Management influences on soil microbial communities and their function in botanically diverse haymeadows of northern England and Wales

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Abstract

The effects of management intensification on the size, activity and structure of soil microbial communities in botanically diverse haymeadows were examined. Paired traditionally managed and intensively managed haymeadows, at three submontane regions in northern England and north Wales, were sampled over four seasons. Management intensification had no significant effect on soil nutrient status, soil microbial biomass and soil microbial activity. Management intensification did influence soil microbial community structure, resulting in a significant reduction in soil fungal biomass, measured as soil ergosterol content, and a decline in the proportion of fungi relative to bacteria in the soil microbial community. Fungi of the genera \textit{Fusarium}, \textit{Mucor}, \textit{Absidia}, \textit{Cladosporium}, \textit{Trichoderma}, \textit{Acremonium}, \textit{Zygorhynchus}, \textit{Phoma} and \textit{Paecilomyces} were commonly isolated from litter and soil of both the traditionally and intensively managed haymeadows of the site tested. Management had a significant effect on the relative isolation frequency of these fungi at this site. All commonly isolated species had proteolytic and urease activity and approximately half had cellulolytic and lignolytic activities. These findings were taken to suggest that although management improvements to submontane haymeadows will induce changes in the size and composition of the fungal community, they do not necessarily influence the functioning of the soil microbial community with respect to soil ecosystem-level processes of organic matter decomposition and nutrient cycling. We suggest that changes in soil microbial communities are related primarily to changes in plant productivity and composition or the form and quantity of fertiliser applied to the site. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Haymeadow; Management intensification; Soil; Ergosterol; Phospholipid fatty acid; Decomposer fungi; Fungal community; Fertilizer

1. Introduction

Traditionally managed haymeadows within submontane regions of northern England and north Wales support, perhaps, the largest diversity of plants of all temperate grasslands (Rodwell, 1992). However, over the last 40 yr some 95% of these traditional flower rich haymeadows have been subjected to intensive grassland agriculture (Porter, 1994), leading to increases in plant productivity, but marked declines in plant species diversity from some 40 plus species to, typically, around 10–15 species m$^{-2}$ (Rodwell, 1992; Smith and Rushton, 1994). Such considerable changes in plant productivity and species composition are likely to strongly influence soil microbial community dynamics, and hence the efficiency of ecosystem func-
Rhinanthus spp., are likely to be highly unpredictable in these grasslands (Shine, 1999). Such ecological effects of plant composition or the litter of different plant species (Wardle and Nicholson, 1996; Wardle et al., 1997) and depending on the traits of the plant species in question (Wardle et al., 1998).

The application of fertilisers to meadows may also directly influence soil microbial community dynamics. For example, studies of grazed, lowland grassland by Lovell et al. (1995) showed that the application of nitrogen fertiliser significantly reduced the size and activity of the soil microbial biomass. It has been suggested that fertiliser N application can have a direct inhibitory effect on the soil microbial community, in particular the decomposer (Arnebrandt et al., 1990; Bardgett et al., 1993) and mycorrhizal fungi (Sparring and Tinker, 1978; Hamel et al., 1994), through the repression of enzyme activity and the build up of recalcitrant and toxic compounds (Fog, 1988). Reductions in microbial biomass in Table 1
Characteristics of traditionally and intensively managed grasslands at three sites

<table>
<thead>
<tr>
<th>Property</th>
<th>Teesdale</th>
<th>Ravenstonedale</th>
<th>Dolgellau</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grid reference</td>
<td>NY817338</td>
<td>NY736033</td>
<td>NY803225</td>
</tr>
<tr>
<td>Altitude (m. a. s. l.)</td>
<td>450</td>
<td>280</td>
<td>180</td>
</tr>
<tr>
<td>Soil type</td>
<td>brown earth</td>
<td>brown earth</td>
<td>brown earth</td>
</tr>
<tr>
<td>Rock base</td>
<td>limestone</td>
<td>limestone</td>
<td>igneous rock/</td>
</tr>
<tr>
<td>Management regime</td>
<td>traditional</td>
<td>intensive</td>
<td>intensive</td>
</tr>
<tr>
<td>Number plant species</td>
<td>33</td>
<td>27</td>
<td>14</td>
</tr>
<tr>
<td>pH</td>
<td>5.9</td>
<td>5.5</td>
<td>5.7</td>
</tr>
<tr>
<td>Soil NH$_4$ (µg g$^{-1}$)</td>
<td>11.7</td>
<td>14.0</td>
<td>13.4</td>
</tr>
<tr>
<td>Soil NO$_3$ (µg g$^{-1}$)</td>
<td>12.3</td>
<td>8.4</td>
<td>21.8</td>
</tr>
<tr>
<td>Manure regime</td>
<td>8 t ha$^{-1}$ y$^{-1}$</td>
<td>–</td>
<td>13 t ha$^{-1}$ y$^{-1}$</td>
</tr>
<tr>
<td>Lime regime t ha$^{-1}$ over last 15 yr</td>
<td>5</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Herbage utilisation</td>
<td>hay</td>
<td>hay</td>
<td>hay</td>
</tr>
<tr>
<td>Date closed off for hay growth</td>
<td>mid May</td>
<td>end May</td>
<td>start May</td>
</tr>
<tr>
<td>Date hay cut</td>
<td>late July</td>
<td>late July</td>
<td>late June</td>
</tr>
<tr>
<td>Cattle grazing</td>
<td>no</td>
<td>after hay cut</td>
<td>after hay cut</td>
</tr>
<tr>
<td>Sheep grazing</td>
<td>for all fields and sites</td>
<td>through out year</td>
<td></td>
</tr>
<tr>
<td>Vegetation</td>
<td>MG2$^a$</td>
<td>MG6$^b$</td>
<td>MG3$^c$</td>
</tr>
<tr>
<td></td>
<td>MG6$^d$</td>
<td>MG5$^e$</td>
<td>MG6$^f$</td>
</tr>
</tbody>
</table>


$^g$ The traditional meadow at Dolgellau was classified as Cynosurus cristatus–Centaurea nigra (MG5a). All fields under improved management (improved fields) were classed as MG6 (Rodwell, 1992).
fertilised grasslands have also been attributed to the acidifying effect of nitrogenous fertilisers (microbial production of nitric acid) in soil (Christie and Beattie, 1989). Information on the relative importance of direct (nutrient availability) and indirect (plant response) effects of fertilisation on grassland soil microbial communities is scarce, although microcosm studies by Bardgett et al. (in press) suggest that changes in plant composition of grasslands may have a greater influence on soil microbial communities than do changes in nutrient availability. Likewise, studies by Wardle and Nicholson (1996) and Wardle et al. (1998) suggest that plant species effects (productivity and species composition) are fundamental in shaping the soil microbial community of grasslands.

Although some research has addressed how changes in agricultural management can affect soil microorganisms (Lovell et al., 1995; Bardgett and Leemans, 1995; Bardgett et al., 1996), little work has considered the effects of management in grasslands of such high botanical diversity, where changes in the plant community in response to management, and hence soil carbon and other nutrient inputs, are so large. One study that has been done on these botanically diverse haymeadows in northern England provides evidence, from a range of sites along gradients of management intensity, that high intensity farming reduces the proportion of fungi relative to bacteria in the soil microbial community (Bardgett and McAlister, 1999); an effect that appears to be common to other temperate grassland systems (Bardgett et al., 1999). The aim of this study was also to confirm that long-term intensive management of haymeadows decreases fungal biomass and the proportion of fungi relative to bacteria within the soil microbial community. However, our principal aim was to see whether observed changes are associated with shifts in fungal community structure and hence the functional capability of the soil with respect to enzyme production. To achieve these aims, we compared measures of soil microbial biomass, fungal-to-bacterial biomass ratios and fungal community structure, and fungal enzyme activities, in adjacent traditionally and intensively managed submontane haymeadows, at different locations in the United Kingdom. Donnison et al. (1999) consider the mechanisms for changes in soil microbial communities with respect to the direct and indirect effects of fertilisers on the soil microbial community, through changes in nutrient availability or plant composition, respectively.

2. Materials and methods

2.1. Study sites and soils

Sites (Table 1) were selected to allow direct comparisons of different management systems at different botanical names in Table 1 follow Clapham et al. (1987). Soils at all sites were sampled in May, July and October 1995, and January 1996. These dates were taken to broadly represent the prevailing climatic conditions of spring, summer, autumn and winter, respectively. In addition soils and surface plant litter at the Dolgelau site in north Wales were sampled in July 1996 to determine the composition of resident fungal communities.

Due to the unique nature of these haymeadows, which are protected under the UK Sites of Special Scientific Interest (S.S.S.I.) legislation, only one grassland of each type was present at each location. Therefore, we were limited to using three permanently located 1 m² quadrats as replicates within each grassland type, at each site. We were confident that these replicates covered the range of variability found between fields within any given location (Bardgett and McAlister, 1999). Soil was sampled for all analyses by taking five randomly located 3.5 cm dia soil cores (10 cm deep) from each quadrat at each sample date. After removal of surface vegetation, soil cores from the same quadrats were bulked and sieved (<6 mm), plant material was removed, and the soil was stored at 4°C (for no more than 24 h) until analyses. Surface plant litter was also stored at 4°C until use.

Soil pH, organic matter (loss on ignition), plant available NO₃⁻ and NH₄⁺ (determined in May and July 1995 and January 1996 only) and total nutrient content (Mg, Ca, N, Na, P and K; determined in October 1995 only) were measured by standard methods (Allen, 1989). Olsen's bicarbonate extractable P (PO₄³⁻) was also measured (Olsen et al., 1954; Allen, 1989; in October 1995 and January 1996 only). Results were expressed on a dry weight basis except for the total soil nutrient analysis where values were expressed as meq% element. Average values for pH and plant available NO₃⁻ and NH₄⁺ are given in Table 1.

2.2. Assessment of soil microbial biomass and activity

Extractable microbial C was measured using the fumigation–extraction technique (Vance et al., 1987). Briefly, soil samples were fumigated with CHCl₃ for 24 h at 25°C. After removal of the CHCl₃, soluble C was extracted from fumigated and unfumigated samples with 0.5 M K₂SO₄ for 30 min on an end-over-end shaker (soil-to-solution ratio 1:4 w/v). Total organic C in filtered extracts was determined by the acid dichromate oxidation method (Tate et al., 1988). Microbial C flush
Frostegård et al. (1993). The fatty acids i15:0, a15:0, basis.
fatty acid methyl-esters was expressed on a dry weight
C20. For each sample, the abundance of individual
methyl ester mix (Supelco) that ranged from C11 to
comparison using standard qualitative bacterial acid
Separated fatty acid methyl esters were identified by
et al. (1959) as modified by White et al. (1979).

2.3. Assessment of the relative contribution of fungi and
bacteria to soil microbial biomass

Lipids were extracted from soil, fractionated and
quantified using the procedure described by Bardgett
et al. (1996), which is based on the method of Bligh
and Dyer (1959) as modified by White et al. (1979).
Separated fatty acid methyl esters were identified by
chromatographic retention time and mass spectral
comparison using standard qualitative bacterial acid
methyl ester mix (Supelco) that ranged from C11 to
C20. For each sample, the abundance of individual
fatty acid methyl-esters was expressed on a dry weight
basis.

Fatty acid nomenclature was used as described by
Frostegård et al. (1993). The fatty acids i15:0, a15:0,
i16:0, 17:0, i17:0, cy17:0, 18:1
these values were used to calculate the ratio of
18:2o6:bactPLFAs, which was taken to represent the
ratio of fungal-to-bacterial biomass in soil (Bardgett et
al., 1996).

2.4. Assessment of fungal abundance and community
composition

Ergosterol was extracted from 1 g dry weight soil
using the procedure described by Frostegård and
Bååth (1996). Dried ergosterol samples were dissolved
in 1 ml methanol (40°C for 15 min; sonicated for 1
min), centrifuged (9000 rev min⁻¹; 5 min) and supernatants
filtered (0.45 mm pore size teflon syringe; Merck, UK).
Ergosterol content of extracts was quan-
tified by high performance liquid chromatography with
methanol as the mobile phase and a reverse phase C18
column (Highchrom, Reading, UK).

Saprotrophic fungi were isolated from soil and sur-
face plant litter collected from the Dolgellau site in
July. Fungi were isolated from litter by a root-washing
technique (Harley and Waid, 1955) adapted for isolat-
ing fungi from plant litter (Bardgett et al., 1993).
Briefly litter was cut into 1–2 mm² fragments and
washed for 5 min in five changes of sterile distilled
water. Fragments were then plated out on Czapek Dox
agar with 1:15,000 w/v rose Bengal (five fragments per
plate; a total of 750 fragments per site) and incubated
at 15°C for 1–3 weeks.

Saprotrophic soil fungi were isolated using the di-
lution plate technique. Soil dilutions were mixed with
molten Czapek Dox agar with 1:15,000 w/v rose
Bengal in Petri dishes. Plates were incubated at 15°C
for 3–7 d. From each replicate sample, 250 colonies
were randomly picked (1500 colonies in total). Fungal
isolates were identified to genus and if possible to
species level. The relative isolation frequency of taxa
isolated was recorded as percentage occurrence.

The diversity of the litter and soil fungal commu-
nities at each site was assessed by calculating values
for the Shannon-Wiener function (H; Margalef, 1958):

\[
H = \sum_{i=1}^{s} p_i \log_2 p_i,
\]

where \( s \) is the number of species and \( p_i \) is the pro-
portion of the total sample belonging to the \( i \)th
species. This function takes two components of species
diversity into account, number of species and evenness
of allotment of individuals among the species (Lloyd

2.5. Determination of enzymatic capacity of commonly
isolated fungi

Commonly isolated fungi (isolation frequency
>5%) and some incidentals were screened for their
enzymatic capabilities. Protease, urease, ligninase and
beta-glucosidase activity were tested as described by
Paterson and Bridge (1994). Cellulase was tested by
the ability of an isolate to clear cellulose medium
(Eggins and Pugh, 1962) and release dye from cellu-
llose azure dye (Paterson and Bridge, 1994).
Phenoloxidase activity was tested as described by
Poppe and Welvaert (1983). Esterase activity was
tested as described by Paterson and Bridge (1994)
and Stalpers (1978). Production of extracellular per-
oxidase, laccase naphthol, laccase guaiacol and acid
phosphatase activity were tested as described by
Stalpers (1978).
2.6. Statistical analysis

Statistical analysis was carried out with SAS software (SAS Institute, Cary, NC). Due to the large number of variates measured and the possibility of correlations between these variates, MANOVA analyses were employed. Where these indicated significant overall differences between managements or sites, univariate ANOVAs and Tukey tests were performed to confirm the source of these differences. Data for each season were analysed separately because incorporating season as an element in the MANOVA analysis would have resulted in an excessive number of degrees of freedom. In addition, experimental limitations, as discussed in the Materials and methods section, meant that our replicate plots within each grassland type were not truly independent with respect to time. Management effects revealed by MANOVA were confirmed by examining the consistency of responses over time at the three sites. Due to the unbalanced nature of the data sets (missing values), general linear models procedures were adopted.

The $\chi^2$ test was used to confirm the null hypothesis that for each method, management practice had no effect on fungal community structure. Tukey's tests (SAS) were used to confirm which individual species were affected by management practice.

3. Results

In May and October, site, management and site management interactions had significant overall effects on soil measurements (Table 2).

3.1. Soil nutrient status and physical properties

Site and management had little or no effect on soil pH, plant available NH$_4^+$ and NO$_3^-$ (not assessed in October) and total soil N and K (assessed in October only). Site had an effect on soil Na concentrations which were lowest at Dolgellau (Table 3). Site–management interactions had effects on soil Ca, Mg, P and PO$_4^{3-}$ levels (Table 3; Olsen's PO$_4^{3-}$ assessed in January and October, other elements in October only). Amounts of Ca and Mg were lowest at Dolgellau and elevated under traditional management at Teesdale. Concentrations of PO$_4^{3-}$ and P were highest under intensive management at Ravenstonedale. Site management interactions also had effects on soil organic matter content in May (Table 4). At this time soils from Teesdale contained higher amounts of organic matter than soils from other sites. Soil organic matter content was slightly elevated under traditional management at Teesdale and Dolgellau but slightly reduced under traditional management at Ravenstonedale.

3.2. Soil microbial biomass and activity

Site management interactions had effects on measures of soil microbial biomass and activity. In both May and October the basal respiration, dehydrogenase activity and microbial C content of soils were

Table 3
Nutrient status of soil in October 1995. Values are given as means ($n = 3$), standard error of the mean is given in parentheses

<table>
<thead>
<tr>
<th>Site/treatment</th>
<th>Na$^a$ (meq%)</th>
<th>Ca$^b$ (meq%)</th>
<th>Mg$^b$ (meq%)</th>
<th>K (meq%)</th>
<th>N (µg g$^{-1}$)</th>
<th>P$^b$ (µg g$^{-1}$)</th>
<th>Olsen's P$^c$ (g dry soil$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Teesdale</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>0.18 (0.03)</td>
<td>20.60 (1.00)</td>
<td>7.40 (0.70)</td>
<td>0.30 (0.03)</td>
<td>0.98 (0.07)</td>
<td>11.93 (0.32)</td>
<td>21.30 (2.10)</td>
</tr>
<tr>
<td>Intensive</td>
<td>0.17 (0.01)</td>
<td>13.60 (0.19)</td>
<td>2.87 (0.02)</td>
<td>0.30 (0.02)</td>
<td>0.50 (0.22)</td>
<td>5.80 (0.57)</td>
<td>18.00 (0.80)</td>
</tr>
<tr>
<td><strong>Ravenstonedale</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>0.17 (0.01)</td>
<td>12.00 (1.00)</td>
<td>3.79 (0.07)</td>
<td>0.33 (0.43)</td>
<td>0.24 (0.20)</td>
<td>11.13 (2.13)</td>
<td>25.80 (1.40)</td>
</tr>
<tr>
<td>Intensive</td>
<td>0.18 (0.02)</td>
<td>14.10 (0.75)</td>
<td>3.12 (0.13)</td>
<td>0.70 (0.17)</td>
<td>0.47 (0.21)</td>
<td>42.90 (3.67)</td>
<td>59.50 (10.40)</td>
</tr>
<tr>
<td><strong>Dolgellau</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>0.15 (0.15)</td>
<td>8.60 (0.70)</td>
<td>0.94 (0.01)</td>
<td>0.30 (0.03)</td>
<td>0.61 (0.27)</td>
<td>0.80 (0.46)</td>
<td>24.30 (0.27)</td>
</tr>
<tr>
<td>Intensive</td>
<td>0.12 (0.02)</td>
<td>8.10 (1.14)</td>
<td>1.34 (0.35)</td>
<td>0.30 (0.14)</td>
<td>0.68 (0.03)</td>
<td>3.60 (0.41)</td>
<td>30.60 (1.75)</td>
</tr>
</tbody>
</table>

$^a$ Univariate ANOVA indicated a significant ($P < 0.05$) effect of site.

$^b$ Univariate ANOVA indicated significant ($P < 0.01$) differences between means.

$^c$ Univariate ANOVA indicated significant ($P < 0.001$) differences between means.
highest at Teesdale and in May dehydrogenase activity and microbial C content were elevated in the traditionally managed site at Teesdale (Table 4; Fig. 1). Basal respiration showed a marked seasonal trend, being greatest at all sites in late spring and apparently declining thereafter (Fig. 1).

### 3.3. Soil microbial community

Ergosterol contents of soils under traditional management were always greater than those under intensive management (Fig. 2). This trend was statistically significant in October. In May, site management inter-
Fig. 2. A comparison of mean and standard errors (n = 3) for soil ergosterol content (µg g⁻¹ d.w. soil) and fungal-to-bacterial PLFA ratios of soils sampled in May, July, October and January from traditional (clear bars) and intensive (full bars) soils at Teesdale, Ravenstonedale and Dolgellau. For ergosterol and fungal-to-bacterial PLFA ratios univariate ANOVAs for individual sample dates indicated significant (P < 0.001) differences between means in May and a significant (P < 0.01) effect of treatment in October.

actions had significant effects on soil ergosterol contents. Concentrations were highest at the Teesdale site and, as in October, amounts were always highest under traditional management (Fig. 2).

With the single exception of the Ravenstonedale site in May fungal-to-bacterial PLFA ratios were always greatest in soils under traditional management (Fig. 2). This trend was statistically significant in October. In May, site management interactions had significant effects on the soil fungal-to-bacterial PLFA ratios. The ratios were greatest at Dolgellau, particularly in soils under traditional management (Fig. 2).

3.4. Fungal community structure at the Dolgellau site

Soils from the traditionally and intensively managed meadows contained 81 and 73 fungal species, respectively. The values for the Shannon–Wiener function for the diversity of these respective fungal communities were 4.81 and 4.84. Litter from the traditionally and intensively managed field contained 62 and 40 fungal species, respectively. The values for the Shannon–Wiener function for these respective communities were 3.63 and 2.91.

Fungal communities of soils and litter differed significantly under the two management systems (\(Z^2, P < 0.001; \) Fig. 3). In particular \(\text{Paecilomyces} \) sp., \(\text{Phoma} \) sp., Unidentified sp. 1 and incidental sp. were significantly more common under traditional management (Tukey’s, \(P < 0.05; \) Fig. 3), whereas, \(\text{Fusarium culmorum}, \text{Plectosphaerella cucumerina}, \text{Phoma exigua} \) and \(\text{Mucor} \) sp 1. were significantly more common under intensive management (Tukey’s, \(P < 0.05; \) Fig. 3).

3.5. Enzymatic activity of fungi

None of the fungi screened positive for phosphatase and aesculin, whereas all fungi screened positive for urease and protease (except an incidental) (Table 5). Some fungi screened positive for cellulase and the enzymes involved in lignin degradation including ligninase, phenoloxidase, peroxidase and laccase (Table 5).

4. Discussion

Our temporal data provides evidence that, although the size and metabolic activity of the soil microbial biomass and total amounts of soil nutrients may not be affected by long-term intensification of haymeadow management, there are large changes in the structure or make-up of the soil microbial community. In particular, intensification of management decreased soil ergosterol content, a sterol specifically found in higher fungi (Newell, 1992), and reduced the fungal-to-bacterial PLFA ratio; an effect that was particularly pronounced in early autumn. It has been proposed that changes in the relative abundance of fungal and bacterial PLFAs can be used as indicators of relative changes in the biomass of these two microbial groups (Frostegård and Bååth, 1996; Bardgett et al., 1996), which constitute some 90–95% of the total heterotrophic metabolism in most soils (Petersen and Luxton, 1982). Therefore, together, these findings (ergosterol and PLFA) provide evidence that intensification of haymeadow management reduces fungal biomass and the proportion of fungi relative to bacteria within the soil microbial community. Similar effects of grassland intensification on the soil microbial community — an increase in the proportion of bacteria relative to fungi — have also been reported by Bardgett et al. (1999) and Bardgett and McAlister (1999) in studies of temperate grasslands in southwest and northern England, respectively. These authors suggested that decomposition processes may be driven more by fungal pathways in low-input or unfertilised grassland systems.

Reductions in soil fungal biomass due to intensive management, at the Dolgellau site, were associated with shifts in the species composition, but not the diversity of the saprotrophic fungal community. In particular, we found that \(\text{Paecilomyces} \) sp., \(\text{Phoma} \) sp., Unidentified sp. 1, and an unidentified sp., were more common under traditional management, whereas, \(\text{Fusarium culmorum}, \text{P. cucumerina}, \text{P. exigua} \) and \(\text{Mucor} \) sp 1. were more common under intensive management. The finding that the composition of the fungal community changed in response to management is consistent with studies of other ecosystems, including grasslands (Bardgett et al., 1993), forests (Arnebrandt et al.,

<table>
<thead>
<tr>
<th>C</th>
<th>P</th>
<th>E</th>
<th>Ph</th>
<th>G</th>
<th>N</th>
<th>Pe</th>
<th>L</th>
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<tbody>
<tr>
<td>(\text{Paecilomyces} ) sp.</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<tr>
<td>(\text{Cladosporium} ) sp.</td>
<td>+</td>
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<tr>
<td>(\text{F. culmorum} )</td>
<td>+</td>
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<td>+</td>
<td>+</td>
<td>+</td>
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<tr>
<td>(\text{P. cucumerina} )</td>
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<td>+</td>
</tr>
<tr>
<td>(\text{Zygomyces} ) sp.</td>
<td>+</td>
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<td>+</td>
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<tr>
<td>(\text{Mucor} ) sp. 1</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<tr>
<td>(\text{P. exigua} )</td>
<td>+</td>
<td>+</td>
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<td>+</td>
<td>+</td>
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<tr>
<td>(\text{Acremonium} ) sp.</td>
<td>+</td>
<td>+</td>
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<td>+</td>
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</tr>
<tr>
<td>(\text{Phoma} ) sp.</td>
<td>+</td>
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<td>+</td>
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<td>+</td>
</tr>
<tr>
<td>Incidentsa</td>
<td>72</td>
<td>94</td>
<td>6</td>
<td>50</td>
<td>39</td>
<td>22</td>
<td>44</td>
<td>0</td>
</tr>
</tbody>
</table>

a A \(\text{Mucor} \) sp. 2, \(\text{Absidia} \) sp., \(\text{E. nigrum}, \text{G. roseum}, \text{Geocladium} \) sp., \(\text{M. nivale}, \text{Trichoderrina} \) sp., \(\text{Sclerotinia} \) sp., \(\text{Verticillium} \) sp. and six unidentified spp. Figures are percentage of isolates scoring positive.
changes in plant community productivity and species diversity, leading to quantitative and qualitative changes in detrital and non-detrital carbon inputs to soil. Although studies have demonstrated that fertilisers may directly influence the soil fungal community (Arnebrant et al., 1990) most work tends to point to a greater role of species changes in the plant community. For example, a microcosm study by Bardgett et al. (in press) suggested that changes in plant composition of grasslands were a more important determinant of soil microbial community structure than were changes in soil nitrogen availability through fertiliser additions. Studies by Wardle and Nicholson (1996) and Wardle et al. (1998) also suggest that plant species effects (productivity and diversity) are fundamental in shaping the soil microbial community of grasslands.

In conclusion, this temporal study has demonstrated that management intensification did not greatly alter the size and total metabolic activity of the soil microbial biomass, but it had an effect on the structure and species composition of the soil microbial and fungal community of haymeadows. The observed microbial community shifts were likely to be related to changes in the productivity and species composition of the plant community, however, further studies are required to substantiate this claim. We have shown that several enzyme activities are ubiquitous to fungi that occur in both traditional and intensively managed haymeadows. Therefore, we provide no evidence to suggest that changes in the species composition of the fungal community will alter the functional capability of the soil microbial community with respect to soil ecosystem-level functions of organic matter decomposition and nutrient recycling.

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Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? J. Ecol. 86, 405–420.


