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Temporal and altitudinal variations in the attached algae of mountain streams in Colorado

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Abstract

Attached algae were examined from eight sites in Central Colorado streams (five sites on St. Vrain Creek and three on the Snake River) between June and November, 1995. The sites ranged in elevation from 1600 m to 3500 m a.s.l.(plains zone to alpine zone). Seasonal variation in algal communities were qualified in forms of species composition and abundance (cell counts and biovolumes). The Ochiai coefficient of similarity was used to estimate degree of similarity between communities at different times, on different streams, and at different locations on the same stream. The composition of communities across streams for alpine and foothills zones was very close, but montane communities differed greatly across streams (similarity <0.1). Temporal variability of attached algae was almost absent in the alpine zone, but was high in other zones. The composition of the alpine community in August developed downstream with a temporal shift: October in the montane and foothills zones, November in the plains zone.

Introduction

Attached algae are a significant source of primary production in many streams, and provide energy for consumers (Lamberti, 1996; Stevenson, 1996). Most publications dealing with attached algae in streams have focused on species composition (e.g. Kawecka, 1981; Ward, 1986; Kawecka & Eloranta, 1987; Pfister, 1992a,b); quantitative studies are scarcer (McConnel & Sigler, 1959; Ward & Dufford, 1979; Keithan & Lowe, 1985; Poff et al., 1990; Uelinger, 1991; Griffith & Perry, 1995). There is little published information on the spatial and temporal variation of the attached algae in mountain streams (Whitford & Schumacher, 1963; Wehr, 1981; Burkholder & Sheath, 1984; Uelinger, 1991; Meegan & Perry, 1996). The recent works on functioning of attached algal communities (Lamberti, 1996; McCormic, 1996; Peterson, 1996; Steinman, 1996; Wellnitz et al., 1996) add some information to knowledge of their dynamics, but deal little with variation in composition. The present work deals with variation of attached algae in two Colorado mountain streams (St. Vrain Creek, the Snake River) as part of an effort to determine the contributions of algae to stream food webs over an altitudinal gradient.

Area of study

A detailed description of St. Vrain Creek is given by Ward (1986). St. Vrain Creek in the area of study begins as a first-order stream at about 3400 m a.s.l. and is a fifth-order stream on the plains near Lyons (1600 m a.s.l.). The riparian communities change from tundra in the alpine zone to fir (*Abies lasiocarpa*) with willow and rose understory in the subalpine zone and then to evergreen pine and spruce forest (*Picea pungens, Pinus ponderosa*, and *Pseudotsuga menzesii*) in the montane and foothills zones. Various shrubs and a few cottonwoods occur in the foothills zone. The riparian vegetation of the plains zone is composed of willow, scattered cottonwood trees, and some srubs and herbaceous plants. The substrate of St. Vrain Creek varies from bedrock, boulders, and cobble at high eleva-

Table 1. Statistical characteristics for algae collected from ten random rocks across St. Vrain Creek at 2426 m a.s.l. in October

Statistic	Mean	St. Dev.	Coeff. Var,%
Cell number per cm^2	503000	319000	63
Biovolume, mm^3 cm^{-2}	0.54	0.29	54
Diatoms, cell cm^{-2}	109000	73000	67
Diatoms, biovolume mm^3 cm^{-2}	0.17	0.12	71
Green algae, cells cm^{-2}	48000	34000	71
Green algae, mm^3 cm^{-2}	0.37	0.27	73
Blue-green algae, cells cm^{-2}	345000	327000	95
Blue-green algae, $mm^3 cm^{-2}$	0.002	0.002	100
Number of species	19	3	16
Most common algae, cells cm^{-2}:			
Achnanthes lanceolata	4000	4000	100
Hannea arcus	90000	63000	70
Phormidium spp.	327000	322000	98
Spirogyra sp.	18000	18000	100
Ulothrix spp.	19000	17000	89

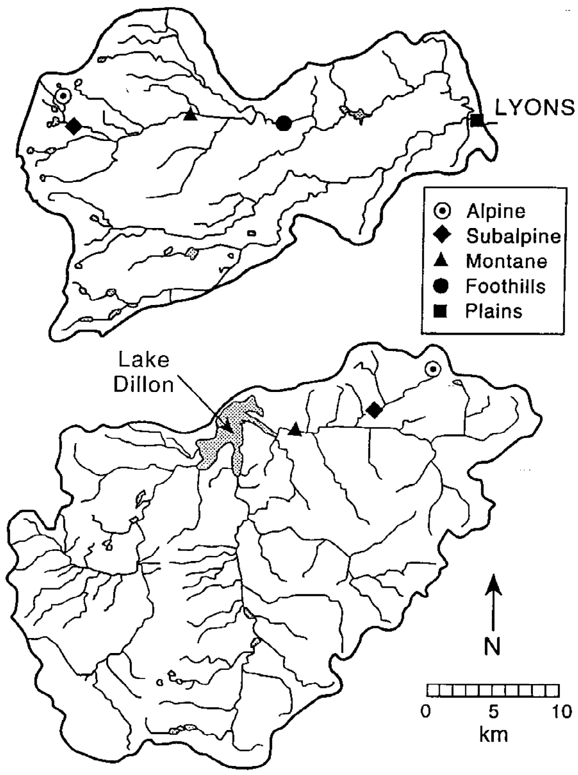

Figure 1. Locations of sampling sites on St. Vrain Creek (top) and the Snake River (bottom).

tion to cobble, gravel, and sand at middle and low elevations.

The riparian vegetation of the Snake River alpine zone consists of herbaceous plants (*Bistorta bistortoides*, *Caltha leptosephala*, and some Compositae), as well as willow. In the subalpine zone evergreen trees (*Picea engelmanii* and *Picea pungens*) dominate, while birch and willow shrubs occur less abundantly. The same vegetation is present in the montane zone, but with the addition of juniper (*Juniperus scopulorum*). The substrate is composed mostly of cobble and gravel. Boulders are present in the alpine zone and sand is present in the montane zone. There is no exposed bedrock in the Snake River.

During the period of investigation, water temperature in summer varied from 4–9 °C at high elevations to 12–17 °C on the plains. Average temperatures in the fall ranged from 3–4 °C to 13–15 °C, correspondingly. Ice melted after the first half of June at high elevation and in April–May at moderate elevation. Concentrations of nutrients in spring were 80–170 μg l^{-1} total inorganic N and 4–5 μg l^{-1} total soluble P at high elevation; 140 μg l^{-1} inorganic N and >50 μg l^{-1} total soluble P at low elevation (J. McCutchan, unpublished).

Material and methods

Samples were collected at five sites on St. Vrain Creek and at three sites on the Snake River (Figure 1) 30 times between June and November 1995. The sites on St. Vrain Creek were alpine (3400 m a.s.l.), subalpine (3150 m), montane (2420 m), foothills (2230 m), and plains (1620 m). The Snake River sites were alpine (3490 m a.s.l.), subalpine (3150 m), and montane (2770 m). Sampling was performed along transects perpendicular to flow. Three rocks were chosen randomly along each transect; each sample for analysis was an aggregation of scrapings from the three rocks. The reason for this approach in collecting samples is high spatial variation among samples from different rocks at the same site, as shown in Table 1. Pooling of samples from three rocks for a site reduces the coefficient of variation from 64–105% to 35–45%. An area of 5.3 cm^2 was scraped on each rock.

The samples were preserved with Lugol's solution. Microalgae were examined at a magnification of 560× with phase contrast for counting cells, measuring, and species identification. For reliable identifica-

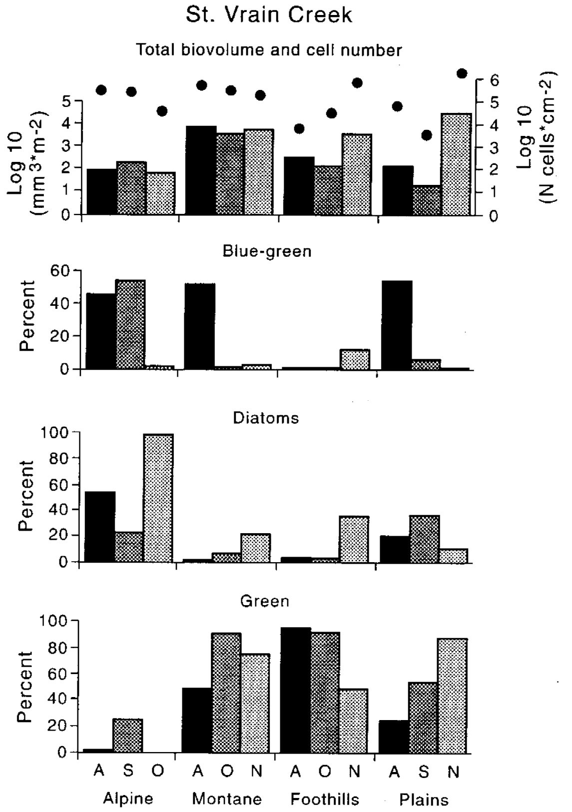

Figure 2. Total biovolume (log $mm^3\ m^{-2}$), cell number (log N cells cm^2), and percentage of main algal groups in total biovolume at four altitudinal zones in St. Vrain Creek, August–November, 1995.

tion of some diatoms (genera *Achnanthes*, *Fragilaria*, *Navicula*, *Nitzschia*, etc.), subsamples were treated with 30% hydrogen peroxide, heated, and mounted on slides. The slides were subsequently examined at 1000×. Cells were enumerated in the volumes of at least 0.04 ml or sometimes as much as in the entire counting chamber for inverse microscope (2.0 ml), depending on the concentration of algae. Biovolumes were estimated according to geometric shapes of cells. Similarity between communities was estimated by the Ochiai coefficient (Van Tongeren, 1995):

$$OS = \Sigma y_{ki} y_{kj} / (\Sigma {y_{ki}}^2 \Sigma {y_{kj}}^2)^{1/2},$$

where y is abundance (number of cells), i and j are samples to be compared (e.g. sites i and j), and k is the species. The coefficient has a potential range of 0 (no similarity) to 1.0 (identical).

Results

St. Vrain Creek

There were four predominant divisions of algae in the stream communities: diatoms (Bacillariophyta), green algae (Chlorophyta), blue-green algae (Cyanophyta), and chrysophytes (Chrysophyta). Variations in relative abundances of these groups are given in Figure 2.

In the alpine zone, blue-green algae dominated. Their percent abundance by cell number varied from about 60 to 98% (August); by biovolume they did not exceed 53%. For diatoms, relative abundance was the highest in October (40%). Green algae did not exceed 1% in cell number, but by biovolume they composed 24% in October.

In the subalpine zone, about 300 m below the alpine site and not far from the treeline, chrysophytes were dominant in August (relative biovolume, 78%). Blue-green and green algae were also present, and increased proportionally in October.

At the montane site, the numerical dominance of blue-green algae dropped from 96% in August to 72% in October and then to 22% in November. Percentage of green algae in total cell counts grew steadily from 3.6% in August to 20% in October and 57% in November. Neither diatoms nor chrysophytes were ever predominant at this site, but their relative abundance increased in late fall.

The algal community in the foothills zone was numerically dominated by blue-green algae from August through October; the highest percentage dominance (about 89%) occurred in September. In August about 23% of cells were green algae.

At the plains site, the blue-green algae were predominant numerically (80–95%) in late summer and early fall. In November, however, their number declined to 10%, while the percentage of diatoms grew to 46%. During the fall months, an increase in the proportion of green algae occurred. The total biovolume of chlorophytes in November was an absolute and relative maximum (29.4 $cm^3\ m^{-2}$, or 89% of biovolume) at this site.

Along with temporal changes at the division level, successional changes occurred within each group of algae. These changes were especially prominent in diatoms (Figure 3a), which showed the greatest species richness and are the best indicators of habitat (Kutka & Richards, 1996; Pan et al., 1996). More than 70 species of diatoms were identified from St. Vrain Creek and the Snake River. Some species were found

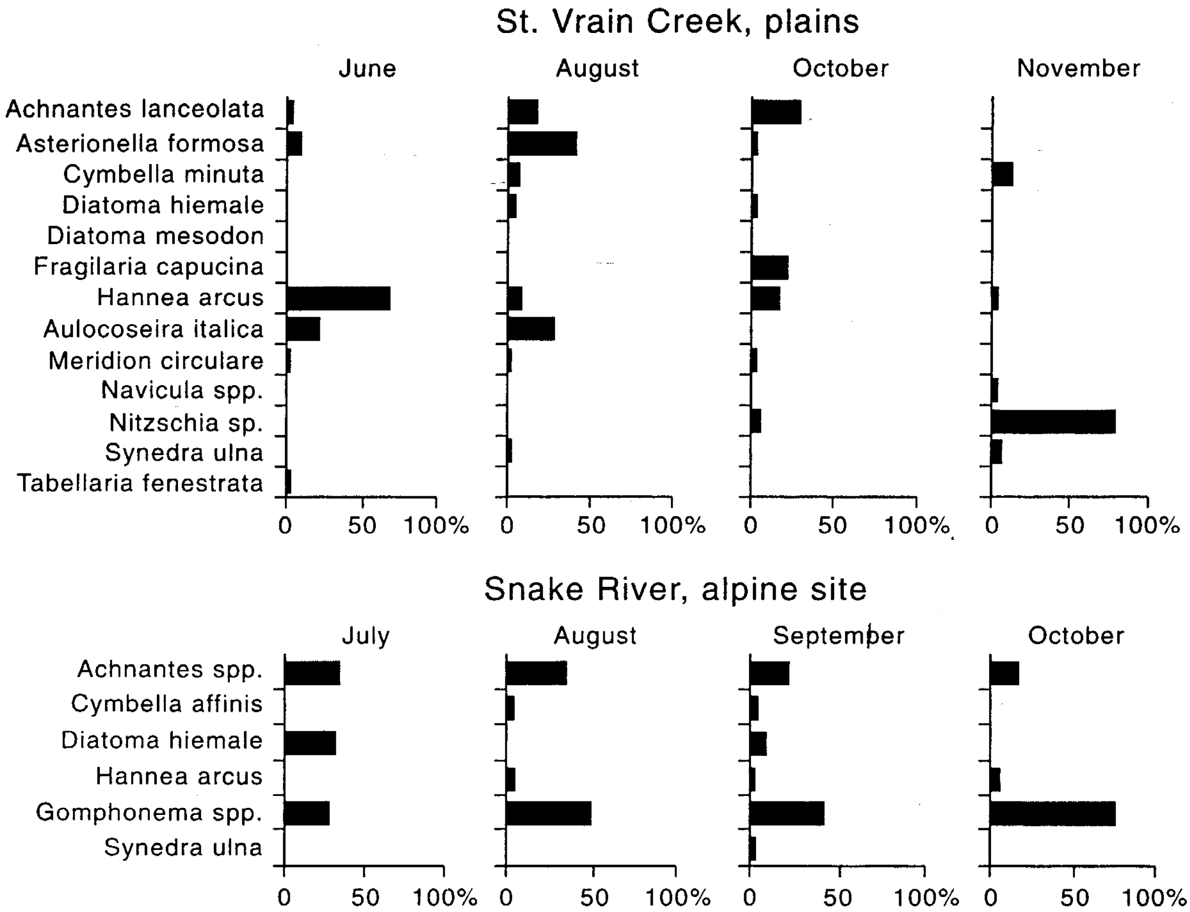

Figure 3. Percentage of dominant (>1%) diatoms in their abundance on St. Vrain Creek at the plains site (A) and on the Snake River at the alpine site (B).

at only one site, while others were found at every site. *Achnanthes lanceolata* (Breb.) Grun. and *Hannea arcus* (Ehren.) Patrick were present at all sites. These two species, together with *Gomphonema* spp. (mostly *G. olivaceum* (Lyngb.) Kutz, *G. intricata* Kutz. and *G. affine* Kutz.), *Diatoma mesodon* (Ehr.) Kutz., and *Achnanthes minutissima* Kutz. were foremost in the diatom communities at high elevation. In August the diatoms were dominated by *Achnanthes lanceolata, Diatoma mesodon, Gomphonema* spp., *Hannea arcus,* and *Achnanthes minutissima*. In September balance shifted to *Gomphonema* spp., *Hannea arcus,* and *Diatoma mesodon*. In October more than one half of diatoms were *Hannea arcus*. The shares of *Diatoma mesodon* and *D. hiemale* (Lyngb.) Heiberg were about equal.

Diatom composition differed from one zone to another. The subalpine August community of *Achnanthes lanceolata, Gomphonema* spp., *Nitzschia* sp., *Hannea arcus,* and *Diatoma mesodon* was replaced by *Hannea arcus, Fragilaria* spp., and *Cymbella minuta* Hilse in October. From the montane zone downstream, the only genus of Centrales found was *Aulacoseira*, which can be planktonic. It amounted to 25% of total diatom number at the plains site in June. Another planktonic diatom, *Fragilaria crotonensis* Kitton, was recorded in the same area. In the montane zone, *Hannea arcus* showed its maximum numerical dominance among diatoms (more than 90% in October-November). Diatom assemblages in the foothills zone were also dominated by *Hannea arcus, Gomphonema* spp., and *Achnanthes* spp.; together these accounted for more than 75% of the total diatom cell number.

In the plains, species composition was different from that of the higher elevations. In August the main dominants among diatoms were *Asterionella formosa*

Hassall and *Aulacoseira italica* (Ehr.) Simmonsen, *Achnanthes* spp., and *Hannea arcus*. In October the percentage of *H. arcus* tripled. The distinguishing features of the November diatom community were the increased amount of *Nitzschia* spp. (*N. dissipata* (Kutz.) Grun., *N. fonticola* Grun., *N. palea* (Kutz.) W. Smith and *N.* spp.), *Navicula cryptocephala* Kutz., *Stauroneis smithii* Grun., and some other cold-season species; the share of *Hannea arcus* dropped to less than 1%, but *Achnanthes* spp. remained important (27%). Blue-green algae were mostly represented by *Phormidium* spp., *Tolypothrix* spp. and *Oscillatoria* spp. *Phormidium* spp. were encountered at all sites but their role was especially significant at high elevations, while *Tolypothrix* spp. were most considerable in the montane zone and below. *Tolypothrix distorta* (Fl. Dan.) Wartm. amounted to about $4*10^5$ cells per cm^2 at the montane site in August (95% of cells; 51% of total biovolume).

Among more than 20 species of green algae only *Ulothrix* spp. and *Spirogyra* spp. exhibited mass development. The remaining green algae species were found only sparsely.

High abundance of chrysophytes at the subalpine site was due to *Phaeodermatium rivulare* Hansg., which is considered by some experts (Pfister, 1992) to be a form of *Hydrurus foetidus* (Vill.) Trev..

Cell abundance varied mostly in the range from 10^4 to 10^5 cells per cm^2. The maximum value ($1.25*10^6$ cells cm^{-2}) was recorded for the plains site in November because of a late fall diatom bloom and a development of green algae; the cell number at the same site in October was rather low ($3.5*10^3$ cells cm^{-2}).

The biovolumes ranged from tens to hundreds mm^3 m^{-2} at the alpine site, but in the subalpine, biovolume was about 8 cm^3 m^{-2} during the fall diatom bloom. In the montane zone, biovolumes were of the order of a few cm^3 m^{-2} (average about 5 cm^3 m^{-2}). The most variable values were observed in the plains. They dropped by an order of magnitude from August to September, but increased drastically to 33 cm^3 m^{-2} in November during mass development of diatoms and green algae (*Ulothrix* spp).

The Snake River

The alpine site on the Snake River is located near Loveland Pass at an elevation of about 3500 m a.s.l.. In summer months at this site, more than a half of the cells were blue-green algae, and 40–45% were diatoms (Figure 4). No green algae were present in July, but in August their percentage was about 5%. In September–October the share of diatoms increased to 70% along with a decrease in blue-green to about 30% and green algae to less than 1%.

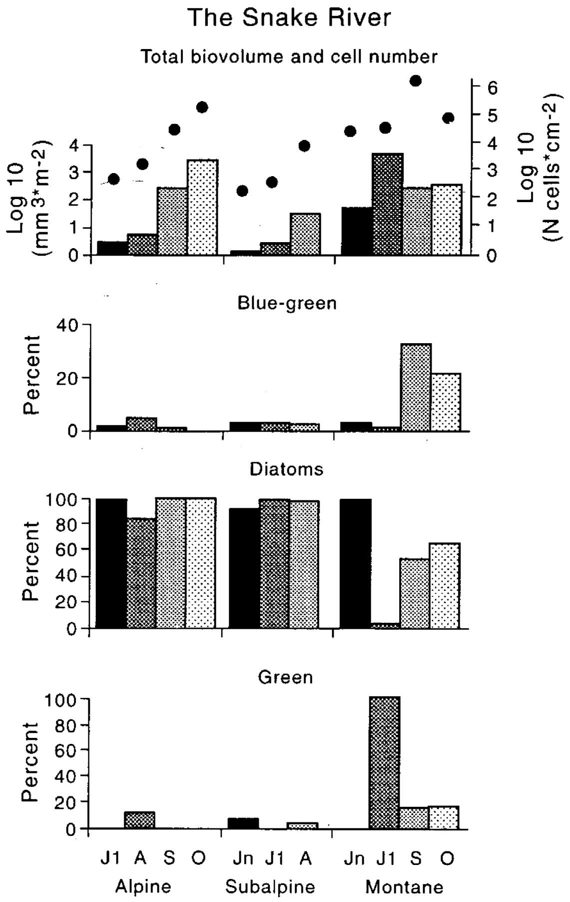

Figure 4. Total biovolume, cell number, and percentage of main algal groups in total biovolume at three altitudinal zones in the Snake River, June–October, 1995.

At the subalpine site during June and July, the microalgae were numerically dominated by diatoms (25–50%) and blue-green algae (36–73%). By biovolume, however, diatoms were always predominant. Numerical percentages of green algae did not exceed 13%. Blue-green algae reached 48–95% at the montane site, but their biovolume did not go beyond 32%. Diatoms dominated biovolume except July, when 98% of biovolume was represented by green algae.

Most of the diatom assemblages in the Snake River were dominated by *Achnanthes* spp., *Gomphonema* spp. and *Fragilaria* spp. Numerically, *Achnanthes* spp. (*A. lanceolata* and *A. minutissima* together) nowhere dropped below 12% of the total diatom number (Figure 3b). At the montane site, *Achnanthes* spp. was more than 90% of total diatom abundance in September–October. *Hannea arcus* was not such a significant component of diatom assemblage as in St. Vrain Creek. It was absent or occasionally present at high elevations until October, when it amounted to about $4{*}10^3$ cells cm^{-2}. Its typical relative abundance was 1–3%, except at the montane site in July, when it reached 16–20%.

Among the blue-green algae, *Phormidium* spp. and *Tolypothrix* spp. were also common, as they were in St. Vrain Creek, but the abundance of *Tolypothrix* spp. did not reach such high values as in the St. Vrain. The chrysophyte *Phaeodermatium rivulare* was almost absent, but the red alga *Audouinella violacea* (Kuetz.) Hamel was more common than in the St. Vrain.

The total cell number of algae in the Snake River was never high. In alpine and subalpine zones it varied from 10^2–10^3 cells per cm^2 in June–August to 10^4–10^5 cells per cm^2 in September–October. At the montane site, the maximum abundance (10^6 cells cm^{-2}) occurred in September. During other months, $2{*}10^5$–$9{*}10^5$ cells cm^{-2} were present.

The total biovolumes in the alpine and subalpine zones during summer months ranged from about 3 to 24 mm^3 m^{-2} and diatoms dominated biovolumes (84–99%). In late fall, algal biovolume reached 2.6 cm^3 m^{-2}. In the montane, maxima of algal biovolume were observed in July and October. The July maximum was created by green algae (*Ulothrix* spp., 98%), and the October maximum was mostly diatoms (63%). The September estimate of biovolume was less by an order of magnitude than the July and October estimates.

Comparison of communities

The Ochiai coefficient of similarity, which is sensitive to composition of communities, allows three kinds of comparisons of algal communities: (1) among streams in the same zone; (2) among zones at the same time in the same stream; (3) among elevations and seasons.

Figure 5a shows that algal communities in St. Vrain Creek and the Snake River are similar in the alpine zone both in summer and autumn. Similarity in the subalpine zone in August and in the montane zone in October was lower. We do not have enough data to compare subalpine communities in autumn and montane in summer.

Comparing the algal communities at different elevations but during the same period of time in St. Vrain Creek demonstrates the higher similarity between the communities in October, as compared to August (Figure 5b). The montane and the plains communities are distinctive.

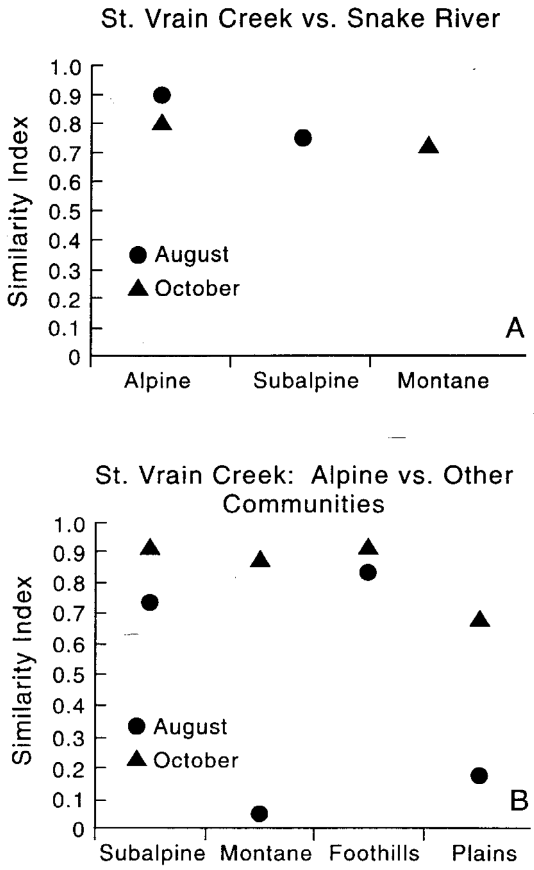

Figure 5. Similarity as shown by the Ochiai coefficient between algal communities in St. Vrain Creek and algal communities in the Snake River at alpine, subalpine, and montane zones (A), and between the St. Vrain alpine and other communities in August ● and October ▲.

Figure 6 demonstrates that algal composition in the alpine zone in August corresponds to those of the montane and the foothills zones in October, and to that of the plains zone in November. Similarity between these communities was 85–95%. In the alpine zone the algal communities of August were quite similar to those of October.

Discussion

Algal communities in streams often are dominated by diatoms in spring, blue-green algae in summer, and green algae later (Whitford & Schumacher, 1963; Al-

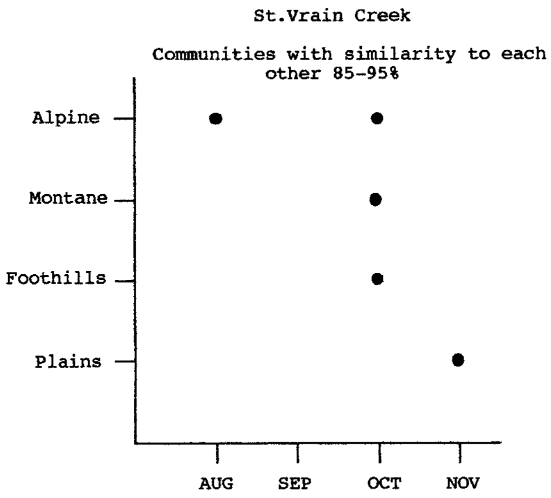

Figure 6. The communities in St. Vrain Creek with mutual similarity (the Ochiai coefficient) exceeding 85%. Each symbol corresponds to an algal community at a particular elevation (y-axis) and in a particular month (x-axis). All pair of these five communities posses similarity exceeding 85%. Thus, the same species composition appears in the alpine zone in August and October, in the montane and foothills zones in October, and in the plains in November.

lan, 1995), but these trends did not always apply to our study sites.

At high elevations, the early summer communities dominated by diatoms were followed in July and August by communities dominated by blue-green algae (Figure 2). Absolute and relative abundance of blue-green algae were constantly higher in St. Vrain Creek than in the Snake River (Figure 4), however. In some cases differences in abundance of blue-green algae might be explained by differences in grazing (Walton et al., 1995). Diatoms contributed the major portion of biovolume in the Snake River during the entire period of study. In St. Vrain Creek diatoms comprised a significant portion (20 to 90% of biovolume) in the alpine zone and in the plains (30%) in autumn. In some other mountain streams, diatoms rarely ever reached 1% of total biomass (Wehr, 1981). Chrysophytes were a significant contributor to biovolume only in the subalpine zone in St. Vrain Creek in August (78%). Dominance by green algae was not observed at high elevations on both streams, notwithstanding the lack of shade, which is considered one of the main factors affecting the development of green algae in streams (Sheath & Burkholder, 1985; Allan, 1995).

In the montane and foothills zones, the major portion of cells belonged to blue-green algae. Green algae dominated biovolume, and increased in abundance in the fall. In the plains zone, blue-green algae were a significant numerical component of algal assemblages during August and September, but in late fall they were replaced by diatoms and green algae, which created the maximum biovolume (33 cm^3 m^{-2}).

The summer biovolumes of algae in the headwaters of the alpine zone were two to three orders of magnitude less than those at medium and low elevations, but they increased in late summer – fall. The late fall peak was characteristic downstream. The autumn maximum was shifted in time from higher elevations to lower. In the montane zone in each stream biovolumes were of the same order of magnitude throughout the period of study. Biovolumes in the montane zone of St. Vrain Creek exceeded those of the Snake River on average by an order of magnitude. Variation in algae abundance was also mentioned for two streams in the Smokey Mountains (Keithan & Lowe, 1985).

Although the background diatom composition was about the same in the two streams, there were differences in dominance at particular elevations and seasons, and between the streams (Figure 3). These differences could be caused by differences in light (Gregory, 1980 in Keithan & Lowe, 1985), substrate (Kutka & Richards, 1996; Lowe et al., 1996), nutrients (Kelly et al., 1995), or flow velocity (Keithan & Lowe, 1985; Allan, 1996). It is apparent that all these multiple covarying factors have complex influence on the whole attached algae communities and should be considered together. But the goal of the present work was to show the pattern without considering environmental factors at this stage of investigation.

Variation in abundance between two streams was more significant as compared to community composition. Algal communities in St. Vrain Creek and the Snake River are similar in the alpine and subalpine zones, but similarity was lower in the montane zone (Figure 5a). Communities from different elevations but in the same stream show more variation in summer than in autumn (Figure 5b). The alpine algal assemblages are almost unchangeable, and are found downstream with a temporal shift of a few months (Figure 6).

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