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RESEARCH PAPER

Radial oxygen loss by the cushion plant *Eriocaulon schimperi* prevents methane emissions from an East-African mountain mire

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Keywords

Bale Mountain National Park; carbon dioxide; Ethiopia; fen; peat; rhizosphere.

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ABSTRACT

- Groundwater-fed fens are known sources of methane (CH₄) emissions to the atmosphere, and these are known to be mediated by the vegetation. In a fen located in the Bale Mountains, Ethiopia, we assessed the effects of a cushion plant (*Eriocaulon schimperi*) and a sedge (*Carex monostachya*) on rhizosphere biogeochemistry.
- Methane and CO₂ concentrations and pH were measured in pore-water at different depths in the profile. Redox potentials and NaCl-extractable element concentrations were analysed in soil samples from sites dominated by either *E. schimperi* or *C. monostachya*. Nutrient and element concentration were analysed in plant tissues.
- At *Carex*-dominated sites, CH₄ concentrations increased from 70 µmol·l⁻¹ at a depth of 10 cm to 130 µmol·l⁻¹ at a depth of 100 cm. CH₄ concentrations at *Eriocaulon*-dominated sites were almost zero (<1 µmol·l⁻¹) to a depth of 100 cm. Simultaneously, soil redox potentials and CO₂ concentrations were higher at *Eriocaulon*-dominated sites, indicating a low potential for CH₄ production and a high potential for CH₄ oxidation.
- *Eriocaulon schimperi* displayed a root investment strategy to cope with the harsh environment, similar to the cushion plant *Astelia pumila* in Patagonian bogs. This strategy is characterised by high root/shoot ratios, high root porosity and density under high redox conditions. Both cushion plant species create an aerobic rhizosphere through radial oxygen loss from deep roots, which strongly reduce CH₄ fluxes to the atmosphere.

INTRODUCTION

It has now widely been accepted that the emission of CH₄ from wetlands is strongly mediated by vegetation type (Ding *et al.* 2004, 2005; Bergström *et al.* 2007; Laanbroek 2010; Lamers *et al.* 2015). A study conducted in ombrogenous and minerogenous peat-forming systems (*i.e.* mires) in southern Finland (Bergström *et al.* 2007) showed that emergent macrophytes, such as *Phragmites australis* and *Equisetum fluviatile* that dominated the littoral zone, emitted about 78% of the total CH₄ efflux of the system, while species with floating leaves, such as *Nuphar lutea*, *Potamogeton natans* and *Sparganium* spp., only emitted about 2%, although the species with floating leaves covered a larger area than the emergent macrophytes. Similarly, it has been shown in an alpine wetland on the Qinghai-Tibetan Plateau, that the emergent macrophytes *Hippuris vulgaris*, *Carex allivescens* and *Scirpus distigmatis* emitted 200, 111 and 11 times more CH₄, respectively, than a submerged vegetation dominated by *Potamogeton pectinatus* (Hirota *et al.* 2004; Duan *et al.* 2005).

These clear differences in CH₄ emissions from different wetland vegetation types result from the cumulative outcomes of biogeochemistry, including microbial activities, species adaptations and climate conditions (Bergman *et al.* 1998, 2000; Cao *et al.* 1998; Aerts *et al.* 1999; Basiliko & Yavitt 2001; Bergström *et al.* 2007; Askaer *et al.* 2011; Bhullar *et al.* 2013). Some authors have suggested that the dominant plant species can be used as a proxy to predict CH₄ fluxes from different wetland types (Ding *et al.* 2005; Dias *et al.* 2010; Couwenberg *et al.* 2011). The production of CH₄ is determined by the concentration of easily degradable organic matter in the soil (Valentine *et al.* 1994; Bergman *et al.* 2000). Wetlands dominated by productive vascular species produce large amounts of readily decomposable litter, which stimulate CH₄ production by methanogenic bacteria, under anoxic conditions (Whiting & Chanton 1993, 2001; Joabsson & Christensen 2001). Thus, CH₄ emission may be facilitated by the transport of methane *via* aerenchyma of higher plants (funnelling effect).

Cushion plants, such as *Eriocaulon schimperi* (Körn. ex Ruhland), *Astelia* and *Donatia* species, form dense vegetation cover

in many parts of the world (Johns *et al.* 2007; Kleinebecker *et al.* 2008; Fritz *et al.* 2011). However, studies on wetlands dominated by cushion plants are limited and are often only descriptive studies, which lack data on soil biogeochemistry (Mark & Bliss 1970; Gibson & Kirkpatrick 1985; John 1988; Gibson 1990; Williams 1991). The vast majority of these studies were carried out in New Zealand and Tasmania, where cushion plants occupy extensive areas. Phillips (1996) mentioned the occurrence of a number of *Eriocaulon* species that form cushion carpets in the highlands of Ethiopia, Kenya, Tanzania and Mozambique. However, from her review, it is in most cases not clearly stated if the *Eriocaulon* species occurs on peat soils or on mineral soils. One species of *Eriocaulon* apparently also occurs in alpine wetlands of the Drakensberg Mountains in South Africa and Lesotho (E. Sieben, Free State University, personal communication).

Despite the extensive occurrence of cushion bogs in Argentina and Chile (Kleinebecker *et al.* 2007, 2008), studies on the role of cushion plants in CH₄ emissions from such bogs are limited. A study from Fritz *et al.* (2011) in Tierra del Fuego, Argentina, illustrated for the first time the important role that cushion plants play in CH₄ emissions from bogs. The cushion plant *Astelia pumila* G.R.Frost.Gaudich can dominate wind-exposed bogs in the eastern part of Tierra del Fuego. By oxygenating the peat soil with its deep roots, it prevents CH₄ accumulation to a depth of 2 m. The authors concluded that *Astelia*-dominated bogs thus keep CH₄ emissions close to zero, in contrast to adjacent *Sphagnum magellanicum*-dominated bogs that emit small amounts of CH₄. So, in general, phanerogamic plant species do not necessarily increase methane emission in mires.

In the present paper, we discuss the role of another cushion species *E. schimperi* on rhizosphere biogeochemistry, including CH₄ levels, in wetland soils of the Bale Mountains in Ethiopia. The occurrence of this cushion plant in groundwater-fed fen systems has been described by Dullo *et al.* (2015). *E. schimperi* in the highlands of Ethiopia has a remarkable morphological resemblance to *A. pumila* in the lowlands of southern Argentina. The species occurs in wetlands at a height of 3000–4000 m a.s.l. and its ecology has not previously been studied.

The aim of the present paper is to investigate if *E. schimperi* shows similar adaptations as *A. pumila* with respect to root depth, root porosity and capacity to release oxygen from the root tips (radial oxygen release; ROL), and to investigate if these root characteristics lead to a fundamental change in peatland biogeochemistry, as was shown for *A. pumila* (Fritz *et al.* 2011). Furthermore, our aim is to investigate if the existence of cushion plants in Bale Mountains is also confined to extremely nutrient-poor and acidic habitats, as was suggested for bogs and blanket bogs in the lowlands of southern Argentina (Kleinebecker *et al.* 2008; Fritz 2012).

Fritz *et al.* (2011) compared rhizosphere biogeochemistry, root shoot ratios and foliar nutrient content of *Astelia*-dominated sites with *Sphagnum*-dominated sites. In the Bale Mountains we compared *E. schimperi*-dominated sites with adjacent *Carex monostachya* A. Rich dominated sites.

Specifically, the following questions are addressed: (i) does the cushion plant *E. schimperi* prevent CH₄ emissions; (ii) if so, what are the functional traits that make *E. schimperi* a suppressor of CH₄ emission in mountain mires; and (iii) is *E. schimperi* also restricted to extremely nutrient-poor habitats?

MATERIAL AND METHODS

Study site

The study was conducted in the Bale Mountains National Park (BMNP) (6°29'–7°10' N, 39°28'–39°57' E), which is located ca. 400 km southeast of Addis Ababa in Ethiopia's moorland eco-region (Fig. 1). Field measurements and data collection were conducted between 4 and 8 April 2013.

The climate of this eco-region is complex, and regularly recorded meteorological data are mostly lacking. The annual rainfall is highest in the southwestern part, reaching a maximum of 2500 mm·year^{−1}, with the dry season lasting only about 2 months. Mean maximum temperature on the mountain peaks is between 6 °C and 12 °C, while mean minimum temperature is between 3 °C and 10 °C. Frost is very common throughout the year, especially during the winter months (November to March; Rundel 1994). An extreme diurnal temperature range of about 40 °C (−15 °C to +26 °C) has been recorded on the Sanetti Plateau of Bale Mountains National Park (Hedberg 1997), which is where the present study was conducted. The Sanetti Plateau is situated at an altitude between 3100 m and 4377 m, with alpine vegetation and almost no trees. The peatlands that we studied were all fed by groundwater and surface water (Dullo *et al.* 2015), so they are fens. *E. schimperi* is locally quite abundant and forms small cushion carpets, mostly at the edge of the peatlands, but also on slightly drained peat surfaces. The wetland studied also includes the tussock-forming species *C. monostachya*, which dominates the wettest parts of the mire. The fen is fed by numerous small streams and springs, which originate from surrounding hills.

We selected three sampling locations, in which we sampled *E. schimperi*-dominated and *C. monostachya*-dominated sites in one large stretch of fen wetland. Sampling sites were chosen to make a comparison between sites with the cushion plant *E. schimperi* and the tussock forming sedge *C. monostachya*. Unlike *Carex*-dominated sites, *Eriocaulon*-dominated sites are not grazed, but rodents may sometimes destroy the cushions by eating the roots, in particular when the water table has dropped (personal observations). In total, there were six sampling locations: three for each vegetation type.

Fig. 1. Position of Bale Mountains in Ethiopia.

Field measurements and sample collection

Redox potential and pH were measured in the field in pore-water using a portable redox-pH multi-meter. Pore-water was collected anaerobically in both *Eriocaulon*- and *Carex*-dominated sites by connecting vacuumed 60-ml syringes to ceramic soil moisture samplers (10 cm Rhizon SMS; Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands). The samplers (pore size: 0.1 μm) were installed at 10, 25, 50 and 100 cm below the soil surface. Samples were kept under anaerobic conditions until analysis. In total 24 pore-water samples were collected (six sampling sites, four depths); samples were stored below 20 °C and brought to the laboratory for further analysis.

In addition, soil samples and samples of *E. schimperi* plants were collected. Soil samples were collected from the top 10 cm to a depth of 60 cm. At each depth, four replicates samples were taken. Twelve replicate cores (10 cm² surface, 30 cm depth) with *E. schimperi* were collected and transported in sealed plastic bags to the laboratory. Due to a combination of high altitude and harsh weather, it was not possible to collect soil cores deeper than 60 cm.

Laboratory analyses

Methane

Methane concentrations in the samples were measured by analysing head space samples on a Hewlett-Packard 5890 gas chromatograph (Avondale, California, USA) equipped with a flame-ionisation detector and a Porapak Q column (80/100 mesh), operated at 120 °C with N as carrier gas, in the laboratory at Radboud University, Nijmegen, the Netherlands (accuracy 0.2 ppm). Bicarbonate and CO₂ concentrations were estimated from pH measurements during sampling and total inorganic C (TIC) measured in the laboratory using an infrared gas analyser (ABB Advance Optima).

Root density and root porosity

Root density (expressed as g·DW·l⁻¹) of *E. schimperi* was determined from six core samples (10 × 10 × 30 cm) collected randomly. Roots were washed thoroughly and dried at 70 °C for 48 h. The porosity of the roots was determined using the microbalance method (Visser & Bögemann 2003) by cutting root samples of 12 cm into 1-cm pieces incrementally from the root base to the apex.

Nutrient and elemental analyses

Nutrient concentrations in plant tissue were analysed using digests of dried samples. Plant material was dried for 48 h at 70 °C and ground into liquid N. Homogenised portions of 200 mg each were digested with 4 ml HNO₃ (65%) and 1 ml H₂O₂ (30%), using an Ethos D microwave lab-station (Milestone srl, Sorisole, Italy). Digests were diluted and concentrations of P, Al, Ca, Fe, Mg, Mn, Na, S, Si and Zn were determined by ICP spectrometry (IRIS Intrepid II; Thermo Electron, Franklin, MA, USA). K was measured on a FLM3 Flame Photometer (Radiometer, Copenhagen, Denmark). Similarly, ICP and AA analysis were used to measure concentrations of nutrients and elements in the soil after extraction of 35 g fresh soil with 100 ml of either 0.2 M NaCl or H₂O. Plant-available P was determined by lactate

extraction (Egnér *et al.* 1960). Concentrations of N and C in *E. schimperi* tissues and peat were measured with a CNS analyser (Model NA 1500; Carlo Erba Instruments, Milan, Italy).

Statistical analyses

The nutrient and element concentrations in pore-water samples and soil extracts between *Eriocaulon*- and *Carex*-dominated sites were compared using the software IBM SPSS Statistics 20 (IBM, Cugago, IL, USA). We used one-way ANOVA and *post-hoc* multiple comparisons of means with the Tukey test. Concentrations of nutrients and elements were set as dependent variables and the depth from where either pore-water samples or soil samples were collected was set as an independent variable. Comparisons were made both to compare mean concentrations of nutrients or elements at the same depth for both species, and among different depths for one particular species.

RESULTS

Root system of *E. schimperi*

Eriocaulon schimperi had a compact rooting zone with a very high root density in the first 30 cm below the soil surface (Fig. 2). Root density decreased below 30 cm and roots extended to a depth of about 60 cm. For the first 10 cm, root density of *E. schimperi* exceeded 10 g·l⁻¹ fresh soil and then decreased to 2 g·l⁻¹ at 30 cm depth, which is still high for such a depth. Possibly the rooting zone of this species extended beyond 50 cm below the surface, albeit with a low density of roots.

In addition, *E. schimperi* invested heavily in root biomass, as the average aboveground to belowground ratio was only 0.10 ± 0.04 (±SE, n = 6); this means that the plant allocates 90% of its biomass below ground. Excluding the rhizomes, it had an average root to shoot ratio of 8.2 ± 1.7 (n = 6). In addition, roots showed high porosity with an average value of 64 ± 4.2% (n = 12) calculated from eight 12-cm long root samples collected from different individual plants of *E. schimperi*. Generally the root porosity of this species tended to decrease toward the root tip.

Fig. 2. Root density of *E. schimperi* presented in g·l⁻¹ fresh soil.

Methane in pore-water

The pore-water found at the two investigated vegetation types, dominated respectively by *E. schimperi* and *C. monostachya*, showed large differences in CH₄ concentrations at different depths. While CH₄ levels for the *Eriocaulon*-dominated sites were extremely low (Fig. 3; <1 µmol·l⁻¹) at both 10 and 25 cm below the surface, *Carex*-dominated sites had concentrations at these same depths of 40 and 90 µmol·l⁻¹, which are 90 and 160 times higher. Down to a depth of 100 cm, CH₄ levels remained lower in the cushion vegetation sites than in the sedge sites. For both vegetation types, CH₄ levels increased with depth.

Redox potential and CO₂

Redox potential (E_h) values at the *Eriocaulon*-dominated sites differed distinctly from those at *Carex*-dominated sites (Fig. 4A). At 10, 25 and 50 cm depth, E_h at *Eriocaulon*-dominated sites remained above 350 mV, indicating the presence of freely available oxygen. At sedge-dominated sites the E_h was always below 300 mV, indicating a low availability of oxygen. At 100 cm depth, E_h values were identical for both species. Similarly, CO₂ concentrations from the two sites differed markedly. *Eriocaulon*-dominated sites had higher levels of CO₂ in the pore-water than *Carex*-dominated sites (Fig. 4B).

There were no notable differences between the two vegetation types in NaCl-extractable nitrate and ammonium, and lactate-extractable P in the soil. At both sites nitrate was depleted from the soil, and ammonium was only present at low concentrations (<3 µmol·g⁻¹·DW). Similarly, plant-available P < 0.01 µmol·g⁻¹·DW soil. A notable difference between the cushion vegetation and sedge vegetation was the significant depletion of Fe, Mn and S at the *Eriocaulon*-dominated sites compared to *Carex*-dominated sites (Table 1).

Elemental concentrations of *E. schimperi*

Eriocaulon schimperi has a N:P ratio of 26 g·g⁻¹, as measured in its green leaves, which indicates P limitation (Güsewell 2004). The concentrations of N, P and K in the living shoots were much higher than those in the roots or dead leaves (Appendix S1). This points to reallocation of these elements

Fig. 3. Methane concentrations in the pore-water at different depths of the peat profile at sites dominated by *C. monostachya* and *E. schimperi*, respectively.

Fig. 4. Redox potentials at cushion plant *Eriocaulon* sites and *Carex* sites A: and concentrations of CO₂ in pore-water from both sites B.

Table 1. NaCl-extractable element concentrations in soil profiles from *Eriocaulon* and *Carex* sites.

veg. type	depth (cm)	Ca	Fe	Mg	Mn	P	S
		µmol·g ⁻¹ ·DW ⁻¹ soil					
<i>Eriocaulon</i>	10	27.27	0.02	8.82	1.11	0.0044	0.94
	30	30.98	0.01	10.56	0.06	0.0079	0.98
	45	23.89	0.01	6.61	0.18	0.0014	0.50
<i>Sedge</i>	10	26.93	0.22	7.91	0.70	0.0044	3.28
	20	18.85	0.10	5.29	0.75	0.0031	3.57
	40	79.24	0.03	27.84	1.07	0.0098	3.81

from the roots to the shoots. Root characteristics and concentration of elements (in µmol·g⁻¹·DW⁻¹) in leaves of *E. schimperi* are presented in Table 2. For comparison, data from the literature on *A. pumila* have been added (Fritz *et al.* 2011). Significant variables are shown in bold.

DISCUSSION

Does *Eriocaulon* suppress CH₄ emission to the atmosphere?

Our research indicates that the cushion plant *E. schimperi* most likely keeps CH₄ levels in the peat low, similar to that reported for another cushion plant, *A. pumila* (Fritz *et al.* 2011). As a result of high root density and high root porosity, *E. schimperi* is able to release sufficient oxygen into the soil to oxidise potential phytotoxins such as sulphide and reduced metals in its rhizosphere. The redox potential of the rhizosphere and to some distance below this zone is above 350 mV, meaning that oxygen is still available around the roots of this plant, and its supply is higher than its consumption. When root density

Table 2. Root characteristics and concentration of elements ($\mu\text{mol}\cdot\text{g}\cdot\text{DW}^{-1}$) in leaves of *E. schimperi* and *A. pumila* ($\pm\text{SD}$). Data derived from the present study and from Fritz (2012).

	<i>Eriocaulon schimperi</i>	<i>Astelia pumila</i>
Shoot/root ratio	0.10 $\pm$ 0.10	
Root biomass density	8.2 $\pm$ 4.3 (n = 6)	2.2 $\pm$ 0.33 (n = 3)
Root biomass m^{-2}	1704 $\pm$ 632 (n = 6)	3590 $\pm$ 550 (n = 3)
Mean root porosity (%)	64	60–70
N	1856 (156)	1014 (104)
P	36 (10)	26 (3)
K	1191 (235)	326 (36)
S	84 (15)	118 (28)
Mg	49 (12)	55 (11)
Mn	2 (1)	11 (5)
Fe	3.2 (1.7)	

decreased (below 50 cm), there was an accompanying rise in CH_4 levels (Fig. 2). At the *Carex*-dominated sites, redox potential values were lower. Concentrations of redox-sensitive metals such as Fe and Mn in the rhizosphere of *E. schimperi* were also very low compared to the *Carex*-dominated sites, which provides further evidence for root oxidation. The high oxygenation of the rooting zone through radial oxygen loss of *E. schimperi* led to almost zero CH_4 concentrations in the pore-water and thus, should lead to zero CH_4 emissions to the atmosphere.

Important functional traits of cushion plants that suppress CH_4 emission

The work of Fritz *et al.* (2011) on *A. pumila* in ombrogenic bogs in Patagonia, Argentina, showed quite similar adaptations as found here for *E. schimperi* in minerotrophic fens in the Bale Mountains. *E. schimperi* has a denser root system compared to *A. pumila*, but the latter has a much more extensive root system on a volume basis (Table 2) because its roots grow much deeper. Except for K the concentration of minerals and nutrients in the shoots are more or less the same. There are more similarities. Both species have root porosities $>60\%$ (Fritz *et al.* 2011) and invest a very large proportion (*E. schimperi* ca. 90%) of their biomass in underground tissue, which not only leads to high radial oxygen loss (ROL), but also enhances peat accumulation from dead roots. In addition, dead leaves remain attached to the shoots for a longer period of time, allowing for internal nutrient reallocation as was shown for N, P and K (Appendix S1). This points to adaptation to very nutrient-poor conditions (Fritz *et al.* 2011). Both *A. pumila*-dominated cushion bogs in Patagonia and *E. schimperi*-dominated fens in the Bale Mountains, show remarkable similarities in nutrient concentrations in their tissue, with high N:P ratios (20 and 26, respectively), which point to P limitation (Güsewell 2004).

The combination of high redox potential, high root density and porosity and high CO_2 concentrations in sites dominated by *E. schimperi* indicates low CH_4 production rates and potentially high CH_4 oxidation rates. In addition, the data suggest high root respiration rates and high peat mineralisation rates, enabling this species to mobilise nutrients. When we further compare the characteristics of *E. schimperi* with those of *A. pumila*, more remarkable resemblances appear. Both species

form very dense cushions and possess leaves that can survive for several years (Phillips 1996). The cushions, formed by tightly clustered *E. schimperi* plants are so strong that it is even possible to walk across them without causing damage or affecting the peat below.

The reasons for low CH_4 emissions in cushion-dominated peatlands may be a consequence of their growth form. Cushion plants form mounds often 15–40 cm above the average groundwater level and they have deep roots with high levels of aerenchyma (Fritz *et al.* 2011; Dullo *et al.* 2015). It is hypothesised that this large root biomass forms an adaptation to nutrient-limited soils, while the bolster/cushion is an adaptation to harsh climate conditions and/or grazing (Billings 1974; Gibson & Kirkpatrick 1985; Cavieres *et al.* 2002, 2007). Due to the micro-relief, CH_4 production is forced deeper into the soil where soil temperatures are low and recalcitrant decomposed organic matter contains a low fraction of easily decomposable C (Fritz 2012). Methanogenesis, normally extensive in the water-saturated zone, becomes further prevented by oxygen released from cushion plant roots, resulting in high redox potentials (Fritz *et al.* 2011; this paper) and the presence of oxygenated soil (pockets). Cushion plants also create conditions ideal for CH_4 oxidation, such as the micro-relief with unsaturated soil thicker than 20 cm that is sufficient to readily oxidise CH_4 formed in deeper layers (Couwenberg & Fritz 2012). CH_4 oxidation close to the roots prevents venting of CH_4 that is still produced in parts of the soil that are fully oxygen-deprived, therefore further decreasing the potential for CH_4 emissions. Hence, this combination of plant resource allocation and root system architecture engineers an environment that inhibits CH_4 production and also stimulates CH_4 oxidation through multiple soil layers. Forming a large aerenchymatous root network provides cushion plants with the advantage of roots with a low cell density (cell respiration) and air-filled roots to facilitate root respiration even at greater depths (>30 cm) in organic soils saturated with water. The transport of oxygen to deeper layers improves uptake of nutrients and minerals from deeper soil layers (Badano & Cavieres 2006). Furthermore, it provides sufficient access to water during episodic drought (induced by weather extremes in cushion plant habitats). Root-contained oxygen (ROL) may simply be a by-product of resource-efficient root architecture and the need for oxygen transport to active root tips. So, despite living in very different habitats, the cushion plants in Patagonia and Bale Mountains have remarkably similar survival strategies and are a good example of ecological convergence in plant species (Reich *et al.* 1997).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Concentration of elements in the tissues of *E. schimperi* (green leaves and roots) and in peat layers to a depth of 30 cm below the soil surface.

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