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Riparian Influences on the Biophysical Characteristics of Seston in Headwater Streams

Abstract

Suspended particles (seston) in streams are an important source of nutrition for many invertebrates, forming a strong trophic link between plant and animal production. In forested regions the management of riparian corridors may alter allochthonous and autochthonous contributions to streams, ultimately changing the biophysical characteristics of seston. This article examines the effects of riparian condition on the biophysical parameters of seston at summer base-flow from 19 small, headwater streams (1st – 3rd order) on the Olympic Peninsula of Washington. Consistent with other studies, seston concentrations and percent of organic matter were not correlated with any single or combination of riparian characteristics. Nevertheless, there are several riparian effects on the biotic characteristics of seston. Chlorophyll-*a* concentrations were generally <1.0 mg Chl-*a*-L⁻¹ but correlated significantly with canopy closure, particularly for streams of 1st and 2nd order. C:N ratios ranged from 7.6 to 25.6 and mean values at coniferous sites were significantly higher than those at alder-dominated deciduous sites or at sites with no appreciable riparian cover. Particle diversity showed that diatoms were a significant proportion of total seston diversity (range = 47-66% of the number of particles), although significantly higher concentrations of diatoms were found in sites lacking canopy cover. Surprisingly, wood particles were not well represented (range 2-4% of seston particles) and wood concentration did not vary by riparian cover type or by any other measured parameter. We conclude that riparian condition affects summer food quality, but not the amount of suspended organic matter.

Introduction

Disturbance in the riparian corridor often causes dramatic shifts in the trophic base of headwater streams. Disturbed streamside forests typically allow greater penetration of direct sunlight and the influx of limiting nutrients such as nitrogen and phosphorus. Ultimately, autochthonous production (e.g., algal growth) increases in these modified systems, and less allochthonous materials are contributed from the riparian corridor. We suspect that these changes are expressed in the type, diversity, and quantity of particulate materials in suspension (i.e., seston).

Positive relationships exist between stream power and seston concentration during storm flows in previously disturbed watersheds (Bilby and Likens 1979, Wallace et al. 1991), but attempts to relate seston concentration during non-storm conditions to stream power, discharge, or any one

physical or biological parameter largely have been unsuccessful (Sedell et al. 1978, Naiman and Sedell 1979, Wallace et al. 1982). Seston concentration and its biophysical characteristics appear to be determined by complex interactions between stream power, availability of material for export, and the efficiency of in-stream retention and processing (Naiman 1982, Golladay et al. 1987, Smock et al. 1989). Changes to the biophysical characteristics of seston relate directly to food quality (e.g., C:N ratio, chlorophyll concentration, particle diversity). In natural systems there are general downstream trends in presumed food quality and direct linkages between seston quality and macroinvertebrate communities (Naiman 1983). For example, in streams originating from lakes, nutrient-rich seston near the outlet supports a rich filter-feeding fauna while high-quality seston and invertebrate assemblages decline in downstream reaches (Maciolek and Tunzi 1968, Oswood 1979). Chlorophyll concentrations tend to increase in larger streams, ultimately declining in deep, turbid rivers (Vannote et al. 1980; Naiman 1983). Also,

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similarity between seston composition and macroinvertebrate gut contents provides the basis for attaching trophic implications to changes in the biophysical characteristics of suspended particles (Fuller and Mackay 1980).

Generally, for the Pacific Coastal Ecoregion and other forested landscapes, base-flow seston concentrations and riparian characteristics are unrelated (Naiman and Sedell 1979, Wallace et al. 1982, Naiman 1983, Webster and Golladay 1984). Even though stormflow, debris dams and macroinvertebrates affect total transport (Wallace et al. 1991, Bilby 1981, Maciolek and Tunzi 1968), the subtle dynamics of seston concentrations at base-flow remain elusive. At the Coweeta Hydrologic Laboratory (North Carolina) a significant proportion of seston is brought into suspension by the activities of macroinvertebrates (Webster 1983, Wallace et al. 1991).

The composition and nutritional content of seston are related to various riparian factors, such as canopy closure and species mix (Maridet et al. 1997). Indeed, seston is suspected to integrate a number of riparian and landscape elements, changing temporally in response to allochthonous inputs and discharge regime. This is especially so in the spatially and temporally dynamic Pacific Northwest of North America where frequently disturbed riparian forests are dominated by red alder (*Alnus rubra*) for as long as 100 yr (Naiman et al. 2000). In contrast, mature riparian zones are generally conifer-dominated or characterized by a heterogeneous array of vegetative communities. The difference in canopy structure between alder-dominated and mature riparian forests is presumed to markedly affect seston characteristics. We thought that some of the changes in seston characteristics would serve as another demonstration of the marked, system-level changes that result from major disturbances in the riparian canopy. While a causal link is not established, this study explores the relationship of riparian condition to the biophysical characteristics of seston at summer base-flow across headwater streams in contrasting stages of recovery from disturbance.

Study Sites

The Olympic Peninsula in western Washington is a highly variable ecological land mass that has evolved unique biotic characteristics since the recession of the Pleistocene glaciers 10,000 yr

ago. Forests on the western slope of the Olympic Mountains receive >500 cm of annual precipitation, more than any region in the conterminous United States (Henderson et al. 1989). However, the mountains are high enough to create a rainshadow resulting in < 50 cm of annual precipitation on the lee side. This climatic and physiographic diversity occurs within a relatively small geographic area (~12,000 km²).

Nineteen streams were chosen to represent a continuum of riparian canopy conditions (Figure 1). The sites were 1st-3rd order streams located within a variety of land ownerships and riparian conditions. Most were on land managed by the USDA Forest Service (USFS; Olympic National Forest); others were within the management boundaries of the USDI National Park Service (NPS; Olympic National Park), the Simpson Timber Company, and the Washington State Department of Natural Resources (DNR). All were between 180 and 915 m elevation; some were low gradient while others, particularly the higher elevation

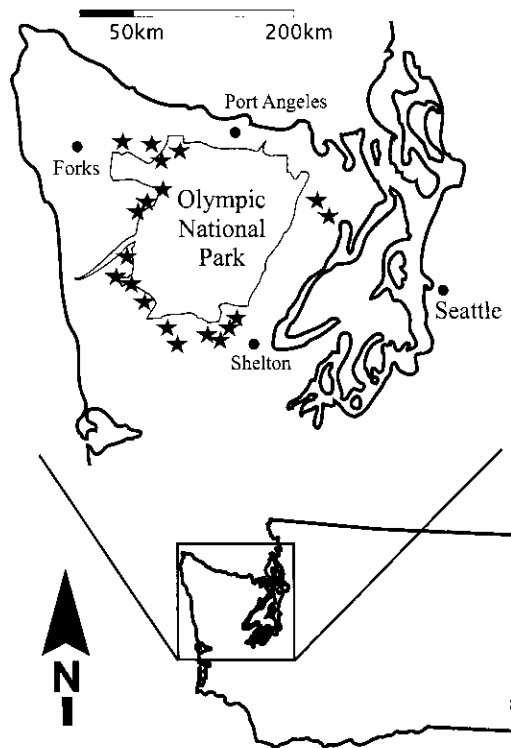


Figure 1. Map of the study sites on the Olympic Peninsula, Washington. [* = study sites]

sites, had gradients >30%. Some had little or no anthropogenic disturbance, while others had experienced recent riparian deforestation. Gradient on these sites ranged from 1-30% and riparian condition represented sites which had not been disturbed in centuries, to sites which were extensively harvested within the past decade.

Methods

Assessing Riparian Condition

We recorded riparian cover type and canopy closure along 200-300 m of the stream site. Each site was initially assessed by determining stream order (Strahler), ordinal aspect, mean slope (degrees), drainage area (ha), mean channel width (m), and year of last major riparian disturbance (either fire or human).

The riparian forest at each site was quantified using systematic plots or belt transects. Different methods were adopted at different physical site types to minimize potential errors, while allowing an accurate representation of the riparian corridor (Husch et al. 1993). The smallest sites were quantified with the random placement of square plots along the channel, while the larger sites were sampled by belt transects parallel to the channel. Forest uniformity along the smallest streams enabled use of the 25 m² plot, which allows both sides of the channel to be sampled within the same plot. On larger streams, belt transect width was equal to the width of the riparian corridor, the riparian extent determined by the slope break and the presumed point at which stream discharge no longer appreciably influenced the structure and composition of riparian vegetation (typically the bankfull width). Tree diameter was used to calculate basal area (BA; m²·ha⁻¹), dominant species (by both density and basal area), and mean diameter (cm). The coefficient of variation (CV) for each parameter provided an index of site heterogeneity.

Sites were grouped into riparian cover types (coniferous, deciduous, no cover) based on total riparian basal area of the dominant tree type. In cases of split dominance in the basal area plots (<10% difference between deciduous and coniferous), dominance from the canopy closure plots was used to determine the riparian cover type.

Canopy closure, a critical function in the hierarchy of in-stream controls, was measured using

a densiometer, with readings taken mid-channel at evenly distributed points along the stream. Mean closure and the coefficient of variation, expressed as the percentage of overhead vegetation covering visible sky, were calculated for each site. Riparian cover type (coniferous, deciduous, no cover) also was noted at each sampling point.

Seston Analyses

Samples were collected at random points in each site during July and August 1997 and 1998. Most samples were filtered on-site, using a hand-operated Nalgene vacuum pump. Filters were returned to the University of Washington for analysis. Typically, 1-L samples were used, but 2-L samples were often taken where seston concentrations were low. The filtered seston was measured for total concentration (mg·L⁻¹ dry weight), organic concentration (mg AFDM·L⁻¹), percent organic matter (%OM), concentration of chlorophyll-*a* (Chl-*a*·L⁻¹), the ratio of carbon to nitrogen (C:N), and visual characterization of particle diversity via scanning electron microscopy (SEM).

Seston concentration and percent organic matter were measured by filtering water samples through pre-ashed, pre-weighed 47 mm glass fiber filters (pore size 1μ). Filters were dried (70°C, 24 hr), weighed, ashed (525°C, 4 hr), and weighed again. Ash-free dry mass (AFDM) was divided by dry seston weight to determine the organic seston fraction for each sample, from which percentages could be obtained. Three replicates were collected for each site on two dates in 1997 and 1998 (once in July and once in August of each sampling year).

Three 1-L grab samples (in the middle of the water column) were taken at each study site for each sampling date for chlorophyll-*a*. Filtered samples were placed on ice and, within two days, the chlorophyll was extracted under refrigeration for 24 hr in a 10 mL solution of 90% acetone, with a 10% solution of MgCO₃ (buffer). After centrifugation, the sample was analyzed in a fluorometer. The resulting measurement was recalculated for expression as concentration (μg Chl-*a*·L⁻¹) and then converted to mg Chl-*a*·g AFDM⁻¹ by dividing μg Chl-*a*·L⁻¹ values by corresponding values for seston concentration (mg AFDM·L⁻¹).

Three replicates were taken from each site during summer 1998 for the carbon-to-nitrogen ratio. Filters were dried (70°C, 24 hr.) and total C and N concentrations determined using an

elemental analyzer. Acetanalide was used as a standard, and calibration curves were built from standards and blanks to determine actual C and N concentrations in each sample.

Scanning electron microscopy was used concurrently with samples taken for the other biophysical parameters to quantify particle diversity. At least three collections were made from each site in July and August 1997 and 1998. Samples on filters were dried (70°C, 24 hr), and a randomly selected section of the filter was cut (15% of the total filter area) and affixed to a mounting stub. The edge of the mounted filter section was then painted with liquid colloidal silver (to increase conductivity), and sputter coated with gold/palladium (60% Au/40% Pd). Four transects 70-120 μm wide were employed on each stub for sampling.

Particles were identified by particle type and recorded in one of three size classes (<15 μm , 15-40 μm , or >40 μm). Individual particles were tallied by size class and relative densities of particles (by size and type) were calculated based on the total area of filter space sampled. An extrapolation was then made based upon total filter surface area to determine the total number and diversity of particles on a per volume basis.

We performed ANOVA and correlation analyses using StatView. The significance level for all analyses was set at $P = 0.05$.

Results

Riparian forests associated with 1st and 2nd order streams were almost indistinguishable from the corresponding surrounding upland or terrestrial forests, whereas sites along the 3rd order streams had a mosaic of patch types and a highly distinct assemblage of typical streamside vegetation. Basal area in individual plots ranged from 0 to 229.7 $\text{m}^2\cdot\text{ha}^{-1}$. Mean basal area within sites ranged from 0 (clearcut sites) to 150.5 $\text{m}^2\cdot\text{ha}^{-1}$ (mature forest). Density was also highly variable, ranging from 0 to 2292 stems $\cdot\text{ha}^{-1}$ in individual plots, to mean density values from 0 (clearcut sites) to 1281 stems $\cdot\text{ha}^{-1}$ (early-successional alder forest). Basal area was not significantly correlated with stem density.

Ten sites were dominated by coniferous cover, six by deciduous cover, and three had no appreciable riparian cover. Canopy closure ranged from

0 - 100% in individual measurements, whereas mean canopy closure values within sites ranged from 0 - 93.6%.

Total seston concentrations ranged from 0.4 to 23.1 $\text{mg}\cdot\text{L}^{-1}$, and mean values ranged from 2.14 to 7.86 $\text{mg}\cdot\text{L}^{-1}$ (Table 1). Organic seston concentrations, expressed as ash-free dry mass per volume of water ($\text{mg AFDM}\cdot\text{L}^{-1}$), ranging from 0.13 to 9.81 $\text{mg AFDM}\cdot\text{L}^{-1}$ and averaging 0.41 to 3.92 $\text{mg AFDM}\cdot\text{L}^{-1}$. The percentage of organic matter ranged from 32% to 55%. Total seston concentration, organic seston concentration and percent organic matter were not significantly related to any riparian parameters, and differences did not exist between riparian canopy cover types.

Chlorophyll-*a* concentrations were < 1.0 $\mu\text{g}\cdot\text{L}^{-1}$, with 32% of all samples having concentrations < 0.1 $\mu\text{g}\cdot\text{L}^{-1}$ (Table 1). Mean chlorophyll-*a* concentrations were < 0.1 $\text{mg}\cdot\text{L}^{-1}$ at 6 of the 19 sites. Chlorophyll concentration was higher in sites with no canopy cover than in the early-successional, deciduous sites ($P < 0.01$) and coniferous sites ($P < 0.001$). There was no significant difference between the coniferous and deciduous site. The primary correlate with chlorophyll-*a* concentration was expected to be canopy closure, because greater closure decreases energy available for photosynthesis. As expected, chlorophyll concentrations were positively correlated with canopy closure across the continuum of sites ($P < 0.001$; Figure 2a).

We separated streams of order 1 and 2 from the 3rd order streams, and we attempted to correlate the chlorophyll concentration of the smaller streams with canopy closure to separate the effects of a natural increase in chlorophyll in larger streams. The correlation from this smaller group was stronger ($P < 0.001$; Figure 2b).

Chlorophyll concentrations were converted from $\text{mg chlorophyll-}a\cdot\text{L}^{-1}$ to $\mu\text{g chlorophyll-}a\cdot\text{g AFDM}^{-1}$ to facilitate comparisons with other studies. Chlorophyll values for all sites remained significantly correlated with canopy closure ($P < 0.05$), and the relationship strengthened when only 1st and 2nd order headwater streams were included ($P < 0.05$).

Carbon to nitrogen ratios (C:N) ranged from 7.55 to 25.58 (Table 1). C:N values were significantly greater at coniferous sites than at the alder-dominated deciduous sites ($P < 0.01$) or at sites with no appreciable riparian cover ($P < 0.05$).

TABLE 1. Mean riparian closure and mean seston parameter values for each site. (BA=Basal Area; Chl-*a*=chlorophyll-*a*; C:N=Carbon-to-nitrogen ratio; AFDM=Ash-free dry mass of the seston).

Site Name	Canopy Closure (%)	Basal Area (m ² /ha)	Density (stems/ha)	Chlorophyll <i>a</i> Concentration (μg/L)	(C:N)	Total Seston Concentration (mg/L)	Organic Seston Concentration (AFDM; mg/L)
Barnes	39.8	73.1	1280.6	0.218	14.57	2.62	1.40
Brown disturbed	57.6	57.1	928.3	0.209	N/A	3.02	1.33
Brown undisturbed	67.4	91.7	358.7	0.136	N/A	4.01	2.52
Camp	46.5	56.7	854.2	0.347	13.76	2.86	1.38
Chester	16	21.8	2037	0.170	12.25	4.04	2.07
DNR 1	0	0	0	0.549	10.98	4.42	2.50
DNR 2	0	0	0	0.371	11.74	3.85	2.48
Gold harvested	0	0	0	0.179	19.71	2.14	1.33
Gold old-growth	93.6	101.5	1076.4	0.028	23.69	2.14	1.42
Hoh	71.9	59.1	445	0.089	18.72	3.80	2.49
LaPoel	90	113.6	466.7	0.046	22.68	3.59	1.59
LeBar disturbed	17.4	58.3	565.7	0.204	17.69	2.17	1.25
LeBar undisturbed	33.6	66	453.7	0.134	23.37	2.17	1.40
Matheny 1	42.5	38.8	1003.7	0.138	16.29	0.64	0.41
Matheny 2	62.4	30.1	421	0.105	18.29	7.86	2.98
Sams	9.8	122.5	321.2	0.125	7.55	6.58	3.92
Simpson control	61.4	52.7	747	0.067	8.81	5.64	3.65
Simpson treatment	77.7	70.3	342	0.041	N/A	1.44	1.44
Sol Duc	79.9	150.5	450.7	0.039	25.58	4.38	1.62

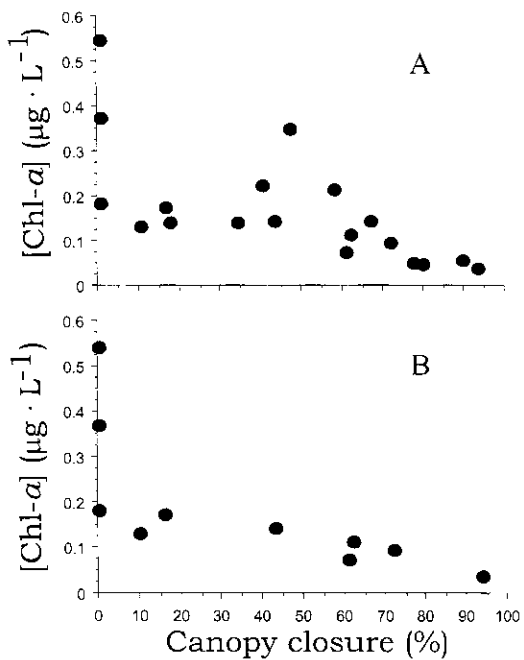


Figure 2. (A) The correlation between the concentration of chlorophyll-*a* (mg · L⁻¹) and canopy closure (%). *P* < 0.001. (B) The correlation between the concentration of chlorophyll-*a* (mg · L⁻¹) and canopy closure (%) for sites of 1st and 2nd order only. *P* < 0.001.

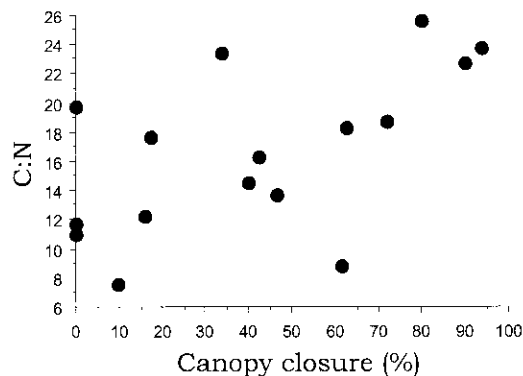


Figure 3. Relationship between base-flow C:N ratio and canopy closure for each site (*P* < 0.001).

No significant difference was observed between sites with deciduous cover and sites with no cover. Considering that riparian vegetation and canopy closure exert considerable control over the nutrient content of particles in streams, C:N ratios were expected to be lower in deciduous or more open canopies. C:N and canopy closure were, in fact, significantly correlated, although there is substantial variance in the relationship (*P* < 0.05; Figure 3).

Surprisingly, concentrations of individual particle types, regardless of size class, were largely unrelated to riparian characteristics. For instance, wood particle concentrations were not correlated with riparian basal area. Wood particle concentrations and proportions also were not different across the three major riparian cover types. The one relationship that did exist, and was expected, was between diatom concentration and canopy closure ($P < 0.05$). Also, as expected, mean diatom concentration for each site was positively correlated with chlorophyll concentration ($P < 0.01$).

Diatoms were the dominant particle across all riparian canopy cover types, ranging from 47 - 66% of the total number of seston particles, even at heavily shaded sites. However, diatoms had greater representation in sites with no cover than in sites with coniferous cover ($P < 0.05$). Further, fecal pellets had greater proportional representation in coniferous sites than at sites with no cover ($P < 0.01$). In both cases, deciduous sites had proportions of these particle types between the values expressed at the other sites, while not being significantly different from either. No differences were detected between proportions of wood, silt, exoskeletons, or other organic matter as a function of any riparian characteristic.

Diatoms, fecal pellets, and organic detritus were important food categories, whereas exoskeletons, wood, and silt were not high quality macro-invertebrate food categories. Grouping particle types into food and non-food categories revealed that the total proportion of foodstuffs was close to three-quarters of the total seston (range = 72-77%), and there was no significant difference in this proportion between coniferous, deciduous, and no cover sites.

Discussion

Riparian forest characteristics influence many biophysical variables associated with seston. Riparian forest cover type and percent canopy cover modify the concentration of chlorophyll-*a*, C:N ratios, and the abundance of specific particles, and particle diversity. Even though many of our results are consistent with previous studies, the lack of any relationship between riparian biomass and seston concentrations or percent organic matter, the abundance of diatoms in heavily shaded

sites, and the paucity of seston wood particles were unexpected.

Seston concentrations reported here are low (relative to other ecoregions) and consistent with other regional results. A negative correlation exists between particulate organic matter concentrations and stream gradient, but the dynamics of base-flow seston concentrations are driven by a combination of stream power, in-stream retention devices, and other biological controls, including the availability of material for transport (Golladay 1997). We found no base-flow patterns in seston concentration (Table 1), underscoring the diversity of forces and processes controlling the concentration of suspended matter at base-flow. Also, riparian characteristics have not been utilized in studies successfully linking base-flow seston concentration to predictor variables. In-stream biological processes, rather than riparian characteristics, likely influence seston concentrations at summer base-flow.

In contrast, the biophysical characteristics of seston appear to be strongly influenced by riparian vegetation. For example, chlorophyll-*a* was negatively correlated with riparian canopy closure at summer base-flow (Figure 2). The correlation strengthens appreciably when only 1st and 2nd order streams are examined, for which the correlation coefficient improved almost 20% (Figure 3). Chlorophyll concentration is typically regarded as an index of primary productivity in streams. Higher concentrations generally indicate a higher quality food source, which can translate into faster growth rates for secondary consumers, such as salmonids (Bisson and Sedell 1984). Chlorophyll concentrations in this study, expressed either as $\mu\text{g Chl-}a\cdot\text{L}^{-1}$ or $\text{mg Chl-}a\cdot\text{g AFDM}^{-1}$, are consistent with previously reported concentrations (Naiman 1983, Naiman and Sedell 1979).

The C:N ratios of seston were partially responsive to riparian conditions (Table 1). Higher ratios (C:N >20) were associated with mature coniferous stands, perhaps due to the higher relative contribution of carbon in litterfall and lower primary productivity at coniferous sites. In contrast, the lower C:N in open canopy sites was due to a combination of greater in-stream primary productivity and lower inputs of refractory allochthonous litter. Further, C:N ratios in open canopy sites were not significantly different from ratios in the deciduous sites likely because of the dominance of

inputs from red alder (*Alnus rubra*), a nitrogen-fixer, at the latter.

The ecological implications of a change in the C:N ratio of seston are similar to the implications associated with the concentration of chlorophyll-*a*. Chlorophyll-*a* and C:N are useful indices of food quality, and the results suggest that disturbed sites with open canopies typically yield a higher quality seston that may translate into more growth in some stream organisms (Gregory et al. 1987, Hartman and Scrivener 1990).

Particle diversity yielded some surprising results, especially the percentage of wood and diatoms in the seston. By proportion, wood represented a small fraction of the seston and did not vary between riparian canopy cover types (Table 1), which may be due to the inability of streams to hold woody particles in suspension at summer base-flow or indirectly to the activities of macroinvertebrates. A significant proportion of the suspended matter is caused by macroinvertebrate feeding activities (Webster 1983, and Wallace et al. 1991). It could be argued that at summer base-flow, wood represents a poor source of food, is largely ignored by feeding organisms, thus, few wood particles are suspended.

Another unexpected result is that diatoms constituted the largest percentage of particles at all sites, even those with dense canopy cover. While significantly higher percentages of diatoms in sites lacking cover certainly supports a trophic shift, it should be noted that a high representation of diatoms at all sites supports the assertion of Naiman and Sedell (1979) that significant primary production occurs under the riparian canopies of even the most densely forested headwater streams. Our results suggest that they may be more abundant than previous studies have shown them to be.

Seston integrates multiple watershed-scale properties and processes, not merely riparian con-

dition. We have shown that, at summer base-flow, many biophysical parameters of seston (e.g., concentration and percent organic matter) were unrelated to selected riparian parameters. Further, factors such as inorganic particle concentration and total foodstuffs (both from the particle diversity analysis) did not differ between site types. C:N was correlated with canopy closure but the relationship was not as strong as other correlations in this study. While the C:N results were generally positive, it may not be a solid biophysical parameter for assessing riparian characteristics, especially in comparison to chlorophyll-*a* results. Overall, only a few biophysical characteristics of seston may be good predictors of specific riparian conditions during summer.

We explicitly assumed that particles do not travel great distances at summer base-flow and that seston characteristics at a given point along a stream represent the surrounding riparian forest. As such, if seston is related to riparian condition, it is important to select biophysical seston parameters that are directly influenced by riparian characteristics, and less so by in-stream processes. Some biophysical parameters that we examined are directly influenced by riparian characteristics (e.g., concentration of chlorophyll-*a*), while others appear to be dictated by a combination of factors, predominantly ones occurring in-channel (e.g., concentration at summer base-flow).

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Literature Cited

- Bilby, R. E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a Cascade mountain stream. *Ecology* 62:1234-1243.
- Bilby, R. E., and G. E. Likens. 1979. Effect of hydrologic fluctuations on the transport of fine particulate organic carbon in a small stream. *Limnology and Oceanography* 24:69-75.
- Bisson, P. A., and J. R. Sedell. 1984. Salmonid populations in streams in clearcut vs. old-growth forests of western Washington. Pages 121-129 *In* W. R. Meehan, J. T. R. McIrell, and T. A. Hanley (editors), *Fish and Wildlife Relationships in Old-Growth Forests*. American Institute of Fishery Research Biologists, Juneau, Alaska.
- Fuller, R. L., and R. J. Mackay. 1980. Feeding ecology of three species of *Hydropsyche* (Trichoptera:Hydropsychidae) in southern Ontario. *Canadian Journal of Zoology* 58:2239-2251.
- Golladay, S. W. 1997. Suspended particulate organic matter concentration and export in streams. *Journal of the North American Benthological Society* 16:122-130.

- Golladay, S. W., J. R. Webster, and E. F. Benfield. 1987. Changes in stream benthic organic matter following watershed disturbance. *Holarctic Ecology* 12:96-105.
- Gregory, S. V., G. A. Lamberti, D. C. Erman, K. V. Koski, M. L. Murphy, and J. R. Sedell. 1987. Influence of forest practices on aquatic production. Pages 233-255. *In* E. O. Salo and T. W. Cundy (editors), *Streamside Management: Forestry and Fisheries Interactions*. Contribution Number 57. Institute of Forest Resources, University of Washington. Seattle, Washington.
- Hartman, G. F., and J. C. Scrivener. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. *Canadian Bulletin of Fisheries and Aquatic Sciences* 223:1-148.
- Henderson, J. A., D. H. Peter, R. D. Lescher, and D. C. Shaw. 1989. Forested Plant Associations of the Olympic National Forest. USDA Forest Service Region 6 Ecological Technical Paper 001-88. Olympia, Washington.
- Husch, B., C. I. Miller, and T. W. Beers. 1993. *Forest Mensuration*, 3rd Edition. Krieger Publishing Company, Malabar, Florida.
- Maciolek, J. A., and M. G. Tunzi. 1968. Microseston dynamics in a simple Sierra Nevada lake-stream system. *Ecology* 49:60-75.
- Maridet, L., M. Phillipe, J. G. Wasson, and J. Mathieu. 1997. Seasonal dynamics and storage of particulate organic matter within bed sediment of three streams with contrasted riparian vegetation and morphology. Pages 68-74 *In* J. Gibert, J. Mathieu, and F. Fournier (editors), *Groundwater Surface Water Ecotones: Biological and Hydrological Interactions and Management Options*. Cambridge University Press, Cambridge, UK.
- Naiman, R. J. 1982. Characteristics of sediment and organic carbon export from pristine boreal forest watersheds. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1699-1718.
- Naiman, R. J. 1983. The influence of stream size on the food quality of seston. *Canadian Journal of Zoology* 61:1995-2010.
- Naiman, R. J., R. E. Bilby, and P. A. Bisson. 2000. Riparian ecology and management in the Pacific coastal rain forest. *BioScience* 50:996-1011.
- Naiman, R. J., and J. R. Sedell. 1979. Characterization of particulate organic matter transported by some Cascade mountain streams. *Journal of the Fisheries Research Board of Canada* 36:17-31.
- Oswood, M. W. 1979. Abundance patterns of filter-feeding caddisflies (Trichoptera:Hydropsychidae) and seston in a Montana (U.S.A.) lake outlet. *Hydrobiologia* 63:177-183.
- Sedell, J. R., R. J. Naiman, K. W. Cummins, G. W. Minshall, and R. L. Vannote, 1978. Transport of particulate organic material in streams as a function of physical processes. *Verhandlungen der Internationalen Vereinigung für Theoretischen und Angewandte Limnologie* 20:1366-1375.
- Smock, L. A., G. M. Metzler, and J. E. Gladden. 1989. Role of debris dams in the structure and functioning of low gradient headwater streams. *Ecology* 70:764-775.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Wallace, J. B., T. F. Cuffney, J. R. Webster, G. J. Lugthart, K. Chung, and B. S. Goldowitz. 1991. Export of fine organic particles from headwater streams: Effects of season, extreme discharges, and invertebrate manipulations. *Limnology and Oceanography* 36:670-682.
- Wallace, J. B., D. H. Ross, and J. L. Meyer. 1982. Seston and dissolved organic carbon dynamics in a southern Appalachian stream. *Ecology* 63:824-838.
- Webster, J. R. 1983. The role of benthic macroinvertebrates in detritus dynamics in streams: a computer simulation. *Ecological Monographs* 53:383-404.
- Webster, J. R., and S. W. Golladay. 1984. Seston transport in streams at Coweeta Hydrologic Laboratory, North Carolina, USA. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 22:1911-1919.

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