

A microbial biomass and respiration of soil, peat and decomposing plant litter in a raised mire

S. Hall¹, D.W. Hopkins²

¹*Biological and Environmental Sciences, University of Stirling, Stirling, UK*

²*Royal Agricultural University, Cirencester, Gloucestershire, UK*

ABSTRACT

We have compared microbial biomass and respiration rates in soils and decomposition of peat materials from the different components of a raised mire system. The microbial biomass in the lagg fen was not greater than that of the mineral soil or the mire expanse, but the respiration rate of the decomposer organisms in the lagg fen exceeded that of either the mire expanse or surrounding mineral soils. The respiration rate of microorganisms in litter recovered from litter bags in the lagg fen was greater than that in the mire expanse, and the microbial biomass of the litter was greater for the lagg fen than for either the mineral soil or the mire expanse. Further, the litter from minerotrophic plants decomposed faster than the ombrotrophic species.

Keywords: carbon; decay; peatland; *Sphagnum*

Globally there is about 1.4×10^{12} t carbon (C) in soils and peats, an amount that exceeds the total amount of C in the terrestrial biomass and the atmosphere combined and peatlands in the northern hemisphere represents about 0.5×10^{12} t C (Kivinen and Pakarinen 1981, Mathews and Fung 1987), as well as sizeable reserves of other elements (nitrogen (N), phosphorus, potassium, magnesium and calcium each of which plays an important role in plant production and litter decomposition in peatlands (Wang et al. 2015). The UK has 15–18% of the world's ombrotrophic (rain-fed) peatland representing approximately 3.2×10^9 t C (Elliot et al. 2015). Peat develops where and when the rate of decay of plant biomass is less than that of primary production. Retarded decomposition is typically the result of cold and wet conditions coupled with acidity (Straková et al. 2011, Elliot et al. 2015) and possibly a lack of inorganic nutrient derived from mineral weathering under ombrotrophic (rain-fed) conditions that occur in raised mires (Ingram 1978).

Raised mires present a particular hydrologic system in which the expanse of the mire develops in a region of water accumulation in the landscape

and becomes ombrotrophic, i.e. receives only meteoric water containing relatively little dissolved nutrients, as the accumulating peat holds water above the altitude of the surrounding fen. At the low-lying interface between the ombrotrophic system and surrounding mineral soils, lagg fen develops and in addition to meteoric water also receives telluric water containing dissolved inorganic nutrients (Ingram 1978, 1982). We hypothesise that decomposition of the peatland plant materials will be greater in the lagg fen than the mire expanse and testing this hypothesis is one objective of this study. The other objective is to contrast the decomposition rates of different peatland plants materials in the raised mire system to assess whether there are interactions between the plant materials and the environmental conditions under which they decompose. These hypotheses are relevant in the context of environmental change because Ward et al. (2015) have shown that plant species has a large effect on decomposition that a one degree increase in temperature. Thus comparing the decomposition of litter from different plant species may help improve understanding of peatland processes.

MATERIAL AND METHODS

Experimental site. Dun Moss is a small (approximately 90 ha), hydrologically-intact raised mire in the southern Grampians of Scotland (56°41'N, 3°21'W; national grid reference NO 167558). The soils or peats were sampled at three locations on three transects each of which started on the mineral soil of the surrounding hill slope, crossed the lagg fen and ended on the mire expanse. Samples were taken from the 0–10 cm depth, which for the mire expanse and the lagg fen represented the aerated or intermittently-saturated layers (acrotelm) that overlay the permanently saturated (catotelm) layer.

Soil/peat sampling. During the early summer (June), three replicate intact blocks of soil or peat were collected in Kubiena tins (5 cm × 5 cm × 5 cm) and dried in an oven at 105°C to estimate bulk density and water contents. Total C and N contents were determined on ball-milled sub-samples of the dried soils or peats using a Carlo-Erba CHN analyzer (CE Instruments, Wigan, UK). The pH values of the soil or peat samples were determined in a 1:2.5 (w:v) suspension of soils or peats to distilled water.

Microbial biomass and respiration determinations. Microbial biomass and respiration were determined using the glucose-induced respiration approach described by Anderson and Domsch (1978) as modified by Hopkins and Shiel (1996). The biomass assay was conducted over 12 h incubation at 20°C and the respiration assay was determined during 12 days' incubation also at 20°C. The respiration assay was used to calculate the rate over two periods, 24–144 h (1–6 days) and 144–288 h (7–12 days).

Vegetation decomposition. Surface vegetation (*Festuca ovina* L., *Juncus effusus* L., *Calluna vulgaris* (L.) Hill, *Hypnum jutlandicum* Holmen & E. Warncke and *Sphagnum papillosum* Lindberg) samples were collected from the different regions of the mire, air-dried and chopped to 2–3 mm lengths.

Samples (1.0 g dry weight) of each chopped vegetation types were weighed into mesh bags with 0.2 mm mesh size made from woven polypropylene. Five replicate mesh bags of each plant species were buried at 4–6 cm depth at each of the nine sampling sites (i.e. three sites on each of three transects). After 12 months, the bags were recovered and the microbial biomass and respiration rates of the decomposer organisms associated with the decomposition of the plant litter (i.e. C mineralization) were determined on the contents remaining in each bag.

RESULTS

Soil and microbial properties. The C and N contents of the hill slope soil were significantly less than those of the lagg fen and mire expanse when expressed on a gravimetric basis, but because of the greater bulk density of the hill slope soil, when expressed per unit volume they were greater for the hill slope soil (Table 1). The total C-to-total N ratio of the hill slope and the lagg fen soils were similar (21.7 and 23.5, respectively), and were much smaller than the C-to-N ratio of the mire expanse soil (31.1). All the soils were intensely acidic (Table 1).

The microbial biomass contents for the hill slope and the mire expanse were not significantly different from each other, but they were significantly greater than that of the lagg fen when expressed on a gravimetric basis (Table 1). However, when expressed per unit volume the biomass content of the hill slope soil was significantly greater than the other two soils types, which did not differ significantly from each other (Table 1). In addition to the differences in absolute C and biomass contents, the ratio of biomass C-to-total C ratio showed marked differences between the soils. The largest microbial amount of biomass C per unit soil

Table 1. Characteristics of surface soil or peat from different parts of the raised mire ecosystem

Soil	Total carbon			Total nitrogen			Microbial biomass carbon			pH		Bulk density	
	(mg C/g)	SE	(mg C/cm ³)	(mg N/g)	SE	(mg N/cm ³)	(mg C/g)	SE	(mg C/cm ³)	SE		(g/cm ³)	SE
Hill slope	254	102	66.0	11.7	2.9	3.0	2.9	0.77	0.76	3.5	0.18	0.26	0.070
Lagg fen	435	40	42.6	18.5	0.6	1.8	1.4	0.18	0.14	3.4	0.17	0.098	0.098
Mire expanse	469	42	28.1	15.1	1.2	0.9	3.3	0.88	0.20	3.3	0.09	0.060	0.060

Each value is the mean of three replicates followed by the standard error (SE)

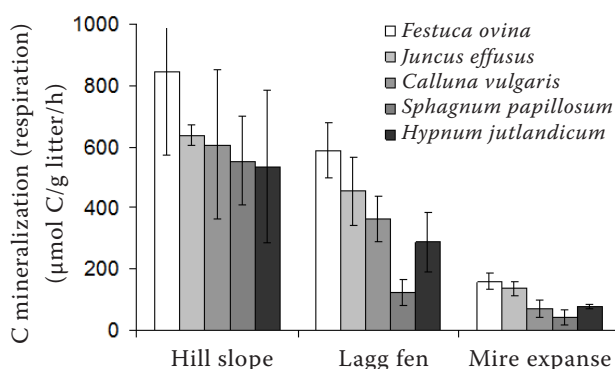


Figure 2. Carbon (C) mineralization (decomposition) rate for decomposer microorganisms associated with the litter from different plant species in soil or peat from different parts of the raised mire ecosystem. Each value is the mean of three replicates and the bars represent \pm standard errors

organic C occurred in the hill slope soil (ratio = 0.011) and was smallest for the lagg fen soil (ratio = 0.0032). The ratio of biomass C-to-total C for the mire expanse was 0.70. This rank ordering of biomass C-to-total C (hill slope > mire expanse > lagg fen) did not follow the rank ordering of the total C-to-N ratios of the soils (hill slope > lagg fen > mire expanse).

When expressed per unit mass, the respiration rates for the soils, whether measured over the 24–144 h or 144–288 h were smallest for the hill slope soil, while the other two soils did not differ significantly (Figure 1). However, when converted to a unit volume basis, the hill slope and the mire expanse did not differ significantly, while the lagg fen had the greatest respiration rate (Figure 2). This large respiration rate for the lagg fen soil was observed despite the small volumetric biomass content (Table 1). Based on the 24–144 h respiration measurements (Figure 2), the biomass specific respiration (respiration rate per unit biomass) for the soils were 51, 357 and 218 $\mu\text{mol CO}_2/\text{mg biomass C/h}$ 180 for the hill slope, lagg fen and mire expanse soils, respectively. The large biomass specific respiration rate for the lagg fen soil was the result of high respiration rate and small biomass, rather than being attributable to a difference in just one of these parameters. In addition, there was no clear relationship between the respiratory quotient and the C-to-N ratio of the soils.

Decomposition of litter. The relative recalcitrance during the early phase of decomposition of litter from the different plant species is indicated

by the respiration rate from litter bags buried in the different soils (Figure 1). In the hill slope soil there were no significant differences in the decomposition rate, whereas in the lagg fen and mire expanses, the rank order for decomposition rate was *F. ovina* > *J. effusus* > *C. vulgaris* > *H. jutlandicum* > *S. papillosum*. In the lagg fen the differences in decomposition between *F. ovina* and all of *C. vulgaris*, *S. papillosum* and *H. jutlandicum* were significant; and those between all of *J. effusus*, *C. vulgaris* and *H. jutlandicum* compared to *S. papillosum* were significant. In the mire expanse, the difference between both *F. ovina* and *J. effusus* compared to *C. vulgaris*, *S. papillosum* and *H. jutlandicum* were significant; and the difference in decomposition between *S. papillosum* and *H. jutlandicum* was also significant (Figure 1). In general, the litter decomposition rates were greatest in the hill slope soil, followed by the lagg fen and then the mire expanse (Figure 1). The only exception to this was the decomposition of *F. ovina* litter in the hill slope and the lagg fen soil, which were not significantly different from each other,

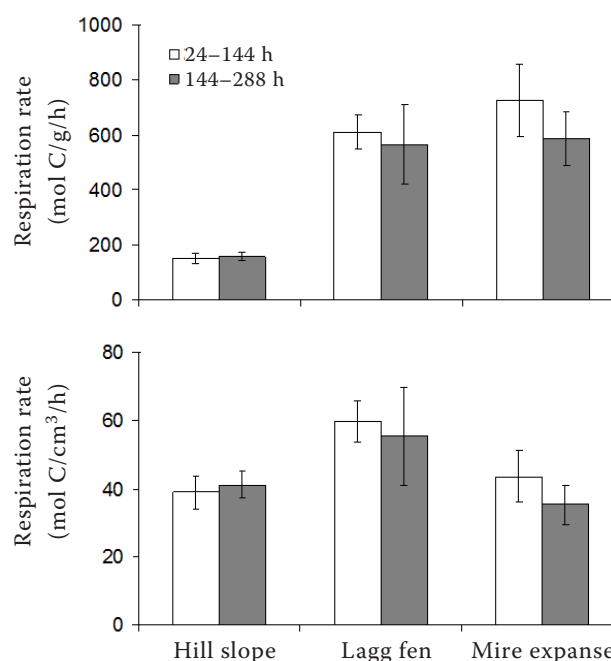


Figure 1. Microbial respiration rates for soil or peat from different parts of the raised mire ecosystem expressed on a gravimetric basis and a volumetric basis. Each value is the mean of three replicates and the bars represent \pm standard errors. The respiration assay was used to calculate the rate over two periods, 24–144 h (1–6 days) and 144–288 h (7–12 days)

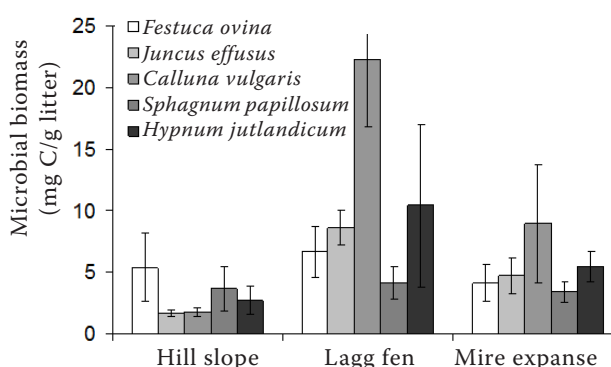


Figure 3. Soil or peat microbial biomass carbon (C) associated with plant litter of plant decomposing in soil or peat from different parts of the raised mire ecosystem. Each value is the mean of three replicates and the bars represent \pm standard errors

although the decomposition rate in the hill slope was greater than that in the lagg fen (Figure 1).

For most of the litter types considered, the amount of biomass was greatest in the lagg fen and least in the hill slope soil (Figure 3). The only exceptions to this were the *F. ovina* litter, which was the fastest decomposing litter, and the *S. papillosum* litter, neither of which had significantly different microbial biomass contents between any of the soils (Figure 3). In the case of the lagg fen, but for neither the hill slope nor 208 the mire expanse, the microbial biomass in the decomposing litter was significantly greater per unit mass than that found in the unamended soil (Table 1). For the hill slope and the mire expanse, the soil microbial biomass contents were similar to the biomass in the litter, despite the significantly different gravimetric C and N contents of the mire expanse.

DISCUSSION

The large differences in bulk density between the soils mean that expressing values on a unit volume basis is the most appropriate to make comparisons between the soils (Hopkins et al. 2009).

All three soil or peat types in the raised mire system have similarly low pH and experience similar temperature regimes, so these two key environmental drivers of decomposition are unlikely to be distinguishing factors between the soils with respect to organic matter decomposition. The supply of mineral nutrients is however likely to be a key driver and is likely to explain in part at

least the faster decomposition of litter in the mineral soil from the surrounding hill slope and the lagg fen as well as the generally larger microbial biomass supported by decomposing litter in the lagg fen. The exception to this was the biomass associated with the *C. vulgaris* litter in the lagg fen, which was significantly larger than that for the other litter types (Figure 3). This larger microbial biomass was not associated with a greater decomposition loss for the *C. vulgaris* litter (Figure 1). Thus conditions in the lagg fen, which could be related to nutrient supply, interacted with the litter to affect the size of the biomass, but there was a still a constraint on decomposition for *C. vulgaris*. Oxygen supply is also a key environmental driver of decomposition, and certainly has a major influence on depressing decomposition deeper in the peat of the mire expanse and the lagg fen (Chivers et al. 2009). However, we have concentrated on the surface layers, which are either permanently above the saturated zone in the case of the mire expanse and the hill slope, or only intermittently saturated and then usually with percolating water in the case of the lagg fen (Ingram 1982).

The size and composition of the decomposer community is also likely to be influential, but this is unlikely to vary independently of the physico-chemical environment, particularly oxygen (Wheatley et al. 1976) and the resource quality (i.e. properties of the plant litter as a substrate for decomposers). When the resource quality is the same but the physicochemical environment differs (i.e. when the microbial biomass of the litter is compared for the same litter in different burial environments), the biomass is greater for the lagg fen compared with the mire expanse. This suggests that the physico-chemical environment is the more influential factor, possibly as suggested above mediated by differential mineral nutrient supply (Wang et al. 2015). It is interesting to note that the biomass in the litter in the mineral soil of the hill slope was consistently smaller than that of the lagg fen. We suggest that this is because litter decomposition in this environment was either faster and the higher quality components had been depleted by the time the biomass was measured.

Comparative information and knowledge about the details of the decomposition of moss biomass is even more scant, such that we have a very poor conception of how these and other cryptogams contribute to major biogeochemical processes.

In this study, we have provided some data to help fill this gap by illustrating the relatively slow rate of decomposition of moss *S. papillosum* and *H. jutlandicum* biomass. These relationships, in which the residues from minerotrophic plants (e.g. *F. ovina* and *J. effusus*) decompose faster than the ombrotrophic species (e.g. *S. papillosum* and *H. jutlandicum*) is consistent with the observations of Bragazza et al. (2007).

The following observations support the hypothesis that decomposition is greater in the lagg fen because of mineral nutrient availability: (i) the greater respiration rate of the decomposer organisms in the lagg fen than of either the mire expanse or the surrounding mineral soils; (ii) the greater respiration rate of microorganisms associated with the litter recovered from litter bags in the lagg fen compared with that in the mire expanses; (iii) the greater microbial biomass of the litter in the lagg fen than the mire expanse; and (iv) the greater rate of decomposition of litter from minerotrophic plants compared to ombrotrophic species.

Acknowledgements

This work was conducted during a research studentship from the UK Natural Environment Research Council to SH. We also thank the landowners for access to the site and Dr H.A.P. Ingram and Dr O.M. Bragg of the University of Dundee for useful discussions.

REFERENCES

- Anderson J.P.E., Domsch K.H. (1978): A physiological method for the quantitative measurement of microbial biomass in soils. *Soil Biology and Biochemistry*, 10: 215–221.
- Bragazza L., Siffi C., Iacumin P., Gerdol R. (2007): Mass loss and nutrient release during litter decay in peatland: The role of microbial adaptability to litter chemistry. *Soil Biology and Biochemistry*, 39: 257–267.
- Chivers M.R., Turetsky M.R., Waddington J.M., Harden J.W., McGuire A.D. (2009): Effects of experimental water table and temperature manipulations on ecosystem CO₂ fluxes in an Alaskan rich fen. *Ecosystems*, 12: 1329–1342.
- Elliott D.R., Caporn S.J.M., Nwaishi F., Nilsson R.H., Sen R. (2015): Bacterial and fungal communities in a degraded ombrotrophic peatland undergoing natural and managed re-vegetation. *PLOS One* 10: e0124726.
- Hopkins D.W., Shiel R.S. (1996): Size and activity of soil microbial communities in long-term experimental grassland plots treated with manure and inorganic fertilizers. *Biology and Fertility of Soils*, 22: 66–70.
- Hopkins D.W., Waite I.S., McNicol J.W., Poulton P.R., MacDonald A.J., O'Donnell A.G. (2009): Soil organic carbon contents in long-term experimental grassland plots in the UK (Palace Leas and Park Grass) have not changed consistently in recent decades. *Global Change Biology*, 15: 1739–1754.
- Ingram H.A.P. (1978): Soil layers in mires: Function and terminology. *Journal of Soil Science*, 29: 224–227.
- Ingram H.A.P. (1982): Size and shape in raised mire ecosystems: A geophysical model. *Nature*, 297: 300–303.
- Kivinen E., Pakarinen P. (1981): Geographical Distribution of Peat Resources and Major Peatland Complex Types in the World. Helsinki, *Annales Academiae Scientiarum Fennicae A III*, 132–160.
- Matthews E., Fung I. (1987): Methane emission from natural wetlands: Global distribution, area, and environmental characteristics of sources. *Global Biogeochemical Cycles*, 1: 61–86.
- Straková P., Niemi R.M., Freeman C., Peltoniemi K., Toberman H., Heiskanen I., Fritze H., Laiho R. (2011): Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water table regimes. *Biogeosciences*, 8: 2741–2755.
- Wang M., Moore T.R., Talbot J., Riley J.L. (2015): The stoichiometry of carbon and nutrients in peat formation. *Global Biogeochemical Cycles*, 29: 113–121.
- Ward S.E., Orwin K.H., Ostle N.J., Briones M.J.I., Thomson B.C., Griffiths R.I., Oakley S., Quirk H., Bardgett R.D. (2015): Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. *Ecology*, 96: 113–123.
- Wheatley R.E., Greaves M.P., Inkson R.H.E. (1976): The aerobic bacterial flora of a raised bog. *Soil Biology and Biochemistry*, 8: 453–460.

Received on May 12, 2015

Accepted on July 28, 2015

Corresponding author:

Prof. David W. Hopkins, Royal Agricultural University, Cirencester, GL7 6JS Gloucestershire, UK
e-mail: david.hopkins@rau.ac.uk