further supports this idea, i.e., in different physical environments (sediment patches) the size discrimination changes.

This community level size discrimination as a process is not really analogous to population level size specificity as in fish feeding. The leaf pack cannot be viewed as a particle by the stream microbes or detritivores. Even the smallest leaf pack is considerably larger than they are. Rather, the leaf pack is an environmental patch, a spatial discontinuity, or a block of resources. Pack size, being a measure of the size of the resource block, can be considered patch size for the biological community of the stream. The theoretical basis for different population level interactions in patches of different sizes is outlined in MacArthur and Pianka (1966).

In this discussion, the prospect of community level discrimination is raised. This is a tenuous area for speculation. It suggests a highly anthropomorphic, superorganism view, with whole communities searching their environment with a giant collective eye. That concept is thoroughly rejected. The community does not make choices. Any behaviors displayed at the community level have been the result of constraints from the physical environment and mechanisms operating at lower levels of organization.

In this study, the process or behavior under examination is the breakdown of leaf litter in a stream, a community level behavior. The highly significant effect of the sediments and pack sizes, demonstrate that there are different degrees of community level behavior associated with the constraints imposed by different environmental patches. To understand the mechanisms of these differences one must look at the lower levels of organization, i.e., populations, individuals, etc. In this context, there is no need to invoke the spectre of the super-organism to explain community level behaviors. The mechanisms for the pack size discrimination at the community level should be sought at the population level and below.

Although elucidating those mechanisms was not the goal of this study, some suggestions will be offered. The different size leaf packs offer different size patches to the organisms comprising the community. These different size packs comprise different types of microhabitats: different degrees of protection from the elements, different accessibility of central leaves, possibly differing oxygen or temperature regimes. These types of microclimatic differences could have dramatic effects on the quality and degree of microbial colonization, the effect of which would have repercussions in the entire scheme of animal feeding and breakdown. No ready explanations suggest themselves for the preeminance of the five gram packs in winter or the one gram packs in spring. It is only speculation to hypothesize that the conditions were particularly good for some heavy feeding in those pack sizes. For instance, if the size of the pack determines the heat content, this could be a factor in the cold winter waters. The one gram pack might be too small to hold sufficient heat to allow the microbes to take hold and grow. The five gram packs might be just large enough to hold the heat needed to allow adequate growth, while having a high enough surface-to-volume ratio to provide sufficient microbial access. In this way a combination of effects can establish one pack size as the optimum site in a given season.

However, this study has shown that a community level process can be effected by the size distribution of the substrate to be processed. The results are clear, pack size is an important determinant of leaf litter breakdown in streams.

Seasonal Effects

The specific within season variations in sediments and pack size effects have been discussed above. It remains to consider the more general question of the between season variation in leaf litter breakdown. In a stream there are several important seasonal trends. The first is the temporal variation in the input of allochthonous organic matter. Particulate organics, like leaves, enter predominantly in the autumn. Additional material is washed in during the spring rains. There is a low level, continuous addition of bud scales, flower petals, etc. from early spring to early fall. The big pulse of particulate organics comes in the fall as leaves [Minshall (1967)]. Fisher (1971) and Fisher and Likens (1972) trace the input of dissolved organics, entering via different water sources. These follow the seasonal pulses in water availability. The availability of water is the second major trend. This is highly variable, with the classic pattern being spring and autumn flooding, separated by moderate water levels in winter and low levels in summer. The third trend is, of course, the temporal changes in ambient temperature. Although the well shaded flowing water of a woodland stream is not subject to the temperature excursions of a standing body of water, there is considerable variation in temperature on a seasonal basis.

The question arises as to whether the community level process of leaf litter decomposition is keyed in to one of these seasonal trends. If the main effect was due to the degree of loading with leaf litter, there might be a community response to food saturation. In this case, the extent of breakdown (both total and percentage) in the experiments could be expected to be inversely related to the natural availability of particulate organics, i.e., least breakdown in the fall, more in the spring, still more in the winter (perhaps roughly the same as spring), and most in the summer. If the effect of catastrophic flooding was the major one, one would expect to see reduced breakdown in the spring and fall, with more in the winter and most in the summer. This is because the flooding would tend to disrupt the community processing capability by the wholesale removal of the processors. If the major effect was temperature, the breakdown should increase with increasing temperature, i.e., winter least, then fall, spring and the most in summer.

The data support the hypothesis that temperature governs the rate of breakdown of leaf litter in Augusta Creek (see Figs. 9 and 10). Table VIII shows the orthogonal contrasts, testing the differences between seasons. The warm seasons, summer and spring, are significantly different from the cool seasons, for all categories tested. The summer always had significantly greater breakdown than the spring. For some classes, winter and fall were indistinguishable. The hypothesis of a thermal regulatory type of control is quite a plausible explanation for these community dynamics, since the community is composed of only poikilothemic organisms.

A possible alternative explanation of these seasonal differences involves the relationship between available detritus and the detritus feeding potential of the stream community. If the seasonal feeding potential (calculated from the life history and population density data of all species present in the stream, together with temperature dependent per capita feeding rates) it should be possible to predict the rate of breakdown of leaf litter in the following way. The availability of suitable detrital food can be determined from the seasonal input of allochthonous organic matter using the model of Boling et al. (1973b). This can be compared to the feeding potential for a given time period. The amount of breakdown should reflect the magnitude of the difference between the available food (gm/m^2) and the feeding potential (gm/m^2) at any given time. The seasonal patterns which would emerge from such data might produce similar patterns to those detected here.

It should be noted that the period of six weeks used in these experiments is adequate for detecting significant loss of weight of Fraxinus americana leaflets. In all seasons evidence of insect feeding was obvious (i.e., skeletonization of leaves, holes from feeding, etc.). This is because of the short time lag in the leaching and microbial colonization steps on this species. However, other species of leaves such as the oaks (Quercus spp.) have longer time lags, and would not evidence the marked losses of weight noted in white ash in the time allowed. Further discussion of the time lags and the grouping of different leaf species can be found in Boling et al. (1973b) and Petersen and Cummins (1973).

Although the study has been carried out in one stream, Augusta Creek, and using one type of leaf, white ash (Fraxinus americana), other studies help to put this work in context. White ash is only one of a broad range of leaf species whose decomposition has been studied in this general manner

[Petersen and Cummins (1973); Kaushik and Hynes (1971); Nykvist (1959a, 1959b, 1961, 1962)]. With these data it is possible to extend the results beyond white ash to the other species whose breakdown rates are known, with appropriate scaling. The scaling will have to be a complex one, simultaneously relating three factors: microbial conditioning rates, breakdown rates, and preferential feeding by detritivores. In addition, such scaling coefficients will have to be temperature dependent. An example of this is presented in Boling et al. (1973b). Another complication is suggested by the work of J. B. Sedall (Oregon State University, personal communication) who has found that leaves that have characteristically slow breakdown rates are broken down faster in mixed leaf packs with other, faster leaves. In addition, Augusta Creek may be considered typical of many temperate zone woodland streams. Therefore, it is hoped that these results may be generalized.

Implications for Community Theory

Several aspects of community theory are broached by this work. Perhaps the most fundamental finding pertains to the hierarchical structure of ecology. Ecologists are used to the step increments in organization: individual, population, community, ecosystem. These results suggest that another level of organization exists, somewhere between the population and the ecosystem. Most ecologists would not hesitate to refer to the "stream community." However, this work has shown that a community dynamic process varies from one sediment patch to another. These differences correlate well with the works of Carpenter (1927), Percival and Whitehead (1927), Thorup (1966), and Mackay and Kalff (1969), who all distinguished different assemblages of populations associated with different sediment types.

If one accepts a behavioral basis for a community definition then there are different communities in each sediment patch. The different degrees of leaf litter processing may not indicate functional differences, but rather behavioral ones, i.e., different magnitudes of the same type of processing. Then, how does one refer to the familiar aggregate stream community? Is it a "megacommunity" or some other such term? There is good intuitive sense in defining communities from a geographical basis. There is a need to retain such useful concepts as a stream, forest or old-field community based on large and significant features of the landscape. Then what should one call the patch-specific assemblages? Root (1973) suggests calling them component communities. These, he argues, are co-adapted to their environment and each other. The morphological adaptations of the stream organisms to their environment are well known (i.e., gill covers in silt, streamlining on rocks, etc.) and the associations are recognizable (for instance, Carpenter's (1927) limnophilous associations, etc. or Hora's (1930) scheme). The sediment-specific communities fit Root's definition of a component community. Then the stream enters his scheme as a compound community -- defined as an array of component communities and their interactions.

In the stream system, sediment particle size appears to be an organizing factor in community dynamics of the former category. Other factors such as mean tide levels in Connell's barnacle studies (1960), annual rainfall, soil moisture are examples of other physical variables which effect community dynamics. It is possible to gain a more complete understanding of community level processes if one understands how they are distributed and dimensioned along the relevant environmental gradients. That such gradients influence the descriptive statistics of the community such as species diversity, is well established [i.e., see Whittaker (1956), Pianka (1966a, 1966b, 1967), Kohn (1967)]. This work extends that relationship to community processes as well.

In addition, the nature of the effect of the physical structure can often be predicted on the basis of current theoretical constructs. As in this work, different community level processes can be expected to increase their rates in direct proportion to the spatial heterogeneity and stability of their environment. Testing and quantifying such relationships can lead to measures of physical structure for use as predictors of community function. The spatial heterogeneity of a system is likely to be an important organizing factor in the community dynamics of an area.

Along this line, a study of the patch specific structure of the environment will help focus the important control factors in community dynamics. The microclimatic differences in degree-days, oxygen availability, shading, etc. can determine significant patch-to-patch variation. This work has shown that such variation does occur in a community level process, leaf litter decomposition in a woodland stream.

Directions

Several lines of research are suggested by this work. One is to elucidate the mechanisms by which such variation in community processes occur. In particular, the role of micro-climates on the dynamics of hyphomycete fungi on leaf litter in streams warrants investigation. Another necessary link is to better characterize the patch-specific distributions of important detritivore species.

For more accurate and comparable studies on spatial heterogeneity effects, it is important to develop some simple measures or indices of environmental heterogeneity for common use. Once in hand, such tools will enable ecologists to study the effects of spatial heterogeneity between and within many different systems.

Summary

1. Sediment type and leaf pack size have significant effects on the breakdown of white ash leaf litter in Augusta Creek.

2. Silt fostered consistently less breakdown than the other more complex, stable sediments.

3. Smaller pack sizes had greater relative breakdown than larger ones. Either the one or five gram size predominated in every season.

4. Seasonal effects were highly significant with the greatest breakdown in summer followed by spring, fall and winter.

5. The implications of this work for community theory are discussed.

APPENDICES

APPENDIX I

FIELD DATA: BIOMASS REMAINING (g.)

APPENDIX I

FIELD DATA: BIOMASS REMAINING (g.)

SUMMER 1972

July 4	Rock	Gravel	Sand	Silt
1g	0.64, 0.79, 0.61	0.69, 0.77, 0.70	0.83, 0.90, 0.79	0.75, 0.79, 0.76
5g	3.86, 3.97, 3.55	3.82, 3.48, 3.62	4.52, 4.08, 4.02	3.48, 3.92, 4.26
10g	7.29, 7.59, 7.51	8.00, 7.29, 7.30	8.31, 7.65, 7.56	4.77, 7.70, 7.68
20g	16.43,14.66,14.99	15.60,17.05,14.82	15.13,15.89,16.11	18.18,15.31,16.52
40g	31.68,32.72,33.26	28.90,29.94,31.13	30.80,31.51,29.96	32.01,32.19,33.80
July 11				
1g	0.51, 0.36, 0.54	0.64, 0.46, 0.36	0.65, 0.62, 0.49	0.71, 0.75, 0.74
5g	4.01, 3.22, 3.50	2.93, 2.74, 3.59	3.80, 3.24, 3.45	3.74, 3.21, 3.89
10g	6.47, 6.94, 8.73	5.04, 6.63, 6.43	6.41, 6.73, 6.82	7.01, 6.97, 7.15
20g	14.61,14.26,12.80	14.42,13.82,14.10	14.09,14.60,14.48	14.16,13.58,15.49
40g	29.47,31.76,28.27	25.61,27.34,30.68	31.00,27.61,27.78	26.14,30.20,27.75
July 18				
1g	0.10, 0.38, 0.26	0.10, 0.38, 0.18	0.15, 0.27, 0.54	0.59, 0.55, 0.61
5g	3.43, 2.47, 3.29	2.63, 2.69, 2.74	2.49, 3.08, 3.38	3.32, 3.32, 3.45
10g	5.85, 5.37, 5.42	4.73, 5.65, 4.97	5.54, 5.59, 6.44	6.81, 6.10, 7.08
20g	13.69, 9.26,13.80	12.49,12.11,12.98	13.24,12.55,12.27	14.27,12.17,13.01
40g	25.82,26.24,23.74	24.11,24.15,24.63	24.25,25.53,25.45	25.52,26.94,27.22
July 25				
1g	0.08, 0.12, 0.38	0.44, 0.25, 0.58	0.00, 0.52, 0.27	0.02, 0.05, 0.26
5g	3.29, 1.81, 1.84	2.98, 2.86, 2.46	2.41, 2.40, 1.77	2.07, 1.08, 2.16
10g	3.37, 5.04, 5.57	6.27, 6.31, 5.82	5.10, 5.39, 6.32	4.31, 4.13, 4.30
20g	10.79,10.02,12.09	12.67,13.56,12.44	13.12,11.74,11.68	11.42,11.02, 8.77
40g	17.95,20.99,23.23	24.68,28.01,25.70	20.81,22.21,24.56	20.11,20.78,21.18
Aug. 1				
1g	0.00, 0.00, 0.10	0.01, 0.00, 0.01	0.07, 0.35, 0.34	0.45, 0.16, 0.55
5g	1.30, 0.88, 0.00	0.05, 1.39, 1.25	2.25, 2.55, 1.96	2.77, 2.52, 3.19
10g	3.31, 3.29, 3.99	3.38, 3.50, 3.95	4.59, 5.27, 4.15	5.80, 2.90, 4.34
20g	8.68, 7.63, 9.48	9.85, 8.71, 8.10	9.08,10.95, 4.81	12.05,12.01,13.04
40g	19.46,18.40,19.15	19.16,18.17,19.52	20.99,22.59,18.90	23.79,24.96,25.02
Aug. 8				
1g	0.00, 0.00, 0.04	0.00, 0.06, 0.04	0.11, 0.23, 0.24	0.00, 0.27, 0.25
5g	0.18, 1.50, 0.83	0.00, 0.00, 0.48	1.43, 0.62, 2.15	2.59, 2.74, 2.20
10g	3.08, 2.90, 3.08	1.97, 3.80, 2.78	3.91, 2.55, 4.08	4.41, 5.86, 2.99
20g	2.31, 8.27, 8.21	7.71, 8.11, 8.15	8.60, 9.43, 8.59	11.28,11.20,11.43
40g	16.27,15.79,15.72	16.52,16.84,13.75	16.97,20.01,19.66	19.63,18.56,21.50

FALL 1972

Oct. 24	Rock	Gravel	Sand	Silt
1g	0.97, 0.93, 0.83	0.89, 0.84, 0.98	0.96, 0.86, 0.99	0.88, 0.96, 0.99
5g	4.12, 4.17, 4.27	3.69, 3.84, 3.86	3.91, 3.90, 3.71	3.92, 4.02, 3.78
10g	8.09, 8.62, 8.16	6.99, 7.93, 7.57	6.38, 7.32, 8.11	7.69, 7.44, 6.77
20g	17.30,15.77,16.78	16.52,15.66,15.75	15.47,15.72,15.46	16.69,15.47,15.81
40g	32.57,32.73,32.45	30.88,29.98,31.32	33.05,31.60,33.18	31.03,31.92,33.22
Oct. 31				
1g	0.69, 0.84, 0.98	0.83, 0.83, 0.95	0.76, 0.89, 0.98	0.98, 0.99, 0.99
5g	3.71, 3.65, 3.71	3.49, 3.59, 3.55	3.78, 3.77, 3.86	4.02, 4.21, 4.53
10g	7.59, 7.83, 7.49	7.62, 7.15, 7.11	7.46, 7.85, 7.67	7.97, 7.44, 7.97
20g	15.62,15.91,15.27	14.53,16.08,14.28	15.72,15.56,15.67	16.11,16.46,15.82
40g	31.17,29.88,31.78	31.13,30.95,32.30	31.09,31.64,31.31	33.25,31.89,33.80
Nov. 7				
1g	0.75, 0.78, 0.76	0.74, 0.70, 0.68	0.78, 0.70, 0.82	0.65, 0.84, 0.85
5g	3.36, 3.42, 3.78	3.27, 3.19, 3.59	3.53, 3.64, 3.47	3.79, 3.56, 3.45
10g	7.50, 7.73, 7.48	7.34, 7.01, 7.15	7.07, 7.09, 7.26	7.24, 7.33, 6.99
20g	14.82,14.77,14.26	14.61,14.81,14.36	15.49,14.83,14.53	15.16,14.47,13.85
40g	29.52,29.80,29.90	29.66,29.21,29.47	28.67,31.95,30.49	30.13,29.49,30.50
Nov. 14				
1g	0.63, 0.83, 0.81	0.69, 0.81, 0.95	0.84, 0.76, 0.89	0.74, 0.92, 0.82
5g	3.47, 3.06, 3.25	3.34, 3.32, 3.26	3.06, 2.76, 3.19	3.38, 3.44, 3.48
10g	7.21, 6.86, 6.89	6.80, 6.83, 7.24	6.90, 6.91, 6.95	7.21, 6.99, 7.02
20g	14.29,13.79,13.61	13.91,13.83,14.12	14.33,14.65,15.89	15.31,15.55,15.20
40g	28.89,27.20,28.13	27.98,28.15,28.46	29.89,29.00,28.38	30.88,29.29,29.86
Nov. 21				
1g	0.70, 0.67, 0.72	0.81, 0.72, 0.69	0.82, 0.78, 0.72	0.71, 0.72, 0.86
5g	3.43, 3.01, 3.34	3.08, 3.63, 3.20	3.04, 3.35, 3.32	3.53, 3.51, 3.27
10g	6.57, 6.51, 5.78	6.28, 6.93, 6.94	6.67, 6.63, 7.89	6.45, 6.79, 6.97
20g	13.85,13.69,13.92	14.69,13.24,12.85	14.62,13.81,13.29	14.62,14.26,13.82
40g	28.25,29.57,26.04	28.11,27.91,27.32	27.23,27.70,29.32	26.95,31.91,29.10
Nov. 28				
1g	0.58, 0.59, 0.69	0.70, 0.50, 0.70	0.68, 0.76, 0.68	0.78, 0.65, 0.71
5g	3.06, 3.06, 2.98	2.75, 2.93, 2.96	3.36, 3.26, 3.13	3.14, 3.39, 3.30
10g	6.39, 6.05, 6.17	6.32, 6.60, 6.18	6.74, 6.64, 6.40	6.67, 6.35, 6.66
20g	13.34,12.40,12.93	12.61,13.50,13.30	14.69,13.52,13.84	14.80,14.49,14.06
40g	27.07,28.00,27.13	28.18,28.48,27.56	28.87,28.49,28.42	27.27,29.53,28.62

WINTER 1973

Jan. 22	Rock	Gravel	Sand	Silt
1g	0.87, 0.74, 0.80	0.81, 0.98, 0.77	0.75, 0.80, 0.72	0.82, 0.79, 0.92
5g	3.40, 3.21, 3.32	3.47, 3.44, 3.49	3.68, 3.44, 3.44	3.12, 3.44, 3.61
10g	8.38, 8.51, 8.34	8.15, 8.04, 7.96	8.26, 7.88, 8.59	8.91, 8.43, 8.20
20g	15.60,15.64,16.02	17.12,16.83,16.28	17.24,16.72,16.92	16.14,15.93,16.75
40g	32.21,32.30,33.51	32.39,32.36,31.95	32.05,30.55,31.10	32.27,32.94,32.04
Jan. 29				
1g	0.79, 0.80, 0.88	0.74, 0.54, 0.76	0.79, 0.87, 0.76	0.82, 0.88, 0.80
5g	3.67, 3.50, 3.29	3.46, 3.40, 3.59	3.44, 3.39, 3.37	3.58, 3.55, 3.12
10g	7.58, 8.12, 7.44	7.62, 8.15, 8.32	8.08, 8.02, 7.79	8.47, 8.51, 8.12
20g	15.93,15.81,15.68	16.09,15.74,16.75	16.18,16.33,15.64	16.35,16.95,16.47
40g	31.91,31.90,30.96	30.59,32.50,32.03	31.76,32.32,31.85	31.52,32.87,31.75
Feb. 5				
1g	0.77, 0.83, 0.69	0.80, 0.92, 0.95	0.88, 0.81, 0.70	0.81, 0.84, 0.77
5g	3.27, 3.23, 3.29	3.23, 3.31, 3.49	3.42, 3.41, 3.46	3.55, 3.53, 3.42
10g	7.75, 7.96, 7.92	7.62, 7.98, 7.93	7.55, 8.06, 7.96	8.58, 8.15, 8.03
20g	15.87,15.27,15.48	15.97,15.62,15.59	15.77,15.44,15.83	16.05,16.10,15.93
40g	31.20,31.04,31.28	31.68,31.23,30.87	31.73,30.73,31.01	31.60,32.32,32.09
Feb. 12				
1g	0.79, 0.71, 0.88	0.85, 0.85, 0.63	0.71, 0.73, 0.68	0.75, 0.73, 0.88
5g	3.17, 3.33, 3.12	3.14, 3.33, 3.20	3.37, 3.04, 3.35	3.45, 3.31, 3.37
10g	7.80, 7.80, 7.52	7.55, 7.70, 7.67	8.00, 7.80, 7.73	7.80, 7.83, 7.89
20g	15.77,14.75,15.19	15.38,15.46,15.90	15.39,15.65,15.29	16.08,15.97,16.21
40g	29.96,29.84,30.26	29.83,30.99,31.46	30.74,29.58,29.87	31.06,31.17,31.96
Feb. 19				
1g	0.55, 0.62, 0.79	0.84, 0.73, 0.66	0.74, 0.79, 0.73	0.85, 0.84, 0.87
5g	3.02, 2.87, 3.04	2.98, 3.14, 2.96	3.21, 3.33, 2.96	3.43, 3.19, 3.48
10g	7.34, 7.74, 7.08	7.12, 7.92, 7.42	7.16, 7.19, 7.04	7.98, 8.14, 8.40
20g	14.40,15.41,15.36	15.03,14.86,14.51	15.07,14.25,14.36	15.99,16.16,16.40
40g	30.27,30.78,28.38	29.74,30.30,29.69	30.67,30.39,29.80	30.57,30.86,30.93
Feb. 26				
1g	0.51, 0.53, 0.60	0.62, 0.68, 0.51	0.57, 0.65, 0.53	0.89, 0.89, 0.73
5g	2.71, 2.95, 3.08	3.07, 3.10, 2.96	2.97, 3.22, 3.10	3.12, 3.29, 3.30
10g	6.89, 7.00, 6.98	7.05, 7.27, 6.79	7.19, 7.09, 7.01	7.46, 7.52, 8.01
20g	14.89,14.08,14.22	14.22,14.26,14.08	13.45,13.93,15.06	15.44,15.80,15.51
40g	28.28,29.38,29.21	28.38,29.17,29.26	28.71,28.71,27.51	29.75,29.20,31.08

SPRING 1973

April 9	Rock	Gravel	Sand	Silt
1g	0.79, 0.79, 0.76	0.84, 0.85, 0.84	0.80, 0.76, 0.83	0.84, 0.88, 0.77
5g	3.91, 3.90, 4.26	4.11, 4.00, 4.34	3.88, 4.09, 3.97	3.94, 4.29, 4.27
10g	7.67, 7.86, 7.62	7.82, 7.68, 7.87	7.70, 7.51, 7.61	8.10, 8.25, 8.37
20g	15.40,14.58,15.85	15.01,15.63,15.54	15.49,15.40,15.26	15.55,16.01,15.41
40g	31.24,32.38,31.46	31.14,31.06,30.47	32.53,31.95,32.13	32.25,33.00,31.95
April 16				
1g	0.67, 0.67, 0.74	0.66, 0.73, 0.76	0.65, 0.68, 0.72	0.82, 0.79, 0.76
5g	3.83, 4.01, 3.79	4.00, 3.88, 4.09	3.66, 3.62, 4.05	4.19, 4.02, 4.14
10g	7.37, 7.19, 7.46	7.45, 7.23, 7.58	7.57, 7.11, 7.21	7.58, 7.90, 7.82
20g	15.21,15.04,14.72	14.98,14.56,14.83	14.65,15.15,14.74	15.30,14.96,14.76
40g	29.72,30.96,29.74	28.92,30.00,30.76	29.31,29.12,29.13	29.80,31.30,31.74
April 23				
1g	0.30, 0.54, 0.46	0.59, 0.67, 0.56	0.57, 0.53, 0.55	0.72, 0.77, 0.78
5g	3.48, 3.75, 3.66	3.46, 3.53, 3.26	3.82, 3.16, 3.35	3.54, 3.70, 3.67
10g	6.79, 6.98, 6.10	6.59, 6.18, 6.94	6.50, 6.96, 7.19	7.13, 7.26, 7.22
20g	13.01,13.47,13.04	14.00,13.25,13.64	13.15,12.66,12.95	14.13,14.67,14.02
40	28.01,25.28,28.19	27.59,28.75,28.27	27.41,27.32,30.11	28.44,27.22,27.74
April 30				
1g	0.21, 0.53, 0.37	0.45, 0.47, 0.42	0.30, 0.29, 0.26	0.61, 0.54, 0.61
5g	2.77, 2.65, 2.98	2.79, 2.94, 2.71	2.70, 2.29, 2.83	3.00, 3.26, 3.13
10g	5.91, 6.64, 6.27	5.38, 6.13, 6.17	5.57, 4.53, 5.37	6.49, 6.30, 6.40
20g	11.22,11.55,11.36	11.53,11.61,11.63	12.45,12.10,11.86	13.23,12.63,12.04
40g	25.00,26.08,22.73	23.39,23.31,26.13	25.82,24.46,22.92	27.77,28.09,26.52
May 7				
1g	0.45, 0.22, 0.27	0.18, 0.33, 0.46	0.60, 0.20, 0.19	0.57, 0.59, 0.51
5g	2.30, 2.69, 2.20	2.63, 2.29, 2.46	2.30, 2.54, 2.42	3.18, 2.88, 2.61
10g	4.67, 5.38, 5.20	5.09, 5.15, 5.34	5.08, 3.80, 4.55	5.99, 5.74, 6.11
20g	11.06,11.43,11.78	11.14,11.92,11.72	10.23,10.50,10.77	12.09,12.13,12.54
40g	22.98,22.92,21.94	22.63,22.60,22.88	22.36,20.81,21.81	24.55,24.75,26.38
May 14				
1g	0.45, 0.11, 0.20	0.13, 0.18, 0.16	0.15, 0.38, 0.28	0.52, 0.58, 0.51
5g	1.98, 1.86, 2.10	2.28, 2.18, 2.44	1.59, 1.61, 2.11	2.56, 2.84, 2.68
10g	4.21, 4.95, 4.55	4.89, 5.00, 5.17	4.88, 4.33, 4.12	4.92, 4.82, 5.80
20g	10.84,10.07,10.45	9.32,10.31,10.35	9.42,10.26,10.74	11.20,10.80,10.63
40g	22.16,21.43,22.00	20.60,19.54,21.44	21.20,21.65,20.91	23.17,23.71,23.44

APPENDIX II

LABORATORY VELOCITY STUDY - WEIGHT REMAINING (g.)

APPENDIX II

LABORATORY VELOCITY STUDY - WEIGHT REMAINING (g.)

	FAST WATER		STANDING WATER	
	1 gram	10 grams	1 gram	10 grams
2 weeks:	.77	7.72	.77	7.91
	.82	7.71	.79	7.82
	.84	7.92	.73	7.84
4 weeks:	.64	7.13	.73	7.14
	.75	7.01	.77	7.32
	.85	7.22	.72	7.40
6 weeks:	.75	6.95	.67	6.92
	.70	6.65	.62	6.85
	.72	7.21	.60	7.30

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