# Recovery of Lotic Periphyton Communities after Disturbance

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ABSTRACT / Periphyton communities represent potentially excellent candidates for assessing the recovery of lotic ecosystems after disturbance. These communities are ubiquitous, relatively easy to sample and measure (in terms of total community biomass), have short generation times, and may influence the recovery rates of higher trophic levels. The first section of this article analyzes how site availability, species availability, and differential species performance influence periphyton successional dynamics. This background information provides a foundation for understanding how periphytic organisms respond after a disturbance. The second section of this article analyzes how periphyton communities respond to four different types of disturbance (flood events, desiccation, organic nutrient enrichment, and toxic metal exposure). Although data are limited, it is concluded that the fast growth rates and short generation times of periphytic organisms, coupled with their flexible life history strategies and good dispersal ability, allow lotic periphyton communities to recover relatively quickly after a disturbance. In addition, disturbance type and severity, local environmental conditions, and site-specific factors also will influence recovery rates.

Future research needs include a better understanding of: (1) what periphyton property(ies) would serve as the best index of recovery; (2) whether or not the robustness of this index varies among different environments and different disturbances; (3) interactions between autotrophs and heterotrophs within the periphyton mat, particularly with respect to nutrient cycling; (4) competitive interactions among organisms; (5) functional redundancy of organisms; and (6) the influence of the riparian zone and channel geomorphology on periphyton recovery rates.

Periphyton communities in lotic ecosystems are complex assemblages comprised of autotrophs (algae) and heterotrophs (fungi, bacteria, protozoa), attached to substrates, and often embedded in a polysaccharide matrix. Periphyton communities possess properties that make them particularly useful in evaluating the rates at which recovery occurs in lotic ecosystems following disturbance. For example, they are ubiquitous and relatively easy to sample and measure (in terms of total community biomass). In addition, compared to terrestrial biota, many periphytic organisms have very short generation times (Cairns 1982, Baars 1983). This permits periphyton growth to be monitored through many generations and different successional seres between disturbance events, potentially resulting in a better understanding of recovery dynamics. Finally, because periphyton is a high-quality food resource for many lotic invertebrates (Lamberti and Moore 1984, Steinman and others 1987a,b), its reestablishment after disturbance may be a critical factor in the recovery rates of higher trophic levels.

Although disturbances come in a wide array of forms, ranging dramatically in terms of space, time, and magnitude (Pickett and White 1985), what constitutes a disturbance is open to question. In this article, disturbance will refer to an event that changes the local environmental conditions and biological properties of the system in question. Different types of disturbances will affect local environmental conditions, and in turn periphyton successional trajectories (Steinman and McIntire 1987), differently. Since these postdisturbance successional trajectories directly influence the course and rate of recovery, an examination of the factors affecting periphyton growth and succession is necessary. Hence, the first part of this article will examine periphyton responses to general causes of succession. In particular, the degree to which site availability, species availability, and differential species performance influence periphyton colonization and growth is discussed. The second part of the article examines how periphyton respond to four different types of disturbance.

KEY WORDS: Desiccation; Disturbance; Floods; Periphyton; Streams; Succession; Toxic pollutants

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## Responses of Periphyton to General Causes of Succession

Pickett and others (1987) proposed a hierarchically structured conceptual framework to analyze successional theory. At the highest level, three basic causes of succession were proposed: site availability, differential species availability, and differential species performance. Although their scheme was designed to examine successional dynamics of terrestrial vegetation, it should be applicable to periphyton communities as well.

### Site Availability

Disturbances can open up new sites for colonization and growth. In lotic ecosystems, disturbances such as floods can increase available space for colonization by physically abrading periphyton from substrates. Anthropogenic disturbances, such as toxic pollutants, also can increase site availability if previously established organisms die and slough from the substrates. However, competition for space may not be as acute among periphytic organisms as among other sessile organisms because many algal and protozoan species: (1) can attach to an already established periphyton mat (Hoagland and others 1982), (2) are motile and can move elsewhere; and (3) can grow unattached within the structurally complex mat (the so-called metaphyton), presumably using the mat as a protective shield to avoid being dislodged by shear stress (Steinman and McIntire 1987). Mucilage exuded by diatoms appears to play a crucial role in this process, as it facilitates adhesion by other cells, increases the surface area available for colonization, and traps metaphytic algal cells (Roemer and others 1984). However, if the disturbance event is great enough to destroy the existing mats, the ability of periphytic organisms to colonize occupied sites becomes a moot point. Rather, factors such as dispersal rate, ability to colonize bare (or almost bare) substrate, and growth rates after establishment become crucial components of periphyton community recovery.

### Species Availability

The rate at which species become available after a disturbance depends both on dispersal ability and the size and type of propagule pool that survived the disturbance. Dispersal ability may be less of a problem in streams than other types of ecosystems because of ease of propagule transport by flowing water. Rushforth and others (1986), for example, found that algae recolonized severely impacted streams and springs of the Mt. St. Helens region within three months of the eruption, whereas the terrestrial landscape was still desolate. However, it is likely that among periphytic species, certain propagules have higher dispersal rates than others. For example, filamentous or colonial organisms should travel shorter distances than single-celled organisms because of their heavier weight and tendency to be retained by substrate structures in streams (personal observation). Among protozoa, dispersal capacities in lakes are thought to be similar (Kuhn and Plafkin 1977), although Henebry and Cairns (1980) noted that organisms from stressed communities should have better dispersal abilities because they are adapted to pioneer episodes of colonization. It is unknown how these patterns relate to dispersal capacities of periphytic protozoan species in lotic systems.

Species availability is reflected in the size and type of the propagule pool, as well as in dispersal properties. For lotic periphyton, there are two potential sources of propagules: (1) those that have traveled downstream or have been transported from an undisturbed area (immigrants); and (2) those that remained attached to the substrate and survived the disturbance (natives). Little attention has been paid to which of these two propagule sources contribute more to periphyton development after a disturbance. Although the two sources are not mutually exclusive, it is hypothesized that the severity of the disturbance and type of organismal growth form will influence their relative contributions to the propagule pool. For example, the more severe the disturbance, the more likely it is that immigrants will contribute to future growth because even firmly attached organisms can be eliminated if the disturbance is sufficiently severe. Alternatively, periphytic organisms that can attach firmly, or that have prostrate growth forms, may remain attached to the substrate during a moderate disturbance (Luttenton and Rada 1986, Robinson and Rushforth 1987) and be able to serve as inoculum for immediate growth and, hence, lead to rapid postdisturbance recovery of biomass.

Overall, streams with high species richness should show faster signs of initial recovery following a disturbance than streams with low richness because the high-richness streams will have a larger available species pool to recolonize substrates for periphyton regrowth. However, recovery to predisturbance levels may take longer in the high-richness streams, especially if the disturbance is severe or covers a large spatial area (Resh and others 1988).

### Species Performance

Differential species performance occurs over two distinct phases of periphyton development: (1) performance with respect to colonization and (2) performance with respect to growth after establishment. Jordan and Staley (1976) and Hoagland and others (1982) working in lentic habitats, and Hudon and Bourget (1981), Korte and Blinn (1983), and Rosowski and others (1986) working in lotic systems, all used scanning electron microscopy (SEM) to note that periphyton succession begins with the development of an organic matrix and a bacterial flora on the substrate, followed by algae and protozoa in several seral stages. Korte and Blinn (1983) observed that organic film, bacteria, and fungal hyphae developed on a substrate's upstream end within one hour of substrate introduction into a stream. However, other studies have shown that an organic coating and bacterial growth need not always precede algal colonization (Perkins and Kaplan 1978, Hamilton and Duthie 1984, Steinman and McIntire 1986, but see Rosowski and others 1986). Peterson and Stevenson (1989) observed that, after a three-day colonization period, two diatoms colonized unconditioned substrates more rapidly than conditioned substrates and suggested competition for nutrients between bacteria and algae was responsible for the negative interaction on conditioned surfaces. Steinman and Parker (1990) failed to find any long-term (>35 day) influence of in situ substrate conditioning on periphyton growth in a heterotrophic woodland stream. More work is needed to assess the importance of organic films as a facilitator of colonization by periphytic organisms.

Species composition of the propagule pool can strongly affect the rate of colonization (cf., Stevenson and Peterson 1989). Intuitively, one would expect a community dominated by pioneer species to be better adapted to colonize new substrates than a community dominated by species characteristic of mature seral stages. In fact, this expectation has been confirmed with protozoan communities in lakes (Henebry and Cairns 1980) and vegetation in tropical rain forests (Opler and others 1975). However, it is not clear if this pattern holds for periphyton in streams, where dispersal is rapid and most species have relatively short generation times. Are there certain features that make some periphytic organisms better colonizers than others? Several researchers have found that the elongate diatom, *Synedra ulna,* rapidly colonizes introduced substrates in streams (Oemke and Burton 1986, Steinman and McIntire 1986, Stevenson 1986, Stevenson and Peterson 1989). This suggests that an elongate shape (which provides a large surface area for attachment and high specific gravity) combined with an ability to exude mucilage may be crucial factors in colonization. However, other studies have shown that small, prostrate diatoms are the first algal immigrants in aquatic ecosystems (Hudon and Bourget 1981, Hoagland and others 1982, Korte and Blinn 1983, Miller and others 1987), which then are followed by larger, upright algal cells. The observation that diatoms are almost always the first algal colonists of introduced substrates in streams (Korte and Blinn 1983, Hamilton and Duthie 1984, Steinman and McIntire 1986, 1987) may be a function of a large diatom species pool (cf., Müller-Haeckel and Hakansson 1978). It also seems probable that their ability to exude mucilage promotes colonization, although Stevenson and Peterson (1989) reported that araphid diatoms had a higher probability of colonizing bare substrates than monoraphid diatoms in a number of different streams.

Abiotic properties, such as the features of a substrate, also can influence colonization rates and patterns. Douglas (1958) reported a positive association between substrate size and degree of colonization, as larger substrates were less likely to be dislodged by flood events. Others have noted greater colonization on substrates with more irregular features (Blinn and others 1980, Stevenson 1983). Hence, under some conditions, colonization may be a relatively passive process with the substrate playing the lead role in influencing colonization patterns.

After colonization, differential species' performance with respect to growth will influence both recovery rates and community structure. Factors of importance include ecophysiology (e.g., production and growth rates), life history strategies (e.g., mode of reproduction), competitive ability, and defense against herbivory (Pickett and others 1987). The information on these topics is limited, and what is available pertains almost exclusively to the algal component of periphyton. As a consequence, parts of the following section are speculative and have an unavoidable autotrophic bias.

*Ecophysiology.* Logistical difficulties in manipulating mats make the determination of production and growth rates of individual species problematic. Although rates can be determined for individual species in culture, it is unlikely that these rates can be extrapolated to natural conditions. There is intuitive appeal in thinking of early colonists as r-strategists (Pianka 1970), with productivity being selected for. Conversely, late colonists can be viewed as K-strategists, with efficiency of resource acquisition and use being selected for. Presumably, competitive pressures for light and nutrients increase as the periphyton mat matures. However, Hamilton and Duthie (1984) found that individual cell production (using track autoradiography) of a pioneer species actually increased over a 23-day experimental period, an unexpected result for a putative r-strategist. They suggested that there was tight nutrient cycling between the algal species and detrital "microcosms" in this nutrient-poor stream, which presumably enhanced the supply rate of nutrients enough to allow cell-specific production to increase over time. Nutrient cycling between periphyton and detritus, as well as within the periphyton mat itself, has received very little attention. In particular, information is needed on whether nutrient regeneration is active (e.g., by grazing) or passive (e.g., cell leakage), the relative roles of heterotrophs vs autotrophs, the fraction of total nutrient demand this process accounts for, and how this fraction changes as ambient nutrient concentrations in the external environment change. If a well-developed periphyton mat is required for tight nutrient cycling, a disturbance that disrupts the integrity of a mat could result in a reduced nutrient flux for periphytic organisms. This, in turn, could retard the recovery rate of periphyton (DeAngelis 1980).

The dominance of filamentous growth forms in late seral stages of periphyton mats (Steinman and McIntire 1986, 1987) may be a result of increased nutrient competition as the mat develops. The ability of filaments to stream out into the current beyond a mat's boundary layer, combined with their high surface area-to-volume (SA:V) ratio, should facilitate the uptake of resources. There may be a trade-off, however: although the filamentous growth form may allow for relatively fast growth rates, it is particularly susceptible to shear stress from the current (Horner and Welch 1981). As a consequence, it may be removed from the substrate before other types of growth forms.

Periphytic bacteria may obtain their nutrition from either photosynthetic metabolites excreted from algae (Haack and McFeters 1982) or the water column (Lock and Ford 1985). The ability of both the polysaccharide matrix to adsorb organic matter and the exoenzymes located within the matrix to process this matter (Lock and others 1984) potentially provides an energy source to bacteria regardless of their location within the mat. Heterotrophic bacteria have been shown to be very efficient at the uptake of inorganic nitrogen in marine environments (Wheeler and Kirchman 1986) and inorganic phosphorus in lentic ecosystems (Currie and Kalff 1984); it is unclear at present whether they exhibit similar abilities in lotic systems or if their uptake rates change as the periphyton communities mature. Diffusion gradients within the mat (Riber and Wetzel 1987) also could influence the distribution of resources and, in turn, the distribution of organisms as a result of nutrient competition.

*Life history strategies.* Many life history strategies exist among periphytic organisms (Bold and Wynne 1985). Life histories are often quite flexible, allowing an organism to reproduce either sexually or asexually or, for certain algal species, allowing unfertilized gametes to develop into new (haploid) individuals (parthenogenisis). Sexual reproduction is presumed to be rare in flowing water environments, since fertilization events that require sperm to travel in the external environment have a low chance of success. Alternatively, asexual reproduction is very common in periphyton. Various types include: zoospores, fragmentation, hormogonia, akinetes, endospores, exospores, statospores, and vegetative cell division. Even among single species, there are often several modes of asexual reproduction. Flexible life history strategies, coupled with the ability to reproduce asexually, may be very important in lotic ecosystems, where disturbance events occur on a frequent basis. Organisms may be able to adjust their life history in accordance with changing environmental conditions brought on by the disturbance. For example, cells may form akinetes to survive periods of desiccation (Morison and Sheath 1985), or after a disturbance, they may reproduce by asexual means in order to grow and quickly reestablish a large population.

*Competitive ability.* Numerous studies have inferred competitive interactions to occur among lotic periphyton species (Klotz and others 1976, Sumner and McIntire 1982, Sheath and Burkholder 1985, Lowe and others 1986, Steinman and McIntire 1986, 1987, Power and Stewart 1987). In mature or structurally complex mats, a large number of species often coexist within small, localized areas, creating a strong potential for competition. Space, light, and nutrients are the three resources most frequently cited as the focus for competition. As mentioned earlier, competition for space may not be as problematic for periphytic organisms as it is for species in other habitats, since some organisms do not need to attach directly to the substrate. However, some studies have indicated that prostrate diatoms, such as *Achnanthes* and *Cocconeis* spp., once attached to a substrate, can reproduce rapidly and form a monolayer of cells that can thereby preclude colonization by other species (Dickman and Gochnauer 1978, Goldsborough and Robinson 1986). In the former study, however, grazing pressure on *Cocconeis* exposed new surfaces for colonization within four weeks, ending this taxon's monopolization of space (Dickman and Gochnauer 1978). Goldsborough and Robinson (1986), however, found that, following short herbicide treatments, *Cocconeis* continued to dominate substrate surfaces throughout the study period (six weeks), suggesting that competition for space can be a relatively long-term event among periphyton.

Mature periphyton communities consist of understory species (usually with prostrate growth forms) and overstory species (usually with filamentous, stalked, or otherwise upright growth forms). This structuring, where overstory species can intercept light that would otherwise reach understory species (Losee and Wetzel 1983), has led investigators to believe that competition for light is an important factor influencing periphyton dynamics and community structure. Hence, understory species are typically perceived as shade tolerant (Hudon and Bourget 1983), where overstory species are viewed as shade intolerant (Steinman and McIntire 1986). However, this view is an oversimplification, because many shade-tolerant species are early colonizers of substrates, when light is abundant. It may be that the superior dispersal and colonization abilities of these pioneer species supercedes any competitive interactions for light, and then as the periphyton in the mat undergo succession, these species are able to persist until light intensity is insufficient for continued growth.

As with competition for light, competition for nutrients by periphyton has been mostly inferred to occur. In this case, inferences are based on indirect evidence and from experimental results obtained using nutrient-diffusing substrates. For example, Hill and Knight (1988) reported that prostrate diatoms reponded positively to nitrate enrichment, although Lowe and others (1986) found no consistent patterns in periphyton growth responses to nutrient enrichments. One way to view nutrient competition in periphyton is with Michaelis-Mentin kinetics. For example, Stevenson (1986) proposed that pioneer species may gain a competitive advantage by sequestering nutrient reserves (presumably by having high $V_{\max}$ rates and being able to sustain them for relatively long periods of time). These species then could draw upon the reserves during later seral stages as competition for nutrients intensified. Conversely, late colonists would have a high affinity for the limiting nutrient (i.e., low $k_s$), which would provide an advantage as competition for nutrients increased. This model presumes that nutrients decrease in concentration as the periphyton community develops (see Hamilton and Duthie 1984). In so doing, it also neglects any nutrient regeneration that may be going on within the mat, such as from herbivore activity (Flint and Goldman 1975, Cuker 1983), algal excretion (Brock and Clyne 1984), or protozoan grazing on bacteria (Caron and others 1988).

*Defense against herbivory.* Prey organisms can defend themselves against herbivores with two strategies: (1) by minimizing the probability that they will be encountered to begin with, or (2) if encountered, by reducing the probability that they will be grazed upon (Lubchenco and Gaines 1981). Many periphytic organisms have small sizes and prostrate growth forms, characteristics that help them avoid encounters with herbivores. For example, the diatoms *Cocconeis placentula* and *Achnanthes lanceolata* persist even under moderate to heavy grazing pressure (Gregory 1983, Steinman and others 1987a) because their close, horizontally oriented attachment to the substrate minimizes their direct exposure to grazer mouthparts. The same mechanism enables some bacteria to avoid being grazed (Dickman 1968). However, other studies have found that these forms can be consumed in large amounts (Brown 1961, Dickman and Gochnauer 1978). It seems likely that whether or not organisms with prostrate growth forms are grazed depends on their location in the periphyton mat. If they are attached to the substrate surface, they may remain invulnerable to grazing; if they grow in clumps (Steinman and McIntire 1987), however, a vertical dimension is created that leaves them vulnerable to grazing. Growth in crevices or fissures in substrates also may enable periphyton to avoid grazers.

Once encountered, prey characteristics such as morphology, chemicals that deter grazing, and nutritional quality can influence the degree to which they are preyed upon. Moderate to heavy grazing pressure usually results in a periphyton community with a simple physiognomic structure and limited biomass (Steinman and others 1987a). At least for disturbances such as floods, recovery times of grazed communities should be short because: (1) predisturbance communities have small biomass levels to begin with, and (2) grazing results in dominance by adnately attached organisms with prostrate growth forms, which are relatively resistant to dislodgement from shear stress and likely to remain attached during a flood disturbance.

## Periphyton Responses to Different Disturbance Types

Periphyton in lotic ecosystems are subject to many kinds of disturbances, including floods, desiccation, organic nutrient enrichment, and exposure to toxic metals. This section will analyze how periphyton respond to these four disturbance types and, in turn, how disturbances affect periphyton communities.

### Floods

This section focuses primarily on high-discharge events that are associated with storm events. Although catastrophic floods (i.e., those with recurrence intervals of 50–100 years) can cause tremendous biological, geological, and socioeconomic damage, their frequency of occurrence is so rare and deviates so greatly from periphyton generation times that they are of limited relevance here. Storm-related high-discharge events not only occur with a frequency that is somewhat similar to periphyton generation times, but they still can have a strong influence on stream biota (Fisher and others 1982), geomorphology (Wolman and Miller 1960), and organic matter storage (Cummins and others 1983). High-discharge events represent a disturbance to periphyton because they can dislodge mats from substrates. Direct shear stress of flow and abrasion by sediments are the primary causes of dislodgement.

Both organismal growth form and environmental conditions can influence the susceptibility of periphyton to removal during high flow. Filamentous growth forms appear to be susceptible to dislodgement if current velocities exceed 50 cm/sec (Horner and Welch 1981). However, filamentous algae that have firm attachment mechanisms can survive floods better than filaments with weak modes of attachment. Power and Stewart (1987) found that the filamentous chlorophyte *Rhizoclonium,* which has specialized basal attachment cells, only decreased fourfold in abundance after a flood, whereas occurrence of *Spirogyra,* which attaches by lateral or terminal hapteroid outgrowths, decreased 20-fold. Alternatively, organisms with prostrate growth forms that reside within the substrate's boundary layer should be able to remain attached at much higher current velocities than filaments (cf., Scrimgeour and Winterbourn 1989). Although filamentous organisms may be more susceptible to scour during high flow, habitats characterized by certain filamentous algae (e.g., chlorophytes) often are characterized by high light and nutrients (Steinman and McIntire 1987). These physical and chemical characteristics promote fast growth rates in periphyton, so recovery rates in these habitats may be faster than in areas where organisms with prostrate growth forms predominate.

Sediments may play an important role as an abrasive force during flood events. As a consequence, knowledge of the stream's and watershed's flood history, which will affect the amount and type of sediment stored in the channel (Cummins and others 1983), may be helpful in assessing the potential damage caused by sediment abrasion. In addition, abrasion is more likely to influence periphyton attached to small, light substrates (e.g., gravel, cobble, twigs) than large, heavy substrates (e.g., boulders) because the former substrates are more likely to be moved by the current (Douglas 1958). Holling (1973) suggested that communities that grow in low-stress, stable environments are more fragile than those that develop in high-stress, unstable environments. Applying this to lotic systems, it may be that periphyton communities that develop in areas of relatively placid flow (e.g., pools, backwaters) are more susceptible to dislodgement during flood events than communities from regions of swift flow (e.g., riffles, cascades).

The recovery of periphyton after a flood will depend upon: (1) propagule abundance, (2) propagule composition, and (3) local environmental conditions. All else being equal, the greater the propagule abundance, the faster the periphyton communities should recover. Unfortunately, few studies analyze pre- or postflood seston for propagule quantity or quality, presumably because of the large volume of water that would need to be filtered. Stevenson and Peterson (1989) reported diatom immigration rates of 50–2500 cells/cm$^2$/day onto bare clay tiles. How representative these colonization rates are for different streams and substrates remains to be investigated. Propagule composition can be important as well, since some periphytic organisms appear to be well adapted for colonizing bare or sparsely colonized substrates, whereas others are effective late colonists (see earlier). Patrick (1967) showed that the potential species pool has a greater effect than size of area in determining the number of species in a diatom community.

Once propagules settle and start to grow following a flood, the successional trajectory will be influenced by local environmental conditions. The main environmental factors that can influence periphyton recovery include current velocity, irradiance, and nutrient levels; other factors such as herbivory, substrate size, and temperature, however, cannot be ignored.

Current velocity may influence lotic periphyton recovery rates in at least three ways. The first is by enhancing algal colonization of primary substrate in low-flow regimes (McIntire 1966, Reisen and Spencer 1970, Stevenson 1983, Steinman and McIntire 1986). This is primarily a physical phenomenon, as cells are more likely to settle out at slow as opposed to fast current velocities. The second is by stimulating growth of established communities at moderate current velocities

(Whitford and Schumacher 1964, McIntire 1966, Horner and Welch 1981), as moderate flow can enhance the exchange rate of nutrients and dissolved gasses between periphytic organisms and the aqueous medium. The third is by dislodging periphyton at high current velocities because of increased shear stress (Douglas 1958, Horner and Welch 1981), thereby resetting the successional process.

Because autotrophic growth is dependent on photosynthesis, the periphyton community should recover to its predisturbance level of biomass more rapidly under higher levels of irradiance and temperature (because photosynthesis is an enzymatically driven process), all other things being equal. Indeed, Grimm and Fisher (1989) reported that resilience of periphyton following flood events was positively associated with high light and warm temperature in a Sonoran desert stream. Irradiance, however, can influence community structure as well as biomass. For example, Steinman and McIntire (1987) reported that relative abundance of chlorophytes was much greater in streams exposed to 150 and 400 $\mu$E/m$^2$/sec than in channels exposed to 15 and 50 $\mu$E/m$^2$/sec. Shortreed and Stockner (1983) also observed increased abundances of filamentous chlorophytes in streams after the riparian vegetation was logged and light levels increased.

Alternatively, prostrate diatoms such as *Achnanthes lanceolata* and *Cocconeis placentula* are often considered shade-tolerant species. It is possible, although untested, that these species actually have faster growth rates in high than low light, but even these faster growth rates under high light cannot match the growth rates of overstory species. As a consequence, they remain in the understory of the mat. This raises the unresolved question of whether light-induced changes in the relative abundances of certain species are the result of competitive interactions among periphyton, or simply different autecological responses by different taxa. Recovery rates of individual taxa may be just as, if not more, important than recovery rates of periphyton biomass if functional redundancy is low in lotic periphyton communities. If separate taxa do indeed play unique functional roles in these communities, a better understanding of the factors influencing periphyton community structure, such as competitive interactions and autecology of key taxa, is necessary.

As with irradiance, periphyton communities should recover more rapidly when nutrient levels in the water are high (DeAngelis and others, 1990). Data from an unpublished study (Table 1, study 10) indicate that periphyton accumulation on bare tiles was greater after 30 days in high-nutrient, ungrazed systems than low-nutrient, ungrazed streams. ATP values also were substantially higher in the high-nutrient than the low-nutrient streams (461 vs 283 ng ATP/cm$^2$, respectively) in study 10. In streams where snail densities were high (studies 11 and 18), nutrient levels had no apparent effect on biomass levels after 30 days. The grazed systems experienced very little reduction in biomass as a result of the scour disturbance and recovered quickly to their predisturbance biomass levels. This appears to be because their biomass levels were very low even before the disturbance, and the prostrate growth form of these organisms was well-adapted to withstand this type of disturbance. If nutrients influenced recovery rates in these streams, they did so before 30 days.

Table 1 lists eighteen studies that have followed periphyton colonization and growth on either bare substrates placed in undisturbed streams or on substrates after a flood or scour event. Since floods act to dislodge periphyton from substrates, the development of periphyton mats on bare substrates in undisturbed streams can serve as an analog of mat development on substrates in flooded streams. Of course, the fact that there will be no organic coating or native propagules on newly introduced substrates may result in slower recovery rates relative to natural substrates. However, substrates newly introduced into an undisturbed stream will be exposed to a larger number of propagules than substrates placed into a recently flooded stream, which may counteract the effect of no conditioning on the substrate.

Table 1 indicates that 30 days after exposure, most substrates accumulated between 0.01 and 0.1 g/m$^2$ of chlorophyll *a*. Of the two studies where chlorophyll *a* values remained below 0.01 g/m$^2$, one system was subjected to intense grazing pressure (study 14). The other was devastated by a debris torrent (study 17), and despite high irradiance levels (due to the removal of riparian vegetation), recovery of chlorophyll *a* was slow. In this case, a limited propagule pool may have retarded short-term recovery rates. Ash-free dry mass (AFDM) values varied to a much greater degree than chlorophyll *a*, ranging from <1 to 145 g/m$^2$. Again, most of the studies in which AFDM values were low were studies of systems where grazing pressure was intense (studies 11 and 12) or where irradiance levels were very low (study 3). Examination of individual experiments indicates that environmental conditions can strongly influence periphyton recovery rates. For example, both light and nutrient levels were positively associated with rates of biomass accumulation in studies by Steinman and McIntire (1987) and Pringle (1987), respectively. Although external factors (e.g.,

Table 1. Biomass accumulation of periphyton communities after ca. 30 days on substrates introduced into undisturbed streams or on substrates from streams disturbed by a flood event

| Habitat | Chlorophyll[a] (g/m$^2$) | AFDM (g/m$^2$) | Light (μE/m$^2$/sec) | SRP (or NO$_3-$N) (μg/liter) | Study |
|---|---|---|---|---|---|
| *Substrates introduced in streams* | | | | | |
| 1. Sycamore Cr., AZ | 1) 0.06[a]<br>2) 0.05[a]<br>3) 0.09[a] | NA[b] | NA | 1) 54<br>2) 340<br>3) (320)[c] | Grimm and Fisher (1986) |
| 2. Artificial channels, OR | NA | 1) 30<br>2) 10 | 450<br>50 | 190 | Steinman and McIntire (1986) |
| 3. Artificial channels, OR | NA | 1) 0.5<br>2) 3<br>3) 18<br>4) 30 | 15<br>50<br>150<br>400 | 100 | Steinman and McIntire (1987) |
| 4. Keough R., British Columbia | 1) 0.05<br>2) 0.03 | NA | 1389[d] | 1) 70<br>2) 40 | Perrin and others (1987) |
| 5. Carp Cr., MI | 1) 0.014[e]<br>2) 0.06 | NA | NA | 1) 2.5<br>2) 12.4 (15.5 × 10$^6$)[f] | Pringle (1987) |
| 6. S. Thompson R., British Columbia | 1) 0.03<br>2) 0.07 | NA | 694[d] | 1) 0.5<br>2) 5.0 | Bothwell (1988) |
| 7. Concrete channels, F.R.G. | NA | 20 | NA | NA | Eichenberger and Wuhrmann (1975) |
| 8. Barnwell Cr., CA | 1) 0.011<br>2) 0.006<br>3) 0.042 | 1) 2.1<br>2) 1.3<br>3) 3.4 | 441[g] | 1) 42 (12)[c]<br>2) (15.5 × 10$^6$)[f]<br>3) (7.5 × 10$^6$)[h] | Hill and Knight (1988) |
| 9. Artificial channels, OR | 1) 0.12<br>2) 0.05 | 1) 75<br>2) 5 | 140<br>30 | NA | McIntire (1968) |
| 10. Artificial channels, TN | 1) .059<br>2) .037 | NA | 150 | 1) 11.0<br>2) 7.3 | Kirschtel (unpublished data) |
| 11. Artificial channels, TN | 1) 0.013[a,i]<br>2) 0.012[a,i] | 1) 2.9<br>2) 3.1 | 150 | 1) 18.3<br>2) 28.1 | Steinman and others (unpublished data) |
| 12. Artificial channels, OR | NA | 1) 43[j]<br>2) 18[k]<br>3) 2[l] | 400 | 200 | Steinman and others (1987a) |
| 13. Artificial channels, OR | 1) 0.70[m]<br>2) 0.43[n]<br>3) 0.01[o] | 1) 36<br>2) 18<br>3) <1 | 400 | 96 | Lamberti and others (1987) |
| 14. Big Sulfur Cr., CA | 1) 0.10[p]<br>2) 0.005[q] | 1) 45<br>2) 18 | NA | NA | Lamberti and Resh (1983) |
| *Substrates in flood-disturbed streams* | | | | | |
| 15. Sycamore Cr., AZ | 0.09 | 110 | 200 | 56 (70)[c] | Fisher and others (1982) |
| 16. Sycamore Cr., AZ | 0.30 | 145 | NA | 42 (63)[c] | Grimm (1987) |
| 17. Quartz Cr., OR | 1) 0.01<br>2) 0.006 | NA | 1) 25<br>2) 1700 | 8 (2)[c]<br>11 (4)[c] | Lamberti and others (unpublished data) |
| 18. Artificial channels, TN | 1) 0.17[r]<br>2) 0.09[r]<br>3) 0.04[s]<br>4) 0.04[s] | 1) 25.2<br>2) 17.9<br>3) 7.4<br>4) 7.8 | 150 | 1) 28.6<br>2) 7.0<br>3) 28.0<br>4) 18.0 | Steinman and others (unpublished data) |

[a] Measurements made at 21 days.

[b] NA = data not available.

[c] N-limited system.

[d] Assumes a 10:14 L:D photoperiod.

[e] Measurements made at 22 days.

[f] PO$_4$-P concentration in nutrient-diffusing substratum.

[g] Assumes a 12:12 L:D photoperiod.

[h] NO$_3-$N concentration in nutrient-diffusing substratum.

[i] Snail (*Goniobasis*) density = 1000/m$^2$.

[j] Snail (*Juga*)-excluded treatment.

[k] *Juga* density = 125/m$^2$.

[l] *Juga* density = 500/m$^2$.

[m] Ungrazed stream.

[n] *Juga* density = 350/m$^2$.

[o] Caddisfly (*Discosmoecus*) density = 200/m$^2$.

[p] Caddisfly (*Helicopsyche*)-excluded treatment.

[q] *Helicopsyche* density = 200/m$^2$.

[r] *Goniobasis*-excluded treatment.

[s] *Goniobasis* density = 1000/m$^2$.

grazing, nutrient availability, light level) may limit the ultimate amount of biomass that can accumulate in a system, it appears that most periphyton communities have the ability to recover quickly to that limit after a flood event (Kaufman 1980).

### Desiccation

Periphyton communities can be subjected to desiccation events as water levels decline. Species that grow near the top of elevated substrates in streams are the first to become emersed as water levels fall and are most likely to have adaptations to desiccation. However, organisms that grow in intermittent streams also must have the ability to survive long periods of exposure or else be good immigrators once flow returns to the stream. Lotic algal species can survive periods of desiccation by producing thick walls (Morison and Sheath 1985), mucilage (Evans 1959, Shephard 1987), zygospores (Evans 1959), or cysts (Evans 1959). Drying also can induce the formation of akinetes, cells that secondarily thicken their walls and accumulate storage products (Coleman 1983).

As a disturbance agent, desiccation may be most influential in systems that normally have year-round flows, but which, because of drought, debris accumulations, or perhaps beaver activity, have flows unexpectedly reduced or eliminated. Among periphytic organisms, those that rarely experience desiccation are less likely to have adaptations to tolerate or survive it than organisms that are occasionally exposed and, hence, are more likely to be eliminated by the event. Both theoretical and empirical work has indicated that an organism that grows in a high-stress environment is more likely to successfully withstand a disturbance, including that of desiccation, than an organism that develops in a low-stress system (Holling 1973, Peterson 1987). Nonetheless, in lotic ecosystems, the ability of many periphytic organisms to form resting spores may be an important feature that enables them to survive desiccation better than most organisms of higher trophic levels.

### Organic Nutrient Enrichment

The introduction of nontoxic organic nutrients to running waters, such as from sewage, can directly impact all types of periphyton. Hynes (1963) presented a general scheme for the biological consequences of organic enrichment to running waters. Directly below the point of introduction, bacterial numbers, including sewage "fungus" (*Sphaerotilus natans*), increase but decline further downstream as organic matter is consumed. As oxygen levels increase further downstream, protozoan populations increase, which feed on the bacteria. Algal populations, especially those of *Cladophora*, increase as oxygen levels build up and inorganic nutrients are released from the remineralized organic matter.

Organic enrichment can have profound effects on periphyton community structure. Protozoan species richness increases in response to a moderate degree of organic pollution (Henebry and Cairns 1980), although at high levels of organic enrichment, richness declines as species such as *Carchesium*, *Urocentrum turbo*, and *Vorticella microstoma* predominate (Hynes 1963, Henebry and Cairns 1980). In terms of diatom community structure, the ultimate response to pollution is reduced species richness, diversity, and evenness (Patrick 1969).

Introduction of nontoxic organic waste usually results in an increase of nonchlorophyllous heterotrophic biomass. Organic enrichment can stimulate autotrophic growth, as well: a gasoline spill in a northern Idaho stream resulted in higher chlorophyll *a* values than in a control reach of the stream 26 days after the spill (Pontasch and Brusven 1987). However, heterotrophic biomass was stimulated to a much greater degree than autotrophic biomass, as measured by an autotrophic index (AI). The AI is calculated as the amount of biomass (as dry mass or ash-free dry mass) divided by the amount of chlorophyll *a* in the community. AI values generally range from 50 to 100 (using dry weight) in unpolluted waters, but can become considerably higher in polluted areas (Weber 1973).

Lock and others (1981a) suggested that petroleum hydrocarbons could stimulate periphytic growth through several mechanisms: they could (1) serve as a carbon source for the heterotrophs, which could lead to increased production and accelerated regeneration of nutrients within the periphyton mat; (2) supply inorganic nutrients that stimulate autotrophic growth; (3) stimulate nitrogen-fixing bacteria, leading to an increased nitrogen supply in the mat; (4) physically enhance the trapping of nutrients through sorptive processes; and (5) contain growth-stimulating compounds, such as trace elements that may stimulate periphytic growth. When periphyton communities grown on bricks were immersed in oils for 1 min, no apparent effects were noted (Lock and others 1981b). The results from these studies suggest that a short catastrophic crude oil spill would have a minimal effect upon established periphyton communities and may actually enhance future growth of periphyton on uncolonized substrates.

Recovery of periphyton communities from nutrient enrichment can occur in two ways: (1) a recovery (in terms of community structure) to a preenrichment state as a result of elimination of the enrichment, or (2) a recovery in downstream sites that is associated with dilution and self-purification of the water. Given the short generation times of periphyton and their good dispersal and colonization abilities, it is expected that once nutrient enrichment to a stream or river ends, it should only take weeks to months for the community to return to the preenrichment state. Pontasch and Brusven (1987) found that the autotrophic index of gasoline-impacted periphyton communities returned to the levels found in the control reach within two months of the spill, although mechanical agitation of the streambed to release trapped hydrocarbons one month after the spill no doubt enhanced recovery. Recovery time may be considerably longer if propagule sources upstream from the disturbance area are impacted (Resh and others 1988). In addition, the larger the area disturbed and more severe the enrichment, the longer it will take for recovery.

Microbial heterotrophs can contribute to the breakdown and removal of organic compounds, thereby helping to purify the running water habitat. In rivers with high discharge and swift currents, physical removal or dilution hastens the system's recovery compared with systems characterized by low discharge and slow flows. In addition, warm temperatures can enhance the biological purification, as bacterial activity, protozoan ingestion rates on bacteria, and bacterial and fungal autolysis are all increased at higher temperatures (Rheinheimer 1985). Biodegradation of synthetic crude oil by periphyton also has been reported (Lock and others 1982), with degradation rates higher at 20°C than 4°C. Although some algal species do not seem to recur after a stream is cleansed of organic pollution (e.g., *Draparnaldia* and *Lemanea*), the overall enrichment of the water often results in an increase in algal species richness (Hynes 1963).

### Toxic Pollutants

Periphyton communities can recover from exposure to toxic pollutants in two ways: (1) through a physiological or genetic adaptation to the existing conditions, or (2) by undergoing a slow successional change after the disturbance ends, which returns the community to its predisturbance structural and functional state. Physiological adaptation occurs within the lifetime of the organism, whereas genetic adaptation may require several generations in the population. Assuming an organism is exposed to a toxic metal, compartmentalization of the toxicant within the cell is a physiological mechanism that can limit its damage. For example, Silverberg (1975) noted that Pb accumulated on the cell walls and within vacuoles of *Stigeoclonium tenue.* Sicko-Goad and Stoermer (1979) reported Pb was concentrated in polyphosphate bodies in the vacuole of *Diatoma tenue,* and Jensen and others (1982) found that Pb and Zn were compartmentalized in the polyphosphate bodies of the unicellular chlorophyte *Chlorella saccharophila* and the diatoms *Navicula incerta* and *Nitzschia closterium.* The ability to sequester toxic metals may be an important factor in allowing certain species to persist in areas where the concentrations of toxic metals is high. Toxicants may have difficulty diffusing through periphyton mats. Rose and Cushing (1970) reported that $^{65}$Zn accumulation in periphyton communities primarily occurred through adsorption to the mat's outer surface. In mats with strong diffusion gradients, toxic metals may never reach the cells located toward the center of the mat.

Genetic adaptation by individual species to heavy metal exposure has been reported for several freshwater green algae: *Scenedesmus* and *Chlorella* (to Ni; Stokes and others 1973), *Chlorella vulgaris* (to Cu; Foster 1977); *Hormidium* spp. (to Zn; Say and others 1977); and *Stigeoclonium tenue* (to Zn; Harding and Whitton 1976). Although some species become less sensitive to certain metals through genetic adaptation, the physiological mechanism(s) responsible in such cases is unknown. Possible mechanisms include cellular exclusion of toxicants (e.g., binding the metal to the cell wall), improved compartmentalization of toxicants (cf., Jensen and others 1982), or enhanced uptake of cations, which can reduce the toxicity of some metals (Shehata and Whitton 1982). Wangberg and Blanck (1988) reported that phosphate concentrations influenced the tolerance pattern of marine periphyton communities to arsenate because arsenate competes with phosphate for sites on the photosynthetic coupling factor.

In situations where exposure to the toxicant ends, the periphyton community may undergo a successional process, bringing it back toward a predisturbance state. The recovery time of periphyton communities exposed to heavy metals may take longer than for the other types of disturbances discussed. Eichenberger and others (1981) noted that algal communities exposed to Co, Cu, and Zn retained an altered taxonomic structure for months after additions of the metals ceased. One reason for this is that the influence of toxicants is likely to remain in the system much longer than that of floods, desiccation, or enrichment. Not only can toxicants be sequestered inside the cells of periphytic organisms (and whatever consumes them), but they can remain in the system if enriched particulate matter enters the sediment pool of the benthos (Hart 1982). In addition, toxicants can adsorb to sediments (Hart 1982) and the polysaccharide matrix of the periphyton mat (Lock and others 1984), from which they can be slowly released over time. Ultimately, the degree to which a metal ion will bind to a surface depends upon the concentration of the reacting species, pH, ionic strength, concentration of competing ions, and the presence of naturally occurring complexation agents (Hart 1982).

The recovery time of periphyton communities exposed to heavy metals may be affected by local environmental conditions. For example, pH has a strong influence on metal toxicity and algal tolerance. Peterson and others (1984) found that the inhibiting affect of Cd and Cu on phosphorus uptake increased markedly with increasing pH over the range of 5.5–8.5. They suggested that competition between $H^+$ and free metal cations for cellular binding sites could explain the higher toxicity at more alkaline conditions. However, the concentration of free metal ions increases as pH decreases. Since free metal ions generally are considered more toxic than organic and inorganic complexes (Sunda and Guillard 1976, Anderson and Morel 1978), there may be confounding effects between higher concentrations of free metal ions (potentially increasing toxicity) and increased competition for cellular uptake sites by $H^+$ (potentially decreasing toxicity) as pH decreases. Alternatively, sedimentation as a result of metal precipitation may inhibit periphyton growth and reduce recovery rates. McKnight and Feder (1984) found that precipitation of hydrous Al and Fe oxides had a more adverse effect on periphyton than high free metal ion concentration. These precipitates destabilized rock surfaces, preventing the development of a stable periphyton community.

Finally, community structure may affect periphyton recovery time. Kaufman (1982) noted that older periphyton communities had a lower resistance (estimated as ATP one day after disturbance divided by ATP on day of disturbance) than younger communities. He attributed the higher resistance of the young communities to their simpler structures. This is analogous to the slower recovery times reported for ungrazed communities relative to grazed communities after a flood event, in that older (or ungrazed) communities are more complex and dynamically fragile (May 1975). In addition, Kaufman (1982) reported that prestressed communities had greater resistance and resilience (estimated as ATP or chlorophyll *a* five or eight days after disturbance divided by ATP or chlorophyll *a* on day of disturbance) than communities with low or no stress history. This finding is consistent with those of Peterson (1987), who found that diatom communities from high-stress environments tolerated periodic desiccation better than those from low-stress environments.

## Summary and Conclusions

The limited amount of experimental data that exists on the postdisturbance recovery properties of lotic periphyton restricts the number of conclusions that can be drawn at present. However, good dispersal abilities, high production rates, short generation times, and flexible life history strategies should enable periphyton biomass to recover rapidly after a disturbance event in most lotic ecosystems. Nevertheless, periphyton recovery patterns also can be influenced strongly by site and disturbance type. For example, local environmental conditions, such as nutrient concentration, light level, grazing pressure, substrate size and composition, propagule abundance and source, sediment load, and stream order, grade, and channel geomorphology all can affect the recovery rates of periphyton. In addition, periphyton communities appear to take longer to recover from exposure to toxic metals than other disturbance types, perhaps because these metals remain in the system a relatively long time. Although communities developing in a high-stress environment appear to be more resistant to disturbance than those growing in a low-stress environment, it is unknown if this resistance applies across a wide spectrum of disturbance types. Indeed, the property that renders heavily grazed periphyton communities resistant to flood events (i.e., dominance by organisms with prostrate growth forms) may make them more susceptible to toxic pollutants (because the community's simple physiognomic structure exposes more organisms to the toxicant).

Periphyton communities are crucial to stream ecosystem recovery because they serve as an important food resource for many invertebrates. Hence, if periphyton recovery is slow following a disturbance, other biological components in streams also may be slow to recover. The high resiliency of periphyton biomass has two important implications. First, fast recovery rates of biomass may, ironically, make biomass a poor endpoint for lotic ecosystem recovery simply because not enough time has elapsed to critically evaluate how the entire ecosystem is recovering. However, this high resiliency may enable periphyton communities to serve as important guideposts indicating what successional trajectory the recovery process is taking. Second, although periphyton biomass appears particularly resilient, it is unknown whether periphyton taxonomic structure and functional processes recover as quickly as biomass. Given our present understanding of periphyton functional redundancy, turnover time, nutrient cycling, and trophic level interactions, any claims of postdisturbance periphyton recovery based solely on biomass measurements seem premature.

## Future Research

If periphyton communities are to serve as a guide in evaluating lotic ecosystem recovery following disturbance, perhaps the most critical research need is to determine what periphyton property(ies) serve as the best index of recovery. At present, it is still not known whether biomass, taxonomic structure, nutrient cycling capacity, or another process makes the best index. Indeed, it seems likely that a "best index" will vary depending on the type of disturbance and stream being studied. Additional research on stream classifications (cf., Frissell and others 1986, Whittier and others 1988, Hughes 1990), may enable us to determine, a priori, whether or not a certain periphyton index is more appropriate to assess resiliency, given a particular stream type. For example, biomass may prove to be the best index of recovery in streams where loss rates are very low during biomass accrual (e.g., low gradient, low grazer densities) and where secondary production is not linked to periphyton production. Alternatively, primary production may be the best index in streams where loss rates are high and secondary production is strongly associated with periphyton photosynthesis.

Based on our current level of ignorance, it seems prudent to gear future research toward both organismal biology and stream ecosystem behavior.

On the organismal scale, we need a better understanding of:

- The interactions between the autotrophic and heterotrophic components within the periphyton mat, particularly with respect to nutrient cycling dynamics. If a disturbance selectively affects one component of the mat more than the other, how will this influence the other part, and what implications will this have for the entire system?
- Functional redundancy in periphyton communities. If it is low, more information is needed on factors controlling taxonomic structure, such as competitive interactions and the autecology of key periphyton species.
- The respective roles of immigrants vs natives in recolonizing substrates, or are differential colonization abilities quickly trivialized by postcolonization processes?
- Why periphytic organisms living in high-stress environments appear to be more resistant to disturbance than those living in low-stress systems. What properties enable organisms to survive stresses and does resistance to one disturbance type convey resistance to other types?

On the ecosystem scale, we need a better understanding of:

- What influence, if any, does the riparian zone and channel geomorphology have on periphyton recovery times. Lamberti and others (1990) reported that retention of particulate and dissolved matter in streams was higher in unconstrained (i.e., broad valley floor) than constrained (i.e., narrow valley floor) reaches. In addition, retention was enhanced by increased geomorphic complexity of channels, diversity of riparian vegetation, presence of woody debris, and heterogeneity in stream hydraulics, sediments, and lateral habitats. These factors profoundly influence macroinvertebrate recovery patterns (Wallace 1990) and presumably could strongly affect periphyton dispersal and colonization rates, thereby affecting periphyton recovery rates after a disturbance.

It is unlikely than any one approach will provide definitive answers about periphyton resistance and resilience to disturbance. However, a multifaceted approach that combines laboratory and field work, descriptive and experimental ecology, and fine-scale and coarse-scale analyses will bring us closer to an understanding of lotic periphyton dynamics.

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