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Thesis 2011-02 of the
Institute of Ecological Science, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands.
ISBN/EAN 978-94-91211-45-4

Cover design & layout	M. Roßkopf
Printing	Ipskamp Drukkers

VRIJE UNIVERSITEIT

Global change and the functional diversity of cryptogams in northern biomes

ACADEMISCH PROEFSCHRIFT

ter verkrijging van de graad Doctor aan
de Vrije Universiteit Amsterdam,
op gezag van de rector magnificus
prof.dr. L.M. Bouter,
in het openbaar te verdedigen
ten overstaan van de promotiecommissie
van de faculteit der Aard- en Levenswetenschappen
op woensdag 29 juni 2011 om 15.45 uur
in de aula van de universiteit,
De Boelelaan 1105

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English summary

Global change and the functional diversity of cryptogams in northern biomes

Climate change in the (Sub)Arctic is expected to be more extreme and rapid compared to other regions on Earth. At these northern latitudes, cryptogams (bryophytes and lichens) are the dominant vegetation component both in terms of abundance and biodiversity, fulfilling important ecosystem functions such as regulation of hydrology, carbon balance, nitrogen fixation and preservation of permafrost. While responses of vascular plants to climate have been studied in much detail, cryptogams have been mostly neglected in these investigations. Here I present a detailed study on cryptogam responses to climate (change), focusing not only on their diversity and abundance in contrasting ecosystems, but also on the consequences these changes may have for the nutrient and carbon economy of the cryptogam community. I focus especially on nutrient cycling processes that are related to the 'afterlife effects' of traits of the cryptogams, through analyzing interspecific variation in nutrient resorption from senescing tissues, quality of the litter remaining and its consequent decomposability.

In chapter 2, peatland cryptogam and vascular plant responses to climate change, both in terms of temperature and soil moisture regimes, were investigated in subarctic Sweden (and partly in Norway), along natural climatic gradients, from micro- to macroscales, and within an *in-situ* warming experiment. Soil moisture and *Sphagnum* growth were significant drivers of vegetation composition, both at smaller and larger spatial scales along natural climatic gradients. The vegetation composition of peatlands within one region, however, was rather stable and not influenced by increasing temperatures. This finding was confirmed by the results of the warming experiment. However, the lack of effect of warming on the vegetation might also have been caused by the rather short-term experimental duration of four years. *Sphagnum* growth, determined by its position on the microgradient and temperature, was a useful tool in separating functional cryptogam groups since the abundances of lichens, liverworts, non-*Sphagnum* mosses and vascular plants were negatively related to *Sphagnum* abundance. Species richness and Shannon index of all cryptogams declined as *Sphagnum* increased in abundance towards the wetter parts of the gradient. This relation was not found for vascular plants, where sedges compensated for the loss of hummock species by increasing in the wetter parts of the

gradient. In conclusion, climate change impacts on subarctic peatlands are strongly determined by moisture and *Sphagnum* growth and, to a lesser extent, by shifts in temperature regimes. However, at the limits of current peatland distribution the positive effect of temperature on *Sphagnum* growth may result in an expansion of peatlands at higher elevations.

Responses of cryptogams and vascular species in (sub)arctic tundra (and forest) to climate change were investigated along two contrasting tundra transects in Alaska and northern Sweden. For these measurements I used the combination of both natural climatic gradients and warming experiments (chapter 3). Here, temperature was an important driver of plant community composition and species richness. Lichens strongly declined in response to higher temperature, followed by non-*Sphagnum* mosses and liverworts while *Sphagnum* showed a high resistance to temperature increases within the Alaskan warming experiment. Responses within experiments were more extreme at colder locations while below the treeline in the birch forest, hardly any changes were observed. Within the Swedish birch forest experiment, amount of litter was the only significant variable determining vegetation composition while soil ammonium was an additional variable in the Alaskan tundra experiment showing higher values in the control plots. Overall, especially dwarf shrubs but also the mosses *Sphagnum girgensohnii*, *Hylocomium splendens* and *Pleurozium schreberi* were positively related to warming, while the majority of cryptogams showed a negative relationship. These responses underlay the phenomenon of arctic greening observed over the last years in many parts of the Arctic. Differences between the two studies (chapter 2 and 3) on climate change and biodiversity were mainly due to the occurrence of a strong biotic driver in peatlands, *Sphagnum* growth, which regulated growth of most other vascular plants and cryptogams. Such a driver was not apparent in the tundra experiments and gradients.

The observed shifts in plant communities from cryptogam- to shrub-dominated tundra, may also affect related processes such as those related to nutrient cycles. In chapter 4, I therefore investigated nutrient resorption efficiencies (RE), i.e. the percentage of nutrients recycled from senescing tissue, in a wide range of cryptogams and vascular plants. In these analyses, I employed a novel method (Fourier transform infrared attenuated total reflectance; FTIR-ATR) to correct for mass loss during senescence based on structural chemistry which is not affected by the resorption process. Mosses, lichens and lycophytes generally showed low nitrogen RE (RE_N < 20%), liverworts and conifers an intermediate RE_N (40%) and monilophytes, eudicots and monocots a high RE_N (> 70%). For P, RE_P appeared higher in eudicots and liverworts than in mosses. Overall, increasing

specialization in conducting tissue from cryptogams to vascular plants seemed to relate to increasing levels of RE. This broadly supported the idea that the evolution of conducting tissues towards specialized phloem has aided land plants to optimize not only their photosynthate transport during organ life, but also their internal nutrient recycling during organ senescence.

Once tissues have senesced, decomposition of the remaining litter will be initiated. To detect general patterns in potential decomposition rates among species and functional or taxonomical species groups, a wide range of mosses and lichens, typical and dominant in the subarctic flora, and a selection of vascular plants, were incubated simultaneously in a 2-year experiment in experimental garden litter beds in northern Sweden (chapter 5). Furthermore, their initial chemical traits determining mass loss rates were investigated. Lichens and vascular plants decomposed generally faster than bryophytes while within cryptogam taxa, species identity was an important determinant of mass loss rates. The exceptional role of *Sphagnum* was once more apparent when screening mass loss rates within bryophytes, as 2-year mass loss of *Sphagnum* mosses was consistently lower than for non-*Sphagnum* mosses or liverworts. The low decomposition rate of *Sphagnum* mosses is an important feature responsible for building up peatlands, but had never been demonstrated without the confounding effects of habitat variation. Using a subset of the large species set, I found that 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. Consequently, predictions about decomposition in the (Sub)Arctic should consider the influence of incubation environment, i.e. ecosystem type, on mass loss rates. Cryptogam mass loss could be predicted very well from infrared spectra (FTIR-ATR) of the initial chemical composition of primary and secondary compounds of the species. This technique thus provides a useful tool in predicting decomposition rates of a larger set of cryptogams. The initial macronutrient concentrations (N, P, carbon and cations) and initial litter pH, however, correlated less well with mass loss. This emphasizes the usefulness of including the complex mobile and structural chemistry, as done by FTIR-ATR, as a standard measurement when considering decomposition of cryptogams.

In the General Discussion (chapter 6), the relationships between cryptogam abundance and diversity changes in the (Sub)Arctic to processes concerning nutrient recycling, i.e. resorption and decomposition, are synthesized at different temporal, spatial or functional scales. Furthermore, additional aspects not covered in this thesis are highlighted. Future

studies should include community-level biotic drivers such as species interactions, competition and facilitation, and evaluate how these affect abundance-weighted processes like decomposition rates. Also, direct climate effects on phenotypic expression of traits of a given species, and on decomposition rate might merit further study. Trophic interactions (herbivory) may counteract climate change-induced shifts in vegetation. Dispersal and reproduction processes will be important for species establishment and disappearance but have not been investigated yet for a larger cryptogam species set. On longer time scales, even evolutionary adaptations to environmental perturbations may be of interest. Shifts in vegetation composition due to climate change may also trigger changes in ecosystem effects of cryptogam species with respect to hydrology, carbon storage, permafrost insulation and N_2-fixation. The measurements conducted in this thesis will help us to identify the consequences of climate change for vegetation composition, specifically cryptogam composition, in the (Sub)Arctic at different temporal, spatial and functional scales. Furthermore, this thesis provides us with the necessary tools to develop predictions about the effects of these vegetation shifts onto ecosystem nutrient and carbon turnover.
In a nutshell we have learned: cryptogam species do matter!

Svensk sammanfattning

Globala förändringar och kryptogamers funktionella diversitet i nordliga biomer

Översättning: Johan Asplund

Klimatförändringar i (sub)arktiska regioner antas bli extremare och snabbare jämfört med andra regioner på jorden. På dessa nordliga breddgrader domineras vegetationen av kryptogamer (mossor och lavar), både m
ed avseende på biomassa och biologisk mångfald. Kryptogamerna utför en mängd viktiga ekosystemfunktioner så som reglering av hydrologin, kvävefixering och bevarandet av permafrost. Kärlväxternas respons på klimatet är väl undersökta, men kryptogamer är i stort sett försummade i dessa studier. Här presenterar jag en detaljerad studie på kryptogamers responser på klimat(förändringar), där jag fokuserar dels på deras abundans och biodiversitet i olika ekosystem men också på vilka konsekvenser förändringar kan ha för närings- och kolhushållningen bland kryptogamerna. Jag lägger ett särskilt fokus på näringscykelprocesser som är relaterade till effekterna av kryptogamernas olika karaktärer. Detta gör jag genom att analysera mellanartsvariationer i näringsresorption från senescenserande vävnad, kvaliteten på återstående förna och dess konsekvenser för nedbrytningsbarheten.

I kapitel 2 studerades kryptogamers och kärlväxters respons på klimatförändringar, med avseende på olika temperatur- och markfuktighetsregimer, på myrar i subarktiska Sverige (samt delvis i Norge). Detta gjordes utmed naturliga klimatgradienter, från mikro- till makroskala, liksom i ett uppvärmningsexperiment i fält. Markfuktighet och *Sphagnum*-tillväxt var viktiga drivkrafter för vegetationens sammansättning, både på större och mindre skalor utmed naturliga klimatgradienter. Vegetationssammansättningen på myrar inom en och samma region var emellertid någorlunda stabil och ej påverkad av stigande temperaturer. Detta bekräftades också av uppvärmningsexperimentet. Den uteblivna effekten av uppvärmning på vegetationen skulle också kunna bero på den relativt korta försöksperioden på fyra år. Tillväxt hos *Sphagnum*, vilket beror på dess position på mikrogradienten och på temperaturen, var en användbar parameter för att separera funktionella grupper av kryptogamer eftersom abundansen av lavar, levermossor, bladmossor (förutom *Sphagnum*) och kärlväxter var negativt korrelerat med *Sphagnum*-

abundans. Artantal och Shannon index för alla kryptogamer minskade då *Sphagnum* ökade i abundans i de blötare delarna av gradienten. Så var emellertid inte fallet hos kärlväxterna då ökningen av halvgräs i gradientens blötare delar kompenserade för förlusten av arter på tuvorna. Sammanfattningsvis, klimatförändringars påverkan på subarktiska myrmarker beror till stor del på fuktighet och *Sphagnum*-tillväxt och i endast mindre grad på temperaturregimer. Ökade temperaturer kan emellertid resultera i att ubredningsgränsen för myrar förskjuts till högre höjd tack vare temperaturens positiva inverkan på tillväxten av *Sphagnum.*

Kryptogamers och kärlväxters respons på klimatförändringar i (sub)arktisk tundra (och skog) studerades utmed två transekter med kontrasterande vegetation i tundran i Alaska och i norra Sverige. Vid dessa mätningar använde jag en kombination av naturliga klimatgradienter och uppvärmningsförsök. Temperaturen var här en viktig drivkraft för vegetationssammansättning och artantal. Lavar minskade kraftigt till följd av ökade temperaturer vid uppvärmningsexperimentet på Alaska, något som bladmossor (förutom *Sphagnum*) och levermossor också gjorde fast i mindre utsträckning. *Sphagnum* var däremot tämligen opåverkad av temperaturökningar. Responser inom experimenten var kraftigare vid kallare lokaler medan förändringar i stort sett uteblev i fjällbjörkskogen nedanför trädgränsen. Vid experimentet i björkskogslokalen i Sverige var mängden förna den enda signifikanta variabeln som förklarade vegetationssammansättningen medan ammonium i jorden var ytterligare en förklarande variabel vid experimentet på tundran i Alaska där ammonium hade högre värden i kontrollytorna. Totalt sett var i synnerhet risbuskar, men även bladmossorna *Sphagnum girgensohnii*, *Hylocomium splendens* och *Pleurozium schreberi,* positivt påverkade av uppvärmning, medan de flesta kryptogamer påverkades negativt. Dessa resultat understöder senare års observationer om ett grönare Arktis. Skillnaden mellan de båda studierna (kapitel 2 och 3) på klimat och biodiversitet berodde till stor del på närvaron av en stark biotisk drivkraft i myrmarker, nämligen *Sphagnum*-tillväxt, som reglerade tillväxten hos de flesta kärlväxter och kryptogamer. En sådan drivkraft var inte närvarande i tundraexperimenten eller i gradienterna.

Den observerade förändringen i vegetationssammansättning från kryptogam- till buskdominerad tundra kan kanske också påverka relaterade processer så som näringscykler. I kapitel 4 studerade jag därför näringsämnens resorptionseffektivitet (RE), andelen näring som återanvänds från vissnande växtdelar, hos ett flertal arter av kryptogamer och kärlväxter. I dessa analyser använde jag en nyutvecklad metod (Fourier transform infrared attenuated total reflectance; FTIR-ATR) för att korrigera för viktförlust under senescens baserat på strukturell kemi vilken inte påverkas av resorptionsprocessen.

Bladmossor, lavar och lummerväxter hade generellt sett en låg RE för kväve (RE_N <20%), levermossor och barrträd hade en medelmåttig RE_N (40%) och ormbunksväxter, trikolpater och enhjärtbladiga växter en hög RE_N (>70%). För fosfor (P) föreföll RE_P högre hos trikolpater och levermossor än hos bladmossor. Ökande specialisering av ledningsväv från kryptogamer till kärlväxter verkade hänga ihop med ökande nivåer av RE. Detta stödjer i stort tanken att evolutionen av ledningsväv mot specialiserad floem har hjälpt landväxter att optimisera transporten av fotosyntesprodukter så väl som den interna näringsåteranvändningen vid senescens.

När vävnaden väl har vissnat startar nedbrytningen av den kvarvarande förnan. För att upptäcka generella mönster i potentiell nedbrytningshastighet bland arter och funktionella eller taxonomiska grupper inkuberades ett brett urval av typiska och dominerande subarktiska mossor, lavar och ett mindre urval kärlväxter simultant under två år i ett förnabäddsexperiment i norra Sverige (kapitel 5). Parallellt studerades de kemiska karaktärer hos den intakta växten som påverkar nedbrytningshastigheten. Lavar och kärlväxter bröts generellt sett ned snabbare än mossor medan arttillhörighet var en viktig faktor för nedbrytningshastigheten inom varje kryptogamgrupp. Återigen utmärkte sig *Sphagnum*-släktets exceptionella roll med betydligt lägre nedbrytningen efter två år jämfört med övriga bladmossor och levermossor. Den låga nedbrytningshastigheten hos *Sphagnum* är en viktig egenskap som är avgörande för torvbildning. Inga tidigare studier har emellertid kunnat visa denna skillnad i nedbrytningshastighet utan att ta hänsyn till samvarierande faktorer så som skillnader i habitat. Genom att använda ett urval av de undersökta arterna kunde jag visa att nedbrytningshastigheten varierade både mellan inkubationsmiljö (näringsrik och näringsfattig björkskog och *Sphagnum*-myrar) och arter. Nedbrytningsmönstret mellan inkubationsmiljöer var inte konsekvent mellan kryptogamarter. Följdaktligen bör prediktioner rörande nedbrytning i (sub)arktiska miljöer ta hänsyn till inkubationsmiljöns, dvs typ av ekosystem, inverkan på nedbrytningshastigheten. Nedbrytning av kryptogamer kan effektivt predikeras utifrån artens ursprungliga kemiska innehåll av primära och sekundära metaboliter med hjälp av dess infraröda spektrum (FTIR-ATR). Denna teknik är således ett utmärkt verktyg för att förutsäga nedbrytningshastigheter för ett stort antal kryptogamer. Startkoncentrationen av makronäringsämnen (N, P, kol och katjoner) liksom förnans pH-värde korrelerade emellertid sämre med viktminskningen. Detta understryker nyttan av att standardmässigt mäta den komplexa mobila och strukturella kemin, med FTIR-ATR, när kryptogamers nedbrytningshastighet studeras.

I den generella diskussionen (kapitel 6) sammanställs förhållandena mellan kryptogamers förändringar i abundans samt diversitet i den (sub)arktiska regionen och processer rörande återanvändning av näringsämnen, dvs resorption och nedbrytning på olika tids-, rumsliga och funktionella skalor. Vidare diskuteras ytterligare aspekter som i övrigt inte behandlas i denna avhandling. Framtida studier bör inkludera biotiska drivkrafter på samhällsnivå som t. ex. interaktioner mellan arter, konkurrens och facilitation samt utvärdera hur dessa påverkar t. ex. nedbrytningshastigheter. Dessutom vore det intressant att studera hur klimatet direkt påverkar fenotypiska uttryck av olika egenskaper hos en given art, liksom hur detta i sin tur påverkar nedbrytningshastigheter. Trofiska interaktioner (herbivori) kan komma att motverka vegetationsförändringar till följd av klimatförändringar. Spridnings- och fortplantningsförmågor kommer att bli viktiga för arters etablering och försvinnande men har ännu inte undersökts bland en större grupp av kryptogamer. På en längre tidskala kan även evolutionära tillpassningar till miljöförändringar vara av intresse. Skiften i vegetationens sammansättning till följd av klimatförändringar kan också utlösa förändringar i hur kryptogamer påverkar ekosystemet med avseende på hydrologi, kolbindning, isolering av permafrost och N_2-fixering. Resultaten av denna avhandling kan hjälpa oss att identifiera de konsekvenser klimatförändringar har på vegetationssammansättningen, särskilt med avseende på kryptogamer, i den (sub)arktiska regionen vid olika tids-, rumsliga- och funktionella skalor. Vidare ger oss denna avhandling nödvändiga verktyg för att utveckla prediktioner rörande hur dessa vegetationsförändringar påverkar närings- och kolomsättningen i ekosystemet.
Till sist vill jag säga: kryptogamer är betydelsefulla!

Nederlandse samenvatting

Global change en de functionele diversiteit van crytogamen in noordelijke biomen

Vertaling: Johannes H.C. Cornelissen

Klimaatsverandering zal in de (sub-)arctische regio waarschijnlijk extremer en sneller zijn dan in andere klimaatsgebieden op Aarde. Cryptogamen (mossen en korstmossen) vormen een hoofdcomponent van de vegetatie op hoge breedtegraden, zowel wat betreft abundantie als biodiversiteit. Ze vervullen daar belangrijke functies in ecosystemen, zoals de regulering van de waterhuishouding, de koolstofbalans, stikstofbinding en de bescherming van de permafrost. De uitvoerige kennis over de respons van vaatplanten op klimaat staat in schril contrast met die van cryptogamen. Mijn proefschrift omvat een gedetailleerde studie van de relatie tussen cryptogamen en (veranderingen in) klimaat, niet alleen wat betreft hun respons in biodiversiteit en abundantie in diverse (sub-)arctische ecosystemen, maar ook wat betreft de consequenties van klimaatsgestuurde veranderingen voor de bijdragen van cryptogamen aan de kringlopen van koolstof en stikstof. Enerzijds zullen die bijdragen bepaald worden door de koolstof- en nutriëntenhuishouding van verschillende soorten, anderzijds door secundaire effecten van hun functionele eigenschappen tijdens en na het afsterven van weefsels. Het gaat dan met name om verschillen in de efficiëntie van nutriëntenresorptie tussen soorten en in de kwaliteit van het resterende strooisel, met de gevolgen daarvan voor hun afbreekbaarheid.

Hoofdstuk 2 behandelt een studie in subarctisch Noord-Zweden (en deels N-Noorwegen), waarbij de respons van zowel cryptogamen als vaatplanten in *Sphagnum*-hoogvenen op klimaatsverandering onderzocht is door de samenstelling van plantengemeenschappen in een *in-situ* opwarmingsexperiment te vergelijken met die langs natuurlijke klimaatsgradiënten; de laatste als ruimtelijke analoog voor veranderingen in de tijd. Bodemvochtregime en de groei van *Sphagnum* (als substraat maar ook concurrent voor andere soorten) waren vooral bepalend voor vegetatiesamenstelling, zowel op micro- als op macroschaal langs de gradiënten. De vegetatiesamenstelling van venen binnen een gebied was tamelijk stabiel en werd niet duidelijk beïnvloed door verschillen in temperatuur. Dit kwam overeen met de bevindingen in het opwarmingsexperiment, hoewel daar ook de korte experimentele duur (4 jaar) een rol kon spelen. *Sphagnum*-groei,

welke was gecorreleerd met de relatieve positie langs microgradiënten van vocht als ook met temperatuur, werkte sterk differentiërend m.b.t. de geassocieerde vegetatie, aangezien de abundanties van korstmossen, levermossen, overige bladmossen en vaatplanten negatief gecorreleerd waren met die van *Sphagnum*. Soortenrijkdom en Shannon diversiteits-index van alle hogere cryptogamen-taxa namen af met toenemende abundantie van *Sphagnum* naarmate de bodem vochtiger werd langs de gradiënt. Bij vaatplanten echter compenseerden toenemende zegges en wollegrassen in de nattere delen van hoogvenen voor het verlies van typische soorten voor (drogere) hoogveenbulten. Concluderend worden effecten van klimaat op plantengemeenschappen vooral bepaald door vochtregimes en *Sphagnum*-groei en in mindere mate door verschillen of veranderingen in temperatuurregimes. Echter, aan de randen van het huidige verspreidingsgebied van hoogvenen kunnen positieve effecten van temperatuur op *Sphagnum*-groei leiden tot expansie van deze venen de berg op.

In hoofdstuk 3 worden ook de effecten van klimaatsverandering op cryptogamen en vaatplanten vergeleken tussen opwarmingsexperimenten en natuurlijke klimaatsgradiënten, maar nu voor toendra i.p.v. hoogveen en met een extra intercontinentale schaaldimensie: Alaska versus Zweden. Temperatuur sprong eruit als belangrijke sturende factor voor vegetatiesamenstelling en soortenrijkdom. Korstmossen namen sterk af met toenemende temperatuur, bladmossen (excl. *Sphagnum*) en levermossen minder sterk, terwijl *Sphagnum* in Alaska erg resistent bleek tegen experimentele opwarming. De sterkste veranderingen in opwarmingsexperimenten waren te meten in de koudere gebieden, terwijl in het berkenbos in Zweden vrijwel geen verandering optrad. Hier was de hoeveelheid strooisel wel onderscheidend, terwijl in het experiment in Alaska ook de hogere beschikbaarheid van ammonium in de bodem van controle-plotjes t.o.v. die in opwarmingsplotjes een significante rol speelde. In het algemeen reageerden met name de struikjes en de mossen *Sphagnum girgensohnii*, *Hylocomium splendens* en *Pleurozium schreberi* positief op opwarming, terwijl de overige cryptogamen een negatieve respons lieten zien. De toename van de struikjes komt overeen met de voor diverse delen van het arctische gebied al eerder beschreven ‘arctic greening’. De verschillen in sturende factoren voor de klimaatseffecten op biodiversiteit tussen de twee onderzoeken hadden alles te maken met de dominantie van *Sphagnum* in de hoogvenen (hoofdstuk 2) t.o.v. de naar verhouding vrijwel *Sphagnum*-loze toendra (hoofdstuk 3).

De verschuivingen in de samenstelling van plantengemeenschappen van cryptogaam-gedomineerde vegetatie richting struik-gedomineerde toendra heeft mogelijke

consequenties voor de nutriëntenkringloop. Hoofstuk 4 behandelt de verschillen in efficiëntie van het terugtrekken van nutriënten uit afstervende fotosynthetiserende weefsels van uiteenlopende soorten en hogere taxa van cryptogamen en vaatplanten (% terugtrekking van stikstof of fosfor = resorptie-efficiëntie RE_N resp. RE_P). Om eventuele massaverliezen mee te nemen in de berekening van % resorptie werden de hoeveelheden N resp. P in verse en afgestorven weefsels steeds uitgedrukt op basis van de hoeveelheid van bepaalde stabiele verbindingen (bijv. lignine, cellulose), welke bepaald werden door middel van state-of-the-art FTIR-ATR (Fourier transform infrared attenuated total reflectance). Bladmossen, korstmossen en wolfsklauwen hadden i.h.a. lage RE_N (< 20%), levermossen en coniferen intermediaire (40%) en varenachtigen en eudicotyle en monocotyle bloemplanten hoge RE_N (> 70%). RE_P leek relatief sterk bij eudicotylen en levermossen en zwak bij bladmossen. In het algemeen was er een positief verband te zien tussen de mate van aanwezigheid of specialisatie van vaatstelsels met RE, zowel binnen cryptogamen als in de evolutionaire lijn van cryptogamen tot en met geavanceerdere vaatplanten. Dit ondersteunde de hypothese dat de evolutie van vaatweefsels richting gespecialiseerd floeem de landplanten heeft geholpen niet alleen om de fotosynthetische productie te faciliteren in nog levende groene weefsels, maar ook om het interne hergebruik van nutriënten gedurende het afsterven van diezelfde weefsels te optimaliseren.

Wanneer de bovengenoemde weefsels eenmaal zijn afgestorven komen deze als strooisel beschikbaar voor afbraak (decompositie). Om algemene patronen te detecteren in de afbreekbaarheid (potentiële decompositiesnelheid) van diverse soorten en functionele groepen, is in hoofdstuk 5 een breed scala aan belangrijke subarctische soorten mossen, korstmossen en vaatplanten vergeleken op de afbreekbaarheid van hun strooisel. Dit gebeurde d.m.v. een 2-jarig experiment in Noord-Zweden, waarin al deze strooisels tegelijkertijd geïncubeerd werden in zogenaamde 'strooiselbedden' in een proeftuin. Ook werden relevante initiële chemische eigenschappen van de diverse soorten strooisel gemeten. Korstmossen en vaatplanten hadden i.h.a. een hogere afbreekbaarheid dan mossen, maar ook binnen ieder van de hoofdtaxa van crytogamen was er belangrijke variatie in afbreekbaarheid tussen soorten. *Sphagnum* bevond zich consequent aan het recalcitrante uiteinde van het gehele afbreekbaarheidsspectrum, ook binnen de mossen. Deze recalcitrantie verklaart onomstotelijk waarom *Sphagnum* zo'n belangrijke bouwer is van veen, terwijl in eerdere studies de effecten van deze recalcitrantie en die van het abiotische milieu op afbraaksnelheid nooit expliciet van elkaar onderscheiden hadden kunnen worden. Een additioneel experiment met minder soorten liet zien dat zowel incubatie-milieu als soort een belangrijke invloed hadden op afbraaksnelheid van

cryptogamen, en dat er interacties waren tussen beide factoren. Dergelijke interacties zijn dusdanig groot dat ze zouden moeten worden meegenomen in voorspellingen over toekomstige afbraaksnelheden van strooisel in (sub-)arctische gebieden. De variatie in afbreekbaarheid tussen soorten kon adequaat verklaard worden m.b.v. FTIR-ATR-spectra die de concentraties van complexe mobiele en structurele chemische verbindingen van het initiële strooisel quantificeren. Deze techniek blijkt dus goed toepasbaar op het verklaren van afbraaksnelheden van uiteenlopende cryptogamen, zeker in vergelijking met conventionele analyses van initiële concentraties aan macronutriënten (N, P, C, kationen) en initiële pH, welke alle veel minder verklarende waarde hadden voor variatie in afbreekbaarheid dan FTIR-ATR.

De Algemene Discussie in hoofdstuk 6 is een synthese van de relaties tussen enerzijds klimaatsgestuurde veranderingen in de abundanties en diversiteit van (sub-)arctische cryptogamen en anderzijds processen in de nutriëntenkringloop, met name resorptie en decompositie. En dit alles op diverse schaalniveaus: tijdsschaal, ruimtelijke schaal en functionele schaal. Ook additionele aspecten van deze thematiek zijn hier voor het voetlicht gebracht. Toekomstige onderzoeken zouden ook ander biotische interacties op de schaal van plantengemeenschappen moeten meenemen, bijvoorbeeld soortsinteracties inclusief concurrentie en facilitatie; en hoe deze zich verhouden tot processen als decompositie, aangezien de hoeveel strooiselmassa per soort een sterk bepalende factor is voor decompositiesnelheid op ecosysteemschaal. Ook directe effecten van klimaat op fenotypische expressie van eigenschappen van een gegeven soort zijn van belang, en hoe die zich vertalen in decompositiesnelheden. Trofische interacties (met name herbivorie) kunnen bepaalde klimaatsgestuurde trends in de vegetatieontwikkeling modereren. Verspreiding van sporen en zaden, en reproductieve processes, zullen uiteindelijk van belang zijn voor de vestiging respectievelijk het verdwijnen van soorten, maar de rol van deze factoren is nog niet onderzocht voor grotere groepen cryptogamensoorten. Over lange tijdsschalen kunnen zelfs evolutionaire adaptaties aan milieuveranderingen een interessante rol spelen. Veranderingen in soortensamenstelling van cryptogamenvegetatie door klimaat kunnen mogelijk ook een trigger vormen voor veranderingen in de ecosysteemfuncties die de cryptogamen verzorgen, met name die van vochtregulering, koolstofopslag, permafrost-isolatie en stikstofbinding. De metingen in dit proefschrift zullen een bijdrage leveren aan het begrijpen en voorspellen van de gevolgen van klimaatsverandering voor cryptogamensamenstelling in (sub-)arctische vegetatie op diverse schalen van tijd, ruimte en functionaliteit. Ook zal dit proefschrift bijdragen aan het verkrijgen van handvaten voor het voorspellen van de verdere consequenties van zulke veranderingen voor subarctische nutriënten- en koolstofkringlopen.

In een notendop: de ene soort cryptogaam is de andere niet waar het gaat over het functioneren van arctische ecosystemen!

Deutsche Zusammenfassung

Globaler Wandel und die funktionelle Diversität von Kryptogamen in nördlichen Biomen

Der Klimawandel in der (Sub-)Arktis wird erwartungsgemäß extremer und schneller verlaufen als in anderen Regionen der Erde. In diesen nördlichen Breiten sind Kryptogamen (Moose und Flechten) die dominante Vegetationskomponente, sowohl im Hinblick auf ihre Häufigkeit als auch auf ihre Artenvielfalt. Sie erfüllen dort wichtige Ökosystemfunktionen wie z.B. die Regulation der Hydrologie, des Kohlenstoffgleichgewichts, der Stickstoff-Fixierung und dienen der Erhaltung des Permafrosts. Während die Reaktionen höherer Pflanzen auf das Klima detailliert untersucht wurden, wurden Kryptogamen in solchen Studien meist ignoriert. In dieser Arbeit wird deshalb eine ausführliche Studie der Reaktion der Kryptogamen auf das Klima (bzw. den Klimawandel) präsentiert, die nicht nur deren Artenvielfalt und Häufigkeit in kontrastierenden Ökosystemen behandelt, sondern auch die Folgen erfaßt, welche diese Änderungen für die Nährstoff- und Kohlenstoffökonomie der Kryptogamengesellschaft haben könnten. Der Fokus liegt dabei speziell auf Nährstoffkreislaufprozessen, die sich auf Charakteristika der Kryptogamen beziehen, die erst mit deren Absterben zu Tage treten. Dazu wurde sowohl die innerartliche Variation der Nährstoffresorption von alterndem Gewebe, als auch die Qualität des verbleibenden Materials sowie dessen Abbaubarkeit untersucht.

Im zweiten Kapitel wurde der Effekt des Klimawandels auf Kryptogamen und höhere Pflanzen in Mooren im subarktischen Schweden (sowie teilweise in Norwegen) entlang natürlicher klimatischer Gradienten untersucht. Dies geschah sowohl im Hinblick auf die Temperatur als auch die Bodenfeuchte. Der Gradient reichte vom Mikro- (innerhalb eines Moores), Meso- (innerhalb einer Region) zum Makromaßstab (überregional). Weiterhin wurden Untersuchungen anhand eines Erwärmungsexperiments im Gelände durchgeführt. Bodenfeuchte und Wachstum von Torfmoosen (*Sphagnum*) waren signifikante Faktoren bezüglich der Vegetationszusammensetzung, sowohl bei kleineren wie auch bei größeren Maßstäben entlang der natürlichen klimatischen Gradienten. Die Pflanzengesellschaften der Moore innerhalb einer Region waren allerdings eher stabil und wurden nicht durch steigende Temperaturen beeinflußt. Dieses Ergebnis wurde durch das Erwärmungsexperiment bestätigt. Der geringe Effekt der Erwärmung auf die Vegetation

könnte jedoch auch durch die eher kurze experimentelle Laufzeit von vier Jahren verursacht worden sein. Das Wachstum von Torfmoosen, beeinflußt durch ihre Lage entlang des Mikrogradienten wie auch die Temperatur, war ein nützliches Hilfsmittel, um funktionelle Gruppen der Kryptogamen zu separieren, da die Häufigkeit der Flechten, Lebermoose, Moose (außer Torfmoosen) und höheren Pflanzen in negativer Beziehung zur Häufigkeit der Torfmoose stand, die im nässeren Bereich zunehmen. Die Artenvielfalt und der Shannon Index aller Kryptogamen stand in umgekehrtem Verhältnis zur Häufigkeit der Torfmoose und nahm ab, während diese zunahm. Diese Beziehung konnte für höhere Pflanzen nicht bestätigt werden, da dort Seggen in den nässeren Bereichen des Gradienten die Stelle der Bultarten einnahmen. Zusammenfassend läßt sich sagen, daß der Effekt des Klimawandels in subarktischen Mooren stark von der Feuchte und dem Wachstum der Torfmoose und weniger durch Veränderungen des Temperaturregimes bestimmt wird. An den Rändern der momentanen Moorerstreckung könnte jedoch der positive Effekt der Temperatur auf das Torfmooswachstum zu einer Expansion der Moore in höheren Lagen führen.

Die Reaktionen der Kryptogamen und höheren Pflanzen in der (sub-)arktischen Tundra (und Wald) auf den Klimawandel wurden entlang zweier in Bezug auf die Vegetation unterschiedlicher Transekte in Alaska und Nordschweden untersucht. Für diese Messungen wurde die Kombination von natürlichen klimatischen Gradienten und Erwärmungsexperimenten verwendet (Kapitel 3). Die Temperatur stellte hier einen wichtigen Einfluß auf die Zusammensetzung der Pflanzengesellschaften und deren Artenvielfalt dar. Flechten nahmen bei steigenden Temperaturen stark ab, gefolgt von Laubmoosen (außer Torfmoosen) und Lebermoosen, während Torfmoose eine hohe Resistenz gegenüber Temperaturerhöhungen innerhalb des Erwärmungsexperimentes in Alaska zeigten. Die Reaktion der Vegetation innerhalb der Experimente war an kälteren Standorten extremer, während unterhalb der Baumgrenze kaum Veränderungen beobachtet wurden. Innerhalb des schwedischen Birkenwaldexperiments war die Bedeckung durch Streu die einzige signifikante Variable, welche die Vegetationszusammensetzung beeinflußte. In Alaska stellte Ammonium im Boden eine zusätzliche Variable war, die in den Kontrollflächen höhere Werte aufwies. Insgesamt profitierten speziell Zwergsträucher, aber auch die Moose *Sphagnum girgensohnii*, *Hylocomium splendens* und *Pleurozium schreberi* von der Erwärmung, während die Mehrzahl der Kryptogamen eine negative Beziehung aufwies. Die Zunahme der Zwergsträucher stimmt überein mit dem in den letzten Jahren beschriebenen Phänomen des ‘arktischen Ergrünens’, welches in vielen Teilen der Arktis beobachtet wurde. Unterschiede zwischen den beiden Studien (Kapitel 2 und 3), den Klimawandel und die

Artenvielfalt betreffend, sind hauptsächlich auf das Wachstum von Torfmoosen in Mooren zurückzuführen. Dieses regulierte das Wachstum der meisten anderen höheren Pflanzen und Kryptogamen. Solch ein regulierendes Element war innerhalb der Tundraexperimente und deren Gradienten nicht vorhanden.

Der beobachtete Wechsel von Kryptogamen- zu Strauch-dominierter Tundra könnte in Folge auch andere Prozesse wie z.B. die Nährstoffzyklen beeinflussen. In Kapitel 4 wurde daher die Effizienz der Nährstoffresorption (RE), d.h. der Anteil der Nährstoffe, der aus dem alternden Gewebe wiederverwendet wird, in einer großen Anzahl von Kryptogamen und höheren Pflanzen untersucht. Bei diesen Analysen wurde eine neue Methode angewendet (Fourier transform infrared attenuated total reflectance; FTIR-ATR), um für den Massenverlust während des Alterungsprozesses zu korrigieren. Diese Methode basiert auf der strukturellen Chemie, die vom Resorptionsprozeß nicht beeinflußt wird. Laubmoose, Flechten und Bärlappgewächse wiesen im Allgemeinen einen niedrigen RE (< 20%) für Stickstoff (N) auf, Lebermoose und Koniferen einen mittleren RE_N (40%), und Monilophyten, Eudikotyledonen und Monokotyledonen einen hohen RE_N (> 70%). Für Phosphor (P) war RE_P höher für Eudikotyledonen und Lebermoose als bei Laubmoosen. Insgesamt schien die zunehmende Differentierung des Leitgewebes von Kryptogamen zu höheren Pflanzen mit zunehmenden Werten von RE verknüpft zu sein. Dies unterstützt im Großen und Ganzen den Gedanken, daß die Evolution des Leitgewebes in Richtung spezialisierten Phloems Landpflanzen nicht nur zu Transport von Photosyntheseprodukten, sondern auch zur internen Nährstoffwiederverwendung während des Alterungsprozesses verholfen hat.

Sobald Gewebe altert, beginnt der Abbau der verbleibenden Materials. Um allgemeine Muster der potentiellen Abbauraten innerhalb der Arten und funktionellen bzw. taxonomischen Artengruppen erkennen zu können, wurde eine breite Auswahl von typischen und dominierenden subarktischen Moosen und Flechten, sowie eine geringere Auswahl an höheren Pflanzen untersucht. Dies geschah mit Hilfe eines zwei-jährigen Abbauexperimentes in Nordschweden, in dem alle Streu gleichzeitig in sogenannten ‚Streuabbaubetten' in einem experimentellen Garten inkubiert wurde (Kapitel 5). Zusätzlich wurden die chemischen Eigenschaften des pflanzlichen Ausgangsmaterials, welche die Abbauraten bestimmen, untersucht. Flechten und höhere Pflanzen bauten sich im Allgemeinen schneller ab als Moose. Innerhalb der Kryptogamengruppen beeinflußte die jeweilige Art die Abbauraten in großem Maße. Die außergewöhnliche Rolle der Torfmoose wurde hier nochmals ersichtlich, da der zwei-jährige Abbau von Torfmoosen deutlich niedriger war als bei den übrigen Laub- oder Lebermoosen. Die niedrige

Abbaurate von Torfmoosen ist ein wichtiges Merkmal, das für den Aufbau der Moore verantwortlich ist. Jedoch wurde diese Eigenschaft bisher noch nicht ohne die überlagernden Effekte demonstriert, die durch unterschiedliche Habitate verursacht werden. Anhand einer begrenzten Auswahl an Arten konnte gezeigt werden, daß der Abbau sowohl durch die Inkubationsumgebung (nährstoffreicher und nährstoffarmer Birkenwald sowie *Sphagnum*-Moore) als auch durch die jeweiligen Arten beeinflußt wurde. Die Abbaumuster der unterschiedlichen Inkubationsumgebungen waren innerhalb der Kryptogamen nicht konsistent. Deshalb sollten Vorraussagen über Streuabbau in der (Sub-)Arktis den Einfluß des jeweiligen Ökosystems auf die Abbauraten in Erwägung ziehen. Der Abbau der Kryptogamen ließ sich sehr gut durch die ursprüngliche chemische Zusammensetzung der Arten, erfaßt durch Infrarotspektren (FTIR-ATR), vorhersagen. Diese Technik ist daher eine ausgezeichnete Methode, um Abbauraten einer größeren Zahl an Kryptogamen vorherzusagen. Die Konzentration der ursprünglichen Makronährstoffe (N, P, Kohlenstoff und Kationen) sowie der anfängliche pH-Wert der Streu korrelierten jedoch weniger gut mit den Abbauraten. Dies unterstreicht den Nutzen der Messung der komplexen mobilen und strukturellen Chemie, wenn Abbauraten der Kryptogamen untersucht werden.

In der Allgemeinen Diskussion (Kapitel 6) werden die Beziehungen zwischen Häufigkeit und Diversität der Kryptogamen in der (Sub-)Arktis mit Prozessen, die sich mit Nährstoffkreisläufen befassen, d.h. Resorption und Abbau, auf unterschiedlichen zeitlichen, räumlichen und funktionellen Ebenen miteinander verknüpft. Zusätzlich werden verschiedene Aspekte diskutiert, die in dieser Arbeit nicht behandelt wurden. Zukünftige Studien sollten biotische Triebkräfte auf Gesellschaftsniveau, wie Arteninteraktionen, Konkurrenz bzw. Förderung, beinhalten und überprüfen, wie diese z.B. Abbauraten beeinflussen. Außerdem wäre es von Interesse zu untersuchen, wie direkte Klimaeffekte den phenotypischen Ausdruck einer gegebenen Art sowie deren Abbauraten beinflussen. Trophische Interaktionen (Herbivorie) könnten eventuell den Klimawandel-bedingten Veränderungen der Vegetation entgegenwirken. Verbreitung und Reproduktion sind wichtige Prozesse für die Etablierung sowie das Erlöschen von Arten. Diese wurden jedoch noch nicht für eine größere Zahl an Kryptogamen untersucht. Auf längere Zeit könnten selbst evolutionäre Anpassungen an Umweltstörungen von Interesse sein. Die durch den Klimawandel bedingten Veränderungen der Vegetation können auch Veränderungen der Ökosystemeffekte der Kryptogamen hervorrufen. Diese umfassen z.B. die Hydrologie, die Kohlenstoffspeicherung, den Schutz des Permafrosts sowie die N_2-Fixierung. Die Messungen, die in dieser Arbeit vorgenommen wurden, werden uns helfen, die Konsequenzen des Klimawandels für die Vegtationszusammensetzung,

speziell der Kryptogamenzusammensetzung, in der (Sub-)Arktis auf unterschiedlichen zeitlichen, räumlichen und funktionellen Skalen zu verstehen und vorherzusagen. Außerdem bietet uns diese Arbeit die notwendigen Werkzeuge, um Vorhersagen über die Effekte dieser Vegetationsveränderungen auf Nährstoff- und Kohlenstoffkreisläufe zu entwickeln.

Zusammenfassend läßt sich sagen: Kryptogamen sind auf den ersten Blick zwar unscheinbar, für das Gesamtökosystem jedoch von größter Bedeutung.

Chapter 1

General Introduction

Ecosystem functions of cryptogams in the (Sub)Arctic

At high northern latitudes, cryptogams, viz. bryophytes and lichens, prevail, by far exceeding vascular plants in terms of biodiversity (Matveyeva & Chernov 2000) and also often in biomass (Wielgolaski *et al.* 1981). Cryptogams can be found as early colonizers under extreme conditions but are also present as a luxuriant ground layer in subarctic forests, their habitats ranging from hostile environments in the high alpine tundra and high arctic polar desert over vast tundra and forest ecosystems in milder environments to peatlands, efficiently storing carbon in peat layers (Longton 1988; Rydin & Jeglum 2006).

The omnipresence of cryptogams in the (Sub)Arctic is mirrored in their importance for ecosystem functioning. In extreme environments, cryptogams are the first to colonize rock and barren soil, preparing the ground for later invasion of less hardy cryptogam species and vascular plants. Especially lichens are known to promote mechanical and chemical weathering of the rock, the latter through their release of organic acids, thereby mobilizing nutrients (Adamo & Violante 2000). Cryptogamic crusts, frequently found in high alpine areas and polar deserts (Gold *et al.* 2001), consist of a complex mixture of free-living nitrogen (N_2)-fixing cyanobacteria, crustose lichens and liverworts. The crust provides shelter, keeping moisture content high and temperatures low while N and organic carbon accumulate (Breen & Lévesque 2008), over time leading to first soil development. Later in succession, N_2-fixing cyanobacteria also are found in symbiosis with larger bryophytes and lichens, such as *Hylocomium splendens*, *Peltigera* spp. and *Nephroma* spp., which together may account for 25-80% of annual N input in tundra ecosystems and 1-20% of total annual plant N uptake (Chapin & Bledsoe 1992). Especially in N-limited ecosystems such as the (Sub)Arctic (Haag 1974; Aerts *et al.* 1992; Shaver & Chapin 1995), this N-input can be of major importance.

A crucial ecosystem function is the storage of carbon, mainly by bryophytes, be it in tundra or, most importantly, in peatlands (cf. Limpens *et al.* 2008). Over centuries to millennia, mosses, specifically *Sphagnum* mosses, have accumulated peat in an area of 346 x 10^6 ha (Gorham 1991). Carbon stored in these peatlands amounts to 600 Gt at northern latitudes, an amount equivalent to all CO_2 stored in the atmosphere (Clymo 1998). But also in arctic tundra, substantial amounts of (moss-derived) carbon are stored

(McGuire *et al.* 2009). Moreover, the moss layer, predominantly covering the surface, insulates the underlying permafrost (Dyrness 1982; Gornall *et al.* 2007), dominant in vast areas of the Russian, Canadian and American Arctic. By now we have learned that both younger and older peat layers (Dorrepaal *et al.* 2009) as well as permafrost (Jorgenson *et al.* 2010) are responsive to climate change; the former by increased carbon mineralization through increasing temperatures and the latter by melting once mosses decrease in abundance (Kade & Walker 2008). Both processes lead to increased emission of the greenhouse gases CO_2 and CH_4 (Updegraff *et al.* 2001; Jorgenson *et al.* 2010), with likely positive feedback to climate warming.

Water retention by cryptogams constitutes another important ecosystem function. Especially *Sphagnum* in peatlands can store vast amounts of water due to both its high tissue water retention capacity and capillary rise of water between its stems (Hayward & Clymo 1982). As a result, these mosses create their own environment where only few other vascular plants and cryptogams are able to compete (cf. Heijmans *et al.* 2002; Hugonnot *et al.* 2003; Malmer *et al.* 2003). Also in tundra and subarctic forests, bryophyte-driven water storage may play an important role by modifying the hydrological regimes in soils (Beringer *et al.* 2001). In conclusion, despite their low stature bryophytes and lichens play a major role in the functioning of (sub)arctic ecosystems with important feedbacks to regional hydrology and even climate.

Assessing climate change impacts on plant communities in the (Sub)Arctic

Climate change in the 21st century is expected to be most drastic in the northern hemisphere (ACIA 2005; IPCC 2007). In the light of the major ecosystem functions cryptogams fulfill in the (Sub)Arctic, it is important to know if and how their communities change as a result of climatic change. As different cryptogam taxa show different ecosystem functions (Cornelissen *et al.* 2007a), investigations at detailed taxonomic and functional levels are needed to understand the possible impact of climate change in the (Sub)Arctic. Unfortunately, studies conducted so far have mainly concentrated on vascular plants (Arft *et al.* 1999; Walker *et al.* 2006), while cryptogams have been largely neglected or were aggregated in major groups (Van Wijk *et al.* 2003; Wahren *et al.* 2005) rather than sampled at species level as done in only a few studies (Molau & Alatalo 1998; Press *et al.* 1998; Jägerbrand *et al.* 2009).

Climate change is expected to affect plant communities both directly and indirectly. Direct effects are manifested in the responses of community composition to increased temperature and changes in precipitation patterns, both as rain and snow (IPCC 2007).

Some bryophytes are not yet, or only for brief periods, at their temperature optimum for photosynthesis (Skre & Oechel 1981) and would benefit to a certain limit from increased temperatures while others are adapted to more extreme i.e. cold environments. Thus, species of a more southerly and low-altitude distribution are expected to increase while species of a more northerly and/or high-altitude distribution might decrease, corresponding to shifts in lichen composition reported from the European temperate zone (Van Herk *et al.* 2002). Increases in rain would lead to increased soil moisture favoring bryophytes without belowground uptake structures such as *Sphagnum*, liverworts and most higher moss taxa. However, increasing evapotranspiration, caused by rising temperatures, might (partly) counteract this development. Increases in snow cover, however, might delay the onset of spring, on the other hand providing an additional water source at sites where water might otherwise be a limiting resource for cryptogam performance. Increasing temperatures might also lead to increased nutrient availability (Rustad *et al.* 2001), both factors favoring certain higher plant groups such as deciduous shrubs and graminoids (Van Wijk *et al.* 2003; Walker *et al.* 2006), and possibly also some faster-growing cryptogams, especially those with conducting tissues promoting uptake and transport of soil water and its nutrients. Where temperature increases lead to soil disturbances via permafrost thaw, ruderal species might appear, taking advantage of this disturbance. The appearance of shrubs and the greening of the Arctic in response to warming is a process well documented (Tape *et al.* 2006; Forbes *et al.* 2010). Slowly-growing cryptogams of low stature can easily be outcompeted by shrubs and other vascular plants through increased shading and litter coverage through increased leaf and litter production of vascular plants (Chapin *et al.* 1995; Cornelissen *et al.* 2001).

Several approaches to investigate climate change impacts on plant communities exist. These include mainly warming experiments, by using transparent open-top chambers (OTCs) (Marion *et al.* 1997), ground heating (Hartley *et al.* 1999) or greenhouses (Bret-Harte *et al.* 2001). These types of experiment offer good replication and reasonably standardized environmental factors among plots, yet they are on shorter temporal scales. Moreover, experimental artifacts such as temperature patterns deviating from climate change predictions (Kennedy 1995), changes in humidity, exclusion of precipitation (greenhouse), wind shelter and barriers for sexual and/or asexual reproduction cannot be excluded. Complementary approaches include recording of vegetation along natural climatic gradients (Gignac & Vitt 1990; Virtanen *et al.* 2006) which operate on larger spatial and temporal scales. However, confounding environmental factors such as changes in pH, soil moisture or underlying geology might be difficult to disentangle. Combining

these two approaches may therefore provide particularly robust insights (Callaghan *et al.* 1999; Cornelissen *et al.* 2001).

Traits of living cryptogams and their litters - implications for nutrient recycling and carbon storage

Cryptogams are not only adapted to extreme temperature and moisture regimes but also to low nutrient availability (Longton 1988; Rydin & Jeglum 2006), a feature of major importance in a highly nutrient-limited system such as the Arctic where low temperatures lead to low mineralization rates (MacDonald *et al.* 1995; Lükewille & Wright 1997; Rustad *et al.* 2001). Fast nutrient uptake and large adsorption surfaces may be important adaptations to survive and compete under these harsh conditions. Cryptogams do indeed show specific adaptations to low nutrient availability as most cryptogams can take up nutrients with their whole shoot or thallus (Nash 1996; Bates 2000), partly even in the form of amino acids (Dahlman *et al.* 2004; Krab *et al.* 2008), which constitute an important N pool in arctic systems (Kielland 1995). Also, they are capable of translocation of nutrients from old dying parts to living material as a result of which nutrients can be re-used (Cornelissen *et al.* 2007a). In contrast with the extensive literature on nutrient retranslocation in vascular plants (Chapin 1980; Reich *et al.* 1992; Killingbeck 1996), retranslocation of nutrients in cryptogams has so far been explicitly shown for a few lichens and bryophytes only (Eckstein & Karlsson 1999; Kytöviita & Crittenden 2007). Whether or not species are more efficient at nutrient translocation may also have strong repercussions for litter quality and, consequently, litter decomposition (Aerts 1997), with a subsequent impact on carbon storage.

As discussed above, climate change is expected to change plant communities drastically in the (Sub)Arctic, promoting certain groups of higher plants which, in comparison to cryptogams, appear to produce relatively easily decomposable plant litter of high quality (see below). If this turns out to be a general pattern, carbon storage will not only decrease as a direct warming response of overall carbon mineralization, but at the same time indirectly, if different and more labile litter will be produced by higher plants. It is also important to investigate the role of interspecific variation in litter decomposability within each of the major taxa (i.e. lichens, bryophytes and vascular plants), which could also be an important driver of soil carbon dynamics. Numerous studies have investigated interspecific variation in vascular plant litter decomposability (Cornwell *et al.* 2008), also in the (Sub)Arctic (Quested *et al.* 2003; Cornelissen *et al.* 2007b), while hardly any work has been done on cryptogams. The few studies that have been conducted concentrated on a few or single species only (Wetmore 1982; Rochefort *et al.* 1990; Hobbie 1996; Coxson

& Curteanu 2002) not allowing for generalizations at this point. For vascular plants we know that chemical traits, such as N, phosphorus and lignin content, determine decomposition rates (Swift *et al.* 1979; Palm & Rowland 1997). Yet so far, predictors of decomposability remain largely unknown for both bryophytes and lichens (Nakatsubo *et al.* 1997; Turetsky *et al.* 2008).

A classification of cryptogam functional groups based on traits and growth forms and their relation to ecosystem functions

As it is impossible to study the response of each individual plant species to environmental change, many attempts have been made to classify vascular plants into functional groups based on a set of similar traits in response to environmental conditions or based on similar effects on ecosystem processes (Gitay & Noble 1997; Lavorel *et al.* 1997). In such classifications, bryophytes and lichens each have mostly been included as one functional group, with the exception of *Sphagnum* mosses whose exceptional ecosystem roles have been recognized early on (Chapin *et al.* 1996). Thus, interspecific differences within the cryptogams concerning their ecosystem functions and traits have been virtually ignored. Depending on the ecosystem processes investigated, classification criteria for functional groups may vary strongly. Obvious criteria could be the N_2-fixing capacity of cryptogams where nutrient economy is concerned. Water relations might be best described by functional groups which are based on increasing degrees of water storage (cf. Smith 1988; Elumeeva *et al.* in press) and conductance efficiency of water-conducting tissues (cf. Hébant 1977). Conducting tissues for transport of photosynthates, on the other hand, may play a role in nutrient resorption and translocation between cryptogam parts. A general classification of cryptogams into functional groups based on a whole set of traits, as might seem the ideal case, might therefore possibly not even serve the envisaged purpose. Rather, functional groups based on specific questions/hypotheses may be more appropriate to answer research questions as concisely as possible.

Aims and outline of this thesis

This thesis investigates both the impacts of climate change on biodiversity of cryptogams in northern biomes and the consequences of these changes for some key ecosystem functions. These ecosystem functions include both the resorption of nutrients from living cryptogams during senescence and the subsequent decomposition of the remaining cryptogam litter. The impact of climate on cryptogams in the (Sub)Arctic, and its possible cascading effects on cryptogam-driven ecosystem functions through their functional traits, is illustrated in Figure 1. By investigating the influence of species composition and diversity across different temporal, spatial and functional scales, the latter from species to

functional groups to larger taxonomical levels, the traits of cryptogams such as nutrient resorption efficiency and decomposability are studied and put into a larger context of environmental (change) drivers and ecosystem carbon and nutrient cycling.

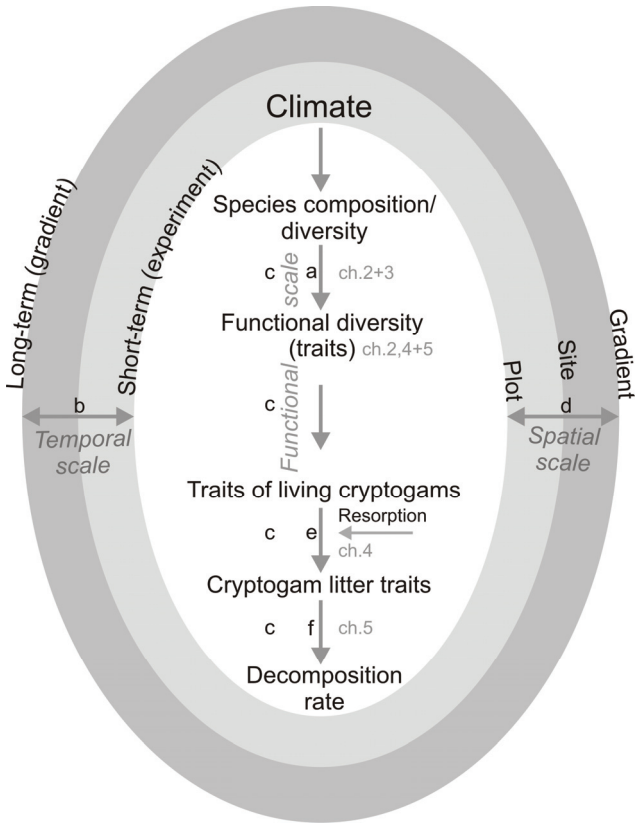

Fig. 1. Climate and its influence on cryptogam diversity and its linkages, through functional traits, to nutrient resorption and litter decomposition at different temporal, spatial and functional scales.

Thus, the specific aims of this PhD study were (i) to identify the consequences of climate change for vegetation composition, specifically cryptogam composition, in the (Sub)Arctic at different temporal, spatial and functional scales and (ii) to investigate the implications of these changes concerning nutrient and carbon fluxes between the primary producers and the decomposition subsystem.

The first main aim of this study is addressed in chapters 2 and 3 (Fig. 1, relation a). Both chapters adopt the approach of combining warming manipulation experiments with natural climatic gradients. This way they study drivers of plant community composition and diversity of cryptogams and vascular plants in northern peatlands in Sweden and

Norway, and in (sub)arctic tundra in Sweden and Alaska at different temporal, spatial and (partly) functional scales.

In chapter 2, I am specifically interested in the main drivers of cryptogam species distribution and how these drivers differ in their relative importance at different temporal (experimental, Fig.1, relation b), spatial (from micro- to macrogradient, Fig.1, relation d) and functional scales (from species level to functional group, Fig.1, relation c). Furthermore, I want to investigate whether the cryptogam species composition and diversity of these peatlands depend strongly on the development of *Sphagnum* as the underlying living substrate. Thereto, a *Sphagnum fuscum*-peatland warming experiment and its related natural climatic gradient have been investigated in subarctic northern Sweden and Norway.

In chapter 3, patterns in biodiversity and abundance changes are subsequently investigated in response to climate change in contrasting tundra ecosystems in subarctic Sweden and arctic Alaska. A wide variety of ecosystems on two continents is chosen since not only climate change is expected to vary among regions (ACIA 2005; IPCC 2007), but also ecosystems differ substantially suggesting a wide variation in ecosystem responses to climate change. Both warming experiments (Fig.1, relation b) in acidic tussock tundra in Alaska, and subarctic tundra and subarctic birch forest in Sweden, and their related natural climatic gradients (Fig.1, relation d) have been sampled. Specifically I am interested in the degree of species turnover, i.e. I hypothesize that only few bryophyte and very few lichen species are able to replace the cold-adapted species that might be lost under warmer conditions.

Chapter 4 deals with the consequences the aforesaid changes in plant community composition may have for nutrient resorption (main question 2, Fig.1, relation e). Thereto, I investigate resorption efficiencies in a wide range of cryptogams and vascular plants. Specifically, I am interested in whether the general lack or low degree of specialisation of conducting tissues in non-vascular cryptogams, as compared to that in vascular plants, has left them less efficient at nutrient resorption. I hypothesize that increasing degrees of differentiation of conducting tissues within basal cryptogam clades have led to increased resorption efficiency, and that this differentiation follows the sequence of phylogenetic branching in the Tree of Life.

In chapter 5, I compare litter quality and potential mass loss rates (decomposabilities) among a wide range of cryptogams, and a few selected vascular plants, in order to assess

the impact changing plant communities may have on nutrient and carbon cycles (Fig.1, relation f). Both standard and novel methods to prepare and incubate cryptogam litters and to monitor their initial chemical traits are applied. These should provide us with the necessary tools to predict cryptogam litter decomposition rates across multiple species.

The concept of functional groups (Fig.1, relation c) is put to the test in chapter 2 where cryptogam growth forms depending on the biotic factor *Sphagnum* growth are developed and compared with increasingly less detailed types of classification. Also chapter 4 investigates the use of functional groups and phylogenetic positions when studying conducting tissues in cryptogams and vascular plants while chapter 5 concentrates on major taxa and the functional group of N_2-fixing lichens concerning their impact on decomposition rates.

In the final chapter (chapter 6, General Discussion), I synthesize the effects of climate change onto vegetation composition in contrasting (sub)arctic ecosystems. The influence of scaling, be it spatial (along gradients), temporal (in climate change experiments) or functional (functional to taxonomical groups), on the output of the analysis is discussed. The consequences of these vegetation shifts are linked to processes such as nutrient resorption and decomposition. Furthermore, other aspects relating to cryptogam community response to climate or their subsequent impact on ecosystem function, not covered or quantified in this thesis, are highlighted. These include biotic interactions (e.g. competition, facilitation, N_2-fixing capacity, herbivory), and abiotic impacts (e.g. on hydrology, permafrost insulation) related to changing plant communities.

References

ACIA (2005) Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.

Adamo, P. & Violante, P. (2000) Weathering of rocks and neogenesis of minerals associated with lichen activity. *Applied Clay Science*, **16**, 229-256.

Aerts, R. (1997) Nitrogen partitioning between resorption and decomposition pathways: a trade-off between nitrogen use efficiency and litter decomposibility? *Oikos*, **80**, 603-606.

Aerts, R., Wallén, B. & Malmer, N. (1992) Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *Journal of Ecology*, **80**, 131-140.

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M. *et al.* (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491-511.

Bates, J.W. (2000) Mineral nutrition, substratum ecology and pollution. *Bryophyte Biology* (eds A.J. Shaw & B. Goffinet), pp. 248-311. Cambridge University Press, Cambridge.

Beringer, J., Lynch, A.H., Chapin, F.S.III, Mack, M. & Bonan, G.B. (2001) The representation of arctic soils in the land surface model: the importance of mosses. *Journal of Climate*, **14**, 3324-3335.

Breen, K. & Lévesque, E. (2008) The influence of biological soil crusts on soil characteristics along a High Arctic glacier foreland, Nunavut, Canada. *Arctic, Antarctic, and Alpine Research*, **40**, 287-297.

Bret-Harte, M.S., Shaver, G.R., Zoerner, J.P., Johnstone, J.F., Wagner, J.L., Chavez, A.S. *et al.* (2001) Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology*, **82**, 18-32.

Callaghan, T.V., Press, M.C., Lee, J.A., Robinson, D.L. & Anderson, C.W. (1999) Spatial and temporal variability in the responses of Arctic terrestrial ecosystems to environmental change. *Polar Research*, **18**, 191-197.

Chapin, D.M. & Bledsoe, C.S. (1992) Nitrogen fixation in arctic plant communities. *Arctic Ecosystems in a Changing Climate* (eds F.S.III Chapin, R.L. Jefferies, J.F. Reynolds *et al.*), pp. 301-319. Academic Press, San Diego.

Chapin, F.S.III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233-260.

Chapin, F.S.III, Bret-Harte, M.S., Hobbie, S.E. & Zhong, H. (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, **7**, 347-358.

Chapin, F.S.III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694-711.

Clymo, R.S. (1998) *Sphagnum*, the peatland carbon economy, and climate change. *Bryology for the Twenty-first Century* (eds J.W. Bates, N.W. Ashton & J.G. Duckett), pp. 361-368. Maney Publishing, Leeds.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A.E. *et al.* (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, **89**, 984-994.

Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A. & During, H.J. (2007a) Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany*, **99**, 987-1001.

Cornelissen, J.H.C., van Bodegom, P.M., Aerts, R., Callaghan, T.V., van Logtestijn, R.S.P., Alatalo, J. *et al.* (2007b) Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters*, **10**, 619-627.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O. *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065-1071.

Coxson, D.S. & Curteanu, M. (2002) Decomposition of hair lichens (*Alectoria sarmentosa* and *Bryoria* spp.) under snowpack in montane forest, Cariboo Mountains, British Columbia. *The Lichenologist*, **34**, 395-402.

Dahlman, L., Persson, J., Palmqvist, K. & Näsholm, T. (2004) Organic and inorganic nitrogen uptake in lichens. *Planta*, **219**, 459-467.

Dorrepaal, E., Toet, S., van Logtestijn, R.S.P., Swart, E., van de Weg, M.J., Callaghan, T.V. *et al.* (2009) Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature*, **460**, 616-619.

Dyrness, C.T. (1982) Control of depth to permafrost and soil temperature by the forest floor in black spruce/feathermoss communities. Research Note PNW-396, pp. 19. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Eckstein, R.L. & Karlsson, P.S. (1999) Recycling of nitrogen among segments of *Hylocomium splendens* as compared with *Polytrichum commune*: implications for clonal integration in an ectohydric bryophyte. *Oikos*, **86**, 87-96.

Elumeeva, T., Soudzilovskaia, N.A., During, H.J. & Cornelissen, J.H.C. (in press) The importance of colony structure versus shoot morphology for the water balance of 22 subarctic bryophyte species. *Journal of Vegetation Science*.

Forbes, B.C., Fauria, M.M. & Zetterberg, P. (2010) Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology*, **16**, 1542-1554.

Gignac, L.D. & Vitt, D.H. (1990) Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of western Canada. *The Bryologist*, **93**, 7-22.

Gitay, H. & Noble, I.R. (1997) What are plant functional types and how should we seek them? *Plant Functional Types: their Relevance to Ecosystem Properties and Global Change* (eds T.M. Smith, H.H. Shugart & F.I. Woodward), pp. 3-19. Cambridge University Press, Cambridge.

Gold, W.G., Glew, K.A. & Dickson, L.G. (2001) Functional influences of cryptobiotic surface crusts in an alpine tundra basin of the Olympic Mountains, Washington, USA. *Northwest Science*, **75**, 315-326.

Gorham, E. (1991) Northern peatlands: role in the carbon cyle and probable responses to climatic warming. *Ecological Applications*, **1**, 182-195.

Gornall, J.L., Jónsdóttir, I.S., Woodin, S.J. & van der Wal, R. (2007) Arctic mosses govern below-ground environment and ecosystem processes. *Oecologia*, **153**, 931-941.

Haag, R.W. (1974) Nutrient limitations to plant production in two tundra communities. *Canadian Journal of Botany*, **52**, 103-116.

Hartley, A.E., Neill, C., Melillo, J.M., Crabtree, R. & Bowles, F.P. (1999) Plant performance and soil nitrogen mineralization in response to simulated climate change in subarctic dwarf shrub heath. *Oikos*, **86**, 331-343.

Hayward, P.M. & Clymo, R.S. (1982) Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. *Proceedings of the Royal Society of London Series B*, **215**, 299-325.

Hébant, C. (1977) The Conducting Tissues of Bryophytes. J. Cramer, Vaduz.

Heijmans, M.M.P.D., Klees, H. & Berendse, F. (2002) Competition between *Sphagnum magellanicum* and *Eriophorum angustifolium* as affected by raised CO_2 and increased N deposition. *Oikos*, **97**, 415-425.

Hobbie, S.E. (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, **66**, 503-522.

Hugonnot, V., Bardat, J. & Boudier, P. (2003) Ecology and distribution of *Jamesoniella undulifolia* (Nees) Mull. Frib. in metropolitan France. *Cryptogamie, Bryologie*, **24**, 341-366.

IPCC (2007) Fourth Assessment report "Climate Change 2007". Cambridge University Press, Cambridge.

Jägerbrand, A.K., Alatalo, J.M., Chrimes, D. & Molau, U. (2009) Plant community responses to 5 years of simulated climate change in meadow and heath ecosystems at a subarctic-alpine site. *Oecologia*, **161**, 601-610.

Jorgenson, M.T., Romanovsky, V., Harden, J., Shur, Y., O'Donnell, J., Schuur, E.A.G. *et al.* (2010) Resilience and vulnerability of permafrost to climate change. *Canadian Journal of Forest Research*, **40**, 1219-1236.

Kade, A. & Walker, D.A. (2008) Experimental alteration of vegetation on nonsorted circles: effects on cryogenic activity and implications for climate change in the Arctic. *Arctic, Antarctic, and Alpine Research*, **40**, 96-103.

Kennedy, A.D. (1995) Temperature effects of passive greenhouse apparatus in high-latitude climate change experiments. *Functional Ecology*, **9**, 340-350.

Kielland, K. (1995) Landscape patterns of free amino acids in arctic tundra soils. *Biogeochemistry*, **31**, 85-98.

Killingbeck, K.T. (1996) Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology*, **77**, 1716-1727.

Krab, E., Cornelissen, J.H.C., Lang, S.I. & van Logtestijn, R.S.P. (2008) Amino-acid uptake among wide-ranging moss species may contribute to their strong position in higher-latitude ecosystems. *Plant and Soil*, **304**, 199-208.

Kytöviita, M.-M. & Crittenden, P.D. (2007) Growth and nitrogen relations in the mat-forming lichens *Stereocaulon paschale* and *Cladonia stellaris*. *Annals of Botany*, **100**, 1537-1545.

Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A. (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution*, **12**, 474-478.

Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J. *et al.* (2008) Peatlands and the carbon cycle: from local processes to global implications - a synthesis. *Biogeosciences*, **5**, 1475-1491.

Longton, R.E. (1988) The Biology of Polar Bryophytes and Lichens. Cambridge University Press, Cambridge.

Lükewille, A. & Wright, R.F. (1997) Experimentally increased soil temperature causes release of nitrogen at a boreal forest catchment in southern Norway. *Global Change Biology*, **3**, 13-21.

MacDonald, N.W., Zak, D.R. & Pregitzer, K.S. (1995) Temperature effects on kinetics of microbial respiration and net nitrogen and sulfur mineralization. *Soil Science Society of America Journal*, **59**, 233-240.

Malmer, N., Albinsson, C., Svensson, B.M. & Wallén, B. (2003) Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. *Oikos*, **100**, 469-482.

Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H. *et al.* (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, **3**, 20-32.

Matveyeva, N. & Chernov, Y. (2000) Biodiversity of terrestrial ecosystems. *The Arctic: Environment, People, Policy* (eds M. Nutall & T.V. Callaghan), pp. 233-273. Harwood Academic Publishers, Reading.

McGuire, A.D., Anderson, L.G., Christensen, T.R., Dallimore, S., Guo, L.D., Hayes, D.J. *et al.* (2009) Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs*, **79**, 523-555.

Molau, U. & Alatalo, J.M. (1998) Responses of subarctic-alpine plant communities to simulated environmental change: biodiversity of bryophytes, lichens, and vascular plants. *Ambio*, **27**, 322-329.

Nakatsubo, T., Uchida, M., Horikoshi, T. & Nakane, K. (1997) Comparative study of the mass loss rate of moss litter in boreal and subalpine forests in relation to temperature. *Ecological Research*, **12**, 47-54.

Nash, T.H.III (1996) Nutrients, elemental accumulation and mineral cycling. *Lichen Biology* (ed T.H.III Nash), pp. 136-153. Cambridge University Press, Cambridge.

Palm, C.A. & Rowland, A.P. (1997) A minimum dataset for characterization of plant quality for decomposition. *Driven by Nature* (eds G. Cadisch & K.E. Giller), pp. 379-392. CABI Publishing, Oxon.

Press, M.C., Potter, J.A., Burke, M.J.W., Callaghan, T.V. & Lee, J.A. (1998) Responses of a subarctic dwarf shrub heath community to simulated environmental change. *Journal of Ecology*, **86**, 315-327.

Quested, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., Aerts, R., Trosien, F. *et al.* (2003) Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology*, **84**, 3209-3221.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**, 365-392.

Rochefort, L., Vitt, D.H. & Bayley, S.E. (1990) Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *Ecology*, **71**, 1986-2000.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E. *et al.* (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543-562.

Rydin, H. & Jeglum, J. (2006) The Biology of Peatlands. Oxford University Press, New York.

Shaver, G.R. & Chapin, F.S.III (1995) Long-term responses to factorial, NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. *Ecography*, **18**, 259-275.

Skre, O. & Oechel, W.C. (1981) Moss functioning in different taiga ecosystems in interior Alaska. I. Seasonal, phenotypic, and drought effects on photosynthesis and response patterns. *Oecologia*, **48**, 50-59.

Smith, R.I.L. (1988) Aspects of cryptogam water relations at a continental antarctic site. *Polarforschung*, **58**, 139-153.

Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) Decomposition in Terrestrial Ecosystems. Blackwell Scientific Publications, Oxford.

Tape, K., Sturm, M. & Racine, C. (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, **12**, 686-702.

Turetsky, M.R., Crow, S.E., Evans, R.J., Vitt, D.H. & Wieder, R.K. (2008) Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. *Journal of Ecology*, **96**, 1297-1305.

Updegraff, K., Bridgham, S.D., Pastor, J., Weishampel, P. & Harth, C. (2001) Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. *Ecological Applications*, **11**, 311-326.

Van Herk, C.M., Aptroot, A. & van Dobben, H.F. (2002) Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *The Lichenologist*, **34**, 141-154.

Van Wijk, M.T., Clemmensen, K.E., Shaver, G.R., Williams, M., Callaghan, T.V., Chapin, F.S.III *et al.* (2003) Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, **10**, 105-123.

Virtanen, R., Oksanen, J., Oksanen, L. & Razzhivin, V.Y. (2006) Broad-scale vegetation-environment relationships in Eurasian high-latitude areas. *Journal of Vegetation Science*, **17**, 519-528.

Wahren, C.H.A., Walker, M.D. & Bret-Harte, M.S. (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, **11**, 537-552.

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M. *et al.* (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 1342-1346.

Wetmore, C.M. (1982) Lichen decomposition in a black spruce bog. *The Lichenologist*, **14**, 267-271.

Wielgolaski, F.E., Bliss, L.C., Svoboda, J. & Doyle, G. (1981) Primary production of tundra. *Tundra Ecosystems: a Comparative Analysis* (eds L.C. Bliss, O.W. Heal & J.J. Moore), pp. 187-225. Cambridge University Press, Cambridge.

Chapter 2

Determinants of cryptogam composition and diversity in *Sphagnum*-dominated peatlands: the importance of temporal, spatial and functional scales

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Journal of Ecology (2009) 97: 299 – 310

Summary

1. Changing temperature regimes and precipitation patterns in the Subarctic will impact on vegetation composition and diversity including those of bryophyte and lichen communities, which are major drivers of high-latitude carbon and nutrient cycling and hydrology.

2. We investigated the relative importance of such impacts at different temporal, spatial and plant functional scales in subarctic *Sphagnum fuscum*-dominated peatlands, comprising both an *in situ* warming experiment and natural climatic and topographic gradients in northern Sweden and Norway. We applied multivariate analyses to investigate the relationships among cryptogam and vascular plant species composition and abiotic (temperature, moisture) and biotic (*Sphagnum* growth) regimes at various scales.

3. At the short-term temporal scale (4-year warming experiment), increased temperature yielded no clear effect on cryptogam or vascular plant species composition. Spatially, direct effects of temperature were decisive for overall species composition across regions (macro-scale) rather than within one region (meso-scale). Moisture and *Sphagnum* growth were drivers of species composition at all spatial scales, and *Sphagnum* growth itself depended on its position on the microtopographic gradient and on temperature.

4. Grouping of bryophytes and lichens at increasing scales of functional aggregation from species, growth form to the major higher taxon level (*Sphagnum*, other mosses, liverworts, lichens) revealed mostly increasing correlation with climate regimes and *Sphagnum* growth. Excluding liverworts from the analysis tended to reduce the correlation.

5. Abundances of lichens, liverworts, non-*Sphagnum* mosses and (to a lesser degree) vascular plants were negatively related to *Sphagnum* abundance. Few cryptogam and vascular plant species showed a positive relationship with *Sphagnum* abundance. Correspondingly, cryptogam species richness and Shannon Index on peatlands strongly declined as *Sphagnum* abundance increased, whilst indices for vascular plants showed no significant relationship.
6. *Synthesis*. Scale, be it spatial or functional, strongly determined which environmental drivers showed the clearest relationships with vegetation composition and diversity. Our findings will help to optimize predictions about long-term effects of climate on peatland vegetation composition, and subsequently its feedbacks to carbon and water cycles, at the regional scale.

Introduction

Climate change at high latitudes, both north and south, is predicted to be of greater impact and progressing more rapidly than in any other region on Earth. In wide regions in the Arctic, not only temperatures but also precipitation are expected to increase (ACIA 2005). In these northern, arctic ecosystems non-vascular cryptogams, i.e. lichens and bryophytes, contribute more to biodiversity than vascular plants (Matveyeva & Chernov 2000). Over extensive areas, cryptogams also exceed vascular plants in abundance and represent the main driver of ecosystem functions (Longton 1997; Cornelissen *et al.* 2007) such as regulation of hydrology (Beringer *et al.* 2001), carbon balance (Rydin & Jeglum 2006), nitrogen fixation (Solheim *et al.* 1996) and preservation of permafrost (Dyrness 1982; Yoshikawa *et al.* 2003). Increasing temperatures and precipitation might induce permafrost melting (Johansson *et al.* 2006; Cheng & Wu 2007), leading, amongst other effects, to a changed hydrology. The growth of cryptogams is highly sensitive to changes in moisture regimes and particularly *Sphagnum* growth is positively related to moisture in the majority of species, albeit in species-specific ways (Weltzin *et al.* 2001; Robroek *et al.* 2007). By building up peat the genus *Sphagnum* accounts for a carbon storage of 600 Gt in northern peatlands, an amount equivalent to all CO_2 stored in the atmosphere (Clymo 1998). Its peat-building ability and increased growth at high moisture regimes may have strong repercussions for the global carbon budget as *Sphagnum* growth may partly counteract the effect of greenhouse gases, thereby making it a potential buffer against climate change.

Given these important roles of cryptogams, and the distinct contributions of different cryptogam species and types to ecosystem functions and climate feedback, predicting the responses of cryptogam diversity and abundance is a high research priority. However,

compared to the great emphasis on vascular plant responses (Arft *et al.* 1999; Van Wijk *et al.* 2004; Walker *et al.* 2006), cryptogams often have been neglected in global change investigations, partly due to difficulties in identification and their small size. From the existing experimental climate manipulation studies we cannot draw conclusions about the general patterns of cryptogam composition or diversity in response to climate change. With few exceptions where cryptogams were identified (partly) to species level (Molau & Alatalo 1998; Press *et al.* 1998; Hollister *et al.* 2005) the existing studies mainly treated bryophytes or lichens as one group (Epstein *et al.* 2004; Wahren *et al.* 2005). Others concentrated on distribution and/or growth of a single species only (Potter *et al.* 1995; Callaghan *et al.* 1997). In contrast to these studies, bryophytes along environmental gradients in peatlands have been studied at species level, focusing on the biodiversity of these systems (e.g. Vitt *et al.* 1995; Gignac *et al.* 1998). Lichens, however, were not included in these studies. Thus, whilst all of the above investigations have addressed components of the large puzzle of peatland cryptogam composition and diversity responses to climatic variation, a more comprehensive and multi-scale study is still lacking.

Climate manipulation experiments and natural climatic gradient studies suggest that the observed responses depend strongly on the temporal, spatial or plant functional scale at which the study is conducted. Short-term experiments were poor predictors of the long-term responses of vascular plants to climate manipulation field experiments (Chapin *et al.* 1995; Shaver *et al.* 2001). This might hold true even more when considering the relatively slowly growing cryptogams. Spatial scales, from local to regional, as demonstrated by Hollingsworth *et al.* (2006), determined the differing environmental drivers of vascular and non-vascular species distribution in a boreal forest (see also Andrew *et al.* 2003). We expect that the magnitude of variation in climatic parameters increases with the coarseness of spatial scale, since microclimate, mesoclimate (as dependent for instance on altitude) and macroclimate (as dependent for instance on maritime influence) each hierarchically contribute their own set of climatic variation to that experienced by any given local community. Epstein *et al.* (2001) showed that by aggregating vascular plant species by species, functional type, life form or vegetation type, functional scale strongly influenced the outcome of the analysis (see also Wright *et al.* 2006). Similarly, Gordon *et al.* (2001) revealed that bryophytes respond to fertilization in different ways, and therefore should not be aggregated into one functional group. Thus, the scale at which a study is conducted, be it temporal, spatial or functional, may determine which environmental drivers are decisive for cryptogam composition and diversity, and to which degree.

The problems associated with scale issues (temporal, spatial or functional) can be overcome in various ways. One approach is to use multi-year experimental manipulations of environment and studies along natural gradients in different regions to explicitly compare responses among different functional grouping schemes. Most climate change studies have been carried out in either experimental setups (Walker *et al.* 2006) or along climatic or hydrological gradients (Gignac & Vitt 1990; Vitt 1990). The combination of approaches may reveal particularly robust insights (Callaghan *et al.* 1999; Cornelissen *et al.* 2001). Here, for the first time, we simultaneously test the importance of temporal, spatial and functional scales as determinants of cryptogam responses to climate. Specifically, we compare the climate responses of cryptogam composition and diversity in subarctic peatlands in an *in situ* warming experiment with natural variation along smaller and larger environmental gradients, and at different levels of species aggregation.

Sphagnum fuscum, of worldwide distribution and one of the most common and abundant bryophytes in boreal-subarctic peatlands (Isoviita 1966), constitutes the dominant peatland cryptogam of both the long-term warming experiment and gradient here. *Sphagnum* growth is known to be strongly influenced by the two direct effects of climate change, increased temperature (Dorrepaal *et al.* 2004) and increased precipitation (Rydin & McDonald 1985) or both (Gunnarsson 2005). The negative and positive interactions of *Sphagnum* with vascular plants have been studied in greater detail (Heijmans *et al.* 2002; Malmer *et al.* 2003) than for cryptogams (Vasander 1981; Hugonnot *et al.* 2003). However, existing studies indicate interactions and dependence of cryptogams on the performance of *Sphagnum* as the underlying growing substrate. Therefore, in the present study we introduced gradients at different scales covering not only the abiotic factors temperature and precipitation, but also the biotic factor *Sphagnum* growth as determinants of species distribution.

We hypothesize that (i) hydrology and temperature, mediated by *Sphagnum* competition, are the main drivers of cryptogam species distribution in *Sphagnum fuscum*-dominated peatlands, (ii) the relative importance of these drivers differs at different spatial, temporal and functional scales and (iii) the cryptogam species composition and diversity of these peatlands strongly depend on the development of *Sphagnum* as the underlying living substrate.

Methods

Central to our study was a climate manipulation experiment on a sloping bog dominated by the peat moss *Sphagnum fuscum*, located in the vicinity of the Abisko Scientific

Research Station, North Sweden and a corresponding climatic natural gradient covering sites from Abisko, North Sweden to Annamo and Andøya, Norway (Fig. 1).

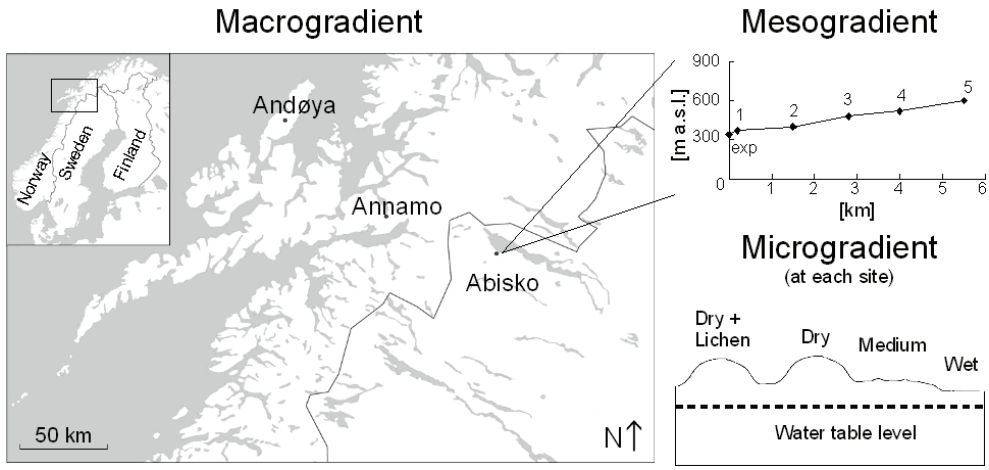

Fig. 1. Location of macrogradient in northern Scandinavia (Andøya, Annamo, Abisko), mesogradient (Abisko: sites one to five), warming experiment and location of plots along the microgradient across macro- and mesogradients.

THE TEMPORAL SCALE STUDY

The experiment at the south shore of Lake Torne (Torneträsk) (68º21'N, 18º49'E, 340 m a.s.l.) was established in June 2000 using open-top chambers (OTC) for passive warming in different seasons and for snow accumulation (details in Aerts *et al.* 2004; Dorrepaal *et al.* 2004). Summer warming was annually from 1 June until the end of September, followed by the winter treatment from the end of September until late April and the spring treatment from late April to 1 June. The winter treatment featured mostly substantial passive snow accumulation, especially in the period January – April, with concomitant buffering of air and soil temperatures (climate details in Aerts *et al.* 2004; Dorrepaal *et al.* 2004). From a larger experimental design, we selected the four combinations of summer, winter and spring treatments which we considered the most relevant for future climate change scenarios: plots with warming all year round, warming in summer and winter, warming in summer only, and the control plots were sampled in 2004 and 2005 (N = 5, Table 1). Vapour pressure deficit did not differ significantly (Dorrepaal *et al.* 2004) in the OTCs *vs.* the control plots.

Table 1. Experimental design and treatment codes used in the climate manipulation experiment (W, warming (with OTC); A, ambient; S, snow accumulation (with OTC); +: treatment applied)

Treatment	Summer	Winter	Spring	Code
1	+	+	+	WSW
2	+	+	-	WSA
3	+	-	-	WAA
4	-	-	-	AAA

THE SPATIAL SCALE STUDY

We studied the effect of spatial scale on cryptogam diversity and abundance at various spatial scales, ranging from macroscale via mesoscale to microscale. The macrogradient consisted of (i) sites from Abisko, Sweden, at altitudes between 370 and 600 m, with a relatively continental climate (annual mean: -0.9 ºC, 301.2 mm, long-term average 1961-1990, continentality index expressed here as eastward distance from ocean: 208 km); (ii) warmer sites in Norway located close to Annamo at about 150 m a.s.l. (68º32'N, 17º13'E, no long-term climate data available, continentality index: 107 km); and (iii) sites on the island Andøya with a typically oceanic climate (annual mean: 4.1 ºC, 870 mm, long-term average 1961-1990, www.met.no, continentality index: 6 km) at about 40 m a.s.l. (69º07'N, 15º52'E). The sites at Abisko, Annamo and on Andøya (Fig. 1) were chosen to aim for the highest similarity in geology and associated abiotic factors such as ion composition of the peat water and soil pH. The mesogradient comprised an altitudinal temperature gradient (370 – 600 m a.s.l.) on the Abisko side of the macrogradient with five sites, chosen at sequentially higher altitudes and thus hypothetically colder than the experiment (which was at the lowest altitude locally, see Appendix S1.1 in Supporting Information). The five sites at 370, 400, 480, 520 and 600 m a.s.l. corresponded to 1973.7, 2085.5, 2060.8, 1806.5 and 1902.3 degree days (measurement see abiotic factors: temperature). The site at the lowest altitude (370 m a.s.l.) displayed degree days which were lower compared to the site at 30 m higher elevation, a phenomenon which is due to the influence of the large water body of Lake Torne (Torneträsk) (T.V. Callaghan, pers. comm.). Also note that the site at the highest altitude was higher in degree days than the site 80 m lower, indicating that local geomorphological and climatic factors, for instance the trapping of cold air in depressions, interfered with the influence of the altitudinal gradient. To study the influence of varying soil moisture on *Sphagnum* and associated cryptogam communities at the microscale, a soil moisture microgradient was established at all sites along the macro- and mesogradients covering the mosaic of plots from (i) very wet hollows (Wet), (ii) medium wet, plane *Sphagnum* surfaces (Medium) to (iii) dry hummocks (Dry) and (iv) dry hummocks in the stage of stagnation in peat production

where *Sphagnum fuscum* is partly dead and lichens start to overgrow the peat mosses (Dry + lichen); for temperature and moisture data see Appendix S1.2.

VEGETATION RECORDING AND PLANT FUNCTIONAL SCALE CLASSIFICATION

Vegetation was recorded in 2004 at the species level by means of the point intercept method (Jonasson 1988). At each microgradient site and each experimental plot, one frame was recorded. The portable aluminium frame covered an area of 50 by 50 cm with nine rows of thirty points each. A bubble level ensured that the frame was horizontal. Two experimental plots were recorded to decide how many points needed to be recorded for an adequate representation of species richness. We chose 270 points for lichens and bryophytes based on species saturation at 270 points per plot in species-rich plots (data not shown). For vascular plants, species saturation occurred at 60 to 150 points (data not shown).The number of hits per plot for vascular plants could thus be reduced to 150. At each point, all hits of vascular plants, lichens and bryophytes were recorded until the pointed tip (Ø < 0.5mm) of the needle touched the ground. Bryophytes, lichens and litter were recorded as first hit only. *Dicranum fuscescens* and *D. elongatum* could not be safely distinguished in the field and were therefore recorded as one species. Tiny liverworts were not further distinguished in the field. *Anastrophyllum minutum*, *Calypogeia sphagnicola*, *Cephalozia bicuspidata*, *Cephalozia leucantha*, *Cephalozia loitlesbergeri, Cephalozia lunulifolia*, *Cladopodiella fluitans* and *Kurzia pauciflora* (or *K. trichoclados*, sterile plants cannot be distinguished) were part of this group. For vascular plants each foliated branch of *Empetrum hermaphroditum* or *Calluna vulgaris* was considered to be one hit since counting every hit leaf would lead to overestimation of abundance. For each vascular plant species the hits per plot were multiplied by 1.8 (270/150 points) to be comparable to the cryptogam data.

Nomenclature followed Hill *et al.* (2006) for all mosses except *Sphagnum*; Daniels & Eddy (1985) for *Sphagna*; Damsholt (2002) for liverworts; Santesson *et al.* (2004) for lichens; and Mossberg & Stenberg (2003) for vascular plants.

The functional scale classification for cryptogams was performed at various levels from species, growth form, major plant taxa to the classification used by Chapin III *et al.* (1996) which is based on vascular plant functional groups and the cryptogam groups *Sphagna*, non-*Sphagnum* mosses and lichens. Species were grouped in growth forms based on their presumed strategy to cope with the growth of *Sphagnum* as the underlying and continuously growing living substrate (species list and classification see Appendix

S2). Liverwort species adapted to active *Sphagnum* growth (erect liverworts) will exhibit vertical growth, which may enable them to keep pace with the growing *Sphagnum* turf, at the same time taking advantage of the micro-habitat created by *Sphagnum*. Albinsson (1997) introduced the term 'compromise strategy' for this adaptation. The 'avoidance strategy', in contrast, is followed by small, prostrate liverwort species that creep over dead *Sphagna* and tend to be typical for peat building stagnation. However, some prostrate liverworts cannot be confined to this avoidance strategy as they occur on living *Sphagna* and exhibit growth rates adapted to the growing *Sphagna* which in turn may be able to uplift them (Albinsson 1997). We classified the liverwort groups with avoidance strategy and those which cannot be confined to the avoidance strategy as prostrate liverworts since their growth form was similar and information on their strategy was not available for all species. We expected erect *vs*. prostrate habit to be relevant for performance in *Sphagnum* turf also for other cryptogams. Thus, cryptogams in our study were grouped into erect and prostrate mosses, liverworts and lichens. We also distinguished crust-forming lichens, which appear indicative of peat building stagnation. Crust-forming lichens also included *Cladonia* cup lichens which, in contrast to other reindeer lichens like *C. arbuscula* that are able to grow upwards as *Sphagnum* advances, are able to build crusts on the peat surface. The moss *Straminergon stramineum* was classified as prostrate, although it exhibits vertical growth inside deeper peat layers. However, attributing this moss to the erect growing mosses such as *Polytrichum* and *Dicranum* seemed unsatisfactory. Vascular plants were grouped into the functional groups of evergreen shrubs, deciduous shrubs, grasses, sedges, forbs and vascular cryptogams (Chapin III *et al.* 1996; Quested *et al.* 2003). Further grouping comprised the major taxa of cryptogams which were defined as *Sphagnum*, mosses, liverworts, lichens and the vascular plant groups used above. The coarsest-scale grouping corresponded to Chapin III *et al.* (1996) with *Sphagnum*, non-*Sphagnum* mosses and lichens as cryptogam groups and the above defined vascular plant functional groups.

THE BIOTIC FACTOR *SPHAGNUM* GROWTH

Sphagnum growth measurements were conducted using the cranked wire method developed by Clymo (1970). In each experimental and microgradient plot, five (experimental plot) or eight (microgradient plot) cranked wires were randomly put out. Measurements were conducted in the summers of 2005 and 2006 starting at the beginning of May and finishing at the end of September. Along the gradient several wires were damaged due to reindeer trampling. The remaining wires (n = 3-8) and the five wires in the experimental plots were averaged before use in the statistical analysis. The temporal differences between sites concerning the measurement of the wires at the beginning and

end of the season were not accounted for, since measurement along the whole gradient always took place within a few days. Furthermore, attributing a growth rate per day would result in a greater error since growth of *Sphagnum* is known to be variable across the growing season and ceases in autumn (own data, not shown, and Dorrepaal *et al.* 2004).

ABIOTIC FACTORS

Temperature

From mid September 2004 until mid August 2005 soil temperature was measured with temperature buttons (MiniTemp Logger, Photologic Ltd., Cobourg, Ontario, Canada) one placed at each site along the macrogradient and in the experimental treatments AAA and WSW. The buttons were protected from moisture damage by putting them into film canisters, sealed with silicone wax. Furthermore, the canister lid was secured with reflecting tape and a thin layer of the surrounding *Sphagna* was arranged on top thus avoiding both heating-up of the canister and human disturbance of the measurement. The top of the canister was at about the same level as the peat surface, integrating temperature over a depth of 0.5 to 5.5 cm in the randomly chosen position at the Dry + lichen, Dry and Medium plots thus only comparing temperature data among the plots which were raised above the water table level. At each site along the macrogradient (except Annamo) and in the same microgradient plots in which the buttons were used the years before, soil temperature was measured at random positions from end of May 2006 until end of August 2006 with two dataloggers and external sensors (Tinytag Plus TGP-0020, PB-5002-1M5 probe, Gemini Data Loggers, Chichester, UK). At Annamo only one logger could be installed. In the warming experiment each of the treatments AAA and WSW was measured in two randomly chosen plots. Soil temperature was recorded at 1 cm depth since we were interested in the effects of temperature on the uppermost growing parts of the cryptogams. The data were averaged per site and treatment. Values for WAA and WSA plots were calculated from the AAA and WSW plots using the appropriate periods for spring, summer and winter treatment when the OTC positions were changed. We used degree days, i.e. the cumulative number of degrees in the measurement period from autumn 2004 to autumn 2006, as a measure for temperature in this study. The temperature threshold at which both bryophytes and lichens might start to be photosynthetically active was estimated to be at 0˚C (Rastorfer 1970; Kappen *et al.* 1996). Consequently, all days of the measurement period with a mean daily temperature exceeding 0˚C were summed resulting in a degree day temperature sum.

Soil moisture and water table level

Soil moisture was manually measured on several days throughout the season by inserting a handheld Time Domain Reflectometry (TDR) soil moisture meter (Trime FM-2, P2G probe, IMKO GmbH, Ettlingen, Germany) vertically into the peat down to 16 cm depth. On each of the four sides of the plot one measurement was taken and all four measurements were averaged. The resulting soil moisture values were averaged for the summers of 2004 through 2006, to account for seasonal variability in peatlands (water table fluctuations see Appendix S3.2). These values were then calibrated for peat soils (Appendix S3.1).

Water table level was recorded at each plot on several occasions. Soil moisture and water table proved to be closely correlated (details see Appendix S3.2). Since not all plots displayed a measurable water table level, soil moisture was used in the analysis.

Nutrient availability

Soil nutrient availability was measured using ion exchange resins in summer 2004 and 2005 according to Weih (1998). The cation (CEM) and anion (AEM) resins were saturated with H^+ using 0.1 M H_2SO_4 and with Cl^- using 2 M NaCl, respectively (Giblin *et al.* 1994). We deviated from Weih (1998) by inserting the resins vertically into the peat at approx. 10 cm depth around 28 May 2006 (± 1d). At the end of the growing season around 16 Sept. 2006 (± 5d), the resins were returned to the laboratory and extracted with 20 mL of 2 M NaCl in 0.1 M HCl (Giblin *et al.* 1994) by shaking for 2 hours. The extracts were subsequently analysed for nitrate, ammonium and phosphate. Ammonium was measured photometrically with an indicator (Tecator Application note AN 134/91) using a flow injection autoanalyzer (Tecator, FIAstar 5020 Analyzer, 5032 Detector Controller, Foss, Rellingen, Germany). Phosphate was analysed photometrically with the molybdenum-blue method (Tecator Application note AN 146/90) using a flow injection autoanalyser (Tecator, Aquatec 5400 Analyser, Foss, Rellingen, Germany). Ca^{2+} and Mg^{2+} were extracted using 2 M HCl. Extracts were subsequently measured by atomic absorption (Varian AAS SpectrAA 220FS, Palo Alto, CA, USA) in an air-acetylene flame under addition of $LaCl_3$ and CsCl to suppress spectral and non-spectral interferences. The difference in exposure time to the soil due to temporal differences in burial and excavation time at each site was not taken into account since the resins were buried and excavated within a few days along all the gradients and at the experiment.

Supplementary to the resin assays, soil cores with a cross-sectional area of 7.55 cm^2 and 10 cm depth per plot were taken during the period of late August to early September 2006

for measurement of extractable nitrate and ammonium. Live roots were removed from the samples before taking an aliquot of soil to be extracted with 1 M KCl solution. The samples were shaken for one hour and subsequently filtered using a Whatman GF/C glass fiber filter. Ammonium and nitrate were measured photometrically by means of the indophenolblue method and the sulfanylamide/naphtyl–ethylene–diamine method, respectively (Skalar SA-40 continuous flow analyzer, Skalar, Breda, The Netherlands). Phosphate was measured photometrically (Shimadzu, UV-1601PC, Shimadzu Corp., Kyoto, Japan) by means of the molybdenum-blue method.

Soil pH was measured in the 1M KCl soil core extracts received for the nutrient analysis using a pH meter (WTW Inolab Level 2 pH meter, Sentix 41 membrane glass electrode, WTW Weilheim, Germany).

STATISTICAL ANALYSIS

Vegetation abundance data from point-intercept recordings were analysed by redundancy analysis (RDA) using CANOCO for Windows 4.5 (Ter Braak & Šmilauer 2002), because the gradients explored in this paper are not sufficiently long to require unimodal methods (gradient lengths for all analyses ranged between 1 and 2). Also, RDA is particularly suited for detecting small systematic changes in the data. Species data were centred and log-transformed prior to analysis. Environmental variables used in the analysis were degree days, soil moisture, *Sphagnum* growth, soil pH, Ca^{2+}, Mg^{2+} and phosphate concentrations (ion resins) and extractable nitrate and ammonium. Only the variables degree days, soil moisture and *Sphagnum* growth yielded a significant result in the Monte Carlo Permutation Test (9999 permutations) and were thus employed in further analysis. When testing the environmental variables for the experiment the plots were freely permuted. Along the gradient one datalogger (or the mean of two dataloggers) per site was used. The plots at each site were therefore not independent and a split-plot design was applied with the sites being the whole plots and the plots within one site the split plots. When testing for effects of degree days, the whole plots were freely permuted and the split plots kept constant. To test for contributions of moisture and *Sphagnum* growth, the whole plots were kept constant and the split plots freely permuted. Variables were tested on entry in the model in a forward selection. To test the influence of grouping (functional scale) of the vegetation data on the analysis, the data were analysed separately at species and higher grouping levels. These groupings (see above) comprised growth forms, major cryptogam taxa and vascular plant groups, and the grouping according to Chapin III *et al.* (1996). In the latter case vascular cryptogams were neglected since they do not appear in their analysis and were represented here by very few data points.

The dependence of *Sphagnum* growth rate on abiotic and partly biotic factors was tested in linear (multiple) regressions (SPSS 14.0 for Windows). Degree days and soil moisture represented the independent abiotic variables whereas the nominal variable microgradient accounted for not only the abiotic factor soil moisture but also the biotic factor of competition/interaction with other cryptogams/vascular plants given a specific microtopographic position. The microgradient consisted of the four categories Dry + lichen, Dry, Medium and Wet with increasing numbers of 1 to 4. The experimental plots were grouped into the Dry + lichen and Dry microgradient categories according to their soil moisture. Lichen cover along the gradient reached up to two hits per plot in the Dry category. Consequently, experimental plots where lichen cover exceeded two hits were allocated to the Dry + lichen category, whereas plots with two or less lichen hits were attributed to the Dry category.

We applied linear regression to test for relationships between major taxa of cryptogams, vascular plant abundance or overall diversity indices compared to *Sphagnum* abundance. *Sphagnum* itself was excluded when calculating the diversity indices species richness and Shannon Index.

Results

TEMPORAL SCALE

There were no significant treatment effects of the 4-yr warming experiment on community composition, as tested in an RDA at species, growth form and major taxa level. However, a trend ($P = 0.096$) could be seen for summer warming when regarding major taxa (Table 2). A further RDA at growth form level showed that the environmental variables moisture and *Sphagnum* growth were significant determinants of community composition ($P = 0.004$ and 0.019, respectively). Degree days were not significant ($P = 0.95$; Table 3).

Table 2. *P*-values of treatment effects on cryptogam and vascular plant composition at different levels of grouping (RDA; Monte Carlo Test: 9999 permutations). Order of the variables entering the model: a – c

Grouping level	Summer warming	Spring warming	Winter snow accumulation
Major taxa	0.096[a]	0.52[b]	0.81[c]
Growth form	0.17[a]	0.67[b]	0.89[c]
Species	0.24[a]	0.94[c]	0.65[b]

Table 3. *P*-values of the first canonical axis and environmental variables (RDA; Monte Carlo Test: 9999 permutations) at species, growth form, major taxa and Chapin III *et al.* (1996) grouping level of the warming experiment and the mesogradient and macrogradient (both including the microgradient). Significant *P*-values are marked with bold letters. Superscript a–c: order of the variables entering the model

Functional scale of diversity		Warming experiment *	Mesogradient (including microgradient) †‡	Macrogradient (including microgradient) †‡
Species	all axes	**0.0386**	**0.0002**	**0.0001**
Growth form		**0.0039**	**0.0005**	**0.0020**
Major taxa		**0.0009**	**0.0003**	**0.0001**
Chapin III *et al.* 1996		**0.0027**	**0.0005**	**0.0001**
Species	Moisture	**0.014**[a]	**0.0004**[a]	**0.0001**[b]
Growth form		**0.004**[a]	**0.0006**[a]	**0.0006**[a]
Major taxa		**0.001**[a]	**0.0004**[a]	**0.0005**[a]
Chapin III *et al.* 1996		**0.005**[a]	**0.015**[b]	**0.0014**[a]
Species	*Sphagnum* growth	0.077[b]	**0.049**[b]	**0.008**[c]
Growth form		**0.019**[b]	**0.015**[b]	**0.006**[c]
Major taxa		**0.0097**[b]	**0.006**[b]	**0.004**[c]
Chapin III *et al.* 1996		**0.011**[b]	**0.003**[a]	**0.009**[c]
Species	Degree days	0.94[c]	0.16[c]	**0.026**[a]
Growth form		0.95[c]	0.64[c]	**0.033**[b]
Major taxa		0.91[c]	0.68[c]	**0.029**[b]
Chapin III *et al.* 1996		0.93[c]	0.69[c]	**0.045**[b]

*: Free permutation

†: Testing of degree days: whole plots permuted at random, split plots constant

‡: Testing of canonical axes, moisture, *Sphagnum* growth: whole plots constant, split plots permuted at random

SPATIAL SCALE

Microgradient

Of the possible independent variables, only the nominal variable, microgradient, explained *Sphagnum* growth significantly ($P = 0.005$; $R^2 = 0.16$), in contrast to moisture ($P = 0.31$; $R^2 = 0.02$) and degree days ($P = 0.30$; $R^2 = 0.02$). In a multiple linear regression, degree days and soil moisture were not related to *Sphagnum* growth ($P = 0.22$; $R^2 = 0.07$) whereas the variables microgradient ($P = 0.001$) and degree days ($P = 0.035$) contributed significantly to the overall significant regression ($P = 0.002$; adjusted $R^2 = 0.21$).

Meso- and macrogradient

Redundancy analysis revealed that for the meso- and the macrogradient soil moisture and *Sphagnum* growth proved to be significant determinants of community composition.

Degree days, however, were only significant at macrogradient scale (Table 3). Abundance of prostrate mosses, sedges, vascular cryptogams and *Sphagna* was positively correlated with moisture for the mesogradient, and negatively with forbs, shrubs, erect mosses, liverworts and grasses (Fig. 2). This relationship was reversed for degree days. Sedges, grasses, vascular cryptogams, prostrate lichens, prostrate mosses and *Sphagna* were positively correlated with *Sphagnum* growth, and shrubs, forbs, erect mosses, liverworts and erect and crust-forming lichens negatively. Along the macrogradient a similar picture was revealed. Prostrate mosses, sedges, *Sphagna* and vascular cryptogams were positively correlated to moisture, degree days and *Sphagnum* growth (Fig. 2), while forbs, shrubs, lichens, liverworts and erect mosses corresponded negatively to the environmental variables. Grasses were negatively related to moisture and degree days, but positively to *Sphagnum* growth.

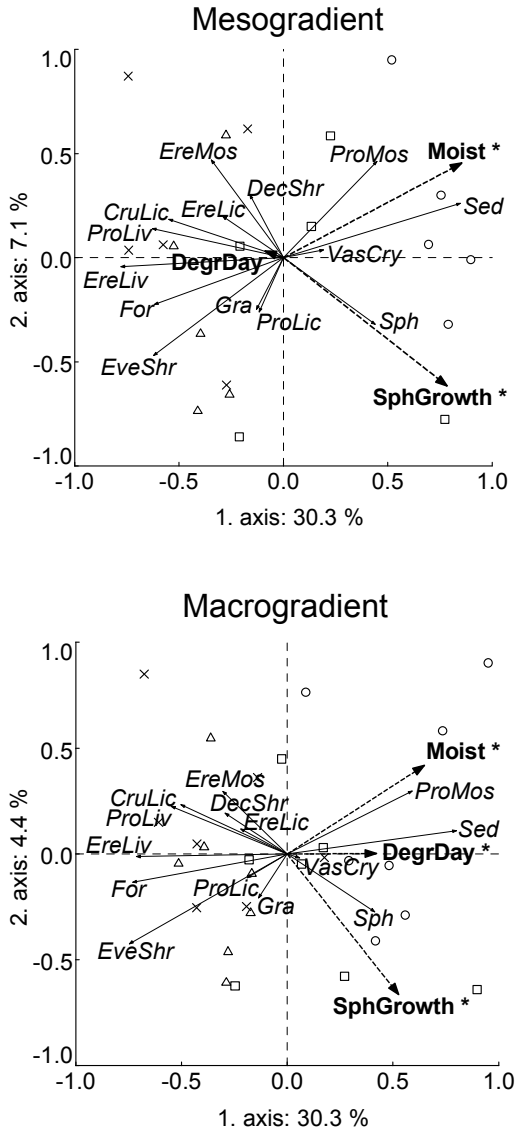

Fig. 2. RDA ordination of the mesogradient and the macrogradient (× Dry + lichen, Δ Dry, □ Medium, ○ Wet). Significant environmental variables are marked with an asterisk (Monte Carlo Test: 9999 permutations; Table 3). Growth form, functional group and environmental variable abbreviations: Sph = *Sphagnum*; Sed = sedge; gra = grass; for = forb; ProLic = prostrate lichen; ProLiv = prostrate liverwort; ProMos = prostrate moss; CruLic = crust-forming lichen; DecShr = deciduous shrub; EreLic = erect lichen; EreLiv = erect liverwort; EreMos = erect moss; EveShr = evergreen shrub; VasCry = vascular cryptogam; Moist = moisture; DegrDay = degree days; SphGrowth = *Sphagnum* growth.

FUNCTIONAL SCALE

When comparing community composition across different plant functional scales, the canonical axes of the RDA were significant at all levels, but to various extents (Table 3). Moisture as an important environmental factor was significant at all scales from temporal (warming experiment) to spatial (both gradients) and functional (all grouping levels). Except for the warming experiment at species level, *Sphagnum* growth showed significance at all temporal, spatial and functional scales whereas degree days were only significant at the macrogradient scale. Grouping species up to major taxa level enhanced the significance of the variable *Sphagnum* growth at all levels and moisture at the experimental level. At the mesogradient level, the significance of moisture decreased when introducing growth forms and was not influenced at major taxa level. For degree days, introduction of growth forms seemed to decrease the significance of the variable at all levels whereas at major taxa level, significance slightly improved. With the exception of the mesogradient scale, where significance of *Sphagnum* growth improved, all variables showed a decrease in significance when applying the Chapin III *et al.* (1996)-grouping, which excludes liverworts from the analysis.

RELATION OF ABUNDANCE OF MAJOR TAXA AND DIVERSITY INDICES VS. *SPHAGNUM* ABUNDANCE

The abundances of all four main taxonomic groups, *viz.* mosses, liverworts, lichens and vascular plants were all highly significantly, negatively correlated with *Sphagnum* abundance (Fig. 3). Dry + lichen plots were located at sites where *Sphagnum* is less abundant whereas plots of high *Sphagnum* abundance tended to be increasingly wet. No clear pattern of the experimental plots concerning treatment was visible.

For the cryptogams, the Shannon diversity and species richness were highly significant and negatively related to the abundance of *Sphagnum* (Fig. 3). With increasing soil moisture, i.e. from Dry to Wet plots, *Sphagnum* abundance increased and Shannon Index and species richness decreased. No clear pattern was observed in the experimental plots. Regarding vascular plants, no significant trend could be observed.

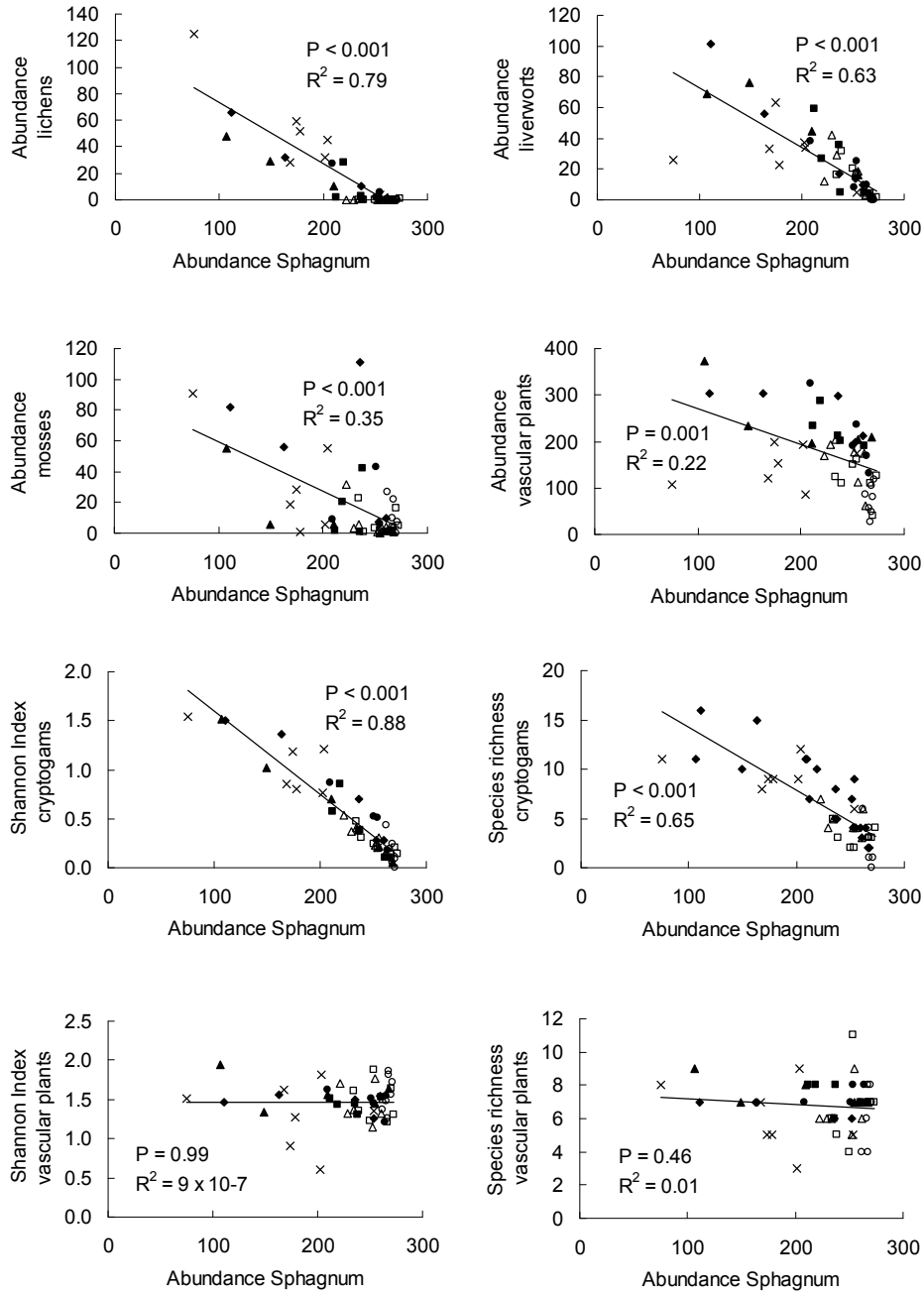

Fig. 3. Relationship of mosses, liverworts, lichens, vascular plants, Shannon Index and species richness (indices excluding *Sphagnum*) of cryptogams and vascular plants *vs.* abundance of *Sphagnum* (× Dry + lichen, Δ Dry, □ Medium, ○ Wet, ♦ AAA, ▲ WAA, ■ WSA, ● WSW, treatment codes see Table 1; n = 48).

Discussion

Our aim was to show how the most important climatic variables (temperature and moisture availability) and the biotic factor *Sphagnum* growth determine the distribution of cryptogams at various spatial, functional and temporal scales in northern peatlands.

We are the first to demonstrate how the importance of these different key determinants of cryptogam composition and diversity in northern *Sphagnum*-dominated peatlands varies according to scales of space and species aggregation. The four-year time scale of our *in situ* climate warming experiment, however, was likely too short to reveal any obvious responses.

THE IMPORTANCE OF TEMPORAL SCALE

The experimental warming treatments did not induce direct changes in vegetation composition (Table 2). However, *Sphagnum* growth, which itself is influenced by temperature, was significant as an environmental driver in the experiment (Table 3). Dorrepaal *et al.* (2004) also showed that *Sphagnum* growth in the same experimental plots increased significantly due to summer warming. The non-responsiveness of the peatland cryptogam composition to summer and spring warming and winter snow accumulation might be due to still prevailing initial heterogeneity among plots (Bates *et al.* 2005), short duration of experimental treatments, growth form and growth rate of cryptogam species and natural succession in mires. The four-year time scale of treatment may have been too short to reveal significant responses of the generally long-lived, slow-growing non-vascular cryptogams. Similarly, in a warming and fertilisation experiment in a boreal mire, there were no responses to experimental treatments over four years, whilst both bryophytes and vascular plants were affected over eight years (Wiedermann *et al.* 2007). Cryptogams growing vertically might have experienced an amplified height increment in response to the experimental treatments. However, proliferation of growing points would take longer to be detectable in the horizontal dimension we measured. Furthermore, the small size of most cryptogams can be expected to result in overall lower growth rates in contrast to vascular plants. Finally, peatlands are subject to natural succession (Gunnarsson *et al.* 2002; Malmer *et al.* 2005), which might impose stronger driving forces on vegetation composition compared to experimental treatments.

THE IMPORTANCE OF SPATIAL SCALE

As we expected, each spatial scale contributed its own environmental variation to the microclimate experienced by a given *Sphagnum* bog community, so that differences between two adjacent communities have come about in a consistently different way than

differences between two distant communities. Despite our efforts to choose sites homogeneous in abiotic factors, the possibility remains that environmental variables other than temperature may have contributed to the overall temperature effect. Differences in salt and N deposition or bedrock geology, although below detection limit, could be influencing vegetation composition. Also, different glacial histories might have influenced re-colonisation, the Caledonian mountain chain in our macrogradient being a possible barrier for spreading plants, shaping plant distribution as we know it today. However, at least the predominant species in our study are of widespread distribution in both Sweden and Norway and, unlike establishment which might be a limiting factor for species distribution, dispersal is unlikely to have put a major biogeographical constraint on present-day vascular plant community composition (cf. Alsos *et al.* 2007).

At the microgradient scale*, Sphagnum* growth depended mainly on microtopography, this factor including moisture and possible species interactions, and, to a lesser extent, on temperature. Correspondingly, Asada *et al.* (2003) reported that growth of *S. fuscum* on hummocks is mainly influenced by precipitation and less by temperature, unless temperatures fall below 0ºC. The positive effect of temperature on growth of *S. fuscum* at low temperatures (as opposed to at higher temperatures; see Robroek *et al.* 2007), has been reported from the Subarctic previously (Sonesson *et al.* 2002; Dorrepaal *et al.* 2004). The importance of microtopography and related soil moisture on the performance of *Sphagna* has been shown in various studies (e.g. Pederson 1975; Rydin 1993). Also, studies of species composition (e.g. Kvillner & Sonesson 1980; Bragazza & Gerdol 1996) recognised microtopography and/or related soil moisture/water table level as the most important factor for bryophyte distribution. Climate change-induced temperature increases can, under subarctic conditions, result in increased growth rates of *S. fuscum* if soil moistures are high enough and the peat mosses are in a favourable topographical position.

As shown for the warming experiment, soil moisture and *Sphagnum* growth were also significant determinants of species distribution at the mesogradient scale in Abisko (Table 3). The altitudinal gradient in Abisko comprises the area of present-day *S. fuscum* distribution here. Temperatures can be expected to vary from 0.9 - 2.3 K on the chosen altitudinal gradient of 230 m (0.4-1K per 100m, Körner 1999), well within predicted climate change scenarios for this century (ACIA 2005). This small temperature range is unlikely to have a clear direct impact on species composition. However, temperature-driven growth enhancement of *Sphagnum* may lead to expansion of small *Sphagnum* islands at the border of present peatland distribution if soil moisture is sufficient. Within current peatlands in Abisko, long-term changes in vegetation composition are likely to be

mainly influenced by hydrology and *Sphagnum* growth which in turn is influenced mainly by microtopography and partly by temperature. Locally, on palsas, temperature-induced permafrost degradation may further influence vegetation composition (Camill 1999; Malmer *et al.* 2005).

At the macrogradient scale, including both the Swedish and Norwegian sites, temperature as an abiotic driver gains significance for species distribution. The 5 K difference in annual mean temperatures between Abisko and Andøya corresponds with the upper end of climate-warming predictions for this century (ACIA 2005). As suggested by our results and previous studies at the climatic macrogradient scale (e.g. Gignac *et al.* 1991; Vitt *et al.* 1995), such a temperature range may well cause changes in cryptogam species composition. Combining the above patterns, we are the first to reveal how the relative contributions of different environmental drivers to cryptogam composition vary with spatial scale.

THE IMPORTANCE OF FUNCTIONAL SCALE

The various functional classification schemes in this study show that species aggregation affects and even enhances the relationships between environmental drivers and cryptogam composition, up to the major taxa level where lichens, liverworts, mosses and *Sphagna* are distinguished within the cryptogam group (Table 3, Fig. 3). Cryptogam species are often single finds in a specific habitat. Summarising similar growth forms can therefore reveal functional responses of species groups with regard to environmental factors which otherwise would remain hidden. For instance, *Sphagnum* growth in the warming experiment only gains significant explanatory power of cryptogam composition when species are aggregated into growth forms (Table 3). Excluding liverworts from the analysis according to the grouping by Chapin III *et al.* (1996) slightly reduces this power. Since identifying cryptogams is a time-intensive and often difficult task, our suggested minimum requirement for understanding peatland cryptogam composition is the distinction of the easily recognised major taxa: lichens, liverworts, mosses and *Sphagna*.

SPHAGNUM DRIVES PEATLAND CRYPTOGAM SPECIES DIVERSITY AND ABUNDANCE

Increasing *Sphagnum* abundance strongly reduces the performance of lichens, liverworts and mosses (Fig. 3). Furthermore, *Sphagnum* growth is a strong driver of cryptogam composition in peatlands (Table 3). Vasander (1981) reported lower growth rates for reindeer lichens than for *Sphagna* (Pakarinen 1978), indicating that lichens can only persist in places where *Sphagnum* ceases growing. The Dry + lichen plots with low

Sphagnum growth rates (Appendix S1.2), likely due to frost disturbance during winter when the hummocks are blown snow-free, confirm this reasoning. Similarly, liverworts can only invade hummocks when *Sphagnum* growth is reduced (Pakarinen 1978; Hugonnot *et al.* 2003). We observed a strong reduction of liverwort abundance in fast-growing *Sphagnum* hollows in Abisko. Mosses, e.g. *Dicranum elongatum*, a typical companion of *S. fuscum* in subarctic mires in the Abisko area, are outcompeted in growth when precipitation increases (Sonesson *et al.* 2002). Accordingly, the highest abundances for non-*Sphagnum* mosses are found in the driest locations (Fig. 3). Negative relations between vascular plants and *Sphagna* (Heijmans *et al.* 2002; Malmer *et al.* 2003) are in our study mainly driven by deciduous and evergreen shrubs compensating for the positive relationship of sedges and vascular cryptogams.

The negative relation of overall Shannon Index and species richness with *Sphagnum* abundance (data see Appendix S1.2) is strongly driven by decreasing cryptogam abundance (Fig. 3). The wetter the plots the fewer cryptogam species are able to compete with *Sphagnum*. In the case of lichens, direct negative effects of substrate moisture are also likely to play a role, since most northern lichens tend to be found in relatively dry (micro-)sites (Robinson *et al.* 1989; Williams & Rastetter 1999). Vascular plant species richness and Shannon Index, however, are unaffected by increasing *Sphagnum* abundance (Fig. 3) as the increasing numbers of sedge species compensate for the decreasing numbers of shrub species in wetter plots. The importance of microtopography for species richness of mosses and liverworts has also been found in swamp forests, where vascular plants were hardly affected by relief either (Økland *et al.* 2008). Thus, in subarctic regions a warmer and wetter climate might locally, depending on microtopography, trigger *Sphagnum*-mediated declines in species diversity. Permafrost thaw and intense rain events, however, may lead to an increase in surface cover of wet graminoid dominated vegetation (Christensen *et al.* 2004) and open water bodies, so that an altogether different vegetation pattern can be expected.

Conclusions

The relative contributions of different climatic (temperature, hydrology) and biotic (*Sphagnum* growth) determinants of peatland vegetation composition in the European Subarctic strongly depend on the scale at which a study is conducted. Soil moisture and *Sphagnum* growth operate as determinants at all spatial scales, whereas temperature only discriminates in a cross-regional comparison. Responses of *Sphagnum* growth or abundance in turn impact strongly on cryptogam diversity and species richness. Peatland cryptogam responses to field manipulations of climate are too slow to reveal substantial

shifts in species composition in short-term (4-yr) experiments. Aggregating species groups at various functional scales helps to summarize the driving forces of cryptogam and vascular plant composition in *Sphagnum*-dominated peatlands. Combining responses and variation of species composition at different temporal, spatial and functional scales will turn out to be most helpful for extrapolating vegetation responses to climate change from the plot to the landscape or regional scale.

Acknowledgements

We would like to acknowledge the Abisko Scientific Research Station which financially supported this work and provided facilities; and several staff members who helped to maintain the experiment. Many thanks to Mats Sonesson for his invaluable discussions and advice concerning the vegetation recording. We are indebted to the Staatliches Museum für Naturkunde Karlsruhe for their generous technical and laboratory support and the provision of work space to S.L.. Many thanks to the FAZIT-STIFTUNG for providing financial support to S.L., enabling completion of this investigation. Ellen Dorrepaal is acknowledged for maintenance of the experiment; Richard S. P. van Logtestijn and Marc Rosskopf for providing technical support. We would like to acknowledge the employees of the Lantbrukskontoret on Andøya for kind permission to work on their peatland property. This study was financed by grant ALW-852.00.070 of the Netherlands Organisation for Scientific Research (NWO).

References

ACIA (2005) *Arctic Climate Impact Assessment: Scientific Report*. Cambridge University Press, Cambridge.

Aerts, R., Cornelissen, J.H.C., Dorrepaal, E., van Logtestijn, R.S.P. and Callaghan, T.V. (2004) Effects of experimentally imposed climate scenarios on flowering phenology and flower production of subarctic bog species. *Global Change Biology*, **10**, 1599-1609.

Albinsson, C. (1997) Niche relations and association analysis of southern Swedish mire hepatics. *Journal of Bryology*, **19**, 409-424.

Alsos, I.G., Eidesen, P.B., Ehrich, D., Skrede, I., Westergaard, K., Jacobsen, G.H. *et al.* (2007) Frequent long-distance plant colonization in the changing Arctic. *Science*, **316**, 1606-1609.

Andrew, N.R., Rodgerson, L. and Dunlop, M. (2003) Variation in invertebrate-bryophyte community structure at different spatial scales along altitudinal gradients. *Journal of Biogeography*, **30**, 731-746.

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M. *et al.* (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491 - 511.

Asada, T., Warner, B.G. and Banner, A. (2003) Growth of mosses in relation to climate factors in a hypermaritime coastal peatland in British Columbia, Canada. *The Bryologist*, **106**, 516-527.

Bates, J.W., Thompson, K. and Grime, J.P. (2005) Effects of simulated long-term climatic change on the bryophytes of a limestone grassland community. *Global Change Biology*, **11**, 757-769.

Beringer, J., Lynch, A.H., Chapin III, F.S., Mack, M. and Bonan, G.B. (2001) The representation of arctic soils in the land surface model: the importance of mosses. *Journal of Climate*, **14**, 3324-3335.

Bragazza, L. & Gerdol, R. (1996) Response surfaces of plant species along water-table depth and pH gradients in a poor mire on the southern Alps (Italy). *Annales Botanici Fennici*, **33**, 11-20.

Callaghan, T.V., Carlsson, B.Å., Sonesson, M. and Temesváry, A. (1997) Between-year variation in climate-related growth of circumarctic populations of the moss *Hylocomium splendens*. *Functional Ecology*, **11**, 157-165.

Callaghan, T.V., Press, M.C., Lee, J.A., Robinson, D.L. and Anderson, C.W. (1999) Spatial and temporal variability in the responses of Arctic terrestrial ecosystems to environmental change. *Polar Research*, **18**, 191-197.

Camill, P. (1999) Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal of Botany*, **77**, 721-733.

Chapin III, F.S., Bret-Harte, M.S., Hobbie, S.E. and Zhong, H.L. (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science*, **7**, 347-358.

Chapin III, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. and Laundre, J.A. (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694-711.

Cheng, G.D. & Wu, T.H. (2007) Responses of permafrost to climate change and their environmental significance, Qinghai-Tibet Plateau. *Journal of Geophysical Research*, **112**, F02S03, doi:10.1029/2006JF000631.

Christensen, T.R., Johansson, T.R., Åkerman, H.J., Mastepanov, M., Malmer, N., Friborg, T. *et al.* (2004) Thawing sub-arctic permafrost: Effects on vegetation and methane emissions. *Geophysical Research Letters*, **31**, L04501, doi:10.1029/2003GL018680.

Clymo, R.S. (1970) The growth of *Sphagnum*: methods of measurement. *Journal of Ecology*, **58**, 13-49.

Clymo, R.S. (1998) *Sphagnum*, the peatland carbon economy, and climate change. *Bryology for the Twenty-first Century* (eds J.W. Bates, N.W. Ashton and J.G. Duckett), pp. 361-368. Maney Publishing, Leeds.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A.E. *et al.* (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, **89**, 984-994.

Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A. and During, H.J. (2007) Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany*, **99**, 987-1001.

Damsholt, K. (2002) *Illustrated Flora of Nordic Liverworts and Hornworts*. Nordic Bryological Society, Lund.

Daniels, R.E. & Eddy, A. (1985) *Handbook of European Sphagna*. Institute of Terrestrial Ecology, Huntingdon.

Dorrepaal, E., Aerts, R., Cornelissen, J.H.C., Callaghan, T.V. and van Logtestijn, R.S.P. (2004) Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-arctic bog. *Global Change Biology*, **10**, 93-104.

Dyrness, C.T. (1982) Control of depth to permafrost and soil temperature by the forest floor in black spruce/feathermoss communities. Research Note PNW-396, pp. 19. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Epstein, H.E., Calef, M.P., Walker, M.D., Chapin III, F.S. and Starfield, A.M. (2004) Detecting changes in arctic tundra plant communities in response to warming over decadal time scales. *Global Change Biology*, **10**, 1325-1334.

Epstein, H.E., Chapin III, F.S., Walker, M.D. and Starfield, A.M. (2001) Analyzing the functional type concept in arctic plants using a dynamic vegetation model. *Oikos*, **95**, 239-252.

Giblin, A.E., Laundre, J.A., Nadelhoffer, K.J. and Shaver, G.R. (1994) Measuring nutrient availability in arctic soils using ion-exchange resins - a field test. *Soil Science Society of America Journal*, **58**, 1154-1162.

Gignac, L.D., Nicholson, B.J. and Bayley, S.E. (1998) The utilization of bryophytes in bioclimatic modeling: present distribution of peatlands in the Mackenzie River Basin, Canada. *The Bryologist*, **101**, 560-571.

Gignac, L.D. & Vitt, D.H. (1990) Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of western Canada. *The Bryologist*, **93**, 7-22.

Gignac, L.D., Vitt, D.H., Zoltai, S.C. and Bayley, S.E. (1991) Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada. *Nova Hedwigia*, **53**, 27-71.

Gordon, C., Wynn, J.M. and Woodin, S.J. (2001) Impacts of increased nitrogen supply on high Arctic heath: the importance of bryophytes and phosphorus availability. *New Phytologist*, **149**, 461 - 471.

Gunnarsson, U. (2005) Global patterns of *Sphagnum* productivity. *Journal of Bryology*, **27**, 269-279.

Gunnarsson, U., Malmer, N. and Rydin, H. (2002) Dynamics or constancy in *Sphagnum* dominated mire ecosystems? A 40-year study. *Ecography*, **25**, 685-704.

Heijmans, M.M.P.D., Klees, H. and Berendse, F. (2002) Competition between *Sphagnum magellanicum* and *Eriophorum angustifolium* as affected by raised CO_2 and increased N deposition. *Oikos*, **97**, 415-425.

Hill, M.O., Bell, N., Bruggeman-Nannenga, M.A., Brugués, M., Cano, M.J., Enroth, J. *et al.* (2006) An annotated checklist of the mosses of Europe and Macaronesia. *Journal of Bryology*, **28**, 198-267.

Hollingsworth, T.N., Walker, M.D., Chapin III, F.S. and Parsons, A.L. (2006) Scale-dependent environmental controls over species composition in Alaskan black spruce communities. *Canadian Journal of Forest Research*, **36**, 1781-1796.

Hollister, R.D., Webber, P.J. and Tweedie, C.E. (2005) The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Global Change Biology*, **11**, 525 - 536.

Hugonnot, V., Bardat, J. and Boudier, P. (2003) Ecology and distribution of *Jamesoniella undulifolia* (Nees) Mull. Frib. in metropolitan France. *Cryptogamie Bryologie*, **24**, 341-366.

Isoviita, P. (1966) Studies on *Sphagnum* L. I. Nomenclatural revision of the European taxa. *Annales Botanici Fennici*, **3**, 199-264.

Johansson, M., Christensen, T.R., Akerman, H.J. and Callaghan, T.V. (2006) What determines the current presence or absence of permafrost in the Torneträsk region, a sub-arctic landscape in Northern Sweden? *Ambio*, **35**, 190-197.

Jonasson, S. (1988) Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, **51**, 101 - 106.

Kappen, L., Schroeter, B., Scheidegger, C., Sommerkorn, M. and Hestmark, G. (1996) Cold resistance and metabolic activity of lichens below 0 C. *Adv. Space Res.*, **18**, 119 - 128.

Körner, C. (1999) *Alpine Plant Life*. Springer, Berlin.

Kvillner, E. & Sonesson, M. (1980) Plant distribution and environment of a subarctic mire. *Ecological Bulletins*, **30**, 97-111.

Longton, R.E. (1997) The role of bryophytes and lichens in polar ecosystems. *Ecology of Arctic Environments* (eds S.J. Woodin and M. Marquiss), pp. 69-96. Blackwell Science, Oxford.

Malmer, N., Albinsson, C., Svensson, B.M. and Wallén, B. (2003) Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. *Oikos*, **100**, 469-482.

Malmer, N., Johansson, T., Olsrud, M. and Christensen, T.R. (2005) Vegetation, climatic changes and net carbon sequestration in a North-Scandinavian subarctic mire over 30 years. *Global Change Biology*, **11**, 1895-1909.

Matveyeva, N. & Chernov, Y. (2000) Biodiversity of terrestrial ecosystems. *The Arctic: environment, people, policy* (eds M. Nutall and T.V. Callaghan), pp. 233-273. Harwood Academic Publishers, Reading.

Molau, U. & Alatalo, J.M. (1998) Responses of subarctic-alpine plant communities to simulated environmental change: Biodiversity of bryophytes, lichens, and vascular plants. *Ambio*, **27**, 322-329.

Mossberg, B. & Stenberg, L. (2003) *Den nya nordiska Floran*. Wahlström & Widstrand, Stockholm.

Økland, R.H., Rydgren, K. and Økland, T. (2008) Species richness in boreal swamp forests of SE Norway: The role of surface microtopography. *Journal of Vegetation Science*, **19**, 67-74.

Pakarinen, P. (1978) Production and nutrient ecology of three *Sphagnum* species in southern Finnish raised bogs. *Annales Botanici Fennici*, **15**, 15-26.

Pederson, A. (1975) Growth measurements of five *Sphagnum* species in south Norway. *Norwegian Journal of Botany*, **22**, 277-284.

Potter, J.A., Press, M.C., Callaghan, T.V. and Lee, J.A. (1995) Growth responses of *Polytrichum commune* and *Hylocomium splendens* to simulated environmental change in the sub-arctic. *New Phytologist*, **131**, 533-541.

Press, M.C., Potter, J.A., Burke, M.J.W., Callaghan, T.V. and Lee, J.A. (1998) Responses of a subarctic dwarf shrub heath community to simulated environmental change. *Journal of Ecology*, **86**, 315-327.

Quested, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., Aerts, R., Trosien, F. *et al.* (2003) Decomposition of sub-arctic plants with differing nitrogen economies: A functional role for hemiparasites. *Ecology*, **84**, 3209-3221.

Rastorfer, J.R. (1970) Effects of light intensity and temperature on photosynthesis and respiration of two east antarctic mosses, *Bryum argenteum* and *Bryum antarcticum*. *The Bryologist*, **73**, 544-556.

Robinson, A.L., Vitt, D.H. and Timoney, K.P. (1989) Patterns of community structure and morphology of bryophytes and lichens relative to edaphic gradients in the subarctic forest-tundra of northwestern Canada. *The Bryologist*, **92**, 495-512.

Robroek, B.J.M., Limpens, J., Breeuwer, A. and Schouten, M.G.C. (2007) Effects of water level and temperature on performance of four *Sphagnum* mosses. *Plant Ecology*, **190**, 97-107.

Rydin, H. (1993) Mechanisms of interactions among *Sphagnum* species along water-level gradients. *Advances in Bryology*, **5**, 153-185.

Rydin, H. & Jeglum, J.K. (2006) *The Biology of Peatlands*. Oxford University Press, New York.

Rydin, H. & McDonald, A.J.S. (1985) Tolerance of *Sphagnum* to water level. *Journal of Bryology*, **13**, 571-578.

Santesson, R., Moberg, R., Nordin, A., Tønsberg, T. and Vitikainen, O. (2004) *Lichen-forming and lichenicolous fungi of Fennoscandia*. Museum of Evolution, Uppsala University, Uppsala.

Shaver, G.R., Bret-Harte, M.S., Jones, M.H., Johnstone, J., Gough, L., Laundre, J. *et al.* (2001) Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology*, **82**, 3163 - 3181.

Solheim, B., Endal, A. and Vigstad, H. (1996) Nitrogen fixation in Arctic vegetation and soils from Svalbard, Norway. *Polar Biology*, **16**, 35-40.

Sonesson, M., Carlsson, B.Å., Callaghan, T.V., Halling, S., Björn, L.O., Bertgren, M. *et al.* (2002) Growth of two peat-forming mosses in subarctic mires: species interactions and effects of simulated climate change. *Oikos*, **99**, 151-160.

Ter Braak, C.J.F. & Šmilauer, P. (2002) *Canoco reference manual and canodraw for windows user's guide: Software for canonical community ordination (version 4.5)*. www.canoco.com, Microcomputer Power, Ithaca, N.Y., USA.

Van Wijk, M.T., Clemmensen, K.E., Shaver, G.R., Williams, M., Callaghan, T.V., Chapin, F.S. III *et al.* (2004) Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, **10**, 105-123.

Vasander, H. (1981) The length growth rate, biomass and production of *Cladonia arbuscula* and *Cladonia rangiferina* in a raised bog in southern Finland. *Annales Botanici Fennici*, **18**, 237-243.

Vitt, D.H. (1990) Growth and production dynamics of boreal mosses over climatic, chemical and topographic gradients. *Botanical Journal of the Linnean Society*, **104**, 35-59.

Vitt, D.H., Li, Y.H. and Belland, R.J. (1995) Patterns of bryophyte diversity in peatlands of continental western Canada. *The Bryologist*, **98**, 218-227.

Wahren, C.H.A., Walker, M.D. and Bret-Harte, M.S. (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, **11**, 537-552.

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M. *et al.* (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 1342-1346.

Weih, M. (1998) Seasonality of nutrient availability in soils of subarctic mountain birch woodlands, Swedish Lapland. *Arctic and Alpine Research*, **30**, 19-25.

Weltzin, J.F., Harth, C., Bridgham, S.D., Pastor, J. and Vonderharr, M. (2001) Production and microtopography of bog bryophytes: response to warming and water-table manipulations. *Oecologia*, **128**, 557-565.

Wiedermann, M.M., Nordin, A., Gunnarsson, U., Nilsson, M.B. and Ericson, L. (2007) Global change shifts vegetation and plant-parasite interactions in a boreal mire. *Ecology*, **88**, 454-464.

Williams, M. & Rastetter, E.B. (1999) Vegetation characteristics and primary productivity along an arctic transect: implications for scaling-up. *Journal of Ecology*, **87**, 885-898.

Wright, J.P., Naeem, S., Hector, A., Lehman, C., Reich, P.B., Schmid, B. *et al.* (2006) Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters*, **9**, 111-120.

Yoshikawa, K., Bolton, W.R., Romanovsky, V.E., Fukuda, M. and Hinzman, L.D. (2003) Impacts of wildfire on the permafrost in the boreal forests of Interior Alaska. *Journal of Geophysical Research*, **108**, 8148, doi:10.1029/2001JD000438.

Appendix S1. Site descriptives, environmental variables and abundance measurements

1.1. Site descriptives

Site	Experiment	Abisko 1	Abisko 2	Abisko 3
Altitude [m a.s.l.]	340	370	400	480
Latitude	68º21'N	68º21'N	68º20'N	68º20'N
Longitude	18º49'E	18º48'E	18º48'E	18º49'E

Site	Abisko 4	Abisko 5	Annamo	Andøya
Altitude [m a.s.l.]	520	600	150	40
Latitude	68º20'N	68º19'N	68º32'N	69º07'N
Longitude	18º50'E	18º51'E	17º13'E	15º52'E

1.2. Mean (SE) of independent, dependent variables and abundance measures along the microgradient and warming experiment. Treatment codes see Table 1 (main manuscript). Measurement of samples at detection limit: d.l.

	Dry + lichen	Dry	Medium	Wet
Explanatory variables				
pH	2.84 (0.03)	2.85 (0.02)	3.02 (0.08)	3.17 (0.11)
Ca [mg/l]	58.18 (16.42)	39.60 (13.09)	53.49 (16.13)	64.71 (14.82)
Mg [mg/l]	27.75 (4.70)	17.94 (3.04)	25.87 (4.82)	35.64 (9.81)
NH4-N [mg/core]	0.0483 (0.0098)	0.0422 (0.0077)	0.0406 (0.0062)	0.0473 (0.0047)
NH4-N [µg/l]	d.l.	d.l.	d.l.	d.l.
NO3-N [mg/core]	0.0012 (0.0005)	0.0010 (0.0002)	0.0014 (0.0004)	0.0013 (0.0002)
NO3-N [µg/l]	d.l.	d.l.	d.l.	d.l.
PO43-P [mg/core]	0.0925 (0.0332)	0.0409 (0.0261)	0.1172 (0.0303)	0.0583 (0.0218)
PO43-P [µg/l]	85.61 (38.16)	90.21 (50.36)	65.08 (29.86)	254.23 (127.40)
Moisture [vol-%]	56.38 (4.47)	52.55 (4.78)	68.89 (5.00)	90.65 (2.35)
Degree days (sum of 2 years)	2112.64 (102.06)	2112.64 (102.06)	2112.64 (102.06)	2112.64 (102.06)
Sphagnum growth [cm]	0.50 (0.10)	0.65 (0.09)	0.98 (0.15)	0.99 (0.13)
Abundance				
Sphagna	179.29 (20.55)	245.00 (6.17)	255.29 (5.81	267.43 (1.11)
Prostrate mosses	3.57 (3.57)	0.29 (0.29)	3.71 (2.10)	7.86 (3.28)
Erect mosses	25.29 (11.84)	7.43 (3.83)	3.43 (1.82)	2.57 (1.43)
Prostrate liverworts	13.29 (6.76)	2.57 (0.75)	1.29 (0.36)	1.14 (0.55)
Erect liverworts	18.29 (3.64)	15.71 (4.89)	11.86 (4.22)	1.14 (0.99)
Prostrate lichens	0.14 (0.14)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Erect lichens	20.00 (10.63)	0.29 (0.29)	0.14 (0.14)	0.00 (0.00)
Crust-forming lichens	29.14 (8.66)	0.14 (0.14)	0.00 (0.00)	0.00 (0.00)
Deciduous shrubs	7.71 (3.88)	15.94 (6.10)	10.29 (6.19)	5.91 (3.51)
Evergreen shrubs	101.57 (13.88)	118.29 (15.28)	72.26 (10.25)	38.57 (8.67)
Grasses	0.00 (0.00)	0.00 (0.00)	0.51 (0.33)	0.00 (0.00)
Sedges	1.80 (0.96)	1.29 (1.02)	5.40 (2.04)	20.83 (3.24)
Forbs	36.77 (6.52)	20.83 (4.86)	28.29 (6.67)	7.97 (2.00)
Vascular cryptogams	0.00 (0.00)	0.00 (0.00)	0.51 (0.51)	1.03 (1.03)
$Diversity_{overall}$				
Species richness	16 (1)	12 (1)	11 (1)	12 (1)
Shannon Index	1.86 (0.13)	1.41 (0.09)	1.27 (0.10)	1.73 (0.06)

1.2. continued

	AAA	WAA	WSA	WSW
Explanatory variables				
pH	2.89 (0.03)	2.87 (0.05)	2.89 (0.06)	2.88 (0.09)
Ca [mg/l]	17.43 (2.87)	16.19 (6.78)	22.32 (7.29)	25.29 (8.96)
Mg [mg/l]	16.77 (1.98)	14.88 (4.39)	21.23 (5.51)	21.56 (6.22)
NH4-N [mg/core]	0.0293 (0.0025)	0.0312 (0.0032)	0.0296 (0.0038)	0.0306 (0.0047)
NH4-N [µg/l]	d.l.	d.l.	d.l.	d.l.
NO3-N [mg/core]	0.0012 (0.0002)	0.0010 (0.0005)	0.0011 (0.0002)	0.0007 (0.0002)
NO3-N [µg/l]	d.l.	d.l.	d.l.	d.l.
PO43-P [mg/core]	0.0555 (0.0337)	0.1228 (0.0574)	0.1068 (0.0334)	0.1559 (0.0920)
PO43-P [µg/l]	132.50	132.50	3.38	106.68
Moisture [vol-%]	39.18 (2.21)	30.22 (3.37)	33.02 (3.19)	34.95 (1.62)
Degree days (sum of 2 years)	1754.67	1799.19	1819.85	1872.19
Sphagnum growth [cm]	0.56 (0.12)	0.77 (0.25)	0.91 (0.06)	0.99 (0.10)
Abundance				
Sphagna	204.60 (29.06)	197.80 (30.80)	233.20 (8.53)	248.80 (10.35)
Prostrate mosses	1.00 (0.63)	0.60 (0.40)	0.00 (0.00)	1.40 (0.93)
Erect mosses	52.20 (20.03)	13.00 (10.09)	13.20 (8.06)	10.80 (6.91)
Prostrate liverworts	30.40 (19.23)	22.80 (12.79)	7.40 (3.33)	11.20 (5.86)
Erect liverworts	9.20 (2.33)	18.80 (8.79)	19.00 (8.26)	5.80 (0.58)
Prostrate lichens	0.60 (0.40)	0.20 (0.20)	0.60 (0.60)	0.60 (0.60)
Erect lichens	19.80 (10.84)	16.60 (9.47)	6.00 (4.79)	6.20 (4.34)
Crust-forming lichens	1.40 (1.40)	0.80 (0.80)	0.00 (0.00)	0.20 (0.20)
Deciduous shrubs	34.20 (12.88)	30.24 (9.48)	19.80 (7.76)	23.40 (10.09)
Evergreen shrubs	192.60 (15.52)	170.64 (27.31)	164.88 (19.77)	148.32 (20.18)
Grasses	1.44 (1.05)	5.76 (2.51)	4.68 (0.72)	3.96 (1.84)
Sedges	3.60 (3.17)	0.36 (0.36)	0.36 (0.36)	3.24 (1.19)
Forbs	31.32 (6.80)	34.92 (6.82)	34.92 (7.30)	31.68 (3.72)
Vascular cryptogams	0.00 (0.00)	1.08 (1.08)	0.36 (0.36)	0.00 (0.00)
$Diversity_{overall}$				
Species richness	17 (3)	16 (2)	15 (2)	15 (2)
Shannon Index	1.91 (0.20)	1.88 (0.21)	1.68 (0.12)	1.58 (0.16)

Appendix S2. Division of species into growth forms (cryptogams) and functional groups (vascular plants)

Growth form	Species	Growth form	Species
Sphagna	*Sphagnum angustifolium*	Prostrate liverworts	*Lophozia binsteadii*
	Sphagnum balticum		*Lophozia ventricosa*
	Sphagnum fallax		*Ptilidium ciliare*
	Sphagnum fuscum		*Riccardia latifrons*
	Sphagnum lindbergii	Erect liverworts	*Mylia anomala*
	Sphagnum magellanicum	Prostrate lichens	*Alectoria nigricans*
	Sphagnum nemoreum		*Cetraria aculeata*
	Sphagnum papillosum		*Flavocetraria nivalis*
	Sphagnum riparium	Erect lichens	*Cetraria islandica*
	Sphagnum russowii		*Cladonia arbuscula* ssp. *arbuscula*
	Sphagnum subnitens		*Cladonia arbuscula* ssp. *mitis*
	Sphagnum subsecundum		*Cladonia* cf. *amaurocraea*
	Sphagnum warnstorfii		*Cladonia* cf. *maxima*
Prostrate mosses	*Hylocomium splendens*		*Cladonia gracilis*
	Pleurozium schreberi		*Cladonia squamosa*
	Loeskypnum badium		*Cladonia stygia*
	Warnstorfia fluitans		*Cladonia uncialis*
	Scorpidium scorpioides		*Flavocetraria cucullata*
	Straminergon stramineum		*Sphaerophorus globosus*
Erect mosses	*Aulacomnium turgidum*	Crust-forming lichens	*Cladonia borealis* or *C. pleurota*
	Dicranum fuscescens		*Cladonia* sp.
	(incl. *Dicranum flexicaule*)		*Cladonia sulphurina*
	Dicranum elongatum		*Icmadophila ericetorum*
	Dicranum groenlandicum		*Ochrolechia frigida*
	Dicranum leioneuron	Deciduous shrubs	*Betula nana*
	Pohlia nutans		*Vaccinium myrtillus*
	Polytrichum strictum		*Vaccinium uliginosum*
	Racomitrium lanuginosum	Evergreen shrubs	*Andromeda polifolia*
Prostrate liverworts	*Anastrophyllum minutum*		*Calluna vulgaris*
	Calypogeia sphagnicola		*Empetrum nigrum* ssp. *hermaphroditum*
	Cephalozia bicuspidata		*Vaccinium microcarpus*
	Cephalozia leucantha		*Vaccinium vitis-idea*
	Cephalozia loitlesbergeri	Grasses	*Calamagrostis lapponica*
	Cephalozia lunulifolia	Sedges	*Carex canescens*
	Cladopodiella fluitans		*Carex chordorrhiza*
	Kurzia pauciflora or *K. trichoclados*		*Carex lasiocarpa*
	Lophozia atlantica		*Carex limosa*

continued

Growth form	Species	Growth form	Species
Sedges	*Carex magellanica* ssp. *irrigua*	Forbs	*Comarum palustre*
	Carex rostrata		*Drosera rotundifolia*
	Carex rotundata		*Pinguicula villosa*
	Eriophorum angustifolium		*Rubus chamaemorus*
	ssp. *angustifolium*	Vascular	*Equisetum arvense* s.l.
	Eriophorum vaginatum	cryptogams	
	Trichophorum cespitosum ssp.		
	cespitosum		

Appendix S3. Measurement and relations of soil moisture and water table level

3.1 Calibration of the Time Domain Reflectometry (TDR) soil moisture meter

For calibrating the TDR soil moisture meter *Sphagnum fuscum* and *Sphagnum riparium* peat of different densities was collected from peatlands in the Abisko area in 2005 and 2006 and transferred into a bucket of known volume. The peat was saturated with water, where-after soil moisture and weight were measured weekly until the peat had completely dried out. The peat was dried at 105ºC. With known volume, weight and an assumed density of water of 1g/cm^3, the mass based volume-% could be calculated for each point of the calibration (Fig S1).

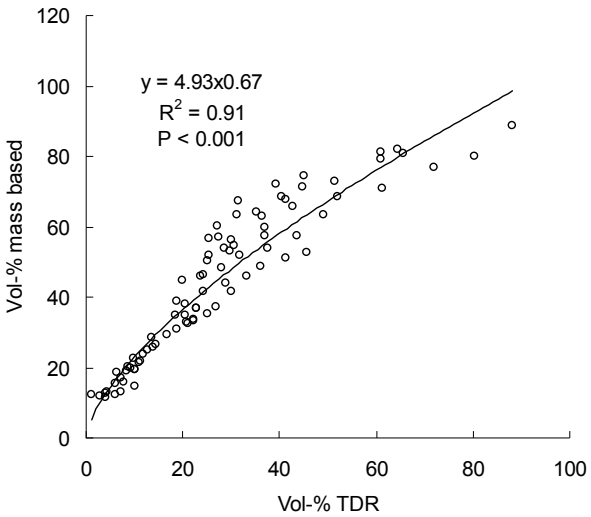

Fig. S1. Calibration: TDR versus mass based measurements of soil moisture (n = 85).

3.2 Measurement of water table level and its relationship to soil moisture

Water table level and soil moisture were recorded simultaneously at each plot. Water-permeable plastic pipes were inserted 40-50cm into the ground in October to guarantee a maximum depth of unfrozen ground. For measuring the water table level a self-made device was used. One wire was connected to the ground, the other attached to a ruler being inserted into the pipe. When touching the water table in the pipe the electric circuit was closed, whereby a beeping sound was produced. The water table level could be calculated as a subtraction of outer distance of the pipe above ground level minus inner distance to water table level.

The water table level in the experiment proved to be too low to be measurable. Thus we tried to predict water table level from soil moisture measurements. Where soil moisture and water table level were measured simultaneously they were included in a dataset to plot soil moisture against water table level. This relationship proved to be significant (Fig S2).

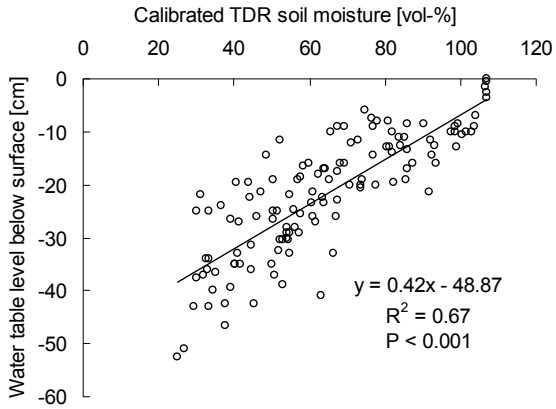

Fig. S2. Relationship water table level – calibrated soil moisture (n = 126).

At the more remote sites in Norway water table level measurements could not be conducted on a regular basis, therefore depth of water table level was mainly measured passively following a modified method developed by Belyea (1999). Plastic sticks onto which PVC tape was attached were put into the ground in October 2005 when the ground was unfrozen and retrieved in the following year in October 2006. The humic acids of the peat water stain the PVC tape at water table level where conditions are anoxic. Often the border between heavily stained and non-stained tape consists of a less stained and spotted zone according to changes in water table depth. This distance was measured with a ruler and the middle point taken as average water table level for one year. PVC tape measurements were in good accordance with water table measured manually during the rest of the year (Fig S3).

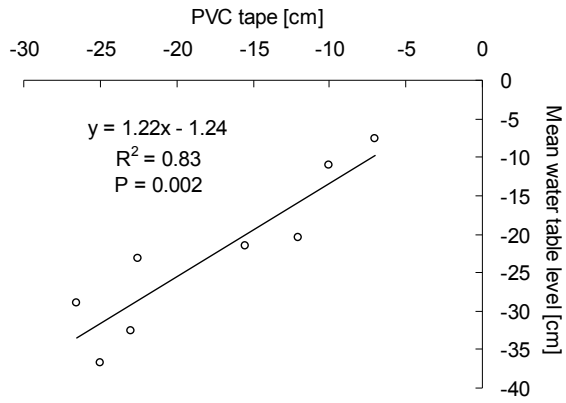

Fig. S3. Relationship of manually measured versus passively measured water table level.

Since calibrated soil moisture is related to water table (Fig S2) and, furthermore, manually and passively measured water table levels are correlated (Fig S3) we assumed that even if measurements of soil moisture could not be conducted at all sites simultaneously, it is valid to take a mean of soil moistures as an estimate of water relations in these peatlands.

References

Belyea, L.R. (1999) A novel indicator of reducing conditions and water-table depth in mires. *Functional Ecology*, **13**, 431-434.

Chapter 3

Consistent negative arctic warming effects on lichen diversity and mixed effects on bryophyte diversity on two continents

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Submitted

Abstract

Little is known about the impact of changing temperature regimes in the (Sub)Arctic on composition and diversity of lichen and bryophyte communities, despite their potentially large role in ecosystem functions with likely feedbacks to climate. Therefore, we investigated changes in diversity and abundance both within *in situ* long-term (9 -16 yrs) warming experiments, ranging from Swedish subarctic birch forest and subarctic/subalpine tundra to Alaskan arctic tussock tundra, and along their related natural climatic gradients. On both continents, lichen diversity responded negatively to experimental warming (with the exception of a birch forest) and to higher temperatures along climatic gradients. Depending on the length of the gradient, bryophyte diversity decreased both with increasing temperatures and at extremely low temperatures. Bryophytes were less sensitive to experimental warming than lichens. Among bryophytes, *Sphagnum* mosses were particularly resistant to experimental warming both in terms of abundance and diversity. Temperature, on both continents, was the main driver of plant community composition within experiments and along gradients, with the exception of the Swedish subarctic birch forest, where amount of litter constituted the best explanatory variable. In the Alaskan acidic tussock tundra experiment, temperature together with soil ammonium availability explained 59% of the variation. Overall, mostly dwarf shrubs (deciduous and evergreen) but also the bryophytes *Sphagnum girgensohnii*, *Hylocomium splendens* and *Pleurozium schreberi* were positively related to warming while the majority of other cryptogams showed a negative relationship. This unique combination of intercontinental comparison, natural gradient studies and experimental studies shows that cryptogam diversity, especially within lichens, is likely to decrease under arctic climate warming. Given the many different functions fulfilled by different cryptogam taxa (e.g.

carbon sequestration, hydrological control, N_2-fixation, trophic interactions), these changes will have important feedback consequences for ecosystem functions and climate.

Introduction

Climate change at high latitudes is expected to be greatest and fastester and more rapid at high latitudes (IPCC 2007), where lichens and bryophytes are greater contributors to biodiversity than vascular plants (Matveyeva & Chernov 2000) and in some areas to aboveground biomass as well (Wielgolaski *et al.* 1981). Moreover, non-vascular cryptogams are a critical control on ecosystem functions (Longton 1997; Cornelissen *et al.* 2007) such as regulation of hydrology (Beringer *et al.* 2001), carbon balance (Rydin & Jeglum 2006), nitrogen (N) fixation (Solheim *et al.* 1996) and preservation of permafrost (Dyrness 1982), their insulation ability minimizing damage to permafrost caused by wildfires (Yoshikawa *et al.* 2003). Given this wide array of ecosystem controls, changes in their abundance and composition may likely impact regional biogeochemistry and even global climate.

Climate change is expected to influence cryptogams through both increased temperature and changing precipitation regimes (Tenhunen *et al.* 1992; Lang *et al.* 2009; Trenbirth & Matthews 2010). Being poikilohydric, both lichens and mosses depend strongly on external water supply, which in turn affects photosynthetic rates (Tenhunen *et al.* 1992). Many moss species exhibit sharp declines in net photosynthesis rates above 20 °C (Oechel & Sveinbjörnsson 1978), *Sphagnum* being an exception showing high rates up to 30 °C (Harley *et al.* 1989). Indeed, *Sphagnum*, in contrast to many other mosses (Hobbie & Chapin 1998), benefits from increasing temperatures as long as moisture availability is sufficient (Gunnarsson 2005; Lang *et al.* 2009). *Sphagnum* may therefore be an exception, being resilient or even reacting positively to climate change.

Yet also indirect effects may trigger changes in species composition. As a combined effect of both increased temperature and increased soil nutrient mineralization (Rustad *et al.* 2001), bigger and faster-growing vascular plant species might outcompete lichens and at least some of the bryophytes, leading to drastic changes in plant community composition (cf. Chapin & Shaver 1985; Molau & Alatalo 1998). Indeed, in response to recent warming, shrub expansion and increased growth have been recorded in various arctic ecosystems (Tape *et al.* 2006; Forbes *et al.* 2010). For cryptogams, contrasting responses to climate change have been reported. Temporal scale studies showed that abundance of mosses in high arctic tundra either increased over the last decades (Hudson & Henry 2009) or remained relatively stable (Prach *et al.* 2010). Similarly, lichen biomass

increased in a short-term warming experiment in Siberia (Biasi *et al.* 2008) while warming decreased the cover of mosses and lichens in standardized warming experiments across the tundra biome (Walker *et al.* 2006), although for mosses the responses were less clear cut than for lichens (Van Wijk *et al.* 2003). Moreover, southerly vascular and cryptogam species might invade into recently still colder ecosystems and outcompete cold-tolerant plants. An indication for this scenario is the recent migration of southerly lichens into the Netherlands where arctic-alpine/boreo-montane species appear to be declining (Van Herk *et al.* 2002).

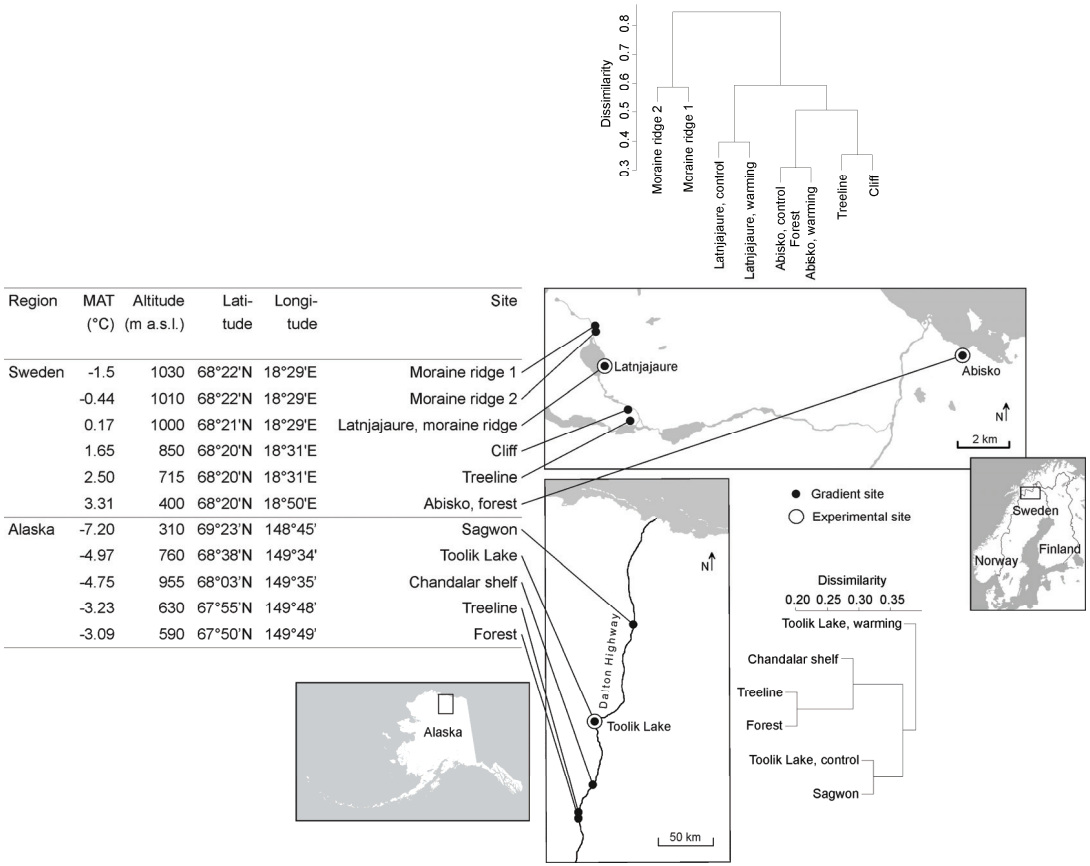
Despite their important ecosystem roles, high-latitude studies of cryptogam responses to climate change have only gained momentum recently (Jägerbrand *et al.* 2009; Lang *et al.* 2009), while those at species (Molau & Alatalo 1998; Press *et al.* 1998; Jägerbrand *et al.* 2009) or genus level are still scarce (Hollister *et al.* 2005). Most studies have treated bryophytes or lichens as one group (Epstein *et al.* 2004; Wahren *et al.* 2005) and concentrated on either experimental setups (e.g. Molau & Alatalo 1998) or climatic gradients (e.g. Virtanen *et al.* 2006; Vonlanthen *et al.* 2008). Yet the combination of biodiversity patterns in space and time, of warming experiment and climatic gradient, may provide robust insights into cryptogam diversity responses to global change (Callaghan *et al.* 1999; Cornelissen *et al.* 2001; Lang *et al.* 2009). Here we take such integration still a step further by comparing patterns of cryptogam diversity in warming experiments and associated gradients in two largely independent regions, i.e. North America and Europe, which together represent some of the most abundant (sub)arctic tundra plant communities. We simultaneously test the impact of climate on (sub)arctic vegetation composition and diversity by studying three *in-situ* warming manipulation experiments and their related natural climatic gradients in northern Sweden and Alaska. This study is the first to report the impact of long-term warming (9 – 16 yr) on (sub)arctic cryptogams. This is especially important when studying slowly growing cryptogams as short-term responses often reveal no significant differences (Jägerbrand *et al.* 2009; Lang *et al.* 2009). In Alaska, the gradient ranged from boreal spruce forest to the coastal plain on the North Slope and included an experiment in acidic tussock tundra, dominated by *Eriophorum vaginatum*. This vegetation type is typical for wide regions of the Alaskan and Siberian Arctic (CAVM Team 2003). In Sweden, the dominant type of tundra is relatively nutrient-poor, showing pH ranges similar to those in Alaskan acidic tussock tundra, and is characterized by dwarf shrubs such as *Betula nana* and Ericaceae. The experiments were located along a strong climatic gradient within subarctic/subalpine tundra and within poor birch forest, both of which are characteristic for wide regions throughout Northern Europe.

We hypothesize (i) that in both time and space, lichens and bryophytes, except *Sphagnum*, generally decline in species diversity and abundance with increasing temperatures as vascular plants increase in abundance; (ii) that there is high turnover of cryptogam community species composition with warming and along temperature gradients, with few bryophyte and very few lichen species likely to replace the many cold-adapted species under warmer conditions.

Materials and methods

LOCATIONS

Central to our study were three warming experiments in Northern Sweden and Alaska embedded in their related natural climatic gradients (locations and site characteristics see Fig. 1).



Region	MAT (°C)	Altitude (m a.s.l.)	Lati-tude	Longi-tude	Site
Sweden	-1.5	1030	68°22'N	18°29'E	Moraine ridge 1
	-0.44	1010	68°22'N	18°29'E	Moraine ridge 2
	0.17	1000	68°21'N	18°29'E	Latnjajaure, moraine ridge
	1.65	850	68°20'N	18°31'E	Cliff
	2.50	715	68°20'N	18°31'E	Treeline
	3.31	400	68°20'N	18°50'E	Abisko, forest
Alaska	-7.20	310	69°23'N	148°45'	Sagwon
	-4.97	760	68°38'N	149°34'	Toolik Lake
	-4.75	955	68°03'N	149°35'	Chandalar shelf
	-3.23	630	67°55'N	149°48'	Treeline
	-3.09	590	67°50'N	149°49'	Forest

Fig. 1 Locations and characteristics of the study sites in Sweden and Alaska. Measurements of MAT (mean annual temperature) see Appendix 1 in Supporting Information. Single linkage clustering for sites is based on the Bray-Curtis dissimilarity measure (see main text).

Experimental warming studies

The Toolik Lake experiment (midarctic, alt. 760 m a.s.l., LTER), in acidic tussock tundra on the North Slope, Alaska, was established in 1989 (16-yr old at sampling). From a larger experimental design we used the warming and control plots (n = 4). From early spring (after snowmelt) to autumn, transparent greenhouses gave passive warming (details in Bret-Harte *et al.* 2001). The Latnjajaure experiment (subarctic/subalpine, alt. 1000 m a.s.l.) in Northern Sweden was established on a poor heath on an acidic moraine ridge in 1995 (9-yr old at sampling) using small transparent open-top chambers (OTC) for passive year-round warming (details in Molau & Alatalo 1998). From the fully factorial design, we used only control and warming plots (n = 4). The Abisko experiment in subarctic Northern Sweden (alt. 400 m a.s.l.) was established in a poor birch forest in 1991 (13-yr old at sampling). Initially, large, transparent open-top polythene tents were placed annually from June to September (details in Wookey *et al.* 1993). From 2000 onwards, warming was applied year-round using large transparent polycarbonate OTCs (details in Makkonen *et al.* 2011). From a larger experimental design, we selected the control and warming plots (n = 6).

Natural climatic gradient studies

The Alaskan gradient stretched c. 140 miles along the Dalton Highway from 67°50'N to 69°23'N, covering altitudes from 310 to 955 m a.s.l.. The Swedish climatic gradient followed mainly an altitudinal profile ranging from 400 to 1030 m a.s.l., compressed within a very narrow latitudinal range in the vicinity of Abisko (68°21'N, 18°49'E). The gradients were chosen for their high internal similarity in geology and associated abiotic factors such as soil ion composition and pH. Thereto, we identified the main vascular plants and cryptogams in the experimental plots and established the plots at four sites along the gradient with some overlap of species composition. At each site, three plots were chosen with maximum inter-plot distance possible, varying between 10 to 40 m, depending on spatial restrictions (valley dimensions, cliff edges, impassable rivers).

VEGETATION RECORDING

Vegetation was recorded by means of the point intercept method (Jonasson 1988). The portable aluminium frame covered 50 by 50 cm with maximum nine rows of thirty points each. A bubble level ensured horizontal positioning. The frame always faced north. In Alaska (summer 2005), two subplots per plot were sampled since the vegetation was patchy and *Eriophorum vaginatum* tussocks, where present, could occupy a large portion of the frame. Every third row was recorded within the frame, resulting in 90 points each (summed before analysis). The southwestern edge of the frame always rested on an

Eriophorum tussock. At each experimental and gradient plot in Sweden (summer 2004), every other row was recorded within the frame resulting in four rows of 120 points. Along the gradient, frames were put out at random. Within experiments, we surveyed the OTC center or the unsampled section in greenhouses. Large patches of bare ground were avoided since our aim was to capture as much of the natural variation in vegetation as possible and, moreover, amount of bare ground was recorded in a more representative way over a larger area (see Appendix 1). At each point, all hits of each vascular plant species were recorded until the pointed tip (Ø < 0.5 mm) of the needle touched the ground. Each bryophyte and lichen species and litter were recorded as first hit only. While recording, every care was taken to avoid moving plants from their original position (for further details concerning sampling technique and species identification see Appendix 2).

ABIOTIC FACTORS

The aim of the abiotic characterisation of the different sampling sites was to compare sites along each of the two gradients for some key climatic and soil parameters in relative terms, not to get a long-term record including the substantial interannual variation. The measurements followed this aim. Temperature, nutrient availability (ammonium [NH_4^+], nitrate [NO_3^-], phosphate [PO_4^{3-}], calcium [Ca^{2+}], magnesium [Mg^{2+}], potassium [K^+]), soil pH, soil moisture, depth of the organic layer, active layer depth (Alaska), ground penetrability (Sweden) and amount of bare ground were recorded within experiments and along gradients in the summers of 2004 to 2006 (for measurement details see Appendix 1).

DATA ANALYSIS

A single linkage clustering based on the Bray-Curtis dissimilarity measure (Faith *et al.* 1987) was carried out, based on average species abundances per site, to obtain an overall picture of vegetation similarities among sites (see Fig 1). This analysis was performed using the Vegan library (Oksanen 2004) in R (Anon. 2004).

The effects of treatment on Shannon Index (Magurran 2004), species richness or abundance (number of hits) for lichens, liverworts, non-*Sphagnum* mosses, *Sphagnum* and vascular plants in warming experiments were tested by one-way MANOVA (Pillai's trace, n = 4-6). Data were checked for normality. Since (M)ANOVA is robust to heterogeneity of variance as long as sample size is nearly equal, we proceeded with analysis (SPSS 15.0 for Windows; SPSS Inc., Chicago, IL, USA) even when homoscedasticity assumptions were not fully met (Zar 1999).

We related species richness, Shannon Index and abundance of lichens, liverworts, non-*Sphagnum* mosses and vascular plants, respectively, to mean annual temperature (MAT; see Appendix 1) by linear and unimodal regressions. Similarly, abundance of each cryptogam group was related to vascular plant abundance.

Vegetation abundance data from point-intercept recordings were analysed by redundancy analysis (RDA) or canonical correspondence analysis (CCA) using CANOCO for Windows 4.5 (Ter Braak & Šmilauer 2002), depending on the length of the gradient (1-3 for the experiments and the Alaskan gradient but > 6 for the Swedish gradient). Species data were centred (and log-transformed for Toolik Lake experiment) before analysis. We selected MAT as the temperature measure. Variables which might be functionally related to MAT were tested using Pearson's correlation and, if significant, excluded (see Appendix 3). The same procedure was applied to other variable sets such as pH, Ca^{2+}, Mg^{2+}, and PO_4^{3-}, NO_3^- and NH_4^+. Thus, variables used in the analysis were MAT, moisture, pH, Ca^{2+}, Mg^{2+}, PO_4^{3-}, NO_3^- and NH_4^+. Altitude, litter, bare ground and K^+ were solely included for Alaska and penetrability for Sweden. Significance of variables was tested with the Monte Carlo Permutation Test (9999 permutations). Since for the experiment at Abisko, none of the available variables proved significant, we reincorporated amount of litter in the variable list which subsequently proved significant. When testing the environmental variables for the experiment, the plots were freely permuted. Since temperature could not be measured in every experimental plot, a dummy variable for temperature represented the warming (1) and control plots (0), respectively, in combination with the other environmental variables. Along the gradient, one datalogger (or the mean of two dataloggers) per site was used. The plots at each site were therefore not independent and a split-plot design was applied with the sites being the whole plots and the plots within one site the split plots. For the gradient analysis, three out of four or six experimental control plots were therefore used to fulfil the requirements of the split-plot-design which allows only equal numbers of plots per site (i.e. three). At Latnjajaure and Toolik Lake, the third control plot was omitted and at Abisko, every second control plot was excluded from analysis. Data for two plots at Latnjajaure in the vicinity of the experiment did not constitute a new site and were excluded. When testing for effects of MAT, the whole plots were freely permuted and the split plots kept constant. Variables were tested on entry in the model by manual selection, and only significant variables were included. The Monte Carlo Test in the CCA for the Swedish gradient revealed that MAT was the only significant variable. Since the resulting graph displayed an arch, we tested for variables other than MAT by including MAT, MAT^2 and MAT^3 as covariables to remove spurious inertia from the analysis. The only resulting significant variable, NH_4^+,

was not included in the final DCCA diagram, since most of its values were (close to) zero and since it contributed little to the explained inertia.

Results

CHANGES IN SHANNON INDEX, SPECIES RICHNESS AND ABUNDANCE IN WARMING EXPERIMENTS

Analysis per experimental site showed that Shannon Index, species richness and abundance of lichens, liverworts and non-*Sphagnum* mosses all significantly decreased in response to warming at Toolik Lake (Fig. 2). Indices for *Sphagnum* and vascular plants remained unchanged. At the high-altitude site at Latnjajaure, Shannon Index, species richness and abundance of lichens significantly decreased with warming while non-*Sphagnum* mosses and liverworts were not affected. *Sphagnum* was absent in the Swedish plots. Abundance of vascular plants increased in response to warming, while Shannon Index and species richness were not affected. At the low-altitude site in Abisko, only Shannon index and species richness of liverworts significantly increased with warming. Abundance of non-*Sphagnum* mosses showed a negative trend in response to warming while all other indices remained unchanged.

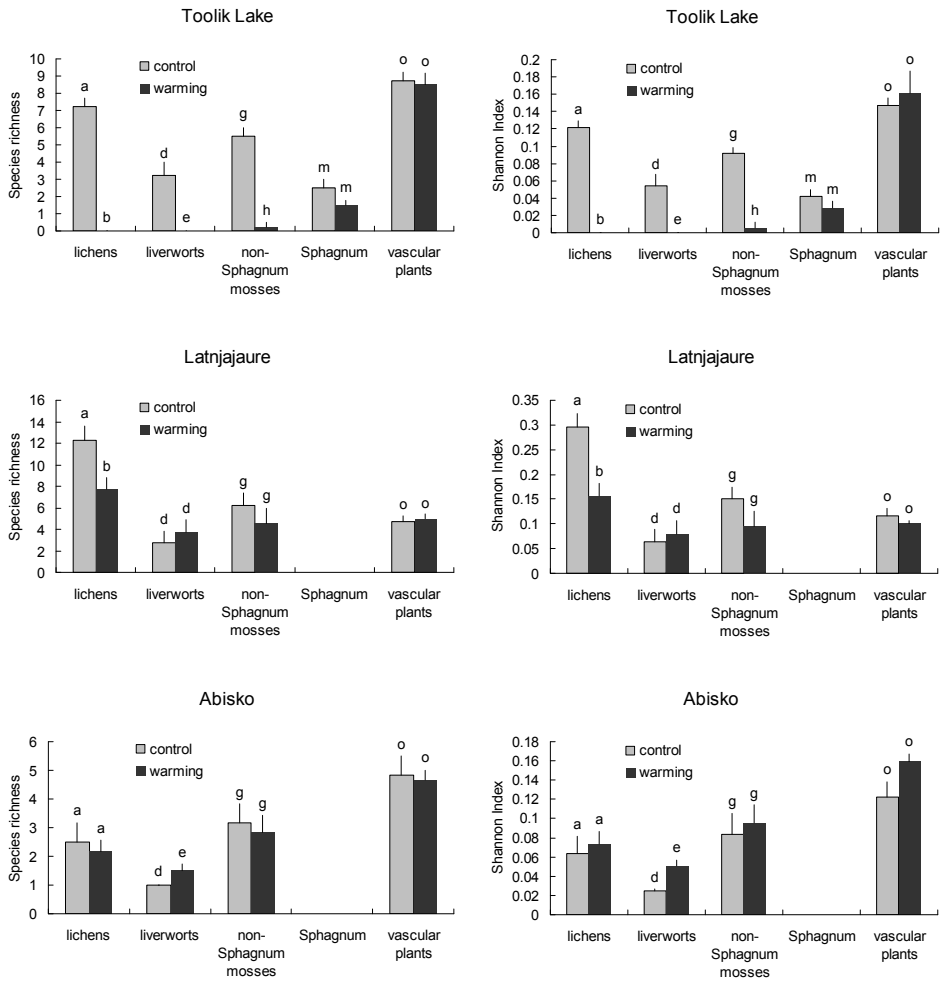


Fig. 2 Effect of warming treatment on species richness, Shannon Index and abundance for lichens, liverworts, mosses and vascular plants (one-way MANOVA, n = 4-6). Different letters indicate differences at P = 0.05; symbols in bold italic mark a trend (P < 0.1). Note that the amount of points, i.e. the area sampled, differed between Alaskan and Swedish sites (see methods).

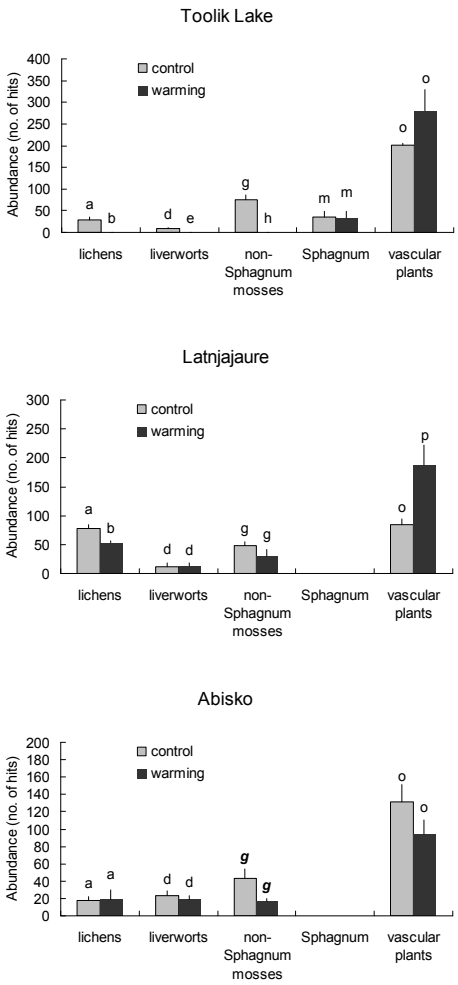


Fig. 2 continued

SHANNON INDEX, SPECIES RICHNESS AND ABUNDANCE ALONG TEMPERATURE GRADIENTS

Shannon Index and species richness of all cryptogam groups declined with increasing MAT along the Alaskan gradient, with lichens showing only a trend for the Shannon Index. For vascular plants, however, no such pattern was found (Fig. 3). Abundance of non-*Sphagnum* mosses (R^2 = 0.09, P = 0.26), lichens (R^2 = 0.005, P = 0.79) or vascular plants (R^2 = 0.08, P = 0.29) was not significantly related to increasing MAT while *Sphagnum* (R^2 = 0.50, P = 0.002) and liverworts (R^2 = 0.79, P < 0.001) were significantly negatively related. Abundances of non-*Sphagnum* mosses (R^2 = 0.33, P = 0.020) and, marginally, of lichens (R^2 = 0.21, P = 0.073) were linearly negatively related to abundance

of vascular plants, while for liverworts (R^2 = 0.06, P = 0.35) and *Sphagnum* (R^2 = 0.003, P = 0.83) no relationship was found.

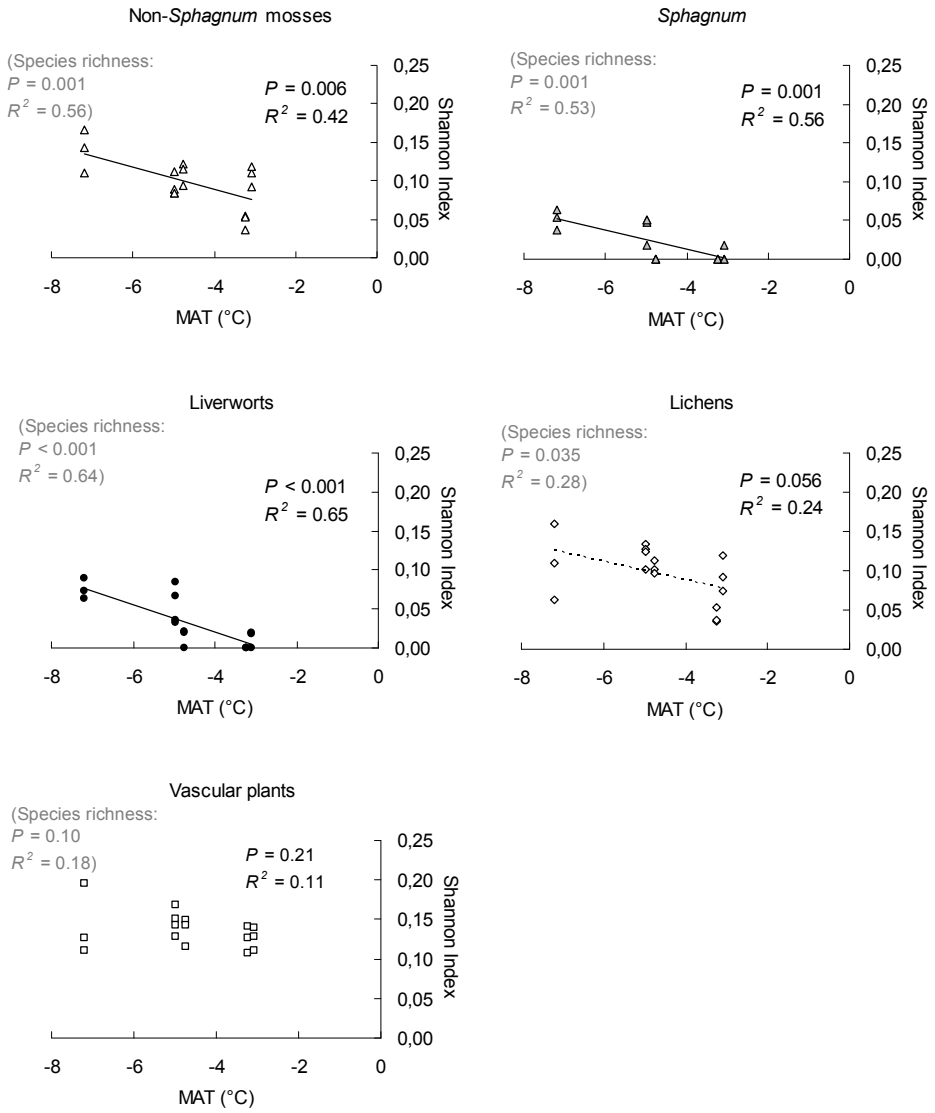


Fig. 3 Shannon Index (and species richness, in parenthesis) versus MAT (°C) for non-*Sphagnum* mosses, *Sphagnum*, liverworts, lichens and vascular plants along the Alaskan gradient (n = 16).

Along the Swedish gradient, Shannon Index and species richness of non-*Sphagnum* mosses and liverworts were best described (trend) by a unimodal curve, showing lowest

values both at high and low MAT (Fig. 4). When excluding the plots with sub-zero MAT, both Shannon Index and species richness of non-*Sphagnum* mosses ($P = 0.013$, $R^2 = 0.33$; $P = 0.003$, $R^2 = 0.43$) and liverworts ($P = 0.012$, $R^2 = 0.34$; $P = 0.008$, $R^2 = 0.36$) decreased significantly linearly with increasing MAT. Shannon Index and species richness of lichens clearly decreased with increasing MAT while vascular plants showed the opposite pattern. The latter group showed no significant relationship (Shannon: $P = 0.36$, $R^2 = 0.05$; species richness: $P = 0.38$, $R^2 = 0.05$) when excluding the plots with negative MAT while the relations for lichens still were significant (Shannon: $P < 0.001$, $R^2 = 0.78$; species richness: $P < 0.001$, $R^2 = 0.81$). Abundance of lichens was linearly negatively related to increasing MAT ($R^2 = 0.83$, $P < 0.001$) and positively for vascular plants ($R^2 = 0.57$, $P < 0.001$) and non-*Sphagnum* mosses ($R^2 = 0.25$, $P = 0.014$), while liverworts showed no relationship ($R^2 = 0.03$, $P = 0.45$). These relations did not change (data not shown) when excluding the plots with negative MAT, except for non-*Sphagnum* mosses which showed no significant relation with MAT anymore ($R^2 = 0.01$, $P = 0.74$). Similarly, abundance of lichens was linearly negatively related to vascular plant abundance ($R^2 = 0.65$, $P < 0.001$), non-*Sphagnum* mosses positively ($R^2 = 0.27$, $P = 0.010$) while liverworts showed no relationship ($R^2 = 0.07$, $P = 0.20$).

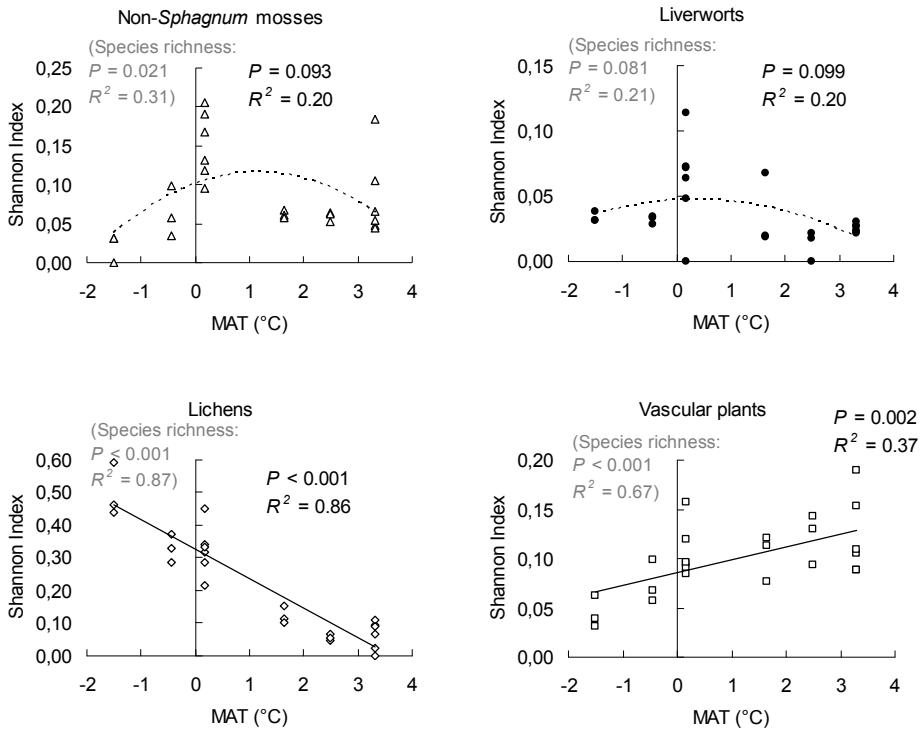


Fig. 4 Shannon Index (and species richness, in parenthesis) versus MAT (°C) for non-*Sphagnum* mosses, liverworts, lichens and vascular plants along the Swedish gradient (n = 24). Types of regression used were similar for Shannon Index and species richness for each group.

DRIVERS OF PLANT COMMUNITY COMPOSITION IN WARMING EXPERIMENTS AND ALONG GRADIENTS

Warming and $NH_4^+{}_{resin}$ (measured with ion resins, see Appendix 1) significantly influenced plant community composition at Toolik Lake (Table 1). $NH_4^+{}_{resin}$ was significantly higher in control plots versus warming plots (F = 21.01, P = 0.004). This relation was also found across experiments for $NH_4^+{}_{soil\ core}$ (measured in soil cores, see Appendix 1) while $NH_4^+{}_{resin}$ showed diverging responses across sites (see Appendix 1). At Latnjajaure, vegetation composition was solely influenced by temperature (Table 1). Vegetation composition at the subarctic birch forest around Abisko, however, correlated with litter amount rather than temperature. While litter was not significantly higher in the Abisko warming versus control plots (F = 0.93, P = 0.36), across all experiments both warming treatment and site identity significantly and positively influenced litter production (see Appendix 1).

Table 1 *P*-values of all canonical axes and environmental variables on cryptogam and vascular plant species composition within experiments and along gradients (RDA, except for Swedish gradient (CCA); Monte Carlo Test: 9999 permutations, n = 4-24; data were log-transformed for the warming experiment at Toolik Lake). Only significant variables were included in the model. Significant *P*-values are marked with bold letters. Superscript a–b: order of the variables entering the model

	Experiment †						Gradient ‡			
	Toolik Lake		Latnjajaure		Abisko		Alaska		Sweden	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
All axes	3.65	< **0.001**	6.93	**0.024**	2.80	**0.007**	9.12	**0.019**	4.45	**0.005**
Temperature §	3.92	**0.026**[a]	6.92	**0.026**			9.12	**0.017**	4.45	**0.005**
$NH_4^+{}_{resin}$	2.43	**0.011**[b]								
Litter					2.80	**0.007**				

† Plots freely permuted.

‡ Testing of annual mean temperature along gradient: whole plots permuted at random, split plots kept constant.

§ MAT for gradient and temperature dummy variable for experiment.

Across experiments, none of the lichen and one moss species were positively related to temperature (Fig. 5). *Sphagnum girgensohnii* (Toolik Lake) and the deciduous dwarf shrubs *Salix pulchra* (Toolik Lake) and *Betula nana* (Latnjajaure) were positively related to warming. No cryptogams were positively related to litter amount while the grass *Deschampsia flexuosa* and the evergreen dwarf shrub *Empetrum hermaphroditum* did.

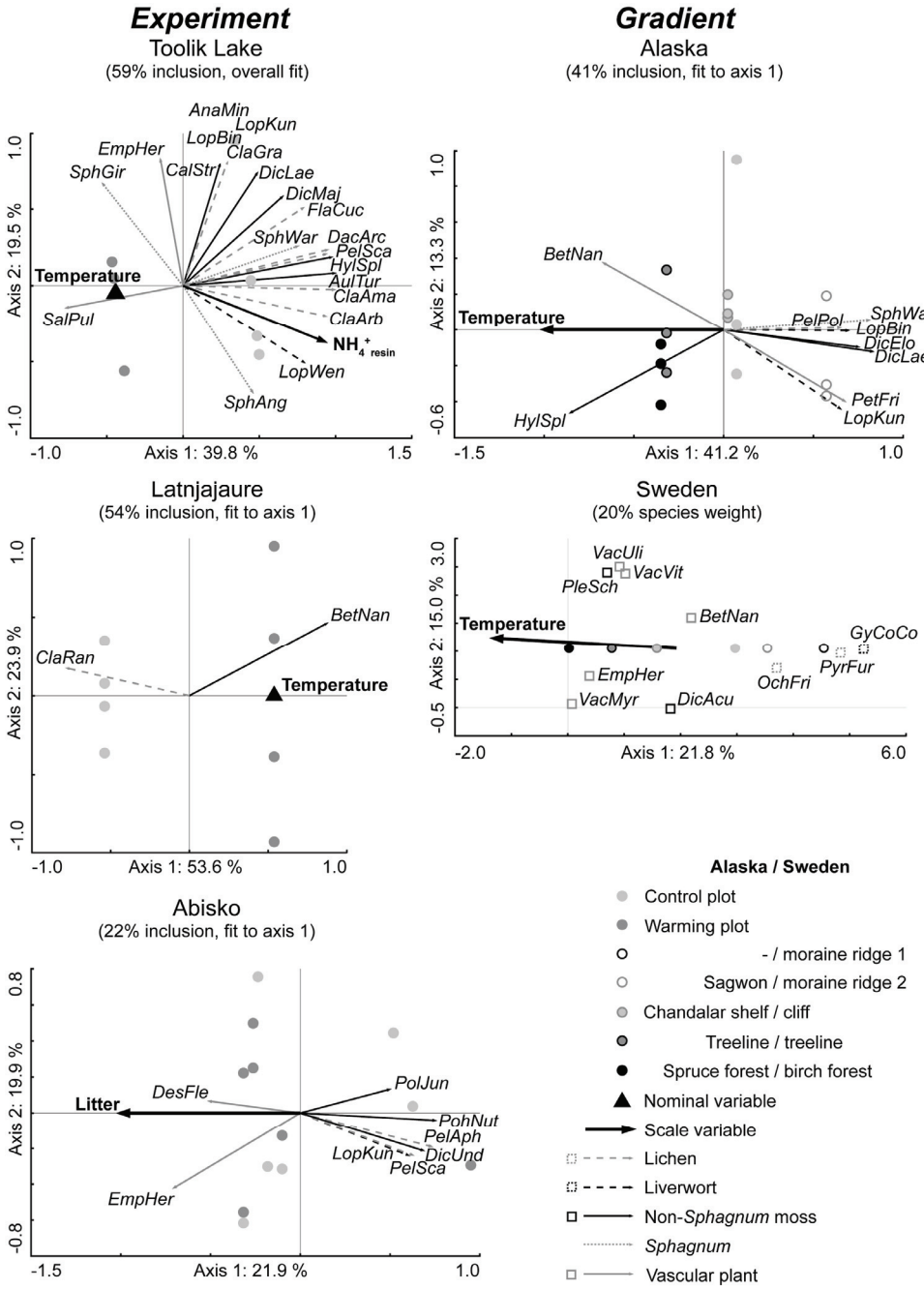

Experiment
Toolik Lake
(59% inclusion, overall fit)
AnaMin
LopKun
LopBin
ClaGra
EmpHer
SphGir
CalStr
DicLae
DicMaj
FlaCuc
SphWar
DacArc
PelSca
HylSpl
AulTur
Temperature
ClaAma
SalPul
ClaArb
NH4+ resin
LopWen
SphAng
Axis 2: 19.5 %
Axis 1: 39.8 %
1.0
-1.0
1.5
Gradient
Alaska
(41% inclusion, fit to axis 1)
BetNan
Temperature
PelPol
SphWar
LopBin
DicElo
DicLae
PetFri
LopKun
HylSpl
Axis 2: 13.3 %
Axis 1: 41.2 %
-0.6
-1.5
Latnjajaure
(54% inclusion, fit to axis 1)
BetNan
ClaRan
Temperature
Axis 2: 23.9 %
Axis 1: 53.6 %
Sweden
(20% species weight)
VacUli
VacVit
PleSch
BetNan
Temperature
GyCoCo
PyrFur
EmpHer
OchFri
VacMyr
DicAcu
Axis 2: 15.0 %
Axis 1: 21.8 %
3.0
-0.5
-2.0
6.0
Abisko
(22% inclusion, fit to axis 1)
DesFle
PolJun
Litter
PohNut
PelAph
LopKun
DicUnd
PelSca
EmpHer
Axis 2: 19.9 %
Axis 1: 21.9 %
0.8
-0.8
Alaska / Sweden
Control plot
Warming plot
- / moraine ridge 1
Sagwon / moraine ridge 2
Chandalar shelf / cliff
Treeline / treeline
Spruce forest / birch forest
Nominal variable
Scale variable
Lichen
Liverwort
Non-Sphagnum moss
Sphagnum
Vascular plant

Fig. 5 (see opposite page) RDA (all except Swedish gradient) and DCCA (Swedish gradient) of warming experiments and climatic gradients in Alaska and Sweden. Temperature is expressed as MAT and displayed as an arrow towards higher temperature along the gradients and as dummy variable indicating the average position of the warming plots for the experiments. Only significant environmental variables are included in each ordination (Monte Carlo Test: 9999 permutations; Table 1). Only those species are shown in the RDA which show a percentage equal to or higher than that explained by the first axis (if one environmental variable present; Latnjajaure 40%, Abisko 22%, Alaska 41%) or than that explained by both axes (if more than one environmental variable present; Toolik Lake 59%). In the DCCA, only species are shown with a species weight equal to or higher than 20%. Species abbreviations in alphabetical order are as follows: AnaMin *Anastrophyllum minutum*; AulTur *Aulacomnium turgidum*; BetNan *Betula nana*; CalStr *Calliergon stramineum*; ClaAma *Cladonia amaurocraea*; ClaArb *Cladonia arbuscula*; ClaGra *Cladonia gracilis*; ClaRan *Cladonia rangiferina*; DacArc *Dactyla arctica*; DesFle *Deschampsia flexuosa*; DicAcu *Dicranum acutifolium*; DicUnd *Dicranum undulatum*; DicElo *Dicranum elongatum*; DicLae *Dicranum laevidens*; DicMaj *Dicranum majus*; EmpHer *Empetrum hermaphroditum*; FlaCul *Flavocetraria cucullata*; GyCoCo *Gymnomitrion corallioides*/*concinnatum*; HylSpl *Hylocomium splendens*; LopBin *Lophozia binsteadii*; LopKun *Lophozia kunzeana*; LopWen *Lophozia wenzelii*; OchFri *Ochrolechia frigida*; PelAph *Peltigera aphthosa*; PelPol *Peltigera polydactylon*-group; PelSca *Peltigera scabrosa*; PetFri *Petasites frigidus*; PleSch *Pleurozium schreberi*; PohNut *Pohlia nutans*; PolJun *Polytrichum juniperinum*; PyrFur *Pyrenopsis furfurea*; SalPul *Salix pulchra*; SphAng *Sphagnum angustifolium*; SphGir *Sphagnum girgensohnii*; SphWar *Sphagnum warnstorfii*; VacMyr *Vaccinium myrtillus*; VacUli *Vaccinium uliginosum*; VacVit *Vaccinium vitis-idaea*.

Along both gradients, temperature significantly determined vegetation composition (Fig. 5). In Alaska, *Betula nana* and the non-*Sphagnum* moss *Hylocomium splendens* were positively related to temperature while all other vascular plants and cryptogams showed a negative relationship. In Sweden, the dwarf shrubs *Vaccinium myrtillus*, *V. uliginosum*, *V. vitis-idaea*, *Empetrum hermaphroditum* and the non-*Sphagnum* moss *Pleurozium schreberi* were positively related to increasing temperatures while the majority of cryptogams showed a negative relationship. *Betula nana*, together with *Dicranum acutifolium*, showed its optimum in the intermediate part of the gradient.

Discussion

GRADIENTS AND EXPERIMENTS – SIMILARITIES AND DIFFERENCES

Between two gradients on two separate continents, differing greatly in species composition, geology and biogeographic history, cryptogam diversity patterns mostly converged. Lichens, and largely also bryophytes (but not vascular plants), decreased with increasing temperatures, if excluding the climatically most extreme and coldest locations in Sweden. The climate amplitude of the gradient played a role in these largely linear relationships, which became curvilinear for bryophytes in Sweden, owing to low diversity at the colder extreme of the gradient. Relations between diversity and MAT were stronger for lichens in Sweden and for bryophytes in Alaska, corresponding with their respective great overall diversity in each (see Appendix 2), each resulting in an enhanced relation

with MAT. Abundance patterns, however, reflected regional differences in species turnover and dominance of different cryptogam groups (see below).

Whilst only temperature was significantly associated with vegetation composition along gradients, within experiments other factors gained in importance. The higher NH_4^+ availability in control plots compared to warming plots at Toolik Lake is intriguing, as warming is usually related to increased mineralization (Rustad *et al.* 2001). However, this effect has been reported earlier (Hartley *et al.* 1999). Explanations may include differences in the size of the microbial biomass between control and warming plots, leading to increased immobilization of N in the latter (cf. Schmidt *et al.* 1999). Also, N_2-fixation by certain lichens (*Peltigera, Nephroma*) and by free-living or moss-associated (e.g. *Hylocomium splendens*) cyanobacteria accounts for 25-80% of annual N input in tundra ecosystems (Chapin & Bledsoe 1992). The decline of these organisms upon warming would reduce plot-level N_2-fixation and thereby possibly NH_4^+ availability, which would then be an effect rather than a cause of cryptogam decline in warmed plots. Also, the short-term warming-induced N mineralization (Rustad *et al.* 2001) depends on the availability of easily decomposable material which by now might be exhausted. The observation of decreasing N in warming plots across experiments, when measured in soil core extracts, provokes future in-depth analysis to estimate the long-term effects of warming on vegetation composition through soil mineralization.

In the Abisko experiment, litter amount rather than temperature was clearly negatively related to all cryptogams. Since litter amount scaled with MAT (see Appendix 3) along the Swedish gradient, temperature might indirectly also be influential here through promoting vascular plant productivity and litter production. Indeed, shading or physical obstruction by vascular plants seems to be the predominant driver of cryptogam species composition, with different impact depending on cryptogam group. Across the whole Alaskan gradient, spaces between *Eriophorum* tussocks can be colonized by cryptogams. *Eriophorum* tussocks and *Betula nana* tend to grow taller towards the South (S.I. Lang, pers. obs.). Therefore, the negative relation of non-*Sphagnum* mosses with vascular plants might be caused by increased litter production towards the South by all vascular plants excluding *Eriophorum vaginatum* ($R^2 = 0.30$, $P = 0.029$), *E. vaginatum* itself not showing a pattern along the gradient ($R^2 = 0.12$, $P = 0.18$). In contrast, along our Swedish gradient, litter cover by vascular plants, although clearly increasing with increasing MAT ($R^2 = 0.76$, $P < 0.001$), does not seem to limit cryptogam abundance generally. Whereas *Eriophorum* tussocks in Alaska cover the ground completely with both living and dead

material, the understorey vegetation at lower elevations in Sweden provides a looser structure under which bryophytes thrive.

Lichens

Lichens showed the strongest decline with increasing temperatures along both gradients and in all experiments except the Abisko one (where no cryptogam group showed strong direct responses to warming), and not a single lichen species was strongly positively related to increasing temperatures. Studies by Chapin *et al.* (1995), Van Wijk *et al.* (2003) and Hollister *et al.* (2005) support these findings. While we can not exclude concomitant other effects of experimental warming, e.g. changes in relative humidity and soil moisture, the latter factor was not significantly different between warming and control plots in the greenhouses (P = 0.78, F = 0.08), and no differences were found for each in similar experiments (Chapin *et al.* 1995). However, exclusion of dewfall in the greenhouses might have negatively affected the cryptogams, which rely mainly on passive uptake of water. Alternatively, increased litter production by shrubs (*Salix pulchra*), which increased in the warming plots as observed in our study (P = 0.04, Kruskal-Wallis), may have outcompeted cryptogams; see also Chapin *et al.* (1995) for extreme birch expansion in the combined fertilisation and warming treatment contributing to cryptogam elimination. Similarly, overgrowth by grasses may have suppressed lichens in two subarctic warming experiments at a treeline and fellfield site (Graglia *et al.* 2001). Indeed, the consistent decline of lichen abundance with vascular plant abundance along our gradients is consistent with other gradients and warming experiments with the exception of the coldest sites with very low vascular plant cover (Cornelissen *et al.* 2001). Here we could take this still a step further by showing that, if crustose lichens are included as done here, this relation even holds true at higher elevations. Thus, we attribute the strong decline of lichens in response to elevated temperatures mostly to increased asymmetric competition by vascular plants and their litter.

Bryophytes

While bryophyte species richness decreased with increasing temperatures along both gradients, the responses within experiments were less clear. At Toolik Lake, non-*Sphagnum* mosses and liverworts disappeared entirely from the experimental plots while in the Swedish experiments, the only changes were a negative trend for non-*Sphagnum* mosses and a marginal increase in liverwort diversity in the warming plots at Abisko. The latter may reflect coincidental differences in initial species composition rather than responses to increasing temperatures. The decreases in abundance in the experiments were only partly reflected along the Alaskan and Swedish gradients since, in Alaska, at least

non-*Sphagnum* moss cover did not depend on MAT whereas abundance of *Sphagnum* and liverworts decreased with increasing temperature. Along the Swedish gradient, abundance of non-*Sphagnum* mosses was positively related to MAT, opposite to measurements in the Abisko experiment, while liverwort abundance along the gradient showed no significant relationship with MAT, in accordance to the Swedish experiments. Comparing the two climatic gradients at species-level, the only mosses positively related to rising temperatures were *Hylocomium splendens* and *Pleurozium schreberi*, with a boreal and boreo-temperate distribution, respectively (Hill & Preston 1998) and well-adapted to warmer and shadier conditions. *H. splendens*, however, which is found at warmer plots along the gradient, was negatively related to warming at Toolik. The observed contrasts between experiment and gradient suggest that experimental artefacts such as effects on humidity and dewfall, protection from wind, or the provision of physical barriers for generative and vegetative reproduction and dispersal, might be responsible for the differences found. However, also the relatively short experimental duration when compared with natural vegetation developed over centuries to millennia, might have a significant impact on the observed discrepancies in our findings.

The persistence of *Sphagnum* (and *Calliergon stramineum*, which is often found growing intermingled with *Sphagnum*, thereby profiting from capillary water held by the latter), even under the severe warming in the Alaskan greenhouses, is of major interest as *Sphagnum* constitutes the dominant moss of today's peatlands and is the predominant contributor to their carbon storage (Rydin & Jeglum 2006). Since acidic tussock tundra has a patchy appearance and since in each warming plot different *Sphagnum* species were present, it seems likely that the species initially present pertained in the plots. This confirms previous reports of the strong performance of *Sphagnum* at relatively high temperatures compared to other northern mosses (see Introduction). Indeed, our multivariate analysis showed that *S. girgensohnii* is positively related to warming. Moreover, this species is often found in slightly drier spots and the above-mentioned ability of *Sphagnum* to hold capillary water may explain its relative independence from precipitation, which was excluded in the Alaskan greenhouses. Since the experiment is located on a gentle slope, *Sphagnum* may either effectively store the run-off water from the surroundings or profit from lateral water flow across the permafrost surface. The diverging responses of mosses to experimental warming are also reflected in a study by Van Wijk *et al.* (2003) and appeared to depend partly on moisture availability in different locations. Interestingly, the wet sedge tundra at Toolik Lake, where *Sphagnum* is present (S.I. Lang, pers. obs.), showed an increase in moss biomass. This emphasizes the importance of moisture for moss growth with rising temperatures and might explain why

Sphagnum, often found in moist or wet locations, seems to benefit from an increase in temperatures (Gunnarsson 2005; Lang *et al.* 2009).

EFFECTS OF WARMING ON COMMUNITY COMPOSITION

In the warming experiments, all on a short time scale in a biogeographic context, the decline of many cryptogam species may not have been compensated (yet) by the arrival and establishments of new ones adapted to warmer climates, either because of natural dispersal limitation or because of the physical barrier imposed by the warming tents. On the other hand, the general relative impoverishment of lichens, and partly bryophytes, with higher temperatures along gradients suggests that dispersal limitations should not be the most decisive driver of cryptogam responses to warming. The multivariate analysis results support our hypothesis that, if dispersal limitations are not strong, only a few moss species and even fewer lichen species are able to replace the many cold-adapted species under warmer conditions. Indeed, only the bryophytes *Sphagnum girgensohnii*, *Hylocomium splendens* and *Pleurozium schreberi*, and not a single lichen species, were strongly positively related to warming. While within experiments, artefacts connected to moisture regimes or humidity might have influenced these results somewhat, the strong relation of cryptogam diversity and composition patterns to temperature along natural gradients is consistent with changes from cryptogam-dominated to shrub-dominated tundra. Shrub expansion has been explained by direct warming promotion of shrubs and positive feedbacks through snow regimes and soil processes (Chapin *et al.* 2005; Sturm *et al.* 2005; Pomeroy *et al.* 2006), even though negative feedbacks through extreme winter events (Bokhorst *et al.* 2009) and grazing by vertebrates (Post & Pedersen 2008) may moderate shrub expansion somewhat. Regional losses in species diversity due to vascular plant expansion, and a shift of cold-adapted plant communities towards higher elevations, may therefore be the result of global warming in the near future.

There are strong indications that cryptogam responses in several warming experiments are not yet at equilibrium. For instance, the initial positive response of lichens to warming at Latnjajaure (Molau & Alatalo 1998), analogue to initial positive effects of warming on lichen biomass in Siberia (Biasi *et al.* 2008), could no longer be detected after five years (Jägerbrand *et al.* 2006; Jägerbrand *et al.* 2009). At Abisko, five years of experimental warming yielded some responses, albeit minor, of a few cryptogam species (*Cladonia rangiferina* and *Cladonia furcata*, *Pohlia nutans*) or species groups (liverworts other than *Lophozia hatcheri* and *Ptilidium ciliare*) while vascular plants were not affected by warming (Press *et al.* 1998). Following the same methodology (see Appendix 2), we could not detect the same responses. However, *Vaccinium myrtillus* had significantly decreased

over time and *Cladonia gracilis* was no longer present in the control plots. That different species come and go with experimental warming over time has also been reported for vascular plants (Chapin & Shaver 1985). Long-term responses might therefore significantly differ from transient responses emphasizing the importance of long-term monitoring in climate change studies.

In conclusion, temperature either directly or indirectly promoted vascular plant productivity, both within experiments and along gradients, while especially lichen abundance and diversity were very sensitive to increases in temperature. Bryophyte abundance and diversity showed mixed responses to temperature and *Sphagnum* resisted even severe experimental warming conditions. Given the many different functions fulfilled by different cryptogam taxa (e.g. carbon sequestration, hydrological control, N_2-fixation, trophic interactions), these responses of cryptogam diversity to warming will have important feedback consequences for ecosystem functions and climate.

Acknowledgements

The Royal Swedish Academy of Sciences subsidized the fieldwork at Abisko by grants to S.I.L.. The National Science Foundation grants #DEB-0423385 and OPP-0807639, given to G.R. Shaver, supported the fieldwork at Toolik Lake. The Staatliches Museum für Naturkunde Karlsruhe provided laboratory support and work space to S.I.L. Marc Roßkopf gave extensive field and technical support, Jim Laundre maintained the Toolik Lake experiment and gave technical help; Richard van Logtestijn and Rob Broekman gave laboratory support. Karin Rebel, Kanchan Shrestha, Kyle Whittinghill, Christina Maki and Marselle Alexander-Ozinskas gave some fieldwork assistance. This study was financed by grant ALW- 852.00.070 of the Netherlands Organization for Scientific Research (NWO) to JHCC.

References

Anon. (2004) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Beringer, J., Lynch, A.H., Chapin, F.S.III *et al.* (2001) The representation of arctic soils in the land surface model: the importance of mosses. *Journal of Climate*, **14**, 3324-3335.

Biasi, C., Meyer, H., Rusalimova, O. *et al.* (2008) Initial effects of experimental warming on carbon exchange rates, plant growth and microbial dynamics of a lichen-rich dwarf shrub tundra in Siberia. *Plant and Soil*, **307**, 191-205.

Bokhorst, S.F., Bjerke, J.W., Tømmervik, H. *et al.* (2009) Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. *Journal of Ecology*, **97**, 1408-1415.

Bret-Harte, M.S., Shaver, G.R., Zoerner, J.P. *et al.* (2001) Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology*, **82**, 18-32.

Callaghan, T.V., Press, M.C., Lee, J.A. *et al.* (1999) Spatial and temporal variability in the responses of Arctic terrestrial ecosystems to environmental change. *Polar Research*, **18**, 191-197.

CAVM Team (2003) Circumpolar Arctic Vegetation Map. Scale 1:7,500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. pp. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Chapin, D.M. & Bledsoe, C.S. (1992) Nitrogen fixation in arctic plant communities. *Arctic Ecosystems in a Changing Climate* (eds F.S.III Chapin, R.L. Jefferies, J.F. Reynolds *et al.*), pp. 301-319. Academic Press, San Diego.

Chapin, F.S.III & Shaver, G.R. (1985) Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, **66**, 564-576.

Chapin, F.S.III, Shaver, G.R., Giblin, A.E. *et al.* (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694-711.

Chapin, F.S.III, Sturm, M., Serreze, M.C. *et al.* (2005) Role of land-surface changes in Arctic summer warming. *Science*, **310**, 657-660.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M. *et al.* (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, **89**, 984-994.

Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A. *et al.* (2007) Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany*, **99**, 987-1001.

Dyrness, C.T. (1982) Control of depth to permafrost and soil temperature by the forest floor in black spruce/feathermoss communities. Research Note PNW-396, pp. 1-19. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Epstein, H.E., Calef, M.P., Walker, M.D. *et al.* (2004) Detecting changes in arctic tundra plant communities in response to warming over decadal time scales. *Global Change Biology*, **10**, 1325-1334.

Faith, D.P., Minchin, P.R. & Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, **69**, 57-68.

Forbes, B.C., Fauria, M.M. & Zetterberg, P. (2010) Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology*, **16**, 1542-1554.

Graglia, E., Jonasson, S., Michelsen, A. *et al.* (2001) Effects of environmental perturbations on abundance of subarctic plants after three, seven and ten years of treatments. *Ecography*, **24**, 5-12.

Gunnarsson, U. (2005) Global patterns of *Sphagnum* productivity. *Journal of Bryology*, **27**, 269-279.

Harley, P.C., Tenhunen, J.D., Murray, K.J. *et al.* (1989) Irradiance and temperature effects on photosynthesis of tussock tundra *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. *Oecologia*, **79**, 251-259.

Hartley, A.E., Neill, C., Melillo, J.M. *et al.* (1999) Plant performance and soil nitrogen mineralization in response to simulated climate change in subarctic dwarf shrub heath. *Oikos*, **86**, 331-343.

Hill, M.O. & Preston, C.D. (1998) The geographical relationships of British and Irish bryophytes. *Journal of Bryology*, **20**, 127-226.

Hobbie, S.E. & Chapin, F.S.III (1998) The response of tundra plant biomass, aboveground production, nitrogen, and CO_2 flux to experimental warming. *Ecology*, **79**, 1526-1544.

Hollister, R.D., Webber, P.J. & Tweedie, C.E. (2005) The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Global Change Biology*, **11**, 525-536.

Hudson, J.M.G. & Henry, G.H.R. (2009) Increased plant biomass in a High Arctic heath community from 1981 to 2008. *Ecology*, **90**, 2657-2663.

IPCC (2007) Fourth Assessment Report: Climate Change 2007. Cambridge University Press, Cambridge.

Jägerbrand, A.K., Alatalo, J.M., Chrimes, D. *et al.* (2009) Plant community responses to 5 years of simulated climate change in meadow and heath ecosystems at a subarctic-alpine site. *Oecologia*, **161**, 601-610.

Jägerbrand, A.K., Lindblad, K.E.M., Björk, R.G. *et al.* (2006) Bryophyte and lichen diversity under simulated environmental change compared with observed variation in unmanipulated alpine tundra. *Biodiversity and Conservation*, **15**, 4453-4475.

Jonasson, S. (1988) Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, **52**, 101-106.

Lang, S.I., Cornelissen, J.H.C., Hölzer, A. *et al.* (2009) Determinants of cryptogam composition and diversity in *Sphagnum*-dominated peatlands: the importance of temporal, spatial and functional scales. *Journal of Ecology*, **97**, 299–310.

Longton, R.E. (1997) The role of bryophytes and lichens in polar ecosystems. *Ecology of Arctic Environments* (eds S.J. Woodin & M. Marquiss), pp. 69-96. Blackwell Science, Oxford.

Magurran, A.E. (2004) Measuring Biological Diversity. Blackwell Science Ltd, Oxford.

Makkonen, M., Berg, M.P., Van Hal, J.R. *et al.* (2011) Traits explain the responses of a sub-arctic Collembola community to climate manipulation. *Soil Biology & Biochemistry*, **43**, 377-384.

Matveyeva, N. & Chernov, Y. (2000) Biodiversity of terrestrial ecosystems. *The Arctic: Environment, People, Policy* (eds M. Nutall & T.V. Callaghan), pp. 233-273. Harwood Academic Publishers, Reading.

Molau, U. & Alatalo, J.M. (1998) Responses of subarctic-alpine plant communities to simulated environmental change: biodiversity of bryophytes, lichens, and vascular plants. *Ambio*, **27**, 322-329.

Oechel, W.C. & Sveinbjörnsson, B. (1978) Primary production processes in arctic bryophytes at Barrow, Alaska. *Vegetation and Production Ecology of an Alaskan Arctic Tundra* (ed L.L. Tieszen), pp. 269-298. Springer, New York.

Oksanen, J. (2004) 'Vegan' Community Ecology Package: ordination methods and other functions for community and vegetation ecologists. University of Oulu, Oulu.

Pomeroy, J.W., Bewley, D.S., Essery, R.L.H. *et al.* (2006) Shrub tundra snowmelt. *Hydrological Processes*, **20**, 923-941.

Post, E. & Pedersen, C. (2008) Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 12353-12358.

Prach, K., Košnar, J., Klimešová, J. *et al.* (2010) High Arctic vegetation after 70 years: a repeated analysis from Svalbard. *Polar Biology*, **33**, 635-639.

Press, M.C., Potter, J.A., Burke, M.J.W. *et al.* (1998) Responses of a subarctic dwarf shrub heath community to simulated environmental change. *Journal of Ecology*, **86**, 315-327.

Rustad, L.E., Campbell, J.L., Marion, G.M. *et al.* (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543-562.

Rydin, H. & Jeglum, J. (2006) The Biology of Peatlands. Oxford University Press, Oxford.

Schmidt, I.K., Jonasson, S. & Michelsen, A. (1999) Mineralization and microbial immobilization of N and P in arctic soils in relation to season, temperature and nutrient amendment. *Applied Soil Ecology*, **11**, 147-160.

Solheim, B., Endal, A. & Vigstad, H. (1996) Nitrogen fixation in Arctic vegetation and soils from Svalbard, Norway. *Polar Biology*, **16**, 35-40.

Sturm, M., Schimel, J., Michaelson, G. *et al.* (2005) Winter biological processes could help convert arctic tundra to shrubland. *Bioscience*, **55**, 17-26.

Tape, K., Sturm, M. & Racine, C. (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, **12**, 686-702.

Tenhunen, J.D., Lange, O.L., Hahn, S. *et al.* (1992) The ecosystem role of poikilohydric tundra plants. *Arctic Ecosystems in a Changing Climate* (eds F.S.III Chapin, R.L. Jefferies, J.F. Reynolds *et al.*), pp. 213-237. Academic Press, San Diego.

Ter Braak, C.J.F. & Šmilauer, P. (2002) Canoco Reference Manual and Canodraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). www.canoco.com, Microcomputer Power, Ithaca.

Trenbirth, H.E. & Matthews, J.A. (2010) Lichen growth rates on glacier forelands in southern Norway: preliminary results from a 25-year monitoring programme. *Geografiska Annaler*, **92A**, 19-39.

Van Herk, C.M., Aptroot, A. & van Dobben, H.F. (2002) Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *The Lichenologist*, **34**, 141-154.

Van Wijk, M.T., Clemmensen, K.E., Shaver, G.R. *et al.* (2003) Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, **10**, 105-123.

Virtanen, R., Oksanen, J., Oksanen, L. *et al.* (2006) Broad-scale vegetation-environment relationships in Eurasian high-latitude areas. *Journal of Vegetation Science*, **17**, 519-528.

Vonlanthen, C.M., Walker, D.A., Raynolds, M.K. *et al.* (2008) Patterned-ground plant communities along a bioclimate gradient in the High Arctic, Canada. *Phytocoenologia*, **38**, 23-63.

Wahren, C.H.A., Walker, M.D. & Bret-Harte, M.S. (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, **11**, 537-552.

Walker, M.D., Wahren, C.H., Hollister, R.D. *et al.* (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 1342-1346.

Wielgolaski, F.E., Bliss, L.C., Svoboda, J. *et al.* (1981) Primary production of tundra. *Tundra Ecosystems: a Comparative Analysis* (eds L.C. Bliss, O.W. Heal & J.J. Moore), pp. 187-225. Cambridge University Press, Cambridge.

Wookey, P.A., Parsons, A.N., Welker, J.M. *et al.* (1993) Comparative responses of phenology and reproductive development to simulated environmental change in sub-arctic and high arctic plants. *Oikos*, **67**, 490-502.

Yoshikawa, K., Bolton, W.R., Romanovsky, V.E. *et al.* (2003) Impacts of wildfire on the permafrost in the boreal forests of Interior Alaska. *Journal of Geophysical Research*, **108**.

Zar, J.H. (1999) Biostatistical Analysis. Prentice Hall, New Jersey.

Appendix S1. Measurement of abiotic factors and effects of experimental warming on nutrients and litter

Measurement of abiotic factors

TEMPERATURE

Soil temperature was measured from end of August 2004 to beginning of August 2005 at Latnjajaure using one temperature button (MiniTemp Logger, Photologic Ltd., Cobourg, Ontario, Canada) at each site along the gradient. The buttons were protected from moisture damage by putting them into film canisters, sealed with silicone wax. They were then buried into the soil until the top of the canister was at about the same level as the soil surface, and subsequently covered with a heavy stone. These precautions were necessary at Latnjajaure since alternating freeze-thaw cycles in winter exert strong forces on equipment, removing loggers from their original position. From end of May 2006 to beginning September 2006 we used dataloggers with an external probe in 1 cm depth (Tinytag Plus TGP-0020, PB-5002-1M5 probe, Gemini Data Loggers, Chichester, UK) since we were interested in the effects of temperature on the surface-dwelling cryptogams. Per experimental treatment two and three loggers were used at Latnjaure and Abisko, respectively. At each gradient site two loggers were used. In Alaska, temperature was measured from mid July 2005 through mid August 2005 with one Tinytag datalogger per plot. From mid August 2005 through end of July 2006, one logger per site/treatment was used. Additionally, in the period of beginning of July 2006 through end of July 2006, at all sites/treatments, one more logger was in place (except at Chandalar shelf). Temperature for plots without loggers was calculated by taking the average of the measurements in nearby plots (if more than one present). As a measure of temperature, we calculated both mean annual temperature (MAT) and degree days, the cumulative number of degrees. MAT and degree days were based on the measurement period from end of August 2004 to beginning of August 2005 in Sweden, and mid August 2005 to end July 2006 in Alaska for MAT. The temperature threshold at which both bryophytes and lichens might start to be photosynthetically active was estimated at 0 °C (Rastorfer 1970; Kappen *et al.* 1996). Consequently, all days of the measurement period with a mean daily temperature exceeding 0 °C were summed resulting in a degree day temperature sum. MAT and degree days were significantly related to depth of the organic layer ($R^2_{MAT} = 0.92$, $P = 0.042$; $R^2_{Degree\ days} = 0.93$, $P = 0.034$; see Appendix 3 in Supporting Information). Since no logger was present in the Abisko plots and the logger in the control plots at Latnjajaure went missing, we calculated MAT and degree days in these plots from the known depth of the organic layer by using the regression in Appendix 3. The additional measurements from the summers 2005 and 2006 in Alaska, and summer 2006 in Sweden, were not included in the calculation of MAT and degree days, but confirmed that within-site differences were indeed small, justifying the overall relationship between sites.

NUTRIENT AVAILABILITY

Soil nutrient availability (ammonium NH_4^+, nitrate NO_3^-, phosphate PO_4^{3-}, magnesium Mg^{2+} and calcium Ca^{2+}; and potassium K^+ in Alaska only) was measured according to Weih (1998) using ion exchange resins, during the summer 2004 and 2005 in Sweden and 2005 and 2006 in Alaska. Soil cores for measurement of extractable NO_3^- and NH_4^+ were taken during the period of mid July (Alaska) to late August (Latnjajaure)/early September (Abisko) 2006.

ION RESINS

The anion exchange membrane (AEM) and cation exchange membrane (CEM) used (product no. 55164 and 55165, respectively, B.D.H., Poole, U.K.) are polystyrene sheets with quarternary ammonium (AEM) or sulphonic acid (CEM) groups attached. The sheets were cut in 1 x 6 cm strips, onto which a fishing line was attached for easy recovery in the field once the resins were buried. CEM and AEM resins were saturated with H^+ using 0.1 M H_2SO_4 and with Cl^- using 2 M NaCl, respectively (Giblin *et al.* 1994), by shaking for 2 h. In

Sweden, resins were put out end July (Latnjajaure)/mid August (Sheffield) and retrieved end of August (Latnjajaure)/end of September (Sheffield) in 2004. Since blanks of NH_4^+ were too high, AEM were brought out again in 2006, starting from end of May/beginning of June and retrieved end of August/beginning of September. In Alaska, resins were brought out mid July to mid August. Since blank values for NH_4^+ were too high, AEM were brought out again in 2006, from beginning of July to end of July 2006. After the incubation period the resins were returned to the laboratory and extracted with 20 mL of 2 M NaCl in 0.1 M HCl (Giblin *et al.* 1994) by shaking for 2 h. The CEM in Alaska, however, were extracted with 2 M HCl since extraction with NaCl in 2005 showed that an overflow of Na superimposes the K spectrum when measuring K^+ by atomic absorption. The extracts were subsequently analysed for NO_3^-, NH_4^+ and PO_4^{3-}. NH_4^+ was measured photometrically with an indicator (Tecator Application note AN 134/91) using a flow injection autoanalyzer (Tecator, FIAstar 5020 Analyzer, 5032 Detector Controller, Foss, Rellingen, Germany). PO_4^{3-} was analysed photometrically with the molybdenum-blue method (Tecator Application note AN 146/90) using a flow injection autoanalyser (Tecator, Aquatec 5400 Analyser, Foss, Rellingen, Germany). Ca^{2+}, Mg^{2+} and K^+ were measured by atomic absorption (Varian AAS SpectrAA 220FS, Palo Alto, CA) in an air-acetylene flame under addition of $LaCl_3$ and CsCl. The difference in exposure time to the soil due to temporal differences in burial and excavation time at each site was not taken into account since the resins were buried and excavated within a few days along all the gradients and at the experiments. Due to logistics, the resins at the Abisko site were excavated from the ground c. two weeks later than the ones at Latnjajaure and its nearby gradient plots. We did not correct for differences in exposure time since the growing season ends much earlier in Latnjajaure compared to Abisko and, because of the colder climate, soil processes are expected to cease as well. The resins are representative for both sites and the gradient for the second half of the growing season.

SOIL CORES

Soil cores with a cross-sectional area of 7.55 cm^2 and 18.86 cm^2 for Sweden and Alaska, respectively, and 5 cm depth per plot were taken during the period of mid July (Alaska) to late August (Latnjajaure)/early September (Sheffield) 2006 for measurement of extractable NO_3^- and NH_4^+. Live roots were removed from the samples before taking an aliquot of soil to be extracted with 1 M KCl solution. The samples were shaken for 1 h and subsequently filtered using a Whatman GF/C glass fiber filter. NH_4^+ and NO_3^- were measured photometrically by means of the indophenolblue method and the sulfanylamide/naphtyl–ethylene–diamine method, respectively (Skalar SA-40 continuous flow analyzer, Skalar, Breda, The Netherlands). PO_4^{3-} was measured photometrically (Shimadzu, UV-1601PC, Shimadzu Corp., Kyoto, Japan) by means of the molybdenum-blue method. Values for NH_4^+ but not for PO_4^{3-} needed to be blank-corrected before further use in analysis. Data were checked for outliers. NH_4^+ (resin) at one control plot at Toolik Lake showed ten times higher values compared to other control plots and was therefore replaced by the mean of the remaining plots. Missing values (resins and soil cores) were replaced by the mean of the remaining plots at one site or treatment.

SOIL PH

Soil pH was measured in the 1 M KCl soil core extracts received for the nutrient analysis using a pH meter (WTW Inolab Level 2 pH meter, Sentix 41 membrane glass electrode, WTW Weilheim, Germany).

SOIL MOISTURE

Soil moisture was measured manually on several days throughout the season by inserting a handheld Time Domain Reflectometry soil moisture meter (TDR Trime FM-2, P2G probe (16cm length) and P2D probe (5cm length), IMKO GmbH, Ettlingen, Germany) into the soil. In Sweden, we used the P2D probe and inserted it vertically into the ground down to 5 cm depth. In Alaska, the P2G probe was used and inserted at an angle of c. 30° into the ground, down to a depth of c. 8 cm. On each of the four sides of the Swedish plots, and in four

places around the two subplots in Alaska, one measurement was taken and all four measurements were averaged. The resulting soil moisture values were averaged for the summers of 2004 through 2005, and 2005 through 2006, for Sweden and Alaska, respectively, to account for seasonal variability in tundra soils. Soil moisture values were separately calibrated for the different types of tundra soils occurring in Sweden and Alaska. To calibrate the TDR soil moisture meter in Alaska, four tundra soil cores, colonized with different mosses (*Dicranum*, *Hylocomium*, *Aulacomnium*, *Sphagnum*), all of which are dominant, were collected around Toolik Lake in 2006 and transferred into water-tight canisters. No mineral soil was included in these cores. The cores were saturated with water, where-after soil moisture and weight were measured weekly during the entire field season. The soil was dried at 105 ºC and the mass based % was calculated for each point of the calibration (Fig 1).

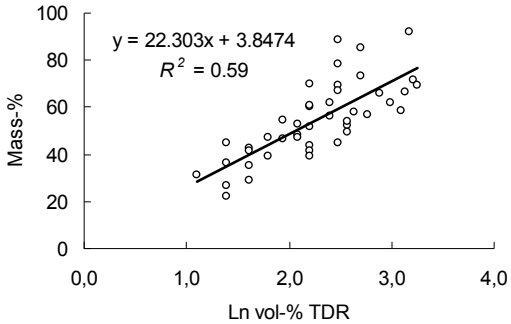


Fig. 1 Mass-based versus ln-transformed TDR-based measurements of soil moisture in Alaska (n = 44).

In Sweden, three tundra soil cores, typical for the gradient, were taken from around Abisko, either colonized with mosses (*Hylocomium*, *Pleurozium*, *Dicranum*) or *Empetrum*. Measurements and calculations equalled those at Toolik Lake (calibration see Fig 2).

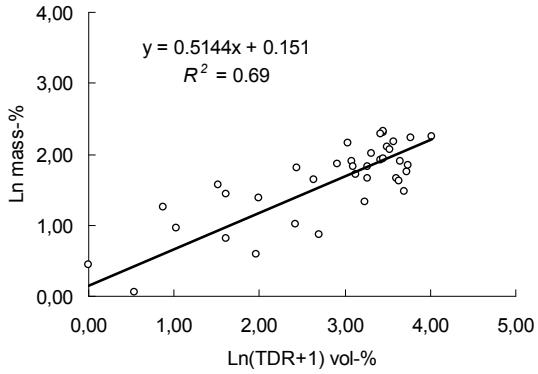


Fig. 2 Mass-based (lnX) versus TDR-based (ln(X+1)) measurements of soil moisture in Sweden (n = 39).

OTHER SOIL MEASUREMENTS

The depth of the organic layer was defined as the humus-rich material on top of the mineral soil. In Alaska, due to patchiness in vegetation caused by *Eriophorum* tussocks, one soil profile of c. 70 cm width was analysed per

site (except for the greenhouse; profiles for control plots were dug outside the experiment to minimize damage). The organic layer depth was measured in several places along the profile wall and the mean taken. In Sweden, vegetation was less patchy and the depth of the organic layer was inferred from soil cores taken for nutrient extractions.

Active layer depth was measured in Alaska towards the end of July in 2006. Since *Sphagnum* was the only surviving bryophyte in the greenhouses, measurements at all sites were conducted below *Sphagnum* to be comparable to each other. A metal pin was inserted into the ground until the frozen ground was reached and depth readings taken starting at the top of the bryophyte layer. Ten measurements per plot were taken and averaged. In Sweden, no permafrost could be measured, being either absent or located too deep in the ground. Instead, end of August until beginning of September 2006, we measured ground penetrability which might be important for plant roots trying to penetrate the soil. A large metal pin was inserted into the ground until a stone was hit or the ground got too dense for further penetration. Four measurements per plot were taken and averaged.

Amount of bare ground was measured beginning of August 2005 in Alaska at all sites using a frame of 1 x 1 m which was subdivided into 10 x 10 cm^2 subquadrats. With the aid of the subquadrats, the percentage of bare ground was recorded close to each vegetation plot in four adjacent quadrats and averaged. In Sweden, 1 m^2 was recorded per experimental plot in late August 2006, this being the maximum area available per plot, while 4 m^2 were covered along the gradient, and subsequently averaged. The amount of stones per plot was measured during the vegetation survey as point intercept hits.

Effects of experimental warming on nutrients and litter

Table 1 Effect of warming treatment and experimental site on $NH_4^+{}_{resin}$, $NH_4^+{}_{soil\ core}$ and amount of litter (two-way ANOVAs, n = 4-6). Significant P-values are marked with bold letters

	$NH_4^+{}_{resin}$		$NH_4^+{}_{soil\ core}$		Litter	
Source	*F*	*P*	*F*	*P*	*F*	*P*
Warming	4.71	**0.041**	9.41	**0.006**	7.51	**0.012**
Site	8.90	**0.001**	3.34	0.054	18.98	**< 0.001**
Warming x site	8.68	**0.002**	1.32	0.289	0.41	0.670

References

Giblin, A.E., Laundre, J.A., Nadelhoffer, K.J. *et al.* (1994) Measuring nutrient availability in arctic soils using ion-exchange resins - a field test. *Soil Science Society of America Journal*, **58**, 1154-1162.

Kappen, L., Schroeter, B., Scheidegger, C. *et al.* (1996) Cold resistance and metabolic activity of lichens below 0°C. *Advances in Space Research*, **18**, 119-128.

Rastorfer, J.R. (1970) Effects of light intensity and temperature on photosynthesis and respiration of two east antarctic mosses, *Bryum argenteum* and *Bryum antarcticum*. *The Bryologist*, **73**, 544-556.

Weih, M. (1998) Seasonality of nutrient availability in soils of subarctic mountain birch woodlands, Swedish Lapland. *Arctic and Alpine Research*, **30**, 19-25.

Appendix S2. Vegetation recording, species identification, species richness and lists for Alaska and Sweden, and experimental warming effects on species abundance at Abisko

Vegetation recording techniques and species identification

For vascular plants, each foliated branch of *Andromeda polifolia*, *Empetrum hermaphroditum*, *Cassiope hypnoides*, *Cassiope tetragona*, *Diapensia lapponica* and *Phyllodoce caerulea* was considered to be one hit since counting every hit leaf would lead to overestimation of abundance. Since the cryptogams *Lophozia lycopodioides* and *Lophozia hatcheri*, *Gymnomitrion corallioides* and *Gymnomitrion concinnatum*, *Cetraria islandica* and *Cetraria ericetorum*, and *Stereocaulon alpinum* and *Stereocaulon paschale* grew intermingled, they could not be safely distinguished in the field and were thus recorded as one species. The same applied to *Peltigera aphthosa* and *Peltigera leucophlebia* where small specimens were not safely distinguishable from each other without apothecia which are rarely present in (sub)arctic ecosystems. At Latnjajaure, the vegetation on moraine ridges consisted partly of a cryptogamic crust, composed of an intimate mixture of crustose lichens (*Pyrenopsis furfurea*), free cyanobacteria and liverworts (*G. corallioides*/*concinnatum*). Since the individual components could not be distinguished in the field, every hit counted as each one lichen and one liverwort while the cyanobacteria were not considered. In Abisko, a caterpillar outbreak in 2003/2004 caused considerable damage in some plots. We therefore included hit leaves of *Empetrum hermaphroditum* that had recently died due to herbivory by caterpillars, causing a characteristic red colour, in the sum of *E. hermaphroditum* hits. Also *Vaccinium myrtillus* showed frequent signs of herbivory. Half-eaten leaves, which would have touched the pin if still intact, were included in its count.

In Sweden, nomenclature followed Hill *et al.* (2006) for all mosses except *Polytrichum* (Long 1985); Damsholt (2002) for liverworts; Santesson *et al.* (2004) for lichens; and Mossberg & Stenberg (2003) for vascular plants. Vascular plants from Alaska were named according to Hultén (1968) and *Sphagnum* according to Crum (1984). Recently newly discovered species of *Sphagnum* not yet covered in Crums flora (1984), *S. tescorum* Flatberg and *S. concinnum* (Berggr.) Flatberg, were considered but not present in this study. Alaskan non-*Sphagnum* mosses were named according to Anderson *et al.* (1990) except *Dicranum* (Hill *et al.* 2006); liverworts according to Damsholt (2002), and lichens according to Santesson (2004) except *Dactylina arctica* (Richards.) Nyl..

Table 1 Species lists and overall species richness for Alaska and Sweden

	Species	Alaska	Sweden
Lichens	*Alectoria nigricans*		+
	Alectoria ochroleuca		+
	Bryocaulon divergens		+
	Cetraria aculeata		+
	Cetraria ericetorum		+
	Cetraria islandica	+	+
	Cetraria nigricans		+
	Cetrariella delisei		+
	Cladonia amaurocraea	+	+
	Cladonia arbuscula	+	+
	Cladonia bellidiflora		+
	Cladonia coccifera		+
	Cladonia ecmocyna	+	
	Cladonia cf. *fimbriata*	+	
	Cladonia furcata		+
	Cladonia gracilis	+	+
	Cladonia cf. *macroceras*		+
	Cladonia cf. *pyxidata/Cladonia chlorophaea*-group		+
	Cladonia rangiferina		+
	Cladonia stygia	+	+
	Cladonia uncialis		+
	Cladonia sp.	+	
	Cladonia sp. *(squamules)*		+
	Dactylina arctica	+	
	Flavocetraria cucullata	+	+
	Flavocetraria nivalis		+
	Lecanora polytropa		+
	Lecidea sp.		+
	Lobaria linita		+
	Nephroma arcticum		+
	Ochrolechia frigida		+
	Peltigera aphthosa	+	+
	Peltigera canina	+	
	Peltigera malacea	+	
	Peltigera polydactylon-group	+	
	Peltigera scabrosa	+	+
	Pertusaria dactylina		+
	Pertusaria oculata		+
	Porpidia flavocaerulescens		+
	Porpidia macrocarpa		+
	Porpidia melinodes		+

Table 1 continued

	Species	Alaska	Sweden
Lichens	*Pseudephebe pubescens*		+
	Psoroma hypnorum		+
	Pyrenopsis furfurea		+
	Rhizocarpon geographicum		+
	Rhizocarpon intermediellum		+
	Solorina crocea		+
	Sphaerophorus globosus		+
	Stereocaulon alpinum		+
	Stereocaulon botryosum		+
	Stereocaulon paschale		+
	Thamnolia vermicularis	+	+
	Umbilicaria proboscidea		+
	Vulpicida pinastri	+	
Liverworts	*Anastrophyllum minutum*	+	+
	Blepharostoma trichophyllum	+	
	Calypogeia sphagnicola	+	
	Gymnomitrion corallioides		+
	Gymnomitrion concinnatum		+
	Lophozia atlantica		+
	Lophozia binsteadii	+	
	Lophozia hatcheri		+
	Lophozia incisa	+	
	Lophozia kunzeana	+	+
	Lophozia lycopodioides		+
	Lophozia polaris		+
	Lophozia ventricosa	+	+
	Lophozia wenzelii	+	+
	Ptilidium ciliare	+	+
	Scapania scandica fo. *parvifolia*		+
	Tritomaria quinquedentata	+	+
Non-*Sphagnum* mosses	*Aulacomnium acuminatum*	+	
	Aulacomnium turgidum	+	+
	Calliergon stramineum	+	
	Ceratodon purpureus	+	
	Dicranum acutifolium	+	+
	Dicranum elongatum	+	+
	Dicranum flexicaule		+
	Dicranum fuscescens	+	+
	Dicranum laevidens	+	
	Dicranum leioneuron	+	
	Dicranum majus	+	

Table 1 continued

	Species	Alaska	Sweden
Non-*Sphagnum* mosses	*Dicranum scoparium*		+
	Dicranum undulatum		+
	Hylocomium splendens	+	+
	Pleurozium schreberi	+	+
	Pohlia nutans	+	+
	Polytrichastrum alpinum var. *alpinum*	+	
	Polytrichum commune		+
	Polytrichum hyperboreum		+
	Polytrichum juniperinum	+	+
	Polytrichum piliferum		+
	Polytrichum strictum	+	+
	Ptilium crista-castrensis	+	
	Racomitrium lanuginosum		+
	Rhytidium rugosum	+	
	Sanionia uncinata	+	
	Tomentypnum nitens	+	
Sphagnum	*Sphagnum angustifolium*	+	
	Sphagnum balticum	+	
	Sphagnum girgensohnii	+	
	Sphagnum russowii	+	
	Sphagnum warnstorfii	+	
Vascular plants	*Andromeda polifolia*	+	
	Arctostaphylos alpinum		+
	Betula nana	+	+
	Calamagrostis lapponica		+
	Calamagrostis sp.	+	
	Carex bigelowii		+
	Carex cf. *bigelowii* x *lugens*	+	
	Cassiope hypnoides		+
	Cassiope tetragona	+	+
	Cornus suecica		+
	Deschampsia flexuosa		+
	Diapensia lapponica		+
	Empetrum hermaphroditum	+	+
	Equisetum arvense		+
	Equisetum sylvaticum		+
	Equisetum variegatum		+
	Eriophorum vaginatum	+	
	Festuca ovina		+
	Ledum palustre	+	
	Linnaea borealis		+

Table 1 continued

	Species	Alaska	Sweden
Vascular plants	*Luzula arcuata*		+
	Pedicularis labradorica	+	
	Petasites frigidus	+	
	Phyllodoce caerulea		+
	Polygonum viviparum	+	
	Rubus chamaemorus	+	
	Salix herbacea		+
	Salix pulchra	+	
	Vaccinium myrtillus		+
	Vaccinium uliginosum	+	+
	Vaccinium vitis-idaea	+	+

Species richness

Lichens	17	46
Bryophytes	35	29
Non-*Sphagnum* mosses	20	16
Sphagnum	5	0
Liverworts	10	13
Vascular plants	15	21

Table 2 Effect of warming treatment on abundance of cryptogams and vascular plants at Abisko. Where variance was homogeneous between the treatments (H), factorial ANOVA was used to test for differences in abundance. Where variance was heterogeneous (h), data were analysed by Kruskal-Wallis. Significant *P*-values are marked with bold letters

Species	Variance	*F*	*P*
Lichens			
Cladonia furcata	h	6.25	0.317
Cladonia gracilis	h	11.33	0.022
Cladonia stygia	h	8.32	0.247
Nephroma arcticum	H	2.50	0.385
Peltigera aphthosa	H	0.54	0.866
Peltigera scabrosa	h	11.79	0.140
Liverworts			
Lophozia lycopodioides/hatcheri	H	0.86	0.362
Lophozia kunzeana	h	16.00	0.140
Ptilidium ciliare	h	6.25	0.317
Non-*Sphagnum* mosses			
Dicranum acutifolium	h	6.25	0.317
Dicranum scoparium	H	4.80	0.174
Dicranum undulatum	h	6.25	0.317
Hylocomium splendens	H	0.74	0.259
Pleurozium schreberi	H	4.09	0.185
Pohlia nutans	H	0.04	0.726
Polytrichum commune	H	0.66	0.773
Polytrichum juniperinum	H	0.48	0.787
Vascular plants			
Arctostaphylos alpinum	h	6.22	0.140
Calamagrostis lapponica	h	9.14	0.140
Deschampsia flexuosa	h	5.65	0.266
Empetrum hermaphroditum	H	1.67	0.365
Equisetum arvense	h	6.25	0.317
Equisetum variegatum	H	3.31	0.484
Festuca ovina	h	6.25	0.317
Linnaea borealis	H	3.85	0.451
Vaccinium myrtillus	h	12.02	**0.045**
Vaccinium uliginosum	H	2.55	0.884
Vaccinium vitis-idaea	h	20.36	0.936

References

Anderson, L.E., Crum, H.A. & Buck, W.R. (1990) List of the mosses of North America North of Mexico. *The Bryologist*, **93**, 448-499.

Crum, H. (1984) Sphagnopsida Sphagnaceae. New York Botanical Garden, New York.

Damsholt, K. (2002) Illustrated Flora of Nordic Liverworts and Hornworts. Nordic Bryological Society, Lund.

Hill, M.O., Bell, N., Bruggeman-Nannenga, M.A. *et al.* (2006) An annotated checklist of the mosses of Europe and Macaronesia. *Journal of Bryology*, **28**, 198-267.

Hultén, E. (1968) Flora of Alaska and Neighboring Territories: A Manual of the Vascular Plants. Stanford University Press, Stanford, California.

Long, D.G. (1985) Illustrated Moss Flora of Arctic North America and Greenland. 1. Polytrichaceae. *Meddelelser om Grønland, Bioscience*, **17**, 9-57.

Mossberg, B. & Stenberg, L. (2003) Den Nya Nordiska Floran. Wahlström & Widstrand, Stockholm.

Santesson, R., Moberg, R., Nordin, A. *et al.* (2004) Lichen-forming and Lichenicolous Fungi of Fennoscandia. Museum of Evolution, Uppsala University, Uppsala.

Appendix S3. Pearson correlations for environmental variables along the Alaskan and Swedish gradient

Pearson correlations Alaska

Table 1 Pearson's correlation for the variables mean annual temperature (MAT), degree days, altitude, latitude, organic layer depth, litter, active layer and bare ground in Alaska

	MAT	Degree days	Altitude	Latitude	Organic layer depth	Litter	Active layer	Bare ground
MAT	1	**.845(**)**	.432	**-.952(**)**	**.957(**)**	.356	**.824(**)**	.497
Degree days	**.845(**)**	1	.096	**-.739(**)**	**.874(**)**	-.014	**.895(**)**	.159
Altitude	.432	.096	1	**-.604(*)**	.179	**.639(*)**	-.094	**.535(*)**
Latitude	**-.952(**)**	**-.739(**)**	**-.604(*)**	1	**-.883(**)**	-.510	**-.687(**)**	**-.655(**)**
Organic layer depth	**.957(**)**	**.874(**)**	.179	**-.883(**)**	1	.245	**.921(**)**	.454
Litter	.356	-.014	**.639(*)**	-.510	.245	1	.022	**.537(*)**
Active layer	**.824(**)**	**.895(**)**	-.094	**-.687(**)**	**.921(**)**	.022	1	.201
Bare ground	.497	.159	**.535(*)**	**-.655(**)**	.454	**.537(*)**	.201	1

* Correlation is significant at the 0.05 level (2-tailed).

** Correlation is significant at the 0.01 level (2-tailed).

Table 2 Pearson's correlation for the variables NH_4^+ resin, NH_4^+ soil core, PO_4^{3-} resin 2005, PO_4^{3-} resin 2006, PO_4^{3-} soil core and NO_3^- soil core in Sweden

	NH_4^+ resin	NH_4^+ soil core	PO_4^{3-} resin 2005	PO_4^{3-} resin 2006	PO_4^{3-} soil core	NO_3^- soil core
NH_4^+ resin	1	.111	.142	**.758(**)**	-.054	-.272
NH_4^+ soil core	.111	1	-.184	.083	.435	-.162
PO_4^{3-} resin 2005	.142	-.184	1	.201	-.034	-.067
PO_4^{3-} resin 2006	**.758(**)**	.083	.201	1	.111	-.243
PO_4^{3-} soil core	-.054	.435	-.034	.111	1	.291
NO_3^- soil core	-.272	-.162	-.067	-.243	.291	1

** Correlation is significant at the 0.01 level (2-tailed).

Table 3 Pearson's correlation for the variables K^+, Ca^{2+}, Mg^{2+} and pH in Alaska

	K^+	Ca^{2+}	Mg^{2+}	pH
K^+	1	.241	.438	.149
Ca^{2+}	.241	1	**.583(*)**	.234
Mg^{2+}	.438	**.583(*)**	1	-.254
pH	.149	.234	-.254	1

* Correlation is significant at the 0.05 level (2-tailed).

** Correlation is significant at the 0.01 level (2-tailed).

Pearson correlations Sweden

Table 4 Pearson's correlation for the variables MAT, degree days, organic layer depth, litter, bare soil, stone, altitude and penetrability in Sweden

	MAT	Degree days	Organic layer depth	Litter	Bare ground	Stone	Altitude	Penetrability
MAT	1	**.969(**)**	**.954(**)**	**.877(**)**	**-.618(**)**	**-.724(**)**	**-.915(**)**	-.181
Degree days	**.969(**)**	1	**.958(**)**	**.875(**)**	**-.492(*)**	**-.607(**)**	**-.917(**)**	-.233
Organic layer depth	**.954(**)**	**.958(**)**	1	**.831(**)**	**-.505(*)**	**-.609(**)**	**-.911(**)**	-.118
Litter	**.877(**)**	**.875(**)**	**.831(**)**	1	**-.625(**)**	**-.777(**)**	**-.716(**)**	-.296
Bare ground	**-.618(**)**	**-.492(*)**	**-.505(*)**	**-.625(**)**	1	**.901(**)**	.404	.237
stone	**-.724(**)**	**-.607(**)**	**-.609(**)**	**-.777(**)**	**.901(**)**	1	**.466(*)**	.098
Altitude	**-.915(**)**	**-.917(**)**	**-.911(**)**	**-.716(**)**	.404	**.466(*)**	1	.157
Penetrability	-.181	-.233	-.118	-.296	.237	.098	.157	1

* Correlation is significant at the 0.05 level (2-tailed).

** Correlation is significant at the 0.01 level (2-tailed).

Table 5 Pearson's correlation for the variables NH_4^+ resin, NH_4^+ soil core, PO_4^{3-} resin, PO_4^{3-} soil core and NO_3^- soil core in Sweden

	NH_4^+ resin	NH_4^+ soil core	PO_4^{3-} resin	PO_4^{3-} soil core	NO_3^- soil core
NH_4^+ resin	1	.044	.099	-.103	-.090
NH_4^+ soil core	.044	1	-.020	**.739(**)**	-.123
PO_4^{3-} resin	.099	-.020	1	.145	.074
PO_4^{3-} soil core	-.103	**.739(**)**	.145	1	-.051
NO_3^- soil core	-.090	-.123	.074	-.051	1

** Correlation is significant at the 0.01 level (2-tailed).

Table 6 Pearson's correlation for the variables Ca^{2+}, Mg^{2+} and pH in Sweden

	Ca^{2+}	Mg^{2+}	pH
Ca^{2+}	1	**.713(**)**	**-.452(*)**
Mg^{2+}	**.713(**)**	1	-.238
pH	**-.452(*)**	-.238	1

* Correlation is significant at the 0.05 level (2-tailed).

** Correlation is significant at the 0.01 level (2-tailed).

Regression MAT and degree days versus organic layer depth along the Swedish gradient

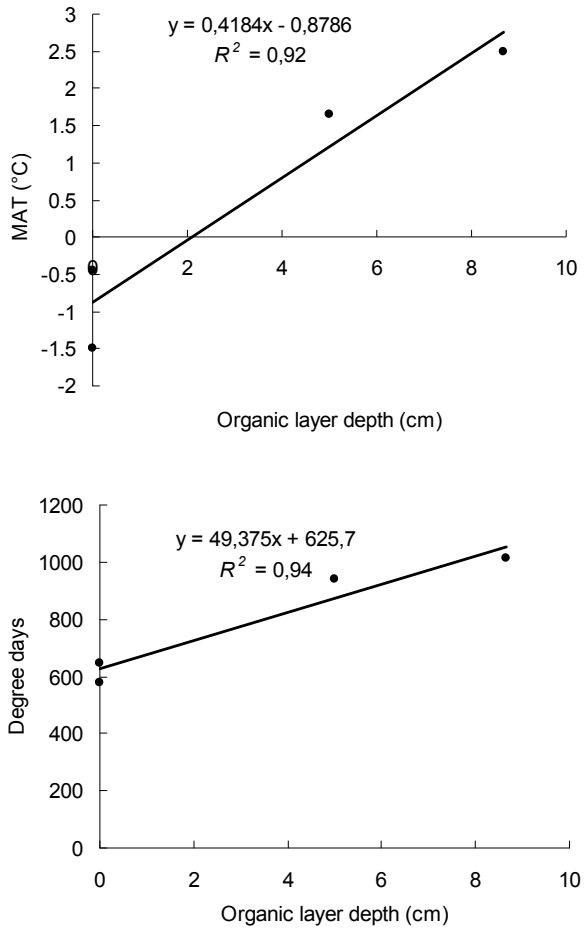


Fig. 1 MAT (°C) and degree days versus organic layer depth (cm) along the Swedish gradient (n = 4).

Chapter 4

Mapping nutrient resorption efficiencies of subarctic cryptogams and seed plants onto the Tree of Life

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Submitted in modified form

Summary

1. Nutrient resorption from senescing photosynthetic organs is a powerful mechanism for conserving nitrogen (N) and phosphorus (P) in infertile environments.

2. Evolution has resulted in enhanced differentiation of conducting tissue, which we hypothesized to have promoted nutrient resorption efficiency (RE, % of nutrient pool exported) as well.

3. Thereto, we compared RE among wide-ranging basal clades from the principally N-limited subarctic region, employing a novel method to correct for mass loss during senescence. Mosses, lichens and lycophytes generally showed low RE_N (< 20%), liverworts and conifers intermediate (40%) and monilophytes, eudicots and monocots high (> 70%). RE_P appeared higher in eudicots and liverworts than in mosses. Within mosses, taxa with more efficient conductance also showed higher RE_N.

4. *Synthesis*. This novel mapping of a physiological process onto the Tree of Life broadly supports the idea that the evolution of conducting tissues towards specialized phloem has aided land plants to optimize their internal nutrient recycling.

Introduction

Plant adaptations to nutrient-poor environments include low nutrient requirements of plant tissues and high tissue longevity together with high resorption of nutrients from senescing parts (Chapin 1980; Reich *et al.* 1992; Aerts 1995; Killingbeck 1996). Although resorption of nutrients, especially nitrogen (N) and phosphorus (P), is a process well-known from higher plants (Aerts 1996; Killingbeck 1996), the controlling factors in nutrient resorption efficiency have remained elusive. While large differences in leaf nutrient resorption have been found among species, differences between plant growth

forms appear inconsistent (Aerts 1996; Killingbeck 1996; Yuan & Chen 2009). Some consistent variation in nutrient RE correlated with taxonomical position was reported by Killingbeck (1996), yet his study included a few seed plants only. Furthermore, environmental conditions have been suggested to influence intraspecific variation in RE (Killingbeck 1996) or may have led to adaptation of whole plant assemblages, as indirectly suggested by the large-scale increase of leaf N resorption efficiency (RE_N) and the decrease of P resorption efficiency (RE_P) of woody plants with latitude (Yuan & Chen 2009). This most likely reflects the predominant N deficiency of ecosystems at high latitudes, where soils are relatively young, as compared to P limitation in ancient soils, which predominate in the (sub-) tropics (Lambers *et al.* 2008). While much work has been done on seed plants, other terrestrial autotrophs have been largely neglected. Only few pteridophytes have been studied (e.g. Headley *et al.* 1985; Killingbeck *et al.* 2002), yet monilophytes other than ferns have been excluded. Moreover, research on variation in and controls on nutrient resorption in cryptogams is still in its infancy (Cornelissen *et al.* 2007), even though bryophytes and lichens are paramount contributors to biomass, especially at higher latitudes where they fulfill important controls on nutrient and carbon cycling (Longton 1997; Cornelissen *et al.* 2007).

Here we introduce a new concept to the debate about what controls nutrient resorption efficiency across taxa by proposing that species' resorption efficiencies are determined more by evolutionary changes in conducting tissues than by current environmental controls. Basic to this concept is that nutrients are translocated via the phloem during senescence (Gan 2007). Differences in conducting tissue should therefore importantly determine the extent of nutrient resorption. What do we know about tissue conductance of the main autotrophic, terrestrial clades of the Tree of Life? While non-vascular cryptogams contain no true sieve elements (SE) (Behnke & Sjolund 1990), conducting tissue as such, albeit simple, have evolved in both liverworts and mosses (Hébant 1977). Phloem emerged in early cryptogams (here: lycophytes or club mosses, monilophytes or ferns and horsetails) but was still relatively primitively built. In contrast, spermatophytes or seed plants (here: conifers, eudicots, monocots) feature a differentiated phloem with sieve cells or tubes accompanied by specialised parenchyma cells (Behnke & Sjolund 1990). Thus, the development of conducting tissue during land plant evolution, from non-vascular cryptogams to tracheophytes (vascular plants), did not only help to bring about increasingly complex plant structures (Behnke & Sjolund 1990) but also efficient transport of a variety of compounds such as photosynthates and amino acids from leaves to other plant parts (Van Bel 2003). We propose that this development also must have offered increasing possibilities of internal nutrient recycling, especially N and P, from

senescing photosynthetic tissues back to other plant parts, thereby helping the plants to gain relative independence from soil nutrient status. In this paper we ask the questions (i) whether the general lack or low degree of specialisation of conducting tissues in non-vascular cryptogams compared to that in vascular plants has left them less efficient at nutrient resorption from senescing parts; and (ii) whether interspecific variation within basal cryptogam clades corresponds with presence/absence or degree of differentiation of conducting tissues as related to their phylogenetic position.

Thus, we hypothesise that the appearance and specialisation of conducting tissues across the autotrophic branches of the Tree of Life has been accompanied by an evolution of increasing nutrient resorption efficiency. We test this new hypothesis across 16 lichen, 27 bryophyte and 25 vascular plant species together comprising the predominant components of the subarctic bogs, mires, tundras and forests of northern Europe, and covering the main basal clades of the Tree of Life present in a subarctic flora. We specifically chose to collect data from one climatic region, thus avoiding confounding effects of strong gradients in climate and nutrient availability and climate (see Yuan & Chen 2009), which in turn might affect nutrient resorption patterns, for instance through luxury consumption. We apply a new methodology to allow fair, calibrated comparisons of mass-loss-corrected nutrient resorption efficiencies among diverse taxa, by expressing nutrient pools of fresh and senesced tissues, respectively, relative to their contents of inert structural chemistry derived from infrared spectra (Fourier transform infrared attenuated total reflectance; FTIR-ATR). To our knowledge, this is the first paper to link a physiological process, nutrient resorption, explicitly to substantial branches of the Tree of Life.

Materials and methods

SAMPLING AND SPECIES CLASSIFICATION

Bryophytes and lichens were sampled in the summer of 2004 mainly around Abisko, Sweden (68º21’N, 18º49’E), but also 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, S Siberia (51º04’N, 85º45’E) in 1999 and stored air-dry. We focused mainly on abundant species (see also Lang *et al.* 2009). For the vascular plants we used an existing database, for which common species were sampled from the predominant ecosystems within 10 km from Abisko in 1998 and 1999 (Quested *et al.* 2003). Since in this dataset no P was measured, we estimated RE_P, with an accuracy of 1%-point, for six vascular plants in the Abisko region from Van Heerwaarden *et al.* (2003b). Together these species were representative of the European subarctic region. For nomenclature see Lang *et al.* (2009).

Phylogeny followed Donoghue (2005). Species were allocated to basal clades, classes, orders and families according to Stevens (2001 onwards) for vascular plants, Goffinet & Shaw (2009) for bryophytes and Lumbsch & Hundorf (2007) for lichens (for the full list see Appendix S1 in Supporting Information). Not all cryptogam classes and orders could be represented by sufficient numbers of species, reflecting their low species richness in the European subarctic flora or the rarity of their occurrence. However, we feel that this imbalance, somewhat constraining detailed statistical analyses (see below) at the finer taxonomic levels, should still be acceptable compared to the disadvantages that would have been associated with adding species from other (climate) regions to artificially top up species numbers per group.

PROCESSING THE CRYPTOGAM SPECIES

After return to the lab, samples were air-dried and kept in paper bags until further preparation. After careful remoistening without producing excess water to avoid leaching, cryptogams were thoroughly cleaned from dirt and other intermingled cryptogam species. Hereafter, liverworts and mosses were visually divided into the living green parts and the recently senesced (brown) parts (see Lang *et al.* 2009). Older, already visibly decomposed parts were not included. Similarly, lichens were divided into the living part and the recently senesced part, the latter with a seemingly softer structure, usually accompanied by a colour change, i.e. a dark brown, black or bleached appearance. For thallose lichens, senesced material was located in the centre of the lichen. In a second dataset, we furthermore distinguished between early and late RE, since the green tissue in mosses often consists of several years' growth. Mosses were visually divided into younger green tissue (bright green), older green tissue (darker green) and the recently senesced parts. Consequently, species that showed no differences in tissue colour were excluded from this dataset, including all sampled liverworts and a few mosses. Younger versus older 'green' tissue of all lichens was identified by its slightly green tinge (depending on thallus colour) versus its mature thallus colour, i.e. brown or yellow.

The influence of choice of material on the magnitude of RE is illustrated in Appendix S2. In general (except for RE_P in lichens), RE was clearly higher in younger parts and lower in older tissue. Consequently, the measure of RE integrating all green tissue (Fig.1), was 10 - 20% lower compared to RE in the youngest tissue. Given also the fact that mosses are known to move photosynthates both upwards into the shoot and downwards into senesced tissue as an energy store (Hakala & Sewón 1992), RE in cryptogams is dependent on the choice of material. In this study, we chose to use RE integrating all green tissue, in accordance with the sampling procedure for evergreen vascular cryptogams (lycophytes).

CALCULATION AND CALIBRATION OF RE

Absolute nutrient concentrations of green versus senesced tissues might give incorrect $RE_{\%}$ depending on the amount of translocation of carbon through plants or fungi (Van Heerwaarden *et al.* 2003a). Since for vascular plants, either area- (all except *Eriophorum vaginatum*) or leaf length-based RE_P (solely *E. vaginatum*) were available as a stable reference (Van Heerwaarden *et al.* 2003b), we combined these measures in the later analysis. We aimed to express nutrient pools based on an immobile fraction, such as total acid-detergent fibers (ADF), lignin or cellulose. The latter occurs in vascular plants, bryophytes as well as in the algal part of lichens and can therefore be used as a stable reference for RE across clades. However, in most cryptogams, especially liverworts, the availability of material was too limited to perform the wet chemical laboratory analyses. Therefore, in a dataset where both wet chemical measurements and infrared measurements were available (n = 14; one moss, 13 vascular plants from contrasting clades), we conducted partial least squares regression (PLS-R) to identify ADF-, lignin- or cellulose-characteristic wavelengths using The Unscrambler v9.2 (CAMO Software AS, Oslo, Norway). Based on significant variables only, which were determined with Jack-knifing (full cross validation), PLS-R was recalculated. In the final model, ADF and lignin were insufficiently described, while PLS-R for cellulose revealed an $R^2_{Calibration}$ of 0.98 and a small root mean square $error_{Calibration}$ of 0.95. In a second, independent dataset, we compared predicted cellulose values with conventional cellulose measurements. The linear relationship was significant (P = 0.003, R^2 = 0.84). However, lichen cellulose content was not equally well expressed for all lichen species (details see Appendix S3). Calibration of lichen REs with Calcium (Ca) content (see Appendix S4), produced the same results for RE (and the interaction term method x lichen order was not significant). We are therefore confident that our results are representative despite the above-mentioned difficulties with cellulose calibration for some lichen species.

Nitrogen $RE_{\%}$ ($RE_{N\%}$) was calculated as $([N_{green}] - [N_{senesced}])/[N_{green}]$ x 100%, with N_{green} and $N_{senesced}$ referring to N in green and senesced tissue, respectively. If calibrated with reference to immobile chemistry, e.g. cellulose, RE_{Nsr} (RE_N with stable reference) was expressed as ([Ngreen]/[cellulose] – [Nsenesced]/[cellulose])/[Ngreen]/[cellulose] x 100%. The corresponding parameters were calculated for P ($RE_{P\%}$ and RE_{Psr}, respectively). For vascular plants, a complete dataset was solely available for green tissue in 1998 and for litter in 1999. We therefore compared $[N_{senesced}]$, and $[N_{senesced}]$/[cellulose] of 1998 versus 1999, for species available in all datasets. Both linear regressions were highly significant, and, in the case of $[N_{senesced}]$/[cellulose], the intercept was close to zero and the slope close to 1 (see Appendix S5). Thus, we concluded that differences in

[$N_{senesced}$] between years were relatively small, allowing a direct comparison of RE across adjacent years.

CHEMISTRY

Nitrogen concentrations of vascular plants were determined from ground samples, using a Tracermass mass spectrometer (Europa Scientific, Crewe, UK). For ADF, cellulose and lignin analyses see Quested *et al.* (2003). P in vascular plants was determined colorimetrically at 880 nm with molybdenum blue (details see Van Heerwaarden *et al.* 2003b). The cryptogam samples, for which the following analyses were carried out, were ground for approx. 2 min using a ball mill (MM 200, Retsch, Haan, Germany) before use in further chemical analysis. For concentrations of Ca and P, subsamples were acid-digested (teflon bomb under addition of 1 ml of the mixture HNO_3/HCl, ratio 4:1) for 7 hours at 140 ºC. After adding 4 ml distilled water, Ca was measured by atomic absorption spectrometry (1100B Spectrometer, PerkinElmer Inc., Waltham, Massachusetts, USA) under addition of 1% $LaNO_3$. For P analyses see above. N was determined by dry combustion with a Carlo Erba NA1500 (Rodana, Italy) elemental analyser. Since cryptogam samples were cleaned meticulously, LOI (mass loss of ignition, at 550 ºC for 4 hours) to correct for extraneous minerals, needed to be determined only for *Racomitrium fasciculare* and the lichen *Solorina crocea*. Both cryptogams originated from environments where contamination by minerals was possible. Molecular structure of the ground cryptogam and vascular plant samples was analysed spectroscopically by FTIR-ATR (Nexus^{TM} 670, ATR cell DuraScope, Thermo Nicolet, Madison, WI, USA) with a resolution of 4 cm^{-1} and 32 scans. Extinction was calculated from infrared spectra followed by ground correction to correct for multiple scattering of light inside the probe. Further details of this methodology are in Lang *et al.* (2009).

DATA ANALYSIS

RE_N of *Cetraria islandica* and RE_P of *Nephroma arcticum* and *Tomenthypnum nitens* were unrealistically very negative and strongly suspected to represent sampling or measurement problems. These outliers were excluded from further analysis. Where necessary, data were ranked to improve normality. The influence of taxonomic level, across basal clades and cryptogam orders and classes, on $RE_{\%}$ and RE_{sr} was tested in several one-way ANOVAs followed by Tukey post-hoc tests using SPSS 15.0 for Windows. The influence of method type on RE was tested in a two-way ANOVA with method type and taxonomical level as between-subject factors. Within lichens, the influence of N_2-fixing ability on RE was tested in a one-way ANOVA. Where Levene's test remained significant despite data transformation, we chose to reduce sample size

randomly down to five (or six) replicates (at basal clade level: RE_P; testing method type and clade: RE_N), since analysis of variance is robust to heterogeneity of variances as long as sample size is nearly equal (Zar 1999). Relating RE to [N_{green}] in linear regression (y = ax + b) would violate the assumptions of independence in statistical tests. Therefore, we compared [$N_{senesced}$] versus [N_{green}] across clades and outlined the isoclines of $RE_{N\%}$ (0, 10, …90), as a function of [N_{green}] and [$N_{senesced}$], in the same graphs. With a positive slope, RE increases if the intercept b > 0 and decreases if b < 0. If b = 0, RE is constant across clades. We also compared $N_{senesced}$/cellulose versus N_{green}/cellulose to evaluate whether results deviated depending on the type of RE_N measure.

Results

RE_N AND RE_P

At a broad taxonomic scale, clade identity influenced both $RE_{N\%}$ and RE_{Nsr} significantly. Lichens (lichenized ascomycetes), mosses and lycophytes showed lower RE_{Nsr} (and $RE_{N\%}$) (< 20%) compared to monilophytes, eudicots and monocots (> 70%) while liverworts held an intermediate position (40%). Conifer RE_{Nsr} and $RE_{N\%}$ did not differ significantly from other basal clades (Fig.1, Table 1). Comparing the two methodologies, clade was a significant determinant of RE_N ($F = 23.72$, $P < 0.001$; ranked) while method type ($F = 0.01$, $P = 0.93$) and the interaction of clade x method type ($F = 0.29$, $P = 0.95$) were not significant. There was a consistent trend for differences in RE_P among clades. These differences are mainly due to the eudicots ($RE_{P\%}$ and RE_{Psr}: 54 and 61%; or angiosperms: 60 and 66%) resorbing more P than mosses (32 and 28%), while lichens (17 and 20%), encompassing a wide data range, were not clearly separated from the other clades. RE_P in liverworts (42 and 50%) was almost as high as in eudicots.

Table 1. Statistical analysis of differences in RE_N and RE_P at clade, class and order level across the autotrophic sections of the Tree of Life (lichenised fungi and plants; n = 2-20). Significant P-values are marked with bold letters. Note that the underlying species sets are more robust for RE_N than for RE_P since RE_P of vascular plant clades encompassed solely eudicots (or angiosperms)

Clade	Taxonomic level	Source	d.f.	F	P
All	Clade	$RE_{N\%}$	7	15.03	**< 0.001**
		RE_{Nsr}	7	19.94	**< 0.001***
		$RE_{P\%}$	2	2.80† (2.62‡)	0.073*† (0.079*‡)
		RE_{Psr}	2	2.88† (3.26‡)	0.068*† (**0.043***‡)
Moss	Class	$RE_{N\%}$	2	3.98	**0.038**
		RE_{Nsr}	2	2.79	0.089
		$RE_{P\%}$	2	0.78	0.47
		RE_{Psr}	2	1.11	0.36
Lichen	Order	$RE_{N\%}$	1	0.10	0.76
		RE_{Nsr}	1	0.45	0.51
		$RE_{P\%}$	1	5.48	**0.036***
		RE_{Psr}	1	3.37	0.089*

* Ranked

† Eudicots

‡ Angiosperms (eudicots and monocots)

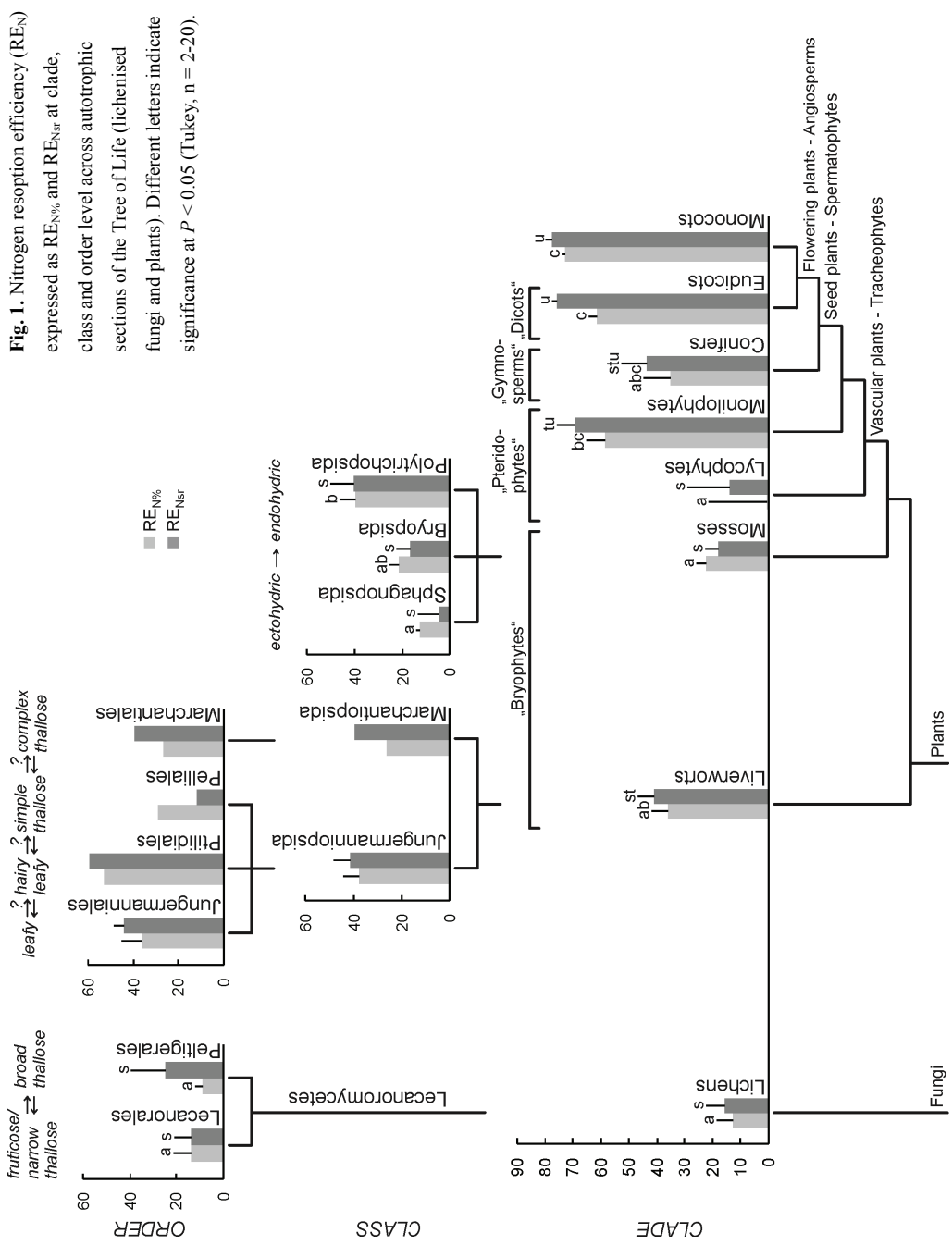


Fig. 1. Nitrogen resoption efficiency (RE_N) expressed as $RE_{N\%}$ and RE_{Nsr} at clade, class and order level across autotrophic sections of the Tree of Life (lichenised fungi and plants). Different letters indicate significance at $P < 0.05$ (Tukey, n = 2-20).

At moss class level, the ectohydric Sphagnopsida showed lower $RE_{N\%}$ compared to the endohydric Polytrichopsida while Bryopsida were intermediate. RE_{Nsr} showed a trend, showing the same pattern as $RE_{N\%}$ for the mean. When comparing the two methods, $RE_{N\%}$ versus RE_{Nsr}, class (F = 6.12, P = 0.005) was a significant determinant of RE_N while method type (F = 0.37, P = 0.55) and their interaction effect (F = 0.11, P = 0.90) were not significant. Neither $RE_{P\%}$ nor RE_{Psr} differed among moss classes.

At lichen order level, $RE_{N\%}$ or RE_{Nsr} of the fruticose and narrow thallose Lecanorales were not significantly different from the broad thallose Peltigerales. $RE_{P\%}$ was significantly higher in the Lecanorales and RE_{Psr} showed the same trend for these groups. N_2-fixing lichens, which were present in both the Lecanorales and Peltigerales, did not show significantly lower RE_N ($RE_{N\%}$: F = 0.96, P = 0.35; RE_{Nsr}: F = 0.19, P = 0.67) whereas RE_P was significantly higher in non-N_2-fixing lichens ($RE_{P\%}$: F = 7.06, P = 0.020; RE_{Psr}: F = 5.89, P = 0.031; ranked).

Whether liverwort taxa representing different growth forms, (hairy) leafy, simple or complex thallose, show differences in RE, remains unsubstantiated as most species in this study belonged to the leafy liverwort order Jungermanniales, while all other orders were represented by only one (Ptilidiales) or very few species in the study area.

THE RELATION OF $N_{SENESCED}$ VERSUS N_{GREEN}

Across clades, linear regressions between $N_{senesced}$ and N_{green}, whether based on percentage or cellulose, were positive and significant (Fig. 2). With increasing [N_{green}] and N_{green}/cellulose, RE increased across clades (intercept of the regression line $b > 0$). Based on [N_{green}] and even more so when looking at N/cellulose, eudicots, monilophytes and monocots showed the highest N_{green} content and highest RE_N while liverworts, conifers, mosses, lichens and lycophytes were located at the lower end of the range.

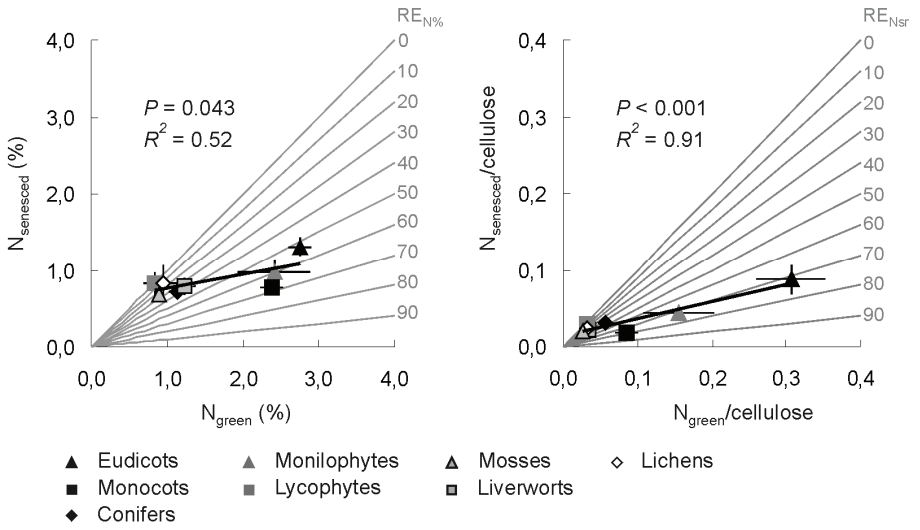


Fig. 2. $N_{senesced}$ (%) versus N_{green} (%), and $N_{senesced}$/cellulose versus N_{green}/cellulose, across the basal clades of the Tree of Life (± SE; n = 8). Isoclines for $RE_{N\%}$ and RE_{Nsr} are outlined in grey.

Discussion

To summarise our main findings, all clades across the Tree of Life resorbed nutrients during organ senescence, but the efficiency differed strongly among clades. Mosses, lichens and lycophytes generally showed low RE_N, liverworts and conifers intermediate and monilophytes, eudicots and monocots high. With reduced numbers of tracheophyte clades (only eudicots or angiosperms present), the pattern for RE_P was similar to RE_N but less clearly expressed. Within mosses, taxa with more efficient conductance also showed higher RE_N. Thus, the variation in nitrogen resorption efficiency in a subarctic flora broadly supports the hypothesis that the evolution of conducting tissues has aided plants to optimise their internal nutrient cycling in terrestrial environments. While we have most confidence for our results for RE as expressed on a stable secondary chemistry basis, derived with our novel application of FTIR-ATR, the general correspondence of the between-clade patterns for RE_{sr} and $RE_{\%}$ show that the larger differences in RE are rather robust to methodological factors (interaction effect of clade x method type is not significant). Below we will discuss our findings in more detail with special focus on the types of conducting system that might support nutrient resorption of autotrophs across the Tree of Life.

CONDUCTIVE SYSTEMS AS VEHICLES FOR NUTRIENT RESORPTION ACROSS AUTOTROPHIC CLADES

The fact that all non-tracheophyte cryptogam clades had distinctly low RE_N compared to seed plants is consistent with the pattern of increasing differentiation of conducting tissue, from lichens, liverworts and moss clades with no or little conducting tissue to the high differentiation of phloem in seed plants, although the apparently lower RE_N of conifers compared to angiosperms might be the results of other traits regulating RE (see below). Though based on fewer clades, the trend for RE_P was similar, with angiosperms showing highest RE_P in comparison to mosses, lichens and, to a lesser extent, liverworts. Our results for monilophytes and lycophytes were surprising, even though the numbers of species represented in this subarctic flora were too low for any firm statements. Still, the lycophytes showed low N resorption while monilophytes had particularly efficient N resorption, even higher than the $RE_{N\%}$ of 52% reported for a temperate fern (Killingbeck *et al.* 2002). The phloem of lycophytes (e.g. *Lycopodium*) differs from other vascular cryptogams in possessing plasmalemma-lined sieve area pores which are wide open, whereas the pores of certain monilophytes, e.g. *Equisetum* and leptosporangiate ferns, are traversed by membranes of endoplasmic reticulum (ER). In sieve tube members of eudicots, ER may play an important role in phloem loading processes (Behnke & Sjolund 1990). However, recent studies suggest ER facilitates the trafficking of proteins between sieve elements (SE) and companion cells (CC) (Van Bel 2003). P-proteins, known from eudicots and many monocots but absent in conifers and mosses, are replaced by refractive spherules in monilophytes but again are absent from lycophytes (Behnke & Sjolund 1990). The functions of P-proteins are subject to debate, but apart from plugging sieve plates upon injury (Behnke & Sjolund 1990), these may include sugar metabolism, transmembrane sugar transport, membrane water permeability and protein degradation (Van Bel 2003). Thus, we speculate that the absence of P-proteins or refractive spherules in conifers and lycophytes may partly explain their low RE. In addition, the evergreen habit of both conifers and lycophytes might compensate for insufficient RE, conserving nutrients by extending their mean residence time (Aerts 1995). Furthermore, the low N concentrations in green tissue found in these clades (Fig. 2), limit the extent of RE (Aerts 1996), given that there is always a pool of N that remains immobile during senescence (Killingbeck 1996). We expected that the emergence of specialized parenchyma cells, 'Strasburger cells' in conifers and CC in angiosperms (Behnke & Sjolund 1990), would lead to increased RE compared to vascular cryptogams. This hypothesis is based on the suggestion by Van Bel (2003) that evolutionary specialization led to increased longitudinal flow in the phloem due to increased porosity of the end walls. Also, most of the cytoplasmic structure is dismantled to decrease mass flow resistance while the

adjacent parenchyma cells gradually take over regulation of functions in the SE (Van Bel 2003). However, RE of monilophytes was equally high as RE in seed plants, possibly owed to the presence of single cytoplasmatic connections between SE and parenchyma cells in this clade (Behnke & Sjolund 1990). It is tempting to assign differences in RE to minor vein type structure and their related phloem loading types, from ancestral symplastic phloem loading (ferns, conifers) to apoplastic or mixed loading in evolutionary young angiosperms (Van Bel 2003). However, in the dicots all three minor vein types are found (Turgeon *et al.* 2001) and, moreover, symplastic phloem loading also occurred in evolutionarily young angiosperms such as *Salix* (Van Bel 2003). Gamalei (1991) suggested evolutionary specialisation of phloem loading in relation to climate. Typical in arctic-alpine tundra is the closed minor vein type, related to apoplastic phloem loading (except trees: symplastic) since symplastic plasmodesmal transport is sensitive to chilling. However, interactions between minor vein type and transported sugar identity on phloem loading type (Van Bel 2003), which is hypothesized to influence hydraulic gradient strength (Holbrook & Zwieniecki 2005), may further complicate the implications for resorption. Analogue to studies on xylem (Roth & Mosbrugger 1996), we can also speculate about possible implications of stelar morphology, from primitive protostele in the earliest land plants (e.g. *Cooksonia*, *Rhynia*) to eustele (e.g. eudicots), on phloem transport properties.

In conclusion, many open questions remain concerning evolution of SEs and their cell biology, pathways and modes of phloem loading, impact of environmental factors on phloem transport and possible adaptation of phloem loading modes to climatic conditions (Van Bel 2003). Yet answering these questions will provide the basis from which we can start to evaluate the factors influencing RE in tracheophytes.

NOVEL SCREENING OF NUTRIENT RESORPTION IN HIGHER CRYPTOGAM TAXA

Our study is the first comprehensive study of nutrient resorption efficiency not only across basal cryptogam and seed plant clades, but also within several non-tracheophyte cryptogam taxa. While for some bryophyte and lichen taxa the subarctic flora did not support sufficient numbers of species for statistically sound comparison, we have quantified some consistent and logical patterns. Despite scattered evidence of N and P translocation, no study so far has investigated RE of a representative number of moss species in order to detect consistent taxonomic variation. Within mosses, translocation has been mainly linked to the endohydric Polytrichales (Collins & Oechel 1974; Reinhart & Thomas 1981) which feature leptoids (Hébant 1977), i.e. conducting tissue, somewhat

comparable to the sieve cells of higher plants. Also, this moss class alone features refractive spherules and callose, associated with plasmodesmata (Ligrone *et al.* 2000), which, in angiosperms, are associated with pores during sieve plate development (Behnke & Sjolund 1990). Indeed, $RE_{N\%}$ in the Polytrichaceae was higher than in other mosses, especially when compared to the ectohydric *Sphagnum*. However, though devoid of leptoids, transport of photoassimilates (Alpert 1989; Hakala & Sewón 1992) or N (Eckstein & Karlsson 1999) has also been reported for *Dicranum*, *Grimmia* and *Hylocomium*, respectively, most likely facilitated by an internal conducting strand of elongated parenchyma cells (Ligrone & Duckett 1994). Moreover, evidence has been found for conducting tissue in the Sphagnales differing from the Bryopsida only in lacking plastid - microtubules associations (Ligrone & Duckett 1998); this conducting tissue might explain P, C and N translocation found for the peat moss *Sphagnum* (Rydin & Clymo 1989; Aldous 2002). We have to be aware that some interspecific variation in RE may be due to environmental factors. Since not all mosses could be collected at the same time, species differences in seasonality of translocation (Skre *et al.* 1983), downwards for storage and upwards for growth, might have contributed to some of the observed variation. Furthermore, cyanobacterial N_2-fixation observed on feather mosses (Zackrisson *et al.* 2009), might have complicated the observed pattern. Indeed, RE_N of these mosses was higher than in most other species of the Bryopsida (data not shown).

We are the first to study RE of N and P in senescing photosynthetic parts of liverworts. With the exception of the complex thallose liverwort *Marchantia* (Rota & Maravolo 1975), little is know about translocation in this clade. Ligrone *et al.* (2000) suggested a microtubule-based translocation system for the marchantialean liverwort *Asterella*. However, liverworts seemed to generally resorb nutrients at rather high rates, comparable to those of conifers and monilophytes. Analogue to mosses, cyanobacterial N_2-fixation is known for a few liverworts (Adams & Duggan 2008) and this might have affected RE. This might also hold for basidiomycetous infections found repeatedly in jungermannialean liverworts, leading to an increase or decrease of the host cytoplasm (Duckett *et al.* 2006). The latter phenomenon has been reported for *Lophozia*, *Barbilophozia* and *Nardia*, all represented in our study. A central strand of conducting tissue has so far only been found for species in the liverwort orders Calobryales, Pallaviciniales (Hébant 1977), Pelliales and Marchantiales (Ligrone *et al.* 2000), of which the latter two were represented in our subarctic flora. The hypothesized link between central strands and RE is in need of explicit comparison across liverwort orders.

This is also the first explicit study of nutrient resorption related to tissue senescence in lichens. Translocation of N and P between fresh tissues has been demonstrated for *Cladonia stellaris*, *Stereocaulon paschale* and *Cladonia portentosa*, respectively (Hyvärinen & Crittenden 2000; Kytöviita & Crittenden 2007), while for *Caloplaca trachyphylla*, transport of carbohydrates has been shown (Bench *et al.* 2002). Translocation in lichens, in which fungal hyphae provide the main structure, can most likely be compared to translocation in (ecto-) mycorrhizal mycelium. Out of three suggested transport mechanisms, diffusion, mass flow along turgor gradients or cytoplasmic streaming through pores of septa (Finlay 1992), the latter seems to be the most likely transport mechanism in lichens (Hyvärinen & Crittenden 2000). Assuming that a similar transport mechanism prevails in all fungal hyphae, we hypothesised that RE would not differ among lichens of different growth forms, when excluding N_2-fixing lichens. Indeed, RE_N did not differ among lichen orders. However, $RE_{P\%}$ was higher in the Lecanorales and seemed to be negatively related to the N_2-fixing ability of lichens. The differences found in RE_P may be due to P in cyanobacteria. Since cyanobacteria are located in cephalodia that are still present in dead lichen tissue, cyanobacterial P might not be accessible during resorption but is left behind in aging lichen tissue. Furthermore, algae in lichens are known to store P as polyphosphate in granules (Guschina *et al.* 2003), complicating the interpretation of the observed pattern. For N_2-fixing lichens, with a constant input of readily available N, one would expect N resorption to be less important than in non-N_2-fixing lichens, analogous to reduced RE_N of N_2-fixing higher plants (Killingbeck 1996). However, N_2-fixing lichens did not differ in RE_N from non-N_2-fixing lichens, which point to a similar transport mechanism across lichen species.

We conclude that the progressive evolution of tissues to facilitate internal transport across the major clades of land plants is, by and large, coupled with their nutrient resorption efficiency during organ senescence. As such, this has led to a lesser dependency of plants on external nutrient supply. While many organism characters have been mapped explicitly onto the Tree of Life before, nutrient resorption may, to the best of our knowledge, represent the first organismal *process* to have been given this treatment. Under the assumption that actual nutrient resorption, which involves several interacting physiological and chemical processes (Gan 2007), is influenced by a myriad of genes (Gan 2007), our approach will also be of great interest for phylogenetic analysis of many other complex organismal processes.

Acknowledgements

The authors would like to acknowledge the Abisko Scientific Research Station which financially supported part of this work. Many thanks to Matthias Ahrens for bryophyte identification, and Adam Hölzer and Rob Broekman for technical support. The authors also acknowledge the Staatliches Museum für Naturkunde Karlsruhe for provision of work space and the FAZIT-STIFTUNG for financial support to S.I.L.. This study was financed by grant ALW-852.00.070 of the Netherlands Organisation for Scientific Research (NWO).

References

Adams, D.G. & Duggan, P.S. (2008) Cyanobacteria-bryophyte symbioses. *Journal of Experimental Botany*, **59**, 1047-1058.

Aerts, R. (1995) The advantages of being evergreen. *Trends in Ecology & Evolution*, **10**, 402-407.

Aerts, R. (1996) Nutrient resorption from senescing leaves of perennials: Are there general patterns? *Journal of Ecology*, **84**, 597-608.

Aldous, A.R. (2002) Nitrogen translocation in *Sphagnum* mosses: effects of atmospheric nitrogen deposition. *New Phytologist*, **156**, 241-253.

Alpert, P. (1989) Translocation in the nonpolytrichaceous moss *Grimmia laevigata*. *American Journal of Botany*, **76**, 1524-1529.

Behnke, H.-D. & Sjolund, R.D. (1990) Sieve elements. Springer-Verlag, Berlin.

Bench, G., Clark, B.M., Mangelson, N.F., St. Clair, L.L.*, et al.* (2002) Use of $^{14}C/C$ ratios to provide insights into the magnitude of carbon turnover in the crustose saxicolous lichen *Caloplaca trachyphylla*. *The Lichenologist*, **34**, 169-179.

Chapin, F.S. III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233-260.

Collins, N.J. & Oechel, W.C. (1974) The pattern of growth and translocation of photosynthate in a tundra moss, *Polytrichum alpinum*. *Canadian Journal of Botany*, **52**, 355-363.

Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A. & During, H.J. (2007) Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany*, **99**, 987-1001.

Donoghue, M.J. (2005) Key innovations, convergence, and success: macroevolutionary lessons from plant phylogeny. *Paleobiology*, **31**, 77-93.

Duckett, J.G., Russell, J. & Ligrone, R. (2006) Basidiomycetous endophytes in jungermannialean (leafy) liverworts have novel cytology and species-specific host

ranges: a cytological and experimental study. *Canadian Journal of Botany*, **84**, 1075-1093.

Eckstein, R.L. & Karlsson, P.S. (1999) Recycling of nitrogen among segments of *Hylocomium splendens* as compared with *Polytrichum commune*: Implications for clonal integration in an ectohydric bryophyte. *Oikos*, **86**, 87-96.

Finlay, R.D. (1992) Uptake and translocation of nutrients by ectomycorrhizal fungal mycelia. *Mycorrhizas in Ecosystems* (eds D.J. Read, D.H. Lewis, A.H. Fitter & I.J. Alexander), pp. 91-97. CAB International, Wallingford.

Gamalei, Y. (1991) Phloem loading and its development related to plant evolution from trees to herbs. *Trees*, **5**, 50-64.

Gan, S. (2007) Senescence Processes in Plants. Blackwell Publishing, Ithaca.

Goffinet, B. & Shaw, A.J. (2009) Bryophyte Biology. University Press, Cambridge.

Guschina, I.A., Dobson, G. & Harwood, J.L. (2003) Lipid metabolism in cultured lichen photobionts with different phosphorus status. *Phytochemistry*, **64**, 209-217.

Hakala, K. & Sewón, P. (1992) Reserve lipid accumulation and translocation of ^{14}C in the photosynthetically active and senescent shoot parts of *Dicranum elongatum*. *Physiologia Plantarum*, **85**, 111-119.

Headley, A.D., Callaghan, T.V. & Lee, J.A. (1985) The phosphorus economy of the evergreen tundra plant, *Lycopodium annotinum*. *Oikos*, **45**, 235-245.

Hébant, C. (1977) The Conducting Tissues of Bryophytes. J. Cramer, Vaduz.

Holbrook, N.M. & Zwieniecki, M.A. (2005) Vascular Transport in Plants. Elsevier Academic Press, London.

Hyvärinen, M. & Crittenden, P.D. (2000) ^{33}P translocation in the thallus of the mat-forming lichen *Cladonia portentosa*. *New Phytologist*, **145**, 281-288.

Killingbeck, K.T. (1996) Nutrients in senesced leaves: Keys to the search for potential resorption and resorption proficiency. *Ecology*, **77**, 1716-1727.

Killingbeck, K.T., Hammen-Winn, S.L., Vecchio, P.G. & Goguen, M.E. (2002) Nutrient resorption efficiency and proficiency in fronds and trophopods of a winter-deciduous fern, *Dennstaedtia punctilobula*. *International Journal of Plant Sciences*, **163**, 99-105.

Kytöviita, M.M. & Crittenden, P.D. (2007) Growth and nitrogen relations in the mat-forming lichens *Stereocaulon paschale* and *Cladonia stellaris*. *Annals of Botany*, **100**, 1537-1545.

Lambers, H., Raven, J.A., Shaver, G.R. & Smith, S.E. (2008) Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology & Evolution*, **23**, 95-103.

Lang, S.I., Cornelissen, J.H.C., Klahn, T., van Logtestijn, R.S.P*., et al.* (2009) An experimental comparison of chemical traits and litter decomposition rates in a diverse

range of subarctic bryophyte, lichen and vascular plant species. *Journal of Ecology*, **97**, 886-900.

Ligrone, R. & Duckett, J.G. (1994) Cytoplasmic polarity and endoplasmic microtubules associated with the nucleus and organelles are ubiquitous features of food-conducting cells in bryoid mosses (Bryophyta). *New Phytologist*, **127**, 601-614.

Ligrone, R. & Duckett, J.G. (1998) The leafy stems of *Sphagnum* (Bryophyta) contain highly differentiated polarized cells with axial arrays of endoplasmic microtubules. *New Phytologist*, **140**, 567-579.

Ligrone, R., Duckett, J.G. & Renzaglia, K.S. (2000) Conducting tissues and phyletic relationships of bryophytes. *Philosophical Transactions of the Royal Society of London Series B*, **355**, 795-813.

Longton, R.E. (1997) The role of bryophytes and lichens in polar ecosystems. *Ecology of Arctic Environments* (eds S.J. Woodin & M. Marquiss), pp. 69-96. Blackwell Science, Oxford.

Lumbsch, H.T. & Huhndorf, S.M. (2007) Outline of Ascomycota - 2007. *Myconet*, **13**, 1-58.

Quested, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., *et al.* (2003) Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology*, **84**, 3209-3221.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**, 365-392.

Reinhart, D.A. & Thomas, R.J. (1981) Sucrose uptake and transport in conducting cells of *Polytrichum commune*. *The Bryologist*, **84**, 59-64.

Rota, J.A. & Maravolo, N.C. (1975) Transport and mobilization of ^{14}C-sucrose during regeneration in the hepatic, *Marchantia polymorpha*. *Botanical Gazette*, **136**, 184-188.

Roth, A. & Mosbrugger, V. (1996) Numerical studies of water conduction in land plants: evolution of early stele types. *Paleobiology*, **22**, 411-421.

Rydin, H. & Clymo, R.S. (1989) Transport of carbon and phosphorus compounds about *Sphagnum*. *Proceedings of the Royal Society of London Series B*, **237**, 63-84.

Skre, O., Oechel, W.C. & Miller, P.M. (1983) Patterns of translocation of carbon in four common moss species in a black spruce (*Picea mariana*) dominated forest in interior Alaska *Canadian Journal of Forest Research*, **13**, 869-878.

Stevens, P.F. (2001 onwards) Angiosperm Phylogeny Website. Version 9. **June 2008**, http://www.mobot.org/MOBOT/research/APweb/.

Turgeon, R., Medville, R. & Nixon, K.C. (2001) The evolution of minor vein phloem and phloem loading. *American Journal of Botany*, **88**, 1331-1339.

Van Bel, A.J.E. (2003) The phloem, a miracle of ingenuity. *Plant, Cell and Environment*, **26**, 125-149.

Van Heerwaarden, L.M., Toet, S. & Aerts, R. (2003a) Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solutions. *Oikos*, **101**, 664-669.

Van Heerwaarden, L.M., Toet, S. & Aerts, R. (2003b) Nitrogen and phosphorus resorption efficiency and proficiency in six sub-arctic bog species after 4 years of nitrogen fertilization. *Journal of Ecology*, **91**, 1060-1070.

Yuan, Z.Y. & Chen, H.Y.H. (2009) Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. *Global Ecology and Biogeography*, **18**, 11-18.

Zackrisson, O., DeLuca, T.H., Gentili, F., Sellstedt, A.*, et al.* (2009) Nitrogen fixation in mixed *Hylocomium splendens* moss communities. *Oecologia*, **160**, 309-319.

Zar, J.H. (1999) Biostatistical Analysis. Prentice Hall, New Jersey.

Appendix S1. List of vascular plant and cryptogam species assessed for nutrient resorption efficiency

Species are sorted according to clades (class and order where appropriate). RE_N was available for all species except *Eriophorum vaginatum*. Shaded species were not used in Figure 1 of the main manuscript. Marked with * are species for which RE_P was available. Species nomenclature follows Hill *et al.* (2006) for mosses except *Sphagnum*; Daniels & Eddy (1985) for *Sphagna*; Damsholt (2002) for liverworts; Santesson *et al.* (2004) for lichens; and Mossberg *et al.* (1992) for vascular plants.

Clade	Class	Order	Species
Lichens	Lecanoromycetes	Lecanorales	*Cladonia uncialis*
			Cladonia amaurocraea
			Cladonia arbuscula
			Cladonia rangiferina
			Cladonia stygia
			Cladonia stellaris
			Cetraria islandica
			Cetrarialla delisei
			Flavocetraria cucullata
			Flavocetraria nivalis
			Alectoria ochroleuca
			Stereocaulon vesuvianum
			Stereocaulon cf.*grande*
		Peltigerales	*Nephroma arcticum*
			Peltigera aphthosa
			Solorina crocea
Liverworts	Jungermanniopsida	Jungermanniales	*Nardia scalaris*
			Barbilophozia atlantica
			Barbilophozia floerkii
			Lophozia lycopodioides
		Ptilidiales	*Ptilidium ciliare*
		Pelliales	*Pellia neesiana*
	Marchantiopsida	Marchantiales	*Marchantia alpestris*
Mosses	Bryopsida		*Cinclidium stygium*
			Dicranum montanum
			Dicranum fuscescens
			Racomitrium microcarpon
			Racomitrium fasciculare
			Racomitrium lanuginosum
			Hylocomium splendens
			Pleurozium schreberi
			Rhytidium rugosum
			Tomenthypnum nitens
			Aulacomnium palustre
			Aulacomnium turgidum

Continued

Clade	Class	Order	Species
Mosses	Bryopsida		*Paludella squarrosa*
	Polytrichopsida		*Polytrichastrum sexangulare*
			Polytrichum strictum
			Polytrichum commune
	Sphagnopsida		*Sphagnum balticum*
			Sphagnum fuscum
			Sphagnum riparium
			Sphagnum teres
Lycophytes			*Diphasiastrum complanatum*
			Lycopodium annotinum
Monilophytes			*Equisetum sylvaticum*
			Gymnocarpium dryopteris
			Matteuccia struthiopteris
Conifers			*Juniperus communis*
			Picea cf. *obovata* x *abies*
			Pinus sylvestris
Eudicots			*Achillea millefolium*
			Astragalus frigidus
			*Betula nana**
			Betula pubescens
			Cornus suecica
			*Empetrum nigrum**
			Epilobium angustifolium
			Filipendula ulmaria
			Populus tremula
			Ribes spicatum
			Rumex obtusifolius
			Salix myrsinites
			Tanacetum vulgare
			Trollius europaeus
			Alnus incana
			*Andromeda polifolia**
			Angelica sylvestris
			Anthriscus sylvestris
			Arctostaphylos alpinus
			Astragalus alpinus
			Bartsia alpina
			Bistorta vivipara
			Caltha palustris
			Cassiope tetragona
			Dryas octopetala

Continued

Clade	Class	Order	Species
Eudicots			*Geranium sylvaticum*
			Lathyrus pratensis
			Orthilia secunda
			Pedicularis hirsuta
			Pedicularis lapponica
			Pedicularis sceptrum-carolinum
			Rhodiola rosea
			Rhododendron lapponicum
			*Rubus chamaemorus**
			Rubus saxatilis
			Salix herbacea
			Salix lapponum
			Salix reticulata
			Solidago virgaurea
			Sorbus aucuparia
			Trifolium pratense
			Vaccinium myrtillus
			*Vaccinium uliginosum**
			Vaccinium vitis-idaea
			Veronica alpina
			Vicia cracca
Monocots			*Calamagrostis lapponica*
			Carex rostrata
			Juncus arcticus
			Carex capitata
			Carex saxatilis
			Carex vaginata
			Deschampsia cespitosa
			Elytrigia repens
			Eriophorum angustifolium
			Juncus trifidus
			Luzula multiflora
			Phleum alpinum
			Eriophorum vaginatum

References

Damsholt, K. (2002) Illustrated Flora of Nordic Liverworts and Hornworts. Nordic Bryological Society, Lund.

Daniels, R.E. & Eddy, A. (1985) Handbook of European *Sphagna*. Institute of Terrestrial Ecology, Huntingdon.

Hill, M.O., Bell, N., Bruggeman-Nannenga, M.A., Brugués, M., Cano, M.J., Enroth, J. *et al.* (2006) An annotated checklist of the mosses of Europe and Macaronesia. *Journal of Bryology*, **28**, 198-267.

Mossberg, B., Stenberg, L. & Ericsson, S. (1992) Den Nordiska Floran. Wahlström and Widestrand, Stockholm.

Santesson, R., Moberg, R., Nordin, A., Tønsberg, T. & Vitikainen, O. (2004) Lichen-forming and Lichenicolous Fungi of Fennoscandia. Museum of Evolution, Uppsala University, Uppsala.

Appendix S2. Early versus late RE in lichens and mosses

Early RE of both N and P in mosses was always higher compared to late RE (Table 1), which even took on negative values (Fig. 1). These might indicate translocation of nutrients into brown moss tissue. Based on upward and downward movement of ^{14}C in the moss shoot, Hakala & Sewón (1992) suggested that senescent moss parts function as an energy store. Early RE in lichens was significantly higher for $RE_{N\%}$ while RE_{Nsr} showed a trend for the same pattern. Early versus late RE_P was not significantly different for lichens.

Table 1. Early versus late $RE_{N\%}$, RE_{Nsr}, $RE_{P\%}$ and RE_{Psr} of mosses and lichens (n = 15; the outliers late RE of *Cetraria islandica* and early RE of *Stereocaulon* cf. *grande* were excluded). Significant *P*-values are marked with bold letters

Clade	Source	d.f.	*F*	*P*
Moss	$RE_{N\%}$	1	18.24	**< 0.001**
	RE_{Nsr}	1	15.55	**0.001**
	$RE_{P\%}$	1	6.83	**0.014**
	RE_{Psr}	1	7.89	**0.010***
Lichen	$RE_{N\%}$	1	25.73	**< 0.001**
	RE_{Nsr}	1	3.61	0.068
	$RE_{P\%}$	1	0.16	0.69
	RE_{Psr}	1	0.11	0.74

* Ranked

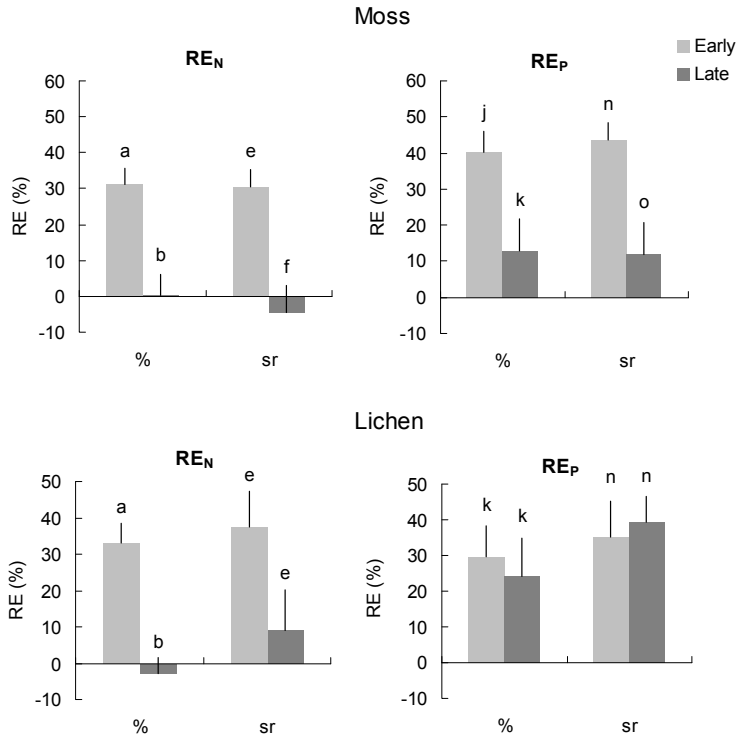


Fig. 1. Early versus late $RE_{N\%}$, RE_{Nsr}, $RE_{P\%}$ and RE_{Psr} for mosses and lichens (Tukey, n = 13-15).

Independent of time, non-N_2-fixing lichens showed significantly higher RE_P (40-50%) compared to N_2-fixing lichens (3-12%) while the interaction of time x N_2-fixation was not significant (Table 2). Possible explanations for this finding are given in the Discussion (see main manuscript).

Table 2. Comparison of N_2-fixation and time of resorption on $RE_{P\%}$ and RE_{Psr} of lichens (n = 15; the outliers late RE of *Cetraria islandica* and early RE of *Stereocaulon* cf. *grande* were excluded). Significant P-values are marked with bold letters

Variable	Source	d.f.	F	P
$RE_{P\%}$	N_2-fixation	1	5.78	**0.024**
	Time	1	0.23	0.63
	N_2-fixation x time	1	0.39	0.54
RE_{Psr}	N_2-fixation	1	8.71	**0.007**
	Time	1	0.67	0.42
	N_2-fixation x time	1	0.51	0.48

References

Hakala, K. & Sewón, P. (1992) Reserve lipid accumulation and translocation of ^{14}C in the photosynthetically active and senescent shoot parts of *Dicranum elongatum*. *Physiologia Plantarum*, **85**, 111-119.

Appendix S3. Prediction of cellulose content inferred from infrared spectra

Table 1. Calibration and prediction of cellulose [%] from infrared spectra (PLS-R, n = 14)

	Cellulose
N	14
No. of PCs*	6
$R^2_{Cal.}$†	0.98
$R^2_{Pred.}$	0.91
$RMSE_{Cal.}$‡	0.95
$RMSE_{Pred.}$	2.02
$Slope_{Cal.}$	0.98
$Slope_{Pred.}$	0.99
$Intercept_{Cal.}$	0.41
$Intercept_{Pred.}$	0.08

* PC: Principal component

† Cal.or Pred.: Calibration or prediction

‡ RMSE: Root mean square error

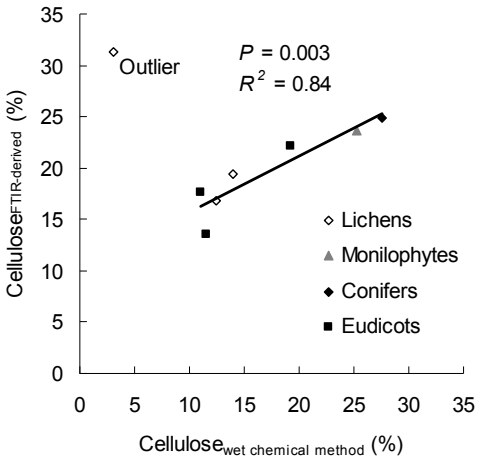


Fig. 1. FTIR-derived versus wet chemical measurements cellulose (n = 7; the outlier was excluded).

Appendix S4. Comparison of RE calibration approaches

Although the pattern for most calibration methods seemed to be similar since none of the interaction terms was significant (Table 1), variation was especially high in RE_{NCa} (Fig. 1). The use of RE_{NCa} for mosses is problematic since Ca is known to either accumulate in old moss tissue (Vitt & Pakarinen 1987), move about mosses (Wells & Brown 1996) or even show no differences to slight decreases in young versus older tissue (Malmer 1993). It therefore provides an unreliable basis in contrast to this method used for vascular plants (Soudzilovskaia *et al.* 2007). Furthermore, in lichens, Ca may occur in trapped particles or as Ca oxalate but is also bound extracellularly (Brown 1987). As older material decomposes, trapped material or Ca oxalate might be lost from the tissue or decomposition of material might create additional exchange sites by increasing the tissue surface. Thus, it seems unsure whether Ca would provide a safe basis for RE.

Table 1. Comparison of measurement type of RE_N at clade, class and order level (ranked; n = 3-20)

Taxonomical level	Source	d.f.	*F*	*P*
Clade	Clade	2	8.94	< 0.001
	Method	2	0.01	0.99
	Clade x method	4	0.39	0.82
Class	Class	2	6.84	0.002
	Method	2	0.30	0.74
	Class x method	4	0.81	0.53
Order	Order	1	1.22	0.28
	Method	2	0.64	0.54
	Order x method	2	1.77	0.19

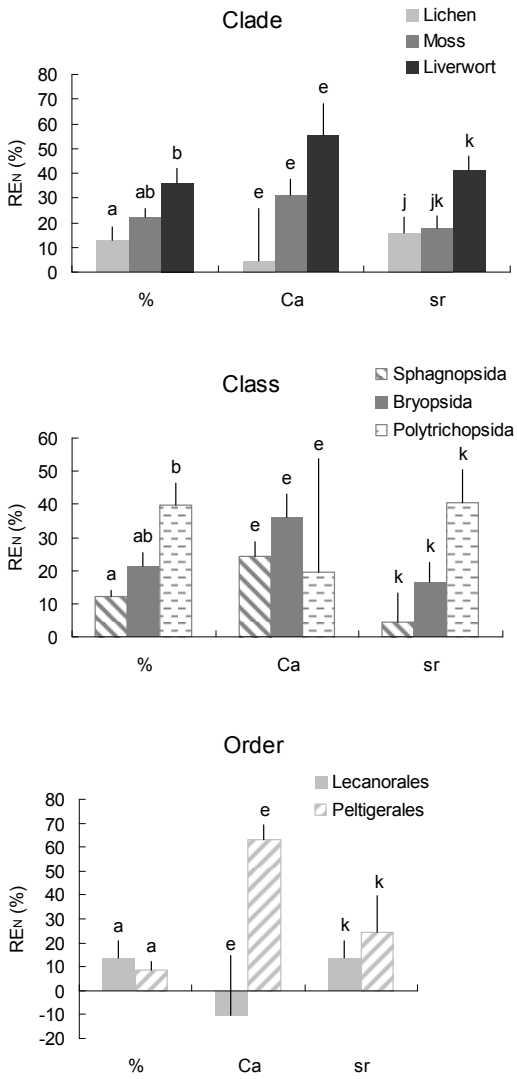


Fig. 1. $RE_{N\%}$, RE_{NCa} and RE_{Nsr} across and within clades. Different letters indicate significance at $P < 0.05$ (Tukey, $n = 3$-20).

References

Brown, D.H. (1987) The location of mineral elements in lichens; implications for metabolism. *Progress and Problems in Lichenology in the Eighties* (ed E. Peveling), pp. 361-375. J. Cramer, Berlin.

Malmer, N. (1993) Mineral nutrients in vegetation and surface layers of *Sphagnum*-dominated peat-forming systems. *Advances in Bryology*, **5**, 223-248.

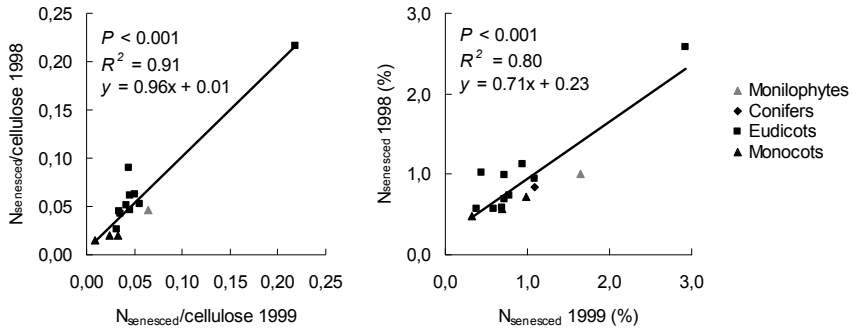
Soudzilovskaia, N.A., Onipchenko, V.G., Cornelissen, J.H.C. & Aerts, R. (2007) Effects of fertilisation and irrigation on 'foliar afterlife' in alpine tundra. *Journal of Vegetation Science*, **18**, 755-766.

Vitt, D.H. & Pakarinen, P. (1987) The bryophyte vegetation, production and organic components of Truelove Lowland. *Truelove Lowland, Devon Island, A High Arctic Ecosystem* (ed L.C. Bliss), pp. 225-244. The University of Alberta Press, Edmonton.

Wells, J.M. & Brown, D.H. (1996) Mineral nutrient recycling within shoots of the moss *Rhytidiadelphus squarrosus* in relation to growth. *Journal of Bryology*, **19**, 1-17.

Appendix S5. Vascular plant [$N_{senesced}$] and [$N_{senesced}$]/[cellulose] of adjacent years

Comparison of [$N_{senesced}$] and [$N_{senesced}$]/[cellulose] of adjacent years (1998 versus 1999, n=15), based on vascular plant data from Quested *et al.* (2003).



References

Quested, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., Aerts, R., Trosien, F. *et al.* (2003) Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology*, **84**, 3209-3221.

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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Journal of Ecology (2009) 97: 886–900

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).

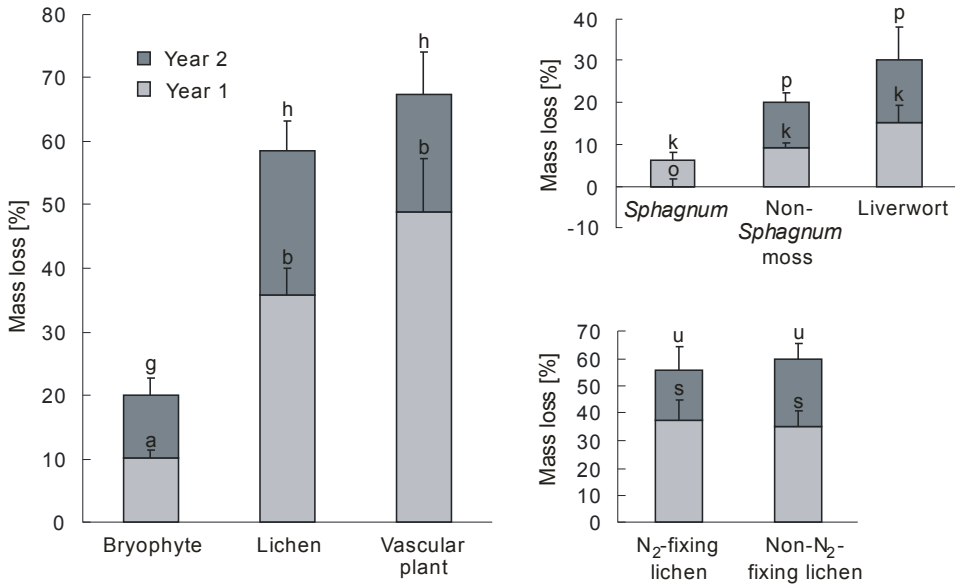

Fig. 1. Comparison of mass loss (+ SE) among the main taxa lichens, bryophytes and vascular plants, and the cryptogam groups *Sphagnum*, non-*Sphagnum* moss, liverwort and N_2-fixing lichen, non-N_2-fixing lichen, after one and two years of decomposition (separate one-way ANOVAs for each harvest, data 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.

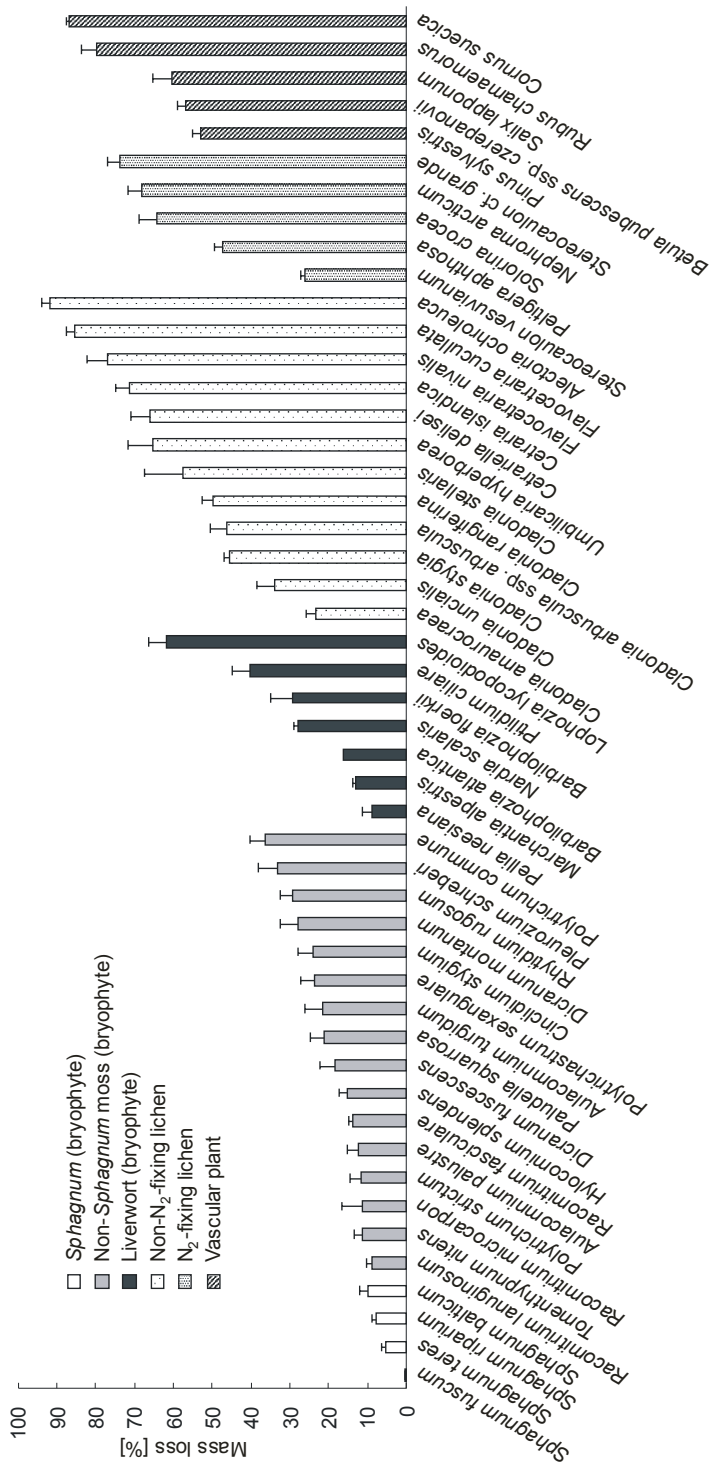

Fig. 2. Two-year mass loss (+ SE) of bryophytes (*Sphagnum*, non-*Sphagnum* moss, liverwort), lichens (non-N_2-fixing lichen, N_2-fixing lichen) and vascular plants in the nutrient-poor birch forest litter bed (n = 1 - 5).

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 ($R^2_{\text{poor birch forest}} = 0.92$, $P = 0.039$; $R^2_{\text{rich birch forest}} = 0.92$, $P = 0.043$; $R^2_{\text{mire}} = 0.92$, $P = 0.041$).

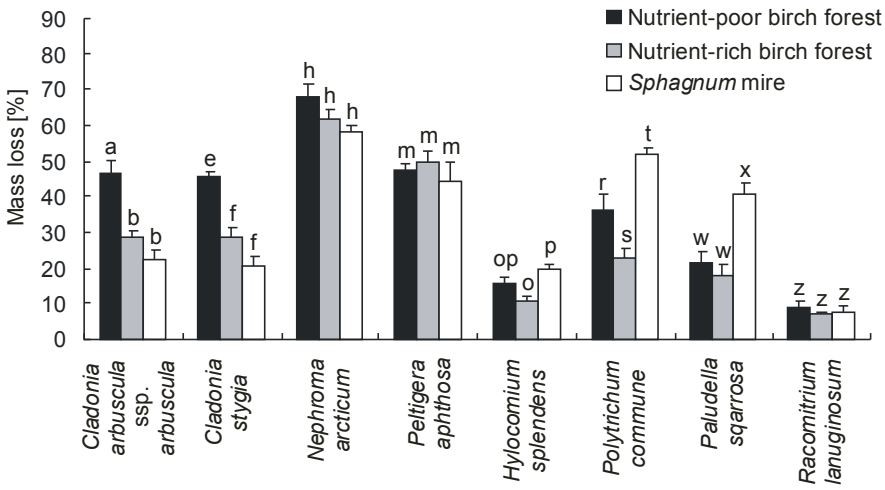

Fig. 3. Effects of nutrient-poor and nutrient-rich birch forest and *Sphagnum* mire litter bed on mass loss (+ SE) of four lichen (left side) and four non-*Sphagnum* moss species (right side) after two years of incubation (one-way ANOVA, data arcsine-square-root transformed, different letters indicate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

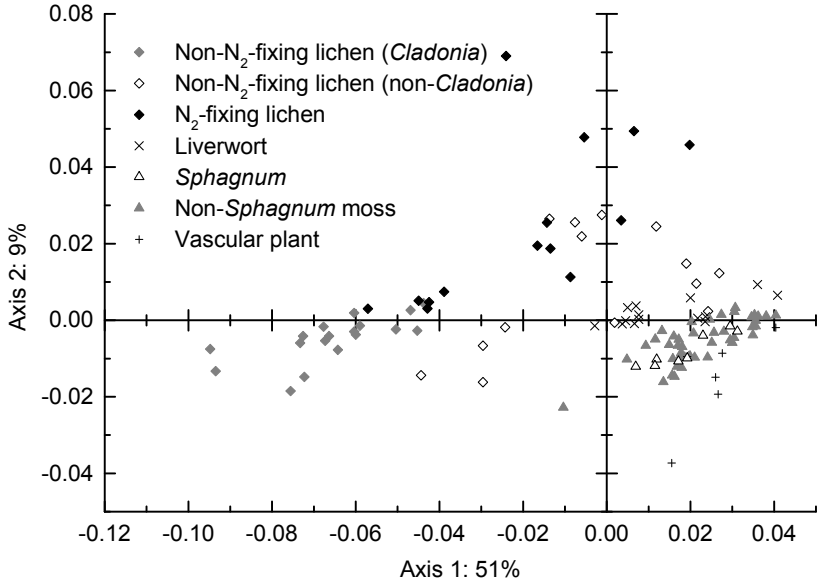

Fig. 4. Differentiation of cryptogam groups and vascular plants by infrared spectra (data untransformed, PCA, $n = 118$).

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)

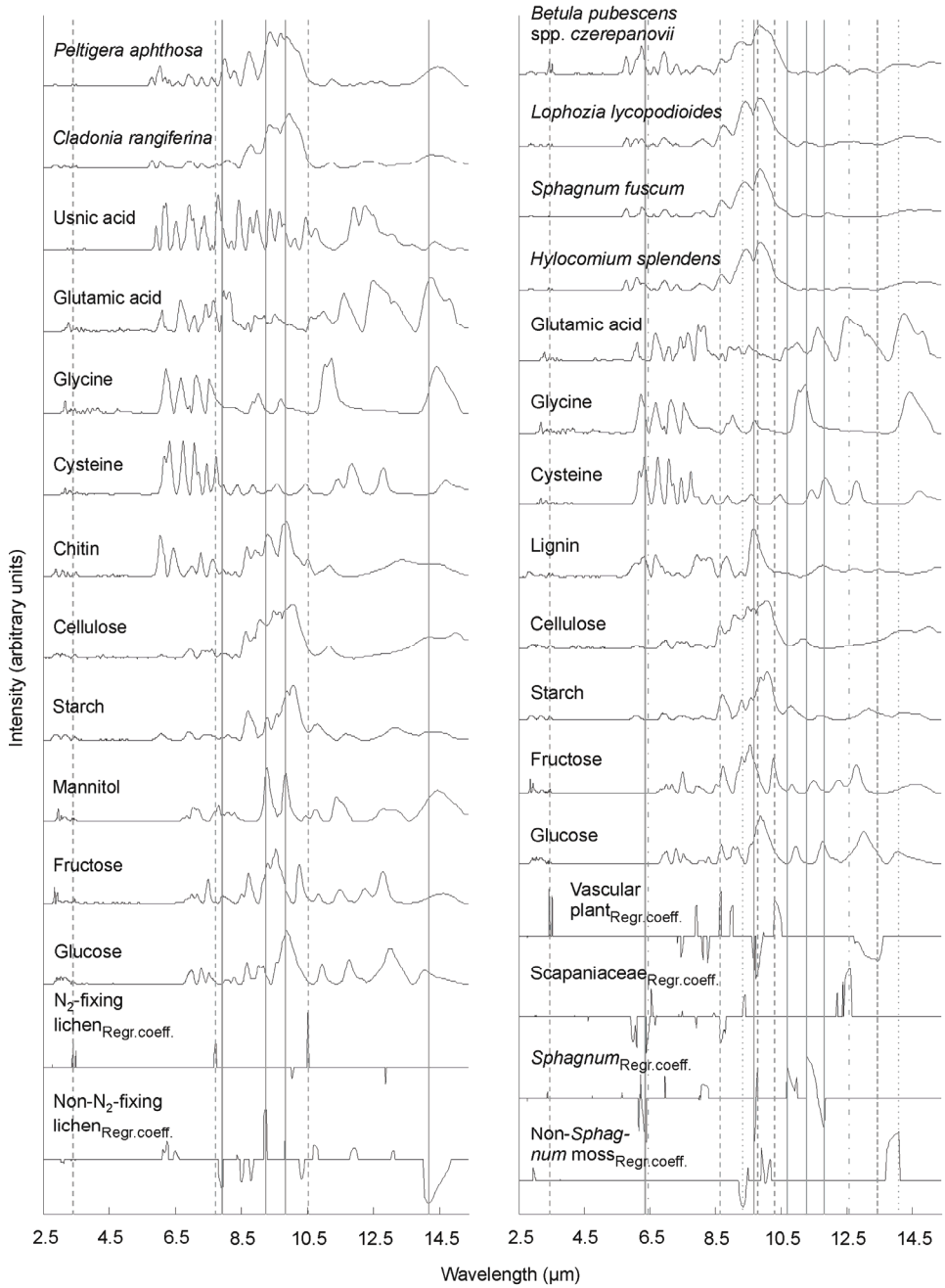

Fig. 5. Cryptogam, vascular plant and reference spectra and regression coefficients (significant coefficients only) of non-N_2-fixing lichens (—) and N_2-fixing lichens (---) (left side), and non-*Sphagnum* mosses (···), *Sphagnum* (—), Scapaniaceae (liverworts, · − ·) and vascular plants (---) (right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

Acknowledgements

The authors would like to acknowledge the Abisko Scientific Research Station, which financially supported this work and provided facilities, and Anne Temesváry and Anders Eriksson who helped to maintain the experiment. Many thanks to Matthias Ahrens who kindly verified bryophyte species identification. The authors are grateful for the generous support by the Fraunhofer Institute for Chemical Technology (ICT) for facilitating the FTIR-ATR measurements. Many thanks to Norbert Leist of the Staatliche

Landwirtschaftliche Untersuchungs- und Forschungsanstalt Augustenberg (LUFA Augustenberg) for advice on the viability test. The authors like to acknowledge A. Hölzer for technical support and the Staatliches Museum für Naturkunde Karlsruhe for generous provision of work space to S.L. Many thanks to the FAZIT-STIFTUNG for financial support enabling completion of this work. This study was financed by grant ALW-852.00.070 of the Netherlands Organisation for Scientific Research (NWO).

References

Aerts, R., Verhoeven, J.T.A. & Whigham, D.F. (1999) Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology*, **80**, 2170-2181.

Asakawa, Y. (1994) Highlights in phytochemistry of hepaticae-biologically active terpenoids and aromatic compounds. *Pure and Applied Chemistry*, **66**, 2193-2196.

Asakawa, Y. (2004) Chemosystematics of the Hepaticae. *Phytochemistry*, **65**, 623-669.

Bakken, S. (1995) Regional variation in nitrogen, protein and chlorophyll concentration in *Dicranum majus* - a reciprocal transplantation experiment. *Journal of Bryology*, **18**, 425-437.

Belyea, L.R. (1996) Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos*, **77**, 529-539.

Benedict, J.B. (1990) Lichen mortality due to late-lying snow: results of a transplant study. *Arctic and Alpine Research*, **22**, 81-89.

Beringer, J., Lynch, A.H., Chapin III, F.S., Mack, M. & Bonan, G.B. (2001) The representation of arctic soils in the land surface model: the importance of mosses. *Journal of Climate*, **14**, 3324-3335.

Brown, D.H. (1987) The location of mineral elements in lichens; implications for metabolism. *Progress and Problems in Lichenology in the Eighties* (ed E. Peveling), pp. 361-375. J. Cramer, Berlin.

Brown, D.H. & Wells, J.M. (1990) The extracellular and intracellular uptake of inorganic chemicals by bryophytes. *Bryophytes: their Chemistry and Chemical Taxonomy* (eds H.D. Zinsmeister & R. Mues), pp. 299-318. Clarendon Press, Oxford.

Chapin III, F.S., Moilanen, L. & Kielland, K. (1993) Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. *Nature*, **361**, 150-153.

Clymo, R.S. (1963) Ion exchange in *Sphagnum* and its relation to bog ecology. *Annals of Botany*, **27**, 309-324.

Clymo, R.S. (1965) Experiments on breakdown of *Sphagnum* in two bogs. *Journal of Ecology*, **53**, 747-758.

Cocchietto, M., Skert, N., Nimis, P.L. & Sava, G. (2002) A review on usnic acid, an interesting natural compound. *Naturwissenschaften*, **89**, 137-146.

Cornelissen, J.H.C. (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology*, **84**, 573-582.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A.E*., et al.* (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, **89**, 984-994.

Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A. & During, H.J. (2007) Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany*, **99**, 987-1001.

Cornelissen, J.H.C., Pérez-Harguindeguy, N., Díaz, S., Grime, J.P., Marzano, B., Cabido, M*., et al.* (1999) Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist*, **143**, 191-200.

Cornelissen, J.H.C., Quested, H.M., Gwynn-Jones, D., van Logtestijn, R.S.P., de Beus, M.A.H., Kondratchuk, A*., et al.* (2004) Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology*, **18**, 779-786.

Cornelissen, J.H.C., Quested, H.M., van Logtestijn, R.S.P., Pérez-Harguindeguy, N., Gwynn-Jones, D., Díaz, S*., et al.* (2006) Foliar pH as a new plant trait: can it explain variation in foliar chemistry and carbon cycling processes among subarctic plant species and types? *Oecologia*, **147**, 315-326.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O*., et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065-1071.

Coulson, J.C. & Butterfield, J. (1978) An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. *Journal of Ecology*, **66**, 631-650.

Coxson, D.S. & Curteanu, M. (2002) Decomposition of hair lichens (*Alectoria sarmentosa* and *Bryoria* spp.) under snowpack in montane forest, Cariboo Mountains, British Columbia. *The Lichenologist*, **34**, 395-402.

Crittenden, P.D. & Kershaw, K.A. (1978) Discovering the role of lichens in the nitrogen cycle in boreal-arctic ecosystems. *The Bryologist*, **81**, 258-267.

Dahlman, L., Persson, J., Palmqvist, K. & Näsholm, T. (2004) Organic and inorganic nitrogen uptake in lichens. *Planta*, **219**, 459-467.

Damsholt, K. (2002) *Illustrated Flora of Nordic Liverworts and Hornworts*. Nordic Bryological Society, Lund.

Daniels, R.E. & Eddy, A. (1985) *Handbook of European Sphagna*. Institute of Terrestrial Ecology, Huntingdon.

Davey, M.C. (1999) The elemental and biochemical composition of bryophytes from the maritime Antarctic. *Antarctic Science*, **11**, 157-159.

Dorrepaal, E., Cornelissen, J.H.C., Aerts, R., Wallén, B. & van Logtestijn, R.S.P. (2005) Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? *Journal of Ecology*, **93**, 817-828.

Duckett, J.G., Russell, J. & Ligrone, R. (2006) Basidiomycetous endophytes in jungermannialean (leafy) liverworts have novel cytology and species-specific host ranges: a cytological and experimental study. *Canadian Journal of Botany*, **84**, 1075-1093.

Erickson, M. & Miksche, G.E. (1974) On the occurrence of lignin or polyphenols in some mosses and liverworts. *Phytochemistry*, **13**, 2295-2299.

Esseen, P.-A. & Renhorn, K.-E. (1998) Mass loss of epiphytic lichen litter in a boreal forest. *Annales Botanici Fennici*, **35**, 211-217.

Faubert, P. & Rochefort, L. (2002) Response of peatland mosses to burial by wind-dispersed peat. *The Bryologist*, **105**, 96-103.

Flanagan, P.W. & Veum, A.K. (1974) Relationships between respiration, weight loss, temperature and moisture in organic residues in tundra. *Soil Organisms and Decomposition in Tundra* (eds A.J. Holding, O.W. Heal, S.F. MacLean Jr. & P.W. Flanagan), pp. 249-277. Tundra Biome Steering Committee, Stockholm.

Gardner, C.R. & Mueller, D.M.J. (1981) Factors affecting the toxicity of several lichen acids: effect of pH and lichen acid concentration. *American Journal of Botany*, **68**, 87-95.

Goffinet, B. & Shaw, A.J. (2009) *Bryophyte Biology*. Cambridge University Press, Cambridge.

Gorham, E. (1991) Northern peatlands: role in the carbon cyle and probable responses to climatic warming. *Ecological Applications*, **1**, 182-195.

Gornall, J.L., Jónsdóttir, I.S., Woodin, S.J. & van der Wal, R. (2007) Arctic mosses govern below-ground environment and ecosystem processes. *Oecologia*, **153**, 931-941.

Gurevitch, J., Curtis, P.S. & Jones, M.H. (2001) Meta-analysis in ecology. *Advances in Ecological Research*, **32**, 199-247.

Gurevitch, J. & Hedges, L.V. (1999) Statistical issues in ecological meta-analyses. *Ecology*, **80**, 1142-1149.

Hakala, K. & Sewón, P. (1992) Reserve lipid accumulation and translocation of ^{14}C in the photosynthetically active and senescent shoot parts of *Dicranum elongatum*. *Physiologia Plantarum*, **85**, 111-119.

Heal, O.W. & French, D.D. (1974) Decomposition of organic matter in tundra. *Soil Organisms and Decomposition in Tundra* (eds A.J. Holding, O.W. Heal, S.F.

MacLean Jr. & P.W. Flanagan), pp. 279-309. Tundra Biome Steering Committee, Stockholm.

Hébant, C. (1977) *The conducting tissues of bryophytes*. J. Cramer, Vaduz.

Hill, M.O., Bell, N., Bruggeman-Nannenga, M.A., Brugués, M., Cano, M.J., Enroth, J.*, et al.* (2006) An annotated checklist of the mosses of Europe and Macaronesia. *Journal of Bryology*, **28**, 198-267.

Hobbie, S.E. (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, **66**, 503-522.

Hobbie, S.E. & Gough, L. (2004) Litter decomposition in moist acidic and non-acidic tundra with different glacial histories. *Oecologia*, **140**, 113-124.

ISTA (2009) Biochemical test for viability. The topographical tetrazolium test. *International Rules for Seed Testing*pp., Bassersdorf.

Johnson, L.C. & Damman, A.W.H. (1991) Species-controlled *Sphagnum* decay on a South Swedish raised bog. *Oikos*, **61**, 234-242.

Kappen, L., Schroeter, B., Scheidegger, C., Sommerkorn, M. & Hestmark, G. (1996) Cold resistance and metabolic activity of lichens below 0°C *Advances in Space Research*, **18**, 119-128.

Krab, E., Cornelissen, G., Lang, S.I. & van Logtestijn, R.S.P. (2008) Amino-acid uptake among wide-ranging moss species may contribute to their strong position in higher-latitude ecosystems. *Plant and Soil*, **304**, 199-208.

Lang, S.I., Cornelissen, J.H.C., Hölzer, A., ter Braak, C.J.F., Ahrens, M., Callaghan, T.V.*, et al.* (2009) Determinants of cryptogam composition and diversity in *Sphagnum*-dominated peatlands: the importance of temporal, spatial and functional scales. *Journal of Ecology*, **97**, 299–310.

Lawrey, J.D. (1983) Lichen herbivore preference: a test of two hypotheses. *American Journal of Botany*, **70**, 1188-1194.

Lawrey, J.D. (1986) Biological role of lichen substances. *The Bryologist*, **89**, 111-122.

Ligrone, R., Carafa, A., Duckett, J.G., Renzaglia, K.S. & Ruel, K. (2008) Immunocytochemical detection of lignin-related epitopes in cell walls in bryophytes and the charalean alga *Nitella*. *Plant Systematics and Evolution*, **270**, 257-272.

Liu, W.Y., Fox, J.E.D. & Xu, Z. (2000) Leaf litter decomposition of canopy trees, bamboo and moss in a montane moist evergreen broad-leaved forest on Ailao Mountain, Yunnan, south-west China. *Ecological Research*, **15**, 435-447.

Lükewille, A. & Wright, R.F. (1997) Experimentally increased soil temperature causes release of nitrogen at a boreal forest catchment in southern Norway. *Global Change Biology*, **3**, 13-21.

Matveyeva, N. & Chernov, Y. (2000) Biodiversity of terrestrial ecosystems. *The Arctic: Environment, People, Policy* (eds M. Nutall & T.V. Callaghan), pp. 233-273. Harwood Academic, Reading.

Meentemeyer, V. (1978) Macroclimate and lignin control of litter decomposition rates. *Ecology*, **59**, 465-472.

Moore, T.R. (1984) Litter decomposition in a subarctic spruce-lichen woodland, eastern Canada. *Ecology*, **65**, 299-308.

Mossberg, B. & Stenberg, L. (2003) *Den Nya Nordiska Floran*. Wahlström & Widstrand, Stockholm.

Murphy, J. & Riley, J.P. (1962) A modified single solution method for the determination of phosphate in natural waters *Analytica Chimica Acta*, **27**, 31-36.

Nakatsubo, T., Uchida, M., Horikoshi, T. & Nakane, K. (1997) Comparative study of the mass loss rate of moss litter in boreal and subalpine forests in relation to temperature. *Ecological Research*, **12**, 47-54.

Nicolai, V. (1988) Phenolic and mineral content of leaves influences decomposition in European forest ecosystems. *Oecologia*, **75**, 575-579.

Olson, J.S. (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, **44**, 322-331.

Opelt, K., Berg, C. & Berg, G. (2007) The bryophyte genus *Sphagnum* is a reservoir for powerful and extraordinary antagonists and potentially facultative human pathogens. *FEMS Microbiology Ecology*, **61**, 38-53.

Pakarinen, P. & Vitt, D.H. (1974) The major organic components and caloric contents of high arctic bryophytes. *Canadian Journal of Botany*, **52**, 1151-1161.

Palm, C.A. & Rowland, A.P. (1997) A minimum dataset for characterization of plant quality for decomposition. *Driven by Nature. Plant Litter Quality and Decomposition* (eds G. Cadisch & K.E. Giller), pp. 379-392. CABI Publishing, Oxon.

Quested, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., Aerts, R., Trosien, F*., et al.* (2003) Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology*, **84**, 3209-3221.

Rice, S.K. (1995) Patterns of allocation and growth in aquatic *Sphagnum* species. *Canadian Journal of Botany*, **73**, 349-359.

Rochefort, L., Vitt, D.H. & Bayley, S.E. (1990) Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *Ecology*, **71**, 1986-2000.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E*., et al.* (2001) A meta-analysis of the response of soil respiration, net nitrogen

mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543-562.

Santesson, R., Moberg, R., Nordin, A., Tønsberg, T. & Vitikainen, O. (2004) *Lichen-forming and Lichenicolous Fungi of Fennoscandia*. Museum of Evolution, Uppsala University, Uppsala.

Scheffer, R.A., van Logtestijn, R.S.P. & Verhoeven, J.T.A. (2001) Decomposition of *Carex* and *Sphagnum* litter in two mesotrophic fens differing in dominant plant species. *Oikos*, **92**, 44-54.

Shaver, G.R. & Chapin III, F.S. (1995) Long-term responses to factorial, NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. *Ecography*, **18**, 259-275.

Sjögersten, S., Turner, B.L., Mahieu, N., Condron, L.M. & Wookey, P.A. (2003) Soil organic matter biochemistry and potential susceptibility to climatic change across the forest-tundra ecotone in the Fennoscandian mountains. *Global Change Biology*, **9**, 759-772.

Sjögersten, S. & Wookey, P.A. (2004) Decomposition of mountain birch leaf litter at the forest-tundra ecotone in the Fennoscandian mountains in relation to climate and soil conditions. *Plant and Soil*, **262**, 215-227.

Socrates, G. (2001) *Infrared and Raman Characteristic Group Frequencies*. John Wiley & Sons Ltd, Chichester.

Solberg, Y.J. (1970) Studies on the chemisty of lichens. IX Quantitative determination of monosaccharides and amino acids in hydrolysates of several Norwegian lichen species. *The Lichenologist*, **4**, 283-288.

Solheim, B., Endal, A. & Vigstad, H. (1996) Nitrogen fixation in Arctic vegetation and soils from Svalbard, Norway. *Polar Biology*, **16**, 35-40.

Sonesson, M. (1972) Studies in production and turnover of bryophytes at Stordalen, 1972. *Swedish Tundra Biome Project. Technical report*, **14**, 66-75.

Stark, S. & Hyvärinen, M. (2003) Are phenolics leaching from the lichen *Cladina stellaris* sources of energy rather than allelopathic agents for soil microorganisms? *Soil Biology & Biochemistry*, **35**, 1381-1385.

Sveinbjörnsson, B. & Oechel, W.C. (1991) Carbohydrate and lipid levels in two *Polytrichum* moss species growing on the Alaskan tundra. *Holarctic Ecology*, **14**, 272-277.

Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in Terrestrial Ecosystems*. Blackwell Scientific, Oxford.

Tolonen, K. (1971) On the regeneration of northeuropean bogs. I. Klaukkalan Isosuo in S. Finland. *Acta Agralia Fennica*, **123**, 143-166.

Turetsky, M.R. (2003) The role of bryophytes in carbon and nitrogen cycling. *The Bryologist*, **106**, 395-409.

Turetsky, M.R., Crow, S.E., Evans, R.J., Vitt, D.H. & Wieder, R.K. (2008) Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. *Journal of Ecology*, **96**, 1297-1305.

Vartia, K.O. (1973) Antibiotics in lichens. *The Lichens* (eds V. Ahmadjian & M.E. Hale), pp. 547-561. Academic Press, New York.

Verhoeven, J.T.A. & Liefveld, W.M. (1997) The ecological significance of organochemical compounds in *Sphagnum*. *Acta Botanica Neerlandica*, **46**, 117-130.

Vitt, D.H. & Pakarinen, P. (1987) The bryophyte vegetation, production and organic components of Truelove Lowland. *Truelove Lowland, Devon Island, A High Arctic Ecosystem* (ed L.C. Bliss), pp. 225-244. The University of Alberta Press, Edmonton.

Vivanco, L. & Austin, A.T. (2008) Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. *Journal of Ecology*, **96**, 727-736.

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., *et al.* (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences USA*, **103**, 1342-1346.

Wetmore, C.M. (1982) Lichen decomposition in a black spruce bog. *The Lichenologist*, **14**, 267-271.

Zar, J.H. (1999) *Biostatistical Analysis*. Prentice Hall, New Jersey.

Zhu, R.-L., Wang, D., Xu, L., Shi, R.-P., Wang, J. & Zheng, M. (2006) Antibacterial activity in extracts of some bryophytes from China and Mongolia. *Journal of the Hattori Botanical Laboratory*, **100**, 603-615.

Zinsmeister, H.D. & Mues, R. (1990) *Bryophytes: their Chemistry and Chemical Taxonomy*. Clarendon Press, Oxford.

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.

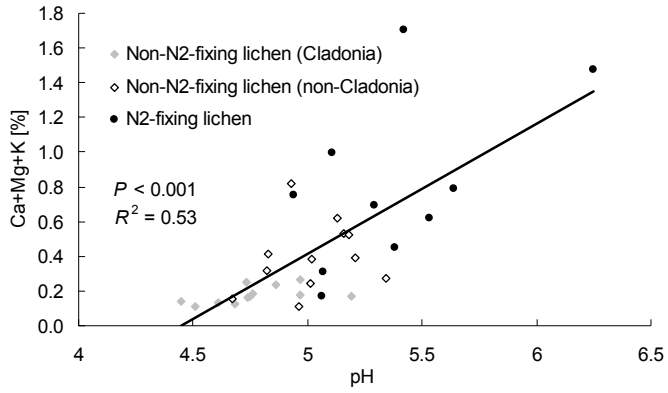

Fig. 1. Relation between pH and the sum of Ca, Mg and K (linear regression, sum of Ca, Mg and K ln-transformed) for non-N_2-fixing (both *Cladonia* and non-*Cladonia*) and N_2-fixing lichens.

Chapter 6

General Discussion

Climate change in the (Sub)Arctic is expected to be more extreme and rapid compared to other regions in the world (IPCC 2007). Tundra and peatlands are the main ecosystem components at these northern latitudes, which are largely dominated by lichens and bryophytes fulfilling important ecosystems functions (see General Introduction, Longton 1988; Rydin & Jeglum 2006). As both biodiversity and vegetation cover in the High North are strongly determined by cryptogams (Wielgolaski *et al.* 1981; Matveyeva & Chernov 2000), investigations of changes of these indices under climate warming are of major importance. These changes in turn may have important repercussions for nutrient recycling. Therefore, the major aims of this thesis were (i) to identify the consequences of climate change for vegetation composition, specifically cryptogam composition, in the (Sub)Arctic at various temporal, spatial and functional scales and (ii) to investigate the implications of these changes concerning nutrient recycling via resorption and decomposition. Below I will discuss whether and to what extent the results presented in this thesis have fulfilled these aims.

Abundance and biodiversity changes in the (Sub)Arctic under climate change

The first aim of this thesis was investigated by combining warming manipulation experiments with natural climatic gradients (see General Introduction, Fig.1, relations a, b, c and d). Studies concentrated on drivers of plant community composition and diversity of cryptogams and vascular plants in northern peatlands in Sweden and Norway, and in (sub)arctic tundra in Sweden and Alaska at different temporal, spatial and functional scales.

CLIMATE CHANGE-INDUCED DRIVERS OF PLANT COMMUNITIES IN SUBARCTIC PEATLANDS

Studying peatlands in times of climate change is of major importance since they both store and still accumulate large amounts of carbon. The genus *Sphagnum* is of particular interest in that respect since it constitutes the dominant peat moss in today's peatlands and its role concerning carbon storage is unsurpassed (Rydin & Jeglum 2006). I found that *Sphagnum*-dominated plant communities in subarctic Sweden were relatively persistent against changes in temperature regimes. This is illustrated in chapter 2 where the

influence of temperature on cryptogam composition in northern *Sphagnum*-dominated peatlands was only apparent across regions. Within one region, however, temperature influenced cryptogam composition only indirectly via *Sphagnum* growth which is partly temperature-dependent (chapter 2, Gunnarsson 2005). Moisture, while being an important determinant of *Sphagnum* growth (Gunnarsson 2005), might be less a limiting factor for this genus than for other cryptogams since *Sphagnum* displays an interesting adaptation to fluctuations in water regimes. Between stems of *Sphagnum*, water can rise by capillary forces and is held between those stems. This, together with the large water storage capacity in hyaline cells, enables *Sphagnum* to act like a sponge (Hayward & Clymo 1982). *Sphagnum* growth constitutes an important driver of plant community composition (chapter 2). This originates from its characteristics to build the 'soil' substrate while at the same time also being a living component of the cryptogam community. Some vascular plants, e.g. the carnivorous genus *Drosera*, are known to adjust their growth patterns to the growth of *Sphagnum*, always growing level with the top of the *Sphagnum* carpet (Rydin & Jeglum 2006). In chapter 2, I could show that this relation is found for a few cryptogams only, while most cryptogams were not able to keep up with *Sphagnum* growth. Thus, the greater the abundance of *Sphagnum* in peatlands, the less lichens, liverworts and non-*Sphagnum* mosses are found. The most important factor influencing peatland vegetation composition, however, was moisture. Since not only temperature but also precipitation regimes are expected to change (IPCC 2007), moisture rather than temperature might be the principal factor responsible for future vegetation shifts in peatlands. However, the range of mean annual temperature within the Abisko region comprised 2.3 °C (data not shown), which is well within the range of current climate projections for this century (IPCC 2007). Temperature increases larger than this range may after all lead to changes in peatland distribution, as was shown across regions with a temperature range of 4 °C (data not shown). Biogeographical differences in species assemblage between regions might be a factor influencing this output yet temperature remained significant even at growth form and major taxa level (chapter 2), thereby correcting for the influence of individual species, typical for a specific region. Also, at the limits of current peatland distribution, temperature may still play an important role in influencing peatland development and expansion. Where moisture is sufficient, *Sphagnum* growth is likely promoted by increasing temperatures at higher elevations possibly leading to an expansion of peatlands at these altitudes.

TEMPERATURE AS THE MAIN DRIVER OF SPECIES COMPOSITION IN (SUB)ARCTIC TUNDRA

In tundra, temperature determined plant community composition along natural climatic gradients even at the regional scale (Swedish gradient, chapter 3). In contrast to *Sphagnum*-dominated peatlands, there is no strong biotic driver (*Sphagnum* growth) controlling vegetation composition but species depend on factors such as temperature, moisture and soil pH. However, vascular plants, promoted through climate warming, have been suggested to be responsible for cryptogam declines as indicated by Cornelissen *et al.* (2001) for lichens. In the warming experiments studied here, bryophytes other than *Sphagnum* were negatively affected by warming as were the lichens which appeared most susceptible. The relative resistance of *Sphagnum* to changes in temperature, as long as moisture is sufficient as discussed above, is also illustrated in chapter 3 where *Sphagnum* was able to survive as the only cryptogam even under severe warming conditions in greenhouses in arctic Alaskan tundra. It is well-known that growth of cryptogams depends on moisture conditions (Longton 1988). As bryophytes and lichens are poikilohydric, they depend almost entirely on external water supply as they do possess no or very simple conducting tissue to actively transport water (Hébant 1977). In contrast to vascular plants with a more sophisticated system for internal water transport (the xylem), cryptogams cannot maintain metabolic activity as well as vascular plants during drought. Bryophytes, often growing in dense mats and supplied with rhizoids, in some species forming a dense tomentum, might sustain metabolic activity longer during times of drought by taking up water from the substrate and by offering a larger water holding capacity than most lichens. Lichens, on the other hand, grow in loose structures and often lack rhizines which intimately connect them to the ground (Smith 1988). As during the coming decades, precipitation regimes are expected to change both during winter and summer (IPCC 2007), moisture might, more than temperature, be the factor determining cryptogam performance. This may hold to a lesser extent for *Sphagnum* as this genus shows a high water holding capacity (see above), probably allowing for its high plasticity as shown in chapters 2 and 3. This water holding capacity is unsurpassed by other cryptogams which might therefore be disadvantaged in times of drought. Indeed, lichens followed by non-*Sphagnum* mosses were the first groups to be affected negatively in climate warming experiments (chapter 3). The loss of cryptogam diversity with warming and the related preferential growth of shrubs under these conditions (chapter 3), are processes taking place already now (Tape *et al.* 2006; Forbes *et al.* 2010). It has been suggested that the deposition of litter on the cryptogam layer by vascular plants, the production of which is promoted through climate warming, might accelerate the disappearance of cryptogams (Chapin *et al.* 1995). However, gradient analysis (chapter 3) showed that, depending on

ecosystem type and bryophyte group, bryophyte abundance was either positively or negatively related to vascular plant abundance or showed no significant relation. Some bryophytes are therefore well-adapted to increasing cover and litter production by vascular plants. Lichen abundance and biomass, however, were always negatively related to vascular plant abundance and biomass, respectively (chapter 3, Cornelissen *et al.* 2001). Also, many cryptogams show a wide range of temperatures where rates of photosynthesis are still comparatively high (Tenhunen *et al.* 1992). However, growth rates of many cold-adapted cryptogam species cannot compete with those of vascular plants. As a result of a combination of the above-mentioned factors, we might have to face severe losses in diversity while cold-adapted cryptogams move further up North or to higher elevations to find refuges still suitable for their existence.

The influence of spatial and temporal scales in climate change investigations

The influence of scaling importantly influenced the analyses both when working along natural climatic gradients and within experiments (see General Introduction, Fig.1, relation b and d). Whether climate warming will be important for vegetation composition and diversity, might depend on the spatial scale at which a study is conducted but also depends on the type of ecosystem, i.e. peatland (chapter 2) versus tundra (chapter 3) investigated in this thesis. Within an established ecosystem, in its optimum range, changes based on temperature regimes might not be apparent as was shown in chapter 2, where peatlands within one region were not significantly influenced by temperature. At the limits of plant distribution, however, e.g. at the limit of current peatland distribution, most future changes might be visible, with peatlands likely expanding towards higher elevations. Also within the subarctic birch forest, experimental warming had almost no effect on plant community composition (chapter 3). Above the treeline in tundra, however, warming induced a loss of cryptogam species while shrubs gained in abundance. Even though conducted at a small spatial scale, the tundra ecosystem in subarctic Sweden was clearly affected by temperature. However, the range of mean annual temperature in the studied peatlands in the Abisko region was 2.3 °C (see above) while it was 4.8 °C in subarctic Swedish tundra and 4.1 °C in arctic Alaska (data not shown). Thus, even though conducted at a smaller spatial scale, the temperature range in Swedish tundra was clearly higher, comparable to the peatland macrogradient with a temperature range of 4 °C (see above), also there significantly influencing vegetation composition.

The influence of temporal scales was most apparent in the peatland experiment conducted at a short time scale. No changes were as yet apparent (chapter 2) while long-term

investigations (9 – 16 yrs) in (sub)arctic tundra (chapter 3) clearly influenced vegetation composition. The 13-yr old experiment in the subarctic forest, however, was likely not hampered by short experimental duration but by its relative resistance to temperature changes.

Since scaling, be it spatial or temporal, importantly influenced the analyses, climate change studies should consider and evaluate their results accordingly. Short-term experiments, especially when dealing with the slowly-growing cryptogams, are unlikely to reveal any significant responses yet. Spatial scales, if comprising a larger temperature range of around 4 °C are more likely to display significant responses in vegetation composition. This temperature range is close to the mean temperature responses predicted in climate change projections for this century (ACIA 2005; IPCC 2007).

Cryptogam functional groups and their usage in climate change investigations

The concept of functional groups (functional scale) has been widely used to simplify and generalize responses of species groups to environmental conditions or to describe their effects on ecosystem processes (Gitay & Noble 1997; Lavorel *et al.* 1997). Where strong biotic drivers exist, e.g. in peatlands where *Sphagnum* growth forces its own growth pattern onto other plants and cryptogams, a functional classification based on this driver was an obvious solution (chapter 2; see General Introduction, Fig.1, relation c). Along the microgradient, from plots overgrown with lichens to wet plots, *Sphagnum* growth increases and only few species are able to keep pace with the constantly growing living soil surface. Other investigations demand different classifications, e.g. based on the existence and increasing specialization of conducting tissue, when resorption efficiencies among species and species groups are compared (chapter 4). Here, taxonomic ranking was the most useful since species are grouped in genera and orders, which show the highest morphological and evolutionary similarities. Ecological functions such as the N_2-fixing capacity cannot clarify the patterns in this case, since transport mechanisms of nitrogen (N) and phosphorus do not differ based on this ecosystem function. Decomposition, on the other hand, might be influenced by N_2-fixation since N levels in senesced tissue are positively related to mass loss rates in cryptogams (chapter 5) and vascular plants (Palm & Rowland 1997). This does not necessarily lead to a clear distinction of decomposition rates between N_2-fixing and non-N_2-fixing lichens, which were indeed not different from each other in this study. On the other hand, a broad taxonomical distinction of the bryophytes into *Sphagnum*, non-*Sphagnum* mosses and liverworts helped to emphasize once more the extraordinary position of *Sphagnum* also when considering mass loss rates.

As yet, we do not have the means to assemble a whole set of similar traits of cryptogams in response to environmental conditions or to group similar effects on ecosystem processes. If this were possible, an objective assessment of the usage of functional cryptogam groups in climate changes studies could be conducted. Until then, the use of functional or taxonomical groups based on a specific research question might be a better approach, if not the only feasible one.

Nutrient resorption in times of climate change

The observed changes in plant community composition from cryptogam-dominated to shrub-dominated tundra, induced by climate change, will also affect processes related to ecosystem nutrient recycling, such as nutrient resorption from senescing tissues and litter decomposition (second aim; see General Introduction, Fig.1, relations c and e). Resorption, the translocation of nutrients from senescing plant parts into roots, stems or fresh tissue, is a process well-known from vascular plants (Chapin 1980; Reich *et al.* 1992; Killingbeck 1996). Cryptogams, however, have hardly been investigated so far (Eckstein & Karlsson 1999; Kytöviita & Crittenden 2007), despite their overwhelming contribution in terms of biomass and abundance in the (Sub)Arctic (Wielgolaski *et al.* 1981; Matveyeva & Chernov 2000). Monitoring nitrogen resorption efficiencies (RE) in a wide range of bryophytes and lichens showed that these were in general lower compared to vascular plants (except lycophytes and liverworts, chapter 4). The evolutionary appearance and increasing specialisation of conducting tissue seemed to relate to increasing levels of RE, also when observed within clades (mosses): from low RE of *Sphagnum* with almost no conducting tissue (Ligrone & Duckett 1998) to highest RE for the Polytrichales (Hébant 1977; Ligrone *et al.* 2000) with a relatively high degree of specialisation in conducting tissues. High RE in vascular plants could be interpreted as an increased ability to efficiently use nutrients in a highly nutrient-limited environment. However, even though cryptogams show overall lower RE, also N levels in their tissues are lower overall (chapter 4), while in vascular plants higher RE is needed to efficiently re-use nutrients to account for the more cost-intensive vascular plant tissue (note that discrepancies in N levels between chapters 4 [high N levels of vascular plants] and 5 [N levels of vascular plants comparable to those of cryptogams] are likely based on interannual variation and the exclusion of N_2-fixers and hemiparasites in the vascular plant dataset in chapter 5). Furthermore, the long lifespan and low nutrient requirements of slow-growing shoots or thalli of many cryptogam species may lead to lower levels of RE, comparable to a reduction of RE in evergreens (Aerts 1995). Long lifespan is a complementary adaptation to conserve nutrients. In conclusion, both vascular plants and cryptogams pursue different strategies to conserve nutrients, which is especially important

in a highly nutrient-limited environment such as the (Sub)Arctic (Arft *et al.* 1999). Interestingly, *Sphagnum*, with almost no conducting tissue (Ligrone & Duckett 1998) and the lowest RE, seems to compensate for this deficiency by showing an extremely high cation exchange capacity and large adsorption surfaces effectively capturing nutrients from the soil solution (Clymo 1963). As different taxa show different N levels in fresh tissues and different levels of RE, this will lead to differences in N litter concentrations. Especially *Salix* spp. and *Betula nana*, the main shrubs responsible for shrub expansion in the (Sub)Arctic, display low N levels in litter, comparable to that in cryptogams (chapter 5). Intermediate N values for these species, however, as found in the dataset underlying Quested *et al.* (2003) used in chapter 4, are likely due to interannual variation. The shift from cryptogam- to shrub-dominated tundra will therefore result in faster internal nutrient recycling (chapter 4) but not necessarily in production of litter with higher N levels. But whether or not any such differences in litter N concentration will lead to differences in their decomposability, will also depend greatly on the structural and mobile defence chemistry of these litters, as will be discussed below.

Decomposition and climate change

After resorption has taken place, leaves (or thalli) are either shed by vascular plants or remain attached to the living parts of the cryptogam while decomposition processes are initiated (see General Introduction, Fig.1, relations c and f). Clear differences can be seen in mass loss rates of the different litters that vascular plants and cryptogams produce (see Bokhorst *et al.* 2007 for an antarctic analogue, albeit with fewer species). Even though litter of vascular plants is not always richer in N than that of bryophytes, mass loss rates of vascular plants are generally higher than those of bryophytes. It is likely that in bryophytes, especially liverworts, a higher percentage of N is used in mobile secondary (defence) compounds (Asakawa 2004), which are not easily digested by the soil fauna or processed by microbes, and which are not withdrawn during the resorption process. Lichens, with high decomposition rates, are only dominant in a few places, while bryophytes are very abundant in many tundra ecosystems. Thus, a decline of bryophytes and an increase in vascular plants will lead to a much faster turnover of nutrients while the slow but continuous organic layer, built up by bryophytes over thousands of years, will cease to increase. In addition, increasing temperatures may accelerate litter decomposition (Cornelissen *et al.* 2007). While there were clear overall differences among vascular plants, bryophytes and lichens, taxonomic identity within cryptogam groups was an important determinant of mass loss rates, too. Especially *Sphagnum*, known for its recalcitrant litter (Hobbie 1996; Scheffer *et al.* 2001), showed the lowest mass loss rates within the bryophytes, and thereby contributes disproportionally to organic matter build-

up in peatlands. Within lichens, especially the Cladoniaceae showed lower decomposition rates. Locally, this might mean that mass loss rates might vary significantly depending on ecosystem type and the species present therein. These substantial interspecific differences in mass loss rates underpin the need for detailed knowledge of species identity when predicting ecosystem responses to climate change. To complicate the pattern, species do not necessarily decompose uniformly in contrasting environments (chapter 5). Therefore, there is still a great need of investigations dealing with cryptogam mass loss rates in various environments. The chemical traits determining mass loss could clearly be described by both standard wet-chemical analyses and FTIR-ATR. The advantages of FTIR-ATR as a novel method to determine primary and secondary chemistry can be seen in its efficiency and its possibility of measuring even very small samples. This is especially important when dealing with the often light-weight cryptogams where standard wet-chemical methods would be strongly disadvantaged. While many variables determining mass loss could be identified (chapter 5, Turetsky *et al.* 2008; Hájek *et al.* online), the influence of the complex secondary chemistry on decomposition still needs to be investigated further. It is likely that these chemical compounds are responsible for the differences in decomposition found in various environments. Soil microbes may be adapted to certain secondary compounds by using them as an energy source (Stark & Hyvärinen 2003). Future studies should therefore concentrate on how fast these communities can adapt to changing environmental conditions, both in terms of temperature and moisture regimes but also in terms of shifting plant communities and their related litters.

Outlook and conclusions

While important effects of climate change on vegetation composition and, thereby, on nutrient recycling have been investigated in this thesis, various other aspects were not covered explicitly, such as feedback from decomposition back to carbon in the atmosphere, with possible effects on global climate itself (Wookey *et al.* 2009). It has been shown that primarily temperature and subsequent shifts in growth form composition (through leaf trait afterlife effects) affect decomposition, while differences in litter quality within species had very little effect (Cornelissen *et al.* 2007). Recalcitrant litter of shrubs, promoted by increasing temperatures (Tape *et al.* 2006), might even constitute a negative feedback to climate warming (Cornelissen *et al.* 2007). However, litter of cryptogams was hardly considered in that study. It seems likely that with the disappearance of cryptogams and their more recalcitrant litters (especially bryophytes), the overall feedback of climate warming onto decomposition might be context-dependent. In *Sphagnum*-dominated systems, the combination of strong resistance to climate change and low decomposability

together would result in carbon sequestration; in certain ecosystems dominated by non-*Sphagnum* mosses the strong decline of mosses would possibly promote carbon turnover. However, this needs to be investigated in future studies. Furthermore, herbivory by muskoxen and caribou might counteract the observed increase in shrubs as was found in a five-year study where warmed plots did not differ from control plots if grazed, while ungrazed but warmed plots shifted from graminoid-dominated toward dwarf birch-dominated (Post & Pedersen 2008). Also, direct climate effects on phenotypic expression of traits of a given species should be investigated further. Reproductive capacity and dispersal of cryptogams may be important determinants of species establishing in new regions where the climate has become or will become benign to them. Perhaps even evolution, generally leading to adaptation to climate change on longer time scales, might be of interest also at intermediate time scales of up to a century. Both topics would be relevant for further in-depth studies. While I studied chronic warming effects on vegetation composition, the influence of extreme winter warming events, possibly leading to shifts in plant communities, should be extended to cryptogams (cf. Bokhorst *et al.* 2008 for vascular plants). Biotic interactions such as competition and facilitation, between vascular plants and cryptogams as well as within cryptogams, might cause shifts in species biomass distributions. We still know very little about how such shifts would affect abundance-weighted processes like decomposition rates (cf. Fortunel *et al.* 2009 for vascular plants). Furthermore, N_2-fixation capacity in cryptogams (Gavazov *et al.* 2010) and how this capacity is influenced by changes in vegetation composition could be of interest in future climate change investigations. Other important aspects (abiotic interactions) not treated here include the effects of changing vegetation composition onto permafrost insulation (Gornall *et al.* 2007). As bryophytes disappear, the active layer will increase (Kade & Walker 2008), releasing larger amounts of the greenhouse gases CO_2 and CH_4 into the atmosphere (Jorgenson *et al.* 2010). Also hydrology, strongly influenced by bryopytes (Beringer *et al.* 2001; Heijmans *et al.* 2004) would be worthwhile investigating. My study focussed on vegetation shifts induced by climate change and its implications for nutrient resorption and decomposition. The most drastic changes in vegetation will likely be visible at the individual limits of the species' ecological optimum range, i.e. at community level at or above treeline, or might be seen at species level for instance in the expansion of peatlands through *Sphagnum*. What is needed in future climate change studies is a linkage between climate change studies and ecosystem traits as mentioned above, which need to be quantified in order to be able to predict effects of climate change onto ecosystem functioning in the (Sub)Arctic. Specifically, interspecific differences in these ecosystem traits might be the key to a deeper understanding of the complex relationships determining the nutrient, carbon and water dynamics of the

(Sub)Arctic and their response in times of climate change. In that sense this thesis, in spite of the complexity of the above mentioned (and further) interacting factors, has added significantly to finding this key. Indeed, it has revealed important new information towards fulfilling the two main aims of this thesis by (i) identifying the likely consequences of climate change for specifically the cryptogam component of vegetation composition in the (Sub)Arctic at various temporal, spatial and functional scales and by (ii) demonstrating the likely implications of these changes for nutrient recycling via nutrient resorption and litter decomposition.

References

ACIA (2005) Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.

Aerts, R. (1995) The advantages of being evergreen. *Trends in Ecology & Evolution*, **10**, 402-407.

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M. *et al.* (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491-511.

Asakawa, Y. (2004) Chemosystematics of the Hepaticae. *Phytochemistry*, **65**, 623-669.

Beringer, J., Lynch, A.H., Chapin, F.S.III, Mack, M. & Bonan, G.B. (2001) The representation of arctic soils in the land surface model: the importance of mosses. *Journal of Climate*, **14**, 3324-3335.

Bokhorst, S., Bjerke, J.W., Bowles, F.W., Melillo, J., Callaghan, T.V. & Phoenix, G.K. (2008) Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland. *Global Change Biology*, **14**, 2603-2612.

Bokhorst, S., Huiskes, A., Convey, P. & Aerts, R. (2007) Climate change effects on organic matter decomposition rates in ecosystems from the Maritime Antarctic and Falkland Islands. *Global Change Biology*, **13**, 2642-2653.

Chapin, F.S.III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233-260.

Chapin, F.S.III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694-711.

Clymo, R.S. (1963) Ion exchange in *Sphagnum* and its relation to bog ecology. *Annals of Botany*, **27**, 309-324.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A.E. *et al.* (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, **89**, 984-994.

Cornelissen, J.H.C., van Bodegom, P.M., Aerts, R., Callaghan, T.V., van Logtestijn, R.S.P., Alatalo, J. *et al.* (2007) Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters*, **10**, 619-627.

Eckstein, R.L. & Karlsson, P.S. (1999) Recycling of nitrogen among segments of *Hylocomium splendens* as compared with *Polytrichum commune*: implications for clonal integration in an ectohydric bryophyte. *Oikos*, **86**, 87-96.

Forbes, B.C., Fauria, M.M. & Zetterberg, P. (2010) Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology*, **16**, 1542-1554.

Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K. *et al.* (2009) Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology*, **90**, 598-611.

Gavazov, K.S., Soudzilovskaia, N.A., van Logtestijn, R.S.P., Braster, M. & Cornelissen, J.H.C. (2010) Isotopic analysis of cyanobacterial nitrogen fixation associated with subarctic lichen and bryophyte species. *Plant and Soil*, **333**, 507-517.

Gitay, H. & Noble, I.R. (1997) What are plant functional types and how should we seek them? *Plant Functional Types: their Relevance to Ecosystem Properties and Global Change* (eds T.M. Smith, H.H. Shugart & F.I. Woodward), pp. 3-19. Cambridge University Press, Cambridge.

Gornall, J.L., Jónsdóttir, I.S., Woodin, S.J. & van der Wal, R. (2007) Arctic mosses govern below-ground environment and ecosystem processes. *Oecologia*, **153**, 931-941.

Gunnarsson, U. (2005) Global patterns of *Sphagnum* productivity. *Journal of Bryology*, **27**, 269-279.

Hájek, T., Ballance, S., Limpens, J., Zijlstra, M. & Verhoeven, J.T.A. (online) Cell wall polysaccharides play an important role in decay resistance of *Sphagnum* and actively depressed decomposition in vitro. *Biogeochemistry*, DOI: 10.1007/s10533-010-9444-3.

Hayward, P.M. & Clymo, R.S. (1982) Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. *Proceedings of the Royal Society of London Series B*, **215**, 299-325.

Hébant, C. (1977) The Conducting Tissues of Bryophytes. J. Cramer, Vaduz.

Heijmans, M.M.P.D., Arp, W.J. & Chapin, F.S.III (2004) Controls on moss evaporation in a boreal black spruce forest. *Global Biogeochemical Cycles*, **18**, doi:10.1029/2003GB002128.

Hobbie, S.E. (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, **66**, 503-522.

IPCC (2007) Fourth Assessment report "Climate Change 2007". Cambridge University Press, Cambridge

Jorgenson, M.T., Romanovsky, V., Harden, J., Shur, Y., O'Donnell, J., Schuur, E.A.G. *et al.* (2010) Resilience and vulnerability of permafrost to climate change. *Canadian Journal of Forest Research*, **40**, 1219-1236.

Kade, A. & Walker, D.A. (2008) Experimental alteration of vegetation on nonsorted circles: effects on cryogenic activity and implications for climate change in the Arctic. *Arctic, Antarctic, and Alpine Research*, **40**, 96-103.

Killingbeck, K.T. (1996) Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology*, **77**, 1716-1727.

Kytöviita, M.-M. & Crittenden, P.D. (2007) Growth and nitrogen relations in the mat-forming lichens *Stereocaulon paschale* and *Cladonia stellaris*. *Annals of Botany*, **100**, 1537-1545.

Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A. (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution*, **12**, 474-478.

Ligrone, R. & Duckett, J.G. (1998) The leafy stems of *Sphagnum* (Bryophyta) contain highly differentiated polarized cells with axial arrays of endoplasmic microtubules. *New Phytologist*, **140**, 567-579.

Ligrone, R., Duckett, J.G. & Renzaglia, K.S. (2000) Conducting tissues and phyletic relationships of bryophytes. *Philosophical Transactions of the Royal Society of London Series B*, **355**, 795-813.

Longton, R.E. (1988) The Biology of Polar Bryophytes and Lichens. Cambridge University Press, Cambridge.

Matveyeva, N. & Chernov, Y. (2000) Biodiversity of terrestrial ecosystems. *The Arctic: Environment, People, Policy* (eds M. Nutall & T.V. Callaghan), pp. 233-273. Harwood Academic Publishers, Reading.

Palm, C.A. & Rowland, A.P. (1997) A minimum dataset for characterization of plant quality for decomposition. *Driven by Nature* (eds G. Cadisch & K.E. Giller), pp. 379-392. CABI Publishing, Oxon.

Post, E. & Pedersen, C. (2008) Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 12353-12358.

Quested, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., Aerts, R., Trosien, F. *et al.* (2003) Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology*, **84**, 3209-3221.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**, 365-392.

Rydin, H. & Jeglum, J. (2006) The Biology of Peatlands. Oxford University Press, New York.

Scheffer, R.A., van Logtestijn, R.S.P. & Verhoeven, J.T.A. (2001) Decomposition of *Carex* and *Sphagnum* litter in two mesotrophic fens differing in dominant plant species. *Oikos*, **92**, 44-54.

Smith, R.I.L. (1988) Aspects of cryptogam water relations at a continental antarctic site. *Polarforschung*, **58**, 139-153.

Stark, S. & Hyvärinen, M. (2003) Are phenolics leaching from the lichen *Cladina stellaris* sources of energy rather than allelopathic agents for soil microorganisms? *Soil Biology & Biochemistry*, **35**, 1381-1385.

Tape, K., Sturm, M. & Racine, C. (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, **12**, 686-702.

Tenhunen, J.D., Lange, O.L., Hahn, S., Siegwolf, R. & Oberbauer, S.F. (1992) The ecosystem role of poikilohydric tundra plants. *Arctic Ecosystems in a Changing Climate* (eds F.S.III Chapin, R.L. Jefferies, J.F. Reynolds *et al.*), pp. 213-237. Academic Press, San Diego.

Turetsky, M.R., Crow, S.E., Evans, R.J., Vitt, D.H. & Wieder, R.K. (2008) Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. *Journal of Ecology*, **96**, 1297-1305.

Wielgolaski, F.E., Bliss, L.C., Svoboda, J. & Doyle, G. (1981) Primary production of tundra. *Tundra Ecosystems: a Comparative Analysis* (eds L.C. Bliss, O.W. Heal & J.J. Moore), pp. 187-225. Cambridge University Press, Cambridge.

Wookey, P.A., Aerts, R., Bardgett, R.D., Baptist, F., Bråthen, K.A., Cornelissen, J.H.C. *et al.* (2009) Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology*, **15**, 1153-1172.

Acknowledgements

"Neither rain nor snow nor gloom of night can stay these messengers about their duty". If expanded to '…neither hail nor grizzlies nor wolves', this motto, from Terry Pratchetts novel 'Going Postal', would most appropriately describe my PhD work. Field work showed its adventurous sides when exploring the Brooks Range, venturing alone into the vast expanses of the Alaskan tundra, or finding my way home through snow storms in the Swedish mountains.

My life in four countries – the Netherlands, Germany, Sweden and Alaska – would be the best way to characterize my PhD. It surely asked for a lot of coordination not only between me and my supervisors but also demanded an immense understanding from family and friends, especially my husband Marc. To bridge the gap between continents or countries was not always an easy task but everybody's commitment, for which I am especially grateful, made this arrangement possible.

A PhD is always an adventurous time, not only in terms of field work. I am glad to say that my supervisors Hans Cornelissen and Rien Aerts successfully accompanied me through the ups and downs of my PhD. I am especially grateful for the invigorating and creative discussions with Hans, who encouraged me to think 'new ideas' and dare to achieve the impossible (and, along the way, translated the English summary into Dutch in my thesis). I am also very grateful to Rien. He showed me how to get things into shape, structure and, in short, bring science down to earth. A big thanks to both of you, I certainly learned a lot during this PhD.

There are a lot of people who helped to finish this thesis. In the Netherlands, I especially want to thank the technicians Richard van Logtestijn, Rob Broekman and Jurgen van Hal for their expert laboratory help and openness when dealing with some of the more unusual requests. Also the staff at the workshop at VU University Amsterdam is gratefully acknowledged for providing the vegetation recording frame and permafrost probes for field work. Many thanks to Cajo ter Braak who introduced me into the world of advanced multivariate statistics; it was good fun collaborating with you. In Alaska, Gus Shaver and Jim Laundre and the staff of Toolik Field Station have helped me greatly by introducing me into the Alaskan ecosystem and setting me up at the research station, always offering help when needed. I also want to acknowledge Terry Callaghan and the staff at the Abisko Scientific Research Station in Sweden for providing help all around my PhD, in the office with computer issues, with the litter experiment and in the workshop. Many thanks to

Johan Asplund who translated the English summary into Swedish, your help is much appreciated. I am also very grateful to Mats Sonesson for sharing his knowledge about point framing, thereby significantly improving my vegetation recording frame. Also people in Germany have greatly contributed to make this thesis happen. Norbert Leist from LUFA Augustenberg introduced me to the seed viability test, and provided me with the necessary chemicals. Thorsten Klahn and Wenka Schweikert from Fraunhofer Institute generously let me use their laboratory equipment and self-developed software, and, by being curious about the unknown, were very helpful when interpreting the FTIR spectra. Last not least, many thanks to Adam Hölzer and Matthias Ahrens from the Staatliches Naturkundemuseum Karlsruhe. Adam Hölzer helped to tackle the more difficult cases of *Sphagnum* identification. However, also laboratory help and the many discussions we had about species and ecology were truly helpful during my stays in Germany. Matthias Ahrens patiently introduced me into the complex world of bryophyte identification, especially the very plastic one in Abisko, and for this I am truly grateful. Last not least, many thanks to all the people who volunteered to assist during field work: Marc, Louise, Helena, Kyle, Marselle, Christina, Kanchan and Karin - you are all gratefully acknowledged. Many thanks also to my paranimphs Richard van Logtestijn and Marika Makkonen. I am glad to have you at my side on the big day.

Last not least, I want to thank all the people in the Netherlands who offered me their friendship during the at times stony path of the PhD. Also a big thanks to my family and friends in Germany for keeping in touch, defying the long distance and infrequent visits. I am also truly grateful to all the people in Sweden and Alaska whom I got to know during field work and who made me feel less abroad but more and more at home wherever I stayed.

The last thanks should go to my husband – who dared to be with a woman who was abroad for all summer and more than half of the winter. Many thanks for being my field assistant and for your excellent support as electrical engineer – it certainly made all technical problems look a lot easier. Without your support, in every respect, this thesis would have been impossible to manage and the biggest thanks will go to you.

List of publications

B.J. Graae, R.Ejrnæs, **S.I. Lang**, E.Meineri, P.T. Ibarra and H.H. Bruun (online) Strong microsite control of plant recruitment in tundra. *Oceologia*, DOI 10.1007/s00442-010-1878-8.

Soudzilovskaia N.A., J.H.C. Cornelissen, H.J. During, R.S.P. van Logtestijn, **S.I. Lang** and R. Aerts (2010) Similar cation exchange capacities among bryophyte species reveal new mechanism of brown moss fen to *Sphagnum* bog succession. *Ecology*, 91, 2716-2726.

Lang S.I., J.H.C. Cornelissen, G.R. Shaver, M. Ahrens, T.V. Callaghan, U. Molau and R. Aerts (2010) Climate change impact on lichen diversity in the (sub)Arctic and implications for carbon and nutrient (re-)cycling. *Conference Proceedings. Bulletin of the British Lichen Society*, 107, 26-27.

Lang S.I., J.H.C. Cornelissen, T. Klahn, R.S.P. van Logtestijn, R. Broekman, W. Schweikert *et al.* (2009) An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. *Journal of Ecology*, 97, 886-900.

Lang S.I., J.H.C. Cornelissen, A. Hölzer, C.J.F. ter Braak, M. Ahrens, T.V. Callaghan*, et al.* (2009). Determinants of cryptogam composition and diversity in *Sphagnum*-dominated peatlands: the importance of temporal, spatial and functional scales. *Journal of Ecology*, 97, 299-310.

Krab E., J.H.C. Cornelissen, **S.I. Lang**, R.S.P. van Logtestijn (2008). Amino acid uptake among wide-ranging moss species may contribute to their strong position in higher-latitude ecosystems. *Plant and Soil*, 304, 199-208.

Douma B., M. van Wijk, **S.I. Lang** and G. Shaver (2007). Carbon and water exchange of arctic mosses. *Plant, Cell and Environment*, 30, 1205–1215.

Cornelissen J.H.C., **S.I. Lang**, N.A. Soudzilovskaia and H.J. During (2007). Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany*, 99, 987-1001.

Lang S.I., M.W. Dees, K. Bockhorst (2007). Life in the Arctic – a struggle for survival. *Arctic Plant Ecology: From tundra to polar desert in Svalbard* (eds. I. G. Alsos, C. Körner, D. Murray), pp 33-54, UNIS online Publication series, Longyearbyen.

Schäfer M., H. Hahn, E. Hoffmann, D. Hilligardt und **S. Lang** (2000). Nassmechanische Ausschleusung von Schadstoffen aus Bioabfall. *Müll und Abfall*, 8, 476 - 483.

Submitted:

Lang S.I., J.H.C. Cornelissen, R.S.P. van Logtestijn, W. Schweikert, T. Klahn, H. Quested, J.R. van Hal and Rien Aerts. Mapping nutrient resorption efficiencies of subarctic cryptogams and seed plants onto the Tree of Life.

Lang S.I., J.H.C. Cornelissen, G.R. Shaver, M. Ahrens, T.V. Callaghan, U. Molau, C.J.F. ter Braak, A. Hölzer and Rien Aerts. Consistent negative arctic warming effects on lichen diversity and mixed effects on bryophyte diversity on two continents.

Curriculum Vitae

Simone Iris Lang was born in Karlsruhe, Germany, on 8th February 1972. After graduating from secondary school at St. Dominikus Gymnasium in 1991, she studied chemistry at the University of Karlsruhe where she obtained her prediploma (equiv B.Sc.). After that she studied geoecology in which she graduated in September 2001 (Diploma, equiv. M.Sc.). During her master study, she investigated how the growth of a carnivorous plant, *Pinguicula vulgaris*, is related to nitrogen compounds and other soil nutrients. This study took place in Northern Sweden under the supervision of Profs. P.S. Karlsson, V. Schweikle and D. Burger, and was funded by the Erasmus programme. From November 2001 to January 2002, she worked as a research assistant supervising a wastewater treatment experiment at the University of Karlsruhe (Institute of Aquatic Environmental Engineering). From February 2002 to February 2004 she worked as a researcher at the Staatliches Museum für Naturkunde Karlsruhe where she investigated pollen cores from a German bog (Blindenseemoor) in the Black Forest. She also studied *Sphagnum* and collected this genus during stays in Sweden and Scotland. In February 2004 she started her PhD research at the Department of Systems Ecology, Vrije Universiteit Amsterdam, the results of which are presented in this thesis. Since February 2008 she has worked both as lecturer and consultant for various organisations. She has also successfully applied for grants from the FAZIT-STIFTUNG to finish her PhD thesis.