

Fen mires with cushion plants in Bale Mountains, Ethiopia

B.W. Dullo^{1,2,4}, A.P. Grootjans^{1,2}, J.G.M. Roelofs², A.F. Senbeta³ and C. Fritz^{2,5}

¹University of Groningen and ²Radboud University of Nijmegen, The Netherlands

³Hawassa University and ⁴Addis Ababa University, Ethiopia

⁵Hochschule Rhein-Waal, Kleve, Germany

SUMMARY

In March 2013 we investigated two small peatlands in the Bale Mountains in central Ethiopia. The mires are located on the Sanetti Plateau at an altitude of approximately 4000 metres above mean sea level (a.m.s.l.). Their vegetation is dominated by tussocky *Carex* species and locally also by a cushion plant *Eriocaulon schimperi*, which occurs elsewhere in eastern Africa in montane areas at altitudes between 2000 and 4100 m a.m.s.l. We studied the vegetation and pore water at different depths. The pore water chemistry suggested that these mires were groundwater fed, but also received water as precipitation and calcium-poor runoff from adjacent hills. The cushion plants (*Eriocaulon schimperi*) on the Sanetti Plateau resemble *Astelia pumila*, a cushion plant that dominates large ‘blanket bog type’ mires in south-west Chile and the south-eastern part of Tierra del Fuego (Argentina). Both species appear to expand in slightly degrading fens or bogs under rather extreme environmental conditions. We also discuss possible evolutionary adaptations within the *Eriocaulon* family to the harsh environment of mountain mires at high altitudes.

KEY WORDS: *Astelia pumila*; erosion; drainage; *Eriocaulon schimperi*; hydrology; over-grazing

INTRODUCTION

Literature on peatlands in the mountain areas of the Ethiopian Plateau is very scarce. Hamilton (1982) studied a three-metre deep peat deposit at 4040 m above mean sea level (a.m.s.l.) on Mount Badda in order to evaluate past climatological changes in this part of Ethiopia. Mount Badda is situated to the north of the Bale Mountains. Umer & Bonnefille (1998) studied a pollen record from a 1.8 m deep mountain mire at Tamsaa (3000 m a.m.s.l.) in central Ethiopia, on the northern side of the Bale Mountains, which showed that peat formation started about 14,000 years ago after the glaciers had melted (Umer *et al.* 2007). Osmaston *et al.* (2005) also discussed the past glaciation of the Bale Mountains, partly on the basis of an analysis of a 2.6 m deep profile of organic matter at Orgoba (4000 m a.m.s.l.) near the town of Goba at the eastern edge of the Bale Mountains.

In March 2013 we visited the Sanetti Plateau, which also forms part of the Bale Mountains (Figure 1). We found some small peatlands that were dominated by sedge vegetation and locally also by cushion plants which strongly resembled *Astelia pumila*, a cushion plant that dominates large ‘blanket bog type’ mires in south-west Chile and the eastern part of Tierra del Fuego (Kleinebecker *et al.* 2008, Fritz *et al.* 2011, Grootjans *et al.* 2014). This cushion plant turned out to be *Eriocaulon schimperi* Körn ex Ruhland. The occurrence of *Eriocaulon schimperi* in

the highlands of Ethiopia has previously been reported by Phillips (1994, 1996) and Edwards *et al.* (1997). This species is restricted to the mountain zones of eastern Africa where it occurs on marshy ground, often near streams or in places with seepage, at altitudes between 2300 and 4100 m a.m.s.l. It is found in Kenya, Uganda, Tanzania, Rwanda, Burundi, western Zaire, Zambia and Malawi (Edwards *et al.* 1997). It is one of more than 400 species and subspecies of the genus *Eriocaulon* which occur in South America, Asia, Africa, North America (less than ten species) and Europe (only one species). *Eriocaulon* species that are related to *Eriocaulon schimperi* also occur in western Africa (Sierra Leone, Cameroon and Equatorial Guinea) and in southern Africa (Mozambique, South Africa; Phillips 1996), but the occurrence of these species on peatlands is not mentioned.

The dominance of cushion plants has often been linked to nutrient-poor soil conditions, which often prevail in rain-fed bog ecosystems (Gibson & Kirkpatrick 1985, Adams 2007) when combined with severe climate conditions (Kleinebecker *et al.* 2008, Fritz 2012). The competition for light by higher plants including trees is low under these conditions, which are unfavourable for their growth. Cushion plants that invest most resources below ground (Gibson 1990, Fritz *et al.* 2011) are supposed to lose competitive strength in nutrient-rich (often groundwater fed) peatlands and in heathlands where

there is an increasing risk of accumulation of plant toxins in the rhizosphere.

In this article we shall investigate whether the mires that we visited on the Sanetti Plateau are rainwater or groundwater fed, and whether *Eriocaulon schimperi* is restricted to peatlands in the Bale Mountains. We shall also compare the characteristics of the cushion plant *Eriocaulon schimperi* in Ethiopia with those of cushion bog plants in Patagonia.

STUDY AREA

The geological formations of the Bale Mountains are older than the Great Rift Valley, which dissects Ethiopia and extends into Mozambique. The mountains were formed due to lava eruptions between 38 and 7 million years BP (Mohr 1963), when the lava covered all underlying rock formations. The main Bale highlands consist of a vast lava plateau with at least six volcanic cones, each rising to more than 4200 metres a.m.s.l., which have been considerably flattened by repeated glaciations (Mohr 1963).

The Bale Mountains National Park (BMNP),

which is located approximately 400 km south-east of Addis Ababa, is the largest continuous area above 3000 m a.m.s.l. in Africa with a total area of about 2220 km² (Yalden 1983, Yalden & Lagen 1992). The National Park lies in the north-western part of the Bale Mountains and encompasses unique flora and fauna. It is divided into five different habitat types, namely: the Northern Grasslands (Gaysay Valley), the Northern Woodlands, the Afro-alpine Meadows (Sanetti Plateau), the Erica Moorlands and the Haremma Forest.

The large variation in habitats combined with the climate, extent and isolation of the Bale Mountains from other Ethiopian highlands west of the Great Rift Valley has resulted in high endemism (Hillman 1988). More than 1300 flowering plant species occur in BMNP, including about 12 % of Ethiopia's endemic flora. Of the 163 endemic plant species, 23 (14 %) are endemic to BMNP. The National Park is well known for its fauna. It is home to 20 mammal species that are endemic to Ethiopia, of which five are found only in the National Park. The Bale monkey (*Chlorocebus djamdjamensis*), Ethiopian wolf (*Canis simensis*), giant mole rat (*Tachyoryctes macrocephalus*) and mountain Nyala (*Tragelaphus buxtoni*) are flagship species for the conservation of

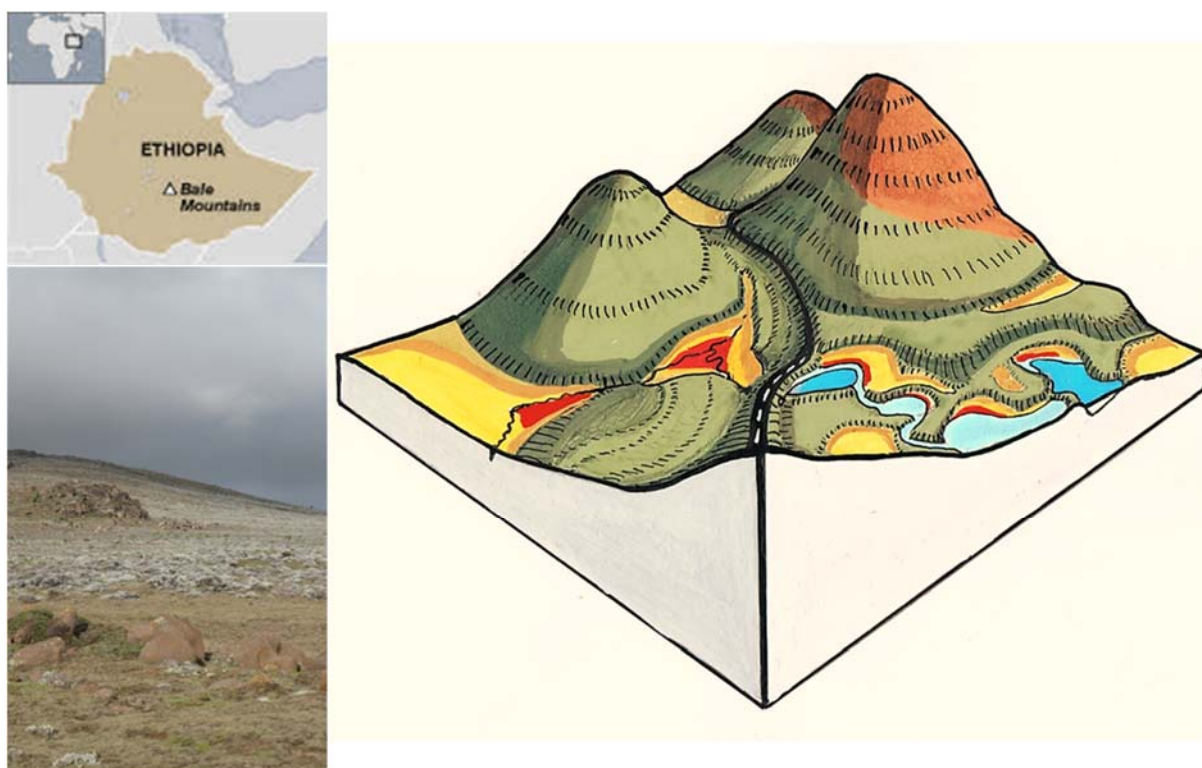


Figure 1. Overview of the Sanetti Plateau (right) in the north-eastern part of the Bale Mountains with low alpine vegetation on the mountains (grey-green), temporary wetlands (blue), wet grasslands (yellow) and peatlands (red). Unvegetated parts of the mountains are shaded brown.

BMNP; however, it hosts 26 % of the endemic fauna including mammals, bovines, hares, rodents, amphibians and reptiles. There are 282 resident bird species in the BMNP including nine of Ethiopia's 16 endemic birds, and about 170 migratory bird species have been recorded here (Hillman 1993).

The Bale Mountains are important for providing water to more than 12 million people in Ethiopia, Somalia and Kenya. They source more than 40 small rivers which contribute to five major rivers, namely the Web, Wabe Shebele, Welmel, Dimal and Genale (Hillman 1986, 1988, 1990). Locally, the countless perennial mountain springs are used by local communities as the sole source of water for their herds.

The climate within the wider area of the Bale Mountains is very variable and few data are available. Annual rainfall is highest in the south-western part, reaching a maximum of 2500 mm year⁻¹, with the dry season lasting only about two months. The maximum annual rainfall is lower at the eastern side and reaches a maximum of only 1100 mm year⁻¹. 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 all year round, especially during the winter months of 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 BMNP (Hedberg 1997).

The present study area is on the Sanetti Plateau, at the centre of BMNP. The altitude of the plateau is 3100–4377 m a.m.s.l. and it has alpine vegetation with almost no trees. It has a high density of rodents (2500 kg km⁻²), a high diversity of birds, and hosts the endemic Ethiopian wolf. The Sanetti plateau was shaped by a series of glaciations which eventually formed flat plateaus with small (temporary) lakes and streams and, locally, even relatively small peatlands (Figure 1).

We investigated two small mires lying close together at 6° 51' 19" N, 39° 53' 39" E, each with an area of about 2 ha. (Figure 2).

METHODS

Field measurements and sample collection

Field surveys, field measurements and data collections were conducted between 04 and 08 April 2013. The thickness of peat above the bedrock was measured by inserting a metal rod. Pore water samples were collected from *Eriocaulon*- and *Carex*-dominated sites (Figure 2) by connecting vacuum

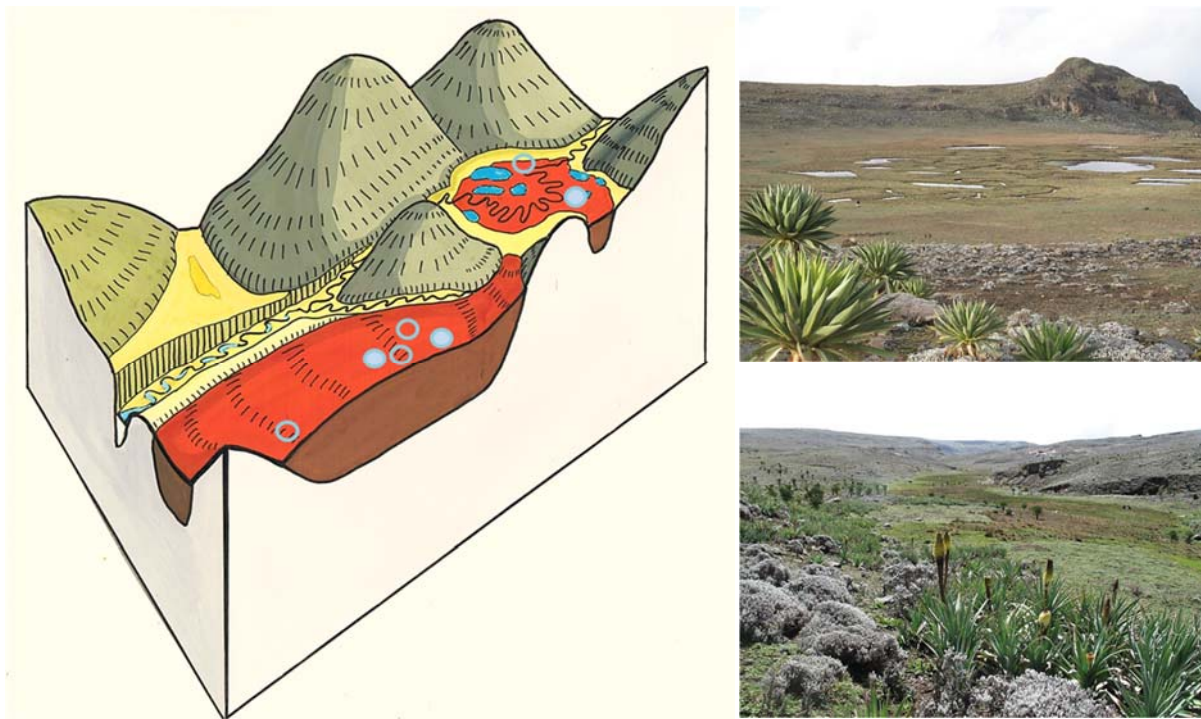


Figure 2. Schematic drawing of the area studied at Bale Mountains National Park (BMNP), Ethiopia (left) and photographs of the study sites (right). Groundwater samples were taken from sites dominated by *Eriocaulon schimperi* (open blue circles) and from sites dominated by sedges such as *Carex monostachya* (filled blue circles). Red shading indicates fen areas and yellow indicates wet grassland.

evacuated 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 depths of 10, 25, 50 and 100 cm below the soil surface. Using separate samples we measured redox potential and pH in the field, with a portable redox-pH multimeter. Pore water was collected anaerobically and kept under anaerobic conditions until analysis. In total, 24 pore water samples were collected (six sampling sites, four depths). The samples were stored below 20 °C and brought to the laboratory for further analysis. In the laboratory, concentrations of P, Al, Ca, Fe, Mg, Mn, Na and S were determined by ICP spectrometry (IRIS Intrepid II, Thermo Electron Corporation, Franklin, MA); K was measured on a FLM3 Flame Photometer (Radiometre, Copenhagen, Denmark); and nitrate, ammonium and phosphate concentrations were measured colorimetrically (Auto Analyser III systems, Bran & Luebbe, Germany).

Data analysis was performed in R. We tested the relationship between plant species cover and pore water composition at different depths. Tests were performed using linear models in R 3.03 (R Core Team 2013) followed by model justification procedures (Crawley 2007). The data for some variables were log-transformed before analysis. We performed a one-way Anova followed by a PostHoc HSD test (Tukey's Honestly Significant Difference test) to highlight differences between individual sites.

RESULTS

Vegetation

The wetland we studied is mainly covered by sedge vegetation dominated by *Carex monostachya*, especially in its wettest parts. The cushion plant *Eriocaulon schimperi* occurs along the fringes of the wetlands and also on slightly drained parts of the peatlands themselves. The two species form patches

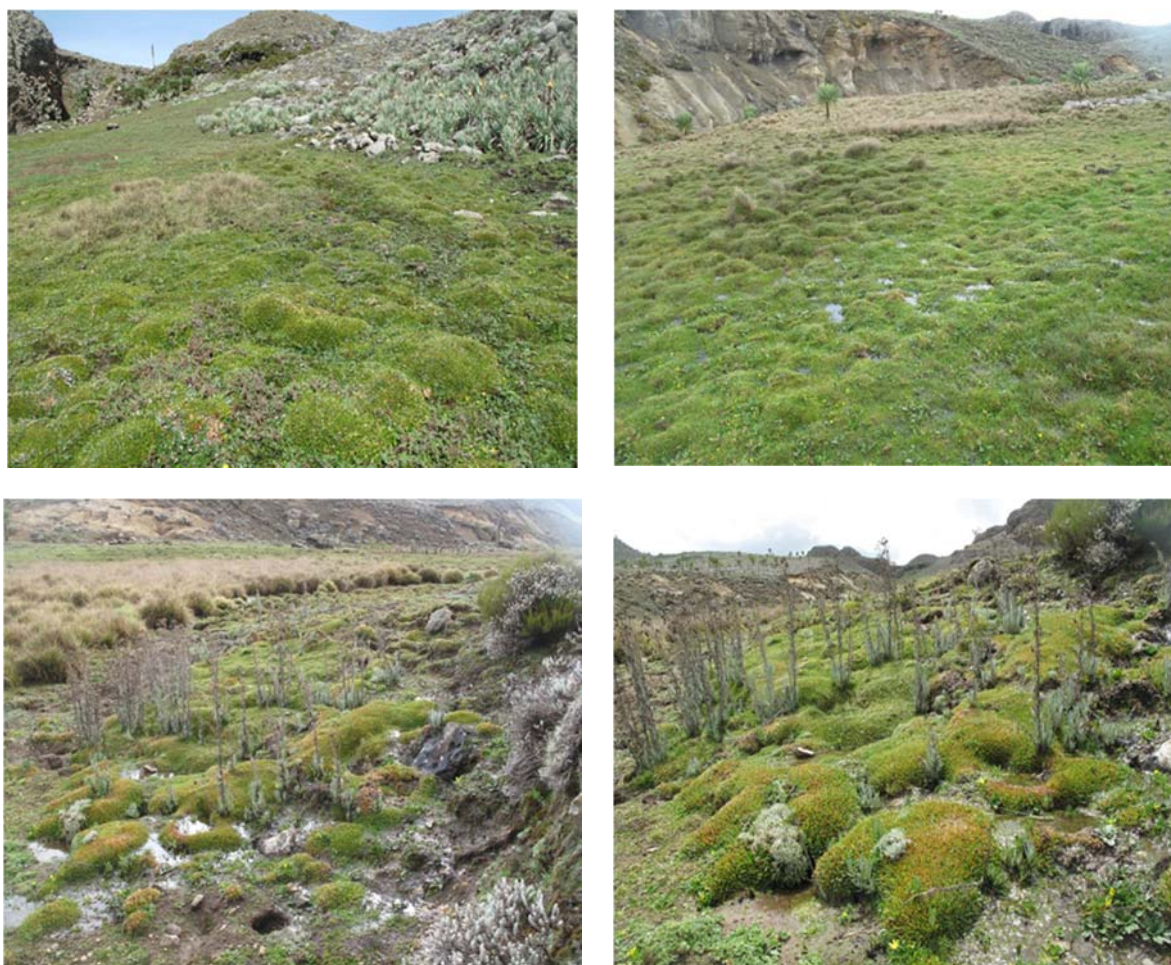


Figure 3. *Eriocaulon* tussocks growing on the mire (upper left and right) and on the spring-fed mineral soils of the sloping flanks of the valley (lower left and right).

of distinct vegetation types with sharp boundaries (Figure 3). Unlike *Carex*-dominated sites, *Eriocaulon*-dominated sites are not grazed but rodents may sometimes destroy the cushions by eating the roots, especially when the peat has been drained (personal observations).

Peat thickness and groundwater composition

Peat thickness at the investigated sites varied between 20 and 190 cm. The deepest peat (240 cm) was found under a small dried-out peat dome in the southern (higher-altitude) peatland. The average peat depth of the two mires was about 130 cm.

The ionic composition of the groundwater showed relatively high values of calcium and magnesium in the deepest samples (1 m below the surface; Table 1, Figure 4). The shallowest samples usually had the lowest values. Iron concentration was sometimes highest in the deepest samples, but sometimes peaked elsewhere in the profile. No consistent patterns were found in the profiles of potassium and sodium values. The highest sulphur values were found in the upper layers of the sedge-dominated sites. In the *Eriocaulon* sites the sulphur concentrations were lower except for one site close to a spring, where the highest values were found at one metre depth.

Mineral composition of soil moisture

Cation concentrations increased with depth, and sites dominated by *Eriocaulon* showed higher

concentrations of calcium, magnesium and potassium than *Carex*-dominated sites ($p < 0.01$). The highest concentrations of calcium (mean $568 \mu\text{mol L}^{-1}$) were found in pore water below the rooting zone of *Eriocaulon* (Table 1). In contrast, iron concentrations were significantly higher below stands dominated by *Carex* ($p < 0.01$). Potassium concentrations were higher in stands of *Eriocaulon* ($p < 0.05$) and showed an increasing trend at depths below 50 cm ($p = 0.056$) for both species. The values for sodium and sulphur showed little variation between sites and species.

Nutrient concentrations and pH

The analyses of plant nutrients in pore water revealed very low concentrations of nitrate, phosphate and ammonium in the *Eriocaulon*- and *Carex*-dominated sites. Ammonium concentrations increased significantly ($p < 0.05$) with depth, showing highest levels well below the rooting zone (depth = 100 cm). The higher ammonium concentrations below stands of *Carex* lacked significant differences ($p = 0.35$). Concentrations of nitrate were lower than those of ammonium at all sites and depths (Table 2). Phosphorus concentrations did not show any trend owing to the large variation in the pore water concentrations. Values of pH ranged from 5.4 to 7.5, indicating that the peatland was circumneutral, although pH was slightly higher at *Eriocaulon*-dominated sites than at sedge-dominated sites (Figure 5).

Table 1. Mean concentrations and standard deviations of means ($n = 3$) of major cations and sulphur in pore water collected at different depths in stands of *Eriocaulon schimperi* and *Carex monostachya*.

Stand type	Depth (cm)	Ca ($\mu\text{mol L}^{-1}$)	Mg ($\mu\text{mol L}^{-1}$)	K ($\mu\text{mol L}^{-1}$)	Na ($\mu\text{mol L}^{-1}$)	Fe ($\mu\text{mol L}^{-1}$)	S ($\mu\text{mol L}^{-1}$)
<i>Eriocaulon</i>	10	255 ± 73	116 ± 37	51 ± 42	389 ± 70	1 ± 1	27 ± 3
	25	366 ± 245	194 ± 136	110 ± 23	578 ± 30	1 ± 0	54 ± 6
	50	366 ± 105	203 ± 83	217 ± 149	575 ± 95	29 ± 42	64 ± 33
	100	568 ± 375	328 ± 174	116 ± 58	518 ± 57	18 ± 19	35 ± 23
<i>Carex</i>	10	250 ± 96	111 ± 38	48 ± 17	415 ± 84	47 ± 70	64 ± 53
	25	175 ± 56	94 ± 20	51 ± 26	437 ± 8	33 ± 28	81 ± 55
	50	212 ± 76	115 ± 25	75 ± 32	387 ± 27	45 ± 39	56 ± 39
	100	224 ± 35	127 ± 8	74 ± 27	419 ± 59	61 ± 42	29 ± 3

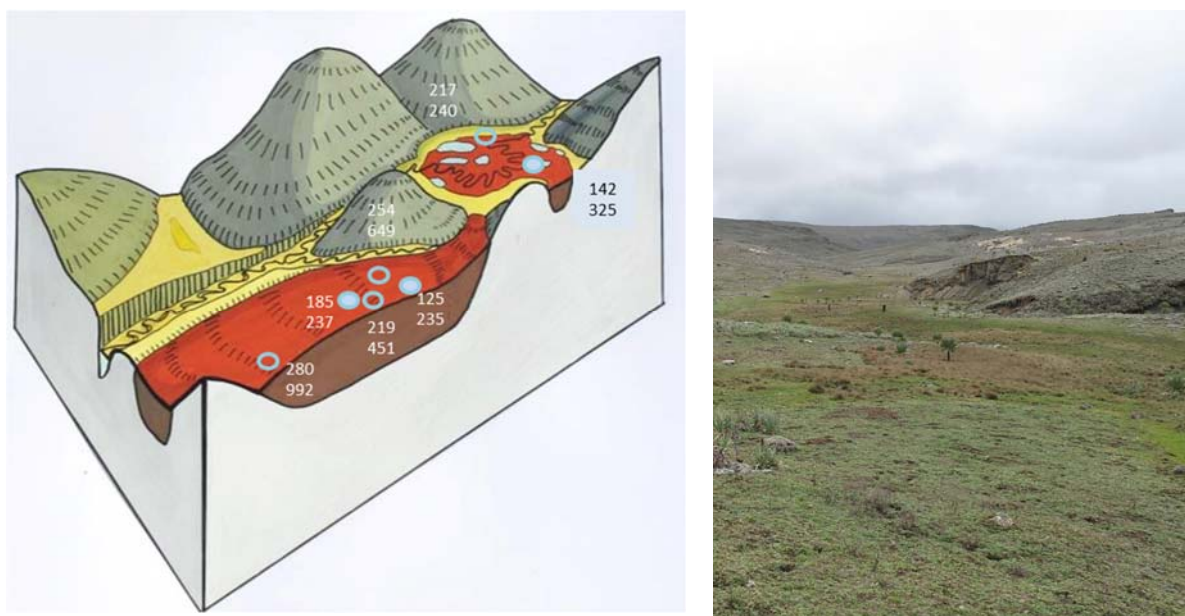


Figure 4. Left: calcium concentration (in $\mu\text{mol L}^{-1}$) measured in the pore water at two depths (25 and 100 cm below surface, respectively) in *Eriocaulon schimperii* sites (open blue circles) and *Carex monostachya* sites (filled blue circles). The photograph on the right presents an overview of the lower mire.

Table 2. Mean pore-water nutrient concentrations ($n=3$) for *Eriocaulon* and *Carex* sites, with their standard deviations.

Depth (cm)	<i>Eriocaulon</i> sites			<i>Carex</i> sites		
	NH_4 $\mu\text{mol L}^{-1}$	NO_3 $\mu\text{mol L}^{-1}$	PO_4 $\mu\text{mol L}^{-1}$	NH_4 $\mu\text{mol L}^{-1}$	NO_3 $\mu\text{mol L}^{-1}$	PO_4 $\mu\text{mol L}^{-1}$
10	1.1 ± 0.4	0.3 ± 0.4	1.6 ± 2.6	2.8 ± 0.8	0.3 ± 0.3	0.6 ± 0.6
25	3.2 ± 2.6	0.6 ± 0.8	0.1 ± 0.1	2.0 ± 0.8	0.1 ± 0.2	0.1 ± 0.1
50	3.2 ± 0.3	0.0 ± 0.0	0.4 ± 0.6	3.0 ± 2.7	0.0 ± 0.0	0.2 ± 0.2
100	3.9 ± 2.7	1.2 ± 2.0	2.0 ± 3.3	6.6 ± 2.3	0.0 ± 0.0	0.3 ± 0.1

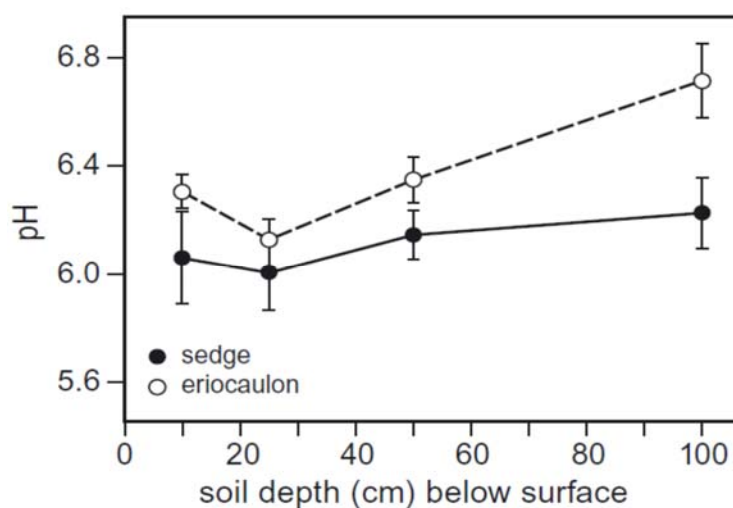


Figure 5. Variation of the pH of pore water with depth in *Carex* (sedge) and *Eriocaulon* vegetation types.

DISCUSSION

Minerotrophic fens in the Bale Mountains

Our results on the pH of the pore water and the mineral concentrations of both the pore water and the soil clearly showed that the wetlands we studied in Bale Mountains National Park are minerotrophic fens. Both fens are influenced by relatively calcium-poor groundwater ($< 1000 \mu\text{mol Ca L}^{-1}$) and the upstream fen also by much precipitation water, which is primarily stored in large surface-water pools. This upstream fen is heavily affected by a small but very erosive stream that has drained most of the peatland, and large sedge tussocks dominate the vegetation. The downstream sloping fen is much better preserved. The erosive stream flows alongside the mire and only slightly influences its lower part. However, some piping was observed in the steepest upstream part of this fen. Here, parts of the fen rapidly lose groundwater through small underground erosion pipes that discharge mineral-poor groundwater at a spring in a lower part of the fen. Small springs of mineral-poor water also occur on the mineral flanks of the mire (EC is about $90 \mu\text{S cm}^{-1}$). Rather mineral-rich groundwater enters the fen at approximately one metre below the surface. The highest calcium values we found were 1 mmol L^{-1} ($= 40 \text{ mg L}^{-1}$). However, most of the groundwater in the fen is relatively calcium-poor with values ranging between 100 and $300 \mu\text{mol L}^{-1}$ ($4\text{--}12 \text{ mg L}^{-1}$).

Eriocaulon schimperi in the Bale Mountains

We found *Eriocaulon schimperi* above the 2000–3000 m altitude range reported by Phillips (1996). The species occurs well above 4000 m in the Bale Mountains and is not restricted to peatlands in our study areas, but also occurs around springs on mineral soils (see also Edwards *et al.* 1997). On the margins of the mire and also on slightly drained parts of the mire *Eriocaulon* cushion plants appear to be able to invade slightly drained mire systems in a similar way to that reported for cushion plants such as *Astelia pumila* and *Donatia fascicularis* in Patagonian raised and blanket bogs (Gibson & Kirkpatrick 1985, Kleinebecker *et al.* 2008, Fritz *et al.* 2011, Fritz 2012). These authors found that the availability of plant nutrients in such rainwater-fed bogs is usually extremely low, and they also have low concentrations of the mineral elements which are potentially phytotoxins, such as Fe, Al, and S. The existence and dominance of cushion plants in such harsh environments makes sense from an evolutionary point of view, since they employ a strong root investment strategy, which provides a competitive advantage in bogs where above-ground competition is low due to low nutrient levels (Fritz

2012). The roots release oxygen *via* radial oxygen loss (ROL), also reducing the potential risks of being exposed to toxic substances such as reduced iron and sulphur species (cf. Lamers *et al.* 2012), thus allowing young roots to explore a large volume of soil when foraging for nutrients (Fritz *et al.* 2011). The iron-rich groundwater of Bale Mountains caused apparently little harm to the roots of *Eriocaulon*. The effective soil oxygenation and, thus, virtual absence of reduced iron in the rooting zone of *Eriocaulon* is highlighted in Table 1. Sedge species tolerate iron concentrations 30–50 times higher than can be tolerated by *Eriocaulon*. Nutrient concentrations, particularly inorganic nitrogen, in the groundwater-fed fens of the Bale Mountains are substantially lower than nutrient concentrations in semi-natural bogs in the European Alps (Bragazza & Gerdol 1999). These nutrient-poor conditions may be a key factor in explaining the occurrence of cushion plants under severe climatic conditions (frequent freezing, high insolation). We concluded that the dense rooting network of *Eriocaulon schimperi* is essential to enable the species to compete successfully for nutrients while avoiding toxic effects similar to those that would be experienced if the alternative nutrient-acquisition strategy found in *Sphagnum* species were adopted (Fritz *et al.* 2014).

Other cushion plants in mountain mires

Cushion plants generally occur in harsh environments which can be very cold and very windy (Billings 1974, Körner 2003). Cushion plants are effective heat and litter traps and store nutrients efficiently (Körner 2003, Fritz 2012). *Eriocaulon schimperi* is one of a limited number of *Eriocaulon* species that have developed into true (dense) cushion plants with hard leaves. Most other *Eriocaulon* species form small rosettes with softer leaves that may, nonetheless, form extensive mats or even loose cushions. Practically all *Eriocaulon* species are associated with wetlands. Some are aquatic plants that grow in shallow water which may temporarily dry up, enabling the plants to flower and form ripe seeds. Many species are terrestrial but restricted to wet soils, often with flowing water on sometimes steep slopes (Moldenke 2014).

Around ten *Eriocaulon* species occur in North America, but although all are restricted to wetlands, none of them are cushion plants. *Eriocaulon decangulare*, for instance, is associated with pioneer stages in *Sphagnum* bogs and intermediate fens. Only one species occurs in Europe (Great Britain and Ireland), namely *Eriocaulon septangulare*, which is a water plant that can form dense mats in bog pools. When the water level drops in summer the species starts to flower. *Eriocaulon decangulare* and

Eriocaulon septangulare are thought to have evolved from a common ancestor some 65 million years ago. After that, North America and Europe began to separate, creating two isolated populations that evolved into separate species. At global scale the genus *Eriocaulon* has developed into species that are adapted to submerged habitats, semi-terrestrial wet habitats, spring-fed sometimes peaty soils and even, at high altitudes, mires (adaptive radiation).

Eriocaulon schimperi bears a remarkable resemblance in morphology and adaptive behaviour to another cushion plant, *Astelia pumila*, which occurs in both the highlands and the lowlands of South Chile and Argentina (Tierra del Fuego) (Figure 6). A recent study in Tierra del Fuego (Fritz *et al.* 2011, Fritz 2012) addressed the functional role of *Astelia pumila*. This plant can dominate wind-exposed bogs in the eastern part of Tierra del Fuego. By oxygenating the peat soil with deep roots, it prevents CH₄ (methane) accumulation to a depth of

almost two metres. In contrast, adjacent bogs dominated by *Sphagnum magellanicum* do emit (small amounts) of CH₄. *Eriocaulon schimperi* in the Bale Mountains has the same adaptation, although the roots effectively prevent CH₄ emissions to a depth of only ~25 cm (Dullo 2014). The two cushion plants are also remarkably similar in terms of the nutrient concentrations in their tissues. Both species appear to be very efficient recyclers of nutrients (Dullo 2014).

Johns *et al.* (2007) report another cushion-forming *Astelia* species (*Astelia papuana*) on Mount Jaya, Papua New Guinea. In the subalpine and alpine zone (3000–4000m) *Astelia papuana* forms hummocks up to 30 cm tall on both flat areas and steep slopes with peat and peaty gravel. Other species, such as *Oreobolus pumila*, also form hard cushion bogs. The soil consists of deep peat with very low mineral concentrations (Johns *et al.* 2007). The above-mentioned studies show that species from very different taxonomic families can end up with very



Figure 6. *Eriocaulon schimperi* in the Bale Mountains (above; photos Ab Grootjans) and *Astelia pumila* in Tierra del Fuego, Argentina (below; photos Christian Fritz).

similar morphological and ecophysiological adaptations to the same (extreme) habitats (convergence).

Threats to minerotrophic fens in BMNP

The main threat to vegetation in the study area is the increase of cattle and sheep grazing on this plateau (Hillman 1988, Stephens *et al.* 2001). We observed that *Carex monostachya* was heavily grazed everywhere but *Eriocaulon schimperi* seemed to be unpalatable since we observed no grazed patches. As the density of grazers in the mountains increases, more biomass from the sedges will be removed and their tussocks destroyed. *Carex monostachya* plays a crucial role in regulating water flow, especially when heavy rainfall leads to flooding. Removal of the tussocks will stimulate erosion. Evidence of erosion is already visible in the field, with erosion gullies exposing deeper soil layers. In addition, higher grazer densities could lead to eutrophication by their dung, which is expected to result in shifts in vegetation composition. Therefore, further research on the wetlands of the Bale Mountains is urgently needed to help us understand the potential effects of grazing on emergent wetland vegetation. This includes addressing questions about how grazing affects further erosion.

ACKNOWLEDGEMENTS

This study was financed by NAM (Nederlandse Aarolie Maatschappij) and the ERA Foundation (Netherlands). The department of Aquatic Ecology and Environmental Biology of Radboud University in Nijmegen, The Netherlands, provided laboratory facilities, technical assistance and accommodation. We also acknowledge the Ethiopian Wild Life Conservation Authority for their permission to conduct this field study in Bale Mountains National Park. We would also like to thank the management of the National Park for providing assistance and allowing us to collect samples. Rodolfo Iturraspe is kindly acknowledged for his comments on an earlier version of this manuscript.

REFERENCES

- Adams, J.M. (2007) *Vegetation-Climate Interaction: How Vegetation Makes the Global Environment*. Springer, Berlin, 82 pp.
- Billings, W.D. (1974) Adaptations and origins of alpine plants. *Arctic and Alpine Research*, 6, 129–142.
- Bragazza, L. & Gerdol, R. (1999) Hydrology, groundwater chemistry and peat chemistry in relation to habitat conditions in a mire on the South-eastern Alps of Italy. *Plant Ecology*, 144, 243–256.
- Crawley, M.J. (2007) *The R Book*. John Wiley & Sons Ltd., Chichester, UK, 942 pp.
- Dullo, B.W. (2014) *Dynamics of Temporal Wetland Under Changing Weather Conditions*. PhD thesis, University of Groningen, 126 pp.
- Edwards, C., Demissew, S. & Hedberg, I. (1997) *Flora of Ethiopia and Eritrea, Volume 6*. Uppsala University, Addis Ababa and Uppsala, 379–380.
- Fritz, C. (2012) *Limits of Sphagnum Bog Growth in the New World: Biochemistry and Ecohydrology of Peatlands in South America and New Zealand*. Dissertation, Radboud University of Nijmegen/University of Groningen, 193 pp.
- Fritz C, Lamers, L.P.M., Riaz, M., Van den Berg, L.J.L. & Elzenga, T.J.T.M. (2014) *Sphagnum* mosses - masters of efficient N-Uptake while avoiding intoxication. *PLOS ONE*, 9, e79991.
- Fritz, C., Pancotto, V.A., Elzenga, J.T.M., Visser, E.J.W., Grootjans, A.P., Pol, A., Iturraspe, R., Roelofs, J.G.M. & Smolders, A.J.P. (2011) Zero methane emission bogs: extreme rhizosphere oxygenation by cushion plants in Patagonia. *New Phytologist*, 190, 398–408.
- Gibson, N. (1990) The environments and primary production of cushion species at Mt Field and Mt Wellington, Tasmania. *Australian Journal of Botany*, 38, 229–243.
- Gibson, N. & Kirkpatrick, J.B. (1985) A comparison of the cushion plant communities of New Zealand and Tasmania. *New Zealand Journal of Botany*, 23, 549–566.
- Grootjans, A.P., Joosten, H., Iturraspe, R., Fritz, C. & Moen, A. (2014) Mires and mire types of Peninsula Mitre, Tierra del Fuego, Argentina. *Mires & Peat*, 14(01), 1–20.
- Hamilton, A.C. (1982) *Environmental History of East Africa. A Study of the Quaternary*. Academic Press, London, 328 pp.
- Hedberg, O. (1997) High-mountain areas of tropical Africa. In: Wielgolaski, F.E. (ed.) *Polar and Alpine Tundra, Ecosystems of the World 3*, Elsevier, Amsterdam, 185–197.
- Hillman, J.C. (1986) *Bale Mountains National Park, Management Plan*. Wildlife Conservation Organisation, Addis Ababa, 250 pp.
- Hillman, J.C. (1988) The Bale Mountains National Park area, southeast Ethiopia, and its management. *Mountain Research and Development*, 8, 253–258.
- Hillman, J.C. (1990) The Bale Mountains National Park area, southeastern Ethiopia, and its management. In: Messerli, B. & Hurni, H. (eds.)

- African Mountains and Highlands, Problems and Perspectives*, African Mountains Association, Walsworth Press, Missouri, 277–286.
- Hillman, J.C. (1993) *Ethiopia: Compendium of Wildlife Conservation Information*. Report to Ethiopian Wildlife Conservation Organisation, Addis Ababa, two volumes, 786 pp.
- Johns, R., Shea, G. & Puradyatmika, P. (2007) Subalpine and alpine vegetation of Papua. In: Marshall, A.J. & Beehler, B.M. (eds.) *The Ecology of Papua, Part 2*, Periplus Editions, Singapore, 1025–1053.
- Kleinebecker, T., Hölzel, N. & Vogel, A. (2008) South Patagonian ombrotrophic bog vegetation reflects biogeochemical gradients at the landscape level. *Journal of Vegetation Science*, 19, 151–160.
- Körner, C. (2003) *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Second edition, Springer, Berlin, 349 pp.
- Lamers, L.P.M., van Diggelen, J.M.H., Op den Camp, H.J.M. *et al.* (2012) Microbial transformations of nitrogen, sulfur, and iron Dictate Vegetation Composition in Wetlands: A Review. *Frontiers in Microbiology*, 3, 156, doi:10.3389/fmicb.2012.00156.
- Mohr, P.A. (1963) *The Geology of Ethiopia*. University College of Addis Ababa, 268 pp.
- Moldenke, H.N. (2014) Additional notes on the Eriocaulacea. LXXXVI. Online at: <http://biostor.org/reference/62873.text>, accessed 27 November 2014.
- Osmaston, H.A., Mitchell, W.A. & Osmaston, J.A.N. (2005) Quaternary glaciation of the Bale Mountains, Ethiopia. *Journal of Quaternary Science*, 20, 593–606.
- Phillips, S.M. (1994) Notes on some *Eriocaulon* species from Ceylon. *KEW Bulletin*, 49, 287–303.
- Phillips, S.M. (1996) *Eriocaulon schimperi* (Eriocaulaceae) and some related species in Eastern Africa. *KEW Bulletin*, 51, 333–342.
- R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. Online at: <http://www.R-project.org>, accessed 24 December 2014.
- Rundel, P.W. (1994) Tropical alpine climates. In: Rundel, P.W., Smith, A.P. & Meinzer, F.C. (eds.) *Tropical Alpine Environments: Plant Form and Function*. Cambridge University Press, 21–44.
- Stephens, P.A., d'Sa, C.A., Sillero-Zubiri, C. & Leader-Williams, N. (2001) Impact of livestock and settlement on the large mammalian wildlife of Bale Mountains National Park, southern Ethiopia. *Biological Conservation*, 100, 307–322.
- Umer, M. & Bonnefille, R. (1998) A late Glacial/late Holocene pollen record from a highland peat at Tamsaa, Bale Mountains, south Ethiopia. *Global and Planetary Change*, 16, 121–129.
- Umer, M., Lamb, H.F., Bonnefille, R., Lézine, A.-M., Tiercelin, J.-J., Gibert, E., Cazet, J.-P. & Watrin, J. (2007) Late Pleistocene and Holocene vegetation history of the Bale Mountains, Ethiopia. *Quaternary Science Reviews* 26, 2229–2246.
- Yalden, D.W. (1983) The extent of high ground in Ethiopia as compared to the rest of Africa. *SINET: Ethiopian Journal of Science*, 6, 35–39.
- Yalden, D.W. & Largen, M.J. (1992) The endemic mammals of Ethiopia. *Mammal Review*, 22, 115–150.

Submitted 21 Sep 2014, revision 24 Dec 2014
Editor: Olivia Bragg

Author for correspondence:

Bikila Dullo, P.O. Box 3434, College of Natural Sciences, Department of Plant Biology and Biodiversity Management, Addis Ababa University, Addis Ababa, Ethiopia.
Tel: +251 919 808306; E-mail: kooket@gmail.com