Global change and the functional diversity of cryptogams in northern biomes

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Chapter 5

An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species

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Summary

1. Climate change in the subarctic is expected to influence vegetation composition, specifically bryophyte and lichen communities, thereby modifying litter decomposition rates and carbon (C) dynamics of these systems with possible feedbacks to climate.

2. In a two-year experiment, we investigated decomposition rates and chemical traits of 27 bryophytes, 17 lichens and 5 vascular plants in litter beds in subarctic Sweden. The majority of the sampled cryptogam species are widespread at higher northern latitudes.

3. Average two-year litter decomposition rates (exponential mass loss constant *k*) of lichen (0.44 ± 0.01) and vascular plant (0.56 ± 0.03) species were higher than that of bryophytes (0.11 ± 0.01), while within main cryptogam taxa, species identity was an important determinant of mass loss rates. At cryptogam group level, two-year litter mass loss of *Sphagnum* was significantly lower than for non-*Sphagnum* mosses and liverworts. Within lichens, N_2-fixing versus non-N_2-fixing lichens showed no variation in decomposability.

4. In a subset of the large species set, mass loss differed both among incubation environments (reflecting nutrient-rich and poor birch forest and *Sphagnum* peatlands, respectively) and species. The pattern of mass loss across incubation environments was not consistent among cryptogam species. N_2-fixing, in contrast to non-N_2-fixing lichens with lower nitrogen (N) levels, displayed similar decomposition rates across incubation environments. Mass loss of non-*Sphagnum* mosses was correlated with initial N irrespective of incubation environment.

5. Litter mass loss of cryptogam taxa could be predicted very well from infrared spectra of the initial chemical composition of the species, by application of Fourier transform infrared using an attenuated total reflectance probe. The initial macronutrient concentrations (N, phosphorus, C and cations) and initial litter pH correlated less well.
6. *Synthesis*. We showed comprehensively that decomposition rates of bryophytes are generally lower than those of lichens and vascular plants. Among bryophyte or lichen species there is also great variation in litter decomposability which depends strongly on species-specific chemistry. Our data will help predict changing land surface feedback to C cycles and climate in cold biomes by understanding long-term climate effects on litter decomposability through shifting vegetation composition.

Introduction

Non-vascular cryptogams, namely lichens and bryophytes, play important roles in ecosystems where environmental stress limits the abundance of vascular plants. At high latitudes, where vascular plant productivity is low, they constitute more than half (Matveyeva & Chernov 2000) of all existing autotrophic species and a substantial proportion of the above-ground biomass. The generally low decomposition rates of bryophytes (Heal & French 1974) also lead to great organic matter accumulation and thereby carbon (C) sequestration of a globally significant magnitude (Gorham 1991). These features are closely linked with other important ecosystem functions fulfilled by cryptogams (Cornelissen *et al.* 2007). Thick layers of live and dead bryophytes, especially peat mosses, control the hydrology of vast peatland areas (Beringer *et al.* 2001) but also preserve permafrost through their temperature-insulating capacity (Gornall *et al.* 2007). The N_2-fixing capacity of some bryophytes (Solheim *et al.* 1996) and lichens (Crittenden & Kershaw 1978) is especially important in these northern ecosystems where nitrogen (N) availability is low. The turnover rates of new N entered into ecosystems via this pathway will depend partly on cryptogam protective secondary chemistry, which may slow down the cryptogams' own decomposition rates. Such chemistry may also inhibit decomposition of other species or influence decomposition indirectly by controlling plant communities, for instance lichen compounds inhibiting moss germination or vascular plant regeneration (Lawrey 1986).

Climate warming is anticipitated to increase soil nutrient mineralization (Lükewille & Wright 1997; Rustad *et al.* 2001), thus providing nutrients in highly nutrient-limited environments such as subarctic ecosystems. As a combined effect of both increased temperature and increased mineralization, bigger and faster-growing vascular plant species might outcompete lichens and bryophytes (Cornelissen *et al.* 2001; Walker *et al.*

2006). Climate warming may also promote *Sphagnum* growth, which will impact on plant community composition (Lang *et al.* 2009). These changes in turn might lead to production of plant litter of different quality and, consequently, different decomposition and mineralisation rates (Hobbie 1996; Quested *et al.* 2003).

Given the paramount importance of bryophytes and lichens in general for the above ecosystems' functions, and the central role their litter dynamics play in these systems, there is a striking lack of information about (i) overall litter decomposability of main cryptogam taxa compared to vascular plants; and (ii) the magnitude and potential importance of interspecific variation in litter decomposability within main cryptogam taxa. This contrasts strongly with our knowledge of vascular plants, where interspecific variation in traits has long been shown to be a major driver of decomposition rates both between and within higher taxa or functional types (Quested *et al.* 2003; Cornelissen *et al.* 2004). And yet, even relatively modest differences in cryptogam decomposability among species or species groups, as related to the species' secondary chemistry, N_2-fixing capacity and structure, may have great implications for regional-scale C sequestration at high latitudes. While poor litter quality has been reported repeatedly for *Sphagnum* (Hobbie 1996; Scheffer *et al.* 2001), there is important interspecific variation in litter decomposability between different *Sphagnum* species (Clymo 1965; Rochefort *et al.* 1990; Johnson & Damman 1991) and likely between different bryophyte species in general (Hobbie 1996; Hobbie & Gough 2004). The distinction between non-*Sphagnum* mosses and liverworts may also be relevant, considering the extensive secondary chemistry of liverworts (Asakawa 2004) which might influence decomposition (Asakawa 1994). However, no comparative studies on a wide range of different bryophyte species are available. Similarly, little is known about interspecific variation in lichen decomposability (Wetmore 1982; Esseen & Renhorn 1998; Coxson & Curteanu 2002). Faster decomposition rates were suggested for N_2-fixing lichens due to their high N content as compared to non-N_2-fixing lichens without additional N input (Crittenden & Kershaw 1978). However, high N concentrations might also reflect high concentrations of defence compounds (Lawrey 1983) inhibiting decomposition. No study comparing these two groups has so far been conducted.

For vascular plants there has been much discussion about interaction effects of litter quality of different species and litter environment (climate, local soil environment) on decomposition rates, which can be important (Vivanco & Austin 2008) or relatively unimportant (Cornelissen *et al.* 1999) depending on the scope and scale of study. Indirect evidence for interaction effects is given in a study by Sjögersten *et al.* (2003) where soil

organic matter, namely polysaccharide-derived O-alkyls and aromaticity, depended on both vegetation type and study region as well as on their interactions. Although existing studies suggest that habitat influences cryptogam decomposition (e.g. Coxson & Curteanu 2002), habitat–species interactions on cryptogam decomposition have been investigated in a few studies only (Belyea 1996; Turetsky *et al.* 2008). There are only few or no robust data to separate (biotic or abiotic) environmental from species-dependent litter quality effects on bryophyte and lichen decomposition rates, respectively, in the literature so far.

In order to underpin and predict broad-scale patterns in decomposability among different bryophytes, lichens and vascular plants, we also have to study the chemical traits that determine litter quality. For vascular plants, simultaneous multi-species screenings for litter decomposability in common garden experiments, particularly litter bed studies *sensu* Cornelissen (1996), have revealed consistent variation in leaf litter decomposability as predicted from functional leaf (or leaf litter) traits (Cornwell *et al.* 2008). In particular, traits related to structural protection (lignin, cellulose and toughness), chemical defence (e.g. polyphenols, tannins), nutrition (N or phosphorus (P)) or pH have been associated with variation in litter decomposability (Palm & Rowland 1997; Cornelissen *et al.* 2006). In contrast to the large body of literature on this topic for vascular plants, it is not known which traits are the better predictors of lichen decomposition rates. The few studies available for bryophytes revealed N and the ratio of metabolic versus structural carbohydrates as positive mass loss predictors for *Hylocomium splendens* (Nakatsubo *et al.* 1997) and *Sphagnum* (Turetsky *et al.* 2008), respectively. Understanding and predicting litter decomposability of wide-ranging cryptogam and vascular species will help to predict C dynamics, ecosystem hydrology and feedback to climate in biomes where environmental change will induce both relative shifts from bryophytes or lichens to vascular plants or *vice versa*, or within cryptogam communities themselves.

Here we present the first-ever multi-species screening of litter decomposability of a wide range of 27 bryophyte and 17 lichen species in a 2-year decomposition experiment in contrasting outdoor litter beds in North Sweden. For comparison we included five vascular plant species known to broadly represent the range of vascular plant litter decomposability (Quested *et al.* 2003). We specifically tested the following hypotheses: (i) Bryophyte and lichen litters are generally less decomposable than vascular plant litter while there is significant and substantial interspecific variation in litter decomposability among bryophyte as well as among lichen species; (ii) The pattern of mass loss across incubation environments is consistent among cryptogam species; (iii) The variation in

litter mass loss between and within main cryptogam taxa can be predicted from the chemistry of the species.

Materials and Methods

LITTER SAMPLING

Bryophytes and lichens were sampled in the summer of 2004 mainly around Abisko, Sweden (68º21'N, 18º49'E) while few were collected on Andøya, Norway (69º07'N, 15º52'E) and in Kilpisjärvi, Finland (69°03'N, 20°50'E). The lichen *Cladonia stellaris* was sampled in the Altai Republic, South Siberia (51º04'N, 85º45'E) in 1999. All samples were air-dried and stored in paper bags until further preparation.

We focussed on abundant species which together were representative of the European subarctic region (Appendix S1). Species nomenclature follows Hill *et al.* (2006) for all mosses except *Sphagnum*; Daniels & Eddy (1985) for *Sphagnum* species; Damsholt (2002) for liverworts; Santesson *et al.* (2004) for lichens; and Mossberg & Stenberg (2003) for vascular plants.

Vascular plant litter was included as a reference to previously conducted decomposition experiments. We included five subarctic species (two woody deciduous, one woody evergreen, two herbaceous species), which together broadly represent the range of vascular plant decomposabilities in a broad screening study (Quested *et al.* 2003; Cornelissen *et al.* 2004). This litter was sampled in the Abisko area in September 2004. One of the woody deciduous species, *Betula pubescens* ssp. *czerepanovii*, suffered from a severe attack by the autumn moth *Epirrita autumnata*. We therefore tried to avoid damaged leaves, since the plants might have developed secondary protective defence compounds.

PREPARATION OF THE LITTER EXPERIMENT

Three litter beds, poor and rich birch forest and a *Sphagnum* mire litter bed, were used for standardized litter incubations (Cornelissen 1996) in the experimental garden of the Abisko Scientific Station (annual mean: -0.9 °C, 301.2 mm, long-term average 1961 - 1990) in subarctic Sweden. Artificial litter bed environments compare to the natural environment as follows. Mass loss in natural birch forest (litter bags placed on top) versus litter bed (placed within litter bed) was ~ 45–50% (Sjögersten & Wookey 2004) versus 60% (own data) for *Betula pubescens* ssp. c*zerepanovii* and ~ 20 versus 34% for *B. nana* (H.M. Quested & J.H.C. Cornelissen, unpublished data). The latter study also showed that litter bags of *Empetrum nigrum* ssp. *hermaphroditum* and *Epilobium angustifolium*,

placed on top, lost 20 - 30% less mass compared to bags placed within the litter bed while the interspecific ranking stayed the same. This indicates that for vascular plants the position of the litter bags, likely due to differences in soil moisture, importantly influenced mass loss while differences between natural versus artificial environment might be less pronounced. Although incubated in different environments, studies in the local Stordalen peatland, with litter bags positioned just below the green moss layer, show one-year mass loss of 7.3, 5.7 and 0% for *Sphagnum riparium*, *S. balticum* and *S. fuscum*, respectively (Sonesson 1972), comparable to 8.9, 7.1 and 0.4% in the poor birch forest litter bed in our study. For cryptogams, decomposition rates should be broadly representative of the natural environment, since they are in the same climate and in their natural position below the living bryophyte carpet.

Nutrient-poor and rich birch forest litter beds were established in October 2004 on sand–gravel beds to allow the litter to settle down over winter. The main nutrient-poor birch forest litter bed, for comparing decomposabilities of the complete species set simultaneously and for doing the methodological checks (see below), contained a matrix of nutrient-poor litter from the locally predominant heath birch forest, mainly consisting of birch leaves (*Betula pubescens ssp. czerepanovii*) and some *Vaccinium vitis-idaea* and *V. myrtillus* leaves. This nutrient-poor litter bed contained 10 compartments of c. 0.65 m^2 each to enable a factorial setup of the experiment, with two harvests with each five replicates (see below for the bryophyte cover on top of the litter bags). The nutrient-rich birch forest litter bed contained birch leaves collected from local meadow birch forest and a large proportion of forbs (e.g. *Trollius europaeus*, *Geum rivale*, *Filipendula ulmaria*). For both litter bed types, we removed all living plant parts as well as dead roots, branches and stones and mixed the leaves thoroughly to ensure a homogeneous incubation environment. The third litter bed consisted of transplanted *Sphagnum balticum* mire cores in drainless plastic trays of 30 x 40 cm and 15 cm height, which had been installed in 2000 and maintained since (Dorrepaal *et al.* 2005). The trays received distilled water during dry periods. Large openings at two sides of the trays ensured the same water table for all trays.

In early May 2005, litter bags of all 27 bryophytes, 17 lichens and five vascular plants, and the litter bags used for methodological tests, were put out in the nutrient-poor birch forest litter bed (957 litter bags, n = 1-5) whereas in the nutrient-rich birch forest and *Sphagnum* mire litter bed, only the subset of each four bryophytes and lichens was used (40 litter bags per litter bed, n = 5). The subset species occurred naturally at least in one of the chosen litter bed environments and were abundant in the area. In the birch forest litter

beds, the litter bags were laid down flat, just without overlap, onto the leaf litter, avoiding the compartment borders (edge effects). The litter bags were re-moistened with distilled water to ensure optimal litter moisture for soil invertebrate action and decomposition. We assumed that in nature cryptogam decomposition mainly takes place under the living cryptogam cover where older bryophyte and lichen segments senesce while still attached to the upper live parts, and where cryptogams are often out-shaded by other cryptogams or vascular plants. Both litter beds were therefore covered with a layer of green bryophytes, which was carefully pressed onto the litter bags to ensure good contact. These bryophytes were taken from the nutrient-poor and rich birch forest in large carpets to facilitate further growth of the moss layer. In the case of nutrient-poor litter we applied a c. 6-cm thick cover of *Hylocomium splendens* with intermingled *Pleurozium schreberi* and for the nutrient-rich litter bed a 2-3 cm thick cover of mainly *Brachythecium salebrosum* with some *B. starkei* and *Rhodobryum roseum*. A large-mesh chicken wire cover protected the litter beds from rodent damage. During extreme sunshine (3 days in July 2005) the beds were shaded with netting on a frame. In contrast to the leaf litter beds, the litter bags in the *Sphagnum* mires were inserted vertically into the peat down to a depth of c. 10 cm (lower edge).

PREPARATION OF THE LITTER

After careful rewetting with distilled water, without producing excess water to avoid leaching, the cryptogam samples were thoroughly cleaned from dirt and non-target cryptogam species using tweezers. In contrast to vascular plants, it is often difficult to determine whether parts of cryptogams are dead (litter) or alive. We checked for (lack of) activity of enzymes in the respiration process by incubating cryptogam material in a 1% solution of 2,3,5-triphenyltetrazolium chloride (ISTA 2009), but the subsequent colour changes in living parts were in most species weak (lichens) or inhibited by chlorophyll (bryophytes). Therefore, true litter was identified species by species. Bryophytes were visually divided into the living green parts and the recently senesced parts and older, already visibly decomposed parts were discarded. For each species we defined specific vertical lengths as live material and recently died material (litter), respectively. Stems of bryophytes may still be alive and not die quickly once buried (Faubert & Rochefort 2002), while outer branches are already starting to decompose (e.g. *Hylocomium splendens*). Therefore, as the main reference litter for bryophytes, litter was frozen for 20 s in liquid N_2 (-196 ºC) to kill any still-living tissues (or 30 s for the rather robust moss *Polytrichum commune*). Before freezing, the material was air-dried to avoid more damage than necessary to kill the tissue. For comparison, we also included a treatment with live material of all species, frozen in liquid N_2.

For lichens it is often difficult to find sufficient true litter. Therefore senescence was accelerated in the lab. Lichens are known to die under snow when hydrated and no light is available or when temperatures are warm during winter since their thalli respire at T =0 ºC but photosynthesis is negligible (Benedict 1990). Thus, we incubated at least partially living lichens at 100% moisture content and 20 ºC in total darkness in an incubation chamber for 63 days from 14 February 2005. Lichens were frequently checked for mould to avoid unforeseen side effects. Most incubated lichens changed visibly, partly in colour and partly in their structure which was seemingly softer. The tetrazolium-test (see above) showed that the fungal part of the lichens was still active and lichen death was only complete in some parts while others were not affected at all. Therefore, after the senescence period, the incubated material was frozen in liquid N_2 (see above) for one minute. Since hydrated antarctic lichens can survive 12h freezing in liquid N_2 (Kappen *et al.* 1996), we cannot guarantee complete tissue death in all species. Still, the incubated-frozen material was used as the main treatment for the litter bed experiment. Since the incubations may have produced artefacts, we also used live and subsequently frozen material as an additional treatment.

For vascular plant litter, easily detachable senesced leaves were hand-picked from living plants in autumn 2005, without any further treatment.

For each species, five replicates (in some species down to two, only one in *Barbilophozia atlantica*) which, depending on the species, weighed between 100 and 200 mg, (down to 50 mg, especially in some liverworts), were pre-weighed and sealed into litter bags. The litter bags, with sizes adjusted to match sample volume and ranging from 9 to 34 cm^2, consisted of polyester with a mesh size of 200 µm. To calculate true dry weight via moisture content, subsamples from each litter sample were weighed, oven-dried at 70 ºC for three days and re-weighed.

HARVEST

Defined bryophyte litter and incubated lichens were harvested after one (May 2006) and two years (May 2007), live material only after the second year. Litter bags were cleaned from soil animals, dirt particles and non-target plant parts (mainly *Equisetum arvense* or roots grown into the bags).

METHODOLOGICAL TESTS

To check for possible methodological artefacts, we complemented the above standard treatments for bryophytes and lichens, respectively, with additional tests using standard

litter (unless otherwise mentioned) of a subset of eight cryptogam species (four bryophytes and lichens each). The species selected to conduct the following tests were abundant in the area and easily collectible: (i) non-freezing, to test whether freezing affected decomposition of the standard litter material (tested on bryophyte litter, incubated lichens and live cryptogam material); (ii) mesh size of 0.9 mm, to test for the effects of excluding some bigger meso-detritivores with 200 µm (Swift *et al.* 1979); (iii) true lichen litter, collected based on its structure and colour suggesting complete senescence, without freezing treatment; (iv) older bryophyte litter (collected from below the upper fresh litter segment), partly decomposed and frozen, to test the influence of young versus older bryophyte litter on decomposition rate; (v) small litter fragments to test for any effects of greater surface area to volume ratio; (vi) low initial litter weight, to test for any effects when using 50 mg versus 100-200 mg samples of the same species.

INITIAL LITTER CHEMISTRY

The undecomposed samples used to determine initial moisture were ground using a ball mill (Mixer Mill MM 200, Retsch, Haan, Germany) before chemical analysis. After digestion of c. 50 mg in 1 mL of a 1:4 mixture of 37% (v/v) HCl and 65% (v/v) HNO_3 in teflon bombs for 4 hours at 140 ºC, 4 mL distilled water were added. P was measured colorimetrically (Shimadzu, UV-1601PC, Shimadzu Corp., Kyoto, Japan) with the molybdenum blue method (Murphy & Riley 1962), and calcium (Ca) and magnesium (Mg) were measured with atomic absorption spectroscopy under addition of 1% $LaNO_3$, and sodium (Na) and potassium (K) with atomic emission spectroscopy (both: 1100B Spectrometer, PerkinElmer Inc., Waltham, Massachusetts, USA). C and N concentrations were determined by dry combustion with a Carlo Erba NA1500 (Rodana, Italy) elemental analyser. Since the samples were cleaned meticulously, LOI (loss on ignition, at 550 ºC for 4 hours) needed to be determined only for *Racomitrium fasciculare* and the lichen *Solorina crocea*, both of which had been collected from environments where contamination by minerals was likely and which showed particularly low C/N values. Tissue pH measurement (WTW Inolab Level 2 pH meter, WTW Sentix Mic electrode, WTW Weilheim, Germany) followed Cornelissen *et al.* (2006). Molecular structure of primary and secondary compounds of the ground samples and reference spectra (see below) was analysed spectroscopically by applying Fourier transform infrared using an attenuated total reflectance probe (Nexus^{TM} 670, ATR cell DuraScope, Thermo Nicolet, Madison, Wisconsin, USA) with a resolution of 4 cm^{-1} and 32 scans. Organic compounds were identified based on Socrates (2001) aided by reference spectra, which included components that are presumably important in decomposition or are typically found in some taxa. Measurements included α-D-glucose monohydrate, D-fructose, mannitol,

starch (potato-derived), L-cysteine, glycine, L-glutamic acid, chitin (crab-derived), cellulose, lignin and usnic acid. We used vascular plant-derived lignin and crab-derived chitin as an approximation of lignin-like components and chitin found in bryophytes and lichens, respectively. As peaks of the majority of plant compounds are overlapping, the resulting mass loss predictors can merely be indicative and need to be verified in further analysis.

DATA ANALYSIS

Some litter bags of *Sphagnum fuscum* showed a slight gain in mass, mainly after two years of incubation, possibly due to accumulation of colloidal matter or absorption of solid organic matter (cf. Johnson & Damman 1991; Dorrepaal *et al.* 2005). Negative mass loss values of *Sphagnum* were set to zero before analysis. Data were checked for normality and mass loss percentages, unless otherwise stated, arcsine($\sqrt{(x/100)}$)-transformed. Since ANOVA was robust to heterogeneity of variance as long as sample size is nearly equal, we proceeded with analysis (spss 14.0 for Windows; SPSS Inc., Chicago, IL, USA) even when homoscedasticity assumptions were not fully met (Zar 1999).

Methodological checks on any effects of freezing, small fragments, low weight, older bryophyte litter or true lichen litter, mesh size and live material on mass loss were done by Independent T-Tests (n = 2 - 5), with 'standard litter' (see above) as the control treatment. Subsequently, data were Bonferroni-corrected across all cryptogams and per main cryptogam group (four bryophytes and lichens each). Effect size L was calculated as $L = \ln(X_t/X_c)$ with X being the mean value of mass loss of treatment (t) and control groups (c). The confidence interval of L was calculated as $\lambda = L \pm C_{\alpha/2}\sigma(L)$ with $\sigma^2(L) = (SD_t)^2/n_tX_t^2 + (SD_c)^2/n_cX_c^2$. $C_{\alpha/2}$ is the two-tailed critical value of the standard normal distribution and n is the number of samples used. L was considered to be significant if its size was larger than the confidence limit (Gurevitch & Hedges 1999; Gurevitch *et al.* 2001).

The effect of time and main taxon (main taxa: bryophytes, lichens, vascular plants) on mass loss was tested in a repeated-measurement ANOVA (data ranked across both harvests, n = 5 - 26). Mass losses of main taxa (n = 5 - 26), cryptogam groups (within bryophytes: *Sphagnum*, non-*Sphagnum* moss, liverwort, within lichens: N_2-fixing lichen, non-N_2-fixing lichen; n = 4 - 16) and *Cladonia* versus non-*Cladonia* species (including or excluding N_2-fixing lichens; n = 6 - 11) were subsequently compared in separate one-way ANOVAs and Tukey tests for each harvest (data ranked, n = 4 - 16). Likewise, untransformed N [%] was compared between N_2-fixing lichens and non-N_2-fixing lichens.

Since Levene proved to be significant for N and the larger variation was found in the group with smaller replication (N_2-fixing lichens), we equalized sample size randomly (n = 5). The exponential mass loss constant k (Olson 1963) was calculated per block of the litter experiment.

Effect of time and species on mass loss were analysed in a repeated-measurement ANOVA (n = 5). Since Levene proved to be significant and sample size was unequal, species with replication below five were excluded. Values for litter bags damaged during harvesting (five species, one litter bag per species) were replaced by averaging the remaining samples.

The effect of group (or species) and litter bed type and their interactions on mass loss was tested in several two-way ANOVAs. Species were first tested across all cryptogams and subsequently within the groups of lichens and mosses followed by a Tukey test (n = 5). Untransformed N [%] of non-N_2-fixing versus N_2-fixing lichens were compared in a one-way ANOVA (n = 2).

Infrared spectra were used to calculate extinction $E = \ln(I_0/I)$, followed by ground correction to correct for multiple scattering of light inside the probe. Ground correction was based on the subtraction of the trajectory described by a disk rolling over the surface of the extinction spectrum (T. Klahn, unpublished method). Principal component analysis (PCA) was applied to show the scattering of cryptogam groups and vascular plants depending on their infrared spectra using The Unscrambler v9.8 (CAMO Software AS, Oslo, Norway). We used partial least squares regression (PLSR) to analyse the relationship between mass loss (ln-transformed; *Sphagnum* arcsine-square-root-transformed) versus macronutrients and pH, and mass loss (ln-transformed; *Sphagnum* and vascular plants arcsine-square-root-transformed) versus infrared spectra. pH and macronutrients were ln-transformed and subsequently 0-1-range-normalized (Min = 0; Max = 1) within each main taxon or cryptogam group before analysis. Only significant variables determined with Jack-knifing (full cross validation) were included in the final regression. Since no valid regression was found for liverworts (Table 4) and a PCA of infrared spectra revealed clustering of liverworts of the Scapaniaceae family, we analysed the liverwort group at family, order and (sub)class level following the classification of Goffinet & Shaw (2009).

Results

METHODOLOGICAL TESTS

One out of four lichen species showed significant differences in mass loss between low initial weight or true litter versus the 'standard' decomposition material (see Appendix S1). The Bonferroni-correction resulted in non-significance for the test of low weight for all cryptogams and at lichen group level, whereas true lichen litter remained significantly different from the standard at both levels of grouping. Testing older bryophyte litter versus standard litter revealed no significant effect. Freezing live material affected only one bryophyte species out of eight cryptogams. After Bonferroni-correction, this result remained significant when regarding the moss group alone, whereas it was non-significant across all cryptogams. Freezing of litter material, fragmentation and mesh size did not affect mass loss significantly compared to the litter standard. Methodological tests, which were significant in the Independent T-Test, also showed significant effect sizes while effect size indicated significance for one additional species when testing older bryophyte litter. Comparing the mass loss of live versus litter material gave significant differences for 2 lichens out of 17, and 7 bryophytes out of 26, while effect size indicated a significant effect for four lichens and nine bryophytes. Differences between live versus litter material were still significant for one lichen and one liverwort after Bonferroni-correction across the whole group of cryptogams or within the groups of lichens and bryophytes separately. The emerging overall pattern is for cryptogam mass loss to be rather robust to the methodological differences. However, when comparing live versus litter material, some species (especially liverworts) seem to be more susceptible than others, and choice of litter material should be carefully considered.

DECOMPOSABILITY AMONG AND WITHIN MAIN CRYPTOGAM TAXA

Time ($F_1 = 104.6$, $P < 0.001$) and main taxa (i.e. bryophytes, lichens, vascular plants; $F_2 = 38.6$, $P < 0.001$), both influenced mass loss rates significantly whereas the interaction of these two factors showed no effect ($F_2 = 0.9$, $P = 0.42$). Both 1-year and 2-year mass loss were similar between lichens and vascular plants whereas bryophytes showed significantly lower values, as indicated also by the mean k values (Fig. 1).

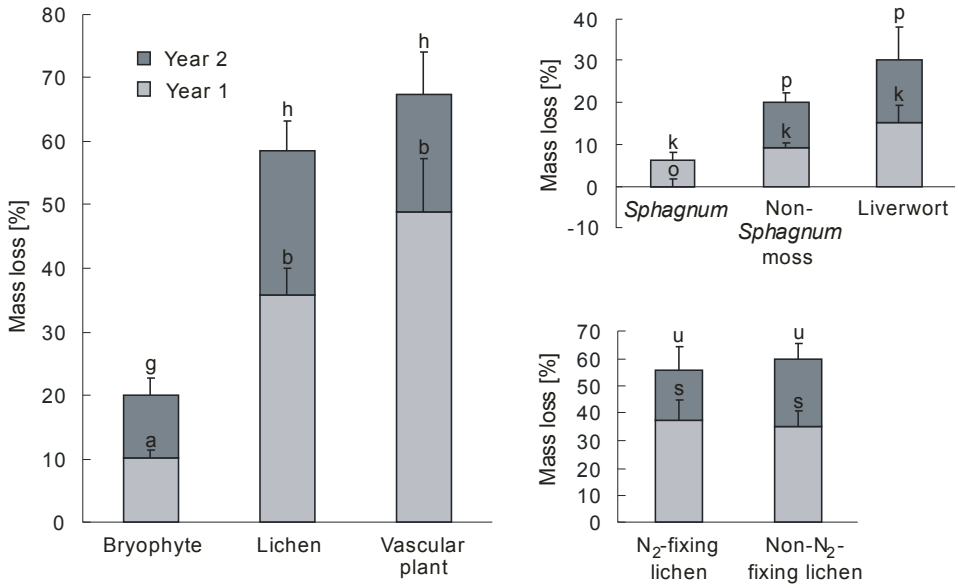

Fig. 1. Comparison of mass loss (+ SE) among the main taxa lichens, bryophytes and vascular plants, and the cryptogam groups *Sphagnum*, non-*Sphagnum* moss, liverwort and N_2-fixing lichen, non-N_2-fixing lichen, after one and two years of decomposition (separate one-way ANOVAs for each harvest, data ranked, n = 5 - 26). Different letters indicate significance at P = 0.05 (Tukey). Note the negative contribution of *Sphagnum* after two years caused by mass gain of some *Sphagnum* species. Decay rate k ± SE [yr^{-1}]: $k_{Bryophyte}$ = 0.11 ± 0.01, k_{Lichen} = 0.44 ± 0.01, $k_{Vascular\ plant}$ = 0.56 ± 0.03, $k_{Non\text{-}Sphagnum\ moss}$ = 0.11 ± 0.01, $k_{Liverwort}$ = 0.19 ± 0.01, $k_{Sphagnum}$ = 0.03 ± 0.01, $k_{N2\text{-}fixing\ lichen}$ = 0.41 ± 0.02, $k_{non\text{-}N2\text{-}fixing\ lichen}$ = 0.45 ± 0.02.

Within the bryophytes, *Sphagnum*, non-*Sphagnum* mosses and liverworts showed no significant differences in 1-year mass loss (F_2 = 2.50, P = 0.10) whereas 2-year mass loss revealed a significantly lower mass loss of *Sphagnum* (negative contribution$_{year2}$ caused by mass gain of some *Sphagnum* species overruling the minute losses of others), compared to either non-*Sphagnum* mosses or liverworts (F_2 = 6.30; P = 0.007). Within the lichens, 1-year (F_1 = 0.27, P = 0.61) and 2-year mass losses (F_1 = 0.04, P = 0.84) of N_2-fixing lichens were not significantly different from non-N_2-fixing lichens despite significant differences in initial N (F_1 = 17.8, P = 0.003). Mean 2-year mass loss, macronutrients and pH are shown in Table 1.

Table 1. Mean (SE) mass loss [%], macronutrients [%] and pH for main taxa and cryptogam groups

Main taxa	Lichen		
Group	All	N_2-fixing lichen	Non-N_2-fixing lichen
Mass loss	57.05 (4.44)	55.90 (8.62)	57.47 (5.37)
pH	5.04 (0.09)	5.44 (0.23)	4.90 (0.06)
Na	0.05 (0.01)	0.03 (0.01)	0.05 (0.02)
K	0.26 (0.07)	0.60 (0.21)	0.14 (0.02)
Ca	0.15 (0.06)	0.27 (0.19)	0.11 (0.04)
Mg	0.07 (0.01)	0.11 (0.02)	0.05 (0.01)
N	0.95 (0.20)	2.19 (0.37)	0.51 (0.06)
C	44.90 (0.30)	46.35 (0.42)	44.38 (0.27)
P	0.10 (0.02)	0.17 (0.08)	0.07 (0.01)
C/N	81.99 (11.03)	24.59 (5.15)	102.49 (10.14)
N/P	15.26 (4.62)	31.62 (16.19)	9.42 (1.18)
C/P	937.02 (175.16)	883.84 (488.89)	956.02 (176.86)

Table 1. continued

Main taxa	Bryophyte				Vascular plant
Group	All	*Sphagnum*	Non-*Sphagnum* moss	Liverwort	All
Mass loss	20.07 (2.51)	5.80 (2.09)	20.07 (2.12)	28.21 (6.91)	67.31 (6.68)
pH	5.34 (0.07)	5.27 (0.19)	5.36 (0.10)	5.30 (0.13)	4.72 (0.31)
Na	0.06 (0.01)	0.03 (0.00)	0.05 (0.02)	0.09 (0.03)	0.02 (0.01)
K	0.20 (0.03)	0.26 (0.04)	0.20 (0.04)	0.18 (0.04)	0.32 (0.10)
Ca	0.52 (0.09)	0.42 (0.08)	0.52 (0.15)	0.55 (0.11)	1.23 (0.55)
Mg	0.15 (0.05)	0.21 (0.03)	0.12 (0.05)	0.19 (0.04)	0.39 (0.10)
N	0.71 (0.04)	0.75 (0.03)	0.66 (0.05)	0.78 (0.11)	0.64 (0.12)
C	45.35 (0.38)	45.49 (0.38)	46.08 (0.40)	43.61 (0.90)	48.46 (2.14)
P	0.05 (0.00)	0.03 (0.01)	0.05 (0.01)	0.04 (0.01)	0.10 (0.05)
C/N	70.65 (4.88)	60.63 (2.10)	76.28 (6.74)	63.50 (10.32)	92.34 (24.24)
N/P	21.71 (3.36)	36.49 (12.22)	15.28 (2.13)	27.95 (8.81)	12.88 (4.47)
C/P	1491.90 (261.98)	2247.10 (771.83)	1303.89 (365.60)	1490.10 (381.26)	1546.89 (942.28)

The differences among species were highly significant within each of the main taxa bryophytes, lichens and vascular plants as well as for the groups *Sphagnum*, non-*Sphagnum* moss, liverwort, N_2-fixing and non-N_2-fixing lichen, with significant time x species interactions for bryophytes, N_2-fixing lichens and liverworts. As an exception, time itself was not a significant determinant of *Sphagnum* mass loss (Table 2).

Table 2. Effect of time and species on mass loss within main taxa and cryptogam groups (repeated-measurement ANOVA, data arscine-square-root-transformed, $n = 5$)

Main Taxa	Group	Source	Df	*F*	*P*
Bryophyte	All	Time	1	177.3	<0.001
		Species	20	31.6	<0.001
		Time x species	20	4.8	<0.001
	Sphagnum	Time	1	0.9	0.36
		Species	3	59.2	<0.001
		Time x species	3	2.0	0.16
	Non-*Sphagnum* moss	Time	1	165.2	<0.001
		Species	14	16.0	<0.001
		Time x species	14	1.6	0.10
	Liverwort	Time	1	103.7	<0.001
		Species	5	51.2	<0.001
		Time x species	5	5.4	0.005
Lichen	All	Time	1	379.8	<0.001
		Species	16	56.7	<0.001
		Time x species	16	1.6	0.11
	N_2-fixing lichen	Time	1	175.9	<0.001
		Species	4	63.4	<0.001
		Time x species	4	3.3	0.032
	Non-N_2-fixing lichen	Time	1	254.5	<0.001
		Species	11	59.0	<0.001
		Time x species	11	0.9	0.56
Vascular plant	All	Time	1	62.1	<0.001
		Species	4	40.1	<0.001
		Time x species	4	2.2	0.11

Within the bryophytes, *Sphagnum* species showed the lowest decomposition rates, with no species exceeding 10% (Fig. 2). Non-*Sphagnum* mosses ranged from 0.2 to 36%, which was lower than mass losses for most of the lichens and lower than for any of the vascular

plants. Liverworts showed a wide range in decomposition rates from 9 to 60%, the high value for *Lophozia lycopodioides* being comparable to mass loss of vascular plants. Low lichen decomposition rates of 20 to 40% were mainly found in the Cladoniaceae, even though up to 50% mass loss was measured in this family. Mass loss of *Cladonia* species was significantly lower compared to non-*Cladonia* species, both when excluding (F_1 = 22.53; P = 0.001) or including N_2-fixing lichens (F_1 = 8.23; P = 0.012). With about 90% mass loss, *Alectoria ochroleuca* even exceeded the mass loss of highly decomposable vascular plants such as the forb *Cornus suecica*. N_2-fixing and non-N_2-fixing lichens both showed a similar range in decomposition, the highest values reached by the latter group.

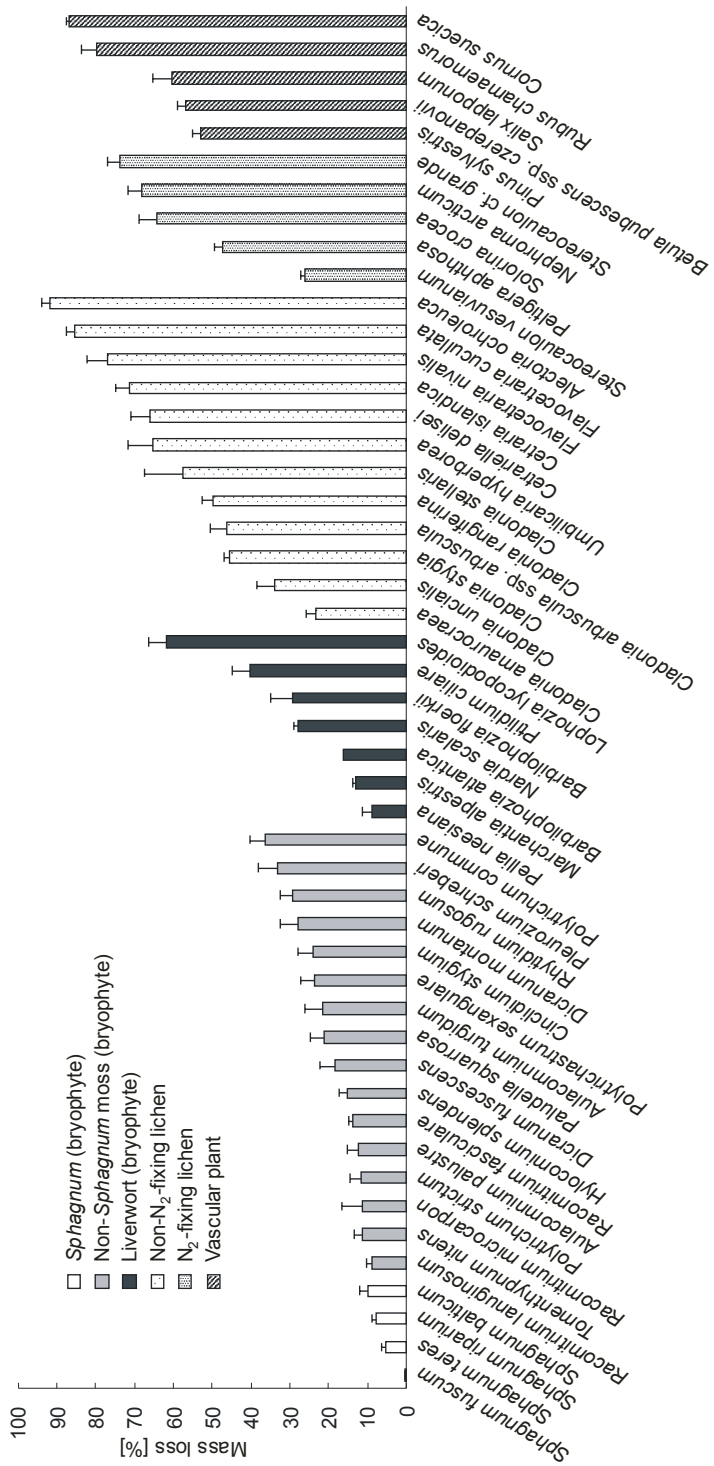

Fig. 2. Two-year mass loss (+ SE) of bryophytes (*Sphagnum*, non-*Sphagnum* moss, liverwort), lichens (non-N_2-fixing lichen, N_2-fixing lichen) and vascular plants in the nutrient-poor birch forest litter bed (n = 1 - 5).

THE INFLUENCE OF LITTER BED TYPE ON DECOMPOSITION

At main taxon level, litter bed type showed a trend ($F_2 = 3.06$, $P = 0.051$) of influencing mass loss, whereas main taxa ($F_1 = 73.93$, $P < 0.001$) and their interaction ($F_2 = 8.69$, $P < 0.001$) were significant determinants of mass loss. At species level, species and litter bed type and their interactions significantly influenced mass loss across all cryptogams and within the non-*Sphagnum* mosses and lichens, respectively (Table 3).

Table 3. Effect of species and litter bed type on mass loss across all cryptogams and within the cryptogam groups non-*Sphagnum* mosses and lichens after two years of incubation (separate two-way ANOVAs, data arcsine-square-root transformed, $n = 5$)

	Source	Df	*F*	*P*
Across main taxa				
All Cryptogams	Species	7	128.14	<0.001
	Litter bed	2	17.15	<0.001
	Species x litter bed	14	11.40	<0.001
Within main taxa				
Non-*Sphagnum* mosses	Species	3	91.40	<0.001
	Litter bed	2	37.73	<0.001
	Species x litter bed	6	6.37	<0.001
Lichens	Species	3	70.94	<0.001
	Litter bed	2	28.93	<0.001
	Species x litter bed	6	4.16	0.002

Of the eight species chosen for this part of the study, lichen and moss species reacted differently to the varying litter bed environments (Fig. 3). The non-N_2-fixing *Cladonia* species showed the highest mass loss when decomposing in nutrient-poor birch forest litter relative to decomposition in nutrient-rich birch forest litter and *Sphagnum* mire. *Cladonia* had significantly lower N ($F_1 = 87.0$; $P = 0.011$) compared to the N_2-fixing lichens *Peltigera aphthosa* and *Nephroma arcticum* which in turn were unaffected by incubation environment showing equally high decomposition rates. Mosses, except *Racomitrium lanuginosum* with overall low decomposition rates independent of the litter bed environment, showed an increase in mass loss when decomposing in *Sphagnum* peat. The nutrient-rich litter bed negatively affected decomposition rates of *Hylocomium splendens* and *Polytrichum commune*. Within each incubation environment, linear regression revealed that moss mass loss was significantly related to cryptogam tissue N ($R^2_{\text{poor birch forest}} = 0.92$, $P = 0.039$; $R^2_{\text{rich birch forest}} = 0.92$, $P = 0.043$; $R^2_{\text{mire}} = 0.92$, $P = 0.041$).

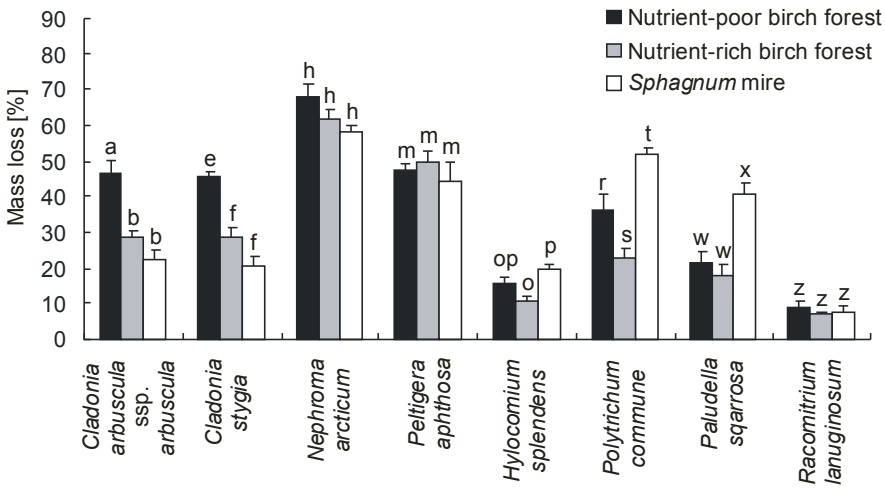

Fig. 3. Effects of nutrient-poor and nutrient-rich birch forest and *Sphagnum* mire litter bed on mass loss (+ SE) of four lichen (left side) and four non-*Sphagnum* moss species (right side) after two years of incubation (one-way ANOVA, data arcsine-square-root transformed, different letters indicate significance at $p < 0.05$ (Tukey), $n = 5$).

THE RELATION OF INITIAL LITTER CHEMISTRY AND DECOMPOSABILITY

Differentiation of cryptogams and vascular plants based on infrared spectra

PCA showed that infrared spectra, despite a certain overlap, clearly differentiated among lichens, liverworts, non-*Sphagnum* mosses and vascular plants, whereas *Sphagnum* species were located within the group of non-*Sphagnum* mosses. Non-N_2-fixing and N_2-fixing lichens were not clearly separated in the PCA (Fig. 4), but all *Cladonia* species were clustered at values below -0.04 along axis 1.

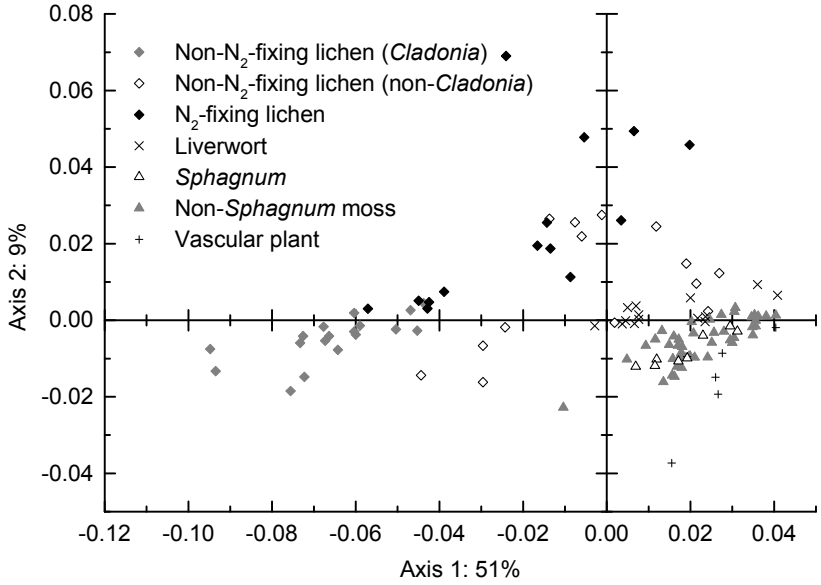

Fig. 4. Differentiation of cryptogam groups and vascular plants by infrared spectra (data untransformed, PCA, $n = 118$).

Infrared spectra in relation to mass loss

Mass loss in relation to infrared spectra showed higher $R^2_{\text{Pred.}}$ values (0.74, 0.43 and 0.70), as opposed to 0.07, 0.12 and 0.46 when using macronutrients and pH (Table 4 and 5), for lichens, bryophytes and vascular plants, respectively. The error of the model ($\text{RMSE}_{\text{Pred.}}$) increased from 0.22, 0.73 and 0.10 to 0.40, 0.90 and 0.18 for the same groups (note the deviating transformations for vascular plants). Further division into N_2-fixing lichens, non-N_2-fixing lichens, *Sphagnum* and non-*Sphagnum* mosses and liverworts enhanced the correlation for all groups except liverworts where no significant variables were found. *Sphagnum* showed a high $R^2_{\text{Pred.}}$ of 0.92 and a very small error of 0.04 (Table 4). Analysing the liverworts at increasing taxonomical levels showed a decrease of $R^2_{\text{Pred.}}$ from family (Scapaniaceae) to order (0.55 to 0.41), followed by a small increase of $\text{RMSE}_{\text{Pred.}}$ (0.42 to 0.44). At subclass and class level, $R^2_{\text{Pred.}}$ increased from 0.61 to 0.83 and $\text{RMSE}_{\text{Pred.}}$ decreased from 0.32 to 0.27. The number of principal components increased from family/order to (sub-)class (details see Appendix S2).

Table 4. Calibration and prediction of mass loss (ln-transformed; *Sphagnum* and vascular plants arscine-square-root-transformed) versus infrared spectra for main taxa and cryptogam groups (PLSR, n = 5–54). PC, principal component; RMSE, root mean square error; Cal or Pred, calibration or prediction

Main taxa	Lichen			Bryophyte				Vascular plant
Group	All	N_2-fixing lichen	Non-N_2-fixing lichen	All	*Sphagnum*	Non-*Sphagnum* moss	Liverwort	All
N	34	10	24	54	8	32	14	5
No. of PCs	4	2	3	3	4	5	-*	2
$R^2_{Cal.}$ ($R^2_{Pred.}$)	0.83 (0.74)	0.96 (0.91)	0.82 (0.75)	0.54 (0.43)	0.98 (0.92)	0.73 (0.60)	-	0.97 (0.70)
$RMSE_{Cal.}$ ($RMSE_{Pred.}$)	0.17 (0.22)	0.09 (0.15)	0.16 (0.20)	0.64 (0.73)	0.02 (0.04)	0.25 (0.31)	-	0.03 (0.10)
$Slope_{Cal.}$ ($Slope_{Pred.}$)	0.83 (0.75)	0.96 (0.97)	0.82 (0.76)	0.54 (0.47)	0.98 (0.93)	0.73 (0.68)	-	0.97 (1.16)
$Intercept_{Cal.}$ ($Intercept_{Pred.}$)	0.68 (1.02)	0.14 (0.11)	0.73 (0.97)	1.33 (1.53)	0.01 (0.02)	0.82 (0.98)	-	0.03 (-0.11)

* No significant variables

Table 5. Calibration, prediction and regression coefficients of mass loss (ln-transformed; *Sphagnum* arscine-square-root-transformed) versus macronutrients [%] and pH (PLSR, chemical variables within main taxa or cryptogam group ln-range-normalized, n = 5–54). Only significant variables are shown. PC, principal component; RMSE, root mean square error; Cal or Pred, calibration or prediction

Main taxa	Lichen		
Group	All	N_2-fixing lichen	Non-N_2-fixing lichen
N	34	10	24
No. of PCs*	1	1	1
$R^2_{Cal.}$***	0.11	0.59	0.46
($R^2_{Pred.}$)	(0.07)	(0.43)	(0.37)
$RMSE_{Cal.}$ ****	0.38	0.29	0.28
($RMSE_{Pred.}$)	(0.40)	(0.38)	(0.32)
$Slope_{Cal.}$	0.11	0.59	0.46
($Slope_{Pred.}$)	(0.06)	(0.37)	(0.39)
$Intercept_{Cal.}$	3.58	1.64	2.20
($Intercept_{Pred.}$)	(3.77)	(2.57)	(2.48)
Regression coefficients k†			
k_0	3.83	3.24	3.48
pH	0.16		0.30
N	0.20	1.06	0.30
C			
P			
K	0.20		0.33
Ca			0.29
Mg			

Table 5. continued

Main taxa	Bryophyte				Vascular plant
Group	All	*Sphagnum*	non-*Sphagnum* moss	Liverwort	All
N	54	8	32	14	5
No. of PCs*	2	2	1	-*	1
$R^2_{Cal.}$***	0.17	0.93	0.41	-	0.58
($R^2_{Pred.}$)	(0.12)	(0.87)	(0.36)		(0.46)
$RMSE_{Cal.}$ ****	0.86	0.03	0.36	-	0.13
($RMSE_{Pred.}$)	(0.90)	(0.05)	(0.39)		(0.18)
$Slope_{Cal.}$	0.17	0.93	0.41	-	0.58
($Slope_{Pred.}$)	(0.13)	(0.82)	(0.37)		(0.41)
$Intercept_{Cal.}$	2.39	0.02	1.74	-	1.75
($Intercept_{Pred.}$)	(2.50)	(0.05)	(1.86)		(2.45)
Regression coefficients k†					
k_0		0.09	2.04	-	3.95
pH				-	
N		0.06	0.42	-	
C	-0.24			-	
P	1.68		0.49	-	0.44
K		0.3	0.32	-	
Ca		-0.04		-	
Mg			0.31	-	

* No significant variables

† $Y_{(2a)} = k_0 + k_1x_1 + k_2x_2 + \ldots + k_nx_n$; x: significant chemical variables (pH to Mg)

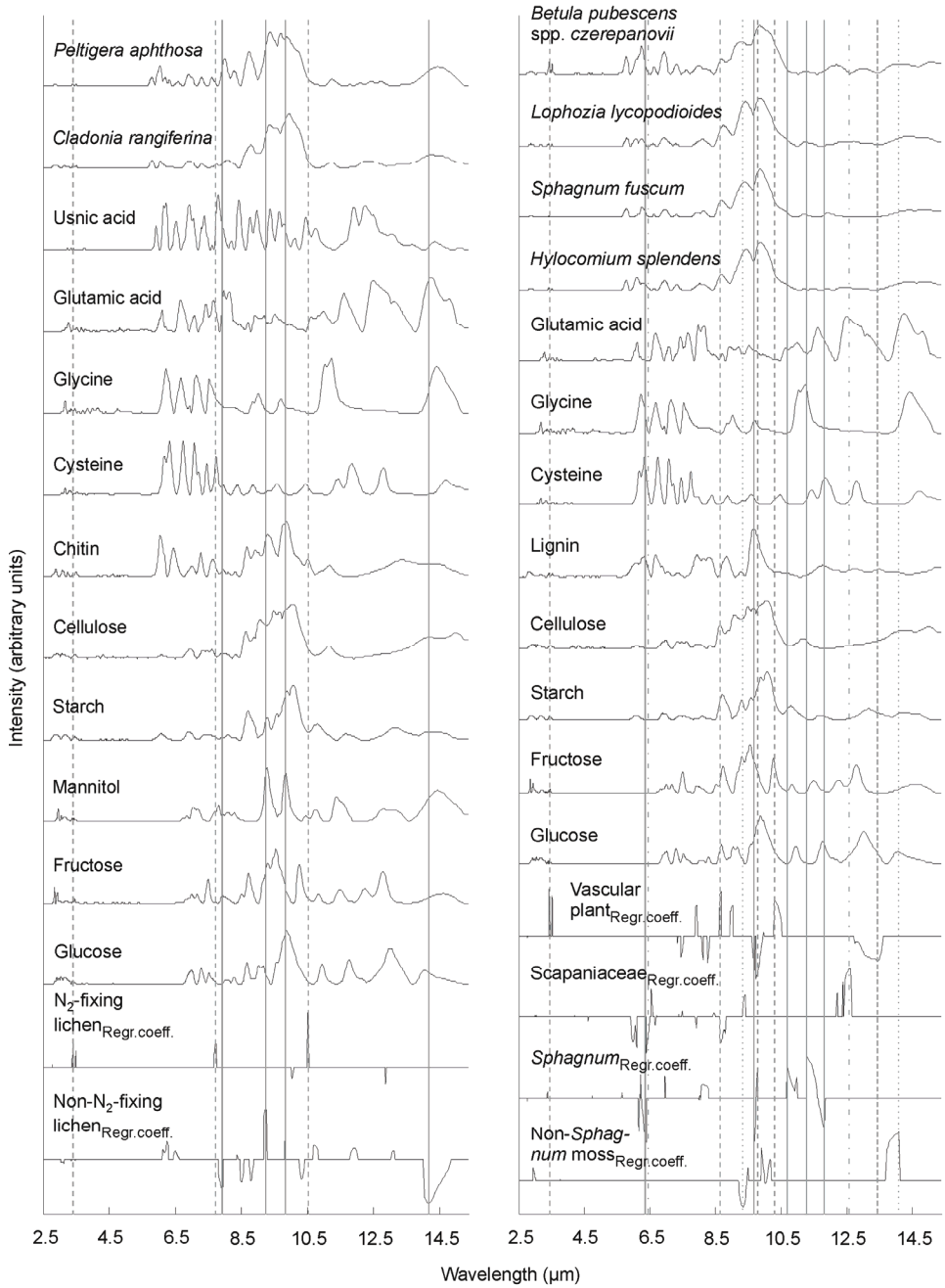

Fig. 5. Cryptogam, vascular plant and reference spectra and regression coefficients (significant coefficients only) of non-N_2-fixing lichens (—) and N_2-fixing lichens (---) (left side), and non-*Sphagnum* mosses (···), *Sphagnum* (—), Scapaniaceae (liverworts, · − ·) and vascular plants (---) (right side). Only larger regression coeffients are marked.

Infrared spectra of structural (cellulose, chitin) and metabolic (sugars, starch) carbohydrates, amino acids (proteins/peptides ~ 6.04, 10.00–10.58, 11.11–12.50, ~13.79/e.g. 7.69–7.87 µm) and aromatic compounds (~ 6.00, 7.75–11.11, 11.11–15.27 µm; e.g. usnic acid, lignin) are shown in Figure 5 (note: absorption bands of compounds are overlapping). Lipids (not shown) absorb at numerous bands (e.g. 3.51, 5.78, 9.22, 10.31, 13.99 µm). Considering solely larger regression coefficients, mass loss of N_2-fixing lichens was positively related to amino acids (proteins, peptides), lipids and structural (~ 3.5, 7.74, 10.54 µm) and metabolic carbohydrates (~ 3.5, 7.74 µm). Mass loss of non-N_2-fixing lichens related positively to structural and metabolic carbohydrates, amino acids and aromatic compounds (9.26, 9.82 µm) while strongly negatively relating to the latter two components (14.01–14.99 µm). Mass loss of non-*Sphagnum* mosses related positively to proteins (amino acids), lipids and aromatic compounds (13.68–14.20 µm) and negatively to carbohydrates (metabolic and structural), amino acids, lipids and aromatic compounds (9.19–9.45 µm). *Sphagnum* mass loss was positively related to proteins (amino acids) and metabolic and structural carbohydrates (10.65–11.63 µm) and negatively to aromatic compounds, proteins (amino acids) and metabolic and structural carbohydrates (6.39, 9.67, 11.81 µm). The liverwort family Scapaniaceae related both positively (12.41–12.71 µm) and negatively (6.40 µm) to proteins (amino acids) and aromatic compounds. Vascular plants were positively related to metabolic and structural carbohydrates, lipids and amino acids (3.43, 3.51, 8.66, 10.33 µm) and negatively to carbohydrates (structural and metabolic), amino acids (proteins) and aromatic compounds (9.77, 12.80–13.65 µm).

Macronutrients and pH in relation to mass loss

Na was not a significant predictor of mass loss and excluded in all regressions (Table 5). Overall regressions for lichens and bryophytes showed low $R^2_{Pred.}$-values. Lichens were significantly positively related to pH, N and K, and bryophytes positively to P and negatively to C. Subsequent analyses of N_2-fixing lichens, non-N_2-fixing lichens, *Sphagnum* and non-*Sphagnum* mosses and liverworts resulted in enhanced correlations, steeper slopes and smaller model errors ($RMSE_{Pred.}$; except liverworts), with *Sphagnum* showing an exceptionally high $R^2_{Pred.}$ of 0.87 and a small error ($RMSE_{Pred.}$) of 0.05. N was significantly and positively related to mass loss in N_2-fixing lichens, while for non-N_2-fixing lichens K, pH, N and Ca showed a positive relation to mass loss of about the same magnitude. *Sphagnum* mass loss related strongly positively to K, to a lesser extent to N, and negatively to Ca. Mass loss of non-*Sphagnum* mosses related positively to P and N, and, to a lesser extent, to K and Mg. For liverworts no significant variables could be determined. Even though the PCA on elemental composition did not reveal any clustering,

we followed the taxonomical classification as suggested for the wavelength data. N and Na were significant determinants of mass loss at family (regression coefficients: $k_0 = 0.35$, $k_N = 0.45$, $k_{Na} = 0{,}35$) and N at order level ($k_0 = 0.52$, $k_N = 0.42$), while at subclass level no such relationship was found. From family to order, $R^2_{Pred.}$ decreased from 0.75 to 0.47, while $RMSE_{Pred.}$ increased from 0.13 to 0.17 (details see Appendix S2).

Discussion

VARIATION IN DECOMPOSABILITY AMONG AND WITHIN MAIN CRYPTOGAM TAXA

Our study is the first to reveal consistent patterns of variation in litter decomposability of a wide range of non-vascular cryptogams when incubated in a standard environment. While there were several significant interactions between litter incubation environment or incubation period and species group identity on mass loss rates, the general pattern was that of a strong influence of cryptogam taxonomic identity on litter mass loss.

Both rapid and slow lichen mass loss, for non-*Cladonia* (Wetmore 1982) and *Cladonia* (Moore 1984), respectively, have been reported in comparison to vascular plants, emphasizing the importance of taxonomic identity. Despite expected antibacterial activity (e.g. Vartia 1973), lichen decomposition rates in our study were generally comparable to those of vascular plants. Stark & Hyvärinen (2003) suggested that the microbial community growing underneath lichens is well adapted to the lichen secondary metabolites, utilizing them as a C source, which might also explain the high turnover rates in our study. Even certain Cladoniaceae, a less degradable group compared to non-*Cladonia* lichens, reached mass losses of up to 50% after two years of incubation. Crittenden & Kershaw (1978) proposed that N_2-fixing lichens exhibit higher N contents and that decomposition rates of N_2-fixers should therefore be greater than those of non-N_2-fixing lichens. In our study, N_2-fixing and non-N_2-fixing lichens alike displayed high decomposition rates in spite of N in N_2-fixing lichens indeed being significantly higher than in non-N_2-fixing lichens. N_2-fixing lichens, as opposed to non-N_2-fixing lichens, decomposed equally well in contrasting litter beds, suggesting that at higher N concentrations the microbial community is not limited by substrate N leading to fast decomposition decoupled from substrate N (Coulson & Butterfield 1978).

Bryophytes, comprising *Sphagnum*, non-*Sphagnum* mosses and liverworts, showed consistently low decomposability compared to vascular plants. This has been shown earlier for *Sphagnum* and single bryophyte species (Hobbie 1996; Aerts *et al.* 1999; Liu *et al.* 2000), but ours is the first explicit and comprehensive test of the general low

degradability of bryophyte litter. Within the Polytrichaceae, mass loss ranged from 10 to 35%, emphasizing that even closely related species can diverge strongly in decomposability. The overall lower decomposition rates found for *Sphagnum* have been attributed to structural, lignin-like and soluble phenolic compounds (Verhoeven & Liefveld 1997), both of which are also found in non-*Sphagnum* mosses (Erickson & Miksche 1974; Zinsmeister & Mues 1990; Ligrone *et al.* 2008), and decomposition-inhibiting bacteria associated with *Sphagnum* (Opelt *et al.* 2007). While most liverworts decomposed slowly too, as related presumably to high contents of secondary metabolites (Asakawa 1994), a few species reached decomposition rates higher than those of any mosses in our study. Despite their suggested antibacterial activity (Zhu *et al.* 2006), oil bodies, known to contain large amounts of terpenoids and aromatic compounds (Asakawa 2004), do not seem powerful enough to inhibit decomposition. This may be due to volatilization of most oil body content within days or weeks after collection. The interaction effect of time and species among liverworts implies a wide heterogeneity of species responses to decomposition over time, possibly due to subgroups within the liverwort group as indicated by chemosystematic differences between, for instance, the Jungermannidae (e.g. *Lophozia lycopodioides*) and Marchantiidae (*Marchantia alpestris*) (Asakawa 2004). While we were able to reveal the importance of species identity on litter mass loss, little is known about the intraspecific variability in mass loss of species growing at contrasting sites or in different geographic regions, with possible feedbacks on chemical composition (cf. Bakken 1995) and, consequently, litter decomposability. Furthermore, little is known about mass loss rates of cryptogam species on longer time scales which could deviate considerably from our shorter-term results.

SPECIES-ENVIRONMENT INTERACTIONS ON MASS LOSS

Mass loss across and within groups was significantly affected by species (or group) identity, litter bed environment (at species level) and their interactions. This contrasts with earlier studies investigating predominantly *Sphagnum* where no significant interaction was found (Belyea 1996; Turetsky *et al.* 2008). The deviating results may be due to the strongly contrasting environments (birch forest vs. mire) used in our study or to the species chosen. Decomposition rates for *Cladonia* species were highest in the nutrient-poor birch forest litter environment where the species naturally occur and microbial communities may therefore be well adapted (Stark & Hyvärinen 2003). In the nutrient-rich birch forest environment, where *Cladonia* species are naturally absent in the Abisko region, accordingly lower mass loss rates were found. Decomposition rates of *Cladonia* species were also lower in the peatland environment. Correspondingly, Tolonen (1971) found subfossil remnants of lichens in peat cores. Wetmore (1982) suggested thallus

structure and firmness of the fungal cortex as determinants for lichen decomposition, while usnic acid content, known for its antibiotic effects (Cocchietto *et al.* 2002), did not determine mass loss of the species in his study. Fumarprotocetraric acid, present in *Cladonia rangiferina* and *C. arbuscula*, is known to be more toxic at lower pH-values (Gardner & Mueller 1981), and possibly also negatively affects decomposition rates. Mass loss rates of *Peltigera aphthosa* and *Nephroma arcticum*, both free of fumarprotocetraric acid and with significantly greater N content compared to the Cladoniaceae, were equally high under all environmental conditions, possibly due to local microbial increases due to high N content (Coulson & Butterfield 1978). Crittenden & Kershaw (1978) proposed leaching and structural damage as possible pathways for N which, in lichens, consists to a large degree of amino acid N (Solberg 1970). In N-limited environments as common in the (High) Arctic (Shaver & Chapin 1995), amino acids are readily taken up by mosses (Krab *et al.* 2008), lichens (Dahlman *et al.* 2004) and vascular plants (Chapin *et al.* 1993). Regarding non-*Sphagnum* mosses, the regression of N versus mass loss proved to be significant, with *Racomitrium lanuginosum* exhibiting extremely low N values (see also Pakarinen & Vitt 1974). In contrast, Turetsky *et al.* (2008) reported *k* values of both *Sphagnum* and non-*Sphagnum* mosses to be positively related to the ratio of metabolic to structural carbohydrates, but not to N. As a peatland hummock-builder, *R. lanuginosum* displayed equally low decomposition rates independent of site which might not only be due to low N values, but also to high values of structural carbohydrates as found in hummock-building *Sphagnum* species (Turetsky *et al.* 2008). In contrast, most of the other non-*Sphagnum* mosses showed a tendency towards increased mass loss rates in the peatland environment. Leaching in the wet mire environment could be a minor cause for enhanced mass loss rates compared to the birch forest, but the low soluble content in mosses (Pakarinen & Vitt 1974; Turetsky 2003) cannot account for more than 1-10% of total mass loss. Maybe more importantly, low moisture could have inhibited moss decomposition (cf. Flanagan & Veum 1974; Meentemeyer 1978), especially in the nutrient-rich birch forest litter bed, where bryophyte cover was thin and might have dried out during warm periods. Furthermore, the habitat-specific soil fauna can be expected to influence decomposition rates to various extents in the contrasting habitats of peat and mineral sites (Coulson & Butterfield 1978). Except for N_2-fixing lichens and *R. lanuginosum*, where mass loss did not vary across habitats, environment influenced decomposition rates of non-N_2-fixing lichens and bryophytes as shown in previous investigations (Coulson & Butterfield 1978; Wetmore 1982; Belyea 1996; Coxson & Curteanu 2002). This complicates predictions of changing decomposition patterns based on species shifts at the landscape level. Future studies should include bacterial, fungal and soil fauna communities of the various ecosystems and investigate a wider range of

cryptogam species, including both *Sphagnum* species and liverworts, in order to unravel the underlying mechanisms of species–environment interactions on cryptogam mass loss.

THE RELATION OF INITIAL LITTER CHEMISTRY AND DECOMPOSABILITY

PCA based on infrared spectra showed a clear separation of lichens, liverworts, mosses (including *Sphagnum*) and vascular plants. Relations of overall lichen or bryophyte mass loss to macronutrients and pH were weak while at cryptogam group level, R^2 improved considerably. The same pattern, although less pronounced, was found for relations of mass loss to infrared spectra. In both analyses, R^2 for liverworts decreased from family to order while R^2 for the genus *Sphagnum* was high. Even with increasing numbers of principal components, regressions were only valid up to class level (Jungermanniopsida) suggesting that Marchantiopsida (*Marchantia alpestris*) show a different decomposition pattern. Taxonomic identity might be important when predicting mass loss, possibly due to differences in carbohydrate partitioning (structural vs. metabolic), as has been suggested for true mosses versus *Sphagnum* species (Turetsky *et al.* 2008). Differences in chemical components, their allocation and respective mass loss might also be related to habitat, as hydric species with a constant nutrient input have been found to show higher protein levels, both higher or lower metabolic carbohydrate content, and, within the genus *Sphagnum*, higher allocation to photosynthetic tissue compared to species from drier habitats (Pakarinen & Vitt 1974; Rice 1995; Davey 1999). Furthermore, availability and type of conductive tissue (Hébant 1977) might influence mass loss, enabling redistribution of easily decomposable components (e.g. Sveinbjörnsson & Oechel 1991; Hakala & Sewón 1992). The lower R^2 for non-*Sphagnum* mosses suggests that indeed further division of this large and heterogeneous group is likely to improve mass loss predictions.

Due to considerable overlap of peaks characterising plant compounds, only indications of possible cryptogam mass loss predictors can be given. Next steps should include analysis of bryophyte and lichen components with conventional laboratory assays, thereby linking wavelengths to chemical compounds. At this stage, we considered compounds as positive or negative mass loss predictors in analogy with predictors known for vascular plants (Palm & Rowland 1997). Metabolic carbohydrates, lipids and proteins as easily decomposable components should be positively related to mass loss, and structural and non-soluble aromatic components negatively. Soluble phenolics, however, may either serve as energy source or inhibit decomposition (Palm & Rowland 1997). N_2-fixing lichens showed mainly positive predictors of mass loss, i.e. metabolic carbohydrates, lipids and amino acids (proteins, peptides). The latter were reflected in the significant relation of mass loss to N, emphasizing the importance of N-limitation in the (sub) Arctic

(Shaver & Chapin 1995). In contrast, non-N_2-fixing lichens revealed also negative predictors, i.e. aromatic compounds (see regression coefficients between 14.01–14.99 µm; but note the positive relation at 9.26, 9.82 µm). Mass loss was further positively determined by N, Ca, K and pH. While the influence of other components (e.g. lichen acids) on pH cannot be excluded, it correlated well with the sum of Ca, Mg and K for vascular plants (Cornelissen *et al.* 2006) and lichens ($P < 0.001$, $R^2 = 0.53$; see Appendix S3). Ca, often present as Ca oxalate crystals (Brown 1987), might positively influence decomposition via the dietary needs of the decomposer community (Swift *et al.* 1979; Nicolai 1988) or provide an indirect positive link to decomposition since both Ca and K were significantly correlated to N ($R^2_{Ca} = 0.54$, $P < 0.001$, excluding *Umbilicaria*; $R^2_K = 0.61$, $P < 0.001$). Similar interconnections have been found for vascular plants (Swift *et al.* 1979).

Since bryophytes generally had low decomposition rates, the chemistry underlying low degradability is of particular interest. Mass losses among *Sphagnum* species as well as among non-*Sphagnum* mosses were negatively related to structural carbohydrates (cf. Turetsky *et al.* 2008) and aromatic compounds, the latter indicating polyphenols substituting lignin in bryophytes (Erickson & Miksche 1974). The positive relation of K to mass loss among *Sphagnum* and non-*Sphagnum* mosses may reflect the mainly intracellular location of K in green shoots, where N, P and metabolic activity are highest (Pakarinen & Vitt 1974; Brown & Wells 1990). Indeed, proteins (N) and lipids (P), and proteins and metabolic carbohydrates, were related to mass loss of non-*Sphagnum* and *Sphagnum* mosses, respectively. Extracellularly located Ca is known to increase in older, less metabolically active tissue (Vitt & Pakarinen 1987) explaining indirectly its negative impact on *Sphagnum* decomposition. This Ca accumulation is mainly attributed to death of tissue providing additional exchange sites (Brown & Wells 1990), which are especially numerous in *Sphagnum* with its high cation exchange capacities (Clymo 1963). Mg, a positive predictor of mass loss for non-*Sphagnum* mosses, might be indirectly linked to decomposition, being the cofactor of the N-rich photosynthetic enzyme Rubisco.

For the liverwort family Scapaniaceae, mass loss was positively related to (N in) proteins, while aromatic compounds (as in non-*Sphagnum* mosses) related both positively and negatively. Structural polyphenolics in liverworts (Erickson & Miksche 1974) are likely to negatively influence decomposition while soluble aromatic liverwort compounds, known to be biologically active (Asakawa 1994), may be antimicrobial in soil or serve as energy source, as suggested for lichens (Stark & Hyvärinen 2003). The positive relation between Na and mass loss might be linked to Na requirements of the decomposer community

(Swift *et al.* 1979). Na availability in liverwort tissue may reflect environmental conditions or, as fungi show high Na levels (Swift *et al.* 1979), relates to basidiomycetous infections, repeatedly found in jungermannialean liverworts (Duckett *et al.* 2006).

The infrared measure was not only faster and easier to conduct, but smaller sample amounts were needed which is of major importance when processing minute samples of liverworts. However, measurements of macronutrients and pH might be easier to achieve and can be used to predict mass loss of cryptogam groups. If FTIR-ATR is not available, including analytical determinations of structural and metabolic carbohydrates, proteins and aromatic compounds (both soluble phenolics and lignin-like compounds) should improve predictions. To investigate if and how initial chemistry of the generally less degradable bryophytes relates to final-stage decomposition, screening multiple species over longer time periods will be necessary.

Conclusions

Understanding and predicting mass loss rates of cryptogams is crucial in cool and cold environments where C stocks in litter are enormous and profound climate change is expected to alter vegetation compositions, their related litter compositions and ultimately the C balance. Our study has shown that both higher taxon and species identity are important determinants of mass loss rates over time, with bryophytes being consistently less degradable across taxa. As the pattern of decomposition across litter bed types was not consistent among cryptogam species, future studies should further investigate the interactions of species identity and environment to fully understand and predict mass loss rates for different ecosystems. Interspecific variation in cryptogam and vascular plant litter mass loss was clearly related to initial litter chemistry. The consistent differences between species-based litter decomposabilities of cryptogam and vascular plant taxa representative of cold northern ecosystems will be most useful in formulating and testing predictions about the consequences of climate-induced shifts in vegetation composition for C cycling.

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Appendix S1. Methodological tests

Table 1. Effect of small fragments, low weight, older bryophyte litter or true litter lichens, mesh size and freezing, respectively, against the standard litter (Independent T-test, data arcsine-square-root transformed, $n = 4 - 5$). Significance marked in bold letters. If not marked otherwise, equal variances (Levene's test) were assumed

	Litter (L) /incubated (I) material	Small fragments					Low weight			
Species	L/I	Df	*T*	*P*	Responsiveness *L*	Confidence limit of *L*	*T*	*P*	Responsiveness *L*	Confidence limit of *L*
Cladonia arbuscula ssp. *arbuscula*	I	8	-0.43	0.68	-0.03	0.13	**-2.50**	**0.04**	**-0.14**	**0.11**
Cladonia stygia	I	8 4.32	1.44	0.19	0.06	0.08	-1.77	0.15*	-0.16	0.16
Nephroma arcticum	I	8	0.18	0.86	0.01	0.09	0.77	0.46	0.04	0.10
Peltigera aphthosa	I	8 4.59	-1.00	0.35	-0.05	0.09	0.91	0.41*	0.09	0.20
Hylocomium splendens	L	8	-1.26	0.24	-0.09	0.15	-0.69	0.51	-0.07	0.20
Paludella squarrosa	L	8	-0.10	0.93	-0.01	0.17	-1.01	0.34	-0.10	0.20
Polytrichum commune	L	8	0.90	0.39	0.07	0.16	0.73	0.49	0.07	0.20
Racomitrium lanuginosum	L	8	-0.28	0.79	-0.02	0.16	-0.63	0.55	-0.04	0.16

* Equal variances not assumed

Table 1. continued

	Litter (L) /incubated (I) material		Older bryophyte litter and true litter lichen				Mesh size			
Species	L/I	Df	*T*	*P*	Responsiveness *L*	Confidence limit of *L*	*T*	*P*	Responsiveness *L*	Confidence limit of *L*
Cladonia arbuscula ssp. *arbuscula*	I	8	-0.17	0.87	-0.01	0.12	-1.46	0.18	-0.08	0.11
Cladonia stygia	I	8 5.05	0.54	0.60	0.05	0.21	-0.49	0.64*	-0.03	0.10
Nephroma arcticum	I	8	1.41	0.20	0.08	0.10	-0.74	0.48	-0.06	0.16
Peltigera aphthosa	I	8 4.51	**6.20**	**<0.001**	**0.25**	**0.08**	-1.28	0.26*	-0.12	0.18
Hylocomium splendens	L	8	0.33	0.75	0.03	0.18	0.27	0.79	0.04	0.30
Paludella squarrosa	L	8	1.84	0.10	0.27	0.30	1.75	0.12	0.27	0.28
Polytrichum commune	L	8	0.04	0.97	0.00	0.16	1.70	0.13	0.14	0.16
Racomitrium lanuginosum	L	8	2.13	0.07	**0.19**	**0.17**	-0.84	0.42	-0.10	0.22

* Equal variances not assumed

Table 1. continued

	Litter (L)/ incubated (I) or life(A) material		Freezing			
Species	L/I or A	Df	*T*	*P*	Responsiveness *L*	Confidence limit of *L*
Cetrariella delisei	I	8	0.63	0.55	0.03	0.09
Cladonia arbuscula ssp. *arbuscula*	A	8	-0.39	0.71	-0.04	0.18
Cladonia stygia	A	8	-0.13	0.90	-0.01	0.15
Cladonia uncialis	I	8	-0.42	0.68	-0.04	0.18
Nephroma arcticum	A	8	-1.34	0.22	-0.05	0.07
Peltigera aphthosa	A	8	-0.60	0.57	-0.03	0.10
Hylocomium splendens	A	8	-0.01	0.99	0.00	0.15
Hylocomium splendens	L	8	0.96	0.36	0.09	0.19
Paludella squarrosa	A	8	**-3.51**	**0.01**	**-0.34**	**0.19**
Paludella squarrosa	L	8	-0.40	0.70	-0.06	0.29
Polytrichum commune	A	8	-0.03	0.98	0.00	0.16
Polytrichum commune	L	8	0.15	0.89	-0.02	0.21
Racomitrium lanuginosum	A	5.96	-0.30	0.77*	-0.05	0.33
Racomitrium lanuginosum	L	8	1.65	0.14	0.34	0.36

* Equal variances not assumed

Table 2. Comparison of bryophyte litter or incubated lichens with live material (Independent T-test, data arcsine-square-root transformed). Significance marked in bold letters, n = 2 - 5. If not marked otherwise, equal variances (Levene's test) were assumed

	Species	Df	*T*	*P*	Responsiveness *L*	Confidence limit of *L*
Lichen (Non-N_2-fixing lichen)	*Alectoria ochroleuca*	8	**2.94**	**0.02**	**0.11**	**0.08**
	Cetraria islandica	8	1.59	0.15	0.10	0.12
	Cetrariella delisei	8	0.24	0.82	0.02	0.15
	Cladonia amaurocraea	8	0.59	0.57	0.05	0.16
	Cladonia arbuscula spp. *arbuscula*	8	1.72	0.12	0.16	0.18
	Cladonia rangiferina	8	0.22	0.83	0.01	0.10
	Cladonia stellaris	8	-1.56	0.16	-0.23	0.26
	Cladonia stygia	8	2.19	0.06	**0.09**	**0.08**
	Cladonia uncialis	8	0.24	0.82	0.02	0.16
	Flavocetraria cucullata	8	-0.64	0.54	-0.02	0.07
	Flavocetraria nivalis	8	1.26	0.24	0.11	0.17
	Umbilicaria hyperborea	8	0.24	0.82	0.02	0.17
Lichen (N_2-fixing lichen)	*Nephroma arcticum*	8	1.79	0.11	0.09	0.09
	Peltigera aphthosa	8	**5.60**	**0.001**	**0.22**	**0.07**
	Solorina crocea	8	2.03	0.08	**0.12**	**0.11**
	Stereocaulon cf. *grande*	8	-0.96	0.36	-0.05	0.11
	Stereocaulon vesuvianum	8	-1.83	0.11	-0.16	0.19
Bryophyte (*Sphagnum*)	*Sphagnum balticum*	4.68	1.76	0.14*	0.17	0.20
	Sphagnum fuscum	8	1.59	0.15	1.52	2.14
	Sphagnum riparium	8	**3.50**	**0.01**	**0.35**	**0.21**
	Sphagnum teres	8	0.00	1.00	0.00	0.25
Bryophyte (non-*Sphagnum* moss)	*Aulacomnium palustre*	8	1.06	0.32	0.17	0.33
	Aulacomnium turgidum	7	-0.64	0.55	-0.09	0.27
	Cinclidium stygium	6	1.81	0.12	0.29	0.34
	Dicranum fuscescens	5	-1.62	0.17	-0.22	0.28
	Dicranum montanum	3.67	-2.79	0.05*	**-0.31**	**0.19**
	Hylocomium splendens	8	0.52	0.62	0.06	0.20
	Paludella squarrosa	8	**3.72**	**0.01**	**0.37**	**0.20**
	Pleurozium schreberi	8	0.03	0.98	0.01	0.22
	Polytrichastrum sexangulare	6	1.69	0.14	0.24	0.30
	Polytrichum commune	8	0.39	0.71	0.04	0.18
	Polytrichum strictum	8	**2.41**	**0.04**	**0.31**	**0.28**
	Racomitrium fasciculare	8	1.97	0.08	**0.28**	**0.24**
	Racomitrium lanuginosum	5.25	0.91	0.41*	0.16	0.32
	Racomitrium microcarpon	8	-0.41	0.69	-0.11	0.48
	Rhytidium rugosum	8	0.00	1.00	0.00	0.17
	Tomenthypnum nitens	8	-0.86	0.42	-0.14	0.33

Table 2. continued

	Species	Df	*T*	*P*	Responsiveness *L*	Confidence limit of *L*
Bryophyte (liverwort)	*Barbilophozia floerkii*	4	**3.48**	**0.03**	**0.39**	**0.25**
	Lophozia lycopodioides	5	1.18	0.29	0.08	0.14
	Marchantia alpestris	8	**6.40**	**<0.001**	**0.97**	**0.49**
	Nardia scalaris	1.36	**10.24**	**0.03***	**0.53**	**0.09**
	Pellia neesiana	3	**3.55**	**0.04**	**0.49**	**0.28**
	Ptilidium ciliare	7	1.67	0.14	0.13	0.14

* Equal variances not assumed

Appendix S2. Calibration, prediction and regression coefficients of liverwort mass loss versus infrared spectra, and macronutrients and pH, at family, order and (sub)class level

Table 1. Calibration/prediction of mass loss versus infrared spectra for liverworts at family, order, subclass and class level (PLS, mass loss ln-transformed, n = 6 - 10)

Liverwort Taxonomy	Family Scapaniaceae	Order Jungermanniales	Subclass Jungermanniidae	Class Jungermanniopsida
N	6	8	10	12
No. of PCs*	3	3	6	6
$R^2_{Cal.}$**	0.93	0.85	0.98	0.97
($R^2_{Pred.}$)	(0.55)	(0.41)	(0.61)	(0.83)
$RMSE_{Cal.}$ ***	(0.14)	0.19	0.06	0.10
($RMSE_{Pred.}$)	(0.42)	(0.44)	(0.32)	(0.27)
$Slope_{Cal.}$	0.93	0.85	0.98	0.97
($Slope_{Pred.}$)	(0.71)	(0.59)	(0.77)	(0.81)
$Intercept_{Cal.}$	0.25	0.54	0.07	0.10
($Intercept_{Pred.}$)	(1.15)	(1.60)	(0.91)	(0.72)

* PC: Principal component

** Cal. or Pred.: calibration or prediction

*** RMSE: root mean square error

Table 2. Calibration, prediction and regression coefficients of mass loss versus macronutrients [%] and pH for liverworts at family, order and subclass level (PLS, mass loss ln-transformed, chemical variables within family, order and subclass ln-range-normalized, n = 6 - 10). Only significant variables are shown

Liverwort	Family	Order	Subclass
Taxonomy	Scapaniaceae	Jungermanniales	Jungermanniidae
N	6	8	10
No. of PCs*	1	1	-**
$R^2_{Cal.}$***	0.92	0.54	-
($R^2_{Pred.}$)	(0.75)	(0.47)	
$RMSE_{Cal.}$ ****	0.06	0.14	-
($RMSE_{Pred.}$)	(0.13)	(0.17)	
$Slope_{Cal.}$	0.92	0.54	-
($Slope_{Pred.}$)	(0.60)	(0.47)	
$Intercept_{Cal.}$	0.06	0.33	-
($Intercept_{Pred.}$)	(0.26)	(0.38)	
Regression coefficients k*****			
k_0	0.35	0.52	-
N	0.45	0.42	-
Na	0.35		-

* PC: Principal component

** No significant variables

*** Cal. or Pred.: calibration or prediction

**** RMSE: root mean square error

***** $Y_{(2a)} = k_0 + k_1x_1 + k_2x_2 + \ldots + k_nx_n$; x: significant chemical variables (pH to Mg)

Appendix S3. Relation between pH and the sum of Ca, Mg and K for non-N_2-fixing and N_2-fixing lichens.

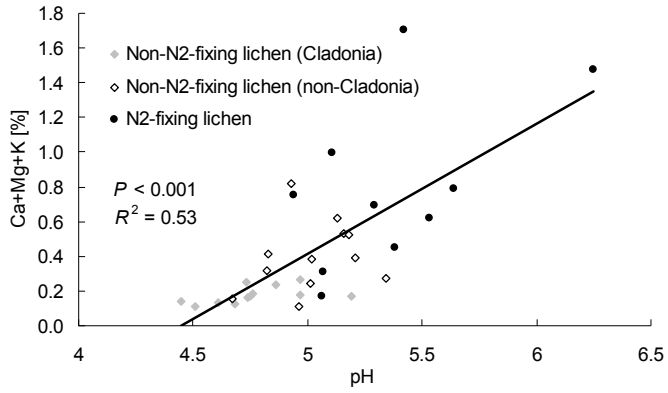

Fig. 1. Relation between pH and the sum of Ca, Mg and K (linear regression, sum of Ca, Mg and K ln-transformed) for non-N_2-fixing (both *Cladonia* and non-*Cladonia*) and N_2-fixing lichens.