ON THE SUMMER REGULATION OF NITROGEN AND
PHOSPHORUS TRANSPORT IN A SMALL STREAM
OF SOUTHWESTERN BRITISH COLUMBIA

by

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ABSTRACT

Patterns of in-stream summer transport of total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) in a high gradient second order stream in southwestern British Columbia were described. Some biological, physical, and chemical processes were also identified and evaluated with respect to their role in regulating in-stream transport of TDN and TDP.

Fifteen water sampling stations were established along an alternating series of open clearcut and densely forest covered drainage areas, each several hundred metres in length. These drainage sections represented young and midsuccesional ecosystems. The furthest upstream section (which was forest covered) and an adjacent downstream open clearcut section each had weirs which were used for comparisons of TDN and TDP export between the successionaly different systems.

Export of TDN was consistently lower from the clearcut section than from the upstream forested section. This indicated that there was consistent in-stream absorption of TDN within the clearcut section. Nitrate flux dominated the absorption of TDN. A pairing analysis of precutting nitrate export data from 1972 with post-treatment export data from 1979 indicated that the absorption of nitrate was due to increased solar radiation reaching the stream channel. It was proposed that the increased light inputs which provided an additional energy input to the stream ecosystem, increased nitrate spiralling rates. Without disruptive stormflow events the net effect was a retention of nitrate within the stream.
Concentrations of TDP were often less than detectable limits so comparisons of P export could not be made.

The TDN data suggested that if nutrient absorption in small watershed streams is widespread, nutrient retention on land may have been overestimated in past small watershed nutrient budget studies.

A further analysis of downstream flux in element concentrations was conducted for all forms of TDN and TDP using three-dimensional images (distance downstream x time x element concentration) from data collected in summer 1979. Nitrate concentrations consistently declined in open sections but increased in densely forest covered sections. Trends in ammonium concentrations were difficult to detect. Orthophosphate levels were rarely greater than the detectable limit of 3 ug/l in all sections. Dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) flux was highly variable with no apparent trend. Nutrient spiralling processes were proposed to explain the flux of each of these forms of TDN and TDP.

An enrichment experiment conducted in a clearcut section of the study stream in mid-summer indicated that rates of disappearance of NO$_3^-$-N, NH$_4^+$-N, and HPO$_4^{2-}$-P from solution were directly related to element concentrations in solution and that relationship could be expressed as fourth, first, and third degree polynomials respectively. Disappearance rates of the three ions were in the order NH$_4^+$-N>HPO$_4^{2-}$-P>NO$_3^-$-N. Reasons for the differences in disappearance rates between elements and element forms were proposed.
The first end-of-summer storm event produced a 20-fold increase in stream discharge at peak flow over summer base flow. This resulted in a 10-fold increase in NO$_3^-$-N concentrations in all stream sections. The increased loading was attributed to flushing of NO$_3^-$-N from land. Stream power was not destructive, however, and NO$_3^-$-N removed from solution increased over that during summer base flow. The increased uptake rates were attributed to an increase in active nutrient processing areas of the stream substrate. DON and DOP concentrations and export increased during the storm but NH$_4^+$-N and HPO$_4^{2-}$-P concentrations did not change. Again, detailed explanations for this element behaviour were proposed.

Results of an enrichment experiment designed to evaluate the role of periphyton in regulation of nutrient transport were insufficient to fully assess the quantitative role of periphyton. Hypotheses were proposed, however, to further evaluate the role of periphyton using alternative methods.

Concluding hypotheses were presented to aid in the development of future research plans.
TABLE OF CONTENTS

ABSTRACT .......................................................... ii
TABLE OF CONTENTS ............................................... v
LIST OF TABLES .................................................... vii
LIST OF FIGURES ................................................... viii
LIST OF APPENDICES ............................................... x
ACKNOWLEDGEMENTS ................................................. xi

CHAPTER 1 INTRODUCTION AND OBJECTIVES ............... 1

CHAPTER 2 REVIEW: Evidence for Nitrogen and Phosphorus Processing in Streams .................. 8
   A. The Concept of Nutrient Processing ................. 9
   B. Uptake and Cycling Routes in the Transport Cycle ................................................. 12
      1. Uptake and cycling by riparian vegetation ...... 15
      2. Uptake and cycling by in-stream autotrophs. 16
      3. Uptake and cycling by immobilization processes .............................................. 21
      4. Sorption to sediments ............................... 23
   C. Element Removal Routes via Redox in the Transport Cycle .................................... 24
   D. Control of Spiralling Rates in the Transport Cycle ............................................. 25

CHAPTER 3 STUDY SITE DESCRIPTION .................. 29
   A. Location ...................................................... 29
   B. Climate ....................................................... 32
   C. Vegetation ................................................... 32
   D. Geology and Soils .......................................... 34
   E. Physical Characteristics of East Creek .......... 35
   F. Stream Hydrology ............................................ 38

CHAPTER 4 SPATIAL AND TEMPORAL VARIATIONS IN NITROGEN AND PHOSPHORUS TRANSPORT .... 41
   A. Introduction ................................................ 41
   B. Materials and Methods .................................. 44
      1. Stream sampling stations ............................ 44
      2. Collection and preservation of water samples ................................................. 45
      3. Laboratory methods ..................................... 47
      4. Rates of nutrient removal from solution ...... 48
      5. Presentation of element concentration data. 53
      6. Solar radiation .......................................... 57
      7. Nitrogen and phosphorus export comparisons. 58
   C. Results and Discussion ................................ 60
      1. Comparison of exports of TDN and TDP between young and mid-successional drainage areas. 60
      2. Consideration of environmental factors regulating export .............................. 65
      3. Variation in transport of all N and P species between all stream sections .......... 70
         a. Consistency of variation directly
<table>
<thead>
<tr>
<th>TABLE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>3-1 Physical characteristics of East Creek in summer 1979.</td>
<td>37</td>
</tr>
<tr>
<td>4-1 Monthly export and differences in export of DON, NO$_3^-$-N and NH$_4^+$-N from East Creek water sampling stations W-1 and W-10 in summer 1979.</td>
<td>61</td>
</tr>
<tr>
<td>4-2 Monthly export and differences in export of DOP and HPO$_4^{2-}$ from East Creek water sampling stations W-1 and W-10 in summer 1979.</td>
<td>62</td>
</tr>
<tr>
<td>4-3 Analysis of differences in export of NO$_3^-$-N from East Creek Sections A and B during summer months of 1972 and 1979.</td>
<td>66</td>
</tr>
<tr>
<td>4-4 Analysis of differences in East Creek stream temperature between Sections A and B before (1972) and after (1979) clearcutting and slashburning.</td>
<td>67</td>
</tr>
<tr>
<td>4-5 Means and standard errors of DON and NO$_3^-$-N concentrations before, during and after enrichment at East Creek sampling stations bordering each of the four different stream sections.</td>
<td>79</td>
</tr>
<tr>
<td>4-6 Mean disappearance rates of inorganic N and P as measured at water sampling stations downstream of the enrichment source during July and August 1979.</td>
<td>86</td>
</tr>
<tr>
<td>4-7 Disappearance rates (mg. N or P/m$^2$/hr$^1$) of ammonium, nitrate and orthophosphate in East Creek section B at selected element concentrations as determined from regression analyses.</td>
<td>93</td>
</tr>
<tr>
<td>4-8 Percent composition of substrate types between water sampling stations in East Creek.</td>
<td>95</td>
</tr>
</tbody>
</table>
### LIST OF FIGURES

<table>
<thead>
<tr>
<th>FIGURE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1 Phosphorus processing in an hypothetical mountain stream.</td>
<td>13</td>
</tr>
<tr>
<td>2-2 Nitrogen processing in an hypothetical mountain stream.</td>
<td>14</td>
</tr>
<tr>
<td>3-1 Study area showing geographic location and location of East Creek in the U.B.C. Research Forest.</td>
<td>30</td>
</tr>
<tr>
<td>3-2 Detailed map of East Creek showing the four sections of different vegetation cover, weir locations and water sampling sites.</td>
<td>31</td>
</tr>
<tr>
<td>3-3 Stream discharge at weir B during summer 1979.</td>
<td>40</td>
</tr>
<tr>
<td>4-1 Schematic diagram of the nutrient solution input apparatus for East Creek.</td>
<td>49</td>
</tr>
<tr>
<td>4-2 Sodium concentrations at each sampling site as determined from 10 sampling occurrences prior to mid-summer enrichment in East Creek, 1979.</td>
<td>51</td>
</tr>
<tr>
<td>4-3 Spatial and temporal trends of NO$_3$-N concentrations (mg/l) in East Creek during summer 1979.</td>
<td>71</td>
</tr>
<tr>
<td>4-4 Spatial and temporal trends of NH$_4$-N concentrations (mg/l) in East Creek during summer 1979.</td>
<td>72</td>
</tr>
<tr>
<td>4-5 Spatial and temporal trends of HPO$_4^{2-}$-P concentrations (mg/l) in East Creek during summer 1979.</td>
<td>73</td>
</tr>
<tr>
<td>4-6 Spatial and temporal trends of DON concentrations (mg/l) in East Creek during summer 1979.</td>
<td>74</td>
</tr>
<tr>
<td>4-7 Spatial and temporal trends of DOP concentrations (mg/l) in East Creek during summer 1979.</td>
<td>75</td>
</tr>
<tr>
<td>4-8 Differences in percent between observed (dilution plus in-stream removal) and expected (dilution only) NO$_3$-N concentrations downstream of enrichment (Site W-3) in East Creek during summer 1979.</td>
<td>82</td>
</tr>
<tr>
<td>4-9 Differences in percent between observed</td>
<td></td>
</tr>
</tbody>
</table>
(dilution plus in-stream removal) and expected (dilution only) NH$_4^+$-N concentrations downstream of enrichment (Site W-3) in East Creek during summer 1979. 83

4-10 Differences in percent between observed (dilution plus in-stream removal) and expected (dilution only) HPO$_4^{2-}$ concentrations downstream of enrichment (Site W-3) in East Creek during summer 1979. 84

4-11 Relationship between concentrations and disappearance rates of NO$_3^-$-N downstream of enrichment in East Creek during summer 1979. 88

4-12 Relationship between concentrations and disappearance rates of NH$_4^+$-N downstream of enrichment in East Creek during summer 1979. 89

4-13 Relationship between concentrations and disappearance rates of HPO$_4^{2-}$-P downstream of enrichment in East Creek during summer 1979. 90

5-1 Periphyton sampling locations in Section B of East Creek.

5-2 Data showing the efficiency of the brushing technique used for removing periphyton from natural rocks. 110

5-3 Significance of differences between means of location and time combinations for standing stock (chlorophyll- a ) of periphyton in the enrichment experiment conducted during summer 1979. 111

5-4 Significance of differences between means of location and time combinations for biomass nitrogen in periphyton in the enrichment experiment conducted during summer 1979. 112

5-5 Significance of differences between means of location and time combinations for biomass phosphorus in periphyton in the enrichment experiment conducted during summer 1979. 113

5-6 Spatial and temporal trends of chlorophyll-a concentrations in Section B of East Creek during summer 1979. 116
LIST OF APPENDICES

A. Source program for three dimensional plotting. 140
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CHAPTER 1

INTRODUCTION AND OBJECTIVES

Small watersheds have often been studied with the aim of assessing flux rates and mechanisms for control of nutrient loss from terrestrial ecosystems. Ecosystem boundaries, based mainly on geomorphological characteristics of a watershed, are easily defined and, therefore, methods which involve quantitative measurements of nutrient transport at ecosystem boundaries or nutrient flux across boundaries are commonly employed.

The budgetary approach, for example, has been widely used. Quantitative differences between inputs from meteorologic, geologic and biologic sources have been compared with exports (mostly in streamwater) leaving the watershed. Such studies have been conducted at various stages in successional development and/or after a specific management action. Work by Likens et al. (1967, 1970) and Bormann et al. (1974) has involved the nutrient budget approach at the Hubbard Brook experimental forest and has contributed to the current understanding of forest biogeochemistry in New England (Bormann et al. 1977, Likens et al. 1977, Whittaker et al. 1979, Bormann and Likens 1979). Similar intensive studies were also carried out in North Carolina (Johnson and Swank 1973), Walker Branch Tennessee (Elwood and Henderson 1975, Henderson and Harris 1975) and at the H.J. Andrews Experimental Forest in Oregon (Fredrikson 1972). Also, in west coast Douglas-fir forests, Brown et al. (1973) and Fredriksen et al. (1975) have evaluated the effects of forest cutting and slashburning...
Another approach utilized to assess element behaviour has been to describe solution chemistry in terms of element concentrations through the hydrologic strata of a small watershed. The various strata may be considered as throughfall, precipitation, surface runoff, forest floor water, mineral soil water, groundwater, and streams. The pattern of nutrient concentrations measured at each level has been termed a water chemistry profile. Although the method cannot be used to quantify nutrient loss, it is considered useful for assessing element behaviour in undisturbed stands (Feller 1974, 1977, Sollins et al. 1980) and changes in element transport as a result of clearcutting and slashburning (Kimmins and Feller 1976).

All the above studies, which have used either the budgetary or the water chemistry profile approach, have provided insight into the control of nutrient export from watersheds. However, only two studies, one by Vitousek and Reiners (1975) and the other by Vitousek (1977) have attempted to provide a widely applicable hypothesis concerning the control of nutrient loss from terrestrial ecosystems. Based on an examination of 47 watersheds, nutrient loss patterns (as measured in streams) were explained as resulting from interactions among four processes: input in precipitation, accumulation in organic matter, input from weathering and concentration of dissolved forms due to transpiration. These authors suggested that:

1. Losses of limiting nutrients are high during and immediately after a disturbance such as clearcutting (when
inputs exceed uptake rates and stream nutrient concentrations are relatively high).

2. That losses diminish to very low levels when terrestrial biomass accumulates and rates of nutrient storage in biomass increases. Stream nutrient levels are low.

3. Losses increase as the system approaches steady state and terrestrial accumulation ceases.

This hypothesis (termed the Vitousek hypothesis) suggests that control of dissolved nutrient concentrations in watershed streams can be explained by changes in element storage in terrestrial biomass during succession. Nutrient losses from mature ecosystems would, therefore, be greater than nutrient losses from early seral ecosystems. In addition, the hypothesis suggests that concentrations of limiting essential nutrients present in streams vary most with terrestrial ecosystem development while concentrations of elements not accumulated in organic matter or those supplied in excess of plant needs vary little with ecosystem development.

There is some evidence other than that contained in the Vitousek studies which is supportive of the Vitousek hypothesis. In western North America for example, litter and mineral soil horizons are highly efficient in retaining nutrients in seral forests (Sollins et al. 1980, Binkley 1980), early seral forests retain nutrients more efficiently than mature forests (Binkley 1980) and the removal of vegetation causes increased nutrient loss rates from soils (Kimmins and Feller 1976, Feller and Kimmins 1981) in the water chemistry profile.

Regardless of these works, however, Bormann and Likens
(1979) have firmly stated that the Vitousek hypothesis is too simplistic and suggest that in the case of nitrogen and cation transport, losses also appear to be controlled by nitrification. For example, Likens et al. (1978) found that plant uptake was insufficient to account for all observed decreases in streamwater NO$_3^-$ concentrations during recovery at Hubbard Brook, implying that other mechanisms were also operating. Also, Johnson and Edwards (1979) found that rates of nitrification (which proceed as a function of the availability of NH$_4^+$) were strongly regulated by the heterotrophic demand for N. Thus, increased activity of heterotrophic soil organisms in the recovery phase of forest growth could account for decreased rates of NO$_3^-$ leaching. In this respect, differences in loss of NO$_3^-$ from different study watersheds have been linked to variation in C/N ratios in both the mineral soil and forest floor (Sollins et al. 1980, Feller and Kimmins 1981).

The above discussion outlines the only two hypotheses proposed by various workers to explain regulation of nutrient loss from terrestrial ecosystems: 1) changes in plant uptake through successional development and, 2) changes in heterotrophic demand for the limiting nutrients. It is important to note that these hypotheses are based on nutrient loss measurements from concentrations in streamwater which is leaving the watershed. The hypotheses imply that terrestrial processes overwhelmingly control nutrient concentrations in streamwater. They do not consider in-stream biological, chemical and physical processes which may also be active in regulating nutrient concentrations in streamwater leaving the
Only recently have in-stream transport and transformations of N and P been assessed in the Hubbard Brook Experimental Forest (Sloane 1979, Meyer and Likens 1979). These studies were based mostly on budgetary measurements to determine net retention patterns of each element over several years. Detailed experiments within these studies to assess the translocation of introduced nutrient forms were only conducted on one to two metres of selected homogeneous substrate types. For example, nutrient solutions were introduced to moss or debris dam substrates and any nutrient uptake occurring over these specific substrates was noted. These data have not been sufficient to evaluate the fate of introduced element species over entire stream reaches and, therefore, cannot be used to assess the seasonal control of element transport in streams as an added mechanism in the control of element export from small watersheds.

The present study provides a quantitative approach to evaluate seasonal in-stream control of element transport by comparing both nutrient concentrations and nutrient export between reaches of a single stream. A method of intensive water sampling along the stream gradient was used throughout the study and became particularly useful for examining the fate of introduced element species over an entire stream reach. Such an approach provided a means of evaluating whether element concentrations in a stream may be controlled by in-stream processes without appeal to control by terrestrial processes.
Two elements were considered for study; N and P. They were chosen primarily because they are considered limiting in terrestrial (nitrogen primarily: Atkinson and Morison 1975) and aquatic (phosphorus primarily: Stockner and Shortreed 1978) ecosystems in southwestern British Columbia. It is most important to understand processes which regulate the ability of a watershed to retain these elements.

The main objective of the study was to determine whether any spatial variations in N and P concentrations along a stream which passed through successively different sections of a watershed could be explained by in-stream control processes in summer. One in-stream component, periphyton, was assessed with respect to its role in the removal of inorganic N and P from solution and thereby its role as a functional in-stream component for control of N and P concentrations.

Specific questions to be asked were:

1. Is there variation in concentrations and transport of dissolved nitrogen and dissolved phosphorus in different sections of a small stream draining successively different drainage areas?
2. If N and P transport does change between successively different drainage areas, what environmental parameter(s) appear to regulate change in N and P species transport?
3. Can one in-stream component, periphyton, be effective in regulating N and P transport?
4. Can in-stream processing of dissolved nitrogen and dissolved phosphorus significantly affect estimates of N and P loss from terrestrial ecosystems which are based on measurements of stream N and P concentrations?
CHAPTER 2

REVIEW: Evidence for Nitrogen and Phosphorus Processing in Streams.

Evidence for element uptake and transformations in a stream ecosystem is by no means contemporary. Neel (1951) reported that both nitrate and phosphate concentrations decreased in streamwater passing over riffles. Madler (1961) made extensive studies of phosphorus in streams and attributed its disappearance over a reach to plant uptake. By applying radiotracer techniques, orthophosphate has been shown to be assimilated and cycled through the food web in streams (Davis and Foster 1958, Foster 1959, Ball and Hooper 1961, Ball et al. 1963, Garder and Skulberg 1966, Nelson et al. 1969, Elwood and Nelson 1972). Increased production of fish due to stream enrichment with fertilizer additions has been shown by Huntsman (1948). From concerns over eutrophication related to sewage and other pollution inputs from runoff, Velz and Gannon (1963) assessed the self-purification potential of streams. Reviews of phosphorus dynamics in running water have been provided by Keup (1968) and Ryden et al. (1973). Van Wazer (1966) provided a comprehensive account of phosphorus chemistry. No review on nitrogen dynamics in streams has yet appeared in the literature.

In spite of this early work the transport and transformations of nitrogen and phosphorus in streams is not well understood. This may be because either single processes have been examined alone (assimilation of $^{32}$P in radiotracer
work for example; Elwood et al. (1980) or the end result of a perturbation is measured with no pretreatment data (e.g. effects of sewage inputs; c.f. Paterson and Nursall (1975), Marcus (1980)) or only one form of the element is measured over a downstream gradient (c.f. Johnson et al. (1976)). These authors have examined isolated pathways but have not integrated their findings to provide an overall pattern of biogeochemical processing. Others have conducted stream nutrient cycling studies with the use of budgets, which, although useful for examining change in net retention or loss of various forms of nutrients (c.f. Sloane 1979), fail to identify the fates of introduced nutrients.

In the following discussion, existing information on the transport and transformations of inorganic N and P in streams is integrated to provide an overall conceptual framework for the present thesis.

A. The Concept of Nutrient Processing.

Small, turbulent mountain streams are highly oxidized environments (Holl 1955: in Hynes 1970), in which inorganic N and P are mainly present in oxidized forms. Dissolved inorganic P is present as orthophosphate, and in small streams of southwestern British Columbia where pH is near neutral (Feller and Kimmins 1979) it has the form, $\text{HPO}_4^{2-}$ (Stumm and Morgan 1970). Oxidized inorganic nitrogen is always present as
nitrate. Ammonium, a reduced form of nitrogen, also persists in streamwater but it is usually in extremely low concentrations. It is generated mostly from mineralization of in-stream organic matter. Input of ammonium from soils is negligible since the strong affinity of ammonium to cation exchange sites in soil greatly retards groundwater losses (Binkley 1980, Sollins et al. 1980).

Each of these inorganic forms of N and P is readily available for uptake by plants or immobilization by microbes and can, therefore, be transformed and/or translocated through the stream ecosystem bound into a variety of size fractions. That is, the element may remain dissolved (<0.45 \mu m) or be incorporated into fine particulate organic matter (FPOM: 0.45 \mu m - 1 mm) in the form of living and dead material sloughed from the stream substrate. Alternatively, it may be incorporated into large particulate organic matter (LPOM: >1 mm) such as aquatic macrophytes.

None of these size fractions of N and P present in a stream is necessarily a result of processes within the stream; they may be introduced from allochthonous sources. Leaf fall is one important source for LPOM (eg. Wetzel and Manny 1972, Suberkropp et al. 1976). Throughfall introduces dissolved organic material (eg. McDowell and Fisher 1976) to solution. These introduced materials which contain N and P are changed in size through transformations by physical, chemical or biological processes during their residence in the ecosystem. This type of conversion from one size class to another, whether it be an increase or decrease in size, is termed element "processing"
The term "nutrient processing", in its relation to streams is a generalized term since it has been used to refer to all lotic processes responsible for transport and transformations of nutrients. It is preferable for the sake of simplification within this study to subdivide it into two groups of biogeochemical cycles as Brock (1979) has done in describing the role of microorganisms in nutrient transformations in lakes. One group involves cyclical transformations of elements and is termed the redox cycle. As the name suggests, an element may enter oxidation processes (nitrification of ammonium for example) and/or reduction processes (ammonification of nitrate for example) within this cycle. Often, the redox processes are significant only when they are catalysed by living microorganisms. The other cycle involves element transport and is termed the transport cycle. Uptake of elements and incorporation into biomass can be considered part of this cycle although it often involves the redox cycle as well. Mineralization of organic matter is one example of the latter, since certain oxidation states of many elements are more volatile or more soluble than other oxidation states (Stumm and Morgan 1970). For the two elements under consideration in this study, both are involved in transport processes in the ecosystem but only nitrogen is involved in the redox cycle.
B. **Uptake and Cycling Routes in the Transport Cycle.**

The processing of $\text{NH}_4^+$, $\text{NO}_3^-$ and $\text{HPO}_4^{2-}$ in a stream potentially begins by following one or a combination of four uptake routes as shown in Figure 2-1 and 2-2:

1. Uptake by riparian vegetation
2. Uptake by in-stream autotrophs
3. Immobilization by microbes in decomposition processes
4. Sorption to sediments

Nitrate can also be denitrified and lost from the system in addition to entering these other routes.
FIGURE 2-1 Phosphorus processing in an hypothetical mountain stream

Input from Allochthonous Sources

Key to abbreviations:
- **DOP** - Dissolved Organic Phosphorus
- **FPOP** - Fine Particulate Organic Phosphorus
- **CPOP** - Coarse Particulate Organic Phosphorus

1 - Uptake
2 - Immobilization
3 - Sorption to Sediments

Recycling in Detritus

Recycling by Periphyton

aquatic macrophyte

export

Input from Allochthonous Sources

HPO$_4^{2-}$
DOP
FPOP
CPOP

riparian 1
FIGURE 2-2 Nitrogen processing in an hypothetical mountain stream

Key to abbreviations:

- **DON** - Dissolved Organic Nitrogen
- **CPON** - Coarse Particulate Organic Nitrogen
- **FPON** - Fine Particulate Organic Nitrogen

1 - Uptake
2 - Immobilization
3 - Sorption to Sediments
4 - N fixation
1. **Uptake and cycling by riparian vegetation.**

No study has yet quantitatively measured nutrient uptake by riparian vegetation. It is extremely difficult to isolate large plants, measure the uptake of a specific nutrient per unit time and extrapolate to a large area. Bormann and Likens (1979) have, however, suggested that riparian uptake may be important in contributing to low nitrate concentrations in mountain streams of New England draining early seral forest stands. However, on the Pacific coast riparian growth may exude more nutrients to streamwater than it removes from solution. Nitrogen fixation by red alder (*Alnus rubra* Bong.) is one local example to support this view. Binkley (1980) and Heatherington (1980) have attributed the considerably greater nitrate concentrations in streams bordered by alder than in those in close proximity to but not actually bordered by alder to be related to input by N-fixation.

Phosphorus flux between the riparian zone and streamwater is also virtually unknown. The potential uptake of phosphorus has been calculated by Meyer (1978) for a New England riparian zone to be 90 mg P/m²/yr¹ or 6% of total fluvial losses. This estimate may, however, be in error since it was based on casual observations that tree root density was about one-tenth of that in the surrounding forest. Root uptake rates were not measured, but were extrapolated from Likens, et al.'s (1977) estimates of uptake in the forest well away from stream banks. Uptake may have been substantially different near the stream where the water regime may have altered uptake rates.
2. **Uptake and cycling by in-stream autotrophs.**

Reports of the significance of uptake by in-stream vascular macrophytes are varied and inconclusive. Root uptake of ammonium and nitrate from solution by aquatic vascular plants has been observed by Toetz (1971, 1974). However, Brink and Widell (1967) and Kaushik *et al.* (1975) have suggested that vascular plants may acquire nitrogen directly from the sediments to which they are anchored and may not be effective whatsoever in removing nutrients from solution. Unlike this uncertainty related to nitrogen uptake, the radiotracer work of Ball and Hooper (1961) clearly showed that phosphorus was taken up from solution and recycled by several species of macrophyte in a small trout stream. Uptake of phosphorus by bryophytes has also been established for a small stream in New England. In that study, Meyer (1979) conducted short term enrichment experiments over bryophyte clumps and found uptake rates up to 20 mg P/m²/min. Variation in the uptake rates was directly related to the enrichment concentration. Sloane (1979) conducted similar experiments and found NO₃⁻ and NH₄⁺ uptake rates of 3.5 and 66 µg N/g AFDW/hr. Respectively (AFDW is the abbreviated term for ash free dry weight). It is difficult, however, to relate these rates to a length of stream channel and, therefore, to estimate their importance relative to other processes since the bryophytes were not widespread and in the case of Sloane's work were not quantified on an area basis.

Measurements of nutrient uptake by the stream periphyton, have been more extensively reported. The term "periphyton" by definition refers to all living plants smaller than bryophytes
and vascular plants attached to the stream substrate (Hynes 1970). Various bacteria, fungi and actinomycetes are virtually always associated with the attached algae (Elwood et al. 1980, Karlstrom 1978, Fenchel 1977) but since they are not considered photosynthetic plants, they have not been considered true periphyton according to this definition. Recent work suggests, however, that they are very much active in mineralization and nutrient uptake in streams, and in some cases more active than algae in nutrient recycling (Fenchel 1977, Elwood et al. 1980). As this role of microbes is now considered of prime importance in nutrient cycling, the definition of periphyton provided by Hynes will be amended for use in this study to include bacteria, fungi and actinomycetes.

A great deal of work in primary productivity and nutrient uptake kinetics has identified algae in the periphyton as the most important component in the self-purification ability of streams. McColl (1974) showed that benthic algae were responsible for downstream dissappearance of phosphate, nitrate, and ammonium in a small New Zealand stream. Increases in algal production as a result of enrichment have also been demonstrated experimentally on the Pacific coast (Cole 1973, Stockner and Shortreed 1978). Also, increases in algal biomass have occurred in response to wastewater inputs (Filip et al. 1975, Hemens and Mason 1968, Marcus 1980, and Paterson and Nursall 1975) and to effects of nutrient movement from land to streams after forest cutting (Hansmann and Phinney 1973, Bormann et al. 1974, Feller: pers. comm.). More definitive assessments of nutrient uptake by benthic algae have been established with the use of
radiotracer techniques. Ball and Hopper (1961) suggested that algae were most important in removing $^{32}$P spikes from solution. Elwood and Nelson (1972) in their work at Oak Ridge, Tennessee developed a method for measuring periphyton (benthic algae in their work) production. They also estimated grazing rates by freshwater gastropods based on $^{32}$P uptake rates and translocation to secondary production. Nelson et al. (1969) suggested that stream bottom areas could be measured based on measuring the assimilation of $^{32}$P into periphyton.

The continuation of radiotracer work has recently brought into question the concept that benthic algae are the most important functional component of periphyton. Elwood et al. (1980) were able to distinguish uptake rates and incorporation of $^{32}$P into microbial and algal components of periphyton and found that uptake rates by microbes far exceeded those in algae primarily because turnover rates of microbes per unit surface area of substrate exceeded those of algae. This is supported by the scanning electron microscope work of Karlstrom (1978) and Dickman and Gochnauer (1978) which showed that periphyton on rocks in streams is not a simple layer of algae but a complex multistory structure, largely composed of organic matter and decomposer microbes. Unicellular algae such as diatoms and some ciliates and flagellates initially colonize a sterile gravel but in so doing their frustules create a rough surface which traps drifting very fine particulate organic matter (VFPOM) and associated decomposing microbes. Eventually the surface area of microbes may far exceed that of algae and potentially achieve functionally greater importance in nutrient uptake and release.
processes than algae. In theory, however, this will only occur where drift of very fine particulate organic matter is ample and biogeochemical characteristics of the stream select for forms of algae which functionally do not overwhelm microbial activity.

The uptake and release of nutrients and transformations which are inherent in such cycling is now termed "nutrient spiralling" (Elwood et al. 1980), a term which emphasizes the concept of reuse in the transport of nutrients downstream. The term is based on observations of periphyton sloughing and mineralization and uptake of remineralized material downstream. Essentially, this process is a continual uptake and release phenomenon which spirals downstream at a rate proportional to uptake rates and release rates (Elwood and Nelson 1972, Elwood et al. 1980). Although the uptake and release process was initially reported from observations of periphyton activity, it is also known to occur through in-stream macrophytes. For example, Stake (1967) found that nitrogen compounds which are taken up by plants in Swedish streams are returned to the water during the same growth period thereby demonstrating a low rate of spiralling (one cycle per year) as opposed to the higher rate discussed by Elwood et al. (1980) for nutrients cycled through periphyton biomass.

Spiralling does not proceed at a constant rate. Rather, it appears to be highly regulated by hydrologic characteristics. Increases in current velocity can increase uptake rates (Whitford 1960, Whitford 1965, Whitford and Schumacher 1961, Whitford et al. 1964, McIntire 1966, Rodgers and Harvey 1976), except in cases where the demand for the element can be
satisfied by molecular diffusion processes alone, as would occur under high nutrient concentrations. Lock and John (1979) have suggested that uptake in moving water could increase up to 120% over that in still water, and, with these same differential flow conditions, up to 360% in water having lower nutrient concentrations. A major reason for the increase has been attributed to the continual resupply of nutrient ions immediately adjacent to the cell walls by the action of moving water. In still water, the nutrient supply at the cell wall is not replenished, a steep concentration gradient is established, a transport limitation of nutrient uptake is enhanced (Gavis 1976) and the cell takes longer to absorb its essential nutrients. Whitford (1960a) and Whitford and Schumacher (1961, 1964) have also shown that cellular respiration increases with greater current velocities, so, increased water movement speeds up the whole cellular metabolism (Odum and Hoskin 1957).

The current required to produce these effects is, however, very low, a minimum threshold being about 5-10 cm/sec (Lock and John 1979). Most mountain streams may have very slow water movement in the interstitial spaces of the substrate gravels so uptake by periphyton below the gravel surface might be low. However, the surface gravels are generally exposed to current velocities considerably greater than the 5-10 cm/sec threshold. Thus, strictly related to water characteristics alone, uptake rates on the surface gravels may be greatest while those in the interstitial spaces (probably associated largely with bacterial activity due to the absence of light) might be lowest.

Although ideal conditions for uptake at the substrate
surface may occur during periods of base flow, high discharge can be most disruptive by removing biomass via sloughing and thereby reduce uptake rates by periphyton. In nutrient enrichment experiments, Meyer (1979) found that efficiencies of phosphorus uptake (downstream reduction in phosphorus concentration as a function of its initial concentration) decreased at discharges greater than base flow. This was attributed to a combination of reduced contact time that a given atom had with the periphyton substrate at high discharge and a reduction in size of the periphyton surface area because of sloughing.

3. **Uptake and cycling by immobilization processes.**

Particulate organic matter, whether it is introduced from allochthonous sources or has sloughed from substrates within the stream (Swanson and Backmann 1976, Naiman and Sibert 1978) will be susceptible to a variety of biochemical breakdown processes. A considerable amount of essential nutrients may be required for these heterotrophic processes. That is, within hours after being introduced to a stream following abscission, a leaf will be leached of some of its N (Triska et al. 1975, Suberkropp et al. 1976, Iversen 1973, Krumholz 1972, Kaushik and Hynes 1971) and P (Meyer 1980) constituents as well as various macromolecules (Krumholz 1972, Triska et al. 1975, Suberkropp et al. 1976). This results in an increased C:N or C:P ratio. The organic matter then becomes largely refractory thereby favouring immobilization as bacteria colonize the particle
surfaces (Triska 1970, Triska et al. 1975, Suberkropp et al. 1976). Much of this "microbially conditioned" (Petersen and Cummins 1974) material gradually becomes more labile as the C:N and C:P ratio decreases and will be either further mineralized in microbially mediated oxidation reactions or processed by animal feeding.

Based on a leaf pack decomposition study in Michigan, Peterson and Cummins (1974) estimated that a microbially-conditioned leaf pack was approximately 78% the original weight of a whole leaf pack and of that conditioned material, 15% entered biochemical oxidation pathways and 21% was processed by animal feeding. Much of the latter, however, would enter oxidation processes upon animal death or in animal faeces. Recycling or spiralling can, therefore, also occur as a result of heterotrophic processes starting either with allochthonous material or organic matter which is produced within the stream; such as that from periphyton production.

Rates of these decomposition processes are regulated at least in part by temperature and by ambient N and P concentrations. For example, Kaushik and Hynes (1971) found about 15% greater rates of decay (measured as weight lost) at 21°C than at 10°C. Also, additions of nitrate and phosphate in stream solution enhanced decay rates by a further 20% over unenriched conditions in the same study. It is likely, therefore, that the presence or absence of a forest canopy which can restrict light and thereby heat inputs to a stream may have a significant impact on heterotrophic spiralling. Also, conditions of nutrient loss from soils can be effective in
determining these spiralling rates.

4. Sorption to sediments.

Debris dams or sections where a stream aggrades and allows accumulation of fine particulate organic matter (FPOM) in addition to silts and sands provide good sites for adsorption reactions. For example, there is a strong tendency for chemical bonding between phosphate ions and metal ions in a solid lattice and sorption of phosphates and polyphosphates onto clay minerals (Stumm and Morgan 1970). Also, Syers et al. (1973) have reported sorption of phosphate groups onto very fine organic particles in lake sediments. Only Meyer (1979) has quantitatively examined these sorption processes in stream sediments and detritus accumulations. Her work at Hubbard Brook showed uptake by sorption to be extremely rapid; silty sediments having a high organic content removed 93% of P from an experimental solution of 1 mg P/l within 5 min. Sandy sediments which had a low organic content were less efficient and removed 19% within 5 min. Sediment which was trapped in bryophyte foliage was also considered active in P removal. In fact, much of P uptake by bryophytes was attributed to sorption processes. The same rapid uptake has been observed by Li et al. (1972) for lake sediments.

The rate of sorption is, however, highly regulated by pH. Meyer (1979) found optimum rates over a pH range of 4-5 below which rates fell dramatically. In addition, Stumm and Morgan (1970) reported that P sorption rates decrease at pH values
greater than 6. In southwestern B.C., stream pH is approximately neutral (Feller and Kimmins 1979) so P sorption may not be significant. Little is known of sorption properties of the nitrogen species except that ammonium is thought to be strongly sorbed to particulate and colloidal particles in alkaline lakes (Wetzel 1975). N sorption in streams has not been investigated.

C. Element Removal Routes via Redox in the Transport Cycle

Of the two elements considered in this study only nitrogen has several oxidation states which are recognized in redox reactions. Of these reactions, the only one which can function in removing N from the stream ecosystem is denitrification. Essentially, it is a type of nitrogen volatilization in which both nitrate and nitrite are reduced aerobically or anaerobically in the presence of organic matter (Keeney 1973, Painter 1970, Alexander 1977, Wetzel 1975). Again, the process is dependent on an adequate accumulation of organic matter. In studies in which denitrification has been detected, that accumulation appears to consist of very fine particulates in a deep muddy matrix. Such a condition was observed by Kaushik et al. (1975) in a small stream in Ontario in which nitrate concentrations were found to consistently decline from 5.2 mg N/l to 2.11 mg N/l over a 2 km reach. Subsequent studies have confirmed that the disappearance was due to denitrification (Sain et al. 1977, Chatarpaul and Robinson 1979). Hill (1979) has also reported denitrification to be responsible for removal
of 75% of daily input of nitrate during the growing season in a low gradient stream in Ontario. Chaturpaul and Robinson (1979) found similar effects in another small Ontario stream as did Toms et al. (1975) in British streams. These works and others have now led to the use of denitrification in summer as a management tool for control of run-off of nitrate from urban and agricultural land in Ontario (Robinson et al. 1979).

D. Control of Spiralling Rates in the Transport Cycle

Stream temperature has already been mentioned as an important regulatory factor in heterotrophic activity of streams, but of greater importance is the ability of streamflow to move or scour organic matter in the watercourse.

The magnitude of streamflow required to move particulate materials in a stream has often been expressed as "stream power" (Leopold et al. 1964). It represents the work rate of flowing water per unit width of stream and is defined by the equation:

\[ w = \frac{pQs}{W} \]

where:

- \( w \) = power per unit width (kg.m\(^{-1}\).s\(^{-1}\))
- \( P \) = density of water
- \( Q \) = discharge (m\(^3\).s\(^{-1}\))
- \( s \) = slope (%)
- \( W \) = width (m)

Debris dams, some aquatic macrophytes (mainly as LPOM) and also periphytic holdfast structures which attach to the stream substrate are structures which resist stream power. When the
retention capacity of these structures exceeds stream power living and detrital organic matter derived either from sloughing of periphyton (Swanson and Backmann 1976, Naiman and Sibert 1978) and/or introduction of allochthonous material will accumulate. Under some conditions the accumulations will form debris dams. Conversely, as discharge increases there is a proportionate increase in stream power and the ability of retention structures to remain effective diminishes. It is no surprise then that FPOM and LPOM transport is significantly related to discharge as has been shown by Fisher and Likens (1973), and supported by Hobbie and Likens (1973), Bormann et al. (1974), Meyer (1978), Bilby and Likens (1979), Holmes et al. (1980) and Cahill et al. (1974).

The magnitude of stream power required to move reactive substrates is, however, not similar for all streams but is related to physical characteristics of a stream (Sedell et al. 1979). Increasing slope will increase the ability of the stream to move material according to the stream power function (Leopold et al. 1964). Width and shape of stream banks will also influence the movement of material; primarily the large particulate organic matter which becomes wedged between banks and initiates build-up of debris dams. The riffle-to-pool ratio is important (Sedell et al. 1979) in that a large number of pools increases the ability of the stream to retain sediment and detritus by a settling action in relatively calm pool water. The presence of pools thus enhances nutrient processing rates (Meyer 1979). All of these variables interact to regulate movement of processing substrates.
On an annual basis, retention structures which regulate movement of particles are often effective in creating a condition in which inputs of LPOM are greater than exports, yet inputs and outputs of total N and P are balanced (Fisher and Likens 1973, Kaushik and Hynes 1971, Sloane 1979, Meyer and Likens 1979, Triska et al. 1979). Changes in size fractions of input materials in the transport cycle are considered the key to understanding these differences. Based on budgetary work, Meyer and Likens (1979) have suggested that \( \text{HPO}_4^{2-} \), DOP and LPOP enter conversion pathways to fine particulate organic phosphorus (FPOP). FPOP exports from a headwater stream are, then, greater than inputs resulting in a balanced input and output budget. This downstream conversion to fine particulates is consistent with the findings of Naiman and Sedell (1979a and b) in their work of tracing particle size transport through stream orders. Meyer and Likens (1979) have also indicated that DP is very rapidly removed from solution by plant uptake and sorption. By turnover in the transport cycle the material was transported downstream as FPP. CPP was reduced in size upon input into the system by physical and biochemical breakdown to be exported primarily as FPP. The export, however, was seasonal in nature. For most days of the year, total P inputs exceeded outputs. Only during high discharge associated with storm events was the annual budget balanced by large losses. Similar findings of retention and in-stream processing during low flow and large losses at high discharge were reported by Sloane (1979) in her N budget at Hubbard Brook and by Triska et al. (1979) in a small stream of the Oregon Cascades.
Flux of organic matter as regulated by stream power would appear to be important as a factor determining rates of nutrient spiralling. Although not yet investigated, it is likely that as POM accumulates during periods of base flow, the relatively low volume of water would allow spiralling frequencies to increase due to the lack of disruptive flows on autotrophic and heterotrophic biomass through which the cycling is mediated. Once removed, by stormflow for example, cycling rates would diminish since that mediating mechanism is partially exported, and as Sloane (1979) concluded from observations of POM export at high streamflow, the system would become a conduit for nutrients lost from land rather than a biochemical reactor.

It should be clear from this review that considerable evidence exists to illustrate that processing of nutrient chemicals transported in water can continue after water has left the mineral soil but before water leaves a watershed. It must be emphasized that unlike the terrestrial ecosystems which streams drain, most plant and microbial biomass in streams turns over relatively rapidly and thereby creates a nutrient spiralling effect which is most important not only in removing nitrogen and phosphorus from solution, but in cyclicly translocating the atoms through various inorganic and organic structures in reduction and oxidation processes. Thus, lotic nutrient cycling appears to be highly dynamic. Much of this behaviour is under the constant influence of stream power which may either enhance cycling under low flow conditions or destroy it during extreme freshet events.
CHAPTER 3

STUDY SITE DESCRIPTION.

A. Location

The study was conducted in East Creek, a small stream near the southern border of the University of British Columbia Research Forest (Fig.3-1), an area of 5157 ha. located approximately 50 km east of Vancouver. East Creek is a second order stream (Strahler, 1957) because of four small intermittent tributaries draining into it, but these can be dry during summer months.

The total reach length was 2475 m within which the stream passed through four different seral stages (Fig. 3-2). The headwaters (section A in this study) originated in a mixed 23-yr-old and 105-yr-old dense second growth stand of Douglas-fir (Pseudotsuga menziesii (Mirb.)Franco) and western hemlock (Tsuga heterophylla (Raf.)Sarg.). 700 m from the headwaters the stream entered an area which was clearcut in 1973 and slashburned in 1974 (section B). A further 400 m downstream, it entered a 500 m section of 25-yr-old Douglas-fir plantation. The remaining section flowed through an undulating area which was clearcut in 1972 and subsequently landscaped in 1973-74 to accommodate light farm equipment for tree planting and intensive stand management.
FIGURE 3-1 Study area showing geographic location and location of East Creek in the U.B.C. Research Forest.
FIGURE 3-2 Detailed map of East Creek showing the four sections of different vegetation cover, weir locations and water sampling sites.

B. Clearcut - 1973
Burned-1974
Planted - 1975.

D. Clearcut - 1972
Landscaped
Planted - 1975.
B. Climate

Climate in the area has been classified as warm maritime-mesothermal (Cfb) according to Koppen (1936). This is a rainy climate with an annual mean precipitation of 220-270 cm. Most precipitation is in the form of rain. At lower elevations, snow may contribute less than 1% of the total annual precipitation (Krajina 1969). As most precipitation occurs in winter, summers are generally characterized by a dry period. Temperatures are mild with an average daily mean of 17°C for July, the warmest month, and 0°C for January, the coldest month.

C. Vegetation

The entire study area lies in the dry subzone of the Coastal Western Hemlock biogeoclimatic zone of British Columbia (Krajina 1969). Klinka (1976) has classified the area into a series of ecosystem units. Under this classification, land adjacent to the stream bed falls under the Ribes - Oplopanax - Western Redcedar type. Mature tree species remaining on the watershed at the time of the study were mainly western hemlock, western redcedar (Thuja plicata Donn) and Douglas-fir. These were second growth and originated mainly from a fire in 1868. Douglas-fir was planted on the cleared watersheds in 1975. The understory and riparian vegetation was diverse and varied, depending on the degree of canopy closure. Within section A and

'Latin names and authorities of trees and minor vegetation as in Hitchcock and Cronquist (1973).
at the extreme downstream end of section C shrubs included *Gaultheria shallon*, *Oplopanax horridus*, *Vaccinium parvifolium* and *Rubus spectabilis*. The ferns *Polystichum munitum* and *Blechnum spicant* as well as many mosses were also common but occurred in patches rather than being evenly distributed. The clearcut area between the two weirs (section B) was in its sixth year of new growth during the study and was dominated by *Blechnum spicant* and *Epilobium spp.* *Alnus rubra* was abundant locally. Riparian vegetation was generally not closed over the stream channel and included *Blechum spicant*, *Epilobium spp.*, and localized *Carex spp.* About half way through section B the stream aggraded slightly and the streambed was covered by *Alnus rubra*, *Acer circinatum*, *Acer macrophyllum* and *Salix spp.* In other areas of the reach these species only occurred occasionally. The streambank in section D was severely disturbed during the landscaping operation in 1974, and, as a result, riparian vegetation lacked diversity. *Alnus rubra*, *Salix spp.*, , and *Carex spp.* which lined the streambank over most of this reach were virtually the only common species present.

Within the stream itself there was a large diversity of plants. Available light was minimal in Section A, so generally a thin periphytic covering (algae, bacteria, and fungi) on the gravel substrate as well as patches of various mosses are all that were noticeable. Algal growths were abundant in section B and included a large variety of species from the *Bacillariophyceae*, *Chlorophyceae* and *Rhodophyceae*. For more details of algal community structure the reader is referred to
the thesis by Wehr (1979). Aquatic vascular plants were also numerous in this section and were dominated by *Carex* spp. The occasional *Salix* spp. was also present. Mosses were noticeable but were certainly not a dominant vegetation group. Section C was virtually devoid of any in-stream macrophytic growth. Only the usual thin covering of periphyton on rock surfaces and localized bryophyte clumps were present. Section D was entirely dominated by a thick diatomaceous covering on the substrate. No macrophytic vegetation was evident.

D. Geology and Soils

Soils in the area are of glacial origin (Roddick 1965) and have been classified as Humo-Ferric Podzols (Canada Soil Survey Committee 1978). Textures range from predominantly loamy sand to sandy loam, with coarse fragments (>2 mm) constituting 50% or more by volume. Adjacent to the stream channels the soils were moist (Lacate 1965) and there was localized waterlogging near outflows of tributary streams. The soils were also deeper near the stream channels than upslope in drier parts of the watershed (Lacate 1965) which accounts for the lack of surficial bedrock within the study area.

The streambed was characterized by acid granitic materials which consisted largely of quartzdiorite, diorite, and gabbro (Roddick 1965). These are poorly soluble materials which contribute little in the way of dissolved minerals to the water (Golterman 1975). Their origin was a granitic bedrock overlain by a layer of compacted basal till, mostly impermeable to water
and which was not penetrated by roots. Material deposited on top of this was the ablation till which was mixed with colluvium in places to form the present soil mantle.

E. Physical Characteristics of East Creek

The major physical characteristics of each of the four sections at the time of the study are summarized in Table 3-1. Each section was composed of a variety of substrates some of which were present as an aftermath of past experimental treatments (Feller, 1974). Section A has always been considered a control area in past work (Feller 1974, Feller 1977, Feller and Kimmins 1979). Streambank tree growth was dense and unmanaged. Only sun flecks penetrated this cover to reach the stream channel. Alternating series of stair-step riffle-pool sequences characterized the channel. Organic debris dams were numerous, having been formed from accumulations of logs, tree trunks, twigs, leaf and needle matter, and decomposing detritus anchored in place by means of fallen trees or branches strung from bank to bank.

In section B, riparian growth consisted of young deciduous vegetation which had not closed over the stream so light inputs to the ecosystem were generally not restricted. Organic debris dams, originating from logging slash, were numerous but were loosely structured and did not create pools behind them. Most of this section was characterized by riffles which flowed over gravel and cobble size rocks (Canada Soil Survey Committee 1978). Several locations on the reach were covered by large
logging slash which was suspended from bank to bank and was not in contact with streamwater at summer base flow.

Section C had fewer debris dams than the upstream sections but individual dams were much larger consisting of stems and branches of fallen trees. Again, they were permeable and did not create upstream pools. Pools were common, however, but had been formed by streamflow erosion of streambanks and gravels of the streambed. Sediment and detritus deposition was common in these during summer. Near the downstream end of Section C was a manmade pond approximately 20 m long, 15 m wide and 1.5 m deep created in the construction of a road crossing shown in Fig.3-2. Detrital sediments lined its basin. The pond outflow entered a culvert which passed under the road and emptied into the original stream channel. Coniferous forest cover over the stream was minimal below the road but dense riparian growth still restricted incoming light. Gravels and cobbles again characterized the substrate in this section but were covered with a thick iron hydroxide - iron bacteria coating.

The riparian growth opened abruptly at the upstream area of section D. Organic debris was absent (relative to upstream) in this section and the substrate consisted of relatively uniformly sized cobbles. The iron hydroxide precipitate extended well into the reach but unlike the other sections, a thick diatomaceous periphyton coating was abundant throughout.
Table 3-1. Physical characteristics of East Creek in summer 1979.

<table>
<thead>
<tr>
<th>FEATURE</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean width (m)</td>
<td>0.8</td>
<td>3.1</td>
<td>3.5</td>
<td>3.7</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>0.09</td>
<td>0.10</td>
<td>0.15</td>
<td>0.08</td>
</tr>
<tr>
<td>Discharge (l.s^-1) Maximum</td>
<td>550</td>
<td>1200</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Discharge (l.s^-1) Minimum</td>
<td>0.2</td>
<td>0.6</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Elevational range (m)</td>
<td>340-300</td>
<td>300-200</td>
<td>200-155</td>
<td>155-140</td>
</tr>
<tr>
<td>Stream gradient (%)</td>
<td>5.7</td>
<td>14.3</td>
<td>7.1</td>
<td>4.3</td>
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<tr>
<td>Watershed area (km²)</td>
<td>44</td>
<td>24</td>
<td>13</td>
<td>21</td>
</tr>
<tr>
<td>Reach length (m)</td>
<td>700</td>
<td>400</td>
<td>500</td>
<td>500</td>
</tr>
<tr>
<td>Freshets per year</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 x base flow</td>
<td>16</td>
<td>16</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>10 x base flow</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Reach order</td>
<td>1</td>
<td>2</td>
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</tr>
<tr>
<td>Substrate type</td>
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<td>gravel/</td>
<td>gravel/</td>
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<tr>
<td></td>
<td>cobble.</td>
<td>cobble.</td>
<td>cobble.</td>
<td>cobble.</td>
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<tr>
<td></td>
<td>organic</td>
<td>logging</td>
<td>erosional</td>
<td>Fe(OH)</td>
</tr>
<tr>
<td></td>
<td>debris.</td>
<td>slash.</td>
<td>pools.</td>
<td>deposits</td>
</tr>
<tr>
<td></td>
<td>riffle-</td>
<td>riffles</td>
<td>riffles</td>
<td>deposits</td>
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<tr>
<td></td>
<td>pool</td>
<td>dominate</td>
<td>dominate</td>
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<td></td>
<td>sequence.</td>
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<tr>
<td>Cross-sectional shape</td>
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<tr>
<td>Time from last freshet to</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>beginning of study (d)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 x base flow</td>
<td>25</td>
<td>25</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>10 x base flow</td>
<td>41</td>
<td>41</td>
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</tr>
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</table>
F. **Stream Hydrology**

Instantaneous discharge measured at the V-notch weir below Section B (Fig.3-2) has ranged from 0.6 to 1200 l/sec since data collections began in 1971. Stream hydrographs have been characterized by high discharges from October until April. This is generally followed by a decline until low flows are reached in May or June and are sustained until the following September. During particularly dry years, the summer base flow may be further reduced through August and early September. Heavy spring and summer runoff or low winter runoff that is typical of many mountain streams in southwestern B.C. does not occur in East Creek because of the lack of a winter snow pack. Anomalous summer storm flow events have occurred, but they appear to be an occasional phenomenon appearing once every several years (Feller 1974). Only one such storm has happened (July 1972) since data collections began.

Stream hydrographs were also characterized by rapid rises and falls in response to individual rainfall events. Feller (1974) followed streamflow responses during an autumn and winter storm and found times to peak discharge to be on the order of 12-16 hours. Further analysis (Feller 1981) has indicated similar time periods for mean annual times to peak discharge for the water years 1972-73 through 1977-78. In addition, once peak flow has occurred or the stream hydrograph indicates stormflow has reached a plateau, flow has appeared to respond to precipitation trends within an hour of their occurrence (Feller 1974). These rapid response times are thought to indicate the importance of soil macrochannels which may be abundant.
throughout the study watershed (Feller and Kimmins 1979).

Clearcutting and slashburning has had no statistically significant effect on annual streamflow and although there were initial increases in peak discharge after cutting, these returned to pretreatment levels by the second year following treatment (Feller 1981). Similarly, the time to peak discharge increased significantly in the first two years following cutting by 6% and 3% respectively. However, starting in the third year (1975), and continuing to the present, times to peak discharge have returned to those characteristic of pretreatment conditions.

Discharge at weir B for the study period is shown in Fig.3-3.
FIGURE 3-3 Stream discharge at weir B during summer 1979.
A. Introduction

In East Creek, several dissolved forms of nitrogen (TDN=<0.45 um) and phosphorus (TDP=<0.45 um) have been recognized as occurring in solution (Feller and Kimmins 1979). TDN is present as nitrate-nitrogen (NO$_3^-$-N), ammonium-nitrogen (NH$_4^+$-N) and, although not measured in past work, dissolved organic nitrogen (DON). The latter is a common constituent of all lotic ecosystems (Hynes 1970, Wetzel 1975, Golterman 1975) and is present mostly as proteins, amino acids and other complex molecules (Stumm and Morgan 1970). A scale showing relative concentrations among each of these three forms is not available for East Creek due to the lack of DON data, but, of the two inorganic species the most oxidized form, nitrate, dominates (Feller 1977, Feller and Kimmins 1979). This is largely related to the 90 to 110% oxygen saturation present throughout the year (Feller and Kimmins 1979). Prior to forest cutting in the drainage area of section B, nitrate nitrogen levels ranged between 0.1 to 0.2 mg.l$^{-1}$ with no seasonal variation or any relationship to discharge (Feller and Kimmins 1979). Similarly, ammonium nitrogen showed no significant trends because concentrations were low (undetectable to 0.05 mg.l$^{-1}$).

TDP does not enter the microbially mediated redox processes which are common to TDN, so TDP is present in only two forms;
orthophosphate and dissolved organic phosphorus (DOP). Again, the dissolved organic form (DOP) was not measured in past work so the relative dominance between this and orthophosphate is not known. Because of the near neutral pH conditions in East Creek (Feller 1974), orthophosphate was present as $\text{HPO}_4^{2-}$ (Stumm and Morgan 1970). Mean annual orthophosphate phosphorus concentrations reported in past work have been very low (eg. $<.005 \text{ mg. l}^{-1}$) and mostly not detectable. Seasonal trends and variation with discharge have also not been apparent.

The relative lack of overstory cover is of considerable interest in this chapter because greater irradiance may increase processing rates, element transport and microbially mediated redox cycles in open sections. One might expect to find lower TDN and TDP concentrations in sections B and D as well as lower export of those dissolved fractions than in sections A and C, primarily due to the effect of different light and temperature conditions on element processing rates. If so, in-stream processing could explain some variation in streamwater N and P concentrations without appeal to terrestrial processes.

This concept of differential TDN and TDP transport forms the basis of questions to be investigated in this chapter:

1. Is there variation in concentrations and export of TDN and TDP between the different sections of East Creek?

2. Can any noticeable differences in TDN and TDP transport between stream sections be explained by available light differences and thereby can variation in ecosystem
energy supply explain differences in TDN and TDP transport?

3. In any sections where declining concentrations of TDN and TDP can be attributed to in-stream processes, what is the rate of incorporation into cycling pathways?

4. Can in-stream processing of dissolved nutrients during a period of intense biotic activity provide an explanation for the regulation of nutrient loss from the East Creek drainage areas?

Each form of TDP and TDN in downstream transport is examined with respect to these questions. In so doing the relative dominance of each in solution is assessed. Downstream change in the N and P transport is discussed by referring to processes in the transport and redox cycles which could be responsible for any observed trends. Hypotheses are thereby proposed as to the fate of TDN and TDP in each section of East Creek.
B. Materials and Methods

1. Stream sampling stations

To achieve the desired objectives of examining nutrient concentrations throughout the gradient of East Creek, several sampling stations were required in each section. This was essentially an extension of the water chemistry profile approach used to trace chemical flux through terrestrial ecosystems (Feller 1977, Binkley 1980). Only at two locations (downstream ends of sections A and B) were continuous measurements of discharge possible using the weir instrumentation established for previous work (Feller 1974). Consequently, element transport was often compared in terms of streamwater concentrations rather than total export.

Vitousek (1977) has indicated that comparison of concentrations will have considerable value provided several important assumptions are satisfied. The sections must receive the same amount of precipitation and precipitation chemistry. Evapotranspiration and chemical flow response characteristics must be similar. If there are differences then variation must be measurable before comparisons can be made. Feller (1974) has tested for variation in precipitation inputs and inorganic nutrient concentrations over the East Creek watershed and found no significant difference between locations for either parameter. The same chemical flow response characteristics have also been noted between sections A and B (Feller 1974).

Early in May 1979, 15 water sampling stations were
established along the entire study reach as shown in Fig.3-2. Site W-1 was the only sampling site in section A and was located at its extreme downstream end. In Section B, W-2 was a reference location used for background water chemistry immediately above the enrichment site at W-3. The downstream flux of nutrients in section B was monitored at the closely spaced sample stations W-4 through to W-10. W-11 was located approximately 50 m from the edge of the clearcut within section C and under a very dense riparian canopy. W-12 and 13 were at the inlet and outlet respectively, of the small pond in section C (Chapter 3), and the remaining two stations were located at the upstream and downstream ends of section D. A broad-crested weir was located at the downstream end of section A (sample location W-1) and a 120° V-notch weir occupied the same position in section B (sample location W-10). Stream heights at the weirs were continuously measured by water level recorders, and stream discharges were obtained from weir rating curves. Weir housings also contained continuous recording water temperature instrumentation (Weather Measure continuous recording thermographs).

2. Collection and preservation of water samples

All sample collections were conducted using new or cleaned (by acid rinse) polyethylene bottles. Sample volumes depended on the particular analysis and number of analyses to be conducted, as discussed below. At all times, sample bottles were rinsed three times with stream water before being filled and the final sample was taken beneath the water surface.
Bottles were also capped beneath the surface to exclude all air bubbles.

Weekly water samples were collected from each sample station in clean 4 litre polyethylene bottles and were transported, unpreserved, in coolers to the B.C. Environmental Laboratory at the University of B.C. for analysis. The time taken from sample collection to arrival at the laboratory was normally less than four hours. However, occasional delays in the field did prevent immediate transport of samples to the government laboratory on the day of collection. In these cases, samples were returned to U.B.C. Forest Ecology Laboratory again within 4 hours of collection, immediately analyzed for pH and electrical conductivity and then stored overnight at 5°C. On the following morning, samples were shipped to the Environmental laboratory and the remaining analyses completed within 8 hours.

Sampling frequency intensified from July 19 to August 26 (once every 1 to 3 days) in order to closely monitor the transport of an enrichment solution being introduced at W-3 (discussed in section B4 following). All of these water samples, which were additional to the weekly collections, were returned in 125 ml polyethylene bottles to the U.B.C. Forest Ecology Lab for analysis. Electrical conductivity and pH determinations were completed within 4 hours of sample collection and then samples were stored at 5°C for up to 2 days before the remaining analyses were completed. Many samples which could not be analyzed within this time were frozen at -15°C for up to eight weeks prior to analysis. This has been found to be an acceptable method of preservation (APHA 1976) and may be
superior to using chemical preservatives (Kluckner et al. 1980).

3. Laboratory methods

In all cases analytical procedures were identical for each laboratory. To be certain results were comparable, however, the same analysis was conducted on several samples in both laboratories. Results indicated no significant difference between laboratories. At the time of analysis, frozen samples were thawed by allowing to stand at room temperature for 24 hours as a standard procedure (Golterman and Clymo 1969).

All anion ($\text{HPO}_4^{2-}$, $\text{NO}_3^- + \text{NO}_2^-$) and $\text{NH}_4^+$ concentrations were determined using a Technicon Autoanalyzer II by standard methods (Technicon Industrial Systems 1973; APHA 1976). Sodium was determined using atomic absorption spectrophotometry (Varian-Techtron Ltd; model AA-5) also by standard methods (APHA 1976).

Samples collected for dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) were filtered through Reeve Angel glass fibre filters (Wetzel and Likens 1979) prior to analysis in order to eliminate the fine particulate fractions. DON was determined by calculating the difference between total Kjeldahl nitrogen (organic constituents plus ammonium) analyzed using a nesslerization method (APHA 1976) and ammonium. Each was determined from subsamples. DOP was also determined by difference between total phosphorus and orthophosphate. Total phosphorus was determined by an initial sulphuric acid digest which released organically bound phosphorus as orthophosphate. This reacted with ammonium molybdate, and through reduction of the ensuing acid, a blue coloured complex was formed and was
analysed colorimetrically in an automated Technicon system (APHA 1976; Brynjolfson 1973).

Electrical conductivity measurements were made with a Radiometer type CDM 2e conductivity meter with a CDC 104 conductivity cell. All measurements were corrected to 25°C based on a calibration curve using 0.01M KCl (APHA 1976). A Radiometer type PHM29 pH Meter with a combined glass-calomel electrode was used for pH measurements.

4. Rates of nutrient removal from solution

A methodological problem encountered in this study involved calculation of in situ rates of removal of dissolved inorganic N and P from solution. Most previous studies have simply introduced a nutrient solution to small sections of a stream over short periods of time by means of a single line feed from a reservoir tank (Sloane 1979, Meyer 1979). Others have relied on upstream water which was high in nutrient concentrations and simply measured decreases in concentrations per unit area of stream substrate (Kaushik et al. 1975). In the present study I could not rely on sufficiently high upstream concentrations of both TDN and TDP, so a long term nutrient addition method was employed.

An apparatus was designed and constructed to provide a continuous and controlled input of a nutrient solution at any specified rate (Fig.4-1). The apparatus was placed in section B as part of the following experimental set-up.

Section B was divided into two subsections: a 230 m upstream control and a downstream treatment section. The
FIGURE 4-1 Schematic diagram of the nutrient solution input apparatus for East Creek.

1. Reservoir tank
2. Gravity feed head tank intake
3. Head tank
4. Float valve head control
5. Gravity feed to orifice
6. Burette orifice support
7. Burette orifice with flow control valve
nutrient solution containing NaNO$_3$ and (NH$_4$)$_2$HPO$_4$ dissolved in a 70 litre reservoir of tap water was continuously introduced into the stream for a 5 week period (July 19 to August 26) at the downstream end of the control section (between W-2 and W-3; Fig.3-2). Outflow from the enrichment device was held constant at a specific rate which increased ambient stream concentrations of NO$_3^-$-N, NH$_4^+$-N and HPO$_4^{2-}$-P at the point of enrichment approximately 20 times and maintained that output 24 hours a day. Intensive water sampling was conducted near the enrichment source to closely monitor and make fine adjustments to the rate of nutrient input.

Sodium was included in the enrichment solution to act as an inert tracer and thereby account for dilution effects. Sodium does not accumulate significantly in plant biomass (Epstein 1972) and so has commonly been used as a hydrologic tracer in other stream studies (Meyer 1978, 1979, Sloane 1979, Gates et al. 1969, McColl 1974). It has also been used to calculate relative rock weathering rates (Johnson et al. 1968) because of its inert properties. During the period of enrichment it was assumed that all increases in sodium concentration in the treatment section were attributable to the enrichment, and all decreases were attributable to downstream dilution from groundwater inputs and longitudinal dispersion effects. This was justified since background sodium concentrations did not change appreciably along the stream reach (Fig. 4-2). Thus, if there were no selective removal of NH$_4^+$-N, NO$_3^-$-N or HPO$_4^{2-}$-P, their downstream concentrations as a proportion of original concentrations at the enrichment site would be equivalent to the
FIGURE 4-2 Sodium concentrations at each sampling site as determined from 10 sampling occurrences prior to mid-summer enrichment in East Creek, 1979.
percent loss of Na written as:

\[
\frac{[\{\text{Na} \}, \text{site } 4] \times 100}{[\{\text{Na} \}, \text{site } 3]} = \frac{[\{\text{N} \}, \text{site } 4] \times 100}{[\{\text{N} \}, \text{site } 3]} 
\]

Where N is a nutrient concentration, site 3 is the enrichment location and site 4 is located downstream.

The difference between measured concentrations of N and P and those predicted from Na concentrations in this equation is attributed to change due to in-stream processes.

Over the entire study period there were 18 episodes in which concentrations of NO\textsubscript{3}^- - N, NH\textsubscript{4}^+ - N and HPO\textsubscript{4}^{2-} - P were measured for comparison with Na concentrations to determine expected (concentrations due to dilution only) and observed (concentrations due to dilution plus uptake) levels over a distance of 495m and the eight downstream sampling stations, all within section B (Fig.3-2).

This method of comparing expected to observed concentrations had several benefits. For example, nutrient removal rates could be calculated for several locations along the entire treatment section so that rates could be compared for substrate types within those locations. Also, the lengthy period of enrichment permitted the sampling of active in-stream processing components over a season.
5. **Presentation of element concentration data**

An important part of this thesis involved developing a method of presenting water chemistry data. Spatial trends in mean nutrient concentrations for the entire experimental time period could easily be expressed on a two-dimensional graph for each nutrient of interest. However, either a storm event, which might significantly change concentrations, or additions of nutrients in section B would bias means and standard errors. A comprehensive interpretation might then require the use of several graphs, each depicting the longitudinal flux in concentrations at appropriate spaces in time. Interpretations of several graphs simultaneously would likely lead to confusion and certainly any temporal trends would be difficult to detect. Similarly, graphs depicting change in concentrations through time for each location and each element of interest would generate 75 curves (5 nutrient forms at 15 sampling locations). Again, the task of extracting temporal and spatial trends from so many graphs would be unquestionably tedious.

A computer program was therefore developed to compile nutrient concentration data over time and location in the stream and then, using computer graphics capabilities, generate a single three-dimensional surface image for each form of nitrogen and phosphorus under study. The program is listed in Appendix A. A detailed description will also be given here, mainly because accurate interpretations of the final plots require an understanding of how the data points are joined in the three-dimensional array.

The program will read concentration data for any number of
variables up to a maximum of twenty. Generally, however, running any more than one variable at a time became far too costly, so even though the program has the potential to plot many variables in one run, this was never attempted. In order to place each data point on a surface grid, information pertaining to a location on the stream reach and points in time were also read in, sorted and scaled to an axis length. Grid axes could then be considered as (1) location, scaled in distances from the furthest upstream sampling point (W-1) and (2) time, scaled in days from when sampling started and (3) element concentrations.

This logical sorting and scaling, however, could not produce a surface with all grid locations filled because plotting hardware requires information at regular intervals along each axis. Since data were collected over irregular distances and because time intervals between sampling were not always consistent, a subroutine was added to interpret and fill in missing grid locations. This worked by using a missing value as a center point to divide the surrounding surface into quadrats. Data points nearest the missing value in each quadrat were averaged and the result assigned to the missing point.

Conceptually, this represented averaging over time and space which does have drawbacks. Although not too obvious on surfaces of low relief, interpolated regions are very apparent on high relief surfaces. Between peaks, a smooth dip is quite common, particularly if the relief is depressed on either side of a ridge (i.e. on the distance axis as shown in Fig.4-3). This might appear to be a serious error in that it was unlikely
that concentrations would smoothly decrease and increase over distance between otherwise irregular peaks. However, the fact that peaks were so irregular and apparently random (in having no trends associated with them on higher relief plots) suggested that there was no predictable interpolating method by which to assign missing values with confidence. The subroutine could have been changed so that it would only average over distance but this would have eliminated any relationship of concentrations at a hypothetical time $x$, for example, being affected by those at time $x-1$. The program was therefore kept as it was, having an integrated temporal and spatial averaging calculation to fill in missing values. The drawbacks mentioned above were considered when interpreting results so that obvious interpolated regions were considered more like geometric linkages rather than being associated with trends in the real data.

After interpolation of missing points on the grid, resolution of the actual plot could be adjusted. That is, at maximum resolution, the plot grid lines were separated by the minimum sampling interval. Over time this was equivalent to one day for a total of 124 days and over distance this represented 15 m (the minimum distance between any two sampling locations) for a total sampling length of 1775 m. This degree of detail would have produced a plot having almost indistinguishable grid lines because they would be so close together. Determining accurate information from such a surface for specific times and locations would have been extremely difficult not to mention the high cost of producing such a plot. Resolution and thereby
cost was reduced to make the plot more manageable by averaging values over both time and distance. The number of grid lines for either or both axes could be preset at a maximum or any number less than that maximum. That is, with a reduction in the number of grid lines, there was a corresponding increase in averaging of both real and calculated data to arrive at a mean estimate to apply to each grid intersection. An assignment of fewer grid intersections, which is synonymous with a reduction in resolution, tends to smooth out the surface whereas greater numbers of intersections (increasing resolution) provides a more jagged and detailed surface. After several trial runs on a remote graphics terminal a resolution was chosen for the final hardcopy plots which provided highly distinguishable grid lines to pick out critical dates and locations and yet minimized averaging in order to emphasize important peaks, ridges, cliffs and trends.

The actual visual image for each plot was generated by calling two plotting routines developed for use on U.B.C plotting hardware by U.B.C. Computing Centre. First "Hide", a routine contained in the program UBC Surface was called to assemble all information and generate the plot in a non-perspective configuration. This was then drawn on blank paper by using the UBC PLOT: Q program. The output was labelled appropriately and photographically reduced to a 8 1/2" x 11" page.
6. Solar radiation

A problem associated with comparing sections of East Creek was obtaining reliable measurements of solar radiation reaching the stream channel. Particularly in sections A and C which had an overstory canopy, shading was highly variable. Some locations were completely shaded by a dense canopy throughout the day, but in others, sun flecks or short periods of unrestricted light were able to reach the stream bed. To provide a reliable estimate of solar radiation under these conditions would have required many solar sensors and recorders. Due to budget limitations this was not possible. A more easily measureable parameter which was directly related to solar radiation was therefore necessary for comparing each section. Stream temperature was the obvious choice based on the work of Brown (1969), who found that the principal source of heat for small mountain streams is solar energy directly striking the stream surface. That is, the rate of heat added is actually an algebraic sum of net radiation (Nr), evaporation (E), convection (H) and conduction (C) written as:

$$\Sigma H = Nr + E + H + C$$

All these energy balance components are extremely small except Nr. So the single parameter, direct solar energy input at the stream surface, is primarily responsible for the net rate of heat added to a stream (Brown 1969, Brown and Krygier 1970). Since convection, conduction or evaporation are very small at the surface of small streams, higher air temperatures which result from forest cutting (as in sections B and D in East Creek) are not the reason why stream temperatures may rise: it
is really direct solar radiation input. Secondly, the negligible values for heat transfer at the air-water interface suggest that heat added to the stream will not be readily dissipated. Most Nr will be stored, causing an increase in water temperature (Brown 1980). Using this argument, stream water temperature was used as an index of solar radiation in this study.

7. Nitrogen and phosphorus export comparisons

In making a comparison of export of nitrogen and phosphorus between study sections A and B, a paired T-test was used to evaluate change in export as a function of factors related to the removal of the forest canopy (one important factor being light inputs to the stream channel). This was accomplished by a comparison of paired differences in exports for each summer month (May through August) for 1972 (year before cutting treatments) and 1979 (post-treatment).

Monthly exports of a nutrient species were determined by multiplying the weighted mean monthly concentration by the total volume of water exported for each month at each of the two weir locations. The weighted mean monthly concentration was determined by:

\[ C_1(K_1/M) + C_2(K_2/M) + C_3(K_3/M) + C_4(K_4/M) \]

where: \( C_1, \ldots, C_4 \) = concentrations in mg/l for each of the 4 weeks of the month.

\( K_1, \ldots, K_4 \) = total discharge for each of the 4 weeks of the month.
To prepare export data for the analysis, the difference in export between the two locations was determined for each month so that export from the upstream weir was expressed as a percent of that from the downstream weir. The null hypothesis stated that tree removal caused no change in the average difference between concentrations in treatment and control sections.

Feller and Kimmins (1981) have substantiated the validity of this test by conducting it on data for several cations for two pretreatment years; 1971/72 and 1972/73. With the absence of any treatment, there was no significant difference (p<.05) in the chosen parameters between years.
C. Results and Discussion

1. Comparison of exports of TDN and TDP between young and mid-successional study sections.

Comparisons of total dissolved nitrogen (TDN) export on a monthly basis for the current study period are shown in Table 4-1. Total dissolved phosphorus (TDP) exports are also shown in Table 4-2 but concentrations were often less than the detectable limit of 3 ug P/l so meaningful comparisons could not be made. These data support observations by Bormann and Likens (1979) and Vitousek (1977) that nitrate nitrogen loss from younger ecosystems is less than that from older ecosystems. It is also apparent, however, that in East Creek nitrate was removed from solution within the stream in transport through the younger system and that the removal process had no relationship whatsoever to control by terrestrial processes. It is important to note here that calculations in both Table 4-1 and 4-2 span the entire study period and in that time 935 g of nitrogen and 149 g of phosphorus in the form of NaNO₃ and (NH₄)₂HPO₄ were added to the middle of section B during the mid-summer nutrient enrichment experiment to be discussed shortly. Apparent instream nitrate absorption is therefore considerably underestimated in Table 4-1.
Table 4-1. Monthly export$^1$ and differences in export of DON, NO$_3^-$-N and NH$_4^+$-N from East Creek water sampling stations W-1 and W-10 in summer 1979.

<table>
<thead>
<tr>
<th>Month/Site</th>
<th>DON</th>
<th>NO$_3^-$-N</th>
<th>NH$_4^+$-N</th>
<th>TDN</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>gm</td>
<td>% total$^2$</td>
<td>gm</td>
<td>% total</td>
</tr>
<tr>
<td>June</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W-1</td>
<td>565.9</td>
<td>52</td>
<td>494.3</td>
<td>45</td>
</tr>
<tr>
<td>W-10</td>
<td>747.2</td>
<td>77</td>
<td>168.1</td>
<td>17</td>
</tr>
<tr>
<td>Diff.$^3$</td>
<td>181.3</td>
<td>326.2</td>
<td>-22.2</td>
<td></td>
</tr>
<tr>
<td>July</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W-1</td>
<td>676.1</td>
<td>61</td>
<td>401.9</td>
<td>36</td>
</tr>
<tr>
<td>W-10</td>
<td>747.2</td>
<td>81</td>
<td>127.7</td>
<td>14</td>
</tr>
<tr>
<td>Diff.$^3$</td>
<td>-71.1</td>
<td>274.2</td>
<td>-8.3</td>
<td></td>
</tr>
<tr>
<td>August</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W-1</td>
<td>355.8</td>
<td>57</td>
<td>253.1</td>
<td>41</td>
</tr>
<tr>
<td>W-10</td>
<td>202.9</td>
<td>65</td>
<td>82.1</td>
<td>26</td>
</tr>
<tr>
<td>Diff.$^3$</td>
<td>152.9</td>
<td>171.0</td>
<td>-13.4</td>
<td></td>
</tr>
<tr>
<td>September$^4$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W-1</td>
<td>1979.0</td>
<td>41</td>
<td>2742.7</td>
<td>57</td>
</tr>
<tr>
<td>W-10</td>
<td>2640.7</td>
<td>61</td>
<td>1528.8</td>
<td>36</td>
</tr>
<tr>
<td>Diff.$^3$</td>
<td>661.7</td>
<td>1213.9</td>
<td>-35.7</td>
<td></td>
</tr>
</tbody>
</table>

$^1$Nutrient solution introduced 230 m downstream of W-1 and 486 m upstream of W-10 from July 19 to August 26.

$^2$Percent total is the weight of the N species expressed as a percent of the total N measured.

$^3$For the difference calculations, positive numbers indicate in-stream retention and negative numbers indicate downstream loss.

$^4$First two weeks of September only.
Table 4-2 Monthly export and differences in export of DOP and HPO$_4^-$ from East Creek water sampling stations W-1 and W-10 in summer 1979.

<table>
<thead>
<tr>
<th>MONTH</th>
<th>SITE</th>
<th>DOP</th>
<th>HPO$_4^-$-P</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>W-1</td>
<td>7.3</td>
<td>&lt; 17.5$^2$</td>
</tr>
<tr>
<td></td>
<td>W-10</td>
<td>8.4</td>
<td>&lt; 25.0</td>
</tr>
<tr>
<td></td>
<td>Difference</td>
<td>-1.1</td>
<td></td>
</tr>
<tr>
<td>July</td>
<td>W-1</td>
<td>5.4</td>
<td>&lt; 12.9</td>
</tr>
<tr>
<td></td>
<td>W-10</td>
<td>5.1</td>
<td>&lt; 19.2</td>
</tr>
<tr>
<td></td>
<td>Difference</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>W-1</td>
<td>1.53</td>
<td>&lt; 6.1</td>
</tr>
<tr>
<td></td>
<td>W-10</td>
<td>6.57</td>
<td>&lt; 12.3</td>
</tr>
<tr>
<td></td>
<td>Difference</td>
<td>-5.04</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>W-1</td>
<td>43.4</td>
<td>&lt; 26.1</td>
</tr>
<tr>
<td></td>
<td>W-10</td>
<td>94.5</td>
<td>&lt; 51.6</td>
</tr>
<tr>
<td></td>
<td>Difference</td>
<td>-51.1</td>
<td></td>
</tr>
</tbody>
</table>

$^1$For the difference calculations, positive numbers indicate in-stream retention; negative numbers indicate downstream loss.

$^2$Actual export was less than these estimates because at least one measurement of HPO$_4^-$ concentrations which contributed to the estimate was less than the detectable limit.
In Table 4-1 the behaviour of nitrate may lead to misinterpretations of TDN flux unless the other nitrogen species are also considered. Ammonium export was minimal compared to either nitrate or DON but it showed a complete reversal of the declining nitrate export trend. For each month, ammonium loads in solution increased within section B. Similarly, DON loss was greater downstream than upstream with the exception of export during August. DON was also the dominant form of TDN in the stream except during the stormflow period of early September. Explanations for these trends and exceptions to them will be assessed later in the thesis but the important point to note here is that although DON generally comprised > 50% of the TDN load, its proportionate increase downstream was less than in-stream absorption of nitrate. It was nitrate, then, which dominated changes in TDN flux in study section B.

While these observations are limited to a single stream, they do present evidence that an exception to the concept of overwhelming control of nutrient loss from watersheds by terrestrial ecosystems does exist. Although regulation of nutrient loss by plant uptake (Vitousek 1977), and heterotrophic demand for N (Likens et al. 1978, Johnson and Edwards 1979, Sollins et al. 1980) on land are well established, the importance of in-stream assimilation must also now be established.

Further analysis of data presented by Feller and Kimmins (1981) has revealed that downstream absorption of nitrate may not be restricted to the summer conditions that prevailed during the study period of this thesis. Based on annual input-output
budgets of drainage sections A and B, there has been a notable increase in \( N (\text{NH}_4^+ + \text{NO}_3^-) \) retention in section B, which was greater than that in section A within four years after clearcutting and slashburning section B.

Implications of the concept that small streams can be active in regulation of nutrient transport are wide-ranging. All studies which have examined nutrient flux in small watersheds or chemical additions to watersheds have based their estimates of nutrient retention on land on chemical flux measurements in the stream at a single weir location. In reality, measurements have reflected the additive effect of terrestrial and in-stream biogeochemical processes. If nutrient absorption in small watershed streams is a general phenomenon, nutrient retention on land may have been considerably overestimated in past studies.

This possible source of error is particularly important since in most studies only inorganic forms of nutrient chemicals have been measured. Clearly, some of this material lost from land may be assimilated within the stream, transformed by in-stream spiralling processes and exported in dissolved or particulate fractions and remain undetectable by the research methods. It is critically important, therefore, to consider some questions which relate not only to the functioning of in-stream processes in the current situation where they are effective, but also to consider factors controlling those processes.
2. Consideration of environmental factors regulating export

Since TDN export from section B is less than from section A, the question that arises is: were these relative differences related to biogeochemical factors associated with change in the successional status of watershed section B or due to in-stream or environmental factors which existed before disturbance? This requires the use of a pairing analysis which compares nitrogen export from each section during the study period with exports from the same months before cutting. Results are shown in Table 4-3. Analysis for nitrate nitrogen only is shown because DON data were not collected before cutting. Orthophosphate levels were largely undetectable in both years so again meaningful comparisons could not be made. Summer months of 1972 and 1979 were selected for comparison.
Table 4-3 Analysis of differences in export of NO$_3$-N from East Creek Sections A and B from summer months in 1972 and 1979.

<table>
<thead>
<tr>
<th>Month</th>
<th>Section</th>
<th>Export (g) 1972</th>
<th>A as % of B</th>
<th>Export (g) 1979</th>
<th>A as % of B</th>
<th>Difference of Percentages</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>A</td>
<td>317.5</td>
<td>32.7</td>
<td>494.3</td>
<td>294.1</td>
<td>261.4</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>971.8</td>
<td></td>
<td>168.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>July</td>
<td>A</td>
<td>3170.0</td>
<td>18.2</td>
<td>401.9</td>
<td>314.7</td>
<td>296.5</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>17374.2</td>
<td></td>
<td>127.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>A</td>
<td>241.9</td>
<td>40.0</td>
<td>253.0</td>
<td>308.2</td>
<td>268.2</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>604.4</td>
<td></td>
<td>82.1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$ts = D/Sd = 275.4/18.6 = 14.8^* \quad P < .0025$

In summer 1972, nitrate exports consistently increased in the downstream direction but this trend completely reversed during this study period. Since the analysis paired differences between locations on the same stream, and thereby eliminated year to year variation in nitrate transport, it is clear that factors related to clearcutting and slashburning (essentially a change in the successional status) were responsible for the dramatic absorption properties in section B.

Clearcutting and slashburning in 1973-74 are known to have had a variety of effects on the stream ecosystem in section B. Moderate increases in nutrient concentrations were noted after disturbance but these returned to pretreatment levels or lower by 1976 (Feller and Kimmins 1981). Streamflows increased but not greatly since only part of the watershed was clearcut.
(Feller 1981). There was also a considerable loading of organic matter from logging slash into the stream and this is presently in a variety of stages of decay. Of greater importance to overall change in stream ecosystem metabolism has likely been the large differences between maximum and minimum temperatures which have been recorded by Feller (unpublished data). Since stream temperature reflects direct solar radiation (Brown 1980), it is clear that any increase in maxima has been primarily due to increases in direct solar radiation reaching the stream channel. A before-and-after-treatment pairing analysis indicates that this has in fact occurred (Table 4-4).

Table 4-4. Analysis of differences in East Creek stream temperature between Sections A and B before (1972) and after (1979) clearcutting and slashburning.

<table>
<thead>
<tr>
<th>Month</th>
<th>Section</th>
<th>1972 Mean Monthly Temperature</th>
<th>1972 Monthly Difference (B-A)=X</th>
<th>1979 Mean Monthly Temperature</th>
<th>1979 Monthly Difference (B-A)=Y</th>
<th>(Y-X)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>7.4</td>
<td>0.7</td>
<td>8.4</td>
<td>2.6</td>
<td>1.8</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>8.2</td>
<td></td>
<td>11.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>9.8</td>
<td>0.1</td>
<td>9.9</td>
<td>2.8</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>9.9</td>
<td></td>
<td>12.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>11.3</td>
<td>0.5</td>
<td>11.9</td>
<td>3.6</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>11.8</td>
<td></td>
<td>15.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>12.4</td>
<td>1.2</td>
<td>13.0</td>
<td>2.8</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>13.6</td>
<td></td>
<td>15.8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\[ ts = D/SD = 3.3^* \quad P < .025 \]

\(^1\)Difference of the monthly differences
Some very clear differences between stream sections A and B have thus been established. Section B presently drains a successional successionally much younger terrestrial ecosystem than does A, and the lack of overstream cover in section B has allowed maximum available light to reach the stream channel, thereby increasing mean monthly stream water temperatures. The stream's absorptive capacity for nitrogen has also been increased enormously as a function of cutting treatments. Clearly, the relationship between available light and absorption of nutrients is important.

Historically, the role of light in the energetics of any ecosystem is one of the most fundamental concepts ever established in the field of ecology. In forest ecosystems, for example, solar energy is fixed in photosynthesis and provides not only the energy required to drive the internal biological functions but is also stored in the form of carbon compounds that make up ecosystem structure. Solar energy thus sustains forest ecosystem processes such as nutrient uptake, decomposition, carbon assimilation, etc. which greatly affect the overall biogeochemistry of the ecosystem.

In stream ecosystems, solar energy has the same role; it drives biological functions and builds ecosystem structure, but depending upon the environment through which the stream drains, there are two pathways for the translocation of that energy. The first is characteristic of forest-covered streams. They derive most of their energy supply from allochthonous sources (Fisher and Likens 1973, Nelson and Scott 1962, Hynes 1963).
Energy fixed by terrestrial vegetation is passed on to the drainage stream as particulate and dissolved organic matter for further biogeochemical processing. P/R ratios remain very low (Hoskin 1959) since the detritus loading is reflected in an excess of community oxygen consumption (R) over oxygen produced in photosynthesis (P). With very low photosynthetic rates, the autotrophic nutrient uptake vector described in Chapter 2 may be very low.

When the forest canopy is removed as in clearcutting, the second pathway for solar energy (direct solar radiation) is available to the stream ecosystem. An increase in light provides a direct addition of energy to the stream metabolism (Odum 1957). Primary production would be enhanced, thereby increasing nutrient uptake. Rates of decomposition and mineralization would increase in importance in response to enhanced metabolic activity.

It is concluded, then, that the higher stream temperatures incurred after logging in this study were not only indicative of greater light inputs but that the added solar energy input induced a shift in stream energy input away from allochthonous material derived from the forest canopy to aquatic plants plus decomposing forest debris introduced from logging. Also, rates of nitrogen assimilation and/or export processes associated with autotrophic production and/or direct volatilization increased in response to increased solar input and were most effective in removing in-stream TDN from section B.
3. Variation in transport of all N and P species between all stream sections

The foregoing discussion has provided evidence of possible mechanisms which explain differences in nitrate transport between individual open and closed canopy sections of East Creek. To expand on these observations and explanations, sampling was intensified to examine the transport of all forms of TDN and TDP through all of the four study sections. The enrichment experiment was also conducted at this time in section B to gain further insight into rates of nutrient assimilation and factors controlling nutrient disappearance. Although the study period was dominated by summer base flows, (Fig.3-3) two major storm events did occur in early September. Any spatial change in TDN and TDP flux as a function of stormflow was examined at that time. All nutrient concentration data are summarized in Fig.4-3 (NO₃⁻-N), Fig. 4-4 (NH₄⁺-N), Fig. 4-5 (HPO₄²⁻-P), Fig. 4-6 (DON) and 4-7 (DOP).
FIGURE 4-3 Spatial and temporal trends of NO$_3^-$-N concentrations (mg./l) in East Creek during summer 1979.
FIGURE 4-4 Spatial and temporal trends of NH₄⁺-N concentrations (mg./l) in East Creek during summer 1979.
FIGURE 4-5 Spatial and temporal trends of $\text{HPO}_4^{--P}$ concentrations (mg/l) in East Creek during summer 1979.
FIGURE 4-6 Spatial and temporal trends of DON concentrations (mg./l) in East Creek during summer 1979.
FIGURE 4-7 Spatial and temporal trends of DOP concentrations (mg/l) in East Creek during summer 1979.
a. **Consistency of variation directly related to overstream cover**

Spatial trends in nitrate concentrations (Fig. 4-3) were consistent throughout the period prior to section B enrichment. Levels over the range of 0.09 to 0.12 mg NO$_3^-$-N/l were characteristic under the forest canopy in Section A but levels dropped to less than the detectable limit of 0.02 mg/l or lower within 100 m in section B. On every sampling occasion these concentrations were consistent at that level through to section C.

In forest covered section C, however, a reversal of trends occurred. Within 180 m downstream of the section B-C boundary, concentrations consistently increased. A peak ranging from 0.08 to 0.10 mg/l was attained within 400 m which then dropped rapidly as the forest canopy opened up into the downstream cleared area (section D). Streamflows can only increase downstream so flow cannot explain the increase in concentrations under the forest canopy. There must have been either net in-stream mineralization and/or nitrogen fixation to contribute to the consistent increases in concentrations.

Trends observed before enrichment were recurrent throughout the enrichment period, but magnitudes of flux increased. This was a period of declining summer base flows and increasing temperatures. By ignoring the cliff in section B caused by nutrient additions, concentrations in water leaving section A were higher by 0.02 to 0.04 mg/l, yet declines to the detectable limit of 0.02 mg/l or lower were maintained within < 100 m of the forest edge. In spite of nutrient additions in section B,
levels lower than the detectable limit were maintained at the base of this section. Increased concentrations were also more pronounced in section C in that a peak of .12 mg/l was attained by mid August.

Also during mid-August, a steep nitrate concentration gradient was established across the pond located between W-12 and W-13 in section C. Streamflows were very low at this time and pond outflow in the surface stream channel disappeared for about two weeks. Flushing rates and mixing in the pond likely decreased, thereby favouring reducing conditions. The increase in ammonium concentrations (Fig.4-4) which must have resulted from ammonification of incoming nitrate and/or release of ammonium from the pond sediments supports this view. Thick formations of a Fe(OH)$_3$ precipitate in the stream channel downstream of the pond indicated a rapid increase in streamwater oxygen in comparison to the low levels in the pond. In section D, concentrations of both nitrate and ammonium ions consistently remained below detectable limits.

Apart from the conditions associated with the pond in section C, ammonium flux over time showed much less variation than did nitrate (Figure 4-4). Virtually no deviation from the detectable limit of .005 mg/l was noted in transport from section A to B. Occasionally, higher concentrations ranging from .008 to 0.19 mg/l were measured at W-1 but these were not consistent. Minor increases from .005 to .010 mg/l were consistent as the water moved from section B to C but returned to the detectable limit in section D.

This relative absence of NH$_4^+$ was likely due to its redox
association with nitrate. Ammonium is a reduced form of nitrogen and unlike nitrate is unstable in the highly oxidized environment of a mountain stream (Stumm and Morgan 1970). Thus, as long as temperatures are greater than 0° C, ammonium is readily oxidized to nitrate. Ammonium can also be removed from solution by biologic uptake which may be enhanced in open sections where autotrophs are potentially more dominant. Also, ammonium is an intermediary in the mineralization of DON and PON. In the absence of light-enhanced uptake processes in section A and C, slight increases in concentrations were likely due to the presence of this transitory mineralization phase.

Orthophosphate-P concentrations (Fig.4-5) at base flow were spatially more consistent than either of the inorganic nitrogen species. Without consideration of the mid-summer enrichment sequence, concentrations were always equal to or less than the detectable limit of .003 mg/l. Variation was undetectable within or between sections. Similarly, DOP concentrations (Fig.4-6) were barely detectable much of the time and variation was minimal. When all DOP data were combined before and during enrichment, the standard deviation was equivalent to the mean of .001 mg/l.

Unlike the temporal and spatial flux of dissolved inorganic forms of N and P, and of DOP, DON transport was highly variable (Fig.4-7), throughout all sections. Both spatial and temporal trends were undetectable. Concentrations of DON were always within detection limits, but the range was enormous, being as low as .01 and as high as 0.59 mg/l. Means and standard errors for the entire data set (before during and after enrichment) at
each sampling location which bordered stream sections are shown in Table 4-5. Nitrate concentrations are included for comparison of relative magnitudes.

Table 4-5. Means and standard errors of DON and NO$_3^-$-N concentrations before, during and after enrichment at East Creek sampling stations bordering each of the four stream sections.

<table>
<thead>
<tr>
<th></th>
<th>W-1</th>
<th>W-10</th>
<th>W-14</th>
<th>W-15</th>
</tr>
</thead>
<tbody>
<tr>
<td>mean DON</td>
<td>0.16</td>
<td>0.08</td>
<td>0.10</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>(0.17)</td>
<td>(0.06)</td>
<td>(0.07)</td>
<td>(0.06)</td>
</tr>
<tr>
<td>mean NO$_3^-$-N</td>
<td>0.09</td>
<td>0.02</td>
<td>0.09</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>(.02)</td>
<td>(.006)</td>
<td>(.05)</td>
<td>(.007)</td>
</tr>
</tbody>
</table>

Unlike nitrate flux, net retention or release of DON was not evident. Variation about the location means was sufficiently large that they could not be considered significantly different (2 factor ANOVA of Table 4-5 data; p<.05). This may suggest that uptake of DON approximated release within the stream. Since DON is thought to be negligible in groundwater, most DON in East Creek was likely derived from leachates of organic matter within the stream substrate. Much of this material can be mineralized by bacterial catalysts to more oxidized nitrogen forms. Some may
form particulates and precipitate out (Lush and Hynes 1974, 1978). Conversely, DON can be introduced to solution from leachable organic matter which was present either as unburned wood slash from clearcutting and slashburning, annually introduced allochthonous material, and/or turn-over of in-stream biota which release DON to solution. Any or all of these factors could have been active in producing the high variability. When recognizing the very patchy distribution of organic matter in each section, and variability in stages of decomposition within patches, a high degree of variation is to be expected. Similar conclusions were reached by Riece (1974) in studies of variation in leaf litter breakdown in a small stream in southern Michigan.

b. Disappearance rates of inorganic TDN and TDP

Beginning on July 19 and ending on August 26 a nutrient solution containing NaNO₃ and (NH₄)₂PO₄ was continuously introduced at W-2 in section B. The magnitude of enrichment relative to ambient concentrations over space and time has already been identified in Figs. 4-4, 4-5, and 4-6 for each of NO₃⁻-N, NH₄⁺-N, and HPO₄²⁻-P respectively. The downstream "cliff" that indicates complete disappearance of all enrichment materials occurred within about 100 m downstream from the enrichment source. Quantitative differences between observed (dilution plus in-stream removal) and expected (dilution only) concentrations expressed as a percent of the original enriched stream concentration are shown in Figs. 4-8, 4-9, and 4-10 for NO₃⁻-N, NH₄⁺-N and HPO₄²⁻-P respectively as determined from
eighteen sampling times over the enrichment period. Complete
\( \text{NH}_4^+ - \text{N} \) disappearance occurred over the shortest downstream
distance (15 to 45 m), \( \text{HPO}_4^{2-} - \text{P} \) over a moderate distance (45 to
75 m) and \( \text{NO}_3^- - \text{N} \) over the longest distance (110 m).
FIGURE 4-10 Differences in percent between observed (dilution plus in-stream removal) and expected (dilution only) \( \text{HPO}_4^{2-} \)-P concentrations downstream of enrichment (site W-3) in East Creek during summer 1979.

A: due to dilution only
B: due to dilution plus in-stream removal processes
FIGURE 4-9 Differences in percent between observed (dilution plus in-stream removal) and expected (dilution only) NH$_4$-N concentrations downstream of enrichment (site W-3) in East Creek during summer 1979.

A. due to dilution only

B. due to dilution plus instream removal processes
East Creek during summer 1979:
Concentrations downstream of enrichment (site M-3) in
in-stream removal and expected (dilution only) NO3-N

FIGURE 4-8 Differences in percent between observed (dilution plus
remaining in solution
Mean disappearance rates and accompanying standard errors between each sampling location were calculated by the following method. The percent loss of material from streamwater as it moved downstream from the enrichment source, corrected for reductions in concentrations due to dilution, was applied to the known rate of input at the enrichment source. This provided a quantitative measure of the weight of material passing the measurement location per unit time (1 hour was arbitrarily chosen). This measure then became the input to the next section with which disappearance over the next section was calculated. These calculations were iterated consecutively downstream until loss of the enrichment solution was no longer detectable. All calculations were corrected for wetted surface area in each section so that results could be expressed on a per unit area basis. Accuracy of all calculations were entirely dependent on accurate knowledge of rates of enrichment input. Since these rates were closely monitored at all times and were always measured during water sample collections, the method was considered reliable.

Means and standard errors of disappearance rates for each interval downstream of enrichment for the 18 sampling times are shown in Table 4-6.
Table 4-6. Mean disappearance rates¹ of inorganic N and P as measured at water sampling stations downstream of the enrichment source during July and August 1979².

<table>
<thead>
<tr>
<th></th>
<th>W-3³ to W-4</th>
<th>W-4 to W-5</th>
<th>W-5 to W-6</th>
<th>W-6 to W-7</th>
<th>W-7 to W-8</th>
</tr>
</thead>
<tbody>
<tr>
<td>NH₄⁺-N</td>
<td>9.4 (3.4)</td>
<td>1.3 (1.2)</td>
<td>0.2 (0.27)</td>
<td>U</td>
<td>U</td>
</tr>
<tr>
<td>NO₃⁻-N</td>
<td>20.7 (8.4)</td>
<td>12.4 (6.8)</td>
<td>6.7 (3.7)</td>
<td>4.5 (2.5)</td>
<td>1.2 (.9)</td>
</tr>
<tr>
<td>HPO₄²⁻-P</td>
<td>8.2 (3.3)</td>
<td>3.4 (1.8)</td>
<td>0.7 (0.3)</td>
<td>U</td>
<td>U</td>
</tr>
</tbody>
</table>

¹Measured as mg.m⁻².hr⁻¹  
²N = 18  
³W-3 is the enrichment location  
⁴U indicates that loss of the enrichment solution was undetectable

Note: Values in brackets refer to 1 S.E.

One overwhelming trend is evident; there were consistent decreases in disappearance rates in the downstream direction. This could be caused either by a decrease in uptake rates or conversion to other chemical species as a function of lower element concentrations in streamwater and/or variation in uptake rates as a function of substrate type (as was discussed in Chapter 2). These will now be examined in detail.
c. **Factors influencing disappearance rates**

i. **Element concentrations**

To examine the relationship of element concentration to disappearance rate, a regression analysis was performed for each of the respective element forms. Nutrient disappearance rates calculated for intervals between each downstream location from the enrichment point over all 18 sampling dates were included in the analysis. This resulted in a total of 100, 60, and 78 data points used for nitrate, ammonium, and orthophosphate regressions respectively. All variances were tested for homogeneity using Bartlett's Test (Sokal and Rohlf 1969) and appropriate transformations were made. Significance of independent variables was determined by a stepwise procedure and the best model was selected by comparing coefficients of determination and standard errors of the estimates. Emphasis was placed on obtaining lowest possible standard errors rather than highest possible coefficients of determination. All regressions were highly significant.

The nitrate disappearance-concentration relationship was best represented by a fourth degree polynomial (Fig.4-11), ammonium by a straight line (Fig.4-12) and orthophosphate by a third degree polynomial (Fig.4-13).
FIGURE 4-13 Relationship between concentrations and disappearance rates of $\text{HPO}_4^{2-}-\text{P}$ downstream of enrichment in East Creek during summer 1979.

$Y = -3.53 - 5.54x - 1.65x^2 - 0.13x^3$

$r^2 = 0.89$

Standard error ($Y$) = 0.46

95% Confidence Limits Included
FIGURE 4-12 Relationship between concentrations and disappearance rates of NH$_4^+$-N downstream of enrichment in East Creek during summer 1979.

\[
y = 15.43x - 1.04
\]
\[
r^2 = 0.95
\]

Standard Error (Y) = 0.28
95% Conf. Limits Included
FIGURE 4-11  Relationship between concentrations and disappearance rates of NO$_3$-N downstream of enrichment in East Creek during summer 1979.

\[ Y = -5.24 + 223x + 1727x^2 + 5941x^3 - 6481x^4 \]

\[ r^2 = 0.89 \]

Standard Error (Y) = 0.23

95% Conf. Limits Included
It is clear that in each case, higher ambient concentrations resulted in more rapid disappearance rates. This trend is similar to the findings of Meyer (1979) who reported greater uptake of orthophosphate at higher concentrations from in-situ experiments in a stream in New Hampshire. It is also well recognized that algae will take up inorganic nitrogen at greater rates as concentrations are increased (Owens and Esaias 1976, Conway et al. 1976). The relationship for this response by a single algal species culture exposed to a single nutrient spike has often been expressed as the Michaelis-Menten equation, a rectangular hyperbola similar to that describing enzyme kinetics; \( V = V_{\text{max}} \cdot \frac{s}{K_s} + s \) where \( V \) is the velocity of uptake, \( V_{\text{max}} \) the maximum velocity; \( s \) the concentration of nutrient, and \( K_s \) the half-saturation constant (the value of \( s \) when \( V = V_{\text{max}}/2 \) (Eppley et al. 1969)). More recent work (Conway et al. 1976) suggests that uptake of a limiting nutrient is better expressed as a third degree polynomial which can be explained by physiological responses of cells to varying nutrient concentrations.

Despite the similarity in form of these relationships to those in the current work, it must be emphasized that they are not directly comparable. Algal physiological research has concentrated on establishing physiological responses of a single species population to varying concentrations. The enrichment experiment reported here has treated an entire stream bed community over a selected reach with a relatively non-varying enrichment concentration of more than one limiting nutrient. The substrate community nearest the enrichment source received a
continuous high level enrichment whereas downstream sections received progressively lower concentrations. The x-axis, viewed left to right, in each of Fig.4-11 to 4-13 can then be considered a downstream gradient from the enrichment source. Uptake rates were greatest nearest the enrichment source and were relatively lower downstream.

Nitrate and orthophosphate uptake saturated at 21.8 mg/m$^2$/hr and 9 mg P/m$^2$/hr respectively with concentrations of 0.42 mg N/l and 0.09 mg P/l respectively. Ammonium uptake saturation was not detected. Uptake at moderate concentrations declined linearly with decreasing nutrient levels with the exception of nitrate. Nitrate uptake changed relatively little over a range of moderate concentrations from approximately 0.1 to 0.19 mg N/l. Above that range a directly proportional relationship was characteristic and below it rates declined exponentially.

Because uptake rates appeared strongly related to concentration, relative differences in the rate of substrate assimilation of nitrate, ammonium and orthophosphate were only comparable at identical element concentrations. These could be extracted from the element regressions. Uptake rates for ammonium, nitrate and orthophosphate at arbitrary concentrations of 0.10, 0.08, 0.06 and 0.04 mg/l respectively are shown in Table 4-7.
In all cases disappearance rates were \( \text{NH}_4^+ > \text{HPO}_4^{2-} > \text{NO}_3^- \).

Ammonium is a preferred nitrogen source to nitrate for algae and bacteria because it is in a reduced state (Owens and Esais 1976, Healey 1973) and nitrate may not be taken up until ammonium supplies are depleted (Healey 1973). Also, ammonium is transient in streams since it is rapidly oxidized to nitrate. The latter may account for the relatively low uptake rates of nitrate at its lower concentrations. It is not only a less preferred nitrogen source for microorganisms but oxidation of introduced ammonium is adding to the nitrate pool.

Rapid orthophosphate uptake is likely related to its high affinity for adsorption on organic particles and also to rapid sorption by algae and bacteria (Gregory 1978). Very low ambient P concentrations in combination with these relatively rapid uptake rates suggests that P is limiting in East Creek. This is in agreement with Stockner and Shortreed (1978) who demonstrated
P limitation in Carnation Creek a coastal stream of B.C. by measuring algal biomass responses to selected N and P additions in troughs. Conway et al. (1976) have suggested that rapid uptake of a limiting nutrient is due initially to the filling of cellular nutrient pools. Harold (1966) and Stewart and Alexander (1971) have shown that P storage is in the form of polyphosphates and these are only degraded to supply metabolic needs when external P again becomes limiting (Baker and Schmidt 1964).

It is likely that the uptake rate-concentration relationship for any nutrient ion can be related to the availability of nutrient ions. At high concentrations, ions per unit volume of water are abundant, and, since the stream is always well mixed, there are more ions available for substrate uptake. Under these conditions uptake rates will continuously increase with increasing concentrations until cellular absorption sites are saturated and no more ions can be removed per unit substrate surface area. Uptake saturation shown in Fig.4-10 and 4-12 may be related to this process.

ii. Substrate type

The proportion of each substrate type between water sampling stations is shown in Table 4-8. The data represents the percent composition of various substrate types as determined from a late summer survey in which the linear composition was measured. Measurements reflect proportions of stream length, not stream area.
Table 4-8. Percent composition of substrate types between water sampling stations in East Creek.

<table>
<thead>
<tr>
<th></th>
<th>BR</th>
<th>MG</th>
<th>MGF</th>
<th>MGL</th>
<th>MGLF</th>
<th>DJ</th>
<th>LF</th>
<th>SLF</th>
<th>F</th>
<th>GL</th>
</tr>
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<tr>
<td>W3-4</td>
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<td>39.7</td>
<td>6.5</td>
<td>42.4</td>
<td>0.0</td>
<td>11.4</td>
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<td>0.0</td>
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<tr>
<td>W4-5</td>
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<td>66.0</td>
<td>5.8</td>
<td>16.7</td>
<td>0.0</td>
<td>11.6</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
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<td>W5-6</td>
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<td>64.5</td>
<td>0.0</td>
<td>14.9</td>
<td>0.0</td>
<td>20.6</td>
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<td>0.0</td>
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<tr>
<td>W6-7</td>
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<td>8.0</td>
<td>12.5</td>
<td>1.5</td>
<td>22</td>
<td>0.0</td>
<td>3.7</td>
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<td>2.5</td>
<td>0.0</td>
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</table>

1Substrate type abbreviations refer to the following associations:

BR  bedrock
MG  mixed gravels and cobble (<25 cm dia)
MGF mixed gravels with fine particulate organic matter
MGL mixed gravels with large particulate organic matter
MGLF mixed gravels with large and small particulate organic matter
DJ  debris jam
LF  large and small particulate organic matter
SLF sand with large and small particulate organic matter
F  fine particulate organic matter
GL  medium sized gravels with large particulate organic matter
Within all sections there was an overwhelming dominance of mixed gravel either with or without particulate organic matter. Debris dams were also abundant in all sections. Most importantly, there were no clear increases or decreases in any substrate component in the downstream direction. Thus, the linear or curvilinear trends in nitrate, ammonium or orthophosphate uptake cannot be explained by variation in substrate composition. However, since gravels dominated the substrate, periphyton which occupy the gravel surfaces may be most important in assimilating introduced nutrients. This is particularly suggestive of the active role of periphyton since Sloane (1979) found organic debris to be highly ineffective in assimilating nitrate from solution.

d. Effect of stormflow

Beginning on September 1, the first frontal storm since late spring produced a nearly constant input of rain to the study area for about 48 hours. Rain subsided to showers through to September 6, but a second storm produced more precipitation on September 8. Total precipitation input for the duration of these disturbances was 130.1 mm. Discharge increased 22 fold over summer base flow both on September 3 and September 8 as shown in Fig.3-3. Water sampling for analysis of TDN and TDP transport at all stations was conducted two days prior to the first storm, during peakflow on September 3 and continued on September 5, 6, 9 and 14 to monitor several phases of both stormflows.

Nitrate responses were most dramatic (Fig.4-3).
Concentrations near the peak of the first stormflow (September 3) increased up to 7 fold over levels noted immediately before the onset of rain. However, by the next sampling episode (September 5) these had returned to low levels even though discharge was still considerably greater than baseflow (Fig.3-3). Large increases in DON were also noted, beginning on the rising limb of the first storm hydrograph (Fig.4-6), but, unlike nitrate flux, high concentrations were maintained through to the last sampling day. Ammonium concentrations changed little during the storm period (Fig.4-4). Corresponding export from W-1 and W-10 and flux through section B increased many fold for all forms of TDN and at each location as shown in Table 4-4 (export in first two weeks of September).

From these observations, changes in TDN flux over what was characteristic in the preceding summer months were apparent. Firstly, the increase in water volumes transported through the entire watershed must have resulted in a mobilization and increased stream loading and export of all forms of TDN. This suggests that as the rate of water movement increases in soils and thereby increases stream volumes, dissolved nutrient chemicals transported in that water and the terrestrial biogeochemical processes controlling those losses can gain increasing importance in the regulation of streamwater chemistry. Most of the mobilized material was likely that which had accumulated in the forest floor, soils, and organic matter of unwetted stream margins due to mineralization and nitrification over the preceding dry weeks. These processes had been proceeding for the duration of the summer, but water
movement had been insufficient to mobilize the end products. Similarly, the stream margins that had been unwetted for most of the summer were exposed to a sudden rise of the stream. Thus, all forms of TDN would be leached from newly wetted streambed organic matter. (c.f. Claridge 1970). These findings support the work of Sloane (1979) and Fisher and Likens (1973) in which terrestrial control of streamwater chemistry on an annual basis is strongly advocated.

The second important point to note is that where the transport of all species of TDN increased, the nature of the increase varied between species. During the rising limb of the hydrograph of the first storm, nitrate was exported in a pulse. Since nitrate is a highly mobile ion, the magnitude of the pulse was likely regulated by the rate of water movement. In the East Creek watershed, rates of water movement are very great indeed during storm activity (Feller 1974). This is thought to be due to channelling of water into macrochannels in the soil matrix (Feller and Kimmins 1979). Thus, short-term mass movement of nitrate, as observed here, is not surprising. Also, the equally rapid return to very low concentrations suggests that all accumulated nitrate was transported through the entire watershed within the short period of the first storm hydrograph, perhaps within the 24 hour period of the rising limb. Increases of DON concentrations were also rapid but in being maintained throughout both storm periods they may reflect a longer term leaching of particulate organic matter, a primary source likely being allochthonous material in streambed margins. Much of this particulate material would likely be moved downstream with
increasing stream power, but in turn would be retained at debris dam structures to continue leaching and enter further processing pathways. This leaching effect is then quite unlike the pulsing nature of nitrate which is not leached, but moved from a storage pool with the passage of water. When that pool is depleted, the pulsing behaviour is no longer apparent and concentrations return to low levels.

Changes in ammonium transport were least dramatic. This might be due to its unstable nature in turbulent water. Concentrations did not change through the stormflow period, but, as a result of increased water flow, transport did increase. Ammonium is not readily mobile in soils so much of the increase must have been derived from in-stream organic matter in a transient stage of mineralization.

The third and final point of difference was a considerable increase in TDN retention in section B. In the first two weeks of September, in-stream retention of TDN increased by 67% over that for the entire month of August (Table 4-1). Since DON and NH$_4^+$ losses from section B increased, the increase in TDN retention was entirely due to a 610% increase in NO$_3^-$-N retention. Clearly, stream power associated with the storm activity was not sufficient to scour and disrupt the assimilation potential of the processing substrates. Quite the opposite occurred. An increase in stream size resulted in water contact affecting a greater substrate area of the streambed. Because the water flow was not destructive, assimilation increased in proportion to the area affected and also to the activation rates of processing substrates (uptake by microbes and periphyton for
example). Working against the increased size of active substrate was a decrease in ion-to-substrate contact time. However, the increase in nutrient ion transport may have overwhelmed any reductions in contact times, so a greater mass of nitrate was available for uptake over an expanded and newly activated surface area.

Change in TDP transport as a function of stormflow was much simpler to interpret. Orthophosphate concentrations essentially didn't change from below detectable limits throughout the entire storm period (Figure 4-5). Thus, meaningful changes in export were undetectable (Table 4-2). DOP concentrations did increase slightly over pre-storm levels (Fig.4-7). This was likely due to increased leaching of organic phosphorus compounds from newly wetted organic matter. The overall effect was a 28 fold increase in export of DOP at W-1 and a 14 fold increase at W-10 (Table 4-2).
CHAPTER 5

THE ROLE OF PERIPHYTON IN CONTROL OF TDN AND TDP TRANSPORT

A. Introduction

The paucity of information on nutrient dynamics in small streams has rendered much of the preceding chapter descriptive. It is clear that East Creek does have internal processes which can influence the flux of TDN and TDP lost from the surrounding terrestrial environment. However, I have provided only a tentative understanding of the regulatory biogeochemical processes involved. Explanations advanced in Chapter 4 must be accepted with due caution and many must be considered only as testable hypotheses. However, Chapter 4 did establish the fundamental importance of light and its role in enhancing TDN and TDP retention in East Creek. Therefore, in those stream sections where direct solar radiation was unimpeded, the following hypothesis concerning TDN and TDP assimilation by periphyton can be proposed:

Within a unit of stream area during summer weather and base flow conditions, the amount of N and P assimilated by periphyton is equal to the total amount of TDN and TDP removed from solution per unit time.

To test this hypothesis, the in-situ nutrient enrichment experiment in section B was designed not only to follow nutrient uptake but also to record change in N and P content in periphyton biomass during a period of summer base flow. Biomass estimates and total nitrogen and phosphorus contents of the periphyton biomass were established in the control (upstream of
enrichment) and treatment (downstream of enrichment) sections before enrichment was begun. Similar measurements were maintained for the five weeks of enrichment and subsequently after enrichment for an additional four weeks. By employing this design, nitrogen and phosphorus assimilated by periphyton in the treatment section (corrected with control levels) could be compared to that artificially introduced in the enrichment solution. The relative importance of periphyton as compared to the "black box" of other processes could then be established for the environmental conditions under which the experiment was run. The fundamental approach was to alter the periphyton metabolism sufficiently to record change in biomass.

B. **Methods and Materials**

1. **Location and description of sampling stations.**

   Early in June 1979, 17 periphyton sampling stations were established in section B as shown in Fig.5-1 (stations labelled with an 'EP' prefix). A length of 10m was used for sampling at each station. These stations were not stratified according to riffle or pool classes. All areas were moderately agitated or had laminar flow characteristics at baseflow during May and so, by the definition of Bishop (1973), were considered riffles. As base flow declined during summer, however, small side pools did form at the stream edges but these were not continuous with the main riffle streamflow and so were not sampled. Also, Wetzel and Likens (1979) have defined pools as areas of deposition. The only site where obvious deposition was noticeable was in the
FIGURE 5-1 Periphyton sampling locations in section B of East Creek.

To Section C

Study Section B
weir pond located at W-10 (Chapter 4).

Five replicate sampling stations were located in the control area upstream of the enrichment site (EP-1 to EP-5), each within a representative riffle section and within easy access of a streamside trail. EP-5 was located immediately upstream of the enrichment source. Stations EP-6 through EP-11 were relatively closely spaced so as to achieve adequate replication in the section where introduced nutrient concentrations declined rapidly (Chapter 4). Enrichment procedures and apparatus described in Chapter 4 also apply to this chapter since both Chapter 4 and Chapter 5 experiments were run concurrently. Initial measurements of nutrient assimilation during the first few days of enrichment indicated that the entire load of introduced N and P was removed from solution within 100 m of the enrichment source. Essentially, this provided 3 nutritionally distinct sections for periphyton sampling which were labelled as follows:


2. Treatment: EP-6 through EP-9; downstream of enrichment and was exposed to up to a 20 times increase in ambient concentrations.

3. Control (2): EP-10 through EP-17; downstream of enrichment but was never affected by above ambient TDN or TDP concentrations.
2. Units of measurement.

In lotic environments, periphyton is collectively made up of both macrophytes (filamentous forms) and microphytes (algal and bacterial unicells). Methods for enumeration of these two groups is very different -- cell counts for unicells (Vollenweider 1969) and plant weight for macrophytes (Mueller-Dombois and Ellenburg 1974, Chapman 1976). In this study, consideration of these traditional techniques was not necessary since the objectives were to: (1) measure any change in periphyton biomass as a collective group, and (2) measure any change in nitrogen and phosphorus stored in the total periphyton biomass as a function of increased TDN and TDP concentrations in solution. For this purpose, total N and P in dried samples was considered an adequate unit of measurement. Dried samples did, however, contain not only algae, fungi and bacteria but also benthic detritus which can be variable by weight between locations and therefore lead to large variation in results. To avoid this problem, the response in algal biomass alone was measured by analysis of chlorophyll concentrations in each sample. Pigment concentration analysis can also be inaccurate, however, in that extraction may not be complete in 90% acetone. Improved extractions have been noted with the use of dimethyl sulfoxide (Shoaf and Liuin 1976) or methanol in place of acetone (Tett et al 1978). However, in spite of these findings, acetone extractions are still widely used (Wetzel and Likens 1979) and were employed in this study. It is assumed that extraneous error in determination of pigment concentration is mostly laboratory-based and constant throughout all analyses.
3. **Field collection of periphyton samples.**

Artificial substrates were not used in this study since they have been found not to be representative (Tippet 1970, Siver 1977, Kann 1978, Tett et al. 1978, Tuchman and Stevenson 1979).

The entire stream was considered a transect along which random sampling could be conducted. Sampling proceeded at each site by, (1) locating the middle of the 10 m long sampling section, (2) flipping a coin to decide whether to sample upstream or downstream of the midpoint and (3) selecting from a random numbers table (Zar 1974) a distance from the midpoint for obtaining the sample. All samples were collected at midstream in order to minimize variation due to current velocity.

At the sampling location a 0.06 m² steel quadrat was placed firmly on the substrate and all surface gravel and cobble was removed from within the quadrat to the depth of subsurface sand and placed in a small bucket containing 1 litre of tapwater. Quadrat size was determined by ensuring that the quadrat surrounded all rock sizes which could be encountered in the sampling program. All material coating the rocks was brushed into the bucket solution using a light duty wire brush. Several trials were made to test the efficiency of this cleaning method by conducting repeated brushings of the same rocks and measuring the dry weight of material removed at each time. After brushing was complete, samples were transferred to 1 litre polyethylene bottles, and immediately placed in an ice chest. All samples were transported to the laboratory live and were processed for...
further analyses upon arrival. Using this method, all 17 stations were sampled over a two day period each week.

4. Laboratory.

Upon arrival in the laboratory samples were partially shredded with forceps and mixed in a 1500 ml capacity glass dish. Two subsamples were extracted; (1) 15 ml for determination of chlorophyll-a concentration, and (2) 500 ml for combined analysis of dry weight and total N and P. The volume of the remaining sample was measured after extraction of subsamples and then discarded. Results of all analyses were corrected to total sample volume and thereby to unit surface area of the stream from which the sample was removed.

Subsamples used for chlorophyll-a analysis were filtered at 0.67 atmosphere through a 0.45 um mesh membrane filter. Acidification was prevented by adding 2 to 3 drops of magnesium carbonate suspension during filtration. Membrane filters were removed from the apparatus, folded in 9 cm diameter Watman #1 papers and transported frozen to the B.C. Environmental Laboratory located on the University of B.C. campus. Within 2 weeks, the chlorophyll-a concentrations were determined from the frozen filters by standard methods of extraction in 90% acetone (APHA 1976, Strickland and Parsons 1972).

The second subsample (500 ml) was filtered through preweighed Reeve Angel 984-H glass fibre filters at 0.67 atmospheres, dried at 50° C for 24 hours and weighed after allowing to cool to room temperature. Weights were corrected for filter weight loss on filtering. After weighing
approximately 0.1 gm of material was removed from each sample filter by scraping with a sharp scalpel and placed in Corning Pyrex digestion tubes for analysis of total N and P by a semimicro Kjeldahl technique. The sample was digested in 5 ml of digestion solution (100 gm potassium sulphate; 1 gm selenium; 1 litre conc. sulphuric acid) for about 24 hours (until solution was clear). The digestion solution was diluted to 50 ml with distilled water and analysed for nitrogen and phosphorus with a Technicon Industrial Automatic Analyser II (Technicon Industrial Systems 1973). Total N and P were corrected to the total dry weight per unit area from which the sample was taken.

5. Statistical Methods.

Log transformed means and standard errors were calculated from the replicate samples for each stream section before treatment, during treatment, and after treatment. Transformations were used for correction of heterogeneous variances. Results were expressed graphically. Also a 2-way ANOVA and F-test was used to aid in identifying any real treatment effects. Factors used in the analysis were location (levels=3; control, treatment and below treatment sections) and time (levels=3; before treatment, during treatment, and after treatment).
C. Results and Discussion

1. Efficiency of organic matter removal from natural rocks.

At each sampling site, the mechanical brushing of rocks to remove periphyton was usually completed in about twenty minutes. This was sufficient time to clean the rocks of the slippery feel caused by cellular excretions (Allen 1971). Repeated brushings of replicate rocks indicated that more than 95% of the total amount of material was removed in the first brushing (Fig. 5-2). This method of brushing to a nonslippery feel was used throughout the sampling program.

2. Periphyton biomass response to enrichment.

Means and standard errors for biomass expressed as weight of chlorophyll-a and N and P content in biomass are shown in Fig. 5-3, 5-4, and 5-5 respectively for each of before, during and after treatment.
FIGURE 5-2 Data showing the efficiency of the brushing technique used for removing periphyton from natural rocks.

n=10
error bars=1 standard error
FIGURE 5-3 Significance of differences between means of location and time combinations for standing stock (chlorophyll-a) of periphyton in the enrichment experiment conducted during summer 1979.

a. Transformed data showing significance of differences

b. Original means

Section: *  
Time: *  
S x T: n.s.  
p<.05

error bar = ± 1 S.E.
FIGURE 5-4 Significance of differences between means of location and time combinations for biomass nitrogen in periphyton in the enrichment experiment conducted during summer 1979.

a. Transformed data showing significance of differences

<table>
<thead>
<tr>
<th>Section:</th>
<th>Time:</th>
<th>S x T:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>*</td>
<td>n.s.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>p &lt; .05</td>
</tr>
</tbody>
</table>

error bar = ±1 S.E.

b. Original means
FIGURE 5-5 Significance of differences between means of location and time combinations for biomass phosphorus in periphyton in the enrichment experiment conducted during summer 1979.

a. Transformed data showing significance of differences

Section: *
Time: *
S x T: n.s.
p<.05
error bar = ±1 S.E.

b. Original means
There was clear spatial separation of each experimental section. The enriched section had greatest biomass throughout the time series, irrespective of nutrient enrichment. The upstream control had least biomass. Nutritionally, however, the section downstream of inorganic treatment effects was least rich throughout the time series, again irrespective of enrichment. Since detailed sampling was not conducted to evaluate biochemical and/or physical characteristics which could have affected periphyton biomass and nutritional status, reasons for the separation are not clear. Many parameters such as variation in lateral shading from riparian vegetation, microenvironmental conditions of substrate and current velocities, slight shifts in channel aspect are just a few which could have contributed to the effects.

A second similarity was that there was a mid-summer decline in periphyton biomass and nitrogen and phosphorus content of the biomass in the two sections not influenced by enrichment. The decline may have been related not only to extremely low nutrient concentrations but also summer base flow was very low (Fig.3-3). Thus, the area of stream in which periphyton could metabolize was considerably reduced over that of the earlier sampling period. Late summer periphyton was influenced by quite opposite environmental conditions. Stormflow effects (Chapter 4) increased stream size, and thereby increased the active substrate surface area. Dissolved inorganic nutrients were also in higher concentrations at that time (Chapter 4). Overall, periphyton standing stocks and nitrogen and phosphorus content increased with near equal magnitudes in all sections in late
summer in comparison with midsummer levels.

The third, and in the context of this thesis, the most important similarity between parameters was that the 20 fold enrichment of N and P did not produce dramatic change in either standing stocks or biomass N and P. Differences in slopes of lines for each section through the time series are apparent but only in the sense that the enrichment lessened the magnitude of the midsummer decline in each parameter. The analyses of variance accompanying Fig.5-3 to 5-5 also indicate that the interaction of the 3 levels for each factor; time and stream section, was not significant. This suggests that treatment effects were inadequate to overcome environmental variation.

Realizing that an F-test is only an aid in analysis the question arises as whether to rely on the statistical significance test or to recognize separation of means and standard errors which are apparent graphically. To resolve this problem a 3 dimensional surface showing temporal and spatial trends was used since it provided a single image, not only of the magnitude of treatment effects, but also the relationship of these effects to environmental variation. It also provided a view of downstream gradients which are otherwise lost in the above analysis. A biological rather than statistical decision could therefore be made to evaluate the significance of enrichment effects. All methods for generating the image are similar to those described in Chapter 4. Since all parameters exhibited similar patterns, the 3-D image for chlorophyll-a only was arbitrarily chosen for discussion and is shown in Fig.5-6.
Clearly, Fig.5-6 shows that although the enrichment appeared to enhance standing stocks, there were sections where environmental variation was excessive throughout the time series. In some locations, biomass increased greatly yet was not at all influenced by increased N and P concentrations. There were obvious increases in standing stock immediately downstream of the enrichment site, but it cannot be concluded that any change in the entire area which was subject to increased N and P availability was caused by enrichment. This is because equally dramatic changes in environmental variation occurred with no relation whatsoever to treatment or location.

It is concluded, therefore, that the quantitative role of periphyton in assimilating nitrate, ammonium and phosphate could not be assessed using the methods employed. The difference between treatment and control means of biomass N and P cannot be conclusively related to treatment and so the amount of N and P introduced to the stream cannot be compared to that in periphyton biomass. The fate of the introduced material therefore remains unclear.

The main purpose of the approach used here was to enrich many fold over ambient concentrations and thereby change the physiological state of the periphyton community to the extent of significantly changing biomass. Since this did not occur, it is also concluded that the magnitude of enrichment was insufficient for the approach that was used. A 50 or perhaps 100 times increase might have been more practical. The 20 times enrichment quite likely changed the physiological activity of the periphyton. However, changes which could include alkaline
phosphatase activity (Perry 1972), N and P turnover (after Elwood et al. 1980), assimilation and uptake rates (Wright and Burnison 1979), or overall productivity (Bott et al. 1978) were not assessed.

In this study, the hypothesis that periphyton were most important in assimilating introduced inorganic nitrogen and phosphorus remains unresolved. The test presented here has been a pioneering step, however, and does identify the need for alternative approaches to the study of periphyton function in nutrient cycling. Tracer levels of radiolabelled materials such as $^{32}$P or $^{14}$C could be used to identify nutrient spiralling rates and magnitudes under various environmental conditions. The relative importance of microorganisms and algae could be assessed with incubation measurements of uptake and turnover using $^{14}$C and $^{3}$H - glucose (Wright and Burnison 1978). If these methods are not feasible, enrichment doses could be used to assess colonization rates as a function of enrichment. Any one of these could contribute to a better understanding of not only periphyton function but also stream ecosystem function in the nutrient cycling of a small watershed.
CHAPTER 6

CONCLUSIONS AND TESTABLE HYPOTHESES

This study has examined an alternative hypothesis concerning the regulation of nutrient loss from small watersheds. During summer months when stream power is low but light inputs and streamwater temperatures are relatively high, the benthic community of a small stream is highly efficient in assimilating dissolved inorganic nitrogen and phosphorus. Rates of assimilation are at least in part regulated by concentrations of dissolved ions in solution. It is also clear that the assimilation of nutrients by a stream ecosystem is related to the intensity of light reaching the stream. Abrupt changes in light inputs which occur in the transition from forested to clearcut sections of a watershed, can result in abrupt changes in assimilation of the inorganic ions. This suggests the following hypothesis:

An increase in solar energy supply to a stream ecosystem increases nutrient spiralling rates and rates of nutrient assimilation. (H1)

The findings in this thesis raise questions as to the seasonality of in-stream control. During fall and winter months, stream power is several times greater than during summer and light inputs and in-stream temperatures are relatively low. These observations lead to the hypothesis that:
Rates of assimilation of introduced inorganic nutrients decline during conditions of low stream temperature and high stream power either in combination or acting alone. (H2)

It is also apparent from this study that expansion of the scope of investigation is necessary. The findings presented here may be unusual since the summer of 1979 was unusually dry (U.B.C Research Forest meteorological data). Stream power, light and temperature may have had extreme values. This leads to the hypothesis that:

The assimilation rate of N and P in East Creek in summer 1979 was not indicative of average nutrient processing conditions for a small stream in southwestern British Columbia. (H3)

Both H2 and H3 could be tested either by tracing the rate of disappearance of introduced nutrients or by tracing rates of recycling in radiotracer pathways under a variety of environmental conditions in successive years. This kind of data may suggest that:

Stream power, light inputs and stream water temperature are the environmental parameters responsible for regulating rates of nutrient spiralling in streams on an annual basis. (H4)

These first four hypotheses identify questions pertaining to the functioning of the stream ecosystem as a single unit. Additional questions are proposed which relate to the functional importance of active nutrient processing compartments within the ecosystem. The present study has suggested that high light
inputs and therefore high stream temperatures can enhance nitrogen retention. Since denitrification is known to be significant only in the presence of deep organic sediments and has not been associated with organic matter accumulations in small turbulent streams, the hypothesis remains that:

Under summer light and temperature conditions, periphyton based spiralling processes regulate nutrient transport in small turbulent mountain streams at base flow. (H5)

Methods for evaluating this problem have been proposed in Chapter 5. H4 assumes of course that:

Denitrification is not active in removing nitrogen from solution in small turbulent mountain streams. (H6)

which could be examined by assessing $^{15}$N activity in laboratory columns (Sain et al. 1977).

Immobilization of dissolved N and P is based mainly on heterotrophic activity, so its importance in regulating nutrient transport may be related to the abundance of organic matter in the stream and to the extent of overstream cover so that:

There is a positive relationship between the amount of refractory organic matter and rates of immobilization and mineralization. (H7)

and

There is a positive relationship between the amount of light-restricting over-stream cover and rates of immobilization and mineralization.
Relative activity measurements (\(^{14}\)C and \(^{3}\)H-glucose) of algae and microorganisms in recirculating chambers might be one method of approaching this problem. The need for a high degree of replication would be a problem not only because of the variation imposed by the radiotracer techniques but also because of the variation inherent in the distribution of organic matter. To avoid this problem of adequate replication of chamber incubations, actual in-situ spikes of \(^{14}\)C and \(^{3}\)H-glucose could be used to assess relative recycling rates (after Elwood et al. 1980).


Toetz, D.W. 1971. Diurnal uptake of NO\textsuperscript{−} and NH\textsuperscript{+} by a Ceratophyllum periphyton community. Limnol. Oceanogr. 16:819-822.


APPENDIX A

THREE DIMENSIONAL PLOTTING ROUTINE

This is the source program for producing 3D perspective plots of a number of successive surfaces whose X axis represents 'Time' (up to 100 days), the Y axis 'Location' N (up to 20) and the variable in question for water chemistry data collected over a time series (day and time of day).

SOME VARIABLE DEFINITIONS:

DIST(I) = Distance to sample station from initial location uppermost on the stream reach.
ZSCALE = Some real number greater than the maximum Z value on the surface to be plotted. ZSCALE sets the height of the reference cliff which is displayed at the extreme sides of each plot. All heights are scaled in relation to ZSCALE.
DAY = Time the program is in starting at 1
NAMOUNT = Counter for the variable plotting
IDIST = Number of the gridline for station allocation
FMT = Logical format to allow data in any format to be used
VAPIVAR = Number of variables
VANLOC = Number of locations
NX = Number of grid lines on 'Distance axis'
DELTAT = Interval between grid lines on 'Time axis'
NY = Number of grid lines on time axis; calculated in the program
DELTAX = Interval between grid lines on distance axis. This is calculated in the program.
VPLOT = Logical variable (T or F) for each of 20 allowed variables. T assignments will be plotted. F's will not.

...........PROGRAM START

REAL Z(20,130,70),DIST(20),ZSCALE(20),VAR(20)
INTEGER FMT(20),DAY,NAMOUNT(20,130,70),IDIST(20)
LOGICAL VAPLOT(20)
COMMON Z

............SET SOME VARIABLES


READ(5,20)FMT,NVAR,NLOC,NX,DELTAT,(DIST(I),I=1,NLOC)
20 FORMAT(20A4/12,2I4,F5.0/20F4.0)
DELTAX=DIST(NLOC)/(NX-1)
C
C............SET GRID LOCATIONS FOR DISTANCE
C
   DO 30 I=1,NLOC
30   IDIST(I)=DIST(I)/DELTAX+2.5
C
C......READ WHICH VARIABLES IN DATAFILE ARE TO BE READ
C
   READ(5,35)(VPLOT(I),I=1,NVAR)
35   FORMAT(20(L1,1X))
C
C.............SET VERTICAL SCALE FOR EACH VARIABLE
C
   READ(5,36)(ZSCALE(I),I=1,NVAR)
36   FORMAT(20F4.0)
C
C.......CHANGE CONCENTRATION UNITS TO INCHES ON PAPER
C
   DO 37 I=1,NVAR
37   ZSCALE(I)=10./ZSCALE(I)
C
C.....ASSIGN MISSING VALUES A LARGE NEGATIVE NUMBER
C
   NX = NX + 1
   DO 38 I=1,NVAR
      DO 38 J=1,NX
         DO 38 K=1,70
            NCOUNT(I,J,K)=0
38      Z(I,J,K)=-1.E30
C
C.........READ IN THE DATA
C
   NY=-1
40   READ(5,FMT,END=60)DAY,ILOC,(VAR(I),I=1,NVAR)
C
C.........SCALES POINTS ON THE TIME AXES
FDAY=DAY
   ITIME=FDAY/DELTAT+2.5
   IF(ITIME.GT.NY)NY=ITIME
C
C....START THE COUNTER APPLYING SEQUENTIAL DISTANCE
C (LOCATION) AND TIME DATA TO THE GRID FOR
C Z VALUES OF EACH VARIABLE
C
   DO 50 I=1,NVAR
      IF(VAR(I).LE.0) GO TO 50
      NCOUNT(I,IDIST(ILOC),ITIME)=
         $NCOUNT(I,IDIST(ILOC),ITIME)+1
      IF(NCOUNT(I,IDIST(ILOC),ITIME).EQ.1)
         $Z(I,IDIST(ILOC),ITIME)=VAR(I)*ZSCALE(I)
         $Z(I,IDIST(ILOC),ITIME)=Z(I,IDIST(ILOC),ITIME)+VAR(I)*ZSCALE(I)
CONTINUE
GO TO 40

C..... AVERAGES HEIGHTS AT THE GRID INTERSECTIONS
C
CONTINUE

DO 70 I=1,NVAR
   DO 70 J=1,NX
   DO 70 K=1,1NY
   70 IF(NCOUNT(I,J,K).GT.1)Z(I,J,K)=
      $Z(I,J,K)/NCOUNT(I,J,K)
   NX=NX+1
   DO 90 I=1,NVAR
   DO 80 J=1,NX
60   Z(I,J,1)=0
   DO 85 J=1,NY
70   Z(I,1,J)=0.
   DO 85 J=1,NY
80   Z(I,1,1)=10.
   Z(I,1,NY)=10.
   Z(I,1,1)=10.
90 CONTINUE
   DO 200 I=1,NVAR
200 IF(VPLOT(I))CALL PERSP(NX,NY,ZSCALE(I),I)
   CALL PLOTND
   STOP
END

SUBROUTINE PERSP

Persp first calls INTER to place interpolated values in the missing data points. Then HIDE (UBC SURFACE, p.12) is called to generate the perspective plots.
PERSP reads input data from logical unit 5, prints a table of the plotted values on unit 6 and sends the generated plot to unit 9 which defaults to -plot#.

SUBROUTINE PERSP(NX,NY,ZSCALE,IVAR)
DIMENSION Z(130,70),Z1(20,130,70)
COMMON Z1
CALL HDCTRL('CLIP','OFF','CROSS','ON
$','TERSE','ON ','XRATIO',40.,
$,'YRATIO',3.5,'ZRATIO',0.2)
   DO 30 I=1,NX
   DO 30 J=1,NY
30   Z(I,J)=Z1(IVAR,I,J)
C FILL IN MISSING DATA POINTS WITH
C INTERPOLATED VALUES.
NXM1=NX-1
CALL INTER(2,NXM1,NY,Z,NX)

C
C PRODUCE PLOT.
CALL HIDE(NX,NY,Z,130)
CALL PLOT(44.,0.,-3)
RETURN
END

C
C
SUBROUTINE INTER

Subroutine INTER generates interpolated
Z values from a set of data points scattered
on a grid. The area surrounding each grid
intersection is divided into four quadrants.
The closest data point in each quadrant is
selected and the value of the intersection is
set equal to the average of the selected data
points weighted by 1/(D*D), where D is the
distance from the data point to the grid
intersection being evaluated. Of the supplied
Z array containing the scattered data points,
only the region between Z(FDAY,*) and Z(LDAY,*),
inclusive, is analysed or searched. All days
less than FDAY or greater than LDAY are ignored.
INTER returns array Z filled with interpolated
values.

SUBROUTINE INTER(FDAY,LDAY,IY,Z,NX)
INTEGER FDAY
REAL Z(130,70),ZTEMP(130,70)
COMMON /A/ SUMS,SWT,K,L

DO 100 K = 2,IY
    DO 100 L = FDAY,LDAY
        SUMS = 0.
        SWT = 0.
        ZTEMP(L,K) = Z(L,K)
        IF(Z(L,K) .NE. -1.E30) GO TO 100
        IF(L .LT. LDAY) CALL QUAD(L+1,LDAY,2,K,Z)
        IF(K .GT. 2) CALL QUAD(FDAY,L,2,K-1,Z)
        IF(L .GT. FDAY) CALL QUAD(FDAY,L-1,K,IY,Z)
        IF(K .LT. IY) CALL QUAD(L,LDAY,K+1,IY,Z)
        ZTEMP(L,K) = SWT / SUMS
    100 CONTINUE

DO 120 K = 2,IY
    DO 120 L = FDAY,LDAY
        Z(L,K) = ZTEMP(L,K)
    120 CONTINUE
RETURN
END
SUBROUTINE QUAD(ILOW, IHIGH, JLOW, JHIGH, Z)
REAL Z(130, 70), ZDIST(130, 70)
COMMON /A/ SUMS, SWT, K, L
MIN = 10000
DO 30 J = JLOW, JHIGH
DO 30 I = ILOW, IHIGH
ZDIST(I, J) = 10000.
IF(Z(I, J) .EQ. -1.E30) GO TO 30
N = (I - L) * (I - L) + (J - K) * (J - K)
ZDIST(I, J) = N
IF(N .LT. MIN) MIN = N
CONTINUE
IF(MIN .GE. 10000) RETURN
TEMP = 1. / MIN
DO 40 J = JLOW, JHIGH
DO 40 I = ILOW, IHIGH
IF(ZDIST(I, J) .GT. MIN) GO TO 40
SUMS = SUMS + TEMP
SWT = SWT + TEMP * Z(I, J)
40 CONTINUE
RETURN
END