Symbiosis of N₂-fixing cyanobacteria and diatoms: A view suggested by N and C isotopic compositions of sedimentary porphyrins

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We have studied biogeochemical responses of past photoautotrophs during the formation of anaerobic sediments based on compound-specific analyses of N and C isotopes of sedimentary porphyrins, molecules derived from chloropigments. Namely, the middle Miocene Onnagawa Formation (northeast Japan), Late Aptian Livello Selli and Late Cenomanian Livello Bonarelli black shales (Italy; OAE-1a and 2, respectively). The mean delta-¹⁵N values of the photoautotrophic community were estimated from the sedimentary porphyrin derived from photoautotrophs in general (i.e., C_{32} DPEP) as +1 per mil (n=1) for the Livello Selli, -2 to 0 per mil (n=4) for the mid-Cretaceous Livello Bonarelli, and -2 to +1 per mil (n=7) for the middle Miocene Onnagawa Formation, respectively. These values strongly suggest that biological N₂-fixation was the dominant source of nitrogen used for the new production in these paleoenvironments. More specifically, diazotrophic cyanobacteria should have played a major role in the primary production because the C₃₂ DPEP porphyrins should have originated from chlorophylls of oxygenic photoautotrophs, and diazotrophic cyanobacteria are thus the only possibility. Such a characteristically low delta-¹⁵N value close to that of diazotrophs was suggested also for a group of marine algae including diatoms (based on the chlorophylls *c*-derived porphyrin C₃₀ 17-nor-DPEP), suggesting that they have utilized regenerated nitrogen from co-existed diazotrophic cyanobacteria or hosted diazotrophic cyanobacteria in their cells. Carbon isotopic signatures of these sedimentary porphyrins indicate that carbon isotopic fractionation during the growth of the photoautotrophs was unusually lower than modern algal communities, which may reflect the unique physiology of cyanobacteria during blooms.

In modern marine environments, diatoms such as *Rhizosolenia* and *Hemiaulus* commonly host endosymbiotic diazotrophic cyanobacteria *Richelia intracellularis* and form blooms in modern oligotrophic ocean (Carpenter, 2002). Although their ecology has not yet well understood, they potentially play major roles in the primary production in stratified surface water. For example, extensive bloom of the *Hemiaulus/Richelia* association was observed in the oligotrophic North Pacific in 1996 where the primary production rate was substantially elevated, comparable to that of the annual mean in coastal upwelling regions (Carpenter et al., 1999). Interestingly, the modern species of diatoms, such as *Rhizosolena* and *Coscinodiscus* that were also reported from the Onnagawa Formation, are indeed known to host cyanobacteria. In the Quaternary Mediterranean sapropels, Kemp et al. (1999) reported that the principal component of export production during the deposition were oligotrophic species of diatoms including *Rezosolenia* and *Hemiaulus*. Furthermore, they are also the principal diatom fossils in the Late Cretaceous arctic black shale (Jenkyns et al. 2004). Although the diatom fossil has not been identified from the OAE black shales including the Livello Selli and Bonarelli, major occurrences of lipid biomarker specifically derived from Rhizosolenid diatoms, C_{25} highly branched isoprenoid, has been reported since the mid-Cretaceous (Sinninghe Damste et al., 2004). Our results thus indicate a potential significance of cyanobacteria-diatom symbiosis in the primary production during the formation of major anaerobic sediments of the geological pasts.

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