Norwegian University
of Life Sciences

Master's Thesis 2017 60 ECTS
The Department of Ecology and Natural Resource Management

INTERNAL AND EXTERNAL FACTORS SHAPING GASTROPOD GRAZING OF OLD FOREST CEPHALO- AND CYANOLICHENS IN BROAD-LEAVED DECIDUOUS FORESTS

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Master of Science in Ecology

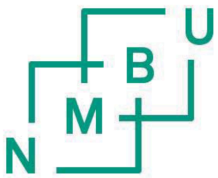
PREFACE

This master thesis was written at the Department of Ecology and Natural Resource management at the Norwegian University of Life Sciences. My field work was done in a deciduous broadleaved old-growth forest at Langangen, Telemark.

I would especially like to thank my main supervisor Yngvar Gauslaa for the valuable feedback and guidance I received at all stages of this project. The field work, analyses and writing were all very stimulating processes thanks to your sincere engagement. Having spoken to other students about their experiences I can affirm that I have been quite privileged to have a supervisor who was always genuinely interested in and excited about the research.

I want to thank my co-supervisor Johan Asplund for all the help with the laboratory analyses and preparations for the field work. Thanks to Knut Asbjørn Solhaug for help with the camera equipment and thanks to Annie Aasen for all your help in the laboratory. Thank you Hanna Lodberg-Holm for your useful comments.

Thanks also to my father for helping me harvest the lichens in the field and for recording field-observations with me at Langangen.



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ABSTRACT

Old forest lichens are used as indicators of continuity and biodiversity in forest ecosystems and are threatened by modern forestry practices. There is a need to better understand what internal and external factors affect their distribution and abundance. This thesis analyses grazing patterns and chemical defence compounds in various species in the old forest lichen genus *Lobaria*. First, in a field experiment, I examined how ecological factors in broadleaved deciduous forests shaped grazing and grazing preference by natural gastropods. The cephalolichen *Lobaria pulmonaria* and the cyanolichen *L. scrobiculata* were transplanted onto tree trunks of *Quercus robur*, *Tilia cordata* and *Acer platanoides* in an old-growth boreonemoral broadleaved deciduous forests at Language, Telemark, Norway for 75 days. Natural lichen grazing was quantified, ecological variables like pH of bark and soil, tree circumference, epiphyte cover etc. were measured in situ. Second, I quantified gastropod grazing using mixed populations of gastropods (*Helicigona lapicida, Cepaea hortensis*) in laboratory experiments on the cephalolichens *L. pulmonaria* and *L. virens*. In this second approach, the lichens had been preconditioned by a growth period of 27 days exposed to three different light/UV-B regimes and several growth variables were measured as part of the work of a previous master´s student. Extractable secondary compounds were analysed from both experiments using high pressure liquid chromatography. In the field experiment Melanin content had no effect on controlled grazing by the gastropods *Helicigona lapicida* and *Cepaea hortensis*. Total CBSCs and lichen growth rates also had no effect on experimental grazing. The minor CBSCs methyl-norstictic and cryptostictic acids were found to decrease in concentration at higher relative thallus area growth rates, which suggests a trade-off between area growth and acid content. *L. pulmonaria* was consistently preferred over *L. scrobiculata* in the natural grazing experiment, which is the opposite of what had been observed in a previous study. Lichenivorous gastropods influence lichen-dominated epiphytic communities on tree trunks, but in more complex ways than was previously thought.

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INTRODUCTION

Old forest lichens are good indicators of both continuity and biodiversity in forest ecosystems where they are threatened by modern industrial forestry. If a goal is to reduce the negative impact of forestry on biodiversity, more knowledge about these indicator species is needed. An underlying question motivating this thesis is: "What drives the abundance and distribution of old forest lichens?". To touch on this question, I have done one field study and one laboratory study. Three old forest species were used in these experiments; the cephalolichens *Lobaria virens, L. pulmonaria* and the cyanolichen *L. scrobiculata*. These are members of the genus *Lobaria* defining a community of old forest lichens named Lobarion (Barkman 1958). Rose (1988) described the Lobarion as the "climax community of epiphytes on the trunks of mature trees in the forest of the Post-glacial (Flandrian) epoch in Europe". Rose (1974) put forward the idea that the presence of a sufficient number of species from the Lobarion community in a forest is "evidence of continuity of the ancient forest canopy at that site". Thus, the community can be thought of as an indicator of forest continuity (Bolli et al. 2008; Rose 1976). The presence of Lobarion is also an indicator of high levels of general biodiversity in a forest (Gauslaa 1994; Nascimbene et al. 2010). The largest primeval beech forest in Europe (Uholka–Shyrokyi Luh , Ukraine) hosts a Lobarion community today (Nadyeina et al. 2014), and *L. pulmonaria* is thought to have survived the last glaciation event within beech forest refugia in the Dinaric Alps (Scheidegger et al. 2012). Abundant herbarium material and historical records indicate that this community was widespread in Europe in the past (Rose 1993). Today, the Lobarion is rare. Requiring forest continuity, Lobarion is threatened by industrial forestry using clear-cuts and short rotational cycles (Campbell & Fredeen 2004; Gauslaa 1994; James et al. 1977; Rose 1993). It is also sensitive to air-borne pollutants and was negatively affected by acid rain (Gauslaa 1995; Gilbert 1986; Mitchell et al. 2005; Nash 2008). Epiphytes in old forests in northern Sweden have been reported to face the risk of extensive extinction due to habitat fragmentation (Berglund & Jonsson 2005), a situation that is probably applicable to Norwegian populations as well. Of the six *Lobaria* species extant in Norway, only *Lobaria hallii* is included in the Norwegian red list (Henriksen et al. 2015), but populations of all *Lobaria* species are apparently declining in Norway. Rose (1988) reported that the "best developed" examples of what he called lowland oceanic forms of the Lobarion could today be seen in Brittany, the coast of Spain and Portugal and in south-west Norway. The remaining European Lobarion communities are of great scientific concern and of high conservation value. The field experiment in this thesis was done in a deciduous forest in Langangen, Norway hosting a sub oceanic lowland Lobarion community.

Ecologists are interested in identifying the specific factors affecting the distribution and abundance of old forest lichens. One important factor is the bark pH of the phorophyte (James et al. 1977). Gauslaa (1985), examining *Quercus*-dominated forests in south-west Norway, gave strong evidence that the Lobarion requires bark pH > 5. Bark pH differs between tree species and lichen elemental composition is modified by bark pH. In Asplund et al. (2015) *Hypogymnia physodes* transplanted on beech trunks that has a higher mean bark pH value, had significantly higher concentrations of Ca, K, Mg and P than transplants on spruce that had lower pH. Tree species, age and size (circumference) are also important factors (Cleavitt et al. 2009; Giorgio et al. 2015; Lie et al. 2009; Nascimbene et al. 2010; Nascimbene et al. 2012).

Older, larger trees with pH > 5 (*Acer platanoides, Tilia cordata, Fraxinus, Quercus* etc.) often support Lobarion species in old stands. Also trees with naturally acidic bark can host these species if the tree is located within a "*Populus* drip zone" (Gauslaa & Goward 2012). Through fall from *Populus* may raise the bark pH on e.g. spruce to levels that can support Lobarion species. Soil pH, known to correlate strongly with bark pH, is another important factor (Gustafsson & Eriksson 1995). But trees with high soil pH also support higher abundance of lichen-feeding gastropods as well, which leads to more grazing (Vatne et al. 2010).

Lichenivory, allelopathy and differing light conditions are factors to which lichens can adapt and/or acclimate to by regulating their production of secondary metabolites. Lichen mycobionts produce more than 800 different Carbon Based Secondary Compounds (CBSCs) (Elix & Stocker-Wörgötter 2008; Huneck & Yoshimura 1996). Their ecological roles have been studied extensively (Gauslaa 2009; Seaward 2008). One example of a CBSC is the brightly coloured ustic acid, which is induced by UV-B radiation (McEvoy et al. 2006; Nybakken & Julkunen-Tiitto 2006). It is found in the cortex of *L. scrobiculata* where it acts as a solar radiation screen (Huneck & Yoshimura 1996; Solhaug & Gauslaa 2012). A cortical pigment that is not a CBSC is the UV-B-induced dark brown melanin that serves a similar function as usnic acid in the cortex of *L. pulmonaria* (Gauslaa & Solhaug 2001). The other CBSCs treated in this thesis are located in the medulla of the lichen have other functions than screening excess solar radiation (Gauslaa et al. 2017). It has recently been suggested that favourable environmental conditions may soften the continuity requirements of the Lobarion, so more research is probably required (Kalwij et al. 2005; Whittet & Ellis 2013). Gauslaa et al. (2006) describes *L. pulmonaria* in Norway as limited by a combination of light availability and desiccation risk. In forest where humidity factors are adequate, *L. pulmonaria* is limited by light availability. Given that enough water is available it can thrive in open areas such as cultural landscapes, whereas young or managed forests usually do not provide enough light. However, desiccation coupled with high light exposure is fatal for this species (Gauslaa & Solhaug 2000). This means that *L. pulmonaria* has "a discrepancy between potential and realized ecological niches".

Lichenivory is an important factor affecting forest lichen distribution and abundance. Gastropods, the focus of this thesis, are among the few organisms that can cause substantial grazing damage to lichens. Grazing may have a negative impact on old forest lichens by constraining their distribution (Asplund et al. 2010; Gauslaa 2008). A negative relationship between grazing and CBSC content, proposed over a hundred years ago (Stahl 1904; Zukal 1895), has been documented in many recent studies (Asplund & Gauslaa 2008; Asplund 2011b; Gauslaa 2005; Nimis & Skert 2006; Pöykkö et al. 2005; Vatne et al. 2011). CBSCs have been shown to increase with thallus age (Asplund & Gauslaa 2007). Therefore, older lichens are better defended than young ones, and grazers selectively feed on younger thalli, limiting the growth and early development of *Lobaria pulmonaria* in natural deciduous forests (Asplund & Gauslaa 2008). Nevertheless it has been shown that lichen fragments may remain at least partly viable after passing through the digestive systems of gastropods (Fröberg et al. 2001) and mites (Meier et al. 2002). Boch et al. (2011) reported that 29% of *L. pulmonaria* survived gut passage of various snail species and regenerated from faecal pellets. Thus, the relationship between lichens and grazers is likely not exclusively antagonistic. Selective uptake of lichen compounds by lichenivorous snails into their

body tissues was discovered by Hesbacher et al. (1995). This means that some CBSCs, like atranorin, are taken up by the organism while others, like usnic acid, pass directly through the digestive system.

Evidence from short-term studies suggests that the compounds defending *L. pulmonaria* from lichenivory are constitutive, meaning their synthesis is not increased as a direct response to grazing (Asplund et al. 2009; Nybakken & Julkunen-Tiitto 2006). Little is known about the mechanisms by which lichens regulate CBSC synthesis in response to environmental stimuli and few experimental studies have related natural grazing to CBSC concentration. The specific objectives of this thesis are:

1. In a natural grazing experiment at Langangen, Norway I aim to relate natural grazing to ecological variables measured in the field and to CBSC concentration in the lichen thalli. I aim to use this field experiment to study factors influencing bark pH, because gastropods are often more abundant on bark with high pH.
    a. I will test the hypothesis that natural grazing decreases with increased CBSCs.
    b. I will also test the hypothesis that natural gastropod grazers prefer *L. scrobiculata* over *L. pulmonaria* (Asplund et al. 2010) due to the fact that *L. scrobiculata* has lower concentrations of CBSCs.

2. In a controlled grazing experiment, I aim to explore the relationships, if any, between growth variables (measured by Kann (2016) and controlled grazing.
    a. I will test the hypothesis that grazers prefer *L. pulmonaria* over *L. virens*, which has been reported in Asplund et al. (2010), and that controlled grazing will decrease with increasing CBSC content.
    b. An increase in melanin production has been assumed to decrease the food quality of fungi by making them less digestible, although some invertebrates do show a preference for melanised fungi (Bonkowski et al. 2000). The *L. pulmonaria* I use in the controlled grazing experiment had previously been exposed to different solar radiation treatments by Kann (2016), and thus synthesized treatment-specific levels of melanins. I will test the hypothesis that gastropod grazing decreases with an UV-B-induced increase in melanin content. This has not been tested before.
    c. I will also explore the relationships between growth variables and CBSC content. It has been shown that the size of the lichen thallus is a good predictor of CBSC concentrations (Asplund & Gauslaa 2007), with larger thalli having more CBSCs. I will test the hypothesis that CBSC content increases with thallus area.
    d. A trade-off has been shown not to occur between relative growth rate or relative thallus area growth rate and CBSC concentration (Bidussi et al. 2013; Gauslaa et al. 2013) and I will test whether this trade-off occurs in studied lichens.
    e. Methyl norstictic and constictic acids are known to increase significantly in concentration when thalli are transplanted from old forest to clear-cut sites (Gauslaa et al. 2013; Nybakken et al. 2007), despite the fact that these CBSCs do not have a role in screening

excess solar radiation. The reason for their increase is unknown. I will test the hypothesis that their concentrations will not be affected by contrasting light regimes.

MATERIALS AND METHODS

LICHENS AND GASTROPODS

The lichen species *Lobaria pulmonaria* (L.) Hoffm., *Lobaria virens* (With.) J.R. Laundon and *Lobaria scrobiculata* (Scop.) DC. were used in the experiments. Lichens, collected at each of two separate locations, were used in two grazing experiments, respectively, one in the lab and one in the field.

On June 27, 2015, *L. pulmonaria* (n=82) and *L. virens* (n=82) were collected in a broad-leaf deciduous forest in Langangen, Norway (59° 06' 43" N, 9° 50' 05" E, 140 m a.s.l.). These lichens were used by Kann (2016) in a growth experiment where she exposed them to three radiation treatments (PAR, PAR+UVA and PAR+UVA+UVB) in open field plots in Ås, Norway (59° 30' N, 10° 47' E, 100 m a.s.l.) for 27 days. Parameters measured by Kann (2016) were: hydrated thallus area (A) and dry mass (DM). Using these parameters, Kann (2016) calculated relative growth rate (RGR = (ln (DM_{end}/DM_{start})) * 1000/Δt (mg g^{-1} day^{-1}) where Δt is the time in days between the start and end) and specific thallus mass (STM=DM/A), and measured chlorophyll *a* fluorescence, CO_2 uptake, melanin content (evaluated as Browning Reflectance Index, BRI) and chlorophyll content. After the experiment, these thalli were put air-dry in a freezer at -18 °C and were given to me for further studies. Some thalli had been subjected to destructive measurements. Therefore, I used a subset (S_1) comprising intact *Lobaria pulmonaria* (n=46) and *Lobaria virens* (n=46) to conduct a grazing experiment in the lab, and had access to the results of Kann (2016).

Six months after the growth experiment of Kann (2016), the S_1 thalli were taken out of the freezer. Each thallus was numbered and put in a paper envelope. A portion (≥30mg) of each air-dry *L. pulmonaria* thallus including both apical and basal parts was weighed (Sartorius Extend, VWR International, Pennsylvania, U.S.A; ±0.1 mg) placed in a numbered Eppendorf vial, and pulverized in a Retsch MM 400 using 6 mm balls (Haan, Germany) at 30x per second for 2 minutes. The vials with ground material were then stored in the refrigerator for later HPLC-analyses. Because the thalli of *L. virens* do not contain any CBSCs, they were not subjected to HPLC analyses. The remaining thalli were put back into their numbered envelopes and stored in the freezer for later use in the controlled grazing experiment.

On December 16, 2015, many *Lobaria pulmonaria* and *Lobaria scrobiculata* thalli were collected from sympatric populations on the same tree trunks *(Quercus)* in an old oak forest in Tysnes, Norway (59° 98' 85" N, 5° 46'68" E, 25 m a.s.l). Their C/N-ratios were 19.2 ± 0.6 *(L. pulmonaria)* and 15.7 ± 0.2 *(L. scrobiculata)* for a random subsample of 15 thalli for each species (Maslach et al., unpubl. data). These thalli were stored air-dry in a freezer at -18 °C for 6 months before I randomly selected 76 thalli of both species (S_2) as the material for the grazing experiment in the field. After removing attached moss and tree bark, these air-dry thalli were weighed, assigned an identity number, wetted and photographed. In order to obtain the dry mass, the lichens

were weighed in the air-dry state (Sartorius Extend, VWR International, Pennsylvania, U.S.A; ± 0.1 mg). 5 additional thalli were oven-dried at 70 °C, and the ratio between air-dried and oven-dried weight was used to calculated. This was then used to convert the air-dried weights to oven-dried weights so that the varying levels of moisture in the lab would not introduce unwanted errors. The thalli were then sewn onto a 2 mm plastic mesh in pairs using a cotton thread for later use in the field experiment. The sequence of thalli used for these pairs was randomized by using the "random number generation" function in Microsoft Excel.

Two common and climbing lichen-feeding snail species were used in experiments, *Cepaea hortensis* and *Helicigona lapicida*. In total, 120 *Cepaea hortensis* were collected from one location in Ås, Norway (59°38'50"N, 10°47'56"E) 9-12 August 2016. The snails were kept in a plastic box outside the north-facing wall of a farmhouse in Ås (59°40'34"N, 10°50'09"E) and fed with *Utica dioica* for approximately one week. In order to habituate the snails to the consumption of lichens, they were given *L. pulmonaria* for two days, after which they starved for one day before the start of the experiment. Likewise, 130 *Helicigona lapicida* were collected from stonewalls surrounding the churchyards of Ås (59°40'17"N, 10°46'07"E) and Frogn churches (59°41'58"N 10°43'24"E) on August 20, 2016.

HPLC ANALYSES

On May 24, 2016 I started preparing thalli from S_1 (*L. pulmonaria* (n=46) for HPLC. The pulverized material was thawed at room temperature for 30 min. 1,5 ml 100% acetone was injected into each vial. The vials were then agitated for 30 min (IKA-WERKE-KS501 digital (Germany)). They were then centrifuged (Eppendorf 5417C, Germany) at 16400 rpm for 8 min in order for the lichen material to sediment. The acetone was then poured into new vials from which it was subsequently evaporated (Eppendorf Concentrator Plus (Germany)). The old vials containing the pellet of pulverized lichen material were then refilled with acetone and the process was repeated. The process was repeated a third and final time using methanol instead of acetone. The new vials containing the concentrated CBSCs were then filled with 1 ml of methanol and treated with ultrasound (VWR-ultrasonic cleaner) and then centrifuged at 16000 rpm for 3 minutes. The liquid was subsequently poured into HPLC-vials and sealed. These were then used in HPLC analysis (Agilent Technologies 1200 series). A detailed description of the methodology can be found in Nybakken et al. (2007).

After analysing the data obtained from the field experiment, quantification of CBSC-concentrations of the S_2 thalli started. On January 26, 2017 I started grinding the lichens, and on January 31 I began the extraction of CBSCs. The HLPC-analyses followed the same procedure as described above.

CONTROLLED GRAZING EXPERIMENT IN THE LAB

The S_1 *L. pulmonaria* (n=46) and *L. virens* (n=46) thalli were taken out of the freezer, dried at room temperature in the lab and weighed (Sartorius Extend, VWR International, Pennsylvania, U.S.A). They were then wetted with deionized water and placed in individual plastic cups containing one snail (*Cepaea hortensis*). The plastic cups were sealed and placed in a temperature-controlled dark room at 16 °C, and left overnight. The snails did not consume much lichen, so the experiment was repeated for two additional nights, this time including one specimen of both snail species (*Cepaea hortensis* and *Helicigona lapicida*) in each sealed cup. Thereafter, the lichens were air dried in individual coffee-filters for four days and weighed. After the experiment, the snails were released to their native ecosystems.

Figure 1. A photo from the controlled grazing experiment. The dark *Helicigona lapicida* and the yellow *Cepaea hortensis* inside a plastic cup with a piece of *Lobaria pulmonaria* thallus.

GRAZING EXPERIMENT IN A NATURAL FOREST AT LANGANGEN, TELEMARK

The lichens *Lobaria pulmonaria* and *Lobaria scrobiculata* (S_2) were transplanted into an old-growth boreonemoral broadleaved forest at Langangen, Telemark, Norway (59°11'40"N, 9°83'45"E; See fig. 2). The study area encompassed forested hills without traces of recent logging. Deciduous (*Acer platanoides*, *Quercus robur*, *Tilia cordata*, *Lanus glutinosa*, *Fraxinius excelsior*, *Betula pendula*, *Populus tremula*) and coniferous trees (*Picea abies* and *Pinus sylvestris*) occurred in varying mixtures and age-structures, interspersed with dead wood in different stages of decomposition. The ground vegetation was herb-rich with e.g. *Hepatica nobile*, *Anemone nemorosa*, *Convallaria majalis*, *Cardamine bulbifera*, *Ranunculus ficaria*, *Galium odoratum*, *Lathyrus vernus*, *Polygonatum multiflorum*, *Lysimachia europaea*, *Viola riviniana*, *Festuca altissima*, *Melica nutans*, *Ranunculus auricomus*, *Scrophularia nodosa* and *Silene dioica*. The bedrock is Larvikite, which is not found any other place on earth other than at the south end of the Oslo Rift. It is an intrusive igneous rock that was formed around 300 million years ago.

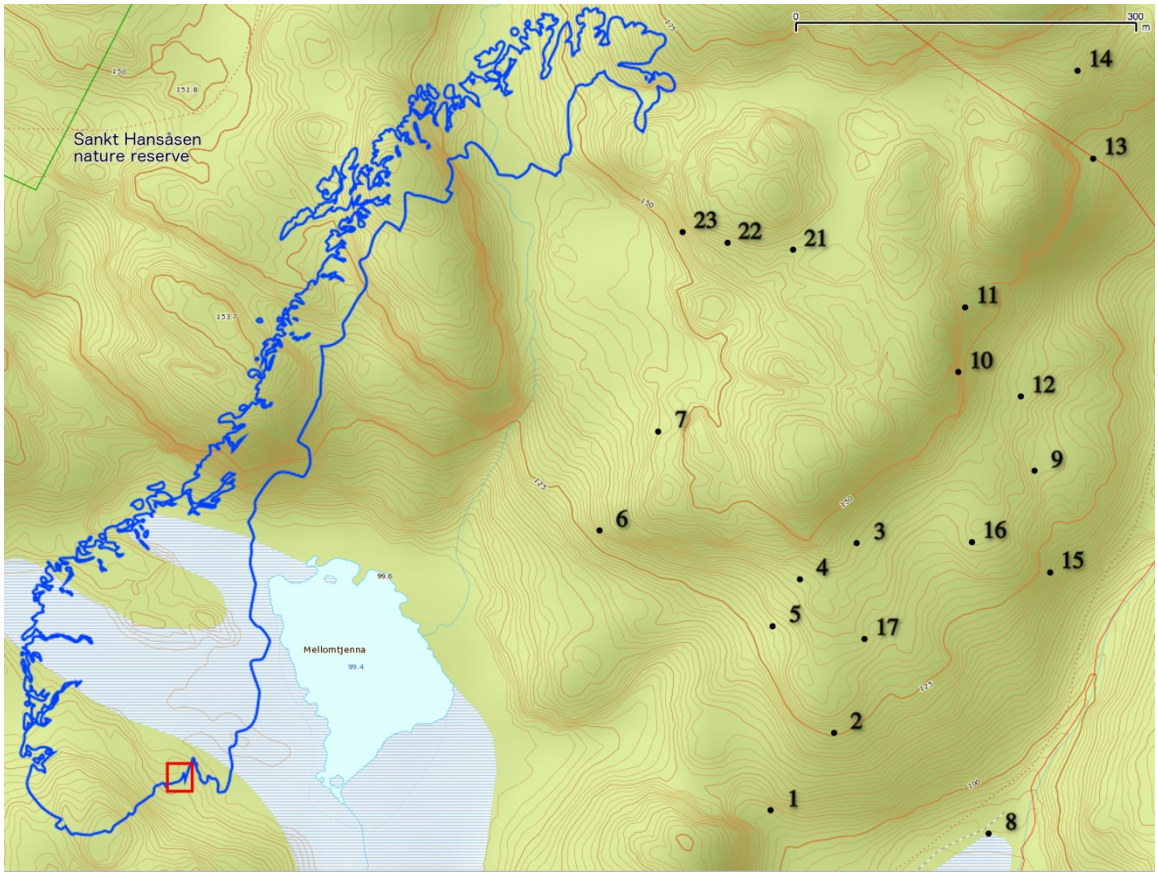


Figure 2. The location of the 23 stands in the field experiment in Langangen, Telemark. In the upper left corner, the border of the Sankt Hansåsen nature reserve (established in 1978) is marked with a green line. The blue map indicates the location of Langangen (59°11'40"N, 9°83'45"E) in Norway.

During 19-22 July 2016, all nets with lichen pairs were fastened with plastic staples (Regur T-37, Germany) onto trees in 23 different stands selected after the following criteria: Each stand should have a mixture of the following three species of tree: *Acer platanoides*, *Quercus robur* and *Tília cordata* in a relatively homogeneous stand with respect to vegetation. Each stand should have similar sized specimens of the three tree species. There should be a distance of at least 100 m between each stand. Within one stand, the selected trees should have similar circumference, but tree size could vary between stands. For each tree, one soil sample was taken (soil depth ~ 5 cm). Bark pH was measured three times on different places on the trunk (at breast-height) with a flat-headed probe (ExStik PH100, Extech Instrument Corporation, U.S.A) after adding 0,1 M KCl to the bark with a spray bottle. Trunk circumference was measured (± 1 cm), the local topographic inclination and m a.s.l. were measured (compass application, Iphone 5S, Apple Corporation, U.S.A). The basal area of tree trunks (m^2 ha^{-1}) was recorded separately for each surrounding tree species, as well as in total for all tree species by point sampling (relascope). The lichen- (micro and macro) and moss-cover (% of tree trunk surface below 2 m height) was visually estimated. One sample was taken of each species of macrolichen for later identification, and their individual percent-cover was estimated.

Figure 3. One plastic mesh bearing *Lobaria pulmonaria* and *Lobaria scrobiculata* transplanted onto a *Quercus robur* trunk with natural populations of *Lobaria virens* at Langangen, Telemark during the field work.

On October 1 and 2, 2016, all transplants were harvested. Thus, their exposure to the environmental conditions of Langangen, including natural gastropod communities, lasted for 75 days. The thalli were dried and weighed in the same way as described above.

On September 22, 2016, 10 ml of each soil sample collected from the individual trees at each of the 23 sites were suspended in 25 ml of deionized water in the lab. The samples were left overnight and the pH was measured the following day with a pH-meter (inoLab pH 720, WTW, Germany).

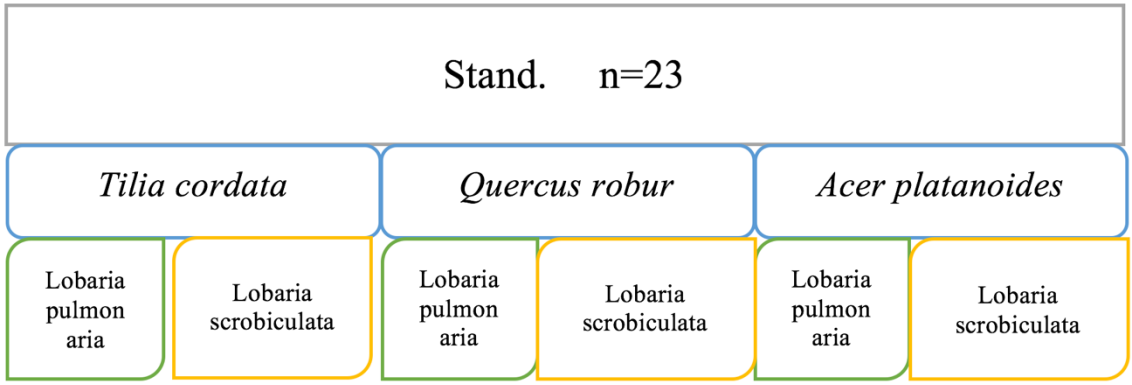


Figure 4. The design of the field experiment. The trunks of each tree species (*Tilia cordata, Quercus robur and Acer platanoides)* are nested within each stand (n=23). All the variables mentioned above were measured for each tree. One of each lichen species (*L. pulmonaria* and *L. virens*) was then fastened to each tree and can be thought of as an experimental treatment.

STATISTICAL ANALYSIS

All statistical analyses were done using RStudio version 1.0.136 (R Development Core Team (2016) and all data management was conducted in Microsoft Excel for Mac version 15.27 (Office 365 Subscription). The data obtained from both the laboratory and field work was first explored with multiple individual correlation matrices (see appendix). The "ggpairs" function from the package "ggplot2" was used for this computation.

Due to the design of the field experiment, where the factor "tree species" was nested within "Stand" (fig. 4) LMEs (Linear Mixed Effects Modeling) were used to treat "Stand" as a random factor. The package "lmer" was used for all LMEs. In order to obtain *P*-values and F-values the "lmerTest" package was used. A likelihood ratio test was performed on the random effects in order to obtain a *P*-value. T-tests were performed several times and when the variables had unequal variance the Welch t-test was used. The data for grazing from the field experiment had to be log-transformed (Log (x+1)) to meet the requirements of the t-tests and LMEs. Since no nesting appeared within the design of the lab experiment these results were analyses using simple linear regression and ANOVA-models in R and no transformations were made since the model requirements were met. An LDA (Linear Discriminant Analysis) was carried out to classify lichen communities on the trees in the field experiment using the "lda" package in R.

RESULTS

CONTROLLED GRAZING EXPERIMENT WITH *LOBARIA PULMONARIA* AND *L. VIRENS* IN THE LAB

This grazing experiment was done twice. Once with only *Cepaea hortensis* and once with *C. hortensis* and *Helicigona lapicida* together. The snails did not graze much on lichens during the first experiment. No significant difference in grazing was found between the two experiments ($F = 1.73$, $p = 0.19$). Therefore, only the combined grazing from both experiments was further analysed. The two snails in combination, *C. hortensis* and *H. lapicida,* used during the grazing experiment, did not discriminate between the lichens *L. pulmonaria* and *L. virens* ($t = 1.0761$, $p = 0.28$). The overall mean grazing was 10 ± 1.4 mg for *L. virens* and 12.2 ± 1.4 mg for *L. pulmonaria*. Gastropod grazing did also not differ between the three solar radiation treatments. Despite the large differences in melanin compounds, RT_AGR and RGR across radiation treatments (see box plots and distribution plots in Appendix 8), neither relative growth rate ($F = 2.1$, $p = 0.14$) nor melanin content assessed as BRI ($F = 0.04$, $p = 0.82$) significantly influenced grazing.

Table 1. Summary statistics for the controlled grazing experiment in the lab. Variables are expressed as means ± 1SE. Grazing by *Cepaea hortensis* and *Helicigona lapicida* on the lichens *Lobaria pulmonaria* and *L. virens* during 24 hrs is reported. Variables marked with "*", BRI (Browning reflectance index) and RGR (Relative Growth Rate), were measured by Kann (2016). Differences in mean values were tested using a two sample *t*-test. Non-integer degrees of freedom are due to unequal variances (Welch *t*-test).

Lichen species:	*L. pulmonaria*	*L. virens*	*t*-value	*p*-value	*d.f.*
PAR					
Grazing, mg	13.3 ± 3.0	8.0 ± 2.0	1.4	0.1	18
Total CBSC, mg g^{-1}	61.2 ± 2.4	-			
BRI*	1.8 ± 0.3	6.9 ± 1.7	2.9	0.01	9.4
RGR*, mg g^{-1} day^{-1}	5.1 ± 0.5	2.0 ± 0.5	4.8	0.00	18
PAR+UVA					
Grazing, mg	11.2 ± 2.4	12.8 ± 2.8	0.4	0.6	24
Total CBSC, mg g^{-1}	57.5 ± 3.5	-			
BRI*	5.2 ± 1.0	4.3 ± 0.5	0.7	0.4	17.7
RGR*, mg g^{-1} day^{-1}	3.4 ± 0.4	1.6 ± 0.3	3.5	0.00	24
PAR+UVA+UVB					
Grazing, mg	12.3 ± 2.3	8.9 ± 2.1	1.0	0.2	24
Total CBSC, mg g^{-1}	60.2 ± 3.8	-			
BRI*	20.4 ± 3.3	7.5 ± 1.6	3.5	0.00	17.2
RGR*, mg g^{-1} day^{-1}	3.1 ± 0.3	1.7 ± 0.2	3.2	0.00	24

The mean concentration of total CBSCs in *L. pulmonaria* from Langangen (S_1) used in the laboratory experiment was 59.5 ± 2 mg g^{-1}, with stictic (31.2 ± 1 mg g^{-1}) and constictic acid 18.2 ± 0.8 mg g^{-1}) as the major CBSCs. The mean concentrations of the minor acids were cryptostictic acid: 3 ± 0.1 mg g^{-1}, norstictic acid: 6.3 ± 0.3 mg g^{-1}, methyl-norstictic acid: 0.52 ± 0.02 mg g^{-1}. Neither the total CBSC concentration nor any individual CBSC concentration (only measured in *L. pulmonaria)* did significantly influence grazing. All linear relationships between controlled grazing and the other variables were non-significant. For complete correlation matrices, see Appendix 7-8. To test for differences in CBSC content within the solar radiation treatments, separate ANOVAs were run. No significant differences were detected. The results of these test are given in table 2 below. STM was found to be a significant predictor of total CBSC (F = -1.82, p = 0.07). Thallus area was significantly correlated with CBSCs (r = -0.58, p = 0.00) but was not a significant linear predictor of CBSCs *(*F = 0.56, p = 0.45). BRI was strongly correlated with Methyl-norstictic acid content (r = 0.52, p = 0.01), RT_AGR (r = -0.58, p = 0.00) and weakly correlated with RGR (r = -0.29, p = 0.1).

Table 2. Mean CBSC concentration ± 1SE in thalli (S_1) collected in Langangen, Telemark, after which they were cultivated for 27 days under three separate light regimes, and finally used in a controlled grazing experiment in the lab. *Lobaria virens* did not contain any CBSCs (and was thus not included in the Table). F-values and p-values are from separate ANOVAs. n = 10 for PAR, n = 13 for PAR+UVA and n = 13 for PAR+UVA+UVB.

Lobaria pulmonaria	**PAR**	**PAR+UVA**	**PAR+UVA + UVB**	F-value	p-value
Constictic acid, mg g^{-1}	19.8 ± 1.2	16.4 ± 1.4	19 ± 1.5	1.50	0.23
Cryptostictic acid, mg g^{-1}	3.1 ± 0.2	3.1 ± 0.2	3 ± 0.2	0.09	0.90
Stictic acid, mg g^{-1}	31.9 ± 1.2	31.3 ± 1.8	30.6 ± 2.2	0.10	0.90
Norstictic acid, mg g^{-1}	6 ± 0.6	6 ± 0.4	7 ± 0.7	0.92	0.40
Methyl-norstictic acid, mg g^{-1}	0.4 ± 0.03	0.5 ± 0.03	0.6 ± 0.05	0.56	0.57
Total CBSC, mg g^{-1}	61.2 ± 2.4	57.5 ± 3.5	60.2 ± 3.8	0.92	0.40

RT_AGR was negatively correlated with Methylnorstictic (r = -0.63) as well as Cryptostictic (r = -0.25) acid (see appendix 08). In order to further investigate these correlations, separate linear regression models were fitted with each acid as dependent variable. A significant negative linear relationship was detected between RT_AGR and Methyl-norstictic acid (p = 0.00; table 3). Cryptostictic acid was also found to have a negative linear relationship to RT_AGR (p = 0.03; table 3). No significant results were obtained for RGR.

Table 3. A summary of the results from general linear models run with RGR and RT_AGR as the predictors of CBSCs in *Lobaria pulmonaria* (S_1) used in the controlled grazing experiment. *F*-values and *p*-values in this table come from separate linear regression models.

Lobaria pulmonaria	**RGR**		**RT_AGR**	
	F-value	*p*-value	*F*-value	*p*-value
Constictic acid, mg g^{-1}	0.2	0.62	0.0	0.77
Cryptostictic acid, mg g^{-1}	2.7	0.10	4.9	0.03
Stictic acid, mg g^{-1}	1.9	0.17	1.1	0.29
Norstictic acid, mg g^{-1}	0.7	0.38	0.6	0.42
Methyl-norstictic acid, mg g^{-1}	1.6	0.21	21.2	0.00
Total CBSC, mg g^{-1}	0.84	0.36	0.54	0.46

NATURAL GRAZING EXPERIMENT WITH *LOBARIA PULMONARIA* AND *L. SCROBICULATA* IN A NATURAL FOREST AT LANGANGEN, TELEMARK

The two lichen species differed significantly in their CBSC concentration. This was apparent in the results of the *t*-tests (table 4). *L. pulmonaria* had consistently higher CBSC concentration than *L. scrobiculata*. Both metascrobiculin and usnic acid were absent in *L. pulmonaria*. *Lobaria pulmonaria* collected from Langangen (S_1) (table 2) and Tysnes (S_2) (table 4) had similar concentrations of CBSCs. *Lobaria virens* collected in Langangen lacked CBSCs and *L. scrobiculata* from Tysnes was only used in the natural grazing experiment.

Table 4. Concentrations (means ± 1SE) of CBSCs in *L. pulmonaria* and *L. scrobiculata* (S_2) collected in Tysnes, Hordaland and used in the grazing experiment in a natural forest in Langangen, Telemark. All results are presented as mg g^{-1}, except for metascrobiculin which is presented as mAU mg^{-1}. Therefore, this concentration is not included in total CBSC. The non-integer degrees of freedom are due to the use of the Welch t-test when variances were not equal.

	L. pulmonaria	*L. scrobiculata*	*t*-value	*p*-value	*d.f.*
Constictic acid, mg g^{-1}	19.4 ± 0.8	9.6 ± 0.6	9.8	0.00	131
Cryptostictic acid, mg g^{-1}	1.3 ± 0.1	0.6 ± 0.0	6.3	0.00	98.6
Stictic acid, mg g^{-1}	27.8 ± 1.2	19.6 ± 0.1	5.9	0.00	131
Norstictic acid, mg g^{-1}	7.2 ± 0.3	4 ± 0.2	10.7	0.00	121.8
Methyl-norstictic acid, mg g^{-1}	0.7 ± 0	0.2 ± 0.0	12.8	0.00	108.7
Usnic acid, mg g^{-1}	-	7.8 ± 0.4	-	-	-
Metascrobiculin, AU mg^1	-	11.0 ± 0.7	-	-	-
Total CBSC, mg g^{-1}	56.3 ± 2.2	41.8 ± 1.7	5.8	0.00	131

The natural gastropod population in the forest sites grazed *L. pulmonaria* consistently more than *L. scrobiculata* on all tree species. (Separate t-tests were carried and gave the following results: *Tilia cordata*: $t = 3.53, p = 0.001$, *Acer platanoides*: $t = 2.22, p = 0.034$ and *Quercus robur:* $t = 2.30, p = 0.025$). Mean grazing calculated across tree species was 139.4 ± 18.0 mg for *L. pulmonaria* and 28.5 ± 3.0 mg for *Lobaria scrobiculata*. Figure 5 may give the impression that *t*-values are inflated or that there is little difference in total grazing between tree species, but this is because the y-axis is logarithmic.

Figure 5. The mean grazed dry mass (*mg*) recorded for *Lobaria pulmonaria* and *Lobaria scrobiculata* (S_2) transplanted onto *Acer platanoides*, *Quercus robur* and *Tilia cordata* in Langangen, Telemark during the natural grazing experiment of 75 days in late summer-early autumn. Grazing is displayed on a logarithmic scale.

To further explore the distinct grazing patterns, correlation matrices were computed for both lichen species (appendices 1 - 6). The significant correlations are presented in table 5. Based on these correlations, a Linear Mixed Effects Model (LME) was fitted to the *L. scrobiculata* grazing data. In this model, stand (one stand is one cluster containing the three studied tree-species, $n = 23$) was treated as a random factor. There was a negative effect on grazing for increasing cryptostictic acid content ($F = 8.90, p = 0.004$) and a positive effect for soil pH ($F = 5.94, p = 0.017$). The random factor of stand was not significant ($p = 1$). As the cryptostictic acid content increases natural grazing is predicted to decrease linearly. An increase in soil pH results in more grazing, according to the model.

Figure 6. Photos of *L. pulmonaria* (left) (170.8 mg grazed) transplanted onto *Acer platanoides* and *L. scrobiculata* (right) (38.2 mg grazed) transplanted onto *Tilia cordata*. Both thalli are examples of heavy grazing by a community of natural inheritors in a broadleaved deciduous old-growth forest at Langangen, Telemark. Each square on the bottom of the photo is 1 mm.

The cortex of both lichen species was grazed intensely, exposing the white medulla that does not contain photobionts nor pigments, but contains CBSCs. The medulla was very rarely grazed but the photos in figure 6 do show some holes where possibly lichenivores have grazed all the way through the thalli.

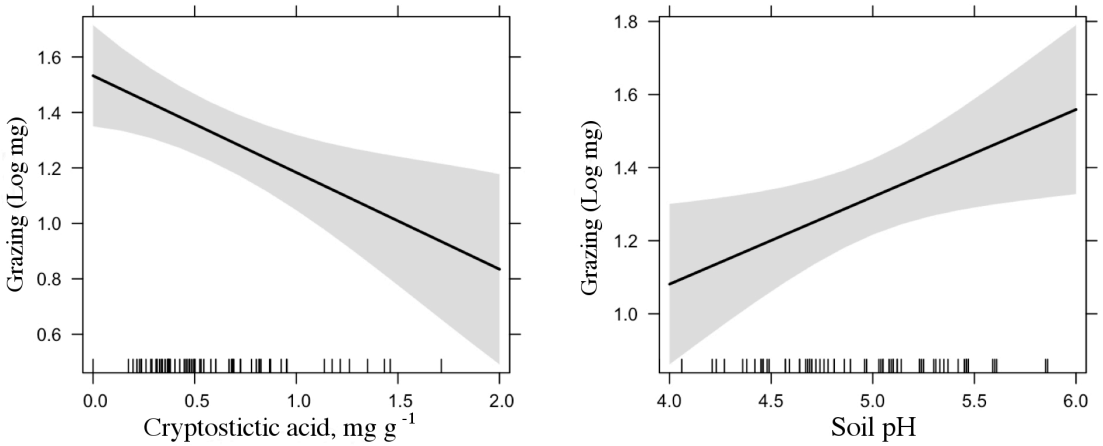


Figure 7. Effect plots from the LME model for *L. scrobiculata* grazing. The data was obtained during the natural grazing experiment at Langangen, Telemark. The grey areas around the line in each figure represents the 95% confidence intervals. The lines on the x-axis are individual observations. Confidence intervals are less narrow for the areas where more observations are clustered together.

Table 5. Pearson correlation coefficients for the natural grazing experiment conducted with *L. pulmonaria* and *L. scrobiculata* in Langangen, Telemark. Levels of significance are indicated as follows: 0.00: "***", 0.01: "**", 0.05: "*" and < 0.1: ".". See Appendices 1-6 for complete correlation matrices. -: not significant; x: not applicable

Parameter	Grazing of *L. pulmonaria*	Grazing of *L. scrobiculata*	Preference for *L. scrobiculata*
CBSCs			
Stictic acid, mg g^{-1}	–	–	–
Constictic acid, mg g^{-1}	–	–	–
Cryptostictic acid, mg g^{-1}	–	-0.32 **	–
Norstictic acid, mg g^{-1}	–	–	–
Methyl-norstictic acid, mg g^{-1}	–	–	–
Usnic acid, mg g^{-1}	x	–	–
M-corbicula, mg g^{-1}	x	0.2 ·	–
Total CBSCs, mg g^{-1}	–	–	–
Environmental variables			
Soil-pH	–	0.26 *	–
Bark-pH	–	–	–
Soil surface inclination (°)	–	0.24 *	–
Meters above sea level, m	–	–	–
Tree circumference, cm	–	–	–
Epiphytic variables			
Cephalolichen-cover, %	–	–	-0.2 ·
Chlorotic-cover, %	0.28 *	–	–
Cyanolichen-cover, %	–	–	–
Naked bark-cover, %	–	–	–
Microlichen-cover, %	–	–	–
Macrolichen-cover, %	–		–
Lichen community	–	–	–
Bryophyte-cover, %	-0.22 ·		
	–	–	–
Relascope sums:	–	–	–
Acer platanoides, m^2 ha^{-1}	–	–	–
Pinus sylvestris, m^2 ha^{-1}	–	–	–
Fraxinus excelsior, m^2 ha^{-1}	–	–	–
Tilia cordata, m^2 ha^{-1}	–	0.26 *	–
Quercus robur, m^2 ha^{-1}	–	-0.28 *	–
Fagus sylvatica, m^2 ha^{-1}	–	–	–
Picea abies, m^2 ha^{-1}	–	–	–
Alnus glutinosa, m^2 ha^{-1}	–	–	–
Populus tremula, m^2 ha^{-1}	–	–	–
Sum total, m^2 ha^{-1}	–	–	–

Using the same approach, an LME was also fitted to the grazing data for *L. pulmonaria*. Chlorolichen cover ($F = 6.86$, $p = 0.01$) was the only significant predictor and the fixed effect was positive, meaning that more grazing occurred on trees which had a higher cover of chlorolichens. The random factor of stand was not significant ($p = 0.6$).

Total CBSC content was not found to have a significant relationship to grazing for any of the two lichen species.

Soil pH, measured at every sampled tree in the forest at Langangen, was modelled using an LME. The effect of the interaction between circumference and metres above sea level was significant ($F = 5.6$, $p = 0.02$). The effect of circumference on m a.s.l on pH was positive for trees with large circumference, but negative for trees with small circumferences. For trees with a circumference of 50 cm there was a predicted decrease in soil pH with an increase in m a.s.l. With elevation increasing from 100 to 180 m a.s.l. the model predicted a decrease of ~ 1 pH unit. For trees with a circumference of 100 or 150 cm there was little effect. For trees that had a circumference of 200 cm, an increase in m a.s.l. had a positive effect on soil pH. At 100 m a.s.l the soil pH was predicted to be ~ 4 and at 200 m a.s.l the model predicted a pH of 5.6. The confidence intervals, at the 95% level are quite large, so the model is not necessarily very accurate. This is due to the fact that my dataset consists of few trees sampled at high altitudes and low altitudes. Most of the trees were sampled at an intermediate altitude at Langangen, Telemark.

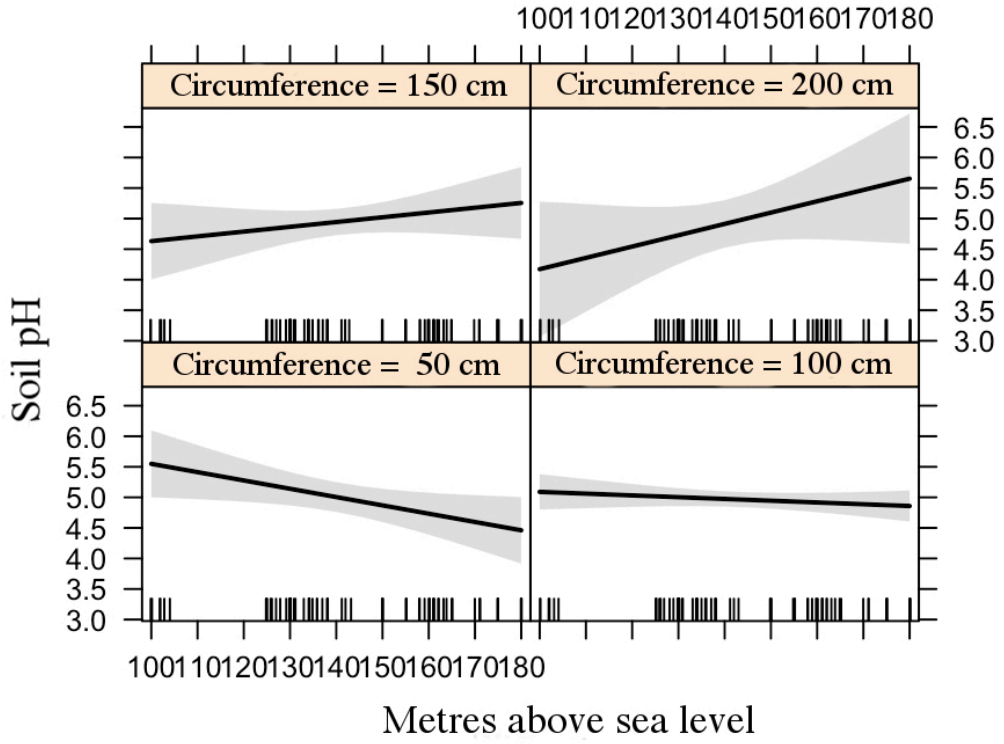


Figure 8. Effect plots from the LME fitted to the soil pH data measured in Langangen, Telemark. At lesser tree circumference the soil pH was predicted to decrease as meters above sea level increase. At greater circumference the effect of

increasing m a.s.l. was predicted to have the opposite effect, increasing the soil pH. Grey areas are confidence intervals (95%) and bars on the x axes are observations. The effect of tree species on each factor measured at Langangen was analysed and the results are presented in table 6. Individual LME models were fitted for each parameter. Tree species was used as a predictor and stand was included as a random factor. The highest number of chlorolichens and greatest chlorolichen- and microlichen-cover, the lowest bryophyte-cover as well as the lowest cyanolichen cover, bark pH and soil pH was recorded on *Tilia cordata*. The highest bark pH, soil pH, cyanolichen cover, bryophyte cover and the greatest total grazing was recorded on *Acer platanoides*. This tree species also had the lowest number of chlorolichens, the lowest chlorolichen- and microlichen cover and the smallest circumference. The highest number of cephalolichens, greatest cephalolichen cover as well as the lowest total grazing was recorded on *Quercus robur*.

Table 6. Measured parameters (means ± 1SE) for all tree species (n=23 for each species) used as hosts for lichen transplants at Langangen, Telemark. Crustose lichens were not included in the mean number of lichens. The F- and p-values are from linear mixed effects (LME) models which included stand as a random variable.

	Tree species			LME		
Parameter	*Quercus robur*	*Tilia cordata*	*Acer platanoides*	*F*-value	Tree species *p*- value	Stand *p*-value
No. of cephalolichens	0.87 ± 0.18	0.04 ± 0.04	0.74 ± 0.19	8.31	0.000	1
No. of chlorolichens	0.87 ± 0.30	1.60 ± 0.41	0.35 ± 0.18	4.08	0.021	1
No. of cyanolichens	0.04 ± 0.04	0.00 ± 0.00	0.17 ± 0.08	4.12	0.020	1
No. of lichen species	1.48 ± 0.26	1.65 ± 0.41	1.13 ± 0.24	1.50	0.229	0.8
Cephalolichchen-cover, %	51.3 ± 10.0	1.3 ± 1.3	44.4 ± 10.1	10.78	0.000	1
Chlorolichen-cover, %	25.2 ± 8.8	54.8 ± 10.3	13.9 ± 7.2	5.66	0.005	1
Cyanolichen-cover, %	1.7 ± 1.7	0 ± 0	10.9 ± 6.1	2.75	0.070	1
Microlichen-cover, %	35 ± 2	46 ± 3	27 ± 4	9.96	0.000	1
Macrolichen-cover, %	12 ± 2	14 ± 3	18 ± 4	1.25	0.292	1
Bryophyte-cover, %	45 ± 2	30 ± 3	50 ± 3	13.76	0.000	1
Bark pH	4.75 ± 0.11	4.66 ± 0.10	5.01 ± 0.12	8.00	0.001	1
Soil pH	4.90 ± 0.08	4.77 ± 0.10	5.23 ± 0.11	2.54	0.086	0.3
Circumference, cm	115.1 ± 7.9	102.4 ± 6.3	96.4 ± 5.1	5.72	0.006	0.00
Basal area, m^2 ha^{-1}	14.17 ± 1.04	13.4 ± 0.8	14.3 ± 1.0	0.78	0.458	0.00
L. scrobiculata preference %	35 ± 6.8	29.7 ± 4.7	37.4 ± 6.21	0.43	0.647	1
Total grazing, mg	72.5 ± 17.8	83.6 ± 16.2	93.5 ± 19.3	3.28	0.040	0.1

As can be seen in appendix 11, bark pH is significantly correlated with soil pH and circumference in the forest at Langangen. A linear mixed effects model was fitted to this data. Tree circumference ($F = 7.18$, $p = 0.009$) and soil pH ($F = 7.6$, $p = 0.007$) were significant positive predictors of bark pH. The random factor of stand ($p = 0.06$) was nearly significant. Bark pH increases with increasing soil pH and with increasing tree circumference.

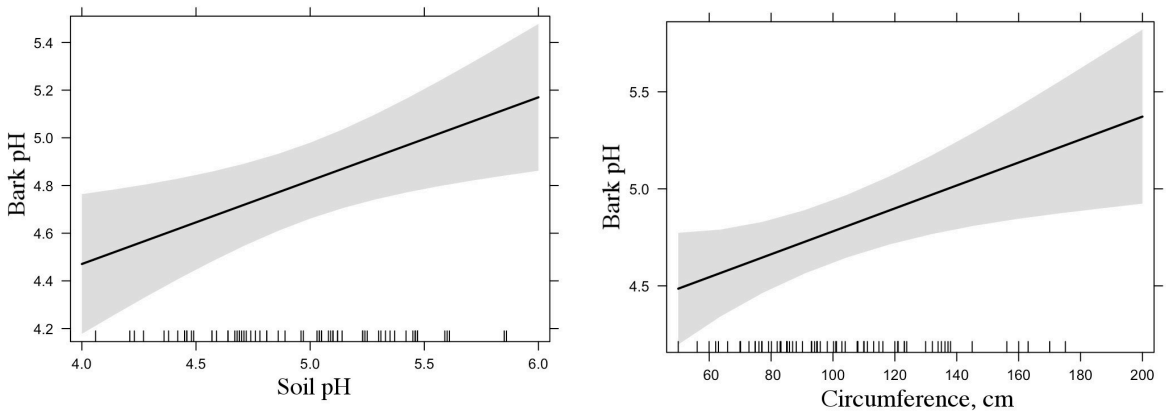


Figure 9. Effect plots from the LME fitted to bark pH data measured in Langangen, Telemark. Left: The relationship between soil pH and bark pH; right: the relationship between trunk circumference and bark pH. Grey areas are confidence intervals (95%) and bars on the x axes are observations.

The presence of specific lichen species was used to classify the sampled trees as presenting a Lobarion community (∑Cephalolichens > 0 or ∑Cyanolichens > 0), a Chlorolichen community (∑Cephalolichens = 0, ∑Cyanolichens = 0 and ∑Chlorolichens > 0) or a Microlichen community (∑Cephalolichens = 0, ∑Cyanolichens = 0 and ∑Chlorolichens = 0). The proportions for all tree species were: Chlorolichen = 29%, Lobarion = 39% and Microlichen = 32%. The proportions for each tree species individually is shown in figure 10, below.

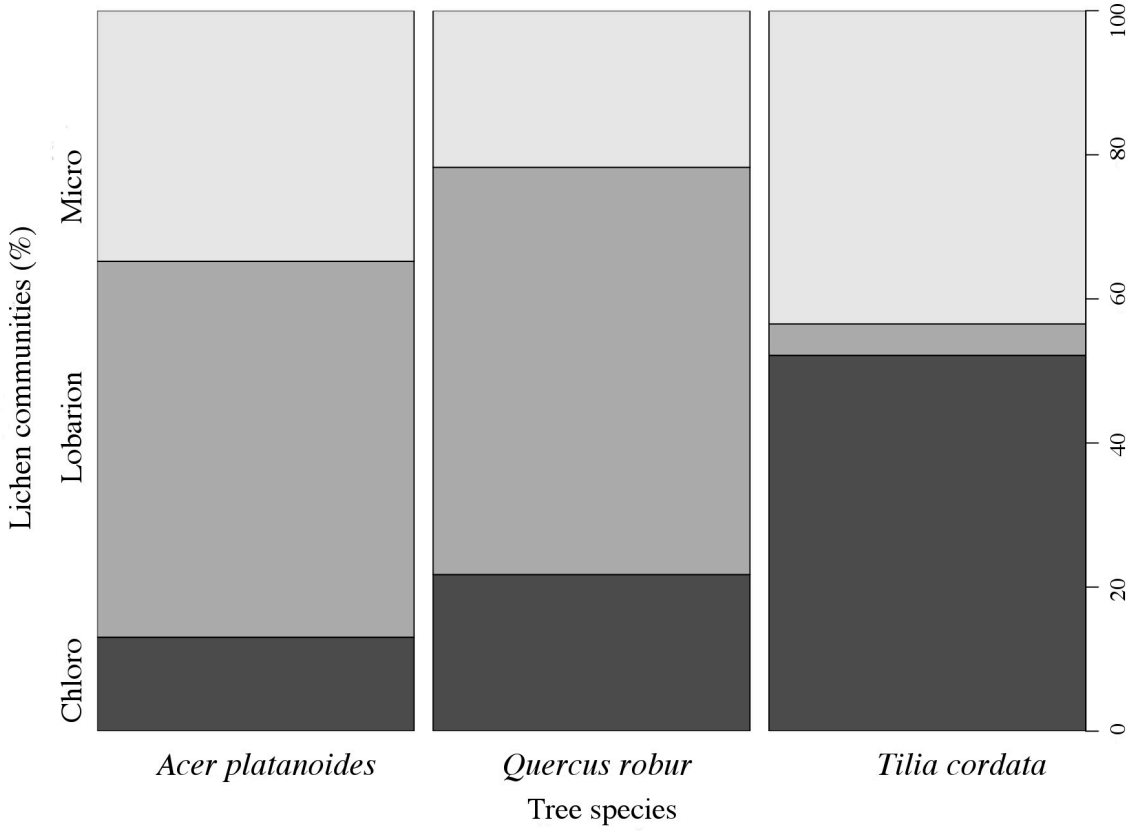


Figure 10. A bar chart showing, for each tree species, the percentage of trees sampled (n = 23 for each species) that presented a chlorolichen, Lobarion or microlichen community.

During the field experiment at Langangen, the lichen diversity was determined on each sampled tree (n=69). All macro lichens were identified and their percentage area cover was assessed. No microlichens were included. All macrolichens were categorized as either chlorolichens (green algal photobiont), cephalolichens (green algal photobiont and cephalodia containing a cyanobacterial symbiont) or cyanolichens (cyanobacterial photobiont). An overview of this diversity-assessment is presented in table 7.

Table 7. The number and mean cover (%) of macrolichen species registered on trees (n=69) at Langangen, Telemark. The tree species are *Acer platanoides*, *Quercus robur* and *Tilia cordata*.

	Quercus robur		*Tilia cordata*		*Acer platanoides*	
Lichen species	**Trees (*n*)**	**Mean (%)**	**Trees (*n*)**	**Mean (%)**	**Trees (*n*)**	**Mean (%)**
Cephalolichens						
Lobaria pulmonaria	13	64	1	30	5	41
L. virens	7	50	0	0	9	82
L. amplissima	0	0	0	0	3	27
Cyanolichens						
Peltigera praetextata	1	40	0	0	4	62
Leptogium lichenoides	0	0	0	0	1	10
Chlorolichens:						
Parmelia sulcata	5	24	5	32	2	65
Evernia prunastri	7	37	11	39	3	47
Ramalina farinaceae	2	20	3	14	1	25
Hypogymnia physodes	4	34	4	24	0	0
Platismatia glauca	1	5	5	25	0	0
Melanelia fuliginosa	0	0	6	20	1	20
Cladonia spp	0	0	3	97	1	5
Usnea subfloridana	1	20	0	0	0	0

An LDA (Linear Discriminant Analysis) was fitted to the lichen community data (figure 10) using tree species, bark pH and moss-cover as the factors used to discriminate between lichen communities. For every tree, the LDA model used information about bark pH, moss-cover and tree species to predict what lichen community is most likely to be present on its trunk. This prediction can later be evaluated using the information from the field about which community was actually present on the tree-trunk. The model either predicts the correct community, or predicts one of the two other possible communities and makes an error. In order to evaluate the model, a confusion matrix is constructed which contrasts all the actual, or correct, classifications with all the predictions made by the LDA model. The model can then be "trained" with a novel dataset and its predictions made more accurate, so that these three simple ecological variables may be used to predict the probable presence of these three lichen communities in forests.

Table 8. Confusion matrix visualizing the performance of the LDA. In total 42/69 (60%) of the trees were correctly classified. The dataset was obtained from the natural grazing experiment at Langangen, Telemark. Correct predictions: Chloro = 55%, Lobarion = 80% and Micro = 43%.

		True		
		Chloro	Lobarion	Micro
Predicted	Chloro	**11**	1	3
	Lobarion	7	**21**	10
	Micro	2	4	**10**

DISCUSSION

An increase in CBSC concentration did not negatively affect grazing in the controlled feeding experiment, although various independent studies (Asplund & Gauslaa 2008; Asplund 2011b; Gauslaa 2005; Pöykkö et al. 2005; Vatne et al. 2011) have documented such a relationship. A mixed population of *Helicigona lapicida* and *Cepaea hortensis* showed no preference for *Lobaria pulmonaria* or *L. virens* although *L. virens* did not contain any CBSCs. Thus, hypothesis 2.a. formulated in the introduction is not supported by my results. Since both lichens were little grazed *L. virens* may have been protected from grazing by an unknown chemical defence. I have no evidence for the identity of this defence. However, the cyanobacteria of *Lobaria scrobiculata* and members of the genus *Peltigera* have been shown to produce a chemical defence based on nitrogen (Kaasalainen et al. 2012), which could be present in *L. virens* as well as in combination with CBSCs in *L. pulmonaria*.

The lack of any significant relationship between grazing and melanin content in controlled grazing experiments, does not support the hypothesis that melanin affects grazing by generalist gastropod lichenivores (Hypothesis 2.b. is rejected). These results may be a consequence of the findings that concentrations of CBSCs of *Lobaria pulmonaria* in the laboratory study did not vary across the three solar radiation treatments (PAR, PAR+UVA, PAR+UVA+ UVB). This is consistent with the well-established hypothesis (Hypothesis 2.e.) that medullary CBSCs are not affected by solar radiation (Asplund 2011b; McEvoy et al. 2007; Nybakken et al. 2007). Specific thallus mass was found to be a good predictor of total CBSCs in *L. pulmonaria*, which is consistent with (Asplund & Gauslaa 2007; Gauslaa et al. 2013; Nybakken et al. 2007). An increase in STM was associated with a decreasing concentration total of CBSCs. Thallus area by itself was not correlated with total CBSC content as reported in (Asplund & Gauslaa 2007). Thus, hypothesis 2.c. is rejected. In my study the results were obtained from an experiment where n=36, while n=67 in the experiment from (Asplund & Gauslaa 2007), and the *L. pulmonaria* thalli used were not subjected to any solar radiation treatments. The range of lichen areas in my study (6.93 – 16.76 cm^2) may not have been sufficient to reveal an existing relationship.

The concentration of the minor CBSC methyl-norstictic acid has previously been found to respond when lichens are transplanted to habitats with more sunlight such as clear-cuts as compared to old forests. Gauslaa et al. (2013); Nybakken et al. (2007) found that it increased significantly, while McEvoy et al. (2007) reported a decrease in its concentration. I found that it did not respond to radiation treatments, but it was positively correlated with melanin concentration ($r = 0.52$, $p = 0.01$). This may indicate that synthesis of this CBSC respond to the same environmental stimuli as melanin production, although available data show contrasting responses to solar radiation treatments. Thus, no clear conclusion could be made.

Relative thallus area growth (RT_AGR) was a good predictor of methyl-norstictic acid and cryptostictic acid content in *L. pulmonaria*. At lower levels of RT_AGR my model predicts higher concentrations of both CBSCs. When the area growth is low, there will likely be an accumulation of photosynthetic that may be converted into CBSC. Thus, a trade off occurs between RT_AGR and CBSC in *L. pulmonaria*, and hypothesis 2.d. is rejected.

The hypothesis that natural grazing at Langangen would decrease with increasing total CBSC was not supported. I thus reject hypothesis 1.a. stated in the introduction. No negative linear relationship was found between grazing and total CBSC concentration. *Lobaria pulmonaria,* with an average CBSC concentration of 56.3 ± 2.2 mg g^{-1}, was grazed consistently more (139.4 ± 18.0 mg) than *Lobaria scrobiculata (*28.5 ± 3.0 mg g^{-1}) which has an average CBSC concentration of 41.8 ± 1.7 mg g^{-1}). Clearly, the best CBSC-defended lichen species was the preferred fodder in the forests at Langangen. This result contrasts the results of Asplund et al. (2010) who showed a clear preference for *L. scrobiculata*, and I thus reject hypothesis 1.b. In Asplund et al. (2010) *Lobaria pulmonaria, L. virens, L. scrobiculata* and *L. amplissima* were transplanted together onto bark of *Fraxinus excelsior* in deciduous forests in Follow, and a 65 ± 3.2% preference was recorded for *L. scrobiculata*. These results were quite different from the mean *L. scrobiculata* preference of 34.0 ± 3.4% recorded here. The total CBSC concentrations reported in Asplund et al. (2010) were higher 68.8 ± 4.4 mg g^{-1} for *L. pulmonaria* and lower (24.8 ± 2.7 mg g^{-1}) for *L. scrobiculata* than the respective concentrations reported here.

It is tempting to infer that my *L. scrobiculata* thalli were grazed less because of their higher levels of CBSCs, but the fact that natural grazers prefer the lichen with higher CBSC content at Langangen complicate such an interpretation. My results are similar to those reported in Gauslaa (2008). He found that the old forest lichen *Pseudocyphellaria crocata* was preferred over *Lobaria pulmonaria* despite having a higher total concentration of CBSCs. Higher stictic acid and constictic acid concentrations negatively impacted grazing in *P. crocata* despite the fact that these were not the major CBSCs in this lichen species. I did find that natural grazing decreased linearly with increasing cryptostictic acid content in in *L. scrobiculata*. In my field experiment, no individual CBSC was found to inhibit grazing of *L. pulmonaria*. In total, the data so far are quite complex and partly contradicting. These diverse results suggest that the herbivore defence of lichens is insufficiently understood, and that there is a need to identify and quantify e.g. N-based defence compounds in these lichens. Kaasalainen et al. (2013) has found that N-based defence compounds are not always present in cephalolichen members of *Peltigera*, which may also be the case in *Lobaria*.

In the various studies cited above, as well as in my own study, lichens were collected from various sites like Langangen, Tysnes and Trøndelag. It is reasonable to assume that lichens from such contrasting ecosystems had experienced different grazing-pressure, those with the highest total CBSC content coming from ecosystems with the most grazing (see table 9). The *Lobaria scrobiculata* used by Asplund et al. (2010) were collected on *Salix caprea* trunks in *Picea* abies dominated forests in Horka, Trøndelag. Gastropods are known to prefer the less acidic bark of deciduous trees from edaphically rich sites over the acidic bark of trees in more acidic coniferous forests (Asplund et al. 2010; Hylander et al. 2005). Therefore, *L. scrobiculata* having its largest populations on spruce branches in Trøndelag presumably does not need a very strong chemical defence. These thalli with low CBSC content were transplanted into *Fraxinus*-dominated stands with an intense grazing pressure, and this might explain why they were grazed so heavily in Asplund et al. (2010). *Lobaria scrobiculata* did not occur naturally in studied stands at Langangen, which is a boreonemoral ecosystem. It has its core habitat in boreal ecosystems and Asplundh et al. (2010) hypothesized that it cannot overcome the grazing-pressure in many coastal

boreonemoral sites. This grazing-pressure is so high because milder temperatures and less acidic soils favour gastropods. Coastal temperate deciduous stands also have a much higher gastropod diversity.

A decline in species diversity from the tropics to the poles is one of the best established patterns in ecology (Willig et al. 2003). The number of gastropod species in Norway follows this pattern as well, so that thalli from Trøndelag come from ecosystems where lichenivorous gastropod communities are less diverse. Vatne et al. (2010) found that the number of gastropod species found in the litter around deciduous trees in calcareous broadleaved forests in southern Norway increased with the counted number of gastropod specimens. Presumably, this relation holds true for Trøndelag as well, which leads to the conclusion that fewer gastropods are present there. Since grazing damage decreases with decreased gastropod abundance, we can expect the Trøndelag site to have a lower grazing-pressure, and the highest grazing pressure is probably in Tysnes.

Table 9. A comparison of the concentrations of CBSCs in *L. pulmonaria* and *L. scrobiculata* from 3 independent studies. "*" indicate results from an experiment with the addition of phosphorous. Only the Tysnes and the Langangen sites are broadleaved deciduous forests, the remaining studies were done in coniferous forests.

Lichen	**Total CBSC**	**Locality**	**Study**
L. pulmonaria	32.4 ± 5.6 mg g^{-1}	Trøndelag	Nybakken et al. (2007)
L. pulmonaria	68.8 ± 4.4 mg g^{-1}	Tysnes	Asplund et al. (2010)
L. pulmonaria	22.2 ± 0.9 mg g^{-1} *	Inland British Colombia	Bidussi et al. (2013)
L. pulmonaria	56.3 ± 2.2 mg g^{-1}	Tysnes, S_2	My study
L. pulmonaria	59.5 ± 2.0 mg g^{-1}	Langangen, S_1	My study
L. scrobiculata	41.8 ± 1.7 mg g^{-1}	Tysnes, S_2	My study
L. scrobiculata	24.8 ± 2.7 mg g^{-1}	Trøndelag	Asplund et al. (2010)

Gauslaa et al. (2013) showed that CBSC concentrations vary seasonally, and that concentrations of all CBSCs were consistently higher during the summer than in winter. This led to the hypothesis that the synthesis of CBSCs is most responsive to change during the summer, which is when grazing mainly occurs. For *L. pulmonaria,* the mean total CBSC concentrations of the thalli used in the controlled grazing experiment (S_1 collected during the summer at Langangen) (59.5 ± 2 mg g^{-1}) barely exceeded those used in the natural grazing experiment (S_2) collected during the winter at Tysnes) (56.3 ± 2.2 mg g^{-1}). Even though the concentrations of S_1 exceeded those of S_2 it was not by as much as could be expected, since winter values can sometimes be 50% of summer values. Thus, when considering seasonal effects, *L. pulmonaria*, like *L. scrobiculata* is better defended (contains higher concentrations of CBSC) in oceanic forests in Tysnes where snails likely are most abundant in terms of species and specimens.

Asplund et al. (2010) recorded grazing not as mg grazed dry matter but as the total area (cm^2) with grazing marks, and only reported grazing preference based on these area data. In fact, this complicates comparisons made with my study, because snails mainly grazed the upper cortex and photobiont layer (fig. 6). I recorded grazing as change in dry matter (mg). The growth that occurred in the field on the transplants,

which may be in the order of 10-25%, is not accounted for and can lead to an underestimation of natural grazing. This source of error is hardly insignificant. Grazing measured as area change is less vulnerable to lichen growth in the field. It is possible that I overestimate the discrepancy between my results and those presented in Asplund et al. (2010).

It is clear that populations of lichens from different habitats have varying concentrations of CBSCs, but how the lichens regulate the synthesis of a majority of these compounds in response to environmental signals is not yet well known. Although interesting, this topic lies beyond the scope of this thesis, and I do not provide evidence that the CBSC content is inducible by environmental factors or differs because of long-term genetic adaptation. Asplund (2011a) describes chemical races of *Lobaria pulmonaria* in North America, but no molecular or qualitatively chemical data has been published that can document adaptations in CBSC concentrations between the regions in Norway.

The different forest ecosystems receiving lichen transplants have different lichenivore-assemblages as well. It is not known if the gastropod-community of Langangen, where I did my experiment is comparable to the one in Follo where the grazing experiment from Asplund et al. (2010) was carried out. The forest at Follo consisted of *Fraxinus excelsior* growing on marine clay sediment, while the forest at Langangen consists of *Acer platanoides*, *Tilia cordata* and *Quercus robur* growing on soils derived in situ from weathering of Larvikite. Different lichenivore-assemblages could well be the cause of the different grazing patterns observed.

My best model for *L. scrobiculata* grazing was an LME where stand was treated as a random factor, and pH and cryptostictic acid concentration were the covariates. There was a negative effect on grazing for cryptostictic acid content ($F = 8.90$, $p = 0.004$) and a positive effect for soil pH ($F = 5.94$, $p = 0.017$). This suggests that natural grazing populations are effectively deterred by cryptostictic acid and that the grazers of *L. scrobiculata* thus require high soil pH. This is a general trend for gastropod grazing seen elsewhere. Although not a significant factor predicting levels of grazing, soil surface inclination was correlated with *L. scrobiculata* grazing ($p = 0.05$). This could be due to the fact that soil pH is known to increase with the slope, because steep terrain it is more exposed to weathering and cations are leach into the soil. Often plants requiring high soil pH can be found in steeper terrain (Gauslaa, personal communication). Therefore it seems likely that gastropods that prefer to feed on *L. scrobibulata* thrive in more steeply inclined terrain. However, no significant correlation was found between soil pH and inclination in my study. This could be because most of the sampled trees were growing on terrain of intermediate inclination.

It is also interesting that, although not a significant predictor in my model, grazing was positively correlated with the relascope sum (m^2 ha^{-1}) of *Quercus robur* ($p = 0.05$) and positively correlated with the relascope sum of *Tilia cordata* ($p = 0.05$). This suggests that if the tree onto which my lichens were transplanted stood in a stand that had a relatively high density of oak trees, it was generally grazed less. This is not strictly related to the effect of pH mentioned earlier, because oak has intermediate values of soil and bark pH, but it might be related to the C/N ratio of litter. *Tilia cordata* was associated with the lowest measured pH in both soil and bark of the tree

species. Yet, higher levels of grazing occurred in stands with relatively higher densities of linden trees. This may occur because gastropods often prefer to feed on leaf litter from *Tilia cordata* (Solhøy, pers communication). It is possible that the mean soil pH of all these tree species was above the lower tolerance limit for natural lichenivore assemblages, but that the litter around linden trees had higher nutritional value (C/N ratio).

Tilia cordata was the tree species on which the Lobarion community was least frequent (fig. 10). It seems plausible that it is favoured by grazers, this reduces the chance for the Lobarion to colonize its stems. *Tilia cordata* has the highest chlorolichen-cover among the studied tree species. The snails that prefer this tree may thus prefer to graze on cyanolichens and cephalolichens rather than on chlorolichens, perhaps because of their requirement for lower C/N ratio food. However, one cannot exclude other factors like e.g. a possibly less favourable elemental composition of *Tilia cordata* bark. Total grazing on my transplanted lichens was highest on the stems of *Acer platanoides* which also had the highest mean values for soil pH, bark pH and cyanolichen cover. The Lobarion community on maples may be so productive and rich in biomass that the local gastropod community cannot eat it all, meaning that there is a kind of saturation.

An LDA model was made to predict the presence of a chlorolichen, microlichen or Lobarion community using tree species, bark pH and moss-cover as discriminating factors. A 60% accurate prediction rate is not very good, but it does illustrate that these factors are important in shaping the tree species-specific lichen communities at Langangen. An ecologist with expert knowledge would probably be better at predicting the occurrence of the Lobarion community than a computer analysing the the discriminating factors in an unexplored forest. Historical factors such as continuity were not included in the model, but would presumably be (Solhaug & Gauslaa 2012) taken into account by an ecologist.

My best model for *L. pulmonaria* grazing was a LME where stand was a random factor and chlorolichen-cover (%) was the covariate ($F = 6.86$, $p = 0.010$). Bryophyte-cover (%) was negatively correlated with grazing, which could be expected because trees with a high bryophyte cover usually do not offer much fodder for gastropods. Chlorolichen-cover was significantly negatively correlated with higher bark and soil pH. Thereby, grazers may limit the chlorolichen cover on studied tree species at Langangen, because they prefer a combination of high bark and soil pH.

The pH of the soil and the circumference of the tree were good predictors for the pH of the bark at Langangen. Larger trees on soils with higher pH were associated with the highest bark pH (e.g. Gauslaa (1985); Gauslaa (1995)) Soils at higher elevations had lower pH (e.g. Gauslaa (1995)), but this was true only when trees had a circumference of 100 or less. The soil pH was predicted to be higher at higher elevations if a tree of large circumference grew there. Wether the tree grows in this soil because it has higher pH or the soil pH is raised because the large trees pump cations through their deeper roots, is an open question. The interactions of ecological factors within natural ecosystems are quite complex.

As can be seen in fig. 6 gastropods grazed the cortex of the lichen thalli more intensively than the medulla, which is consistent with the fact that the medulla is

where most of the CBSCs assumed to deter grazing are located (Asplund 2011b). The preference for the cortex of lichens by grazing gastropods has been well documented (Gauslaa et al. 2010). It could be possible that I did not detect a relationship between grazing and total CBSC content because the gastropods consistently avoided the medulla. Snails in natural habitats that are presumably rich in alternative food sources would avoid the lichen medulla to an even greater extent than snails do in a laboratory setting like the one in Asplund (Asplund 2011b). Laboratory conditions with starving snails could lead to more grazing of lichens with high CBSC content, as long as they avoid the medulla. We do not yet know which snail species that heavily graze on *Lobaria* spp in natural ecosystems, they may well be slugs like *Lehmannia marginata* and *Arion fuscus*. In general, a mixed population of *Helicigona lapicida* and *Cepaea hortensis* did not graze much in the laboratory experiment (10 ± 1.4 mg for *L. virens* and 12.2 ± 1.4 mg for *L. pulmonaria*). Gauslaa (2005) also recorded low levels of *L. pulmonaria* grazing by *C. hortensis*: 7.6 ± 1.4 mg for acetone-rinsed thalli (CBSC-deficient) and 2.2 ± 1.0 mg for control-thalli (CBSCs present). Even though the mixed grazing in my experiment was slightly higher than in the experiment of Gauslaa (2005), it is still low compared to the 78.5 ± 8.7 mg (acetone-rinsed) and 42.0 ± 9.6 mg (control) mg of e.g. *Cladonia arbuscula* that were grazed by *C. hortensis* in the experiment from Gauslaa (2005). Neither *C. hortensis* nor *H. lapicida* were optimal snails for use in controlled grazing experiments with *Lobaria pulmonaria*. However, they are more simple to collect and to handle than slugs. Vatne et al. (2010) collected and identified snails in litter around 33 decidous trees with the Lobarion community in southern Norway. A total of 28 snail species was observed and only 0.7% of the 1709 specimens sampled were C. hortensis. Furthermore, *H. lapicida* was not found. The sampling method used in Vatne et al. (2010) could not provide an adequate characterization of the diversity of climbing snails since only litter was sampled. Gastropods that likely feed on *Lobaria spp*. are *Clausilidae spp*., and slugs like *Lehmannia marginata* or *Arion fuscus* (Yngvar Gauslaa, personal communication). *C. hortensis* and *H. lapicida* used in my controlled feeding experiment are considered lichen feeding specialists (Anette Bauer, pers. communication) that are easy to work with and to collect in greater numbers, which is probably not the case for the gastropods feeding on *Lobaria* species. Other invertebrates like oribatid mites, springtails (Collembola) or psocids (Psocoptera) (Pettersson et al. 1995; Seyd & Seaward 1984) also graze on lichens, but their grazing has not been distinguished from that of gastropods in this study. Baur et al. (2000) was able to link specific grazing marks to specific lichen species by using SEM images, but that was not an option for this thesis.

THE STATUS OF THE STUDY AREA FROM A CONSERVATION PERSPECTIVE

After having spent time in the forest at Langangen, and observed the abundance of a rich Lobarion community in forests that can be considered old-growth forests with dead wood of various degradation stages, I believe that a strong case can be made for protecing this forest. The nearby Sankthansåsen Nature Reserve has much younger forests, and therefore it does not have a lichen community as rich as the non-protected neighbouring old-growth forests I studied. If the two sites could be combined to form a single reserve this would probably be the optimal situation since it would possibly allow the Lobarion community to spread naturally.

CONCLUSION

Melanin content, CBSC content and growth variables were shown to have no effect on controlled grazing by the two generalist gastropods *Cepaea hortensis* and *Helicigona lapicida*. The gastropods did not show any clear preference for *Lobaria pulmonaria* or *Lobaria virens*. CBSC content in *L. pulmonaria* did not respond to solar radiation treatments, but the minor methyl-norstictic acid and cryptostictic acid decreased with increased relative thallus area growth rate (RT_AGR). The concentration of methyl-nostictic acid positively correlated with melanin content. Natural populations of gastropods at Langangen consistently preferred *L. pulmonaria* over *L. scrobiculata,* despite the fact that *L. pulmonaria* had higher concentrations of CBSCs known to deter grazing. Different lichen populations have different grazing defense levels. Therefore, grazing preferences can be population dependent. At the same time, different ecosystems also host different gastropod communities. Thereby the complexity in gastropod-lichen relationships is high, and much of the variation in responses could not be accounted for. An additional N-based defence mentioned in the literature could also contribute to the unexpected preference, but no evidence for such a defence is presented here. Lichen feeding gastropods influence lichen-dominated epiphytic communities on tree trunks, but in more complex ways than previously thought.

APPENDIX

The distributions of all measured variables from field and lab experiments, as well as all correlations between these variables, are presented as appendices. The Pearson correlation coefficients and the results of a two-tailed significance test performed for each correlation are given. Levels of significance are as follows: $P<0.001$: "***", $P<0.01$: "**", $P<0.05$: "*" and $P< 0.1$: "·". Matrices are presented in the following order. First, two matrices for each of the transplanted lichen species, *Lobaria pulmonaria* (Appendices 1 and 2) and *Lobaria scrobiculata* (Appendices 3 and 4). Appendices 1 and 3 report grazing and other ecological variables measured in the field, appendices 2 and 4 report grazing and the CBSC concentrations. CBSC and field variables were given in separate matrices because transplants were collected in another forest stand. Earlier transplantation studies have shown that medullary CBSCs do not respond to changed habitat conditions within a three months period, meaning that there are no functional relationships between stand variables in the stands used for transplantation and the concentration of CBSCs (McEvoy et al. 2007). Appendices 5 and 6 report species-wise correlation matrices for the same lichen species, but only the variables grazing and relascope sum in total and for individual trees. Appendices 7 and 8 report matrices for *Lobaria virens* and *Lobaria pulmonaria,* respectively, from the grazing experiment in the laboratory.

The following tables explain each **v**ariable included in the correlation matrixes in appendices 1-8. For a more precise definition and additional information about how the measurements were obtained see Materials and Methods.

Legends for Appendices 1 and 2: *LOBARIA PULMONARIA* natural grazing experiment:

Ecological variables	*CBSCs*
1. Tree. *Acer platanoides* (A), *Quercus robur* (Q) *and Tilia cordata* (T)	**1. Tree.** A, Q and T
2. LogGR: Natural grazing, mg (log-transformed)	**2. LogGr:** Natural grazing, mg (log-transformed)
3. Spref: Grazing preference for *L. scrobiculata*, %	**3. CON:** Constictic acid, mg g^{-1}
4. CE: Cephalolichen cover on tree trunks, %	**4. CRY:** Cryptostictic acid mg g^{-1}
5. CH: Chlorolichen cover on tree trunks, %	**5. STIC:** Stictic acid mg g^{-1}
6. CY: Cyanolichen cover on tree truns, %	**6. NOR:** Norstictic acid mg g^{-1}
7. No: No lichen cover, %	**7. MET:** Methyl norstictic acid mg g^{-1}
8. Micro: Microlichen cover, %	**8. CBSC:** Total CBSCs, mg g^{-1}
9. Macro: Macrolichen cover, %	**9. Spref:** Grazing preference for *L. scrobiculata*, %
10. Moss: Moss cover, %	
11. Soil: Soil pH	
12. Bark: Bark pH	
13. M.a.s.l.: Meters above sea level, m	
14. Circ: Tree circumference, cm	
15. Incl: Inclnation of soil surface, °	
16. R.Sum: Relascope sum, m^2 ha^{-1}	

17. Comm: Lichen community. Only chlorolichens are present (C), Lobarion (L) and only microlichens (M).

Legends for Appendices 3 and 4: ***LOBARIA SCROBICULATA*** natural grazing experiment:

Ecological variables	*CBSCs*
1. Tree. *Acer platanoides* (A), *Quercus robur* (Q) *and Tilia cordata* (T)	**1. Tree**. *A, Q and T*
2. LogGR: Natural grazing, mg (log-transformed)	**2. LogGR:** Natural grazing, *mg* (Log-transformed)
3. Spref: Grazing preference for *L. scrobiculata*, *%*	**3. CON:** Constictic acid, *mg* g^{-1}
4. CE: Cephalolichen cover on tree trunks, *%*	**4. CRY:** Cryptostictic acid, *mg* g^{-1}
5. CH: Chlorolichen cover on tree trunks, *%*	**5. STIC:**Stictic acid, *mg* g^{-1}
6. CY: Cyanolichen cover on tree truns, *%*	**6. NOR:** Norstictic acid, *mg* g^{-1}
7. No: No lichen cover, *%*	**7. MET:** Methyl norstictic acid**,** *mg* g^{-1}
8. Micro: Microlichen cover, *%*	**8. USN:** Usnic acid, *mg* g^{-1}
9. Macro: Macrolichen cover, *%*	**9. M.SC:** M-scrobiculin, *mg* g^{-1}
10. Moss: Moss cover, *%*	**10. CBSC:** Total CBSCs, *mg* g^{-1}
11. Soil: Soil pH	**11. Spref:** *Lobaria scrobiculata* preference, *%*
12. Bark: Bark pH	
13. M.a.s.l.: Meters above sea level, m	
14. Circ: Tree circumference, cm	
15. Incl: Inclination of soil surface, °	
16. R.Sum: Relascope sum, m^2 ha^{-1}	
17. Comm: Lichen community. Only chlorolichens are present (C), Lobarion (L) and only microlichens (M).	

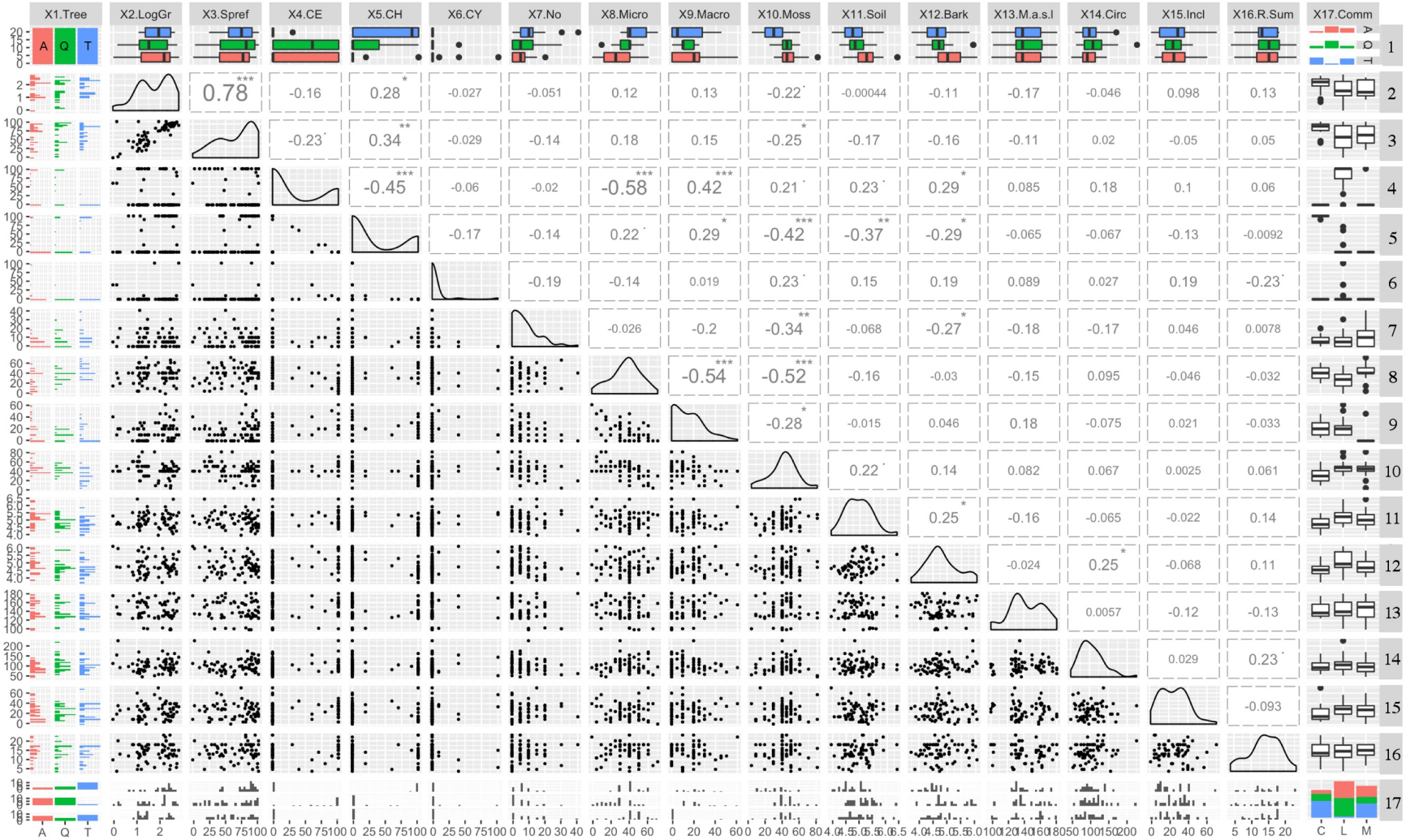
Legends for Appendices 5 and 6: ***L. PULMONARIA*** and ***L. SCROBICULATA*** natural grazing experiment:

Grazing and Relascope sums
1. LogGr: Natural Grazing, *mg* (Log-transformed)
2. Spref: *Lobaria scrobiculata* preference, *%*
3. Acer: *Acer platanoides, m^2 ha^{-1}*
4. Pinus: *Pinus silvestris, m^2 ha^{-1}*
5. Frax: *Fraxinus excelsior, m^2 ha^{-1}*
6. Tilia: *Tilia cordata, m^2 ha^{-1}*
7. Quercus: *Quercus robur, m^2 ha^{-1}*
8. Fagus: *Fagus sylvatica, m^2 ha^{-1}*
9. Picea: *Picea abies, m^2 ha^{-1}*
10. Alnus: *Alnus incana, m^2 ha^{-1}*
11. Populus: *Populus tremula, m^2 ha^{-1}*
12. R.Sum: Sum total, *m^2 ha^{-1}*

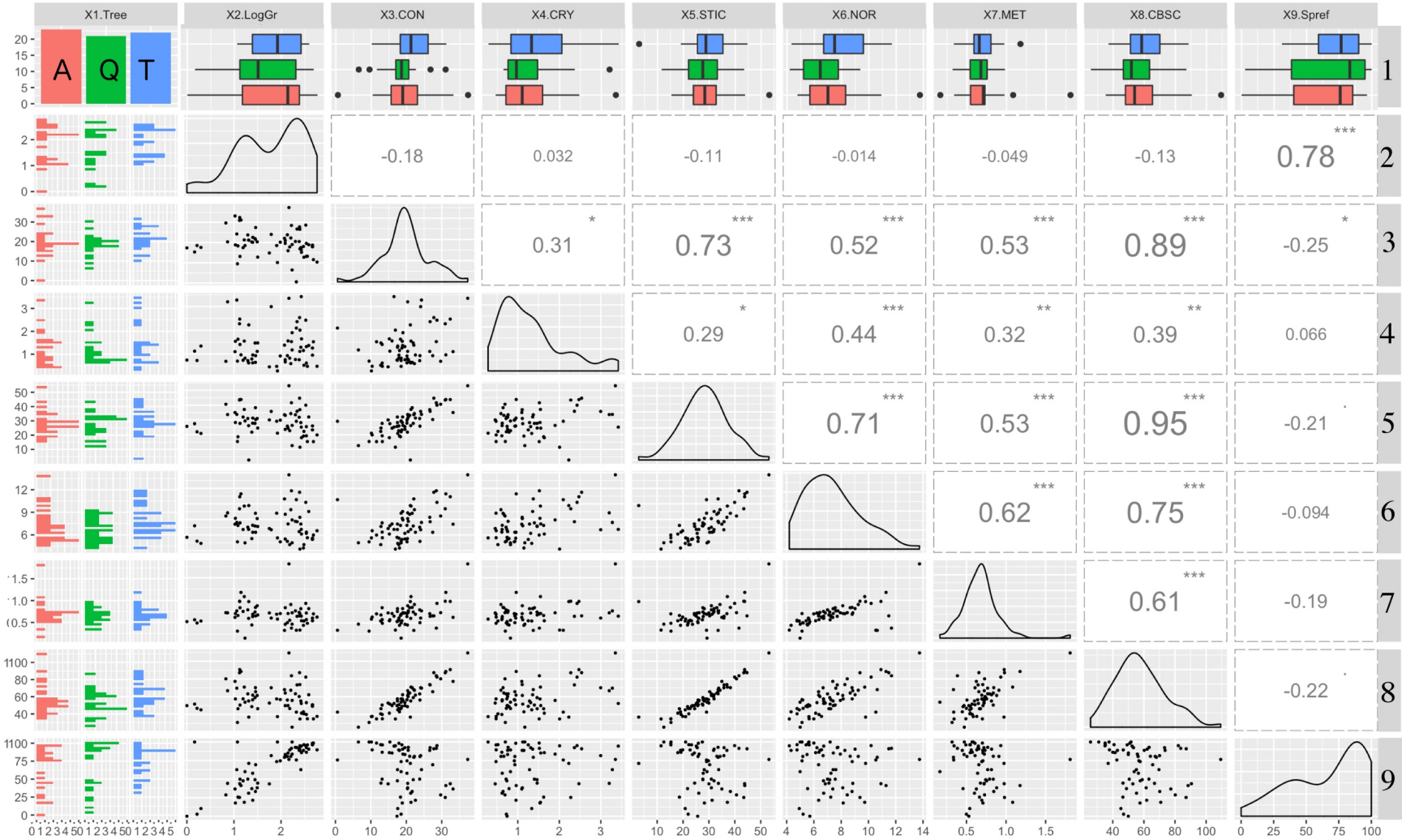
Legends for Appendices 7 and 8: ***LOBARIA VIRENS*** and ***L. PULMONARIA*** controlled grazing experiment in the lab:

Lobaria virens	***Lobaria pulmonaria***
1. Treatment: Treatments (PAR, PAR+UVA, PAR+ UVA+UVB)	**1. Treatment:** Treatments (PAR, PAR+UVA, PAR+ UVA+UVB)
2. Grazing: Controlled Grazing, *g*	**2. Grazing:** Controlled Grazing, *g*
3. DM: Thallus dry mass, *mg*	**3. CON:** Constictic acid, $mg\ g^{-1}$
4. RGR: Relative growth rate, $g\ g^{-1}\ d^{-1}$	**4. CRY:** Cryptostictic acid, $mg\ g^{-1}$
5. RLAGR: Relative thallus area growth rate (RT_AGR), $mm^2\ cm^{-2}\ day^{-1}$	**5. STI:** Stictic acid, $mg\ g^{-1}$
6. Area: Thallus area, mm^2	**6. NOR:** Norstictic acid, $mg\ g^{-1}$
7. STM: Specific thallus mass, $mg\ DM\ mm^{-2}$	**7. MET:** Methyl norstictic acid, $mg\ g^{-1}$
8. BRI: Browning reflectance index	**8. CBSC:** Total CBSCs, $mg\ g^{-1}$
	9. DM: Dry mass, *mg*
	10. RGR: Relative growth rate, $g\ g^{-1}\ d^{-1}$
	11. RLAGR: Relative thallus area growth rate (RT_AGR), $mm^2\ cm^{-2}\ day^{-1}$
	12. Area: Thallus area, mm^2
	13. STM: Specific thallus mass, $mg\ mm^{-2}$
	14. BRI: Browning reflectance index

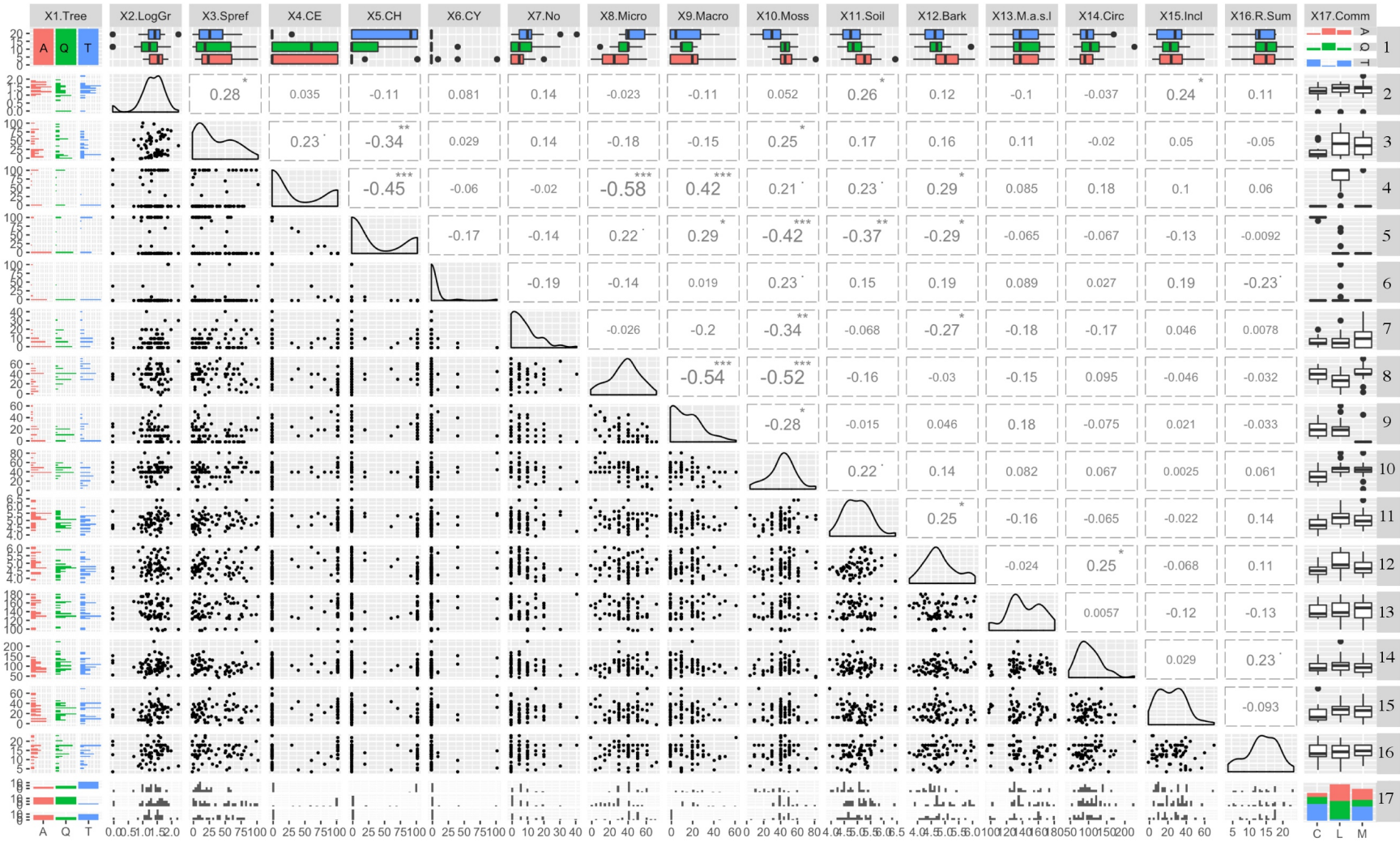
APPENDIX 1: Correlation matrix for grazing by natural populations of gastropods and other field variables recorded in broadleaved deciduous forests at Langangen. Lichen species: *Lobaria pulmonaria*.
Ecological variables were measured at Langangen, Telemark, Norway (59°11'40"N, 9°83'45"E), during the field experiment that lasted from 19. July to October 1, 2016.



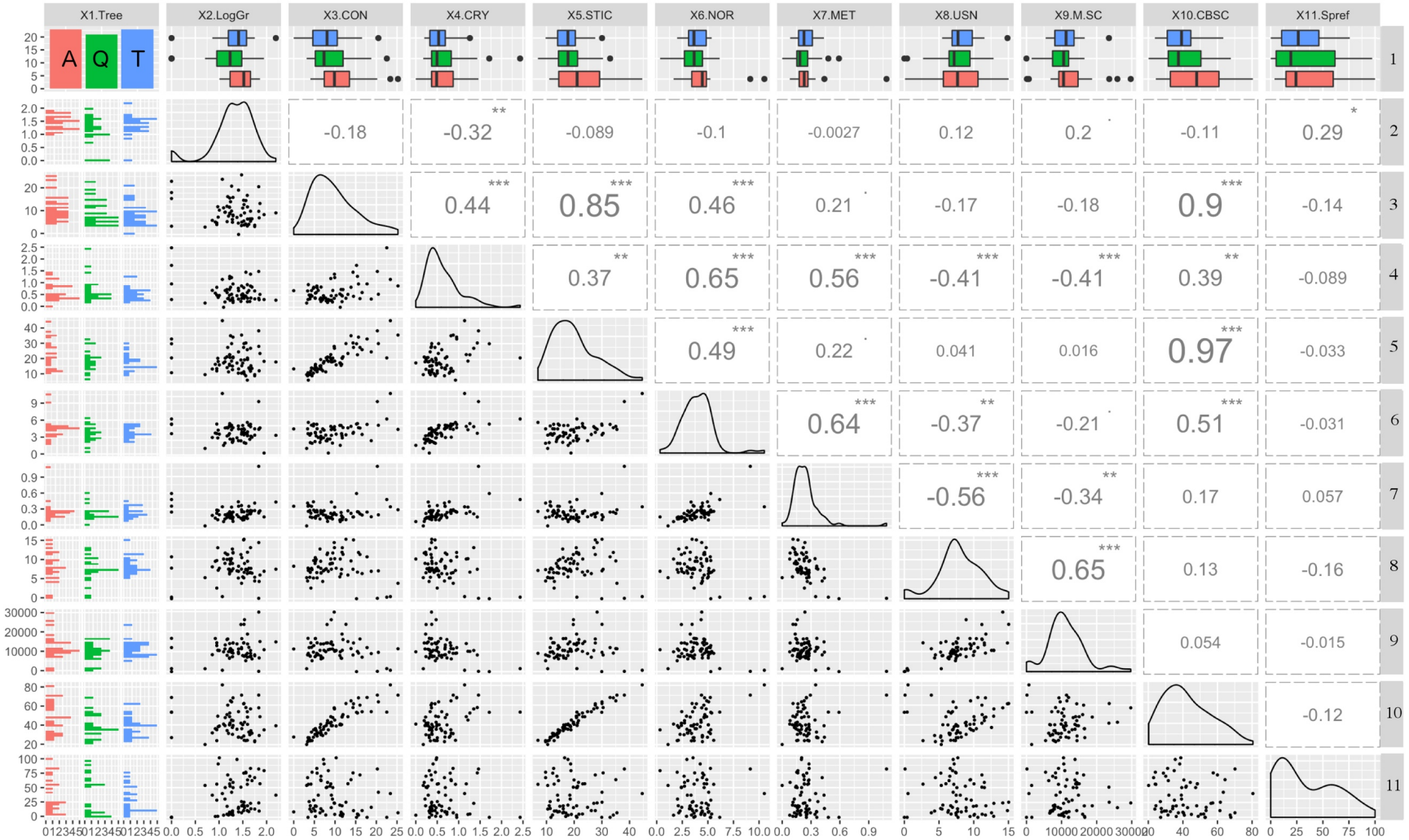
APPENDIX 2: Correlation matrix for grazing by natural populations of gastropods in broadleaved deciduous forests at Langangen and CBSCs. Lichen species: *Lobaria pulmonaria.* The field experiment at Langangen, Telemark, Norway (59°11'40"N, 9°83'45"E) lasted from 19. July to October 1, 2016.



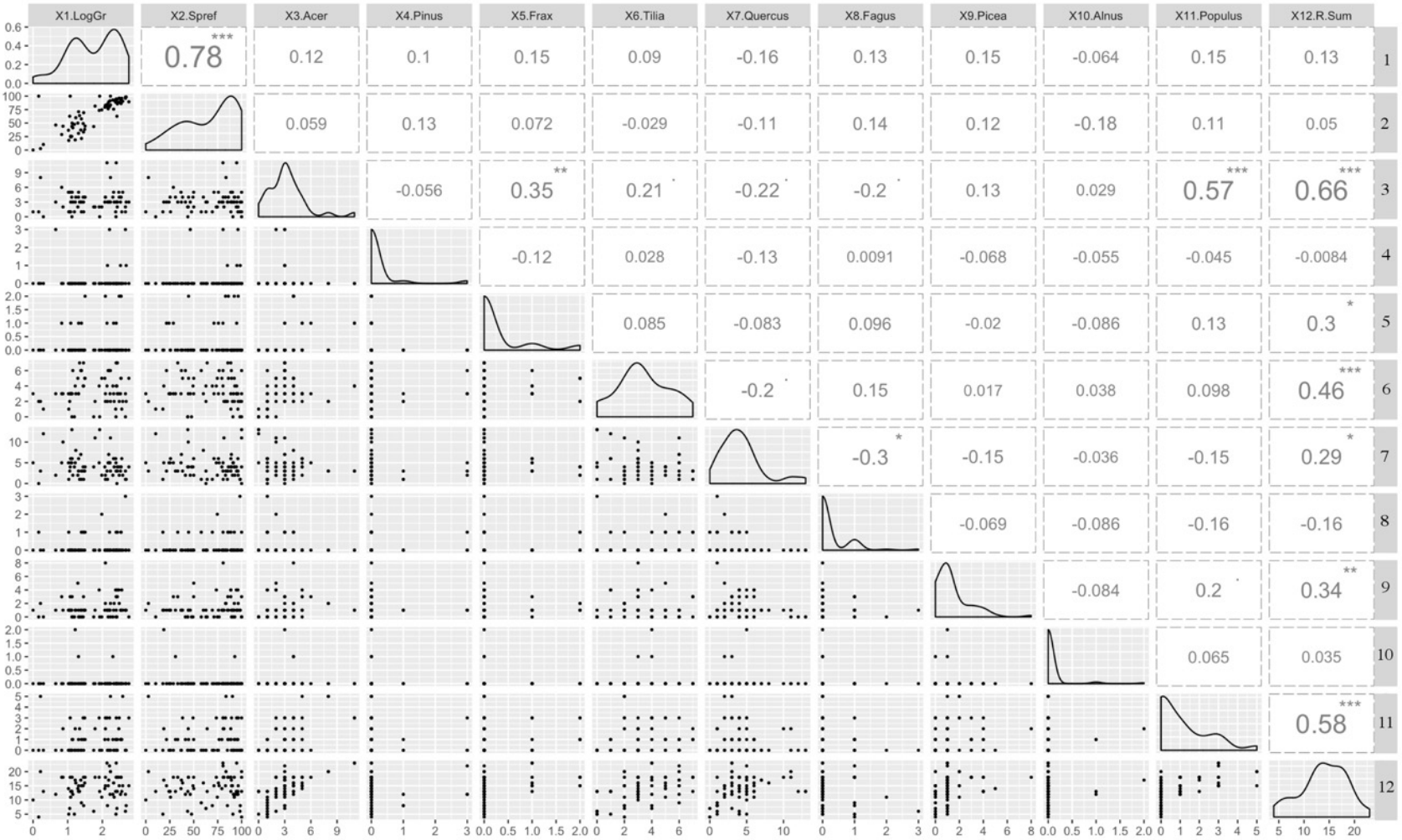
APPENDIX 3: Correlation matrix for grazing by natural populations of gastropods and other field variables recorded in broadleaved deciduous forests at Langangen. Lichen species: *Lobaria scrobiculata*.
Ecological variables were measured at Langangen, Telemark, Norway (59°11'40"N, 9°83'45"E), during the field experiment that lasted from 19. July to October 1, 2016. The CBSCs were measured in the laboratory.



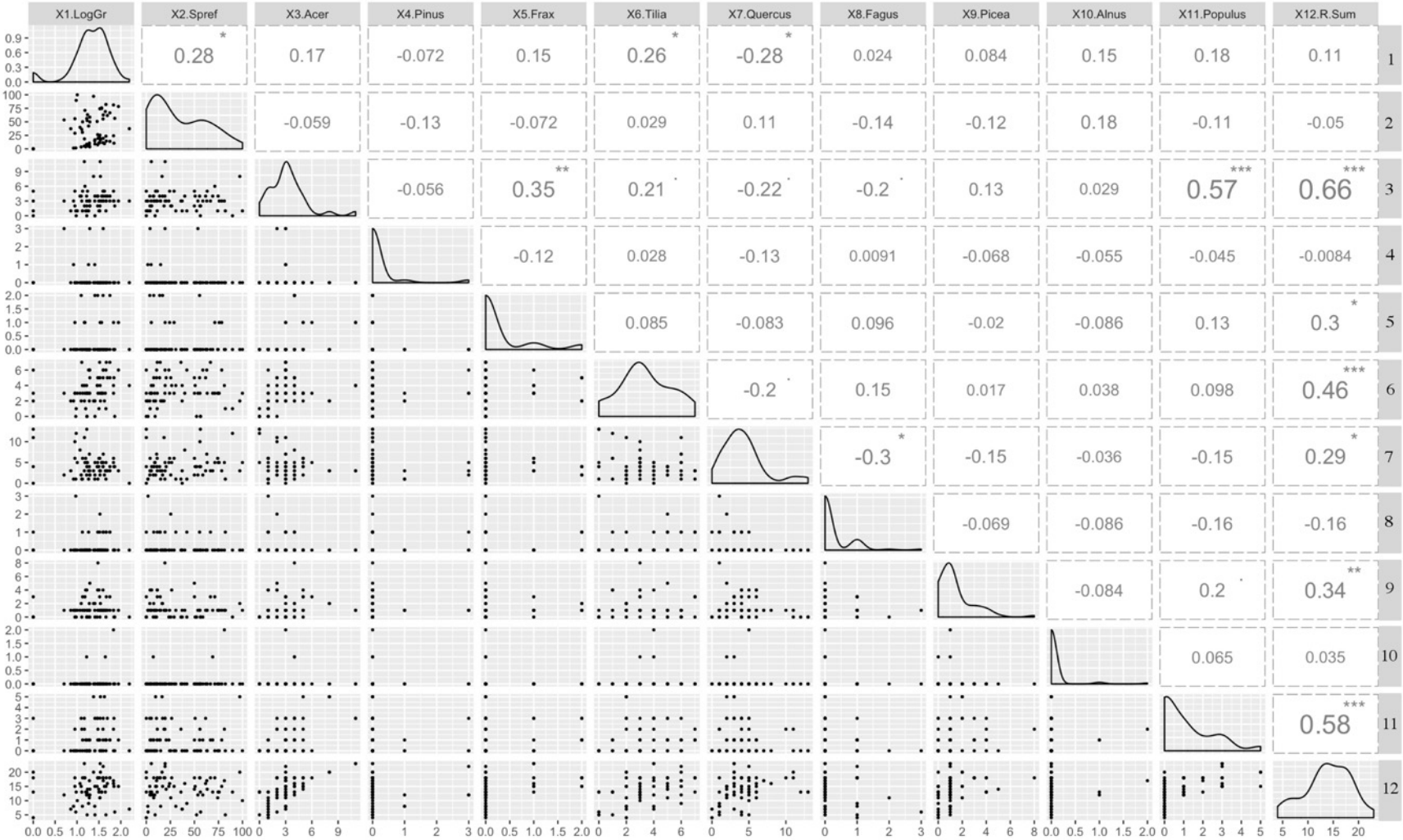
APPENDIX 4: Correlation matrix for grazing by natural populations of gastropods in broadleaved deciduous forests at Langangen and CBSCs. Lichen species: *Lobaria scrobiculata.* The field experiment at Langangen, Telemark, Norway (59°11'40"N, 9°83'45"E) lasted from 19. July to October 1, 2016. The **CBSCs**.were measured in the laboratory.



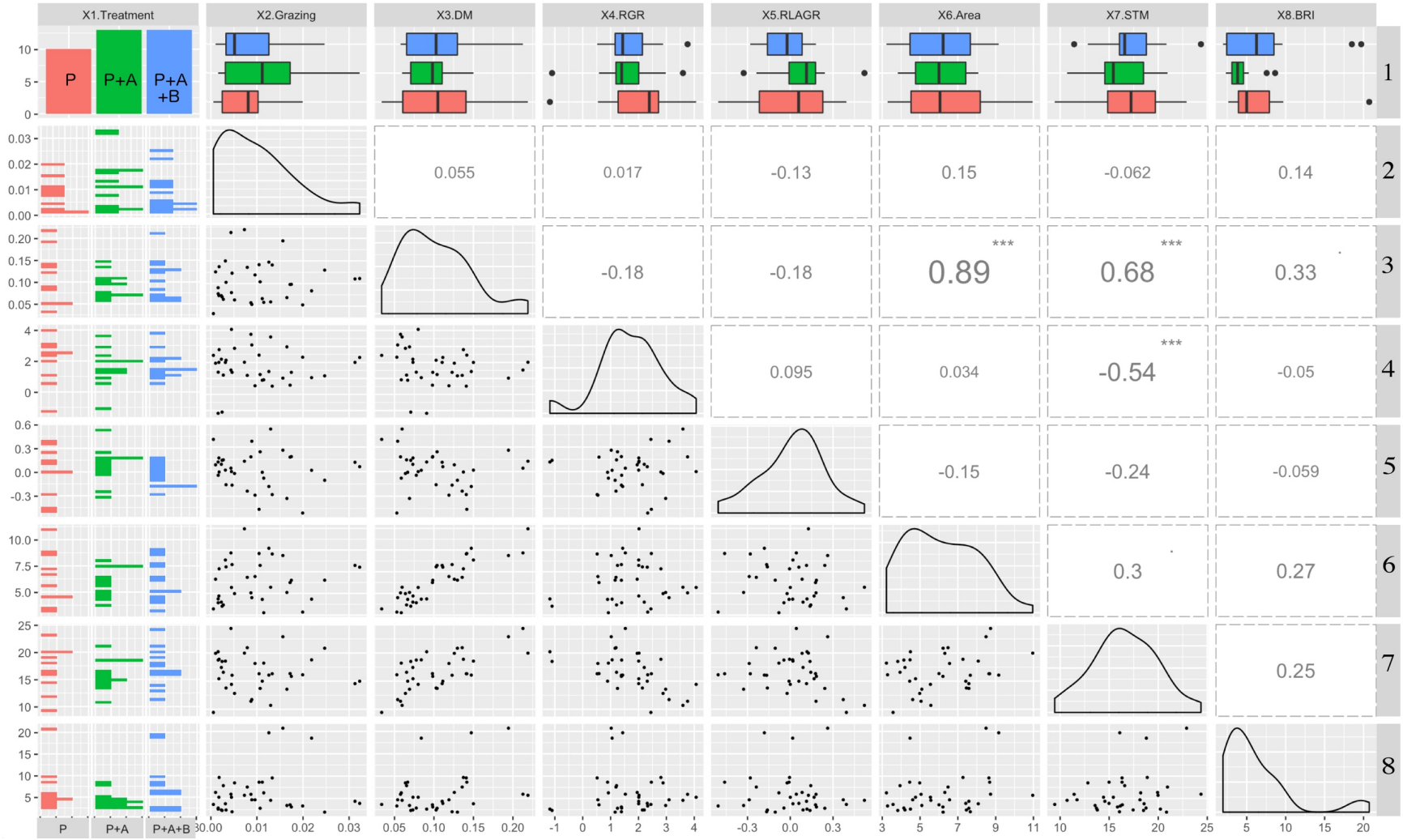
APPENDIX 5: Correlation matrix for grazing by natural populations of gastropods in broadleaved deciduous forests at Langangen and Relascope sums. Lichen species: *Lobaria pulmonaria.* The Relascope sums were measured in the field, at Langangen, Telemark, Norway (59°11'40"N, 9°83'45"E), during the field experiment that lasted from 19. July to October 1, 2016.



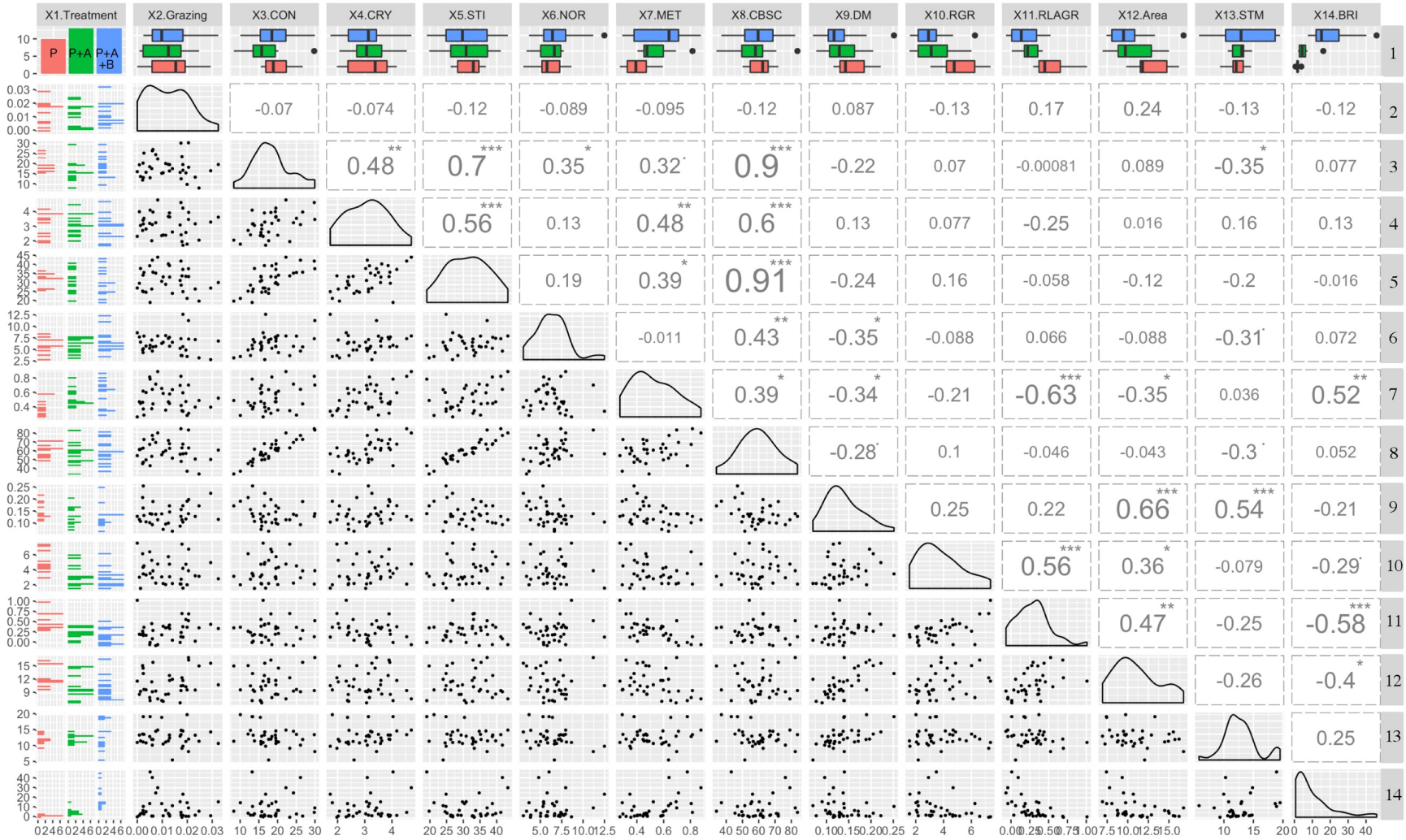
APPENDIX 6: Correlation matrix for grazing by natural populations of gastropods in broadleaved deciduous forests at Langangen and Relascope sums. Lichen species: *Lobaria scrobiculata.* The Relascope sums were measured in the field, at Langangen, Telemark, Norway (59°11'40"N, 9°83'45"E), during the field experiment that lasted from 19. July to October 1, 2016.



APPENDIX 7: Correlation matrix for grazing by the gastropods *Helicigona lapicida* & *Cepaea hortensis* and CBSCs measured in the laboratory. Lichen species: *Lobaria virens*. Variables 3 - 9 measured by Kann (2016).



APPENDIX 8: Correlation matrix for grazing by the gastropods *Helicigona lapicida* & *Cepaea hortensis* and CBSCs measured in the laboratory. Lichen species: *Lobaria pulmonaria*. Variables 3 - 9 measured by Kann (2016).



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