Lichen-gastropod interactions

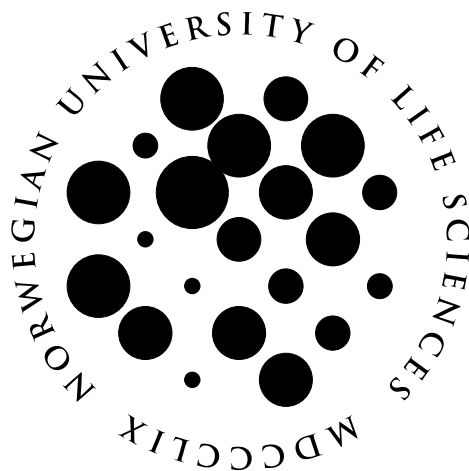## Chemical defence and ecological consequences of lichenivory

Lav-snegle interaksjoner – kjemisk forsvar og økologiske konsekvenser av lavbeiting

Philosophiae Doctor (PhD) Thesis

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TABLE OF CONTENTS

LIST OF PAPERS

This thesis consists of the following papers that are referred to by the roman numerals (I-VII)

Paper I   Nybakken, L., *Asplund, J.*, Solhaug, K.A. & Gauslaa, Y. (2007) Forest successional stage affects the cortical secondary chemistry of three old forest lichens. *Journal of Chemical Ecology*, **33**:1607-1618.

Paper II   *Asplund, J.*, Solhaug, K.A. & Gauslaa, Y. (2009) Fungal depsidones - an inducible or constitutive defence against herbivores in the lichen *Lobaria pulmonaria*? *Basic and Applied Ecology*, **10**:273-278.

Paper III   *Asplund, J.* & Gauslaa, Y. (2010) The gastropod *Arion fuscus* prefers cyanobacterial to green algal parts of the tripartite lichen *Nephroma arcticum* due to low chemical defence. *Lichenologist*, **42**:113-117.

Paper IV   *Asplund, J.*, Solhaug, K.A. & Gauslaa, Y. (2010) Optimal defense – snails avoid reproductive parts of the lichen *Lobaria scrobiculata* due to allocation of secondary compounds. *Ecology*, doi:10.1890/09-1829.

Paper V   *Asplund, J.* & Gauslaa, Y. (2007) Content of secondary compounds depends on thallus size in the foliose lichen *Lobaria pulmonaria*. *Lichenologist*, **39**:273-278.

Paper VI   *Asplund, J.* & Gauslaa, Y. (2008) Mollusc grazing limits growth and early development of the old forest lichen *Lobaria pulmonaria* in broadleaved deciduous forests. *Oecologia*, **155**:93-99.

Paper VII   *Asplund, J.*, Larsson, P., Vatne, S. & Gauslaa, Y. (2010) Gastropod grazing shapes the vertical distribution of epiphytic lichens in forest canopies. *Journal of Ecology*, **98**:218-225.

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ABSTRACT

Herbivory are considered a significant factor regulating plant communities. Some mammals, e.g. reindeers, substantially influence lichen-dominated communities. The impact on lichens posed by invertebrate grazers is less known. Therefore this thesis aims to study interactions between lichens and lichenivorous gastropods. The most important objective is to quantify variations in lichen defence compounds and to test how this variation affects grazing patterns.

Lichens synthesize a large variety of carbon-based secondary compounds with various biological roles. According to recent literature, cortical compounds function as solar radiation screens. This thesis has provided new and strong experimental field and laboratory evidence for the hypothesis inferring lichenivore defence of some medullary compounds. Medullary compounds in *Lobaria pulmonaria* were not induced by lichenivory, consistent with a constitutive type of defence. In this species, the chemical defence increased with thallus age. As a consequence gastropods limit the early development of *L. pulmonaria* by preferring juvenile thalli. In general, chemical defence varies between different tissues in a lichen thallus. For example, in the tripartite (green algal with cyanobacteria in cephalodia) *Nephroma arcticum* gastropods readily consume the compound-deficient cephalodia and avoid the green algal tissues. In *Lobaria scrobiculata*, gastropods avoid the well-defended soralia (structures with asexual symbiotic diaspores) compared to less defended non-reproductive tissues. The latter finding is consistent with the optimal defence theory that predicts allocation of defence compounds in proportion to risk of a specific plant part to be attacked and its value to plant fitness. Finally, a field experiment suggest that climbing gastropods determine the lower distribution limit of four species of old forest lichens along a vertical canopy gradient and influence the spatial pattern of susceptible lichen species. By selective grazing of lichen species, gastropods can shape epiphytic lichen communities in some broad-leaved deciduous forests.

SAMMENDRAG (NORSK)

Laver er symbiotiske organismer som består av en heterotrof sopp og en autotrof alge og/eller en blågrønn bakterie. Slike plantelignende organismer vokser langsomt, lever lenge, tåler ulike former for stress, og dominerer ofte i habitat hvor karplanter er mindre vanlige. Slike egenskaper gjør dem sårbare for beiting. Beitende dyr påvirker sammensetningen av ulike plantesamfunn, og rein er kjent for å kunne endre sammensetningen av lavsamfunn. I hvilken grad snegler (Gastropoda) påvirker laver er imidlertid lite kjent. Denne avhandlingen har som mål å studere samspillet mellom laver og lavetende snegler. En viktig problemstilling er å studere lavers beiteforsvar i form av karbonbaserte lavsyrer og undersøke hvordan disse påvirker beitende snegler. Noen lavsyrer er lokalisert i overbarken over algene. Disse induseres av solstråling og er kjent for å beskytte fotobionten mot sterkt lys. Lavsyrene i margen derimot fungerer ofte som et beiteforsvar. Lavsyrene i lungenever (*Lobaria pulmonaria*) beskytter mot beiting, men viste seg ikke å bli påvirket av beiting. Indusert forsvar er vanlig hos planter, men noen arter har konstant høyt beiteforsvar. Det viste seg at lavsyrer ofte er ujamnt fordelt mellom ulike organer i laven, og dette påvirker sneglenes beitemønster. Storvrenge (*Nephroma arcticum*) har nitrogenfikserende blågrønne bakterier i spesielle strukturer, cefalodier. Disse mangler lavsyrer og blir ofte beitet, mens resten av thallus vanligvis blir forlatt ubeitet. Forsvarsstoff hos en plante antas å bli fordelt til de mest utsatte og verdifulle delene av planten med hensyn til artens konkurranseevne (teorien om optimalt forsvar). En slik seleksjon har skjedd hos flere lavarter. Skrubbenever (*Lobaria scrobiculata*) har høy konsentrasjon av forsvarsstoffet metascrobiculin i sine vegetative reproduksjonsorgan (soral). Som resultat unnviker sneglene soralene. Men om lavsyrene fjernes ved uskadelig acetonvasking, er det soralene som blir foretrukket av beitende snegl. Videre varierer lavsyrekonsentrasjonen med lavens alder hos lungenever. Svært små lungeneverindivid viste seg å være dårlig forsvart. Som resultat ble unge individ av denne arten i stor grad beitet. Dette kan hemme etableringsfasen som ofte er et sårbart ledd i lavens livssyklus. Klatrende snegler viste seg å påvirke den nedre utbredelsesgrensa av en del lavarter på trestammer i edelauvskog. Arter som ofte ble beitet vokste høyere på trestammen eller i spesielle mikrohabitat som er mindre attraktive for sneglene., mens mindre populære laver ofte vokste helt ned til stammebasis. Dette tyder på at snegler kan påvirke epifyttiske lavsamfunn og begrense enkelte lavarter utbredelse i trærne.

SAMMANFATTNING (SVENSKA)

Lavar är symbiotiska organismer bestående av en svamp och en fotosyntetiserande alg och/eller cyanobakterie. Dessa växtliknande organismer är långlivade, stresståliga och dominerar ofta på platser där kärlväxter är mindre vanliga. Därför riskerar de att utsättas för predation. Växtätare påverkar sammansättningen av olika växtsamhällen. På samma sätt har renar stor påverkan på lavar. I vilken grad snäckor och sniglar (Gastropoda) påverkar lavar är emellertid mindre känt. Denna avhandling syftar således till att studera samspelet mellan lavar och lavätande gastropoder samt hur lavarnas försvarsämnen varierar och hur detta påverkar lavkonsumtion. Lavar producerar stora mängder sekundära kolföreningar, sk lavsyror, som har visat sig skydda laven mot evertebrater. Vissa lavsyror är placerade i barken och kring algerna där de skyddar algerna från starkt solljus och de ökar i koncentration med ökande ljus. De betesskyddande lavsyrorna, som ofta är placerade i märgen, påverkas däremot ej av solljus. Lavsyrorna i lunglav (*Lobaria pulmonaria*) induceras ej av betning. Inducerat försvar är annars vanligt hos växter även om många växter har konstant höga försvarshalter. Vidare visade sig lavsyorna variera mellan olika organ i laven något som också påverkar hur laven betas. Norrlandslav (*Nephroma arcticum*) har kvävefixerande cyanobakterier i interna samlingar (cephalodier). Dessa saknar helt försvarsämnen och betas således i stor utsträckning medan övriga bålen oftast lämnas orörd. Försvarsämnen hos växter har antagits vara fördelade så att de försvarar de delar som är mest utsatta och dessutom viktigast för artens fitness, "duglighet" (teorin om optimalt försvar). En sådan selektion har också skett hos flera lavarter. Skrovellav (*Lobaria scrobiculata*) har hög koncentration av försvarsämnet meta-scrobiculin i soralen (vegetativa förökningsorgan). Tillföljd av detta undviks dessa organ av snäckor men då lavsyrornas avlägsnats, genom att skölja laven med aceton, är det istället soralen som i första hand attackeras. Vidare varierar lavsyrorna med ålder på laven. Mycket unga individer av lunglav visade sig vara dåligt försvarade. Tillföljd av detta betas unga individer av laven i större utsträckning, vilket kan hindra etableringen som är en begränsande del av denna rara arts livscykel. Klättrande gastropoder kan också förklara den vertikala fördelningen av lavarter längs trädstammar. De arter som ofta betas växer högre upp på stammen medan mindre populära arter gärna växer ända ned till trädbasen. Således tycks gastropoder kunna påverka lavsamhällen och begränsa enstaka lavarters utbredning.

1 INTRODUCTION

A lichen is a symbiotic organism in which a fungus (mycobiont), a green alga and/or a cyanobacterium (photobionts) form an intimate biological union. Such organisms are long-lived and stress-tolerant in habitats where plants often are less abundant, but may face various environmental challenges, like lichenivory.

Herbivory is considered a significant regulating factor in plant communities (as reviewed by Huntly 1991; Olff & Ritchie 1998; Augustine & McNaughton 1998). Herbivores can impact plant communities via a few general processes. They influence growth, recruitment, and mortality rates of plants by affecting plant density, frequency, or other neighbourhood traits, or by modifying competition. Herbivores may increase, offset, or generate reciprocal negative interactions (competition) among plants. Herbivory is highly variable in space and in time. Spatial and temporal patterns of herbivory can generate structures in plant populations and strongly shape community dynamics. However, lichenivores' influence on species composition and structure in lichen-dominated communities is little studied and poorly understood.

Lichens are the main source of food for reindeer/caribou during winter (Danell et al. 1994). Hence, studies on lichenivory have mainly focused on these economically important animals (as reviewed by Richardson & Young 1977). Several studies have, for example, dealt with the reindeer's effect on species composition (e.g reviews by Suominen & Olofsson 2000; van der Wal 2006) or with the nutritional value of lichens (e.g. Storeheier et al. 2002). Lichens are low in proteins and nutrients, still reindeers depend on them as winter forage.

In addition to reindeers and other vertebrates, a number of terrestrial invertebrates, e.g. Acari, Collembola, Coleoptera, Gastropoda, Lepidoptera and Psocoptera, feed on lichens (Gerson & Seaward 1977). Gastropod-lichen interactions have only been given some attention (see cited references of Baur et al and Lawrey).

Considering the many lichenivorous animals, lichens depend on various mechanisms that offer lichenivore protection. Apart from the low nutritional value, many lichens invest much carbon into chemical defence (section 1.1).

1.1 Ecological role of lichen compounds

More than 800 mycobiont-derived secondary metabolites are described from lichens; many are unique to lichens even though some are known from plants and non-lichenized fungi (Huneck & Yoshimura 1996; Huneck 2001). Most compounds are polyphenols bio-synthesized through the acetyl-polymalonyl pathway, but some through the shikimic acid pathway and the mevalonic acid pathway (Elix & Stocker-Wörgötter 2008). The lichen compounds, which are almost insoluble in water, are deposited as crystals outside fungal hyphae and photobiont cells (Honegger 1986). The concentration is usually in the range of 1-5% per thallus dry weight but concentrations up to 30% have been measured (Huneck 1973). The lichen compounds are not evenly distributed within the thallus (as reviewed by Elix & Stocker-Wörgötter 2008). For instance, orange anthraquinone derivatives and the yellow pigmented usnic acid that occur in many lichens species are mainly restricted to the upper cortex (Fig. 1). Meanwhile many of the colourless depsides and depsidones are restricted to the medullary layer. In addition, lichen compounds vary both quantitatively and qualitatively between different thallus parts as well as between different individuals.

The diversity and the high concentration of lichen compounds suggest that these sub-stances do have an adaptive value. There is currently strong experimental evidence for a number of functional roles (sections 1.1.1 & 1.1.2). The same compound can even have different functional roles. For example, certain compounds have been found to protect both against lichenivores and gram-positive bacteria (Lawrey 1989). Living, air-dry lichens tolerate rinsing in 100% acetone without adverse effects on any of the lichen symbionts (Solhaug & Gauslaa 1996, 2001). As acetone does not enter the membranes of desiccated cells, the extracellular lichen compounds can be extracted and quantified. In this way, various hypotheses can be directly tested. For instance, lichen pairs with and without lichen compounds can be offered lichenivores to test the lichenivore defence hypothesis.
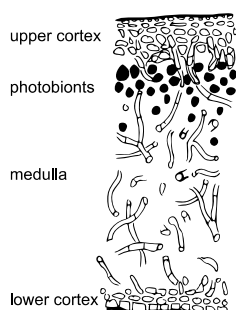

Fig. 1. Cross-section of a stratified (heteromerous) lichen thallus. The uppermost layer is formed by densely agglutinated fungal hyphae building a protective outer layer called the cortex. Loosely interwoven hyphae forms the medulla which occupies the major part of the thalline volume. The photobiont layer is localized in the very upper part of the medulla.

1.1.1 Lichenivore defence

The lichenivore defensive role of lichen compounds was suggested as early as 1895 by Zukal. In contrast, Zopf (1896), who served potato slices smeared with pure lichen compounds to snails, argued that these compounds did not deter grazing snails. A few years later Stahl (1904) found that removal of lichen compounds by a sodium bicarbonate solution made the lichen more attractive to the snail *Cepaea hortensi*s. In more modern times this hypothesis has been further tested and the empirical evidence is now strong. Several authors have tested the lichenivore defence role by removing lichen compounds with acetone (Paper III,VI; Reutimann & Scheidegger 1987; Gauslaa 2005; Pöykkö et al. 2005). Others have given the test animals the choice between artificial food (or vegetables) with and without added lichen compounds (Paper VII; Slansky 1979; Lawrey 1983a; Blewitt & Cooperdriver 1990; Hätscher et al. 1991; Emmerich et al. 1993; Giez et al. 1994; Gauslaa 2005; Clark et al. 1999; Reutimann & Scheidegger 1987). A third group of studies have compared the lichenivores preferences for lichens with different lichen compounds (Lawrey 1980, 1983b; Rambold 1985; Benesperi & Tretiach 2004; Nimis & Skert 2006).

The infestation of the polyphagous beetle (Coleoptera) *Lasioderma serricorne* in the lichen herbarium at the University of Trieste gave Nimis & Skirt (2006) the opportunity to assess the levels of damage to different species and to see if damage was related to lichen chemistry. Nearly 1500 specimens of 50 species were examined and a number of lichen compounds were found to deter the beetle. In addition, pruinose lichens with a layer of calcium oxalate crystals were resistant against beetle attacks. However, calcium oxalate crystals did not deter gastropods from feeding on tropical foliicolous lichens (Lücking & Bernecker-Lücking 2000). Gauslaa (2005) conducted another overall assessment of the effectiveness of the chemical defence of different lichen species. In his study 17 lichen species were tested for the deterrent effect of their lichen compound by using the acetone-rinsing technique. The majority of the tested species were well defended chemically. However, compounds produced by members of the Parmeliaceae, a chemically diverse family, were more deterring than those produced by members of Physciaceae and Teloschistaceae. Studied members of the former family dominate nutrient-poor habitats, in contrast with those from the two latter families. Therefore, Gauslaa (2005) suggested that the effectiveness of the lichen compounds in each group is related to nutrient availability and that lichens in nutrient-rich habitat are protected in some unknown way. In contrast, Lawrey (1983a) found that lichens high in N, P, K and Ca were better defended. He argued that

element-rich species invest in more defence as their biomass is more costly to replace. Apart from deterring animals, lichen compounds may also reduce the growth rate and survival of various insects (e.g. Slansky 1979; Blewitt & Cooperdriver 1990; Emmerich et al. 1993; Pöykkö et al. 2005). Furthermore, some compounds may even attract lichenivores. The oribatid mite *Fuscozetes setosus* was attracted by lichen compounds (atranorin, norstictic acid and an unidentified substance) in *Cladonia symphycarpa* (Reutimann & Scheidegger 1987). However, in the same study the oribatid mite *Carabodes intermedius* was deterred by these substances when applied to filter paper. Conclusively, several, but not all, lichen compounds have been proved to deter various invertebrates. In general, medullary compounds are more likely to deter grazing than cortical compounds (Gauslaa 2009).

There is some discrepancy regarding the deterring power of certain lichen compounds. Some of the differences are most likely lichenivore-dependent. For instance, usnic acid seems to deter coleopteran and lepidopteran grazing (e.g. Proksch & Hesbacher 1997; Nimis & Skert 2006), but not grazing by gastropods such as *Helicigona lapicida* and *C. hortensis* (Paper IV; Proksch & Hesbacher 1997). There is a bias towards chlorolichens in grazing experiments preconditioning thalli by acetone rinsing. However, the few studied cyanobacterial or tripartite lichens, *Lobaria pulmonaria* (Paper VI; Gauslaa 2005), *Nephroma arcticum* (Paper III) and *Lobaria scrobiculata* (Paper IV), do have lichenivore-deterrent lichen compounds. Furthermore, Benesperi & Tretiach (2004) found that the snail *Cantareus aspersa* and the slug *Arion* sp. preferred species of *Peltigera* without lichen compounds over related species with lichen compounds. However, many cyanobacterial lichens are deficient or low in lichen compounds (Krog et al. 1994). Still, they are rarely grazed despite their high content in nitrogen (Palmqvist et al. 1998). Furthermore, cyanobacterial lichens often grow in habitats preferred by many gastropods like lower parts of tree trunks in damp and mineral-rich forests. Thus, other factors than carbon based secondary compounds must reduce lichen palatability in such species.

Many lichens within the cyanobacterial lichenized fungal suborder Peltigerineae produce superoxide ($O_2\cdot^-$) at high rates (Beckett et al. 2003), a production that is induced by wounding (Beckett & Minibayeva 2003). Reactive oxygen species, such as $O_2\cdot^-$, may defend plants from herbivore attack (Bi & Felton 1995). Furthermore, *Nostoc* spp. in some lichen symbioses can produce hepatotoxic microcystin as shown for *Protopannaria pezizoides* and

Peltigera leucophlebia (Oksanen et al. 2004; Kaasalainen et al. 2009). In addition, some cyanolichens are mechanically protected, e.g. *Collema* spp. are generally avoided by snails, presumably due to their gelatinous nature when moist (Smith 1921; Baur et al. 1995).

Possible nitrogen-based defence compounds in green-algal as well as in cyanobacterial lichens, are carbohydrate-binding proteins. These compounds, the so-called lectins, have been suggested to play a role during the early stages of symbiont interactions (e.g. Bubrick et al. 1985; Kardish et al. 1991; Lehr et al. 2000). Many highly abundant plant lectins combine a plant defensive role with other functional roles (Peumans & Van Damme 1995). Recently, lectins from lichens and non-lichenized fungi have been shown to be toxic to insects (Hamshou et al. 2009; Silva et al. 2009).

In addition to chemical defence compounds, other factors such as surface toughness or energy and nutrient composition may also control lichen palatability. Furthermore, palatable species may escape from lichenivory by having high dispersal rates and/or high growth rates allowing quick replacement of lost tissues. For instance, partly grazed thalli of *Aspicilia calcarea*, *Tephromela atra* and *Verrucaria nigrescens* regenerated within a year (Fröberg et al. 2006). However, regenerated thalli were thinner than ungrazed ones. Additionally, Gauslaa et al. (2006) showed that moderate grazing did not affect subsequent growth rates of *L. pulmonaria*. Moreover, cortex of *Flavoparmelia baltimorensis* removed by *Hypogastrura packardi* (Collembola) in the autumn was replaced by midsummer (Hale 1972).

1.1.2 Additional functions

Many lichen compounds, such as atranorin and chloroatranorin, usnic acids, anthraquinones, xanthones and pulvinic acid derivatives, are restricted to the upper cortex just above the photobiont cells (Elix & Stocker-Wörgötter 2008). These compounds colour the lichen cortices yellow, orange, gray or brown and are capable of screening sunlight before it reaches the high light susceptible photobiont cells. The concentration of light-screening compounds such as usnic acid, parietin, atranorin and melanic compounds increase with increasing light availability (e.g. Rundel 1969; Gauslaa & Solhaug 2001; Gauslaa & Ustvedt 2003; Solhaug et al. 2009). Such variations also occur on a temporal scale in *Xanthoria parietina* where the parietin concentration is twice as high in the summer as in winter (Gauslaa & McEvoy 2005). Cortical compounds strongly absorb UV-B

light (Huneck & Yoshimura 1996; Gauslaa & Solhaug 2001) and are therefore assumed to protect against UV-B (Rikkinen 1995). However, it's uncertain how susceptible lichens are to UV-B. Acetone-rinsed *X. parietina* and *L. pulmonaria* low in UV-B absorbing vertical pigments grew rapidly under high UV-B levels (Larsson et al. 2009). But, DNA damage following high UV-B levels has been reported (Buffoni Hall et al. 2003). Instead, protection by cortical compounds against excess photosynthetically active radiation (PAR) is backed with supporting evidence (Solhaug & Gauslaa 1996; Gauslaa & Solhaug 2004; McEvoy et al. 2007a). PAR and UV-B are strongly correlated in natural ecosystems, hence the similar responses.

Other suggested functional roles of lichen compounds include allelopathy, mineralization of essential elements, regulation of photobiont metabolism, defence against microorganisms and pathogens (as reviewed by Rundel 1978; Lawrey 1986, 1995, 2009). Moreover, some lichen compounds possibly improve gas exchange by their hydrophobic properties (Huneck 2003). Lately, acidity tolerance has been shown to correlate with lichen compounds (Hauck & Jürgens 2008; Hauck et al. 2009). Lichen compounds may also protect lichens from toxic metals by immobilization in fungal cell walls (Hauck & Huneck 2007a, b).

In conclusion, lichen compounds may serve to protect lichens from chemical, physical and biotic threats. Considering the multiple functions of several compounds, one hypothesis is that lichen compounds represent an adaptation to a stressful life in extreme environments regardless of the type of stress (Lange 1992).

1.2 Lichen–gastropod interactions

1.2.1 Lichenivory

Lichenivory is found in several ecosystems and at least 64 species of terrestrial gastropods worldwide have been reported to consume lichens (Appendix). For instance, gastropods feed on calcicolous lichens in limestone grasslands (e.g. Fröberg et al. 1993) or rocky deserts (Shachak et al. 1987) and on epiphytic lichens (Fig. 2) primarily in broadleaved forests (e.g. Gauslaa et al. 2006) but also to a lesser extent in the boreal zone (personal observation). In addition, some marine and freshwater gastropods are lichenivorous (Schmid 1932; Colman 1940; Fletcher 1973).

Fig. 2. Grazed *Lobaria pulmonaria* and the snail *Anguispira alternata*. On *Acer* sp. in Petitcodiac, New Brunswick, Canada. Photo: Johan Asplund.

A few snail species are specialized lichen-feeders or feed predominantly on lichens (e.g. Kerney 1999), making them dependent on lichens as a food resource. Some snails even have specialized radulae enabling them to graze off epi- and endolithic lichens from rockfaces (Schmid 1929; Breure & Gittenberger 1981). Another example of possible co-evolution is that *X. parietina* provides *B. perversa* with all essential elements and nutrients necessary for snail growth and reproduction (Baur & Baur 1997).

Co-existing snail species may prefer different lichen species, and the most preferred lichen causes the greatest weight increase in juvenile snails (Baur et al. 1992, 1994; Fröberg et al. 1993). Thus, the net food quality of a lichen species varies between snail species. In other words, the snails have different abilities to deal with secondary compounds and/or physical characteristics or different degrees of utilization of the energy and nutrients of the lichens. Baur et al. (1994) discuss that the differential growth rates of snail species, raised on the same lichen diet, could reflect an evolved niche divergence as a result of previous avoidance of competition. As an alternative, they propose that the observed pattern results from independent, species-specific adaptations to different diets.

Lichens regenerated after grazing damage may severely differ in morphology from ungrazed ones. Such alterations have even led lichenologists to describe lichen thalli of one species as two separate taxa (Schade 1933, 1963; Wirth 1980). Yet, grazing marks on lichens are usually over-looked. Gastropods leave species-specific grazing marks depending on their size and the type of radulae (Baur et al. 2000). *Helicigona lapicida* is a very eager lichen-feeder and shows little discrimination between different thallus parts in contrast to some Clausiliidae snails. This makes it hard to use this species in studies of preference as it passionately grazes on the first object it encounters (personal observation). It is, however, deterred by lichen compounds like the other gastropod species tested (Arionidae: *Arion fuscus*, Clausiliidae: *C. bidentata, Cochlodina laminata, Macrogastra plicatula*, Helicidae: *Arianta arbustorum, C. hortensis* Limacidae: *L. marginata*, unpubl. data). Moreover gastropods have species-specific grazing patterns. *Helicigona lapicida* removes pieces of the thallus perpendicularly to the thallus surface (personal observation; Baur et al. 2000). Snails of the family Clausiliidae remove the upper cortex and partly the photobiont layer, and when grazing is severe, they feed also on the medulla (personal observations; Baur et al. 2000). *Cochlodina laminata* avoids the medulla of *L. pulmonaria* and *L. scrobiculata* but removes entire parts perpendicularly in acetone-rinsed compound-deficient lichen specimens (unpubl. data). This suggests that their avoidance of the medulla in the two *Lobaria* species is due to its content of stictic acid derivatives. Likewise lepidopteran larvae avoid the medulla of *Cladonia* spp. likely due to the fumarprotocetraric acid in this layer (Hesbacher et al. 1995; Bačkor et al. 2003). This pattern was also observed with *F. baltimorensis*, containing medullary protocetraric acid, after grazing by Collembola (Hale 1972). However, it has not yet been experimentally tested that these compounds deter the arthropods from feeding on the medulla. *Cepaea hortensis* restricts its grazing to the lower side of the cyano-

lichen *L. scrobiculata* (unpubl. data). In contrast, green algal lichens are commonly grazed from the upper side suggesting that this species prefer green algal photobionts (unpubl. data). The removal of the upper cortex exposes the medulla to various microorganisms. A higher exposure of the medulla may explain why Baur et al. (1995) found that lichenicolous fungi were restricted to heavily grazed parts of *A. calcarea* and *X. parietina*.

Snails with rock-scraping radulae can weather rocks at a rate of 0.7 to 1.1 metric tons ha^{-1} yr^{-1} while feeding on lichens (Shachak et al. 1987). Hence snails contribute to soil formation at a rate similar to that of windborne dust deposition. Consequently, lichenivorous gastropods can have a significant role in ecosystem processes.

1.2.2 Dispersal

Lichen dispersal by invertebrates has been briefly reviewed by several authors (Bailey 1976; Gerson & Seaward 1977; Seaward 2008). However, the number of experimental studies is scarce and very few have studied lichen dispersal by gastropods. Epizoochory have been observed with Gastropoda, Hymenoptera, Psocoptera, Neuroptera, Lepidoptera, Collembola, Coleoptera, Arachnida and Acari (Smith 1921; Bailey 1976; Gerson & Seaward 1977; Henderson & Hackett 1986). However, zoochory probably plays a minor role compared to anemochory (wind dispersal). Stubbs (1995) reports an average dispersal distance of merely 3.8±2.2 cm, by one species of oribatid mites. Ants have higher mobility allowing longer dispersal distances of diaspores. Six out of ten ants (*Acanthomyops niger*) collected from a tree trunk carried soredia (asexual symbiotic diaspores; Bailey 1970). Lorensson & Mattsson (1999) noted soredia on ants on the ground and observed a relationship between the distribution of ants and lichens. Soredia and lichen fragments also adhere to the mucus of gastropods and are in that way dispersed (Peake & James 1967). Moreover, the gastropods' mucus might increase the diaspores adhesion to the substrate. The immobilization of lichen diaspores have been shown to be a limiting factor for lichen establishment (Scheidegger et al. 1995; Hilmo & Såstad 2001). In fact, an adhesive agent (the hydrogel Ac-Di-Sol®) increased the establishment of transplanted isidia (asexual symbiotic diaspores) by a factor of 41 (Lidén 2009).

Gastropods (as well as other invertebrates) may possibly disperse lichens by endozoochory. McCarthy & Healy (1978) observed both photobiont cells and intact ascospores in faecal pellets of the lichen-feeding slug *Limax flavus*. Later, Fröberg et al. (2001)

showed that photobiont cells from *X. parietina* still had chlorophyll fluorescence activity after passing through the digestive tract of *H. lapicida*. In addition, faecal pellets of lichenivorous mites (*Trhypochtonius tectorum* and *Trichoribates trimaculatus*) have been found to contain both viable and regenerating ascospores and photobiont cells of *X. parietina* (Meier et al. 2002). Photobionts and spores dispersed within a faecal pellet may lead to the growth of new lichen thalli.

More importantly, gastropod grazing generates lichen fragments of various sizes, which can be redistributed vertically or horizontally. Small fragments, as well as faecal pellets containing photobiont cells, fungal hyphae or spores, can subsequently be dispersed by wind or birds over short or long distances. Hence, gastropods might indirectly play an important role in lichen dispersal. Lichens may also indirectly disperse snails, as snails can be attached to small pieces of lichens dispersed by wind (B. Baur unpubl. data cited by Baur & Baur 2000).

1.2.3 Shelter and camouflage
In addition to food, lichens provide gastropods with shelter from predators and desiccation. For instance, *B. perversa* seek protection under *X. parietina* that also serves as a food supply (Baur & Baur 1997). Some snails may also use lichens to conceal themselves. The snail *Napaeus barquini* actively covers its shell with lichens (Allgaier 2007). This camouflage can also serve as a food reserve as the snail grazes from its own shell in lack of food. Such camouflage can also occur on other species in this genus (Alonso et al. 1995). In addition, some lichens grow on the shell of snails (Gerson & Seaward 1977). However, in these cases the snails hardly actively camouflage themselves.

In summary, lichens are important organisms for a number of terrestrial gastropods as they constitute an important food source and may provide shelter for these animals. The extent of lichenivory, and the ecological consequences, may occasionally be extensive. Thus, lichen-gastropod interactions deserve further attention.

2 OBJECTIVES

The aim of this thesis was to study interactions between lichens and lichenivorous gastropods, mainly from a lichen perspective. Such interactions include variation in lichen chemical defence, how lichen compounds regulate lichenivory and how lichenivory shapes lichen communities.

The specific questions addressed in this thesis are:

1)   Do abiotic and biotic factors control the concentration of lichen compounds?
- Abiotic: light availability (Paper I)
- Biotic: gastropod grazing (Paper II)

2)   How do lichen compounds vary between different structures within a thallus? Do such variations affect the grazing pattern of lichenivorous gastropods?
- Green algal *vs.* cyanobacterial thallus parts (Paper III)
- Optimal defence theory: reproductive *vs.* somatic thallus parts (Paper IV)

3)   Does the concentration of lichen compounds vary with the age of the thallus? (Paper V)

4)   What are the ecological consequences of lichenivory?
- Juvenile thallus development (Paper VI)
- Effect on horizontal distribution of lichens (Paper VI)
- Effect on vertical distribution of lichens (Paper VII)

3 METHODS

3.1 Study species

This thesis deals with ten lichen species (Table 1). Nine of these are epiphytic, but *N. arcticum* is terricolous and all species but *U. longissima* also grow on rocks. *Pseudocyphellaria crocata* (VU) and *Usnea longissima* (EN) are red-listed in Norway (Timdal et al. 2006). The *Lobaria* species are rare and threatened in many parts of the world presumably due to high susceptibility to commercial forestry (e.g. Campbell & Fredeen 2004) and air pollution (e.g. Gilbert 1986; Gauslaa 1995).

Table 1 Studied lichen species and the respective lichen compounds identified in the studies

Lichen species	Identified lichen compounds	Paper
Lobaria amplissima (Scop.) Forssell	Metascrobiculin, Pseudocyphellarin A, Atranorin (trace)	VII
L. pulmonaria (L.) Hoffm.	Stictic acid, constictic acid, norstictic acid, peristictic acid, cryptostictic acid, methylnorstictate	I,II,V-VII
L. scrobiculata (Scop.) DC	Stictic acid, usnic acid, peristictic acid, meta-scrobiculin, constictic acid, norstictic acid, methylnorstictate, unknown derivatives	IV,VII
L. virens (With.) J.R.Laundon	Atranorin (trace)	VII
Nephroma arcticum (L.) Torss.	Phenarctin, nephroarctin, usnic acid, methyl gyrophorate	III
Usnea longissima Ach.	Usnic acid, diffractaic acid	I
Pseudocyphellaria crocata (L.) Vain.	Tenuiorin derivatives, constictic acid, stictic acid	I

Two snail species and one slug were used in lab feeding experiments. The snail *Cepaea hortensis* (O.F. Müller, 1774) is a generalist living in woods, grassland, hedges and dunes (Kerney & Cameron 1979). This 14-20 mm wide species was used in Paper IV and have been used earlier in lichen-feeding experiments (Stahl 1904; Gauslaa 2005). *Arion fuscus* (O.F. Müller, 1774) (previous *A. subfuscus* (Draparnaud, 1805)), a common 50-70 mm long slug that inhabits woods, pastures, gardens, hedges and dunes throughout Europe, was used in Paper III (Kerney & Cameron 1979). This species feeds predominantly on fungi (including lichens) but also green plants and animals (Andersson et al. 1980). The 15-17 mm long fusiform snail *Cochlodina laminata* (Montagu, 1803) lives in shaded places in woods and often climbs trunks in wet weather to feed on lichens (Kerney & Cameron 1979). It was used in Paper IV. In addition to mentioned species, *Balea perversa* (Linnaeus 1758), *Clausilia bidentata* (Ström, 1765), *Columella edentula* (Draparnaud, 1805), *Helicigona lapicida* (Linnaeus, 1758), *Lehmannia marginata* (O.F. Müller, 1774), *Macrogastra* (W Hartmann, 1841) sp., and *Vertigo pusilla* (O.F. Müller, 1774) were observed on studied lichen transplants in natural environments.

3.2 Chemical analysis

Concentration of lichen compounds were analysed with high pressure liquid chromatography (1100 Series HPLC, Agilent Technologies, Waldbronn, Germany). The extraction protocols and the HPLC method are given in the respective papers.

3.3 Quantification of grazing

Grazing was quantified both as biomass consumed (Paper III, VI) and as area grazed (Paper III, IV, VII). Biomass consumed is a straight forward and quick assessment. In long-term grazing experiments, lichen growth will obscure the results unless the grazing is severe. Area grazed was assessed by polygon delineation in ArcGIS™ (ESRI®, Redlands, CA, USA), from georeferenced photographs of the lichens (Fig. 3). This is much more time consuming but lichen growth is less likely to influence the results. On the other hand, the depth of the grazing is not accounted for by this method. Quantifying grazing on different parts of a single thallus, as was done in Paper III & IV, is only possible with polygon delineation.
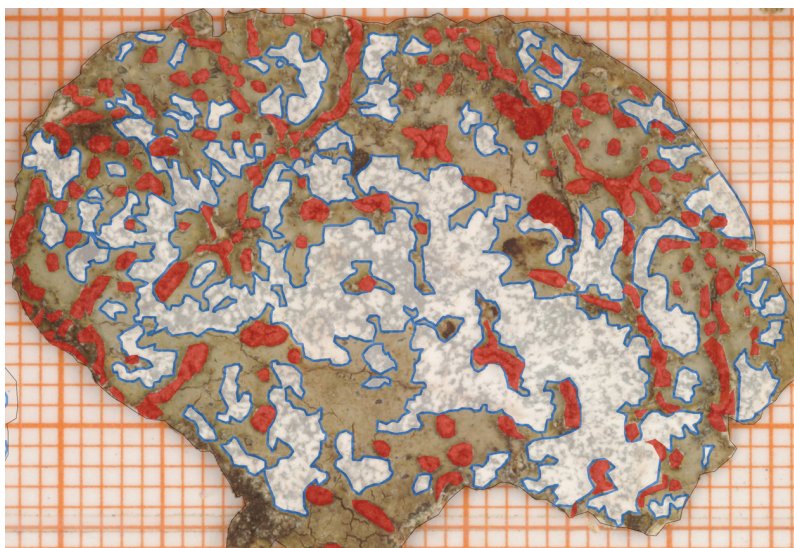

Fig. 3. Example of grazing quantification by polygon delineation. Grazing marks are marked with transparent white with blue outline while the soralia of this *L. scrobiculata* thallus is marked with red. Soralia were delineated from the pre-experiment photograph (not shown). Photo: Johan Asplund.

3.4 Acetone rinsing

Lichen compounds were removed, or reduced in concentration, from living thalli by acetone rinsing (Solhaug & Gauslaa 2001). Air-dry thalli were left in excess acetone for 20 minutes. This procedure was repeated three to four times and the thalli were thereafter left for 24 h for residual acetone to evaporate.

3.5 Experimental setup

Paper I dealt with *U. longissima*, *P. crocata* and *L. pulmonaria* transplanted along a natural shade-sun gradient comprising three successional stages in boreal spruce forests (dense young forest, open old forest and clear-cut). The lichens were transplanted at three boreal sites dominated by *Picea abies*. The Atlantic location was in Namsos, Nord-Trøndelag, W Norway (Fig 4A, 64°25´N 11°27´E, 30 m a.s.l.) in rainforests with a few scattered *Betula pubescens* and *Alnus incana*. The suboceanic location was in Siljan, Telemark, SE Norway (Fig. 4B, 59°22´N 9°45´E, 500 m a.s.l.) with a few trunks of *B. pubescens* and *Sorbus aucuparia*. The third location, Kullbäcksliden, near Umeå, Västerbotten, N Sweden (Fig.
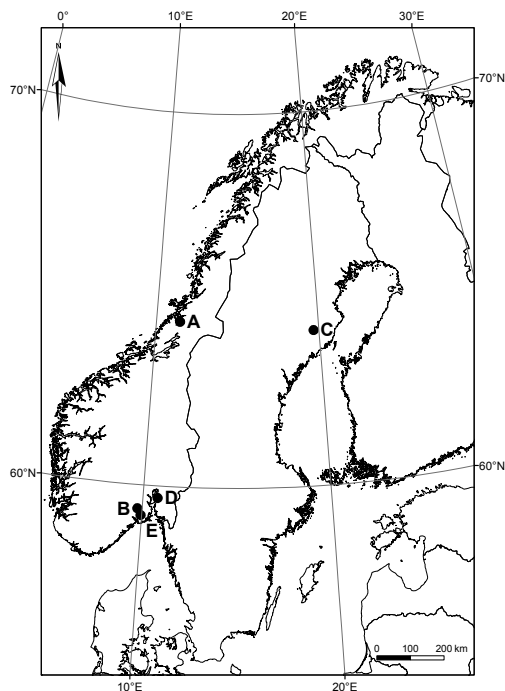

Fig. 4. Fennoscandia with study sites. Capital letters localities named in the text.

4C, 64°10´N 19°40´E, 250 m a.s.l.), represented the most continental climate and had scattered *Pinus sylvestris*, *B. pubescens*, *Salix caprea*, *S. aucuparia* and *Populus tremula*. After the 111 day transplantation period extractable lichen compounds were quantified with HPLC and the melanic pigmentation was quantified by measuring the reflectance from the lichen surface. *Lobaria pulmonaria* and *P. crocata* were only analyzed from the atlantic locality while *U. longissima* were analyzed from all localities.

Paper II & VI analysed *L. pulmonaria* transplanted to broadleaved deciduous forests with high populations of lichenivorous gastropods. One forest, located at Bekkevoll, Frogn, Akershus SE Norway (Fig. 4D, 59°43´N 10°43´E, 20 m a.s.l.), had a poor epiphytic lichen flora with no *L. pulmonaria*. However, the species occur naturally in the landscape. The second site, located in Jordstøyp Nature Reserve, Kvelde, Larvik, Vestfold S Norway (Fig. 4E, 59°12´N 9°57´E, 300 m a.s.l.), had a species rich lichen flora including the study species. Transplantation stands were put up in pairs (with or without gastropod exclosure). Half of these pairs were placed under a shading canopy while the others were more exposed to light in canopy gaps. Mature thalli (± acetone rinsing) and bark pieces each with

33±2.3 juvenile thalli (mean±SE; size <5 mm) of *L. pulmonaria* were transplanted to the stands. Mature thalli were weighed and juvenile thalli were counted before and after the 104 day transplantation period to quantify grazing (Paper VI). In addition, depsidone concentration was quantified in mature thalli to determine if the lichen compounds are induced by grazing (Paper II).

In paper III cephalodia (including upper and lower cortex) and purely green algal thallus of *N. arcticum* were separated and analysed for lichen compound concentration. *Nephroma arcticum* has *Coccomyxa* sp. (green alga) as the main photobiont. In addition, the cyanobacterium *Nostoc* sp. is localized in scattered large internal structures (cephalodia). In addition, we let the mycophagous slug *A. fuscus*, which co-occur with *N. arcticum* throughout its distribution range, graze on acetone rinsed and control thalli. The amount of grazing on the respective thallus structure was quantified with polygon delineation.

Paper IV quantified the concentration of lichen compounds in soralia (structures with soredia) and somatic parts of *L. scrobiculata*. Usnic acid and metascrobiculin were separately applied to filter paper to test their respective deterrent effect by letting *C. hortensis* choose between filter paper with and without lichen compounds. Subsequently, we gave *C. laminata* acetone rinsed and control thalli of *L. scrobiculata* to determine the preference for reproductive and somatic tissues in the presence and absence of lichen compounds.

Paper V quantified defence compounds in thalli of *L. pulmonaria*, ranging from 0.08 to 550 mg in size, from two *P. tremula* trunks in an old and open oligotrophic *P. abies* forest at Kollåsen, Ski, Akershus SE Norway (Fig. 4D, 59°45′N, 10°57′E, 200 m). Thalli with a weight less than 10 mg were pooled in size-dependent batches. Subsequently the concentration of lichen compounds was quantified using HPLC.

In paper VII four *Lobaria* species (*L. scrobiculata L. amplissima*, *L. pulmonaria* and *L. virens*) were transplanted together on *Fraxinus excelsior* trunks at 0.5, 3 and 6 m above ground. The lichens were transplanted to five sites in the hemiboreal region in Akershus, SE Norway (Fig. 4D): Askehagen (one site, 59°40′N, 10°46′E, 100 m a.s.l.), Bekkevoll (two sites 100 m apart, 59°43′N, 10°43′E, 20 ma.s.l.) and Pollevann (two sites 100 m apart, 59°44′N, 10°45′E, 10 m a.s.l.). In addition, the height above the ground of naturally oc-

curring *Lobaria* species were registered on tree trunks along a coastal section from eastern to western parts of S Norway.

4 RESULTS AND DISCUSSION

4.1 Quantitative studies of lichen compounds

4.1.1 External factors

Usnic acid, the major cortical, secondary compound in *U. longissima*, showed significantly higher concentration in the clear-cut than in the two forested stands (Paper I). *Pseudocyphellaria crocata* and *L. pulmonaria*, lacking extractable secondary compounds in the cortex, significantly increased their amounts of cortical melanins in well-lit stands. These results (Paper I) suggest a common functional role of usnic acid and melanins as light screening compounds (see section 1.1.2). In general, the medullary compounds did not increase with increasing light availability, which is supported by a number of other studies (e.g. Stephenson & Rundel 1979; Bjerke et al. 2005; McEvoy et al. 2007a). The contrasting main responses of cortical and medullary compounds suggest that these two compound groups have different functions. However, some individual medullary compounds did show stand-specific responses, particularly in *P crocata*, although these trends were generally weak or with contrasting directions. In *U. longissima*, the medullary depside diffractaic acid responded in an inverse pattern to the cortical dibenzofuran usnic acid. In clear-cuts, where much carbon is spent for new growth as well as for synthesis of usnic acid, the production of diffractaic acid probably has lower priority.

Likewise, *N. arcticum* collected in lowland spruce forests had lower concentrations of the depsides phenarctin and nephroarctin compared to thalli collected at an alpine exposed heath and subalpine birch forest, while usnic acid occurred in higher concentrations in the latter habitats (McEvoy et al. 2007b). Swanson et al (1996) found lower levels of medullary compounds in *Umbilicaria americana* in sites at higher elevations, where UV irradiance was more intense. The concentration of the medullary depsidone norstictic acid was negatively correlated with the yearly amount of light reaching the lichen *Parmotrema hypotropum* on a tree trunk (Armaleo et al. 2008). In contrast, the levels of the cortical depside atranorin increased with increasing light. Armaleo et al. (2008) argues that the increase of norstictic acid with decreasing irradiance is explained with lower temperatures and higher water potential in these thalli. This explanation is given some support in the literature as barbatic pathway compounds increased at lower temperatures (Culberson et

al. 1983). However other medullary compounds seem to increase with increasing temperatures (Hamada 1982a; Culberson et al. 1983; Bjerke et al. 2003). Furthermore, medullary compounds in *N. arcticum*, *U. americana* and *L. pulmonaria* decreased with increasing altitude (Swanson et al. 1996; McEvoy et al. 2007b; Vatne 2009), presumably due to decreasing temperature. In conclusion, medullary compounds are hardly directly affected by light but sometimes by other factors co-varying with light availability.

Neither grazing nor canopy openness had significant effects on the concentrations of stictic acid and related depsidones in *L. pulmonaria* (Paper II). Furthermore, the ratio between the depsidone concentrations of acetone rinsed and controls remained the same before and after 3 months grazing. Hence, I found no evidence that gastropod grazing induces or stimulates the synthesis of depsidones in *L. pulmonaria*. Instead, the results are consistent with a constitutive type of defence. Nybakken & Julkunen-Tiitto (2006) found no effect of artificial grazing (clipping) on the concentration of several medullary depsidones in three mat-forming *Cladonia* species under laboratory conditions. However, the lack of response in this case may occur because artificial grazing lacks signal elicitation (Baldwin 1990; Lehtilä & Boalt 2004). A constitutive type of defence in lichens with high concentration of lichen compounds is likely because these high levels may decrease the benefit of induced defence (Herms & Mattson 1992). *Lobaria pulmonaria* contains various stictic acid derivatives that have been shown to protect the species from snails (Gauslaa 2005). Induced defence is widespread in plants (Karban & Baldwin 1997), but many secondary plant substances are not induced by grazing (Herms & Mattson 1992). The only observation of induced lichenivore defence is from *Cladonia bacilliformis* and *C. norvegica* (Timdal 1989). In these two species the red rhodocladonic acid was exclusively synthesised around cavities formed by mites on the lower side of basal squamules.

4.1.2 Intrathalline variations
The concentration of lichen compounds was higher in thallus parts without cephalodia than in adjacent cephalodial thallus parts (Table 1 in Paper III). The cephalodia themselves lack lichen compounds (Renner 1980) and any substances observed in cephalodial thallus parts are produced in the fungal tissues below and/or above the cephalodia. The lack of lichen compounds in the cephalodia may be caused by different fungal metabolism within this tissue (Renner 1982). Renner (1982) proposed that these differences are caused

by adaptations of the mycobiont to take up and transfer ammonium ions released by N_2-fixing *Nostoc*.

In intact thalli *A. fuscus* fed mainly on cephalodia while green-algal thallus parts were avoided. However, after lichen compounds had been removed by acetone rinsing the snails did not discriminate between green-algal and cyanobacterial parts (Fig. 2 in Paper III). Thus, it is not the cyanobacteria *per se* that are preferred but the lack of defence compounds in their immediate surroundings. Besides, in the lichen compound-deficient *Sticta canariensis* gastropods prefer the green algal-morphotype to the cyanobacterial one (James & Henssen 1976). On the other hand, *Nostoc* sp. in lichen symbiosis can in some cases produce hepatotoxic microcystins which might protect the cephalodia against invertebrate grazing (Kaasalainen et al. 2009).

The secondary chemistry varies both quantitatively and qualitatively between reproductive and somatic parts of lichens (e.g. Paper IV; Imshaug & Brodo 1966; Culberson 1969; Brodo & Hawksworth 1977; Brodo 1984; Botnen & Tønsberg 1988; Tønsberg 1992; Hyvärinen et al. 2000). This pattern has been suggested to be a case of optimal defence (Hyvärinen et al. 2000). The optimal defence theory (ODT) is developed and widely used for plants (Zangerl & Bazzaz 1992). It predicts that defence compounds within a plant are allocated in proportion to the risk for a specific plant tissue being attacked and this tissue's value in plant fitness (McKey 1974; Rhoades 1979). However, the empirical evidence is lacking, as one needs to measure the benefit of defence to prove the hypothesis. This cannot easily be done in plants as one needs to offer conspecific pairs of natural control specimen and defence-deficient individual to herbivores (Hamilton et al. 2001). However, the acetone rinsing technique provides the tools to fully test this hypothesis. *Lobaria scrobiculata* contained five times as much meta-scrobiculin in the soralia as in the somatic parts of the thallus (Fig. 1 in Paper IV). In contrast, the cortical usnic acid, which did not deter snails, was absent in the soralia, and concentration of the stictic acid related compounds did not differ between thallus structures. *Cepaea hortensis* avoided filter paper to which purified meta-scrobiculin had been applied, suggesting that this substance deters gastropods. Furthermore, *C. laminata* avoided the highly protected soralia in control thalli but preferred the soralia after the lichen compounds had been removed. In conclusion, *L. scrobiculata* allocates their defence to the soralia which are more likely to be attacked. They are valuable for the fitness of the lichen as suggested by ODT. Moreover the cyanolichen

P. crocata has the pulvinic acid derivative calycin restricted to the soralia (Paper I). In a transplantation study involving this species, Gauslaa (2008) observed that the soralia were avoided by grazing gastropods. The allocation of defence in the soralia suggests that also the diaspores and perhaps even the early stages of juvenile thallus development are well defended. This would be favourable for the establishment of the lichen. However, juvenile thalli were poorly defended in *L. pulmonaria* (Paper V). On the other hand, *L. pulmonaria* contains only the stictic acid related compounds, which showed no variation between reproductive and somatic tissues (data not shown).

4.1.3 Life-stage variations

The lichen compounds concentration in *L. pulmonaria* correlated positively with thallus size (Paper V). Lichen compounds have been shown earlier to correlate with thallus size or age within a number of lichen species (Table 1). However, the direction of the trend varies between lichen species and compound. Sometimes the same lichen compounds can show opposite responses in different lichens.

Table 2 Studies on the correlation between age and lichen compounds concentration. ↗ denotes increasing concentration with age, while ↘ denotes the opposite, and – denotes no correlation

↗↘ Lichen	Compound	Parts measured	Reference
↗ *Cladonia cristatella*	condidymic acid	development stage	(Culberson et al. 1983)
↗ ------	didymic acid	development stage	(Culberson et al. 1983)
↗ *C. rangiferina*	protocetraric acid	intrathalline	(Mirando & Fahselt 1978)
↗ *Letharia vulpina*	atranorin	intrathalline	(Stephenson & Rundel 1979)
↗ *Lobaria pulmonaria*	stictic acid derivatives	thalli of various age	(Paper V)
↘ *Cladonia* spp.	atranorin,	intrathalline	(e.g. Fedoseev & Yakimov 1960; Mirando & Fahselt 1978)
↘ ------	fumarprotocetraric acid	intrathalline	
↘ ------	usnic acid	intrathalline	
↘ *L. vulpina*	vulpinic acid	intrathalline	(Stephenson & Rundel 1979)
↘ *Ramalina siliquosa*	salazinic acid	intrathalline	(Hamada 1982b)
↘ *Vulpicida pinastri*	pinastric acid	thalli of various age	(Golojuch & Lawrey 1988)
↘ ------	vulpinic acid	thalli of various age	(Golojuch & Lawrey 1988)
– *C. cristatella*	barbatic acid pathway	development stage	(Culberson et al. 1983)
– *Lasallia papulosa*	gyrophoric acind	thalli of various age	(Culberson & Culberson 1958)
– *Tephromela atra*	alectoronic acid	thalli of various age	(Hesbacher et al. 1996)
– ------	atranorin	thalli of various age	(Hesbacher et al. 1996)
– ------	α-collatolic acid	thalli of various age	(Hesbacher et al. 1996)

A positive trend, as with *L. pulmonaria*, can possibly be explained with the growth-differentiation hypothesis (Herms & Mattson 1992), which suggests that early allocation of energy is insufficient for both growth and secondary metabolites. On the other hand, the optimal defence theory explains the higher concentration of light-screening compounds in apical parts of *Cladonia* spp. However, in this genus age also correlates with the vitality which might affect secondary chemistry. Golojuch & Lawrey (1988) argues that younger tissues should be better defended because of their peripheral position which makes them more likely to be attacked. However, this should only be the case for young versus old parts within a single thallus. Contrary, small thalli are probably less likely to be encountered by lichenivores than big ones. However, predation on a small thallus is likely more devastating for the individual lichen. The consequences of the poor defence in juvenile *L. pulmonaria* were later studied in gastropod-rich forests (Paper VI).

4.2 Ecological consequences of gastropod grazing

4.2.1 Effect on growth and early development

The old forest lichen *Lobaria pulmonaria* is limited by dispersal due to various ecological factors at the stand level (Werth et al. 2006). Considering the low concentration of defence compounds in juvenile *L. pulmonaria* thalli, invertebrate grazing may be one limiting factor for the establishment phase. Almost 50% of juvenile thalli on transplanted bark pieces in deciduous forests were lost during one summer with free access for gastropods, compared to only 10% loss when gastropods where excluded (Paper VI). When bark pieces with juvenile thalli were transplanted at a lichen-rich site the loss was below 20% in stands with free access for natural gastropod populations. Likewise, Scheidegger (1995) found a high loss of transplanted *L. pulmonaria* diaspores partly due to invertebrate grazing. In mature lichens the grazing was significantly higher on the acetone rinsed thalli, providing field evidence for a lichenivore defensive role of the depsidones that has earlier only been shown in lab experiments (Gauslaa 2005). In acetone rinsed thalli the concentration of lichen compounds were reduced to 36% of original concentration (Paper II). Hence, compound concentration after rinsing was approximately the same as in the juveniles. Consequently, the biomass grazed on acetone rinsed thalli was equivalent to the loss in number of juvenile thalli (Fig. 1 & 4 in Paper VI). Thereby, the high loss of juvenile thalli was likely due to poor defence.

Grazing on juvenile thalli has presumably a greater effect for the species at a population level than grazing on mature thalli, as it limits the establishment rather than just the growth of already reproducing individuals. Besides, mature thalli have an ability to regenerate after lichenivore damage (Hale 1972; Fröberg et al. 2006; Gauslaa et al. 2006). Consequently gastropods may have a great impact in regenerating lichen communities even at a low biomass consumption level. Also for plant communities, the effect of gastropods has been suggested to be weakly coupled to the quantity consumed (Hanley et al. 1995). Instead it depends on the affected life stage and preferred tissue type of the individual plant.

4.2.2 Effect on species distribution

Lichenivorous gastropods discriminate between different lichen species (e.g. Fröberg et al. 1993). Thus, they can potentially alter the relative abundance between lichen species. Given that gastropods do play a role in restricting lichens, one would expect a relationship between grazing pressure and species composition. Species composition in epiphytic communities varies along a complex environmental gradient from the ground to the top of the forest canopy. Likewise, the grazing pressure from invertebrates presumably also varies across this gradient. Hence, this gradient may be shaped by a combination of invertebrate grazing, bark properties and microclimatic factors. Natural gastropod populations clearly discriminated between species (paper VII). They grazed mostly on *L. scrobiculata* (65±3.2% of the total grazing per mesh) followed by *L. amplissima* (28±3.1%), *L. pulmonaria* (4.6±1.1%) and finally *L. virens* (2.9±0.9%). In addition, gastropod grazing increased with increasing proximity to the ground. Measured gastropod preferences among studied *Lobaria* species reflect the ranges of these lichens in forest canopies. The highly palatable *L. scrobiculata* occurs mainly in localities with low gastropod abundance, such as boreal forests and on bark with slightly lower pH. The second most palatable species, *L. amplissima*, occurs in gastropod-rich localities, but above the lower parts of the trunk. *Lobaria pulmonaria* and *L. virens* frequently grow down to a level of <1 m above the ground. Hence, climbing gastropods likely play a role in shaping the lichen community along a vertical gradient in forest canopies restricting the spatial pattern of susceptible lichen species. Fletcher (1973) found no lichen species in territories grazed by *Patella* spp, suggesting that marine snails have an important role in limiting the initial colonization of lichens on seashores.

Gastropod grazing has been proposed as an explanation for the decline, and in some cases disappearance, of *P. crocata* from its southern localities, where lichenivorous gastropods are more abundant (Gauslaa 2008). Gastropod grazing is probably not the sole reason for local extinction of species, but may be an important contributing factor. In localities with few individuals stochastic grazing events likely have large effects. For example, *Arion fuscus* has been observed heavily grazing on the rare and declining *Erioderma pedicullatum* in Nova Scotia, Canada (Dogett 2007). However, it is uncertain if grazing poses a threat to the few remaining populations. Reduced vitality of lichens may raise their palatability, and thereby increase the risk of local extinction. For instance in Paper VII we found that grazing marks of *L. virens* was restricted to high light-damaged parts. Lichens of low vitality may have lower concentration of defensive compounds (Follman & Schulz 1993). On the other hand, *H. lapicida* avoided dead *L. scrobiculata* killed by excess temperature in a lab feeding experiment (unpubl. data).

Herbivores are generally considered to increase plant diversity by causing disproportionate mortality or tissue loss rates of certain plant species that would be dominant in the absence of herbivores (e.g. reviews by Huntly 1991; Olff & Ritchie 1998). Hence, one possible effect of lichenivory could be increased diversity of lichen species. However, this is probably only true in lichen communities with pronounced competition for the substrate and where few species are dominant. This is the case in foliicolous lichen communities where psocopteras, but not gastropods, feed on large sized species and thus enhance diversity (Lücking & Bernecker-Lücking 2000). Conversely, Baur et al. (1995) studied 12 calcareous stone walls and found no correlations with lichen diversity and frequency of the two lichen-feeding snails *B. perversa* and *C. clienta*. However, grazing was more frequent on dominant species and species richness tended to decrease with increasing proportion of area covered by the dominant *A. calcarea*.

4.3 Variation in grazing pressure
The grazing pressure varies on both local and larger scales. The frequency of grazing marks on *L. pulmonaria* is higher in temperate broadleaved forests than in boreal *P. abies* forests due to higher abundance of lichenivorous gastropods in the former type (Gauslaa et al. 2006). However, grazing pressure also varies between different broadleaved deciduous forests. For example, lichens transplanted to a site rich in *Lobaria* spp. were less grazed than those transplanted to a lichen-poor site (Paper VI). The higher availability of

other lichens probable decreased the interest in transplanted thalli. Gastropods often show patchy occurrences within forests due to small-scale differences in micro-climate, habitat heterogeneity or a patchy distribution of food (Ledergerber et al. 1997; Kleewein 1999), causing grazing pressure to vary substantially even on a spatial scale of a few metres (Paper VI, VII). For instance, *L. pulmonaria* placed under more shading canopies experienced far more grazing than thalli at nearby, but more open locations. Likewise, Vatne (2009) found a negative correlation with direct site factor and cover of grazing marks on naturally occurring *L. pulmonaria*. In shady positions the desiccation is slower allowing longer periods of gastropod activity (Kerney & Cameron 1979). The grazing pressure may also vary between years (Gauslaa, personal communication), probably because of climatic differences.

5 CONCLUSION AND FUTURE PERSPECTIVES

Several medullary lichen compounds protect against lichenivores. This defence is most likely constitutively expressed and is not induced by grazing (as evidenced for *L. pulmonaria* in Paper II). The defensive compounds are disproportionally distributed within the lichen thallus. Consequently, gastropods selectively graze on specific parts of a lichen thallus. Thallus parts with high concentrations of chemical defence are frequently avoided and lichenivores usually stop feeding when reaching the medulla, where most of the defence is situated. Moreover, lichens may allocate defence to valuable parts in order to increase their fitness. Hence, defence theories developed for plants also apply to lichens. In fact, lichens are well suited study organisms to test such theories as their defensive compounds easily can be removed. However, allocations to specific thallus parts may not always be metabolically possible, evidenced by high grazing of compound-deficient cephalodia containing valuable N-fixing cyanobacteria. Furthermore, gastropods show preferences for specific lichen species that partly can be explained by their different defence compounds. As a result, lichenivorous gastropods likely play a significant role in shaping lichen communities, by reducing juvenile development for certain species. This suggests that herbivore-induced processes shaping plant communities are also created by gastropods in lichen communities.

Future perspectives:
- More studies on how biotic and abiotic as well as genetic factors affect lichen compounds are needed.

- Other factors (apart from lichen compounds) determining lichen palatability needs to be further tested. For instance how does composition of proteins, carbohydrates and various elements affect lichen palatability? How does surface toughness affect lichenivory? Do nitrogen-rich lichens have N-based defences?

- Lichen palatability in relation to available foods deserves further attention. Does the availability of certain food types affect the grazing pressure on lichens? Does the configuration of the lichen community affect the grazing pressure on a given species? For instance, *L. pulmonaria* is more grazed in the absence of *L. scrobiculata.*

- The knowledge of temporal/seasonal differences in grazing pressure needs to be expanded.

- The effect of climate change on gastropod grazing needs further attention.

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APPENDIX. Terrestrial gastropods known to feed on lichens.

Gastropod	Lichen	References
⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯*SNAILS*⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯⋯		
ACHATINELLIDAE		
Achatinella vulpina	–	(Schmidt 1936)
BULIMULIDAE		
Oxystyla undata	*Graphis* sp., *Buella parasema*, *Lecanora pallida*, *Pertusaria amara*	(Plitt 1934)
CHONDRINIDAE		
Abida secale	–	(Peake & James 1967)
Chondrina avenacea	*Verrucaria calciseda*, *Protoblastenia rupestris*	(Schmid 1929; Gittenberger 1973)
C. clienta	20 species listed	(e.g. Fröberg et al. 1993)
CLAUSILIIDAE		
Balea perversa	*Aspicilia calcarea*, *Caloplaca variabilis*, *Lobaria pulmonaria*, *Physcia adscendens*, *Rinodina immersa*, *Staurothele* cf. *guestphalica*, *Tephromela atra*, *Verrucaria muralis*, *V. nigrescens*, *Xanthoria parietina*	(Baur et al. 1994; Fröberg et al. 1993, 2006; Gauslaa et al. 2006; Baur & Baur 1997)
Clausilia bidentata	*Aspicilia calcarea*, *L. pulmonaria*, *Protoblastenia rupestris*, *Verrucaria glaucina*, *V. nigrescens*	(Fröberg et al. 1993; Gauslaa et al. 2006)
C. dubia	–	(Peake & James 1967)
C. parvula	–	(Baur et al. 2007)
Cristataria genezarethana	–	(Heller & Dolev 1994)
Macedonica zilchi	–	(Irikiov & Mollov 2006)
Neostyriaca corynodes	–	(Baur et al. 2007)
DISCIDAE		
Discus rotundatus	–	(Peake & James 1967)
D. ruderatus	*L. pulmonaria*	Personal observation
ENIDAE		
Ena montana	–	(Peake & James 1967)
Euchondrus albulus	endolithic species	(Shachak et al. 1987)
E. desertorum	endolithic species	(Shachak et al. 1987)
Merdigera obscura	–	(Peake & James 1967)
Napaeus barquini	*Pertusaria* sp. among others	(Allgaier 2007)
HELICIDAE		
Arianta aethiops	–	(Baur et al. 2000)
A. arbustorum	*Parmelia sulcata*, *X. parietina*	(Gauslaa 2005)
A. chamaeleon	–	(Ledergerber et al. 1997)
Cantareus aspersa	*Peltigera* spp.	(Benesperi & Tretiach 2004)

Gastropod	Lichen	References
Cepaea hortensis	*Anaptychia runcinata, Cladonia arbuscula, C. rangiferina, Evernia prunastri, Flavoparmelia caperata, Hypogymnia physodes, Hypotrachyna revoluta, L. pulmonaria, Parmelia saxatilis, P. sulcata, Parmelina tiliacea, Parmotrema chinense, Physcia aipolia, Physconia distorta, Platismatia glauca, Vulpicida pinastri, X. parietina*	(Gauslaa 2005)
C. nemoralis	-	(Peake & James 1967)
Cornu aspersum	-	(Peake & James 1967; Iglesias & Castillejo 1999)
Chilostoma cingulatum	10 different species	(Zopf 1907)
Helicigona lapicida	*L. pulmonaria* and 15 other species	(Fröberg et al. 1993; Gauslaa et al. 2006)
Iberus gualtieranus	-	(Moreno-Rueda & Díaz-Fernández 2003)
Levantina caesareana	*Caloplaca alociza*	(Danin 1986)
Sphincterochila boissieri	*Buellia* sp.	(Yom-Tov & Galun 1971)
HELICODONTIDAE		
Helicodonta obvoluta	-	(Peake & James 1967)
HYGROMIIDAE		
Cernuella virgata	-	(Peake & James 1967)
Trochoidea seetzeni	*Buellia* sp.	(Yom-Tov & Galun 1971)
HYGROMIIDAE		
Helicella caperata	-	(Peake & James 1967)
LAURIIDAE		
Lauria cylindrica	-	(Peake & James 1967)
ORTHALICIDAE		
Drymaeus inglorius	-	(Schmidt 1936)
POLYGRIDAE		
Mesodon normalis	-	(Foster & Stiven 1996)
Mesodon thyroidus	*Dimeralla pineti*	(Norden 2008)
Polygyra thyroides	*Sticta herbacea*	(Wolf & Wolf 1939)
Triodopsis Platysayoides	Crustose lichen	(Dourson 2008)
PUPILLIDAE		
Pupilla muscorum	-	(Peake & James 1967)
PYRAMIDULIDAE		
Pyramidula rupestris	*Protoblastenia rupestris, Verrucaria calciseda*	(Peake & James 1967)

Gastropod	Lichen	References
VERTIGINIDAE		
Columella edentula	*Lobaria* spp.	(Paper VII)
Vertigo alpestris	-	(Peake & James 1967)
V. pusilla	-	(Paper VII)
V. pygmaea	-	(Peake & James 1967)

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Gastropod	Lichen	References
ARIONIDAE		
Ariolimax columbianus	-	(Schmidt 1936; Richter 1979; Harper 1988)
Arion ater	-	(Peake & James 1967)
A. fasciatus	-	(Peake & James 1967)
A. subfuscus/fuscus	*Erioderma pedicellatum, N. arcticum*	(Paper III; Dogett 2007)
A.intermedius	-	(Peake & James 1967)
Geomalacus maculosus		(Boycott & Oldham 1930)
LIMACIDAE		
Deroceras agreste	-	(Schade 1933)
D. reticulatum	-	(Peake & James 1967)
Lehmannia macroflagellata	-	(Pokryszko & Maltz 2007)
L. marginata	*H. physodes, L. pulmonaria, Pertusaria pertusa*	(Graham 1955; Coker 1967; Andersson et al. 1980; Gilbert 1989)
Limacus flavus	*Lecania erysib, Verrucaria* sp.	(Graham 1955; McCarthy & Healy 1978)
Limax cinereoniger	-	(Graham 1955; Peake & James 1967)
L. maximus	-	(Peake & James 1967)
L. sarnensis	*Pseudevernia furfuracea*	(Nitz et al. 2009)
Limax sp.	*Peltigera* spp.	(Benesperi & Tretiach 2004)
Malacolimax tenellus	-	(Peake & James 1967; Andersson et al. 1980)
PHILOMYCIDAE		
Pallifera varia	*Aspicilia cinerea, A. gibbosa, Lasallia papulosa, Ochrolechia yasudae, Pertusaria* sp., *Pseudoparmelia baltimorensis, Xanthoparmelia cumberlandia*	(Lawrey 1980)