Environmental and Experimental Botany 90 (2013) 43–52

Contents lists available at SciVerse ScienceDirect

Environmental and Experimental Botany

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

Boreal peatland ecosystems under enhanced UV-B radiation and elevated tropospheric ozone concentration

Riikka Rinnan[a,b,c,*], Sanna Saarnio[d,e], Jaana K. Haapala[d], Sami K. Mörsky[a], Pertti J. Martikainen[a], Jouko Silvola[d], Toini Holopainen[a]

[a] Department of Environmental Science, University of Eastern Finland, Kuopio Campus, PO Box 1627, FI-70211 Kuopio, Finland
[b] Terrestrial Ecology Section, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark
[c] Center for Permafrost (CENPERM), University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark
[d] Department of Biology, University of Eastern Finland, Joensuu Campus, PO Box 111, FI-80101 Joensuu, Finland
[e] Finnish Environment Institute, the Joensuu Office, PO Box 111, FI-80101 Joensuu, Finland

ARTICLE INFO

Keywords:
Sphagnum
Eriophorum
Warnstorfia
Net ecosystem CO_2 exchange
Soil microbial community
Methane emission

ABSTRACT

Boreal peat-forming wetlands, mires, are globally important sources of methane and sinks for CO_2. As peatland vegetation plays a significant role regulating the exchange of these greenhouse gases, we have assessed the responses of the dominant plants and ecosystem functions to increasing tropospheric ozone concentration and enhanced ultraviolet-B (UV-B) radiation in long-term experiments, the results of which are summarized in this review. The dominant sedge, *Eriophorum vaginatum*, and especially the *Sphagnum* mosses common on peatlands, appear fairly tolerant to the future predicted ozone levels. Similarly, UV-B radiation only caused few alterations in the carbohydrates and pigments of the dominant sedge, *Eriophorum russeolum*, and had no effects on the dominant moss species of the experimental site, *Warnstorfia exannulata*. Surprisingly, there were alterations in organic acid concentrations in the peat pore water and peat microbial community composition in both experiments. Elevated ozone caused a transient decrease in ecosystem-level gross photosynthesis and methane (CH_4) emission, which shifted to a slight increase later on. Enhanced UV-B decreased dark ecosystem respiration and increased CH_4 emission in the course of the six measurement years. The emission of isoprene was increased by both ozone and UV-B during warm weather periods, suggesting interactive effects with temperature. All in all, we suggest that ozone and UV-B have limited effects on the carbon cycle in boreal peatlands, because other environmental factors, such as temperature, water level and photosynthetically active radiation more strongly regulate CO_2 and CH_4 exchange rates.

1. Introduction

1.1. Boreal peatland ecosystems

Boreal and subarctic peatlands cover less than 3% of the global land surface (Joosten, 2009), but these peat-forming ecosystems constitute a substantial part of the landscape of the Northern Hemisphere. For example, in Finland they cover one third of the total land area (Turunen et al., 2002).

Boreal peatlands are characterized by a high groundwater table, which causes anoxic conditions in the submerged peat layer. Due to the anoxia, decay of soil organic matter is slowed down and the rate of net primary production typically exceeds the rate of decomposition. These ecosystems therefore serve as a net sink for CO_2. The C pool in boreal and subarctic peatlands is estimated at 270–370 Pg (Turunen et al., 2002), which equals to 35–50% of the present day atmospheric C pool (Denman et al., 2007).

Besides being sinks for CO_2, peatlands are the most important natural source of another greenhouse gas, CH_4, and the emission of CH_4 is mediated by vegetation in various ways. Methane is produced in the anoxic peat by methanogenic archaea using either hydrogen and CO_2 or acetate as precursors (Boone, 1991). As acetate partly originates from plant root exudation, vegetation can indirectly affect the CH_4 production rates (Ström et al., 2003). The produced CH_4 moves to the atmosphere by diffusion, ebullition, and via plant-mediated transport (Joabsson et al., 1999). A significant part of the produced CH_4 is oxidized by methanotrophic bacteria

Abbreviations: AOT_{40}, accumulated ozone exposure over a threshold of 40 ppb; CH_4, methane; NEE, net ecosystem exchange; O_3, ozone; OTC, open top chamber; P_G, gross photosynthesis; PLFA, phospholipid fatty acid; ROS, reactive oxygen species; R_{TOT}, total dark respiration; UV-B, ultraviolet-B; VOC, volatile organic compounds.

* Corresponding author at: Terrestrial Ecology Section, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. Tel.: +45 51827039; fax: +45 35322321.
E-mail address: rikkar@bio.ku.dk (R. Rinnan).

0098-8472/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.envexpbot.2012.10.009

in the aerobic peat layer and within plants (Hornibrook et al., 2008).

The vegetation of boreal peatlands consists of a continuous moss layer, sedges (*Cyperaceae* Juss.) and dwarf shrubs (Gorham, 1991). The abundance of trees depends on the peatland type. Peat mosses (*Sphagnum* sp.) dominate the ground-layer in nutrient-poor peatlands, whereas true mosses (mostly of the family *Amblystegiaceae* G. Roth) are abundant in rich fens (Vitt, 2006). Mosses absorb water and nutrients straight to the leaves and stem, as they lack a developed root system (Brown, 1982).

The root system of the vascular plants growing on peatlands can account to more than half of the total plant biomass (Wallén, 1986; Saarinen, 1996). The roots and rhizomes of sedges can penetrate deep into the anoxic peat thanks to the specialized tissue, aerenchyma, which transports oxygen down to the rhizosphere (Schütz et al., 1991). The same tissue functions as an escape route for CH_4 from the peat to the atmosphere (Whiting and Chanton, 1996).

In addition to the greenhouse gases CO_2 and CH_4, boreal peatland ecosystems are significant sources of various reactive hydrocarbons, VOCs, to the atmosphere (Tiiva et al., 2007a; Faubert et al., 2010a; Holst et al., 2010). Of the common plant species, *Sphagnum* mosses and sedges (*Carex* sp., *Eriophorum* sp.) are isoprene emitters (Ekberg et al., 2009, 2011). Dwarf shrubs emit a variety of mono- and sesquiterpenes (Faubert et al., 2012) and peat, especially when submerged by high water table, is a net source of various VOCs (Faubert et al., 2010b, 2011).

1.2. Ozone and UV-B radiation

The concentrations of O_3 have been decreasing in the upper atmosphere, but increasing in the lower atmosphere (The Royal Society, 2008), leading to two separate environmental problems and an array of research projects assessing the effects of these problems on plants and ecosystem functions.

Ground-level O_3, i.e. tropospheric O_3, is one of the most phytotoxic air pollutants causing the most damage to plants (for a review on tree responses, see Wittig et al., 2009). It is formed in photochemical reactions involving nitrogen oxides, carbon monoxide and VOCs (Fowler et al., 1998). These precursors originate from both biogenic and a wide variety of anthropogenic sources, such as burning of fossil fuels, land use change and chemical solvents, and they can be transported over considerable distances leading to elevated O_3 concentrations also in remote areas.

The depletion of the stratospheric O_3 column due to manmade chloride and bromide compounds (e.g. CFCs) has led to increased fluxes of UV-B (280–320 nm) radiation to the biosphere. Ozone depletion occurs mainly above the polar regions, where the stratospheric temperatures are low enough and the relative isolation of the polar air masses provide suitable conditions for the atmospheric processes destroying O_3 (WMO, 2007). Vegetation absorbs most of the incident UV-B radiation, which targets among others DNA, proteins and membrane lipids in plant cells (Jansen et al., 1998). In addition to the direct damage to the biomolecules, UV-B radiation can induce formation of ROS in the chloroplasts as a result of over-excitation of PSII (photo-oxidation) (Mackerness, 2000). The ROS induction creates a similar mechanism as the oxidative stress response under O_3 exposure (Long and Naidu, 2002).

The responses of forest trees, crops and natural vegetation to the elevated tropospheric O_3 concentrations have been reviewed elsewhere (Felzer et al., 2007; Manninen et al., 2009; Wittig et al., 2009). Effects of solar UV-B radiation on terrestrial ecosystems have been recently summarized by Ballaré et al. (2011). How polar vegetation responds to enhanced UV-B has been reviewed by Newsham and Robinson (2009), the responses of cryptogams, including mosses, by Björn (2007) and the responses of deciduous trees and shrubs by Julkunen-Tiitto et al. (2005).

Fig. 1. Boreal peatland microcosms in outdoor ozone exposure. The microcosms with intact vegetation and a 40 cm-deep peat layer were cored in May 2003 and installed into the ground of the experimental fields. The microcosms were exposed either to ambient or elevated ozone concentration (four replicate exposure fields) from mid-May to early October 2003–2006 (see Mörsky et al., 2008 for a technical description). The achieved increase in the ozone treatment was 1.7–1.9 times the ambient ozone concentration. Photos by Sami Mörsky.

This review focuses on the responses of boreal peatland vegetation and ecosystems to elevated O_3 and UV-B radiation. A large part of the published data on this topic stems from the UVOCARB project, which assessed relationships between CO_2 and CH_4 exchange and vegetation in UV-B or O_3 exposed boreal peatland ecosystems during the past decade. The UVOCARB project was initiated after the first findings were obtained under controlled conditions (Niemi et al., 2002a, b, c; Rinnan et al., 2003), in order to gain long-term evidence that would increase our understanding of the effects of O_3 and UV-B on functioning of the peatland ecosystem. In contrast to the earlier studies using growth chamber O_3 exposure for a duration of up to 8 weeks (Niemi et al., 2002a), peatland microcosms were now placed into an open-field O_3 exposure for four years (Fig. 1; Mörsky et al., 2008). The peatland microcosms represented a common oligotrophic peatland type dominated by *Sphagnum* mosses and a sedge *Eriophorum vaginatum*.

The UV-B exposure with peatland microcosms (Niemi et al., 2002c) was in the new project updated to a field experiment, where a long-term modulated exposure system was built on a natural fen in Sodankylä, Northern Finland (Fig. 2; Tiiva et al., 2007a). This flark fen was dominated by a brown moss, *Warnstorfia exannulata* and a sedge *Eriophorum russeolum*. In this review, we summarize the main results of the UVOCARB project (Tables 1 and 2) and compare them to other reports on effects of O_3 and UV-B on peatland ecosystems.

We expected that elevated O_3 concentration would not have significant effects on *Sphagnum* mosses, but that O_3 would alter morphology and functioning of the dominant *Eriophorum* species with further effects on ecosystem level CO_2 exchange and CH_4