**NOSTOC (CYANOPHYTA) PRODUCTIVITY IN OREGON STREAM ECOSYSTEMS: INVERTEBRATE INFLUENCES AND DIFFERENCES BETWEEN MORPHOLOGICAL TYPES**

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**ABSTRACT**

Nostoc parmelioidees colonies housing dipteran larvae (Cricotopus) had higher rates of weight specific photosynthesis than colonies without the larvae. A change in colony shape, which allowed the algae to be exposed to higher light intensities, occurred in the presence of the larvae. This change in morphology together with potential nutrient additions by the larvae and other effects may have caused the increase in photosynthetic rates. Nostoc colonies were typically found in open areas of small streams in western Oregon mountains where the ability to respond to high light would be advantageous in supporting the metabolically expensive process of nitrogen fixation.

Key index words: Algal-invertebrate interactions; blue-green algae; chironomid; Cricotopus nostocicola; Nostoc parmelioidees; stream algal productivity

Several groups of algae exhibit different morphological stages in their life cycle. Of the macroalgae, the heteromorphic mode of existence is most frequently found in the Chlorophyta, Phaeophyta, and Rhodophyta (Lubchenco and Cubit 1980). However, also members of the Cyanophyta (cyanobacteria), particularly species of Nostoc, are polymorphic (Lazaroff 1973). The ecological advantages of these different morphological types have not always been clear, although in marine macroalgae it has been suggested as an adaptation to fluctuations in grazing pressure (Lubchenco and Cubit 1980).

An unusual mutualistic relationship and perhaps a rare example of co-evolution among stream plants and animals (Gregory 1983), exists between two species of chironomid midges, Cricotopus (nostocicola and fuscata) (Diptera: Chironomidae), and a nitrogen-fixing, blue-green alga, Nostoc parmelioidees, in western mountain streams (Wirth 1957, Brock 1960). During the early summer, females lay eggs on the surface of developing Nostoc colonies. After hatching, larvalae bore into the colony and eventually a single larva is housed, until emergence of the adult, within the colony. The midges appear host-specific; that is, they have not been observed in the freeliving state or in other plants, and by later instars, do not move from colony to colony. Upon entry of the midge, the Nostoc colonies which house the midges change in shape from globose, essentially spherical macrocolonies to flattened, more erect forms resembling discs or small “ears.” The Nostoc colony resumes its globose form and decomposes after emergence of the adult midge.

Both Nostoc ears and unoccupied spheres are present throughout the year in Oregon streams which have abundant Nostoc parmelioidees, although ears are more prevalent in summer and spheres in winter (Ward, unpublished data). This relationship allows the larvae to grow in a protected environment with a readily available, high nitrogen food source within the colony. The advantages to the algal colonies, which are being consumed from the inside out, have been less obvious, although the larva may on occasion aid in attaching the colony to the substrate. We present evidence that the ear-shaped Nostoc colonies with the Cricotopus midge have much higher photosynthetic rates year round than the globose, spherical colonies and suggest that the midge provides the stimulus for the change in colony shape, which together with the presence of the midge, allows the alga to exist in and respond to a high light regime.

**MATERIALS AND METHODS**

Seasonal and diel measurements of Nostoc primary productivity were made in “Nostoc Creek,” a second order mountain stream located in the H. J. Andrews Experimental Forest in the Cascade mountains of central Oregon. This creek is an unnamed tributary of Lookout Creek on U.S. Forest Service maps. One bank of the stream is adjacent to an oldgrowth of Douglas fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophylla) forest; whereas, the other side abuts an experimentally logged and subsequently thinned section with fewer trees. Because of the thinning, parts of the stream surface are unshaded and receive full sunlight from about 11:00 to 15:00 h with some seasonal variation. The stream is shallow (<0.25 m) and has a rocky substrate to which the Nostoc colonies attach (Fig. 1).

Primary productivity measurements were made by incubating rocks with attached Nostoc colonies in approximately 1.5 L Plexiglas® recirculating chambers (modified from Bott et al. 1978). Rocks were placed in the chamber with streamwater, injected with 4.0 mL NaHCO₃ (5.12 µCi/mL), sealed, and set in the stream near the site of rock collection. After 3 to 4 h, the rocks were removed, rinsed with nonradioactive stream water, placed in plastic Zip-loc® bags and returned to the laboratory in the dark in an ice chest. At the laboratory, the Nostoc colonies were removed from the rocks, the two types of colonies were separated, dried to constant weight and stored in a desiccator. Preliminary
treatment bottles were injected to yield a final added concentration in µg/L of: 100, NH₃-N (added as NH₄Cl), 50, PO₄-P (added as K₂HPO₄·3H₂O); 5, Mo (added as Na₂MoO₄·2H₂O); and 5, Fe (added as FeCl₃). Streamwater contained 35 µg PO₄-P·L⁻¹, and 5 µg NH₃-N·L⁻¹. NO₃-N concentrations were below the limit of detection (<2 µg/L).

RESULTS AND DISCUSSION
Seasonal changes in rates of primary production in shaded and open areas of Nostoc Creek indicated consistently higher rates of photosynthesis/algal dry weight associated with Nostoc colonies containing the chironomid midge compared to colonies without the midge (Fig. 2). These increases were most apparent in the open area which received maximum radiation with maximum photosynthetic rates of ears greater than six times that of Nostoc spheres incubated in the same chamber (August 1981). In shaded areas, photosynthetic rates of ears were maximally three times that of spheres in September 1981 and April 1982. Photosynthetic rates of Nostoc apparently responded more to changes in irradiance than temperature since photosynthetic rates remained high on sunny days in winter months (e.g. December 1981). Rates of photosynthesis depicted in this figure represent the physiological responses of the algae and not estimates of total carbon input seasonally to the stream reach, since the values were not corrected for total biomass/stream area. Algal biomass in many Cascade mountain streams decreases in the winter months because of heavy precipitation and subsequent scouring and rearrangement of rocky substrates (Rounick and Gregory 1981). However, those Nostoc colonies that remain, appear photosynthetically adapted to a wide temperature range (7–15°C).

Comparison of photosynthetic rates of ears versus spheres over a 24 h period on a sunny day in August (1980) further demonstrated that colonies with midgets were much better able to respond to midday high light intensities than spheres (Fig. 3). Photosynthetic rates of Nostoc ears much more closely paralleled incoming solar irradiance than those of the spheres. Light and photosynthetic data for Nostoc ears and spheres from Figure 3 were subjected to linear regression. The r² value for ears was 0.98 compared to 0.45 for spheres. This response may be due to a decrease in self-shading associated with a disc-shaped, flattened colony compared to a spherical colony. For both ears and spheres, maximum photosynthetic rates occurred between 14:00 and 17:00 unlike the mid-afternoon photosynthetic depression, typically reported for other aquatic plant communities (e.g. phytoplankton and aquatic macrophytes) and attributed to photorespiration (Hough 1974, Wetzel 1983).

The exact metabolic cues for the change in Nostoc shape and the physiological differences are unknown, but we suggest that the potential effects of the midge on the Nostoc colonies may include some...
or all of the following. First, the *Cricotopus* midge may cause the algal colony to change from a globose form to a flattened, thinner, more erect form with a higher surface area to volume ratio. This form, which extends away from the rock, is exposed to higher light intensities than the spheres which are more closely appressed to the rock surface. The flattened shape would decrease the distance from the surface of the colony to the interior, which together with altered flow patterns around the thallus, may facilitate nutrient (particularly CO₂) transport. Second, midge respiration could supply an endogenous source of CO₂, increasing levels of free CO₂ within the colony and augmenting CO₂ for carbon fixation. Paerl (1983) has shown that internal cells of *Microcystis* colonies can become CO₂ limited. Third, the midge may release other inorganic or organic nutrients which stimulate photosynthetic rates. Our initial experiments with nutrient addition bioassays (ammonium-nitrogen, molybdate, iron, and orthophosphate) did not significantly (at 5% level, one-way ANOVA) increase rates of photosynthesis over the control in either ears or spheres. There may be combinations of other inorganic or organic nutrients not tested which may cause a response, or longer experiments may be necessary. Fourth, grazing by the midge may remove the senescent or dead algal material within the colony thereby stimulating apparent photosynthetic rates per unit algal weight. Our data initially favor mechanism one with some support for mechanisms two and four. Additional experimental work with nutrient additions are needed before eliminating mechanism three. The effects of the midge on *Nostoc* photosynthesis suggested here are in agreement with earlier reports on invertebrate effects on algae (Brock et al. 1969, Hargrave...
Fig. 3. Diel changes in rates of photosynthesis of Nostoc colonies with and without the Cricotopus midge compared to changes in solar radiation on 14 August 1980. Horizontal bars indicate period of incubation.


General characteristics of Nostoc and chironomids make these organisms particularly adaptable to the scenario described here. The success of the relationship suggests several requirements for both organisms. For example, bacteria frequently exhibit pleomorphism (plasticity in form) in response to changing environmental conditions and blue-green algae (cyanobacteria) are physiologically and structurally similar to bacteria. Nostoc species in general also exhibit polymorphism or formation of different morphological stages in their life cycles (Lazaroff 1973). Other blue-green algal forms (Aphanizomenon flos-aquae) have been shown to respond to the presence of an invertebrate (Daphnia pulex) by changing colony shape in planktonic situations (Lynch 1980). Therefore, members of this group are genetically predisposed to respond to environmental variations by changing morphology. Not all animals do as well consuming blue-green algal material as the Cricotopus midge discussed here. Studies addressing ingestion and assimilation of blue-green algae by aquatic invertebrate grazers produce no clear pattern of suitability of these algae as a food source in lentic or lotic systems, although they are frequently regarded as toxic or unpalatable (reviewed by Porter and Orcutt 1980, Gregory 1983). In our study, gut analyses of Cricotopus revealed numerous remains of lysed vegetative cells and intact heterocytes. The midge was feeding directly on the trichomes with no apparent toxic effect, and had little difficulty in assimilating the blue-green algal material. Other studies have indicated that chironomids can ingest
and assimilate blue-green algae easily (Izvekova 1971, Kehde and Wilhm 1972). Possibly some chironomids have special digestive enzymes or gut flora with enzymes enabling rapid digestion of the blue-green algal material.

Besides the physiological implications for both the midge and the alga, the results of the Nostoc-Cricotopus association suggest important ecosystem modifications with regard to nutrient inputs, apparently linked to the ability of the Nostoc colony to respond to and utilize high light intensities. All of the factors influencing distribution of Nostoc ears in Oregon streams are not clearly understood, but there is a strong, positive correlation between Nostoc distribution and open-canopied first or second-order streams which have been clear-cut, or streams in second growth watersheds (<55 years since clear-cutting) with an alder-dominated riparian zone (Ward 1985). These ecosystems are characterized by nitrogen-limited with high concentrations of both inorganic and organic phosphorus (PO₄-P > 35 μg/L; organic P = 26–80 μg/L). The Nostoc ears function in supplying these streams with nitrogen, made possible by the metabolically expensive and high energy requiring process of nitrogen fixation. The presence of the Cricotopus midge apparently triggers a change in morphology which appears to enhance the ability of the Nostoc colony to respond to the metabolic requirements of this process. Linkages between the Cricotopus life cycle (e.g. site and timing of egg deposition) and Nostoc ear distribution, and the exact metabolic cue for the proposed midge-induced change in Nostoc shape, are areas which need further investigation.

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