

2-6-2014

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Abstract

The role of abiotic processes on dissolved organic matter (DOM) production is often underappreciated. However, abiotic processes appear to be especially important in subsoils where, with increasing depth, microbial activity declines and soil organic matter (SOM) becomes a progressively more important contributor to DOM. Within three soil depths (20, 40, and 60 cm) in a temperate forest, soil temperature was positively associated with dissolved organic carbon (DOC) concentration ($R^2 = 0.23\text{--}0.77$) and the DOM humification index ($R^2 = 0.35\text{--}0.72$) for soil solutions in slow and fast flowpaths. With increasing soil temperature from 5 to 24 °C, average DOC concentrations increased by 86% at 20 cm, 12% at 40 cm and 12% at 60 cm soil depths. Our data suggest that DOM supply, especially in subsoils, is temperature dependent. We attribute this to the influence of temperature on DOM replenishment through direct processes such as SOM dissolution, diffusion and exchange reactions as well as indirect processes such as rhizodeposition and exoenzyme activity. In contrast, negative relationships ($R^2 = 0.71\text{--}0.88$) between temperature and nitrate concentrations in subsoil suggested that the temperature-dependent supply of DOM drives microbial processes such as dissimilatory and assimilatory nitrate consumption.

Disciplines

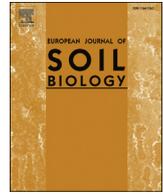
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This article is published as Toosi ER, Schmidt JP, Castellano MJ. 2014. Soil temperature is positively associated with dissolved organic carbon supply and negatively associated with soil solution nitrate. *European Journal of Soil Biology* doi: [10.1016/j.ejsobi.2014.01.003](https://doi.org/10.1016/j.ejsobi.2014.01.003). Posted with permission.

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Soil temperature is an important regulatory control on dissolved organic carbon supply and uptake of soil solution nitrate



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ARTICLE INFO

Article history:

Received 6 October 2013

Received in revised form

20 December 2013

Accepted 14 January 2014

Available online 6 February 2014

Handling editor: Yakov Kuzyakov

Keywords:

Dissolved organic matter (DOM)

Flowpath

Nitrate

Soil temperature

Subsoil

Solubilization

Abiotic processes

ABSTRACT

The role of abiotic processes on dissolved organic matter (DOM) production is often underappreciated. However, abiotic processes appear to be especially important in subsoils where, with increasing depth, microbial activity declines and soil organic matter (SOM) becomes a progressively more important contributor to DOM. Within three soil depths (20, 40, and 60 cm) in a temperate forest, soil temperature was positively associated with dissolved organic carbon (DOC) concentration ($R^2 = 0.23\text{--}0.77$) and the DOM humification index ($R^2 = 0.35\text{--}0.72$) for soil solutions in slow and fast flowpaths. With increasing soil temperature from 5 to 24 °C, average DOC concentrations increased by 86% at 20 cm, 12% at 40 cm and 12% at 60 cm soil depths. Our data suggest that DOM supply, especially in subsoils, is temperature dependent. We attribute this to the influence of temperature on DOM replenishment through direct processes such as SOM dissolution, diffusion and exchange reactions as well as indirect processes such as rhizodeposition and exoenzyme activity. In contrast, negative relationships ($R^2 = 0.71\text{--}0.88$) between temperature and nitrate concentrations in subsoil suggested that the temperature-dependent supply of DOM drives microbial processes such as dissimilatory and assimilatory nitrate consumption.

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1. Introduction

Dissolved organic matter (DOM) is a small but highly dynamic OM pool that links the C cycle among terrestrial, atmospheric, and aquatic systems [13]. Plant tissues (above- and below-ground) and soil organic matter (SOM) are the two primary sources of DOM, but their relative contribution to DOM varies along the soil profile [32,33]. Lysimeters sample DOM representing the residual products of interactions among biological activities and non-biological processes.

Despite the well-established paradigm that suggests extracellular enzymes break down SOM into soluble (assimilable) compounds [24], recent research suggests that in many soil conditions SOM is solubilized primarily as a result of abiotic processes (e.g. [12]). This argument (i.e. decomposer-substrate disconnection) is based on the poor energy tradeoff of enzymatic OM depolymerization under many soil conditions and specifically the rare occurrence of a combination of favorable soil conditions for activity of a

diverse microbial community that is essential for SOM decomposition [1,8,22]. On the other hand, microorganisms and their exoenzymes are not only inherent components of soil, but are largely dormant in most soil conditions. Thus, even when highly reduced, the activities of exoenzymes and decomposer community often with diverse functions (i.e. functional redundancy) may still substantially contribute to SOM break down [14]. As a result, it is extremely difficult to directly determine the relative importance of biotic and abiotic processes to SOM solubilization in real soil conditions.

Temperature directly and indirectly regulates DOM production through its influence on biological activities and physico-chemical processes [23,24]. We examined the influence of temperature on the pool size and complexity of DOM and inorganic N in soil solutions primarily associated with fast and slow flowpaths (i.e. DOM collected from zero-tension and tension lysimeters, respectively). Sources of DOM and microbial activity vary with soil depth and flowpaths, with fast flowpaths often containing greater proportions of plant-derived DOM (e.g. Refs. [5,11,18,34]). Thus, we hypothesized that the influence of soil temperature on DOM pool size and complexity varies with depth and flowpaths such that the effect of temperature is greater in slow flowpaths and subsoils where biological activity is relatively low.

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Table 1
General physico-chemical properties of the soil (data are mean \pm STDER; $n = 3$).

Depth (cm)	Texture	TOC ^a	TN ^b	C/N	pH	EC ^c
0–20	Loam	91.9 \pm 1.9	4.82 \pm 0.3	19.1 \pm 0.9	4.7 \pm 0.6	0.47 \pm 0.06
20–40	Loam	10.8 \pm 0.4	0.69 \pm 0.06	15.5 \pm 1.4	4.8 \pm 0.4	0.22 \pm 0.03
40–60	Loam	2.6 \pm 0.2	0.24 \pm 0.04	10.5 \pm 1.6	4.7 \pm 0.4	0.18 \pm 0.03

^a Total organic C (g kg⁻¹).

^b Total N (g kg⁻¹).

^c m mho cm⁻¹.

2. Materials and methods

The study site was located within a long-term research watershed operated by the USDA in Pennsylvania, USA [4]. In 2009, we installed tension and zero-tension lysimeters at 20 (A horizon), 40 and 60 cm (B horizon) depths in a mixed oak-hickory forest that had not been harvested for >50 years. The soil is categorized as Typic Dystrudept. General soil properties are shown in Table 1. Within each of three replicate plots, three subreplicate zero-tension and tension lysimeters were installed along with one moisture-temperature sensor at each depth (Decagon Devices, USA). Within each soil depth, average soil temperature and moisture between each sampling event was used for analyses [16]. Lysimeters were sampled every 10–14 d or after rain events during the sampling period (Mar–Oct 2011), but there were occasions where soil was frozen or too dry. Depending on soil moisture conditions for a given depth, 6 to 14 sampling events were conducted. Tension and zero-tension lysimeters preferentially collect soil solutions that represent different sources and transport kinetics and are primarily associated with slow and fast flowpaths, respectively [5,9,34]. Soil solutions were filtered (0.45 μ m), acidified and analyzed for concentration of C (Shimadzu TOC_{CPN}, Japan)

and nitrate (Lachat flow injection analyzer). A humification index (HI) was determined as an indicator of the degree of humification based on the DOM fluorescence property [19]. The HI was determined as below using an excitation wavelength of 254 nm and emission range of 300–480 nm (Jobin–Yvon Horiba Fluoromax, Japan):

$$HI = \left(\sum I_{300-345} - \sum I_{435-480} \right) / \left(\sum I_{300-345} + \sum I_{435-480} \right) \quad [1]$$

where I is the fluorescence intensity for the given wavelengths. The HI varies from 0 to 1 with higher HI values indicating a larger proportion of humified compounds or an increased degree of humified OM.

All statistical analyses were carried out using SAS 9.2. Linear regression analyses were used to explore across-soil depth relationships between soil temperature and nitrate, DOC, and humification index. Regression lines were shown when $P \leq 0.05$.

3. Results and discussion

3.1. Influence of temperature on DOC, HI, and nitrate

Soil temperature was positively associated with DOC concentration ($R^2 = 0.23$ – 0.77 , $P \leq 0.05$) and complexity (HI) of DOM ($R^2 = 0.35$ – 0.72 , $P \leq 0.05$) for both lysimeter types (Fig. 1). Although soil temperature was positively correlated with nitrate sampled from zero-tension lysimeters at 20 cm, it was negatively correlated with nitrate sampled from the tension lysimeters at 40 cm and both lysimeter types at 60 cm. The regression coefficients among these variables were i) higher for DOM sampled

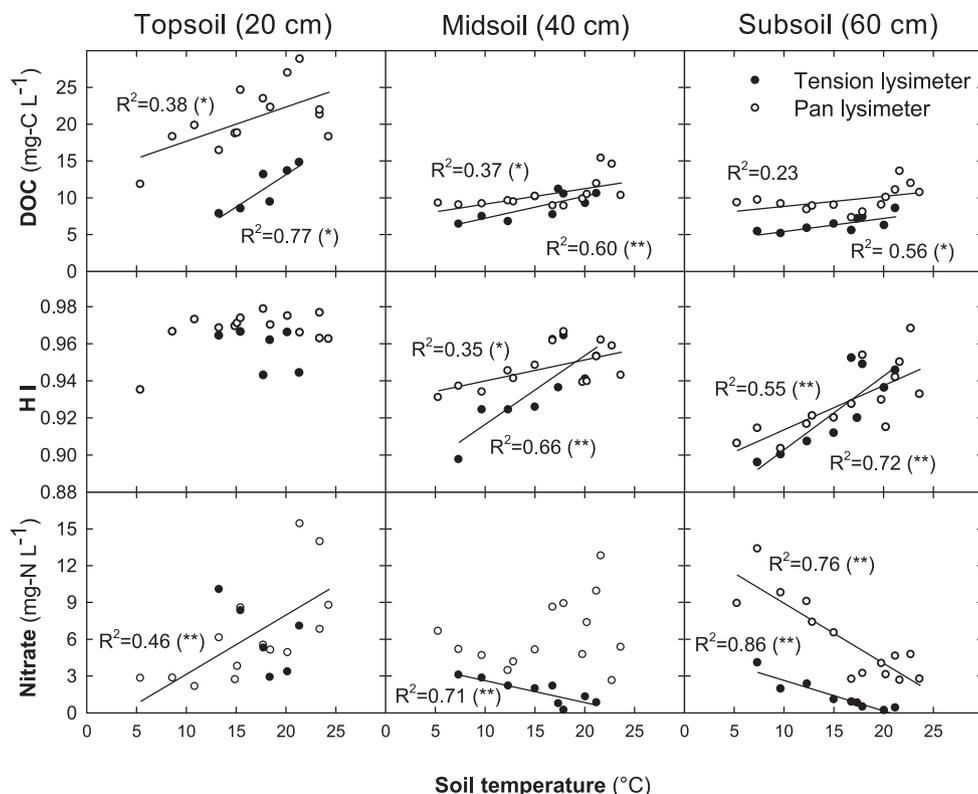


Fig. 1. Regression coefficients between dissolved organic carbon (DOC), humification index (HI) and soil solution nitrate with soil temperature. * and ** indicate P values ≤ 0.05 and ≤ 0.01 , respectively.

from tension lysimeters and ii) increased with soil depth for HI (Fig. 1).

Under favorable conditions, increasing soil temperature (10–30 °C) enhances microbial activity, resulting in accelerated SOM solubilization that is subsequently assimilated or mineralized [2,3,24]. However the energy budget theory of microbially driven SOM depolymerization suggests that the consistently larger DOM pool at greater soil temperatures (Fig. 1) could not have been microbially produced without being consumed [2,8]. Moreover, soil often becomes drier at higher temperatures [6], which is consistent with our data (Toosi et al., 2014, in revision) and suggests a lack of simultaneous occurrence of optimum soil moisture and temperature for microbial activity. Previous research suggested reduced influence of soil temperature on microbial respiration with increasing soil depth [21]. For example [7], showed that below topsoil both temperature fluctuations and the positive relationship between soil temperature and CO₂ production decreased with soil depth, ultimately resulting in no relationship at 60 cm depth.

The release of microbial necromass may contribute to the increasing DOC pool at higher temperatures (drier soil conditions) [3]. However, microbial biomass is comprised of low humified components, which is inconsistent with the positive relationship between HI and soil temperature (Fig. 1). Further, given the very small size of microbial biomass in subsoil, microbial necromass is unlikely to be a considerable source of DOM at elevated temperatures. The lack of significant relationship between HI and soil temperature at 20 cm, may be due to complicated DOM dynamics and diverse sources (i.e. throughfall and litter leachate).

Our soil moisture data along with DOM properties showed that DOC leaching was not a likely source of DOC in subsoil for the majority of the sampling period because DOC concentrations tended to be high when soils were warm, but relatively dry (Toosi 2014, in revision). Leaching of DOM from aboveground vegetation occurs during wet seasons and contributes to subsoil DOM mainly through the addition of non-humified DOM with low HI [11,34]. In contrast, a growing body of evidence suggests that in forest soils with increasing soil depth, a greater portion of DOM is produced *in situ* from SOM and rhizodeposition [10,17,34]. Temperature affects these processes through a number of mechanisms (i.e. desorption, dissolution, diffusion, activity of exoenzymes, and rhizodeposition).

3.2. Direct influence of temperature

Increasing strength of relationships between soil temperature and HI with increasing soil depth may be related to changes in DOM source through the greater contribution of SOM (more humified) to subsoil DOM. Subsoil OM comprises greater proportions of highly processed, microbially derived compounds with greater solubility [26,36]. The rate of SOM dissolution and diffusion within the soil solution increases with temperature. Temperature also increases the rate of exchange reactions between dissolved fresh organic compounds and humified SOM, a process that has been suggested as a source of subsurface DOM [15,34]. Finally, increasing soil temperature favors desorption of humified OM (high HI) from mineral surfaces [25]. Together, it appears that soil temperature, particularly at greater soil depths, can affect DOM pool size and complexity through enhanced dissolution, diffusion, and exchange reactions [25,27,31,34].

3.3. Indirect influence of temperature

Increasing temperature enhances the activity of exoenzymes through desorption and diffusion and reactions rates with substrate, and thus, indirectly enhances break down of SOM and its release in to soil solution [14,30]. On the other hand, temperature

enhances rhizodeposition, a substantial source of labile DOM with low HI [17,29]. Because subsoil DOC and HI concomitantly increased with temperature, our data suggest that temperature-induced rhizodeposition was either not an important contributor to subsoil DOC or rhizodeposits were rapidly decomposed during which HI increased [28]. The rapid decomposition of rhizodeposits is consistent with increased biological N demand and the decrease in soil solution nitrate. Alternatively, the concomitant increase in DOM pool size and HI, along with nitrate reductions may have been due to enhanced microbially-driven solubilization of SOM and biological N demand that occurs following greater rhizodeposition (priming) at higher temperature [13,37]. Finally, higher temperature may have promoted sorption of “low molecular weight root exudates” onto mineral surfaces, and desorption of humified OM from these surfaces, resulting in greater HI of DOM [25]. Rhizodeposition however, may play a small role in DOM supply in subsoil due to lower distribution and activity of fine roots at soil depth.

In conclusion, solute retention time, diffusion and biological activities vary between fast and slow flowpaths, with fast flowpaths often containing greater microbial diversity, root activity and proportions of plant-derived DOM [5,18,20]. However, the consistent influence of temperature on DOC and HI suggests a consistent effect of temperature on DOM supply (particularly in subsoil), regardless of lysimeter type which is regarded as a proxy of flowpath. Nevertheless, all relationships (Fig. 1) were stronger for slow flowpaths, which is in line with reported lower temporal variability for DOM sampled from slow compared to fast flowpaths [34,35]. Soil temperature within 5–25 °C appeared to regulate subsoil DOM production primarily through i) physico-chemically mediated release of SOM into the soluble pool and ii) rhizodeposition. In turn, negative relationships between subsoil temperature and nitrate suggest DOM production regulated microbial processes that produce and consume nitrate, including heterotrophic consumption of ammonium prior to nitrification as well as assimilatory and dissimilatory nitrate uptake. Together, these data constitute an important field observation that is consistent with a growing body of evidence that suggests under many soil conditions microorganisms play a minor role in DOM production, but act as a major sink for the produced DOM [12,16,27,31]. Given the dearth of *in situ* observations, especially for subsoil, these findings call for further attention to temperature effects on DOM supply and decomposition.

Acknowledgment

We would like to thank Dr. A. Clapp for providing access to spectrofluorometer and Dr. M. Thompson for his helpful comments. We appreciate Amanda Oswald for laboratory and Michael Reiner, Sarah Fishel, David Otto, and Todd Strohecker for field assistance. The research was funded by a USDA AFRI grant.

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