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Lichen-plant interactions

Sergio E. Favero-Longo & Rosanna Piervittori

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Abstract

Controversial data on the pathways and effects of lichen growth on and near bryophytes and vascular plants are reviewed. In most cases, plants which are used as growth substrates positively influence lichen mineral nutrition and are poorly affected by lichen overgrowth, but several reports of negative relationships, including lichen parasitism and allelopathic interferences, prevent generalizations. The allelopathy of terricolous lichens against neighboring plants has been suggested by *in vitro* investigations, and a multidirectional phytotoxic mode of action has been shown for lichen secondary metabolites. Recent researches on field settings, instead, offer little support of lichen allelopathy, and plant allelopathy against lichens has so far been neglected. A comparison with lichen-rock interactions indicates that a common set of physical and chemical factors can explain the heterogeneous reciprocal effects that exist between lichens and plants, which depend on the species involved, and highlights gaps that need further studies.

Keywords: allelopathy, epiphytes, lichen-rock interactions, lichen secondary metabolites, plant health, terricolous lichens,

Introduction

Land plants, including bryophytes and vascular plants, are both growth substrates of lichens and their potential competitors in colonizing soil surfaces (van Halowyn and Lerond [1993 Van Halowyn, C](#) and [Lerond, M](#). 1993. *Guide des Lichens*, Paris: Édition Lechevalier.). Several studies have been performed on lichen-plant interactions, but their different aims and experimental approaches have often resulted in seemingly contradictory data which support long-term controversies on the lichen effect on plants and the plant effect on lichens. The recognition of a negative impact of air pollution on lichens soon strengthened the assertion of their fundamental dependence on the atmosphere and of their use of plants as mere points of support (Richard 1891 in Grilli [1892 Grilli, C](#). 1892. *Osservazioni sopra una questione di fisiologia vegetale relativa ai licheni per O.J. Richard*, Castelplanio: Tipografia Luigi Romagnoli. ; Acloque [1893 Acloque, A](#). 1893. *Les Lichens. Étude sur l'anatomie, la physiologie et la morphologie de l'organisme lichénique*, Paris: J.B. Baillièrre et Fils. ; Nylander [1896 Nylander, W](#). 1896. *Les lichens des environs de Paris*, Paris: Typographie Paul Schmidt.), as epiphytes (*sensu* Barkman [1958 Barkman, JJ](#). 1958. *Phytosociology and ecology of cryptogamic epiphytes*, Assen, , The Netherlands: van Gorcum & Comp. N.V.). However, the penetration of lichen hyphae within bryophyte and plant tissues was also observed early on, a fact that suggested parasitic relationships (Zukal [1879 Zukal, H](#). 1879. *Das Zusammenleben von Moos und Flechte*. *Oesterr Botan Zeitschrift*, 29: 189–191. ; Fink [1913 Fink, B](#). 1913. The nature and classification of lichens-II. The lichen and its algal host. *Mycologia*, 5: 97–166.) and justified the practice of some orchard owners in Europe and North America to destroy lichens with biocides (e.g., copper sulphate) in order to have lichen-free, more robust fruit trees (Hale [1967 Hale, ME](#). 1967. *The biology of lichens*, London: Edward Arnold (Publishers) Ltd.). It has been recognized for a long time that nutrient dissolution from the plant substrate provides mineral nutrition to epiphytic lichen communities (Des Abbayes [1951 Des Abbayes, H](#). 1951. *Traité de Lichénologie*. *XLI*, Paris: Lechevalier Éditeur. ; Nash [2008 Nash TH III](#). 2008. *Lichen biology*, 2nd ed. Chapter 12. Nutrients, elemental

accumulation, and mineral cycling . Cambridge, , UK : Cambridge University Press . 234 251 .), but the inhibition of lichens by bark compounds has also recently been claimed (Koopmann et al. [2007 Koopmann, R, Stevens, H, Franzen-Reuter, I, Frahm, JP and Grote, M.](#) 2007. *In vitro* inhibition of soredial growth in the epiphytic lichen *Physcia tenella* (Ascomycetes: *Lecanorales*) by a variety of bark phenols. *Lichenologist.*, 39(6): 567–572.). Several *in vitro* studies suggest that competitive relationships between terricolous lichens and plants depend on allelopathic interferences (Lawrey [1984 Lawrey, JD.](#) 1984. *Biology of lichenized fungi*, New York: Praeger Publishers. , [1986 Lawrey, JD.](#) 1986. Biological role of lichen substances. *Byrologist.*, 89(2): 111–122. , [2009 Lawrey, JD.](#) 2009. *Diversity of defensive mutualisms. Chapter 11. Chemical defense in lichen symbiosis*, 167–181. London: Taylor and Francis Group.), but recent ecological investigations do not support this finding (Kytöviita and Stark [2009 Kytöviita, MM and Stark, S.](#) 2009. No allelopathic effect of the dominant forest-floor lichen *Cladonia stellaris* on pine seedlings. *Funct Ecol.*, 23: 435–441.).

This body of controversial information on lichen-plant interactions is somewhat similar to that pertaining to lichen interactions with mineral substrates, which different authors have associated to biodeterioration or bioprotection effects. In this case, however, recent improvements in the knowledge of the factors involved in lichen colonization of rocks have allowed researchers to explain the heterogeneous effects observed, which depend on the different deteriogenic abilities of the lichen species and the different physico-chemical features of the mineral substrates (e.g., St Clair and Seaward [2004 St Clair, LL and Seaward, MRD.](#) 2004. *Biodeterioration of stone surfaces. Lichens and biofilms as weathering agents of rock and cultural heritage*, Dordrecht: Kluwer Academic Publishers. ; Piervittori et al. [2009 Piervittori, R, Favero-Longo, SE and Gazzano, C.](#) 2009. Lichens and biodeterioration of stonework: A review. *Chem Today.*, 27(6): 8–10.). We hypothesize that the observed heterogeneity of reciprocal effects of lichens and plants could be similarly explained if the factors involved in their interaction were considered altogether in the context of each case study.

This paper critically reviews literature which has, in various ways, considered the pathways and effects of lichen growth on and near bryophytes and vascular plants. The factors involved in the lichen-plant interactions, which have received different emphasis in old and recent investigations from the ultrastructural to the ecosystem level, are discussed, with particular attention to allelopathic interferences.

Land plants as growth substrates for lichens

Lichen growth on bryophytes

Bryophytes host about 350 bryosymbiotic fungal species, including lichenized ones (musci-colous lichens), which display pathogenic, parasitic, saprophytic and commensal interactions to various extents (Stenroos et al. [2009 Stenroos, S, Lukka, T, Huhtinen, S, Döbbeler, P, Myllys, L, Syrjänen, K and Hyvönen, J.](#) 2009. Multiple origins of symbioses between ascomycetes and bryophytes suggested by a five-gene phylogeny. *Cladistics.*, 25: 1–20.). Lichen overgrowth on mosses has frequently been correlated to high light and low moisture conditions (During and van Tooren [1990 During, HJ and van Tooren, BF.](#) 1990. Bryophyte interactions with other plants. *Bot J Linn Soc.*, 104: 79–98. ; Sedia and Ehrenfeld [2003 Sedia, EG and Ehrenfeld, JG.](#) 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey Pineland. *Oikos.*, 100: 447–458.).

Although no biological relationships generally exist between most musci-colous lichens and the bryophytes on which they grow (Poelt [1985 Poelt, J.](#) 1985. Über auf Moosen parasitierende Flechten. *Sydowia.*, 38: 241–254.), some epiphytic species display obligate specificity to their phorophyte (i.e., host plant, *sensu* Barkman [1958 Barkman, JJ.](#) 1958. *Phytosociology and ecology*

of cryptogamic epiphytes, Assen, , The Netherlands: van Gorcum & Comp. N.V.) (During and van Tooren [1990 During, HJ](#) and [van Tooren, BF](#). 1990. Bryophyte interactions with other plants. *Bot J Linn Soc.*, 104: 79–98.) and some species have been shown to kill their moss substrate by modifying microclimatic factors (e.g., light irradiance; Jahns [1982 Jahns, HM](#). 1982. The cyclic development of mosses and the lichen *Baeomyces rufus* in an ecosystem. *Lichenologist.*, 14: 261–265.). A similar process likely accounts for the development of the multi-layered polar cryptogamic vegetation, which, in the late successional stage, displays moribund mosses covered by fruticose and crustose lichens (Lewis Smith [1972 Lewis Smith, RI](#). 1972. Vegetation of the South Orkney Islands with particular reference to Signy Island. *British Antarctic Survey Scientific Rep.*, 68: 1–124. ; Longton [1988 Longton, RE](#). 1988. *Biology of polar bryophytes and lichens*, Cambridge, , UK: Cambridge University Press. ; Øvstedal and Lewis Smith [2001 Øvstedal, DO](#) and [Lewis Smith, RI](#). 2001. *Lichens of Antarctica and South Georgia*, Cambridge, , UK: Cambridge University Press.). Moreover, the hyphae of a small group of species cover the cell walls of mosses and liverworts with appressoria-like structures and, in some cases, penetrate them with haustoria; they grow inside the leaf cells and develop ascocarps within/between the leaves (Döbbeler and Poelt [1981 Döbbeler, P](#) and [Poelt, J](#). 1981. *Arthopyrenia endobrya*, spec. nov. eine hepaticole Flechte mit intrazellulärem Thallus aus Brasilien. *Pl Syst Evol.*, 138: 275–281. ; Poelt [1985 Poelt, J](#). 1985. Über auf Moosen parasitierende Flechten. *Sydowia.*, 38: 241–254. ; During and van Tooren [1990 During, HJ](#) and [van Tooren, BF](#). 1990. Bryophyte interactions with other plants. *Bot J Linn Soc.*, 104: 79–98.). Such lichens, which mainly belong in lichenized Lecanoromycetes, generally display a strong specialization towards their hosts and behave as (necrotrophic-) parasites (Poelt [1985 Poelt, J](#). 1985. Über auf Moosen parasitierende Flechten. *Sydowia.*, 38: 241–254. ; Stenroos et al. [2009 Stenroos, S, Lukka, T, Huhtinen, S, Döbbeler, P, Myllyls, L, Syrjänen, K](#) and [Hyvönen, J](#). 2009. Multiple origins of symbioses between ascomycetes and bryophytes suggested by a five-gene phylogeny. *Cladistics.*, 25: 1–20.). The clinging of hyphae to moss cells has been correlated, in the case of the crustose *Amphiloma lanuginosum* (syn. *Lepraria membranacea*) on *Grimmia* sp., to the dissolution of the pectinized region of the cell wall (McWhorter [1921 McWhorter](#) . 1921 . Destruction of mosses by lichens . *Bot Gaz* . 72 : 321 325). The hyphal penetration through the cell wall has been related, in the case of the foliose *Peltigera canina*, to the production of multiple isoforms of β -1,4-glucanase (de los Ríos et al. [1997 de los Ríos, A, Ramirez, A](#) and [Estévez, P](#). 1997. Production of several isoforms of β -1,4-glucanase by the cyanolichen *Peltigera canina*. *Physiol Plant.*, 100: 159–164.). The crustose *Ochrolechia frigida* colonizes its moss substrate as a gelatinous aposymbiotic prothallus which behaves, in various ways, in its early stages of development, as a saprotroph, a commensal, a biotrophic or necrotrophic parasite: hyphae grow in the moss tissues, penetrate and actively kill the cells, efficiently overgrow the organic substrate and provide a favorable microhabitat for the development of the lichenized thallus and its ascocarps (Gassmann and Ott [2000 Gassmann, A](#) and [Ott, S](#). 2000. Growth strategy and the gradual symbiotic interactions of the lichen *Ochrolechia frigida*. *Plant Biol.*, 2: 368–378.). *O. frigida* is thus parasitically or saprotrophically supplemented by nutrients and thus less dependent on the short-term photosynthetic activity of its photobionts in arctic-alpine climates (Gassmann and Ott [2000 Gassmann, A](#) and [Ott, S](#). 2000. Growth strategy and the gradual symbiotic interactions of the lichen *Ochrolechia frigida*. *Plant Biol.*, 2: 368–378.).

Lichen growth on mature bryophytes can thus be associated, depending on the species involved, to: (a) no biological interaction (most cases), (b) an indirect interaction through the modification of climate factors, or (c) parasitic or saprotrophic interactions. A parasitic stage was also hypothesized early on for mycobiont mycelia growing on moss protonemata, before the establishment of the symbiosis with their algal photobionts (Bonnier [1889 Bonnier, G](#). 1889. Germination des lichens sur les protonemas des mousses. *Rev Gén Bot.*, 1: 165–169.). However, the growth, in the laboratory, of the mycobionts of *Cladonia foliacea* and *C. grayi* on protonemata does not lead to the formation of appressoria or an increase in hyphal lateral branching, which characterize the early

contact stages of fungi with symbiotic green algae, and the growth of protonemata slows down only upon incubation with *C. foliacea* (Giordano et al. [1999 Giordano, S, Alfano, F, Basile, A and Castaldo Cobianchi, R](#). 1999. Toxic effects of the thallus of the lichen *Cladonia foliacea* on the growth and morphogenesis of bryophytes. *Cryptogamie Bryol.*, 20(1): 35–41. ; Joneson and Lutzoni [2009 Joneson, S and Lutzoni, F](#). 2009. Compatibility and thigmotropism in the lichen symbiosis: A reappraisal. *Symbiosis.*, 47: 109–115.).

Lichen growth on vascular plants

Lichens use living plants, dead wood and plant detritus as substrates (van Halowyn and Lerond [1993 Van Halowyn, C and Lerond, M](#). 1993. *Guide des Lichens*, Paris: Édition Lechevalier.). Lichen species are rarely found on both live and dead (decorticate-) wood: logs, snags, stumps and branches often host characteristic communities that include many specialized species (epixylic or lignicolous lichens), depending on the type of wood and on the stage of decay (Brodo et al. [2001 Brodo, IM, Duran Sharnoff, S and Sharnoff, S](#). 2001. *Lichens of North America*, New Haven: Yale University Press. ; Caruso et al. [2008 Caruso, A, Rudolphi, J and Thor, G](#). 2008. Lichen species diversity and substrate amounts in young planted boreal forests: A comparison between slash and stumps of *Picea abies*. *Biol Conserv.*, 141: 47–55. ; Nascimbene et al. [2008 Nascimbene, J, Marini, L, Motta, R and Nimis, PL](#). 2008. Lichen diversity of coarse habitats in a *Pinus-Larix* stand in the Italian Alps. *Lichenologist.*, 40(2): 153–163. ; Osyczka and Wee, grzyn [2008 Osyczka, P and We, grzyn, M](#). 2008. Lichens on lignum in the coastal regions of west Spitsbergen (Svalbard). *Biologia.*, 63(6): 1069–1072. ; Spribille et al. [2008 Spribille, T, Thor, G, Brunnell, FL, Goward, T and Björk, CR](#). 2008. Lichens on dead wood: Species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. *Ecography.*, 31: 741–750.).

The growth of lichens on living plants, which was first reported by Theophrastus when he introduced the term ‘lichen’ (Hawksworth and Hill [1984 Hawksworth, DL and Hill, DJ](#). 1984. *The lichen-forming fungi*, Glasgow and London: Blackie.), involves both pteridophytes (e.g., Roberts et al. [2005 Roberts, NR, Dalton, PJ and Jordan, GJ](#). 2005. Epiphytic ferns and bryophytes of Tasmanian tree-ferns: A comparison of diversity and composition between two host species. *Austral Ecol.*, 30: 146–154.) and phanerogams, with different communities occurring on fronds/leaves (foliicolous l.) and shoots (corticolous l.) (van Halowyn and Lerond [1993 Van Halowyn, C and Lerond, M](#). 1993. *Guide des Lichens*, Paris: Édition Lechevalier.).

Do plants influence foliicolous lichen communities?

More than 800 species from various lineages of lichen forming fungi grow on the surface of living pteridophyte fronds (e.g., Nowak and Winkler [1975 Nowak, R and Winkler, S](#). 1975. Foliicolous lichens of Chóco, Colombia, and their substrate abundances. *Lichenologist.*, 7: 53–58. ; Farkas [1987 Farkas, E](#). 1987. Foliicolous lichens of the Usambara Mountains, Tanzania I. *Lichenologist.*, 19(1): 43–59. ; Weber [1993 Weber, WA](#). 1993. Additions to the Galápagos and Cocos Islands lichen and bryophyte floras. *Bryologist.*, 96(3): 431–434. ; Gradstein et al. [1996 Gradstein, SR, Hietz, P, Lücking, R, Lücking, A, Sipman, HJM, Vester, HFM, Wolf, JHD and Gardette, E](#). 1996. How to sample the epiphytic diversity of tropical rain forests. *Ecotropica.*, 2: 59–72.) and phanerogam leaves (Lücking [2008 Lücking, R](#). 2008. *Foliicolous lichenized fungi*, New York: Botanical Garden Press.). They are largely confined to and characterize tropical rain forests, but also subordinately occur in extratropical regions (Lücking [2008 Lücking, R](#). 2008. *Foliicolous lichenized fungi*, New York: Botanical Garden Press.). Foliicolous lichen communities seem to be poorly influenced by the phorophyte species, as also suggested by the complete life cycles, including reproductive stages, observed on plastic cover slips during *in situ* controlled experiments (Sanders [2002 Sanders, WB](#). 2002. *In situ* development of the foliicolous lichen *Phyllophiale* (Trichotheliaceae) from propagule

germination to propagule production. *Am J Bot.*, 89(11): 1741–1746. , [2005 Sanders, WB](#). 2005. Observing microscopic phases of lichen life cycles on transparent substrata placed *in situ*. *Lichenologist.*, 37(5): 373–382.). Nevertheless, slight differentiation has been observed in some cases, which has been assigned to leaf characteristics, such as surface structure and longevity (Nowak and Winkler [1975 Nowak, R](#) and [Winkler, S](#). 1975. Foliicolous lichens of Chóco, Colombia, and their substrate abundances. *Lichenologist.*, 7: 53–58. ; Pinokiyo et al. [2006 Pinokiyo, A, Singh, KP](#) and [Singh, JS](#). 2006. Leaf-colonizing lichens: Their diversity, ecology and future prospects. *Curr Sci.*, 90(4): 509–518. ; Lücking [2008 Lücking, R](#). 2008. *Foliicolous lichenized fungi*, New York: Botanical Garden Press.), while chemical influences have never been invoked. A predominance of some foliicolous species on fern fronds, with respect to dicotyledonous leaves, has also been reported (Nowak and Winkler [1975 Nowak, R](#) and [Winkler, S](#). 1975. Foliicolous lichens of Chóco, Colombia, and their substrate abundances. *Lichenologist.*, 7: 53–58.). Hairs and glands have been suggested to retard epiphyll colonization, while recent experiments have shown that drip tips can favor lichen colonization by influencing water drainage (Lücking [2008 Lücking, R](#). 2008. *Foliicolous lichenized fungi*, New York: Botanical Garden Press.).

How do lichens colonize and affect leaves?

All foliicolous species colonize the upper surface of leaves (epiphyllous), with the exception of *Strigula janeirensis*, which has been reported on the lower surface (hypophyllous) (Pinokiyo et al. [2006 Pinokiyo, A, Singh, KP](#) and [Singh, JS](#). 2006. Leaf-colonizing lichens: Their diversity, ecology and future prospects. *Curr Sci.*, 90(4): 509–518.). As they also colonize plants of economic value, such as coffee, tea, cacao and rubber, they are generally considered as pests by tropical farmers (Hale [1967 Hale, ME](#). 1967. *The biology of lichens*, London: Edward Arnold (Publishers) Ltd. ; Honegger [2006 Honegger, R](#). 2006. *Fungi in the environment. Chapter 9, Water relations in lichens*, 185–200. Cambridge, , UK: Cambridge University Press.). Eufoliicolous taxa are restricted to leaves: they mostly display thin crustose thalli adnate to the substrate, are poor in or lack secondary metabolites, exhibit shorter life-cycles and higher growth rates than other ecological groups of lichens, and thus adapt to the ephemeral nature of leaves which rarely exceed 24–36 months of lifetime (Grübe and Lücking [2002 Grübe, M](#) and [Lücking, R](#). 2002. Fine structures of foliicolous lichens and their lichenicolous fungi studied by epifluorescence. *Symbiosis.*, 32: 229–246. ; Lücking [2008 Lücking, R](#). 2008. *Foliicolous lichenized fungi*, New York: Botanical Garden Press.). The use of clear nail varnish has been suggested as an efficient way of removing foliicolous thalli from their substrate, without leaving lichen material behind (Grübe [2001 Grübe, M](#). 2001. A simple method to prepare foliicolous lichens for anatomical and molecular studies. *Lichenologist.*, 33: 547–550.): A thin layer of mucilage, probably produced by papillose appendages that grow from the lowermost hyphal layer, only contributes to the adhesion of thalli to leaves, but the leaves are not penetrated (Modenesi et al. [1986 Modenesi, P, Lajolo, L](#) and [Dondero, G](#). 1986. Acid carbohydrates in the hypothallus of *Catillaria boutellei* (Desm.) Zahlbr. *A histochemical localization. Cryptogamie Bryol Lichénol.*, 7: 1–10. ; Grübe and Lücking [2002 Grübe, M](#) and [Lücking, R](#). 2002. Fine structures of foliicolous lichens and their lichenicolous fungi studied by epifluorescence. *Symbiosis.*, 32: 229–246.). Only some species of *Strigula* grow below the cuticle layer, where their photobiont *Cephaleuros* lives as a parasite of the leaf tissue; some of them have been observed to damage their living substrate, but their potential semiparasitic lifestyle still needs further investigation (Lücking [2008 Lücking, R](#). 2008. *Foliicolous lichenized fungi*, New York: Botanical Garden Press.). Pseudofoliicolous lichens, including filamentous and small-foliose species, grow and reproduce on different substrates, including leaves, while facultative foliicolous lichens mainly grow on other substrates and are only occasionally found on leaves, on which they do not reproduce (Sérusiaux 1977 in Lücking [2008 Lücking, R](#). 2008. *Foliicolous lichenized fungi*, New York: Botanical Garden Press.).

Cover values of around 50% of the leaf surface can determine a light interception that ranges from 30–70%, which is significantly lower than that of other lichen groups, e.g., saxicolous. Interestingly, some plants, i.e., *Calamus australis* (Arecaceae) and *Lindsayomyrtus racemoides* (Myrtaceae), display significantly higher chlorophyll contents and lower saturation irradiance in areas covered by lichens, indicating the acclimatation of leaves to lichen shading (Anthony et al. [2002 Anthony, PA, Holtum, JAM and Jackes, BR](#). 2002. Shade acclimation of rainforest leaves to colonization by lichens. *Funct Ecol.*, 16: 808–816. ; Moore [2003 Moore, PD](#). 2003. Shady deals with lichens. *Nature.*, 421: 591–593.).

As in most cases the physical interaction between thalli and leaves is scarce and the latter balance the indirect effects due to light interception, the occurrence of foliicolous lichens on plants mostly appears to be a neutral factor for plant health.

Do plants influence corticolous lichen communities?

The occurrence of a distinctive set of lichen species on the bark of different plant species in the same sites highlights the influence of the substrate on the composition of corticolous communities (Lawrey [1984 Lawrey, JD](#). 1984. *Biology of lichenized fungi*, New York: Praeger Publishers. ; Brodo [1973 Brodo, IM](#). 1973. *The lichens. Chapter 12, Substrate ecology*, 401–441. New York: Academic Press. ; van Halowyn and Lerond [1993 Van Halowyn, C and Lerond, M](#). 1993. *Guide des Lichens*, Paris: Édition Lechevalier. ; Brodo et al. [2001 Brodo, IM, Duran Sharnoff, S and Sharnoff, S](#). 2001. *Lichens of North America*, New Haven: Yale University Press. ; Nash [2008 Nash TH III](#) . 2008 . *Lichen biology* , 2nd ed . Chapter 12. Nutrients, elemental accumulation, and mineral cycling . Cambridge, , UK : Cambridge University Press . 234 251 .). Bark properties, including texture, chemistry and water holding capacity, mainly determine different communities on different phanerogamic trees (e.g., lichens of the acidic bark of conifers and *Betula*; lichens of the more neutral bark of *Fraxinus* and *Tilia*) (Nash [2008 Nash TH III](#) . 2008 . *Lichen biology* , 2nd ed . Chapter 12. Nutrients, elemental accumulation, and mineral cycling . Cambridge, , UK : Cambridge University Press . 234 251 .) in the same way that rock properties, including surface roughness, mineral composition and internal porosity, determine saxicolous communities (e.g., Brodo [1973 Brodo, IM](#). 1973. *The lichens. Chapter 12, Substrate ecology*, 401–441. New York: Academic Press.). It is worth noting that some corticolous species have been reported more on the tree fern trunks of *Dicksonia antarctica* than on other rainforest phanerogamic trees (Ford and Gibson [2000 Ford, S and Gibson, M](#). 2000. Lichens of the soft tree-fern *Dicksonia antarctica* Labill. in Victorian rainforests. *Victor Natural.*, 117(5): 172–179.). Moreover, epiphytic communities are influenced to a great extent by variations in microclimates, both vertically along the trunk and between the different tree fractions (e.g., trunk, branches). These variations are determined by interactions between the regional climate, tree architecture and bark properties (van Halowyn and Lerond [1993 Van Halowyn, C and Lerond, M](#). 1993. *Guide des Lichens*, Paris: Édition Lechevalier. ; Caruso and Thor [2007 Caruso, A and Thor, G](#). 2007. Importance of different tree fractions for epiphytic lichen diversity on *Picea abies* and *Populus tremula* in mature managed boreonemoral Swedish forests. *Scand J Forest Res.*, 22: 219–230.). The position of a branch along the tree trunk influences the accumulation of fruticose lichen biomass, which decreases from the top of the tree to the base (Arseneau et al. [1998 Arseneau, MJ, Ouellet, JP and Sirois, L](#). 1998. Fruticose arboreal lichen biomass accumulation in an old-growth balsam fir forest. *Can J Bot.*, 76: 1669–1676.).

Crustose and foliose lichens, appressed to the bark, significantly profit from nutrients dissolved from the substrate and are thus affected by the bark chemistry and pH, which, in live trunks, ranges from acidic to around neutral (Barkman [1958 Barkman, JJ](#). 1958. *Phytosociology and ecology of cryptogamic epiphytes*, Assen, , The Netherlands: van Gorcum & Comp. N.V.). In particular, epiphytic lichens seem to obtain phosphorous and potassium as leachates from other canopy

components (Nash [2008 Nash TH III](#) . 2008 . *Lichen biology* , 2nd ed . Chapter 12. Nutrients, elemental accumulation, and mineral cycling . Cambridge, , UK : Cambridge University Press . 234 251 .) and thalli of the lower canopy display higher mineral contents than those of the upper canopy (Pike [1978 Pike, LH](#). 1978. The importance of epiphytic lichens in mineral cycling. *Bryologist.*, 81(2): 247–257.).

How do corticolous lichens colonize bark?

Few corticolous lichen species develop thalli that are immersed in bark (endo- or hypo-phloedal) (Büdel and Scheidegger [2008 Büdel B. Scheidegger C](#). 2008 . *Lichen biology* , 2nd ed . Chapter 4, Thallus morphology and anatomy . Cambridge, , UK : Cambridge University Press . 40 68 .): light penetration through the transparent outer bark cells allows the photobionts to photosynthesize (Brodo et al. [2001 Brodo, IM, Duran Sharnoff, S and Sharnoff, S](#). 2001. *Lichens of North America*, New Haven: Yale University Press.). Hyphae intermingled with the bark cells characterize the ‘cortex’ of endophloedal Trypetheliaceae (e.g., *Melanotheca*, *Trypethelium*), which produce a pseudostroma that includes their fruiting bodies in a pustule primary composed of bark cells altered by the hyphae, and which possibly derive some of their nourishment from their host (Johnson [1940 Johnson, GT](#). 1940. Contributions to the study of the Trypetheliaceae. *Ann Miss Bot Gard.*, 27: 1–44.). ‘Endophloedal thalli’, however, are often confined to the corky outer periderm layers and separated from the living and photosynthetic phelloderm by suberized cork cells (Brodo [1973 Brodo, IM](#). 1973. *The lichens. Chapter 12, Substrate ecology*, 401–441. New York: Academic Press.).

Most corticolous lichens develop thalli which superficially occur on bark (epiphloedal). Contrasting observations on mycobiont penetration within bark have been reported since the end of the 19th century and have supported the divergent opinions on the lichen use of the plant substrate as a mere point of support, in the absence of hyphal penetration, or as a nutritional source contacted by penetrating hyphae (Fink [1913 Fink, B](#). 1913. The nature and classification of lichens-II. The lichen and its algal host. *Mycologia.*, 5: 97–166. ; Tobler [1925 Tobler, F](#). 1925. *Biologie der Flechten. Entwicklung und Begriff der Symbiose*, Berlin: Verlag von Gebruder Borntraeger. ; Johnson [1940 Johnson, GT](#). 1940. Contributions to the study of the Trypetheliaceae. *Ann Miss Bot Gard.*, 27: 1–44. ; Brodo [1973 Brodo, IM](#). 1973. *The lichens. Chapter 12, Substrate ecology*, 401–441. New York: Academic Press. ; Brodo et al. [2001 Brodo, IM, Duran Sharnoff, S and Sharnoff, S](#). 2001. *Lichens of North America*, New Haven: Yale University Press.). A decrease in hyphal penetration with an increase in the proportion of lichen bulk above the substrate was initially suggested (fruticose<foliose<crustose species; Fink [1913 Fink, B](#). 1913. The nature and classification of lichens-II. The lichen and its algal host. *Mycologia.*, 5: 97–166.), but this has not been confirmed from observations concerning a lack of penetration by crustose thalli of *Lecanora carpinea* within the bark of *Populus tremula* (Solhaug et al. [1995 Solhaug, KA, Gauslaa, Y and Haugen, J](#). 1995. Adverse effects of epiphytic crustose lichens upon stem photosynthesis and chlorophyll of *Populus tremula* L. *Bot Acta.*, 108: 233–239.). Moreover, only a superficial invasion of the periderm has been observed for foliose species of *Physcia*, *Dirinaria* and *Hypogymnia* (Brodo [1973 Brodo, IM](#). 1973. *The lichens. Chapter 12, Substrate ecology*, 401–441. New York: Academic Press.), while the attachment structures of common foliose (*Parmelia s.l.* sp. pl.) and fruticose (*Ramalina* and *Usnea* sp. pl.) species penetrate deeply through the cork, cortex, phloem and cambium of different plant species (Porter [1917 Porter, L](#). 1917. On the attachment organs of the common corticolous Ramalinae. *Proc Roy Irish Acad, Sect. B.*, 34: 17–32. , [1919 Porter, L](#). 1919. On the attachment organs of the common Parmeliae. *Proc Roy Irish Acad Sect. B.*, 34: 205–211. ; Brodo [1973 Brodo, IM](#). 1973. *The lichens. Chapter 12, Substrate ecology*, 401–441. New York: Academic Press. ; Legaz et al. [1988 Legaz, E, Perez-Urria, E, Avalos, A and Vicente, C](#). 1988. Epiphytic lichens inhibit the appearance of leaves in *Quercus pyrenaica*. *Biochem System Ecol.*, 16(3): 253–259.).

Hyphae of the fruticose *Evernia prunastri* penetrate within oaks (*Quercus pyrenaica*, *Q. rotundifolia*), beech (*Fagus sylvatica*) and birch (*Betula pendula*) down to the xylem vessels, widely occupy the intracellular spaces and penetrate the cells (Ascaso et al. [1980 Ascaso, C, Gonzales, C and Vicente, C](#). 1980. Epiphytic *Evernia prunastri* (L.) Ach.: Ultrastructural facts. *Cryptog Bryol Lichénol.*, 1(1): 43–51. ; Orús and Ascaso [1982 Orús, MI and Ascaso, C](#). 1982. Localización de hifas liquénicas en los tejidos conductores de *Quercus rotundifolia* Lam. *Collect Bot.*, 13(1): 325–338. ; Monsó et al. [1993 Monsó, MA, Legaz, ME and Vicente, C](#). 1993. A biochemical approach to the hemiparasitic action of the epiphytic lichen *Evernia prunastri* on *Betula pendula*. *Ann Bot Fenn.*, 30(4): 299–303.).

The lichen colonization patterns on bark therefore vary according to the different lichen and plant species involved. As the abundance and type of internal discontinuities have been shown to control the depth and pattern of penetration of saxicolous lichens within different lithotypes (Piervittori et al. [2009 Piervittori, R, Favero-Longo, SE and Gazzano, C](#). 2009. Lichens and biodeterioration of stonework: A review. *Chem Today.*, 27(6): 8–10. and references therein), the influence of different bark tissues on the hyphal penetration pattern is in particular worth further investigation. Moreover, as an abundance of free living fungi beneath corticolous lichens has been invoked for a long time (Kaufert [1937 Kaufert, F](#). 1937. Factors influencing the formation of periderm in aspen. *Am J Bot.*, 24: 24–30.), and molecular analyses have shown the occurrence of a rich fungal diversity beneath saxicolous thalli (Bjelland and Ekman [2005 Bjelland, T and Ekman, S](#). 2005. Fungal diversity in rock beneath a crustose lichen as revealed by molecular markers. *Microb Ecol.*, 49: 598–603.), the identity of hyphae observed within bark covered by lichen thalli is also worth further checks through molecular analysis. It is worth noting that the ‘lichen identity’ of the hyphae observed beneath *Evernia prunastri* was established because of the abundant occurrence of concentric bodies (Ascaso et al. [1980 Ascaso, C, Gonzales, C and Vicente, C](#). 1980. Epiphytic *Evernia prunastri* (L.) Ach.: Ultrastructural facts. *Cryptog Bryol Lichénol.*, 1(1): 43–51.), which, however, have also more recently been reported in non-lichenized fungi (Ahmadjian [1993 Ahmadjian, V](#). 1993. *The lichen symbiosis*, New York: John Wiley & Sons. ; Honegger [2006 Honegger, R](#). 2006. *Fungi in the environment. Chapter 9, Water relations in lichens*, 185–200. Cambridge, , UK: Cambridge University Press.).

To what extent do corticolous lichens affect plant health?

Corticolous lichens play different actions on plants, ranging from mechanical to chemical processes. Superficial arching of the periderm layers immediately below the fruiting bodies and, subordinately, below the areolae was accurately described and illustrated by Fry ([1926 Fry, EJ](#). 1926. The mechanical action of corticolous lichens. *Ann Bot.*, 40: 397–417.) and correlated to the mechanical action of expanding and contracting thalli during the absorption and loss of water, respectively. Such a process, which is interestingly similar to that described by the same author concerning the mechanical defoliation of rocks by saxicolous lichens (Fry [1924 Fry, EJ](#). 1924. A suggested explanation of the mechanical action of lithophytic lichens on rocks (shales). *Ann Bot.*, 38: 175–196. , [1927 Fry, EJ](#). 1927. The mechanical action of crustaceous lichens on substrata of shale, schist, limestone and obsidian. *Ann Bot.*, 41: 437–459.), has not been correlated to negative effects on plant health.

The covering of *Populus tremula* by the crustose *Lecanora carpinea* has been shown to reduce light transmission through the phellem to about one fourth and to halve the photosynthetic rate of bark (Solhaug et al. [1995 Solhaug, KA, Gauslaa, Y and Haugen, J](#). 1995. Adverse effects of epiphytic crustose lichens upon stem photosynthesis and chlorophyll of *Populus tremula* L. *Bot Acta.*, 108: 233–239.). Interestingly, *P. tremula* displays a lower chlorophyll a/b ratio in lichenized areas, which indicates adaptation to shading and, consequently, a neutral effect of lichen cover (Solhaug et

al. [1995 Solhaug, KA](#), [Gauslaa, Y](#) and [Haugen, J](#). 1995. Adverse effects of epiphytic crustose lichens upon stem photosynthesis and chlorophyll of *Populus tremula* L. *Bot Acta.*, 108: 233–239.).

Some corticolous lichens possess the needed enzymes to attack the plant substrate. The secretion of laccases by the foliose *Pseudocyphellaria aurata* has been suggested to assist the attachment of lichens to their lignin-rich substrate (Laufer et al. [2006 Laufer, Z](#), [Beckett, RP](#), [Minibayeva, FV](#), [Lüthje, S](#) and [Böttger, M](#). 2006. Occurrence of laccases in lichenized ascomycetes of the *Peltigerinae*. *Mycol Res.*, 110: 846–853.). The production of β -1,4-glucanase and a polygalacturonase by *Evernia prunastri* supports the enzymatic decomposition of cellulose and of the pectin (rhamnogalacturonide fraction) of the primary cell walls of oak tissues (Yagüe et al. [1984 Yagüe, E](#), [Orús, MI](#) and [Estevez, MP](#). 1984. Extracellular polysaccharidases synthesized by the epiphytic lichen *Evernia prunastri* (L.) Ach. *Planta.*, 160: 212–216.). The consequent hyphal inter- and intracellular penetration has been correlated to defoliation and vigor decrease of oaks induced by allelopathic processes (see the dedicated section below), while its influence on the nutritional lifestyle of lichens has not been investigated. Only in the case of the hyphal penetration by *Ochrolechia frigida* inside the vascular tissues of dwarf shrub branches and in the leaves of *Carex* spp., has the final destruction of the tissue structure been hypothetically correlated to the activation of a saprotrophic nutrition (Gassmann and Ott [2000 Gassmann, A](#) and [Ott, S](#). 2000. Growth strategy and the gradual symbiotic interactions of the lichen *Ochrolechia frigida*. *Plant Biol.*, 2: 368–378.).

The carbon-nutrition of lichens from vascular plants is thus not experimentally supported and the evidence of a direct negative effect of corticolous lichens on plant health is limited to a few specific cases. On the other hand, corticolous lichens, regardless of their hyphal penetration, may indirectly affect their plant substrate by harboring insects. It is worth noting that epiphytic lichens provide favorable conditions for the oviposition of the hemlock looper *Lambdina fiscellaria* (Lepidoptera), which is a devastating defoliator of coniferous forests in North America (Hébert et al. [2003 Hébert, C](#), [Jobin, L](#), [Auger, M](#) and [Dupont, A](#). 2003. Oviposition traps to survey eggs of *Lambdina fiscellaria* (Lepidoptera: Geometridae). *J Econ Entomol.*, 96(3): 768–776.). However, in many cases, abundant corticolous colonization is a consequence and not a driving factor of defoliation, as exemplified by the *Bryoria* colonization of defoliated, moribund parts of black-spruce trees infested by spruce budworms *Choristoneura fumiferana* (Lepidoptera; Simard and Payette [2003 Simard, M](#) and [Payette, S](#). 2003. Accurate dating of spruce budworm infestation using tree growth anomalies. *Ecoscience.*, 10(2): 204–216.).

Land plants as lichen neighbors on soil

Lichens are known to trap seeds (Sedia and Ehrenfeld [2003 Sedia, EG](#) and [Ehrenfeld, JG](#). 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey Pineland. *Oikos.*, 100: 447–458.). The fruticose saxicolous lichen *Niebla ceruchoides* has even been shown to increase seed germination, growth and the survival of *Dudleya* plants (Crassulaceae) by increasing water availability, offering a nutrient enriched seed bed and protection from herbivores (in turn *Niebla* thallus is fragmented and dispersed by the expanding plant caudex; Riefner and Bowler [1995 Riefner, RE Jr](#) and [Bowler, PA](#). 1995. Cushion-like fruticose lichens as *Dudleya* seed traps and nurseries in coastal communities. *Madrozo.*, 42: 81–82.). Some epiphytic lichens (*Parmotrema tinctorum*, with lecanoric acid, and *P. rigidum*) speed up the colonization by epiphytic *Tillandsia* (Bromeliaceae) on its most common host *Quercus virginiana* and increase the number of seeds that adhere to the trunk of other unusual host trees (Callaway et al. [2001 Callaway, RM](#), [Reinhart, KO](#), [Tucker, SC](#) and [Pennings, SC](#). 2001. Effects of epiphytic lichens on host preference of the vascular epiphyte *Tillandsia usneoides*. *Oikos.*, 94: 433–441.). However, in most cases, vascular plants have rarely been observed to massively overgrow terricolous lichen carpets and in many cases are absent from the vicinity of lichen patches, suggesting some adaptive strategies of the symbiotic slow-

growing organisms against their higher-biomass producing competitors (Pyatt [1967](#) [Pyatt, FB](#). 1967. The inhibitory influence of *Peltigera canina* on the germination of graminaceous seeds and the subsequent growth of the seedlings. *Bryologist.*, 70: 326–329. ; Hobbs [1985](#) [Hobbs, RJ](#). 1985. The persistence of *Cladonia* patches in closed heathland stands. *Lichenologist.*, 17(1): 103–109. ; Sedia and Ehrenfeld [2005](#) [Sedia, EG](#) and [Ehrenfeld, JG](#). 2005. Differential effects of lichens, mosses and grasses on respiration and nitrogen mineralization in soils of the New Jersey Pinelands. *Oecologia.*, 144: 137–147. ; Lawrey [2009](#) [Lawrey, JD](#). 2009. *Diversity of defensive mutualisms. Chapter 11. Chemical defense in lichen symbiosis*, 167–181. London: Taylor and Francis Group.). In this context, a physical inhibition of seedling establishment by *Cladonia rangiferina* was described long ago: the expansion of thalli, driven by morning dew, pulls the seedlings completely out of the ground, breaking their root connection and preventing their establishment (Allen [1929](#) [Allen, AE](#). 1929. Influence of *Cladonia* ground cover on the establishment of seedlings. *Ecology.*, 10(3): 354–355.). Root penetration within a biological crust predominantly composed of *Diploschistes muscorum* is significantly lower than that observed within a bare soil, with a consequent lowering of seedling establishment (Deines et al. [2007](#) [Deines, L](#), [Rosentreter, R](#), [Eldridge, DJ](#) and [Serpe, MD](#). 2007. Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. *Plant Soil.*, 295: 23–35.). Moreover, a low organic matter content and low rates of net mineralization, mainly limited to nitrification, make the soils beneath lichen mats nutrient-poor as bare soils and less suitable for vascular plant invasion than those covered by mosses, which have higher organic matter accumulation and ammonium production rates (Sedia and Ehrenfeld [2005](#) [Sedia, EG](#) and [Ehrenfeld, JG](#). 2005. Differential effects of lichens, mosses and grasses on respiration and nitrogen mineralization in soils of the New Jersey Pinelands. *Oecologia.*, 144: 137–147.).

On the other hand, as significantly higher values of seed germination are detectable on bare soils than on live lichen clumps, but not on dead lichen clumps, a biotic factor clearly yields the inhibitory effect of lichen thalli (Zamfir [2000](#) [Zamfir, M](#). 2000. Effects of bryophytes and lichens on seedling emergence of alvar plants: evidence from greenhouse experiments. *Oikos.*, 88: 603–611.), i.e., the release of secondary compounds that have an allelopathic effect (see below).

Allelopathic effects of lichens on land plants

Lichen secondary metabolites, secreted by mycobionts and tolerated by photobionts through exclusion or detoxification mechanisms (Takahagi et al. [2008](#) [Takahagi, T](#), [Endo, T](#), [Yamamoto, Y](#) and [Sato, F](#). 2008. Lichen photobionts show tolerance against lichen acids produced by lichen mycobionts. *Biosci Biotechnol Biochem.*, 72(12): 3122–3127. with references therein), determine allelopathic effects on bryophytes and vascular plants which have been extensively examined both focusing on the inhibition of spore/seed germination and, subordinately, of other growth stages (e.g., moss sporeling growth, seedling and root elongation, mitosis in root tips, coleoptile section extension, leaf initiation) (e.g., Lawrey [1984](#) [Lawrey, JD](#). 1984. *Biology of lichenized fungi*, New York: Praeger Publishers. , [1986](#) [Lawrey, JD](#). 1986. Biological role of lichen substances. *Bryologist.*, 89(2): 111–122.). Researches have dealt both with the effects of terricolous lichen metabolites on plants, to explain the competition for soil surfaces, and with the effects of corticolous lichens on the health of their phorophytes. As in the case of plant-plant interactions (Inderjit et al. [2005](#) [Inderjit, Weston LA](#) and [Duke, SO](#). 2005. Challenges, achievements and opportunities in allelopathy research. *J Plant Interact.*, 1(2): 69–81.), lichen allelopathic interferences have mainly been observed *in vitro*, while few examples have been reported in natural settings.

To what extent do lichen metabolites affect bryophytes?

The allelopathic effect of lichens on bryophytes has been inferred from *in vitro* experiments that have assayed spores of different moss species with terricolous lichen metabolites at different concentrations. Compounds extracted from *Cladonia* species, such as usnic acid, inhibit spore germination of several moss species to various extents (Lawrey [1977](#) [Lawrey, JD.](#) 1977. Adaptive significance of *o*-methylated lichen depsides and depsidones. *Lichenologist.*, 9: 137–142. ; Giordano et al. [1999](#) [Giordano, S](#), [Alfano, F](#), [Basile, A](#) and [Castaldo Cobianchi, R.](#) 1999. Toxic effects of the thallus of the lichen *Cladonia foliacea* on the growth and morphogenesis of bryophytes. *Cryptogamie Bryol.*, 20(1): 35–41. ; Glime [2007](#) [Glime JM](#) 2007 . Bryophyte ecology . 1 . Physiological ecology. E-book sponsored by Michigan Technological University and the International Association of Bryologists . Accessed from the website: <http://www.bryoecol.mtu.edu/>). In most cases, the toxic effect on *Funaria hygrometrica* spores is exerted at concentrations of $2.7 \cdot 10^{-3}$ M and, in some cases, $2.7 \cdot 10^{-4}$ M, by reducing percent germination and sporeling growth: the relative toxicity of the different compounds depends on the pH, with vulpinic acid being the most toxic over all the pH tested (Gardner and Mueller [1981](#) [Gardner, CR](#) and [Mueller, DMJ.](#) 1981. Factors affecting the toxicity of several lichen acids: Effect of pH and lichen acid concentration. *Am J Bot.*, 68(1): 87–95.). *O*-methylated compounds, such as evernic and squamatic acids, strongly inhibit the spore germination of mosses such as *F. hygrometrica*, *Ceratodon purpureus* and *Mnium cuspidatum* (Lawrey [1977](#) [Lawrey, JD.](#) 1977. Adaptive significance of *o*-methylated lichen depsides and depsidones. *Lichenologist.*, 9: 137–142.). However, *O*-methylated stictic acid has been shown to be poorly effective in spore inhibition (Gardner and Mueller [1981](#) [Gardner, CR](#) and [Mueller, DMJ.](#) 1981. Factors affecting the toxicity of several lichen acids: Effect of pH and lichen acid concentration. *Am J Bot.*, 68(1): 87–95.), thus highlighting a poor correlation between toxicity and chemical structure (Lawrey [1984](#) [Lawrey, JD.](#) 1984. *Biology of lichenized fungi*, New York: Praeger Publishers. , [1986](#) [Lawrey, JD.](#) 1986. Biological role of lichen substances. *Bryologist.*, 89(2): 111–122.).

Secondary metabolites may contribute, together with the modification of microclimate conditions (see the dedicated section above), to the detrimental effects which, in some cases, characterize lichens that overgrow bryophytes, but the allelopathic interference has never been addressed in natural settings. On the other hand, it is worth noting that some lichen metabolites extracted from *Cladonia foliacea*, e.g., arabitol and mannitol, exert a stimulating effect on moss growth. This may also explain the increasing development of gametophytes cultured with *C. foliacea* thalli from the third week to 2–3 months, following an initial inhibition, during the first two weeks, associated with cytological alterations (e.g., a granular appearance of cytoplasm, changes in chloroplast shape) (Giordano et al. [1999](#) [Giordano, S](#), [Alfano, F](#), [Basile, A](#) and [Castaldo Cobianchi, R.](#) 1999. Toxic effects of the thallus of the lichen *Cladonia foliacea* on the growth and morphogenesis of bryophytes. *Cryptogamie Bryol.*, 20(1): 35–41.).

To what extent do lichen metabolites affect the germination and growth of vascular plants?

Water extracts of terricolous lichens, including several *Cladonia* species and the foliose *Peltigera canina*, have been shown, *in vitro*, to reduce the seed germination of several vascular plants, including Gymnosperms (e.g., *Pinus sylvestris*) and Angiosperms, trees, shrubs, forbs and grasses (Pyatt [1967](#) [Pyatt, FB.](#) 1967. The inhibitory influence of *Peltigera canina* on the germination of graminaceous seeds and the subsequent growth of the seedlings. *Bryologist.*, 70: 326–329. ; Lawrey [1984](#) [Lawrey, JD.](#) 1984. *Biology of lichenized fungi*, New York: Praeger Publishers. ; Hobbs [1985](#) [Hobbs, RJ.](#) 1985. The persistence of *Cladonia* patches in closed heathland stands. *Lichenologist.*, 17(1): 103–109. ; Sedia and Ehrenfeld [2003](#) [Sedia, EG](#) and [Ehrenfeld, JG.](#) 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey Pineland. *Oikos.*, 100: 447–

458.). Growth parameters, e.g., root elongation, are even more sensitive to allelopathic effects than seed germination (Peres et al. [2009 Peres, MTLP, Mapeli, AM, Faccenda, O, Gomes, AT and Honda, NK](#). 2009. Allelopathic potential of orsellinic acid derivatives. *Braz Arch Biol Technol.*, 52(4): 1019–1026.): in multi-assay laboratory experiments, the growth of forbs and grasses has been inhibited by most of the tested, purified lichen metabolites at concentrations ranging from 10^{-3} to 10^{-9} M, while stimulation effects have been reported for a few compounds at lower concentrations (Lawrey [1984 Lawrey, JD](#). 1984. *Biology of lichenized fungi*, New York: Praeger Publishers. and references therein; Nishitoba et al. [1987 Nishitoba, Y, Nishimura, H, Nishiyama, T and Mizutani, J](#). 1987. Lichen acids, plant growth inhibitors from *Usnea longissima*. *Phytochemistry.*, 26(12): 3181–3185. ; Cardarelli et al. [1997 Cardarelli, M, Serino, G, Campanella, L, Ercole, P, De Ciccio Nardone, F, Alesiani, O and Rossiello, F](#). 1997. Antimitotic effects of usnic acid on different biological systems. *Cell Mol Life Sci.*, 53: 667–672. ; Rojas et al. [2000 Rojas, IS, Latina-Hennsen, B and Mata, R](#). 2000. Effect of lichen metabolites on thylakoid electron transport and photophosphorylation in isolated spinach chloroplasts. *J Nat Prod.*, 63: 1396–1399. ; Peres et al. [2009 Peres, MTLP, Mapeli, AM, Faccenda, O, Gomes, AT and Honda, NK](#). 2009. Allelopathic potential of orsellinic acid derivatives. *Braz Arch Biol Technol.*, 52(4): 1019–1026.). Some authors have suggested that the chemical structure, e.g., the number and length of alkyl groups bonded to the benzene rings and to phenolic oxygen, is important in terms of activity (Nishitoba et al. [1987 Nishitoba, Y, Nishimura, H, Nishiyama, T and Mizutani, J](#). 1987. Lichen acids, plant growth inhibitors from *Usnea longissima*. *Phytochemistry.*, 26(12): 3181–3185. ; Peres et al. [2009 Peres, MTLP, Mapeli, AM, Faccenda, O, Gomes, AT and Honda, NK](#). 2009. Allelopathic potential of orsellinic acid derivatives. *Braz Arch Biol Technol.*, 52(4): 1019–1026.). However, other evidence, e.g., the inhibitory effect of methyl-orsellinate, which has only one methyl substitution, on the radicle growth of *Amaranthus hypochondriacus* (Amaranthaceae) and *Echinochloa crusgalli* (Poaceae) (Rojas et al. [2000 Rojas, IS, Latina-Hennsen, B and Mata, R](#). 2000. Effect of lichen metabolites on thylakoid electron transport and photophosphorylation in isolated spinach chloroplasts. *J Nat Prod.*, 63: 1396–1399.), would seem to suggest that a direct correlation between toxicity and chemical structure, as previously discussed for bryophytes, cannot be claimed (Lawrey [1986 Lawrey, JD](#). 1986. Biological role of lichen substances. *Byrologist.*, 89(2): 111–122.). The different effects of lecanoric acid (extracted from the foliose *Parmotrema tinctorum*) and its orsellinate derivatives on the germination and growth of *Lactuca sativa* (poorly affected) and *Allium cepa* (strongly affected) have highlighted that the allelopathic action of certain metabolites can vary to a great extent between different plant species (Peres et al. [2009 Peres, MTLP, Mapeli, AM, Faccenda, O, Gomes, AT and Honda, NK](#). 2009. Allelopathic potential of orsellinic acid derivatives. *Braz Arch Biol Technol.*, 52(4): 1019–1026.).

The heterogeneity of effects recorded *in vitro*, which depend on the metabolite and plant species tested, the concentration assayed and the developmental parameter considered, is similar to that recorded for *in vitro* tests of biodeterioration studies, which show the effect of different lichen secondary metabolites on different lithotypes, ranging from actively leaching to neutral (Chen et al. [2000 Chen, J, Blume, HP and Beyer, L](#). 2000. Weathering of rocks induced by lichen colonization – a review. *Catena.*, 39: 121–146.). When considering the interaction of lichens with both biotic/plant and abiotic/rock substrates, generalization on the allelopathic or deterioration effects of secondary metabolites should therefore be avoided.

How do corticolous lichens exert an allelopathic effect?

The hyphal penetration of the fruticose *Evernia prunastri* within the xylem vessels of oaks determines defoliation and a decrease in vigor of colonized plants as a result of the mycobiont release of secondary metabolites which are translocated with the xylem sap and induce allelopathic processes (Legaz et al. [2004 Legaz, ME, Monsó, MA and Vicente, C](#). 2004. Harmful effects of

epiphytic lichens on trees. *Recent Res Devel Agron Hortic.*, 1: 1–10.). Such effects were first suggested after performing advanced microscopical observations on hyphal penetration together with physiological investigations and correlating the results of *in vitro* assays with analyses of field samples (Legaz et al. [2004 Legaz, ME, Monsó, MA and Vicente, C.](#) 2004. Harmful effects of epiphytic lichens on trees. *Recent Res Devel Agron Hortic.*, 1: 1–10.).

Evernic acid, which is secreted by *E. prunastri* together with atranorin, chloroatranorin and usnic acid, has caused changes in the internal organization of isolated chloroplasts of spinach and oak (*Q. rotundifolia*) in *in vitro* tests at 35.5 μM : these changes include lowering of the number of grana per chloroplast section, of thylakoids per grana and of the height of grana stacks (Rapsch and Ascaso [1985 Rapsch, S and Ascaso, C.](#) 1985. Effect of evernic acid on structure of spinach chloroplasts. *Ann Bot.*, 56: 467–473. ; Ascaso and Rapsch [1986 Ascaso, C and Rapsch, S.](#) 1986. Ultrastructural changes in chloroplasts of *Quercus rotundifolia* Lam. in response to evernic acid. *Ann Bot.*, 57: 407–413.). Similar changes, including a lower percentage of stroma area occupied by grana, a lower number of thylakoids forming grana, a smaller grana width and a higher starch content, have been observed on the chloroplasts of the leaves of twigs colonized by *E. prunastri* in the field (Ascaso and Rapsch [1985 Ascaso, C and Rapsch, S.](#) 1985. Chloroplast-ultrastructure and chlorophyll content in leaves from *Quercus* branches with and without epiphytic lichen thalli. *Plant Cell Environ.*, 8: 651–656.). Evernic acid has been shown, *in vitro*, to induce the reduction of the total chlorophylls, chlorophyll *a* and *b* in spinach and oak chloroplasts (Ascaso and Rapsch [1985 Ascaso, C and Rapsch, S.](#) 1985. Chloroplast-ultrastructure and chlorophyll content in leaves from *Quercus* branches with and without epiphytic lichen thalli. *Plant Cell Environ.*, 8: 651–656. ; Bouaid and Vicente [1998 Bouaid, K and Vicente, C.](#) 1998. Chlorophyll degradation effected by lichen substances. *Ann Bot Fenn.*, 35: 71–74.). This effect has also been detected in the leaves of lichenized oak twigs (Ascaso and Rapsch [1985 Ascaso, C and Rapsch, S.](#) 1985. Chloroplast-ultrastructure and chlorophyll content in leaves from *Quercus* branches with and without epiphytic lichen thalli. *Plant Cell Environ.*, 8: 651–656.) and explained in relation to the chelation of magnesium by this chemical (Rapsch and Ascaso [1985 Rapsch, S and Ascaso, C.](#) 1985. Effect of evernic acid on structure of spinach chloroplasts. *Ann Bot.*, 56: 467–473.). Moreover, evernic acid *in vitro* inhibits the photolytic capacity of *Q. rotundifolia* chloroplasts (Hill reaction), possibly because of manganese chelation (Orús et al. [1981 Orús, MI, Estévez, MP and Vicente, C.](#) 1981. Manganese depletion in chloroplasts of *Quercus rotundifolia* during chemical simulation of lichen epiphytic states. *Physiol Plant.*, 52: 263–266.). It also leads to the disappearance of the absorbance maximum at 430 nm and a displacement from 665–675 nm of the absorbance maximum in the red zone, indicating some substitutions of the pyrrolic rings (Bouaid and Vicente [1998 Bouaid, K and Vicente, C.](#) 1998. Chlorophyll degradation effected by lichen substances. *Ann Bot Fenn.*, 35: 71–74.). In a mixture with usnic acid, atranorin and chloroatranorin, it yields the formation of paracrystalline structures and other morphological alterations in the chloroplasts (Ascaso et al. [1983 Ascaso, C, Orús, I and Estévez, P.](#) 1983. Chloroplast crystalloids and other alterations in response to lichen substances. *Photosynthetica.*, 17(2): 198–203.).

However, lichen phenolics, including evernic acid derivatives, which have been detected in the xylem sap of oak branches colonized by *E. prunastri* in samples collected in winter (without leaves) and in the leaf ribs in samples with leaves, have never been detected in mesophyll (Avalos et al. [1986 Avalos, A, Legaz, ME and Vicente, C.](#) 1986. The occurrence of lichen phenolics in the xylem sap of *Quercus pyrenaica*, their translocation to leaves and biological significance. *Biochem System Ecol.*, 14(4): 381–384.). Moreover, no detectable differences have been observed between leaves with and without evernic acid in their ribs in the ability to carry out electron transport from PSII (Avalos et al. [1986 Avalos, A, Legaz, ME and Vicente, C.](#) 1986. The occurrence of lichen phenolics in the xylem sap of *Quercus pyrenaica*, their translocation to leaves and biological significance. *Biochem System Ecol.*, 14(4): 381–384.). The fact that photosynthesis is not inhibited depends on

the absence of phenolic penetration of the photosynthetic tissues (Legaz et al. [1988 Legaz, E, Perez-Urria, E, Avalos, A and Vicente, C](#). 1988. Epiphytic lichens inhibit the appearance of leaves in *Quercus pyrenaica*. *Biochem System Ecol.*, 16(3): 253–259.), and some of the results on the uncoupling effects of evernic acid as an inhibitor of PSII (Orús et al. [1981 Orús, MI, Estévez, MP and Vicente, C](#). 1981. Manganese depletion in chloroplasts of *Quercus rotundifolia* during chemical simulation of lichen epiphytic states. *Physiol Plant.*, 52: 263–266.) possibly depend on a sensibilization of chloroplasts which has been induced by the use of bicarbonate as a phenol solvent (Avalos et al. [1986 Avalos, A, Legaz, ME and Vicente, C](#). 1986. The occurrence of lichen phenolics in the xylem sap of *Quercus pyrenaica*, their translocation to leaves and biological significance. *Biochem System Ecol.*, 14(4): 381–384. ; Legaz et al. [1988 Legaz, E, Perez-Urria, E, Avalos, A and Vicente, C](#). 1988. Epiphytic lichens inhibit the appearance of leaves in *Quercus pyrenaica*. *Biochem System Ecol.*, 16(3): 253–259. ; Legaz et al. [2004 Legaz, ME, Monsó, MA and Vicente, C](#). 2004. Harmful effects of epiphytic lichens on trees. *Recent Res Devel Agron Hort.*, 1: 1–10.). On the other hand, the accumulation of evernic acid in the apical zones of branches without leaves and in the buds of oaks and birches indicates an acropetal translocation of this chemical (Avalos et al. [1986 Avalos, A, Legaz, ME and Vicente, C](#). 1986. The occurrence of lichen phenolics in the xylem sap of *Quercus pyrenaica*, their translocation to leaves and biological significance. *Biochem System Ecol.*, 14(4): 381–384. ; Monsó et al. [1993 Monsó, MA, Legaz, ME and Vicente, C](#). 1993. A biochemical approach to the hemiparasitic action of the epiphytic lichen *Evernia prunastri* on *Betula pendula*. *Ann Bot Fenn.*, 30(4): 299–303.), which inhibits bud differentiation and retards leaf initiation by affecting oxidative phosphorylation and inducing a respiratory depletion (Legaz et al. [1988 Legaz, E, Perez-Urria, E, Avalos, A and Vicente, C](#). 1988. Epiphytic lichens inhibit the appearance of leaves in *Quercus pyrenaica*. *Biochem System Ecol.*, 16(3): 253–259.). The parallel accumulation of usnic acid in the buds further decreases leaf growth, as this lichen metabolite conjugates auxin through an esterification reaction (Legaz et al. [2004 Legaz, ME, Monsó, MA and Vicente, C](#). 2004. Harmful effects of epiphytic lichens on trees. *Recent Res Devel Agron Hort.*, 1: 1–10.). All these processes likely explain the frequently reported ‘defoliation’ of lichen colonized trees rather than an accelerated senescence of leaves induced by photosynthesis inhibition. Evidence of hyphal penetration within bark and the secretion of allelopathic metabolites make thus *E. prunastri* a lichen species that certainly has a harmful effect on trees. Similar processes may also explain the negative effect on tea plants of corticolous lichens, which suppress the growth of adventitious shoots (Asahina and Kurokawa [1952 Asahina, Y and Kurokawa, S](#). 1952. On the harmful effect of epiphytic lichens upon the higher plants. *Miscel. Report Res Inst Natl Res.*, 25: 83–86.).

Has the allelopathic action of terricolous lichens on plants been assessed in natural settings?

The effect of lichen metabolites on soil functions and tree growth has only recently been explored in relevant ecological studies, and the results of these studies suggest that the emphasis on lichen allelopathy at the ecosystem level should be moderated (Kytöviita and Stark [2009 Kytöviita, MM and Stark, S](#). 2009. No allelopathic effect of the dominant forest-floor lichen *Cladonia stellaris* on pine seedlings. *Funct Ecol.*, 23: 435–441.). Stark and colleagues (2007) have observed that the secondary metabolites of *Cladonia stellaris*, i.e., usnic and perlatolic acids, are poorly leached from thalli during natural rainfall events, that even after prolonged water immersions concentrations of the metabolites are quite negligible in soils beneath lichen mats and that soil microbial respiration is not affected by the far larger concentrations of usnic acid than those expected in soils.

Moreover, usnic acid has no effect on the nitrogen uptake and growth of pine seedlings: the addition of thallus fragments of *C. stellaris* even increases the biomass accumulation of mycorrhizal pine seedlings and the nitrogen acquisition of non-mycorrhizal seedlings, because of the potential rapid decomposition of Cladoniaceae in soil releasing nitrogen (Kytöviita and Stark [2009 Kytöviita, MM](#)

and [Stark, S.](#) 2009. No allelopathic effect of the dominant forest-floor lichen *Cladonia stellaris* on pine seedlings. *Funct Ecol.*, 23: 435–441.). As usnic acid does not exert a toxic effect, the lichen mat inhibition of pine seedlings may derive from other chemicals in water extraction or from physical effects on the moisture and temperature of soils ([Kytöviita and Stark 2009](#) [Kytöviita, MM](#) and [Stark, S.](#) 2009. No allelopathic effect of the dominant forest-floor lichen *Cladonia stellaris* on pine seedlings. *Funct Ecol.*, 23: 435–441.). Accordingly, these authors have suggested that the antimicrobial and allelopathic interpretation of lichen secondary metabolites in natural systems should be re-evaluated, and that there are better grounds to consider their role on light filtering and anti-herbivore protection. On the other hand, it is worth noting that the joint mixture of chemicals is important to explain the allelopathic interference in natural settings and the possibility that many chemicals may induce an inhibitory effect on higher plant growth at low concentrations ([Inderjit et al. 2005](#) [Inderjit, Weston LA](#) and [Duke, SO.](#) 2005. Challenges, achievements and opportunities in allelopathy research. *J Plant Interact.*, 1(2): 69–81.). Research on the allelopathic effect of lichen species in the field should thus take into account the complete chemosyndromes and the synergic action of all metabolites. As external stress factors, such as drought or pollution, have also been shown to reduce the effect of lichen mats in suppressing seed germination ([Hawkes and Menges 2003](#) [Hawkes, CV](#) and [Menges, ES.](#) 2003. Effects of lichens on seedling emergence in a xeric Florida shrubland. *South Nat.*, 2(2): 223–234.), a wider spectrum of environmental conditions should also be taken into account in field studies on the allelopathic action of terricolous lichens.

Do mycorrhizal fungi mediate the effects of terricolous lichens on plants?

The effect of lichen mats on seedling growth has also repeatedly been correlated to the allelopathic effect of lichen metabolites on mycorrhizal fungi which support plant nourishment ([Kytöviita and Stark 2009](#) [Kytöviita, MM](#) and [Stark, S.](#) 2009. No allelopathic effect of the dominant forest-floor lichen *Cladonia stellaris* on pine seedlings. *Funct Ecol.*, 23: 435–441.). Water extracts from terricolous lichens, including several *Cladonia* species and the fruticose species *Cetraria islandica* and *Stereocaulon paschale*, inhibit the growth of an extensive set of mycorrhizal fungi in pure cultures: mycorrhiza formation and phosphorous absorption by pine and spruce seedlings are reduced to various degrees, depending on the mycorrhizal fungus species and on the different lichen extracts, while stimulation effects have rarely been observed ([Brown and Mikola 1974](#) [Brown, R](#) and [Mikola, P.](#) 1974. The influence of fruticose soil lichens upon the mycorrhizae and seedling growth of forest trees. *Acta Forestalia Fenn.*, 141: 5–23.). The results obtained with purified compounds, however, are contradictory: usnic acid at 10–50 mg/l inhibits the growth of *Pisolithus tinctorius* ([Goldner et al. 1986](#) [Goldner, WR,](#) [Hoffman, FM](#) and [Medve, RJ.](#) 1986. Allelopathic effects of *Cladonia cristatella* on ectomycorrhizal fungi common to bituminous strip-mine spoils. *Can J Bot.*, 64: 1586–1590.), while it was barely effective in [Brown and Mikola's](#) study, only reducing the growth of *Paxillus involutus*, i.e., the only species affected by all the treatments. The growth of *Pinus banksiana* and *Picea glauca* transplants and seedlings also reduces following mulching with *Cladonia rangiferina* or *C. alpestris*; the phosphorous accumulation by the plants decreases ([Fisher 1979](#) [Fisher, RF.](#) 1979. Possible allelopathic effects of reindeer-moss (*Cladonia*) on Jack Pine and White Spruce. *Forest Sci.*, 25(2): 256–260.).

On the basis of field studies, it can be stated that ectomycorrhizal infection of the roots of oak seedlings and arbuscule formation within *Schizachyrium* (Poaceae) roots are significantly lower in plants growing on lichen mats ([Sedia and Ehrenfeld 2003](#) [Sedia, EG](#) and [Ehrenfeld, JG.](#) 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey Pineland. *Oikos.*, 100: 447–458.). Moreover, the removal of lichens improves the species diversity of ectomycorrhizal communities and favors a higher morphotype distribution and short root conditions ([Brown and Mikola 1974](#) [Brown, R](#) and [Mikola, P.](#) 1974. The influence of fruticose soil lichens upon the mycorrhizae and seedling growth of forest trees. *Acta Forestalia Fenn.*, 141: 5–23. ;

Markkola et al. [2002 Markkola, AM, Ahonen-Jonnarth, U, Roitto, M, Strömmer, R and Hyvärinen, M](#). 2002. Shift in ectomycorrhizal community composition in Scots pine (*Pinus sylvestris* L.) seedling roots as a response to nickel deposition and removal of lichen cover. *Env Poll.*, 120: 797–803.).

A negative effect of terricolous lichens on mycorrhizal fungi and, consequently, on plant nutrition is thus consistently supported by both *in vitro* and field data, but the differences observed between case studies, which depend on the lichen metabolites, plant and mycorrhizal fungus species considered, prevent generalized quantifications of the phenomenon. It is worth noting that a clear stimulating effect of lichen extracts from the fruticose *Alectoria sarmentosa*, *Bryoria fuscescens* and *B. fremontii* has even been reported on the growth of the ascomycete *Gremmeniella abietina*, which has caused serious epidemics on *Pinus sylvestris* (Kaitera et al. [1996 Kaitera, JA, Helle, T and Jalkanen, RE](#). 1996. The effect of *Alectoria sarmentosa*, *Bryoria fuscescens*, and *Bryoria fremontii* extracts and usnic acid on the growth of *Gremmeniella abietina* in vitro. *Can J Bot.*, 74: 352–359.).

What is the phytotoxic mode of action of lichen metabolites?

Although the characterization of the phytotoxic mode of action of lichen secondary metabolites has been limited (Duke et al. [2002 Duke, SO, Dayan, FE, Rimando, AM, Schrader, KK, Aliotta, G, Oliva, A and Romagni, JG](#). 2002. Chemicals from nature for weed management. *Weed Sci.*, 50: 138–151. ; Takahagi et al. [2006 Takahagi, T, Ikezawa, N, Endo, T, Ifuku, K, Yamamoto, Y, Kinoshita, Y, Takeshita, S and Sato, F](#). 2006. Inhibition of PSII in atrazine-tolerant tobacco cells by barbatic acid, a lichen-derived depside. *Biosci Biotechnol Biochem.*, 70(1): 266–268.), a significant body of data is available on usnic acid and, subordinately, on other compounds. The extensive knowledge of the antibiotic properties of usnic acid and of its potential medical applications (Cocchietto et al. [2002 Cocchietto, M, Skert, N and Nimis, PL](#). 2002. A review of usnic acid, an interesting natural compound. *Naturwissenschaften.*, 89: 137–146. ; Guo et al. [2008 Guo, L, Shi, Q, Fang, JL, Mei, N, Ali, AA, Lewis, SM, Leakey, JEA and Frankos, VH](#). 2008. Review of usnic acid and *Usnea barbata* toxicity. *J Env Sci Health, Part C.*, 26: 317–338.) likely explains the focusing of research on the phytotoxicity of this compound, although it has more difficulty in crossing chloroplast membrane than other chemicals, such as atranorin (Bouaid and Vicente [1998 Bouaid, K and Vicente, C](#). 1998. Chlorophyll degradation effected by lichen substances. *Ann Bot Fenn.*, 35: 71–74.).

As previously mentioned concerning the effects of evernic acid injected by *Evernia prunastri* into living tissues of its phorophytes, usnic acid also displays a multidirectional toxic effect on both the photosynthetic and respiratory pathways, and also on the transpiration and phytohormonal regulation of plant growth (Vavasseur et al. [1991 Vavasseur, A, Gautier, H, Thibaud, MC and Lascève, G](#). 1991. Effects of usnic acid on the oxygen exchange properties of mesophyll cell protoplasts from *Commelina communis* L. *J Plant Physiol.*, 139: 90–94. ; Legaz et al. [2004 Legaz, ME, Monsó, MA and Vicente, C](#). 2004. Harmful effects of epiphytic lichens on trees. *Recent Res Devel Agron Hortic.*, 1: 1–10. ; Latkowska et al. [2006 Latkowska, E, Lechowski, Z, Bialczyk, J and Pilarski, J](#). 2006. Photosynthesis and water relations in tomato plants cultivated long-term in media containing (+)-usnic acid. *J Chem Ecol.*, 32: 2053–2066.). Plants cultivated with usnic acid (20 or 30 μ M) have demonstrated lower photosynthetic (about –40%) and respiratory (down to –80%) activities than the controls and displayed a reduction in their chlorophyll and carotenoid contents (Vavasseur et al. [1991 Vavasseur, A, Gautier, H, Thibaud, MC and Lascève, G](#). 1991. Effects of usnic acid on the oxygen exchange properties of mesophyll cell protoplasts from *Commelina communis* L. *J Plant Physiol.*, 139: 90–94. ; Latkowska et al. [2006 Latkowska, E, Lechowski, Z, Bialczyk, J and Pilarski, J](#). 2006. Photosynthesis and water relations in tomato plants cultivated long-term in media containing (+)-usnic acid. *J Chem Ecol.*, 32: 2053–2066.). The proliferation of

Nicotiana tabacum cultured cells is inhibited by usnic acid concentrations of 5–50 µg/ml, and by five times lower concentrations in the case of mesophyll leaf protoplasts; non-inhibiting concentrations exert a stimulatory effect (Cardarelli et al. [1997 Cardarelli, M, Serino, G, Campanella, L, Ercole, P, De Cicco Nardone, F, Alesiani, O and Rossiello, F.](#) 1997. Antimitotic effects of usnic acid on different biological systems. *Cell Mol Life Sci.*, 53: 667–672.).

(–)-Usnic enantiomer has a greater phytotoxic activity, bleaches the cotyledonary tissues of cucumber seedlings and induces the decrease in chlorophyll and carotenoids in lettuce seedlings more than (+)-usnic acid (Romagni et al. [2000 Romagni, JG, Meazza, G, Nanayakkara, NPD and Dayan, FE.](#) 2000. The phytotoxic lichen metabolite, usnic acid, is a potent inhibitor of plant p-hydroxyphenylpyruvate dioxygenase. *FEBS Lett.*, 480: 301–305.). As membrane leakage depends on light, the destabilization of the photosynthetic apparatus has been correlated to the irreversible inhibition by both (–)-usnic acid (IC₅₀=70 nM) and (+)-usnic acid (one order of magnitude less active) of the p-hydroxyphenylpyruvate dioxygenase (HPPD), which catalyzes the synthesis of plastoquinone (PQ): This process stops the synthesis of carotenoids, which usually quench excess photoexcitation energy, and increases the susceptibility of chlorophyll and membranes to degradative processes driven by highly reactive singlet oxygens (Romagni et al. [2000 Romagni, JG, Meazza, G, Nanayakkara, NPD and Dayan, FE.](#) 2000. The phytotoxic lichen metabolite, usnic acid, is a potent inhibitor of plant p-hydroxyphenylpyruvate dioxygenase. *FEBS Lett.*, 480: 301–305.). Moreover, the inhibition of photosynthetic electron transport by usnic acid has been observed in illuminated mesophyll cell protoplasts from *Commelina sativa* (usnic acid 4 µM) (Vavasseur et al. [1991 Vavasseur, A, Gautier, H, Thibaud, MC and Lascève, G.](#) 1991. Effects of usnic acid on the oxygen exchange properties of mesophyll cell protoplasts from *Commelina communis* L. *J Plant Physiol.*, 139: 90–94.) and in isolated chloroplasts from *Spinacia oleracea* (Inoue et al. [1987 Inoue, H, Noguchi, M and Kubo, K.](#) 1987. Site of inhibition of usnic acid at oxidizing side of photosystem 2 of spinach chloroplasts. *Photosynthetica.*, 21(1): 88–90. ; Endo et al. [1998 Endo, T, Takahagi, T, Kinoshita, Y, Yamamoto, Y and Sato, F.](#) 1998. Inhibition of photosystem II of spinach by lichen-derived depsides. *Biosci Biotechnol Biochem.*, 62(10): 2023–2027.), *Quercus rotundifolia* (Orús et al. [1981 Orús, MI, Estévez, MP and Vicente, C.](#) 1981. Manganese depletion in chloroplasts of *Quercus rotundifolia* during chemical simulation of lichen epiphytic states. *Physiol Plant.*, 52: 263–266.) and *Lycopersicon esculentum* (Latkowska et al. [2006 Latkowska, E, Lechowski, Z, Bialczyk, J and Pilarski, J.](#) 2006. Photosynthesis and water relations in tomato plants cultivated long-term in media containing (+)-usnic acid. *J Chem Ecol.*, 32: 2053–2066.): the electron flow has been indicated to be blocked at the oxidizing side of P680 of PSII due to usnic binding to the secondary electron donor (Inoue et al. [1987 Inoue, H, Noguchi, M and Kubo, K.](#) 1987. Site of inhibition of usnic acid at oxidizing side of photosystem 2 of spinach chloroplasts. *Photosynthetica.*, 21(1): 88–90.); inhibition of the electron flow by chelating manganese divalent ions and by disturbing the electron flow from the water-splitting catalytic centre to PSII has also been suggested to predispose chlorophylls to photoinhibitory damage as a manganese supply has reversed the inhibition in some experiments (Orús et al. [1981 Orús, MI, Estévez, MP and Vicente, C.](#) 1981. Manganese depletion in chloroplasts of *Quercus rotundifolia* during chemical simulation of lichen epiphytic states. *Physiol Plant.*, 52: 263–266.), but this phenomenon has not always been observed (Vavasseur et al. [1991 Vavasseur, A, Gautier, H, Thibaud, MC and Lascève, G.](#) 1991. Effects of usnic acid on the oxygen exchange properties of mesophyll cell protoplasts from *Commelina communis* L. *J Plant Physiol.*, 139: 90–94.). Usnic acid also inhibits the oxidative phosphorylation pathway and, to a lesser extent, it prevents the redistribution of reduced intermediates towards an alternative oxidase (Vavasseur et al. [1991 Vavasseur, A, Gautier, H, Thibaud, MC and Lascève, G.](#) 1991. Effects of usnic acid on the oxygen exchange properties of mesophyll cell protoplasts from *Commelina communis* L. *J Plant Physiol.*, 139: 90–94.).

Furthermore, usnic acid at a concentration of 20–50 μM causes a decrease in the transpiration rate, which has been correlated to an increase in stomatal diffusive resistance, a reduction in stomatal density, and a decrease in root hydraulic conductance in tomato, sunflower and maize; however, the interaction mechanisms have not been fully explained (Lascève and Gaugain [1990 Lascève, G and Gaugain, F.](#) 1990. Effects of usnic acid on sunflower and maize plantlets. *J Plant Physiol.*, 136: 723–727. ; Latkowska et al. [2006 Latkowska, E, Lechowski, Z, Bialczyk, J and Pilarski, J.](#) 2006. Photosynthesis and water relations in tomato plants cultivated long-term in media containing (+)-usnic acid. *J Chem Ecol.*, 32: 2053–2066. ; Lechowski et al. [2006 Lechowski, Z, Mej, E and Bialczyk, J.](#) 2006. Accumulation of biomass and some macroelements in tomato plants grown in media with (+)-usnic acid. *Environ Exp Bot.*, 56: 239–244.). As previously mentioned, the conjugation of auxin by usnic acid has been reported to cause a modification of the phytohormonal regulation of leaf growth (Legaz et al. [2004 Legaz, ME, Monsó, MA and Vicente, C.](#) 2004. Harmful effects of epiphytic lichens on trees. *Recent Res Devel Agron Hortic.*, 1: 1–10.).

With regard to the other metabolites that have been investigated about the phytotoxic mode of action, barbatic, lecanoric (depsides) and gyrophoric acid (tridepside) have been shown to interrupt the photosynthetic electron transport by binding the secondary quinone acceptor (barbatic acid on tobacco cells) (Takahagi et al. [2006 Takahagi, T, Ikezawa, N, Endo, T, Ifuku, K, Yamamoto, Y, Kinoshita, Y, Takeshita, S and Sato, F.](#) 2006. Inhibition of PSII in atrazine-tolerant tobacco cells by barbatic acid, a lichen-derived depside. *Biosci Biotechnol Biochem.*, 70(1): 266–268.), by inhibiting the electron transfer between P680 and Q_A on the reducing side of PSII (gyrophoric acid on spinach chloroplasts) or by acting at the water splitting enzyme level (lecanoric acid on spinach chloroplasts) (Rojas et al. [2000 Rojas, IS, Latina-Hennsen, B and Mata, R.](#) 2000. Effect of lichen metabolites on thylakoid electron transport and photophosphorylation in isolated spinach chloroplasts. *J Nat Prod.*, 63: 1396–1399.). Other depsides, including atranorin and nephroarctin, have not shown any inhibitory activity, while evernic acid and sphaeosporin have shown a strong inhibition activity, which is limited to the reducing and oxidizing side of P680, respectively (Endo et al. [1998 Endo, T, Takahagi, T, Kinoshita, Y, Yamamoto, Y and Sato, F.](#) 1998. Inhibition of photosystem II of spinach by lichen-derived depsides. *Biosci Biotechnol Biochem.*, 62(10): 2023–2027.). Dual inhibition on both the reducing and oxidizing sides of P680 has been demonstrated to be common for lichen depsides (Takahagi et al. [2008 Takahagi, T, Endo, T, Yamamoto, Y and Sato, F.](#) 2008. Lichen photobionts show tolerance against lichen acids produced by lichen mycobionts. *Biosci Biotechnol Biochem.*, 72(12): 3122–3127.). Analogues of lichen-derived antraquinones, such as emodin and rhodocladonic acid, have been shown to cause malformation and to determine bleaching in grasses, the former inhibiting the PSII in thylakoids isolated from spinach and corn, while the mode of action of the latter has not been clarified (Romagni et al. [2004 Romagni, JG, Rosell, RC, Nanayakkara, NPD and Dayan, FE.](#) 2004. *Allelopathy, chemistry and mode of action of allelochemicals. Chapter 1, Ecophysiology and potential modes of action for selected lichen secondary metabolites*, 13–33. Boca Raton, FL: CRC Press.).

As *in vitro* studies highlight the possibility of usnic acid and other metabolites of multidirectionally affecting plant metabolism (photosynthesis, respiration, transpiration, hormonal regulation), a research approach similar to that followed about evernic acid (see the dedicated section above), which associated *in vitro* assays with physiological and ultrastructural analyses of field samples, appears as particularly suitable to understand the effective phytotoxic mode of action of lichen compounds in natural settings. This information may further support the recent suggestion of using lichen compounds, which are chemically simple and are possibly easily synthesized in the laboratory, as herbicides (Dayan and Romagni [2001 Dayan, FE and Romagni, JG.](#) 2001. Lichens as a potential source of pesticides. *Pest Outlook.*, 12: 229–232. ; Duke et al. [2002 Duke, SO, Dayan, FE, Rimando, AM, Schrader, KK, Aliotta, G, Oliva, A and Romagni, JG.](#) 2002. Chemicals from nature for weed management. *Weed Sci.*, 50: 138–151.). However, the different effects, ranging

from inhibition to stimulation, that have been observed on different tested plants (Peres et al. [2009](#) [Peres, MTLP](#), [Mapeli, AM](#), [Faccenda, O](#), [Gomes, AT](#) and [Honda, NK](#). 2009. Allelopathic potential of orsellinic acid derivatives. *Braz Arch Biol Technol.*, 52(4): 1019–1026.) will also have to be taken into account.

The reverse side of the medal: plant allelopathic effects on lichens

Investigations on plant allelopathy against lichens are scarce and the few that exist focused on the effects of bark substances on corticolous lichens. A variety of monomeric phenolic acids, aldehydes and alcohols (including catechol, benzoic acid, salicin, gallic acid, catechin), derived from the hydrolytic decomposition in the stem flow of bark phenolic glycosides (including salicylates as tremulacin, salicortin), flavonoids and tannins of *Populus×canadensis*, has been shown to inhibit the soredial growth of the foliose *Physcia tenella* in natural concentrations, suggesting a role of plant metabolites in the regulation of corticolous lichen colonization (Koopmann et al. [2007](#) [Koopmann, R](#), [Stevens, H](#), [Franzen-Reuter, I](#), [Frahm, JP](#) and [Grote, M](#). 2007. *In vitro* inhibition of soredial growth in the epiphytic lichen *Physcia tenella* (Ascomycetes: *Lecanorales*) by a variety of bark phenols. *Lichenologist.*, 39(6): 567–572.). Water-based bark extracts have also been reported to enhance or inhibit lichen ascospore germination, depending on the extract and the lichen species tested (Pyatt [1973](#) [Pyatt FB](#) . 1973 . The lichens . Chapter 4 , *Lichen propagules* . New York : Academic Press . 117 145 .; Ostrofsky and Denison [1980](#) [Ostrofsky, A](#) and [Denison, WC](#). 1980. Ascospore discharge and germination in *Xanthoria polycarpa*. *Mycologia.*, 72: 1171–1179.), and tree bark alkaloids have been shown to be potentially lichenocidal or lichenostatic compounds as they inhibit the lichen photobiont *Scenedesmus obliquus* (Lawrey [1984](#) [Lawrey, JD](#). 1984. *Biology of lichenized fungi*, New York: Praeger Publishers.).

As investigations on the effects of plant compounds on terricolous lichens may involve experimental difficulties (e.g., to evaluate a reduction in lichen growth), the action of plants as neighbors of lichens on soil is an open research question. Advances in mycobiont culture techniques, which have recently allowed lichen interactions with mineral substrates to be investigated in controlled conditions (Piervittori et al. [2009](#) [Piervittori, R](#), [Favero-Longo, SE](#) and [Gazzano, C](#). 2009. Lichens and biodeterioration of stonework: A review. *Chem Today.*, 27(6): 8–10.), may represent a suitable technique to examine the action of plant metabolites (e.g., root exudates) on the mycobionts of terricolous lichens.

Conclusions

The reviewed body of information on lichen-plant interactions supports our hypothesis that the heterogeneity of reciprocal effects that exist between lichens and plants depends on the degree of involvement and effectiveness, in a relationship between a certain lichen species and a certain plant species, of a common set of physical and chemical factors, as in the case of the interactions of saxicolous lichens with mineral substrates (Gazzano et al. [2009](#) [Gazzano, C](#), [Favero-Longo, SE](#), [Matteucci, E](#), [Roccardi, A](#) and [Piervittori, R](#). 2009. Index of lichen Potential Biodeteriogenic Activity (LPBA): A tentative tool to evaluate the lichen impact on stonework. *Int Biodeter Biodegr.*, 63: 836–843.). It is worth noting that the hyphal penetration and the secretion of metabolites, which in the single case of *Evernia prunastri* on oaks have been shown to determine allelopathic interferences and, consequently, a negative effect of corticolous colonization on plant health (Legaz et al. [2004](#) [Legaz, ME](#), [Monsó, MA](#) and [Vicente, C](#). 2004. Harmful effects of epiphytic lichens on trees. *Recent Res Devel Agron Hortic.*, 1: 1–10.), are the same factors which control the physical disaggregation and chemical deterioration of rocks by saxicolous lichens

(Piervittori et al. [2009 Piervittori, R, Favero-Longo, SE](#) and [Gazzano, C](#). 2009. Lichens and biodeterioration of stonework: A review. *Chem Today.*, 27(6): 8–10.). Moreover, the influence of bark on corticolous lichen communities depends on the physical and chemical surface properties (i.e., texture, water holding capacity and chemistry) which are similar to those that control the saxicolous communities on rocks (i.e., roughness, internal porosity and mineral composition) (Brodo [1973 Brodo, IM](#). 1973. *The lichens. Chapter 12, Substrate ecology*, 401–441. New York: Academic Press.). Secondary metabolites, which in the case of saxicolous lichens determine biodeterioration through ion leaching from minerals (Chen et al. [2000 Chen, J, Blume, HP](#) and [Beyer, L](#). 2000. Weathering of rocks induced by lichen colonization – a review. *Catena.*, 39: 121–146.), are involved in the relationship of muscicolous, corticolous and terricolous lichens with plants, as both growth substrates and neighbors on soil, causing alleopathic interferences (Legaz et al. [2004 Legaz, ME, Monsó, MA](#) and [Vicente, C](#). 2004. Harmful effects of epiphytic lichens on trees. *Recent Res Devel Agron Hortic.*, 1: 1–10. ; Lawrey [2009 Lawrey, JD](#). 2009. *Diversity of defensive mutualisms. Chapter 11. Chemical defense in lichen symbiosis*, 167–181. London: Taylor and Francis Group.). Enzymatic processes are involved in hyphal adhesion on and penetration within plant tissues (de los Ríos et al. [1997 de los Ríos, A, Ramirez, A](#) and [Estévez, P](#). 1997. Production of several isoforms of β -1,4-glucanase by the cyanolichen *Peltigera canina*. *Physiol Plant.*, 100: 159–164. ; Laufer et al. [2006 Laufer, Z, Beckett, RP, Minibayeva, FV, Lüthje, S](#) and [Böttger, M](#). 2006. Occurrence of laccases in lichenized ascomycetes of the *Peltigerinae*. *Mycol Res.*, 110: 846–853.) as well as they have been recently suggested to explain carbonate dissolution by endolithic lichens (Tretiach et al. [2008 Tretiach M, Favero-Longo SE, Crisafulli P, Gazzano C, Carbone F, Baiocchi C, Giovine M, Modenesi P, Rinino S, Chiapello M, Salvadori O, Piervittori R](#). 2008. How do endolithic lichens dissolve carbonates? Tempe: ABLIS and IAL. Lichenological abstracts. The 6th IAL Symposium, (Asilomar, CA, USA) ; 72).

Frequent questions, such as those on the effect of corticolous colonization on plant health, cannot therefore be solved by generalizing the lichen-plant reciprocal effects, but it is necessary to examine, in each case study, the overall factors which act at the lichen interface with any biotic or abiotic substrate: (a) the factors that determine the lichen effects on plants, such as hyphal penetration and organization within the plant tissues, thallus expansion/contraction according to the hydration state, interference on microclimatic conditions, physical support to pathogenic insects, epiphytic plants or non-lichenized fungi, enzymatic processes and secretion of secondary metabolites (Table 1), and (b) the factors that influence the lichen colonization on/near plants, such as physical and chemical surface properties of leaves and bark and release of compounds supporting lichen nutrition or exerting alleopathy (Table 2).

Table 1. Effects of physical and chemical factors related to the lichen colonization on/near land plants and, for comparison, on rocks. °,general pattern; *,exception to the general pattern; #,information based on single/few investigations; n.i., non-investigated; -,the involvement of this factor is not possible; [...], notes.

Effects of lichens on ...				
	... land-plants used as growth substrates	... land-plants being lichen neighbors on soil	... rocks	
	- bryophytes	- vascular plants		
Lichen factors	(muscolous lichens)	(follicolous L.)	(corticulous L.) (terricolous L.) (saxicolous L.)	
Hypal penetration and organization within the substrate	<ul style="list-style-type: none"> ° no effects * except in the case of some lichen species behaving as parasites 	<ul style="list-style-type: none"> [no penetration] * except in the case of some species of <i>Strigula</i> possibly living as semi-parasites 	<ul style="list-style-type: none"> ° endophloematic thalli: suberification of cork cells ° epiphloematic thalli: no effects * except in the case of <i>Ochrolechia frigida</i> (destruction of the penetrated tissues) and of <i>Evernia prunastri</i> (injection of allelopathic metabolites within the xylem vessels of oaks) 	<ul style="list-style-type: none"> ° physical disaggregation at the lichen-rock interface
Thallus expansion/contraction according to the hydration state	n.i.	n.i.	# periderm arching	
Interference on microclimatic conditions	# light interception causing moss death	# light interception causing leaf acclimatation (e.g., higher chlorophyll contents)	# light interception causing bark acclimatation (lower chlorophyll a/b ratio)	
Physical support to other organisms	n.i.	n.i.	<ul style="list-style-type: none"> ° pathogenic insects, epiphytic plants, non-lichenized fungi 	
Enzymatic processes	# hyphal penetration through the cell walls (β -1,4-glucanase)	n.i.	# thallus attachment (laccases); cell wall decomposition (β -1,4-glucanase and polygalacturonase)	
Secretion of secondary metabolites	° allelopathic inhibition of germination and growth assessed <i>in vitro</i> , but studies are needed in natural settings	[poorness or absence of secondary metabolites]	<ul style="list-style-type: none"> ° allelopathic effects of <i>Evernia prunastri</i> on oaks (defoliation, decrease in vigor) 	
			<ul style="list-style-type: none"> ° allelopathic inhibition of germination and growth assessed <i>in vitro</i>, but not supported by studies in natural settings ° allelopathic effects on mycorrhizal fungi assessed <i>in vitro</i> and in the field 	
			<ul style="list-style-type: none"> ° mechanical defoliation ° modifications of e.g., moisture supporting rock deterioration ° non-lichenized fungi and other rock-inhabiting microorganisms # dissolution of carbonates (carbonic anhydrase) ° chemical deterioration of minerals 	

Table 2. Effects of plant- and, for comparison, of rock-related factors on lichens.
°,general pattern; *,exception to the general pattern; #,information based on single/few investigations; n.i., non investigated; -,the involvement of this factor is not possible.

Effects of plants ...		Effects of rocks on ...
... used as growth substrates on being neighbors on soil on
Plant/rock factors	... muscicolous lichens	... terricolous l.
Physical and chemical surface properties	<p>... foliicolous l.</p> <p>° no effect * but in some cases a slight community differentiation has been related to the surface structure and longevity of leaves</p> <p>n.i.</p> <p>* but some species display specificity to their phorophyte</p> <p>n.i.</p>	<p>... corticolous l.</p> <p>° influence on the community composition of bark properties, as texture, water holding capacity and pH</p> <p>° influence on the community composition of rock properties, as surface roughness, internal porosity and mineral composition</p> <p>n.i.</p> <p>° contribution to the lichen mineral nutrition of ion leaching from the plant substrate</p>
Release of inorganic compounds	n.i.	n.i.
Release of organic compounds	n.i.	n.i.
		° contribution to the lichen mineral nutrition of ion leaching from the plant substrate

As plants are living organisms and they should be expected to respond to lichens in a more complex way than rocks, further investigations on the potential plant factors which modulate the type of physico-chemical, trophic and/or competition relationships with lichens seem necessary to clarify the plant perspective of the interaction (*sensu* Mayer [1989 Mayer, AM](#). 1989. Plant-fungal interactions: A plant physiologist's viewpoint. *Phytochemistry*, 28(2): 311–317.) and to explain any differences in behavior between different plant species (e.g., Peres et al. [2009 Peres, MTLP, Mapeli, AM, Faccenda, O, Gomes, AT and Honda, NK](#). 2009. Allelopathic potential of orsellinic acid derivatives. *Braz Arch Biol Technol.*, 52(4): 1019–1026.). Only in a few cases plant responses have so far been described, including adaptation of their photosynthetic functions (Solhaug et al. [1995 Solhaug, KA, Gauslaa, Y and Haugen, J](#). 1995. Adverse effects of epiphytic crustose lichens upon stem photosynthesis and chlorophyll of *Populus tremula* L. *Bot Acta.*, 108: 233–239. ; Anthony et al. [2002 Anthony, PA, Holtum, JAM and Jackes, BR](#). 2002. Shade acclimation of rainforest leaves to colonization by lichens. *Funct Ecol.*, 16: 808–816.) or physical compartmentalization of hyphae (Brodo [1973 Brodo, IM](#). 1973. *The lichens. Chapter 12, Substrate ecology*, 401–441. New York: Academic Press.). No investigation has examined whether the hyphal growth within plant tissues is modulated by the tissue organization, as textural features control hyphal penetration within rocks, or by metabolic responses. Moreover, the allelopathic effects of plant metabolites on terricolous lichens have been disregarded completely. On the other hand, in the case of allelopathic interferences, the lichen perspective should also be revisited: *in vitro* evidence of lichen allelopathy against plants and their mycorrhizal partners has been poorly supported by recent research in natural settings (Stark et al. [2007 Stark, S, Kytöviita, MM and Neumann, AB](#). 2007. The phenolic compounds in *Cladonia* lichens are not antimicrobial in soils. *Oecologia.*, 152: 299–306.), which suggests the need to reduce emphasis on the allelopathic effect of lichen secondary metabolites.

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