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The biology and ecology of the liverwort *Cephaloziella varians* in Antarctica

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Abstract: The biology and ecology of *Cephaloziella varians*, the most widespread and abundant liverwort in Antarctica, are reviewed. A description of the species is given, together with information on its geographical distribution, reproduction, habitats, associated organisms and responses to environmental stresses. Characteristics of its photosynthetic physiology are also presented, including data on oxygen evolution rates and chlorophyll *a* fluorescence parameters. Substratum and tissue chemistry, water relations and pigments are discussed, along with recent data demonstrating that the dark pigment in the apical leaves of *C. varians* is the anthocyanidin riccionidin A. Recent studies showing that the ericoid mycorrhizal symbiont *Rhizoscyphus ericae* is present in the tissues of the plant at a wide range of locations in the maritime and sub-Antarctic are also described. It is evident, from the literature reviewed, that *C. varians* has several adaptations that enable it to survive in the Antarctic biome, explaining its survival at higher latitudes than any other hepatic. The species' major adaptations include the synthesis of riccionidin A in apical leaves, enabling efficient heat absorption and protection from photoinhibition, and the presence in stems and rhizoids of fungal hyphae, which are potentially beneficial to the hepatic's nutrition and possibly also synthesize cryoprotectants.

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Introduction

Of the 27 species of liverwort that are known from Antarctica, only one, the leafy liverwort *Cephaloziella varians* (Gottsche) Steph., occurs in the continental Antarctic (Bednarek-Ochyra *et al*. 2000). This species, which is the commonest and most widespread liverwort in Antarctica, is the only hepatic to occur at latitudes above 70°S. Only 22 native species of moss, and no higher plant species, have been recorded beyond this latitude (Ochyra *et al*. 2008). Terrestrial habitats beyond 70°S present some of the most hostile conditions for plant life on Earth, including very low winter temperatures, extended periods of ice- and snow-cover and darkness, extreme aridity, wide diurnal and annual variations in temperature and solar radiation exposure, and, in summer, frequent freeze-thaw cycles. However, despite the occurrence of *C. varians* in such extreme habitats, the reasons for its success in the Antarctic biome remain obscure.

This article has two aims. The first is to collate the available information from the literature on *C. varians*. A description of the hepatic and its reproduction is given, together with information on the habitats in which it occurs, its photosynthesis, pigments, water relations, responses to changing environmental conditions and its associated organisms. The second aim of the article is to attempt to identify the adaptations that have led to the success of *C. varians* in the Antarctic terrestrial biome.

The format of this paper is based upon that of the *Biological Flora of the British Isles* series published in *Journal of Ecology*, initiated by the late Professor Arthur Willis of the University of Sheffield.

Geographical distribution

Cephaloziella varians occurs in the sub-, northern and southern maritime and continental Antarctic (Fig. 1a). Geographical definitions of each of these four regions are given in Table I. The species is widespread throughout the sub- and maritime Antarctic, occurring at Heard Island, South Georgia, Bouvetøya and the South Sandwich, South Orkney and South Shetland islands, and along the western Antarctic Peninsula to the eastern coast of Alexander Island (Fig. 1a & b). It is the only hepatic known from continental Antarctica, where it occurs at coastal locations in Victoria, Wilkes, Princess Elizabeth and Mac Robertson lands (Fig. 1a). Its southernmost known location is at 77°S, at Granite Harbour in Botany Bay, Victoria Land (Seppelt & Green 1998). The species usually occurs within 2 km of the coast and at low (< 350 m) altitudes, although it is present on Mount Melbourne in the continental Antarctic on heated ground at an altitude of 2700 m (Smith 2007). For the precise locations of *C. varians* collections from the Antarctic, see Ochyra & Váňa (1989a, 1989b) and Bednarek-Ochyra *et al*. (2000).

Outside Antarctica, *C. varians* is present in mountainous regions, including the Alps, Pyrenees and Carpathians ranges, and in New Zealand, Alaska, Canada, Greenland, Sweden, Iceland and the Russian Arctic (Schuster & Damsholt 1974, Schljakov 1979, Söderström 1995, Konstantinova & Potemkin

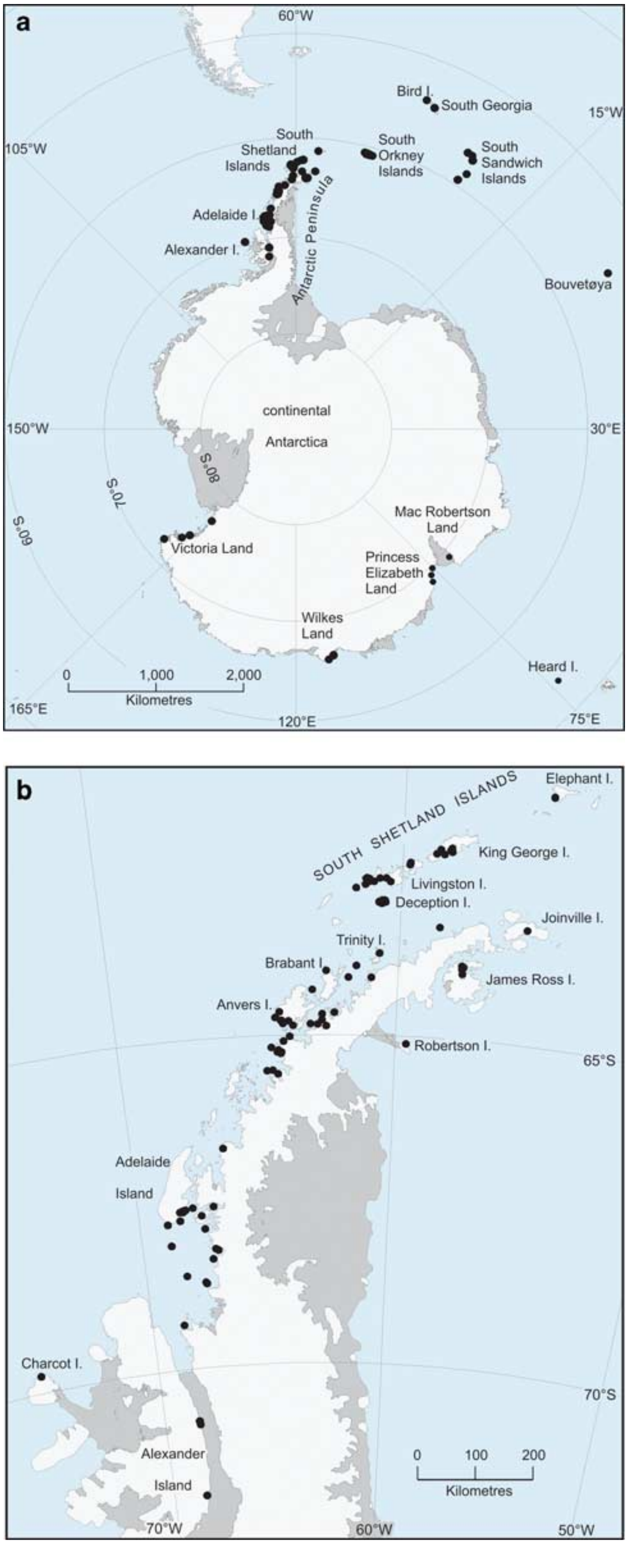

Fig. 1. The distribution of *Cephaloziella varians* in **a.** sub-, maritime and continental Antarctica, and **b.** the South Shetland Islands and Antarctic Peninsula. Data from the Antarctic Plant Database (http://www.antarctica.ac.uk/Resources/BSD/PlantDatabase/) and Bednarek-Ochyra *et al.* (2000).

1996, Bednarek-Ochyra *et al.* 2000). It is frequently recorded in the Arctic as *C. arctica*, which is considered to be synonymous with *C. varians* (Ochyra & Váňa 1989a). In agreement with this, Ochyra & Váňa (1989b) note that *C. varians*, together with four other Antarctic hepatics (*Anthelia juratzkana* (Limpr.) Trevis., *Barbilophozia hatcheri* (Evans) Loeske, *Lophozia excisa* (Dicks.) Dumort. and *Scapania obcordata* (Berggr.) Arnell), belongs to a bipolar floristic element. They note that these taxa may have attained their southern range by long-range dispersal, rather than by fragmentation of their original ranges.

Species description

A detailed description of the species is given by Bednarek-Ochyra *et al.* (2000), from which much of the following is derived. Plants very small and delicate, with stems 2–8 (-12) mm in length, usually creeping or semi-erect and sparsely or lateral-intercalary branched. Leaves 100–250 µm in length, plane or concave, barely overlapping, typically 1.5–2 times as wide as the stem, transversely or subtransversely inserted, distinctively bilobed to 0.5–0.7 of length (Fig. 2a & b). Lobes ovate to ovate-triangular, erect or incurved and 6–10 cells wide at their base. Leaf cell dimensions *c.* 12–15 × 10–13 µm. Leaves and stems smooth. Rhizoids hyaline, typically occurring at base of stem. Oil bodies frequent in cells (Post & Vesk 1992).

Leaves and stems slightly lustrous, especially in damp locations, and exceptionally variable in colour, ranging from deep violet to black, brown-green, green and yellow-green (Seppelt & Green 1998, Bednarek-Ochyra *et al.* 2000, Newsham *et al.* 2005). Considerable variation in pigmentation can occur within a given location: sun-exposed plants are deeply-pigmented (Fig. 2a), but plants growing in shaded habitats are uniformly green (Fig. 2b). Observations suggest that deeply-pigmented plants in the maritime Antarctic typically occur in unshaded habitats at the southern end of the species' range (Bednarek-Ochyra *et al.* 2000, Newsham *et al.* 2005), possibly reflecting the more continental climate in this region, which is typified by extended periods of cloudless skies during summer (see *Effects of solar radiation*, below).

Reproduction

Autoecious or pseudodioecious. Male inflorescence terminal, becoming intercalary, bracts imbricate, monandrous and saccate at base, in 4–10 pairs. Female inflorescences on elongated shoots, bracts broadly ovate, and bracteoles, which are smaller than bracts, mostly bilobed. Perianths obloid to obloid-clavate, formed by thick-walled rectangular cells in the apical region. Capsule ovoid-elliptical, rounded at apices with bistratose walls. Epidermal cells of capsule with nodular thickenings and inner cells with semi-annular narrow bands. Spores 9–12 µm in diameter, delicately verruculose (Bednarek-Ochyra *et al.* 2000, Smith & Convey 2002).

Table I. Regions of Antarctica in which *C. varians* occurs and their climates. Adapted from Smith (1984).

Region	Localities	Climate
sub-Antarctic	South Georgia, Bird and Heard islands	cool oceanic climate, annual mean air temperature > 0°C, mean monthly air temperatures > 0°C for at least six months, coldest monthly mean air temperature rarely < -2°C, precipitation > 900 mm per annum
northern maritime Antarctic	Bouvetøya, South Sandwich, South Orkney and South Shetland islands, western Antarctic Peninsula and offshore islands to 66°S	cold moist maritime climate, mean monthly air temperature > 0°C for 3–4 months, rarely < -10°C in winter, precipitation 350–500 mm per annum, with much falling as rain during summer
southern maritime Antarctic	western Antarctic Peninsula and offshore islands from 66°S to 72°S and north-east coast of Peninsula to 63°S	cold dry maritime climate, mean monthly air temperature > 0°C for 1–2 months, rarely < -15°C in winter, precipitation < 350 mm per annum, with only occasional rain
coastal continental Antarctic	coastal regions of Greater Antarctica	cold, arid climate with mean monthly air temperatures > 0°C for 0–1 months, winter mean air temperature of between -5 and -25°C, precipitation 100–150 mm, but rain very rare

Elaters free, bispiral and 7–8 μm in diameter. Gemmae two-celled, 15–25 μm in length, 10–15 μm in width (Fig. 2a, inset), borne on the margins of leaves and formed frequently in the natural environment. Vegetative reproduction also by branch fragmentation (Seppelt & Green 1998).

Although the species is almost entirely sterile in the Antarctic natural environment, sporophytes have been observed in populations on the South Shetland Islands, in the Marguerite Bay region and on Alexander Island in the southern maritime Antarctic since the mid 1990s, possibly as a consequence of climate warming in the maritime Antarctic (Smith & Convey 2002). Mean spore counts per capsule from these locations are 23 750 and 14 000, respectively. Sporophytes are also occasionally found on plants in geothermally-heated habitats in the South Sandwich Islands (Convey *et al*. 2000).

Chromosomes $n = 18$ $(16 + 2\,\mathrm{m})$, based on material from South Georgia and King George Island (Newton 1980, Ochyra *et al*. 1982). The smallest of the nine pairs of chromosomes are unique in being composed of two unequal m-chromosomes (Newton 1980).

History

Cephaloziella varians was originally described as *Jungermannia varians* by Gottsche (1890) from material collected by H. Will at South Georgia during the German Polar Year Expedition in 1882–83. It was later assigned to *Cephalozia varians* by Stephani (1901), based on material from the Gerlache Strait collected by E. Racovitza of the Belgian Antarctic Expedition in 1897–99. Stephani (1905) subsequently assigned the species to *Cephaloziella varians*.

Taxonomic placement

There is considerable phenotypic plasticity between populations of *C. varians* from different locations in the Antarctic, which has led to the elevation of several different names for the taxon from the biome (e.g. Grolle 1972,

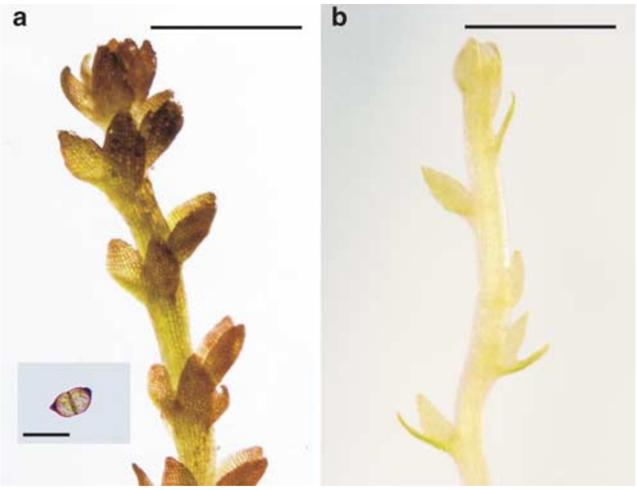

Fig. 2. Micrographs of **a.** sun-exposed, and **b.** shade-adapted forms of *Cephaloziella varians*. Bars are 500 μm. Inset in **a.** is a gemma. Bar in inset is 25 μm. Material collected from Léonie Island, Ryder Bay, south-western Antarctic Peninsula.

Fig. 3. A darkly pigmented colony of sun-exposed *Cephaloziella varians* growing amongst shoots of the moss *Sanionia uncinata* at Rothera Point on Adelaide Island. The colony is *c.* 100 mm in width.

Table II. pH and organic matter content of substrata on which *C. varians* occurs at a range of maritime and sub-Antarctic locations. Data are means of 5–8 replicates ± SD.

Location	Latitude and longitude	pH (H_2O)	organic matter (%)[1]
Schlieper Bay, South Georgia	54°00'S, 38°04'W	4.917 ± 0.387	94.39 ± 0.78
Foca Point, Signy Island[2]	60°42'S, 45°39'W	5.866 ± 0.398	90.05 ± 2.40
Factory Bluffs, Signy Island[2]	60°43'S, 45°36'W	5.046 ± 0.154	93.59 ± 1.59
Rothera Point, Adelaide Island	67°34'S, 68°07'W	5.346 ± 0.098	94.73 ± 0.66
Ablation Valley, Alexander Island	70°55'S, 68°20'W	6.467 ± 0.218	34.49 ± 9.21
Moutonnée Valley, Alexander Island	70°55'S, 68°20'W	6.880 ± 0.085	23.68 ± 5.93

[1] 550°C for 2 h, [2] South Orkney Islands

Schuster & Damsholt 1974, Fulford 1976, Schuster 1980). The species has frequently been referred to in the literature as *Cephaloziella exiliflora* (Tayl.) Steph. (e.g. Seppelt 1983, Williams *et al*. 1994, Seppelt & Green 1998), but it is now accepted that all Antarctic *Cephaloziella* should be referred to *C. varians*, with *C. exiliflora*, a distinct species with larger leaves, vestigial underleaves and red-brown pigmentation, being restricted to Australasia (Ochyra & Váňa 1989a, Bednarek-Ochyra *et al*. 2000).

Nucleotide sequence data for a specimen of *C. varians* from New Zealand are deposited in GenBank under accession numbers AY608222, DQ439689, AY608074 and AY607953 (Davis 2004, Forrest *et al*. 2006). These nucleotide sequences are of 26S large subunit ribosomal RNA, the ribulose biphosphate carboxylase (*rbc*L), small ribosomal protein (*rps*4) and the CD122 photosystem II 32 kDa protein (*psb*A) genes, respectively. Based on these data, Forrest *et al*. (2006) place *C. varians* in a clade of leafy liverworts including *C. hirta* Schuster and species of *Cephalozia*, *Stenorrhipis*, *Scapania*, *Diplophyllum*, *Tritomaria*, *Anastrophyllum,* *Tetralophozia*, *Herzogobryum*, *Nowellia*, *Schiffneria*, *Odontoschisma* and *Adelanthus*.

Microhabitat

Substratum

Cephaloziella varians forms dense compact mats (Fig. 3), often of a few square metres in area, on the surface of moribund mosses, or more usually intertwined with the shoots of other bryophytes. The species occurs predominantly in moist to wet habitats, normally on acidic substrata with pH values of 4.9–6.9 (Table II). Davis (1986), Wynn-Williams (1988) and Smith (1990) similarly report pH values of 4.8–5.1 for mixed bryophyte communities in which *C. varians* occurs on Signy Island in the South Orkney Islands, at Rothera Point on Adelaide Island and on Bailey Peninsula in Wilkes Land, continental Antarctica. However, the species also occurs on more alkaline soils, such as those derived from marble on Signy Island, with pH values of up to 8.2 (Smith 1972). The substrata on which *C. varians* occurs are variable in their organic matter content, with between 24% and 95% loss on ignition (LOI) for material from Bird Island to Moutonnée Valley on Alexander Island, with more mineral substrata being encountered at more southerly locations (Table II). Roser *et al*. (1992) and Melick & Seppelt (1992) report 95% and 88% LOI for the substratum under *C. varians* from Bailey Peninsula, whilst Wynn-Williams (1988) reports 91% and 87% LOI for peat under *C. varians* at Signy and Adelaide Islands, respectively. LOI values of between 3.3% and 96.4% are reported by Smith (1972) for soils on which *C. varians* occurs at Signy Island. *Cephaloziella varians* is also present on geothermally-heated ground, where soil surface temperatures reach 25–35°C, on Mount Melbourne in Victoria Land, on Deception Island, and on Leskov, Visokoi, Candlemas

Table III. Extractable elements (mg 100 g^{-1} dry weight) in substrata on which *C. varians* occurs. Data for Factory Bluffs and the Bailey Peninsula are means of 5–7 replicates ± SD. Other data are single measurements.

Location	Latitude and longitude	Element						
		Na	K	Ca	Mg	P	NO_3-N	NH_4-N
Factory Bluffs, Signy Island[1]	60°43'S, 45°36'W	16 ± 14	10 ± 6	30 ± 24	19 ± 14	10 ± 1	2.0 ± 3.7	1 ± 1
Gourlay Peninsula, Signy Island[1]	60°44'S, 45°35'W	-	23	60	-	20	0.5	61
Uruguay Island[2]	65°14'S, 64°14'W	50	35	88	140	9	< 0.1	10
Cape Tuxen[2]	65°16'S, 64°08'W	32	38	100	100	13	< 0.1	24
Bailey Peninsula, Wilkes Land	66°17'S, 100°32'E	19 ± 7	20 ± 9	123 ± 48	80 ± 38	21 ± 21	0.11 ± 0.11	6 ± 5
Rothera Point, Adelaide Island	67°34'S, 68°07'W	50	120	220	180	9.5	2.3	53
Jenny Island[2]	67°44'S, 68°23'W	75	19	150	110	8	< 0.1	7
Lagotellerie Island[2]	67°53'S, 67°24'W	73	18	490	190	14	1.0	2
Refuge Islands (largest)[2]	68°21'S, 67°10'W	27	44	180	60	12	< 0.1	52

Data, which were all analysed by the same analytical chemistry facility, are from Holdgate *et al*. (1967), Wynn-Williams (1988) and Smith (1990, 1996). [1] South Orkney Islands. [2] Sites for which soil chemical data are reported by Smith (1996) for *Polytrichum strictum*, *Sanionia uncinata* and *Bryum pseudotriquetrum*/*Brachythecium austrosalebrosum*, but at which *C. varians* also occurs (R.I.L. Smith, personal communication 2009). Dashes indicate missing data.

Fig. 4. *Cephaloziella varians* growing in meltwater channels with mixed mosses on the north-facing slopes of Moutonnée Valley on Alexander Island (71°S), close to the southernmost limit of the species' range in the maritime Antarctic.

and Bellingshausen islands in the South Sandwich Islands (Longton & Holdgate 1979, Broady *et al*. 1987, Convey *et al*. 2000, Smith 2005, Convey & Smith 2006).

Concentrations of extractable elements in substrata on which *C. varians* occurs are highly variable (Table III), and, in broad terms, not limiting for plant growth (Allen 1989). For the nine locations for which data are available, moderate to high concentrations of sodium, potassium, calcium, magnesium, phosphorus and ammonium have been recorded in soil on which the species occurs (Table III). Low concentrations of nitrate (< 0.2 mg 100 g^{-1} dry weight; Allen 1989) have been recorded in soil at five of the nine locations for which data are available (Table III).

Topography

Cephaloziella varians usually occurs on level or gently-sloping ground, commonly along rills, meltwater flushes, seepage channels and in sheltered depressions that are irrigated with meltwater during summer (Smith 1990, Bednarek-Ochyra *et al*. 2000). It often occurs on north-facing slopes, which are exposed to more solar radiation than south-facing areas, and where meltwater channels are more frequent (Fig. 4). The species is also found in drier habitats, such as on rock ledges or in crevices and fissures.

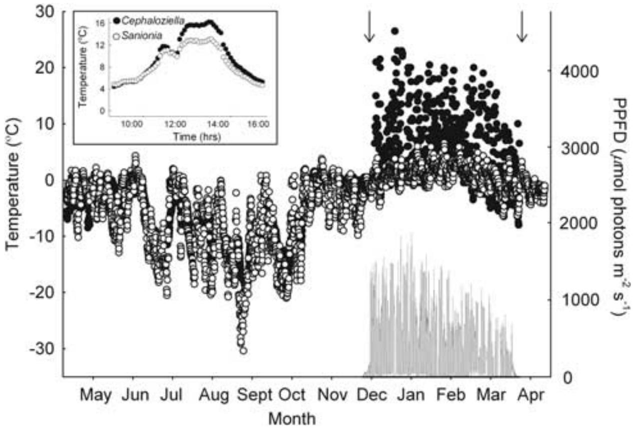

Fig. 5. Temperature of (●) sun-exposed *Cephaloziella varians* and (○) air (left axis) and (—) photosynthetic photon flux density (PPFD; right axis) between May 2006 and April 2007 at Rothera Point on Adelaide Island. Data were recorded every 3 h. Plant temperature was measured by button loggers (SL51 Smart Button Logger, Status Instruments, Tewkesbury, UK) inserted into mats and air temperature was measured in the shade by two platinum resistance thermometers (PT100; Labfacility Ltd., Teddington, UK). PPFD was measured with a Skye SKP 215 sensor (Skye Instruments Ltd., Llandrindod Wells, UK). Arrows mark the period when plants were free from snow and ice. *Inset* shows temperatures of sun-exposed *C. varians* and the moss *Sanionia uncinata* at Rothera Point between 09h00 and 16h00 on 27 November 1999. The two colonies were separated by *c*. 0.2 m.

Climate and plant temperature

Cephaloziella varians occurs in a wide range of Antarctic habitats, in which mean monthly air temperature can exceed freezing point for several months each year, but can fall to -25°C or below in winter (Table I). Precipitation in these environments varies widely between *c*. 100 mm and > 900 mm water equivalent per annum (Table I). Rainfall, particularly at more southerly latitudes, can be very rare, with any precipitation usually falling as snow. The temperature within a mat of *C. varians* varies widely, and often on a diurnal basis: at Rothera Point in the southern maritime Antarctic, mat temperature can reach 27°C at solar noon during the summer, and often exceeds air temperature by 20°C, but frequently falls to below freezing point at night (Fig. 5). After the first snowfalls of autumn, mat temperature declines to near freezing point, closely tracking air temperature, and can fall to -30°C during winter (Fig. 5). The high temperatures attained by sun-exposed shoots during the summer relative to air temperature are apparently due to their purple-black pigmentation, which enables efficient heat absorption: under clear skies, the temperature of *C. varians* mats can be up to 4°C higher than that of nearby *Sanionia uncinata* (Hedw.) Loeske shoots (Fig. 5, inset), which are light green in colour (Fig. 3).

Light environment

Cephaloziella varians experiences wide fluctuations in its light environment in the Antarctic. At Signy Island, the length of the growing season, when plants are not covered by snow and ice, is approximately six months (Wynn-Williams 1980), whereas at a more southerly site, Rothera Point, the season rarely lasts for more than four months. Plants at the latter site become covered with snow and ice

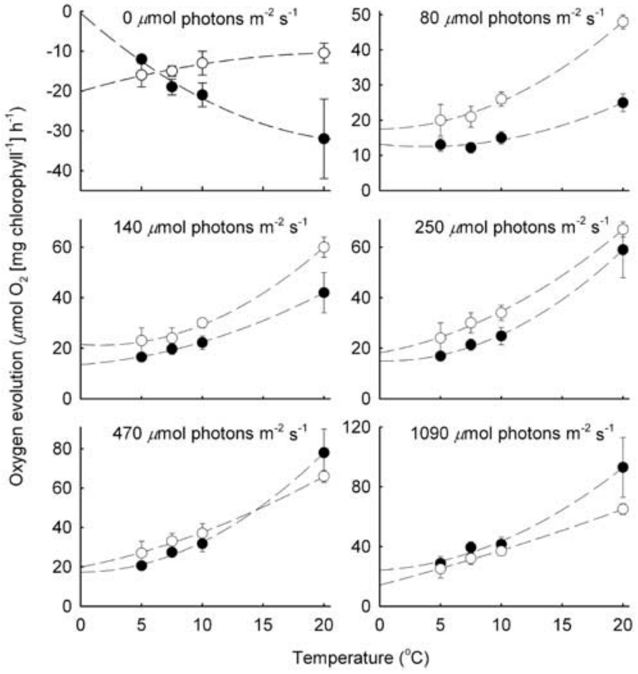

Fig. 6. Oxygen evolution of (●) sun-exposed and (○) shade-adapted forms of *Cephaloziella varians* as a function of temperature at irradiances of 0, 80, 140, 250, 470 and 1090 μmol photons $m^{-2}\,s^{-1}$. Data for 20°C are means of measurements for December and February from Post & Vesk (1992). All other data are from Snell *et al*. (2009). Bars are S.E.M.

in the autumn, with photosynthetic photon flux density (PPFD) incident on the mats falling to close to zero when the depth of snow over them exceeds *c*. 200 mm. This depth of snow is usually maintained for approximately eight months. Mild spells, when air temperatures can reach freezing point, do occur during winter (Fig. 5), but mats usually remain covered with snow and ice. In contrast, after snowmelt has occurred during the late spring, PPFD often reaches 1500 μmol photons $m^{-2}\,s^{-1}$ at solar noon (Fig. 5), and plants are exposed to almost continual daylight. However, low solar elevation angles during the early hours of the morning in the summer cause PPFD to fall to 20–40 μmol photons $m^{-2}\,s^{-1}$ (Snell *et al*. 2007).

The exposure of plants to UV-B radiation (280–315 nm) can also vary widely, both as a consequence of changes in solar elevation angles and, in recent decades, anthropogenic depletion of ozone in the stratosphere. The daily mean biologically effective dose of UV-B radiation in the southern maritime Antarctic during late spring and early summer, when plants emerge from melting snow and ice, is *c*. 3 kJ m^{-2} under undepleted ozone columns (*c*. 350 Dobson Units, DU). However, when depletion of the gas occurs in the stratosphere to 200 DU, the daily dose of biologically effective UV-B radiation to which plants are exposed can reach 10.3 kJ m^{-2} (Newsham *et al*. 2002), which is three fold higher than the mean dose of UV-B received by plants in the region in midsummer, when ozone depletion does not occur. *Cephaloziella varians* is able to respond rapidly to these changes in UV-B exposure (see *effects of solar radiation*, below).

Photosynthesis, fluorescence measurements and net primary production

For *C. varians* growing *in situ*, the maximum quantum yield of photochemistry (F_v/F_m) is 0.4–0.6 (Snell *et al*. 2007, 2009), although values of this parameter can fall to 0.1–0.2 (Newsham *et al*. 2002). Given that F_v/F_m values are typically 0.7–0.8 for most plant species growing under optimal conditions, the low values of this parameter indicate that *C. varians* is probably under constant physiological stress in the natural environment. Non-photosynthetic quenching (*qN*), derived from fluorescence measurements, is 0.02–0.05 for the sun-exposed form of *C. varians* but 0.17 for the shade form of the species, which is attributable to increased heat dissipation from chloroplasts in cells lacking dark pigmentation (Snell *et al*. 2009).

The shade-adapted and sun-exposed forms of *C. varians* also display different gas exchange characteristics. At low irradiances (80–250 μmol photons $m^{-2}\,s^{-1}$), the shade form of the species evolves significantly ($P < 0.05$) more oxygen than the sun-exposed form at temperatures of between 5°C and 20°C (Fig. 6). In contrast, at a temperature of 20°C and at higher irradiances (470–1090 μmol photons $m^{-2}\,s^{-1}$), the sun-exposed form evolves significantly ($P < 0.05$) more oxygen than the shade form (Fig. 6). Oxygen evolution of the shade form saturates at PPFD of 200–400 μmol photons $m^{-2}\,s^{-1}$, whereas that of the sun-exposed form apparently does not saturate at < 1090 μmol photons $m^{-2}\,s^{-1}$ (Post & Vesk 1992, Snell *et al*. 2009). Gas exchange of *C. varians* is closely and positively associated with temperature, with sun-exposed and shade forms evolving up to 93 and 65 μmol O_2 (mg chlorophyll^{-1}) h^{-1} at 20°C, respectively (Fig. 6). At present, the reduction in the dark respiration rate of sun-exposed *C. varians* at higher temperatures, and the lower dark respiration rate at 7.5–20°C of sun-exposed, compared with shade-adapted plants (Fig. 6), remain anomalous.

Davis (1981) gives estimates of net primary production for *C. varians* of between 58 and 98 g dry weight $m^{-2}\,yr^{-1}$ on Signy Island. However, these data should be regarded as approximations, as they are not based on empirical measurements.

Chloroplast ultrastructure

The chloroplasts of *C. varians* are spherical to slightly oval, and show little variation between different parts of the plant in size, shape or thylakoid content. Chloroplasts show marked differences between sun-exposed and shade-adapted forms of the species: in those of the former plants, the thylakoid system consists of sparsely-arranged elongated grana, usually comprising two or three thylakoids distributed evenly throughout the stroma. In those of shade-adapted plants, the thylakoid system is more extensive, with grana consisting of usually more than eight thylakoids (Post & Vesk 1992). Thylakoids occupy 19% and 39% of the total chloroplast volume in sun-exposed and shaded plants, respectively (Post & Vesk 1992).

Pigments

Chlorophylls

Roser *et al.* (1992) report a chlorophyll *a* concentration of 0.29 mg g^{-1} (fresh weight) in tissues of *C. varians* sampled from the Bailey Peninsula in Wilkes Land. Post & Vesk (1992) similarly report total chlorophyll (*a* and *b*) concentrations of 0.21 and 0.38 mg g^{-1} (fresh weight) respectively in the sun-exposed and shade-adapted forms of *C. varians* from the Clarke Peninsula, also in Wilkes Land. Similar values of 0.20 and 0.33 mg total chlorophyll g^{-1} (fresh weight) have been measured in sun-exposed and shade-adapted plants at Léonie Island in Ryder Bay, south-western Antarctic Peninsula, respectively (K.K. Newsham, unpublished data). Total chlorophyll concentrations in *C. varians* from Rothera Point of 1.2–3.3 mg g^{-1} (dry weight) are also reported by Newsham *et al.* (2005) and Snell *et al.* (2007, 2009). The chlorophyll *a*/*b* ratios of plants from sun-exposed and shaded habitats, which vary between 2.1 and 2.4, do not differ (Post & Vesk 1992, Snell *et al.* 2007).

Carotenoids

The concentration of total carotenoids in *C. varians* tissues typically varies between 0.15 and 0.45 mg g^{-1} (dry weight) (Newsham *et al.* 2002, Snell *et al.* 2007, 2009), with increased concentrations of carotenoids in plants exposed to high levels of solar radiation (see *Effects of solar radiation*, below). HPLC analyses indicate that lutein is the most abundant carotenoid in the tissues of *C. varians*, forming 76% of the total mass of carotenoids (Newsham *et al.* 2002). Neoxanthin, zeaxanthin, antheraxanthin, β,β-carotene and violaxanthin are also relatively common, forming 10.3, 8.0, 1.4, 0.6 and 0.5% of the total mass of carotenoids, respectively. The carotenoids α- and β,ε-carotene and their derivatives are present in *C. varians* tissues at low ($< 0.1\%$) concentrations (Newsham *et al.* 2002).

Non-photosynthetic pigments

Post & Vesk (1992) isolated the dark pigment present in the tissues of *C. varians* sampled from Clarke Peninsula in Wilkes Land. The pigment was dark under ultraviolet light, had an R_f value of 0.7 and similar mobility on thin layer chromatography plates to anthocyanins. Post & Vesk (1992) concluded that it was an anthocyanin-like pigment. The pigment, which is located in the walls of apical cells of sun-exposed leaves (Fig. 7), has a peak of absorption at 495 nm and minor peaks at 240, 281 and 330 nm. A later study (Snell *et al.* 2009) showed the pigment, which has a molecular weight of 285, to be riccionidin A ($C_{15}H_9O_6$; Fig. 7, inset), a red to purple anthocyanidin found in the cell walls of *Rhus javanica* L., a vascular plant, and four other liverworts, including *Ricciocarpos natans* (L.) Corda and *Marchantia polymorpha* L. (Kunz *et al.* 1994, Taniguchi *et al.* 2000). In the absence of an authenticated standard of riccionidin A, comparisons were made between the anthocyanidin extracted from Antarctic *C. varians* and that from north European *R. natans* and *M. polymorpha*. Snell *et al.* (2009) found that the molecular masses, spectral profiles and elution times of the pigments from the three hepatics matched, and concluded that riccionidin A is present in *C. varians* tissues. The anthocyanidin is present at concentrations of *c.* 2 μmol g^{-1} (dry weight) in sun-exposed plants (Post & Vesk 1992, Snell *et al.* 2009).

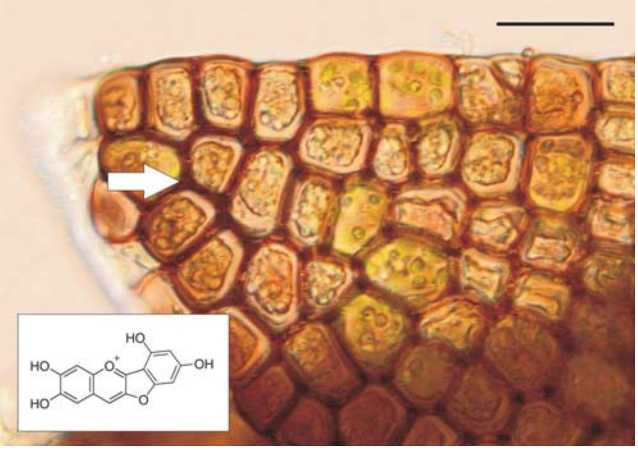

Fig. 7. Micrograph of sun-exposed *Cephaloziella varians* leaf, showing dark pigmentation in cell walls (arrow). Bar is 20 μm. Inset shows molecular structure of riccionidin A.

Other flavonoids are also synthesized by *C. varians*. HPLC analyses have shown there to be at least six, and possibly as many as nine, other acidified methanol-extractable flavonoids within the tissues of *C. varians*, none of which have sugar attachments (T. Kokubun, personal communication 2009). In common with riccionidin A, these compounds tend to be localised in apical leaves, which have the highest exposure to solar radiation, but, unlike the anthocyanidin, are present in the cytosol, rather than the cell wall (Snell 2007). The absolute concentrations of these pigments, which vary widely depending on exposure to solar radiation, are currently unknown, but total absorption of acidified-methanol extracts over the UV-B waveband is *c.* 3–6 mg^{-1} dry weight (Newsham *et al.* 2002, 2005, Snell *et al.* 2009).

Table IV. Carbon, nitrogen, phosphorus and potassium concentrations in *C. varians* tissues at a range of maritime and sub-Antarctic locations. See Table II for latitudes and longitudes of locations. Data are means of 5–8 replicates ± SD.

Location	C (%)[1]	N (%)[1]	P (%)[2]	K (%)[2]
Schlieper Bay, South Georgia	46.93 ± 0.58	2.52 ± 0.19	0.026 ± 0.003	0.392 ± 0.040
Foca Point, Signy Island[3]	42.82 ± 0.34	2.30 ± 0.15	0.024 ± 0.004	0.165 ± 0.016
Factory Bluffs, Signy Island[3]	46.48 ± 0.22	2.26 ± 0.11	0.025 ± 0.002	0.136 ± 0.018
Rothera Point, Adelaide Island	47.88 ± 0.25	1.58 ± 0.25	0.016 ± 0.003	0.263 ± 0.045
Ablation Valley, Alexander Island	32.65 ± 3.18	1.18 ± 0.15	0.009 ± 0.001	0.299 ± 0.030
Moutonnée Valley, Alexander Island	30.70 ± 1.00	1.39 ± 0.20	0.010 ± 0.001	0.463 ± 0.040

[1] Elementar Vario EL elemental analyser, [2] Perkin Elmer DRC11 ICP-MS, [3] South Orkney Islands

Carbohydrates

Sucrose, trehalose and glucose are reported by Roser *et al.* (1992) to be the only sugars in the tissues of *C. varians* sampled from Bailey Peninsula. Concentrations of these carbohydrates are 3.3, 2.0 and 1.3 mg g^{-1} (dry weight), respectively (Roser *et al.* 1992). A separate study, also on plants from Bailey Peninsula, reports concentrations of sucrose, trehalose, fructose and glucose of 4.3, 1.1, 0.2 and 0.2 mg g^{-1} (dry weight), respectively (Melick & Seppelt 1992). Of the polyols, trace levels of arabitol and ribitol (total 0.5 mg g^{-1} dry weight) and higher levels of mannitol (1.7 mg g^{-1} dry weight) are present in *C. varians* tissues sampled from the field. Laboratory-grown plants contain 10.2 mg g^{-1} (dry weight) of mannitol (Roser *et al.* 1992).

Tissue chemistry

Carbon, nitrogen, phosphorus and potassium concentrations of *C. varians* plants sampled from Bird Island and Signy, Adelaide and Alexander islands in the sub-, northern and southern maritime Antarctic vary between 31 and 48%, 1.2 and 2.5%, 0.009 and 0.026% and 0.14 and 0.46% (dry weight), respectively (Table IV). Reductions occur in the concentrations of the former three elements in *C. varians* tissues at more southerly locations (Table IV). Bokhorst *et al.* (2007) report a δ^{15}N value of 11.9 for *C. varians* growing on a soil with a δ^{15}N value of 14.0.

Water relations

Cephaloziella varians is poikilohydric, and is thus unable to control water loss from its tissues. The water content of tissues is high, owing to the damp environments that the species inhabits, with the substrate below *C. varians* becoming sufficiently waterlogged for decomposition to be inhibited and for methanogenesis to occur (Wynn-Williams 1980, 1988, Yarrington & Wynn-Williams 1985, Davis 1986). Roser *et al.* (1992), Melick & Seppelt (1992) and Post & Vesk (1992) report water contents of 76–80% (fresh weight) of plants from continental Antarctic locations. Similarly, the water contents of plants at Signy and Adelaide islands are 68% and 88% (fresh weight), respectively (Davis 1981, K.K. Newsham, unpublished data). Smith (1972) and Davis (1986) report water contents for substrata under plant communities in which *C. varians* occurs at Signy Island of between 16% and 1125% (dry weight). Water evaporation rates for vegetation in which *C. varians* occurs on Bailey and Clark peninsulas in continental Antarctica are 27 and 38 mg h^{-1} (Smith 1990).

Response to environment

Effects of freeze-thaw cycles

Plants of *C. varians* subjected to a daily freeze-thaw cycle (between -15°C and 4°C) for 16 days lose 29% of low molecular weight carbohydrates after leaching with water, compared with plants not subjected to freeze-thaw events, which lose 10% of carbohydrates (Melick & Seppelt 1992). This loss is largely accounted for by an increase in sucrose in the leachates. Changes in the freezing points of material subjected to freeze-thaw are not observed, however: after 16 days, those of the control and freeze-thawed material are -5.4°C and -5.3°C, respectively (Melick & Seppelt 1992). These relatively high ($>$ -9°C) freezing points suggest that *C. varians* does not avoid freezing, but rather tolerates the freeze-thaw process. The species is able to survive for long periods at temperatures below freezing point: Longton & Holdgate (1967) and Bednarek-Ochyra *et al.* (2000) document the growth of *C. varians* after plants had been frozen at up to -20°C for three and 20 years, respectively.

Effects of snowmelt

Snell *et al.* (2007) report a rapid increase from 0.18 to 0.45 in the maximum quantum efficiency of photosystem II (F_v/F_m), and an 88% increase in the concentrations of chlorophyll *a* and *b*, during the first 24 h after *C. varians* emerges from snow. However, there is little evidence of increased concentrations of photoprotective pigments in *C. varians* as it emerges from melting snow and ice at the end of spring (Snell *et al.* 2007).

Effects of solar radiation

Several studies demonstrate that the morphology and pigmentation of *C. varians* responds to solar radiation. In the sun-exposed form, apical leaves tend to be more closely

Fig. 8. Mats of *Cephaloziella varians* exposed to reduced (left) or full (right) solar UV-B radiation for three weeks under Plexiglas screens covered with Mylar polyester or Plexiglas screens only, respectively. The green shoots in the right hand mat are of the moss *Bryum pseudotriquetrum*. Reproduced from Snell (2007).

spaced than in the shade form, and overlap each other slightly (Post & Vesk 1992). The shade form of the species has elongated internodes and may have smaller leaves. Sun-exposed leaves have thick cell walls, particularly on the abaxial surface.

Post & Vesk (1992) report that apical leaves of *C. varians* from sun-exposed habitats accumulate higher concentrations of an anthocyanin-like pigment (riccionidin A; see *non-photosynthetic pigments*, above) than those from shaded habitats. They also show that sun-exposed plants have lower concentrations of chlorophyll and higher carotenoid/chlorophyll ratios than shade-adapted plants. The accumulation of riccionidin A in apical leaves is owing to exposure to solar UV-B radiation (Newsham *et al*. 2005): the pigment is lost within approximately three weeks when UV-B radiation exposure is reduced to 30% of that in sunlight, achieved by placing Mylar polyester screens over plants in the natural environment (Fig. 8). If the species is then exposed to an abrupt increase in solar UV-B exposure by removing the screens, the anthocyanidin is resynthesized within 48 h at a mean air temperature of 0.9°C (Snell *et al*. 2009), with a visible darkening of its tissues during this period. Snell *et al*. (2009) estimate that a minimum of 1.85% of the carbon fixed in photosynthesis is used to synthesize riccionidin A during this period.

Cephaloziella varians displays rapid responses to changes in UV-B exposure arising from ozone depletion, with concentrations of UV-B screening pigments (putative colourless flavonoids) tracking solar UV-B irradiances, implying that plants respond rapidly (within 24 h) to UV-B exposure (Newsham *et al*. 2002). Concentrations of carotenoids, notably neoxanthin, violaxanthin and lutein, are also positively associated with the flux of UV-B radiation in sunlight (Newsham *et al*. 2002).

Associated organisms

Bryophytes and vascular plants

Cephaloziella varians is frequently associated with many other bryophyte species in the Antarctic (Ochyra *et al*. 2008). It is a common member of the short moss cushion and turf sub-formation, the tall moss turf sub-formation and the bryophyte carpet and mat sub-formation (Smith 1996). It also occurs amongst the two native Antarctic vascular plant species, *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl., and in the grass and cushion chamaephyte sub-formation, usually in well-drained habitats (Ochyra & Váňa 1989a). Although *C. varians* is often sparsely distributed amongst other bryophytes, it can form almost pure stands of up to 2–3 m^2 in area and attains covers in mixed bryophyte communities of 13% at Signy Island (Wynn-Williams 1980, Davis 1981) and 65% on Bailey Peninsula (Smith 1990).

Invertebrates

Many invertebrates occur amongst the shoots of *C. varians* and in the substratum beneath them. *Cryptopygus antarcticus* Willem, a widespread maritime Antarctic collembolan, is frequent in mats of *C. varians* at Signy Island and at Rothera Point. At the latter site, unidentified bdelloid rotifers, the nematodes *Aphelenchoides haguei* Maslen, *Coomansus gerlachei* (de Man) Jairajpuri & Kahn, *Eudorylaimus pseudocarteri* Loof, *E. coniceps* Loof, *Plectus antarcticus* de Man, *P. belgicae* de Man and *Rhyssocolpus paradoxus* (Loof) Andrassy, and the tardigrades *Diphascon* and *Echiniscus* spp., *Hypsibius* cfr. *dujardini* Doyère and *Macrobiotus furciger* Murray, are frequently found in the substratum beneath *C. varians* (Newsham *et al*. 2006, N.R. Maslen, personal communication 2009). As yet, there is little to suggest that any of these invertebrates are specific to substrata under *C. varians*.

Fungi

Microscopic examination of *C. varians* from the Antarctic almost invariably reveals fungal hyphae ramifying through the shoot. Williams *et al*. (1994) were the first to report the presence of fungi in the tissues of the species. They documented dark septate hyphae and rudimentary coils, resembling those formed by ericoid mycorrhizal fungi in the hair roots of ericaceous plants, in the rhizoids of *C. varians* from Bailey Peninsula and Botany Bay, both in the continental Antarctic. Subsequently, Chambers *et al*. (1999) sequenced the Internal Transcribed Spacer (ITS) region of a fungus isolated by Williams *et al*. (1994) from plants on Bailey Peninsula and found that it displayed $< 2.1\%$ divergence from that of the type culture of *Rhizoscyphus ericae* (Read) Zhuang & Korf., a widespread mycorrhizal fungus in heathland and boreal ecosystems (Smith & Read 2008).

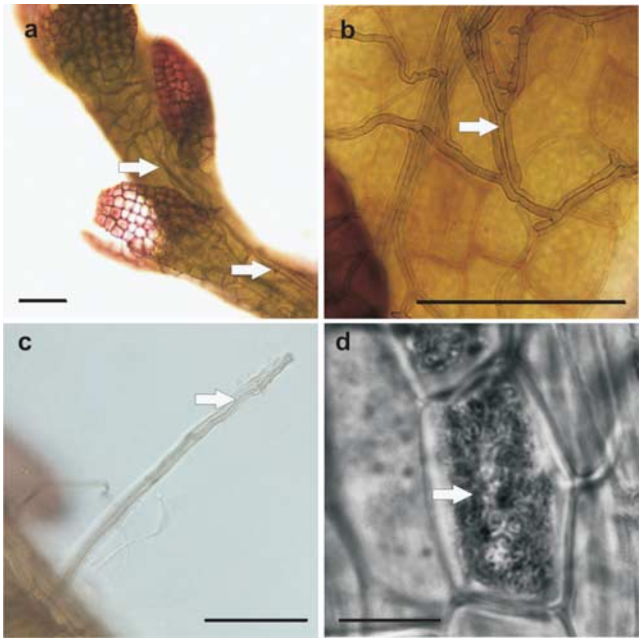

Fig. 9. Micrographs of **a.** fungal hyphae in *Cephaloziella varians* shoot (arrows), **b.** hyphae forming strands on shoot surface (arrow), **c.** hypha colonizing a rhizoid (arrow), and **d.** hyphal coil in axial cell (arrow). Bars in a–d are 80, 50, 25 and 10 μm, respectively. Reproduced, with permission from Wiley-Blackwell, from Upson *et al*. (2007).

Further studies revealed that *R. ericae* is abundant in the tissues of *C. varians* along a 1875 km transect from Bird Island in the sub-Antarctic, through to Coronation, Lynch and Signy islands in the South Orkneys, King George and Livingston Islands in the South Shetlands, and Adelaide and Alexander islands, off the south-western Antarctic Peninsula (Upson *et al*. 2007). Analyses of ITS1-5.8S-ITS2 and 28S large subunit sequences indicated that isolates are 98–99% similar to those of *R. ericae* from North America, Australia and Europe (Upson *et al*. 2007). Fungal hyphae ramify through the tissues of the plant almost to the apical meristem, forming strands of hyphae on the shoot surface, and also frequently colonize rhizoids (Fig. 9a–c). Hyphal coils, similar to those observed by Williams *et al*. (1994) in plants from Bailey Peninsula, are also formed by *R. ericae* in the axial cells of axenically-grown plants (Fig. 9d).

Although *R. ericae* is widespread in the rhizoids of *C. varians* in the maritime and sub-Antarctic, other apparently non-pathogenic fungi also colonize the tissues of the plant. Sequencing of fungal 18S small subunit genes amplified directly from *C. varians* from Adelaide Island reveals a diverse fungal community, including sequences conspecific with a large group of fungi nested within the Chaetothyriales, and those similar to *Rhizoscyphus* spp. and *Phialocephala fortinii* Wang & Wilcox (Jumpponen *et al*. 2003). Mats of *C. varians* from the Terra Firma Islands in southern Marguerite Bay, off the south-western Antarctic Peninsula, yield nematode-trapping ring fungi (Duddington *et al*. 1973). Geothermally-heated soils under *C. varians* on Mount Melbourne also yield *Mucor*, *Penicillium* and *Cryptococcus* spp. (Broady *et al*. 1987).

Algae, cyanobacteria and protozoa

The microalga *Stichococcus bacillaris* Nägeli is frequently isolated from *C. varians* mats at Rothera Point and Signy Island, and the foliose alga *Prasiola crispa* (Lightf.) Kütz. is also commonly found growing amongst mats of *C. varians* at these locations. Broady *et al*. (1987) report the alga *Chlorella* cf. *reniformis* Watan., the testate amoeba *Corythion dubium* Taranek., and the cyanobacteria *Gloeocapsa magma* (Bréb.) Holl., *Tolypothrix bouteillei* (Bréb. & Desm.) Lemm. and *Stigonema ocellatum* Thuret, to be present with *C. varians* in geothermally-heated soils on Mount Melbourne.

Disease

No specific reports of any pathogens on *C. varians* exist in the literature. However, rings formed by *Thyronectria antarctica* occur in mats of *C. varians* in the northern maritime Antarctic (R.I.L. Smith, personal communication 2009). A species of *Pythium*, which bears phylogenetic affinities to snow moulds and causes dieback symptoms in *Deschampsia antarctica* (Bridge *et al*. 2008), is present in mats of *C. varians* at Adelaide Island, as is *Phoma herbarum* Westend (Hughes *et al*. 2003), a globally-distributed weak fungal pathogen.

Adaptations of *C. varians* to the Antarctic natural environment

In their review of the phytogeography of Antarctic hepatics, Bednarek-Ochyra *et al*. (2000) note that (*the*) *distribution pattern of liverworts in the maritime Antarctic implies that particular species differ markedly in their tolerance of severe environmental conditions, and there are only a very few which have adapted physiologically to very low temperatures and long periods of continual daylight*. *Cephaloziella varians* is clearly one such species: from the literature reviewed above, it is evident that it tolerates a range of stresses in the Antarctic natural environment. The foremost of these are the wide diurnal (20–30°C) and annual (50–60°C) fluctuations in temperature to which the species is exposed, the absence of solar radiation for several months each year, and exposure to high irradiances of solar radiation, including damaging shortwave UV-B radiation, during the brief growing season.

What adaptations does *C. varians* possess in order for it to survive these hostile conditions? Although the photosynthesis of the species displays rapid responses to snowmelt, enabling it to maximize carbon acquisition during the short growing season (Snell *et al*. 2007), it seems unlikely that the ability of the species to fix carbon is substantially greater than that of other bryophytes in

Antarctica. Assuming a photosynthetic quotient of 1 for Antarctic bryophytes (Longton 1974), the estimated carbon fixation rates of the species (up to 87 and 57 μmol CO_2 g^{-1} dry weight h^{-1} at 10°C for the sun-exposed and shade forms; Snell *et al*. 2009) is similar to that of other hydric species of Antarctic mosses and liverworts (33–83 μmol CO_2 g^{-1} dry weight h^{-1} at 10°C; Davey & Rothery 1997). The concentrations of chlorophylls in its tissues (0.2–0.4 mg g^{-1} fresh weight) are also similar to those of other Antarctic mosses (0.3–0.9 mg g^{-1} fresh weight; Rastorfer 1972, Roser *et al*. 1992).

Although the concentrations of photosynthetic pigments in the tissues of *C. varians* apparently do not differ from those of other Antarctic bryophytes, it is probable that the flavonoid pigments synthesized by the species play a significant role in its survival in the natural environment. Of note is the presence of riccionidin A in sun-exposed apical leaves: this anthocyanidin enables efficient heat absorption by *C. varians* tissues, increasing their temperature by several degrees relative to associated moss species. The shading of chloroplasts by this flavonoid most probably also reduces photoinhibition at high irradiances, with the oxygen evolution of shade-adapted plants, which lack the pigment, saturating at 200–400 μmol photons m^{-2} s^{-1}, but that of sun-exposed plants, which possess the pigment, not becoming saturated at irradiances of $<$ 1090 μmol photons m^{-2} s^{-1} (Post & Vesk 1992, Snell *et al*. 2009). Two other Antarctic hepatics, *Lophozia excisa* and *Barbilophozia hatcheri*, which extend to *c*. 68°S on the south-western Antarctic Peninsula, also synthesize dark pigments in apical leaves (Bednarek-Ochyra *et al*. 2000), which might similarly contribute to tolerance of high solar radiation exposure in the southern maritime Antarctic. Tolerance of high irradiance, although not ascribed to dark pigmentation, has been put forward as a reason for the success of *Deschampsia antarctica* and *Colobanthus quitensis* in the Antarctic natural environment (Smith 2003). Riccionidin A and other colourless flavonoids, which most probably scavenge free radicals during periods of high solar radiation exposure, are aglycones, and can thus be synthesized at a low metabolic cost to *C. varians* (Snell *et al*. 2009). Furthermore, the colourless flavonoids synthesized by the species appear to protect photosystem II from rapid changes in UV-B exposure during periods of ozone depletion in the stratosphere over the Antarctic (Newsham *et al*. 2002).

Another key adaptation of *C. varians* appears to be its association with the mycorrhizal symbiont *Rhizoscyphus ericae*. This fungus, which facilitates the uptake of nitrogen by the roots of ericaceous plants in acidic, nutrient-poor soils at lower latitudes (Smith & Read 2008), has a widespread and consistent association with *C. varians* throughout the maritime Antarctic (Chambers *et al*. 1999, Upson *et al*. 2007). At present, the nature of any possible benefit to *C. varians* from *R. ericae* is unclear, but the formation in the cells of axenically-grown plants of hyphal coils, which maximise the surface area of contact between symbionts in ericoid mycorrhizas (Smith & Read 2008), is suggestive of active nutrient exchange between the liverwort and the fungus (Upson *et al*. 2007). However, with the exception of nitrate at some locations, inorganic nutrient availability in soils on which *C. varians* occurs in the Antarctic is within the range of that considered to be optimal for plant growth at lower latitudes (Holdgate *et al*. 1967, Allen 1989). Nutritional benefits of *R. ericae* colonization to *C. varians* might hence not be expected under such conditions of optimal inorganic nutrient supply. Resynthesis experiments under axenic conditions are hence required to resolve the question of whether *R. ericae* enhances the flow of nitrogen into the tissues of *C. varians* or not, and whether the liverwort benefits from its association with the fungus in this way in the natural environment.

A further adaptation enabling the survival of *C. varians* in the Antarctic terrestrial biome is the presence of cryoprotectants, notably sucrose, mannitol and trehalose, in its tissues. The last is an effective cryoprotectant that is considered to confer desiccation tolerance and osmotic protection on a range of Antarctic plants and animals by stabilizing cell membranes during dehydration (Montiel 2000). The presence of cryoprotectants in the tissues of *C. varians* might explain the survival of the liverwort for several years at temperatures below freezing point (Longton & Holdgate 1967, Bednarek-Ochyra *et al*. 2000) and the ability of the species to remain frozen in a dehydrated state during winter in the natural environment. Previous studies suggest that polyols are synthesized by leafy liverworts, and not by their associated fungi (Christie *et al*. 1985). However, the presence in *C. varians* of mannitol, a sugar alcohol frequently used as a fungal storage compound, at 60 times greater concentrations than in those of associated mosses, and at similar concentrations to those in lichens, suggests that fungi present in *C. varians* may benefit the liverwort by synthesizing polyols in its tissues (Roser *et al*. 1992).

Further comparative studies between *C. varians* and other Antarctic hepatics are required to determine the precise reasons for the success of the species in the high maritime and continental Antarctic. At present, however, it seems likely that the presence in *C. varians* of riccionidin A, colourless flavonoids, cryoprotectants and fungal symbionts account, at least in part, for the remarkable geographical range of the hepatic and its tolerance of environmental stresses in the Antarctic terrestrial biome.

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