Long-Term Consequences of Grazing and Burning on Northern Peatland Carbon Dynamics

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ABSTRACT

Using a 50-year-old field experiment, we investigated the effects of the long-term land management practices of repeated burning and grazing on peatland vegetation and carbon dynamics (C). Plant community composition, C stocks in soils and vegetation, and C fluxes of CO_2, CH_4 and DOC, were measured over an 18-month period. We found that both burning and grazing reduced aboveground C stocks, and that burning reduced C stocks in the surface peat. Both burning and grazing strongly affected vegetation community composition, causing an increase in graminoids and a decrease in ericoid subshrubs and bryophytes relative to unburned and ungrazed controls; this effect was especially pronounced in burned treatments. Soil microbial properties were unaffected by grazing and showed minor responses to burning, in that the C:N ratio of the microbial biomass increased in burned relative to unburned treatments. Increases in the gross ecosystem CO_2 fluxes of respiration and photosynthesis were observed in burned and grazed treatments relative to controls. Here, the greatest effects were seen in the burning treatment, where the mean increase in gross fluxes over the experimental period was greater than 40%. Increases in gross CO_2 fluxes were greatest during the summer months, suggesting an interactive effect of land use and climate on ecosystem C cycling. Collectively, our results indicate that long-term management of peatland has marked effects on ecosystem C dynamics and CO_2 flux, which are primarily related to changes in vegetation community structure.

Key words: carbon controlled burning; CH_4; CO_2; DOC; fire; grazing; land use; microbial biomass; moorland; photosynthesis; peat; respiration; vegetation.

INTRODUCTION

Peatland ecosystems are one of the most important stocks of terrestrial carbon (C), accounting for an estimated one third of all global soil C stocks (Gorham 1991). Northern peatlands develop under conditions of waterlogging, low nutrient availability and low temperatures that limit the activity of

decomposer organisms leading to an accumulation of organic matter (Bubier and others 1998; Maltby and Immirzi 1993). These C rich ecosystems are currently considered to be net sinks for atmospheric carbon dioxide (CO_2) (Maljanen and others 2001; Martikainen and others 1995; Charman 2002; Roehm and Roulet 2003), with C inputs from plant photosynthesis exceeding losses from plant and soil respiration. However, there is concern that climate change and disturbances such as wildfires may increase rates of decomposition, resulting in

peatlands becoming a net C source (for example, Roulet and others 2007; Nykanen and others 2003; Turetsky and others 2002). Climate is recognized as the primary driver of peatland CO_2 production, with changing temperatures (Lafleur and others 2001; Updegraff and others 2001) and hydrology (Freeman and others 1997, 2004a, b; Lafleur and others 2003; Silvola and others 1996) having the potential to increase decomposition rates. This is important considering that climate change scenarios predict that greatest global temperature increases will occur at higher latitudes (IPCC 2001, 2007), where high C storage ecosystems, such as peatlands and boreal forests, are located.

Land use also represents a globally important driver of ecosystem structure and function (Vitousek and others 1997) with implications for biogeochemical cycling (Chapin and others 1997; Bardgett 2005). For example, land-use change is identified as a cause of soil C losses over the last century, primarily as a result of deforestation in the tropics (Houghton 2003; Schimel 1995). For the most part, northern peatlands remain relatively unaffected by direct human activity except in areas of high population density such as northern Europe where they can be under considerable pressure. In the UK and other parts of Europe, for example, upland peatlands are generally considered to be of limited agricultural value (Heal and Smith 1978), although they have historically been used for forestry, as a source of fuel or horticulture medium, for livestock grazing and game bird breeding, and for recreational use. There is evidence that the removal of peat for fuel or horticulture drastically reduces C storage (Immirzi and others 1992) and afforestation has been shown to increase soil microbial activity and C loss through decomposition (Brake and others 1999; Maljanen and others 2001; Martikainen and others 1995). In the UK low-density sheep grazing has been occurring for over 2,000 years and habitat management for game birds, which necessitates periodic controlled burning, since the early 1800s (Simmons 2003). Both practices are recognized as important drivers of vegetation change (Miles 1988; Bardgett and others 1995), holding back natural vegetation succession to woodland below the tree line (Gimingham 1960; Rodwell 1991). Also, both grazing (Diaz and others 2007; Bardgett and others 1998, 2001, 2005; Bardgett and Wardle 2003) and burning (Bergner and others 2004; Treseder and others 2004; Wardle and others 2003) are known to directly affect plant community composition and indirectly affect the activity of decomposer organisms, thereby potentially altering ecosystem C fluxes.

Many studies have considered the effects of intensive land uses including drainage, forestry and restoration on northern peatland C dynamics (for example, Freeman and others 2004a, b; Nieminen 2004; Strack and others 2004). Less, however, is known about the combined effects of low-density grazing and controlled fires that are a feature of upland peatlands. Rough livestock grazing is recognized as the primary driver of habitat form and function with an estimated 14,150 km^2 (that is, approximately 10%) of England and Wales being subjected to low-density sheep grazing (Bardgett and others 1995). Habitat management for game bird populations (Red Grouse, *Lagopus lagopus*) is also a feature of many UK peatlands where the land is often too poor for agriculture (Simmons 2003). In England and Wales alone, this activity occupies 400,000 ha, making grouse shooting worth more than £10 million y^{-1}. Managed burning in the English uplands is now widespread on peatland with 17% of the area of this habitat having been burned within the previous four years, equivalent to 114 km^2 y^{-1} (Yallop and others 2006). There has also been a significant increase in the extent of new burns (from 15.1 to 29.7%) in the past 20 years (Yallop and others 2006). Despite the prevalence of grazing and controlled burning, the interactive effects of these land uses on ecosystem carbon dynamics are not well understood.

In this study, we examined the long-term consequences of regular disturbance from the practices of controlled vegetation burning and sheep grazing (in isolation and in combination) on vegetation community composition, C stocks, dissolved organic carbon (DOC), carbon dioxide (CO_2) and methane (CH_4) fluxes. We determined C stocks in peat and vegetation, and measured C fluxes from a 50-year-old factorial burning and grazing field experiment, established at Moor House National Nature Reserve (NNR) in northern England in 1954 (Hobbs 1984; Garnett and others 2000). The use of long-term field experiments is widely recognized as being of great value for investigating effects of land management and biodiversity on ecosystem properties, including plant productivity and nutrient cycling (Tilman and Downing 1994; Bardgett and others 1997; Silvertown and others 2006; Spiegelberger and others 2006). This unique 50-year experiment was used to test the hypothesis that long-term land use practices of burning and grazing will reduce ecosystem C stocks and increase gross CO_2 fluxes as a result of changes in vegetation composition and soil biological activity. Previous studies have examined the effects of burning and/or grazing on plant productivity and composition (Heal and Smith 1978; Hobbs 1984;

Rawes [1983]; Rawes and Hobbs [1979]) and soil C storage (Garnett and others [2000, 2001]) in isolation, but, as far as we are aware, no studies have taken an integrated approach to examine how grazing and burning affect both soil and vegetation properties and ecosystem C cycling. We aim, therefore, to provide a greater understanding of how long-term grazing and burning control C dynamics in these C rich ecosystems.

MATERIALS AND METHODS

Study Site and Experimental Design

The experiment is located on an area of acidic ombrogenous upland blanket peat at Moor House NNR, in the North Pennines of northern England (54°65′N, 2°45′W), formally a site for the International Biological Programme (Heal and Perkins [1976]). The climate is described as sub-arctic oceanic with mean monthly temperature of approximately 10°C and average annual precipitation of 1,900 mm (see http://www.ecn.ac.uk). The experiment extends across an area of 1 km^2 and consists of four replicate treatment blocks on a 10° southeast facing slope, at an altitudinal range of 590–630 m (Hobbs [1984]). The peat, belonging to the Winter Hill Association (Soil Survey of England and Wales) is 1–2 m thick (Garnett and others [2000]) and the vegetation is classified as *Calluna vulgaris–Eriophorum vaginatum* blanket mire, *Empetrum nigrum* ssp *nigrum* sub-community M19b according to the UK National Vegetation Classification (NVC) (Rodwell [1991]). The experiment is composed of fully factorial experimental plots that have been subjected to a range of burning and grazing treatments since 1954. At the time of this study, the site was 9 years into a 10-year burning cycle, and grazing levels were low, estimated at 0.04 sheep ha^{-1} in the summer. In 1954 when the experiment was started, the whole area underwent a controlled burn. Each block is composed of six 10 by 30 m treatment plots. Within each block, the plots were subjected to different burn cycles: every 10 years, every 20 years or, not burned since 1954 (Rawes and Hobbs [1979]) and half of the treatment plots are fenced off to prevent grazing. This study used only the ten-year burn and unburned treatments, for both grazed and ungrazed areas, to give a 2 × 2 factorial design of four different land use treatment combinations, with four repetitions of each ($n = 16$ total). Treatments studied were as follows: (1) no burn and ungrazed; (2) 10-year burn and ungrazed; (3) no burn and grazed; and (4) 10-year burn and grazed.

Vegetation Community Composition

Vegetation community composition was determined by measuring the quantity (g dry weight) of live aboveground shoots for each species present. Material was collected from an area 25 cm^2 within each replicated treatment plot at quarterly intervals in April 2003 (spring), August 2003 (summer), November 2003 (autumn), February 2004 (winter), and May 2004 (spring), and dried at 105°C before weighing. Results were subsequently grouped into the three functional types present: graminoids (dominant species *E. vaginatum*), ericoid sub-shrubs (dominant species *Calluna vulgaris*) and bryophytes (dominant species *Pleurozium schreberi*).

Carbon Stocks

Sampling of C stocks in the peat horizons was divided into three categories: (1) organic ('*O*') horizons to a depth of 1 m; (2) *F* and *H* horizons (Avery [1980]); and (3) litter. For the purposes of this study, *F* and *H* horizon samples included living plant roots and associated mycorrhizal fungi; the litter layer included loose plant litter on the peat surface plus standing dead plant material. Samples were collected from a randomly selected area within each sampling plot ($n = 16$) in May 2004. Litter and the *F* and *H* horizon material was collected from an area measuring 25 cm^2. Peat '*O*' horizon cores 1 m deep and 5 cm × 5 cm in diameter were taken using a metal peat square corer (Cuttle and Malcolm [1979]). All samples were oven-dried at 105°C to ascertain dry weights. Sub-samples of peat material and aboveground vegetation were then ground and stored in airtight glass vials. A 20-mg sample of each was subsequently analyzed for total C and N by oxidative combustion, followed by thermal conductivity detection using an Elementar Vario EL analyzer. Total C and N stocks for peat and vegetation were calculated using the dry weights, C and N content, and, for the peat '*O*' horizon, bulk density measurements at 10-cm depth increments.

Peat Microbial Properties and N Availability

Peat was sampled at quarterly intervals to measure microbial properties and N availability. Five cores of 3-cm diameter and 10-cm depth were collected from a randomly selected area within each field-sampling plot in August 2003 (summer), November 2003 (autumn), February 2004 (winter) and May 2004 (spring). Cores were stored in airtight polythene bags at 4°C and then bulked, homogenized and any root material removed immediately prior

to analysis. Samples were analyzed for N availability by measuring the concentration of inorganic N (NH_4^+ and NO_3^-), potential rates of N mineralization and water extractable dissolved organic N (DON). Additional measurements of total water extractable organic C (TOC) and microbial biomass C and N were made. All procedures were in accordance with those in Bardgett and others (2002). Briefly, inorganic N concentration was measured by potassium chloride (KCl) extraction, followed by measurement of the concentration of ammonium–N (NH_4^+–N) and nitrate–N (NO_3^-–N) by colorimetric technique (Ross 1992), on a continous flow stream AutoAnalyser (Bran and Luebbe, Northampton, UK). This method was repeated on a second set of samples after incubation at $25°C$ for 14 days. Potential N mineralization was then calculated as the difference between the incubated and non-incubated sample results (Ross 1990). Soil microbial biomass C and N was measured by fumigation-extraction (Brookes and others 1985; Vance and others 1987), using ethanol-free chloroform ($CHCl_3$) as the fumigant following by extraction with potassium sulphate (K_2SO_4). Resultant filtrates were analyzed for extractable microbial C using a Shimadzu 5000A TOC analyzer (Shimadzu, Milton Keynes, UK). Extractable microbial biomass N was measured from the filtrate that had first undergone oxidation with potassium persulphate ($K_2S_2O_8$), by mixing 1.5 ml filtrate with 4.5 ml of 0.165 M $K_2S_2O_8$ then autoclaving for 30 min at $121°C$ (Ross 1992). These autoclaved samples were analyzed for NH_4^+–N and NO_3^-–N by colorimetric technique, as above. Extractable microbial biomass C and N flush was calculated by subtracting the results of the non-fumigated from the fumigated samples. Values were then converted using extraction coefficients to take into account incomplete extraction (Vance and others 1987) of 0.35 for K_{ec} (Sparling and others 1990) and 0.54 for K_{en} (Brookes and others 1985).

Trace Gas Fluxes

The study of C fluxes concentrates on CO_2, which constitutes the main land to atmosphere exchange of C in peatlands (Johnson and others 2000; Moore and others 2002), but also considers CH_4 and DOC. Measurements of CO_2 and CH_4 fluxes were made between May 2003 and September 2004 at approximate monthly intervals using a calibrated static chamber approach (Livingston and Hutchinson 1995). This technique is commonly used in peatland and high latitude systems where rates of biological activity can be very low (Nykanen and

others 2003; Waddington and Roulet 2000). A pair of plastic base rings, of 30-cm diameter and 20-cm height, were sunk into randomly located areas within each sampling plot in May 2003. The upper part of each chamber (height 35 cm) was constructed from 30-cm diameter plastic soil pipe and clear plastic plant cloches (Haxnicks, UK) fitted with a self sealing rubber septa for gas collection. One of the pair of chamber lids was left clear to allow penetration of light to measure net CO_2 fluxes from the processes of both respiration and photosynthesis. The other was covered to block out photosynthetically active radiation (PAR), thus measuring gross CO_2 fluxes of ecosystem respiration only. The gross flux of respiration measured in this experiment represents both above- and belowground components, that is, plant shoots and roots, soil microbes, mycorrhizal fungi and soil fauna. Gross photosynthetic fluxes were estimated from the difference between the net flux and the respiration flux, using the light and dark chamber technique (Heikkinen and others 2002; Nykanen and others 2003).

Sampling commenced at 12 noon ± 1 h by sealing a chamber lid onto its base ring using a rubberized band. A 20-ml sample of gas was collected through the septum, using a 20-ml luer lock syringe fitted with a 0.5-mm needle, flushed three times before the final filling. Gas samples were transferred into evacuated 12-ml exetainers (Labco Ltd, UK) for storage at field sampling temperature prior to laboratory analysis. A repeat gas sample was taken from each chamber after approximately 2 h duration, with the exact times noted. The exetainers were checked for leakage over an 8-week storage period and there was no statistically significant change in CO_2 concentrations. Climatic and physical conditions in the field were recorded for each sampling visit. This included soil, air and chamber temperatures, measured using a 'Tinyview' temperature logger (Gemini Data Loggers, UK); PAR recorded at vegetation height using a PAR sensor (Skye Instruments, UK); and water table levels from 16 randomly placed dip wells using a meter rule. Use was also made of data collected at the Moor House Automatic Weather Station (AWS) maintained by the UK Environmental Change Network (ECN), in accordance with standard protocols (Sykes and Lane 1996).

All gas samples were analyzed upon return to the laboratory for CO_2 and CH_4 concentrations by gas chromatography, on a Perkin Elmer Autosystem XL GC with Flame Ionization Detector (FID) containing a methanizer. The injector temperature was $150°C$, the detector temperature was $350°C$ and a

2 m Poropak Q 50–80-mesh column in the oven was operated at 40°C. Results were calibrated against certified gas standards comprising 500 ppm CO_2 and 10 ppm CH_4 in N_2 (Air Products, UK). Gas fluxes were adjusted for differences in field sampling temperatures and calculated on a per hour basis using the difference in concentrations between start and end times (Holland and others 1999).

Soil Solution DOC

Soil water samples were collected monthly between June 2003 and May 2004 at depths of 10 cm below the surface (where water table levels fluctuated seasonally) and 50 cm below the surface (below normal water table level). Access to the two depths was from a 60-cm deep plastic bin sunk into the soil through which collection tubes containing glass wool as a filter were inserted horizontally into the soil to approximately 20 cm away from the bin. The soil solution was collected by low suction pressure, applied using luer lock syringes attached to the free end of the length of plastic tubing. All water samples were double filtered within 48 h of collection. A GFC filter paper (Whatman, UK) rinsed with deionized water was used as a coarse pre-filter, followed by final filtering using 0.45-µm cellulose nitrate filter paper (Whatman, UK). Filtered samples were stored in glass containers at 4°C prior to chemical analysis. All samples were analyzed on a Skalar continuous flow colorimetric system (Skalar BV, Netherlands) by the phenolthalein indirect method, with a detection limit of 0.5 mg l^{-1}, in accordance with standard protocols.

Statistical Analysis

All statistical analyses were carried out using SAS V9.1, Enterprise 3.0. Carbon fluxes of CO_2, CH_4 and DOC were analyzed using a mixed model ANOVA, with repeated measures. Soil microbial activity and total C stocks in soils and vegetation were analyzed by ANOVA using generalized linear models. Residuals plots for all data were checked for normality, and any set of non-normal variables were log transformed before final analysis. Correlations were made by Spearman ranking.

RESULTS

Vegetation Community Composition

Changes in the relative contribution of the three plant functional groups present were observed due to burning and grazing (Figure 1), with the greatest
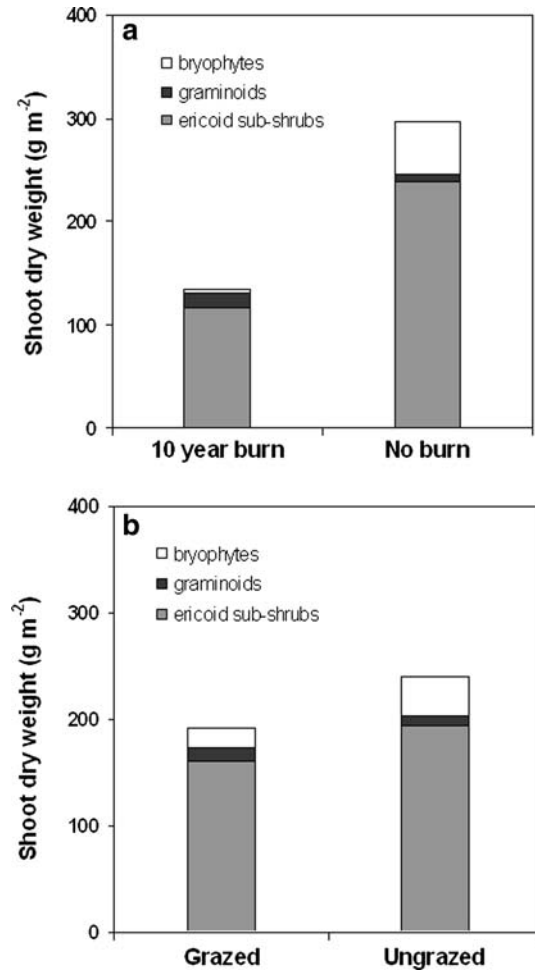

Figure 1. Live vegetation shoot biomass for (**a**) burn and no burn treatments and (**b**) grazed and ungrazed treatments, subdivided into the three plant functional groups. Values are means of all quarterly measurements (dry weight g m^{-2}).

effects being due to burning (Figure 1A). Burning increased the biomass of graminoids by 88% relative to unburned controls ($F_{1,71} = 7.18$, $P = 0.009$), but reduced the biomass of shrubs and bryophytes by 51% ($F_{1,72} = 26.56$, $P < 0.0001$) and 92% ($F_{1,54} = 38.76$, $P < 0.0001$), respectively. The change in vegetation composition due to grazing was similar (Figure 1B), but of smaller magnitude. An 18% reduction in shrub biomass ($F_{1,72} = 4.18$, $P = 0.05$) and a 47% reduction in bryophytes ($F_{1,54} = 6.15$, $P = 0.02$) relative to ungrazed plots was observed, and there was no effect of grazing on the biomass of graminoids ($F_{1,71} = 0.98$, $P = 0.33$).

Carbon Stocks

Peat and vegetation C stocks, split between the burning and grazing treatments, are shown in Ta-

Table 1. Total C and N Stocks in Soils and Vegetation

	Total C storage (kg m^{-2})	Total N storage (kg m^{-2})	C:N ratio
Peat 'O' horizons to 1 m depth			
Burn	50.409 (±0.728)	1.3460 (±0.0396)	37.5
No burn	49.625 (±0.676)	1.3224 (±0.0324)	37.5
Grazed	49.942 (±0.745)	1.3266 (±0.0381)	37.6
Ungrazed	50.076 (±0.660)	1.3413 (±0.0340)	37.3
ALL (mean)	**50.010** (±0.496)	**1.3340** (±0.0254)	**37.5**
F and H horizons			
Burn	0.114 (±0.004) *	0.0036 (±0.0003) *	31.7
No burn	0.281 (±0.027) *	0.0074 (±0.0007) *	38.0
Grazed	0.213 (±0.096)	0.0060 (±0.0021)	35.5
Ungrazed	0.182 (±0.072)	0.0050 (±0.0017)	36.4
ALL (mean)	**0.198** (±0.035)	**0.0055** (±0.0009)	**36.0**
Litter			
Burn	0.079 (±0.001)	0.0023 (±0.0001)	34.3
No burn	0.085 (±0.024)	0.0026 (±0.0009)	32.7
Grazed	0.070 (±0.009)	0.0020 (±0.0003)	35.0
Ungrazed	0.095 (±0.015)	0.0030 (±0.0005)	31.7
ALL (mean)	**0.082** (±0.008)	**0.0025** (±0.0003)	**32.8**
Vegetation (live shoots)			
Burn	0.069 (±0.007) **	0.0013 (±0.0001) **	53.1
No burn	0.157 (±0.009) **	0.0027 (±0.0002) **	58.1
Grazed	0.099 (±0.010) *	0.0018 (±0.0002) *	55.0
Ungrazed	0.127 (±0.011) *	0.0022 (±0.0002) *	57.7
ALL (mean)	**0.113** (±0.008)	**0.0020** (±0.0001)	**56.5**
Total			
Burn	50.671 (±0.74)	1.353 (±0.04)	37.5
No burn	50.148 (±0.74)	1.335 (±0.03)	37.6
Grazed	50.324 (±0.86)	1.336 (±0.04)	37.7
Ungrazed	50.480 (±0.76)	1.352 (±0.04)	37.3
ALL (mean)	**50.403** (±0.55)	**1.344** (±0.03)	**37.5**

Values are mean ± SE, **significant difference at the P < 0.001 level, *significant difference at the P < 0.05 level.

ble 1. Differences in C stocks were observed in the aboveground vegetation and upper peat horizons only. The F and H horizon of burned plots contained 60% less C ($F_{1,16} = 8.59$, $P = 0.011$) than the unburned controls. For aboveground vegetation, the greatest change in C stocks was due to burning, with a 56% reduction relative to the unburned control. In addition, the C:N ratio of plant shoots was greater in the burned plots than in the unburned controls, being 58.1 and 53.1, respectively, which can be largely attributed to the changes in relative contribution of the three plant functional groups present (Figure 1A). Grazing also reduced the amount of C contained within aboveground vegetation by 22% ($F_{1,74} = 7.99$, $P = 0.006$) relative to the ungrazed control. Neither burning nor grazing affected total ecosystem C storage when sampled to a depth of 1 m. This was due to the greatest stocks (over 99%) being contained within the soil 'O' horizon, which was unaffected by either burning or grazing.

Soil Microbial Properties and Nutrient Availability

Burning and grazing had a limited influence on soil microbial properties (Table 2). The only significant response was a 50% greater microbial biomass C:N ratio during the spring and summer in burned compared to unburned controls ($F_{1,48} = 9.98$, $P = 0.0033$). Although not significant, rates of N mineralization were 20–30% lower after burning ($F_{1,64} = 3.79$, $P = 0.058$) for all sampling dates except summer (Table 2).

Seasonal differences in soil N availability were detected across all treatments. For example, concentrations of inorganic N in soil were twice as high in spring and summer than at autumn and winter sampling dates ($F_{3,63} = 15.40$, $P < 0.0001$). Potential N mineralization was greatest in the winter and lowest in spring ($F_{3,63} = 8.22$, $P = 0.0002$), and water extractable DON peaked in spring ($F_{3,64} = 55.64$, $P < 0.0001$). DOC concentrations

Table 2. Seasonal Soil Microbial Activity

Variable	August 2003	November 2003	February 2004	May 2004
Inorganic N (μg N cm^{-3})	3.22 ($\pm$0.41)a	1.48 ($\pm$0.07)b	1.73 ($\pm$0.21)b	3.27 ($\pm$0.27)a
N mineralization (μg cm^{-3} day^{-1})	0.94 ($\pm$0.08)ab	0.86 ($\pm$0.14)bc	1.33 ($\pm$0.10)a	0.59 ($\pm$0.06)c
Water extractable C (μg C cm^{-3})	177.63 ($\pm$6.69)a	133.62 ($\pm$8.92)b	91.95 ($\pm$4.59)c	225.00 ($\pm$8.74)d
Water extractable N (μg N cm^{-3})	3.12 ($\pm$0.23)a	9.96 ($\pm$1.30)b	10.30 ($\pm$1.74)b	39.14 ($\pm$5.55)c
Microbial biomass C (μg C cm^{-3})	499.40 ($\pm$3.30)ab	725.50 ($\pm$93.40)a	550.10 ($\pm$56.10)a	420.00 ($\pm$42.10)b
Microbial biomass N (μg N cm^{-3})	31.29 ($\pm$3.25)a	70.52 ($\pm$6.89)b	65.98 ($\pm$6.89)b	66.70 ($\pm$7.40)b

Values are mean ± SE. Within each variable, values with the same letter are not significantly different at the P < 0.05 level.

were greatest in spring and summer, but lowest in winter ($F_{3,64}$ = 59.18, P < 0.0001). Seasonal patterns were also detected for soil microbial biomass (Table 2); in summer, microbial biomass N fell to below half the value of all other sampling dates ($F_{3,62}$ = 8.64, P = 0.0001). Microbial biomass C was only weakly affected by season, being maximal in autumn. As a result, microbial C:N was greatest in summer and lowest in spring ($F_{3,48}$ = 12.43, P < 0.0001).

Ecosystem CO$_2$ Fluxes

Burning and grazing had significant effects on net and gross CO$_2$ fluxes (Table 3). The greatest effects were observed in the burning treatment (Figures 2, 3), where rates of respiration and photosynthesis were greater relative to unburned treatments ($F_{1,213}$ = 13.46, P = 0.002 for respiration and $F_{1,207}$ = 27.53, P < 0.0001 for photosynthesis). Grazing increased rates of respiration ($F_{1,213}$ = 3.93, P = 0.063) and photosynthesis ($F_{1,207}$ = 10.81, P = 0.003) relative to ungrazed plots, but to a lesser extent than the burning treatment (Figure 3). Net CO$_2$ fluxes were also affected by burning ($F_{1,230}$ = 17.43, P = 0.0002), with burned plots acting as a slightly larger sink for CO$_2$ than the unburned plots for 14 out of the 15 sampling dates. The grazing treatment similarly affected net fluxes ($F_{1,230}$ = 8.47, P = 0.0059), with grazed plots acting as greater net sinks for CO$_2$ than ungrazed plots for 10 of the 15 dates sampled. There were no interactive effects of burning and grazing on gross or net CO$_2$ fluxes ($F_{1,213}$ = 3.51, P = 0.076 for respiration, $F_{1,207}$ = 2.95, P = 0.098 for photosynthesis, $F_{1,207}$ = 0.15, P = 0.701 for net flux). Significant interactions occurred between the date of sampling and burning ($F_{1,213}$ = 2.28, P = 0.009 for respiration, $F_{1,207}$ = 1.87, P = 0.038 for estimated photosynthesis and $F_{1,230}$ = 2.24, P = 0.010 for net flux). Interactions between sampling date and grazing were only significant for net

Table 3. Effects of Sampling Date, Burning and Grazing on CO$_2$ Fluxes

Source of variation	df	F	P
Respiration			
Sampling date	14	43.19	**<0.0001**
Burning	1	13.46	**0.0017**
Grazing	1	3.93	0.0625
Burning × grazing	1	3.51	0.0759
Burning × sampling date	14	2.28	**0.0087**
Grazing × Sampling date	14	0.88	0.5868
Estimated photosynthesis			
Sampling date	14	52.31	**<0.0001**
Burning	1	27.53	**<0.0001**
Grazing	1	10.81	**0.0031**
Burning × grazing	1	2.95	0.0979
Burning × sampling date	14	1.87	**0.0380**
Grazing × sampling date	14	0.97	0.4933
Net flux			
Sampling date	14	14.25	**<0.0001**
Burning	1	17.43	**0.0002**
Grazing	1	8.47	**0.0059**
Burning × grazing	1	0.15	0.7010
Burning × sampling date	14	2.24	**0.0104**
Grazing × sampling date	14	2.83	**0.0012**

P values in bold are statistically significant (P < 0.05)

CO$_2$ fluxes ($F_{1,230}$ = 2.83, P = 0.001). In all cases, the increases in CO$_2$ fluxes due to burning and grazing were greatest during spring and summer and lowest during the winter months.

Seasonality accounted for more variation in CO$_2$ flux than did the land-use treatments (Table 4); we detected significant temporal variation for net ($F_{14,230}$ = 14.25, P < 0.0001) and gross fluxes of respiration ($F_{14,213}$ = 41.39, P < 0.0001), and for photosynthesis ($F_{14,207}$ = 52.31, P < 0.0001). Gross CO$_2$ fluxes were lowest during the winter and greatest during the summer, peaking at 746.7 ($\pm$64.9) mg m^{-2} h^{-1} for respiration and −912.6 ($\pm$87.9) mg m^{-2} h^{-1} for estimated photosynthesis in August 2003. Respiration and photosynthesis
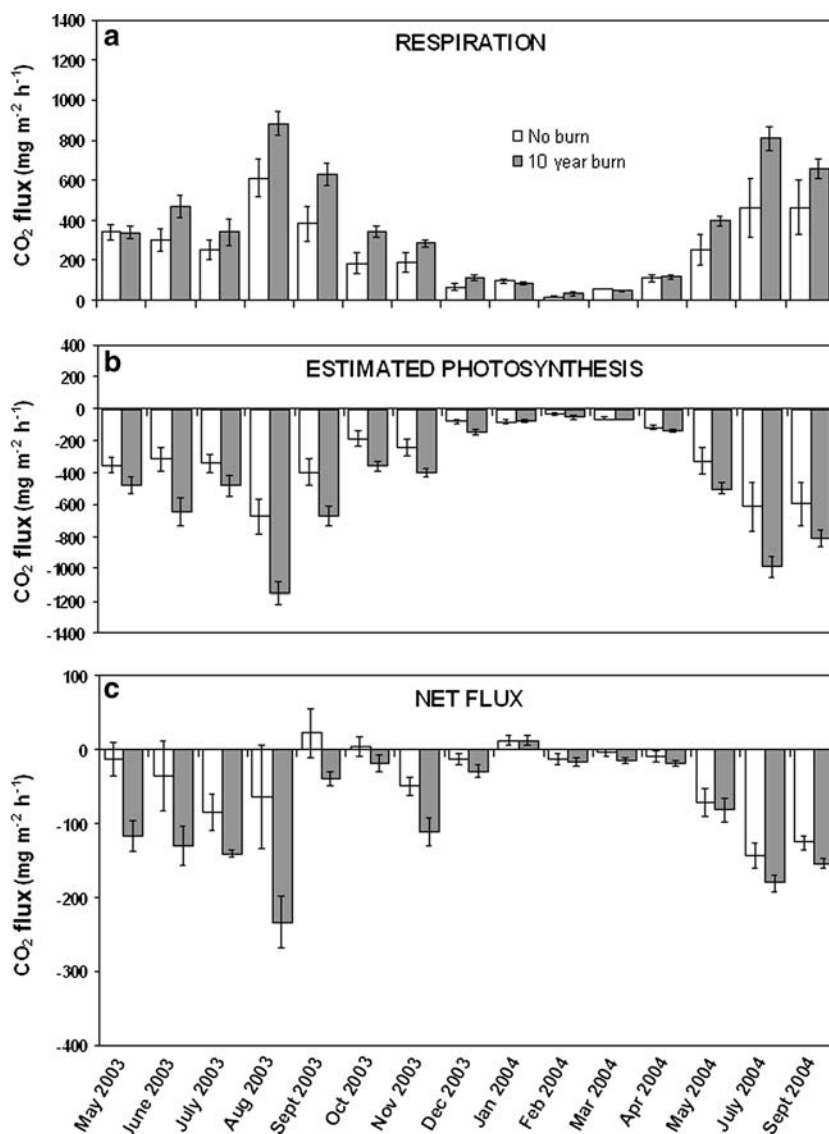
Figure 2. CO_2 fluxes: (**a**) respiration, (**b**) estimated photosynthesis and (**c**) net, for all sampling days, showing comparisons between 10-year burn and no-burn treatments. Values are mean ± SE. *Positive values* indicate a release of CO_2 and negative numbers, an uptake of CO_2.

were roughly in equilibrium from late autumn to early spring, as evidenced by the net CO_2 flux of around zero for most of the sampling dates (Figures 2, 3). During the summer, however, negative net fluxes indicated that the field site was a sink for CO_2 at the peak of primary productivity. Correlations between CO_2 fluxes and a range of environmental variables measured on the day of sampling show that both net and gross CO_2 fluxes were most strongly correlated with temperature and solar radiation (Table 4).

CH₄ Fluxes and DOC in Soil Solution

Burning reduced net CH_4 fluxes on 12 out of the 15 sampling dates, with a mean reduction of 12% relative to unburned plots ($F_{1,206} = 5.46$, $P < 0.0207$). Grazing had a greater effect, signifi-

cantly increasing CH_4 effluxes on all sampling dates, with an average increase of 115% relative to ungrazed plots ($F_{1,206} = 23.43$, $P < 0.0001$). There was a significant interaction between burning and grazing ($F_{1,206} = 13.70$, $P = 0.0003$) with the lowest CH_4 fluxes occurring in the no burn, ungrazed plots. CH_4 fluxes varied with the seasonal sampling date ($F_{14,206} = 6.33$, $P < 0.0001$) and correlated most strongly with soil temperature (Table 4). Greatest fluxes were observed during summer (Figure 4). As well as the land use and seasonal effect, a significant difference between the four sampling blocks occurred ($F_{3,206} = 6.16$, $P = 0.0006$) with the lower altitude block having a greater net CH_4 flux than the other three blocks.

DOC was only affected by grazing, with greater concentrations at 10 cm depth relative to ungrazed plots ($F_{1,171} = 6.72$, $P = 0.011$). This effect was

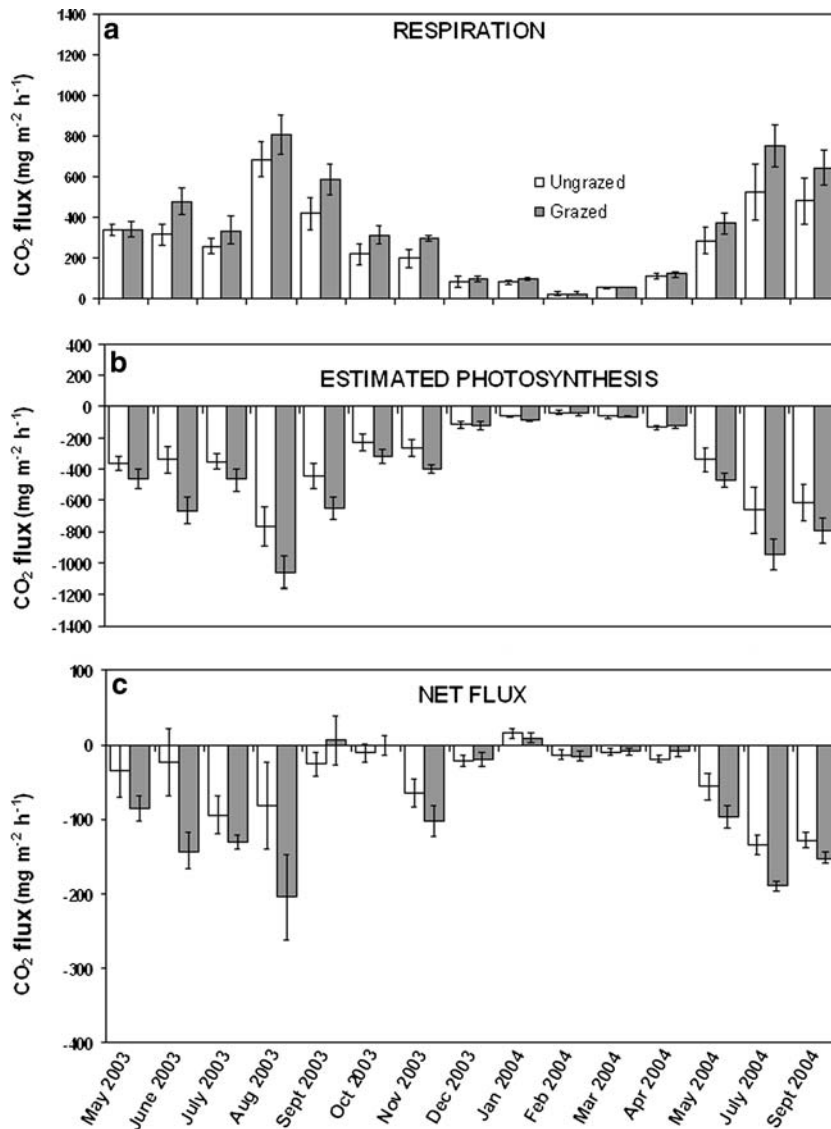**Figure 3.** CO_2 fluxes: (**a**) respiration, (**b**) estimated photosynthesis and (**c**) net, for all sampling days, showing comparisons between grazed and ungrazed treatments. Values are mean ± SE. *Positive values* indicate a release of CO_2 and negative numbers, an uptake of CO_2.

small (∼7%) and inconsistent over time, being detected at only 7 of the 12 sampling dates. There was much temporal variation in DOC at both 10 cm depth ($F_{11,171}$ = 51.39, $P < 0.0001$) and 50 cm depth ($F_{11,181}$ = 8.64, $P < 0.0001$), reaching their maximum in summer when concentrations were greater at 10 cm than 50 cm depth (Figure 5). DOC was most strongly correlated with soil temperature and water table levels but there was no significant effect of grazing and burning treatment on water table depth (Table 4).

DISCUSSION

The unique Hard Hill 50-year burning and grazing experiment provided an opportunity to investigate effects of land-use disturbances on peatland C dynamics. Our results show that long-term land management has significantly affected both the surface storage and flux of C in peatland, and that these effects are strongly related to the changes in vegetation that result from burning and grazing. Furthermore, we found that different management regimes have contrasting effects on C dynamics, which appear to relate to the intensity of disturbance and the magnitude of vegetation change.

Management practices of regular burning and grazing reduced aboveground C by 56 and 22%, respectively, and reduced C storage in the surface *F* and *H* horizons by 60% in the case of burning. This reduction in surface C, however, was not detected in terms of total ecosystem storage, presumably because the bulk of C (99%) in these ecosystems is at depth. Overall, regular burning (that is, 10-year cycle) led to a loss of 167 g C m^{-2} from the peat surface and 88 g C m^{-2} from aboveground vege-

Table 4. Climatic Variables and their Correlation with C Fluxes

|	Air temperature (°C)	Soil temperature (°C)	PAR (µmol m^{-2} s^{-1})	Water table (cm below surface)	Rain 1 week prior to sampling (cm)
Sample date					
May 2003	17.4	8.8	899	9.3	0.11
June 2003	18.5	10.4	1,270	17.1	0.07
July 2003	12.3	11.6	275	16.9	0.11
August 2003	23.6	12.5	1,573	13.8	0.23
September 2003	10.6	9.8	840	28.6	0.02
October 2003	6.3	6.4	203	4.2	0.13
November 2003	10.8	6.7	443	7.1	0.33
December 2003	−0.9	1.1	285	7.1	0.10
January 2004	4.3	3.5	128	4.2	0.86
February 2004	−0.7	1.5			0.45
March 2004	1.1	0.4	295	5.1	0.42
April 2004	3.4	2.5	450	3.0	0.27
May 2004	13.7	8.2	1,740	16.5	0.00
July 2004	17.0	10.4	1,647	3.9	0.00
September 2004	14.4	10.1	1,303	7.7	0.21
Correlation coefficient (R^2)					
Respiration (mg m^{-2} h^{-1})	**0.687**	**0.699**	**0.527**	**0.390**	**−0.370**
Photosynthesis (mg m^{-2} h^{-1})	**−0.731**	**−0.752**	**−0.575**	**−0.418**	**0.387**
Net CO$_2$ flux (mg m^{-2} h^{-1})	**−0.566**	**−0.592**	**−0.516**	−0.231	0.213
Net CH$_4$ flux (mg m^{-2} h^{-1})	**0.280**	**0.365**	**0.235**	0.074	−0.078
DOC at 10 cm depth (mg l^{-1})	**0.505**	**0.667**	0.115	**0.545**	−0.302
DOC at 50 cm depth (mg l^{-1})	**0.478**	**0.627**	0.047	**0.436**	−0.304

R^2 values in bold are statistically significant (P < 0.05).
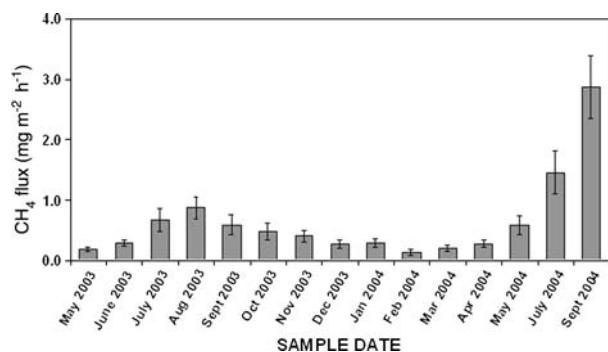
Figure 4. CH$_4$ fluxes integrated across all land-use treatments. Values are mean ± SE.

tation. Assuming losses of this size after every 10-year burning event, the total C loss attributable to burning is estimated to be 25.5 g C m^{-2} y^{-1}. This compares to an estimated peat C loss of 73 g C m^{-2} y^{-1} suggested by Garnett and others (2001) at the same field site, measured 3 years into the 10-year cycle, using spheroidal carbonaceous particles as a marker to date soil accumulation after burn events. The surface peat and litter hosts the majority of living organisms and is the most bio-

logically active zone of the peatland (Collins and others 1978; Cole and others 2000; Charman 2002). Therefore, disturbances in this zone are likely to be of high significance for ecosystem C dynamics. The lack of effect of land use on total ecosystem C storage was not unexpected, because over 99% of total C is contained within the deep peat organic horizons, which have been accumulating at the site over five to six thousand years (Heal and Perkins 1976).

Fluxes of CO$_2$ from peatland were strongly affected by the long-term burning and grazing treatments (Figures 2, 3). Both the gross CO$_2$ fluxes of respiration and photosynthesis increased as a result of 10-year burning, indicating a long-term acceleration of C processing rates at the ecosystem scale. Burning also created a greater net sink for CO$_2$ by increasing photosynthesis at a greater rate than respiration, as shown by the net CO$_2$ flux results (Figure 2). The effects of grazing on CO$_2$ fluxes were similar to those from burning, but of a lower magnitude. Grazing stimulated rates of biological processes, as evidenced by the increase in respiratory and photosynthetic fluxes, and grazing also reduced net CO$_2$ flux. There were no signifi-
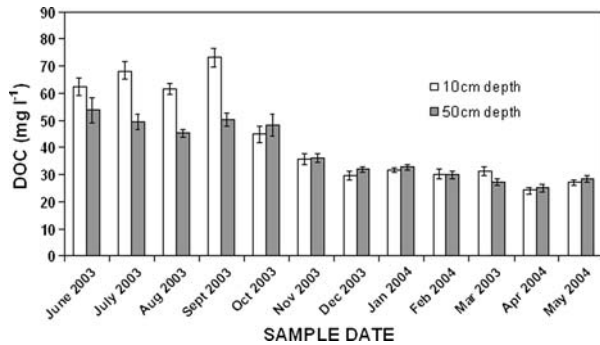
Figure 5. DOC concentration is soil solution integrated across all land-use treatments; *Open box* 10-cm depth. *Filled box* 50-cm depth. Values are mean ± SE.

cant interactions between burning and grazing. Collectively, these observations suggest that long-term disturbance from burning and grazing increases ecosystem process rates and gross CO_2 fluxes, and reduces net ecosystem CO_2 efflux, and that extent of effect is related to the level of disturbance. This is in agreement with findings by Wardle and others (2003) and DeLuca and Zouhar (2000), who similarly observed increases in ecosystem process rates related to C cycling in boreal forests subject to higher fire frequency.

Long-term peatland burning and grazing significantly altered the relative contribution of the three dominant plant functional groups present. Graminoids, which have a relatively fast recovery time after disturbance, were favored over slow-growing shrubs and bryophytes in both burned and grazed treatments (Figure 1). Changes in vegetation composition have the potential to alter the rate of ecosystem processes through differences in plant functional traits such as nutrient use efficiency and leaf life span (Aerts and others 1999; Westoby and others 2002), tissue phenolic and lignin content (Bardgett 2005; Hobbie 1992), or litter nutrient content (Hector and others 2000; Melillo and others 1982; Wardle and others 1997). Consistent with this, we found that burning reduced the C:N ratio of vegetation and the peat *F* and *H* horizon relative to unburned controls. This was attributed to differences in the C and N content of individual species present within the plant community, that is, the replacement of C rich, N poor shrubs, such as *Calluna vulgaris*, with relatively N rich graminoids such as *E. vaginatum*. The lower C:N ratio of vegetation is likely to enhance the decomposability of litter in burned treatments, which in turn could feedback to the plant community via enhanced nutrient cycling, thereby stimulating rates of primary productivity. Despite these changes in

resource quality, we detected no overall response in either peat microbial biomass or nutrient availability after burning and grazing, aside from an increase in peat microbial biomass C:N ratio during the spring and summer in burned plots relative to controls (Table 4). This suggests that the peat decomposer community was not particularly sensitive to either land use or consequent changes in vegetation community composition. This result is perhaps surprising, given that previous studies have shown these measures to be responsive to the manipulation of plant functional groups, including ericaceous shrubs, in boreal ecosystems (Wardle and Zackrisson 2005).

Although peatland CO_2 fluxes were responsive to burning and grazing, the main factor controlling both gross and net fluxes of CO_2 was seasonal changes in climate. An interaction between the effects of land use and seasonality was also seen, evidenced by the more pronounced increase in CO_2 fluxes in burned and grazed plots during the growing season, when fluxes were of a higher magnitude. We found that CO_2 fluxes correlated most closely with temperature and PAR, which is consistent with many other peatland studies across the northern hemisphere (Aurela and others 2001; Bubier and others 1999; Keller and others 2004; Updegraff and others 2001; Waddington and Roulet 2000). A distinct seasonal pattern was observed, with the greatest rates of respiration and photosynthesis being during the growing season, between May and September. Maximum gross CO_2 fluxes were recorded when air and soil temperatures were maximal in August 2003, when air temperature reached 23.9°C, far in excess of the average of 16.1°C for all other sampling days. In contrast, the relative difference in soil temperature was small, at 12.5°C, compared to the growing season average of 10.2°C. This indicates that the high respiration flux in August 2003 was likely accounted for by an aboveground plant response to air temperature. Lowest respiration and photosynthetic fluxes were recorded out of the plant-growing season between December 2003 and April 2004, during the winter and early spring. These findings suggest that effects of land use on peatland C dynamics might be greater as a consequence of predicted climate change.

Peatland C fluxes as CH_4 and DOC are considerably smaller than CO_2 (Johnson and others 2000; Moore and others 2002), but are nevertheless important. CH_4, for example, is a trace gas with a global warming potential that is 62 and 23 times greater than CO_2 over a period of 20 and 100 years, respectively (IPCC 2001). In our study system,

fluxes of CH_4 were always positive, that is, the system was always a source of CH_4, as would be expected for a wetland ecosystem (Alm and others 1997; Clymo and Pearce 1995; Martikainen and others 1995). Results show a small, but significant, reduction in CH_4 flux due to burning and a larger increase due to grazing. These patterns are difficult to explain, although in general, data indicated a high degree of spatial variability in CH_4 fluxes across the site. Differences in CH_4 fluxes might be due to spatial patterns of vegetation. Higher emissions have been reported when graminoids such as the sedge *E. vaginatum* are present within the plant community, because increased root exudates stimulate microbial activity and aerenchyma act as a conduit for CH_4 release (Greenup and others 2000; Marinier and others 2004). However, at the study site, a greater abundance of graminoids occurred in burned as well as the grazed treatment plots, so this probably does not explain the difference in CH_4 fluxes seen here. There is also some evidence that CH_4 is oxidized in dry areas such as hummocks (Clymo and Pearce 1995). This may explain why burned areas, which are more likely to have *Eriophorum* tussocks, show a lower CH_4 efflux. But, it cannot explain why grazing increased CH_4 flux because grazing also favored graminoid growth.

DOC export in streams is considered to be important in peatland catchments (Dawson and others 2002; Hope and others 1997), and is reported to have been increasing in recent years in the UK (Freeman and others 2001a; Worrall and others 2004). This is a concern not only for reduced terrestrial C storage, but also for water quality, as many peatland areas are reservoir catchments. We found that burning did not influence DOC release, whereas grazing produced a small increase in DOC at shallower soil depth. Our findings indicate, therefore, that in this peatland, the release of DOC is controlled primarily by climate rather than by land use.

As with CO_2, there was a pronounced seasonal pattern in both CH_4 and DOC fluxes. For CH_4 this correlated positively with soil temperature, which upholds the view that temperature is the most important climatic variable controlling CH_4 fluxes (Bellisario and others 1999; Updegraff and others 2001). Release of C in the form of DOC was also correlated with seasonal climatic variables, with greater concentrations observed at high temperatures (particularly soil temperature) and low water table levels. In agreement with other studies (Dawson and others 2002; Freeman and others 2001a; Moore 1998), DOC concentrations were greatest during the summer months and in the top few centimetres of ground. This implies a link between DOC production and aerobic conditions when microbial activity is not constrained by being water logged. The importance of biological processes to DOC release are being increasingly recognized as it becomes clear that abiotic conditions alone cannot fully explain changes in DOC concentration in peatlands and their drainage waters (Freeman and others 2004a, b; Worrall and others 2004). DOC concentration can be increased by enhanced biological activity in soils by a range of mechanisms cited in recent literature, including: increased soil enzyme activity due to soil aeration through the enzymatic latch mechanism (Freeman and others 2001a, b); an increase in soil faunal activity, especially of enchytraied worms (Cole and others 2002); and a change in plant productivity affecting root exudates (Freeman and others 2004a, b).

Overall, the use of a long-term field experiment has enabled us to demonstrate a hierarchy of factors controlling C dynamics in this ecosystem. Although seasonal climatic conditions were the most important controlling factors, the long-term land management practices of controlled burning and grazing were also influential, with burning having the greatest influence on C stocks and fluxes. Furthermore, we detected an interaction of land use with climate, indicating that the effects of land-use practices on peatland C fluxes are likely to be influenced by future climate change. At the time of the field survey, the site was 9 years into a 10-year burning cycle, a period widely considered appropriate by UK grouse moorland land owners operating such burning cycles. However, this time scale is not sufficient to allow a full recovery to a pre-burn state, as evidenced by the fact that vegetation biomass, plant species composition and CO_2 fluxes had not returned to their pre-burn levels (Hobbs 1984). We argue that the increases in CO_2 fluxes observed as a result of land use are largely attributable to changes in vegetation, as evidenced by the pronounced changes in vegetation community composition and the minimal response of the belowground community. Our findings highlight the potential for changes in vegetation resulting from long-term management to strongly regulate ecosystem C dynamics in C-rich peatland.

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