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

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Abstract

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, Molinia, or Sphagnum. 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 under each type of vegetation cover. The composition of the living biomass, the bulk SOM and some extractable fractions of 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 modifications in the SOM potential to last induced by climate change.

1 Introduction

Heathland vegetation covers approximately 60 % of Norway's ice-free land. 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 the Norwegian C balance and the water quality of lakes and rivers. This consideration is valid also at a larger scale, since heathlands represent a significant portion of the northern regions of America, Europe, and Asia.

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). In some environments, however, 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 humification processes (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 water rich 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 and soil depth to bedrock – of three vegetation types, which are dominated by the heather *Calluna*, the moor grass *Molinia*, and the peat moss *Sphagnum*. 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 forming histosols where Sphagnum grows (Strand et al., 2008). Field studies on the 0–10 cm depth interval revealed that DOC and dissolved organic nitrogen (DON) concentrations increased in the order Sphagnum < Molinia < Calluna in spite of the similar SOM content (Vestgarden et al., 2010). Laboratory experiments with intact soil columns finally showed that milder winters cause a decrease in the release of CO_2, DOC, DON and ammonium (NH_4^+) compared to winters with severe frost, and that the soil loss of CO_2, DOC, DON and NH_4^+ is highest under Molinia and lowest under Sphagnum, with Calluna in between (Vestgarden and Austnes, 2009). Relatively little work has focused on the solid phase of SOM in these environments, most of the research having chiefly focused on SOM storage (e.g., Berendse et al., 1994; Kopittke et al., 2013).

In the present study we report an in situ investigation of the relationships between vegetation cover, 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 litter decomposition rate. Furthermore, the composition of the aboveground biomass, the bulk SOM and some extractable fractions of 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 occurs as pockets in small 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 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* spp. L) at poorly drained sites, and moor grass (*Molinia caerulea* (L) Moench) at intermediately drained sites (Fig. 1a and b). These dominant vegetation types are interspersed in the area, forming a patchwork dictated by topography, which in turn is a driving factor of soil water supply. At the Calluna sites Calluna was virtually 100 % of the vegetation cover. At the Molinia

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sites some *Calluna*, Erica (*Erica tetralix* L), and Nartecium (*Narthecium ossifragum* (L) Huds) were associated with Molinia but, on a visual basis, amounting to no more than 5 % of the total cover. At the Sphagnum sites, Sphagnum 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, Sphagnum and Molinia, respectively. Further pictures and information on vegetation and soils at Storgama are reported in Strand et al. (2008).

2.2 Vegetation and soil sampling

Three sampling sites per dominant vegetation were chosen within an area of about a couple of hectares. At each location, we sampled the living biomass of the dominant vegetation within approximately a square meter. 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. At the same places a soil pit was opened to check the depth to bedrock, which varied from 35 to 50 cm. We focused our attention on the uppermost soil layer, where we expected the closest relationship between SOM quality and the current vegetation. Undisturbed soil samples, to be used for extraction of the circulating solution, were taken by completely inserting 7.0 cm high and 4.6 cm in inner diameter, rigid cylinders into the ground, after litter removal. The filled cylinders were carefully extracted from the soil and, once the ends were sealed with plastic lids, placed in a cooling box. Two replicates each profile were collected giving a total of 18 cylinders. The samples were stored at 4 °C, for a maximum of one week, until they were processed further. Disturbed soil samples were taken adjacently to the holes left by the cylinders and were used for determining soil C, N, and pH, and for performing NMR analyses of SOM.

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2.3 Soil water analysis

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 filter. One 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). These C and N fractions were assumed to represent DOC – since inorganic C was not compatible with the low pH of these soils – and total dissolved N (TDN), respectively. 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 ($\pi - \pi^*$ 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 2000 g and filtration through 0.45 µm filters, 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 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 $\mathrm{g\,L^{-1}}$ of α-D glucose ($R^2 = 0.9907$).

2.4 Total C, N and pH analysis

Aboveground vegetation and soil samples were oven-dried (60 °C) to constant weight and finely ground to be analysed for C and N by dry combustion using a LECO® CHN1000 Analyser. Soil pH was determined potentiometrically in a 1 : 2.5 V/V distilled water suspension.

2.5 Nuclear magnetic resonance spectroscopy

The chemical structure of the aboveground vegetation (one composite sample per dominant species) and SOM (one composite bulk soil sample per profile, hence three 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 paramagnetic iron 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 40 000, 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 per cent 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), di-O-alkyl C (90–110 ppm, mainly from polysaccharides), H- and C-substituted aromatic C (110–140 ppm), O-substituted aromatic C (140–160 ppm, mainly from lignin

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structures, tannins, polyphenols), and carboxyl C (160–190 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. Twigs of Calluna, leaves of Molinia, and Sphagnum capitula were collected at the end of the growing season in late September. This material, which represented the most recently formed biomass, was dried at 40 °C and used for filling 10 × 12 cm nylon netting bags (0.5–1 mm mesh), with 3.0 g Calluna, 2.0 g Molinia, or 1.0 g Sphagnum, respectively. The Calluna and Molinia material had to be cut into pieces smaller than 6 cm to fit into the bags. In November, 32 litterbags of each litter type were installed on the ground at each sampling site (reciprocal experiment design), except for 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 foreign material, dried at 40 °C to initial moisture 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). Effects of vegetation and decomposition site on soil pH and SOM were tested by analysis of variance (General Linear Model, GLM). Pairwise comparisons were done by the Tukey's Simultaneous test.

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3 Results

Analysis of the initial litter material confirmed that there were marked differences in composition between vegetation types. The C concentration in the biomass increased significantly in the order Sphagnum < Molinia < Calluna, whereas the C / N ratio increased in the order Molinia < Sphagnum < Calluna (Table 1), suggesting a parallel increase in intrinsic recalcitrance to decomposition. Belowground, Calluna, and Molinia mimicked the composition of the aboveground biomass (Table 1), which is a sort of guarantee about the fact that using the above biomass only, and not the roots as well, does not lead to major errors in the litterbags experiment.

Concerning the soil, the measured pH values, all much below neutrality (Table 2), ensured that all C there measured was in organic forms. We can not exclude that part of the measured N was inorganic N, namely NH_4^+ fixed in the interlayer of micas, which are abundant in granitic bedrocks. Assuming that all N is organic, the C / N ratio of the SOM was higher under Calluna than under the other two vegetation types, hence reflecting the trend observed for the aboveground biomass. However, it must be noted that, in the case of SOM, the differences among vegetation types were much smaller than between their biomasses, and, anyway, they were not statistically significant.

Soil properties under different vegetation types were fairly similar, except for Calluna, which differed significantly from Molinia and Sphagnum in terms of SON, HWN and HW-C/N ratio (Table 2).

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 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.

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

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compositions for Molinia and Sphagnum with respect to Calluna. The spectrum of the Calluna biomass is dominated by signals between 60 and 104 ppm, characteristic of polysaccharides; the relatively high intensity in the alkyl C region (0–50 ppm) is 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 with respect to both Calluna and Sphagnum, suggested respectively the occurrences of less hemicellulose and some crystalline cellulose. 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. Overall, the NMR investigation revealed that Calluna and the related SOM were richer in alkyl C and poorer in O-alkyl C than the corresponding specimens from Molinia and Sphagnum (Fig. 2 and Table 3). NMR spectra also revealed that the residues of all three dominant plants, once in soil, experienced a significant increase in the alkyl C contribution and a concomitant decrease in the O-alkyl C one, most probably as a result of a faster decay of carbohydrates than of other C forms and the synthesis of alkyl carbon from the biodegradation of carbohydrate and aromatic fractions (Baldock et al., 1992). Noteworthy differences in the spectral features between the aboveground biomass and soil were observed in the aromatic region as well. 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. 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 Sphagnum on the one hand, and Calluna and Molinia on the other, were lower but 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 if it was 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 drastic 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 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). Significant site effect in terms of C / N ratio were observed for the Molinia litter only, with significantly higher values under Sphagnum than under 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 SOM chemical structure appeared to partly maintain memory of the original composition of the parent vegetation. Hence, for example, the abundance in alkyl C in the Calluna biomass relative to the other two vegetation types was reflected in the SOM. Nevertheless, the accumulated SOM could be the result of multiple changes in vegetation cover in the area, hence, partly unrelated to the current vegetation cover, although there is no direct or indirect evidence in this regard. Furthermore, input of wind-blown or water-transported material could not be excluded at any site.

Sphagnum showed a composition potentially more prone to decay than Calluna and Molinia. Nevertheless, the topsoil associated to Sphagnum was richer in SOM than the ones supporting the other vegetation types, which is clearly a result of the prevailing anoxic conditions under Sphagnum. 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). Soil drainage is of course also a driving factor of decomposition processes and, thus, of both SOM quantity and quality. 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). As for DOC, total dissolved nitrogen (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 between vegetations. 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), but is much lower than that reported by Wieder and Starr (1998) for sphagnum peat soils. 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, except in the Sphagnum soils, where this proportion was lower.

The NMR spectra showed clear structural differences in the initial litter quality (Fig. 2 and Table 3), which led to expect some discrepancy in decomposition rate between vegetations. In particular, the Calluna biomass, was characterised by an intense signal of lipids, which has been correlated to slow decomposition rates in heathland ecosystems (van Vuuren and van der Eerden, 1992; van Vuuren and Berendse, 1993). The alkyl C / O-alkyl C ratio, which generally increases as decomposition proceeds due to both a prevailing decrease in carbohydrates (O-alkyl C) and a release of hydrophobic by-products of decomposition (alkyl C), was significantly higher under Calluna than under Molinia and Sphagnum. Hence, on the basis of the NMR spectra, Calluna appeared to be potentially more recalcitrant to decomposition than Molinia and Sphagnum. However, this was not confirmed by our litterbags experiment, where 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 it was placed (Fig. 3). A possible explanation for the intrinsic resistance of Sphagnum could be that, in this type of vegetation, a consistent portion of polysaccharides are sphagnan pectin-like, which, unlike the rest of polysaccharides, are hard to decompose (Verhoeven and Toth, 1995; Scheffer et al., 2001; Hajek et al., 2011).

In addition to a “vegetation effect”, the litterbags experiment showed some “site effect” or “home-field advantage”, i.e. more rapid decomposition when litter was placed beneath the plant species it derived from than beneath a different plant 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 Molinia litter showed significant environment-induced advantage under Sphagnum compared to under itself just after six months of trial (Fig. 3). Unexpectedly, the largely oxidising Calluna soils preserved Sphagnum and Molinia from decay better than the moister soils where they were growing. This finding leads to hypothesise the action of some antibiotic substances from Calluna. In this regard, Handley (1963) in his investigations on the suppression of tree growth on Calluna heathland found in the raw humus some water soluble-substances that inhibited the development of mycorrhizal hymenomycetes. Since the inhibiting factor seemed to be associated with the Calluna roots, the author suggested an endophyte in the roots as the excretory agent of the antibiotic substances.

In our litterbag experiment, 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 its tissues 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,

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Molinia is a grass that wilts at the end of the growing season. The Molinia sampled for basic characterisation was still with active photosynthesis, i.e. when the C / N ratio is in fact much lower than in the later period, when Molinia was sampled for filling the litterbags and it had already wilted. On the other hand, Calluna is an evergreen and no great difference in C and N concentrations occurs through the season, while sphagnum does not fall in the group of evergreens but does not wilt and its C / N ratios does not show great seasonal variations. Anyway, an outcome of the litterbags experiment is that the C / N ratio is not a powerful enough predictor of decay, and evidently other compositional variables and environmental factors play a major role. The anoxic conditions imposed by prolonged water saturation, commonly offered by the Sphagnum soils and expected to have considerable influence in slackening litter decomposition, actually appeared to be irrelevant in preserving organic residues during our one-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. Scheffer et al. (2001) studied how the decomposition process in fens is influenced by the transition from a vascular plant-dominated system to a Sphagnum-dominated system. To this end, they carried out a two-year long reciprocal litterbag experiment using *Carex diandra*, *C. lasiocarpa*, *Sphagnum papillosum* and *S. squarrosum* in a fen dominated by Sphagnum species and a fen without Sphagnum. The decomposition rate hardly differed between the two sites and was highest for the Carex litter types and lowest for the Sphagnum ones, indicating that decomposition was controlled more by intrinsic differences in litter quality than by the environment.

5 Conclusions

We found that in the variegated 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 quality of parent vegetation. A “vegetation effect” on litter decomposition rate was clear, Sphagnum remnants being much more refractory independently of the environmental conditions they underwent, which varied 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 environmental changes such as global warming and higher concentration of rainfall 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 ability to resist decomposition under the two replacing types of vegetation, Molinia and Calluna, at least over a relatively short term. Medium to long-term experiments addressing this issue are needed.

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Table 1. Carbon and nitrogen concentrations and C/N ratio of the dominant plant species in the Storgama area. The material was sampled in early autumn with still active photosynthesis. Values in parentheses are standard deviations of six independent replicates.

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

Table 2. Selected topsoil properties 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	$\mathrm{g\,kg^{-1}}$	373.6 (140.9)	436.8 (101.4)	459.1 (73.0)
SON	$\mathrm{g\,kg^{-1}}$	16.3 (7.0)^{b}	22.3 (3.1)^{ab}	25.7 (5.0)^{a}
soil C / N-ratio		24 (5)	20 (2)	19 (4)
DOC	$\mathrm{mg\,L^{-1}}$	86.0 (49.2)	174.5 (138.3)	53.5 (47.5)
TDN	$\mathrm{mg\,L^{-1}}$	4.4 (3.7)	9.9 (9.9)	3.4 (3.0)
C / N-ratio soil water		23 (7)	27 (19)	16 (3)
Hydrophobicity index		0.772 (0.014)^{a}	0.692 (0.021)^{b}	0.740 (0.015)^{c}
HWC	$\mathrm{g\,kg^{-1}}$	16.3 (6.5)	20.7 (8.4)	20.7 (7.8)
HWN	$\mathrm{g\,kg^{-1}}$	0.68 (0.34)^{a}	1.43 (0.64)^{b}	1.54 (0.31)^{b}
HWC / HWN-ratio		26 (7)^{a}	15 (3)^{b}	13 (4)^{b}
HWcarb–C	$\mathrm{g\,kg^{-1}}$	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 water; 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.

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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)	Carbonyl 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.

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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.

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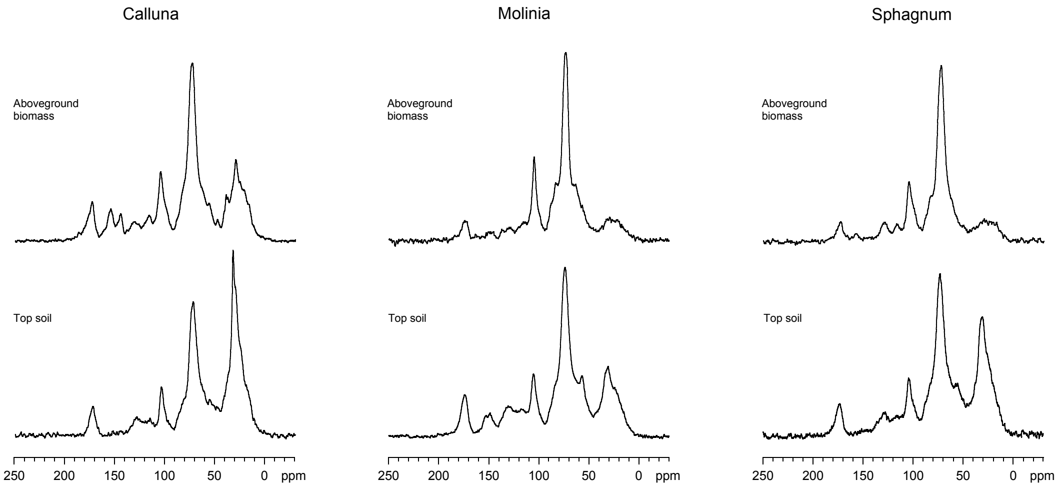

Figure 2. ^{13}C CPMAS NMR spectra of the aboveground biomass of the dominant plant species and the underlying soil.

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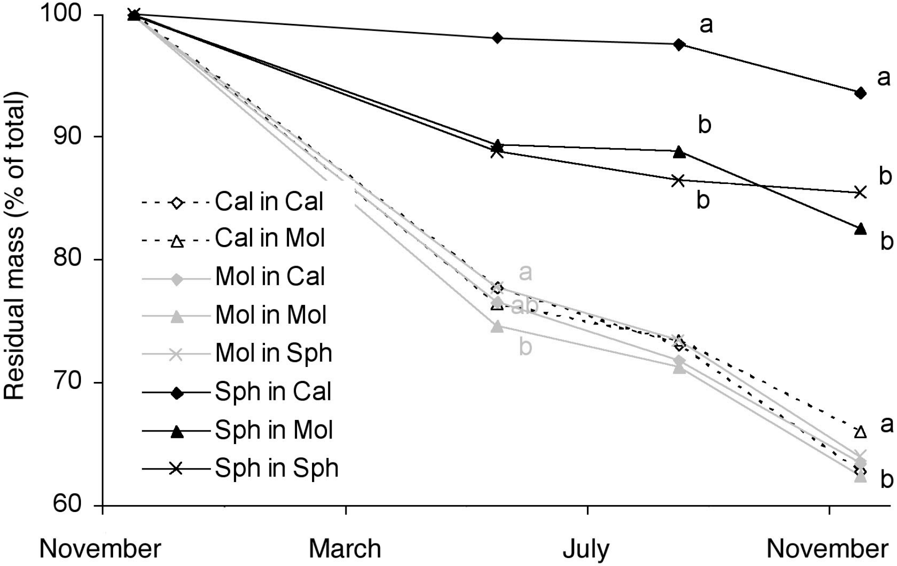

Figure 3. Residual mass in buried litterbags as a function of time for different combinations of litter and vegetation cover. Cal in Cal means *Calluna* litter decomposing in soil under *Calluna*, Cal in Mol means *Calluna* litter decomposing in soil under *Molinia*, and so on. Lower case letters indicate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

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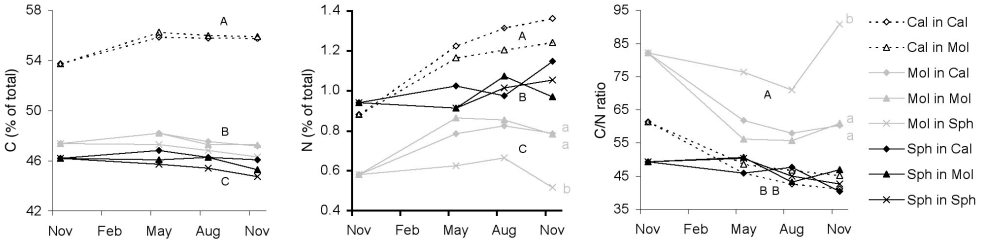

Figure 4. Carbon and nitrogen concentrations and C / N ratio in decaying biomass of the trial of Fig. 4 as a function of time for different combinations of litter and vegetation cover. Cal in Cal means *Calluna* litter decomposing in soil under *Calluna*, Cal in Mol means *Calluna* litter decomposing in soil 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.