

AN ABSTRACT OF THE THESIS OF

Martin Dieterich for the degree of Doctor of Philosophy in Entomology presented on December 7, 1992.

Title: Insect Community Composition and Physico-Chemical Processes in Summer-Dry Headwater Streams of Western Oregon

Abstract approved: Redacted for Privacy

N. H. Anderson

Seven streams, one of them permanent, were studied in western Oregon, USA. The research was designed to assess the value of summer-dry headwaters for conservation oriented landscape management. Streams were categorized primarily according to exposure (forest versus meadow sites) and secondarily according to flow duration (ephemeral = short-flow versus temporary = long-flow sites). Ephemeral streams have discontinuous flow and last less than three months annually. Temporary streams have continuous flow for more than five months each season.

Ephemeral forest streams were highly efficient at filtering road-generated sediment. Uptake lengths for suspended sediment were short (36 m - 105 m) at moderately elevated input concentrations. As a result of the filtration mechanism, filtration efficiency is expected to increase as annual flow duration decreases.

Injection experiments yielded nitrate uptake rates of almost 1% per m of temporary stream channel. Exchange with subsurface flow was the most important route for nitrate removal from the water column. Biological uptake was insignificant in a light-limited forest stream, whereas a considerable amount of nitrate was retained by the biota in a nutrient-limited meadow channel.

At least 207 insect species were collected from the summer-dry streams. Species richness recorded from temporary forest streams exceeded that in an adjacent permanent headwater and there was high overlap between the fauna of the permanent and the temporary streams. Species richness in ephemeral channels was only 1/4 to 1/3 of that in long-flow forest streams.

Multivariate analysis of community structure revealed flow duration and microhabitat pattern (riffle - pool) as the most important environmental factors determining faunal composition in temporary forest streams. Summer drought conditions at the sample sites also were important.

By providing habitat and contributing to water quality in permanent downstream reaches, summer-dry streams have the potential to serve multiple purposes in conservation management. Their value from a conservation perspective is unexpectedly high. Landscape management therefore should be directed toward the preservation and protection of ephemeral and temporary streams.

**Insect Community Composition and Physico-Chemical Processes
in Summer-Dry Streams of Western Oregon**

by

Martin Dieterich

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed December 7, 1992

Commencement June 1993

APPROVED:

Redacted for Privacy

Professor of Entomology

Redacted for Privacy

Head of Department of Entomology

Redacted for Privacy

Dean of Graduate School

Date thesis is presented December 7, 1992

ACKNOWLEDGEMENTS

Many people at different academic institutions have made extremely valuable contributions to this thesis. However, first and foremost I want to thank my wife Petra for her patience over all these years of long office and laboratory hours.

I am indebted to Dr. N. H. Anderson, my academic advisor at Oregon State University. He contributed his experience and broad knowledge of aquatic entomology at every stage of this thesis.

My thanks go to the faculty, students and staff at the OSU Department of Entomology, who were willing to put up with me and never refused to help and discuss whatever problem there was. Specifically I want to thank Dr. J. D. Lattin for his advice on issues concerning insect conservation, Dr. P. B. McEvoy who taught me much about ecology, Dr. D. McIntire (Dept. of Botany and Plant Pathology) and Dr. B. McCune (Dept. of General Science) for their instructive comments on the analysis of community data, Dr. G. Spycher (Dept. of Forest Science) who provided software and computer access and Dr. P. List (Department of Philosophy) for long discussions on environmental ethics and the philosophy of science. Dr. S. Gregory, Dr. M. Resche and R. Wildman let me use equipment. T. Anderson and J. DiGiulio helped with experiments.

For the identification of insects I have to thank Dr. L. Ferrington (Chironomidae), Dr. G. W. Byers (Tipulidae), Dr. B. Sinclair (Empididae, Clinocera), Dr. A. Borkent (Ceratopogonidae), Dr. D. Curry (Simuliidae) and R. Wisseman (Trichoptera).

I want to express my sincere appreciation to Dr. J. Schwoerbel (University of Freiburg) for his willingness to help as an adviser in Germany. Without him this thesis could not have been accomplished.

This work was supported by a Baden-Württemberg State grant (Landesgraduiertenförderungsgesetz) given to me through the Albert-Ludwigs Universität, Freiburg.

TABLE OF CONTENTS

1. INTRODUCTION	
1.1. A Conservation Perspective.....	1
1.2. Review of Summer-Dry Stream Research.....	4
1.3. Thesis Structure and Objectives.....	8
2. CHARACTERIZATION OF STUDY AREA AND STUDY SITES	
2.1. Study Area.....	11
2.2. Study Streams.....	17
Precipitation, Discharge and Flow Regime.....	17
Width, Slope and Velocity.....	22
Temperature, pH and Oxygen.....	22
Channel Bed Structure.....	25
Microbial Respiration.....	26
Vegetation.....	28
Input and Retention of Allochthonous Material...	30
2.3. Discussion.....	33
3. NITRATE AND SEDIMENT DYNAMICS IN SUMMER-DRY STREAMS	
3.1. Introduction.....	39
3.2. Materials and Methods.....	43
Nitrate Sampling.....	43
Solute Injection Experiments.....	44
Sediment Retention.....	48
3.3. Results.....	50
Nitrate Dynamics.....	50
Injection Experiments.....	55
Sediment Dynamics and Retention.....	61
3.4. Model for Suspended Sediment Retention.....	72
Model Parameters.....	72
Constraints and Assumptions.....	75
Experimental Runs of the Model.....	77
3.5. Discussion.....	80

4. COMPARATIVE ANALYSIS OF SUMMER-DRY STREAM COMMUNITY PATTERNS	
4.1. Introduction.....	90
4.2. Methods.....	94
4.3. Computations.....	96
Diversity and Evenness.....	98
Similarity.....	99
Classification (Cluster Analysis).....	103
Multi-Response Permutation Procedure (MRPP) ...	104
Ordination.....	106
4.3. Results.....	108
General Findings.....	108
Comparison between Study Sites.....	113
Comparison between FLC and FLR Sample Sites ...	124
4.4. Discussion.....	132
Species Richness and Abundances.....	132
Multivariate Analysis.....	138
General Characteristics of Summer-Dry Streams	145
Applicability.....	148
5. CONSERVATION VALUE, THREATS AND MANAGEMENT	
5.1. Conservation Value.....	150
5.2. Threats.....	152
5.3. Management.....	154
7. BIBLIOGRAPHY.....	157
8. APPENDIX.....	169

LIST OF FIGURES

FIGURE		PAGE
2. 1	The western United States with the study area in Oregon (arrow)	12
2. 2	The study area northwest of Corvallis, Oregon	15
2. 3	Correspondence between precipitation and discharge in two summer-dry streams (October 1988 to July 1990)	18
2. 4	Drying patterns of 5 summer-dry streams	20
2. 5	Comparison of water temperature in PERM and FLR	24
2. 6	Leaf input and retention in summer-dry forest streams (FLC and FLR)	33
3. 1	Diel fluctuations in nitrate concentrations [$\mu\text{g/l}$]	52
3. 2	Discharge and nitrate patterns (FLC and FLR)	54
3. 3	Nitrate export from headwater streams	55
3. 4	Fertilization Experiment in FLC (left column) and MLR (right column).	56
3. 5	Effect of fertilization on microbial respiration	60
3. 6	Sediment concentrations (site FSC)	62
3. 7	Sediment export via FSC	64
3. 8	Suspended sediment retention (FSC and FSL)	67
3. 9	Suspended sediment deposition in leaf packs (FSC and FSL)	68
3.10	Effect of forest road sediment on stream bed structure	71
3.11	Alteration of single variables in the sediment retention model	79
4. 1	Emergence trap design	95
4. 2	Comparison between study sites (streams)	123
4. 3	Comparison between sample sites (forest long-flow streams)	125

4. 4	Polar ordination of FLC and FLR sample sites (Endpoints objectively selected).	129
4. 5	Polar ordination of FLC and FLR sample sites (endpoints of first axis subjectively selected).	131

LIST OF TABLES

TABLE	PAGE
1. 1 Definition of terms	5
2. 1 Water quality data for Berry Creek, Oregon (1959-63)	13
2. 2 Nomenclature of study streams near Corvallis, Oregon	16
2. 3 Summer moisture conditions at sample sites	20
2. 4 Physical parameters characterizing the study streams near Corvallis, Oregon	23
2. 5 Composition of stream bed substrate	26
2. 6 Respiration associated with organic substrates	27
2. 7 Vegetation along the study streams in McDonald forest near Corvallis, Oregon.	29
2. 8 Litterfall collections from summer-dry stream channels in McDonald forest near Corvallis, Oregon (01/09/89 - 25/11/89)	31
3. 1 N-NO ₃ concentrations [μ g/l] in the study streams	51
3. 2 Solute retention in FLC and FLR	58
3. 3 Sediment removal from the water column	65
3. 4 Sediment retention in leaf packs	70
3. 5 Model parameters	73
3. 6 Basic setting of constants and variables for the model runs.	77
4. 1 Level of systematic resolution for different groups	97
4. 2 Effect of relativization on similarity measures	100
4. 3 Species numbers in summer-dry streams	110
4. 4 Habitat association of taxa collected	111
4. 5 Microhabitat association of summer-dry stream taxa	113
4. 6 Species richness in different summer-dry streams	114

4. 7	Invertebrate abundance in leaf pack collections	115
4. 8	Insect abundance in emergence collections	117
4. 9	Effect of drought on insect abundances	118
4.10	Diversity and Evenness in community samples from summer-dry streams	120
4.11	Comparison of species identity and percent similarity between streams	121
4.12	Correspondence of faunistic classification and classification based on environmental parameters (MRPP-analysis)	126
4.13	Ranking of environmental parameters	127

Insect Community Composition and Physico-Chemical Processes in Summer-Dry Headwater Streams of Western Oregon

Chapter 1

INTRODUCTION

1.1. A Conservation Perspective

This study of invertebrate communities and physico-chemical processes in summer-dry headwater streams was designed and conducted from a conservation perspective. The researcher's perspective determines the questions to be asked or the hypotheses to be tested in a scientific project. While an agricultural economist might focus on monetary gains or losses associated with temporary and ephemeral streams in rural landscapes, the conservation biologist will address largely different issues while working on the same system. In addition, if the question of these studies was to evaluate whether summer-dry streams should be preserved, the economist and biologist may reach contradicting conclusions, because their judgements are based on different objectives.

Conservation has been championed by naturalists and scientists for centuries; names like Saint Francis of Assisi, John Muir, August Thienemann and Aldo Leopold come to mind. However, it is only since the early 1980's that conservation biology has started to emerge as a scientific discipline (Soulé, 1986). By then, ecological theories important for species conservation such as the theory of island biogeography had been developed. Books like Ehrlich's *Extinction* (1981) helped focus public attention

on what has become known as the "extinction crisis". Thus, an environment fruitful for the establishment and growth of a new branch of biology began to take shape.

Because of its closeness to often emotional public debates, conservation biology remains a questionable field for proponents of "pure" science - that is, science apparently free of values and independent of societal processes. By the same token, conservation biologists are frequently seen by fellow scientists as being supportive of special interests and therefore as being subjective in their judgments. However, generating controversy and taking sides do not in themselves imply the abandonment of scientific objectivity in methods selected for a study, nor in conclusions drawn from results.

The discussion of topics that are as unscientific as ethics in major conservation biology journals and textbooks - Arne Naess' discussion of the intrinsic value concept in Soulé (1986) is a striking example - adds to the suspicions of purists. However, as Kuhn (1962) has shown, science is not "pure" in the positivist sense. Subjectivity and values will be part of science as long as it remains a human enterprise. There is a range for the need to make subjective decisions in experimental design and interpretation of data between sciences, but this does not predetermine the quality of results. The discussion of values in conservation biology is an expression of the practical need to find ethical justification beyond utilitarianism in a field that focusses on the preservation of biological diversity. The lack of a comparable discussion in other areas of biology indicates that these fields can exist within a mainstream utilitarian framework. It does not indicate the absence of a value base in areas such as biochemistry, genetics or physiology. After all, research in these fields commonly is justified as promoting human welfare through medical progress or through

contributions to higher yield food production.

Applied conservation research frequently focusses on endangered species as the basic unit of inquiry. Biology and population dynamics under different environmental regimes are studied to gain insight into possible causes for decline. In fact, Murphy (1989) rather narrowly defines conservation biology as applied population biology. A discomfoting aspect of this kind of research lies in its a posteriori character. Research and protection are initiated after habitat alteration has driven a species toward the brink of extinction. At this point, cause - effect relationships for the decline cannot be established directly any more and favorable habitat conditions are often difficult to reconstruct. The focus on endangered species therefore represents a damage-control approach.

In contrast, using habitat as the basic study unit may allow for an a priori conservation strategy. That is, if specialized species and their habitat requirements are identified before changes in land use go into effect, then landscape planning may be enacted to prevent or moderate impacts on such organisms independent of whether they are listed as being endangered.

Studying habitat prior to major anthropogenic alteration also is important in that it provides the basis to directly gauge human impacts on the environment, that is to establish cause - effect relationships. Therefore, habitat oriented studies are essential for the improvement of management strategies designed and implemented to maintain a high overall biodiversity.

The "value" of a habitat in a conservation perspective is based on its provision of a living space for organisms as well as its influence on physico-chemical processes within the larger landscape or ecosystem context. For example, in an agricultural landscape, hedges can provide a refuge for a number of animals and plants and at the same

time act as wind-breaks, thus minimizing erosion and reducing local temperature fluctuations. Similarly, summer-dry streams can be expected to provide habitat and at the same time influence water chemistry as well as food availability in permanent downstream reaches.

1.2. Review of Summer-Dry Stream Research

Summer-dry streams have attributes that make them ideal habitats for evaluation from a conservation perspective. They have received surprisingly little attention in limnological studies (D.D. Williams, 1987; Boulton and Suter, 1986). "The extent of limnological references to temporary waters is not in accord with their widespread occurrence and abundance, ecological importance, nor limnological interest" (W.D. Williams, 1985). Therefore temporary and ephemeral streams afford a high potential for faunistic surprises, that is, the occurrence of presumably rare taxa and even undescribed species. Furthermore, due to their presence in all kinds of landscapes and their transitional position between terrestrial and aquatic systems, they provide a prime target for improvements in landscape management that affect both lotic and terrestrial environments.

From a researcher's perspective, summer-dry headwaters offer the advantage of being easily accessible even during flood events. Experiments can be set up while the streams are dry. These experiments then "will be initiated 'naturally' when flow resumes" (Boulton and Suter, 1986). The aquatic invertebrate fauna is expected to be less diverse than that of permanent streams. This allows for a more complete and in-depth assessment of governing processes and the communities inhabiting these sites.

The terms "intermittent", "temporary" and "ephemeral" describe summer-dry lotic systems. There is considerable inconsistency between authors in the use of these terms. In this thesis I will follow the terminology suggested by Legier and Talin (1973) to distinguish between ephemeral and temporary streams and that of Delucchi and Peckarsky (1989) to distinguish between temporary and intermittent channels (Table 1.1). More terms specifically coined for this study and a summary of acronyms used is given in the appendix (Table A.5).

Williams and Hynes (1977) give a general overview of hydrological and physical features common to summer-dry streams and conclude that fluctuations of physical and chemical parameters are far greater in such streams than in

Table 1.1: **Definition of Terms.** The definitions follow those given by Legier and Talin (1973) and Delucchi and Peckarsky (1989).

Stream Type	Definition	Insects
Intermittent	Permanent lotic section present above summer-dry section. Recolonization by drift possible. Flow continuous, over 5 months.	Ephemeroptera, Plecoptera, Trichoptera and Diptera
Temporary (= long-flow)	No permanent lotic section present over entire channel length. Permanent pools or seeps may be present. No recolonization by drift. Flow continuous, over 5 months ¹ .	Ephemeroptera, Plecoptera, Trichoptera and Diptera
Ephemeral (= short-flow)	No permanent lotic section present over entire channel length. Permanent pools or seeps may be present. No recolonization by drift. Flow discontinuous (after storms), less than 3 months ¹ .	Chironomidae, Simuliidae and Coleoptera.

1 : Streams with flow for 3 - 5 months are intermediate.

permanent channels. Temperature as well as period and range of flow are cited as examples for physical parameters, but no examples of variable chemical parameters are given. In an intermittent stream in southern France the stagnant summer pool period was variable with respect to chemical and physical factors, whereas the spring run-off period was found to be stable (Legier and Talin, 1973). Einfeld (1983) measured seasonal patterns of nitrate and phosphate in a permanent and an intermittent section of the Mauchach, a creek in south-west Germany. Fluctuations in chemical parameters at the intermittent sites were high but at least partly attributed to influx of insufficiently purified sewage.

Most studies of ephemeral and temporary streams focus on the fauna associated with these habitats. Boulton and Suter (1986) report a general "trend of increasing species richness with increasing permanence" for Australian summer-dry streams. Delucchi (1988) compared the community structure of adjacent temporary, intermittent and permanent streams. Einfeld (1983) looked at differences in benthic community composition between sample sites on the Mauchach. The hyporheic fauna of the Mauchach at summer-dry locations was compared with that in permanently flooded sites by May (1983).

Studies on the fauna of intermittent and summer-dry streams rarely attempt to associate community structure with habitat parameters. Instead the main focus is on life cycle strategies, especially on adaptations to survive the summer drought (Legier and Talin, 1973; Butcher, 1979; Boulton and Lake, 1988). Williams and Hynes (1976) as well as Legier and Terzian (1981) provide a classification of animals in temporary and intermittent streams according to summer drought survival strategies. However, most species inhabiting summer-dry lotic systems are also found in adjacent permanent waters (Delucchi and Peckarsky, 1989;

Knight and Gaufin, 1967; Clifford, 1966). Growth rates and development did not differ between temporary and permanent streams for species present in both habitats (Delucchi and Peckarsky, 1989). Paradoxically, ecological generalization appears to be the best specialization for life in temporary habitats (Wiggins et al., 1980; Boulton and Suter, 1986). Another important attribute of species common in temporary streams was found to be their low affinity to enter the drift (Delucchi, 1989). This is in agreement with Dance and Hynes (1979) who without further explanation state that "resistance to drifting may be advantageous to many inhabitants of temporary streams".

Only limited work has been conducted on temporary and ephemeral streams in Oregon, although the large number of summer-dry channels and the distinct, predictable change between dry and wet seasons make the Pacific Northwest a very suitable place to study these habitats in an environment comparatively undisturbed by human impacts. Tew (1971) conducted a faunistic survey of a temporary headwater stream located in a meadow just north of McDonald Forest, Benton County. Butcher (1979), working in the Blue Mountains of eastern Oregon, compared drought effects on Ephemeroptera, Plecoptera and Trichoptera in 6 streams, one of them temporary. Lehmkuhl (1971) published a note on life cycles of two stoneflies from temporary streams just south of Corvallis. Müller (1990) did research on leaf degradation rates and sediment transport in some of the streams studied for this thesis.

1.3. Thesis Structure and Objectives

The objective of this study is to assess the functions of summer-dry headwater streams as part of a larger drainage system. The inclusion of temporary and ephemeral channels in management strategies will depend on a better understanding of their habitat value and their role in a watershed context. They are believed to be important for conservation management because of their omnipresence and their potential for serving multiple functions. Such functions include:

1. Providing habitat for specifically adapted aquatic and terrestrial organisms.
2. Providing corridors managed primarily for biological diversity in otherwise intensively cultivated landscapes.
3. Reducing the input of nutrients (nitrate) and sediment into permanent channels thereby serving buffer functions in the transition zone between terrestrial and aquatic habitats.
4. Providing temporary water storage and thereby lessening peak flows in permanent streams during severe storm events.

The thesis focuses on the potential habitat and buffer functions of summer-dry streams. It is structured into three largely independent units, each with separate Methods, Results and Discussion sections. Chapter 2 describes and compares the study sites in detail. The remaining chapters provide the basis for evaluating the significance of summer-dry streams within a conservation perspective.

Chapter 3 addresses the potential of temporary and ephemeral streams to enhance habitat in downstream reaches by: 1) limiting the amount of fine sediment transported in

the water column; and 2) buffering against high levels of nitrate input into permanent channels. The chapter is an observational and experimental unit addressing the following questions:

1. To what extent can ephemeral streams retain fine sediment washed from forest roads, and what are the possible retention mechanisms?
2. What is the pattern of nitrate levels over time and space in temporary headwater streams?
3. To what extent can temporary streams moderate pulse-type nitrate inputs and what are the retention mechanisms?

Chapter 4 compares arthropod community patterns within and between summer-dry streams. Between-stream comparison serves to classify the communities of distinctly different stream types. Within-stream comparison elucidates community patterns along environmental gradients. The chapter is largely observational and addresses the following question:

1. Are there differences in macroinvertebrate species composition between the streams selected and between sites within a given channel; if so, can these differences be related to factors such as duration of flow, stream-bed structure, food availability, or presence/absence of a canopy?

In the course of this study a vast amount of autecological information was also generated. This will be published later in the form of scientific papers.

Summer-dry streams appear to be a case of a habitat too insignificant to warrant specific consideration in land-use concepts. However, these systems may serve important functions in a landscape. This research project was conducted in order for these functions to become obvious before too many such microhabitats have been

destroyed or critically altered out of ignorance. The data gathered in this study will provide basic knowledge about the general significance of temporary and ephemeral streams in a conservation perspective. It is the goal that the findings of this research will be applied toward improved landscape management - improved toward a healthier environment. After all, as Murphy (1990) points out, applicability is a basic characteristic of conservation research.

Chapter 2

CHARACTERIZATION OF STUDY AREA AND STUDY SITES

2.1. Study Area

The headwater streams studied are located in, or adjacent to, the McDonald-Dunn Forest north of Corvallis, Benton Co., Oregon (Fig. 2.1). The Forest, which is owned and managed by Oregon State University, is part of the eastern foothills of the Oregon Coast Range.

Closeness to Corvallis was an important consideration in choosing the study area. Establishing the field sites in the university forest only 5 km from the OSU campus allowed for 3 - 5 visits weekly during the flow period. The frequent visits helped to improve the general understanding of the summer-dry stream systems. Furthermore, research efforts could be geared toward key events such as flow initiation, floods or premature drought and timing of experiments could easily be adjusted to specific system patterns such as discharge.

The climate in the Pacific Northwest is characterized by warm, dry summers and wet, mild winters (Waring and Franklin, 1979). There is a very distinct and predictable seasonality in rainfall patterns. Annual precipitation in McDonald-Dunn Forest averages about 1000 to 1500 mm (Hall and Alaback, 1982). Streams typically exhibit several peak flows in winter, while flow is much decreased in summer and fall (Anderson and Wold, 1972).

All study streams are located in soils of the Dixonville-Philomath and Price-Ritner associations. These brown to dark brown soils are deep to moderately deep, well

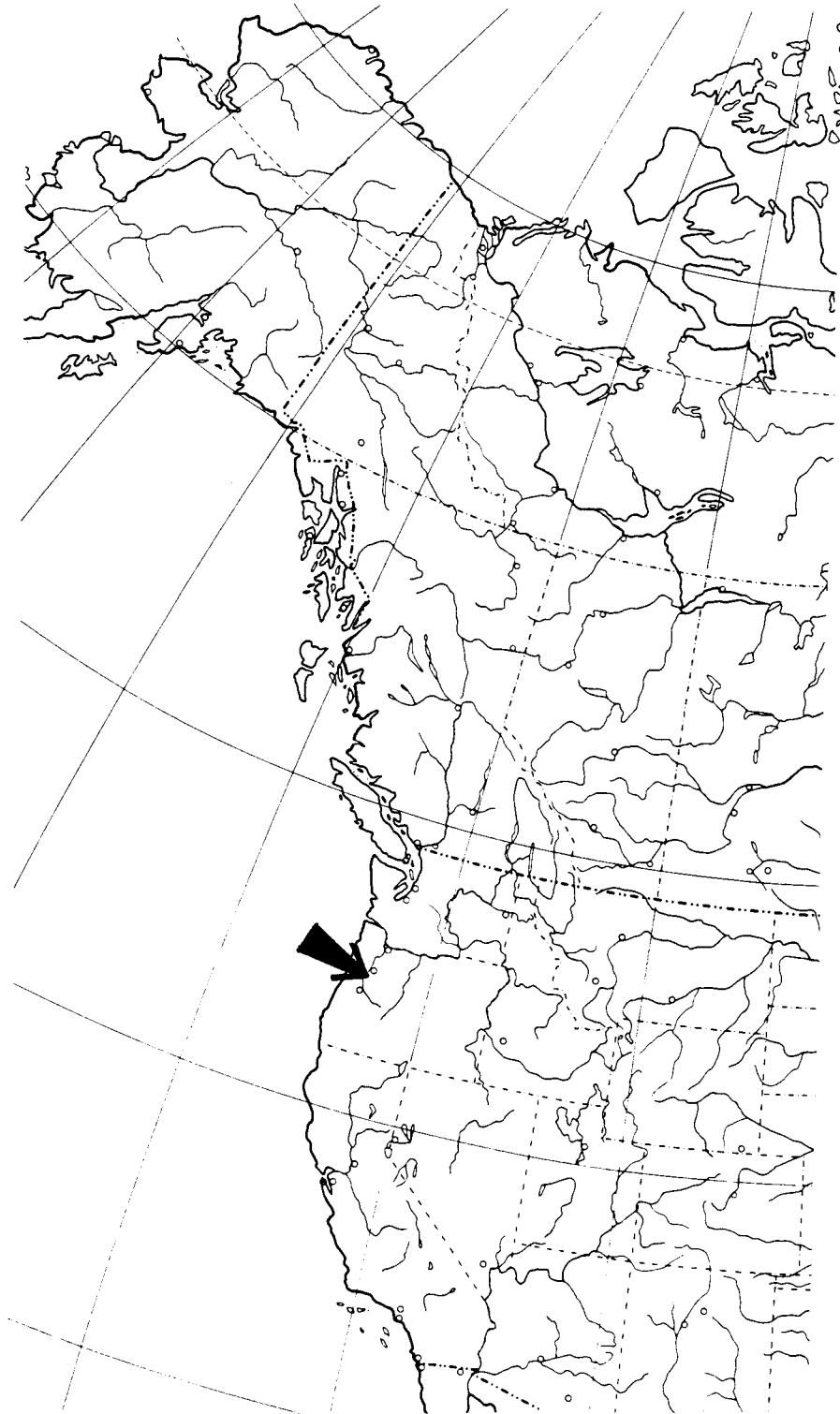


Figure 2.1: The Western United States with the Study Area in Oregon (Arrow).

drained silty clay loams. They were formed from basic igneous basalts of the Siletz River Volcanic series (Knezevich, 1975).

Table 2.1 summarizes water quality data for Berry Creek. This is a second-order stream draining part of the

Table 2.1: Water Quality Data for Berry Creek, Oregon (1959-63). Data are averages of yearly measurements in fall, winter and spring (after Warren et al., 1964). If not indicated otherwise, values are mg/l.

Parameter	Fall	Winter	Spring
pH	7.5	7.3	7.4
Conductance [$\mu\Omega$]	124	86	92
Dissolved solids	91	65	70
Hardness (CaCO_3)	50	33	36
Silica (SiO_2)	24	22	22
Calcium (Ca)	12	8	9
Iron (Fe)	0.12	0.15	0.17
Magnesium (Mg)	4.8	3.1	3.6
Sodium (Na)	6.0	4.1	4.4
Potassium (K)	0.5	0.3	0.2
Bicarbonate (HCO_3^-)	67	45	51
Carbonate (CO_3^{2-})	0.0	0.0	0.0
Sulfate (SO_4^{2-})	1.3	1.4	0.8
Chloride (Cl^-)	5.8	3.8	3.4
Fluoride (F^-)	0.05	0.07	0.06
Nitrate (NO_3^{2-})	0.18	0.13	0.10
Phosphate (PO_4^{3-})	0.13	0.02	0.09

study area. Data from Berry Creek are considered to be representative for lotic systems in the McDonald-Dunn Forest vicinity (Müller, 1990).

The characteristic vegetation of the area is coniferous forest. All forest streams are situated within the Abies grandis - Brachypodium sylvaticum association as determined by Hubbard (1991). This plant community is at the "dry end" of the environmental gradient for plant associations found in McDonald Forest. Douglas fir (Pseudotsuga menziesii) and grand fir (Abies grandis) are the dominant conifers in this association. Bigleaf maple (Acer macrophyllum) is the dominant deciduous tree in the forest and Oregon white oak (Quercus garryana) is common. Oregon white ash (Fraxinus latifolia) is only found occasionally, and red alder (Alnus rubra) is absent from the association. Poison oak (Rhus diversiloba) and trailing blackberry (Rubus ursinus) are the most common shrubs, while false brome (Brachypodium sylvaticum), an invading grass native to Europe, dominates the herbaceous layer.

Four summer-dry streams in, or adjacent to, the Oak Creek watershed in the southern part of McDonald Forest were selected for study in 1987. Limited sampling was conducted in a first-order permanent stream in the same area (Fig. 2.2). The food base for the biota in the heavily shaded forest streams is allochthonous material, mainly maple leaves. For comparison, two unshaded meadow channels were included in the study in 1988. One of these is located in the Oak Creek valley and the other along Tampico Road, to the north of McDonald-Dunn Forest in the Berry Creek watershed (Fig. 2.2).

Besides the presence or absence of a canopy, the streams differ in the duration of the flow period. Continuous flow from about mid-November to May characterizes two of the forested sites and the unshaded stream north of Tampico Road. Flow in the other channels is discontinuous

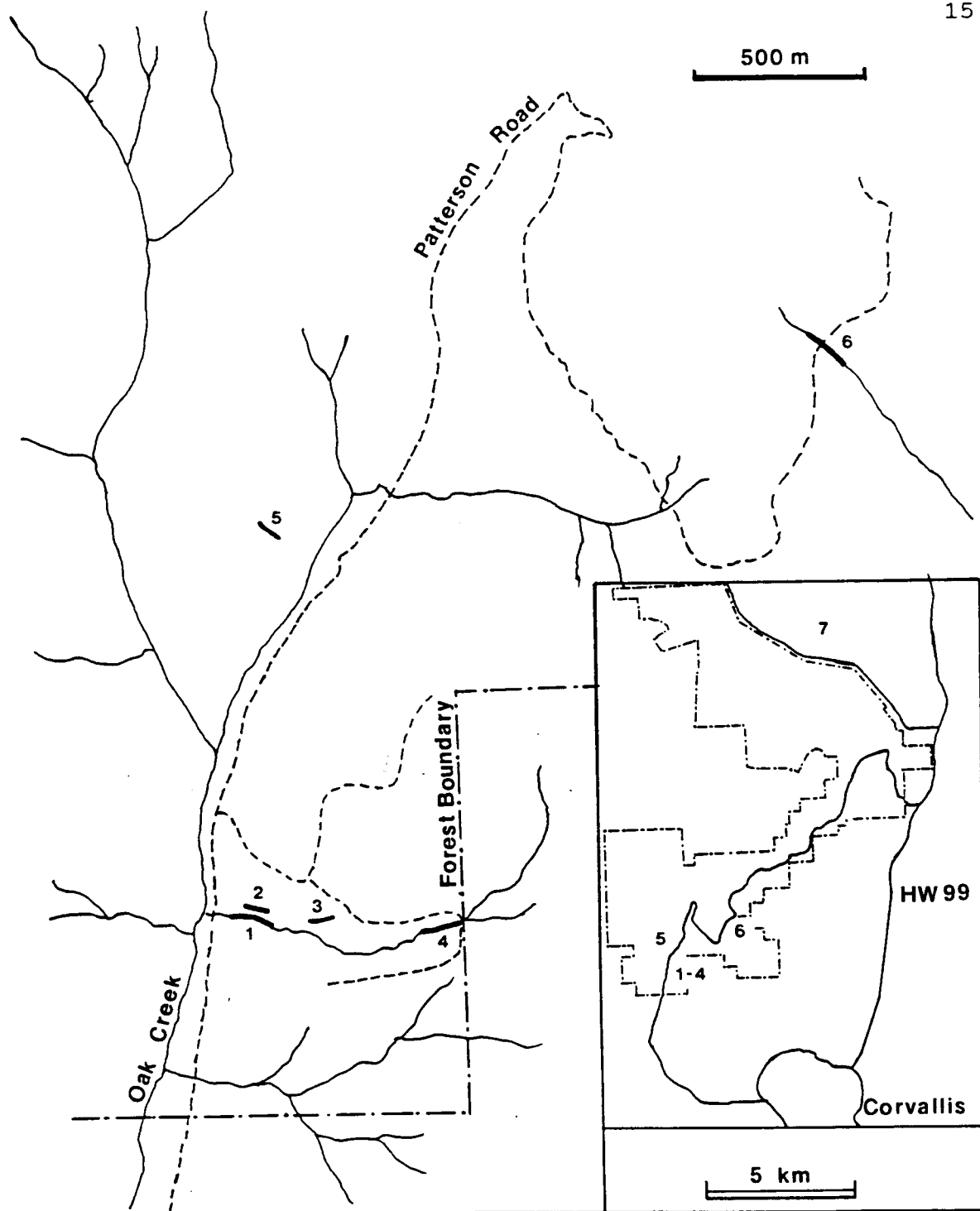


Figure 2.2: The Study Area Northwest of Corvallis, Oregon. Insert map shows outline of McDonald-Dunn Forest, and relation of stream 7 (MLR) to the other streams. Study sites are:
 1 = PERM; 2 = FSE; 3 = FSC; 4 = FLC;
 5 = MSC; 6 = FLR; 7 = MLR.

Table 2.2: Nomenclature of Study Streams near Corvallis, Oregon.

Location	Flow Regime	Stream Bed	Abbreviation
Forest	Long-flow	Clay	FLC
Forest	Long-flow	Rock	FLR
Forest	Short-flow	Clay	FSC
Forest	Short-flow	Experimental ¹	FSE
Meadow	Long-flow	Rock	MLR
Meadow	Short-flow	Clay	MSC

1: A flow extension experiment was conducted in this stream.

and restricted to periods of 3 - 4 months in winter and early spring. Channels also differ in the amount of rocky sediments present in the stream bed. The nomenclature used for the study sites reflects the physical differences described above (Table 2.2).

Study reaches of 160 m in temporary streams (long-flow streams) and 80 m in ephemeral streams (short-flow streams) were selected. Within each reach, five sample sites were chosen at random. Another five sites were added so that the following criteria were met for each stream: (a) sites with maximum and minimum duration of flow are included; and (b) riffles and pools are equally represented. Only five randomly selected sample sites were established in the first-order permanent stream (PERM).

A sample site was 2 m of stream channel. It contained

artificial substrates to sample the benthic community and an emergence trap to collect adults. In addition, a number of physical parameters characterizing the study streams were measured at the sample sites.

2.2. Study Streams

Precipitation, Discharge and Flow Regime

Three rain gauges were used to measure precipitation over the 2-year study period. Gauges were placed at sites MLR, FLR and in the Oak Creek valley close to streams PERM, FSC, FSE and FLC. To put the rainfall during the study period into a long-term perspective, data from the Oregon State University weather station at Hyslop Farm were obtained. Yearly precipitation was between 1100 and 1250 mm for the gauges near the study sites, while only 900 to 950 mm were measured at Hyslop Farm. The total precipitation at the long-term monitoring station was 200-250 mm below the 1951-1980 average in the 2 years of the study. Annual precipitation at all gauges was about 50 mm higher during 1988-89 as compared to the following season.

Stream discharge was measured using timed collections into a bucket. In some of the streams a temporary V-notch weir was installed to facilitate measurements. Maximum discharge was highest in FLC (27.7 l/s) and lowest in the ephemeral MSC, where a maximum discharge of 1.7 l/s was observed (Table 2.3).

Stream discharge closely reflects precipitation patterns, except at the beginning of the wet season (Fig. 2.3). After the summer drought the terrestrial system needs approximately 200 mm of precipitation before flow resumes in late fall. The soil at that point becomes almost water

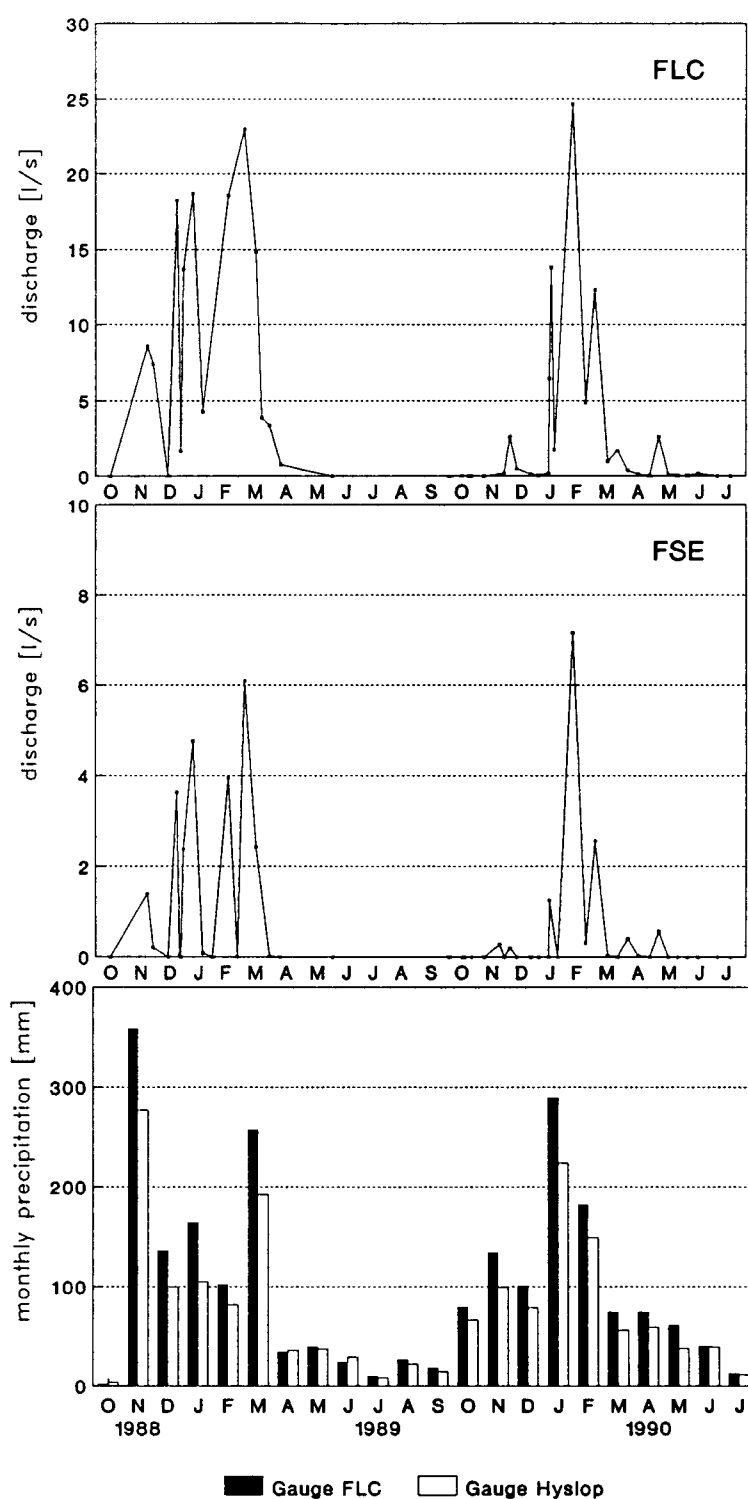


Figure 2.3: Correspondence between Precipitation and Discharge in two Summer-Dry Streams (October 1988 to July 1990). Discharge is given as point measurements, precipitation is a monthly total.

saturated and the groundwater level has risen high enough to support drainage via temporary and ephemeral channels.

Flow duration in MLR was considerably shorter than in either FLC or FLR over the 2-year study period. On the average, water was present at the meadow stream sample sites for 137 days as compared to 246 and 228 days at FLC and FLR sample sites.

Rainfall in November and December 1989 was insufficient to create saturated soil conditions. Consequently, significant portions of the channels were subjected to an early winter drought (Fig. 2.3). By January 1990 the groundwater was finally recharged enough to sustain continuous flow in the temporary systems. Thus, the flow period in all streams was shorter in 1989-90 than in the winter and spring of 1988-89. In MLR flow duration in 1989-90 was only 72% of that of the previous year. The impact of shorter flow duration on the fauna is discussed in chapter 4.

Fig. 2.4 illustrates the drying patterns of the streams studied. Ephemeral streams dry out rather rapidly over most of the channel reach, but small areas retain water for a considerably longer period. These seep areas often stay moist even after the surface water has disappeared.

Temporary forest streams have sections that go dry rapidly and, at the other extreme, typically retain summer pools or even small segments with permanent trickles. Overall, the long-flow forest streams dry out more gradually than do their ephemeral counterparts; seeps and moist sections are retained year around in addition to permanent trickles and pools.

In contrast to the forest streams, the meadow channels do not retain permanent sections with water or even permanent seeps. Instead they go dry rather rapidly over the entire channel reach. Although the stream is not

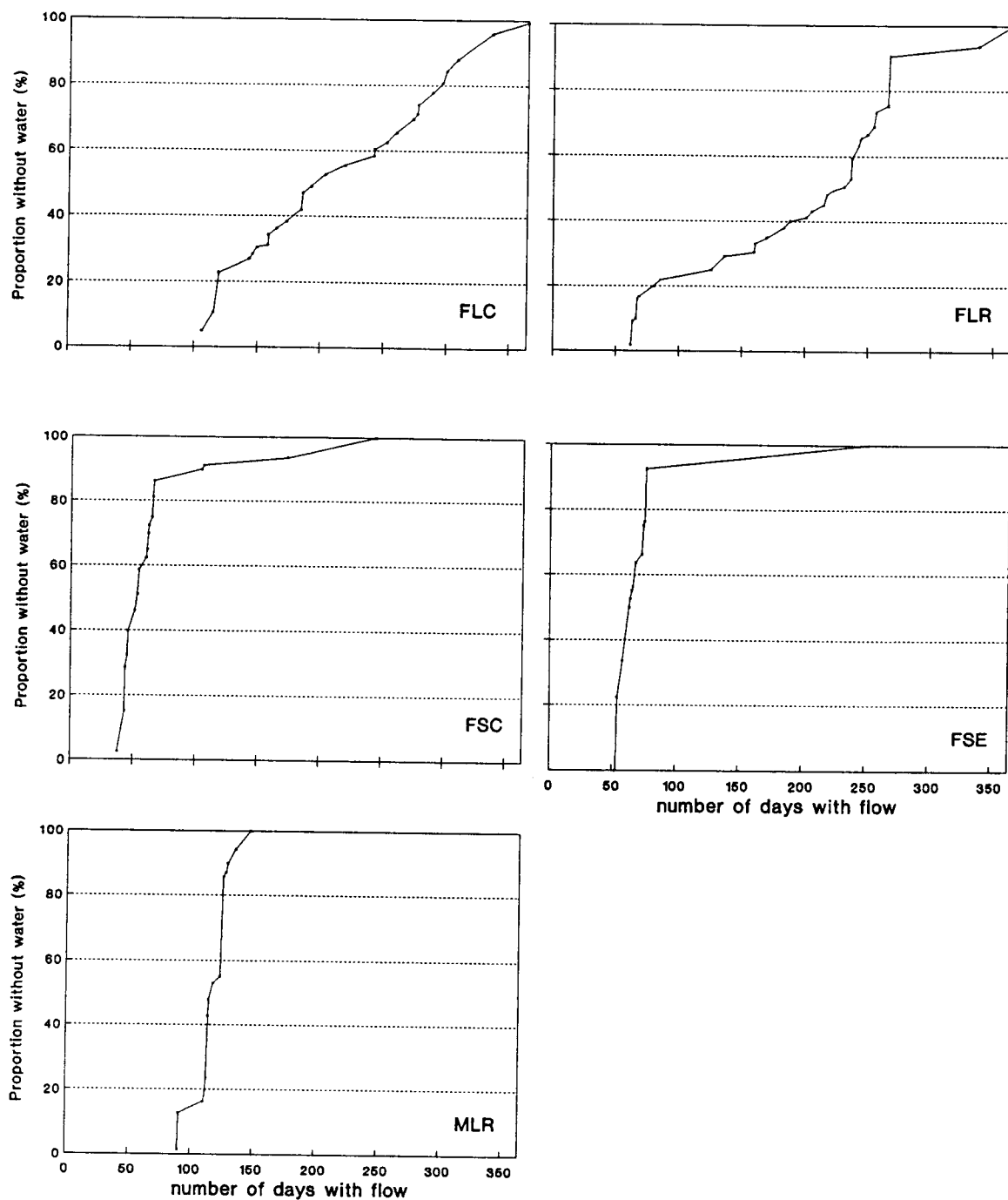


Figure 2.4: Drying Patterns of 5 Summer-Dry Streams. Drying patterns are expressed as proportion of the study reach without surface water after a given number of days (average over 2 seasons).

included in Figure 2.4 the drying pattern of MSC closely resembles that of MLR except for the shorter flow period in the former. However, the dense vegetation in the channel bed of MSC made it difficult to precisely determine whether or not flow had ceased in a given section of the study reach. Consequently no continuous data referring to drying patterns were collected there.

Table 2.3 describes summer drought conditions at FLC, FLR and in seep sites of short-flow forest streams (SEEP). All sample sites not explicitly listed in the table were dry in late summer 1990. FLC and FLR compare well in that sample sites in both channels represent a range of summer drought conditions from 'dry' to 'water' (permanent sites).

Table 2.3: Summer Moisture Conditions at Sample Sites.
Streams and sample sites not explicitly listed were dry (score = 1) during summer.

FLC S1	4	FLR S1	3.5	FSC S7	2	FSE S9	4
FLC S2	1	FLR S2	4.5	FSC S8	4.5	FSE S10	2
FLC S3	1	FLR S3	1				
FLC S4	4	FLR S4	2.5				
FLC S5	5	FLR S5	1				
FLC S6	5	FLR S6	1				
FLC S7	1	FLR S7	1				
FLC S8	1	FLR S8	3.5				
FLC S9	2	FLR S9	1				
FLC S10	4	FLR S10	5				

Scores:
1 = dry
2 = moist
3 = saturated
4 = seep
5 = water

Width, Slope and Velocity

Data describing channel width and slope for all study streams are summarized in Table 2.4. Velocity was measured with a battery powered, portable flow-meter in temporary systems only.

The long-flow forest streams are about double as wide as their meadow counterpart. In fact, at the mid-water line MLR is even narrower than the short-flow forest streams. Although slope of FLR is considerably more and slope of MLR is considerably less than that of any other channel, average velocities between FLR and MLR are not different (Table 2.4). Rather, difference in slope is better reflected in the range of velocities measured in the streams.

Temperature, pH and Oxygen

Mean water temperature as well as maximum and minimum temperatures from December 1989 to April 1990 are listed in Table 2.4. Temperatures were obtained from all streams in 10-day intervals. The average and the maximum are highest for the temporary meadow site (MLR). Temperatures as high as 17.5°C were recorded there in mid-April, when flow had ceased in most of the unshaded study reach and the channel began to dry up. Maximum temperatures in the summer-dry forest streams were measured in July/August 1990. Water temperatures in seemingly stagnant pools then did not exceed 15°C, in spite of air temperatures commonly rising well above 30°C.

Table 2.4: Physical Parameters Characterizing the Study Streams near Corvallis, Oregon.

Parameter	PERM	FLC	FLR	FSC	FSE	MLR	MSC
Elevation [m] ¹	165	253	378	197	163	110	186
Width [cm] ²	104	104	94	68	63	46	42
Slope [%] ³	9	11	20	13	12	5	11
Discharge [l/s] ⁴	57.6	24.7	11.6	5.2	7.2	10.3	1.7
Velocity [m/s] ⁵							
average	----	0.19	0.23	----	----	0.24	----
	----	0.86	0.72	----	----	0.32	----
	----	0.00	0.08	----	----	0.14	----
pH ⁶							
average	7.67	7.64	7.25	7.39	7.46	7.25	7.19
maximum	7.99	8.10	7.68	7.75	7.84	7.99	7.50
minimum	7.27	7.12	6.79	7.00	7.13	6.99	6.95
Temperature ⁷							
average	7.4	8.1	7.9	8.2	7.8	10.1	8.3
maximum	10.0	10.5	10.0	10.5	10.0	17.5	11.0
minimum	4.0	6.0	7.0	6.0	6.0	5.5	6.5

1: Elevation is given for the mid study reach.

2: Measured for active channel bed in 5 m intervals along each study reach.

3: Average over the total study reach.

4: Maximum discharge values.

5: Measured at each long-flow stream sampling site during a single afternoon (13/03/91).

6: Measurements cover period from 06/12/89 - 26/07/90.

7: Based on 15 measurements for long-flow streams and 10 measurements for short-flow streams during the 1989-90 flow period (30/11/89 - 28/04/90).

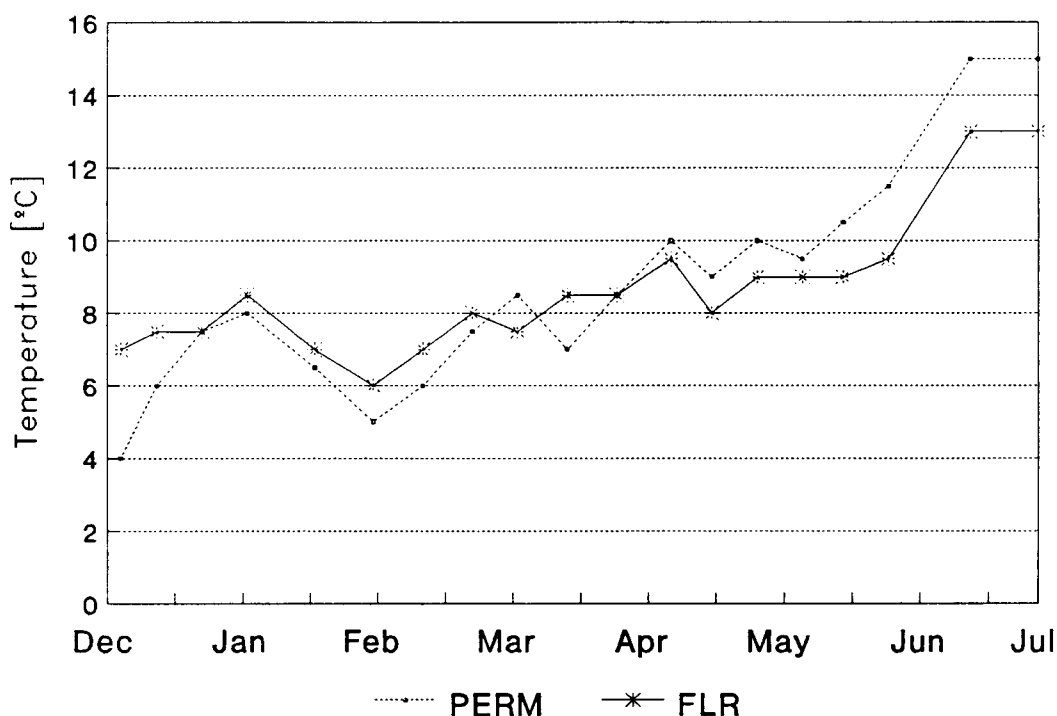


Figure 2.5: Comparison of Water Temperature in PERM and FLR
Measurements were taken at slightly irregular intervals between 18/12/89 and 15/07/90.

Temperature fluctuations were less pronounced in the temporary forest streams than in the permanent channel. This is exemplified in a comparison of temperature patterns in PERM and FLR (Fig. 2.5). During winter, the water in PERM is cooler than that in FLR, while in summer this relationship is reversed. Using a simple linear regression model, air temperature explained more of the variation in the water temperature pattern in Perm ($R^2 = 0.90$, $p < .01$) than in FLR ($R^2 = 0.65$, $p < .01$) or any other summer-dry forest stream.

To determine pH, water samples were collected in 250-ml plastic bottles. The bottles were transferred to the laboratory where the pH was measured immediately with a Beckmann 45 pH-meter. The pH values during the 1989-90 flow period were found to be alkaline on the average, although slightly acidic conditions did occur at times in FLR and MLR (Table 2.4). The pH values were stable within 1 unit in all streams over the course of the year. No diel pH fluctuations were observed in samples taken from the temporary sites in 4-hour intervals between 08:00 and 20:00.

Oxygen content in the water was measured in the field with a YSI Oximeter. Repeated measurements during the main flow period in winter and spring yielded oxygen at saturation concentration in all streams. However, measurements in fall revealed an oxygen gradient in the permanent FLC pools. Oxygen levels in the leaf litter at the pool bottom were only 13% of the saturation concentration, whereas just above the litter layer 41% saturation and just below the water surface 60% saturation was measured.

Channel Bed Structure

The channel bed surface at each sample site (2 m of channel) was characterized by determining percent cover of clay, rock, wood and macrophytes. Cover was estimated visually in July 1990 shortly after flow had ceased and before any major litter input covered the ground. Stream-bed composition, averaged for the 10 sample sites in each stream, is given in Table 2.5. The results reflect the initial characterization of stream beds into those mostly composed of rocky sediments (MLR, FLR) and those dominated by clay (FSC, FLC). MSC was exceptional in that plant cover (largely grasses) was higher than 80%.

Table 2.5: Composition of Stream Bed Substrate. Percent cover by different substrate types was estimated in summer (July 1990). Listed is the average sample site substrate composition for each summer-dry stream.

Stream	Clay	Rock	Wood	Plants ¹
FLC	63	26	6	5
FLR	15	69	4	12
FSC	79	0	10	11
FSE	68	11	9	12
MLR	11	87	0	2
MSC	19	0	0	81

1: This includes moss and grass growing in the stream bed.

Microbial Respiration

Microbial respiration associated with leaf material and fine particulate organic matter (FPOM) was measured as an index of food quality available for the shredder and collector functional feeding groups. FPOM was obtained by decanting organic material from sediment fractions retained on U.S.A. Standard sieves sizes 53 μm , 106 μm and 250 μm . The decanted material was oven dried and well mixed. Approximately 2 g of the FPOM was placed into a 100 μm -mesh Nitex bag. Similarly, 5 leaf pieces, each 1 cm^2 in size, were transferred into a Nitex bag. All pieces were cut from 5 oven-dried leaves. These leaves had been softened in tap water for 24 hours before they were cut into the small

pieces. Each of the 5 leaves contributed 1 piece (1 cm^2) to each of the bags.

Ten bags with leaf material and 10 bags with FPOM were exposed for 6 weeks in the forest streams. The bags were divided between 2 pools in each stream. Due to drought conditions bags were only recovered from one pool in FSC and FSE.

After removal from the streams, bags were stored on ice for transport to the laboratory. Substrates were transferred from the bags into the chambers of a Gilson

Table 2.6: Respiration Associated with Organic Substrates.

Substrates (leaf disks and FPOM) were exposed for 6 weeks in the forest streams and then incubated in a respirometer. Respiration rates are expressed as $\mu\text{l O}_2$ consumed per mg of substrate over a 72hr incubation period (SD in brackets).

Stream	n	FPOM	Leaf disks
FLC	10	0.58 (0.08)	9.66 (1.15)
FLR	10	0.57 (0.22)	11.59 (3.92)
FSC	5	0.65 (0.10)	10.31 (1.21)
FSE	5	0.50 (0.04)	7.78 (0.17)

Analysis of Variance Summary:

Source	df	SS	MS	F	P
Stream	3	19.16	6.39	2.06	<.12
Substrate	1	1321.01	1321.01	425.43	<.01
Str*Sub	3	23.36	7.79	2.51	.07
Error	50	155.26	3.11		

Differential Respirometer within 2 hours of collecting. After a preincubation period to adjust temperature inside the chambers to that of the milieu, samples were incubated for 24h at 10°C and the amount of O₂ consumed was measured. Microbial activity was computed as μl O₂ consumed per weight of organic material (FPOM or leaf) over a 72hr incubation period.

Respiration rates of leaf material were significantly higher than those found for FPOM (Table 2.6). No significant differences in respiration rates were found between organic material from different streams (Table 2.6). Therefore, food quality is considered to be similar in all forest streams.

Vegetation

Although all the forest streams are located within the Abies grandis - Brachypodium sylvaticum association, there are distinct differences in vegetation density and species composition along the study reaches (Table 2.7).

Red alder, otherwise a dominant component in riparian plant communities of the Pacific Northwest, is only found along the first-order permanent stream. Bigleaf maple and, to a somewhat lesser extent, Oregon white ash provide most of the leaf material to the summer-dry systems. Shrub vegetation, mainly vine maple (Acer circinatum) and ocean-spray (Holodiscus discolor), is present along all streams, but particularly dense along FLC. Shrubs contribute a significant portion to the total leaf input into that channel. The herbaceous layer along the forest streams is generally sparse and does not appear to significantly add to the food base in the streams. However, false brome has invaded several sections of the FSC channel and one

Table 2.7: Vegetation along the Study Streams in McDonald Forest near Corvallis, Oregon. Abundance is expressed in categories: absent (0); rare (1); common (2); dominant (3).

Species	FLC	FLR	FSC	FSE	PERM
Trees					
<u>Alnus rubra</u>	0	0	0	0	2
<u>Fraxinus latifolia</u>	2	1	1	1	2
<u>Acer macrophyllum</u>	3	2	2	2	2
<u>Pseudotsuga menziesii</u>	1	2	2	2	1
Shrubs					
<u>Osmaronia cerasiformis</u>	1	0	0	0	1
<u>Sambucus glauca</u>	1	0	0	0	1
<u>Acer circinatum</u>	3	1	0	1	3
<u>Physocarpus capitatus</u>	2	1	0	0	1
<u>Holodiscus discolor</u>	2	1	0	0	1
<u>Rhamnus purshiana</u>	1	0	0	1	1
<u>Rubus sp.</u>	1	1	1	0	1
<u>Corylus cornuta</u>	2	0	2	2	2
<u>Symphoricarpus albus</u>	1	2	2	2	1
<u>Rhus diversiloba</u>	0	1	3	1	0
Ferns					
<u>Polystichum munitum</u>	2	2	3	2	2
<u>Athyrium filix-femina</u>	0	0	1	0	0

isolated area in the FSE stream bed. It may thus contribute to channel stability there.

MLR drains a grassland community dominated by introduced plants, most of them pioneer species as classified by Oberdorfer (1983). Insufficient density of plant cover allows for spots of bare soil to be apparent throughout the meadow. Cynosurus echinatus, Phleum pratense, Agrostis stolonifera, Poa pratensis, Bromus mollis, Deschampsia cespitosa and Dactylus glomerata are some of the grasses found in the meadow. These grasses are characteristic of clay soils. They show a wide amplitude with respect to moisture requirements, but tend to occur on nutrient-rich soils in Europe (Oberdorfer, 1983). Within the forbs, Prunella vulgaris indicates nutrient-rich conditions (Oberdorfer, 1983) and Eriophyllum lanatum is typically found on dry sites (Niehaus, 1976). Achillea millefolium and Senecio jacobaea, which are also part of the meadow community, have wide amplitudes with respect to nutrients and moisture.

The plant community in the meadow drained by MSC is characterized by species preferring moist, often nutrient-rich clay soils such as false brome, Festuca rubra and Plantago lanceolata. In contrast to the land surrounding MLR the plant cover is dense here and bare soil is not exposed.

Input and Retention of Allochthonous Material

Framed rectangular screens (1 m * 0.5 m) were used to collect litter falling into the forest streams. Ten litter traps were assigned to each stream. Traps were placed in the dry channel in early September 1989. A systematic sampling design as described in Cochran (1977) was used to select sites. Thus, litter traps were spaced evenly over

the entire study reach. They covered 6.25% of the total reach in long-flow streams and 12.5% of the total reach in ephemeral channels. Litter was removed from the traps just prior to the onset of flow in late November 1989. The

Table 2.8: Litterfall Collections from Summer-dry Stream Channels in McDonald Forest near Corvallis, Oregon (01/09/89 - 25/11/89). Values given are the mean and range [g/m²] for ten traps per stream.

Stream	Leaves	Needles	Other
	Maple	Other	
FLC			
average	152.4	76.5	5.7
maximum	361.4	127.1	13.2
minimum	15.1	21.1	1.8
FLR			
average	90.1	6.9	40.1
maximum	179.3	16.8	77.5
minimum	26.3	1.0	14.8
FSC			
average	73.5	22.5	15.5
maximum	270.6	65.6	44.8
minimum	9.5	0.2	1.2
FSE			
average	132.6	17.8	3.6
maximum	261.4	59.3	7.0
minimum	21.7	2.8	0.3

organic material was sorted into categories, oven dried and weighed on a Mettler electrobalance.

The data on litter inputs are summarized in Table 2.8. Maple leaves were the dominant component in all cases. Leaf input ranged from 95 g/m² in FSC to 230 g/m² in FLC. The dense shrub vegetation alongside FLC is reflected in the large amount of non-maple leaves collected there. FLR had the highest needle input of all channels (40 g/m²). Input levels of litter were highly variable between sample sites, thus causing a very high standard error for the mean input. Inferential statistics therefore did not yield significant differences between study sites although such differences were obvious.

To estimate within-channel litter retention, all organic material left in a 1-meter stretch just upstream of 5 litter trap sites in FLC and 3 sites in FLR was collected after the first major flood. The litter was washed, sorted, dried and weighed as described above. Average litter weights in traps and adjacent channel sections were compared to assess Coarse Particulate Organic Matter (CPOM) retention rates in FLC and FLR.

Only 14% of the initial leaf input remained in the FLC channel after the first flood, whereas 29% was retained in FLR. Thus, in spite of higher original input rates into FLC, the amounts of leaf material available to the temporary stream biota were similar in both streams (Fig. 2.6).

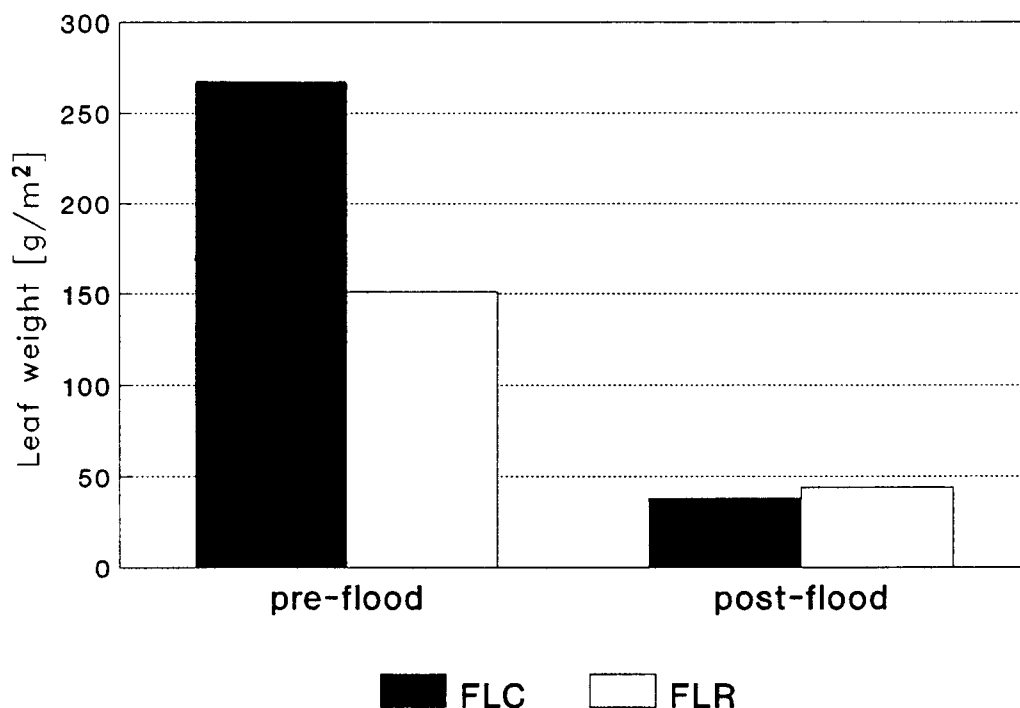


Figure 2.6: Leaf Input and Retention in Summer-dry Forest Streams (FLC and FLR). Average leaf weight [g/m²] in litter traps (pre-flood) and channel bed (post-flood).

2.3. Discussion

Summer-dry streams in Oregon are situated in a unique climate. The distinctness of the wet and dry seasons and the predictability of the winter rains have given rise to the characteristic evergreen forests of the Pacific Northwest (Waring and Franklin, 1979). The regularity in the occurrence of the catastrophe - the drought from the "perspective" of the aquatic organisms - presumably allows for the development of characteristic biota in summer-dry

streams there. In contrast, if flow initiation and flow duration are less predictable, community composition in temporary streams is expected to be less characteristic and to resemble that typical for early successional stages. That is, there would be considerable randomness in the structure and composition of such communities dominated by opportunist taxa with short life cycles.

In the absence of alder the summer-dry stream biota have to achieve rapid development on food of mainly medium quality. Alder leaves are consumed fast by stream organisms (Cummins, 1974). Breakdown rates for maple are medium (Webster, 1983). Grafius and Anderson (1979) observed delayed development of the caddisfly Lepidostoma quercina then larvae had to switch to maple leaves as higher quality alder food became scarce. Similar observations on the shredder caddisfly Potamophylax cingulatus are reported by Otto (1974).

Clearly, high quality food from shrubs and some ash also reaches the channels. But 70% to over 90% of the leaf litter falling into the temporary and ephemeral streams in McDonald Forest is medium quality maple. Similarly, in Virginia hardwoods Webster et al. (1990) found 80% to 98% of the leaf material falling into high gradient headwater streams to be of medium or low food quality. Contrary to the above, Richardson (1992) reports >90% of the litter input into 3 second order creeks in western British Columbia to be composed of high quality alder, vine maple, blackberry and willow leaves.

In addition to the comparatively poor food quality, the quantity of the litter input into the McDonald Forest streams was also low. Only FLC is at the low end of the annual input range of 200 to 800 g of CPOM per m² considered to be typical for small streams (Richardson, 1992). All other sites are below the 200 g/m² threshold.

Low quantities of litter input into temporary headwaters as compared to higher order downstream reaches have previously been reported by Cushing (1988).

Low inputs as well as the inferior nutritional value of the leaves falling into small summer-dry streams result from the lack of a typical riparian vegetation along these sites. Rather, the vegetation accompanying such headwaters is an integral part of the forest association. Distinct riparian strips usually are developed along third-order streams. As is apparent in the comparison between Webster et al. (1990) and Richardson (1992), first- and second-order streams are transitional and may differ considerably with respect to quantity and especially quality of the allochthonous inputs.

Although PERM is still too small for a typical riparian zone to have developed, there is more deciduous vegetation along its course than would typically be found within the forest. Elements of the riparian belt along PERM extend into its temporary headwater section, which is FLC, and allow for more deciduous vegetation there as compared to other summer-dry streams. Similarly, FSE is located only 50 m north of PERM in the transition zone between riparian and forest vegetation. Litter input into this stream therefore is higher than that into FLR or FSC.

While litter input into the study streams was low, standing stocks of CPOM in FLC and FLR are well within the autumn range of 30 - 150 g/m² given for small mountain streams by Stewart and Davies (1990). Naiman and Sedell (1979) found 397 g/m² of CPOM (wood particles > 10 cm diameter omitted from the analysis) in autumn samples from Devils Club Creek, a first-order Cascade mountain stream. This included 74 g/m² of leaf material. However, they apparently sampled when the loading of the systems with litter was at a maximum. That is, they sampled after the

leaves had fallen, but before the first flood had occurred. This points to a general difficulty in comparing CPOM standing stocks. In order to allow for between-study comparisons, data on CPOM standing stocks should be given with reference to flood events, especially the number and severity of floods since the peak litter input in autumn, rather than being related to season alone.

High retentiveness is a general feature of headwater streams (Bilby and Likens, 1980). It allows for relatively large quantities of allochthonous material to be present in summer-dry streams in spite of low input. Retention rates observed in this study were between 20% (FLC) and 35% (FLR) of the original loading. These findings agree well with results from second-order headwater streams in British Columbia, where based on a comparison between model predictions of benthic CPOM and actual standing crop, retention rates between 6% and 30% were calculated (Richardson, 1992).

The higher retentiveness of FLR as compared to FLC results from differences in channel morphology between both streams. There are more and more efficient retentive structures in FLR because the stream is narrow and less deeply incised than is FLC. In FLC wood across the channel frequently is stored above the water line and therefore does not function as retentive device. The difference in retentiveness between FLC and FLR allows for an approximately equal CPOM availability and thus similar food bases in both streams.

Surprisingly, during the flow phase the permanent stream displayed larger temperature fluctuations and higher correlations of air temperature with water temperature than did either FLC or FLR. This finding is best explained by the lack of large rocks in the bed of the summer-dry channels and by the close groundwater connection, which buffers these streams against the impacts of fluctuations

in air temperature. In PERM a relatively wide channel combined with the predominantly rocky stream bed catalyzed heat exchange during periods of low flow. Rocks which are partly submerged and partly exposed to the air mediate the heat transfer which cannot be buffered as efficiently by groundwater exchange in PERM as compared to the temporary streams. This shows that summer-dry streams do not necessarily exhibit a higher fluctuation in physico-chemical parameters as postulated by Williams and Hynes (1977). Rather, the degree of groundwater connectedness is needed to qualify statements about parameter variability in summer-dry streams.

This study was designed to investigate differences in community structure and nutrient retention between different types of streams. Exposure, flow duration and channel bed sediment composition were used as parameters to define stream types. However, factors such as channel slope and flow duration were not uniform within 'types' and contributed to unwanted variation. This raises questions concerning the validity of a comparison which is assumed to show the effects of different exposure, flow duration or sediment types on community structure.

The considerable difference in channel slope between sites is not apparent in average velocities for the long-flow streams. Rather, difference in slope is reflected in the range of velocities measured in these systems. Numerous falls of various sizes and few steep riffles (chutes) give FLR and FLC a stair-step structure. Thus, much of the energy in these channels is dissipated in perpendicular falls. Pools tend to be formed at the base of these falls. Velocities between the steps, and that is about 90% of the channel length, are similar to those measured in MLR. The effect of slope therefore is not that it calls for adaptations to high velocities in organisms inhabiting FLC and FLR. However, it provides the basis for a broader range

of distinct habitat types (pool - riffle), whereas the study reach in MLR is a more or less uniform glide.

While slope differences are not expected to severely hamper a comparison between FLC, FLR and MLR, variation in flow duration between these sites is more critical. However, differences in flow duration between the long-flow streams are less pronounced than the data of average water presence at the sample sites suggest. After cessation of visible flow the forest streams dry up rather slowly and areas with seemingly stagnant water remain for 2-3 months. In MLR there is a rapid transition from the lotic to the terrestrial stage. In a typical year the actual lotic phase in the forest streams therefore is only about 4 - 6 weeks longer than in MLR.

The higher average temperatures in the meadow stream will likely allow for more rapid larval development there, so that in biological terms the difference in flow duration should be even less pronounced than the 4 - 6 weeks would suggest. This presumption is supported by the occurrence of rather large Rhyacophila and Limnephilus caddisflies, which can successfully complete their life cycles in MLR.

In regular years MLR therefore can be expected to provide a good comparison for canopy effects to FLR and FLC. However, as will be discussed in more detail in chapter 4, early drought in the 1989-90 season pushed MLR below the flow duration threshold characteristic for temporary streams. During that season the faunistic comparison between long-flow sites of different exposure was considerably hampered.

Chapter 3

NITRATE AND SEDIMENT DYNAMICS IN SUMMER-DRY STREAMS

3.1. Introduction

During their period of flow, summer-dry headwater streams become an integral part of a catchment's drainage system. It is then that biological and physical processes in these small channels contribute to water and habitat quality in permanent downstream reaches, in lentic systems into which many streams discharge and in groundwaters to which they are connected. There is a potential for significant impacts, because headwater streams "represent the maximum interface with the landscape" (Vannote et al., 1980). Their small size translates into a high channel surface/water volume ratio. Thus, in relative terms, the exchange surface and the biologically active boundary layer between sediment and water column are large. At the same time the density of retention devices in small streams is high (Bilby and Likens, 1980) and because velocity is low, the downstream movement of particles is slow (Naiman et al., 1987). Large exchange surface and long particle residence time cause a short nutrient turnover length in headwaters (Stream Solute Workshop, 1990; Minshall et al., 1983). The short nutrient turnover length, particularly the possibility of a considerable transfer of nutrients from the aquatic to the terrestrial environment, mediates a more efficient use of materials in the overall watershed.

This chapter is concerned with the role of summer-dry headwaters in determining water and habitat quality in

higher order streams. The transport of nitrate in temporary streams (long-flow streams) and the retention of sediment in ephemeral streams (short-flow streams) was studied to gain insight into retention mechanisms and to quantify the amount of solutes and fine sediment which can be removed from the water column. Knowledge of retention mechanisms and removal capacities provide the baseline to assess the potential of ephemeral and temporary streams to contribute to water and habitat quality in permanent downstream reaches.

Nitrate was chosen as the exemplary compound to study nutrient dynamics because of its importance for eutrophication¹. Eutrophication is of specific concern for conservation-oriented management because the shift toward higher primary production in eutrophic streams is accompanied by considerable changes in the fauna "from that typical of cool, stony streams to that characteristic of river shoals" (Hynes, 1969). In terms of invertebrate functional feeding groups this corresponds to a shift from a shredder- to a grazer/collector-dominated community (Cummins and Klug, 1979).

From a practical point of view, nitrate provides a relatively simple model of retention processes because

1

Eutrophication is the increase in primary production as a result of increased nutrient availability (Schwoerbel, 1987). In the context of streams, Hynes (1969) suggests the usage of the term enrichment because eutrophication "which was coined for application to lakes, has acquired so many connotations to aging and evolution of the environment that it cannot properly be applied to running water". While Hynes raises a valid point other authors have been less restrictive and applied the term 'eutrophication' to all bodies of water (e. g. Rohlich, 1969; Schwoerbel, 1987). Since I am not aware of a German term equivalent to enrichment in the sense of Hynes, eutrophication as used in this thesis will apply to standing and running waters.

losses through volatilization, adsorption to the sediment and transformation driven by the redox potential of the milieu are negligible in oxygen-saturated waters. In addition cost of analysis at a high sensitivity level is comparatively low.

Nitrate concentrations in streams can fluctuate on a spatial and on a temporal scale. Considerable longitudinal fluctuations of nutrient levels between sites located within the same channel were observed (Jacobs and Gilliam, 1985; Triska et al., 1990). On the temporal scale, Cooper (1990) measured a 72-fold range of nutrient concentration over a one-year period in a small headwater stream. He sampled from a single site and NO_3 concentrations in the water were found to be correlated with discharge and macrophyte abundance (Cooper, 1990).

Several studies have been conducted on the removal of nitrate from small streams. For a temporary headwater in the North Carolina Coastal Plain, Jacobs and Gilliam (1985) report a significant decrease of nitrate concentrations in the water column between sample sites closest to, and most distant from an agricultural production area. They attribute their observations to denitrification processes in the stream and floodplain sediments (Jacobs and Gilliam, 1985). McColl (1974) applied pulse injection of a solution containing nitrate, ammonium and other nutrients to a small semi-natural stream. He measured rapid removal of ammonia from the water column. Nitrate was removed less efficiently. However, the author did not consider the possibility of nitrification, which may have masked nitrate uptake within the system.

Primary producers are the most important biological sink for dissolved nutrients such as nitrate or phosphate. Aquatic macrophytes have been shown to remove nitrate efficiently from the water column (Vincent and Downes,

1980; Reddy and De Busk, 1985). However, no aquatic macrophytes were present in the study sites. But in the case of the forest streams the root systems of terrestrial plants were well developed beneath the channel beds. The root zone is potentially effective in modifying the chemical composition of groundwater that flows through riparian areas (Swanson et al., 1982). Nitrate uptake by trees is considered to be a "major component of nutrient exchange between streams and floodplains" (Trotter, 1990). Thus, via the root system, terrestrial macrophytes may contribute significantly to the 'self-purification' process in temporary headwater streams.

Gregory (1980) demonstrated that uptake by periphyton caused a diel pattern of nitrate concentration in unshaded or partly shaded Cascade Mountain streams. In an artificially lighted first-order channel located in an old growth forest, addition of nitrate resulted in increased periphyton standing crop and gross primary production. Nitrate addition to unlighted regions of the same stream did not yield any significant effect. Working with experimental flumes, Triska et al. (1983) found significant nitrate uptake by an immature algal community. Uptake rates decreased as the periphyton community matured.

Suspended sediment is present in every surface water as a result of natural erosion (Sorensen et al., 1977). Land-use practices can significantly increase the amount of soil particles in lotic systems (for a recent review see Campbell and Doeg, 1989). Erosion from road surfaces is an especially important source of fine sediment in streams (Reid and Dunne, 1984).

The effect of suspended sediment on freshwater biota was reviewed by Sorensen et al. (1977) and more recently by Rivier and Sequier (1987). The main effects include a decrease of primary production through abrasion and shading of periphyton, and the loss of invertebrate habitat and

spawning gravel through smothering and clogging of substrates (Milner et al., 1981).

Water depth is the main determinant for the settling rate of suspended sediment (Reynolds et al., 1990). This rate is largely independent of current velocity (Reynolds et al., 1990) and "even the finest of particles must deposit everywhere in a stream under all conditions of velocity and turbulence" (Graham, 1990). Thus, fine particles accumulate in still water sections not because of higher settling rates, but because flow conditions there do not allow for them to be swept up into suspension again (Graham, 1990).

Swanson et al. (1982) point out that in-stream storage of sediment in general is a poorly understood process in need of more research. None of the work published to date on summer-dry streams addresses the question of sediment retention within such channels. Considering that ephemeral and temporary headwaters are rather shallow systems with low current velocities, such streams can be expected to retain suspended sediment far more effectively than does a river such as the Waitaki in New Zealand, where Graham (1990) computed a settling rate only slightly more than 10% for silt over a 60 km stretch.

3.2. Materials and Methods

Nitrate Sampling

Water samples were taken in acid-washed 250-ml plastic bottles from all streams to investigate seasonal variation in nitrate concentration. Sampling was accomplished during the 1989-90 season and immediately before and after the onset of flow in late fall 1990. Pre-

flow samples were from pools which began to appear in the channels after heavy autumn rains had recharged the groundwater reservoir.

Additional sampling was conducted to allow an assessment of daily variations in nitrate levels. These samples were collected in 4hr intervals over a 12hr period in the permanent and the temporary streams.

Samples were stored on ice in the field. In the laboratory they were filtered through Whatman GF/A Glass Microfibre filters and then analyzed for nitrate within five days of sampling. Nitrate concentrations were determined by the Cd-reduction method (APHA, 1985) with a Technicon AutoAnalyzer II by the Cooperative Chemical Analytical Laboratory of the USDA Forest Service and Oregon State University.

Solute Injection Experiments

Solute injection experiments lasting for 120 minutes were conducted in April/May 1991 at study sites FLC and MLR. A solution containing nitrate (40-45 mg/l) as reactive solute as well as rhodamine (12 mg/l) and chloride (6.6 g/l in MLR and 1.2 g/l in FLC) as passive tracers was dripped into the streams. Drip rate was kept constant at ca. 100 ml/min in MLR. Initial drip rate in FLC was also ca. 100 ml/min, but it was increased after 40 minutes to about 150 ml/min. Water samples were taken in 2.5 to 20 minute intervals about 3 m below the injection location (S_0) and at a sampling station (S_D) 25 m downstream in FLC or 40 m downstream in MLR.

Samples from the injection experiments were treated and analyzed for nitrate as described above. A fluorometer was used to measure rhodamine content. Chloride

concentrations were determined according to the ferric thiocyanate method described by Bergmann and Sanik (1957) and modified by Resche (M. Resche, pers. communication). This analysis required 125 μ l of a saturated solution of mercuric thiocyanate and 125 μ l of 0.25 M ferric ammonium sulfate to be added to 750 μ l sample solution. The aliquots then were well mixed and kept at room temperature for 10 minutes. Finally chloride concentrations were determined colorimetrically at 460 nm in a spectrophotometer.

Expected nitrate levels at the downstream stations $S_{(D)}$ were computed for a given solute input at $S_{(I)}$, the station just below the injection site. The computation gauges the loss of in-stream nitrate resulting solely from groundwater exchange processes over the experimental reach. Rhodamine loss was used to obtain an estimate for the exchange rate between stream water and subsurface flow. This assumes that rhodamine is not removed from the water column by adsorption, transformation or biological uptake. To approximate diffuse input from the groundwater over the experimental reach, the nitrate concentration in the subsurface reservoir was estimated from pre-treatment levels at $S_{(I)}$ and $S_{(D)}$ according to:

$$NO_{3(D)} = NO_{3(I)} * (1 - R_{loss}) + NO_{3(sub)} * (R_{loss} + (D_{(D)}/D_{(I)} - 1)) / R_{tot} \quad (1)$$

with: $R_{tot} = (1 - R_{loss}) + (R_{loss} + (D_{(D)}/D_{(I)} - 1))$
 $D_{(D)}/D_{(I)} \approx 1$

Solved for $NO_{3(sub)}$:

$$NO_{3(sub)} = (NO_{3(D)} - NO_{3(I)} * (1 - R_{loss})) / R_{loss} \quad (2)$$

where: R_{loss} : $R_{(D)} / R_{(I)}$, i.e. rate of Rhodamine lost over the experimental reach (25 m or 40 m)
 $D_{(Z)}$: Discharge at $S_{(D)}$ or $S_{(I)}$.
 $\text{NO}_{3(\text{sub})}$: Nitrate concentration in subsurface pool
 $\text{NO}_{3(Z)}$: In-stream nitrate concentration at stations $S_{(D)}$ or $S_{(I)}$ (equilibrium concentrations: pre-experiment or experimental plateau)

Having estimated $\text{NO}_{3(\text{sub})}$, the expected nitrate concentration at the downstream stations ($\text{exp NO}_{3(D)}$) can be computed as:

$$\text{exp NO}_{3(D)} = (1 - R_{\text{loss}}) * \text{NO}_{3(I)} + R_{\text{loss}} * \text{NO}_{3(\text{sub})} \quad (3)$$

To statistically test for nitrate removal over the experimental reach, nitrate/passive tracer ratios were computed. Ratios were obtained separately for the injection and the downstream sampling site according to the general formula:

$$Q_{(Z)} = (\text{Nitrate}_{(Z)} - \text{BG Nitrate}_{(Z)}) / (\text{Tracer}_{(Z)} - \text{BG Tracer}_{(Z)}) \quad (4)$$

where BG abbreviates pre-treatment 'BackGround' concentration of a solute. A value of $Q_{(D)} < Q_{(I)}$ results from biological uptake of nitrate over the experimental reach, whereas $Q_{(D)} > Q_{(I)}$ indicates nitrate influx from subterranean sources or tracer uptake.

Nutrient uptake length (S_w) and nutrient turnover time (k_c) were computed to provide values for general model parameters. These values can be used for between-study comparison of stream retention efficiency. S_w is the average distance a molecule travels before being taken up in the system and k_c measures the rate at which a solute is

taken up in a given time interval.

S_w can be determined from the nitrate plateau concentrations (corrected for background) at the downstream stations using a log-transformation of the general decay function (Stream Solute Workshop, 1990):

$$S_w = x / (\ln (NO_{3(D)} - BG \ NO_{3(D)}) - \ln (NO_{3(0)} - BG \ NO_{3(0)})) \quad (5)$$

where $x = 25 \text{ m (FLC)}$ or 40 m (MLR)

Median residence time (MRT) of water in an experimental reach was estimated as the time when solute concentrations reached 1/2 of the maximum plateau levels (corrected for background) at the downstream sampling stations. The average of the inverse of the MRTs for the 3 solutes was then used as an estimate of velocity (u) and k_c was obtained by solving the relationship:

$$S_w = u / k_c$$

for k_c :

$$k_c = u / S_w \quad (6)$$

During the injection trials 16 cellulose strips (weight ca. 0.2 g each) enclosed in 100 μm nitex bags were exposed in the channels. The strips provided a standard substrate to assess the microbial response to fertilization in the streams by measuring respiration rates.

An equal number of bags with cellulose were placed above and within the experimental reaches 30 min after initiation of drip. Substrates were exposed until the end of the experiment (total exposure 90 min). Bags containing the strips were then collected, stored on ice, and rushed

to the laboratory. Within two hours of removal from the stream, the cellulose strips were placed into a Gilson-Differential Respirometer and incubated in 2 ml of pre-filtered (Whatman GF/A Glass Microfibre Filter) water from PERM. Respiration rates were measured for 72 hours at 8°C.

Sediment Retention

Retention of sediment was studied in FSC and in an adjacent ephemeral stream with similar physical characteristics (FSL). The work was initiated shortly after the construction of a forest road. Both streams are crossed within a 100 m stretch of this road. To estimate sediment input into FSC and FSL, samples were obtained daily during the period of heavy road use by log trucks. Water was collected from the unimpacted channel segment above the road, the roadside ditch and the culvert immediately below the road. In addition several serial samples were obtained from both channels 25 m, 50 m, 75 m and 100 m below the culvert.

To analyze for sediment content, water samples were first filtered through a 53 μm USA Standard Testing Sieve. For the purpose of this study, material retained in the 53 μm sieve is defined as non-suspended sediment. Subsequently, 5 subsamples of different volumes (10 - 250 ml) were taken from the already filtered water. The subsamples were washed through a pre-weighed Whatman GF/A Glass Microfibre Filter (pore size 1.6 μm). As defined by Sorensen et al. (1977), sediment retained on the glass microfibre filter represents the suspended sediment fraction (53 μm > suspended sediment > 1.6 μm). The remaining filtrable residue (sediment < 1.6 μm) will be referred to as ultra-fine sediment. Non-suspended sediment and glass microfibre filters loaded with suspended sediment

were oven dried in aluminum pans for 48 hours at 45°C and then weighed. To quantify amounts of ultra-fine solids, three 25 ml aliquots of water having passed a glass microfibre filter were evaporated in pre-weighed aluminum pans in a drying oven. The pans were weighed again after the water had evaporated and the non-filtrable residue content was determined.

All weights were obtained on a Mettler Electrobalance. Weights are reported in mg/l as subsample average (suspended sediment fraction and ultra-fine solids fraction) or total weight of sediment in a sample (non-suspended sediment fraction).

The sediment trapped in leaf packs otherwise used as colonizing substrate for invertebrates (see chapter 4) was weighed to obtain a measure for sediment deposition on the stream bed. Packs were exposed in the channels above the road (control) and below the road (treatment) during the period of intense road usage in early spring. Distances from the road in the treatment sections were 63 - 136 m in FSC and 12 - 64 m in FSL. After 2 weeks of exposure, leaf packs were pulled from the streams, stored in plastic bags and transported to the laboratory. Packs were then washed over a 53 μm Standard Testing Sieve and the wash water containing the suspended sediment and ultra-fine solids fraction was collected in a bucket. Weights of non-suspended sediment, suspended sediment and ultra-fine sediment were obtained as described above.

To further assess the impact of sediment deposition, a core sample was taken at a site of mass mayfly emergence before and after construction of the forest road. Sample volume was 269.5 cm^3 ($38.5 \text{ cm}^2 * 7 \text{ cm}$). Both samples were fractionated using a series of Standard Testing Sieves of different mesh sizes. Fractions were dried at 45°C for 72 hours and weighed. Organic content for each fraction was

determined by burning in a Thermolyne Furnace at 500°C for 12 hours.

3.3. Results

Nitrate Dynamics

The nitrate dynamics in the summer-dry streams was investigated during 1989 and 1990. Nitrate levels were consistently low in both meadow sites (MLR and MSC) and in the short-flow forest channel (FSC). No values are given for FSE because flow was increased there in 1989 by rerouting of water from PERM. Nitrate levels fluctuated considerably over time and between different locations within a reach in the long-flow forest streams (FLC and FLR) (Table 3.1). In both these streams peak nitrate concentrations were measured before the onset of flow. Pre-flow samples were taken in early November 1990 from small pools. These pools began to appear in the formerly dry channels as the water table had risen enough after several weeks with rain. Elevated nitrate concentrations persisted for about a month into the flow period (Table 3.1).

The permanent forest stream (PERM) was intermediate with respect to nitrate concentrations (Table 3.1). Moderately elevated levels of nitrate were recorded there in winter and spring. However, on the temporal scale the increase in nitrate concentration in PERM lagged behind the maximum values in FLC and FLR (Table 3.1).

Samples obtained in June 1990 had increased nitrate concentrations compared with previous months (Table 3.1). These samples were taken after several days with rain. Stream discharge, which previously had declined steadily for six weeks, at that time began to rise slightly as compared

Table 3.1: N-NO₃ Concentrations [$\mu\text{g/l}$] in the Study Streams. Day column indicates the number of days elapsed after flow resumption. Two locations separated by 114 m (FLC₁₂ and FLC₁₂₆) and 90 m (FLR₄₀ and FLR₁₃₀) were sampled in temporary forest streams. The abbreviation n.f. indicates no flow.

Site	preflow 02/11/90	2 days 26/11/90	20 days 13/12/89	90 days 23/02/90	125 days 27/03/90	190 days 19/06/90
FLC ₁₂	15	12	8	10	3	8
FLC ₁₂₆	256	166	82	61	27	64
FLR ₄₀	817	354	152	59	65	174
FLR ₁₃₀	26	239	100	58	37	79
FSC	n.f.	n.f.	12	15	16	n.f.
MLR	n.f.	n.f.	4	3	4	n.f.
MSC	n.f.	n.f.	8	9	n.f.	n.f.
PERM	4	9	52	59	31	47

compared to the preceding days.

While in-stream nitrate concentrations fluctuated considerably over the year, no significant daily rhythm was found (Fig. 3.1). Nitrate concentrations were constant in all streams between 08:00 and 20:00 during the mid- to late-flow period.

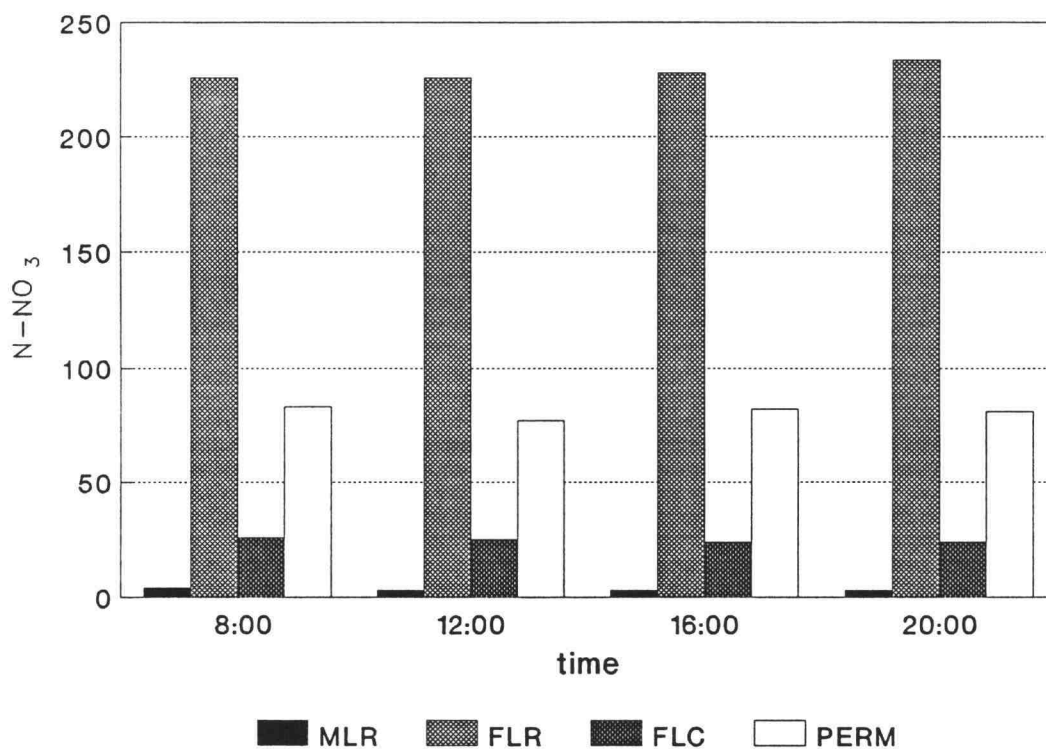


Fig. 3.1: Diel Fluctuations in Nitrate Concentrations [$\mu\text{g/l}$]. The series was measured on April 23rd, 1991.

Nitrate concentrations were not correlated with discharge during the first part of the flowing season. In MLR nitrate concentrations were always 3 or 4 $\mu\text{g/l}$ at discharge values ranging between 0.1 and 3 l/s. In PERM and FLC nitrate levels were almost identical for days 20 and 90, while discharge differed by 10-fold (PERM) and 20-fold (FLC). In FLR nitrate measurements were constant from late February to the end of March (days 90 to 125 after resumption of flow) while discharge fluctuated between 0.1 and 6 l/s (Fig. 3.2).

In FLC and PERM, both of which drain rather deep soils, there was an indication for a correlation between

discharge and nitrate concentrations in the water during the second half of the flowing season. In FLC where, due to injection trials, three data points are available between days 125 and 190 after onset of flow, discharge was negatively correlated to nitrate concentrations in the water for that period ($R^2 = .99$; $p < .05$). Similarly, nitrate concentrations increased in PERM as flow decreased between days 125 and 190. However, in FLR, which drains a shallow soil and flows on bedrock for some of its channel length, increased nitrate concentrations in June 1990 coincided with an increase in discharge in that stream after a period of rain (Fig. 3.2).

Nitrate export rates from a given system, calculated as product of in-stream nitrate concentration and discharge, were greatest early in the season. The permanent stream exhibited the highest and MLR the lowest export rates (Fig. 3.3). Higher export rates from PERM, in spite of typically lower nitrate concentrations as compared to FLR and FLC, were a result of the relatively high flow rates in this stream. In PERM and FLC the negative correlation between discharge and dissolved nitrate concentration caused export rates to be constant later in the season (days 120 to 190). In FLR nitrate export increased between March and June, whereas consistently low nitrate levels in MLR translated into decreased export rates as the season progressed and flow decreased (Fig. 3.3).

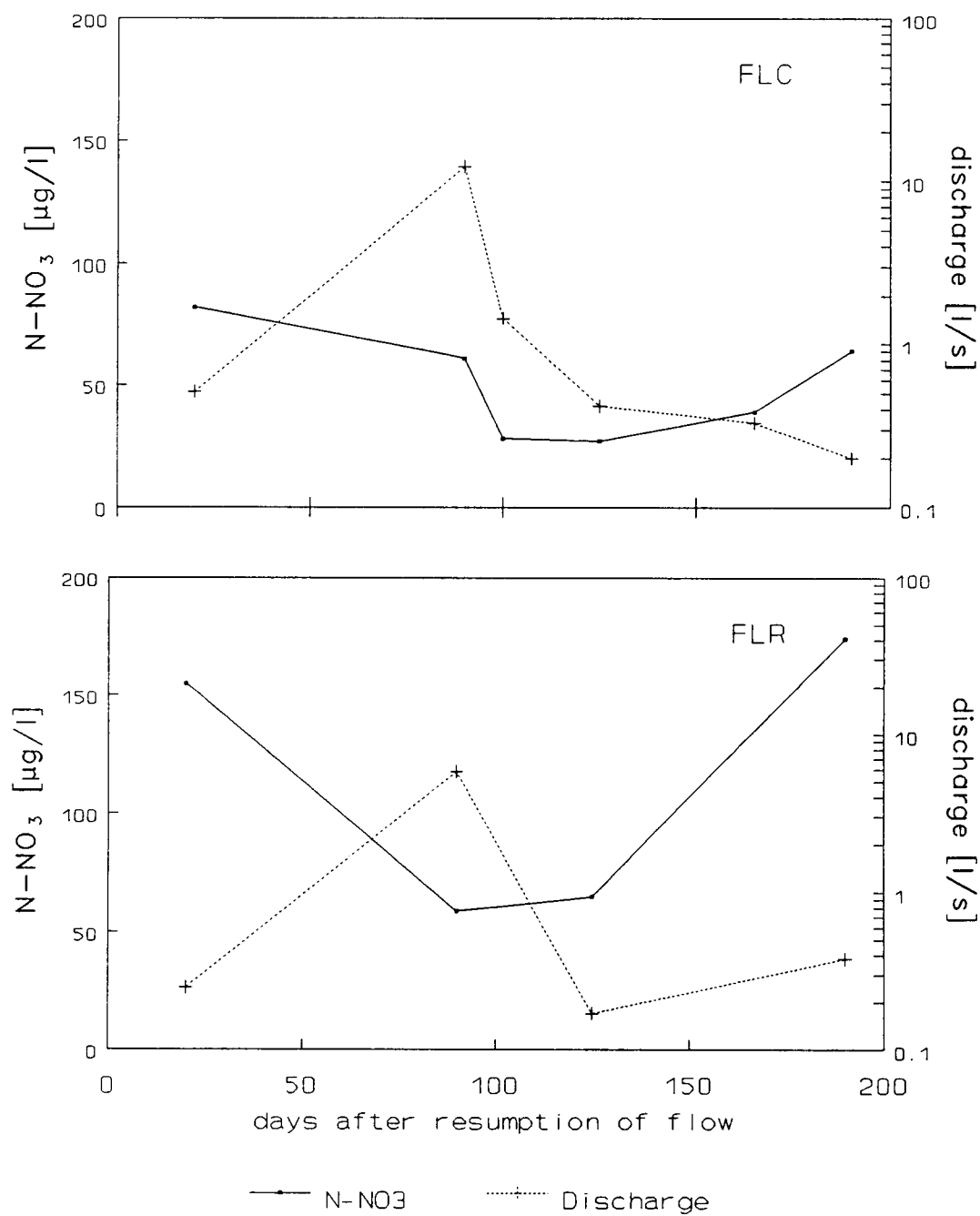


Fig. 3.2: Discharge and Nitrate Patterns (FLC and FLR).
 Time period covered is from 13/12/89 - 19/06/90
 (20 - 190 days after resumption of flow).

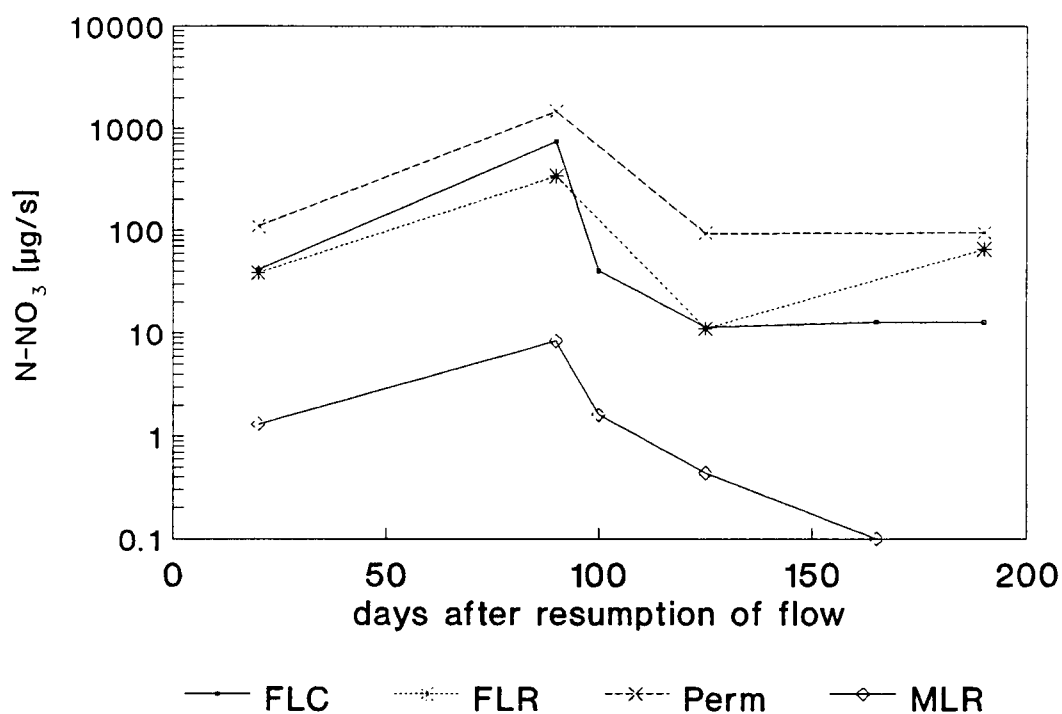


Fig. 3.3: Nitrate Export from Headwater Streams. Export is calculated as product of discharge and N-NO_3 concentration. Time period covered is from 13/12/89 - 19/06/90 (20 - 190 days after resumption of flow). MLR dried up by day 165.

Injection Experiments

The results of the injection experiments are illustrated in Fig. 3.4. The separate charts show solute concentrations at minutes after drip initiation at the injection sites ($S_{(0)}$) and at the sampling stations ($S_{(D)}$). The differences in plateau concentrations between $S_{(0)}$ and $S_{(D)}$ are a measure of the retention of a given solute in each of the study streams.

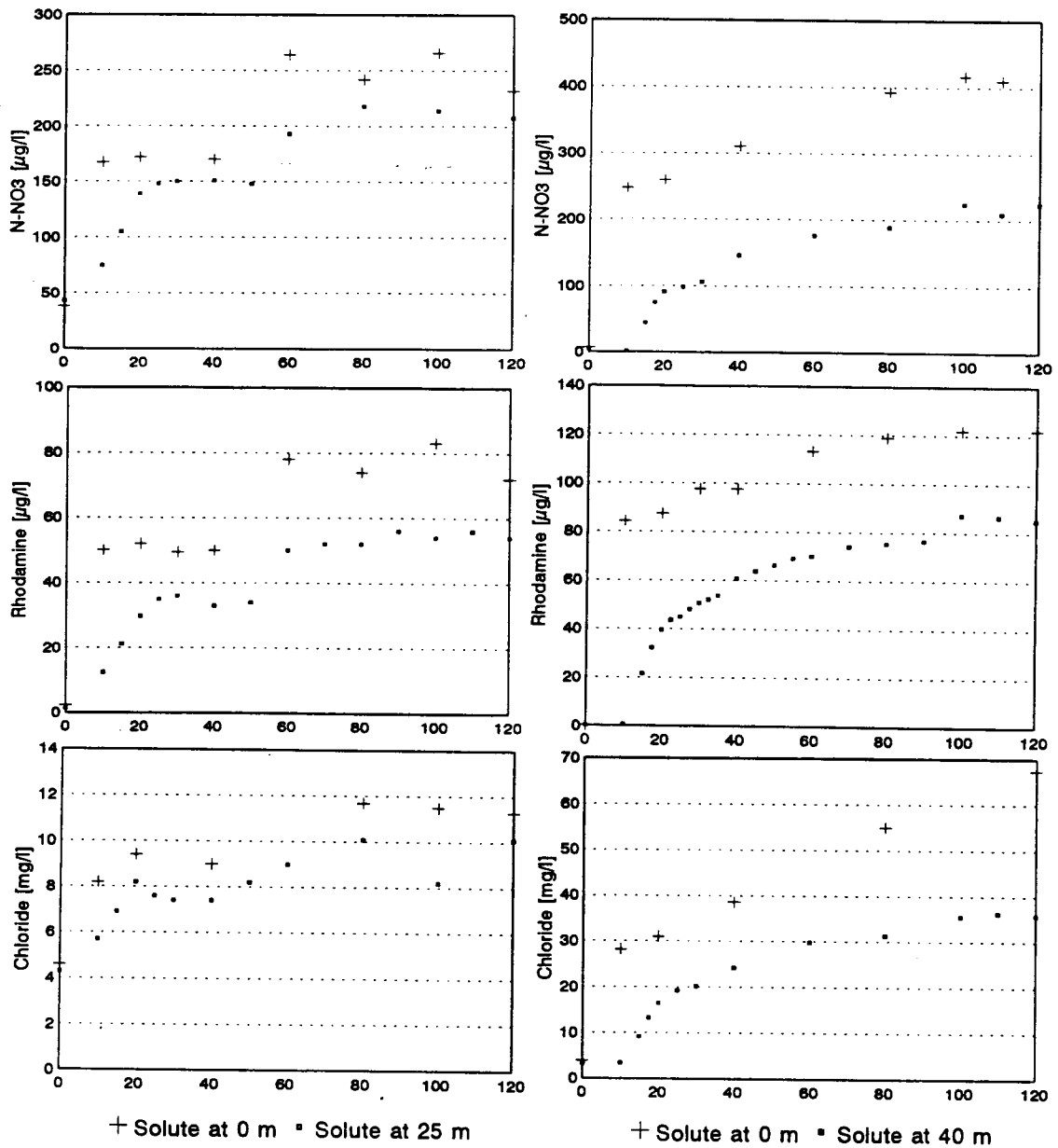


Fig. 3.4: Fertilization Experiments in FLC (Left Column) and MLR (Right Column). In FLC the amount of solutes injected was increased at $t = 40'$. Note the different scales for solutes in FLC and MLR.

In the forest stream (FLC) drip rates were increased at $t = 40$ minutes into the experiment to examine possible saturation induced limitations on uptake rates. The two resulting plateau levels (P_I and P_{II}) at the sampling station 25 m downstream from the injection site were established 20-30 minutes after initiation of drip or increase of drip frequency (Fig. 3.4). Removal rates of all solutes were similar for both plateau concentrations. This indicates a linear relationship between solute concentrations and uptake capacity. That is, the solute concentrations used in the experiment did not saturate the uptake capacities of the system.

Solute plateau concentrations at the meadow stream (MLR) sampling station located 40 m downstream from the injection site were established about 100 minutes after initiation of drip. For unknown reasons no plateau concentration was obtained for chloride just below the injection site in this stream. It therefore was estimated from initial solute concentrations in the drip solution to be 56.9 mg/l.

Solute concentrations corrected for background decreased about 20% - 30% over 25 m in FLC and between 28% - 46% over 40 m in MLR (Table 3.2). The drop of passive tracer concentrations (rhodamine and chloride) in the water column was high in spite of constant or decreasing flow rates between injection and sampling sites. Passive tracer loss corresponded to stream water - subsurface flow exchange rates of 0.8% (FLR) and 0.75% (MLR) per meter of channel. Exchange with subsurface flow therefore was the most important route for solute removal in FLC and MLR.

Uptake distances (S_w) were less than 120 m for all solutes in both channels. Nitrate in MLR had an uptake distance of less than 65 m. This is within the range of headwater stream uptake distances reported elsewhere for

Table 3.2: Solute retention in FLC and MLR. Rhodamine loss from the water column quantifies the stream - groundwater exchange. Negative values in the second data column indicate that Rhodamine was lost at a higher rate than Nitrate or Chloride.

Solute	Site	$\Delta\%$ Solute	$\Delta\%$ exp. - meas.	S_w [m]	MRT [s/m]	k_c [l/min]
N-Nitrate	FLC _{PI}	19.3	- 8.76	119.05	32.4	0.017
	FLC _{PII}	20.0	- 8.97	113.64		0.018
	MLR	46.2	17.72	64.52	46.3	0.024
Chloride	FLC _{PI}	20.4	- 4.96	108.70	26.7	0.018
	FLC _{PII}	23.6	- 8.70	92.59		0.022
	MLR	37.9	8.27	83.30	39.6	0.019
Rhodamine	FLC _{PI}	31.1		65.79	31.5	0.030
	FLC _{PII}	29.3		71.43		0.028
	MLR	28.6		117.65	33.4	0.013

$\Delta\%$ Solute : Difference (%) corrected for background in solute concentration between injection site ($S_{(I)}$) and sampling site ($S_{(D)}$).

$\Delta\%$ exp. - meas. : Difference (%) between solute concentration expected at $S_{(D)}$ (solute background concentration and import via subsurface flow included) and solute concentration measured at $S_{(D)}$.

S_w : Solute uptake length.

MRT : Median residence time of a solute in the experimental reach.

k_c : Uptake rate based on average MRT of all solutes (all solutes used to estimate velocity).

phosphate (Newbold et al., 1983; Mulholland et al., 1985) and nitrate (Triska et al., 1990). Considering the short uptake distances, uptake rates (k_c) were surprisingly low (Table 3.2). But median residence times (MRT) for molecules of more than 30 s per meter of channel allowed for short uptake distances in spite of low uptake rates.

The measured concentrations of nitrate and chloride at the downstream sampling station in FLC were higher than the computed values for the expected concentration of these solutes would suggest. That is, the rhodamine losses overestimate the actual exchange rate between stream water and subsurface flow by about 5% - 9% (Table 3.2). This indicates that rhodamine is not a truly passive tracer in FLC. Sorption to sediment (Bencala et al., 1983; Munn and Meyer, 1988) and organic matter (S. Gregory, pers. communication) was found to significantly reduce rhodamine concentrations in the water column of headwater streams. Such interactions of rhodamine with the sediment are poorly understood, however, and depend on site-specific conditions (Bencala et al., 1983).

Due to dye retention in the channel and the presence of nitrate in the subsurface flow recharging the stream, the $N-NO_3$ /rhodamine ratio at $S_{(0)}$ was significantly smaller than that at $S_{(D)}$ ($P < .01$) in FLC.

The data obtained from the injection experiment do not indicate any biological uptake of nitrate in the forest stream. Nitrate was lost from the water column at rates equal (chloride) or lower (rhodamine) than those of the passive tracers. However, bacterial respiration on colonisation substrates was significantly higher ($P < .05$) in the fertilized channel section as compared to the reach where nitrate had not been added (Fig. 3.5). Thus, there was a biological response to nitrate addition in FLC. Within the short time frame of the injection experiment,

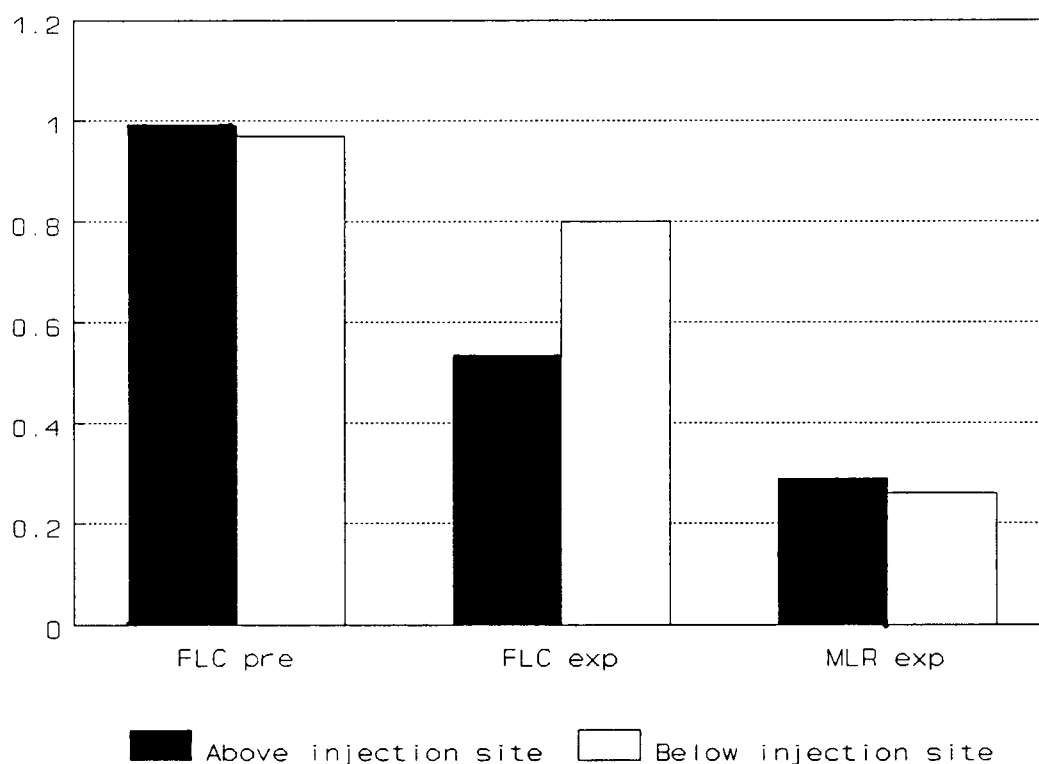


Fig. 3.5: Effect of Fertilization on Microbial Respiration. Respiration [$\mu\text{g O}_2/\text{g}\cdot\text{h}$] associated with cellulose substrates exposed in FLC and MLR prior (pre) and during the fertilization experiment (exp). Incubation time was 576 degree hours. FLCexp and MLRexp were incubated at 8°C for 72 hours, FLCpre was incubated at 4°C for 24 hours and at 10°C for 48 hours.

this response did not contribute significantly to the removal of nitrate from the water column.

In contrast to FLC, nitrate was more efficiently removed from the water column in MLR than were the passive tracers (Table 3.2). The removal rate of nitrate was 18%

above that of rhodamine and 8% higher than that of chloride (based on the estimated chloride plateau level at $S_{(0)}$ of 56.9 mg/l). The $N-NO_3$ /rhodamine ratio at $S_{(0)}$ was significantly larger than that at $S_{(0)}$ ($P < .05$). This indicates more removal of nitrate as compared to passive tracers over the study reach. Denitrification is assumed to be negligible in MLR, because this stream carried oxygen-saturated water and lacked any signs of anaerobic sediment. Therefore, biological uptake was a major mechanism of nitrate removal from the water column in the nitrogen-limited meadow stream.

In contrast to the situation found in FLC, microbial activity on colonization substrates did not differ between treated and untreated reach in MLR (Fig. 3.5). Filamentous green algae appear to be the primary biological sink for nitrate there. Such algae occurred in high densities in this unshaded stream, but were absent from forest channels.

Sediment Dynamics and Retention

The sediment loads in FSC and FSL were related to road usage. Peak inputs occurred when traffic on the forest road was highest during a five-day period in January 1989. At that time logs were removed from a harvest unit in an adjacent watershed. Road repair (spot graveling) and limited road use continued until mid February and ceased thereafter.

During the period of heavy road use (20 - 30 passes per day), levels of ultra-fine solids, suspended and non-suspended sediment were up to 70-fold higher in the section of FSC impacted by the road as compared to the natural channel (Fig. 3.6). The maximum concentration of suspended sediment in the ditch was 7260 mg/l. Sediment content in

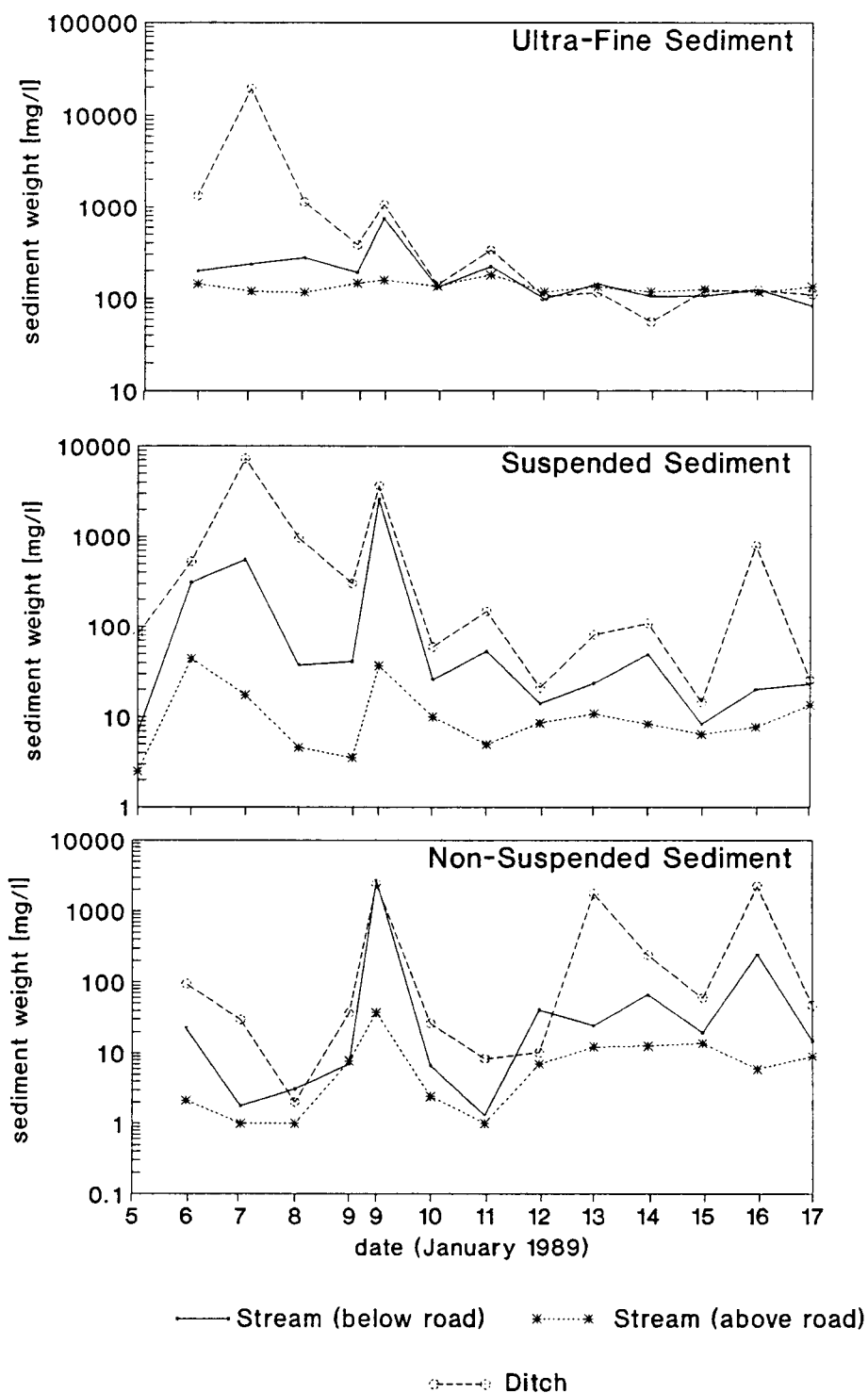


Fig. 3.6: Sediment Concentrations (Site FSC). Data points represent daily samples except that two samples were taken on 09/01/89 at 12:00 and 16:00.

the water was highly variable during the period of heavy road use and closely linked to precipitation events. As a result of this variability, it is not possible to estimate overall sediment input into the ephemeral streams by integration between spot measurements.

The pool of suspendable sediment on the road decreased rapidly after traffic ceased on January 9th. A storm event on the same day produced high overall export rates of particulates from the system (Fig. 3.7). Consequently, until the ditch dried up on January 17th, sediment levels in the stream section below the road were still elevated, but for most of the time remained within a range that could also be found in the unimpacted section of FSC (Fig. 3.6).

At moderately elevated particle concentrations in mid-February, uptake length for ultra-fine sediment was 818 m (16/02/89) and 267 m (19/02/89) in FSC, 350 m (16/02/89) and 401 m (19/02/89) in FSL. For these dates 70-90% of the variation in ultra-fine solids concentrations can be explained by distance from input with a linear regression model (Table 3.3). At low turbidities no significant negative correlation between distance from input and the concentration of ultra-fine solids was found in FSL. In fact, in FSC there was evidence for a positive correlation between distance from input and ultra-fine sediment concentrations at low turbidities (Table 3.3). This positive correlation occurred after the road had not been used over a two-week period and ultra-fine solids levels in the ditch water were below those in the section of FSC above the road.

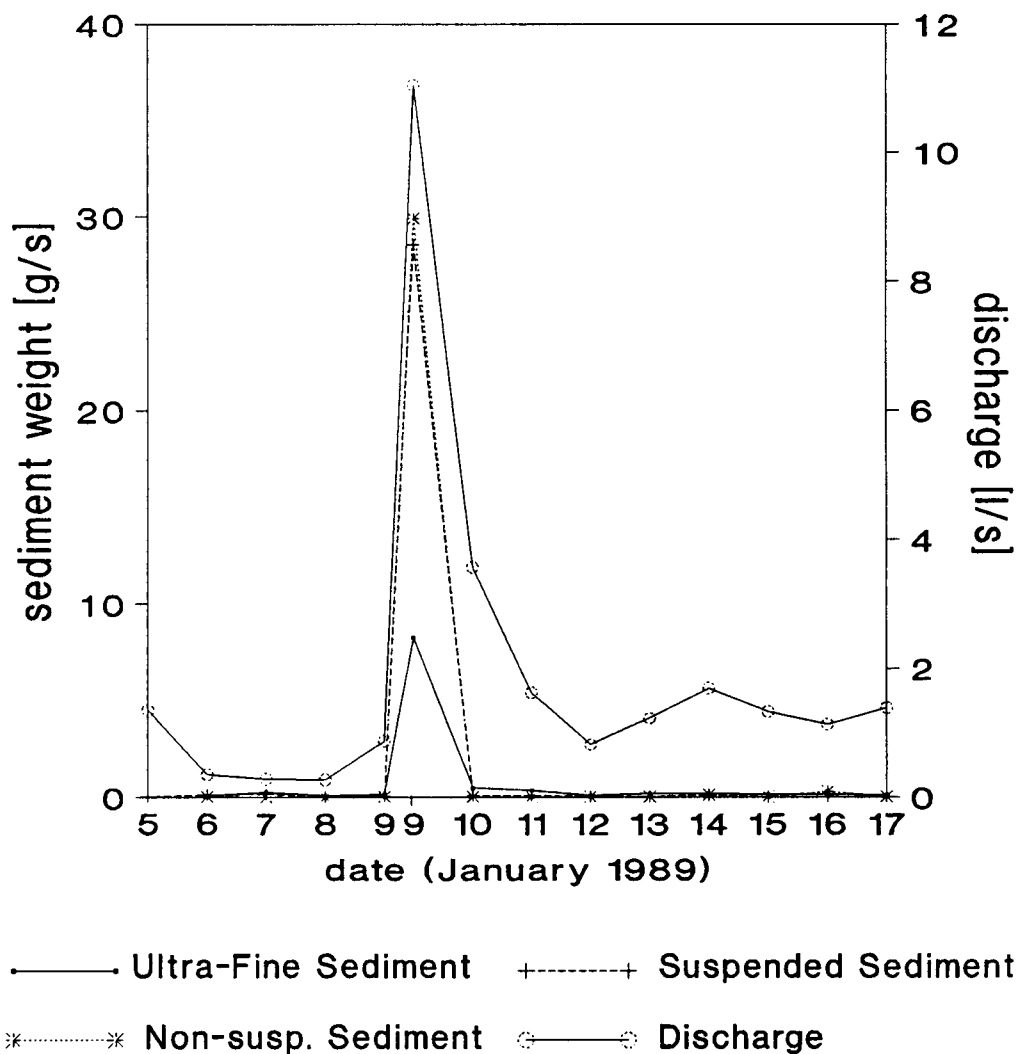


Fig. 3.7: Sediment Export via FSC. Export [g/s] is calculated as product of sediment concentration in the water and discharge.

Slopes of the regression lines describing the relationship between ultra-fine solids in the water and distance from input were highly correlated with initial input concentrations at the culvert in FSL ($R^2 = .95$; $p < .01$). This indicates increasing retention efficiency as

Table 3.3: Sediment Removal from the Water Column. Linear regression analysis of sediment concentration in the water as a function of distance from input.

Date	Site	df	Non-suspended sediment			Suspended sediment			Ultra-fine sediment		
			slope	R ²	P	slope	R ²	P	slope	R ²	P
21/01/89 ¹	FSC	2	+0.08	0.12	n.s.	-0.23	0.76	<.07	+0.70	0.75	<.08
	FSL	2	+0.53	0.73	<.08	-0.10	0.78	.06	+0.12	0.17	n.s.
01/02/89 ¹	FSC	2	-1.77	0.58	n.s.	-0.22	0.82	<.05	+0.30	0.68	<.10
	FSL	3	-1.31	0.94	<.01	-0.37	0.70	<.05	-0.09	0.08	n.s.
16/02/89 ²	FSC	2	-0.29	0.55	n.s.	-2.03	0.90	<.05	-0.33	0.70	<.09
	FSL	3	-0.38	0.53	<.09	-0.99	0.98	<.01	-0.60	0.91	<.01
19/02/89 ²	FSC	2	-0.33	0.66	<.10	-2.39	0.95	<.01	-0.96	0.90	<.05
	FSL	3	-0.15	0.58	<.08	-1.87	0.95	<.01	-0.71	0.83	<.05

1: Date with low sediment input levels.

2: Date with elevated sediment input levels.

sediment concentration in the water increases. As might be expected from the above, the same relationship was less significant in the case of FSC ($R^2 = .69$; $p < .09$).

In both study streams the concentration of suspended sediment in the water decreased with distance from the source (Fig. 3.8). Uptake length (S_w) at moderately elevated suspended sediment concentrations (16/02/89 and 19/02/89) was 36 m and 64 m in FSC, 71 m and 105 m in FSL. Linear regression models relating suspended sediment concentration in the water to distance from input explained 70-80% of the variation in the data at low input levels (less than 50 mg/l) and at least 90% of the variation when sediment concentrations were moderately elevated at the culvert (more than 150 mg/l) (Table 3.3).

Slopes of the regression lines describing the relationship between suspended sediment in the water and distance from input were positively correlated with suspended sediment concentrations just below the road crossing in the case of FSC ($R^2 = .90$; $p < .05$). In FSL this correlation was not significant but still evident ($R^2 = .69$; $p < .09$).

Correlations for non-suspended sediment in the water column in relation to distance from input tended to be weaker than those for ultra-fine and suspended sediment (Table 3.3).

Deposition in leaf packs, which is independent of small-scale temporal variation in the discharge regime, strongly supports the conclusion that suspended sediment is efficiently retained in ephemeral streams (Fig. 3.9). Amounts of suspended sediment trapped in leaf packs were significantly correlated to distance from input in all stream sections impacted by road run-off (Table 3.4).

R^2 and p-values were particularly high for the series of packs exposed in FSC during the period of intense road use

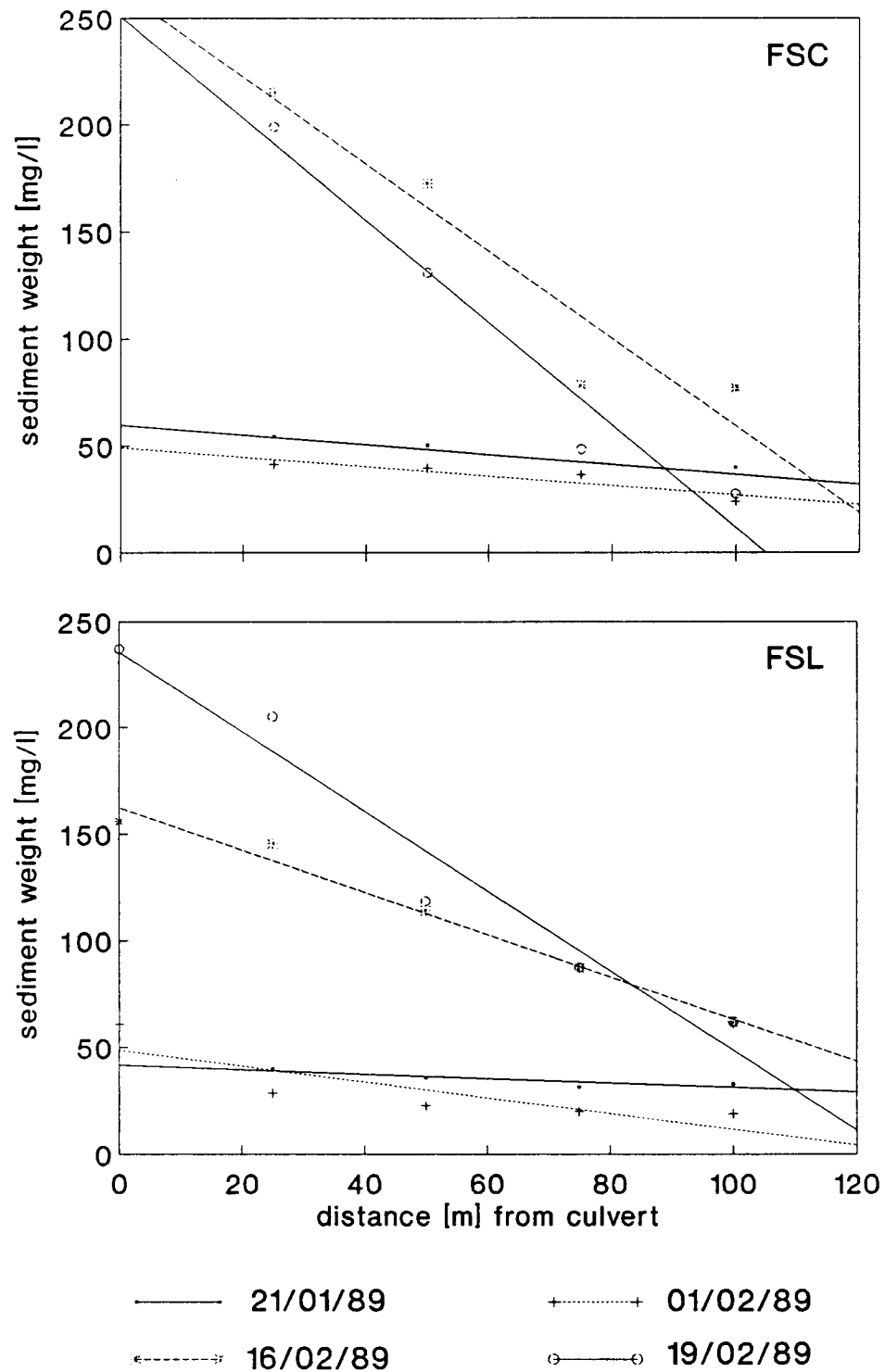


Fig. 3.8: Suspended Sediment Retention (FSC and FSL).
 Regression of suspended sediment in the water
 against distance from input (culvert).

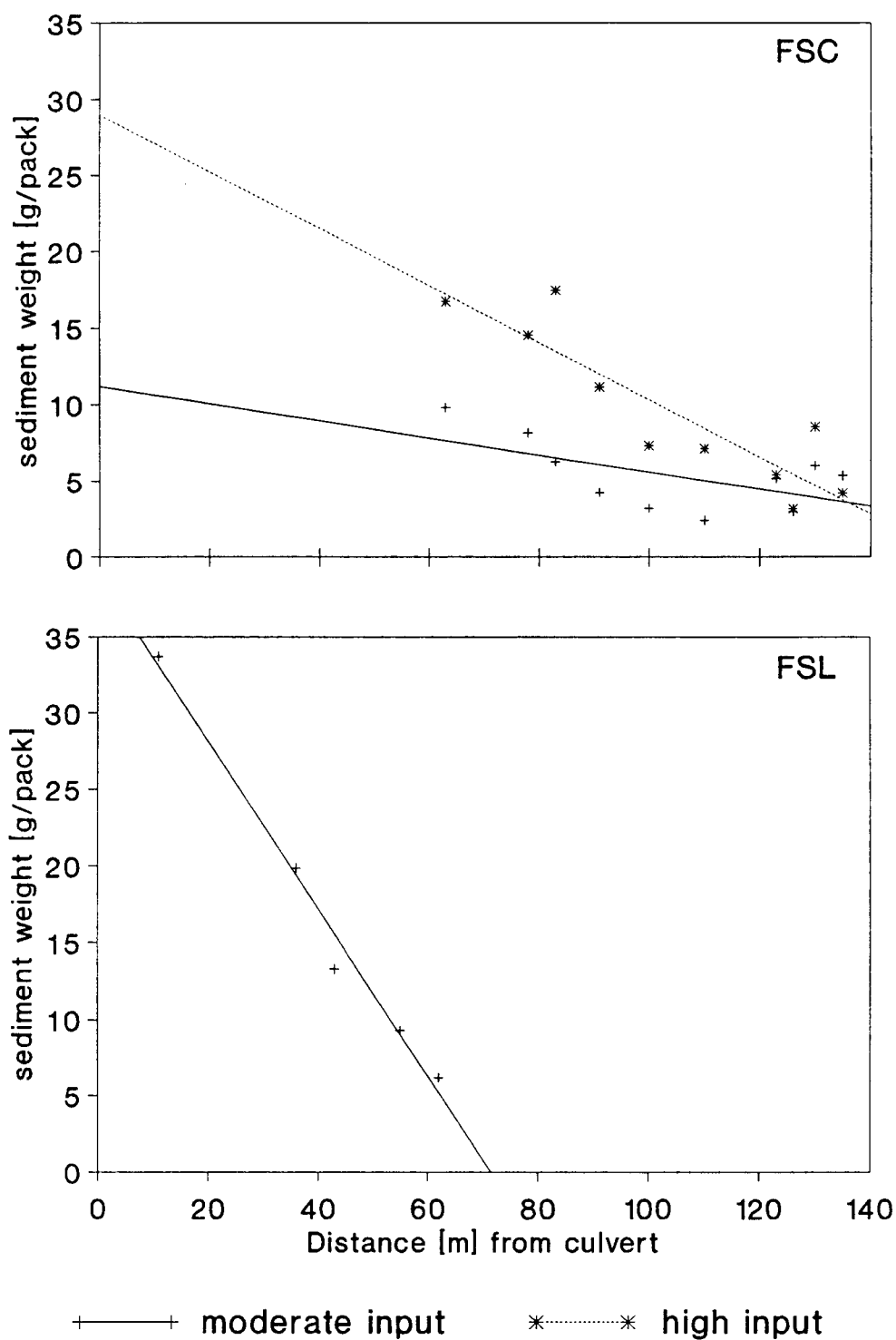


Fig. 3.9: Suspended Sediment Deposition in Leaf Packs (FSC and FSL). Regression of suspended sediment [g/pack] trapped over a 15-day exposure period.

in January 1989 and for the series of packs exposed close to the culvert in FSL. The correlation was looser as input levels decreased and as distance from the source of sediment input increased (packs in FSL were placed 11 m to 62 m below the intersection of road and channel, while packs in FSC were located 63 m to 130 m below the road). During the period of moderate input in February, distance from the culvert accounted for 99% of the variation in the weight of suspended sediment trapped in the FSL packs ($p < .01$). At the same time only 35% of the variation was accounted for by distance from input in FSC packs ($p < .05$). However, negative correlations were high for sediment trapped in FSC packs during the period of maximum input in January ($R^2 = .80$; $p < .01$). This and the slopes of the regression lines in Fig. 3.9 clearly illustrate the importance of initial input concentrations for the closeness of the correlation and the efficiency with which suspended sediment is retained.

Given that sediment retention data are arranged against distance from the uppermost location in the study reach (point 0) and therefore at the same time against upstream distance from the culvert, no correlations were evident for leaf packs in unimpacted control sections of FSC and FSL (Table 3.4).

No correlation was found between non-suspended sediment retention in leaf packs and distance from input. However, non-suspended sediment weight in the leaf pack closest to the culvert in FSL (11 m from the culvert) was the highest for all packs exposed in all streams. Non-suspended sediment weight in this pack was 10-fold higher than that of the leaf pack next in the downstream direction (35 m from the culvert). This illustrates that sediment $> 53 \mu\text{m}$ is retained very quickly in the system. Therefore, at distances which provide a suitable scale for describing

Table 3.4: Sediment Retention in Leaf Packs. Linear regression of suspended sediment retained in relation to leaf pack distance from input.

Date	Site	Impact	Suspended sediment		
			df	R ²	P
19/01/89	FSC _b	yes	8	0.80	<.01
24/02/89	FSC _a	no	3	0.01	n.s.
	FSL _a	no	3	0.01	n.s.
	FSC _b	yes	8	0.35	<.05
	FSL _b	yes	3	0.99	<.01

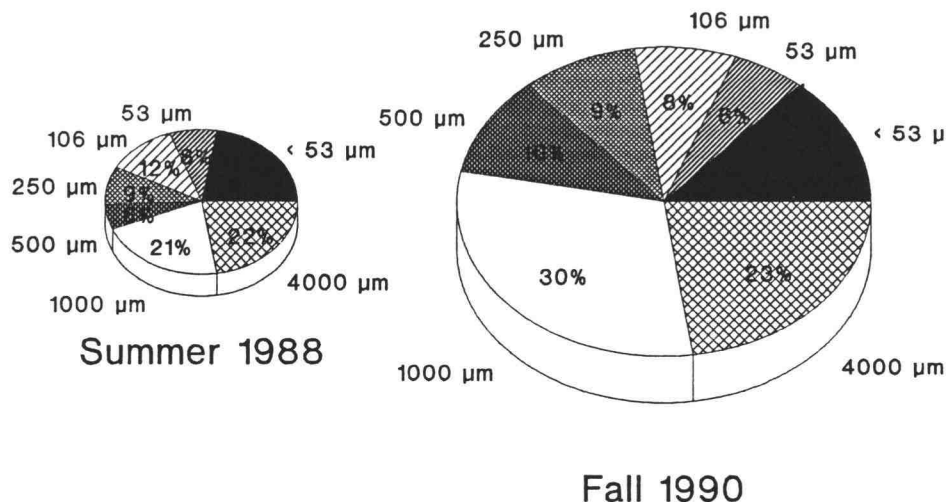
a: Stream section above the road (not impacted)

b: Stream section below the road (impacted)

the retention of suspended sediment, no effect is obvious with respect to the deposition of larger sediment particles.

The comparison between 2 core samples taken in FSC from the same location (FSC S8) prior to the construction of the road and after completion of the logging operations illustrates sedimentation impacts on the lotic habitat. Sediment was more densely packed in the 1990 core sample from FSC as compared to the pre-impact sample taken in summer 1988. Core weight increased more than 4.5 times as compared to the pre-disturbance levels. Particle size distribution was similar for both cores (Fig. 3.10), but the overall organic content decreased from 34% to 22%, with fractions .250 mm and 4 mm contributing most to that decrease (Fig. 3.10).

a.) Particle Size Distribution



b.) Organic Matter Content in Sediment Fractions

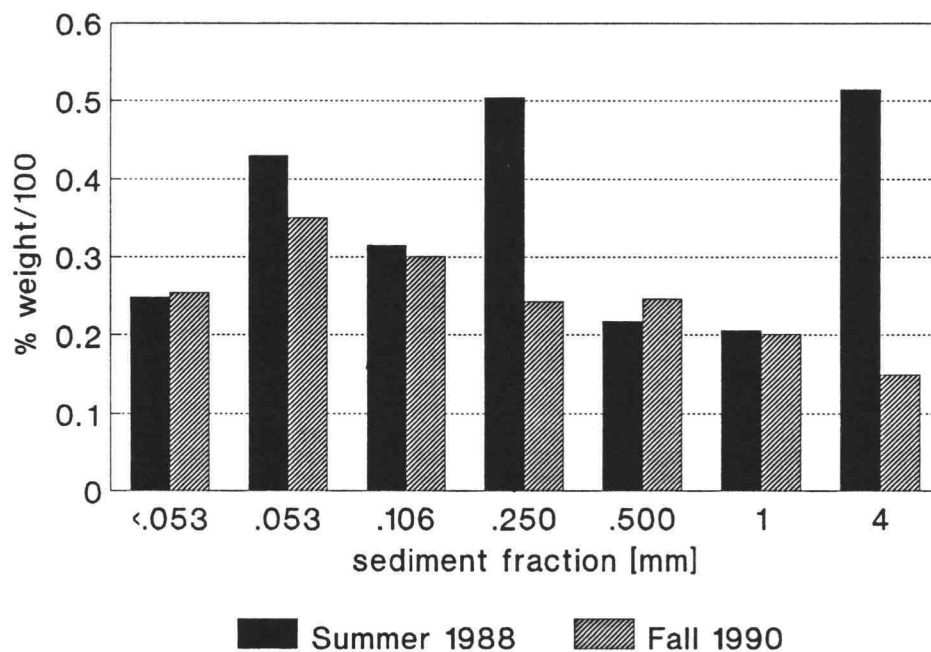


Fig. 3.10: Effect of Forest Road Sediment on Stream Bed Structure. Core samples were taken at FSC S8 before construction of the forest road (summer'88) and after completion of the logging operations (fall '90). The size of the pies is proportional to the total weight/volume of the two cores.

The FSC core samples were taken at a unique site of Paraleptophlebia gregalis mass emergence. Approximately 10 000 adults/m² emerged from the small pool in 1988. At that time the habitat for mayfly larvae on the pool bottom exhibited a distinct 3-dimensional character as a result of the loose packing of sediment. That is, the larvae could readily move within the sediment. Visual estimates of larval densities therefore generally were low. Emergence collections from the same site were 1 450 adults/m² in 1990. Although there is no control for treatment effects due to the uniqueness of the habitat, this suggests that sedimentation resulting in more densely packed sediment on the pool bottom negatively affected the mayfly population.

3.4. Model for Suspended Sediment Retention

Model Parameters

A model was developed to assess the potential of ephemeral streams to retain suspended sediment generated by the use of forest roads. The model allows one to gauge the importance of different variables for sediment input rate and retention capacity. Variables included in the estimation of in-stream sediment concentrations were: (1) intensity of road use; (2) length and slope of road segment drained; (3) precipitation intensity (as estimated from discharge); (4) suspended sediment uptake length (S_w); and (5) distance of sampling point from road intercept (site of sediment input). These variables and other model parameters are briefly explained in Table 3.5.

Table 3.5: Model Parameters.**State Variables**

Sed_x	Suspended sediment concentration [mg/l] in the water at distance x from input.
Sed_b	Suspended sediment background concentration [mg/l] (values obtained from the unimpacted system).
Sed_0	Suspended sediment concentration [mg/l] at input site (culvert).

Input Variables

G	Road gradient [m/m]
L_s	Length of road segment draining toward a given input point.
U	Number of passages over a given road segment (road use variable).
W	Average discharge in ditch draining a given road segment (representing precipitation intensity).
t_L	Time [h] since last use of road (time elapse variable).
x	Distance (channel length) [m] from site of suspended sediment input.
C_D	Dilution coefficient (ratio discharge ditch/discharge unimpacted stream).

Parameters

a_1	Modifier constant; maximum amount of sediment that can be generated in the ditch with a given road gradient, road segment length, traffic and precipitation intensity.
c_1	use constant; maximum amount of sediment that can be generated by road traffic.
c_2	time lag constant; hours it takes for suspended sediment to be washed off the road at a given ditch discharge (precipitation intensity).
S_w	Average distance [m] a particle travels in the water column (uptake length).

The basic model equation is a decay function multiplied by the sediment concentration at the culvert outflow (Sed_0) and corrected for suspended sediment concentrations found in unimpacted systems (Sed_B):

$$Sed_x = Sed_B + Sed_0 * e^{-x/S_w} \quad (1)$$

Sed_B and S_w were measured in the field or directly derived from the data. The sediment concentration at the culvert efflux was computed according to:

$$Sed_0 = G * L_s * C_D * (a_1 (1 - e^{-c_1 U W}) * (e^{-c_2 L W})) \quad (2)$$

Reid and Dunne (1984) found that road gradient (G) and segment length (L_s) together explained only 3% of the variation in sediment input from a forest road. They saw this as an indication of a compensatory relationship between increasing segment length and decreasing slope. The model is designed to accommodate this observation in the input part. The dilution coefficient (C_D) simply is the proportion of water contributed by the roadside ditch to the total outflow at the culvert. The remaining elements in the equation to compute Sed_0 are a saturation and a decay function. The saturation function estimates sediment in the ditch as a function of road use and discharge (precipitation). The decay function estimates the depletion of the sediment pool on the road as a function of time elapsed since last use and discharge.

The constants a_1 , c_1 and c_2 were estimated. Field observations suggested that the sediment pool on the road was largely depleted within 3 - 5 days after last use during the rainy season in winter. Thus, a value accommodating this observation was attributed to c_2 . Conservative estimates were used for a_1 and c_1 ; that is,

these constants were estimated with respect to encompassing the highest sediment levels observed assuming low traffic frequencies and no prior depletion of the sediment pool on the road. Model computations therefore will tend to overestimate actual sediment input levels. Estimation of constants was particularly difficult because at times of highest input no clear distinction could be made between suspended sediment introduced to the road surface by truck traffic and sediment introduced with gravel used to repair the road. However, specific experiments could be designed to obtain more accurate estimates of these parameters.

Constraints and Assumptions

The model has several constraints and is based on a number of assumptions that limit its accuracy. It is extremely static with respect to temporal variations. Road use is separated in time from wash-off, thus inputs cannot be well predicted for road use during rainy periods even if a better estimate of constants was available. Equations to gauge sediment concentrations in roadside ditches if logging operations are conducted during periods with rain were developed by Reid and Dunne (1984). They, however, did not attempt to consider the depletion of the on-road sediment pool as traffic ceases.

The stream is modeled as a continuous "filter" system with retention rates independent of channel slope, microhabitat patterns or vegetation. The close correlation between distance from culvert and sediment content in the water at high initial input levels confirms this to be a realistic assumption.

Potential suspended sediment sources other than the road surface such as road cuts are ignored in the model. Data presented by Reid and Dunne (1984) and findings in my

study suggest that, barring catastrophic events, sediment input from sources not related to road use is probably less than 10% in forest areas for which this model applies. It therefore can be ignored in a simple simulation.

A less obvious assumption of the model is that use is assumed to produce an even spread of fine sediment on the road independent of distance from landings and turning areas. These areas are point sources of fine sediment, because they are frequently used by off-road vehicles (landings) or because they are not entirely graveled (turning areas). Consequently, the development of an on-road fine sediment gradient over distance from landings and turning areas appears probable. The shape of this gradient may be determined by traffic intensity; higher use leads to a more even distribution of the sediment over larger stretches of forest road. No data base is available to quantify this likely phenomenon which, on the other hand, could be accounted for by altering the specific model constants a_1 and c_1 on an empirical basis.

Retention values of suspended sediment in the streams are assumed to stay constant, i.e. they are considered to be independent of original input. As has been shown above, this assumption is not realistic. However, inaccuracies may be ameliorated by scaling S_w with respect to high input levels so that the possible over- or underestimation of retention will only affect low sediment level situations. But it should be noted that for low input concentrations the model will clearly overestimate the potential of ephemeral streams to retain sediment if in fact S_w is scaled with respect to high input levels.

Experimental Runs of the Model

Experimental runs of the model were conducted to explore the effects of: (1) road use patterns; (2) time lag after last use; (3) different discharge regimes; and (4) different uptake lengths on suspended sediment content in the water column at different distances from input. Such runs allow one to examine simple cause/effect relationships in order to investigate the importance of different variables on sediment content in the water. Within the framework of assumptions and constraints, the runs also provide an estimate of the length of ephemeral stream channel that is necessary to remove road-generated suspended sediment from the aquatic environment. Model runs were performed with a consistent set of values for all except one of the variables (test variable). Table 3.6 lists the basic setting of variables and constants.

Table 3.6: Basic Setting of Constants and Variables for the Model Runs.

Constants		Variables	
Sed_B	= 10.00 [mg/l]	U	= 10.00
a_1	= 200.00	t_L	= 0.00 [h]
c_1	= 0.25	W	= 0.50 [l/s]
c_2	= 0.04	S_w	= 70.00 [m]
S_w	= 70.00 [m]		
L_s	= 205.00 [m]		
C_D	= 0.20		
G	= 0.12		

If the uptake length (S_w) is small, then suspended sediment concentration in the water is largely determined by the decay function of the model. Thus, the problem of inaccurate estimation of input function parameters is minimized. However, at uptake lengths of >500 m, initial inputs largely govern sediment concentrations in any given section of the stream (Fig. 3.11).

On the input side, the model runs suggest that suspended sediment concentrations are especially sensitive to changes in stream discharge and use patterns at low discharge and road use levels (Fig. 3.11). Similarly, comparatively small differences in lag time early after flow resumption translate into large differences in sediment input, whereas at lag times larger than 72 hours sediment depletion from the road surface has progressed sufficiently to minimize effects from further variation in lag time (Fig. 3.11).

The model does reflect the two general patterns found for sediment retention in this study. That is, the slope of the regression line, calculated to illustrate sediment retention in the system, increases with increased input and decreases with distance from the culvert outflow. This is not surprising, because the model was developed based on the field observations made during this study. The model runs only illustrate that the translation of field observations into abstract mathematical language can be accomplished in the way proposed here. The degree of universality of this translation must be put to further empirical tests, especially with respect to situations where, at high S_w values, the import part rather than the decay function drives the model.

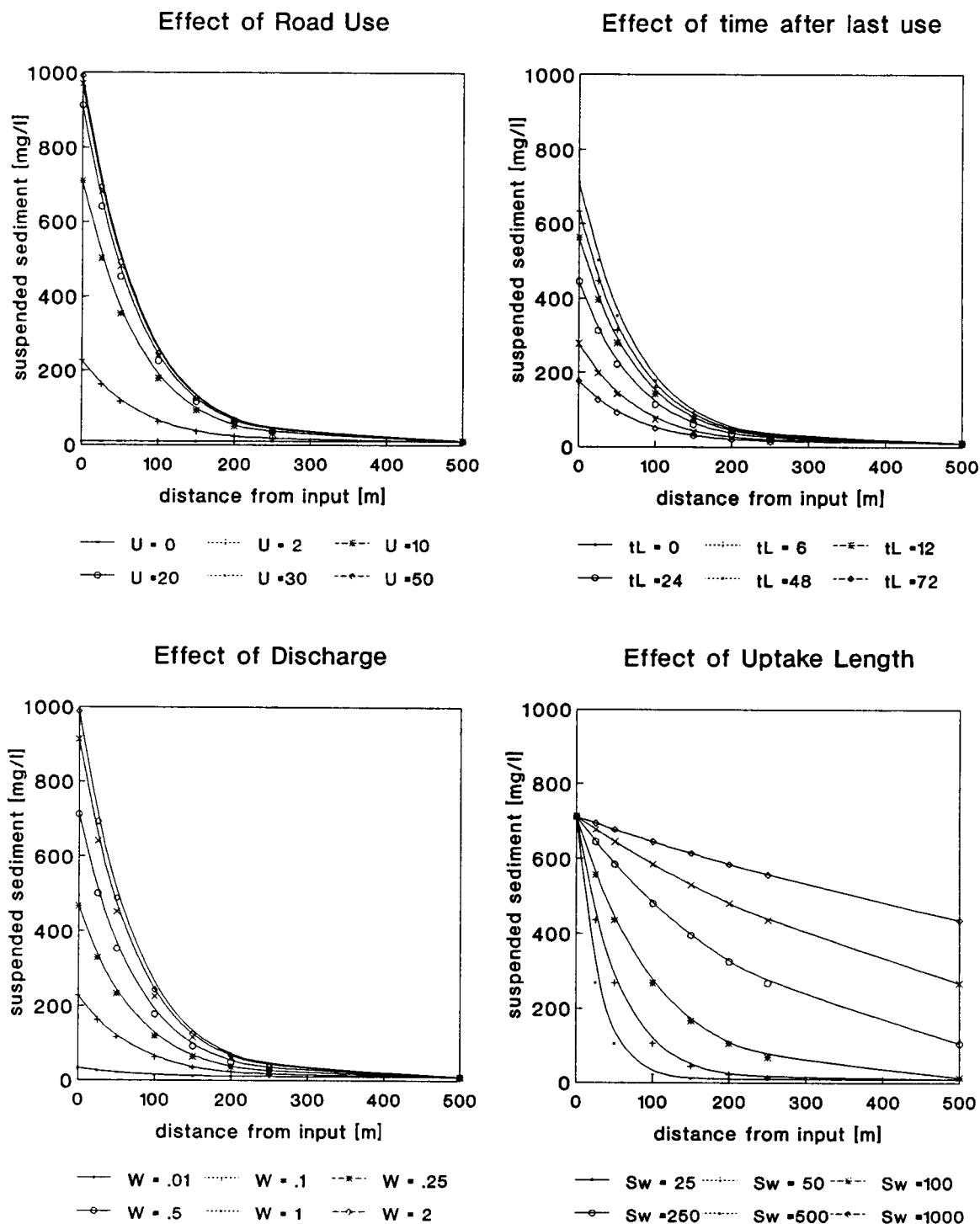


Fig. 3.11: Alteration of Single Variables in the Sediment Retention Model. Curves are predicted sediment concentrations in the water at different distances from the road. For detailed explanation of all model variables see tables 3.5 and 3.6.

3.5. Discussion

The study of nitrate and sediment dynamics in summer-dry streams confirms the close interconnection of small headwaters - temporary or not - with the terrestrial system that they drain. This coupling with the terrestrial environment gradually loosens with increasing stream order, thereby promoting regularities along a gradient of increasing stream size, such as those expressed in the "River Continuum Concept" (Vannote et al., 1980). Summer-dry headwater streams represent the upper boundary of that gradient.

However, the tight connection of headwaters to the terrestrial system not only gives rise to regularities but also can generate patchiness, as the physical and chemical features of low order streams closely reflect small-scale soil, geomorphological or vegetational differences within the landscape. Such patchiness is evident in the nitrate patterns observed in the forest streams where considerable fluctuations of nitrate were measured on a spatial as well as on a temporal scale.

No attempt was made to gather data linking nitrate concentrations in the stream to soil nitrogen parameters. The vegetation in the meadow system mainly consists of introduced species which in Europe are typically found on nutrient-rich soils, but the sparsity of the plant cover and the consistently low in-stream nitrate concentrations suggest that the meadow stream drains a nitrogen-limited grassland on an impoverished soil. This grassland, as well as the temporary stream draining it, depend on atmospheric nitrate inputs. Weekly N-NO_3 concentrations in the rainwater at Hyslop Farm 8 km northeast of Corvallis ranged between $21 \mu\text{g/l}$ and $83 \mu\text{g/l}$ (average $54 \mu\text{g/l}$) from January to April 1989 (NADP, 1990). Denitrification and uptake by

the terrestrial community are believed to reduce the nitrate content in the rain water to the very low concentration of 3-4 $\mu\text{g/l}$ as it moves towards the temporary stream. Absence of a diel fluctuation in N-NO_3 concentration in MLR is further evidence that the lotic system is nitrate limited at all times (Fig. 3.1).

Similarly, the short-flow sites FSC and MSC mainly drain surface or shallow subsurface flow and therefore reflect nitrate concentrations in the precipitation more than those in the terrestrial system. Triska et al. (1990) found nitrate concentrations in a headwater stream in northwest California to be low, when the soil was saturated and rain was "quickly converted to discharge by rapid, shallow, subsurface runoff".

Both temporary forest streams display a pattern of early season nitrate flushing from the soil. Patrick and Wyatt (1964) as well as Reddy and Patrick (1975) report increased loss of nitrate from soils exposed to cycles of drying and wetting. Drying creates aerobic conditions that promote nitrification, whereas in soils at $> 60\%$ of their water-holding capacity denitrification is the dominant transformation process (Alexander, 1977). Thus, nitrate formed in forest soils under aerobic conditions in summer, appears in the stream water immediately before and after resumption of flow. Subsequently, flushing progressively depletes the nitrate pool in the soil. In addition, after the water saturated soil becomes anaerobic, denitrification may further contribute to decreased nitrate export from the terrestrial system to the stream.

The differences of nitrate concentrations between and within each of the temporary forest streams may be connected to differences in geomorphological or hydrological parameters, or a combination of both. FLR is a fairly young system in geological terms (C. Frissell, pers.

communication). The stream drains shallow soils and flows on or close to bedrock for some of its length. FLC drains deeper soils in an older valley (C. Frissell, pers. communication). Deep soils provide more favorable conditions for the establishment of anaerobic zones. Denitrification activity in these anaerobic zones may buffer against high nitrate peaks, such as those observed in FLR just before and early into the flowing season.

In addition, water routing through the soil may contribute to the dissimilarities in nitrate patterns between FLC and FLR. Hornberger et al. (1991) showed that water transport in forest soil is controlled by "preferred paths". The contraction and expansion of these paths as regulated by precipitation may determine the overall efficiency of nitrate flushing as well as the extension of the water-saturated, anaerobic zone in the soil.

In the second half of the flowing season, nitrate concentration in FLC and PERM increased with decreasing discharge. Triska (1990) attributes the increase of nitrate concentrations in summer to a proportional increase in the amount of water with long residence time in the soil to the stream flow. The groundwater is nitrate rich, whereas the contribution of nitrate depleted, shallow subsurface-flow decreases as the dry season progresses.

The interpretation of the results obtained for FLR is hampered by the lack of samples taken from that stream between days 90 and 190 after resumption of flow. Increased nitrate concentrations were observed in June after stream discharge had risen following a period of late spring rain. As at the beginning of the flowing season, the increase in nitrate more than anything may have resulted from flushing of the nutrient from the soil. Thus, flushing from the soil and the relative contribution of groundwater to stream flow are perceived as the main determinants of in-stream nitrate concentrations.

The injection experiments provide additional evidence for the close interconnectiveness of terrestrial environment and temporary headwater streams. Solute loss in FLC and MLR is attributed mainly to groundwater exchange facilitated by a large water-soil boundary surface, rather than to biological processes. Passive tracer removal indicates that during average flow ca. 20% of the stream water was exchanged over a 25 m reach in FLC and ca. 30% of the stream water was exchanged over a 40 m reach in the case of MLR.

Biological retention differed strongly between the forest and the meadow stream. In-stream nitrate concentrations were consistently low in the meadow channel, while a high standing stock of algal biomass was present. Nitrogen availability therefore is believed to limit primary production in MLR. Newbold et al. (1982) argue that the influence of biological processes on the concentration of a given nutrient increases as that nutrient becomes more limiting to system productivity. Thus, in MLR biological uptake plays an important role in the removal of nitrate from the water column.

In contrast, primary production is light-limited in forested headwater streams and therefore insensitive to nutrient enrichment (Gregory, 1980; Lowe et al., 1986). McIntire and Phinnney (1965) conducted a laboratory study of periphyton productivity in artificial channels using water from a small first-order permanent stream adjacent to FLC. In their study the factor limiting periphyton primary production was light rather than nitrate or phosphorous.

Light limitation of primary production in FLC, FLR and PERM also causes the lack of a diel pattern in nitrate concentrations. Gregory (1980) found no such pattern in a heavily shaded first-order headwater in the Oregon Cascades, whereas in a fifth-order creek the daily fluctuation in nitrate concentration was 25 $\mu\text{g/l}$.

While biological uptake was not measurable in FLC, microbial respiration on cellulose colonization substrates was enhanced by fertilization. Kaushik and Hynes (1971) showed that microbial protein associated with dead leaves was significantly higher in samples where nitrate had been added to the water as compared to untreated controls. It is not clear from their findings, whether nitrate addition actually increased overall microbial populations in the system or if it facilitated colonisation of substrates otherwise lacking nitrogen compounds. If, in fact, microbial populations increase as a direct effect of nitrate injection to the system, then some nitrate will be immobilized through incorporation into living tissue. However, this possible immobilization pathway was not apparent from the injection experiment data. Possibly, the quantities of nitrate retained within the microbial community are too small to be detectable on the rather crude scale of an injection experiment and the duration of the experiment was insufficient to allow for a significant increase in microbial biomass and thus biological uptake capacity.

The question of seasonal variation in nutrient uptake was not addressed in this study. Such variation was reported for phosphate uptake (Elwood et al., 1983; Mulholland et al., 1985) and nitrate (Triska et al., 1990). Triska et al. (1983) found higher nutrient uptake rates for immature as compared to mature algal communities. Therefore, somewhat higher biological retention of surplus nitrate would be expected in MLR early in the season, when the algal community is most immature. In FLC, nitrate concentrations are elevated when light energy reaching the stream (i.e. the potential for primary productivity) is highest. With the progressing season, nitrate becomes scarcer between February and May, but so does available light due to increased shading by riparian vegetation.

Thus, under natural conditions FLC at all times carries an excess of nitrate with respect to what can be utilized by primary producers in the stream. The potential for seasonal variation in the uptake of surplus nitrate therefore is small.

Ephemeral streams effectively retain sediment. The suspended sediment fraction appears to be suited best to demonstrate retention as a function of distance from input for the 100 m scale used in this study. Correlations were tight and significant even if suspended sediment input was low. Uptake lengths were short (between 35 m and 105 m) at moderate input levels and likely would be even shorter if input concentrations were high. This is because the determination of uptake length (S_w) neglects the resuspension of particles. At high sediment concentrations this is a valid assumption, as the contribution of the resuspension process to the amount of sediment transported in the water becomes negligible as compared to the deposition process. Thus, if sediment input is high, the values for uptake length are shortest and the correlation between sediment content in the water and distance from its source is tight and highly significant. In the unimpacted system there is a dynamic equilibrium between deposition and resuspension. Microhabitat and flow characteristics induce local fluctuations in levels of deposition and resuspension. Therefore correlations between distance from input and sediment concentrations are less tight and less significant at low input levels.

Considering the high sediment retention efficiency of the short-flow streams, increased distance of a sampling reach from the forest road can simply be viewed as a substitute for lower in-stream sediment concentration. Therefore, correlations between sediment levels and distance from input become less evident as sample reaches

are further removed from the road.

The non-suspended sediment fraction, comprising size classes 53 μm and larger, probably is too heterogenous to yield clear-cut correlations between sediment content in the water and distance from input. Furthermore, large amounts of non-suspended sediment are deposited within the uppermost section of the impacted reach, thus not allowing for a clear longitudinal deposition gradient to be formed further downstream. Rather, amounts of sediment trapped in leaf packs vary primarily according to microhabitat characteristics (riffle - pool).

The behavior of the ultra-fine solids is rather interesting because at times positive correlations were observed between sediment concentrations in the water and distance of sampling points from the road. The positive correlations occurred, after the road had not been used for two weeks. As the pool of ultra-fine solids on the road became depleted, the water in the ditch carried lower loads of ultra-fine particles than did the water in the undisturbed section of FSC. The addition of ditch water therefore diluted the ultra-fine particles in the channels to concentrations below those found in unimpacted reaches of the short-flow streams. Hence, the recovery of FSC to its 'natural' state consisted in an enrichment of the ditch water with ultra-fine solids. This enrichment process is reflected in the positive correlation between distance from input and amount of ultra-fine sediment in the water.

Overall, ephemeral headwater streams are highly efficient at filtering sediments from the water column. This efficiency results from the number of retentive structures in these channels - primarily organic debris - and, more importantly, from the pattern of width expansion and contraction which these streams display as immediate response to precipitation. For example, discharge increased by a factor of 10 between 12:00 h and 16:00 h on January

9th, 1989. The rapid increase in discharge caused a considerable widening of the otherwise narrow and shallow channel. During the process of lateral expansion water movement at the "wave-front" is mostly vertical into the soil (rolling flood-wave). Therefore a considerable proportion of the sediment in the stream water is actually filtered through the soil rather than being flushed out with the current. Bilby and Likens (1979) found that seston concentration peaks during a flood occurred before the discharge maximum. Assuming a similar behavior for small, inorganic sediment particles adds to the overall efficiency of a filtration process coupled to lateral expansion of the stream. Sediment concentration under this assumption is highest during the early flood stage. That is, filtration potential and turbidity are at a maximum simultaneously. Finally, the rapid recession of stream width after floods minimizes resuspension and adds further to the filtration efficiency of the system.

Field observations after the first year of road use suggest that fine sediment deposited in a summer-dry stream may be transformed or incorporated into larger, non-suspendable soil particles during the dry season. Thus, rather than being temporarily stored in the stream, fine sediment can be removed permanently from the aquatic environment. This amounts to a seasonal regeneration of the fine sediment filtration and storage capacity of summer-dry streams.

The results from runs of the model illustrate the importance of uptake length (S_w) for the retention efficiency of a system. The significance of input levels in determining in-stream sediment concentrations decreases as uptake length decreases. Uptake length decreases with decreasing stream size. Therefore, the smallest streams are most retentive and best suited to protect higher order

lotic systems from unwanted input of fine particles.

This study reveals two general problems in estimating the retentiveness of a stream ecosystem. One problem is that uptake length (S_w), the central parameter describing retentiveness, varies not only with season but also with initial concentration of solute molecules or particles in the water column. Models therefore, while being helpful in describing general patterns and key parameters, can only be used to a very limited extent for predictive purposes on a spatial or temporal scale. Ultimately, model parameters will have to be estimated specifically for sites and for seasons to quantify retentiveness. This, however, appears to be a general problem in field ecology.

Secondly, retentiveness in the context of stream systems is defined in rather vague terms. It is the "net difference between input and transport" (Stream Solute Workshop, 1990). In this view, elements are retained as they are transferred from the flowing water (export mode) into a stationary phase. However, from a practical point of view, it is usually difficult to decide whether, and to what extent, nitrate lost to subsurface flow or groundwater is retained within the watershed. In this case retention can be realized as uptake by terrestrial plants or as a general increase of residence time without incorporation into biological systems. In addition, nutrients such as nitrate can be retained in the biota in the form of energy, while the nitrogen molecule itself is lost to the atmosphere (denitrification).

The question of whether nitrate lost to subsurface flow will end up in deep groundwater reservoirs, terrestrial plants, microflora or in the atmosphere is important if the role of temporary streams in the landscape is to be assessed. If temporary or ephemeral streams just help to channel nitrate from surface water to groundwater

systems, then the problem of nitrate pollution has not been solved, but just been shifted elsewhere. More research in this field is needed. Because of the small catchment area they drain, summer-dry headwaters are particularly well suited to study both the interdependency of terrestrial and aquatic ecosystems and the connectiveness between surface run-off and subsurface flow including groundwater reservoirs.

Chapter 4

COMPARATIVE ANALYSIS OF SUMMER-DRY STREAM COMMUNITY PATTERNS

4.1. Introduction

Communities are more than an assemblage of species (Begon et al, 1986). They reflect and integrate present environmental conditions, biological relationships and the history of a habitat. Communities therefore cannot be understood or predicted solely from the physical demands of their parts. They have to be studied as entities. However, it is difficult to find consistent patterns of cause and effect in community structure, mainly because of the number and wide variety of factors which shape the biota. This range of factors renders replication in community studies to imperfection. That is, random variation in community pattern cannot be clearly separated from variance due to differences in genetic composition of populations, biotic interactions, environmental factors or history of an area.

But are there distinct communities in the first place? Gleason (1926) and Peus (1954) oppose the notion that organisms are organized in distinct, well defined packages called communities. In their view, species are simply arranged along environmental gradients according to their physiological needs. Therefore, discrete communities with distinct boundaries, more than anything, are artificial constructs.

Kühnelt (1960) rejects this as an "extreme autecological view" that ignores synecological

interactions. Friederichs (1960) argues that the evolution of organisms is closely tied to interactions between species. Thus, if species coevolve, the synecological component can hardly be ignored when assemblages of organisms are to be understood. Therefore biological communities are not a fictitious construct. Rather, they are a necessary outcome of the evolutionary process. Carrying the importance of biological interactions furthest, Clements (1916) conceived of the community as a sort of superorganism with well defined boundaries.

The views of Clements (1916) and Gleason (1926) represent extremes. But they are not mutually exclusive (Richardson, 1980; Liss et al., 1986). They are complementary instead (Verdonschoot, 1990). Organisms respond to environmental gradients, but they also rely on biological interactions. If there is a high degree of interaction between species, Clements' (1916) organismic view may better describe the nature of the community and community boundaries will be more obvious. If such assemblages are largely determined by underlying physical parameters, Gleason's (1926) perception of gradual change of species arrangement in space and time may be more appropriate and community boundaries will be obscure.

The Clements - Gleason controversy provides an important insight into the nature of ecological knowledge. More than in most other scientific disciplines, ecological information is context bound because processes are not governed by a single universal law. Findings depend on the specific framework of a study (location, organisms studied, seasonality etc.) and contradictory results are possible and frequent. Only if limitations for the applicability of information can be given, will ecological knowledge be gained. Broad scale community research is an excellent tool to build a basic framework which allows one to assess the limits for the applicability of information generated in a

study.

The broad scale study of communities also is a prerequisite to formulate and investigate hypothesis about community components. Only if important players and driving processes are recognized can questions of relevance be asked. The design of community studies therefore should always be flexible, allowing for the adaptability of sampling schemes and strategies.

For conservation management the work of Braun-Blanquet (1928) on the classification of plant communities clearly demonstrated the value of an approach which tries to define and distinguish between characteristic associations of organisms. It has been successfully applied to gauge human-induced changes of plant community structure in central Europe. Whether analogous faunistic assemblages can be defined is questionable and judgement ultimately will rely on the development of a large enough data base generated by a number of broad scale community studies.

Probably the most promising characterizations of habitat using faunistic accounts have been provided for lotic environments. Saprobic systems and indices derived from the work of Kolkwitz and Marsson (1908, 1909) have been and are widely used to assess water pollution in streams. Illies and Botosaneanu (1963) classified stream reaches by the occurrence of indicator fish. Within the framework of the 'River Continuum Concept' Vannote et al. (1980) proposed an approach based on functional feeding groups to typify stream sections from the headwater to the mouth.

If conservation biology is to succeed in moving from damage control to more preventive strategies, potential candidates susceptible to alteration of the environment will have to be recognized before hand. Community studies are the prime tool to assess a species rarity, niche breadth and susceptibility to change within a natural

assemblage and consequently to scale habitats with respect to their importance for conservation management.

Cluster analysis and ordination are widely used to describe community pattern. These methods are complementary (Gauch, 1982). Both approaches require subjective choices and/or interpretations before and/or after applying an algorithm to the data. Furthermore, ordination algorithms are based on the rather unrealistic assumption of linearity or at least monotonicity of a species response to an environmental gradient. "That environmental gradients appear in ordination at all seems close to miraculous" (Beals, 1984). However, in spite of their limitations, ordination and cluster analysis can greatly facilitate the interpretation of complex community data sets. They are the best tools to display recognizable pattern in community studies.

This chapter describes and compares the animal communities found in McDonald Forest summer-dry streams. As is expressed in the acronyms used for the streams (Table 2.2), the sites studied differ in exposure, flow duration, and stream bed sediment composition.

It is hypothesized that insolation is the most important physical determinant of community structure in summer-dry streams, because the presence or absence of a canopy along the channels determines the food base of the organisms therein. Diversity and species richness is expected to decrease with decreasing flow duration, that is, as the harshness of the environment increases for the aquatic organisms, fewer species will be capable of colonizing the streams. Lastly, rocky sediment is expected to add to the structural diversity of the temporary stream habitat, thereby allowing for higher species richness and diversity in FLR as compared to FLC.

While the main focus is on between-stream comparisons, the within-stream pattern of species distribution will also

be examined for temporary (long-flow) forest streams. Community pattern in these streams will be related to differences in environmental parameters and the importance of different parameters for community structure will be assessed.

4.2. Methods

Collection methods were chosen to allow for semi-quantitative to quantitative sampling, while minimizing the amount of habitat disturbance. This permitted repeated collections from pre-determined sample sites. An effort was made to live-trap animals in order for them to be released after inspection.

Collections were obtained from sample sites selected according to the description in Chapter 2. A sample site is 2 m of stream channel. It contains: (1) sediment baskets dug into the stream bed; (2) leaf packs attached to the ground; and (3) an emergence trap.

Both sediment baskets and leaf packs were used to sample the benthic community in the different streams. Two pairs of sediment baskets were dug into the stream bed adjacent to each other prior to the onset of flow. The inner basket of each pair was filled with substrate (approx. 150 cm³) from the surrounding channel bed and was used as the sample unit. The outer basket permanently remained in the stream as the receptacle for the sampler. Leaf packs each contained 5 maple leaves of about equal size (ca. 5 g of leaf material). Leaves for the packs were collected on the ground next to the study sites in late fall.

Leaf packs and the contents of the sediment baskets were transferred into plastic bags and stored on ice for the transport to the laboratory. Leaves and sediments were then washed over a series of sieves and animals retained by mesh sizes $250\ \mu\text{m}$ and larger were determined and counted.

The sampling schedule for both types of benthos collections was irregular and adapted to flow conditions. In general, leaf packs or sediment baskets were only taken from sites with flow or water-saturated soil after 15 - 20 days of exposure.

To obtain a quantitative sample of the emerging adults, five traps (Fig. 4.1) were placed into every study stream. Each emergence trap covered $0.15\ \text{m}^2$ ($0.5\ \text{m} * 0.3\ \text{m}$)

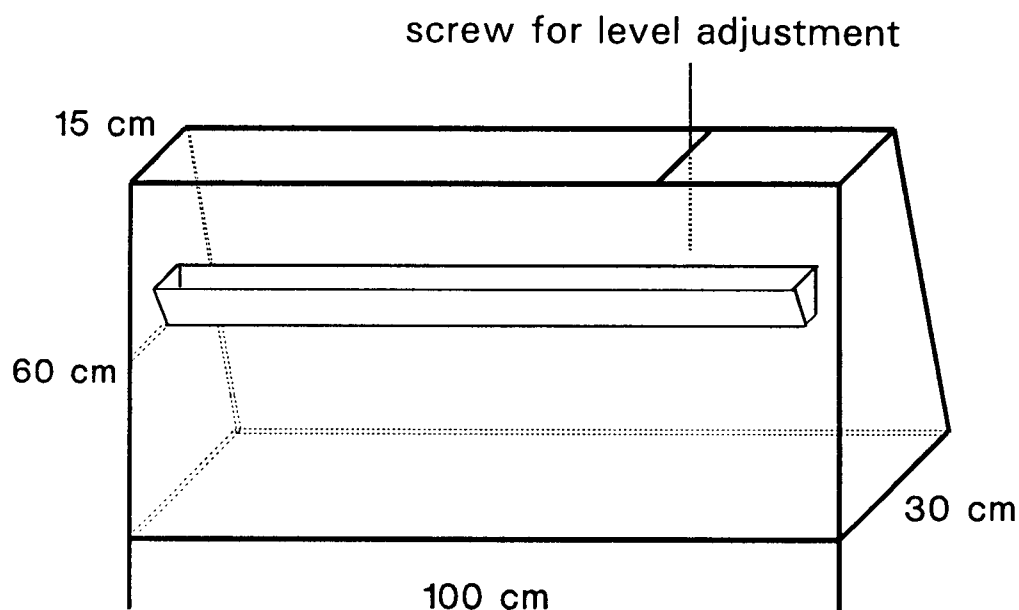


Figure 4.1: Emergence Trap Design. Traps in temporary streams were 100 cm long, traps in ephemeral streams were 50 cm long.

in ephemeral (short-flow) channels and 0.3 m² (1.0 m * 0.3 m) in temporary (long-flow) streams. Insects were collected in a gutter installed in the top section of the trap. The gutter contained ethyleneglycol ('anti-freeze') as a preservative.

Traps were emptied at 10 - 15 day intervals during the flow period and in 4 - 6 week intervals thereafter. Traps were moved between sample sites after each trapping period during the lotic phase, but were permanently installed over seep areas and pools in summer and fall. This allowed for collections from all sample sites in spite of only 5 traps being operated at a time in each stream.

Depending on the availability of keys and 'experts' for the different groups, the determination of animals was either to family, genus or species (Table 4.1).

4.3. Computations

Diversity, evenness, species identity, faunistic similarity and cluster analysis were used to describe and compare community structure between study sites (between-stream comparison). The seep areas of the forest short-flow channels (sample sites 7 and 8 in FSC, sample sites 9 and 10 in FSE) were considered a separate unit (SEEP).

The FLC and FLR sample sites were pooled for a second analytical step. Clustering, ordination and the Multi-Response Permutation Procedure (MRPP) were applied to explore patterns of community structure between the 20 sites and to relate such patterns to underlying differences in environmental parameters.

Table 4.1: Level of taxonomic resolution for different groups. The + indicates determination to species, - indicates determination to genus or family, 0 indicates no collection.

Group	Larvae	Adults
Ephemeroptera	+	+
Plecoptera	+	+
Trichoptera	+	+
Coleoptera	+ /-	+
Minor groups ¹	+	+
Diptera		
Tipulidae	+ /-	+
Trichoceridae	0	+
Dixidae	+ /-	+
Simuliidae	-	+
Psychodidae	+	+ /-
Chaoboridae	+	+
Chironomidae	-	-
Ceratopogonidae	+ /-	+ /-
Ptychopteridae	+	+
Pelecorhynchidae	+	0
Empididae	+ /-	+
Dolichopodidae	-	+

1: Odonata, Megaloptera, Heteroptera, Hymenoptera

Diversity and Evenness

The usefulness of diversity as a measure of stability has been questioned (Goodman, 1975; Washington, 1984) mainly because diversity is also considered to be linked to disturbance (Begon et al., 1986). However, while disturbance appears to cause diversity, diversity in return is not necessarily an indicator for disturbance. Diversity may also result from long term evolution in stable habitats (tropics) or from accelerated speciation by genetic drift and adaptive radiation in previously uncolonized areas with low competitive interactions (Hawaiian Islands). Without further qualification of the concept, diversity in itself therefore does not provide information on the conservation value, history, or state of a given habitat or ecosystem. Nevertheless, diversity indices can be useful to describe community structure, especially if viewed in connection with species richness and the evenness with which individuals are distributed among taxa.

A simple qualitative index of diversity is the number of species found in a community. However, species richness is strongly determined by the presence of rare taxa. But it does not account for abundances.

In order to incorporate abundances into the diversity measure the Shannon-Wiener index is commonly used in ecological studies. This index is computed as:

$$H_s = - \sum p_i * \ln p_i \quad (1)$$

with $p_i = n_i/N$.

The desirable properties of the Shannon-Wiener index are: (a) H_s is at a maximum ($H_{s(max)}$) if all species in a sample are equally abundant; (b) the value of H_s increases

sample are equally abundant; (b) the value of H_s increases with the number of species in the sample; (c) the weight given to each taxon ($\ln p_i$) reflects the actual abundance better as compared to Simpson's index which also is frequently used in community studies; and (d) rare taxa contribute more to the diversity measure as compared to most other indices.

Evenness is H_s relativized in reference to $H_{s(max)}$. It provides a measure of equitability for the distribution of individuals among taxa:

$$E = H_s / H_{s(max)} \quad (2)$$

where: $H_{s(max)} = \ln S$

Similarity

Species identity will be used to compare species composition between study sites (streams). It is a simple qualitative measure of similarity between communities.

Species identity is computed as:

$$I_{sp} = 2 S_c / (S_j + S_k) \quad (3)$$

where S_c = number of species common to collections j and k

S_j = number of species in collection j

S_k = number of species in collection k

Before calculating quantitative measures of similarity between collections, a rather subjective choice has to be made as to whether computations should be based on absolute or relativized data sets. Relativized data only allow one

to compare the faunistic structure between collections. Sample weights are identical; that is, they are independent of absolute numbers of individuals caught. In contrast, if similarities are calculated on the basis of absolute numbers, differences between collections become a function of density and structure. This is illustrated in the example given in Table 4.2.

In this study sampling effort differed between streams. More collections were obtained from temporary forest channels as compared to other sites because flow duration in these streams was longest. Benthic samples occasionally were washed out and consequently lost. A few emergence traps were found tipped over for unknown reasons.

Table 4.2: Effect of relativisation on similarity measures.

a.) abundance of 3 species in 3 collections

species	collection		
	C1	C2	C3
sp.1	1	2	10
sp.2	3	6	30
sp.3	6	12	60

b.) similarity between collections

combination	similarity	
	relativized	not relativized
C1-C2	1	.66
C1-C3	1	.18
C2-C3	1	.33

More importantly, although emergence traps covered a uniform area of 0.15 m² (ephemeral streams) or 0.3 m² (temporary streams) this did not necessarily correspond to an equal area of lotic habitat being sampled because of the channel narrowness during medium and low flow. Therefore, the use of absolute numbers in the analysis would be misleading.

Since this study explicitly focuses on a comparison of community structure and because of the skew in absolute counts, abundance data were generally relativized with reference to the total collection from a given study site (stream) or sample site (row total in the site X species data matrix).

In order to characterize sites environmentally, measurements such as velocity and slope have to be transformed to a scale which allows for a comparison. Such a common scale for all parameters can be obtained by relativizing of each parameter in reference to the sum of all measurements for that parameter. Similarity measures between sites which are based on environmental parameters therefore are computed from data relativized with respect to the parameter total for all sites (column total in the site X environmental parameter matrix).

Percent similarity (PS) was chosen as the measure of faunal or environmental distance between study sites (streams) and sample sites. Consequently, all classifications (cluster analysis) and ordinations were derived from distance matrices based on the percent similarity measure.

Percent similarity between two collections is calculated as:

$$PS = 2 \sum \min(P_{ij}, p_{ik}) / \sum (P_{ij} + P_{ik})$$

For relativized data: $\Sigma(P_{ij} + P_{ik}) = 2$

and $PS = \Sigma \min(P_{ij}, P_{ik})$. (4)

Percent similarity is a much less abstract distance measure than is Euclidean Distance (ED). Equal relative abundances of species in PS directly translate into complete similarity for that segment of the communities to be compared. In the multi-dimensional species space of ED it translates into an abstract change in the distance between sample points.

Furthermore, in the case of sparse matrices (matrices containing many zeros) ED will treat joint absence of species as an indicator of similarity between samples. For all practical purposes, more often than not joint absence of taxa is affected by chance (rare species) or results from response to different rather than identical environmental parameters. This rare species default in ED is largely compensated for by the tendency to downweigh the importance of rare taxa for sample distances inherent in the ED algorithm. Yet, this results in the compensation of a default by an additional distortion.

In contrast to the above, the PS measure does not treat joint absence as similarity between samples and taxa are not weighed according to their abundances. Gauch (1982) considers percent dissimilarity, which is equivalent to PS, as the best distance measure available for ordination.

Gauch (1973a,b) showed that dissimilarity measures tend to be increasingly distorted with respect to accurately representing ecological distance as samples become less similar. This distortion is not limited to the PS measure, however, but affects ED in a similar way (Gauch, 1973a).

Classification (Cluster Analysis)

From the design of this study as a comparison of streams differing considerably with respect to major environmental parameters (exposure, flow duration, sediment composition), classification appears to be the 'natural' first approach to data analysis. It was used to compare between study sites (streams) and to analyze within stream sample site patterns.

The "average distance" method was applied to generate the cluster hierarchy. Before formation of a new cluster, the average of all distances (similarities) between each point in one cluster and each point in the other is computed (Pielou, 1984). Samples or clusters separated by the smallest average distance then are fused at each of the consecutive steps.

In contrast to some other polythetic agglomerative clustering methods "average distance" linking can be used on PS distance matrices. It does not produce inversions and it does not depend on single "extreme" points for the determination of closest entities.

Gauch (1984) recommends the use of divisive rather than agglomerative clustering, particularly the TWINSpan algorithm. However, according to B. McCune (pers. communication) TWINSpan doesn't seem to produce empirically good results. Pielou (1984) considers the TWINSpan ordination-space partitioning "a much more 'rough and ready' method" as compared to agglomerative techniques.

Since clustering and ordination are considered to be complementary approaches in community analysis (Gauch, 1984) it seems appropriate to keep both routes separate. TWINSpan is a clustering method applied to data which have already been subjected to an ordination. The clustering is performed on an artificial, two dimensional environmental space. In contrast, agglomerative methods apply the

clustering algorithm directly to the multi-dimensional species space. and the analysis therefore incorporates the complete information in the original data set. The preference for agglomerative clustering is also supported by the close correspondence of distance measures and ecological separation for similar samples. Therefore, the danger of early misclassifications, which Pielou (1984) considers the most serious drawback of agglomerative clustering, is small.

The distance on the cluster dendrograms used to present the results is Wishart's (1979) objective function. The objective function measures information loss (increase in error sum of squares) as agglomeration proceeds (McCune, 1990). The advantage of the method is that 'reversals' in the clusters are not possible, the disadvantage is the abstract, non-linear nature of the measure.

Multi-response permutation procedure (MRPP)

The MRPP was used in connection with cluster analysis: (a) to test for correspondence of site separation based on insect community composition and site separation based on environmental parameters; and (b) to rank environmental parameters according to their contribution to the above correspondence.

The MRPP procedure was developed by Mielke et al. (1981). It allows to test whether the partition of a priori classified groups is statistically significant. MRPP is relatively free of assumptions but requires considerable computer capacity.

Following Mielke et al. (1981) and Biondini (1985) the MRPP algorithm is best explained by considering a comparison between two clusters (A and B) of 7 community samples (sites). Each of the 7 samples is further

characterized by two environmental measurements (x_1 and x_2). Assume that the cluster analysis based on community data assigns 4 samples to cluster A and 3 samples to cluster B. This cluster structure is then imposed on the site similarity matrix computed on the basis of the environmental measurements. A combined weighted average of within-cluster sample distances is computed. This weighted average is then compared to distances obtained if the 7 samples are randomly attributed to a 2-cluster structure with one 4 and one 3 sample cluster. Given 7 samples partitioned into two subgroups with 4 and 3 elements there are $M = 7!/(4!3!) = 35$ possible ways of clustering and therefore 35 weighted means of within-cluster distances. As shown by Mielke et al. (1981) the distribution of the 35 weighted averages can be approximated by a Pearson Type III distribution and a t-statistic can be computed for the weighted average distance of the cluster structure derived from the community data.

Correspondence analysis is used as initial step in assessing the importance of different environmental parameters for the composition of temporary stream macroinvertebrate communities. All faunistic cluster structures not containing a cluster with a single entity are imposed on the environmental data set to determine the structures for which site separation according to fauna and site separation according to environmental parameters correspond best. Clusters containing only one sample have a within-cluster distance of zero. Therefore the MRPP can not be applied to structures with 'monotypic' clusters.

In a second analytical block ('omission analysis') single environmental parameters are omitted from the MRPP performed on a selected cluster structure derived from the preceeding correspondance analysis. Change of within-cluster distance as parameters are omitted is used to gauge

the importance of each environmental parameter for the correspondence between fauna and habitat. Factors which result in the highest increase of within-cluster distance when omitted (i.e. parameters which contribute most to the tightness of clusters) are ranked as most important in this respect.

The selection of an environmental parameter based cluster structure for the omission analysis is subjective. However, in order to obtain the finest possible resolution with respect to the contribution of environmental parameters to the composition of the animal communities, the following criteria should be used in the selection process: (1) maximization of the number of clusters; and (2) maximization of the separation between clusters (minimum p-value). Thus, the ideal choice for the omission analysis would be a cluster structure with many separate clusters and the smallest available p-value. In practice there often is a need to compromise between the above criteria.

The environmental parameters used in the omission analysis were those obtained for each sample site as described earlier (chapter 2). They are: (1) number of days with flow; (2) summer drought condition (index); (3) current velocity; (4) site specific slope; (5) percent of stream bed covered with clay; (6) percent of stream bed covered with rock; (7) percent of stream bed covered with plants (moss and grass); and (8) percent of stream bed covered with wood.

Ordination

Ordination was applied to a comparatively 'homogenous' data set containing samples from FLC and FLR only. The purpose of the ordination was to investigate differences of

community structure within temporary forest streams in more detail. If possible, such differences were to be linked to underlying variation in environmental parameters.

Polar ordination (PO) was chosen as analytical tool, because it allows the investigator to either apply an algorithm in order to objectively place the ordination axis or, if so desired, to subjectively select the axis endpoints. Via subjective endpoint selection, a recognized environmental gradient can be imposed upon the data set. The arrangement of samples along that gradient can then be investigated and the significance of the gradient can be tested by regression of site scores against site-specific environmental parameter values.

Endpoints to be subjectively imposed in the PO analysis were composites of: (1) collections from all PERM sample sites; and (2) collections from all ephemeral stream sample sites (except seep sites and sites affected by experimental flow extension). That is, a gradient of flow duration was imposed on the faunistic data set.

PO was developed by Bray and Curtis (1957). Therefore it is frequently called Bray-Curtis ordination in the literature. As explained in more detail by Beals (1984), given that the variance-regression method is used for endpoint selection, the resulting ordination axis will be placed through the longest extension of the cloud of sampling points in species space. All samples are then projected onto this axis to obtain the ordination scores.

Beals (1984) found that PO empirically yielded results which in most cases were superior to arrangements by any other ordination technique. The main critique commonly raised against PO is its dependance on only 2 samples for the placement of the axis. Gauch (1982) states that while PO "remains of interest" Detrended Correspondence Analysis (DCA) is the more advanced and preferable method. Therefore DCA analysis were performed parallel to PO with objective

endpoint selection. DCA ordinations generally were similar to PO results. Without being discussed in any detail the DCA results will be presented at the appropriate places in the results section.

4.3. Results

General Findings

The benthic collection yielded 23 700 organisms about 38% of which were determined to species. The corresponding values for the emergence collection are 81 600 individuals with about 25% included in the faunistic analysis of between and within channel differences (see Table A.3 in the appendix for a list of taxa).

First-instar larvae of Ostrocerca foersteri and Soyedina interrupta, as well as first and second instar Paraleptophlebia were omitted from the analysis. There are samples with almost 400 first instar O. foersteri. This 'clumping' is not as much a reflection of larval habitat favorability as it reflects closeness of a sampling device to a clutch of eggs. The larvae appear to disperse rather fast, because no such 'clumping' was observed in later instars. Very early instar Paraleptophlebia could not be accurately determined to species and therefore were excluded from the computations.

The high numbers of organisms collected result from a considerable sampling effort in the small streams. Overall, 97 basket samples and 338 leaf pack samples were taken over the two-year study period. At the same time exposure of emergence traps totaled 2934 m² * days, which corresponds to over 8 m² of channel continuously covered for a one-year

period.

A minimum of 231 species were present in the collections, 207 of which were found in summer-dry streams. This includes 13 species of Chironomidae recognized as separate taxa by L. Ferrington, who upon returning the material wrote that species identifications are likely to "meet with little success. Your material is quite interesting, to state it mildly, and I expect that many taxa will be undescribed or poorly described" including the possibility of an undescribed Tanytarsini genus. Because of the taxonomic problems associated with the group, no effort was made to identify midges to species and the Chironomidae were omitted from the detailed analysis.

The emergence collection yielded the highest number of taxa (192 species). Leaf packs and basket samples combined contained 108 species. The discrepancy between emergence and benthic collections is largely a result of insufficient taxonomic resolution of the Diptera larvae. Whereas a considerable number of species found in leaf packs were absent from the sediment basket collections, only Polycentropus denningi, five tipulid species and the pelecorrhynchid Glutops were found in basket samples but not in leaf packs.

New species are reported for several groups (Table 4.3). This includes a rather large and conspicuous mayfly (Ameletus), a caddisfly (Genus Rhyacophila), at least two craneflies (Tipulidae), a ceratopogonid, several chironomids and several Empididae in the genus Clinocera.

Tipulidae (59 species) were the group with highest species richness in the samples (Table 4.3). However, more than 50% of the cranefly taxa were represented by 5 or fewer individuals in the collection. Trichoptera (26 species) were the second most important contributor to species richness (Table 4.3).

Table 4.3: Species numbers in summer-dry streams

Taxonomic group	no. species	new species
Ephemeroptera	8	1
Plecoptera	21	0
Minor groups ¹	4	0
Trichoptera	26	1
Coleoptera	17	1(?)
Diptera		
Tipulidae	59	2 + 4(?)
Trichoceridae	4	0
Simuliidae	8	2(?)
Psychodidae	5	0
Ceratopogonidae	16	1
Dixidae	4	0
Chironomidae ³	13 ⁺	several
Empididae	18	5
Minor Groups ²	4	0
TOTAL	207 ⁺	10 ⁺ + 7(?)

1: Odonata, Heteroptera, Megaloptera, Hymenoptera

2: Chaoboridae, Pelecorynchidae, Dolichopodidae

3: Chironomidae were not identified to species, but at least 13 different taxa were recognized.

Of all the taxa encountered in the study, 52% showed a preference for the ephemeral and temporary stream habitats, 24% were found to be equally common in summer-dry and permanent streams and 24% preferred or were limited to the permanent site (Table 4.4). Empididae, Ceratopogonidae and Tipulidae showed the highest overall affinity to

Table 4.4: Habitat Association of Taxa Collected. Values are number of species.

Taxonomic group	habitat association scores										
	n.s.	permanent							temporary		
	0	1	2	2.5	3	3.5	4	4.5	5	5.5	6
Ephemeroptera	1	5	0	1	2	0	2	0	2	0	0
Plecoptera	0	5	5	0	6	0	6	2	0	0	0
Minor groups	0	1	0	1	1	0	0	0	0	1	0
Trichoptera	3	9	3	0	4	0	3	3	8	0	0
Coleoptera	1	3	2	0	5	0	3	4	1	0	0
Diptera											
Tipulidae	20	0	1	0	13	5	2	14	5	0	0
Trichoceridae	0	0	0	0	0	0	2	0	2	0	0
Simuliidae	1	2	0	0	2	0	2	0	2	0	1
Psychodidae	2	0	0	0	3	0	0	1	0	0	0
Ceratopogonidae	3	0	2	0	1	0	2	6	2	0	0
Dixidae	0	0	0	3	1	0	0	0	0	0	0
Empididae	4	0	0	0	3	0	2	8	0	0	0
Minor groups ²	1	1	0	0	1	0	1	0	0	0	0
TOTAL	36	26	13	5	42	5	25	38	22	1	1

1: Odonata, Heteroptera, Megaloptera, Hymenoptera

2: Chaoboridae, Pelecorynchidae, Dolichopodidae

Habitat Association Scores:

0 = insufficient information for score (n.s. = no score)

1 = obligate permanent stream

2 = facultative permanent stream

3 = permanent and temporary stream

4 = facultative temporary stream

5 = obligate temporary stream

6 = obligate ephemeral stream

summer-dry streams. Only one species (Greniera sp., Simuliidae) was found to depend on ephemeral sites. It can be assumed, however, that a number of chironomids would have to be added to that list.

There is considerable overlap between the fauna of the summer-dry streams and that of the permanent site (PERM). Habitat association scores were attributed to 152 species found in ephemeral or temporary streams (Table 4.4). Eighty-six percent of these taxa were also encountered in the permanent headwater. This includes 2 species classified as obligate temporary stream inhabitants (> 99% of the individuals were collected from temporary sites).

The temporary streams in the forest are characterized by two distinct aquatic habitat phases. The winter flow period, when these systems exhibit the physical characteristics of small first-order permanent streams, and the summer seep and pool period. A separate fauna is associated with both phases although there is overlap. Semivoltine lotic species (Sweltsa fidelis, Calliperla luctuosa) survive the summer drought in pools and seeps. Some taxa can thrive during both habitat phases but are distinctly more common in winter and spring (Paraleptophlebia gregalis, Ameletus n. sp.). Some seep-associated species will appear as early-instar larvae during spring flow, but complete most of their growth in the summer (many Tipulidae).

The number of aquatic species encountered was higher for the winter-flow period as compared to the records for summer pools and seeps (Table 4.5). In summer, more species were present in pools than in seeps. Littoral and hyporheic taxa are poorly represented in the list. However, many of the rare species could not be associated to a microhabitat type and some of them would likely fall into the above categories.

Table 4.5: Microhabitat Association of Summer-Dry Stream Taxa. Values are number of species associated with a microhabitat.

Taxonomic group	winter (flow-period)			summer (drought)	
	benthic	littoral	hyporheic	seep	pool
Ephemeroptera	6	0	0	0	2
Plecoptera	18	0	1	6	3
Minor groups ¹	2	0	0	0	1
Trichoptera	22	0	0	10	2
Coleoptera	18	8	0	1	2
Diptera					
Tipulidae	31	0	0	4	24
Trichoceridae	0	4	0	0	0
Simuliidae	9	0	0	0	0
Psychodidae	1	0	0	3	0
Ceratopogonidae	8	0	0	1	7
Dixidae	4	0	0	0	0
Empididae	13	0	0	2	2
Minor groups ²	2	0	1	1	1
TOTAL	134	12	2	28	43

1: Odonata, Heteroptera, Megaloptera, Hymenoptera

2: Chaoboridae, Pelecorynchidae, Dolichopodidae

Comparison between Study Sites

Species richness was about 25% higher in both temporary forest streams as compared to the permanent headwater (Table 4.6). It was lowest in the ephemeral

Table 4.6: Species Richness in Different Summer-Dry Stream Types. Emergence, benthic, drift and qualitative collections combined.

Taxonomic Group	FLC	FLR	SEEP	FSC	FSE	MLR	MSC	PERM
Ephemeroptera	6	5	2	0	1	2	0	10
Plecoptera	16	12	8	2	8	3	0	17
Minor groups ¹	2	3	2	0	1	1	1	3
Trichoptera	14	15	7	1	5	8	1	17
Coleoptera	5	5	4	2	2	14	5	5
Diptera								
Tipulidae	33	40	23	11	24	14	6	16
Trichoceridae	3	4	3	1	3	2	3	1
Simuliidae	7	5	2	3	2	6	2	2
Psychodidae	4	3	3	1	2	2	2	1
Ceratopogonidae	13	14	11	8	9	9	3	8
Dixidae	4	4	2	2	3	1	1	4
Empididae	11	14	6	5	7	5	6	5
Minor groups ²	3	2	1	0	0	1	0	2
TOTAL	121	126	74	36	67	68	30	91

1: Odonata, Heteroptera, Megaloptera, Hymenoptera

2: Chaoboridae, Pelecophrynchidae, Ptychopteridae, Dolichopodidae

channels and somewhat intermediate in seep areas (SEEP) and the temporary meadow stream (MLR). Experimental flow extension in FSE doubled species richness there in comparison to the untreated short-flow sites (Table 4.6).

Since no sediment baskets had been exposed in PERM,

Table 4.7: Invertebrate abundance in leaf pack collections. Data relativized to sampling effort (no. individuals/pack).

Taxonomic Group	FLC	FLR	SEEP	FSC	FSE	MLR	MSC	PERM
Ephemeroptera	14.0	9.8	9.4	0.0	0.1	0.1	0.0	8.2
Plecoptera	9.7	7.5	3.8	0.5	0.6	0.8	0.0	15.8
Minor groups ¹	0.1	0.2	0.1	0.0	0.1	0.0	0.2	0.2
Trichoptera	2.4	1.0	3.9	0.0	0.4	1.8	0.0	5.4
Coleoptera	2.3	5.4	20.3	14.0	7.5	2.3	6.1	1.0
Diptera								
Tipulidae	0.6	0.8	1.3	0.0	0.4	0.1	0.0	1.2
Trichoceridae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Simuliidae	0.6	0.1	0.3	0.0	0.3	1.0	0.1	0.1
Psychodidae	0.3	0.2	1.6	0.0	0.1	0.0	0.0	1.1
Ceratopogonidae	0.0	0.7	0.6	0.1	0.1	1.7	0.0	0.3
Dixidae	1.3	1.3	1.1	0.0	0.1	0.0	0.0	1.1
Chironomidae	57.9	54.0	14.6	3.0	7.4	48.8	9.0	58.1
Empididae	0.2	0.4	0.2	0.0	0.2	0.5	0.0	0.3
Minor groups ²	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3
Pleuroceridae	0.3	0.0	0.0	0.0	0.0	0.0	0.0	16.5
TOTAL	89.6	81.2	57.1	17.7	17.3	57.1	15.4	118.0

1: Megaloptera

2: Ptychopteridae, Chaoboridae, Dolichopodidae

only leaf pack samples were considered in the quantitative comparison of benthic communities. The highest invertebrate abundances were found in PERM. In this stream the

pleurocerid snail Juga silicula was second only to the midges in numerical abundance (Table 4.7) and probably represented > 90% of the invertebrate biomass. The presence of J. silicula in permanent streams and its absence from temporary waters is likely one of the most significant biological differences between such systems in the Pacific Northwest. Among the summer-dry streams, the long-flow forest sites came close to the overall abundance of benthic insects in PERM. In contrast, insect abundances in short-flow channels were only about 1/5 of those in FLC or FLR. The seep areas and MLR had intermediate densities of insects (Table 4.7).

Chironomid midges were the most abundant benthic group in the temporary systems and in PERM. However, in ephemeral streams Coleoptera were important. This was due to the extremely large numbers of the littoral Hydraena vandeykei collected there. Mayflies were more abundant in benthic collections from long-flow forest streams as compared to PERM, while Plecoptera and Trichoptera larvae were more common in PERM than in the temporary channels (Table 4.7).

Abundance patterns in the emergence collections were similar to those for the benthos samples (Table 4.8). PERM and FLC yielded the highest numbers of insects. The number of insects in ephemeral streams fluctuated considerably between sites. Fewer animals were collected from MLR than from any other stream except FSC, mainly as a result of drought conditions in the second sampling season.

With the exception of the SEEP sites, chironomid midges contributed between 74% (FLC and FLR) and 87% (MSC) of the total collection. In SEEP, 44% of all animals caught in emergence traps were midges and 32% were mayflies. The high mayfly numbers in SEEP result from mass emergence of Paraleptophlebia gregalis at FSC S8. During pre-study sampling approximately 10 000 animals/m² were trapped

Table 4.8: Insect abundance in emergence collections.
 Data relativized to sampling effort.
 (no. individuals/m²*day)

Taxonomic group	FLC	FLR	SEEP	FSC	FSE	MLR	MSC	PERM
Ephemeroptera	4.22	1.12	7.31	0.00	0.00	0.53	0.00	3.95
Plecoptera	3.90	1.82	2.20	0.39	1.23	0.33	0.00	1.63
Minor groups ¹	0.02	0.04	0.01	0.00	0.00	0.01	0.00	0.06
Trichoptera	0.13	0.27	0.22	0.00	0.02	0.06	0.01	0.18
Coleoptera	0.01	0.01	0.04	0.00	0.02	0.51	0.39	0.01
Diptera								
Tipulidae	0.29	0.48	0.57	0.33	1.20	0.16	0.34	0.21
Trichoceridae	0.03	0.03	0.02	0.04	0.03	0.02	0.08	0.01
Simuliidae	0.31	0.15	0.11	0.40	0.18	0.33	0.74	0.01
Psychodidae	0.72	0.80	0.76	0.20	0.65	0.03	0.25	0.48
Ceratopogonidae	0.24	1.24	1.32	0.33	0.20	0.72	0.11	0.52
Dixidae	0.22	0.11	0.24	0.04	0.07	0.00	0.00	1.11
Chironomidae	29.75	18.10	10.17	6.91	14.15	10.67	14.65	38.46
Empididae	0.11	0.17	0.20	0.13	0.18	0.06	0.28	0.09
Minor groups ²	0.01	0.01	0.03	0.00	0.00	0.00	0.00	0.08
TOTAL	39.95	24.35	23.07	8.76	17.92	13.44	16.86	46.80

1: Odonata, Heteroptera, Megaloptera, Hymenoptera

2: Ptychopteridae, Chaoboridae, Dolichopodidae

at that site over a six week period. Numbers of adult mayflies collected at FLR were lower than might have been expected from the benthic results, while FLC and SEEP still yielded more individuals than PERM (Table 4.8). More Plecoptera and Trichoptera were found in emergence collections from FLC, FLR and SEEP than in the PERM

samples. This reverses the observations made for benthic collections. In the benthic collections stoneflies and caddisflies were more common in PERM than in any of the temporary streams. Beetle abundance was considerably lower in emergence samples than in the benthic collections because the littoral H. vandykei was rarely encountered in emergence traps (Table 4.8).

Dry weather in February and March 1990 temporarily caused cessation of flow in parts of the long-flow streams. The effect was severe in MLR where average flow at the study sites dropped from about 140 days in 1988-89 to 95 days in the following year. Average annual flow decreased only slightly or remained constant in the other channels (Table 4.9). The total collection from MLR was 73% lower in 1989-90 as compared to the preceding season and species richness dropped from 49 to 24 taxa. All faunistic groups

Table 4.9: Effect of Drought on Insect Abundance.

Percent change in flow duration (days with flow at sample sites) and decrease or increase (%) of numbers collected in emergence traps between the 1988-89 and the 1989-90 seasons.

	FLC	FLR	SEEP	FSC	MLR	MSC
Flow duration	- 5	- 4	- 1	1	-31	---
EPTC-Group ¹	-48	-19	-25	-59	-45	-48
Chironomidae	60	98	32	56	-74	84
Other Diptera	2	18	77	84	-89	-22
TOTAL	24	63	32	62	-73	65

1: Combined collection of Ephemeroptera, Plecoptera, Trichoptera and Coleoptera.

were negatively affected by the drought (Table 4.9). In the other channels, the combined collections of Ephemeroptera, Plecoptera, Trichoptera and Coleoptera (EPTC-group) decreased in the 1989-90 season. However, in terms of numbers this loss was overcompensated by increased abundances of Diptera in the samples. Consequently, in spite of the losses in the EPTC-group, the total number of insects collected in these streams was higher during the season affected by the drought (Table 4.9).

Diversity and evenness tend to be higher in temporary streams (including PERM) than in ephemeral channels, but there is no clear pattern (Table 4.10). With the exception of FSC and FSE, the diversity and evenness indices are similar for benthos and emergence samples. However, the ranking from most to least diverse stream changes. PERM has the most diverse benthic fauna, but FLR is the most diverse site based on emergence collections (Table 4.10). The difference in diversity between benthic and emergence samples for FSC and FSE is caused by the different abundances of the littoral H. vandykei in the two collection types. H. vandykei comprised 95% of the total benthic catch in FSC and 82% in FSE. In the emergence collections from short-flow sites the eudominance¹ of the ground dwelling H. vandykei is not apparent and therefore the diversity values are considerably increased.

Species identity matrices show the same general patterns for benthic and emergence samples (Table 4.11). The highest species identity values were recorded among FLC and FLR. Values were also high between both temporary forest channels and SEEP, as well as between both long-flow forest sites and PERM. Species identity between PERM and

¹ Eudominance is a term frequently used in the German literature. It describes proportional abundances of > 30% in faunistic collections.

Table 4.10: Diversity and Evenness in Community Samples from Summer-Dry Streams. Diversity was computed according to the Shannon-Wiener formula ($H_s = - \sum p_i * \ln p_i$).

a.) Benthic samples (leaf packs and sediment baskets combined).

Index	FLC	FLR	SEEP	FSC	FSE	MLR	MSC	PERM
H_s	2.08	2.39	1.73	0.35	0.94	2.70	0.67	2.75
$H_{s(max)}$	3.85	3.87	3.37	2.20	3.00	3.30	2.57	4.04
E	0.54	0.62	0.51	0.16	0.31	0.82	0.26	0.68

b.) Emergence samples

Index	FLC	FLR	SEEP	FSC	FSE	MLR	MSC	PERM
H_s	1.92	3.12	1.77	2.90	2.22	2.65	0.97	2.86
$H_{s(max)}$	4.69	4.74	4.17	3.47	4.09	3.93	3.30	4.29
E	0.41	0.66	0.42	0.84	0.54	0.67	0.29	0.67

its temporary headwater section (FLC) was higher than that between PERM and FLR. FSE, the site with experimental flow extension, displays higher species identities to forest temporary streams (including SEEP and PERM) than does FSC. The two meadow sites were most distant from the forest systems in faunal composition and the least species overlap was observed between PERM and the meadow sites (Table 4.11).

There are differences in the faunistic similarity between benthic and emergence collections (Table 4.11). As explained above, these differences are mainly driven by the

Table 4.11: Comparison of Species Identity and Percent Similarity between Streams.

a.) Benthic samples

Species identity							
	FLR	SEEP	FSC	FSE	MLR	MSC	PERM
FLC	.70	.56	.24	.35	.21	.19	.60
FLR		.62	.25	.41	.19	.33	.53
SEEP			.41	.61	.21	.42	.44
FSC				.53	.38	.25	.18
FSE					.21	.24	.26
MLR						.29	.17
MSC							.17

Percent Similarity							
	FLR	SEEP	FSC	FSE	MLR	MSC	PERM
FLC	.56	.38	.10	.15	.07	.07	.20
FLR		.51	.21	.25	.13	.21	.15
SEEP			.54	.63	.14	.53	.09
FSC				.86	.11	.88	.03
FSE					.11	.83	.04
MLR						.16	.02
MSC							.02

b.) Emergence samples

Species identity							
	FLR	SEEP	FSC	FSE	MLR	MSC	PERM
FLC	.74	.54	.41	.59	.31	.28	.54
FLR		.59	.36	.53	.29	.24	.47
SEEP			.37	.58	.29	.30	.41
FSC				.59	.29	.41	.27
FSE					.27	.34	.39
MLR						.38	.05
MSC							.12

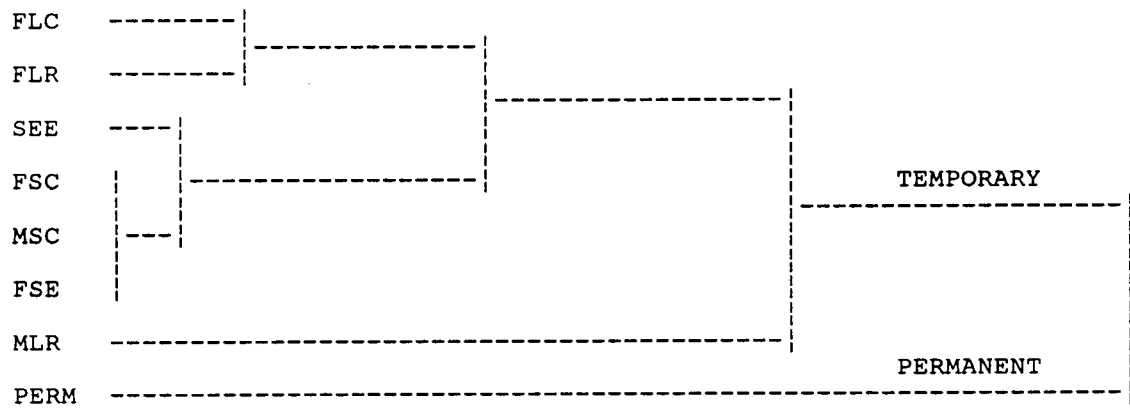
Percent Similarity							
	FLR	SEEP	FSC	FSE	MLR	MSC	PERM
FLC	.50	.57	.22	.45	.03	.02	.23
FLR		.50	.34	.36	.05	.07	.28
SEEP			.26	.26	.03	.03	.21
FSC				.46	.12	.30	.08
FSE					.07	.15	.09
MLR						.23	.00
MSC							.01

large number of Hydraena vandykei in benthic samples from all ephemeral streams. The scarcity of the same species in emergence samples shifts the similarity structure between the short-flow channels. While these streams are highly similar for benthic collections (83-88% similarity), correspondence in faunal composition drops to 15-46% similarity for the emergence collections.

Similarity was highest between temporary forest streams (except the similarities between benthic collections from ephemeral channels). Faunal correspondence between forest streams decreased as differences in flow duration increased along a PERM - temporary streams - SEEP - ephemeral streams axis. Independent of flow duration, meadow and forest streams were most dissimilar. As is the case for long-flow and short-flow forest streams, similarity between the two meadow sites was low (16% for benthic samples and 23% for emergence samples). However, MSC was more similar to MLR than any other stream for both the benthic and the emergence collection.

The cluster analysis summarizes the similarity patterns between streams. Figure 4.2 illustrates the trend for samples to be classified primarily according to exposure (meadow vs. forest clusters) and secondarily according to flow duration (FLC, FLR, SEEP = long-flow cluster; FSC, FSE = short-flow cluster; Perm = permanent stream). This tendency is especially well reflected in the classification of the emergence samples. The clustering according to flow duration overrides the forest - meadow classification structure in the case of the benthic collections because of high numbers of H. vandykei at site MSC.

a.) Benthic collection



b.) Emergence collection

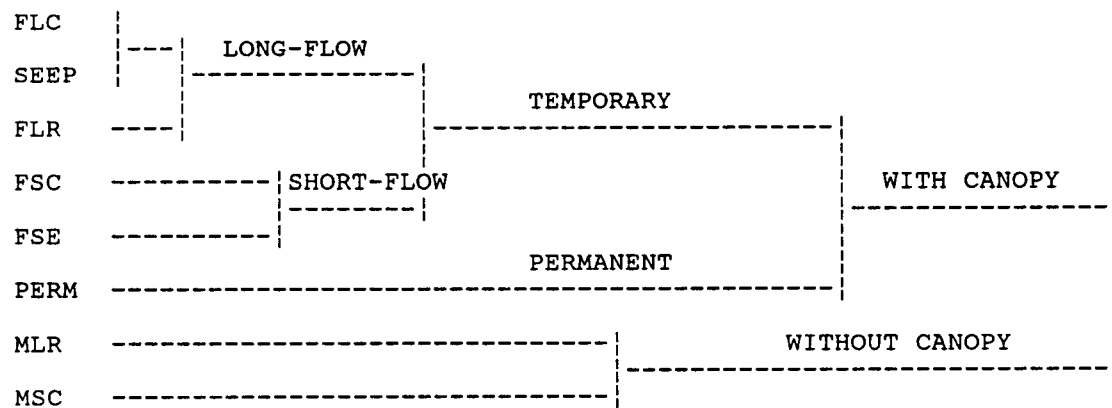


Figure 4.2: Comparison between Study Sites (Streams).
Cluster analysis of benthic and emergence samples.

Comparison between Sample Sites

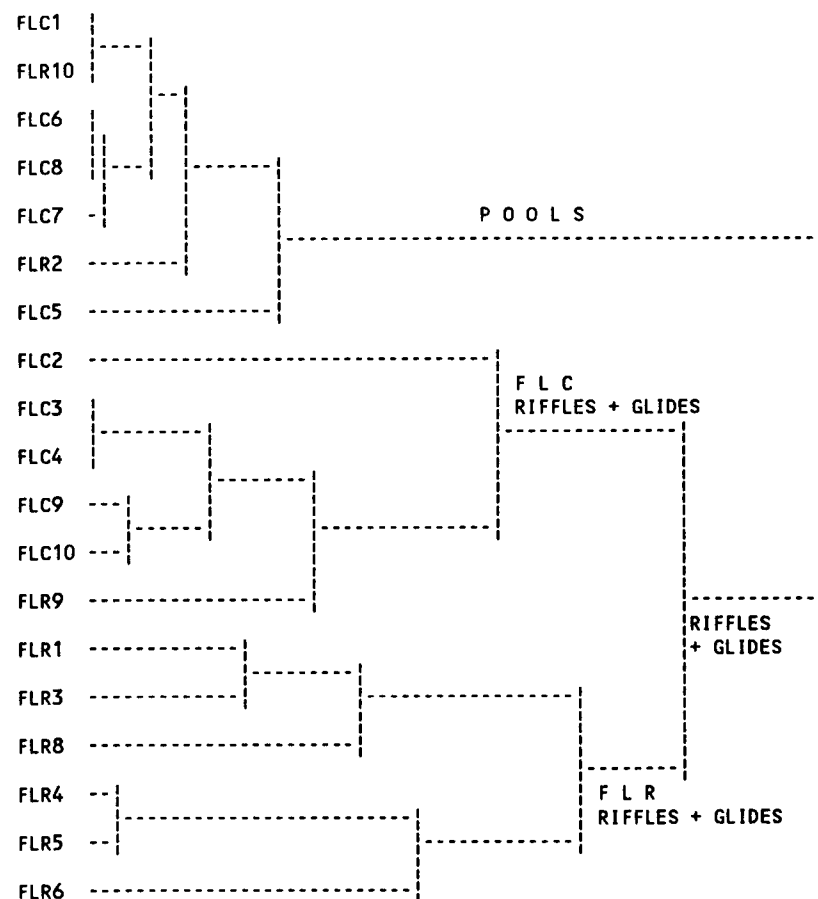
Community patterns were investigated at the sample site level of resolution for the two temporary forest streams (FLC and FLR). The sample sites of both streams were pooled and subjected to multivariate analysis. For practical purposes, FLR S7 was treated as an outlier and omitted from the data set in the general part of the analysis. This site has flow for only about 70 days each year thereby exhibiting typical short-flow characteristics. To investigate the importance of flow duration on faunal composition, FLR S7 was included.

The clustering of FLC and FLR sample sites yields a similar classification pattern for benthic and emergence samples. However, the benthic sample clusters are interpretable over two dichotomies in reference to environmental parameters, whereas the emergence samples can be interpreted over 3-4 dichotomies (Fig. 4.3).

Both cluster structures show an initial split into pool and riffle/glide sample sites. At the second dichotomy FLC and FLR samples are separated. The emergence samples can be further classified into a group of summer dry sites versus sites that retain moisture during the dry season (Fig. 4.3).

The difference in interpretability between emergence and benthic collections follows from the sampling scheme. Sampling continued year around in the case of the emergence collections, but was restricted to the flow period in the case of the benthic collections. Thus, the faunistic classification based on benthic samples does not reflect the summer habitat conditions at the sample sites. These are the habitat conditions which provide the interpretation at the 3rd dichotomy in the cluster structure derived from the emergence collections.

a.) Benthic collection



b.) Emergence collection

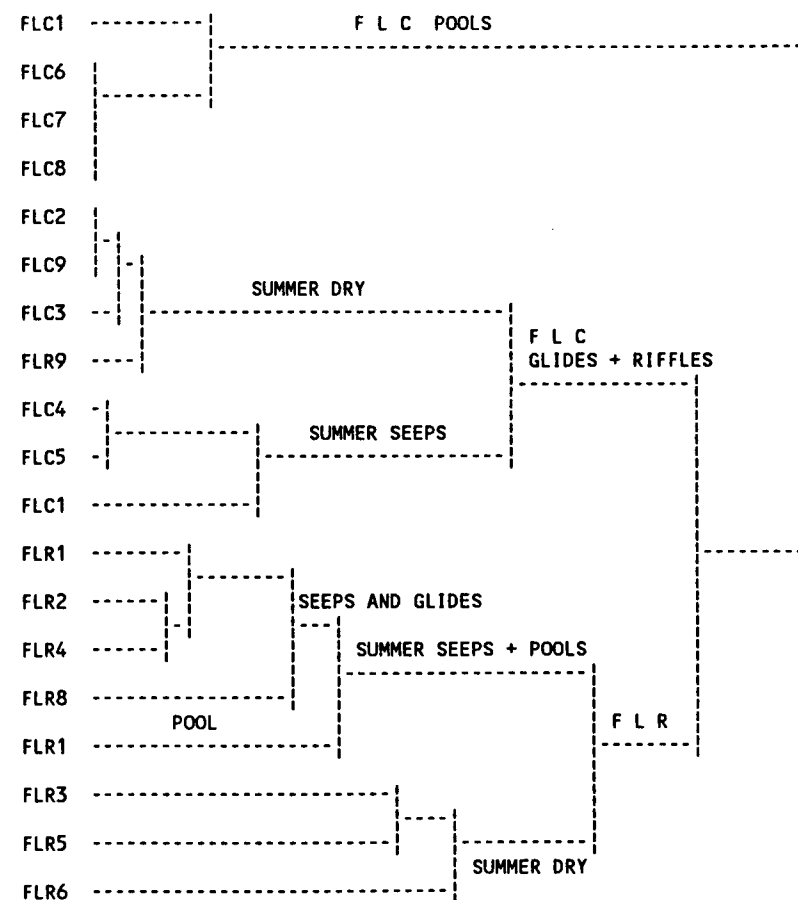


Figure 4.3: Comparison between Sample Sites (Forest Long-Flow Streams). Cluster analysis of benthic and emergence samples.

Given the results of the clustering based on fauna, correspondence analysis was performed for the 2, 3 and 4 cluster structure in the case of the benthic samples and for the 2, 3, 4 and 5 cluster structure in the case of the emergence samples. The benthic 5 cluster structure and the emergence 6 cluster structure each contain an entity with only one sample.

The correspondence between benthic classification and underlying environmental parameters is highest for the 2 cluster structure (Table 4.12). It decreases with increasing cluster numbers. For emergence samples the 2 and 5 cluster structures represent correspondence between fauna and environmental parameter based classification of sample sites about equally well (Table 4.12).

The benthic 3 cluster structure and the emergence 5 cluster structure were chosen for the two separate omission analysis. The omission analysis ranks days with flow and summer drought conditions as the most important factors determining community composition. Current velocity and percent stream bed covered with plants or wood were least important (Table 4.13). Only the rank of site-specific

Table 4.12: Correspondence of Faunistic Classification and Classification Based on Environmental Parameters (MRPP-analysis).

no. clusters	p-values	
	benthic	emergence
2	0.0012	0.0054
3	0.0085	0.0508
4	0.0370	0.0401
5	---	0.0056

Table 4.13: Ranking of Environmental Parameters. Parameters are ranked according to their contribution to cluster tightness in the environmental-parameter-based cluster structure corresponding to the faunistic classification of sample sites. Ranks are assigned with respect to increase or decrease of cluster compactness (within cluster distance) following the omission of a single environmental parameter.

a.) Benthic samples (faunistic 3 cluster structure imposed)

Parameter omitted	distance change	rank
days with flow	0.0389	1
summer drought conditions	0.0123	2
current velocity	-0.0128	6
site specific slope	0.0113	3
percent dirt	0.0079	4
percent rock	0.0058	5
percent plant	-0.0256	7
percent wood	-0.0391	8

b.) Emergence samples (faunistic 5 cluster structure imposed)

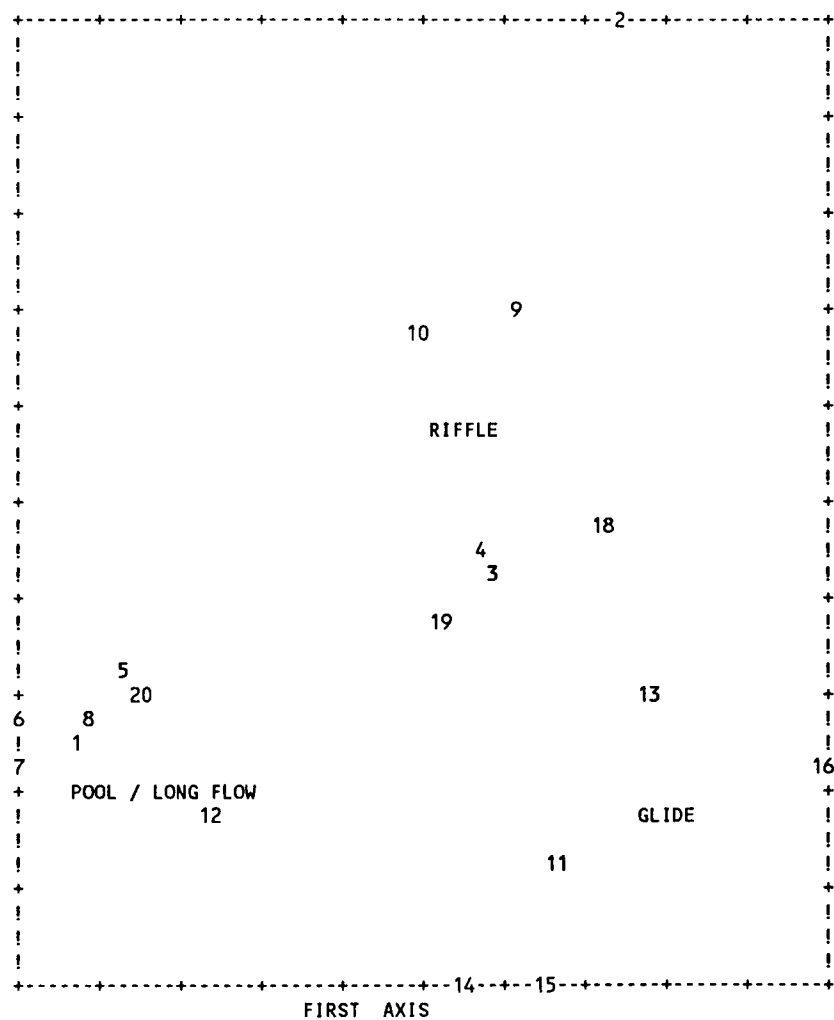
Parameter omitted	distance change	rank
days with flow	0.0412	1
summer drought conditions	0.0244	2
current velocity	-0.0061	6
site specific slope	-0.0051	5
percent dirt	0.0128	3
percent rock	0.0103	4
percent plant	-0.0397	7
percent wood	-0.0422	8

slope was inconsistent between both analysis. While it was ranked the 3rd most important factor in determining the faunal composition of benthic samples, it was ranked 6th for emergence samples.

The polar ordination with objective selection of axis endpoints revealed a somewhat distorted pool/long-flow - riffle/short-flow gradient for the benthic collections in the first dimension. The gradient is distorted in that neither the most distinct riffles such as FLR S3 (13), nor the site with shortest flow (FLC S3 (3)) were selected as one of the axis endpoints (Figure 4.4). The gradient underlying the second axis can not be interpreted in ecologically meaningful terms. The first axis extracts 43% of the information in the data set and Paraleptophlebia gregalis is the taxon with the highest correlation to axis 1 ($R^2 = 0.9$). The DCA structure is quite similar to that generated by PO, except that the second axis can be interpreted as separating FLC and FLR samples. The DCA Eigenvalue for axis 1 is 0.42 (42% of the information in the data set is extracted by the first axis) and P. gregalis displays the highest correlation to it ($R^2 = 0.9$).

The PO applied to the emergence samples reveals a distorted short-flow - long-flow gradient in the first axis (permanent pools FLC S6 and FLR S10 arranged toward the center) and a pool - riffle gradient in the second axis. The first axis extracts 33% of the information in the data set and is correlated highest to the distribution of Ostrocerca foersteri in the samples ($R^2 = .88$). The second axis extracts 31% of the information in the data set. P. gregalis is the taxon with the highest correlation to that axis ($R^2 = 0.82$). DCA results are very similar to those obtained by PO, although somewhat more information is retained in the first axis (40%).

a.) Benthic collection



b.) Emergence collection

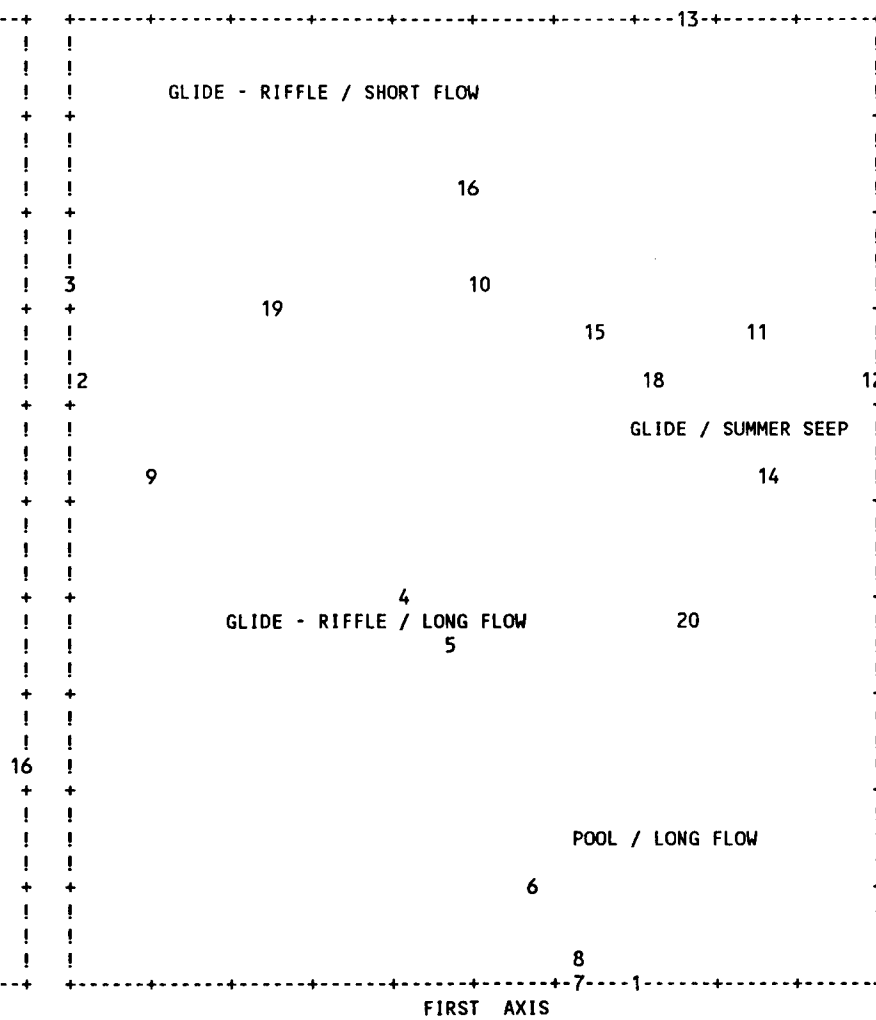


Figure 4.4: Polar Ordination of FLC and FLR Sample Sites (Endpoints Objectively Selected). (FLC: 1- 10; FLR: 11-20; FLR S7 omitted).

Figure 4.5 illustrates the PO results with subjective endpoint selection for benthic and emergence samples. Endpoints of the first axis are the composite of all short-flow stream collections (21) and the composite of all PERM collections (22). In both cases the second ordination axis (endpoints objectively selected) cannot be related to any environmental gradient.

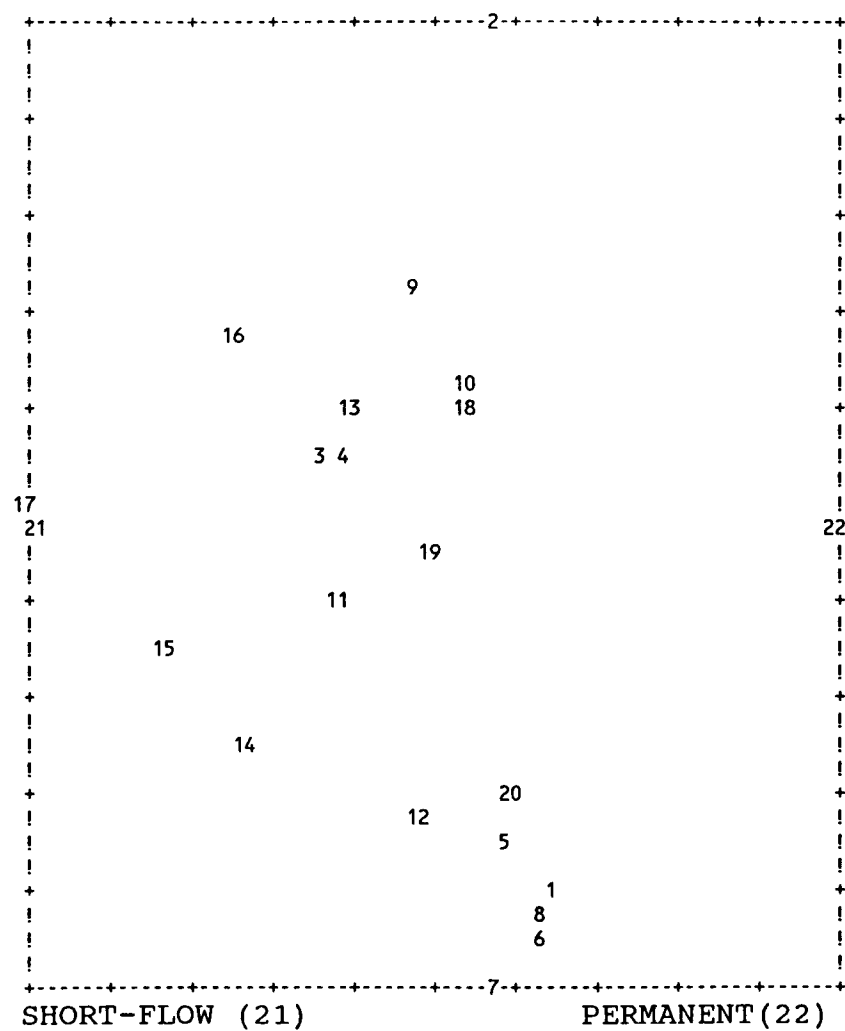
The ordination with selected endpoints performed on benthic samples extracts 23% of the information in the data set in the first axis and 25% in the second axis. Hydraena vandykei, the eudominant taxon in benthic samples from ephemeral streams, is negatively correlated to the first axis ($R^2 = 0.79$).

In the corresponding analysis for emergence samples 16% of the information in the data set is captured in the subjectively selected axis while the second axis extracts 24%. None of the common mayfly or stonefly species is highly correlated to the first axis. However, the tipulid Molophilus spiculatus, which is common in FLC and FLR, is negatively correlated to the flow duration gradient ($R^2 = 0.60$).

The ordination scores for the sample sites in the PO with selected endpoints are correlated with the number of days with flow for the benthic collections ($R^2 = 0.35$, $P < .01$). However, the correlation was much weaker if FLR S7, the site exhibiting ephemeral conditions, was omitted from the regression ($R^2 = 0.18$, $P = .06$) and no apparent correlation was found after omission of the 3 sites with shortest flow ($R^2 = 0.07$, $P > .10$).

First-axis ordination scores for the emergence collections were highly correlated to flow duration at the sample sites ($R^2 = 0.78$, $P < .01$). This was the case even as the outlier FLR S7 was removed from the data set ($R^2 = 0.73$, $P < .01$). In fact, successive omission of

a.) Benthic collection



b.) Emergence collection

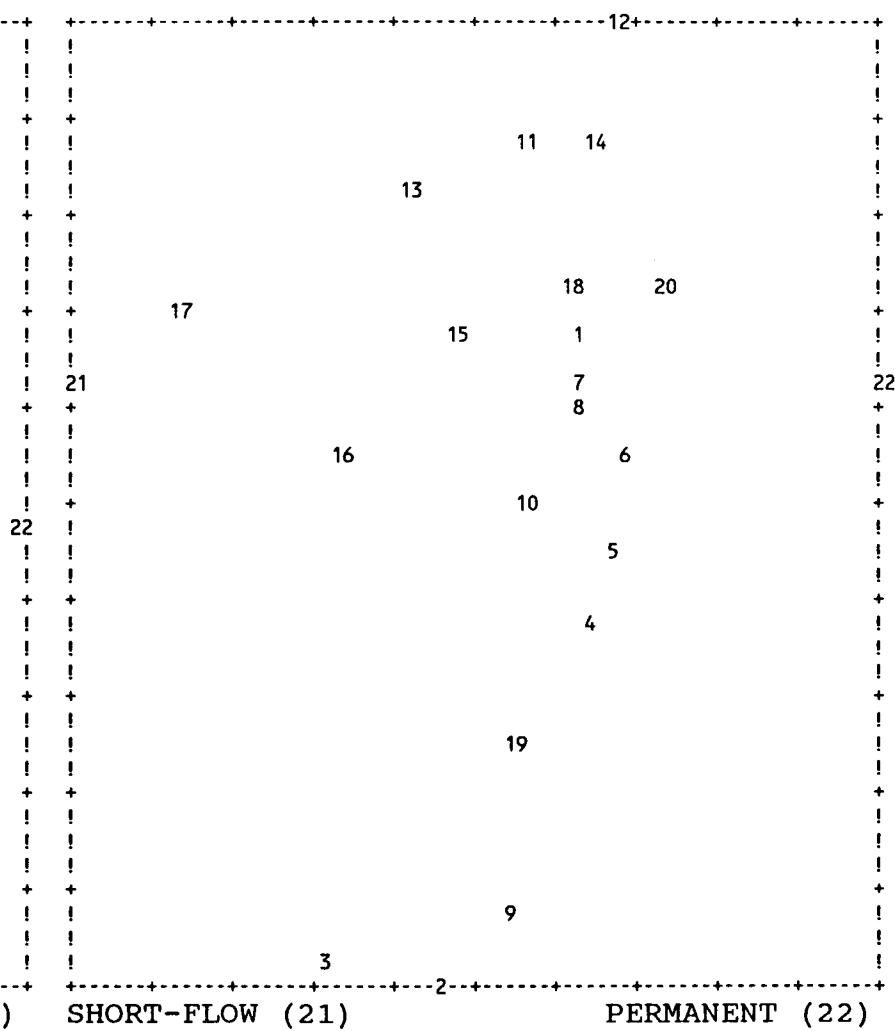


Figure 4.5: Polar Ordination of FLC and FLR Sample Sites (Endpoints of First Axis Subjectively Selected). (FLC: 1-10; FLR: 11-20).

sample sites with shortest flow did not considerably alter the coefficient of determination or the significance for the slope of the regression line.

Duration of flow therefore is a significant factor determining community composition not only between short-flow and long-flow streams but even within streams classified as temporary.

4.4. Discussion

Species Richness and Abundance

Species richness and abundance in western Oregon summer-dry streams were surprisingly high. However, in the absence of standardized designs, abundances obtained in this study cannot be properly judged within the context of other research. Even the qualitative comparison of species richness is hampered by differences in methodology, sampling scheme and taxonomic resolution (Boulton and Lake, 1988).

Lake et al. (1986) suggest that temporary streams in Australia are richer in species than similar systems elsewhere in the world. Australian studies yielded between 131 species in a stream with 7 months of flow and 166 species in a stream with flow over a 9-month period. These counts include Chironomidae (Boulton and Suter, 1986).

In Europe, Legier and Talin (1973) found between 42 and 80 insect species in benthic samples from temporary streams in the Provence. Morrison (1990), studying drought effects on headwaters located in a mature Scottish forest, reported 23 species of Ephemeroptera, Plecoptera and Trichoptera from benthic collections in one of his sites.

Williams and Hynes (1976) examined two meadow streams

in Ontario with flow over 7 - 8 months. They found up to 36 insect species (Chironomidae excluded). Midges not considered, intense benthic sampling yielded 37 species in the temporary section of a forest stream in the same province (Mackay, 1969). Based on studies of California summer-dry streams, Abell (1984) concludes that 15 - 35 insect taxa are characteristic for sites with 7 - 8 months of steady flow, while 0 - 5 species are typical for ephemeral systems.

In the McDonald Forest area the emergence study by Kraft (1963) yielded 116 species of non-midge insects from Berry Creek, a second order woodland stream with permanent flow. Kerst and Anderson (1974) collected 43 stonefly taxa in emergence traps exposed over 45 months in Oak Creek. During the same long-term project 28 caddisfly species were recorded over a 20-month period (Anderson and Wold, 1972). Tew (1971) collected 58 species, 9 of which were midges, in a temporary stream located in a meadow adjacent to MLR.

The extensive review shows that species richness in FLC and FLR, the long-flow streams located in McDonald forest, compares well to that in Australian temporary streams. It appears to be considerably higher than in other parts of North America or in Europe. It is particularly noteworthy that the number of insect taxa in the temporary forest streams is higher than that in permanent headwaters of the same area.

Species richness largely followed the patterns initially predicted for the different types of summer-dry streams. FLR had more species than FLC and more taxa were found in long-flow streams as compared to ephemeral channels. Furthermore, species richness declined by more than 50% as MLR was pushed toward ephemeral conditions during the drought of 1989/90.

The distinct and predictable change between wet and

dry season, which Waring and Franklin (1979) point out as the unique climatic feature shaping the vegetation in the Pacific Northwest, is considered to be a key factor for the species richness observed in western Oregon temporary streams. While the change of physical conditions in these systems is dramatic within a season, the habitat parameters are very consistent between seasons.

Thienemann (1932) proposes that species richness in harsh environments is closely correlated to the persistence of such habitats. In that sense, temporary streams with unpredictable flow regimes only exist for a single season, while temporary streams in the Pacific Northwest have existed for several thousand years. In a more traditional evolutionary view, the predictable presence of these habitats allowed for the radiation of organisms into the harsh temporary stream environment via the development of specific adaptations.

While adaptive radiation may contribute somewhat to species richness in western Oregon temporary streams, the wide overlap between the fauna of temporary and permanent lotic systems suggests a different mechanism to be more important. Rather, organisms from permanent headwaters with accidental preadaptations can readily colonize the temporary stream environment (Clifford, 1966). Such preadaptations include: (1) univoltinism combined with rapid growth in winter and spring; (2) larval feeding independent of fast currents; and (3) egg deposition in moist habitats in early summer.

Univoltinism and rapid spring growth are necessary to complete the life cycle during the lotic phase of temporary headwaters. Currents in these streams are low for most of the season, thus the habitat is not well suited for filter feeders such as Hydropsychidae. Egg deposition in moist habitats in early summer allows adults to "recognize" the temporary stream habitat. Earlier in the year, temporary

streams are not distinguishable from permanent headwaters because of similar flow conditions. Later in the year streams with sufficient flow duration and streams with a flow period too short for successful larval development will both be dry. Data on egg diapause, searching behavior of females and larval drift support this scenario (Dieterich, unpublished data). In this model the predictability of the moisture regime in late spring and early summer is a direct key for successful colonization of the temporary stream environment from a large pool of potential colonizers.

The large pool of potential colonizers partly explains the large number of species in western Oregon temporary streams. However, it does not account for the higher species richness in FLC and FLR than in the permanent headwater (PERM). The higher number of species in temporary sites is surprising at first sight, although species richness in long-flow systems has been reported to be as high as that in adjacent first-order streams (Legier and Talin, 1973; Boulton and Suter, 1986).

While lacking many structural features of higher order permanent streams, FLC and FLR are highly heterogenous environments on a temporal scale. Clifford (1966) and Williams (1987) differentiate between two distinct faunistic groups in temporary streams: the winter fauna associated with the flow phase and the summer fauna associated with stagnant pools. Such summer pools "invite colonization from many purely lentic forms" (Williams and Hynes, 1977). In FLC and FLR not only one but two summer habitat types are apparent. The pools, characterized by Coleoptera and midges of the subfamily Chironomini, and the seeps characterized by a number of Tipulidae and otherwise rarely collected Diptera such as Glutops.

PERM lacks many of the features causing heterogeneity in higher-order streams. Medium to large sized rocks,

occasional openings in the canopy or a distinct riffle - pool structure are absent. On the other hand, PERM also lacks the temporal heterogeneity of FLC and FLR. The general lack of heterogeneity in PERM, which is a rather typical first-order stream in the Coast Range, results in a relatively low species richness there as compared to higher-order permanent streams or its own temporary headwater section (FLC).

Species richness in MLR, the long-flow meadow stream, is lower than that in the temporary forest sites. In contrast to FLC and FLR, spring flow ceases rapidly over the entire length in MLR. No pools or seeps remain during the summer. Thus, the site lacks the pool and seep component in its fauna, which contributes 1/3 to the overall species richness in FLC and FLR.

The long duration of the dry season causes low species richness in ephemeral streams (Williams and Hynes, 1976; Abell, 1984). According to Thienemann's second biocenotic principle (Thienemann, 1920) species richness is negatively correlated to the harshness of an environment. The pool of species capable of colonizing summer-dry streams decreases as the duration of seasonal flow shortens. Ultimately only ubiquitous taxa with extremely short life cycles, mobile taxa which can migrate between sites (Coleoptera adults) or taxa with increasingly sophisticated adaptations to survive prolonged periods of drought can colonize short-flow channels.

Thus far the discussion has focussed on the qualitative species richness measure. However, two observations concerning abundance patterns also warrant attention. Firstly, the dramatic shift in abundances between the two field seasons in MLR and secondly the high number of stonefly and caddisfly larvae in benthos collections from PERM as compared to the abundance of these taxa in the emergence collection.

The drought in 1990 pushed the flow duration in MLR below the threshold for temporary stream biota. MLR in that year turned into a stream with ephemeral characteristics. Faunistically, these are reduced insect abundance and lack of representatives in the mayfly, stonefly and caddisfly groups. Two species of Plecoptera were still collected from MLR in the 1989-90 season. Thus, flow duration was still too long for the transformation from a long-flow (temporary) to a short-flow (ephemeral) site to be complete. The observations made in this study suggest that for meadow streams approximately 90 days of annual flow is the upper threshold for ephemeral systems, whereas 130 days is the lower threshold for streams to be classified as temporary. Flow duration of 90 to 130 days results in sites with intermediate faunal characteristics. Similarly, for the summer-dry streams in the forest flow duration of 100 to 145 days will result in intermediate faunal characteristics. This defines the thresholds for ephemeral and temporary forest streams. Additional research specifically focussing on the threshold levels will be necessary to get more accurate and reliable estimates. The somewhat faster development of organisms in MLR could be either a result of better food quality or slightly higher average temperatures in that stream or a combination of both. The possible temperature effect suggests that threshold levels defining ephemeral versus temporary streams should be related to degree days rather than simple temporal measurements. Unfortunately, the success of research directed to establish more precise 'class boundaries' for ephemeral and temporary systems will largely depend on unpredictable climatic factors determining flow duration.

Benthic samples yielded considerably higher abundances of Plecoptera and Trichoptera in PERM as compared to FLC, FLR and SEEP. In contrast, for the emergence samples

stonefly and caddisfly abundances in PERM were lower than in any of the long-flow forest streams or the SEEP site. This is a strong indication for higher survival rates of stoneflies and caddisflies in temporary streams as compared to the permanent headwater. However, only a species-based comparative analysis of survival rates for different larval stages could yield conclusive results in this context.

Multivariate Analysis

There is good correspondence in species identity patterns for benthic and emergence samples. However, in the case of the percent similarity measure, differences between collection types are apparent.

Merritt and Cummins (1984) characterize artificial substrates including leaf packs as qualitative or semi-quantitative sampling devices. Mobile taxa such as the pool-dwelling 'swimmer' Ameletus are not adequately represented in benthic samples. Especially in deeper pools Ameletus moved away from the colonization substrates prior to and during the recovery of leaf packs or sediment baskets. Only 92 Ameletus larvae, most of them early instars, were present in benthic collections, while 808 adults were caught in emergence traps. The large pool FLC S1 yielded just 1 larva but more than 250 adults.

Leaf packs also provide food and shelter for some organisms, but shelter only for most others. Therefore shredders may be overrepresented in leaf pack collections.

A general difficulty with benthic samples is the identification of immature animals. With the notable exception of early-instar Paraleptophlebia larvae, Ephemeroptera, Plecoptera and Trichoptera generally could be identified to species in this study. However, in the case of the Diptera, identification of larvae frequently

was not possible even for late instars.

Clumping of early-instar larvae also may severely distort benthic community patterns. To ameliorate distortions, early-instar Ostrocerca and Soyedina were omitted from the analysis. However, this does not eliminate the potential for less obvious clumping effects in other taxa.

The interpretation of the results of this study was impaired by the mass occurrence of Hydraena vandykei in leaf packs and sediment baskets. As indicated before, the different percent similarity patterns between benthic and emergence samples are primarily a result of the overwhelming number of H. vandykei in benthic samples from the ephemeral streams. This minute beetle occupies the littoral zone closest to the waterline (Perkins, 1976). It is a litter dweller which, according to my observations, can enter the stream at sites of litter accumulations. Since the species is littoral rather than lotic, factors such as riffle - pool structure, velocity or stream bed composition will likely not affect its distribution. Thus, the presence of H. vandykei can obscure patterns displayed by the lotic community in the multivariate analysis.

Furthermore, while Hatch (1961) only recognizes H. vandykei in western Oregon, Perkins (1980) recently described a number of new species. My identifications are based on the Hatch collection and other reference material in the Systematic Entomology Laboratory, Oregon State University. The determinations in these collections may not be accurate. Therefore, there is some ambiguity in the H. vandykei determinations.

H. vandykei is rarely caught in emergence traps. Therefore the emergence collection data are less ambiguous and focus more on the in-stream fauna. On the other hand, they almost lack the eudominant littoral element of the ephemeral and temporary stream communities.

A number of gravid Soyedina interrupta and Ostrocerca foersteri females were collected in the emergence traps. Direct observations suggest that females in these species search for appropriate oviposition sites by walking along the streams or in the drying stream beds. When disturbed, they hide in the litter rather than flying away. Thus, secondary catch of egg-bearing females is an additional distortion in the emergence results. However, this distortion is usually small (< 5% of the total collection for a species) and yields valuable information on life cycle strategies.

Neither emergence collections, which Merritt and Cummins (1984) list among the quantitative sampling methods, nor benthic collections accurately represent the fauna associated with summer-dry streams. Rather, emergence and benthic sampling is complementary. But all things considered, the more quantitative emergence collections can be expected to better reflect the overall (summer and winter fauna combined) structure of the community than do the more qualitative benthic collections, especially in the light of the benthic sampling being restricted to the lotic phase of the summer-dry streams in this study.

Species identity patterns for the benthos and emergence collections, and the clustering of study sites (streams) based on emergence collections, reveal insolation as the most important environmental factor shaping summer-dry stream communities. Flow duration is less important. Similarly, Hawkins (1983) found the presence or absence of a canopy to be more important for explaining the community structure in Oregon permanent streams, than other physical parameters such as substrate type.

In the cluster analysis based on benthic samples, flow duration is more important for the community structure than is insolation. The ephemeral sites form a distinct cluster, independent of the presence or absence of a canopy. This is

a direct result of the eudominance of H. vandykei at these sites. In each of the ephemeral streams the littoral beetle comprised more than 80% of the total collection, while in seep sites (SEEP) 49% of the animals caught were H. vandykei.

It is somewhat discomfoting that the analysis of the benthic samples is governed by the distribution of a single species which is not even a lotic taxon. But H. vandykei depends on temporary stream habitats just as much as the truly aquatic species and therefore cannot be ignored in the analysis of summer-dry stream communities. In fact, H. vandykei may serve as an indicator for flow duration in summer-dry streams. Not only was it more common in ephemeral as compared to temporary streams. The distribution of H. vandykei also was highly correlated to decreasing flow duration within the temporary forest channels.

Presence or absence of a canopy is the most important environmental factor determining the structure of the lotic community. Flow duration is the most important environmental factor determining the distribution and relative abundance of H. vandykei in the samples. Thus, in the light of the biological knowledge concerning H. vandykei, the results of the cluster analysis based on benthic and emergence collections are not contradictory. To ask whether summer-dry stream community structure is primarily determined by canopy or flow duration more than anything is a case of a question inappropriate to be answered at the whole community level.

Cluster analysis on FLC and FLR sample sites yielded riffle-pool structure and summer-drought conditions as important determinants of community composition. Benthic samples were not taken during the summer. Therefore a separation of sites according to summer drought conditions is apparent only for the emergence collection. No flow

duration effect was revealed in the cluster structures. But classification may not be the appropriate technique to analyze a rather uniform flow duration gradient.

Both, flow duration and riffle - pool structure are usefull for the interpretation of the ordination results. In the ordinations with objectively selected endpoints the pool sites group toward one endpoint of either the first or second ordination axis, but the opposite end is less well defined. This reflects the lack of a distinct riffle habitat in the temporary streams where the channel gradient is high enough for riffles to be formed, but velocity is generally low.

According to the omission analysis, flow duration and summer drought conditions are the most important environmental parameters shaping community composition at the FLC and FLR sample sites. Omission of days with flow had a similar effect on cluster tightness in the analysis based on benthic samples and in the analysis based on emergence samples. Omission of summer-drought conditions also decreased the tightness of the cluster structure for both collection types, but the effect was stronger in the case of the emergence samples. This is in agreement with the more integrative nature of the emergence collections, which sample winter and summer fauna while the benthos is sampled only during the lotic phase. However, the appearance of the summer-drought effect in the results of the ranking procedure based on benthic samples demonstrates that summer-drought conditions affect larval distribution patterns even during the lotic phase. Larvae of semivoltine lotic species (Sweltsa fidelis, Calliperla luctuosa) are more common in areas with summer seeps. Furthermore, the typical summer fauna begins to appear toward the end of the flowing season and is then sampled in the benthic collection.

Only in the case of the benthic samples was

microhabitat somewhat important for cluster tightness. But current velocity and site specific slope are rather indirect measures for the riffle - pool structure in streams. The ranking procedure therefore may not be suited to detect the importance of microhabitat for animal abundances at the sample sites.

This points to a general ~~def~~ fault of the ranking procedure based on the MRPP algorithm. Different measurements used to describe a specific microhabitat may not always equally well describe the actual physical conditions of the environment. In addition, the biological response to such factors usually will not be linear. This causes within cluster variation in the MRPP and potentially affects the ranking of parameters.

Furthermore, in the case of the temporary streams, emergence collections integrate the highly dissimilar faunas associated with summer and winter habitat types, while environmental parameters will either describe winter or summer habitat conditions. This will also tend to increase the within cluster variation in the classification of sample sites. If a parameter describing lotic conditions (e.g. duration of flow) is correlated to a parameter describing summer habitat conditions (e.g. summer-drought conditions), then the distortion by increased variation will be less severe and the actual importance of the factor in question may be overestimated using the MRPP ranking approach. This effect may have contributed to the high ranking of summer-drought conditions and number of days with flow in the ranking analysis conducted in this study.

However, the importance of summer-drought conditions and days with flow for macroinvertebrate community composition in temporary streams is supported by cluster analysis results, as well as by the significant correlation between days with flow and the ordination scores of sample sites on the 'flow duration axis' in the PO with

subjectively selected endpoints. Whether flow duration or microhabitat structure is more important for the structure of macroinvertebrate communities in temporary forest streams cannot be decided conclusively. But it is safe to state that microhabitat pattern and flow duration are the most important factors in this respect.

An analysis of short-flow sites similar to that performed for the long-flow streams was not possible due to a lack of taxonomic resolution. That is, only if the Chironomidae had been determined to species could a more detailed analysis on ephemeral streams have been performed. Future research on community structure in short-flow streams therefore will have to focus on the midge fauna.

The multivariate analysis of the faunistic data in this study was successful in that results were generally interpretable. Furthermore, different analytical pathways yielded similar or complementary results. The same general patterns were found if the analysis was based on different data sets (benthic vs. emergence), although there were differences in resolution. The correspondence analysis based on the MRPP procedure proved to be a promising approach in gauging the importance of different environmental factors for community structure, especially if such factors can be directly quantified. Smith et al. (1990) recently suggested a similar technique as the basis for a unified approach to statistical analysis of multivariate data.

If important factors for community structure (key factors) can be defined, then species susceptible to changes in key factors can be identified via correlation to appropriate ordination axis. This may provide a basis for an indicator species concept in conservation biology, which does not solely depend on observational, often inconsistent evidence of species distribution between habitats.

The complementary nature of the multivariate results

is a reflection of the complementary nature of the competing views on community structure. Communities change along environmental gradients. This rate of change is not constant. The lack of uniformity in the rate of community change along an environmental gradient is the basis for the definition of characteristic community types. However, as the multivariate analysis on the fauna of FLC and FLR sample sites has shown, community types themselves are not uniform. Rather, they continue to change at low rates along the environmental gradient in question.

General Characteristics of Summer-Dry Streams

The summer drought accounts for the perceived harshness of the environment in ephemeral and temporary streams. With increasing duration of the drought the environment becomes less favorable for aquatic organisms until finally only short-lived Diptera or mobile Coleoptera can utilize the habitat.

Some authors (e.g. Williams and Hynes, 1977) consider large fluctuations in chemical and physical parameters an additional obstacle which has to be overcome by organisms colonizing temporary streams. However, this study shows that if these systems are tightly connected to subsurface waters, fluctuations in physical and chemical parameters during the lotic phase are small, except for a possible nutrient peak at the onset of flow.

A number of factors make summer-dry streams a favorable environment for organisms which can overcome the restrictions imposed upon aquatic life by the summer drought. Even during peak flows, velocities in the summer-dry headwaters of the Pacific Northwest were comparatively low. Stream edge refugia were always close because channel width rarely exceeded 60-80 cm. Therefore, flush-out of

animals which causes high mortality in streams in the southwestern United States (Clifford, 1966), does not occur. Consequently, drift collections were extremely low even during the peak flood event in the 1989-90 season (Dieterich, unpublished data).

Biological parameters which contribute to habitat favorability for insects in summer-dry streams include the lack of fish predation and the absence of competition by the snail Juga silicula. Fish predation can be an "important determinant of insect community structure in running waters" (Flecker, 1984). Williams and Hynes (1979) found diets of fish in temporary streams to be largely composed of insects. Plentiful food supply in these systems was considered to be an important factor for rapid growth of fish (Williams and Hynes, 1979). Abell (1984) distinguishes between different types of summer pools. He contrasts those with an assemblage of adult beetles, dragonflies and Heteroptera to those occupied by fish. The fish in such pools "consume everything that is soft enough to chew" (Abell, 1984).

The absence of fish does not completely eliminate vertebrate predation in the temporary streams. In spring, the rough-skinned newt (Taricha granulosa) was commonly encountered in the large FLC pools. Lugthart and Wallace (1992) expect larval salamanders to be of "primary importance in terms of predation on aquatic macroinvertebrates" and Taylor (1984) found that while diet in adult T. granulosa depends on prey availability, insects generally are of great importance.

The rough-skinned newt is a sit-and-wait predator. Thus, the very agile mayflies Paraleptophlebia gregalis and especially Ameletus may become easy prey to the salamanders. In contrast, the small stonefly shredders are closely associated with leaf litter at pool edges and in general are more common in glide/riffle sections than in

pools. They therefore are less susceptible to Taricha predation. The potential vulnerability of the two most common mayfly taxa may help explain the relatively low numbers of Ephemeroptera emerging from the temporary streams as compared to PERM.

Juga silicula is considered to be a "competitive dominant" in some Pacific Northwest streams (Hawkins and Furnish, 1987). This pleurocerid snail prefers to feed on periphyton, but readily consumes leaves and other detritus when algae are scarce (Hawkins and Sedell, 1981). In the well shaded headwater stream PERM, Juga silicula can be observed grazing on rocks and other surfaces, but it also consumes large quantities of leaf material and therefore impacts all feeding guilds.

In an experimental channel in the Oak Creek watershed, Hawkins and Furnish (1987) examined competitive effects of Juga silicula on other stream invertebrates. They found Sweltsa, Malenka/Zapada, Paraleptophlebia and Lepidostoma to be more common in the shaded channel where Juga had been removed as compared to the shaded channel without snail removal. The effects of Juga shredding in PERM are illustrated in that it was virtually impossible to condition leaf packs over a 20-day period there, because leaves were rapidly skeletonized. If packs were exposed in FLC or FLR for conditioning, no damage caused by shredders was apparent. Similarly, leaf litter was rarely seen in PERM from April to November, while plenty of leaf material was present in the summer-dry streams during the entire flowing season.

Lack of high current velocities combined with the closeness of refugia, reduced predator pressure, and lack of competition by Juga silicula may all contribute to summer-dry streams being habitats superior to permanent headwaters for organisms which can overcome the drought-imposed restrictions. In the streams surveyed in this

study, the protection from flush-out and the absence of Juga are particularly important. Fish predation does not explain differences between the long-flow sites and PERM, because fish were absent from the permanent as well as the temporary headwaters.

The price temporary stream inhabitants pay for the superiority of the habitat is the risk of unexpected drought. Such droughts will occasionally occur even in the predictable climate of the Pacific Northwest. Plasticity in habitat selection can be viewed as a means of protection from drought effects at the species level. The consequences of this hierarchical view of adaptability in the context of evolutionary biology will be discussed elsewhere.

Applicability

A range for the applicability of the results has to be given in order to gain ecological knowledge from the information obtained in a study. Giving a range of applicability for results requires the comparison to other research. Some of this was done in the previous section. Comparing the findings of this study to other research was hampered because work on summer-dry streams often lacks qualitative exactness in defining the settings of a study. Grubb (1988) views this as a general problem in ecological research. Without such exactness the speculative nature of comparisons is unnecessarily high.

In order to make research more comparable the characterization of summer-dry stream habitats has to include stream order, discharge, average temperature and other standard physico-chemical descriptors. This study suggests that seasonal predictability and some measure of connectiveness between stream flow and subsurface flow also are important. Flow duration, moisture conditions during

the period of most severe drought, exposure (presence or absence of a canopy), and a riffle - pool characterization will be needed for the specific sample sites.

Two general patterns suggested by earlier work on summer-dry stream communities that were confirmed in this study are: (1) the decrease in species richness with decreasing flow duration and temporal habitat heterogeneity; and (2) a large proportion of the temporary stream fauna is comprised of facultative species.

However, the predictable pattern of distinct wet and dry seasons will likely cause differences in community structure between summer-dry streams in the Pacific Northwest and elsewhere in the world. Lack of predictability is expected to result in a fauna dominated by opportunistic species with short life cycles. Thus, the temporary stream fauna under unpredictable climatic regimes would be less characteristic and differences in community structure along the flow duration or other environmental gradients would be less distinct. This would not exclude the possible occurrence of a few highly adapted species. Adaptations would include drought-resistant life stages, that could be activated in response to appropriate moisture conditions. Individuals then would mature rapidly when conditions were favorable. The numbers of obligate temporary stream species in the Ephemeroptera, Plecoptera and Trichoptera would not be expected to be high in temporary streams located in parts of the world with unpredictable climatic patterns.

Chapter 5

CONSERVATION VALUE, THREATS AND MANAGEMENT

5.1. Conservation Value

Summer-dry streams influence the habitat conditions further down the drainage network in permanent lotic systems. This study shows that ephemeral channels are highly efficient at filtering fine sediment from the water column. Filtration efficiency is related to the degree of longitudinal and latitudinal expansion and contraction of the active channel in response to precipitation. The more ephemeral the streams are, the more efficient they will be at retaining fine sediment. There is a potential for permanent sediment removal from the aquatic phase via physical and biological processes during the dry season, when ephemeral streams become an integral part of the terrestrial environment.

The fertilization experiments demonstrate the importance of temporary streams in removing nutrients from the aquatic environment. Although this research has focussed on long-flow sites, the results are believed to be applicable to ephemeral systems, too. The removal of nutrients such as nitrate from the water column is greatly facilitated by long solute residence times. Removal is accomplished through exchange with subsurface flow. In addition, uptake by in-stream vegetation can be important if algal production is limited by nutrients rather than by light.

Summer-dry streams provide pathways for the direct

transfer of nutrients from the aquatic to the terrestrial system. Nutrients exported into subsurface flow can be absorbed by the rhizomes of terrestrial plants. The nutrients retained as algal biomass will provide food accessible to terrestrial organisms once the streams dry up.

Temporary streams also provide habitat for a large number of species. Only a few taxa are obligate temporary stream inhabitants, but many of the facultative species probably would have intrinsic rates of increase (r) that are too small to sustain durable populations in permanent streams alone. Such species use the temporary systems as "mass cropping" sites, thereby pushing the overall r for a regional population to or above the critical value of 1.

It follows from the above that the value of summer-dry streams as viewed from a conservation perspective is rather high. Probably unexpectedly so. The reason for this high value differs somewhat between short-flow and long-flow streams. Both stream types provide important links for the direct nutrient transfer from the aquatic to the terrestrial environment, thereby conditioning water chemistry in permanent downstream reaches. Ephemeral channels can be very efficient filters of fine sediment, but they offer a rather poor habitat with few specialized species. Temporary streams are expected to be far less efficient at filtering fine sediment from the water column, but they provide invertebrate habitat similar in quality to that of permanent systems.

5.2. Threats

The threats to summer-dry stream habitats are numerous. Global climatic change can alter the discharge pattern and its predictability. Extended periods of drought would likely result in a top-down shift of flow duration. That is, some permanent streams would dry up during the summer, temporary channels would be pushed toward the ephemeral category and ephemeral channels might completely cease to flow. Increase of drought periods in this scenario would ultimately result in a lower density of summer-dry streams.

Besides the global threat, there are currently numerous land use practices which contribute to the deterioration of summer-dry stream environments on a local scale. Some of these were discussed by Abell (1984).

Forestry practices can significantly alter the integrity of ephemeral and temporary stream habitats and sediment-retention capacities. Clear-cut harvesting often causes summer-flow to increase for several years (Beschta, 1990; Rothacher, 1970). In the case of the summer-dry streams this translates into an increase in flow duration. The increase in flow duration can improve habitat quality as it tends to allow for more species to utilize the temporary channels. However, there will also be a tendency towards permanency for long-flow streams connected to subsurface flow. Seep areas in particular are affected by this transformation.

Except for two permanent pools, FLC was dry over the entire study reach in the summers of 1987 and 1988. After clearcut harvesting in parts of its watershed in spring 1989, a short section with permanent flow developed in the stream in the vicinity of one of the sample sites (FLC S6). Juga snails, which had maintained a small population in an upstream seep, began to appear in that section in 1990 and

became increasingly more common by 1992 (Dieterich, personal observation). Over time, the immigration of permanent stream taxa presumably would replace the obligate temporary stream species. However, exact predictions referring to the resiliency of temporary stream species under permanent flow conditions go beyond the scope of this study, but it should be noted that the effects of an increase in stream flow may be both beneficial or detrimental from a conservation perspective.

The removal of deciduous trees and shrubs along temporary streams, which is the usual practice under clear-cut management regimes, has considerable negative effects on the habitat value of the system. It removes the food base for the shredder-dominated aquatic community. This study shows that the fauna of temporary headwaters lacking a canopy is quite different from that of forest streams. The latter not only support more taxa, but a considerable proportion of the species there is highly characteristic for the temporary stream environment. In contrast the fauna of meadow streams, at least in the Pacific Northwest, appears to be dominated by generalists. Tew (1971) reports 83% of the species found in a temporary stream in a meadow adjacent to MLR to be "the result of aerial movements of adults from permanent waters."

Removal of the deciduous canopy along ephemeral streams is expected to reduce the sediment retention capacities of these sites because considerable amounts of sediment are trapped in the thick litter layer characteristically present on the stream beds of short-flow channels.

Agricultural practices pose even more of a threat to summer-dry streams than does forest management. Irrigation can lower groundwater tables and thus cause ephemeral or temporary channels to dry up completely. Grazing, with subsequent erosion and gully formation, has the same effect

in areas where streams recharge the groundwater. This effect is frequently observed in eastern Oregon.

To obtain large and uniform fields, small summer-dry stream channels are commonly filled up and replaced by drainage pipes. Such practices eliminate the whole system and with it the buffer capacities of these channels. For the same purpose and to secure rapid drainage of agricultural land, the meandering pattern of small headwaters is often "streamlined". This decreases the residence time of solutes and therefore the retention capacity of the systems.

The measures described above result in temporary streams with significantly reduced or completely eliminated habitat as well as nutrient and sediment retention functions. The loss of the temporary stream "buffer" will have negative effects on water and habitat quality in permanent waters.

5.3. Management

The large number of summer-dry streams in a wide variety of landscapes makes these systems a prime target for conservation management. In forested areas, to preserve the habitat value and fine sediment filtration function is of primary importance. In agricultural landscapes, nutrient removal frequently will be the main focus.

To preserve the habitat value and sediment retention functions of summer-dry streams, it is important to protect the deciduous vegetation along these sites. This mainly requires careful planning of timber harvests. That is, ephemeral and temporary channels have to be mapped prior to the logging. Cutting, as well as the removal of timber, has to be accomplished without impacting the integrity of the

temporary stream system and its accompanying vegetation. This includes the careful selection of channel crossings, which should not be established over seeps or wet spots. Overall, the above calls for logging management to be carefully adapted to a particular landscape rather than to available machinery and thus highest possible efficiency.

Temporary stream management in agricultural lands will primarily attempt to increase the nutrient removal capacities of these systems and, somewhat less importantly, will try to establish habitat for species characteristically occurring in the summer-dry streams. In general, increase of channel length will be a first management goal. Increase of channel length not only provides additional aquatic habitat, it also increases water and solute residence times in a given stream section. This study suggests that residence times are a key to high nutrient removal rates in temporary streams.

Leaving an area of unused land along the temporary channels will significantly improve their function as nutrient sinks and provide refuge for terrestrial organisms in agricultural landscapes. Smith (1989) found that 67% of the nitrate and 55% of the phosphate were removed from agricultural run-off in a small buffer zone (retired pasture) along a headwater stream. Peterjohn and Correll (1984) consider removal of diffuse-source pollutants in riparian forests to be "of ecological significance to receiving waters."

Once nutrients have reached the channel, both in-stream plants and riparian vegetation can be important routes for solute removal from the water. The most effective way to remove nutrients depends on the degree of exchange between stream run-off and subsurface flow. If these exchange rates are high, terrestrial vegetation will be important and an appropriate canopy providing a dense root system in the soil near and under the stream should be

established. If exchange rates are small, algae should be allowed to grow in the streams without being limited by light availability. Thus, a dense canopy is not desirable. For most practical applications a mixture between areas with and without canopy may be best.

Summer-dry headwaters are not spectacular landmarks like whitewater streams or mountain lakes in the Cascades. But, as this thesis illustrates, the small channels at the temporal edge between aquatic and terrestrial systems provide important functions in healthy landscapes. It is to be hoped, that summer-dry streams will receive the attention they warrant. After completing this thesis, that is the challenge I face: to educate about the importance, value and management of ephemeral and temporary headwaters. This thesis is only a first step. It was worth the time invested only if the results ultimately will be applied toward a better landscape management. After all, to recall Murphy (1990), applicability is the basic characteristic of conservation research.

BIBLIOGRAPHY

- Abell, D. L., 1984: Benthic invertebrates of some California intermittent streams. Pages 46-60 in Jain, S. and P. Moyle (eds.): Vernal pools and intermittent streams Institute of Ecology Publication No. 28, UC Davis.
- Alexander, M., 1977: Introduction to soil microbiology. John Wiley and Sons, New York.
- Anderson, N. H. and J. L. Wold, 1972: Emergence trap collections of Trichoptera from an Oregon Stream. Can. Ent., 104:189-201.
- APHA, 1985: Standard methods for the examination of water and wastewater. 16th edition. American Public Health Association, Port City, Maryland, USA.
- Baldwin, E. M., 1964: Geology of Oregon. Edwards, Ann Arbor.
- Beals, E. W., 1984: Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. Advances in Ecological Research, 14:1-55.
- Begon, M., J. L. Harper and C. R. Townsend, 1986: Ecology. Blackwell Scientific, Sunderland Massachusetts, USA.
- Bencala, K. E., R. E. Rathbun, A. P. Jackman, V. C. Kennedy, G. W. Zellweger and R. J. Avanzino, 1983: Rhodamine WT dye losses in a mountain stream environment. Water Res. Bull., 19:943-950.
- Bergmann, J. G. and J. Sanik, 1957: Determination of trace amount of chlorine in Naphta. Analytical Chem., 29:241-243.
- Beschta, R. L., 1990: Effects of fire on water quantity and quality. Pages 219-231 in Walstad, J. D., S. R. Radosevich and D. V. Sandberg: Natural and prescribed fire in Pacific Northwest forests. Oregon State University Press, Corvallis.
- Bilby, R. E. and G. E. Likens, 1979: Effect of hydrologic fluctuations on the transport of fine particulate organic carbon in a small stream. Limnology and Oceanography, 24: 69-75.

- Bilby, R. E. and G. E. Likens, 1980: Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology*, 61:1107-1113.
- Biondini, M. E., 1985: Secondary successional patterns in a sagebrush (*Artemisia tridentata*) community as they relate to soil disturbance and soil biological activity. *Vegetatio*, 60:25-36.
- Boulton, A. J. and P. J. Suter, 1986: Ecology of Temporary Streams - an Australian Perspective. Pages 313-327 in de Deccker, P. and W. D. Williams (eds.): *Limnology in Australia*. CSIRO/Junk Publishers, Melbourne and The Netherlands.
- Boulton, A. J. and P. S. Lake, 1988: Australian temporary streams - some ecological characteristics. *Verh. Internat. Verein. Limnol.*, 23:1380-1383.
- Braun-Blanquet, J., 1928: *Pflanzensoziologie: Grundzüge der Vegetationskunde*. Springer, Berlin.
- Bray, J. R. and J. T. Curtis, 1957: An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.*, 27:325-349.
- Butcher, M. K., 1979: Drought effects on stream insect populations. MS Thesis, Central Washington University.
- Campbell I. C. and T. J. Doeg, 1989: Impact of timber harvesting and production on streams: a review. *Aust. J. Mar. Freshwater Res.*, 40:519-539.
- Clements, F. E., 1916: *Plant succession: Analysis of the development of vegetation*. Carnegie Institute of Washington Publication, No.242. Washington D.C.
- Clifford, H.F., 1966: The ecology of invertebrates in an intermittent stream. *Indiana Lakes Streams*, 7:57-98.
- Cochran, W. G., 1977: *Sampling Techniques*. J. Wiley & Sons, N.Y.
- Cooper, A. B., 1990: Nitrate depletion in the riparian zone and stream channel of a small headwater catchment. *Hydrobiologia*, 202:13-26.
- Cummins, K. W., 1974: Structure and function of stream ecosystems. *BioScience*, 24:631-641.

- Cushing, C. E., 1988: Allochthonous detritus input to a small, cold desert spring-stream. *Verh. Int. Verein Limnol.*, 23:1107-1113.
- Dance, K. W. and H. B. N. Hynes, 1979: A continuous study of the drift in adjacent intermittent and permanent streams. *Arch. Hydrobiol.*, 87:253-261.
- Delucchi, C. M., 1988: Comparison of community structure among streams with different temporal flow regimes. *Can. J. Zool.*, 66:579-586.
- Delucchi, C. M., 1989: Movement patterns of invertebrates in temporary and permanent streams. *Oecologia*, 78:199-207.
- Delucchi, C. M. and B. L. Peckarsky, 1989: Life history patterns of insects in an intermittent and a permanent stream. *J. N. Am. Benthol. Soc.*, 8:308-321.
- Einfeld, R., 1983: Untersuchungen zur Chemie und tierischen Besiedlung der Mauchach, eines periodisch versickernden Baches der Baar. MS Thesis, Albert-Ludwigs Universität, Freiburg.
- Elwood, J. W., J. D. Newbold, R. V. O'Neill and W. Van Winkle, 1983: Resource spiralling: an operational paradigm for analyzing lotic ecosystems. Pages 3-27 in T. D. Fontaine and S. M. Bartell (eds.): Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan.
- Flecker, A. S., 1984: The effects of predation and detritus on the structure of a stream insect community: a field test. *Oecologia*, 64:300-305.
- Friederichs, K., 1960: Kolloquium über Biozönose-Fragen: Schlußwort. *Z. angew. Ent.*, 47:110-116.
- Gauch, H. G., 1973a: The relationship between sample similarity and ecological distance. *Ecology*, 54:618-622.
- Gauch, H. G., 1973b: A quantitative evaluation of the Bray-Curtis ordination. *Ecology*, 54:829-836.
- Gauch, H. G., 1982: Multivariate analysis in community ecology. Cambridge University Press, Cambridge, UK.
- Gleason, H. A., 1926: The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, 53:7-26.

- Goodman, D., 1975: The theory of diversity-stability relationships. *Quarterly Rev. Biol.*, 50:237-266.
- Grafius, E. and N. H. Anderson, 1979: Population dynamics, bioenergetics and role of Lepidostoma quercina (Trichoptera: Lepidostomatidae) in an Oregon woodland stream. *Ecology*, 60:433-441.
- Graham, A. A., 1990: Siltation of stone-surface periphyton by clay sized particles from low concentration in suspension. *Hydrobiologia*, 199:107-115.
- Gregory, S. V., 1980: Effects of light, nutrients and grazing on periphyton communities in streams. Ph. D. Thesis, Oregon State University, Corvallis.
- Grubb, P. J., 1989: Toward a more exact ecology: a personal view of the issues. Pages 3-29 in Grubb, P. J. and J. B. Whittaker (eds.): Toward a more exact ecology. *Symposia of the British Ecological Society*, 30. Blackwell Scientific Publications, Oxford.
- Hall, J. K. and P. B. Alaback, 1982: Preliminary checklist of the vascular flora of MacDonald and Paul Dunn State Forests. Spec. Publ. 3, Forest Research Lab, OSU.
- Hatch, M. H., 1961: The beetles of the Pacific Northwest. Part III. Pselaphidae and Diversicornia. Univ. Wash. Publ. Biol., 16:i-ix, 1-503; 66 pl.
- Hawkins, C. P. and J. R. Sedell, 1981: Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology*, 62:387-397.
- Hawkins, C. P., M. L. Murphy, N. H. Anderson and M. A. Wilzbach, 1983: Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. *Can. J. Fish. Aquat. Sci.*, 40:1173-1185.
- Hawkins, C. P. and J. K. Furnish, 1987: Are snails important competitors in streams? *Oikos*, 49:209-220.
- Hornberger, G. M., P. F. Germann and K. J. Beven, 1991: Throughflow and solute transport in an isolated sloping soil block in a forest catchment. *J. Hydrology*, 124:81-99.
- Hubbard, C. J., 1991: A plant association classification for McDonald-Dunn Forest. MS Thesis, College of Forestry, Oregon State University, Corvallis.

- Hynes, H. B. N., 1963: The biology of polluted waters. Liverpool University Press, Liverpool.
- Hynes, H. B. N., 1969: The enrichment of streams. Pages 188-196 in Rohlich, G. A. (ed.): Eutrophication: causes, consequences, correctives. National Academy of Sciences, Washington.
- Illies, J. and L. Botosaneanu, 1963: Problèmes et méthodes de la classification et de la zonation écologique des eaux courantes, considérées surtout du point de vue faunistique. Mitt. int. Verein theor. angew. Limnol., 12:1-57.
- Jacobs, T. C. and J. W. Gilliam, 1985: Headwater stream losses of nitrogen from two Coastal Plain watersheds. J. Environ. Qual., 14:467-472.
- Kaushik, N. K. and H. B. N. Hynes, 1971: The fate of the dead leaves that fall into streams. Arch. Hydrobiol., 68:465-515.
- Kerst C. D. and N. H. Anderson, 1974: Emergence patterns of Plecoptera in a stream in Oregon, USA. Freshwat. Biol., 4:205-212.
- Knezevich, C. A., 1975: Soil survey of Benton County area, Oregon. USDA, Soil Conservation Service, Washington D.C.
- Knight, A. W. and A. R. Gaufin, 1967: Stream type selection and association of stoneflies (Plecoptera) in a Colorado River drainage system. J. Kans. Ent. Soc., 40:347-352.
- Kolkwitz, R. and M. Marsson, 1908: Ökologie der pflanzlichen Saprobien. Ber. Dt. Bot. Ges., 261:505-519.
- Kolkwitz, R. and M. Marsson, 1909: Ökologie der tierischen Saprobien. Int. Revue Ges. Hydrobiol., 2:126-152.
- Kraft, G. F., 1963: Seasonal occurrence and distribution of insects in Berry Creek. Ph. D. Thesis, Oregon State University, Corvallis.
- Kühnelt, W., 1960: Kolloquium über Biozönose-Fragen: 1. Diskussionsbeitrag. Z. angew. Ent., 47:91-95.
- Kuhn, T. S., 1962: The Structure of Scientific Revolutions. University of Chicago Press, Chicago.

- Lake, P. S., L. A. Barmuta, A. J. Boulton, I. C. Campbell, and R. M. St. Clair, 1986: Australian streams and Northern Hemisphere stream ecology: comparisons and problems. *Proc. Ecol. Soc. Aust.*, 14:61-82.
- Legier, P. and J. Talin, 1973: Comparaison des ruisseaux permanents et temporaires de la Provence calcaire. *Ann. Limnol.*, 9:273-292.
- Legier, P. and E. Terzian, 1981: Les milieux aquatiques temporaires de Provence: Resistance des invertébrés à l'assèchement des habitats. *Ecol. Mediterr.*, 7:113-129.
- Lehmkuhl, D. M., 1971: Stoneflies (Plecoptera: Nemouridae) from temporary lentic habitats in Oregon. *Am. Midl. Naturalist*, 85:514-515.
- Liss, W. J., L. J. Gut, P. H. Westigard and C. E. Warren, 1986: Perspectives on arthropod community structure, organization, and development in agricultural crops. *Ann. Rev. Entomol.*, 31:455-478.
- Lowe, R. L., S. W. Golladay and J. R. Webster, 1986: Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. *J. N. Am. Benth. Soc.*, 5:221-229.
- Lugthart, G. J. and J. B. Wallace, 1992: Effects of disturbance on benthic functional structure and production in mountain streams. *J. N. Am. Benthol. Soc.*, 11:138-164.
- Mackay, R. J., 1969: Aquatic insect communities of a small stream on Mont St. Hilaire, Quebec. *J. Fish. Res. Bd. Canada*, 26:1157-1183.
- May, G., 1983: Die Besiedlung des Interstitials der Mauchach, eines periodischen Baches im Muschelkalk der Baar. MS Thesis, Albert-Ludwigs Universität, Freiburg.
- McColl, R. H. S., 1974: Self-Purification of small freshwater streams: phosphate, nitrate and ammonia removal. *N. Z. J. Marine and Freshwater Research*, 8:375-388.
- McCune, B., 1990: Multivariate Analysis on the PC-ORD system. Department of General Science, Oregon State University, Corvallis.
- McIntire, C. D. and H. K. Phinney, 1965: Laboratory studies of periphyton production and community metabolism in lotic environments. *Ecol. Monographs*, 35:237-258.

- Merritt, R. W., K. W. Cummins and V. H. Resh, 1984:
Collecting sampling and rearing methods for aquatic
insects. Pages 11-26 in Merritt, R. W. and K. W. Cummins
(eds.): An introduction to the aquatic insects of North
America, second edition. Kendal/Hunt, Dubuque, Iowa.
- Mielke, P. W., K. J. Berry and G. W. Brier, 1981:
Application of Multi-Response Permutation Procedures
for examining seasonal changes in monthly mean sealevel
pressure patterns. Monthly Weather Review, 109:120-126.
- Milner, N. J., J. Sculling, P. A. Crisp and D. T. Crisp,
1981: The effects of discharge on sediment dynamics and
consequent effects on invertebrates and salmonids in
upland rivers. Appl. Ecol., 6:153-20.
- Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott,
J. R. Sedell, C. E. Cushing and R. L. Vannote, 1983:
Interbiome comparison of stream ecosystem dynamics.
Ecol. Monographs, 53:1-25.
- Morrison, B. R. S., 1990: Recolonisation of four small
streams in central Scotland following drought conditions
in 1984. Hydrobiologia, 208:261-267.
- Müller, H., 1990: The role of sediment abrasion in leaf
decomposition processes. MS Thesis, Albert-Ludwigs
Universität, Freiburg.
- Mulholland, P. J., J. D. Newbold, J. W. Elwood and
L. A. Ferren, 1985: Phosphorus spiralling in a woodland
stream: Seasonal variations. Ecology, 66:1012-1023.
- Munn, N. L. and J. L. Meyer, 1988: Rapid flow through the
sediments of a headwater stream in the southern
Appalachians. Freshwater Biology, 20:235-240.
- Murphy, D. D., 1989: Conservation and confusion: wrong
species, wrong scale, wrong conclusions. Conservation
Biology, 3:82-84.
- Murphy, D. D., 1990: Conservation Biology and scientific
method. Conservation Biology, 4:203-204.
- NADP, 1990: Precipitation chemistry in the United States
1989. U.S. Geological Survey, Task group on deposition
monitoring.
- Naiman, J. R. and J. R. Sedell, 1979: Benthic organic matter
as a function of stream order in Oregon. Arch.
Hydrobiol., 87:404-422.

- Newbold, J. D., J. W. Elwood, R. V. O'Neill and A. L. Sheldon, 1983: Phosphorous dynamics in a woodland stream ecosystem: A study of nutrient spiralling. *Ecology*, 64:1249-1265.
- Newbold, J. D., R. V. O'Neill, J. V. Elwood and W. van Winkle, 1982: Nutrient spiralling in streams: implications for nutrient limitation and invertebrate activity. *Am. Naturalist*, 120:628-652.
- Niehaus, T. F., 1976: A field guide to pacific states wild-flowers. Houghton Mifflin, Boston.
- Oberdorfer, E., 1983: Pflanzensoziologische Exkursionsflora. Verlag Eugen Ulmer, Stuttgart.
- Otto, C., 1974: Growth and energetics in larval populations of Potamophylax cingulatus (Steph.) (Trichoptera) in a south Swedish stream. *J. Anim. Ecol.*, 43:339-361.
- Patrick, W. H. and R. Wyatt, 1964: Soil nitrogen loss as a result of alternate submergence and drying. *Soil Sci. Soc. Am. Proc.*, 28:647-653.
- Perkins, P. D., 1976: Psammophilous aquatic beetles in southern California: a study of microhabitat preferences with notes on responses to stream alteration (Coleoptera: Hydraenidae and Hydrophilidae). *Coleopt. Bull.*, 30:309-324.
- Perkins, P. D., 1980: Aquatic beetles of the family Hydraenidae in the western hemisphere: classification, biogeography and inferred phylogeny (Insecta: Coleoptera). *Quaest. Ent.*, 16:3-554.
- Peterjohn, W. T. and D. L. Correll, 1984: Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. *Ecology*, 65:1466-1475.
- Peus, F., 1954: Auflösung der Begriffe "Biotop" und "Biozönose". *Dtsche. Ent. Z. (N. F.)*, 1:273-308.
- Pielou, E. C., 1984: The interpretation of ecological data. J. Wiley & Sons, N.Y., USA.
- Reddy, K. R. and W. H. Patrick, 1975: Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil. *Soil Biol. Biochem.*, 7:87-94.

- Reddy, K. R. and W. F. De Busk, 1985: Nutrient removal potential of selected aquatic macrophytes. *J. Environ. Qual.*, 14:459-462.
- Reid, L. M. and T. Dunne, 1984: Sediment production from forest road surfaces. *Water Resources Research*, 20:1753-1761.
- Reynolds, C. S., M. L. White, R. T. Clarke and A. F. Marker, 1990: Suspension and settlement of particles in flowing water: comparison of the effects of varying water depth and velocity in circulating channels. *Freshwater Biol.*, 24:23-34.
- Richardson, J. L., 1980: The organismic community: Resilience of an embattled ecological concept. *BioScience*, 30:465-471.
- Richardson, J. S., 1992: Coarse particulate detritus dynamics in small, montane streams of southwestern British Columbia. *Can. J. Fish. Aquat. Sci.*, 49:337-346.
- Rivier, B. and J. Sequier, 1985: Physical and biological effects of gravel extraction in river beds. Pages 131-146 in Alabaster, J. S. (ed.): *Habitat modification in Freshwater Fisheries*. Butterworths, London.
- Rohlich, G. A., 1969: Introduction, summary and recommendations. Pages 3-13 in Rohlich, G. A., (ed.): *Eutrophication: causes, consequences, correctives*. National Academy of Sciences, Washington.
- Rothacher, J., 1970: Increase in water yield following clear-cut logging in the Pacific Northwest. *Water Resour. Res.*, 6:653-658.
- Schwoerbel, J., 1987: Einführung in die Limnologie (6. Aufl.). UTB 31, Fischer Verlag, Stuttgart.
- Smith, C. M., 1989: Riparian pasture retirement effects on sediment, phosphorus, and nitrogen in channelised surface run-off from pastures. *New Zealand J. Marine Freshw. Res.*, 23:139-146.
- Smith, E. P., K. W. Pontasch and J. Cairns Jr., 1990: Community similarity and the analysis of multispecies environmental data: a unified statistical approach. *Wat. Res.*, 24:507-514.

- Sorensen, D. L., M. M. McCarthy, E.J. Middlebrooks and D. B. Porcella, 1977: Suspended and dissolved solids effects on freshwater biota: a review. Ecological Research Series, EPA-600/3-77-042.
- Soulé, M. E., 1986: Conservation Biology and the "Real World". Pages 1-12 in M.E. Soulé (ed.): Conservation Biology. Sinauer Publishers, Sunderland.
- Stewart, B. A. and B. R. Davies, 1990: Allochthonous input and retention in a small mountain stream, South Africa. *Hydrobiologia*, 202:135-146.
- Stream Solute Workshop, 1990: Concepts and dynamics for assessing solute dynamics in stream ecosystems. *J. N. Am. Benthol. Soc.*, 9:95-119.
- Swanson, F. J. and R. L. Fredriksen, 1982: Sediment routing and budgets: implications for judging impacts of forestry practices. Pages 129-137 in Swanson, F. J., R. J. Janda, T. Dunne and D. N. Swanston (eds.): Sediment routing and budgets in forest drainage basins. USDA Forest Service, General Technical Report, PNW-141.
- Swanson, F. J., S. V. Gregory, J. R. Sedell, and A. G. Campbell, 1982: Land-Water interactions: the riparian zone. Pages 267-291 in R. L. Edmonds (ed.): Analysis of coniferous forest ecosystems in the Western United States. US/IBP Synthesis Series 14. Hutchinson Ross Publishing Company, Stroudsburg, PA.
- Taylor, J., 1984: Comparative evidence for competition between the salamanders Ambystoma gracile and Taricha granulosa. *Copeia*, 1984:672-683.
- Tew, M. P., 1971: The species composition and adaptations of insects in an intermittent stream in Western Oregon. MS Thesis, Oregon State University, Corvallis.
- Thienemann, A., 1920: Die Grundlagen der Biozönotik und Monard's faunistische Prinzipien. Festschr. f. Zschokke 4. Basel.
- Thienemann, A., 1932: Die Bedeutung des Zeitfaktors für die Besiedlung extremer Lebensstätten. *Jenaische Z. Naturwiss.*, 67:70-79.

- Triska, F. J., V. C. Kennedy and R. J. Avanzino, 1983: Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. Pages 129-159 in T. D. Fontaine and S. M. Bartell (eds.): Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor.
- Triska, F. J., J. H. Duff and R. J. Avanzino, 1990: Influence of exchange flow between the channel and hyporheic zone on nitrate production in a small mountain stream. Can. J. Fish. Aquat. Sci., 47:2099-2111.
- Trotter, E. H., 1990: Spatial and temporal patterns of nitrogen uptake by riparian plants. Bull. N. Am. Benthol. Soc., 7:93.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell and C. E. Cushing, 1980: The River Continuum Concept. Can. J. Fish. Aquat. Sci., 37:370-377.
- Verdonschot, P. F., 1990: Ecological characterization of surface waters in the province of Overijssel (The Netherlands). Research Institute for Nature Management, Province of Overijssel.
- Vincent, W. F. and M. T. Downes, 1980: Variation in nutrient removal from a stream by watercress (Nasturtium officinale R. Br.). Aquatic Botany, 9:221-235.
- Waring, R. H. and J. F. Franklin, 1979: Evergreen coniferous forests of the Pacific Northwest. Science, 204:1380-1385.
- Warren, C. E., J. H. Wales, G. E. Davis and P. Doudoroff, 1964: Trout production in an experimental stream enriched with sucrose. J. Wildlife Management, 28:617-660.
- Washington, H. G., 1984: Diversity, biotic and similarity indices. Water Res., 18:653-694.
- Webster, J. R., 1983: The role of benthic macroinvertebrates in detritus dynamics of streams: a computer simulation. Ecol. Monographs, 53:383-404.
- Webster, J. R., S. W. Golladay, E. F. Benfield, D. J. D'Angelo and G. T. Peters, 1990: Effects of forest disturbance on particulate organic matter budgets of small streams. J. N. Am. Benthol. Soc., 9:120-140.

- Wiederholm, T., 1984: Responses of aquatic insects to environmental pollution. Pages 508-557 in Resh, V. H. and D. M. Rosenberg (eds.): The ecology of aquatic insects. Praeger, New York.
- Wiggins, G. B., Mackay, R. J. and I.M. Smith, 1980: Evolutionary and ecological strategies of animals in annual temporary pools. Arch. Hydrobiol. Suppl., 58:97-206.
- Williams, D. D. and H. B. N. Hynes, 1976: The ecology of temporary streams. I. The fauna of two Canadian streams. Int. Rev. Gesamten Hydrobiol., 61:761-787.
- Williams, D. D. and H. B. N. Hynes, 1977: The ecology of temporary streams. II. General remarks on temporary streams. Int. Rev. Gesamten Hydrobiol., 62:53-61.
- Williams, D. D. and H. B. N. Hynes, 1979: The ecology of temporary streams. III. Temporary stream fishes in southern Ontario, Canada. Int. Revue ges. Hydrobiol., 64: 501-515.
- Williams, D. D., 1987: The Ecology of Temporary Waters. Croom Helm, London & Sydney.
- Williams, W. D., 1985: Biotic adaptations in temporary lentic waters with special reference to those in semiarid regions. Pages 85-110 in Davies, B. R. and R. D. Walmsley (eds.): Perspectives in Southern Hemisphere Limnology. Junk, Dordrecht.
- Wishart, D., 1969: An algorithm for hierarchical classifications. Biometrics, 25:165-170.

A P P E N D I X

Table A.1: Suspended Sediment Concentrations [g/l] in the Water Column ($1.6 \mu\text{m} < \text{Suspended Sediment} < 53 \mu\text{m}$)
 Subscriptes indicate distance [m] of sample site from the culvert.

Site	Date			
	21/01/89	01/02/89	16/02/89	19/02/89
FSC ₂₅	54.4	41.2	215.2	199.1
FSC ₅₀	50.3	39.6	172.6	130.9
FSC ₇₅	36.3	36.5	78.3	48.4
FSC ₁₀₀	39.9	24.1	77.1	27.5
FSL ₀	----	60.7	155.8	237.2
FSL ₂₅	40.0	28.6	145.5	205.3
FSL ₅₀	36.0	22.7	114.2	118.6
FSL ₇₅	31.5	19.9	87.2	87.7
FSL ₁₀₀	32.9	18.9	61.2	62.3

Table A.2: Sediment Retention in Leaf Packs. Sediment [g/pack] trapped in impacted stream sections at different distances [m] from the road crossing.

Site	Distance [m]	Date	
		13/01/89	24/02/89
FSC S1	63	16 746	9 813
FSC S2	78	14 519	8 150
FSC S3	83	17 471	6 305
FSC S4	91	11 147	4 231
FSC S5	100	7 315	3 210
FSC S6	110	7 127	2 411
FSC S7	123	5 415	5 171
FSC S8	126	3 163	2 988
FSC S9	130	8 551	6 022
FSC S10	135	4 185	5 396
FSL S6	11		33 707
FSL S7	36		19 844
FSL S8	44		13 286
FSL S9	54		9 305
FSL S10	62		6 172

Table A.3: List of Taxa and Abbreviations.

Rules for the coding of taxa:

1. Codes are comprised of six letters: the three initial letters of the generic name and the three initial letters of the species name.
2. If a name refers to larval collections only, the capitalized letter "L" replaces the 6th letter of the code.
3. If a taxon cannot be attributed a species name the genus with the extension sp. is given. The letters spe are used instead of the initial three letters of the species name in the code in this case.
4. If a taxon has been determined to the generic level only and no attempt for a species level determination was made, the genus without the spe extension is given. The six initial letters of the generic name are the code.
5. Larvae are listed separately where no association to adults is possible.
6. The character "*" preceeding larval taxa indicates the entity is counted as separate taxon at a study site only if the number of adult taxa in the group is smaller than the number of larval taxa at that site.
7. The total number of taxa collected (all sites including PERM) is given for orders or families. The number of taxa in that group found in temporary streams is given in brackets.

Superscripts:

- 1: early instar larvae present
- 2: found in qualitative samples within the sampling area of a given stream.
- 3: found in qualitative samples outside the sampling area of a given stream
- 4: found only in drift samples

TAXON	ABBREV	FLC	FLR	FSC	FSE	MLR	MSC	Perm
-------	--------	-----	-----	-----	-----	-----	-----	------

Ephemeroptera

Siphonuridae

Ameletus n.sp.	amensp	+	+	+	+	0	0	+
Ameletus sp.	amespe	0	0	0	0	+	0	0

Baetidae

Baetis bicaudatus	baebic	+	+	0	0	0	0	0
Baetis sp.	baespe	+	+	0	0	0	0	+
Centroptilum elsa	cenels	0	0	0	0	+	0	0

Heptageniidae

Cinygma integrum	cinint	+	0	0	0	0	0	+
Cinygmula	cinula	0	0	0	0	0	0	+
Epeorus	epeoru	0	0	0	0	0	0	+
Ironodes	ironod	0	0	0	0	0	0	+

Leptophlebiidae

Paraleptophl. debilis	pardeb	+	+	0	0	0	0	+
P. gregalis	pargre	+	+	+	+	0	0	+
P. temporalis	partem	0	0	0	0	0	0	+

Ephemerellidae

	epheme	0	0	0	0	0	0	+
Total	13(8)	6	5	2	2	2	0	10

Odonata

Cordulegastridae

Cordulegaster dorsalis	cordol	0	+	0	0	0	0	+
------------------------	--------	---	---	---	---	---	---	---

Gomphidae

Octogomphus specularis	octspe	0	0	0	0	0	0	+
Total	2(1)	0	1	0	0	0	0	2

Plecoptera


Pteronarcyidae

Pteronarcella regularis	ptereg	0	0	0	0	0	0	+
-------------------------	--------	---	---	---	---	---	---	---

Peltoperlidae

Yoraperla brevis	yorbre	+	+	0	+	0	0	+
------------------	--------	---	---	---	---	---	---	---



TAXON	ABBREV	FLC	FLR	FSC	FSE	MLR	MSC	PERM
<u>Trichoptera</u>								
								
Philopotamidae								
Dolophilodes sisko	dolsis	+	+	0	+	0	0	0
Wormaldia anilla	worani	+	0	0	0	0	+	+
W. occidea	worocc	+	+	0	+	0	0	0
Polycentropidae								
Polycentropus denningi	polden	0	+	0	0	0	0	0
Hydropsychidae								
Arctopsyche sp.	arcspe	+	0	0	0	0	0	0
Parapsyche elsis	parels	0	0	0	0	0	0	+
Homoplectra sp.	homspe	0	0	0 ³	+	0	0	0
Rhyacophilidae								
Rhyacophila ecosa	rhyeco	+	0	+	0	0	0	+
R. fenderi	rhyfen	+	+	0	0	0	0	+
R. grandis	rhygra	+	+	0	+	0	0	+
R. narvae	rhynar	0	0	0	0	0	0	+
R. norcuta	rhynor	0	0	0	0	+	0	0
R. oreta	rhyore	+	+	0	+	0	0	+
R. (?)viquaea	rhyviq	+	0	0	0	0	0	0
R. willametta	rhywil	0	+	0	0	0	0	0
R. n.sp.	rhynsp	+	+	0	0	0	0	+
Glossosomatidae								
Anagapetus sp.	agapet	0	0	0	0	0	0	+
Brachycentridae								
Micrasema bacro	micbac	0	0	0	0	0	0	+
Lepidostomatidae								
Lepidostoma hoodi	lephoo	0	+	0	0	0	0	+
L. jewetti	lepjew	+	+	+	+	0	0	0
L. roafi	leproa	0	0	0	0	0	0	+
L. unicolor	lepuni	0	0	0	0	0	0	+
L. sp.	lepspe	0	0	0	0	+	0	0
Limnephilidae								
Pseudostenoph. edwardsi	pseedw	+	0	+	0	0	0	0
Clostoea disjuncta	clodis	+	0	+	+	+	0	0
Hesperophylax alaskensis	hesala	0	0	0	0	+	0	0
Limnephilus aretto	limare	0	0	0	0	+	0	0
L. nogus	limnog	0	+	0	0	+	0	+
L. occidentalis	limocc	0	+	0	0	+	0	0
L. sitchensis	limsit	0	+	0	0	+	0	0
L. sp.	limspe	0	0	0	0	0	0	+

TAXON	ABBREV	FLC	FLR	FSC	FSE	MLR	MSC	PERM
Psychoglypha avigo	psyavi	+	+	0	0	0	0	+
Goeracea genota	goegen	0	+	0	0	0	0	0
Calamoceratidae								
Heteroplect. californica	hetcal	0	0	0	0	0	0	+
Total	34(26)	14	15	4	7	8	1	17

Coleoptera

Dytiscidae

Agabinus glabrellus	agagla	0 ⁴	0	0	0	0	0	0
Agabus confertus	agacon	0 ⁴	0	0	0	0	0	0
A. lugens	agalug	+	+	+	0	+	0	0
A. walsinghami	agawal	0	0	0	0	+	0	0
Agabus (larvae)	agabuL	+	0	0	0	+	0	0
Hydroporus planiusculus	hydpla	+	+	+	+	+	+	0
Hydroporus (larva) *	hydpol	+	0	+	+	+	+	+

Hydrophilidae

Anacaena limbata	analim	0	0	0	0	+	+	+
Crenitis dissimilior	credis	0	0	0	0	+	+	0
C. rufiventris	creruf	0	0	0	0	+	0	0
Cymbiodyta imbellis	cymimb	+	+	+	0	+	0	0
C. pacifica	cypac	0	0	0	0	+	0	0
Elophorus	elopho	0	0	0	0	+	+	0
Enochrus carinatus	enocar	+	0	0	0	0	0	0
Hydrobius (larva)	hydroL	+	0	0	0	0	0	+
Laccobius californicus	laccal	0	0	0	0	+	+	0

Hydraenidae

Hydraena vandykei	hydvan	+	+	+	+	+	+	0
Hydraena (larva) *	hydraL	+	+	+	+	+	0	0
Ochthebius discretus	ochdis	0	0	0	0	+	0	0

Psephenidae

Acneus	acneus	+	0	0	0	0	0	+
--------	--------	---	---	---	---	---	---	---

Scirtidae

Elodes	elodes	0	+	0 ³	0	0	0	0
--------	--------	---	---	----------------	---	---	---	---

Elmidae

Heterlimnius koebeli	hetkoe	0	0	0	0	+	0	+
Heterlimnius (larva)	heterL	0	0	0	0	0	0	+
Lara avara	larava	0	0	0	0	+	0	0
Total	17(17)	7	5	4	2	14	6	5

TAXON	ABBREV	FLC	FLR	FSC	FSE	MLR	MSC	PERM
<u>Hymenoptera</u>								
Sulcarius nigricornis	sulnig	+	+	+	0	+	0	0
Total	1(1)	1	1	1	0	1	0	0
 <u>Diptera</u>								
<u>Tipulidae</u>								
Holorusia rubiginosa	holrub	+	+	0	0	0	0	0
Tipula albofasciata	tipalb	0	+	0	+	0	0	0
T. aspersa	tipasp	0	+	+	0	+	0	0
T. continentalis	tipcon	0	+	0	0	0	0	0
T. miseranda	tipmis	0	+	0	0	0	0	+
T. pacifica	tippac	+	0	0	0	0	0	+
T. streptocera	tipstr	0	+	0	+	0	0	0
T. (Lunatipula) sp.	tiplun	0	0	0	0	+	0	0
T. (Pterelachisus) sp.	tippte	0	+	0	0	0	0	0
T. (Sinotipula) sp.	tipsin	+	0	0	0	0	0	0
T. sp.	tipspe	+	0	0	0	0	0	0
T. sp. L1 *	tiponL	0	+	0	0	0	0	0
T. sp. L2 *	tiptwL	+	+	0	0	0	0	0
T. sp. L4 *	tipfoL	0	0	0	0	+	0	0
T. sp. L6 *	tipsiL	0	0	0	0	+	0	0
T. sp. L7 *	tipseL	0	0	0	0	+	0	0
Austrolimnophila badia	ausbad	0	+	0	0	0	0	0
Cheilotrichia sp.	chespe	+	+	+	+	0	0	0
Dactyl. pteropoecilla	dacpte	+	+	+	+	0	0	0
D. pteropoec. (larva)*	dacptL	0	0	0	+	0	0	0
Dicranopt.stenophallus	dicste	0	+	+	0	0	0	0
Dicranota cayuga	diccay	0	+	+	+	+	0	0
D. cazieriana	diccaz	+	+	0	0	0	0	0
D. maculata	dicmac	+	+	+	0	0	0	0
D. megalops	dicmeg	0	0	+	0	0	0	0
D. polymeroides	dicpol	+	+	0	+	0	0	+
D. subapterogyne	dicsub	+	+	0	+	0	0	0
D. nr. vanduzei	dicvan	+	+	0	+	0	+	+
Dicranota (larvae)*	dicraL	+	+	+	+	+	+	+
Erioptera cana	erican	0	+	0	0	0	0	0
E. dulcis	eridul	0	0	+	+	0	0	0
E. n.sp.nr. margarita	erimar	+	+	+	+	0	0	0
E. oregonensis	eriore	0	+	0	0	0	0	0
E. (Psiloconopa) sp.	eripsi	+	+	0	0	0	0	+
E. sp.1	erione	+	+	0	+	0	0	0
E. sp.2	eritwo	+	0	0	0	0	0	0
Erioptera (larvae) *	eriopL	0	0	0	0	+	0	0
Gonomyia gonocephala	gonpol	0	0	0	0	+	0	0
Hexatoma (larvae)	hexato	0	0	0	0	0	0	+

TAXON	ABBREV	FLC	FLR	FSC	FSE	MLR	MSC	PERM
Limnophila nr.aldrichi	limald	0	0	0	+	0	0	+
L. nycteris	limnyc	+	0	+	+	0	0	0
L. occidens	limocc	0	+	+	0	0	0	+
L. oregonensis	limore	0	0	+	0	0	0	0
L. rubra	limrub	0	+	+	+	0	0	0
L. nr. vancouverensis	limvan	0	0	0	0	0	+	0
L. (Prionolabis) n.sp.	limnsp	0	0	+	+	0	0	0
L. sp.	limspe	0	0	0	+	0	0	0
L. sp. L1 *	nopone	+	+	+	+	0	0	0
L. sp. L2 *	noptwo	+	+	+	+	+	0	+
L. sp. L3 *	nopthr	0	+	0	+	0	0	0
L. sp. L4 *	nopfiv	0	0	+	0	0	0	0
Limonia duplicata	limdup	0	+	0	0	0	0	0
L. infuscata	liminf	+	+	0	0	0	0	0
L. libertoides	limlib	0	0	0	0	0	+	0
L. nebeculosa-sciophilalimneb	limneb	+	+	+	+	0	0	+
L. stigmata	limsti	+	+	+	+	+	+	0
L. sp. L1 *	onione	0	0	0	+	+	0	0
L. sp. L2 *	onitwo	0	0	+	+	+	0	0
L. sp. L3 *	onithr	0	+	0	0	0	0	0
Lipsothrix fenderi	lipfen	+	0	0	0	0	0	0
L. nigrilinea	lipnig	0	+	+	+	0	0	+
Molophilus bispinosus	molbis	0	0	0	0	+	0	0
M. sackeniana	molsac	+	+	+	+	0	0	+
M. spiculatus	molspi	+	+	+	+	0	0	+
M. sp.	molspe	0	0	0	+	0	0	0
Ormosia nr.brachyrhabdaormbra	ormbra	+	0	+	0	+	+	0
O. nr. furibunda	ormfur	+	0	0	+	0	0	0
O. fusiformis	ormfus	+	0	0	0	0	0	0
O. manicata	ormman	+	+	+	+	+	0	0
O. sp.	ormspe	0	0	0	0	0	0	+
Ormosia (larva) *	ormosL	0	0	0	0	0	0	+
Paradelphomyia pacificaparpac	parpac	0	+	+	0	0	0	0
Pedicia bicomata	pedbic	+	+	+	+	0	0	+
P. disphana	peddis	+	+	0	0	0	+	+
P. obtusa	pedobt	+	+	0	0	0	0	0
P. septentrionalis	pedsep	+	+	+	+	+	0	0
P. sp. L1 *	pedonL	0	+	0	+	0	+	0
P. sp. L2 *	pedtwL	+	+	+	+	0	0	+
P. sp. L4 *	pedfoL	0	+	0	+	0	0	0
Ulomorpha sierricola	ulosie	+	+	+	+	0	0	+
Total	61(59)	32	39	25	28	14	6	16

TAXON	ABBREV	FLC	FLR	FSC	FSE	MLR	MSC	PERM
Trichoceridae								
Paracladura trichoptera	partri	+	+	+	+	0	0	+
Trichocera colei	tricol	0	+	0	+	+	+	0
T. columbiana	triumb	+	+	0	+	0	+	0
T. hyaloptera	trihya	+	+	0	+	+	+	0
Total	4(4)	3	4	1	4	2	3	1
Chaoboridae								
Eucorethra underwoodi	eucund	+	+	+	0	0	0	0
Total	1(1)	1	1	1	0	0	0	0
Psychodidae								
Pericoma *	perico	+	+	+	0	+	0	+
Pericoma sp.1 (larvae)	peronL	+	+	+	+	0	0	+
Pericoma sp.2 (larvae)	pertwL	+	+	+	+	0	0	0
Pericoma sp.3 (larvae)	perthL	+	0	0	0	0	0	0
Psychoda *	psycho	+	+	+	+	+	+	+
Psychoda sp.1 (larvae)	psyonL	+	+	0	0	0	+	0
Psychoda sp.2 (larvae)	psytwL	0	0	0	0	0	+	0
Total	5(5)	4	3	2	2	2	2	1
Ceratopogonidae								
Dasyhelea sp.1	dasone	+	+	+	+	0	0	+
Dasyhelea sp.2	dastwo	+	+	+	+	0	0	0
Dasyhelea sp.3	dasthr	+	+	0	0	0	0	+
Dasyhelea sp.4	dasfor	0	+	0	0	0	0	0
Dasyhelea (larva) *	dasyhL	0	+	+	+	0	0	0
Atrichopogon	atrich	+	+	+	+	+	0	+
Atrichopogon (larva) *	atricL	0	+	+	0	0	0	0
Forcipomyia sp.A1	forone	+	+	+	+	0	+	+
Forcipomyia sp.A2	fortwo	+	+	+	+	0	0	+
Forcipomyia sp.L1 *	foronL	+	0	0	0	+	0	0
Forcipomyia sp.L2 *	fortwL	0	+	+	+	0	+	0
Ceratoculicoides	cerato	+	+	+	+	+	+	0
Ceratopogon	cerpog	0	0	0	0	+	0	0
Culicoides sp.1	culone	+	+	+	+	+	+	0
Culicoides sp.3	culthr	+	0	+	+	+	0	0
Isohelea	isohel	+	+	0	+	+	0	0
Mallochohelea	malloc	+	+	+	0	0	0	+
Neurohelea	neuhel	+	+	0	+	0	0	0
Palpomyia sp.A1	palone	+	+	+	+	0	0	+
Palpomyia sp.A2	paltwo	0	+	0	0	0	0	0
Palpomyia sp.L1 *	palonL	+	+	+	0	+	0	+
Palpomyia sp.L2 *	paltwL	0	+	+	0	+	0	+
Total	16(16)	13	14	11	11	9	3	8

TAXON	ABBRE	FLC	FLR	FSC	FSE	MLR	MSC	PERM
Simuliidae								
Greniera sp.	grenie	+	+	+	+	+	+	0
Prosimulium dicum	prodic	+	0	0	0	0	0	0
P. esselbaughi	proess	+	+	0	0	0	0	0
P. fulvithorax	proful	+	+	0	0	+	0	0
P. impostor	proimp	+	0	+	0	+	0	0
P. mixtum group	promix	0	0	0	0	0	0	+
Simulium (Eusim.) sp.	simeus	0	0	0	0	0	0	+
S. nebulosum	simneb	0	0	0	0	+	0	0
Stegopterna	stegop	+	+	+	+	+	+	0
Twinnia nova	twinov	+	+	0	0	+	0	0
Simuliidae (larvae) *	simuli	+	+	+	+	+	+	+
Total	10(8)	7	5	3	2	6	2	2
Chironomidae¹								
Boreochlus			+		+			
Brillia								
Bryophaenocladus								
Corynoneura			+		+			
Limnophyes			+		+			
Metriocnemus								
Parakiefferiella								
Parametriocremus			+					
Parochlus kiefferi								
Pseudosmittia								
Tanytarsus								
Ptychopteridae								
Ptychoptera townesi	ptytow	0	0	0	0	0	0	+
Total	1(0)	0	0	0	0	0	0	1
Dixidae								
Dixa hegemonica	dixheg	+	+	+	+	0	0	+
D. lobata	dixlob	+	+	+	+	0	0	+
D. rathyme	dixrat	+	+	0	+	0	0	+
Dixa (larvae) *	dixaL	+	+	+	+	+	+	+
Meringodixa (larvae)	merinL	+	+	0	0	+	0	+
Total	4(4)	4	4	2	3	1	1	4
Pelecorhynchidae								
Glutops (larvae)	glutoL	+	+	0	0	0	0	0
Total	1(1)	1	1	0	0	0	0	0

TAXON	ABBREV	FLC	FLR	FSC	FSE	MLR	MSC	PERM
Dolichopodidae								
Dolichopus sp.1	dolone	+	0	0	0	+	0	0
D. sp.2	doltwo	0	0	0	0	0	0	+
Dolichopus (larvae) *	dolicL	0	0	0	+	+	0	0
Total	2(2)	1	0	0	1	1	0	1
Empididae								
Chelifera	chelif	0	0	0	+	0	0	+
Chelifera (larvae) *	cheliL	+	+	0	+	0	0	+
Clinocera lineata	clilin	+	+	0	+	0	+	0
C. sp.1	clione	+	+	0	0	+	0	0
C. sp.3	clithr	+	+	+	+	+	0	+
C. sp.4	clifor	0	0	0	0	0	+	0
C. sp.5	clifiv	+	+	0	0	+	0	0
C. sp.6	clisix	0	+	0	0	0	0	0
Clinocera (larvae) *	clinoL	+	+	+	+	+	0	0
Dolichocephala	dolich	+	+	+	+	+	+	+
Hemerodromia	hemero	+	+	+	0	0	0	+
Oreogeton	oreoge	0	+	+	0	0	+	+
Oreothelia	oreoth	0	+	0	0	0	0	0
Rhamphomyia sp.1	rhaone	+	+	+	+	+	+	0
R. sp.2	rhatwo	+	0	+	+	0	0	0
R. sp.3	rhathr	+	+	0	+	0	0	0
R. sp.4	rhafor	0	+	0	+	0	0	0
R. sp.5	rhafiv	0	0	0	0	0	+	0
R. sp.6	rhasix	+	0	+	0	0	0	0
R. sp.7	rhasev	0	+	0	0	0	0	0
Rhamphomyia (larvae) *	rhampL	+	+	+	+	0	0	0
Total	18(18)	11	14	7	8	5	6	5
Gastropoda								
Pleuroceridae								
Juga silicula	jugsil	+	0	0	0	0	0	+
Total	1(1)	1	0	0	0	0	0	1

1: Chironomidae were identified by L. Ferrington from a small sample of the total collection. Only a few specimens were returned with site labels. Sites could only be given for these specimen. Information on sites therefore can not be used for the establishment of distributional patterns between streams.

Table A.4: Habitat Association Scores (HAS) and Microhabitat Association Indices (MAI) of Species Inhabiting Summer-Dry Streams in Western Oregon.

Description of the Codes

1. Habitat Association Scores (HAS)

- 0 = insufficient information for score.
- 1 = obligate permanent stream.
- 2 = facultative permanent stream
- 3 = permanent and temporary stream
- 4 = facultative temporary stream
- 5 = obligate temporary stream
- 6 = obligate ephemeral stream

2. Microhabitat Association Indices

Winter habitat: b = benthic
 l = littoral
 h = hyporheic

Summer habitat: s = seep
 p = pool
 d = dry channel (pupa)

Listing of a species in several microhabitats is possible. Scores in brackets indicate that species were occasionally collected in that microhabitat, but were more commonly encountered in a different microhabitat.

	HAS	MAI
<u>Ephemeroptera</u>		
Siphonuridae		
Ameletus n.sp.	5	b, (p)
Baetidae		
Baetis bicaudatus	4	b
Baetis sp.	3	b
Centroptilum elsa	5	b
Heptageniidae		
Cinygma integrum	2-3	b
Cinygmula	1	b
Epeorus	1	b
Ironodes	1	b
Leptophlebiidae		
Paraleptophlebia debilis	3	p, (b)
P. gregalis	4	b
P. temporalis	1	b
 <u>Odonata</u>		
Cordulegastridae		
Cordulegaster dorsalis	2-3	b
Gomphidae		
Octogomphus specularis	1	b
 <u>Plecoptera</u>		
Pteronarcyidae		
Pteronarcella regularis	1	b
Peltoperlidae		
Yoraperla brevis	3	b, s

	HAS	MAI
Nemouridae		
Malenka bifurcata	4	b, s
M. cornuta	2	b, (s)
Ostrocercia dimicki	3	b
O. foersteri	4	b
Podmosta obscura	3	b
Soyedina interrupta	4	b, s
S. producta	4	b, s
Zapada cinctipes	2	b, (s, p)
Leuctridae		
Megaleuctra sp.	4-5	b, s, p
Despaxia augusta	3	b, p, (s)
Moselia infuscata	1	b
Paraleuctra occidentalis	2	b
P. sara	2	b
Capniidae		
Capnia umpqua	3	
Mesocapnia projecta	2	b
Perlidae		
Calineuria californica	1	b
Perlodidae		
Chernokrillus misnomus	4	
Calliperla luctuosa	4	b, p, (s)
Isoperla marmorata	1	b
Chloroperlidae		
Sweltsa borealis	1	h
S. fidelis	4-5	b, s, (p)
S. fraterna	3	h
<u>Heteroptera</u>		
Gerris remigis	3	p
<u>Megaloptera</u>		
Protochauloides spenceri	5-6	b

	HAS	MAI
<u>Trichoptera</u>		
Philopotamidae		
Dolophilodes sisko	5	b, d
Wormaldia anilla	1	b
W. occidea	4-5	b, s, (h?)
Polycentropidae		
Polycentropus denningi	5	s, (p)
Hydropsychidae		
Arctopsyche sp.	1	b
Parapsyche elsis	1	b
Homoplectra sp.	5	b
Rhyacophilidae		
Rhyacophila ecosa	4-5	b, p, s
R. fenderi	4-5	b, s, (p)
R. grandis	2	b
R. narvae	1	b
R. norcuta	3	b
R. oreta	3	b, s
R. willametta	2	b
R. n.sp.	4-5	b, s
Glossosomatidae		
Anagapetus sp.	1	b
Brachycentridae		
Micrasema bacro	1	b
Lepidostomatidae		
Lepidostoma hoodi	2	b
L. jewetti	5	b, p, s
L. roafi	1	b
L. unicolor	1	b
Limnephilidae		
Pseudostenophylax edwardsi	4	b
Clostoea disjuncta	5	b
Hesperophylax alaskensis	5	b
Limnephilus aretto	0	b
L. nogus	3	b
L. occidentalis	4	b, s
L. sitchensis	4	b
Psychoglypha avigo	3	b, p
Goeracea genota	5	b, s
Calamoceratidae		
Heteroplectron californica	1	b

	HAS	MAI
<u>Coleoptera</u>		
Dytiscidae		
A. lugens	3	b
A. walsinghami	4-5	b
Agabus (larvae)	3	b
Hydroporus planiusculus	4-5	b,p
Hydroporus (larva) *	4-5	b,(s,p)
Hydrophilidae		
Anacaena limbata	3	b,l
Crenitis dissimilor	4-5	b,l
C. rufiventris	0	b,l
Cymbiodyta imbellis	5	b,l,s,p
C. pacifica	3	b
Elophorus	4	b
Hydrobius (larva)	2	b
Laccobius californicus	5	b,l
Hydraenidae		
Hydraena vandykei	4	l
Hydraena (larva) *	4	l
Ochthebius discretus	3	l
Psephenidae		
Acneus	2	b
Scirtidae		
Elodes	4	s,(b)
Elmidae		
Heterlimnius koebeli	1-2	b
Heterlimnius (larva)	1	b
Lara avara	1	b
<u>Hymenoptera</u>		
Sulcarius nigricornis	5	s

	HAS	MAI
<u>Diptera</u>		
Tipulidae		
Holorusia rubiginosa	3	b,s
Tipula albofasciata	4-5	s,(b)
T. aspersa	4	s
T. continentalis	0	s,(b)
T. miseranda	3	b
T. pacifica	3	b
T. (Lunatipula) sp.	0	b
T. (Pterelachisus) sp.	0	b,s
Austrolimnophila badia	3	b
Cheilotrichia sp.	4-5	
Dactylolabis pteropoecilla	4-5	b
Dicranopt.stenophallus	3-4	s
Dicranota cayuga	3-4	0
D. cazieriana	4-5	b,s
D. maculata	4-5	b
D. megalops	5	b,s
D. polymeroides	3	b,s
D. subapterogyne	4-5	b
D. nr. vanduzei	3	b
Erioptera cana	3	b,s
E. dulcis	4-5	s
E. n.sp.nr. margarita	5	s,(p)
E. oregonensis	3	b
E. (Psiloconopa) sp.	3	
E. sp.1	4-5	
Gonomyia gonocephala	0	b
Limnophila nr.aldrichi	2	b
L. nycteris	4-5	b
L. occidens	3-4	b,s
L. rubra	4-5	b,(s,p)
L. nr. vancouverensis	0	b,s
L. infuscata	0	b
L. libertoides	0	b,s
L. nebeculosa-sciophila	3	b
L. stigmata	5	b
Lipsothrix fenderi	3	s,(p)
L. nigrilinea	3	p,(s)
Molophilus bispinosus	0	b
M. sackeniana	3-4	s,(b,p)
M. spiculatus	5	b,s
Ormosia nr.brachyrhabda	4-5	b,(s)
O. fusiformis	0	b,(s)
O. manicata	4-5	b
Paradelphomyia pacifica	4-5	s,p
Pedicia bicomata	3-4	b,s,(p)
P. disphana	4	s,(b)
P. obtusa	4-5	p,s
P. septentrionalis	5	p,s,(b)

	HAS	MAI
Ulomorpha sierricola	3	s, h, (b)
Trichoceridae		
Paracladura trichoptera	4	1
Trichocera colei	5	1
T. columbiana	4	1
T. hyaloptera	5	1
Chaoboridae		
Eucorethra underwoodi	3	p
Psychodidae		
Pericoma sp.1 (larvae)	3	b, s
Pericoma sp.2 (larvae)	4-5	s
Psychoda sp.1 (larvae)	3	s, (b)
Ceratopogonidae		
Dasyhelea sp.1	4	b, (s)
Dasyhelea sp.2	4-5	b, s
Dasyhelea sp.3	2	b
Atrichopogon	4-5	0
Atrichopogon (larva) *	0	b, s
Forcipomyia sp.A1	4	s, (b)
Forcipomyia sp.A2	3	
Forcipomyia sp.L1	0	b
Forcipomyia sp.L2	0	s
Ceratoculicoides	4-5	
Culicoides sp.1	5	b
Culicoides sp.3	4-5	
Isohelea	5	b
Mallochohelea	2	b, p, s
Neurohelea	4-5	
Palpomyia sp.A1	4-5	
Palpomyia sp.L1	0	s
Palpomyia sp.L2	0	b, s

	HAS	MAI
Simuliidae		
Greniera sp.	6	b
Prosimulium dicum	3	b
P. esselbaughi	4	b
P. fulvithorax	4	b
P. impostor	5	b
P. mixtum group	1	b
Simulium (Eusim.) sp.	1	b
S. nebulosum	0	b
Stegopterna	5	b
Twinnia nova	3	b
Ptychopteridae		
Ptychoptera townesi	1	b
Dixidae		
Dixa hegemonica	3	b, (s,p)
D. lobata	2-3	b, (p)
D. rathyme	2-3	b, (p)
Meringodixa (larvae)	2-3	b
Pelecorhynchidae		
Glutops (larvae)	3	s,h
Dolichopodidae		
Dolichopus sp.1	0	b
D. sp.2	1	b
Empididae		
Chelifera	3	b, (s)
Clinocera lineata	4-5	
C. sp.1	4-5	b
C. sp.3	4	b
C. sp.4	0	b,s,p
C. sp.5	4-5	b
Dolichocephala	4	
Hemerodromia	3	b
Oreogeton	3	b
Oreothelia	0	b
Rhamphomyia sp.1	4-5	b
R. sp.2	4-5	b
R. sp.3	4-5	b
R. sp.4	4-5	b
R. sp.6	4-5	0

Table A.5: List of Acronyms and Thesis Specific Terms.

TERM	EXPLANATION	PAGE
a.) Study Sites (Streams)		
FLC	<u>F</u> orest <u>L</u> ong-flow <u>C</u> lay: Forest stream with continuous flow over 5 months and clay as the main component of the channel bed substrate.	16
FLR	<u>F</u> orest <u>L</u> ong-flow <u>R</u> ock: Forest stream with continuous flow over 5 months and channel bed substrate mainly composed of rocks.	16
FSC	<u>F</u> orest <u>S</u> hort-flow <u>C</u> lay: Forest stream with continuous flow for less than 3 months and clay as the main component of the channel bed substrate.	16
FSE	<u>F</u> orest <u>S</u> hort-flow <u>E</u> xperimental: Forest stream with continuous flow for less than 3 months and clay as the main component of the channel bed substrate. Experimental flow extension was conducted here.	16
FSL	<u>F</u> orest <u>S</u> hort-flow <u>L</u> ower: Forest stream with continuous flow for less than 3 months and clay as the main component of the channel bed substrat. Adjacent to FSC. Used to study sediment retention in ephemeral streams, no faunal sampling	48
SEEP	Combination of 4 <u>seep</u> sites treated as separate entity in the community analysis. FSC and FSE each contributed two sites to this entity.	96
MLR	<u>M</u> eadow <u>L</u> ong-flow <u>R</u> ock: Meadow stream with continuous flow over 5 months and channel bed substrate mainly composed of rocks.	16
MSC	<u>M</u> eadow <u>S</u> hort-flow <u>C</u> lay: Meadow stream with continuous flow for less than 3 months and channel bed substrate mainly composed of clay.	16
PERM	<u>P</u> ermanent first-order headwater stream in the Oak Creek watershed.	16

b.) Specific Terms

Ephemeral (= short-flow) stream	Stream with discontinuous (sporadic) flow after rain. Flow for less than 3 months each season.	5
Temporary (= long-flow) stream	Stream with continuous flow for more than 5 months each season.	5
Study site	Stream	14
Sample site	2 m of stream channel where samples were collected	16
Non-suspended Sediment	Sediment of size class 53 μm and larger.	48
Suspended sediment	Sediment of size class 53 μm > suspended sediment > 1.6 μm .	48
Ultra-fine sediment (= Ultra-fine solids)	Sediment of size class < 1.6 μm .	48

c.) Acronyms used in chapter 3

k_c	Uptake rate = nutrient turnover time [1/sec]. Particles being taken up per unit time.	46
MRT	Median Residence Time [sec/m]. Time a particle remains in a channel section.	47
S_w	Uptake length [m]. Average distance a particle or solute travels in the water column.	46
$S_{(I)}$	Sample site just below the location for solute injection (solute injection experiment).	44
$S_{(D)}$	Downstream sample site: 25 m from the solute injection site in FLC, 40 m from the solute injection site in MLR (solute injection experiment).	44

d.) Acronyms used in chapter 4

DCA	Detrended correspondence analysis. Ordination technique which maximizes the correspondence between sample site and species scores through continuous iterations.	107
PO	Polar ordination. Ordination technique which places the ordination axis through two sample sites. Selection of sites can be objective (different methods) or subjective.	107
MRPP	Multi response permutation procedure. Used to test the correspondence between the classification based on faunistic collections and the classification based on environmental parameters.	104