Litter decomposition rate and soil organic matter quality in a patchwork heathland of Southern Norway

Norwegian heathland soils, although scant and shallow, are major reservoirs of carbon (C). We aimed at assessing whether vegetation cover and, indirectly, its driving factor soil drainage are good proxies for soil organic matter (SOM) composition and dynamics in a typical heathland area of Southern Norway consisting in a patchwork of three different types of vegetation, dominated by Calluna (*Calluna vulgaris* (L) Hull), Molinia (*Molinia caerulea* (L) Moench), or Sphagnum (*Sphagnum capillifolium* (Ehrh.) Hedw.). Such vegetation covers were clearly associated to microtopographic differences, which in turn dictated differences in soil moisture regime, Calluna growing in the driest sites, Sphagnum in the wettest, and Molinia in sites with intermediate moisture.

Litter decomposition was followed over a period of 1 year, by placing litterbags filled with biomass from each dominant species in each type of vegetation cover. The composition of the plant material and SOM were investigated by chemical methods and solid-state ^{13}C nuclear magnetic resonance (NMR) spectroscopy.

Litter decomposition was faster for Molinia and Calluna, irrespective of the vegetation cover of the site where they were placed. Sphagnum litter decomposed very slowly, especially under Calluna, where the soil environment is by far more oxidising than under itself. In terms of SOM quality, Calluna covered areas showed the greatest differences from the others, in particular a much higher contribution from lipids and aliphatic biopolymers, apparently related to biomass composition.

Our findings showed that in the studied environment litter decomposition rate and SOM composition are actually dependent on vegetation cover and/or soil drainage. On this basis, monitoring changes in the patchwork of vegetation types in boreal heathlands could be a reliable cost-effective way to account for climate change induced modifications to SOM and its potential to last.

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1. Introduction

Heathland vegetation covers approximately 60% of Norway's land area. Norwegian heathland soils, although scant and shallow, are so rich in organic matter that they represent a stock of carbon (C) at least one order of magnitude larger than the aboveground vegetation they sustain (Rosberg et al., 1981). To predict the ecological effects of climate and land use changes, it is essential to understand the nature and environmental dependencies of soil organic matter (SOM) in these widespread systems. In fact, any change influencing their SOM stocks and dynamics may have major consequences for both C balance and the water quality of lakes and rivers (Stuanes et al., 2008).

Following changes in SOM stocks is not a simple task, and several approaches have been proposed for this purpose (*e.g.,* Johnson and Curtis, 2001; Trumbore, 2009; Chiti et al., 2011). The current common belief is that environmental and biological factors predominate on the molecular structure in controlling SOM stability (Kleber, 2010; Kleber et al., 2011; Schmidt et al., 2011); however, in some environments, vegetation cover is a good proxy for soil C dynamics, since it controls the input and quality of litter (De Deyn et al., 2008). In turn, vegetation depends, among other factors, on soil drainage, which also influences litter decay and SOM transformation (Wickland et al., 2010), so representing another possible proxy for SOM storage.

Although present-day vegetation may be different from the one the underlying SOM originated from (Chambers et al., 1999; Hjelle et al., 2010), many studies have demonstrated that the most active part of SOM is the youngest (*e.g.,* Leavitt et al., 1996; Trumbore, 2000; Chiti et al., 2009). Trumbore (2000) found that the average age of the carbon dioxide (CO_2) released by decomposition processes in boreal forest soils is 30 years, and 50-60% of total soil respiration arises from SOM with mean residence time less than 1 year. The dominant contribution of recently synthesized organic matter to soil respiration was also assessed by Certini et al. (2003) for forests in temperate regions. Theoretically, the moister and colder the pedoclimate, the better preserved the dead biomass in soil (Hobbie et al., 2000; Hicks Pries et al., 2013). Hence, the wet boreal heathlands are environments where the investigation of a possible relationship between vegetation covers and SOM dynamics is particularly meaningful. Here, due to the intense leaching, lost dissolved organic C (DOC) may be much older than the respired C (Karltun et al., 2005), rendering any possible relationship between present day vegetation and bulk SOM quality less clear. Nonetheless, in the uppermost soil, where SOM is younger and less degraded than below, such relationship is expected to be strong enough.

In Southern Norway, heathland areas are in most cases characterised by the alternate occurrence – essentially dictated by the soil drainage, in turn controlled by topography, particle size distribution, and soil depth to bedrock – of three vegetation types, which are dominated by the heather Calluna (*Calluna vulgaris* (L) Hull), the moor grass Molinia (*Molinia caerulea* (L) Moench), and the peat moss Sphagnum (*Sphagnum capillifolium* (Ehrh.) Hedw.). Such different vegetation types are cause and effect of the properties and behaviour of the underlying soil. This is undoubtedly true for the soil profile morphology and the sequence of horizons, generally ranging from the O-E-Bhs soil sequum of Calluna-sustaining podzols to multiple H horizons consisting histosols where Sphagnum grows (Strand et al., 2008).

In this study we report an *in situ* investigation of the relationships between vegetation cover, initial litter decay rate and soil organic matter composition for a typical montane heathland area in Southern Norway where the alternation between Calluna, Molinia, and Sphagnum occurs on decametric scale. The objective of the study was to assess whether in this environment the current vegetation cover is a good proxy for SOM quality and dynamics. To this end, litter decomposition was followed over a period of 1 year, by placing litterbags filled with biomass from each dominant species under each type of vegetation cover, so as to simulate the effects of possible climate change induced shift of vegetation on early stages of litter decomposition. Furthermore, the composition of the aboveground biomass and the bulk SOM were investigated by chemical methods and solid-state ^{13}C nuclear magnetic resonance (NMR) spectroscopy.

2. **Materials and Methods**

2.1. Study site

The study area, Storgama (59°02’47”N, 8°39’37”E), is located in the Telemark county, southern Norway, at an elevation of 560-m above sea level. The mean annual precipitation in Storgama for the period 1961-1990 was 994 mm, the mean annual air temperature for the same period was 5.0 °C. Approximately 30 % of the area is barren granite bedrock and boulders, and soil often occurs as pockets in depressions in the bedrock surface (Fig. 1a). The average soil depth generally varies between 10 and 35 cm but greater thicknesses, up to 100 cm, do occur. According to the U.S. Soil Taxonomy (Soil Survey Staff, 2010) and moving from drier to wetter locations, soils are Lithic Haplorthods, Lithic Udipsamments, Lithic Endoaquents, and Lithic Haplosaprists. Although there are some scattered or vaguely grouped Scots pines (*Pinus sylvestris* L) and Downy birch trees (*Betula pubescens* Ehrh), the vegetation is largely dominated by heather (*Calluna vulgaris* (L) Hull) at well drained sites, peat moss (*Sphagnum capillifolium* (Ehrh.) Hedw.) at poorly drained sites, and moor grass (*Molinia caerulea* (L) Moench) at intermediately drained sites (Figs. 1a and 1b). These dominant vegetation types are interspersed in the area, forming a patchwork dictated by topography, which in turn is a driving factor of water supply. At the Calluna sites *Calluna vulgaris* was virtually 100 % of the vegetation cover. At the Molinia sites some Calluna, Erica (*Erica tetralix* L), and Nartecium (*Narthecium ossifragum* (L) Huds) were associated with *Molinia caerulea* but, on a visual basis, amounting to no more than 5 % of the total cover. At the Sphagnum sites, *Sphagnum capillifolium* covered the entire surface except for a few scattered individuals of Molinia, Erica and Calluna. Hereafter, we will refer to such vegetation assemblages simply as Calluna, Molinia and Sphagnum, respectively. Further pictures and information on vegetation and soils at Storgama are reported in Strand et al. (2008).

2.2. Vegetation sampling and analysis

Three sampling sites per dominant vegetation were chosen within an area of approximately one hectare. At each location, three soil pits were dug down to bedrock, which was 35 to 50 cm deep. All the vegetation above the pit had been previously sampled and divided according to species. In the case of Calluna, the woody stems and branches were separated from the leaves and flowers. Capitula and the five upper centimetres were used to represent the whole Sphagnum material. Visible roots were picked out from the soil samples and separated according to species when possible. The aboveground biomass and the roots were analysed for C and N by dry combustion on oven-dried (60 °C to constant weight) and finely ground samples using a LECO® CHN1000 Analyser. The aboveground biomass also underwent NMR investigation.

2.3. Soil sampling and analysis

We focused our attention on the uppermost soil layer, where we expected the closest relationship between SOM quality and current vegetation. Two undisturbed soil samples, to be used for soil solution extraction, were taken by completely inserting 7.0 cm high and 4.6 cm in inner diameter, rigid cylinders at about five cm depth in each soil profile. The filled cylinders were carefully extracted from the soil and placed in a cooling box after sealing the ends with plastic lids. The samples were stored at 4 °C, for a maximum of one week, until they were processed further. Two standard disturbed soil samples were taken near the holes left by the cylinders and used for C, N, and pH determination, and NMR analysis. As for the plant material, soil C and N concentrations were measured by dry combustion on oven-dried and ground samples, while soil pH was determined potentiometrically in a 1:2.5 V/V distilled water suspension.

The soil-containing cylinders were inserted in two-compartment buckets and centrifuged at 4620 *g* for 20 min, following the method described by Giesler et al. (1996). The obtained solution was filtered through a 0.45 μm membrane filter (Millipore). An aliquot of the filtrate was analysed for total C (Shimadzu TOC-V element analyser) and, after oxidation by peroxodisulphate (NS4743 1975), for total N (FiaSTAR, Tecator Spectrophotometer system). Another aliquot of the filtrate was used to measure hydrophobicity, by determining the ratio between the absorbances of the solution at 285 and 254 nm using an UV-VIS spectrophotometer (UV-1201 Shimadzu). These two absorbances are, in fact, correlated to hydrophobic C (π-π^* electron transitions occur at ~285 nm for a number of aromatic substances, as described in Chin et al. 1994) and total C (Brandstetter et al., 1996), respectively.

After centrifugation the soil was immediately passed through a 2 mm-mesh sieve. Two grams of the moist sieved soil was treated as in the second step of the procedure proposed by Ghani et al. (2003) to obtain hot-water extract (80 °C for 16 h). After centrifugation for 20 min at 2,000 *g* and filtration through 0.45 μm membrane filters (Millipore), the extract was analysed for total C (HWC), total N (HWN), and carbohydrate C (Carb-C). HWC and HWN were determined by the same method as DOC and total dissolved nitrogen (TDN), while the analysis of Carb-C was done according to the “direct determination” method proposed by

Safarík and Santrucková (1992). In brief, 1 mL of the extract was combined in a polyethylene tube with 1 mL 5% phenol solution and 5 mL concentrated sulphuric acid and immediately shaken on a vortex mixer. The absorbance of the mixture was read after 1 h at 485 nm on a UV-VIS spectrophotometer (UV-1201 Shimadzu). A calibration curve was built with the following standards: 0.00, 0.05, 0.10, 0.25, 0.40 g L^{-1} of α-D glucose (R^2=0.9907).

2.5. Nuclear magnetic resonance spectroscopy

The chemical structure of the aboveground vegetation (one composite sample per dominant species, after removal of stems and coarse branches in the case of Calluna) and SOM (one composite sample per soil pit; hence, three samples per vegetation type) was investigated by solid-state ^{13}C nuclear magnetic resonance (NMR) spectroscopy using the cross polarization with magic angle spinning (CP MAS) technique. Prior to analysis, soil samples underwent 2 % HF treatment according to Skjemstad et al. (1994) in order to remove possible paramagnetic oxides, which cause broadened resonances and signal loss. NMR spectra were obtained by a Bruker AMX 300-WB spectrometer equipped with a 4 mm CP MAS probe. The operating frequencies were 300.13 and 75.47 MHz for ^{1}H and ^{13}C, respectively; the $\pi/2$ pulse was 3.4 μs on the ^{1}H channel. A contact time of 2 ms and a relaxation delay of 4 s were used. The MAS speed was set to 8 kHz and the number of scans recorded ranged between 4800 and 40000, depending on the sample. The chemical shifts were referenced to tetramethylsilane (TMS) using adamantane as external standard. Seven chemical-shift regions of the NMR-spectra, corresponding to the main C forms, were integrated and expressed as percent contribution to total area subtended by the spectrum between 0 and 220 ppm. The seven regions account for alkyl C (0-45 ppm, mainly comprising lipids, waxes, resins, suberin), methoxyl and N-alkyl C (45-60 ppm, comprising the methoxy group of guaiacyl and the two methoxy groups of syringyl lignin moieties at ~56 ppm), O-alkyl C (60-90 ppm, carbohydrates, mainly cellulose and hemicellulose, with contributions from carbohydrate carbons bonded to one oxygen), di-O-alkyl C (90-110 ppm, mainly from polysaccharides, with contributions from anomeric carbons of carbohydrates, *i.e.*, bonded to two oxygens), H- and C-substituted aromatic C (110-140 ppm), O-substituted aromatic C (140-162 ppm, mainly from lignin structures, tannins, polyphenols), and carboxyl C (162-190 ppm, esters, acids and amides); no carbonyl intensity in the 190-220 ppm region, ascribable to aldehydes and ketones, was detected.

2.6. Litter decomposition

Litter decomposition was determined *in situ* by the litterbag technique. Recently formed aboveground biomass of Calluna, Molinia, and Sphagnum (approximately, the top 5 cm), were collected at the end of the growing season in late September. This material was oven dried (35 °C to constant weight) and used for filling 10 x 12 cm nylon mesh bags (0.5-1 mm mesh), with 3.0 g Calluna, 2.0 g Molinia, or 1.0 g Sphagnum. In November, 32 litterbags of each vegetation type were installed on the surface of each sampling site, except Calluna under Sphagnum, since a substitution of Calluna by Sphagnum was judged to be highly improbable. Eight to ten litterbags per type of content were sampled from each site after 6, 9 and 12 months of decomposition. The removed litterbags were cleaned of plant remnants and other minor foreign material by gently using a soft brush, oven dried (35 °C to constant weight) and weighed for determining mass loss. Their content was thus ground and analysed for carbon and nitrogen as described for the vegetation and soil samples.

2.7. Statistics

All statistical analyses were performed using the software program SAS (SAS Institute, Inc., 1990, Cary, NC). After checking the dataset for normality and variance heterogeneity, effects of vegetation and decomposition site on soil pH and SOM were tested by one-way analysis of variance (General Linear Model, GLM). Two separate one-way ANOVAs were performed on litterbags data: one assessing differences in decomposition rate between the three litter types disregarding the dominant vegetation effect, the other assessing differences between the vegetation types disregarding the litter effect. Pairwise comparisons were done by the Tukey's Simultaneous test.

3. Results

The experimental data set indicated marked differences in composition among the dominant plant species. The C concentration in the aboveground biomass increased in the order Sphagnum<Molinia<Calluna, whereas the C/N ratio increased in the order Molinia<Sphagnum<Calluna, with most interspecific differences being significant (Table 1). Belowground, Calluna, and Molinia also showed different composition, hence reflecting the aboveground biomass (Table 1).

Concerning the soil, the measured pH values, all much below neutrality (Table 2), ensured that all C there present was in organic forms. The N content of Sphagnum was significantly higher than that of Calluna, although there were no differences in terms of C/N ratio. The latter, clustering around 20, was in all cases much smaller than the C/N ratio of the respective dominating plant species.

There was a large variability in soil DOC and TDN concentrations, and vegetation types did not show any significant difference with respect to these two variables (Table 2). On the contrary, the hydrophobicity index was significantly different in soils under the three types of vegetation, being highest for Calluna and lowest for Molinia. This difference indicates that a greater proportion of DOC under Calluna was hydrophobic. For the rest, the only other significant differences were in terms of HWN and HW-C/N ratio between Calluna, on the one hand, and Molinia and Sphagnum, on the other (Table 2).

The ^{13}C CPMAS NMR spectra of the aboveground biomass and soil are shown in Fig. 2, and the relative contributions of the different chemical shift regions are reported in Table 3. The NMR spectra of the aboveground vegetation suggested more similar compositions for Molinia and Sphagnum with respect to Calluna. The spectrum of the Calluna biomass was dominated by signals between 60 and 104 ppm, characteristic of polysaccharides; the relatively high intensity in the alkyl C region (0-50 ppm) was due to lipids and aliphatic biopolymers. The spectrum also revealed the presence of lignin and tannins, as indicated by the lignin methoxyl carbon signal at 56 ppm, and the distinct aromatic peaks at 145 and 155 ppm, typical of condensed tannins. The sharp peak at 172 ppm is normally assigned to the carboxyl C of hemicellulose esters, but may also have contributions from amides (Forte et al., 2006). The spectra of Molinia and Sphagnum aboveground biomasses showed the same dominant polysaccharide features of Calluna in the 50-110 ppm range, but a significantly lower intensity of signal in the alkyl and aromatic C regions, which means lower contribution of lipids and lignin/tannins, respectively. In the case of Molinia, the slightly narrower signals in the 60-100 ppm region and the relatively smaller peak shoulder at about 103 ppm compared with both Calluna and Sphagnum, suggested the occurrence of less hemicellulose and some crystalline cellulose, respectively. Sphagnum did not show the typical lignin signals, in agreement with the common lignin-free composition of bryophytes (Kļaviņa et al., 2012). The only aromatic signals in the sphagnum spectrum were due to unsubstituted or C-substituted aryl C at 130 and 117 ppm, while the signal at 158 ppm was ascribable to phenolic structures. In the case of Calluna, the two sharp tannin peaks at 145 and 155 ppm observed in the aboveground biomass spectrum were totally absent in the SOM spectrum. In the case of Molinia, differently from the other two vegetation types, the relative contribution of aromatic C significantly increased in soil compared to that observed in the aboveground biomass. In the case of Sphagnum, no major changes occurred in the aromatic region, except for the absence in the soil spectrum of the signal at 158 ppm detected for the aboveground vegetation (Fig. 2). The alkyl C/O-alkyl C ratio increased for all vegetation types on passing from the intact biomass to its decomposition products in soil (Table 3), with large differences in absolute values between Calluna, on the one side, and Molinia and Sphagnum, on the other side.

The *in situ* decomposition study using litterbags showed that the litter mass remaining after one year of decomposition varied between 62 and 66% in the case of Molinia and Calluna and 83 and 94% for Sphagnum (Fig. 3). The discrepancy between the couple Calluna-Molinia and Sphagnum was lower, although significant, in the intermediate stages of the experiment. After six months, Calluna showed significantly lower mass loss than Molinia under itself, while at the end of the experiment Calluna resulted to be better preserved than Molinia only under Molinia (Fig. 3).

In terms of relative C content of the residual litter, Calluna did not change throughout the 12 months of the experiment, while Molinia and Sphagnum experienced a marked decrease compared to the original value (Fig. 4). Relative concentrations of N in the litter changed more than the C ones. Except for Sphagnum under itself or under Molinia, all litters increased their N content from November to May; later, all of them increased until August, with the exception of Sphagnum under Calluna and Molina under itself; finally, in the period from August to November, N concentration continued to increase in Calluna, whereas it decreased in Molinia and showed an irregular trend in Sphagnum (Fig. 4). These C and N trends implied progressive, although slight, decrease in C/N ratio for Calluna and Sphagnum, and a sharper decrease for the same ratio for Molinia until August, after which it increased (Fig. 4). Contrary to Calluna and Sphagnum, Molinia degraded maintaining significantly higher values of C/N ratio under Sphagnum than under the other types of vegetation (Molinia and

Calluna). At the end of the experiment, in November, the C/N ratio in Molinia under Sphagnum was even higher than the original value.

4. Discussion

In the heathland environment of Storgama, the composition of SOM appeared to partly reflect that of the parent vegetation. Hence, for example, the abundance in alkyl C in the Calluna biomass relative to the other two vegetation types was transferred to the SOM. Nevertheless, SOM accumulated over a long period of time; as a consequence, it could be the result of multiple changes in vegetation cover in the area and, thus, be partly unrelated to the current vegetation cover. Actually, there was no direct or indirect evidence in this regard, but inputs of wind-blown or water-transported material cannot be excluded at any site.

Sphagnum showed a composition potentially more prone to decay than Calluna and Molinia. Nevertheless, there were no significant differences in the SOM content of the topsoil of the three vegetation covers. Evidently, the prevailing anoxic conditions limited decomposition at the Sphagnum sites. This is in accordance with several studies that used the type of vegetation cover as a proxy for carbon dynamics, based on the consideration that vegetation chiefly reflects the soil moisture regime (Bridgham et al., 2008; Couwenberg et al., 2011; Delarue et al., 2011), which is in turn a driving factor of litter decomposition (Hobbie et al., 2000; Laiho 2006). Large variability in DOC concentrations and no significant effect of vegetation was observed (Table 2). It must be noted, however, that our study shows the conditions only at one sampling occasion, *i.e.* at the end of the growing season, when DOC concentrations are affected by a considerable contribution from senescing plant material. The measured DOC concentrations were generally in agreement with those recorded in autumn using zero tension lysimeters in soils at Storgama and other Norwegian heathland areas (Strand et al., 2002; Vestgarden et al., 2010), although DOC concentrations in centrifuged and freely drained soil solutions are not directly comparable (Giesler et al., 1996). Similarly to DOC, TDN showed a large variability and no apparent correlation with vegetation. The relatively small amount of water extracted by centrifugation limited the number of possible analyses, preventing N speciation. TDN therefore included both organic N and inorganic N, the latter amounting to 25-50% of TDN in soil water from southern Norway (Austnes et al., 2008; Kaste et al., 2008).

The hydrophobicity index of soil water differed significantly among vegetation types. Apparently, Calluna released DOC with the highest proportion of hydrophobic organic compounds, perhaps mostly arising from tannins and decomposition of lignin (Dilling and Kaiser, 2002), which are indeed important components of the Calluna litter (Fig. 2).

Hot water C approximately amounted to 4.5% of SOC in all samples, irrespective of vegetation. This percentage is in the range reported by von Lützow et al. (2007). Significantly lower amounts of HWN were extracted from the Calluna soils compared to the Molinia and Sphagnum ones, which also implied significantly higher HWC / HWN-ratio for Calluna (Table 2). We did not partition HWN, however Curtin et al. (2006) demonstrated that it is mainly organic and, in suborder, NH_4-N generated by hydrolysis of heat-labile organic N. The quality of the hot water extract rather well discriminated Calluna from Molinia and Sphagnum. Some authors have proposed hot water extraction of SOM as a method to measure the labile SOM pool (Chodak et al., 2003; Ghani et al., 2003; Curtin et al., 2006); however, other authors consider this method not selective enough for this purpose (Landgraf et al., 2006; von Lützow et al., 2007). In our case, approximately half the C extracted by hot water belonged to carbohydrates.

The NMR spectra showed clear structural differences in aboveground plant material (Fig. 2 and Table 3). In particular, Calluna was richer in alkyl C and poorer in O-alkyl C than Molinia and Sphagnum, as well reflected in the alkyl C / O-alkyl C ratio. The richness in alkyl C has been correlated to slow decomposition rates in heathland ecosystems (van Vuuren and van der Eerden, 1992; van Vuuren and Berendse, 1993). However, in our litterbags experiment there were little and variable differences between the mass losses of Calluna and Molinia, and both of them were much higher than the one in Sphagnum wherever the latter was placed (Fig. 3). A possible explanation for such short-term resistance of Sphagnum to degradation could be that this type of vegetation is particularly rich in sphagnan pectin-like polysaccharides, which, unlike the other types of polysaccharides, induce processes that prevent organic matter decay (Hájek et al., 2011; Ballance et al., 2012). Moreover, it must be considered that Sphagnum might have experienced a "non-additive" pattern of mass loss, *i.e.* a decomposition behaviour sometimes observed in litter mixes that deviates from the response predicted for the individual species because of the influence of the other species present in the mix (Gartner and Cardon, 2004). In this case, the necromasses of Molinia and, in particular, Calluna could have partly inhibited the decomposition of the Sphagnum in the litterbags.

In addition to a "vegetation effect", the litterbags experiment showed some "site effect", *i.e.* more rapid decomposition when litter was placed beneath the parent vegetation rather than beneath other species (Ayres et al., 2009; Perez et al., 2013; Wang et al., 2013). In fact, for Sphagnum the mass loss was significantly lower when it decayed under Calluna than under Molina or Sphagnum (Fig. 3). Calluna was better preserved under Molinia than under itself at the end of the trial, while, after six months only, Molinia litter showed significant environment-induced advantage under Sphagnum compared to under itself (Fig. 3). Unexpectedly, the well drained Calluna soils preserved Sphagnum and Molinia from decay better than the moister soils where they were growing, perhaps as an effect of a seasonal drought.

The enclosure of litter inside mesh bags may actually change its overall decomposition rate and its C and N percent concentrations compared to non-bagged substrate (Berhe, 2013). However, we must confidently assume that in our experiment such a bagging effect is uniform through the samples, also because the bags are very similar. On this basis, Molinia showed an initial C/N ratio much higher than the ones of Calluna and, especially, Sphagnum (Fig. 4), which suggested a more marked intrinsic resistance of Molinia to decay. Noteworthy is the difference in C/N ratio between the aboveground Molinia biomass analysed for basic characterisation (data of Table 1) and the Molinia used in the litterbags experiment (30 vs. circa 80). Actually, Molinia is a grass that wilts at the end of the growing season, when we sampled the material to be inserted in the bags, while the Molinia sampled for basic characterisation was still with active photosynthesis, when the C/N ratio is relatively low (Taylor et al., 2001). On the other hand, Calluna is an evergreen and no great seasonal changes in C and N concentrations occur, while Sphagnum, although it is not an evergreen, does not wilt and its C/N ratio is rather constant throughout the year. Our litterbags experiment showed that the C/N ratio is a poor predictor of decay in this environment. The anoxic conditions imposed by prolonged water saturation, commonly occurring in the Sphagnum soils and expected to have considerable influence in slackening litter decomposition, on the contrary appeared to be irrelevant in preserving organic residues during a 1-year long experiment (Fig. 3). In this regard, during a 3-year study in heathlands on *Molinia caerulea* and *Erica tetralix*, van Vuuren and Berendse (1993) did not find any site effect and litter quality appeared to be the sole driving factor. Also Scheffer et al. (2001), studying the decomposition process in fens dominated by Sphagnum species or without Sphagnum, concluded that decomposition was controlled more by intrinsic differences in litter quality than by the environment.

The NMR investigation revealed that soils, compared to the litter they receive, showed significantly higher contribution of alkyl C and lower contribution of O-alkyl C (Fig. 2 and Table 3), most probably as a result of a faster decay of carbohydrates than of other C forms and the synthesis of lipids from the biodegradation of carbohydrate and aromatic fractions (Baldock et al., 1992). The alkyl C / O-alkyl C ratio, which generally increases as decomposition proceeds, was significantly higher in the Calluna soil than under Molinia and Sphagnum.

5. Conclusions

We found that in the varied heathland of Storgama there were many significant differences in terms of SOM composition between the Calluna dominated areas and the interspersed Sphagnum-covered areas. Most differences were clearly due to the litter quality. A “vegetation effect” on the early stage of litter decomposition rate was clear, Sphagnum remnants being much more stable independently of the environmental conditions they underwent, which differed especially in terms of soil drainage. Hence, overall, vegetation appeared to be a good proxy for SOM quality. On this basis, monitoring the distribution of vegetation types in heathlands of Norway and elsewhere could be of particular interest for assessing the consequences of climate change on SOM stocks and dynamics. In the plausible scenario of a less continuous rainfall supply and a consequent contraction of Sphagnum-covered areas, the Sphagnum-released litter seems to have good short-term ability to resist decomposition under the two replacing types of vegetation, Molinia and Calluna. Long-term experiments addressing this issue are needed.

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Figures captions:

Figure 1. a) A general view of the study area, Storgama, showing soil occurring in pockets and small depressions at the bedrock surface; note that close up vegetation at the bottom right is dominated by *Molinia caerulea* (L), the understorey of pines beyond is *Calluna vulgaris* (L) Hull, the basin in the background is covered by *Sphagnum* spp. **b**) A rare coalescence of the three dominant species, *Calluna vulgaris*, on the left, *Sphagnum* spp. L, at the bottom, and *Molinia caerulea*, on the right.

Figure 2. ^{13}C CPMAS NMR spectra of the aboveground biomass of the dominant plant species and soil.

Figure 3. Residual mass in the litterbags as a function of time for different combinations of litter and vegetation cover. Cal in Cal means *Calluna* litter decomposing under *Calluna*, Cal in Mol means *Calluna* litter decomposing under *Molinia*, and so on. Error bars are standard deviations, while lower case letters indicate significant differences ($p<0.05$) between same litters decomposing under different types of vegetation. The trial was one year long.

Figure 4. Carbon and nitrogen concentrations and C/N ratio in decaying biomass in the litterbags as a function of time for different combinations of litter and vegetation cover. Cal in Cal means *Calluna* litter decomposing in soil under *Calluna*, Cal in Mol means *Calluna* litter decomposing under *Molinia,* and so on. Upper case letters indicate significant differences ($p<0.05$) between different litters, whereas lower case letters indicate significant differences between same litters decomposing in soils covered by different types of vegetation.

Fig 1 a, b

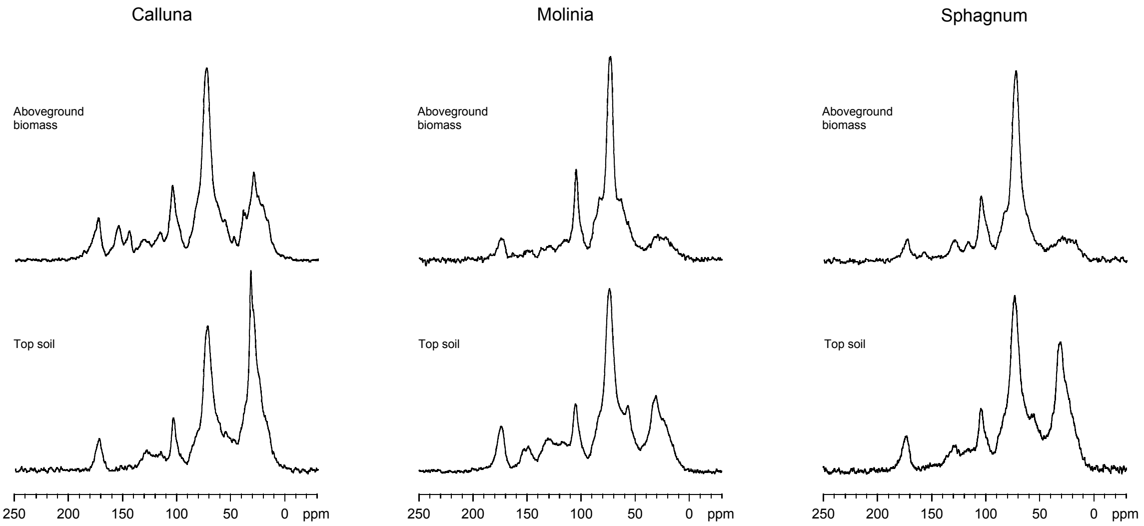
Calluna
Molinia
Sphagnum
Aboveground biomass
Aboveground biomass
Aboveground biomass
Top soil
Top soil
Top soil
250
200
150
100
50
0
ppm
250
200
150
100
50
0
ppm
250
200
150
100
50
0
ppm

Fig. 2

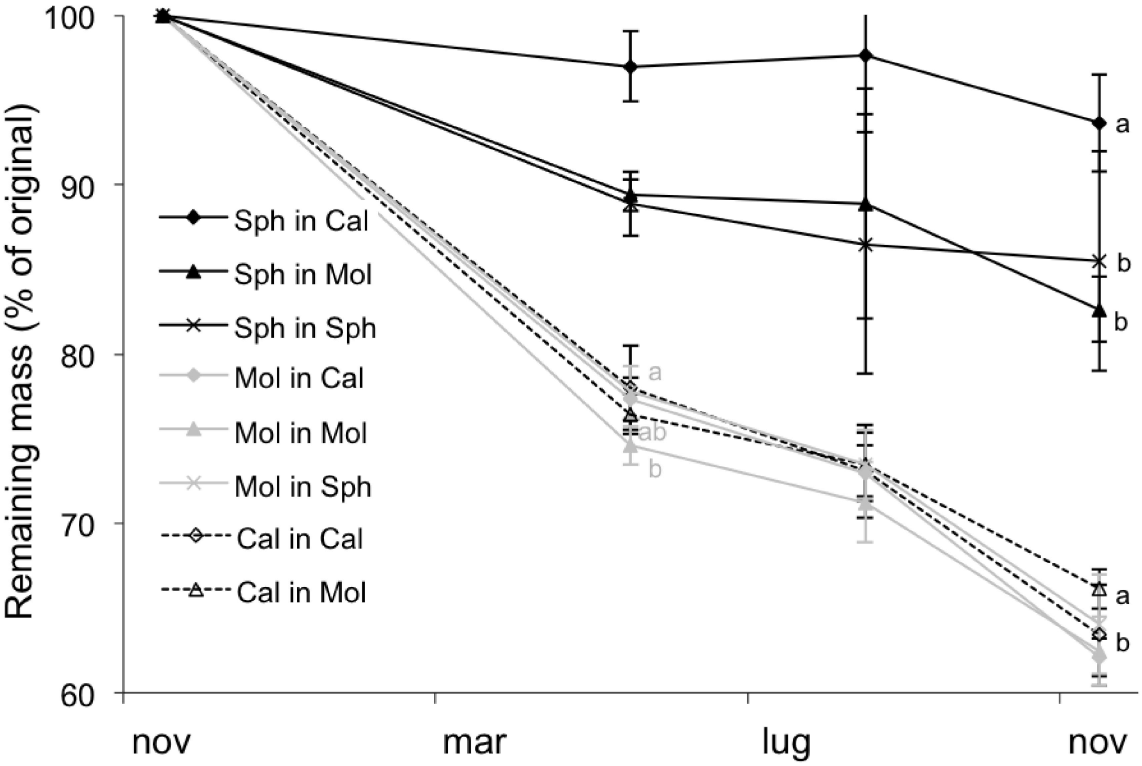
100
90
80
70
60
Remaining mass (% of original)
nov
mar
lug
nov
Sph in Cal
Sph in Mol
Sph in Sph
Mol in Cal
Mol in Mol
Mol in Sph
Cal in Cal
Cal in Mol
a
b
b
a
ab
b
a
b

Fig. 3

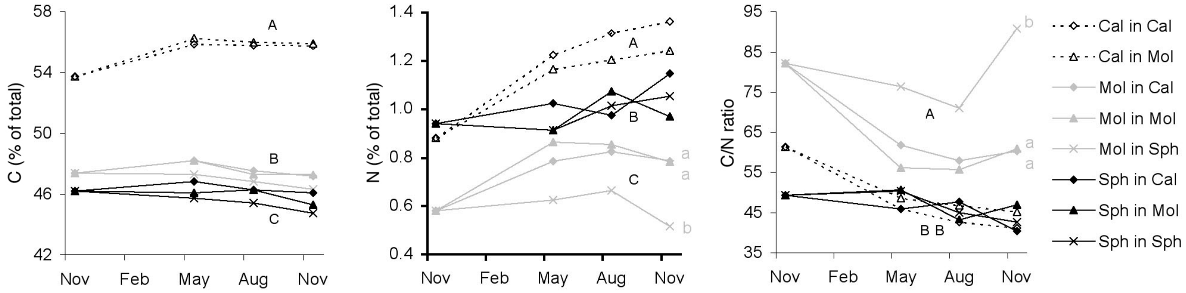
58
54
50
46
42
C (% of total)
A
B
C
Nov
Feb
May
Aug
Nov
1.4
1.2
1.0
0.8
0.6
0.4
N (% of total)
A
B
C
a
a
b
Nov
Feb
May
Aug
Nov
95
85
75
65
55
45
35
C/N ratio
A
B B
b
a
a
Nov
Feb
May
Aug
Nov
Cal in Cal
Cal in Mol
Mol in Cal
Mol in Mol
Mol in Sph
Sph in Cal
Sph in Mol
Sph in Sph

Fig. 4

Table 1. Carbon and nitrogen concentrations and C/N ratio of the dominant plant species in the Storgama area. Values in parentheses are standard deviations of six independent replicates. Lower case letters indicate significant differences ($p<0.05$), with above and below ground vegetation treated separately.

Vegetation	C	N	C/N ratio
	g kg^{-1}	g kg^{-1}	
Aboveground:			
Calluna leaves and flowers	536.0 (3.2) a	9.3 (1.0) b	58.3 (5.8) b
Calluna stems and branches	522.6 (4.8) b	3.9 (0.2) c	135.6 (6.2) a
Molinia	487.0 (0.9) c	16.8 (4.1) a	30.3 (7.2) d
Sphagnum	473.9 (9.3) d	11.6 (1.2) b	41.4 (5.0) c
Belowground:			
Calluna roots	528.6 (15.6) a	9.2 (2.6) b	60.4 (13.6) a
Molinia roots	499.9 (5.4) b	15.6 (5.2) a	36.4 (15.5) b

Table 2. Selected properties of the topsoil according to dominant vegetation. Values in parentheses are standard deviations of six independent replicates. Lower case letters indicate significant differences ($p<0.05$).

		Calluna		Molinia		Sphagnum	
pH		4.2 (0.2)		4.3 (0.1)		4.3 (0.0)	
SOC	g kg^{-1}	373.6 (140.9)		436.8 (101.4)		459.1 (7.3)	
SON	g kg^{-1}	16.3 (7.0)	b	22.3 (3.1)	ab	25.7 (5.0)	a
C/N-ratio soil		24 (5)		20 (2)		19 (4)	
DOC	mg L^{-1}	86.0 (49.2)		174.5 (138.3)		53.5 (47.5)	
TDN	mg L^{-1}	4.4 (3.7)		9.9 (9.9)		3.4 (3.0)	
C/N-ratio soil solution		23 (7)		27 (19)		16 (3)	
Hydrophobicity index		0.772 (0.014)	a	0.692 (0.021)	b	0.740 (0.01	c
HWC	g kg^{-1}	16.3 (6.5)		20.7 (8.4)		20.7 (7.8)	
HWN	g kg^{-1}	0.68 (0.34)	a	1.43 (0.64)	b	1.54 (0.31)	b
HWC/N-ratio		26 (7)	a	15 (3)	b	13 (4)	b
HWcarb–C	g kg^{-1}	8.6 (3.9)		11.1 (5.0)		10.1 (3.8)	
HWcarb–C/HWC	%	52 (4)		52 (11)		49 (7)	

SOC = soil organic carbon; SON = soil organic nitrogen; DOC = dissolved organic carbon; TDN = total dissolved nitrogen; Hydrophobicity index = hydrophobicity index of soil solution; HWC = carbon in the hot-water extract; HWN = nitrogen in the hot-water extract; HWC/N-ratio = carbon to nitrogen ratio in the hot-water extract; HWcarb–C = carbohydrate carbon in the hot-water extract; HWcarb–C/HWC = percent carbohydrate carbon to total carbon in the hot-water extract.

Table 3. Relative intensities, expressed as per cent of total area between 0 and 190 ppm, of seven main chemical shift regions of CP MAS ^{13}C NMR spectra and the ratio between the Alkyl C and the O-alkyl C related signals for aboveground vegetation and topsoil.

Vegetation	Sample	Alkyl C (0-45 ppm)	Methoxyl and N-alkyl C (45-60 ppm)	O-alkyl C (60-90 ppm)	di-O-alkyl C (90-110 ppm)	H-, C-substituted aromatic C (110-140 ppm)	O-substituted aromatic C (140-162 ppm)	Carboxyl C (162-190 ppm)	Alkyl C/O-alkyl C (0-45 ppm/60-110 ppm)
Calluna	Aboveground	24	6	39	11	7	7	6	0.5
	Top 10-cm soil*	42 ± 1	8 ± 1	29 ± 3	7 ± 1	8 ± 1	2 ± 1	4 ± 1	1.2 ± 0.1
Molinia	Aboveground	12	8	51	14	8	3	4	0.2
	Top 10-cm soil*	28 ± 5	9 ± 1	33 ± 4	8 ± 1	11 ± 1	5 ± 1	6 ± 1	0.7 ± 0.2
Sphagnum	Aboveground	13	7	51	14	8	2	5	0.2
	Top 10-cm soil*	30 ± 10	7 ± 2	36 ± 10	8 ± 2	9 ± 1	3 ± 1	7 ± 2	0.7 ± 0.3

* These values are means of three independent samples±standard deviation