Ecological Engineering 118 (2018) 191–200

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

Coupled UV-exposure and microbial decomposition improves measures of organic matter degradation and light models in humic lake

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ARTICLE INFO

Keywords:
Brownification
DOC
Groundwater
Photo-bleaching
Lake restoration
Plant recovery

ABSTRACT

Increasing terrestrial input of colored dissolved organic matter (CDOM) to temperate softwater lakes has reduced transparency, distribution of pristine rosette plants and overall biodiversity in recent decades. We examined microbial and UV-induced reduction of absorption by CDOM and dissolved organic carbon pools (DOC) in humic water from a groundwater-fed softwater lake as well as groundwater received from surrounding heathland and coniferous forest. An experimental setup that mimics naturally coupled continuous UV-exposure and microbial degradation was introduced and compared with experiments applying a single initial or no UV-exposure. We found that decreases of CDOM and DOC concentrations were negligible in groundwater and very small in lake water over 30 days in the absence of UV-exposure. Initial UV-exposure increased degradation rates, but further degradation ceased after 20 days preventing determination of the natural time course of degradation. Coupled continuous UV-exposure and microbial degradation showed high and constant degradation of CDOM (340 nm) over 30 days removing 87% of the initial absorption in heathland groundwater, and 20% in forest groundwater and lake water. Declines in DOC concentrations over 30 days were 34%, 28% and 13% of the initial levels in heathland groundwater, forest groundwater and lake water, respectively. Model estimates showed that a shift in land use from a forest dominated to a heathland dominated catchment could increase lake transparency from 0.6 to 2.5 m. and expand plant-covered area from 3 to 35%. The main time delay to a new steady state of better light climate would be degradation of soil organic pools and exchange of groundwater magazines, while the delay in the lake water after a complete shift to inflow of CDOM-poorer groundwater would last only 1–2 years. Consequently, changes in CDOM levels in groundwater input should have relatively rapid and marked influence on light conditions and plant distribution in shallow softwater lakes.

1. Introduction

Dissolved organic carbon (DOC) in lake water originates from primary production within the lake (autochthonous) and external input (allochthonous) from the surrounding terrestrial environment (Kragh and Sondergaard, 2004; Lampert, 1978; Sondergaard et al., 2000). The pool of autochthonous DOC in lakes is mainly of recent origin containing small amounts of structural material and more labile compounds resulting in faster turnover rates compared to allochthonous compounds (Sondergaard and Middelboe, 1995). Allochthonous input is frequently the main contributor to the DOC content in small lakes having a large contact zone with the terrestrial surroundings relative to lake surface area and a fast renewal of the lake water (Sand-Jensen and Staehr, 2007). Allochthonous DOC input derives from terrestrial primary producers and has undergone photochemical changes (Opsahl and Benner, 1998; Wetzel et al., 1995) as well as biological transformations (Agren et al., 2008; Marín-Spiotta et al., 2014; McCallister and Giorgio, 2008) before entering the lake via groundwater or surface water. The DOC input to groundwater fed lakes has primarily undergone biological transformation due to the lack of UV-exposure in soil water.

DOC undergoes all kinds of production, transformation and degradation processes in the terrestrial-aquatic continuum. It has a strong impact on the physiochemical and biological characteristics of lakes. The pool of DOC in lakes is rarely constant and particularly the labile DOC compounds undergo marked temporal variations, for example, as a result of bursts of release from phytoplankton blooms followed by fast degradation of labile compounds (Baines and Pace, 1991; Sondergaard et al., 2000). Much of the DOC pool in lakes (commonly 50–70%) is composed of colored organic material (Gelbstoff or CDOM; (Aiken et al., 1985)), which is primarily refractory complex substances of low N and P cssontent deriving from partial soil degradation of cellulose, hemicellulose and lignin from terrestrial plants before entering the lake.

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https://doi.org/10.1016/j.ecoleng.2018.04.018
Received 7 December 2017; Received in revised form 28 March 2018; Accepted 19 April 2018
Available online 14 May 2018

The inverse relationship between the concentration of each compound and its rate of degradation (Hopkinson et al., 2002; Ogura, 1972; Sondergaard et al., 1995) reflects that the degradation rate is an essential determinant of the resulting concentration.

CDOM is very important for the light climate and thermal structure in lakes (Jones, 1998; Williamson et al., 1999). CDOM components are responsible for shielding organisms against harmful UV-exposure (Arrigo and Brown, 1996; Bricaud et al., 1981) and CDOM competes with pigment absorption in photoautotrophs for primary production (Krause-Jensen and Sand-Jensen, 1998). Brown-colored lake waters have a very restricted photic zone for pelagic and benthic photoautotrophs (Jones, 1992), and high nutrient levels are required for phytoplankton to form high biomasses capable of absorbing a substantial proportion of the incoming light (Krause-Jensen and Sand-Jensen, 1998). Moreover, refractory allochthonous CDOM promotes sedimentation of fine flocculent particles (von Wachenfeldt and Tranvik, 2008) that can further reduce growth and survival of rooted plants by smothering their surfaces (Barko et al., 1991).

During the recent decades, an increase in DOC has been observed in freshwaters across Europe and North America (Freeman et al., 2001; Monteith et al., 2007). Increasing water color and DOC concentration have been correlated with higher precipitation (Hongve et al., 2004), but climatic factors alone cannot be the main driver behind this change in CDOM and DOC (Evans et al., 2006). Studies have documented that high acid deposition and low soil pH can change the molecular size of organic compounds and make them less aromatic and hydrophobic, thereby decreasing the content and mobility of CDOM compounds (Ekstrom et al., 2011; Evans et al., 2012). These processes contributed to reduced CDOM leaching and the development of more transparent waters in acidified catchment soils (Hultberg and Grennfelt, 1986). Recent detailed evaluations have documented, however, the prominent influence of changes in land use, catchment vegetation and drainage have showed profound effect on the CDOM in lakes (Kristensen et al., 2017; Kritzberg, 2017). In particular, coniferous forest plantations lead to high groundwater concentrations of CDOM (Kristensen et al., 2017). This increase in terrestrially derived CDOM, known as brownification, has occurred to the extent that light limitation presently reduces the abundance of submerged lake vegetation (Sondergaard et al., 2013) and induces profound changes of food webs (Seekell et al., 2015; Solomon et al., 2015). This development has also taken place in low-alkaline lakes (< 1 meq. L^{-1}, Arts (2002)) located on sandy sediments with conifers or heathland vegetation along the West coast of Denmark and the Netherlands (Brouwer et al., 2002) leading to deterioration of some of the few oligotrophic lakes with a pristine vegetation of small rosette species in the two countries. For ecosystem ecology and nature conservation it is, therefore, essential to evaluate sources to brownification and processes reducing it.

In the present study, a new experimental design was applied to obtain a better understanding of the interaction between photobleaching and microbial degradation of CDOM in a mixed water column. Traditionally these experiments have involved an initial UV-exposure until a certain proportion of CDOM-absorbance had vanished (Moran et al., 2000). UV-exposure for a specific time period (Helms et al., 2008; Vachon et al., 2017) or a continued UV exposure throughout the study (Helms et al., 2014; Obernosterer and Benner, 2004) to the entire sample volume have also been applied. The traditional approach with UV-exposure followed by gradual microbial degradation in darkness of the generated degradable carbon results in first order degradation kinetics. In our novel design, however, a small fraction of the water was exposed to UV-light and circulated directly to a reservoir chamber for bacterial mineralization in a continuous loop to mimic the natural situation with water constantly being transported from deeper layer to UV-exposure at the surface. This approach yields a continuous input of degradable carbon from the large pool of refractory CDOM and may result in different degradation kinetics over the 30-days experiments. Jones et al. (2016) also used a recirculation approach, but used high UV-exposure and ran experiments over a short period of only four days. Furthermore, our design used water circulation and UV-exposure estimated from *in situ* measurements in a dose that is not harmful for the bacteria.

The experiment was carried out on lake water and on groundwater below the two main vegetation types in the catchment, coniferous forest and heathland. While DOC mineralization in groundwater is restricted to microbial degradation due to lack of UV-exposure, lake water is exposed to UV-light enhancing the degradation of CDOM by photobleaching (Del Vecchio and Blough, 2002; Goldstone et al., 2004). When CDOM absorbs UV-light, the molecular and optical properties change (Bertilsson and Tranvik, 2000) resulting in transformation of refractory CDOM to more labile DOC as well as lesser refractory CDOM enhancing microbial degradation (Kragh et al., 2008; Mopper, 2002; Moran and Zepp, 1997). The new experimental design offers a better understanding of how color absorption decreases in a lake, where constant input of previously none UV-exposed water releases labile compounds for bacterial degradation, compared to most previous experiment applying a single, initial UV-dose.

Our objective was to study the decrease in DOC concentrations and spectral light absorption of CDOM in the two main groundwater inputs and in the water of a humic softwater lake by using the new experimental design and comparing it with results obtained with a single or no UV-exposure. The obtained degradation rates were used in a theoretical model to estimate future scenarios for the light environment in the lake in which the main input of CDOM-rich coniferous groundwater is shifted to CDOM-poorer heathland groundwater and, thereby, potentially improves the vertical light penetration and cover of submerged vegetation.

2. Materials and methods

2.1. Study site and water sampling

Lake water and groundwater was collected in Lake Tvorup Hul and in the surrounding catchment in Nationalpark Thy in NW-Jutland, Denmark (56°91′N, 8°46′E). Lake Tvorup Hul is a mainly groundwater fed small (surface area 4 ha), shallow lake (mean depth 2.5 m, maximum depth 7.5 m) with a water retention time of about 1 year (Kristensen et al., 2017). Lake Tvorup Hul is an oligotrophic kettle lake, which before 1990 had transparent waters and a high diversity of submerged rosette species, including the nationally threatened species, *Isoetes echinospora* and *Subularia aquatica* (Naturstyrelsen, 2011). Over the past three decades, the lake has experienced increasing inputs of CDOM from the surrounding coniferous forest and heathland leading to profound brownification, decline of depth penetration and richness of submerged plants as well as loss of the above-mentioned nationally threatened species.

To reduce brownification, the Danish Nature Agency restructured ditches and closed surface drainage inlets to the lake already in 1992 and by-passed the former surface inflow of humic-rich water. The water sources to the lake today are small amount of surface water during snow melt and exceptional high rainfall and a greater amount of groundwater with high concentrations of humic substances from the two main vegetation types, coniferous forest and heathland in the catchment.

Water was collected at 1 m depth in the lake and in groundwater wells below the coniferous forest and heathland. The groundwater was collected in autumn 2015 and the lake water in February 2016 before the spring development of phytoplankton. Groundwater was collected from wells with water inflow at 2 m depth that were emptied twice before sampling to ensure that only “fresh” groundwater was retrieved. All samples were kept in darkness, at low temperatures (5 °C) in large, acid-rinsed containers (10 L) for less than 6 months until start of each experimental run. Experimental water consisted of 90% GF/F (0.7 µm nominal pore size GF/F) filtered water to remove all heterotrophic