

Ecology of Algae in Two Forested Streams at Shillong (Meghalaya)

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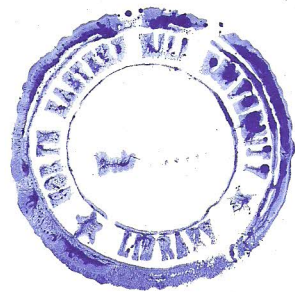
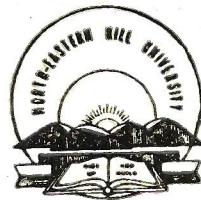
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THIS THESIS SUBMITTED IN FULFILMENT OF THE DEGREE OF

Doctor of Philosophy

IN

Botany



**NORTH-EASTERN HILL UNIVERSITY
SHILLONG**

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Dedicated
to
My Parents



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I certify that the thesis entitled "Ecology of algae in two forested streams at Shillong (Meghalaya)" submitted by Miss Jayashree Rout, M.Sc. for the Degree of Doctor of Philosophy of the North-Eastern Hill University, Shillong, embodies the record of original investigation carried out by her under my supervision. She has been duly registered and the thesis presented is worthy of being considered for the award of the Ph.D. Degree. The work has not been submitted for any Degree of any other University.

Signature of the Supervisor

Date : 28 November, 1991

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Preface

The realization of significance of autotrophy in streams has led to a resurgence of interest on periphytic algal communities of these systems. Whereas the corpus of information on stream algae of North America and Europe appears to be quite impressive, similar details about tropical streams are still scanty. It is of particular concern that literature on stream algae of the entire Indian subcontinent is virtually non-existent. The generation of relevant information about algae of Indian streams becomes imperative in view of the ongoing rapid depletion of forest cover, and the necessity of evolving judicious strategies for the management of these endangered ecosystems.

The work presented in this thesis deals with the study of algal ecology of two pristine streams draining forested areas at Shillong. The thesis has been divided into eight chapters. The first chapter ('General Introduction') discusses the current status of the subject, and the reasons for taking up the present work. This is followed by a brief account of the study area in Chapter 2. The detailed studies of epilithic algae in relation to physico-chemical characteristics of stream water are given in Chapter 3. Similar studies for epipellic algal assemblages constitute the next chapter. Chapter 5 deals with laboratory bioassay for assessing the nutrient limitation in selected streams. Since light conditions are highly variable in forested streams, the influence of light on periphytic algae colonizing artificial substrata has also been studied (Chapter 6). Chapter 7 discusses preliminary survey of the ability of stream algae to tolerate desiccation. Each chapter includes 'Discussion'; however, a brief general discussion is also given (Chapter 8) to assimilate the information gathered in various chapters. This is followed by 'Summary' and 'Literature Cited'.

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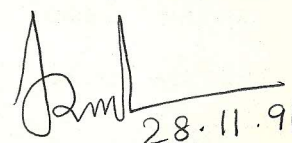
Mr. Ganesh Sharma has kindly helped me in field studies. I would like to appreciate the help of my lab colleagues Dr. A.K. Singh, Miss Mita Ghosh, Mr. Norbert Noraho and Mr. Nabendu Sengupta. I am thankful to my friends, Debjani, Raja, Bisnu, Arun, Jharna (Chakravorty), Beena, Sarfaraj, Saroj, Uttam and others who have helped me in all possible ways. I appreciate Dr. Surendra Singh and Dr. Girish Panda for their keen interest in my research work.

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(JAYASHREE ROUT)

Chapter 1

GENERAL INTRODUCTION

Streams and rivers constitute one of the major features of most landscapes, although their total area is about one-thousandth of that of the land surface (Hynes 1970). In spite of representing a small fraction of the total global area under water, the significance of streams is enormous. Streams are the most convenient and cheap source of water for domestic and industrial requirements particularly in the hilly regions. Irrigation and artificial impoundment of streams have aided in increasing local water supplies. The sound land-use practices trap stream water at or near its source for maximum usefulness to plants, animals, and man. Hydroelectric power generation is advancing day by day by damming the large streams and rivers. In addition, streams, serve as a repository of waste materials in many parts of the world. Another extremely important role of streams lie in the hydrologic cycle.

All rivers essentially originate as streams which, in turn, receive water from various sources. Streams may depend on glacial melting, which is not, as a rule, a common source of water for streams. During rainy seasons the surface runoff contributes

substantially to total volume of stream water. The perennial streams mostly originate from springs. Ground water is the major source of water for such streams. In springs, physico-chemical characteristics of water do not fluctuate much, whereas variations are tremendous in case of ponds, lakes, rivers and coastal waters. The cold water springs usually maintain a temperature ranging from 9° to 18°C, while hot springs characterised by extremely high temperature (up to 90°C, Castenholz & Wickstrom 1975) are mostly volcanic in origin and provide a steady state microcosm of extreme conditions. They have a high concentration of dissolved salts (Hynes 1970). In contrast, most cold water springs have high concentrations of Ca^{++} and HCO_3^- ions (Whitton 1975). Whatever may be the source of water in streams, they find their way to major rivers which, in turn, lead ultimately to the sea. Estuary is a good example of a coupled system between freshwater of the river and saltwater of the sea that achieves a good balance between physical and biotic components, and thereby a high rate of biological productivity which is undoubtedly unique.

Lotic systems, including streams, have several characteristic features that distinguish them from lakes and other standing bodies of water. The differences are due mainly to the following : (i) water current is much more of a major controlling and limiting factor in rivers and streams and the velocity of current varies depending on the steepness of the surface gradient, the roughness of the stream or river bed and the depth and width; (ii) in smaller streams, water is subjected to a greater variety of movements and to a more thorough mixing than the standing bodies of water; (iii) streams are more apt to be highly turbid than lentic systems at

least seasonally; (iv) oxygen content in unpolluted streams is usually higher than in lentic waterbodies; (v) there is little or no thermal or chemical stratification in streams and other lotic systems, and (vi) lotic systems exhibit a great variety of physical, chemical and biological conditions as these systems are greatly influenced by the landscape through which they traverse. Owing to these characteristics, especially the land-water interlinkage, a stream or a river is said to constitute an open ecosystem in contrast to standing bodies of water. In lotic systems the prominent zonation is longitudinal, whereas in lakes and ponds it is horizontal. Moreover, the communities show older stages from source to mouth in lotic systems, while successive zones from middle to shore are characteristic of standing waters. The physico-chemical environment of streams differ from rivers in two main respects; the former habitats are shallower with much faster flow rates in comparison to the latter.

Streams may be conveniently viewed as the processors of natural organic matter which for small, shaded, cool headwater streams (in the range of first to third order) is derived from the watershed. Recent years have witnessed another very significant change in perspective from that of viewing streams, or different stretches within a stream, as individual entities to that of an integrated view popularly called as the "River Continuum Concept (RCC)" (Vannote et al. 1980, Newbold et al. 1982, Minshall et al. 1985). This concept provides a framework for integrating predictable and observable biological features of lotic systems. A critical reassessment of the concept has been made recently by Bott et al. (1985) in their investigation addressed at evaluation of the

chemical, geomorphological, physical and biotic factors that are most strongly related to benthic community metabolism in temperate stream systems. Yet another significant feature in stream ecology is the critical linkage between stream and its landscape characteristics, and the importance in terrestrially derived organic matter on stream dynamics (Hynes 1963). The permeability of soil, slope of valley and precipitation characteristics are found to greatly influence the pattern of flow, dissolved organic matter and the concentration of nutrients in stream ecosystems. The term "Nutrient Spiralling" (Webster 1975), characteristic of running waters refers to the joint processes of transport and cycling of nutrients. The inefficiency of storage and processing of organic matter provides energy and inorganic nutrients for downstream communities. Vannote et al. (1930) have suggested that downstream communities are structured to capitalize on these inefficiencies of upstream processing. In every reach some material is processed, some stored, and some released. The amount released in this fashion has been used in calculating stream efficiency (Fisher 1977). It is extremely significant to note that biogeochemical cycle is an important phenomenon operative in lotic ecosystems with streams being no exception. Based on biological productivity streams are broadly classified into oligotrophic, mesotrophic and eutrophic categories. Oligotrophic streams are characterised by low nutrient supply in relation to the volume of water they contain. Eutrophic streams lie at the other end of the spectrum with high nutrient supply. Mesotrophic streams occupy an intermediate position between these two extremes with respect to nutrient supply, depth, biological productivity, water clarity and oxygen depletion. The eutrophic streams and rivers have high

nutrient supply resulting in a high production at all levels of food chain, shallow depth and low transparency due to excessive plant growth.

Many headwater streams are strongly influenced by the riparian vegetation which reduces autotrophic production by shading and contributes large amounts of allochthonous detritus. As the stream size increases, the reduced importance of terrestrial organic input coincides with enhanced significance of autochthonous primary production and organic transport from upstream. In this way stream metabolism shifts from heterotrophy to autotrophy with increased P/R ratio. The zone through which this shift occurs is primarily dependent upon the degree of shading (Minshall 1978). In deciduous forests and some coniferous forests, the transition probably occurs at order 3. At higher elevations and latitudes, and in xeric regions where riparian vegetation is restricted, the transition to autotrophy may be at order 1. Deeply incised streams, even with sparse riparian vegetation, may be heterotrophic due to side slope ("canyon") shading.

Autotrophy plays a major part in the trophic economy of a wide variety of streams, and large rivers which are not disturbed by man (Minshall 1973). Total gross primary production here exceeds community respiration on an annual basis and accretion (storage of excess photosynthate) and/or export (transportation of biomass out of the system) occurs.

Algae are the main autotrophs in stream ecosystems. Bacteria and aquatic fungi also seem to be of significance in performing the

vital role of transforming organic matter to inorganic form which may then be used again by the producers. Different types of invertebrates including molluscs, aquatic insects, annelids, rotifers, protozoans, helminths, and fishes are important biotic components of stream systems. Stream algae mainly provide the complex organic molecules for the vast range of animals. In addition, some 50-90% of oxygen in streams is estimated to come from algal growth (Cloud 1968). Stream algae may be used as ecological indicators. They are now being increasingly used in field bioassays with a view to gain relevant information about the availability of nutrients and other chemicals to algae and their different stimulatory and inhibitory effects and pollution in streams (Squires et al. 1979 b, Economou-Amilli 1980, Lampkin & Sommerfeld 1982, Heinonen 1984, Stevenson 1984 a, Leland & Carter 1985, Deniseger et al. 1986, Beamish et al. 1987, Singh & Gaur 1989).

Although phytoplanktonic assemblages are often found in slow flowing rivers, they are generally absent in streams. If present, they occur in pools along the bank of streams. Due to maintenance of high flow rate, streams favour those algae which are capable of attaching themselves to substrata. For algae forming a slimy layer on various substrata, the terms "periphyton" and "Aufwuchs" have been frequently used (see Otten & Willemsse 1988). Some workers even use the term "benthic" for such assemblages (Keithan et al. 1988, Stevenson et al. 1991). The periphytic algal communities encountered in streams, are the epilithon (algae attached to stones, pebbles, and large rocks), the epipelon (algae lying freely in sediment), the epipsammon (algae attached to sand grains), the

epiphyton (algae attached to plant surfaces), and the epizoon (algae on the surfaces of animals). The macroalgae of streams include the members of Rhodophyta, Phaeophyta, Chlorophyta and Cyanophyta, whereas the diatoms and coccoid algae mainly constitute the microalgal component of streams.

Algal flora attached to sand grains is fairly extensive in streams, but has as yet been studied less than any other algal community. Small coccoid Cyanophyta and Chlorophyta members often occupy the hollows of the grains but the most conspicuous components are often diatoms, either adnate to the surface or raised on very short mucilage stalks. Harper (1969) found that the epipsammic diatoms from a freshwater site showed very little movement, e.g., Amphora ovalis var. pedilulus moved on an average $1.7 \mu\text{m s}^{-1}$, whilst the epipellic diatom Navicula oblonga averaged $11 \mu\text{m s}^{-1}$. Harper & Harper (1967) surmised that it is essential for diatoms to attach to a surface even when moving. The mineralogy and microtopography of sand grains influence the epipsammic assemblage (Krejcki & Lowe 1936). These workers found stalked diatoms mainly on "hills" or exposed portions of sand particles. In contrast, motile prostrate diatoms were predominant in crevices and depressions. Miller et al. (1987) believe that the epipsammion represent a specialised community capable of existence in highly variable environments. According to them disturbance probably plays an important role in structuring this community and keeps it in a pioneering state. Krejci & Lowe (1987) studied temporal variations in epipsammic community of a brook. The persistence of common epipsammic algae in the assemblage led them to support the idea developed from the RCC that species comprising

riverine benthic assemblages continually persist and rarely become completely absent.

The epipelon is another widespread community occurring in regions where sediment accumulate and on to which light penetrates. The species are almost all microscopic and the associations rich and widespread. They live on and in the surface layers of sediment and cannot withstand long periods of darkness and anaerobic conditions (Moss 1977). Many diatoms, coccoid green and blue-green algae and euglenoids are found in epipellic assemblages. In order to avoid burial in continuously depositing sediment, many epipellic algae are capable of movement (Harper 1977). This attribute enables them to regain to the surface layer for utilizing light energy. During dark period, these algae move in to the sediment once again. The epipellic algae derive their nutrients from water as well as the sediment (Round 1981).

In streams with moderate or low flow conditions several macrophytic species as also large filamentous algae occur abundantly. These serve as ideal hosts for many epiphytic algae. According to Round (1981) epiphytic algae prefer those host plants which do not produce mucilage, tannin and phenolic substances. The epiphytic communities are dominated by diatoms together with small filamentous algae. The exact nature of relationship between epiphytes and their hosts has remained a subject of great dispute. Cattaneo and Kalff (1977) found similar epiphyton densities on natural and artificial plants and concluded that macrophytes are neutral substrates for the epiphyton. This viewpoint was subsequently criticised by Gough & Gough (1981) who found

differences in epiphyton composition on morphologically similar macrophytes. Recently, Blindow (1987) has made similar observations. Preliminary studies have shown the transfer of nutrients and photosynthetically fixed carbon from the epiphyton to host (see Darley 1982), although this aspect warrants more sincere researches.

The epilithon of running waters have received very little attention. Macroscopic growths of species such as Cladophora glomerata, Lemanea fluviatilis, Batrachospermum boryanum, Chaetophora incrassata and Ulothrix sp. are common on rocks in many fast flowing waters (Hynes 1970, Round 1981). Several microalgae, notably diatoms, also occur abundantly in epilithic assemblages. Slower flow tends to result in silt deposition on the stones and this hampers the growth of the epilithon. The pattern of algal colonization of rock surfaces varies depending on the microenvironmental situations. The pioneering algal species are mainly attached to the rock substrata in prostrate position. When the community matures, the late-comers organize themselves in erect position, an adaptation to probably avoid light and nutrient limitation (Hudon & Bourget 1981). The vertical overgrowth in advanced stages of colonization is suggestive of competition for space in the periphyton (Hoagland et al. 1982). Increase in thickness of periphytic biofilm is very likely to produce a gradient of growing conditions within the assemblage (Lock et al. 1984). If such is the case, the algae located within each of these strata may experience entirely different growing conditions. Cells in the lower strata may be exposed to low light and nutrient levels, whereas the cells in the upper strata are benefited by high

light intensities and abundant supply of nutrients. Hudon et al. (1987) observed increased accessory pigment concentration in the lower strata and called it an adaptation to low light conditions. Paul & Duthie (1989) speculated that the overstory extracts nutrients from water, whereas the understory helps in recycling nutrients as organic complexes within the periphyton.

Scanning electron microscopy (SEM) has been used to more precisely describe the three dimensional organisation of microcommunities on the surfaces of aquatic macrophytes (Allanson 1973, Sieburth & Thomas 1973, Sieburth et al. 1974), wood discs (Cundell & Mitchell 1977), rocks (Perkins & Kalpan 1978), slate tiles (Dickman & Gochner 1978), plastic panels (Hudon & Bourget 1981), glass slides (Maszaleck et al. 1979, Hoagland et al. 1982) and fine plankton netting (Winterbourn 1990). A series of seral stages during the colonization were described by Hudon and Bourget (1981), Hoagland et al. (1982) and Korte and Blinn (1983). Jorgensen and Revsbech (1983) analysed the microzonation within the cyanobacterial mats using SEM and have also described a microelectrode for measuring photosynthetic rate of algal mats. The importance of mucilage secretion by long stalked diatoms (Cymbella affinis and Gomphonema olivaceum) has been explained in context of their autoecological role in the development of spatially complex periphyton communities (Roemer et al. 1984, Lock et al. 1984). On the other hand, the synecological observations (e.g., biofilm-substrate interfaces, spatial relationships, community sloughing) are used together with the autecological data to interpret the structural integrity of these microcommunities (Lock et al. 1984,

Sinsabaugh et al. 1991). The spiralling concept of nutrient reutilization in running waters was assessed in view of the changing physiology of microorganisms comprising a developing biofilm (Paul & Duthie 1989). The immigration of algae on to the substratum is related to current velocity and the stage of assemblage development. The autogenic modification of substratum surface condition is related with immigration rates and current velocity in the later stages of the community development (Stevenson 1981). Temporal variations in immigration due to variability of algal drift have been observed (Müller-Haeckel & Håkansson 1978). Current velocity controls the rate of nutrient supply to cells. Stimulatory effects of water current on nutrient uptake, productivity and respiration have been observed by Whitford (1960), Whitford & Schumacher (1961 & 1964), Pfeifer & Mcdiffett (1975) and Lock & John (1979).

Researches on the structure and functioning of stream ecosystems with emphasis on origin of organic and inorganic resources escalated markedly in the last fifteen years or so. Much of these recent investigations focused on energy flow and carbon fluxes, being stimulated by the concept of streams as systems processing organic matter. The measurements of chlorophyll a content as an indicator of relative benthic primary producer biomass is an important parameter in stream ecology. Studies on chlorophyll a and periphytic metabolism in temperate, subarctic and antarctic streams have been described in detail (Stockner & Shortreed 1976, Pennak & Lavelle 1979, Sumner & Fisher 1979, Bott & Ritter 1981, Minshall et al. 1983, Keithan & Lowe 1985, Bott et al. 1985, Brown & King 1987, King & Cummins 1989 a, b, c, Howard-

Williams & Vincent 1989, LaPerriere et al. 1989). Various methods have been proposed by different workers for assessing the contribution of primary producers to stream ecosystem metabolism (Bott et al. 1978). Changes in dissolved oxygen levels over a 24 h cycle at two points along a stream (upstream-downstream method; e.g., Hall 1971), or in plexiglass chambers containing natural periphytic assemblage under in situ condition (Rodgers et al. 1978, Keithan & Lowe 1985, Mullholland et al. 1986) have been recommended. Tracer technique involving the use of ^{14}C is also available for measuring algal photosynthesis and primary production in closed chambers placed under in situ condition (Bott et al. 1978). Laboratory streams have been successfully employed by researchers particularly Max L. Bothwell and C. David McIntire to elucidate various ecological and physiological aspects of lotic algae. Bothwell (1985) and Freeman (1986) have carried out comprehensive sets of assays to isolate the limiting nutrient in continuous-flow troughs in lab channels and rivers, respectively, and Aizaki (1978), Aizaki & Sakamoto (1989) and Horner et al. (1983) have demonstrated correlations between dissolved inorganic phosphorus concentrations with algal biomass in both streams and laboratory channels. Recently, Bothwell (1989) has carried out continuous-flow trough experiments to demonstrate the different processes of nutrient saturation of periphytic growth rates and areal biomass.

Knowledge about stream algae has not advanced much due to methodological problems. Quantitative methods for studying algal periphyton of streams have been reviewed and discussed by several workers (Cooke 1956, Lund & Talling 1957, Blum 1960, Sládečková

1962, Hynes 1970, Weitzel 1979, Aloi 1990). Algal distribution on natural substrata lying in the stream bed is extremely patchy due inter alia to variability in size, shape and nature of substratum, and the pattern of water flow around them (Round 1981). Recently, De Nicola and McIntire (1990) have suggested that in cobble riffle areas of natural streams, the interaction between current flow and substratum relief has the potential to create patches of algae which are different in biomass and taxonomic composition. Thus the study of stream algae by quantitative techniques offer formidable difficulties (Hynes 1970). The technical difficulties are mainly associated with accurate quantitative removal of algae from uneven and rough surfaces of natural substrata. This problem has prompted many workers to use artificial substrata (Cooke 1956, Blum 1960, Lund & Talling 1957, Sládečková 1962). They believe that almost anything left for a while in a stream becomes covered with algae. The importance of substratum properties on periphyton formation has been discussed by Linskens (1963), Luther (1976), and Luning (1985), in case of natural substrata, and Hoagland et al. (1982), Hamilton (1985) and Edyvean et al. (1985) for artificial substrata. The materials used as artificial substrata are wood, slate, clay, concrete, asbestos, asbestos-cement, sheets of metals, celluloid, a great number of organic plastics and glass (Aloi 1990). Nevertheless, the glass slide method has been used successfully in various comparative studies (Sládeček & Sládečková 1964, Stockner & Armstrong 1971, Weitzel 1979, Patrick & Roberts 1979, Hunter 1980, Marcus 1980, Munteanu & Maly 1981, Bamforth 1982, Oemke & Burton 1986). Although many investigators have assumed that algal communities on glass substrata are identical to the naturally occurring epilithic or epiphytic communities, few have verified

this. Stockner & Armstrong (1971) found diatom communities on glass slides and rocks to have similar seasonal periodicity, but there were differences in species abundances and biomass. Korte & Blinn (1983) found plexiglass to be more suitable for microbial colonization than aluminium. Fairchild & Lowe (1984) and Fairchild et al. (1985) described a new method for in situ bioassay of nutrient limitation. This method involves the use of clay flower pots filled with agarized nutrient solution. Periphytic algae growing on the surface of such pots placed in situ respond to nutrients diffusing from tiny pores in the wall of the pots. A similar nutrient-diffusing substratum composed of agar-consolidated sand and nutrients in a petri dish is useful in sampling periphyton that grow on sandy bottoms (Pringle & Bowers 1984). Grimm & Fisher (1986), Pringle (1987) and Hill & Knight (1988) have used nutrient diffusing substrata to assess the response of periphytic algae to nutrient enrichment.

The position and exposure period are extremely important if artificial substrata are to be employed for different purposes. A horizontal position may be preferred when studying the influence of light on periphyton composition. For studying the effect of current velocity on periphyton colonisation all possible positions are preferred (Munteanu & Maly 1981, Stevenson 1984). In short-term experiments the rates of photosynthesis, respiration, nitrogen fixation and nutrient uptake can be measured for a period less than 24 h (Hansmann et al. 1971, Elwood & Nelson 1972, Bothwell 1988). Whereas, for long-term experiments the exposure period of 1 wk (Kesler 1981, Sumner & McIntire 1982), or 14 d (Patrick et al. 1954, Castenholtz 1960), or even a month (Brown & Austin 1971, Lowe

Gale 1980, Hunter 1980) have been recommended for sampling the equivalent of the "mature" community occurring on natural substrata in streams. The rock substrata permit the best growth of algae in general, whereas sandy bottoms are unfavourable for algal attachment, and sandy streams tend to be poor in epilithic algae. Owing to formidable difficulties in obtaining a representative sample of stream algae from natural substrata, limited success has been achieved in identifying the factors governing their ecology. Blum (1957) had for the first time applied the transect method of terrestrial plant ecologists to stream algae. Hynes (1970) has considered this method to be worthy of further use, and has advocated the need for refinements. Inspired by earlier works (Blum 1956, Descy 1973, Saunders & Eaton 1976), Holmes & Whitton (1981) have extensively used the line transect method to study the ecology of algae of Tees river in England. This method gave satisfactory results to Sheath & Burkholder (1985) and Sheath et al. (1986 b) also, but it is time consuming and difficult to apply in extensive sampling programmes.

As in other aquatic environments, stream algae are affected by an array of factors including current speed (McIntire 1966, Stevenson 1983, 1984 b, Keithan & Lowe 1985, Steinman & McIntire 1986, Biggs & Close 1989), pH (Hancock 1973, Van Dam et al. 1981, Maurice et al. 1987), light intensity (Brylinsky & Mann 1973, Busch 1978, Sumner & Fisher 1979, Gregory 1980, Keithan & Lowe 1985, Steinman & McIntire 1986), temperature (Patrick et al. 1969), nutrients (Stockner & Shortreed 1978, Crawford 1979, Marcus 1980, Peterson et al. 1983, Pringle & Bowers 1984, Grimm & Fisher 1986, Lowe et al. 1986), and dissolved and particulate organic inputs

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originating from riparian vegetation which may have a detrimental or beneficial effect on stream algae (Larson 1978). Superimposed on these primary factors are intensity and periodicity of rainfall, which can cause scouring and rearrangement of stream surfaces, and the effects of herbivores which can influence algal biomass, rates of primary production, and community structure (Gregory 1983, Lamberti & Resh 1983, Mulholland et al. 1983). Physical parameters have commonly been shown to be the most important factors controlling algae of heavily shaded streams at both the structural and functional levels (Minshall 1978, Vannote et al. 1980). Typically light is the principal factor limiting algal productivity in streams with dense tree canopies (Hill & Knight 1988), or in streams traversing through deep canyons (Blinn et al. 1981). A number of studies discuss the importance of light energy on the growth of lotic algae (Minshall 1978, Eloranta & Kunnas 1979, Vannote et al. 1980, Homles & Whitton 1981, Sheath et al. 1986, Steinman & McIntire 1987). The effect of light intensity on algal production has been determined in several Oregon streams (Gregory 1980, Lyford & Gregory 1975, Murphy & Hall 1981). Sheath and Burkholder (1985) observed the fate of green algae in the Rhode Island streams subjected to dense riparian shading. Photoperiod, the length of time light reaches the primary producers per day, is important in periphyton productivity and abundance (Byers 1963, McIntire & Phinney 1965).

The importance of immigration, growth and competition for nutrients and light in benthic diatom succession was studied in experimental channels of a low nutrient stream (Stevenson et al. 1991). Succession rates were greater in NP-enriched than control

channels. The density-dependent decreases in nutrient availability in benthic mats were greater in NP-enriched than in control channels. They have found that shading during the later stages of community development reduced algal standing crop. A substantial proportion of benthic diatoms can detach from substrata and drift downstream (Stevenson 1990), which can be a response to unfavourable habitat conditions (Bothwell et al. 1989). According to Stevenson et al. (1991), the ability to detach from substratum and immigrate rapidly may be an important adaptation. Thus diatoms may escape from resource limited conditions deep inside a mat, drift downstream, and reattach to the surface of another mat, where they may again be exposed to nutrients in the water column.

Productivity of stream algae is influenced by several other physical factors: temperature (Dillard 1969, Kilkus et al. 1975, Darley 1982), current velocity (Whitford & Schumacher 1961, 1964, Munteanu & Maly 1981, Antoine & Benson-Evans 1982, Peterson 1987), substratum composition (Bott 1983) and disturbance (Fisher 1983). Patrick (1971), Tuchman & Blinn (1979) and Blinn et al. (1989) reported the relationship between water temperature and the structural composition of the diatom community. Deniseger et al. (1986) found that low temperature and high flow were limiting to algal biomass accrual. Many previous studies have shown that current velocity can influence the structure and dynamics of lotic algal assemblages (Whitford 1961, 1964, Munteanu & Maly 1981, Horner & Welch 1981, Antoine & Benson-Evans 1982, Stevenson 1983, Peterson 1986, 1987, Steinman & McIntire 1986, Peterson & Stevenson 1989). Floods have been shown to reduce species number and diversity of stream communities and these changes depend upon local flood

frequency (Siegfried & Knight 1977, Gray & Fisher 1981, Fisher et al. 1982, Power & Stewart 1986). Fisher et al. (1982), Power & Stewart (1986) and Fisher & Grimm (1988) have described the alteration in algal assemblage structure and decrease in biomass following flash floods. Many of these workers relate reduction in algal biomass at high flows to scouring action of water current. The effect of drying has not received due attention of stream researchers, but disruption of the structure, function and dynamics of stream communities during drought condition have been reported (Fritsch 1944, Evans 1958, Hostetter & Hoshaw 1970, Peterson 1987).

Many researchers have emphasized that chemical factors are more important than physical variables in determining the structure and function of stream algal assemblages. Several studies on nutrient dynamics of stream ecosystems showed P and N to be the principal nutrients limiting algal growth (Sommerfeld et al. 1974, Gregory 1980, Grimm et al. 1981, Elwood et al. 1981, Peterson et al. 1983, Triska et al. 1983). Supplementation of these nutrients during in situ bioassays enhanced algal growth to a great extent (Wuhrmann & Eichenberger 1975, Fairchild et al. 1985, Pringle & Bowers 1987, Lowe et al. 1986, Pringle et al. 1986, Munn et al. 1989, Hart & Robinson 1990). Unforeseen natural events also influence significantly the chemical budget of streams (Martin 1979) and this, in turn, may adversely affect algae.

The pH exerts considerable influence on stream algae. Many genera like Lemanea, Batrachospermum and Stigeoclonium occur at wide range of pH, others however show preferences for a particular pH (Hynes 1970). Low pH has been found to reduce the diversity of

periphytic diatom assemblages (Descy 1979, Maurice et al. 1987). It has been suggested that acidic conditions reduce the availability of nutrients to algae of various groups. The preference of blue-green algae for high pH is particularly marked (Brock 1973).

Seasonal variations in stream algal communities have been studied in Europe, Japan and North America, and long lists of the times of occurrence of various algal species have been published (e.g., Budde 1928, 1932, Wehrle 1942, Mack 1953, Guntow 1955, Blum 1957, Koboyasi 1961, Bursche 1962). Johansson et al. (1977) gave a complete bibliography of algal studies in running waters. In temperate regions standing crop of periphyton exhibits systematic seasonal variations. Maximum biomass often occurs during the summer, whereas the minimum occurs during the winter (Flemer 1970, Lyford & Gregory 1975, Stockner & Shortreed 1976). The summer maxima is mainly associated with increase in temperature, light intensity and photoperiod and low flow, whereas the winter minima is due mainly to physical removal of periphyton, abrasion, increased grazing pressure, decreased temperature and light intensity and shorter photoperiod. Spring and summer maxima were reported by Sabater (1990) in a limestone stream in Spain. Reports of winter maxima (Tominaga & Ichimura 1966) and autumn maxima (Ertl et al. 1972) emphasize low flow during these periods. Growths of benthic diatoms are characteristic of chalk-streams during the spring (Westlake et al. 1972, Marker 1976). In chalk-streams, Casey et al. (1981) related the changes in silicon concentration to the seasonal cycle of diatoms. Seasonal succession of algae in a eutrophic stream in southern England was

studied by Moore (1977 c). Similar studies have been made in temperate region by other workers (Douglas 1958, Marker 1976, Jones 1978, Wilhm et al. 1978, Anderson 1984, Holmes & Whitton 1981, Rounick & Gregory 1981, Wehr 1981, Lamberti & Resh 1987, Lay & Ward, 1987, Biggs & Close 1989, Sabater 1990).

1.1 Present Study

The present work has been guided by the consideration that the ecology of stream algae does not seem to have been studied properly in the entire Indian subcontinent, although efforts have been made to investigate the ecology of phytoplankton in Indian rivers (Iyengar & Venkataraman 1951, Roy 1965, Lakshminarayan 1965 a & b, Venkateswarlu 1969, 1976, 1983, Venkateswarlu et al. 1987 a & b, Reddy & Venkateswarlu 1987, Rai et al. 1987). Limited efforts have been made on floristics and other aspects of algae of thermal springs (Gonzalves 1947, Chatterjee & Guha 1964, Sarkar & Rai 1964, Thomas & Gonzalves 1965 a-g, Prasad & Srivastava 1965, Vasistha 1968, Jana 1973, 1978, Saha & Dutta 1983, Jha 1985, Singh 1991).

The data presented in this dissertation deal with a detailed study of algal communities in two pristine forested streams. Epilithic algal assemblages of the selected streams were studied with respect to biomass, species composition and diversity. Temporal variations in the structure of epilithic assemblages have been followed and their relationships with physico-chemical characteristics of the environment have been explored using canonical correspondence analysis. Likewise, the epipellic algal assemblages of the selected streams were also studied. Laboratory bioassay experiments were carried out to define the nutrients

limiting algal growth in selected streams. Since shading often limits the growth of periphytic algae in streams, effect of different light conditions on periphytic assemblages was studied using glass slides as the artificial substrata. Some short-term experiments have also been carried out to understand the response of stream periphyton to desiccation, and changes in desiccated assemblages after rewetting.