

## Lichens and ultramafic rocks: a review

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**Abstract:** Floristic, vegetational and ecological features of lichens in ultramafic environments are reviewed using a wide range of literature dating from the beginning of the 20th century. Co-presence of acidophytic (silicolous) and basiphytic (calicolous) species and the occurrence of species characterized by particular (disjunct) distribution patterns are features of lichens in ultramafic environments. It is not possible to detect consistent trends in data on other broadly accepted features, such as paucity of species, low cover and the occurrence of particular ecotypes because of the influence of several environmental factors in addition to the substratum. Some recent data about physico-chemical interactions between saxicolous lichens and ultramafic rocks are also reported.

**Key words:** lichens, serpentinite, ultramafic environments

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### Introduction

Ultramafic rocks are plutonic rocks with more than 90% modal mafic (ferromagnesian) minerals and essentially consist of olivine, orthopyroxene, clinopyroxene and hornblende. Spinel, garnet, biotite, magnetite, or chromite may also be present in small amounts. Their modal classification is based on the proportion of the major minerals. In particular, peridotites are distinguished from pyroxenites and hornblendites by containing more than 40% olivine. Further subdivisions and specific names are based on the relative amount of orthopyroxene, clinopyroxene and hornblende (Streckeisen 1973; Le Maitre *et al.* 2002). From a chemical point of view, ultramafic rocks would also be considered ultrabasic as they contain less than 45% by weight SiO<sub>2</sub> (Le Maitre *et al.* 2002).

Ultramafic rocks occur in layered igneous complexes which have been derived by fractional crystallization of tholeiitic (basaltic) magmas (e.g. Skaergaard, Greenland; Stillwater, USA; Bushveld, South Africa; Skye and Rhum, Scotland) (Best 2003 and refer-

ences therein). Ultramafic rocks are also common in Alpine-type ophiolite suites, a rock association thought to represent 're-worked' oceanic crust (O'Hanley 1996; Le Maitre *et al.* 2002), which includes an ultramafic complex capped by gabbroic and mafic sheeted dykes and volcanic complexes (Coleman 1977). In these suites, hydration of the igneous minerals (serpentinization) changes the ultramafic protolith into serpentinite, a metamorphic rock mainly consisting of serpentine (antigorite, lizardite, chrysotile) ± magnetite. Additional phases such as diopside, Ti-clinohumite, brucite, minor Fe-Ni alloys and sulfides may occur locally (Coleman 1977; O'Hanley 1996). Ophiolite complexes are known in almost every orogenic belt on earth. They occur in the Alpine-Himalayan belt (e.g. Pyrenees, Alps, Apennines, the Balkans chains), in the Appalachian-Caledonian-Uralian belt (e.g. Chic-Chocs Mountains, Appalachians, Canada; Lizard peninsula, England), and in the Circum-Pacific orogenic belt (e.g. Western USA coast).

In both igneous layered complexes and ophiolite suites, ultramafic rocks are often closely associated with mafic rocks [i.e. rocks having <90% modal mafic minerals, and commonly being mesocratic or melanocratic

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(Le Maitre *et al.* 2002)] such as gabbro and basalt, and their metamorphic products (e.g. metagabbro, metabasalt, amphibolite, eclogite). Chemically, gabbro and basalt are basic rocks [45–52% wt SiO<sub>2</sub> (Le Maitre *et al.* 2002)], with higher aluminium and calcium contents which, besides different mineral assemblages, lead to different ecological conditions (e.g. O’Hanley 1996).

Ultramafic rocks are associated with unique ecosystems in which characteristic plant communities develop in response to geochemically induced stresses (Pichi-Sermolli 1948; Brooks 1987; Baker *et al.* 1992). These include high concentrations of heavy metals (Ni, Cr and Co), a scarcity of macronutrients (particularly nitrogen) and high Mg/Ca ratios (Brooks 1987). The vegetation is characterized by (i) low numbers of individuals and species, (ii) the occurrence of ecotypes which differ ecologically and, sometimes, also morphologically from the original type [serpentinomorphoses such as stenophyllism, glabrescence, plagiotropism, nanism, a high root:shoot ratio, glaucescence (Pichi-Sermolli 1948)], (iii) the co-presence of acidophytic and basiphytic species, (iv) the abundant presence of species characterized by disjunctive distributions, (v) the presence of typically xerophytic species, and (vi) the dominance of certain families or genera (Rune 1953).

Some species on ultramafics show an exceptional capacity for the hyperaccumulation of metals, particularly nickel, in epigeal parts through chelation and selective compartmentalization mechanisms. This characteristic may be a detoxification response to relatively high concentrations of metals in the substratum (e.g. Brooks 1987; Baker *et al.* 1992; Krämer *et al.* 2000). For example more than 320 species show dry-matter concentrations of nickel in excess of 1000 µg g<sup>-1</sup> (Reeves *et al.* 1999).

Although there is extensive literature on the flowering plants of ultramafics (Brooks 1987; Baker *et al.* 1992), only limited data exist for cryptogams, particularly lichens (Purvis & Halls 1996). The aim of this review is to summarize present knowledge of lichens in ultramafic habitats and to evaluate

how far lichens match the principal ecological characteristics of phanerogamic vegetation of ultramafics. Most of the literature pertaining to lichens on ultramafics considers ophiolite suites (i.e. serpentinites) as opposed to layered igneous complexes (i.e. non-serpentinized ultramafic rocks). This is a reflection of the wide global distribution of ophiolites and consequent ease of access for study, compared with the local occurrence of layered igneous complexes such as those on the island of Rhum (Scotland).

### Floristic, vegetational and ecological features

Two hundred and fifty saxicolous and terricolous species which have been recorded at least twice from ultramafic rocks are listed in Table 1. A predominance of particular lichen families or genera has not been noted in the literature and none is evident from this list of species.

### Relative abundance of lichens

The paucity of lichens has been generally accepted as a recurrent feature of ultramafic environments (Purvis & Halls 1996; Gilbert 2000) possibly because of the high concentrations of Mg and Ni and the low availability of macronutrients (Bates 1978). However, only a few authors have provided detailed data documenting the paucity and low cover of lichen species.

A low cover on ultramafics has been reported several times for saxicolous lichens (Suza 1927; Gilbert 1983; Sirois *et al.* 1987), but only once for terricolous lichens (Gilbert 1983). In contrast, high percentage cover values for saxicolous lichens on serpentinites have been reported from Germany [85–95% (Wirth 1972)] and North-Western Italy [from >35% (Gallo & Piervittori 1991) to >90% (Piervittori *et al.* 2004)], and also for saxicolous lichens on mafic rocks such as basalts [e.g. >85%, (Wirth 1972)].

The data from the main floristic studies, based on samples from areas of very different size, show that the number of species varies from 8 to 227 (Table 2). Diversity is even

TABLE 1. *Lichen species reported from ultramafic environments*

Species	References*
<i>Acarospora fuscata</i> (Schrad.) Th. Fr.	a, i, o, t
<i>A. smaragdula</i> (Wahlenb.) A. Massal. subsp. <i>smaragdula</i>	k, l, r
<i>A. veronensis</i> A. Massal.	e, f
<i>Acrocordia macrospora</i> A. Massal.	r, s
<i>Agonimia tristicula</i> (Nyl.) Zahlbr.	k, l
<i>Alectoria ochroleuca</i> (Hoffm.) A. Massal.	m, q
<i>Amandinea punctata</i> (Hoffm.) Coppins & Scheid.	l, o, r, t
<i>Anaptychia nuncinata</i> (With.) J. R. Laundon	k, l, r
<i>Arctoparmelia centrifuga</i> (L.) Hale	d, i, m
<i>Aspicilia caesiocinerea</i> (Malbr.) Arnold	e, f, g, o, q, r, t
<i>A. cinerea</i> (L.) Körb.	d, e, f, g, i, o, r, t
<i>A. crusii</i> Klement	e, f, g
<i>A. gibbosa</i> (Ach.) Körb.	a, c
<i>A. haeyrenii</i> (H. Magn.) Räsänen	d, i
<i>A. polychroma</i> (Anzi) Nyl.	c, e, f, g
<i>A. serpentinicola</i> (Suza) Räsänen	d, e, f, g
<i>Bacidia bagliettoana</i> (A. Massal. & De Not.) Jatta	a, k
<i>B. scopulicola</i> (Nyl.) A. L. Sm.	n, r
<i>Baeomyces rufus</i> (Huds.) Rebert.	a, d, i, j, m
<i>Bellemerea diamarta</i> (Ach.) Hafellner & Cl. Roux	m, q
<i>Belonia russula</i> Nyl.	m, q
<i>Biatora vernalis</i> (L.) Fr.	d, i, m
<i>Buellia aethalea</i> (Ach.) Th. Fr.	c, k, r, t
<i>B. dispersa</i> A. Massal.	m, r
<i>B. leptoclinoides</i> (Nyl.) J. Steiner	r, s
<i>B. ocellata</i> (Flot.) Körb.	c, k, r
<i>B. spuria</i> (Schaer.) Anzi	c, o, r
<i>B. stellulata</i> (Taylor) Mudd	o, r
<i>Caloplaca ammiospila</i> (Wahlenb.) H. Olivier	m, q
<i>C. aractina</i> (Fr.) Häyrén	a, h, k
<i>C. arenaria</i> (Pers.) Müll. Arg.	q, u
<i>C. citrina</i> (Hoffm.) Th. Fr.	i, n, r, t
<i>C. crenularia</i> (With.) J. R. Laundon	e, f, g, k, l, u, r
<i>C. holocarpa</i> (Ach.) A. E. Wade	l, m, t
<i>C. marina</i> (Wedd.) Du Rietz	k, r
<i>C. obliterans</i> (Nyl.) Blomb. & Forssell	i, q
<i>C. pyracea</i> (Ach.) Th. Fr.	a, e
<i>C. saxicola</i> (Hoffm.) Nordin	k, u
<i>Candelariella aurella</i> (Hoffm.) Zahlbr.	c, g, i, n, q, t, u
<i>C. vitellina</i> (Hoffm.) Müll. Arg.	a, c, d, e, g, h, i, m, o, p, q, r, t
<i>Catillaria chalybeia</i> (Borrer) A. Massal.	c, k, l, n, t
<i>C. lenticularis</i> (Ach.) Th. Fr.	o, k, l
<i>C. leucophaeotera</i> (Nyl.) Vain. var. <i>serpentina</i>	d, i
<i>Cetraria ericetorum</i> Opiz	i, m, q
<i>C. islandica</i> (L.) Ach.	a, i, m, q
<i>Cladonia acuminata</i> (Ach.) Norrl.	i, m
<i>C. amaurocraea</i> (Flörke) Schaer.	d, i, m, q
<i>C. arbuscula</i> (Wallr.) Flot. subsp. <i>arbuscula</i>	a, i
<i>C. arbuscula</i> (Wallr.) Flot. subsp. <i>mitis</i> (Sandst.) Ruoss	a, m
<i>C. carneola</i> (Fr.) Fr.	a, i, m
<i>C. cenotea</i> (Ach.) Schaer.	a, d, i, m
<i>C. cervicornis</i> (Ach.) Flot subsp. <i>verticillata</i> (Hoffm.) Ahti	a, d, i
<i>C. cervicornis</i> (Ach.) Flot. subsp. <i>cervicornis</i>	r, k
<i>C. chlorophaea</i> Flörke s. lat.	a, d, g, i, m, r, t

TABLE 1. *Continued*

Species	References*
<i>C. coccifera</i> (L.) Willd.	a, d, i, m
<i>C. coniocraea</i> (Flörke) Spreng.	a, g, i, m, o, t
<i>C. cornuta</i> (L.) Hoffm.	a, d, i
<i>C. crispata</i> (Ach.) Flot.	a, d, i, m
<i>C. cyanipes</i> (Sommerf.) Nyl.	i, m
<i>C. decorticata</i> (Flörke) Spreng.	a, m
<i>C. deformis</i> (L.) Hoffm.	a, m
<i>C. digitata</i> (L.) Hoffm.	a, m
<i>C. fimbriata</i> (L.) Fr.	a, d, g, t
<i>C. furcata</i> (Huds.) Schrad.	a, g, i, k, m, t
<i>C. glauca</i> Flörke	a, m
<i>C. gracilis</i> (L.) Willd.	a, i, m, q
<i>C. macilenta</i> Hoffm. subsp. <i>macilenta</i>	a, c, i, m
<i>C. phyllophora</i> Hoffm.	a, m
<i>C. pleurota</i> (Flörke) Schaer.	a, m, q
<i>C. pyxidata</i> (L.) Hoffm.	a, d, g, i, m, o, q, r
<i>C. rangiferina</i> (L.) F. H. Wigg.	a, d, i, m, q
<i>C. rangiformis</i> Hoffm.	a, g, k, r
<i>C. silvatica</i> (L.) Rab.	a, d
<i>C. squamosa</i> Hoffm. var. <i>squamosa</i>	a, i, m
<i>C. stellaris</i> (Opiz) Pouzar & Vězda	d, i, m
<i>C. subulata</i> (L.) F. H. Wigg.	a, g, m
<i>C. sulphurina</i> (Michx.) Fr.	i, m
<i>C. symphyocarpia</i> (Flörke) Fr.	a, k
<i>C. turgida</i> Hoffm.	a, d, i, m
<i>C. uncialis</i> (L.) F.H.Wigg.	a, d, i, m, q
<i>Collema flaccidum</i> (Ach.) Ach.	a, b
<i>C. furfuraceum</i> (Arnold) Du Rietz	k, l
<i>Degelia atlantica</i> (Degel.) P. M. Jørg. & P. James	k, r
<i>Dermatocarpon luridum</i> (With.) J. R. Laundon var. <i>luridum</i>	i, m, u
<i>D. minutum</i> (L.) W. Mann	a, b, e, g, o, r
<i>Dibaeis baeomyces</i> (L. fil.) Rambold & Hertel	a, j, q
<i>Diploicia canescens</i> (Dicks.) A. Massal.	k, r
<i>D. subcanescens</i> (Werner) Hafellner & Poelt	k, r
<i>Diploschistes muscorum</i> (Scop.) R. Sant.	a, d, g
<i>D. scruposus</i> (Schreb.) Norman	a, c, d, i, o, u
<i>Diplotomma alboatrum</i> (Hoffm.) Flot.	o, t
<i>D. chlorophaeum</i> (Leight.) Szatala	f, k
<i>Dirina massiliensis</i> Durieu & Mont. f. <i>massiliensis</i>	k, r
<i>Ephebe lanata</i> (L.) Vain.	e, m, r
<i>Flavocetraria cucullata</i> (Bellardi) Kärnefelt & Thell	m, q
<i>F. nivalis</i> (L.) Kärnefelt & Thell	m, q
<i>Flavoparmelia caperata</i> (L.) Hale	c, k
<i>Fuscopannaria leucophaea</i> (Vahl) P. M. Jørg.	a, d, m, o
<i>F. praetermissa</i> (Nyl.) P. M. Jørg.	d, i, m, q
<i>Haematomma ochroleucum</i> (Neck.) J. R. Laundon var. <i>ochroleucum</i>	d, i
<i>Heterodermia obscurata</i> (Nyl.) Trevis.	c, k, r
<i>H. speciosa</i> (Wulfen) Trevis.	c, d, k
<i>Hypogymnia physodes</i> (L.) Nyl.	a, i, m, t
<i>H. viitata</i> (Ach.) Parrique	d, i, m
<i>Icmadophila ericetorum</i> (L.) Zahlbr.	i, m
<i>Ionopsis lacustris</i> (With.) Lutzoni	d, l
<i>Lecania cuprea</i> (A. Massal.) van den Boom & Coppins	q, r
<i>L. erysibe</i> (Ach.) Mudd	e, f, k, l

TABLE 1. *Continued*

Species	References*
<i>Lecanora albescens</i> (Hoffm.) Branth & Rostr.	f, n
<i>L. campestris</i> (Schaer.) Hue	a, r, t
<i>L. cenisia</i> Ach.	d, q, u
<i>L. dispersa</i> (Pers.) Sommerf.	l, n, t
<i>L. gangaleoides</i> Nyl.	k, r
<i>L. intricata</i> (Ach.) Ach.	a, q, t
<i>L. kulturalensis</i> Vain.	d, i
<i>L. muralis</i> (Schreb.) Rabenh. subsp. <i>muralis</i>	a, d, e, f, g, i, t
<i>L. polytropa</i> (Hoffm.) Rabenh. var. <i>polytropa</i>	a, d, i, m, o, t, u
<i>L. rupicola</i> (L.) Zahlbr.	a, k, o, q, r, u
<i>L. sulphurea</i> (Hoffm.) Ach.	a, l, r
<i>L. umbrina</i> (Ach.) A. Massal.	q, t
<i>Lecidea atrobrunnea</i> (Lam. & DC.) Schaer.	o, u
<i>L. bullata</i> (Körb.) Th. Fr.	q, t
<i>L. confluens</i> (Weber) Ach.	c, q, u
<i>L. fuscoatra</i> (L.) Ach.	a, k, o, t
<i>L. lapicida</i> (Ach.) Ach. var. <i>lapicida</i>	g, q
<i>L. plana</i> (J. Lahm) Nyl.	d, i
<i>L. tessellata</i> Flörke	m, o, t
<i>Lecidella anomaloides</i> (A. Massal.) Hertel & H. Kiliass	d, f, g, i, t, u
<i>L. asema</i> (Nyl.) Knoph & Hertel var. <i>asema</i>	k, l, n, r, t, u
<i>L. carpathica</i> Körb.	a, d, g, h, i, m, o, q, t
<i>L. scabra</i> (Taylor) Hertel & Leuckert	k, l, n, r, t
<i>L. stigmatea</i> (Ach.) Hertel & Leuckert	d, e, i, k, l, m, n, o, q, t
<i>L. viridans</i> (Flot.) Körb.	r, t
<i>L. wulfenii</i> (Hepp) Körb.	m, q
<i>Lecidoma demissum</i> (Rutstr.) Gotth. Schneid. & Hertel	m, q
<i>Lepraria incana</i> (L.) Ach.	i, m, t
<i>L. lobificans</i> Nyl.	r, t
<i>L. neglecta</i> (Nyl.) Lettau	d, g, q
<i>Leptoloma membranaceum</i> (Dicks.) Vain.	a, d, f
<i>Leptogium corniculatum</i> (Hoffm.) Minks	n, o
<i>L. tenuissimum</i> (Dicks.) Körb.	n, t
<i>Lobothallia radiosa</i> (Hoffm.) Hafellner	c, e, f
<i>Melanelia fuliginosa</i> (Duby) Essl. subsp. <i>glabratula</i>	a, k, t
<i>M. subaurifera</i> (Nyl.) Essl.	a, n
<i>Micarea lignaria</i> (Ach.) Hedl. var. <i>lignaria</i>	j, q
<i>Miriquidica garovaglii</i> (Schaer.) Hertel & Rambold	q, u
<i>Mycobilimbia berengeriana</i> (A. Massal.) Hafellner & Wirth	i, m
<i>M. hypnorum</i> (Lib.) Kalb & Hafellner	i, l, m
<i>Mycobilimbia pilularis</i> (Körb.) Hafellner & Türk	d, i
<i>M. tetramera</i> (De Not.) Vitik <i>et al.</i>	d, i
<i>Myxobilimbia sabuletorum</i> (Schreb.) Hafellner	i, k, m
<i>Neofuscelia loxodes</i> (Nyl.) Essl.	a, t
<i>N. pulla</i> (Ach.) Essl. s. lat.	a, c, g, p
<i>N. verruculifera</i> (Nyl.) Essl.	c, f
<i>Nephroma arcticum</i> (L.) Torss.	i, m
<i>N. parile</i> (Ach.) Ach.	d, i
<i>Ochrolechia parella</i> (L.) A. Massal	c, f, r
<i>O. tartarea</i> (L.) A. Massal.	d, i
<i>O. upsaliensis</i> (L.) A. Massal.	m, q
<i>Parmelia saxatilis</i> (L.) Ach.	a, d, f, g, i, k, m, q, t

TABLE 1. *Continued*

Species	References*
<i>P. sulcata</i> Taylor	a, m, l, t
<i>Parmeliella triptophylla</i> (Ach.) Müll. Arg.	d, i
<i>Parmotrema chinense</i> (Osbeck) Hale & Athi	c, k, r
<i>P. reticulatum</i> (Taylor) M. Choisy	k, r
<i>Peltigera aphthosa</i> (L.) Willd.	i, m
<i>P. canina</i> (L.) Willd.	a, d, i, m
<i>P. didactyla</i> (With.) J. R. Laundon	a, d, i, t
<i>P. leucophlebia</i> (Nyl.) Gyeln.	d, i
<i>P. malacea</i> (Ach.) Funck	a, d, i
<i>P. polydactylon</i> (Neck.) Hoffm.	a, d, m
<i>P. rufescens</i> (Weiss) Humb.	a, d, i, j
<i>P. scabrosa</i> Th. Fr.	d, m
<i>Pertusaria amara</i> (Ach.) Nyl.	d, i
<i>P. chiodectonoides</i> A. Massal.	c, l
<i>P. pseudocorallina</i> (Lilj.) Arnold	q, r
<i>Phaeophyscia endococcina</i> (Körb.) Moberg	m, q
<i>P. orbicularis</i> (Neck.) Moberg	a, i, l, n, t
<i>P. sciastra</i> (Ach.) Moberg	a, d, i, n, q
<i>Physcia adscendens</i> (Fr.) H. Olivier	a, n, o, r, t
<i>P. caesia</i> (Hoffm.) Fürnr.	a, c, d, e, f, g, i, m, n, q, r, t
<i>P. dubia</i> (Hoffm.) Lettau	a, e, k, m, q, r, t
<i>P. tenella</i> (Scop.) DC.	a, c, k, n, t
<i>Physconia distorta</i> (With.) J. R. Laundon	c, o
<i>P. grisea</i> (Lam.) Poelt subsp. <i>grisea</i>	o, t
<i>P. muscigena</i> (Ach.) Poelt var. <i>muscigena</i>	m, q
<i>Placidium lachneum</i> (Ach.) de Lesd.	k, o
<i>Placynthiella uliginosa</i> (Schrud.) Coppins & P James	a, i, g
<i>P. nigrum</i> (Huds.) Gray	m, o, q
<i>Polyblastia cupularis</i> A. Massal.	l, m
<i>Polysporina simplex</i> (Davies) Vězda	p, q, r, t
<i>Porina chlorotica</i> (Ach.) Müll. Arg.	r, t
<i>Porpidia cinereoatra</i> (Ach.) Hertel & Knoph	a, d, i, l, m, r
<i>P. crustulata</i> (Ach.) Hertel & Knoph	d, e, i, k, l, m, q, r, t
<i>P. macrocarpa</i> (DC.) Hertel & A. J. Schwab	c, g, j, m
<i>P. nadvornikiana</i> (Vězda) Hertel & Knoph	v, w
<i>P. speirea</i> (Ach.) Kremp.	c, u
<i>P. tuberculosa</i> (Sm.) Hertel & Knoph	i, m, q, t
<i>Protopannaria pezizoides</i> (Weber) P.M. Jørg. & S. Ekman	d, i, l, m, q
<i>Protoparmelia badia</i> (Hoffm.) Hafellner	a, o, q, u
<i>Psoroma hypnorum</i> (Vahl) Gray	a, m
<i>Pyrenocollema halodytes</i> (Nyl.) R. C. Harris	n, r
<i>Pyrenopsis triptococca</i> Nyl.	r, s
<i>Ramalina pollinaria</i> (Westr.) Ach.	a, d, i
<i>R. siliquosa</i> (Huds.) A. L. Sm.	k, l, r
<i>R. thrausta</i> (Ach.) Nyl.	d, i
<i>Rhizocarpon badioatrum</i> (Spreng.) Th. Fr.	a, d, i
<i>R. cinereovirens</i> (Mull. Arg.) Vain.	d, m
<i>R. distinctum</i> Th. Fr.	a, g, p, t
<i>R. effiguratum</i> (Anzi) Th. Fr.	e, f
<i>R. eupetraeum</i> (Nyl.) Arnold	o, t
<i>R. geminatum</i> Körb.	e, f
<i>R. geographicum</i> (L.) DC. subsp. <i>geographicum</i>	a, b, c, d, e, f, g, i, m, o, p, q, t, u

TABLE 1. *Continued*

Species	References*
<i>R. hochstetteri</i> (Körb.) Vain.	d, i, m
<i>R. obscuratum</i> (Ach.) A. Massal.	a, f, g, r, t
<i>R. petraeum</i> (Wulfen) A. Massal.	k, q, r
<i>R. richardii</i> (Nyl.) Zahlbr.	k, l
<i>R. viridiatrum</i> (Wulfen) Körb	h, g, o, r
<i>Rimularia insularis</i> (Nyl.) Rambold & Hertel	a, q
<i>R. confragosa</i> (Ach.) Körb.	d, g, l, q, t
<i>R. gennarii</i> Bagl.	l, k, n, t
<i>R. oxydata</i> (A. Massal.) A. Massal.	k, t
<i>R. santorinensis</i> J. Steiner	r, s
<i>Scoliciosporum umbrinum</i> (Ach.) Arnold	a, k, l, m, q, r, t
<i>Spilonema revertens</i> Nyl.	d, i, n
<i>Sporastatia testudinea</i> (Ach.) A. Massal.	q, u
<i>Staurothele ambrosiana</i> (A. Massal.) Zschacke	q, t
<i>Stereocaulon alpinum</i> Laurer	i, m
<i>S. paschale</i> (L.) Hoffm.	d, i, m
<i>S. subcoralloides</i> (Nyl.) Nyl.	i, m
<i>S. tomentosum</i> Fr.	d, i, m
<i>Sticta canariensis</i> Delise	r, s
<i>Tephromela atra</i> (Huds.) Hafellner var. <i>atra</i>	a, i, l, m, o, q, r, t
<i>Thermutis velutina</i> (Ach.) Flot.	c, d, i
<i>Trapelia coarctata</i> (Sm.) M. Choisy	a, d, i, j, q, r, t
<i>T. involuta</i> (Taylor) Hertel	j, r, t
<i>Trapeliopsis granulosa</i> (Hoffm.) Lumbsch	a, d, i, m, t
<i>Tremolecia atrata</i> (Ach.) Hertel	m, q, u
<i>Umbilicaria cylindrica</i> (L.) Duby var. <i>cylindrica</i>	q, u
<i>U. deusta</i> (L.) Baumg.	i, q
<i>Verrucaria caerulea</i> DC.	l, q
<i>V. maura</i> Wahlenb.	n, r, n
<i>V. muralis</i> Ach.	o, r, t
<i>V. nigrescens</i> Pers.	e, l, o, q
<i>V. viridula</i> (Schrad.) Ach.	c, o
<i>Xanthoparmelia conspersa</i> (Ach.) Hale	a, c, f, g, t
<i>X. somloensis</i> (Gyeln.) Hale	d, e, f, g, i, p
<i>X. tinctina</i> (Maheu & Gillet) Hale	c, k
<i>Xanthoria candelaria</i> (L.) Th. Fr.	a, n
<i>X. elegans</i> (Link) Th. Fr. subsp. <i>elegans</i>	a, i, m, q, u
<i>X. parietina</i> (L.) Th. Fr.	a, c, r, t
<i>X. soredata</i> (Vain.) Poelt	i, m, q

\*a: Suza, 1927; b: Lammermayr, 1934; c: Sambo, 1937; d: Hakulinen, 1958; e: Krause & Klement, 1958; f: Krause & Klement, 1962; g: Ritter-Studnička & Klement, 1968; h: Wirth, 1972; i: Takala & Seaward, 1978; j: Gilbert, 1983; k: Gilbert & James, 1987—Lizard; l: Gilbert & James, 1987—Keen of Hamar; m: Sirois *et al.*, 1987; n: Ryan, 1988; o: Sigal, 1989; p: Gallo & Piervittori, 1991; q: Hafellner, 1991; r: Sánchez-Biezma *et al.*, 1996; s: Sánchez-Biezma *et al.*, 2001; t: Kossowska, 2001; u: Piervittori *et al.*, 2004; v: Vězda, 1972; w: Sánchez-Biezma & López de Silanes, 1999. Nomenclature follows Nimis & Martellos (2003), Brodo *et al.* (2001) and Wirth (1995).

higher on ultramafics than on mafic rocks of adjacent areas, for example on the Lizard, England, *c.* 70 species on gabbros and *c.* 200

species on serpentinites (Gilbert & James 1987); at Mont Albert, Canada, *c.* 120 on amphibolite and *c.* 150 on serpentinite

TABLE 2. Number of lichen species listed in ultramafic areas

Reference	Locality	Area (ha)†	Altitude (m)	No. species
Zahlbrückner 1907	Greece, Cyclades, Tinos	–	–	19
Sambo 1927	Italy, Tuscany, M.te Ferrato	c. 1400	100–422	100
Suza 1927*	Czech Republic	–	–	121
Hakulinen 1958	Finland	–	–	99
Krause & Klement 1962	Greece, N Eubea	c. 45000 (massenkalk, serpentin, schiefer)	0–500	113
Takala & Seaward 1978	E Finland—Kaavi region	c. 500	–	123
Gilbert 1983 *	UK, Scotland, Rhum	3000	0–812	21
Gilbert & James 1987	UK, Cornwall, Lizard Peninsula	c. 2500	0	227
Sirois <i>et al.</i> 1987	Canada, Appalachians, mont Albert	1600	900–1150	157
Ryan 1988	USA, Washington, Fidalgo Island	c. 5	0–	61
Sigal 1989	USA, California,	–	150–1900	76
Gallo & Piervittori 1991	Italy, Piedmont, Monti Pelati	c. 200	400	8
Hafellner 1991	Austria, E-Alps, Steiermark	–	1630–2060	149
Kossowska 2001	Poland, Lower Silesia	–	–	84
Sánchez-Biezma <i>et al.</i> 2001	Spain, Sierra A Capelada	–	80–613	106
Piervittori & Favero-Longo 2002	Italy, Aosta Valley, Mt. Avic	3500	1400–3000	90
Piervittori <i>et al.</i> 2004	Italy, Aosta Valley, Mt. Avic	150	2600–3000	60

\*Publications in which paucity of lichen species is clearly noted.

†Estimated.

(Sirois *et al.* 1987); and at Mont Avic, Italy, 28 species on metagabbros, 42 species on serpentinites (Piervittori *et al.* 2004). According to our observations, we maintain that ultramafic outcrops are more easily colonized by saxicolous lichens because they undergo pedogenic processes more slowly and, consequently, are colonized less successfully by flowering plants despite their chemical features (Piervittori *et al.* 2004). On the other hand, the absence of certain species on serpentinites that commonly occur on mafics in adjacent areas [amphibolites (Suza 1927); andesites and amphibolites (Yoshimura & Yamanaka 1962); basaltic lavas (Gilbert & James 1987); amphibolites (Sirois *et al.* 1987); Mg-metagabbros (Piervittori *et al.* 2004)], has often been noted, particularly in saxicolous communities. The paucity of foliose species has been reported from several localities (Wirth 1972; Sirois *et al.* 1987) but not invariably (Gallo & Piervittori 1991). Rare species or new records of lichens have been

frequently reported on serpentinites (Takala & Seaward 1978; Gilbert & James 1987; Sirois *et al.* 1987; Sánchez-Biezma *et al.* 1996; Kossowska 2001; Piervittori *et al.* 2004). However, these discoveries are perhaps indicative of the extent of previous fieldwork as much as the influence of the substratum.

In alpine areas, differences between serpentinites and non ultramafic populations are less marked perhaps because the effects of high altitude dominate over geochemical factors in these habitats (Hafellner 1991; Piervittori *et al.* 2004).

### Serpentinophytic species

Various lichen species have been reported as restricted to ultramafic rocks (Suza 1927; Lammermayr 1934; Ritter-Studnička & Klement 1968; Sirois *et al.* 1987; Sigal 1989; Sánchez-Biezma & López de Silanes 1999) (Table 3). However, most of these species are poorly differentiated from related species



TABLE 3. *Lichen species regarded as exclusive to ultramafic rocks*

Lichen species regarded in the past as exclusive to serpentinites	References
<i>Acarospora suzai</i> Magnusson*†	Magnusson 1924; Wirth 1972; Hafellner 1991
<i>Aspicilia crusii</i> Klem.*	Krause & Klement 1958; Ritter-Studnička & Klement 1968; Hafellner 1991
<i>Aspicilia polychroma</i> (Anzi) Nyl. var. <i>ochracea</i> Anzi*†	Anzi 1860; Krause & Klement 1958; Ritter-Studnička & Klement 1968 Huuskonen 1949 (in Hafellner 1991); Ritter-Studnička & Klement 1968; Wirth 1972; Hafellner 1991
<i>Aspicilia serpentinicola</i> (Suza) Räs.*	Räsänen 1947; Hafellner 1991
<i>Lecanactis serpentinicola</i> Räsänen*	Suza 1930 (in Hafellner, 1991); Wirth 1972; Hafellner 1991
<i>Lecanora dvorakii</i> Suza*†	Anzi 1868; Hafellner 1991
<i>Placidopsis dermatocarpoides</i> Anzi*	Servit 1936 (in Hafellner 1991); Hafellner 1991
<i>Polyblastia suzae</i> Servit*	Sánchez-Biezma & López de Silanes 1999
<i>Porpidia nadvornikiana</i> (Vězda) Hertel & Knoph	Ritter-Studnička & Klement 1968
<i>Rhizocarpon sphaericum</i> (Schaer.) Mig.*†	Mayrhofer & Poelt 1979; Hafellner 1991
<i>Rinodina serpentina</i> Mayrhofer & Poelt*†	Poelt 1975; Hafellner 1991
<i>Squamarina serpentina</i> Poelt*	Servit 1952 in Hafellner 1991
<i>Verrucaria serpentinicola</i> Servit*	

\*Species which have also been recorded on other mafic rocks.

†Species still not considered to be valid taxa.

and many of them have also later been found on basic siliceous substrata (Wirth 1972; Hafellner 1991). Some of these species have been considered characteristic of the habitat and used for the syntaxonomic definition of serpentiniculous lichen communities. Krause & Klement (1958, 1962) described in the Balkan Peninsula the association *Aspicilietum ochraceae* with *Aspicilia crusii*, *A. polychroma* var. *ochracea*, *A. serpentinicola*, *Caloplaca festiva*, *Placodium diffractum*, *P. subcircinatum*, *Rhizocarpon sphaericum*, as characteristic species. Wirth (1972) described in Germany the association *Aspicilietum serpentinicolae* with *Aspicilia serpentinicola* as characteristic and *Acarospora suzai*, *Caloplaca festiva*, *C. fuscoatra*, *C. irrubescens*, *Candelariella vitellina*, *Lecidella carpathica*, *Rhizocarpon viridiatum*, as companions. Other syntaxonomic groupings are: *Parmelietum conspersae* Klement 1931 (characteristic species: *Parmelia conspersa*, *P. glomellifera*) and *Staurotheletum fissae* Klement 1931 (characteristic species: *Staurothele fissa*, *Verrucaria silicea*).

### Serpentinomorphosis

There have been only a few reports of serpentinomorphoses in lichens. Suza (1927), the first to study lichens colonizing ultramafic rocks, mentioned the occurrence of stenophyllum in certain species (Rune 1953). Sambo (1937) described *Diploschistes ocellatus* DC. var. *serpentinicola* present on the serpentinites of Monte Ferrato (Tuscany, Italy) as being characterized by underdeveloped slender thalli and by smaller and less frequent apothecia (dwarfism). These observations have not been confirmed by more recent workers (Krause & Klement 1958; Wirth 1972; Hafellner 1991).

Accumulation of Fe by species occurring on ultramafic rocks from Bosnia and Lapland has been reported to produce ochraceous forms of *Aspicilia polychroma* [var. *ochracea* (Krause & Klement 1958)], *Lecidea macrocarpa* [f. *oxydata* (Ritter-Studnička & Klement 1968)], and *Lecidea lapicida* [f. *ochromeliza* (Räsänen 1953 in Purvis & Halls 1996)]. This phenomenon is also reported by Sánchez-Biezma Serrano

and co-authors (2001). Rust coloured forms, however, have also been frequently reported from many different rocks containing mafic minerals (Purvis & Halls 1996 and refs. therein).

### Characteristic vegetation

If the evidence for serpentinophytes and 'serpentinomorphoses' is scant, the hypothesis that certain species are characteristic of ultramafics, albeit limited to a certain geographical area, is more substantive. In adjacent areas, characterized by the occurrence of mafic and ultramafic rocks, Suza (1927), Sirois *et al.* (1987), Sánchez-Biezma Serrano *et al.* (2001) and Piervittori *et al.* (2004) have all reported the existence of a characteristic lichen flora on each substratum. For example, Sirois *et al.* (1987) reported that 40.1% of species were restricted to ultramafics, while 22.3% of species were limited to amphibolite; Sánchez-Biezma Serrano (2001) noted that 16% of species were limited to ultramafics and Piervittori *et al.* (2004) reported that 31.4% of species were limited to ultramafics while 11.4% were confined to metagabbros. Some of these authors noted a stronger relationship between saxicolous lichens and ultramafic substrata than between terricolous lichens and ultramafics (Sirois *et al.* 1987; Piervittori *et al.* 2004).

Locally differentiated lichen communities have been reported on different ultramafic rocks of Unst (Shetland, UK) by James & Purvis (Proctor 1992). Moreover, the lichen vegetation of the serpentinized harzburgite and dunites of Unst appears similar, though poorer, than that of serpentinites outcropping on the Lizard peninsula (Cornwall, UK) (Gilbert & James 1987; Gilbert 2000). An even lower number of species has been reported from the non-serpentinized ultramafic rocks of the layered igneous complex of Rhum (Scotland, UK) (Gilbert 1983). In California, serpentinized dunites host a poorer lichen flora than other serpentinized ultramafics (Sigal 1989).

Sometimes the xerophytic character of ultramafic lichen communities has been

noted (Suza 1927; Krause & Klement 1958; Piervittori *et al.* 2004), and the poverty of flowering plants in some areas appears to promote a photophilic lichen flora (Sánchez-Biezma Serrano *et al.* 2001; Piervittori *et al.* 2004).

### Co-existence of silicolous and calcicolous species on ultramafics

As is the case for flowering plants, a broad co-existence of silicolous and calcicolous species has been reported for the lichen flora of ultramafic environments (Sambo 1927; Krause & Klement 1958, 1962; Jørgensen 1974 in Purvis & Halls 1996; Takala & Seaward 1978; Sirois *et al.* 1987; Gilbert & James 1987; Ryan 1988; Kossowska 2001). This co-existence obviously depends on the chemical composition of the ultramafics, which contain a higher concentration of Si (absent in limestone or dolostone), Ca and Mg than basic, intermediate ( $52 < \text{SiO}_2 < 63\%$  wt as granites) and acid rocks ( $\text{SiO}_2 > 63\%$  wt as quartzites). Prevalence of a silicolous component in lichen communities is stressed by several authors (Suza 1921 in Purvis & Halls 1996; Ritter-Studnička & Klement 1968; Gilbert 1983; Gilbert & James 1987; Hafellner 1991; Sánchez-Biezma Serrano *et al.* 2001; Piervittori *et al.* 2004), although in some cases the strongest acidophytic component (e.g. *Rhizocarpon geographicum* s.l.) is absent (Yoshimura & Yamanaka 1962; Wirth 1972; Gilbert & James 1987; James & Purvis in Proctor 1992; Kossowska 2001). The number of 'calciphilous' species has been reported to be enhanced by the occurrence of ornithocoprophilous species (Suza 1927; Piervittori *et al.* 2004) which often favour calcareous substrata.

### Ultramafics and distribution

*Porpidia nadvornikiana* (Vězda) Hertel & Knoph, has been recorded in Europe only at two very disjunct sites, both on ultramafic rocks: the East Sudety Mountains (Czech Republic) and the Sierra do Careón (Spain) (Sánchez-Biezma & López de Silanes 1999).

Similarly *Cladonia praetermissa* var. *modesta* Kantvilas has been reported only on ultramafic soils in East Africa (Mt. Kenya) and on peaty and inorganic soils on ultramafics in Australia and Tasmania (Kantvilas 1991).

The latitudinal limits of some lichen species occur in areas with serpentinized ultramafic rocks, perhaps suggesting that the substratum provides particularly favourable growth conditions or freedom from competition (Sambo 1927; Wirth 1972; Gilbert 2000). For example, some Mediterranean species occurring in Britain (*Solenospora liparina*, *Collema latzelii*) are confined to the Lizard serpentinites (Gilbert 2000). *Lichinella stipatula*, *Toninia cinereovirens* and *Caloplaca rubelliana* have their northermost limit of distributions on ultramafics of Central Europe (Wirth 1972). There are only a few reports concerning the influence of ultramafic rocks on altitudinal distribution of lichens, for example Sigal (1989) reported eight species on serpentinites at lower altitudes than on non-ultramafic rocks.

### Lichen-ultramafic substrata interactions

#### Effects of heavy metals

There are very few studies of the accumulation of heavy metals in lichens on ultramafics. However, Paribok & Alexeyeva-Popova (1966) reported high concentrations of Fe, Ni, Cr, Co, Pb and Sn in the ash from lichens on ultramafic soils in the Polar Urals. High concentrations of metals in rocks colonized by crustose lichens may induce the mycobiont to activate detoxification mechanisms. Various authors (Sambo 1937; Wilson *et al.* 1981; Purvis 1984; Garty 1993; Sayer & Gadd 1997) have suggested that the production of oxalic acid, given its chelating activity, is a detoxification mechanism. A detoxification mechanism was attributed to the production of copper oxalate (mooloite) and manganese oxalate (allivarite) within lichen thalli growing on substrata rich in Cu and Mn, respectively (Purvis 1984; Wilson & Jones 1984). Similarly the presence of magnesium oxalate dihydrate (ghushinskite)

in thalli colonizing ultramafic rocks was postulated as a detoxification mechanism (Sambo 1937; Wilson *et al.* 1981), although the product was not consistently present. Calcium oxalate monohydrate and dihydrate (whewellite and weddellite, respectively) accumulate in lichen thalli, not only on strictly calcareous rocks, but also on other substrata including ultramafics (Wilson *et al.* 1981; Adamo *et al.* 1993; Adamo & Violante 2000). Sayer & Gadd (1997) suggested that the biocrystallization of the products functions as a detoxification mechanism for excess Ca, while Wadsten & Moberg (1985) considered these crystalline products to be a water and Ca reserve necessary for the survival of the symbiosis.

#### Weathering action of lichens

Mineralogical and structural characters of ultramafic rocks determine the intergranular and intragranular passageways for hyphal penetration. Foliated serpentinites are usually penetrated along the foliations which follow the orientation of the serpentine minerals. The cleavage planes of pyroxenes represent the main passageways for the penetration of hyphae into the massive serpentinites. The depth of penetration of hyphae into serpentinites often reaches 2 mm and is comparable with data obtained from other rocks (R. Piervittori, unpublished data).

Lichen growth on serpentinites promotes biogeochemical processes which influence the weathering rate of the original mineral in the rocks and the appearance of new minerals (Wilson *et al.* 1981; Adamo *et al.* 1993). The primary phases may be completely altered by lichen action; for example, in a Scottish serpentinite, serpentine was completely depleted of Mg for 200 µm beneath lichen thalli (Wilson *et al.* 1981). Many secondary minerals, often characterizing serpentine soils (vermiculite, illite, montmorillonite), are very common beneath lichens (R. Piervittori, unpublished data). As discussed above, the production of oxalic acid by the lichen mycobionts promotes the deposition of Ca- and Mg-oxalates (whewellite, weddellite and glushinskite) (Sambo

1937; Wilson *et al.* 1981; Adamo *et al.* 1993).

### Conclusions and perspectives

Until now lichens on ultramafics have been considered an interesting subject because of the particular ecological features determined by the chemical properties of the mineral substrata.

Some characteristics of lichens in ultramafic environments, such as the co-presence of acidophytic (silicolous) and basiphytic (calicolous) species and the occurrence of species characterized by particular distribution areas, match some of the main ecological features of flowering plants. Other typical characteristics of phanerogams on ultramafics, however, such as the paucity of species, low cover, and the occurrence of particular ecotypes, are not consistent features of lichen communities on ultramafics, possibly because of the influence of several other environmental factors in addition to the substratum. These characteristics clearly need further investigation.

High concentrations of heavy metals in lichen thalli on ultramafic substrata deserve further study. The unusual chemical composition of ultramafics make these substrata interesting habitats for the study of tolerance and detoxification mechanisms in lichens. For example, there is very little information on the physiological responses of lichen symbionts to the high concentration of metals such as magnesium and nickel in ultramafics.

Beyond the ecological and physiological significance of lichen growth in ultramafic habitats, some ultrabasic rocks, particularly serpentinites, are noteworthy as sources of asbestiform minerals, investigated intensively for their importance for human health. In this context, with regard to the bioweathering action, our group is examining lichen interactions with asbestos-rich serpentinites (Favero-Longo *et al.* 2004) to discover if lichen action could significantly modify the pathogenetic effects of asbestos minerals.

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