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Didymosphenia geminata: Algal blooms in oligotrophic streams and rivers

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[1] In recent decades, the diatom *Didymosphenia geminata* has emerged as nuisance species in river systems around the world. This periphytic alga forms large “blooms” in temperate streams, presenting a counterintuitive result: the blooms occur primarily in oligotrophic streams and rivers, where phosphorus (P) availability typically limits primary production. The goal of this study is to examine how high algal biomass is formed under low P conditions. We reveal a biogeochemical process by which *D. geminata* mats concentrate P from flowing waters. First, the mucopolysaccharide stalks of *D. geminata* adsorb both iron (Fe) and P. Second, enzymatic and bacterial processes interact with Fe to increase the biological availability of P. We propose that a positive feedback between total stalk biomass and high growth rate is created, which results in abundant P for cell division. The affinity of stalks for Fe in association with iron-phosphorus biogeochemistry suggest a resolution to the paradox of algal blooms in oligotrophic streams and rivers.

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1. Introduction

[2] Periphyton growth in flowing waters is typically stimulated by enrichment of nitrogen, phosphorus (P), or both nutrients [Dodds *et al.*, 2002]. At regional to global scales, nutrient inputs, primarily from anthropogenic sources, lead to eutrophic conditions that favor algal blooms with undesirable consequences [Schindler *et al.*, 2008; Galloway *et al.*, 2008]. Since the mid-1980's, the diatom *Didymosphenia geminata* has dramatically expanded its range by colonizing oligotrophic rivers worldwide [Bothwell *et al.*, 2009; Blanco and Ector, 2009; Kilroy *et al.*, 2009; Kirkwood *et al.*, 2007; Kawecka and Sanecki, 2003]. In New Zealand, *D. geminata* spread to at least 32 watersheds on the South Island since 2004 [Kilroy *et al.*, 2009], resulting in 10 and 6 fold increases in periphyton ash free dry mass and chlorophyll *a*, respectively. Studies of rivers in North America report similarly high biomass [Kirkwood *et al.*, 2007; Kumar *et al.*, 2009]. Blooms of *D. geminata* in oligotrophic streams and rivers

present a counterintuitive result, because a bloom implies access to sufficient nutrients to sustain growth. The goal of this study is to examine how high algal biomass is attained under low P conditions.

[3] Attached algae, including attached diatoms, are able to exploit phosphorus through a variety of means [Pringle, 1990] including use of enzymes such as alkaline phosphatase [Ellwood and Whitton, 2007] and luxury consumption and storage [Kilham *et al.*, 1977]. Furthermore, heterotrophic bacteria associated with the attached algae are primary drivers of respiration, nutrient cycling and decomposition in stream ecosystems [Ardon and Pringle, 2007]. Not only do heterotrophic bacteria control physiological processes, they have the ability to influence hydrologic exchange of material available at the scale of the biofilm within large river beds [Battin and Sengschmitt, 1999]. Most of the biomass of the benthic mats formed by *D. geminata* is attributed to mucopolysaccharide stalks. The stalks are composed of sulfated polysaccharides, uronic acid and proteins with ionic cross-bridging with calcium (Ca²⁺) [Gretz, 2008], and adhere the diatom cells to substrates in high flow conditions, with recent investigations suggesting that the stalks are involved in efficient nutrient cycling [Kirkwood *et al.*, 2007], including direct uptake of P [Ellwood and Whitton, 2007]. While there is a rich literature on the role of biofilms and nutrients in algal colonization and succession [Korte and Blinn, 1983; Pringle, 1990; Stevenson *et al.*, 1991] there has been no investigation of the role of bacterial biofilms on the formation of algal blooms in low nutrient rivers.

2. Materials and Methods

2.1. Site Description

[4] The study was conducted in Rapid Creek - an oligotrophic montane stream in western South Dakota, where *D. geminata* blooms were first observed in 2002. This creek regularly experiences extensive *D. geminata* blooms, with 30–100% coverage of the streambed over a 5–10 km reach, for over four months of the year [Larson and Carreiro, 2008] despite low nutrient concentrations in surface waters. The total dissolved P in creek water is very low with total Nitrogen (N):P molar ratio near 30:1. Rapid Creek has a regulated flow and receives water from the hypolimnion of Pactola Reservoir.

2.2. Water Quality and Mat Nutrient Content

[5] Water quality of Rapid Creek was measured using standard wet chemical technique [Lachat Instruments, 2010]. Parameters measured included: Soluble Reactive Phosphorus (SRP), total P, total N, NH₄⁺, Nitrate-Nitrite, total Kjeldahl Nitrogen, Silica, SO₄²⁻, soluble sulfides (S²⁻), and total Fe

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Table 1. Chemical Characteristics of Water and Algal Mats From Rapid Creek, SD (mean \pm s.e.m., $n = 3$)^a

	TP	SRP	TN	SO ₄ ²⁻	Si	Fe	DO	pH	*S ²⁻
Water (mg/L)	0.02 (0.008)	0.004 (0.0006)	0.31 (0.09)	42.55 (4.01)	11.7 (0.26)	0.31 (0.07)	9.5 (1.13)	7.8 (0.3)	<0.01
Algal Mat (mg/Kg)	1120 (135)	ND	3000 (300)	ND	ND	93303 (10203)	ND	ND	0.63 mg/L (0.02)

^aTP = total P, SRP = Soluble Reactive Phosphorus, TN = total N, Silica (Si), DO = dissolved oxygen, ND = No data. *Soluble sulfide (S²⁻) concentrations in the algal mats were measured after incubating the mats in creek water for 21 days.

(TFe). pH, and dissolved oxygen (DO) in creek water were measured in situ using a Hydrolab. *Didymosphenia geminata* mats were assayed for TP, TFe after wet digestion, and TN, Total Carbon (C) content of the mats was assayed on a Flash E1112 CHNSO Thermo Finigan Elemental Analyzer.

2.3. P and Fe Adsorption in *D. geminata*

[6] P and Fe adsorption in the mats was experimentally tested by incubating 3 gm of washed (in deionized water) and unwashed mats from Rapid Creek in solutions containing 1000 mg/L P and 250 mg/L Fe, respectively. All incubations were poisoned to minimize biological uptake of P and Fe. Samples spiked with P, Fe, or both were rinsed with deionized water to remove unincorporated P and Fe prior to further analyses. TP and TFe on the mats were subsequently measured using wet digestion techniques [Lachat Instruments, 2010].

2.4. Scanning Electron Microscope (SEM) Examination

[7] An SEM examination and spot elemental analyses of washed *D. geminata* stalks that were spiked with Fe and P, and unspiked controls, was conducted with a Zeiss Supra40VP variable pressure field emission SEM with a PGT energy-dispersive X-ray (EDX) system on a glass slide mount under 15 keV accelerating voltage, 12 Pa chamber pressure VP; a 35° take-off angle, with a live time of around 115 seconds and an SEM magnification of 2380X.

2.5. Presence of Iron and Sulfate Reducers

[8] Presence of iron and sulfate reducers in interstitial water of *D. geminata* mats was confirmed by expelling the interstitial water from freshly collected *D. geminata* mats from Rapid Creek, SD. Interstitial water from each replicate mat was used to inoculate media singularly enriched in Fe³⁺ [Lovley and Phillips, 1986] or SO₄²⁻ [Sani et al., 2001]. Bacterial growth was measured as an increase in total protein concentration [Sani et al., 2002, 2005] in live incubations over killed controls. Presence of reduced Fe [Sani et al., 2002] and soluble sulfides [Sani et al., 2005] under anaerobic incubation confirmed the presence of iron and sulfate reducing bacteria.

3. Results and Discussion

[9] Total P, total N and total Fe of *D. geminata* mats from Rapid Creek are presented in Table 1. At 1,120 and 93,303 mg/Kg, the concentrations of P and Fe are comparable to those in lacustrine sediments [Holcomb, 2002] and those of non-marine mineral wetlands with high P-sorption capacity [Sundareswar and Morris, 1999]. The potential for the stalks to sequester Fe and P from ambient water was quantified by spiking washed (in deionized water) and unwashed stalks with Fe and P, then measuring the adsorbed Fe and P content (Figure 1). Particulate mineral matter, including Fe, within the mat was reduced by washing the stalks (Figure 1a).

Spiking the washed and unwashed stalks with Fe resulted in Fe adsorption to the stalks, with greater amounts adsorbed to the unwashed stalks. The washed and unwashed stalks also adsorbed significant amounts of P (Figure 1b), with a greater affinity for P in the presence of Fe (Figure 1b). Spot elemental analyses of the stalks revealed that Fe and P are co-localized (see Figure S1 of the auxiliary material), likely by sorbed Fe acting as a metal bridge between the stalk and dissolved P.¹ We interpret these results to mean that soluble Fe is adsorbed onto the stalk, where oxidized conditions in the surface layer facilitate the formation of Fe-oxyhydroxide. In this amorphous form, Fe has a strong affinity for P, and as a result, effectively strips P from the surrounding water. The

¹Auxiliary materials are available in the HTML. doi:10.1029/2010GL046599.

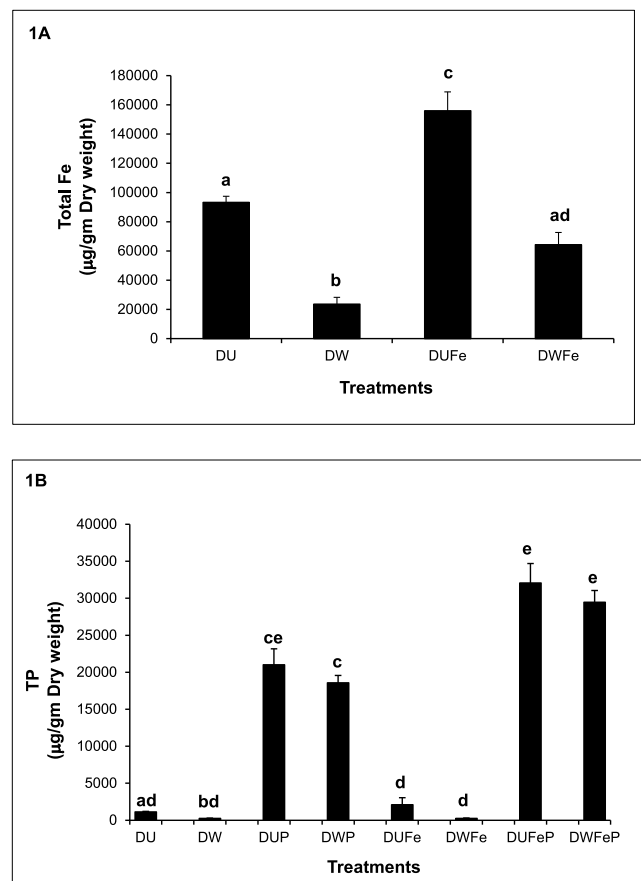


Figure 1. (a) Total Fe and (b) total P concentrations (mean \pm s.e.m. $n = 3$) of *D. geminata* stalks that were either untreated (U), washed to remove particulate matter (W), spiked with Fe (UFe and WFe), inorganic P (UP and WP), or both (UFeP and WFeP). Means of treatments were significantly different at $\alpha \leq 0.05$, as indicated by different letters.

co-occurrence of P and Fe is consistent with other studies on mineral sediments [Sundareswar and Morris, 1999; Paludan and Morris, 1999]. Thus, the mucopolysaccharide stalks function to concentrate P and Fe. Unlike the periphyton of Everglades wetlands where P is rapidly taken into the biological pool (86%) [Scinto and Reddy, 2003], P sorption in *D. geminata* mats is primarily an abiotic process, rather than direct biological uptake.

[10] We propose that adsorbed P becomes bioavailable through the following biogeochemical processes within the mat biofilm. As the mats develop, new stalks are produced at the surface and older stalks with bound Fe and P are displaced to the inner regions of the mat. In Rapid Creek, thick (2–4 cm) mats develop a redox gradient, in which the surface is oxidized as a result of photoautotrophy, while the inner and bottom regions of the mats are reduced, a feature observed in other microbial mats [Pierson et al., 1999; Roden et al., 2004; Baumgartner et al., 2006]. In the absence of oxygen, microbes can utilize other electron acceptors such as oxidized Fe (Fe^{3+}) and SO_4^{2-} for respiration, resulting in the generation of reduced Fe (Fe^{2+}) and soluble sulfides (S^{2-}), respectively.

[11] We tested for the evidence of the proposed process by determining the presence of Fe^{3+} and SO_4^{2-} reducing microbes. We observed significantly greater microbial growth, as compared to sterilized (killed) controls, when interstitial water from the mats was incubated anaerobically in media singularly enriched with Fe^{3+} or SO_4^{2-} as the sole electron acceptor [Pierson et al., 1999; Roden et al., 2004]. For Fe^{3+} rich media, total protein concentration (mean \pm s.e.m.), was significantly greater in live incubation than killed controls ($90.02 \text{ mg/L} \pm 2.32$ vs. 21.38 ± 2.68 , $n = 3$, $p < 0.0001$). The presence of Fe^{3+} reducers was confirmed by monitoring the production of reduced Fe (Fe^{2+}), which was significantly greater in live incubations ($1.95 \text{ mg/L} \pm 0.33$ vs. 0.2 ± 0.009 , $n = 3$, $p = 0.0058$). When SO_4^{2-} is abundant (Table 1), microbial sulfate reduction can dominate anaerobic respiration resulting in production of soluble sulfides (S^{2-}) within the mat. The presence of SO_4^{2-} reducers in the mat was similarly confirmed by monitoring bacterial growth and sulfide production in media where SO_4^{2-} was provided as the sole electron acceptor. Total protein and soluble sulfide concentrations were significantly greater in live incubations versus killed controls (total protein: 89.63 ± 1.33 vs. 26.80 ± 7.13 , $n = 3$, $p < 0.001$; S^{2-} : $5.6 \text{ mg/L} \pm 0.22$ vs. 0.23 ± 0.06 , $n = 3$, $p < 0.0001$). In the reduced zones of the mats both reduced Fe and sulfides are present [Fe^{2+} ($0.94 \text{ mg/L} \pm 0.04$; $n = 3$), S^{2-} ($0.27 \text{ mg/L} \pm 0.01$; $n = 3$)], because of an abundance of Fe on the mats and SO_4^{2-} in the creek water (Table 1). Reduction of Fe either directly by Fe^{3+} reducing microbes or as a result of changes in redox conditions in the mats due to the production of sulfides from microbial sulfate reduction, results in release of bound P from the Fe-oxyhydroxide pool. Additionally, when soluble sulfides are present, they interact with reduced Fe to form iron monosulfides FeS (Figure 2b) effectively competing with P for Fe and retarding the re-oxidation of Fe^{2+} to Fe^{3+} . This process is well documented in benthic systems where redox gradients develop across the sediment water interface, but was considered unlikely to occur in lotic habitats where hydrodynamic conditions are generally unfavorable for the development of such redox gradients. Our study demonstrates that the redox driven Fe-S-P coupling also occurs in lotic habitats, when inter-

actions between *D. geminata* mats and the hydrodynamic environment results in very low velocities around the mat where redox stratification can then occur [Larned et al., 2011]. Indeed, the concentration of biologically available P in the interstitial water of *D. geminata* mats was at least an order of magnitude greater than the concentration in surface water, and increased 200-fold upon incubation in the laboratory. Such an ability of biofilms to control the hydrologic exchange of interstitial waters has been demonstrated [Battin and Sengschmitt, 1999]. Although we have demonstrated the presence of active Fe^{3+} and SO_4^{2-} reducers in *D. geminata* mats, the identity and source of these microbes remain unknown. Nevertheless, it is clear that these microbes play a central role in nutrient cycling within the biofilm.

[12] We conceptualize the autotrophic-heterotrophic couple (Figure 2c) as a biogeochemical process by which P is solubilized from the mucopolysaccharide stalks. In addition, other processes potentially act to increase P availability. For example, we observed that the activity of phosphatase enzymes in the surface of mats was high ($3.74 \text{ } \mu\text{mol/mg dry/hr} \pm 0.51 \text{ s.e.m.}$), consistent with suggestions that organic P is important in *D. geminata* blooms [Ellwood and Whitton, 2007]. Since activity of phosphatases is negatively correlated with the concentration of bioavailable P, the high phosphatase activity despite the high concentration of total P in the mat indicates that P sequestered on the surface of the mats is in a non-bioavailable pool [Paludan and Morris, 1999], which could be subsequently solubilized by microbial processes.

[13] Phosphorus limitation has been shown to promote stalk elongation in *D. geminata* [Kilroy and Bothwell, 2010], while P enrichment results in greater cell division and retardation of stalk production [Bothwell and Kilroy, 2011]. Blooms occur primarily in oligotrophic streams and rivers, where P availability typically limits primary production. This observation causes us to reach an interesting conclusion. Because a bloom consists of stalk material which only forms in low P conditions, and cell division that occur under P-replete conditions: the stalks function in obtaining P, while the bioavailability of P in the mat is regulated by autotrophic-heterotrophic coupling within the biofilm. We propose that, at least in *D. geminata*, these processes create a novel positive feedback between total stalk biomass and cell division rates, leading to the seemingly paradoxical formation of blooms in oligotrophic streams and rivers. Further work should investigate how P availability in the mats varies spatio-temporally due to changes in redox potential. For example, it is likely that stalk production and cell division are temporally separated as a function of diurnal changes due to photosynthesis leading to pulsing of bio-available P. Furthermore, we suggest that mucopolysaccharides may have a role in nutrient adsorption for diatom species, in general. While *D. geminata* may be unusual for its high biomass in low nutrient systems, our results suggest that the mucopolysaccharide stalks, tubes, tufts, and pads of diatoms may play a role in P adsorption across different aquatic habitats.

4. Fe Concentrations and Distribution of *D. geminata* Blooms

[14] While previous studies have attributed *D. geminata* blooms to various factors including flow rates, climatic

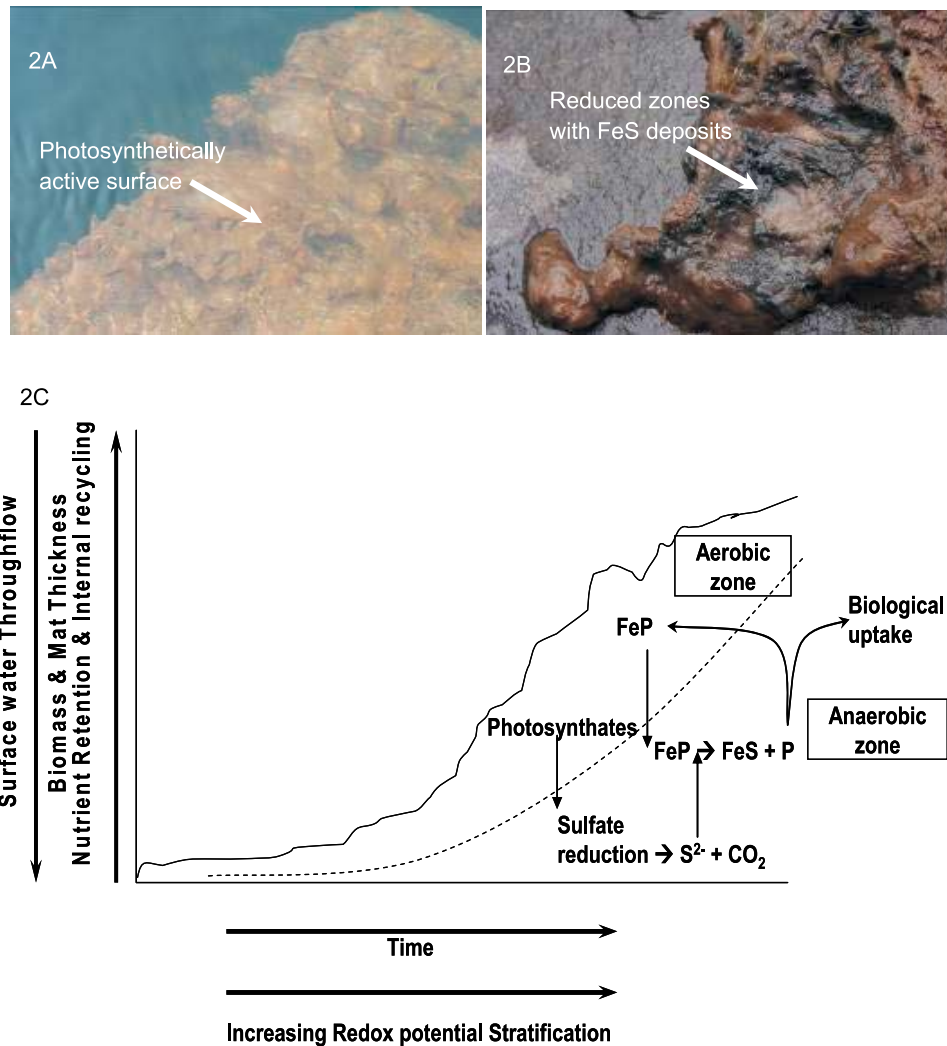


Figure 2. (a) Photographs of *D. geminata* mat in Rapid Creek showing photosynthetically active aerobic surface. Note that O₂ bubbles produced by photosynthesis and trapped within the mat is visible. (b) The underside of the mat revealing black material indicative of reducing conditions and deposition of iron monosulfides (FeS). (c) Illustration of a conceptual biogeochemical process – the Fe-P-S couple – by which sequestered P is solubilized. See text for explanation.

variables, and genetic strains [Kilroy *et al.*, 2009; Kumar *et al.*, 2009; Kirkwood *et al.*, 2009], our findings suggest that Fe reactivity and availability may also be a key factor in determining its distribution (Table S1 of the auxiliary material). For example, the occurrence of blooms downstream of reservoirs may be related to the release of water rich in Fe and P from the hypolimnion of stratified lakes. However, not all rivers with high Fe concentrations have, or will be susceptible to *D. geminata* blooms, because the reactivity of soluble Fe is variable, for example, due to the presence of chelators such as dissolved organic carbon. While our study presents a mechanism by which P is enriched in *D. geminata* mats, the reasons for the sudden onset of the blooms across the globe remains unclear. Undoubtedly, while human vectors play an important role in the spread of this invasive species [Bothwell *et al.*, 2009], watershed processes [Sherbot and Bothwell, 1993] determine the ability of the alga to form blooms in oligotrophic rivers. Reducing the reactivity of Fe and other cations in streams to minimize P sequestration potential of *D. geminata* mats may present a viable management option to mitigate the bloom of this invasive species.

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