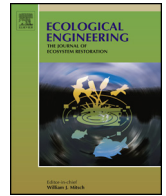




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# Investigating whether light intensity can modify decomposition rates in peatlands through control of the ‘enzymic latch’

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### ABSTRACT

Root exudates released by vascular plants contain significant amounts of photosynthetically-derived low molecular weight carbon compounds and gases, such as oxygen. These compounds are reported to have a priming effect on the activity of soil microbes which, in turn, release extracellular soil enzymes. Rates of root exudation are known to correlate positively with photosynthesis rates. As such, we hypothesized that phenol oxidase activity in the rhizosphere of peatland plants could be manipulated by varying the intensity of light to which above ground biomass is exposed, in line with recent solar radiation management proposals of geoengineers. Since phenol oxidase plays a pivotal role in regulating biodegradation in peat soils, through a mechanism widely known as the ‘enzymic latch’, this approach was thought to have potential as an ecoengineering strategy designed to enhance carbon sequestration in these environments. Our experiment however, found little relationship between phenol oxidase activity and light intensity level for any of the plants analysed, although significant differences in enzyme activity were observed between plant species. It is argued therefore, that encouraging the growth of particular plant species may be more effective at enhancing carbon sequestration in peatlands than manipulating ambient light levels.

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## 1. Introduction

Peatlands have sequestered vast stores of carbon over millennia due, primarily, to the accumulation of partially decomposed organic matter in anoxic soils (Clymo, 1984) and it is estimated they continue to do so at an average rate of 0.05, to 0.096 Pg (1 Pg =  $10^{15}$  g) of carbon per year (Yu et al., 2010; Clymo et al., 1998; Gorham, 1991). Decomposition of some soil organic matter (SOM) does take place in peatlands though – to varying degrees – releasing carbon in aqueous (dissolved organic carbon, DOC), solid (particulate organic carbon, POC) and gaseous forms such as carbon dioxide (CO<sub>2</sub>) and methane (CH<sub>4</sub>; Freeman et al., 2001a,b; Gorham, 1991; Worrall et al., 2003). The flux of these latter two key greenhouse gases (GHGs) between peatlands and the atmosphere has a significant effect on the Earth’s climate. Globally, these wetlands currently act as a net sink for atmospheric CO<sub>2</sub> (Kayranli et al., 2010) and crucially, unlike other ecosystems (such as forests) they are potent long term repositories for this carbon

(Dunn and Freeman, 2011; Freeman et al., 2012; Holden, 2005). The actual mechanism allowing this carbon accretion, the ‘enzymic latch’ (Fenner and Freeman, 2011; Freeman et al., 2001b), is so called because the sequestration results from a suppression of the normal enzymic decomposition pathways. This unusual stalling of SOM breakdown is the result of a disproportionate concentration of enzyme-inhibitory phenolic compounds in the peat-matrix. These accumulate due to constraints on phenol oxidase enzymes (Freeman et al., 2001b) which impede activities of the major agents of decomposition; namely, hydrolase enzymes (Freeman et al., 2004). Removal of these limitations on phenol oxidases, such as oxygen availability, temperature and pH, can initiate a biogeochemical cascade of degradation (Fenner and Freeman, 2011; Freeman et al., 2001a, 1997, 2004). Conversely, manipulation or strengthening of this enzymic latch has the potential to promote enhanced peatland carbon sequestration (Freeman et al., 2012). Such amplified suppression of decomposition in peat-soils would increase SOM accumulation, maximise the carbon storage intensity per unit area of peatlands and offer a new approach to geoengineering – acting as a cost efficient CO<sub>2</sub> removal (CDR) scheme (Royal Society, 2009). We propose one method for doing this involves altering the amount of light available for photosynthesis to peat-

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land plants. Preventing optimal rates of photosynthesis would decrease root exudation and thus further lower phenol oxidase activity in the rhizosphere.

Root exudation is part of the rhizodeposition process of plants and involves the release of ions (eg.  $H^+$ ), inorganic acids, oxygen, water and a wide-variety of carbon-based compounds, depending on the species of plant and its age, along with external factors such as biotic and abiotic stresses (Badri and Vivanco, 2009; Bais et al., 2006). Known as the 'rhizosphere priming effect' (RPE; Kuzyakov, 2002) these rhizodeposits are known to affect microbial communities and their activities in the soil surrounding the roots (Shackle et al., 2000) – an area known as the rhizosphere. Amplified rhizodeposition has been shown to increase microbial activity in the rhizosphere (Oger et al., 2004), and as most phenol oxidases in peat-soil are produced by bacteria (Burke and Cairney, 2002) and fungi (Thormann, 2006; Fenner et al., 2005), it is likely these enzymes will be affected too. Previous studies have shown that increased rates of photosynthesis increase rhizodeposition (Graham et al., 1982; Rovira, 1969); therefore by repressing photosynthetic activity, by altering the amount of light reaching peatland plants, it may be possible to curtail microbial activity and the production of phenol oxidase. The enzyme's activity may also be suppressed under sub-optimal photosynthesising conditions due to increased soil hypoxia, as oxygen (essential for phenol oxidase activity) is also a common root exudate (Bertin et al., 2003). The release of oxygen from the roots of some wetland plants, known as radial oxygen loss (ROL) has been shown to be correlated to photosynthetic activity (Lai et al., 2012). We hypothesise that higher rhizodeposition will lead to higher extracellular phenol oxidase activity.

The intensity of the light, or photon flux density (PFD), which promotes optimal rates of photosynthesis, is different depending on the plant species. Increasing the PFD beyond this point results in photosynthetic saturation, as the rate of photosynthesis does not increase, and eventually photoinhibitory damage, due to the over excitation of the photosynthetic reaction centres (Björkman and Demmig-Adams, 1994). It was not known what the optimal PFD for photosynthesis was for the two vascular plant species used in our study so  $750 \mu\text{mol m}^{-2} \text{s}^{-1}$  was selected as it was the average light intensity during the growing season at the chosen blanket bog site in North Wales, UK (personal communication, CEH 2013).

Being a dominant peatland plant, the effect of light on *Sphagnum* mosses was also investigated. As bryophytes, they do not have roots in the same way as vascular plants, however; they do exude organic carbon which can increase microbial activity in the peat-soil (Fenner et al., 2004; Shackle et al., 2000). And with bryophytes being generally shade-loving plants (Davey and Rothery, 1997), it was hypothesised that phenol oxidase activities would be highest in bryophytic plants grown under lower light conditions, as they would reach photosynthetic saturation, or even be affected by photoinhibitory damage, at higher PFDs.

To investigate how varying the light intensity would affect phenol oxidase activities in the rhizosphere of peatland plants through rhizodeposition, intact peat mesocosms were collected from a blanket bog in the UK and grown for six weeks under experimental conditions in a specially constructed growth room. If it was discovered that altering the PFD reaching peatland plants could increase the levels of carbon sequestered by peatlands, it would require methods to shade or intensify vast areas of land. However, as an ecoengineering or 'geoengineering' project this may not be conceivable, in terms of physical practicability and/or expense, when compared to other Solar Radiation Management (SRM) methods currently being considered. These include increasing the albedo of the desert, stratospheric aerosols and even the manufacture and release of space-based reflectors (Royal Society, 2009). Indeed one of the unintended consequences of some SRM projects may be a reduction in the Photosynthetically Active Radiation (PAR) reaching

peatlands, creating the potential for additional carbon sequestration through a lowering of rhizosphere priming.

## 2. Methods

Mesocosms of peat-soil ( $22,800 \text{ mm}^2 \times 220 \text{ mm}$ ) and vegetation, were collected at the start of the summer from the Migneint Valley in North Wales, UK. The area is a  $200 \text{ km}^2$  Special Area of Conservation, incorporating one of the largest areas of blanket bog in Wales. The area is 460 m above sea level and is predominantly a *Sphagnum*-rich, *Calluna vulgaris* (common heather) and *Eriophorum vaginatum* (hare's-tail cotton grass) dominant blanket mire, with acid grasses on drier hillslopes, and *Juncus effusus* (soft rush) in riparian areas. The underlying geology of the ombrotrophic bog is a mixture of acid and basic volcanic rocks, Ordovician shales and mudstones. Annual rainfall is 2400 mm and in the peat the water table is usually within 100 mm of (and often at) the ground surface. The study area has a pore water pH, at a depth of 100 mm, in the range of 4.1–5.1. The mean peat depth across the site is 2000 mm (Evans et al., 2012).

The mesocosms (held within black plastic containers) were collected so that they were dominated by one of the three experimental vegetative species – according to a score of 5 on the Braun-Blanquet cover-abundance scale (Wikum and Shanholtzer, 1978). The species studied were mixed *Sphagnum* moss species, *Calluna vulgaris* and *Eriophorum vaginatum*: referred to as *Sphagnum*, *Calluna* and *Eriophorum* (respectively) throughout this study. All groups of mesocosms containing one of the species were taken from an area of approximately  $25 \text{ m}^2$  and the entire study area was approximately  $100 \text{ m}^2$ .

Using one of the plastic containers with both ends removed as a guide each monolith was carefully extracted, to ensure the surface vegetation was kept intact and compaction of the soil was avoided to prevent any changes to its physical structure.

Once the mesocosms had been collected (a total of 45, consisting of 15 *Sphagnum*, 15 *Calluna* and 15 *Eriophorum*) they were returned to the laboratory, approximately 30 miles from the study site. They were placed in a climate controlled room (set to  $18^\circ\text{C}$ ) with commercially available growth lights, set to give 12 h conditions of  $1000 (\pm 20) \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR and 12 h of darkness, for one week (a Techone 600 w Energy Saving Digital Electronic Ballast fitted with a high pressure sodium a dual spectrum lamp). Soil samples were taken, 4 g, from a depth of 50 mm within the mesocosms, using a 10 mm soil-borer and taking care to minimise any disturbance to the vegetation or soil structure.

The mesocosms of each species were then split into three groups randomly assigned a light regime (with  $n = 5$ ) for the next six weeks which meant they were either kept under the full  $1000 (\pm 20) \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR conditions, or they were shaded – using horticultural mesh – so they received  $750 (\pm 20) \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR or  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR (Fig. 1). The levels of PAR were measured using a LI-250A Light Meter, from a set point above the mesocosms regularly throughout the experiment. All other conditions were kept the same. Water levels in the mesocosms were checked daily and kept consistent with the level of the water table in field at time of collection, using laboratory prepared distilled water.

The activity of extracellular phenol oxidases in the peat-soil from the different mesocosms was determined every week using 10 mM L-DOPA (dihydroxy phenylalanine) (Sigma-Aldrich Co., Ltd, Dorset) solution as a substrate, based on the procedure of Pind et al. (1994), Williams et al. (2000) and Dunn et al. (2014). Peat samples for the analyses were taken randomly from a depth of 5 cm from every mesocosm.

The concentration of water extractable phenolics from the peat samples were assayed every week using a modified version of the

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