Polar Biol (2016) 39:511–521
DOI 10.1007/s00300-015-1803-z

ORIGINAL PAPER

Usnea antarctica, an important Antarctic lichen, is vulnerable to aspects of regional environmental change

Stef Bokhorst[1,4] · **Peter Convey**[2] · **Ad Huiskes**[3] · **Rien Aerts**[4]

Received: 22 May 2015 / Revised: 6 October 2015 / Accepted: 7 October 2015 / Published online: 13 October 2015

Abstract Studies of cryptogam responses to climate change in the polar regions are scarce because these slow-growing organisms require long-term monitoring studies. Here, we analyse the response of a lichen and moss community to 10 years of passive environmental manipulation using open-top chambers (OTCs) in the maritime Antarctic region. Cover of the dominant lichen *Usnea antarctica* declined by 71 % in the OTCs. However, less dominant lichen species showed no significant responses except for an increase in *Ochrolechia frigida*, which typically covered dying lichen and moss vegetation. There were no detectable responses in the moss or associated micro-arthropod communities to the influence of the OTCs. Based on calculated respiration rates, we hypothesise that the decline of *U. antarctica* was most likely caused by increased net winter respiration rates (11 %), driven by the higher temperatures and lower light levels experienced inside the OTCs as a result of greater snow accumulation. During summer, *U. antarctica* appears unable to compensate for this increased carbon loss, leading to a negative carbon balance on an annual basis, and the lichen therefore appears to be vulnerable to such climate change simulations. These findings indicate that *U. antarctica* dominated fell-fields may change dramatically if current environmental change trends continue in the maritime Antarctic, especially if associated with increases in winter snow depth or duration.

Keywords CO_2 · Gas fluxes · Micro-arthropods · Snow · *Usnea antarctica* · Winter

Introduction

The Antarctic Peninsula has been one of the regions of the world experiencing relatively fast regional climate warming over recent decades (Turner et al. 2009, 2013) and, due to its relatively simple ecosystems (Convey 2013), serves as an early warning system in understanding species and ecosystem responses to climate change. Terrestrial ecosystems in the Antarctic are dominated by mosses and lichens, with only two vascular plants present in localised areas of the maritime Antarctic (western Antarctic Peninsula region and associated outlying islands) (Convey 2013). The latter have undergone increases in population size over recent decades, and this spread is interpreted to be linked to the strong regional warming trend (Fowbert and Smith 1994; Grobe et al. 1997; Parnikoza et al. 2009; Torres-Mellado and Casanova-Katny 2011). However, the response of mosses and especially lichens to environmental change is often much harder to determine due to their slower growth rates (Lindsay 1973). Studies performed in the Arctic suggest that lichens are likely to decline in

---

Electronic supplementary material The online version of this article (doi:10.1007/s00300-015-1803-z) contains supplementary material, which is available to authorized users.

✉ Stef Bokhorst
Stefbokhorst@hotmail.com

[1] Department of Arctic Ecology, Norwegian Institute for Nature Research (NINA), 9296 Tromsø, Norway

[2] British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

[3] Royal Netherlands Institute for Sea Research, Korringaweg 7, P.O. Box 140, 4400 AC Yerseke, The Netherlands

[4] Department of Systems Ecology, Institute of Ecological Science, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

response to increased competition from vascular plants (Cornelissen et al. 2001), although winter climate change studies often show opposite patterns (Bjerke et al. 2011). Direct measurements of lichen and moss responses to climate warming without the confounding presence of vascular plants are sparse and often short term (Bokhorst et al. 2007a) and have not helped to clarify their predicted response under future climate scenarios (Lang et al. 2012). Mosses and lichens play a vital role in many ecosystems and in ecosystem service provision across the world, for instance as sinks for carbon in northern tundra regions (Cornelissen et al. 2007), suppliers of nitrogen to boreal forests (Lindo et al. 2013), food for vertebrates (Berg et al. 2011) and as a habitat and food source for many invertebrates (Gerson and Seaward 1977; Bokhorst et al. 2007b; Salmane and Brumelis 2008; Bokhorst et al. 2014, 2015). In the Antarctic context, the latter is particularly important, as soil invertebrates are the only macroscopic terrestrial faunal group (Convey 2013). Any changes in moss and lichen community composition and abundance are therefore likely to have major implications for the terrestrial fauna and food web of Antarctic ecosystems.

Since 2003, a passive experimental environmental manipulation study has been operated in a moss-dominated and a lichen-dominated community on Signy Island in the northern maritime Antarctic (Bokhorst et al. 2007a). During the early years of this study, no response to the experimental manipulation was observed in the moss community while, in the lichen community, some deterioration of the dominant lichen *Usnea antarctica* was reported (Bokhorst et al. 2007a, 2012), along with a decline in the abundance of micro-arthropods (Bokhorst et al. 2008). The lichen decline was suggested to be caused by the thicker snow pack that accumulates inside the manipulation chambers (open-top chambers, OTCs) in winter, which insulates the vegetation against the extremes of winter temperatures (Bokhorst et al. 2011, 2013). However, this ‘protection’ allows for more physiological activity during the winter period when it is hard for primary producers to acquire resources due to the low light levels. Therefore, respiration rates in the vegetation may increase during winter, using up stored resources, which may be hard to compensate for during the short periods of activity possible during the summer growing season when mosses and lichens are also often subject to considerable periods of desiccation stress (Schroeter et al. 1995; Kappen 2000). The decline in the micro-arthropod community was proposed to be directly linked to the decline in a potential food source (*U. antarctica*) (Bokhorst et al. 2007b, 2008). The lack of decline in the moss community was assumed to indicate the buffering capacity of the thick moss layer has on water availability for its own growth and that of the micro-arthropods living among them. Therefore, if the moss vegetation and associated micro-arthropods are less affected by water stress during the summer months (Bokhorst et al. 2007a), they may be able to compensate for increased winter respiration rates and even then increase in abundance due to the opportunities provided by the warmer summer temperatures generated by the OTCs. However, whether any of these changes hold in the longer term is unknown, as it is also recognised that such field manipulation approaches can generate more extreme responses and artefactual results in the shorter term (Kennedy 1995; Bokhorst et al. 2011, 2013).

After 10 years of year-round OTC manipulation at Signy Island, we here report on the impacts on the contained cryptogam and micro-arthropod communities. We hypothesised that: (1) based on the initially observed declines of lichens in OTCs (Bokhorst et al. 2007a), the lichen community will deteriorate further following longer-term warming but that any impact on the moss community will be much less due to the larger water availability in the deeper moss turf; (2) the lichen decline in the fell-field community is driven by a negative carbon balance caused by higher winter respiration rates due to warmer (and longer duration) sub-nivean temperatures inside OTCs; and (3) the micro-arthropod community will decline in tandem with the lichens, whereas the warming in the moss community is likely to increase their abundance by reducing temperature limitation on growth and reproduction.

Materials and methods

Study site

The study site was located on Signy Island, in the northern maritime Antarctic South Orkney Islands (60°71′S 45°59′W), on the north facing ‘back slope’ area near the British Antarctic Survey (BAS) Signy Research Station. Signy Island has an annual mean temperature of around −2 °C and receives about 400 mm year^{-1} of precipitation of which most falls as snow (Walton 1982; Royles et al. 2013). Two distinct vegetation types have developed on the back slope area: (1) a moss community dominated by *Polytrichum strictum* Brid. (63 % cover) and *Chorisodontium aciphyllum* (Hook. f. & Wils.) Broth. in Engl. (76 % cover), which has accumulated to a depth of approximately 20 cm, underlain by a base layer of quartz–mica–schist and (2) a fell-field lichen community dominated by *U. antarctica* Du Rietz (>50 % cover) on the same rock type. The two study sites were c. 50 m apart (Bokhorst et al. 2007a).

Environmental manipulation study

During the austral summer of 2003, six open-top chambers (OTCs) (Bokhorst et al. 2013) were deployed in each vegetation type (moss and lichen), where they remained year-round until December 2013. The design of the hexagonal OTCs was based on the widely used ITEX chambers (Marion et al. 1997). Passive warming chambers, such as OTCs, tend to affect various micro-climatic conditions besides temperature (Bokhorst et al. 2013) but remain a widely used and most reliable tool in remote locations such as the Antarctic. To minimise confounding effects on other micro-climatic variables besides temperature, larger chambers are most suitable (Bokhorst et al. 2011). Therefore, we deployed relatively large-sized OTCs, measuring 1.8 m from opposite corners and 1.6 m from opposite sides at the top and 0.5 m high. Each OTC had a neighbouring control plot in a split plot design. The placement of OTC and control plots was randomised to avoid any possible consistent effects of OTCs on the neighbouring control plots, for instance by wind or snow. Temperatures (°C) in the air (+5 cm), at the soil surface and deeper in the soil (−5 cm) were recorded using copper–constantan thermocouples, and soil water content (Water Content Reflectometer CS616, Campbell Scientific UK) was measured at hourly intervals year-round in three paired plots of each vegetation type. In addition, we measured photosynthetically active radiation (PAR; μmol $m^{-2}s^{-1}$) at the soil surface in one OTC and control plot for each vegetation type (SKP215 Campbell Scientific UK). All data were recorded on a CR10X Storage module (Campbell Scientific, UK). Precipitation was recorded with a self-registering heated precipitation gauge (PLUVIO, OTT Hydrometrie) that recorded weight increments at hourly intervals in the vicinity (50 m) of the experimental plots. Due to intermittent power shortages and damage to sensors, micro-climatic recordings are incomplete for many of the later years. Therefore, we focus here on micro-climate differences for the years 2009–2011, regarded to be representative, as these had the most complete data sets available across entire years. OTC effects on the micro-climate in the early years of the experiment (2003–2005) were reported by Bokhorst et al. (2007a).

Vegetation survey

To quantify changes in the cryptogam communities in OTCs and control plots across time, we measured the percentage cover of each lichen and moss species through the point-intercept method in fixed 30 cm × 30 cm quadrats in each of the plots established in 2003. The presence/absence of each species was noted for 121 points at 2.5-cm intervals in the fixed quadrats. In one of the paired OTC–control plots of the fell-field vegetation, the vegetation quadrat could not be accurately relocated in 2013 and therefore was not quantified.

Usnea antarctica carbon balance

To quantify potential changes in the carbon budget of *U. antarctica*—the most dominant of the lichen species in the fell-field community on Signy Island (Bokhorst et al. 2007a) and an abundant lichen throughout the maritime Antarctic (Øvstedal and Smith 2001)—due to OTC effects on the micro-climate, we calculated potential annual photosynthesis and respiration rates using the CO_2 response curves in relation to temperature and PAR described by Schroeter et al. (1995). For these calculations, we used the hourly temperature data of individual plots ($n = 3$ for both OTCs and control plots) and PAR values from one paired plot of OTC and control. We used five PAR categories (<5, 5–100, 100–300, 300–500 and >500 μmol m^{-2} s^{-1}) to calculate CO_2 fluxes. To achieve realistic calculations of annual CO_2 flux rates, we set a number of restrictions: (1) the lower temperature limit was set to −10 °C as the temperature response curves had a polynomial shape and lower temperatures would have resulted in increased respiration values, which is unrealistic considering the limited CO_2 efflux rates at very low sub-zero temperatures for lichens (Schroeter and Scheidegger 1995); (2) summer CO_2 flux rates were limited to periods with precipitation events, as drought is the main limiting factor for lichen physiological activity (Schroeter and Scheidegger 1995; Schroeter et al. 1997; Kappen 2000; Schroeter et al. 2010). If precipitation was recorded during a specific hour, irrespective of the amount, the corresponding CO_2 flux for that data point was included in the calculations; (3) during the snow cover period between April and September, we included all CO_2 flux values, as the sub-nivean micro-climate provides high relative humidity allowing lichen physiological activity (Kappen et al. 1995); (4) these calculations were limited to 2004, 2005, 2009 and 2010, the years with the most complete micro-climatic recordings. Although there are clear limitations to these calculations, they permit comparison of the potential carbon budget of *U. antarctica* between OTCs and control plots in a consistent manner and allow a test of Hypothesis 2.

Micro-arthropod abundance

To quantify changes in the abundance and diversity of the micro-arthropod community in response to the warming treatment, we collected vegetation and underlying soil using a PVC corer (7 cm diameter). In the moss community, we collected the top 5 cm and in the lichen community all lichens and the first cm of soil and loose gravel in the lichen community of each plot. Micro-arthropods were extracted in a modified Tullgren extractor for 48 h. Collembola and Acari were identified to species level except for smaller Prostigmata, which were grouped together.

Statistics

Micro-climate differences between OTCs and control plots were compared across seasons using monthly mean values to calculate a seasonal mean (summer: December–February, autumn: March–May, winter: June–August, and spring: September–November). We used repeated-measures ANOVA with treatment (OTC vs. control plots) within a plot as a within-subject factor to test for significant differences between OTCs and control plots. As only minor, non-significant, differences were found in the soil moisture data, we only present the summer mean values. To quantify changes in cryptogam species cover, we used repeated-measures ANOVA on the point-intercept data from 2003 to 2013. Differences in total and individual species abundances of micro-arthropods between OTCs and control plots were quantified through one-way ANOVA. Potential differences in the calculated values of photosynthesis, respiration and the net annual carbon budget between treatments were tested using repeated-measures ANOVA. Log transformations were applied where necessary, and homogeneity of variance was compared using Levene's test. All analyses were carried out in SPSS 21.0 (SPSS Inc., Chicago, IL, USA).

Results

Impact of OTCs on micro-climate

Mean summer air temperature warming achieved by OTCs was relatively low and amounted to 0.3 and 0.7 °C in the lichen and moss communities, respectively (Table 1). The strongest warming took place during winter reaching on average 1.0 °C higher in the OTCs compared to controls, most likely as result of snow accumulation inside OTCs. At the soil surface, summer warming reached 0.7 and 0.2 °C in the lichen and moss communities, respectively, and strongest warming also occurred during winter, 0.9 and 0.2 °C. At 5 cm in the soil, summer warming by OTCs was 0.6 and 0.3 °C in the lichen and moss communities,

Table 1 Effect of open-top chambers (OTCs) on the micro-climate of the lichen and moss communities

OTC effect (OTC-C)	Lichen community			Moss community		
	2009	2010	2011	2009	2010	2011
Air temperature (°C)						
Summer	0.4 (0.2)	0.4 (0.4)	0.1 (0.3)	0.6 (0.1)*	0.9 (0.1)*	0.6 (0.1)*
Autumn	0.8 (0.0)*	−0.2 (0.3)	0.0 (0.1)	0.7 (0.6)	0.5 (0.4)	0.4 (0.1)
Winter	1.0 (0.3)*	0.1 (0.3)	1.0 (0.5)	0.5 (0.3)	0.6 (0.3)	1.8 (1.0)
Spring	0.0 (0.2)	0.1 (0.2)	0.1 (0.1)	−0.9 (0.3)	0.3 (0.2)	0.5 (0.1)
Soil surface (°C)						
Summer	0.6 (0.0)*	0.8 (0.3)*	0.8 (0.1)*	0.2 (0.2)	0.3 (0.0)*	0.1 (0.0)
Autumn	0.7 (0.2)	0.3 (0.2)	0.7 (0.2)	0.0 (0.2)	−0.2 (0.1)	0.2 (0.1)
Winter	0.8 (0.3)	0.3 (0.3)	1.6 (0.6)	0.1 (0.1)	0.3 (0.1)	0.3 (0.2)
Spring	0.0 (0.1)	0.3 (0.1)	0.6 (0.2)	−0.5 (0.1)*	0.1 (0.1)	0.0 (0.1)
Soil (°C)						
Summer	0.5 (0.1)	0.7 (0.5)	0.5 (0.3)	0.2 (0.4)	0.5 (0.4)	0.3 (0.5)
Autumn	0.7 (0.3)	0.5 (0.1)*	0.7 (0.1)*	1.0 (1.1)	0.5 (0.7)	0.8 (0.6)
Winter	0.6 (0.2)*	0.3 (0.2)	1.1 (0.0)*	0.7 (0.6)	0.9 (0.8)	2.9 (1.6)
Spring	−0.6 (0.3)	0.0 (0.1)	0.1 (0.3)	−1.0 (0.2)*	0.7 (0.7)	0.7 (0.6)
Soil moisture (%)	−6.5 (4.5)	−18.4 (1.0)	−20.3 (0.0)	−17.5 (4.5)	−19.4 (3.5)*	−17.4 (4.6)
PAR (%)						
Summer	3.4	5.6	3.6	−10.0	−1.3	−10.2
Autumn	−39.2	−3.3	−12.1	−1.9	−11.6	−3.5
Winter	−37.6	−59.9	−84.4	−52.5	−51.1	−70.3
Spring	−32.0	−10.2	−19.4	−66.3	−10.7	−7.6

* Indicate significant $P < 0.05$ differences between OTC and control plots. Values are mean of $n = 3$ with SE in brackets. Note that due to some sensor damage some mean values are based on $n = 2$. Soil moisture is shown for summer mean values only. PAR data are calculated from $n = 1$ in an OTC and control plot of each vegetation type. Spring PAR values for 2010 and winter values of 2011 were consistently lower in OTCs compared to control plots ($P < 0.05$) when combining moss and lichen PAR recordings

respectively, while during winter, warming effects of 0.7 and 1.5 °C were recorded. Soil moisture was reduced, but not always significantly so, during the summer months, with 6–20 % lower mean values recorded in OTCs compared to control plots (Table 1). PAR showed small non-significant changes between OTCs and control plots, ranging between 10 % lower and 5 % higher mean values during summer (Table 1). Larger differences (up to -84 %) were recorded between OTCs (2.5 μmol m^{-2} s^{-1}) and control plots (11.0 μmol m^{-2} s^{-1}) in winter, again indicating snow accumulation inside OTCs. In addition, freeze–thaw cycles were often reduced during late winter inside the OTCs (see Online Resource 1), indicating that OTCs were accumulating more snow than the surrounding non-manipulated habitats.

Response of the lichen community to warming

There were strong responses by parts of the lichen community to the OTC manipulation (Table 2; Fig. 1). The cover of the dominant lichen species *U. antarctica* declined by 71 % in the OTCs following 10 years of warming, while reducing by only 16 % in the control plots (Fig. 2a). The percentage cover of the lichen *Ochrolechia frigida* increased (Tukey HSD $P < 0.01$) from 1.3 % (SE ±0.9) to 14.3 % (±2.2) in the OTCs between 2003 and 2013 while showing no significant change in the control plots (4.1 ± 1.7 %–4.6 ± 1.9 %) (Fig. 2b). The other lichen and moss species, which have a low cover in this ecosystem, showed no significant changes in response to the OTC manipulation (Table 2, Online Resource 2). On average, photosynthetic rates of *U. antarctica* were lower (6 %) in the OTCs compared to control plots while respiration increased (11 %) (Table 3; Fig. 3). The changes in photosynthetic and respiration rates resulted in a decreased net carbon budget for *U. antarctica* in the OTCs compared to control plots, and in overall carbon loss during 2005 and 2009 (Fig. 3c), and this may have been the underlying cause for the cover declines observed in the OTCs.

Total Collembola and Acari abundance were not affected by the warming treatment (Table 4). However, the abundance of the less common collembolan *Folsomotoma octooculata* decreased by 71 % ($P < 0.05$) in the OTCs compared to control plots.

Response of the moss community to warming

There were no species-specific changes in the bryophyte community in response to the OTC treatment (Table 2). However, there were overall declines of 68 ± 7 % and 51 ± 11 % in *P. strictum* cover in the control plots and OTCs, respectively (Fig. 4, Online Resource 2). The liverwort *Cephaloziella varians* had invaded two of the OTC plots replacing *P. strictum*, covering up to 9 % of the surface (Fig. 4), while this was not observed in the control plots. There were no abundance differences for Collembola and Acari between control plots and OTCs in the moss community (Table 4).

Discussion

We found a clear contrast between Antarctic moss and lichen communities in their response to 10 years of experimental field environmental manipulation mimicking long-term climate change scenarios. The currently widespread and common lichen *U. antarctica* was very vulnerable to the applied manipulation, while none of the

Table 2 ANOVA statistics (*F* and *P* values) of cryptogam responses to 10 years' manipulation using open-top chambers on Signy Island

		Treatment		Time		Treatment × time	
		F	*P*	*F*	*P*	*F*	*P*
Lichen community		(*df* 1,8)					
Ochrolechia frigida	L	3.8	0.088	16.0	0.004	14.0	0.006
Cladonia gracilis	L	1.5	0.262	0.0	0.895	2.3	0.171
Sphaerophorus globosus	L	0.0	1.000	0.1	0.786	0.0	0.892
Cetraria aculeata	L	0.9	0.379	0.1	0.745	1.4	0.272
Usnea antarctica	L	0.0	0.960	33.6	0.000	18.7	0.003
Andreaea depressinervis	M	2.3	0.165	1.4	0.263	1.4	0.263
Polytrichum strictum	M	1.4	0.265	4.2	0.075	1.7	0.223
Moss community		(*df* 1,10)					
Chorisodontium aciphylum	M	1.9	0.198	1.5	0.256	0.0	0.867
Polytrichum strictum	M	0.8	0.390	54.0	0.000	0.7	0.437
Cladonia gracilis	L	1.8	0.205	2.6	0.135	2.5	0.142

Analyses are based on the percentage cover data from the start of the environmental manipulation (2003) and after 10 years (2013) in open-top chambers and control plots for the lichen ($n = 5$) and moss community ($n = 6$). *L* lichen, *M* moss

Fig. 1 Cover of the fruticose lichen *U. antarctica* inside an open-top chamber on Signy Island at the start of the environmental manipulation in 2003 (*left*) and after 10 years of the study (*right*). Distance between metal pegs is 30 cm

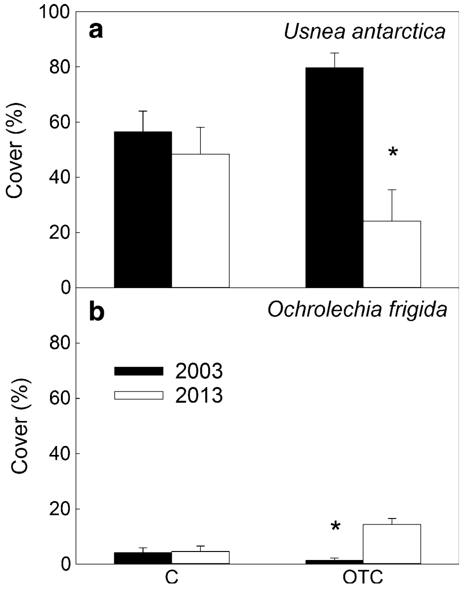

Fig. 2 Lichen cover changes following 10 years of manipulation using OTCs on Signy Island. **a** Percentage cover of the lichens *U. antarctica* and **b** *O. frigida* in control plots (C) and open-top chambers (OTC) from surveys taken in 2003 and 2013. *Bars* are mean of $n = 5$ with SE as *error bars*. *Asterisk* indicate significant ($P < 0.05$) differences between years

moss species showed detectable responses. The response of the lichen community is in line with reports from the Arctic (Wahren et al. 2005) but also provides a clear account of lichen responses to climate change without confounding effects from vascular plants (Cornelissen et al. 2001), thereby highlighting the vulnerability of lichens to future environmental change. The very limited response detected in the micro-arthropod community is likewise consistent with results obtained in a 3-year manipulation experiment on High Arctic Svalbard (Webb et al. 1998), indicating that these organisms are resistant or resilient to the magnitude of micro-climatic changes induced by the OTC methodology on this experimental timescale.

Cryptogam response to climate warming

In support of Hypothesis 1, the dominant lichen *U. antarctica* declined under the climate change simulation while the moss community was unchanged. The limited response by the moss vegetation to warming indicates that this community is relatively resistant to climate change, probably as a result of the larger water availability in the deeper moss turf. The large decline of the moss *P. strictum*

Table 3 ANOVA statistics (F and P values) of *U. antarctica* CO_2 fluxes from Signy Island in open-top chambers and control plots

	Treatment		Time		Treatment × time	
	$F_{(1,4)}$	P	$F_{(3,12)}$	P	$F_{(3,12)}$	P
Photosynthesis	70.5	0.001	2789.9	<0.001	7.6	0.004
Respiration	124.8	<0.001	102.7	<0.001	2.2	0.146
Net carbon budget	230.3	<0.001	50.2	<0.001	2.5	0.107

Analyses are based on data from 4 years and 3 replicate plots for each treatment

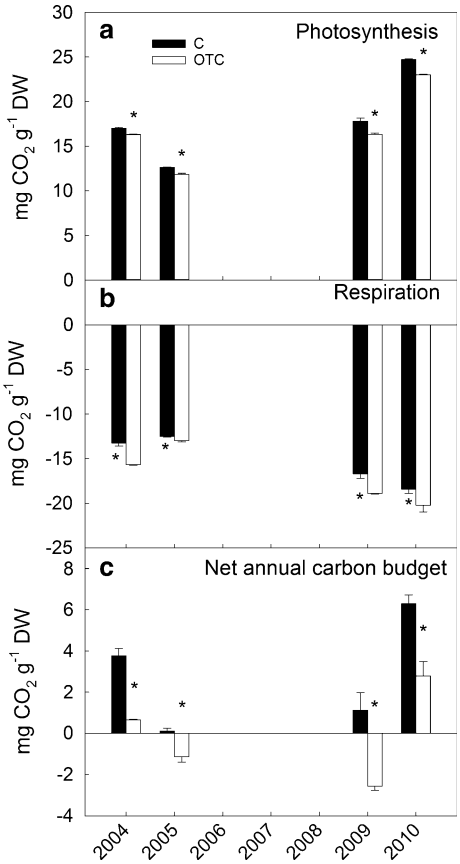

Fig. 3 Annual CO_2 gas fluxes of *U. antarctica* in control plots (C) and open-top chambers (OTCs). Values are based on calculations of CO_2 exchange using hourly temperature and photosynthetically active radiation data from six experimental plots on Signy Island and CO_2 response curves of *U. antarctica* quantified by Schroeter et al. (1995). *Bars* are mean of $n = 3$ with SE as *error bars*. *Asterisk* indicate significant ($P < 0.05$) differences between years

over time was unrelated to the influence of OTCs, indicating either that there was a natural turn over in the moss community (Collins 1976) or that local environmental conditions in this part of Signy Island are becoming less favourable for this moss species. Large changes in precipitation regime are predicted for the Antarctic Peninsula region (Thomas et al. 2008; Turner et al. 2009, 2013) and have already been implicated in affecting moss growth in the South Orkney Islands (Royles et al. 2012, 2013). Together with invasion of non-native or expansion of native vascular plants, these changes may well lead to outcompeting of these moss communities in the near future if regional climate warming becomes more intense (Day et al. 2009; Hill et al. 2011).

The lichen decline was driven by that of the dominant species *U. antarctica*, while many other sub-dominant crustose lichens in this community did not respond significantly to the OTC treatment (Online Resource 2), indicating that not all lichens were vulnerable to these climate change scenarios. In addition, the initially less common *O. frigida* increased, as has also been reported in a long-term warming study in the Arctic (Wahren et al. 2005). *O. frigida* typically can be found overgrowing dead mosses and lichens, and its increase may at least in part be in response to the high mortality of *U. antarctica*. The experimental manipulation remained in place year-round, typically resulting on average in temperature increases of less than 1.0 °C. These changes are well within the current annual temperature variation for these Antarctic lichens and should therefore not provide a problem for their survival. However, maximum short-term temperatures (i.e. extreme events) have been reported to increase in OTCs (Bokhorst et al. 2011), which could have negatively affected the physiology of lichens (Schroeter et al. 1995). Furthermore, some drying of the soil was also measured inside the OTCs which, although often not reaching significance, could have placed additional restrictions upon the already limited water supply for their contained terrestrial communities (Kennedy 1993; Convey et al. 2014). In addition, the 16 % decline of *U. antarctica* observed in

Table 4 Abundance (ind. × 1000 m^{-2}) of microarthropods following 10 years' manipulation using OTCs

	Lichen community		Moss community	
	C	OTC	C	OTC
Collembola				
Cryptopygus antarcticus	16.6 (6.6)	22.2 (5.9)	34.9 (9.2)	19.3 (5.6)
Folsomotoma octooculata	1.8 (0.5) a	0.5 (0.2) b	0.0	0.0
Acari				
Prostigmata	0.3 (0.1)	0.6 (0.2)	0.6 (0.2)	2.4 (1.4)
Stereotydeus villosus	0.1 (0.1)	0.6 (0.2)	0.0	0.04 (0.04)
Alaskozetes antarcticus	0.1 (0.1)	0.0	0.0	0.0
Gamasellus racovitzai	0.4 (0.3)	0.5 (0.2)	0.2 (0.1)	0.3 (0.1)

Significant ($P < 0.05$) differences between treatments are indicated by different letters. Values are mean of $n = 6$ with SE between brackets. *C* control, *OTC* open-top chamber

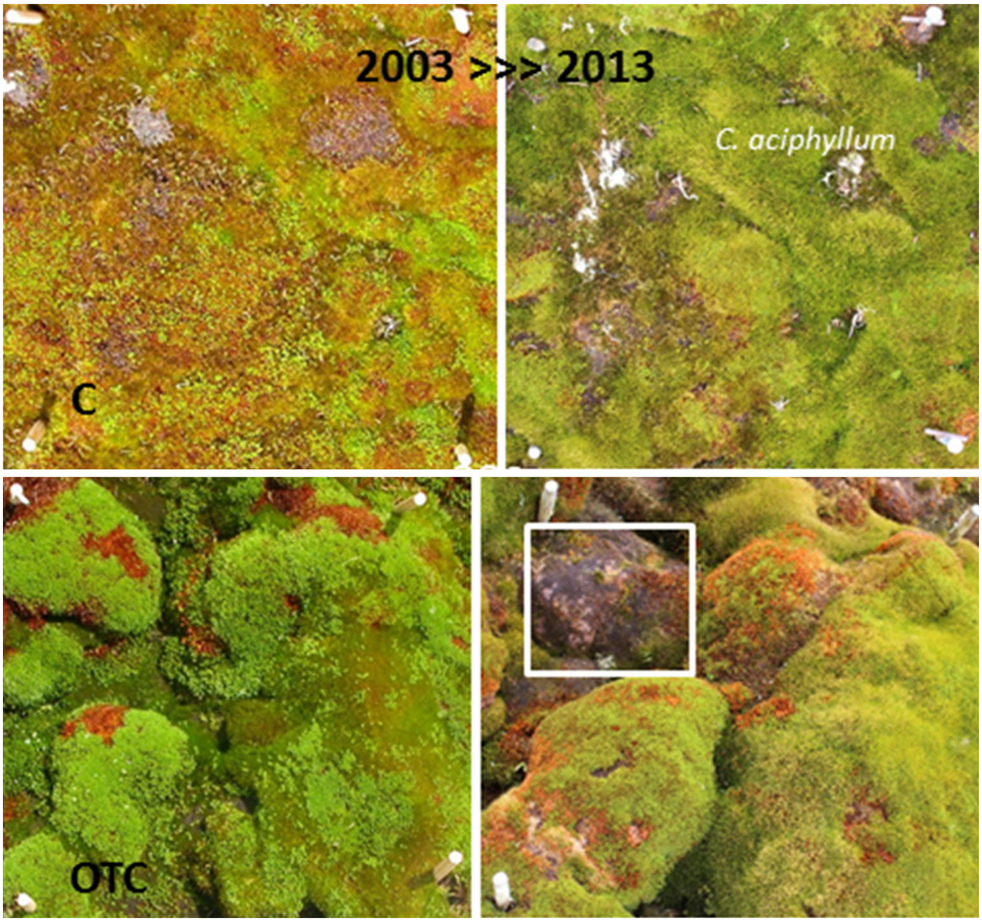

Fig. 4 Shifts in the moss community on Signy Island between 2003 and 2013. The *top photograph* shows the decline of *P. strictum*, while *C. aciphyllum* remains dominant in the control plots. The *lower pictures* show the invasion of the liverwort *Cephaloziella varians* (*white square* of the *lower right figure*) in an OTC where previously *P. strictum* was growing. Although this only occurred in one OTC, it indicates the start of a community shift. The distance between the wooden pegs is 30 cm

the control plots may indicate that conditions are already becoming unfavourable for this lichen on Signy Island.

Although the warming achieved with the OTCs was on average not particularly high, it was most apparent during winter due to thicker snow insulation inside the OTCs (as confirmed by the much lower PAR values during this period), reduction in freeze–thaw cycles and the loss of deep-freezing temperatures (Bokhorst et al. 2011). Therefore, changes in the winter temperature and light regime due to snow accumulation were the most likely cause underlying the observed lichen decline inside the OTCs. Similar lichen declines have been reported in several Arctic studies, particularly in those that led to alterations in snow regimes (Benedict 1990, 1991; Wahren et al. 2005). The assumed underlying cause of these declines is the depletion of stored carbon through increased winter respiration (Benedict 1991; Kappen 2000), itself resulting from the increased insulation and higher temperatures provided by the deeper snow pack (Kappen 1993). Therefore, it is possible that the same mechanism, carbon depletion due to increased winter respiration, also affected *U. antarctica* inside the OTCs, a proposition which is supported by the CO_2 calculations.

Carbon budget of *U. antarctica* under climate warming

In support of Hypothesis 2, there was a potential negative carbon balance for *U. antarctica* based on the calculated CO_2 flux rates. The differences in carbon balance of *U. antarctica* between OTCs and control plots were primarily driven by increased winter respiration rates (11 %), themselves most likely a direct result of the higher winter temperatures in combination with lower light levels (Schroeter et al. 1995) due to the build-up of a thicker snow pack inside OTCs (Bokhorst et al. 2013). In addition, the decrease in growing season photosynthetic rates, although small, reduced the total carbon uptake. These combined effects resulted in a lower net carbon uptake and for some years a negative carbon balance for *U. antarctica* inside the OTCs. Furthermore, the lower photosynthetic rates may have been a consequence of the lichen mycobiont parasitising the photobiont as stored carbon became depleted, as suggested by (Gannutz 1970). Some evidence for deterioration of the photobiont was observed in 2005 when *U. antarctica* thalli showed a reduction (42 %) in chlorophyll content inside the OTCs compared to control plots (Bokhorst et al. 2012), indicating that it was performing poorly, as would be consistent with parasitisation by the mycobiont. The calculated CO_2 flux rates here were much lower compared to the maximum potential rate identified by Schroeter et al. (1995) (323 mg CO_2 g^{-1} dw $year^{-1}$) and reflect the limitation of carbon uptake by the infrequent occurrence of precipitation for lichen hydration in our calculations. Although Antarctic lichens can withstand particularly harsh climatic conditions, the OTC treatment appears to greatly affect the performance of *U. antarctica* through relative minor changes in temperature, light availability and water availability during different parts of the year, indicating that some Antarctic lichens may be very vulnerable to season-specific climatic changes.

Micro-arthropod response to OTC manipulation

The micro-arthropod communities were little affected by our climate manipulations. Neither the most dominant springtail in this ecosystem, *C. antarcticus* (Bokhorst et al. 2008), nor any of the mite species, showed any detectable response to the 10-year manipulation. However, the significant decline in numbers of the less common springtail *F. octooculata* in the lichen OTCs may provide some support for Hypothesis 3. These findings are inconsistent with the previously reported declines of *C. antarcticus* in various passive warming treatments as a result of desiccation (Convey et al. 2002) or the increased abundance observed under summer warming with water additions (Day et al. 2009). The limited response in our OTCs used on Signy Island indicates that the climate manipulations were not strong enough to have an impact on the micro-arthropod community, indicating that this group of invertebrates appears relatively resistant. Initial declines in *C. antarcticus* abundance following 2 years of warming in these OTCs (Bokhorst et al. 2008) may therefore be an example of an artefactual response, or there may be inter-annual variation in the micro-arthropod response depending on the ambient temperature and moisture conditions experienced. The latter explanation would suggest that the micro-climate of the OTCs was only capable of affecting these organisms during unfavourable ambient weather conditions, resulting in abundance declines from which the population could recover during better years. The lack of response by the micro-arthropod community to the massive decline in *U. antarctica* suggests that the species involved either do not depend on this lichen for food (Bokhorst et al. 2007b), or were not limited by food availability despite the decline (Davis 1981). It may also be possible that micro-arthropods could benefit from the increase in the lichen *O. frigida*. Overall, the minimal responses identified here in either the moss community or the micro-arthropods of both vegetation communities suggest that both these important elements of Antarctic terrestrial ecosystems have considerable resistance to changes in abiotic and biotic conditions under current change scenarios.

In conclusion, the regionally important lichen *U. antarctica* appears very sensitive to changes in winter snow depth and associated alterations in light levels and temperature regime. As climate change is likely to affect the precipitation patterns along the Antarctic Peninsula, *U. antarctica* dominated fell-field communities may drastically change in floristic composition during the coming decades.

Acknowledgments We are very grateful for the logistical support provided by the British Antarctic Survey. We thank Mark van de Wouw and Simon Hernimon for their help in establishing this experiment in the field. Special thanks to Roger Worland for managing the micro-climate logging system for many years in our absence. This study was initiated through financial support by the Netherlands Polar Programme (NPP-NWO 851.20.016), and SB was supported by an Antarctic Science Bursary for the 2013/2014 field season. PC is supported by NERC funding to the BAS core ‘Biodiversity, Evolution and Adaptation programme’. This work also forms an output of the SCAR programme ‘State of the Antarctic Ecosystem’.

References

Benedict JB (1990) Experiments on lichen growth 1. Seasonal patterns and environmental controls. Arctic Alp Res 22:244–254

Benedict JB (1991) Experiments on lichen growth 2. Effects of a seasonal snow cover. Arctic Alp Res 23:189–199

Berg A, Gunnarsson B, Ostlund L (2011) ‘At this point, the lichens in the trees are their only means of survival’: a history of tree cutting for winter reindeer fodder by Sami people in Northern Sweden. Environ Hist 17:265–289

Bjerke JW, Bokhorst S, Zielke M, Callaghan TV, Bowles FW, Phoenix GK (2011) Contrasting sensitivity to extreme winter warming events of dominant sub-Arctic heathland bryophyte and lichen species. J Ecol 99:1481–1488

Bokhorst S, Huiskes A, Convey P, Aerts R (2007a) The effect of environmental change on vascular plant and cryptogam communities from the Falkland Islands and the Maritime Antarctic. BMC Ecol. doi:10.1186/1472-6785-7-15

Bokhorst S, Ronfort C, Huiskes A, Convey P, Aerts R (2007b) Food choice of Antarctic soil arthropods clarified by stable isotope signatures. Polar Biol 30:983–990

Bokhorst S, Huiskes AHL, Convey P, Bodegom PMv, Aerts R (2008) Climate change effects on soil arthropod communities from the Falkland Islands and the Maritime Antarctic. Soil Biol Biochem 40:1547–1556

Bokhorst S, Huiskes AHL, Convey P, Sinclair BJ, Lebouvier M, van de Vijver B, Wall DH (2011) Microclimate impacts of passive warming methods in Antarctica: implications for climate change studies. Polar Biol 34:1421–1435

Bokhorst S, Bjerke JW, Tømmervik H, Preece C, Phoenix GK (2012) Ecosystem response to climatic change: the importance of the cold season. Ambio 41:246–255

Bokhorst S, Huiskes AHL, Aerts R, Convey P, Cooper EJ, Dalen L, Erschbamer B, Gudmundsson J, Hofgaard A, Hollister RD, Johnstone JF, Jonsdottir IS, Lebouvier M, Van de Vijver B, Wahren C-H, Dorrepaal E (2013) Variable temperature effects of Open Top Chambers at polar and alpine sites explained by irradiance and snow depth. Glob Change Biol 19:64–74

Bokhorst S, Wardle DA, Nilsson M-C, Gundale MJ (2014) Impact of understory mosses and dwarf shrubs on soil micro-arthropods in a boreal forest chronosequence. Plant Soil 379:121–133

Bokhorst S, Asplund J, Kardol P, Wardle AD (2015) Lichen physiological traits and growth forms affect communities of associated invertebrates. Ecology 96:2394–2407

Collins NJ (1976) Growth and population dynamics of the moss *Polytrichum alpestre* in the maritime Antarctic. Oikos 27:389–401

Convey P (2013) Antarctic ecosystems. In: Levin SA (ed) Encyclopedia of biodiversity, vol 1. Elsevier, Waltham, pp 179–188

Convey P, Pugh PJA, Jackson C, Murray AW, Ruhland CT, Xiong FS, Day TA (2002) Response of Antarctic terrestrial microarthropods to long-term climate manipulations. Ecology 83:3130–3140

Convey P, Chown SL, Clarke A, Barnes DKA, Bokhorst S, Cummings V, Ducklow HW, Frati F, Green TGA, Gordon S, Griffiths HJ, Howard-Williams C, Huiskes AHL, Laybourn-Parry J, Lyons WB, McMinn A, Morley SA, Peck LS, Quesada A, Robinson SA, Schiaparelli S, Wall DH (2014) The spatial structure of Antarctic biodiversity. Ecol Monogr 84:203–244

Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik DS, Hobbie SE, Press MC, Robinson CH, Henry GHR, Shaver GR, Phoenix GK, Jones DG, Jonasson S, Chapin FS, Molau U, Neill C, Lee JA, Melillo JM, Sveinbjornsson B, Aerts R (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? J Ecol 89:984–994

Cornelissen JHC, Lang SI, Soudzilovskaia NA, During HJ (2007) Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. Ann Bot 99:987–1001

Davis RC (1981) Structure and function of two Antarctic terrestrial moss communities. Ecol Monogr 51:125–143

Day TA, Ruhland CT, Strauss SL, Park JH, Krieg ML, Krna MA, Bryant DM (2009) Response of plants and the dominant microarthropod, *Cryptopygus antarcticus*, to warming and contrasting precipitation regimes in Antarctic tundra. Glob Change Biol 15:1640–1651

Fowbert JA, Smith RIL (1994) Rapid population increases in native vascular plants in the Argentine Islands, Antarctic Peninsula. Arctic Alp Res 26:290–296

Gannutz TP (1970) Photosynthesis and respiration of plants in the Antarctic Peninsula area. Antarct J 5:49–52

Gerson U, Seaward MRD (1977) Lichen-invertebrate associations. In: Seaward MRD (ed) Lichen ecology. Academic Press, London, pp 69–119

Grobe CW, Ruhland CT, Day TA (1997) A new population of *Colobanthus quitensis* near Arthur Harbor, Antarctica: correlating recruitment with warmer summer temperatures. Arctic Alp Res 29:217–221

Hill PW, Farrar J, Roberts P, Farrell M, Grant H, Newsham KK, Hopkins DW, Bardgett RD, Jones DL (2011) Vascular plant success in a warming Antarctic may be due to efficient nitrogen acquisition. Nat Clim Change 1:50–53

Kappen L (1993) Plant activity under snow and ice, with particular reference to lichens. Arctic 46:297–302

Kappen L (2000) Some aspects of the great success of lichens in Antarctica. Antarct Sci 12:314–324

Kappen L, Sommerkorn M, Schroeter B (1995) Carbon acquisition and water relations of lichens in polar regions—potentials and limitations. Lichenologist 27:531–545

Kennedy AD (1993) Water as a limiting factor in the Antarctic terrestrial environment—a biogeographical synthesis. Arctic Alp Res 25:308–315

Kennedy AD (1995) Simulated climate-change—are passive greenhouses a valid microcosm for testing biological effects of environmental perturbations. Glob Change Biol 1:29–42

Lang SI, Cornelissen JHC, Shaver GR, Ahrens M, Callaghan TV, Molau U, Ter Braak CJF, Hölzer A, Aerts R (2012) Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. Glob Change Biol 18:1096–1107

Lindo Z, Nilsson M-C, Gundale MJ (2013) Bryophyte-cyanobacteria associations as regulators of the northern latitude carbon balance in response to global change. Glob Change Biol 19:2022–2035

Lindsay DC (1973) Estimates of lichen growth rates in the Maritime Antarctic. Arctic Alp Res 5:341–346

Marion GM, Henry GHR, Freckman DW, Johnstone J, Jones G, Jones MH, Levesque E, Molau U, Molgaard P, Parsons AN, Svoboda J, Virginia RA (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. Glob Change Biol 3:20–32

Øvstedal DO, Smith RIL (2001) Lichens of Antarctica and South Georgia. University Press, Cambridge

Parnikoza I, Convey P, Dykyyz I, Trokhymets V, Milinevsky G, Tyschenko O, Inozemtseva D, Kozeretska I (2009) Current status of the Antarctic herb tundra formation in the Central Argentine Islands. Glob Change Biol 15:1685–1693

Royles J, Ogée J, Wingate L, Hodgson DA, Convey P, Griffiths H (2012) Carbon isotope evidence for recent climate-related enhancement of CO_2 assimilation and peat accumulation rates in Antarctica. Glob Change Biol 18:3112–3124

Royles J, Amesbury MJ, Convey P, Griffiths H, Hodgson DA, Leng MJ, Charman DJ (2013) Plants and soil microbes respond to recent warming on the Antarctic Peninsula. Curr Biol 23:1702–1706

Salmane I, Brumelis G (2008) The importance of the moss layer in sustaining biological diversity of Gamasina mites in coniferous forest soil. Pedobiologia 52:69–76

Schroeter B, Scheidegger C (1995) Water relations in lichens at subzero temperatures—structural changes and carbon dioxide exchange in the lichen *Umbilicaria aprina* from continental Antarctica. New Phytol 131:273–285

Schroeter B, Olech M, Kappen L, Heitland W (1995) Ecophysiological investigations of *Usnea antarctica* in the Maritime Antarctic. 1. Annual microclimatic conditions and potential primary production. Antarct Sci 7:251–260

Schroeter B, Kappen L, Green TGA, Seppelt RD (1997) Lichens and the Antarctic environment: effects of temperature and water availability on photosynthesis. In: Lyons WB, Howard-Williams C, Hawes I (eds) Ecosystem processes in Antarctic ice-free landscapes. Balkema Publishers, Rotterdam, A.A, pp 103–117

Schroeter B, Green TGA, Pannewitz S, Schlensog M, Sancho LG (2010) Fourteen degrees of latitude and a continent apart: comparison of lichen activity over two years at continental and maritime Antarctic sites. Antarct Sci 22:681–690

Thomas ER, Marshall GJ, Mcconnell JR (2008) A doubling in snow accumulation in the western Antarctic Peninsula since 1850. Geophys Res Lett. doi:10.1029/2007GLO32529

Torres-Mellado GA, Casanova-Katny MA (2011) Antarctic hairgrass expansion in the South Shetland archipelago and Antarctic Peninsula revisited. Polar Biol 34:1679–1688

Turner J, Bindschadler R, Convey P, di Prisco G, Fahrbach E, Gutt J, Hodgson D, Mayewski P, Summerhayes C (2009) Antarctic climate change and the environment. Scientific Committee on Antarctic Research. Victoire Press, Cambridge

Turner J, Barrand NE, Bracegirdle TJ, Convey P, Hodgson DA, Jarvis M, Jenkins A, Marshall GJ, Meredith MP, Roscoe H, Shanklin J (2013) Antarctic climate change and the environment: an update. Polar Rec 50:237–259

Wahren CHA, Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and a winter snow manipulation experiment. Glob Change Biol 11:537–552

Walton DWH (1982) The Signy Island terrestrial reference sites: XV. Micro-climate monitoring, 1972–1974. Br Antarct Surv B 55:111–126

Webb NR, Coulson SJ, Hodkinson ID, Block W, Bale JS, Strathdee AT (1998) The effects of experimental temperature elevation on populations of cryptostigmatic mites in high Arctic soils. Pedobiologia 42:298–308