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# Continuous production- degradation of dissolved organic matter provides signals of biogeochemical processes from terrestrial to marine end-members

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## Introduction

Photosynthesis powered by sunlight, which involves plants and microorganisms in terrestrial soils and phytoplankton in fresh and marine waters, is one of the most important biogeochemical processes occurring in the environment. It constantly controls the production of most natural organic matter (NOM), which is a fundamental constituent of all ecosystems of our planet. Dissolved organic matter (DOM) is generated from NOM in terrestrial soils depending on three key sets of properties, i.e. physical, including temperature and moisture, chemical, which comprise nutrient availability, amount of available oxygen and redox activity, and microbial, such as microfloral succession patterns and availability of aerobic and anaerobic microorganisms. Terrestrial DOM is then partially transferred to surface waters

through surface runoff and groundwater leaching (Kritzberg et al., 2004; Catalán et al., 2016; Zark and Dittmar, 2018; Mostofa et al., 2019; Mohinuzzaman et al., 2020; Yi et al., 2021). Differently, autochthonous aquatic DOM originates from phytoplankton in surface water (Yamashita and Tanoue, 2004; Zhang et al., 2009; Guidi et al., 2016; Flemming et al., 2016; Shammi et al., 2017a; Igarza et al., 2019; Yang et al., 2021). Thus, a complex mixture of terrestrial and aquatic DOM occurs in surface-water environments (Kritzberg et al., 2004; Zark and Dittmar, 2018; Yi et al., 2021), which can be efficiently characterized on the basis of fluorescence properties (FDOM) and discriminated by excitation-emission matrix (EEM) fluorescence spectroscopy coupled with parallel factor (PARAFAC) modeling (Yamashita and Tanoue, 2004; Zhang et al., 2009; Shammi et al., 2017a; Mohinuzzaman et al., 2020; Yang et al., 2021; Yi et al., 2021). However, a clear, holistic understanding of terrestrial (allochthonous) and autochthonous aquatic DOM components is still lacking, as well as that of their sources and simultaneous production-degradation processes and pathways during transport from soil to sea through freshwater bodies, and their biogeochemical links.

## Transformation of DOM from land source to marine environments

Based on the most recent research results, a detailed picture is provided in Figure 1 and summarized below. Soil DOM is universally recognized to be mostly composed of humic substances (HS), including humic acids (HA), fulvic acids (FA) and protein-like substances (PLS) (Figures 1A–C, forest soil), of which the fluorescence peaks are discussed in detail elsewhere (Mohinuzzaman et al., 2020). Terrestrial HS are partially released into ambient freshwaters *via* groundwater leaching and surface runoff (Figures 1D, E, F). In particular, the two terrestrial components FA and PLS are entirely degraded (Mostofa et al., 2019) due to their lability in photochemical and microbial degradation processes (Figure 1), and only the HA fraction persists during transport from soil to streams to coastal seawater (Mostofa et al., 2019), possibly due to its macromolecular structure (Senesi and Loffredo, 1999; Mohinuzzaman et al., 2020).

In a study on the fluorescence behavior of the terrestrial HA fractions of DOM along their flow (soil → stream → river →

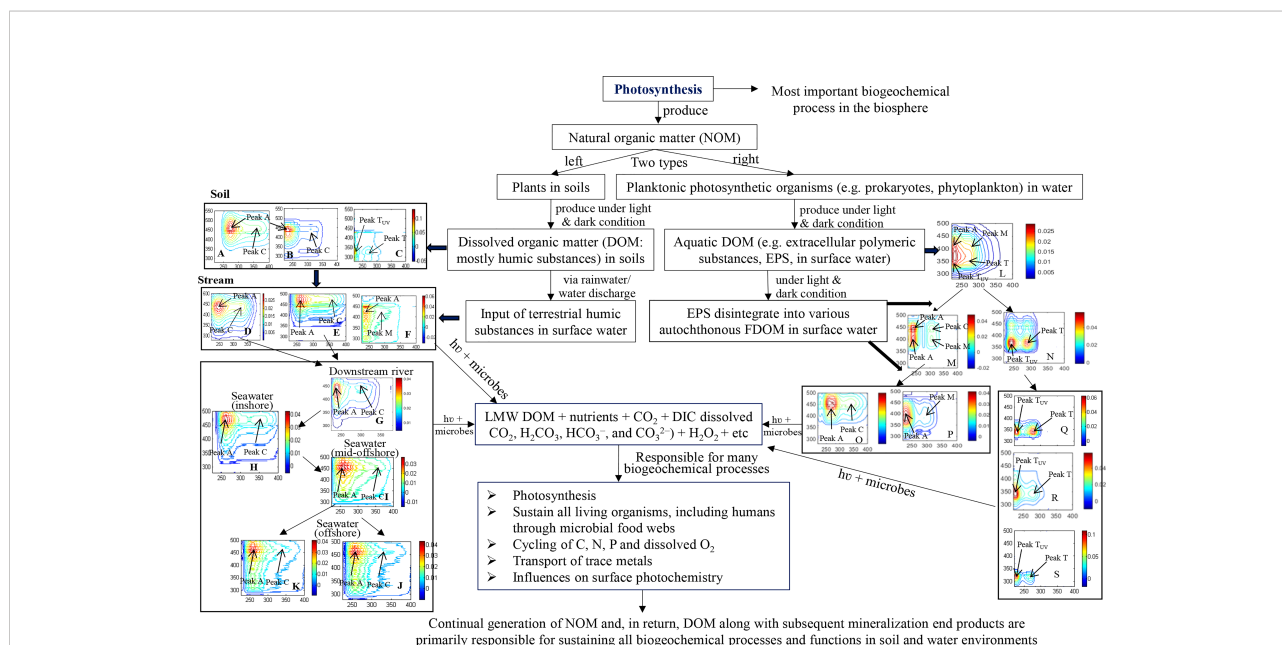


FIGURE 1

Flow diagram of the overall sequential constant photosynthetic production of natural organic matter (NOM) from terrestrial plants, animals and microorganisms in soils, and from planktonic photosynthetic organisms in waters. Figure 1, left: origin of soil humic substances [humic acids-HA (A), fulvic acids-FA (B) and protein-like substances-PLS (C)] from terrestrial NOM and their subsequent runoff/leaching into surface waters, first into streams [terrestrial HA-like (D), terrestrial FA-like (E), terrestrial PLS-like (F)], then into downstream river (only terrestrial HA-like substances, (G), then into inshore seawater ((H), 0–10 m depth) and mid-offshore seawater ((I), 0–10 m depth), and finally into offshore upper ((J), 0–15 m) and deeper (K), 20–300 m) seawaters in Seto Inland Sea. Figure 1, right: origin of extracellular polymeric substances (EPS, (L) from phytoplankton and their subsequent degradation, first into a combined form of autochthonous HA-like substances (AHLs) of C- and M-types (M) and a newly-released autochthonous protein-like substances (APLS, (N), then into their individual components, i.e. AHLs into C-type (O) and M-type (P) and APLS into protein-like substances (Q), tryptophan-like substances (R), tyrosine-like substances (S), etc. During all transformation described above for the two DOM systems mineralization end products are constantly produced, with the exception of terrestrial HA-like substances that ultimately did not degrade entirely, whereas autochthonous DOM is entirely degraded over one diurnal 24-h cycle by daytime sunlight-induced and nighttime microbial degradation.

sea), a red-shift from shorter to longer wavelength excitation-emission (Ex/Em) peak maxima has been measured when reaching the sea (peak C: stream 330/455; river 315/402; sea 350/473; peak A: stream 250/455; river 240/402; sea 260/473 nm) (Figure 1) (Mostofa et al., 2019; Mohinuzzaman et al., 2020). This red-shift can be ascribed to salinity effects occurring when terrestrial HAs reach seawater, possibly due to the formation of stable complexes with metal ions (Wu et al., 2004; Plaza et al., 2006; Mostofa et al., 2013; Mostofa et al., 2019). After reaching the sea, the water flows in the offshore direction determine a gradual blue shift of fluorescence peaks (C and A) toward wavelengths (325/461 and 255/461 nm in surface waters and 345/462 and 255/462 nm in deeper waters, respectively) that are shorter than those appearing for inshore to mid-offshore sea waters (345/461 and 260/461 nm, respectively). Apparently, a gradual transformation of terrestrial HA-like substances occurs along their transport in soil, stream, river, and then to coastal, mid-shore and offshore seawaters, where HA reach a relatively chemically recalcitrant nature. This behavior is confirmed by radio-carbon dating, which shows an increase of  $^{14}\text{C}$  ages from soil to inland waters and then to marine waters (Catalán et al., 2016). Importantly, photochemical and microbial degradation processes along with hydrological processes, particularly carbonate and silicate weathering, would play important roles in overall transformation processes along with transport of chemical species (Catalán et al., 2016; Igarza et al., 2019; Mostofa et al., 2019; Liu et al., 2020; Zhong et al., 2020; Yi et al., 2021).

## Origin of autochthonous DOM from planktonic communities and its transformation

Differently, autochthonous DOM originates from photochemical processes and microbial respiration from planktonic photosynthetic organisms (Yamashita and Tanoue, 2004; Zhang et al., 2009; Flemming et al., 2016; Guidi et al., 2016; Shammi et al., 2017a; Yang et al., 2021; Yi et al., 2021). The latter are thought to be responsible for approximately 50% of oceanic primary production and fuel the global biological carbon pump in marine environments (Guidi et al., 2016). Extracellular polymeric substances (EPS) are primarily originated from the plankton community and are considered the early-stage of newly-formed DOM (Flemming et al., 2016; Shammi et al., 2017a). EPS are not yet converted into individual organic components and are composed mainly of polysaccharides, proteins, nucleic acids, lipids, surfactants and humic-like substances (Flemming et al., 2016). The fluorescence moieties, mostly protein-like and humic-like fractions in EPS are firstly transformed into the following components, which can be monitored/detected by EEM-PARAFAC: (i) a combined form of autochthonous humic-like substances (AHLS) of C- and M-

types, and (ii) newly-released autochthonous protein-like substances (APLS) (Shammi et al., 2017a; Yang et al., 2021). Successively, AHLS evolve into their individual forms, i.e. C- and M-types, whereas APLS are gradually transformed into individual protein-like, tryptophan-like, tyrosine-like and phenylalanine-like substances (Figure 1) (Yang et al., 2021). All these substances are commonly detected in surface waters, particularly in stagnant waterbodies such as ponds and lakes, but also in estuaries and oceans (Yamashita and Tanoue, 2004; Shammi et al., 2017a; Yang et al., 2021; Yi et al., 2021). Finally, all individual components are photochemically and microbially degraded into low molecular weight (LMW) DOM and mineralized end-products, including gaseous  $\text{CO}_2$ , dissolved inorganic carbon (DIC) and nutrients (e.g.,  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$ ) (Figure 1) (Igarza et al., 2019; Yang et al., 2021; Yi et al., 2021). Differently, the carbohydrates and lipids moieties in EPS do not show any fluorescence, but undergo hydrolysis along with photochemical and microbial degradation/mineralization in surface waters (Zhang and Bishop, 2003; Adav et al., 2008; Shammi et al., 2017b). Details about the origin of autochthonous DOM and its subsequent daytime photoinduced and nighttime microbial degradation are extensively discussed elsewhere (Yang et al., 2021).

## Discussion

On the basis of results described above, the features of the two mentioned DOM systems and their biogeochemical transformation processes can be summarized as follows. Terrestrial FA-like and PLS-like fractions are extensively degraded along their transport, whereas terrestrial HA-like substances are only partially degraded by both photochemical and microbial processes (Amador et al., 1989; Catalán et al., 2016; Mostofa et al., 2019), due to their macromolecular size (Senesi and Loffredo, 1999; Mohinuzzaman et al., 2020). Therefore, the macromolecular size of HA is only one feature that would possibly account for its recalcitrant nature, and so can be used to determine the radio-carbon dating (Catalán et al., 2016; Tadini et al., 2018). Furthermore, various long-chain aliphatic and aromatic organic acids are produced by the photoinduced degradation of humic substances extracted from lakes and prolonged irradiation, which leads to a decrease of their concentrations and concomitant mineralization to end-products (Corin et al., 1996). Similarly, many aliphatic and aromatic byproducts were found to derive from aquatic DOM upon pyrolysis (Leenheer and Croué 2003). Studies also shows that various carboxylic acids (oxalic, malonic, formic, acetic, etc) are often major byproducts of the photoinduced degradation of DOM, which amounts to approximately 25.0–34.4% in surface waters (Bertilsson et al., 1999; Bertilsson and Tranvik 2000; Ma and Green, 2004). Simultaneously, EPS of planktonic origin are rapidly converted into AHLS and APLS, which are further

transformed into individual components that are finally degraded to produce LMW DOM and mineralized end-products (Yang et al., 2021).

The entire degradation of autochthonous aquatic FDOM has been shown to occur within a 24-h cycle under high air/water temperatures during summer, but not during low-temperature months (Yang et al., 2021). Similar results have been obtained for Antarctic glacial environments where exudates from primary production are utilized by heterotrophs within 24 h and support bacterial growth demands (Smith et al., 2017). As well, similar complete photoinduced degradation of humic-like fractions to EPS have been detected experimentally within 58 h, together with a decreasing DOC concentration of approximately 38.4%, from a very high ( $308.97 \pm 1.20 \text{ mgL}^{-1}$ ) initial DOC concentration (Shammi et al., 2017b).

Thus, the key difference between terrestrial (allochthonous) and aquatic (autochthonous) DOM is that the latter is entirely degraded within a 24-h diurnal period during summer, whereas in the case of terrestrial DOM only the FA-like and PLS-like fractions (but not the HA-like ones) can be completely degraded in waterbodies. The mineralization end-products of both allochthonous and autochthonous DOM are produced continuously under both daytime sunlight-induced degradation and nighttime microbial degradation. In particular, *in-situ* solar irradiation experimental studies showed that the dissolved inorganic carbon (DIC: dissolved  $\text{CO}_2$ ,  $\text{H}_2\text{CO}_3$ ,  $\text{HCO}_3^-$ , and  $\text{CO}_3^{2-}$ ) photoproduction rate is much lower in river waters (0.04–0.22 mg/L) than in lake waters (0.21–0.73 mg/L), whereas DOC concentrations vary respectively from 33.22–33.22 mg/L and 1.88–2.40 mg/L (Ma and Green, 2004). Similar results for DIC have been obtained for humic lake waters (0.086–0.41 mg C/L day) for *in-situ* photo-irradiation samples (Granéli et al., 1996). Moreover, several experimental studies also showed that autochthonous fluorescent aromatic amino acids (e.g. tryptophan, tyrosine and phenylalanine), PLS and humic-like substances can produce dissolved inorganic nitrogen such as  $\text{NH}_4^+$  and  $\text{NO}_x^-$  in surface waters (Bushaw et al., 1996; Berman and Bronk, 2003; Stedmon et al., 2007; Zhang et al., 2021). As these end-products act as nutrients, they continuously fuel the reproduction of photosynthetic planktonic organisms in surface waters and simultaneously contribute to global carbon cycling as well as to climate change (Mopper et al., 1991; Bushaw et al., 1996; Moran and Zepp, 1997; Berman and Bronk, 2003; Zhong et al.,

2020; Mostofa et al., 2013). In conclusion, the continuous production of NOM and its transformation/mineralization represent the primary backbone process in the cycles of carbon, nitrogen, phosphorus, dissolved oxygen and trace metals and in sustaining life of all living organisms, including humans, thus it is of key importance to deepen their understanding, in particular because climate warming determines longer stratification periods to occur in surface waters during summer.

## Author contributions

KMG designed and conceived the project. HS, KMG, C-QL contributed the key data sources. JY, MM, YL, XY conducted the EEM-PARAFAC analysis. KMG, NS wrote the manuscript. DV and S-LL reviewed & edited the manuscript. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

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