Above-ground biomass accumulation patterns in moorlands after prescribed burning and low-intensity grazing

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Abstract

Shrub-dominated ecosystems such as moorlands are recognized internationally as cultural landscapes with high biodiversity conservation value. These ecosystems are commonly managed using prescribed burning to reduce the impact of wildfires, increase biodiversity and ecosystem productivity for grazing. Given that ecosystem responses are sensitive to the above-ground balance within the vegetation, knowledge of the above-ground biomass accumulation patterns on moorlands is an important issue for planning management action. Here, we used the replicated long-term manipulative grazing and burning experiment at Moor House (UK) to explore the cumulative effects of multiple fires and low-grazing. The study comprised a comparison between no-burn reference plots (no-burn since ca. 1923) and an experiment where all plots were burned in 1954/55. Within the experiment, the effects of low sheep grazing vs. no grazing and three burning rotations were tested (no-burn since 1954/55, repeat-burning at 10- and 20-year intervals). We hypothesized that prescribed burning and grazing will interact, affecting both the above-ground biomass and vegetation height. The results reveal that although the main above-ground biomass was constrained in three fractions (litter, *Calluna* and bryophytes) there was no significant effect of sheep-grazing or its interaction with prescribed burning (graze×burn) on any biomass variables or vegetation height. Significant reductions in above-ground biomass and vegetation height were only produced by repeated burning. There were no significant differences in biomass or vegetation height between the no-burn since 1954/55 treatment and reference plots. Moreover, *Calluna* biomass and vegetation height showed a positive significant asymptotic association with time since the last burn with an asymptote at 20 and 15 years after fire, respectively. This work demonstrates that burning rotations lower than 20 years reduced the above-ground biomass and vegetation height on this moorland compared to stands unburned for more than 50 years. In order to maximize the C fixation, fire return intervals should be around the *Calluna* biomass accumulation asymptote 20 years since last fire. Furthermore, the vegetation height asymptote of 36 cm, indicating when the vegetation is at its maximum stage, could be a useful tool for guiding when to implement prescribed burning for carbon accumulation purposes.

Highlights:

- The effect of prescribed burning and low-grazing pressure in moorlands was assessed
- We examined the vegetation height and above-ground biomass accumulation patterns
- Repeated burning produce reductions in vegetation height and above-ground biomass
- Low sheep-grazing has no effect on any biomass variables
- Fire-return interval must be around 20 years since burning to maximize C fixation

Keywords:, Fire, return interval, *Calluna vulgaris*, litter, sheep grazing, shrub-dominated ecosystems.

Introduction

For many shrub-dominated ecosystems around the world, prescribed burning, the deliberate application of fire under specific conditions (Fernandes and Botelho, 2003), is a widely-used management tool to reduce the impact of wildfires, prevent succession to woodlands, improve wildlife habitats, or increase biodiversity and ecosystem productivity for grazing livestock (Pakeman et al., 2003; Calvo et al., 2005; Borghesio, 2009; Keeley et al., 2012; Lee et al., 2013a). As these benefits usually last for only a few years after fire, repeated prescribed burning is needed for effective management (Ascoli et al., 2009). Therefore, prescribed burning planning requires an understanding of the vegetation response to repeated burning, which involves the implementation of long-term monitoring programs (Fernandes et al., 2013). These long-term monitoring programs help to unravel the potential consequences of the use of prescribed burning on ecosystems, their recovery and their carbon balance (Ascoli et al., 2009; Velle et al., 2012), as well as to define the most effective rotation interval required under present and future global climatic change scenarios (Keeley, 2005). Unfortunately, despite the importance of having well-designed management plans, there is a lack of long-term empirical studies testing the effects of repeated prescribed burning on shrub-dominated ecosystems (e.g. Boer et al., 2009).

One of the main difficulties in prescribed burning practices is to quantify the patterns in above-ground carbon balances. Many complex interactions may exist between fire and other management practices where biomass is consumed, such as with grazing. It is well known that grazing is an important biomass consumer in many terrestrial ecosystems and it can interact with fire in many shrub-dominated ecosystems (Rigolot et al., 2002; Ascoli et al., 2013; Johansson and Granström, 2014). Grazing can also influence the above-ground biomass accumulation patterns after fire, which are primarily controlled by a balance between plant growth, litter production (both negatively affected by grazing; Evlagon et al., 2012) and decomposition rates (positively affected; Riggan et al., 1988). This is especially true in the early post-fire years when pasture quality is greatest (Fuhlendorf et al., 2009). As a consequence, prescribed burning might be expected to be implemented in grazed systems at longer time intervals as grazing slows down the biomass accumulation (Johansson and Granström, 2014). However, despite the great interest in prescribed burning as a management tool in shrub-dominated ecosystems, there are few studies that investigate the post-fire biomass accumulation patterns under the influence of grazing (but see Rigolot et al., 2002, Ascoli et al., 2013). Studies of the interactions between plant growth rates and management treatments such as grazing and repeated burning are essential for developing appropriate management strategies within shrub-dominated ecosystems. Indeed, repeated prescribed burning along-side grazing are the predominant tools for the management of north-west European moorlands (Harris et al., 2013a; Lee et al., 2013b; Velle et al., 2014).

In Great Britain upland moors, many of them growing on blanket bog (ombrotrophic mire) have a very high conservation value of international significance (Bain et al., 2011; Lee et al. 2013a). These moors are currently cultural landscapes that have been created and maintained by anthropogenic activity, mainly sheep grazing and prescribed burning (Rosenburgh et al., 2013). Whilst fire has been used for hundreds, perhaps thousands of years (Simmons, 2003), its use has increased in the last 200 years to enhance the productivity of the moors for sheep grazing and especially for red grouse (*Lagopus lagopus scoticus* Latham) (Harris et al., 2011a; Lee et al., 2013a). Nowadays, approximately, 65% of British upland moors are managed using prescribed burning for the benefit of red grouse (Sotherton et al., 2009). Hence, their sustainable management is important in terms of both the local economy and biodiversity (Harris et al., 2011a).

Prescribed burning will inevitably affect the vegetation carbon balance from the moorland systems as the fire moves through it. Carbon balance will depend on the biomass consumed by the fire (initial instantaneous loss) and the ecosystem resilience (Mitchell et al., 2000), i.e. the time it takes for the ecosystem to recover via plant growth and biomass accumulation during the inter-fire interval. Where prescribed burning is done carefully within the approved burning season (winter months in Great Britain; Anon, 2007), using “cool burn” or “pressurized fuel-assisted” burning (Harris et al., 2011a), these losses should be minimized as some vegetation remains after the fire and the peat should be left relatively unaffected. After burning there is often relatively rapid vegetation recovery and hence carbon accumulation during the post-fire succession, and the overall aim should be to produce a balanced budget over a specified time period. In this sense, there is still little information available in moorlands subjected to prescribed fires, being often conflicting. In a moorland area in central England, Allen et al. (2013) used a modelling approach to predict that over a 50 year period the longer the fire-rotation interval, greater the accumulation of above-ground biomass (vegetation and litter). However, Clay et al. (2010) observed, in terms of carbon budgets, that prescribed burning can reduce global C releases in comparison to long-term unburned areas; i.e., taking into account fluvial and gaseous fluxes such as dissolved organic carbon, particulate organic carbon, excess dissolved CO_2, release of CH_4, net ecosystem respiration of CO_2, and uptake of CO_2 through primary productivity. Therefore, that knowledge of the above-ground biomass accumulation patterns on moorlands is fundamental for global change research, and for planning management action; therefore, further research is needed to disentangle the effect of different fire rotation intervals in defining above-ground biomass as C sink and source. Undoubtedly, such knowledge will assist in determining the fire rotation interval that optimizes C fixation by means of vegetation growth.

As far as moorland conservation management in Great Britain is concerned, a major issue that needs to be addressed is a quantification of the effects of low-intensity grazing, current on many moorland ecosystems, and repeated prescribed burning on the above-ground biomass during the prescribed burning/post-fire recovery cycle. To address this, we measured above-ground biomass within the replicated long-term manipulative grazing and burning experiment at Moor House National Nature Reserve (Rawes and Hobbs, 1979; Lee et al., 2013a). This experiment has a history of approximately 90 years of known low-grazing pressure and fire rotations at different intervals (10, 20 and 56/57 years). This experiment, therefore, represents a unique opportunity to quantify the cumulative effects of multiple fires and low-grazing on biomass accumulation and its related parameters such as the dry weight of component fractions (e.g. *Calluna vulgaris* (L.) Hull, litter, bryophytes, graminoids and other vascular plants) and vegetation height. For all of these measures we assessed the effect of (a) grazing (grazing *vs*. no grazing), (b) the different rotation intervals (short-, long-, and unburned for 50+ years) and their interaction. In addition, we modelled plant growth through time since the last burning; as both the total accumulated, and as the absolute growth rate (AGR).

Essentially, our aim is to determine what is the optimal fire return time based on the biomass patterns found. For that, we made a comparison of biomass accumulation with literature sources and we tested two main hypotheses: First, that the shorter fire return-intervals will produce greater reductions in above-ground biomass and vegetation height. Second, it has been shown that grazing slows down the above-ground biomass accumulation by consumption, especially in early post-fire years when pasture quality is greater (Velle et al., 2012; Johansson and Granström, 2014); therefore, we expect that biomass reduction by grazing will be greater in shorter fire return-intervals.

Material and methods

Study area

The study site is within the Moor House National Nature Reserve (hereafter referred as Moor House, Table 1), which is located in the northern Pennines, a range of hills that form the backbone of England (54°41'34.4"N, 2°24'28.1"W). The experimental site is on the eastern side of Hard Hill, a gently-sloping, high-level plateau (600-650 m; Heal and Smith, 1978); and it is situated on blanket bog (>50 cm peat, the widely-accepted definition for blanket peat in the UK; Costigan et al., 2005). The vegetation at Moor House can be described as *Calluna vulgaris-Eriophorum vaginatum* blanket mire (M19) and *Eriophorum vaginatum* blanket and raised mire (M20) communities within the British National Vegetation Classification (NVC; Rodwell, 1991). Thus, the most common species are *Calluna vulgaris*, *Eriophorum vaginatum* L., *Pleurozium schreberi* (Brid.) Mitt. and *Sphagnum capillifolium* (Ehrh.) Hedw. Here, *Calluna* was the dominant species in the vegetation sampled (i.e. biomass and height); with no presence of other woody shrub species. The climate is oceanic/sub-arctic rather than temperate, cool, wet and windy (abridged for Heal and Smith's (1978) description of the Moor House climate). The January and July mean temperatures at Moor House are 2.7°C and 14.4°C, respectively. The Moor House annual precipitation is 1314 mm (data derived from UK Meteorological Office 5-km monthly gridded climatic data averaged between 1961-2005; Perry and Hollis, 2005), and precipitation was much greater in winter (January mean = 130 mm) compared to summer (July mean = 82 mm).

Experimental design

The experimental design is detailed in Marrs et al. (1986). Briefly, the experiment was set up on Hard Hill at Moor House in 1954/5 and was designed to test the effects of low-intensity grazing vs. no sheep grazing in combination with three prescribed burning rotations (a 10- and 20-year rotation plus a no-further-burn treatment). In 1954/5 four replicate moorland blocks (A-D), each 90 m × 60 m, were burned along an elevational gradient (A = NY743330; B = NY740330; C = NY736330; D = NY738331). Blocks A, B and D were burned in 1954 and block C in 1955. At the start of the experiment the vegetation was considered to have remained unburned for at least 30 years (Rawes and Hobbs, 1979). Within each block, two main-plot treatments (60 m × 30 m) were allocated randomly, these treatments were: sheep grazing and no sheep grazing, referred to here as Grazed (G) and Enclosed (E), respectively (Table 1). The sheep grazing pressures have varied during the experimental period, but have always been low. The densities on this moorland type vegetation were estimated at ca. 0.1-0.3 sheep ha^{-1} in the 1960s when the overall sheep grazing density over the entire reserve was 15,400 sheep in the summer months, an average of 4.4 sheep ha^{-1} across all vegetation types (Rawes and Welch, 1969). The formalization of grazing rights under the Commons Registration Act (1965) was completed for Moor House in 1972 and grazing was then restricted to 7,000 sheep, a halving of sheep numbers (2 sheep ha^{-1}). There was a further reduction in sheep numbers following the foot and mouth outbreak in 2001 when some grazing rights were extinguished and a new stocking density of 0.5 sheep ha^{-1} established over the whole moor. Hence the already light stocking density present when the experiment was set up has been reduced on two occasions during the study to an approximate 15-fold reduction.

Within each main-plot, three burning-rotation treatments were allocated randomly to sub-plots (30 m × 30 m), these were: (i) Short-rotation burning approximately every 10 years (S), (ii) Long-rotation burning approximately every 20 years (L), and (iii) No burning since 1954/5 (N). Prescribed burning in the weather conditions prevailing at Moor House is very difficult and in some years burning is impossible, accordingly burning timings could not be applied fully in accordance with the planned schedule but were applied as follows: 1954/55 (All), 1965 (S), 1975 (S & L), 1984 (S), 1995 (S & L) and 2006 (S). Thus, the experimental data here represents six burns in S, three burns in L and one burn with subsequent recovery after 56/7 years (N) since the start. However, since monitoring was done in 2011 the years between sampling and last burn for each treatment were: S=5 years, L=16 years and N=56/57 years since the last burn (Table 1). In addition to the formal experiment, each block had an associated unburned reference plot (denoted R, 10 m × 10 m) set up outside the burn area delimited in 1954/5, but sheep grazed. The exact positions of these unburned reference controls have been lost over time but in 2011 the approximate positions of these plots were relocated using a combination of map locations and aerial photography to ensure they were placed outside the original burn areas. We accept they may not be in identical positions but they are extremely close. These reference plots were deemed to have remained unburned for at least ca. 87 years, although the exact date of the last burn remains unknown; for calculation purposes we have assumed the elapsed time since last burn was 90 years.

Biomass monitoring after prescribed burning experiments

In July 2011, above-ground biomass was harvested from each of the 28 sub-plots (Table 1). In each sub-plot, three 0.25 m^2 quadrats were sampled in the buffer zone surrounding the vegetation monitoring plot to minimise disturbance to ongoing research. In each quadrat, first the vegetation height was measured with a ruler (cm) in five points (i.e. centre and the four quadrat corners), and then plot average was taken. Here, vegetation height was predominantly dictated by *Calluna* height. Afterwards vegetation was harvested to 2 cm from the solid peat surface and separated crudely in the field into two fractions (*Calluna* and the remainder). In the laboratory, the two fractions from each sample were re-sorted to produce a sample of *Calluna* and remaining vegetation per plot; the *Calluna* sample was then oven-dried and weighed. The remaining vegetation was then quartered; one quarter selected randomly was retained for further separation and the other three-quarters oven-dried and weighed. The retained quarter was separated into four fractions: litter, bryophytes, graminoids and a combined fraction containing all other vascular plants. The litter was distinguished from live material by absence of chlorophyll. In these vegetation samples *Calluna* was the only shrub species detected. All fractions were then oven-dried and weighed. The proportions of each fraction in the sub-sample were applied to the entire sample to derive component weights.

Data analyses

Biomass data from all burns were converted to g m^{-2} dry weight. Unfortunately, the statistical design at Moor House was unbalanced (no enclosed reference plot) so the data were, therefore, analyzed as follows: First, a comparison of burning treatment effects on vegetation height and biomass variables (total, *Calluna*, litter and bryophytes biomass) in the grazed plots. Here, the data for all four grazed treatments (S, L, N, R) were compared using Linear Mixed-effects models to account for the spatial structure of the data (random effects); Block/Plot/Sampling quadrat. We accept that the R treatment was not positioned randomly within the experimental design. Second, a comparison of the formal experiment was done. Here, the R treatment was excluded and the effects of grazing (G, E) and burning rotation (S, L, N) and their interactions on vegetation height and biomass variables (total, *Calluna*, litter and bryophytes biomass) were assessed using the same methodology. In both analyses the biomass of graminoids and the combined fraction containing other vascular plants were not analyzed statistically, because these fractions were detected in less than 20% of the plots.

Afterwards, we analyzed the plant growth through elapsed time since the last burning using two variables: *Calluna* biomass and vegetation height. An understanding of growth is essential to understand ecological processes including the interactions between plants and factors affecting communities such as grazing and burning. Here, these relationships were assessed using non-linear mixed models based on the idea that plant size may approach an asymptote because of limiting below-ground resources or ontogenetic changes (Paine et al., 2012). In the case of *Calluna* non-linear mixed Gompertz growth curves were fitted; the choice of Gompertz curves was to maintain consistency with previous published works on British heath/moorland areas (Chapman et al., 1975; Miller, 1979). The Gompertz regression model (function "SSgompertz") full equation is $y = Asym \times \exp(-b2 \times b3^{Age})$, where y is biomass variables, Asym is the asymptote, b2 is the y-intercept and b3 determines the rate at which the asymptote is reached. Vegetation height was modelled using a non-linear logistic function (function "SSlogis") where the full equation is $y = Asym / (1 + \exp((xmid - Age) / scal)))$, where y is the vegetation height, Asym is the asymptote, xmid is the inflection point of the curve and scal determines the scale parameter of the age since the last burning parameter. In all non-linear analyses, the spatial structure of the data and treatments applied (grazing and burning) were included as random factors; Block/Graze/Burning/Sampling. Next, the absolute growth rate (AGR, biomass = g m^{-2} $year^{-1}$; height = cm $year^{-1}$) were derived from the non-linear models fits using the methodologies and scripts described in Paine et al. (2012). These growth rates were expressed as functions of time since the last burning and their confidence intervals were derived from population prediction intervals (Paine et al., 2012). Because the litter, bryophytes, graminoids and other vascular plants group biomass showed no change since the time of last burning (continuous values along the sequence, $P > 0.050$); the total biomass pattern was controlled mainly by the Calluna biomass pattern. As a consequence only a detailed description of *Calluna* biomass change is reported.

All statistical analyses were performed in the R statistical environment (version 3.1.0 R Development Core Team, 2014); Linear and non-linear Mixed-effects modelling was performed using the "nlme" package (Pinheiro et al., 2014).

Results

Biomass distribution within the vegetation

The biomass distribution within the vegetation at Moor House showed that there were three main fractions; litter, *Calluna* and bryophytes; these fractions represented almost 97% of the total biomass (Fig. 1). Litter was the most abundant biomass fraction (36% - 67%) followed by *Calluna* (5% - 43%) and bryophytes (6% - 27%). The other two fractions, either the graminoids or other vascular plants biomass, made up a trivial contribution to the total biomass. Graminoid biomass was more abundant in short-rotation treatments (S) independent of grazed treatment (ES = 1.1% and GS = 0.7%), whereas the biomass of other vascular plants was only abundant in short rotation enclosed plots (ES = 0.9%). At the same time, there were few differences in the distribution of the three main biomass fractions (litter, *Calluna* and bryophytes) between grazing treatments (E vs. G), although there were consistent differences between burning treatments (Fig. 1). *Calluna* biomass was greater at the longer rotation interval treatment (N, followed by L and S), whereas bryophytes biomass was greater in the shortest rotation interval (S).

Burning rotations effects on biomass and height in the grazed plots

As expected, there were no significant differences between the no-burn since 1954/55 treatment (N) and reference plots (R) on any of the five biomass and height measures considered ($P > 0.050$, Table 2). In contrast, the short- and long- burning rotation treatments (S and L) produced significant reductions of total biomass compared to the reference plots ($P < 0.050$, Table 2). These reductions were greatest in the short-term rotation treatment (S) which had the lowest biomass value (S = 1198 ± 165 g m^{-2}) followed by long-term rotation (L = 1593 ± 119 g m^{-2}). Indeed, the short-rotation treatment was the only burning treatment that reduced *Calluna* biomass and vegetation height compared to the reference plots (R, $P < 0.001$, Table 2). In contrast, bryophytes biomass was only reduced by the long-term rotation treatment (L; $P = 0.043$), whereas, the litter biomass was not affected by any burning rotation ($P > 0.050$).

Grazing and burning rotations effects on biomass and height in the formal experiment

Within the formal experiment, the grazing treatments showed no effect on their own nor in interaction with prescribed burning (graze × burn) on any biomass variables or height ($P > 0.050$). Significant differences were only found in four biomass variables (total, *Calluna* and bryophytes biomass and height) with respect to the prescribed burning rotations ($P < 0.050$).

The results were similar to the previous analysis; prescribed burning rotation treatments S and L produced reductions on biomass in comparison with the no-burn since 1954/55 treatment (N) ($P < 0.050$). Total biomass was lower in short rotations than in no burn treatments (N = 2037 ± 25 vs. S = 1342 ± 194, t-value = -3.57, P = 0.002), *Calluna* biomass was reduced by burning rotation (N = 833.70 ± 70.25 vs. L = 656.98 ± 81.39 vs. S = 83.50 ± 81.39, F-value = 46.44, $P < 0.001$), bryophytes biomass was reduced by long-rotation burning (N = 415.52 ± 106.80 vs. L = 166.10 ± 113.25, t-value = -2.26, P = 0.041) and vegetation height by short-rotation burning (N = 35.83 ± 1.28 vs. S = 22.29 ± 1.81, t-value = -7.48, $P < 0.001$). Litter biomass showed no response to burning rotation ($P > 0.050$).

Calluna *biomass and height accumulation patterns through time*

The non-linear mixed-effects analysis showed that *Calluna* and vegetation height had a positive asymptotic association with elapsed time since the last burning (Table 3, Fig. 2). Both variables increased with elapsed time since the last burning until they stabilized. *Calluna* biomass reaches an asymptote of 795.87 ± 80 g m^{-2} approximately at 20 years after fire and vegetation height reaches an asymptote of 36.31 ± 0.84 cm approximately at 15 years after fire (Table 3). The AGR peak for *Calluna* was at 8 years after the last fire with a value of 76.08 g m^{-2} $year^{-1}$, whereas the AGR peak for vegetation height was earlier at 4 years, with a value of 4.61 cm $year^{-1}$ (Fig. 2b, d).

Discussion

Biomass distribution within the vegetation and comparison with literature sources

The data collected at Moor House provides comprehensive information on above-ground biomass budgets during the prescribed burning/post-fire recovery cycle on high-elevated moorlands. The above-ground material was accumulated almost entirely in three biomass component fractions: litter, *Calluna* and bryophytes, with negligible amounts of graminoids and other vascular plant species. This almost certainly reflects the impact of severe climate and the lack of exposure to pollutants as other moorlands (Tallis, 1988; Caporn and Emmett, 2009; Lee et al., 2013a). Moor House being colder, wetter and less polluted have a lower productivity (e.g. *Calluna* biomass), more litter and peat accumulation than low-land moorlands where productivity should be enhanced by the drier (less water-logged), warmer conditions and a greater nitrogen loading (Lee et al., 2013b; Table 4). At the same time, Moor House has retained a substantive bryophyte component including the peat-forming *Sphagnum* species (Rawes and Hobbs, 1979; Lee et al., 2013b) probably because of a lack of exposure to present and past pollutants (nitrogen deposition; Tallis, 1988; Caporn and Emmett, 2009; Lee et al., 2013a) which has favoured the biomass increases of bryophytes in this ecosystem and especially under the shorter-rotation intervals (S). On the other hand, the deep litter layer acts as an inhibiting recolonization *sensu* Connell and Slatyer (1977), reducing the development of graminoids and other vascular plants groups (Lee et al., 2013a), as a result their above-ground biomass in all blocks was trivial (<1.2%).

The lower productivity is supported by evidence from other studies, it is clear that the total biomass data for older stands at Moor House that ranged from 2076-2223 g m^{-2} were considerably lower than comparable data from the literature (5,240-10,000 g m^{-2}; Table 4). Literature values for younger moorland stands at Teesdale, Kincardineshire or Dartmoor were within the same orders of magnitude as the Moor House total biomass values for greater age ranges (Moor House=2076-2223 g m^{-2} at age range 56/57-90 years *vs.* younger Moors=1820-2930 g m^{-2} at age range 6-25 years; Table 4). The vegetation at Moor House does not appear to follow the traditional *Calluna* four-phase, life-cycle model of Watt (1947, 1955),where the transition from mature to degenerate phases involves the older branches falling over with gaps being created in the middle (Barclay-Estrup & Gimingham, 1969). At Moor House, the degenerate phase does not appear to be pronounced rather the mature phase continues vertically and with horizontal growing along the ground and through other vegetation; the stems adventiously rooting in the bryophyte/litter layer. This was first noted by Forrest's (1971) observations that at Moor House the moorland vegetation was in a presumed steady-state but the degenerate phase of *Calluna* was seldom seen. It will be interesting to monitor these patterns in the future especially if either conditions become warmer and drier as a result of climate change, or there is a reduction in burning management.

Burning rotations effects on biomass and height

This study has provided a detailed long-term insight into the above-ground biomass dynamics of high-land moorland communities in Great Britain managed using repeated prescribed burning rotation intervals. Our results indicate that the shorter fire return-intervals (5 years-S and 16 years-L after last fire) produced greater *Calluna* biomass and height reductions in comparison with unburned controls (56/57 years-N and 90 years old-R), and this was equal independently of the type of analysis done (grazed plots or formal experiment); hence, Hypothesis 1 is accepted with respect to burning rotations. As expected, when the fire frequency increased there is a reduction of the dominance of *Calluna* (Littlewood et al., 2010; Allen et al., 2013). In contrast, short-burning rotations do not optimize the C fixation based on vegetation growth as the *Calluna* biomass asymptote is held at 20 years, equal to long-rotation burning treatment in this moor. However, short rotations appears to be associated with an increase in peat-forming species (*Eriphiorum* spp. and *Sphagnum* spp.; Lee et al., 2013a), being fundamental for moorland diversity and conservation, and also for carbon fixation in the peat (Lee et al., 2013a). It seems that no burning for more than 50 years (N and R treatments) will produce a stand dominated mainly by *Calluna* and litter with low biomass of bryophytes and other vascular plant species, and with a community composition changing towards *Calluna vulgaris-Hypnum jutlandicum* with a reduction of peat forming species (Lee et al., 2013a). However, it is important to consider in the interpretation of results that differences in biomass accumulated or height can also be attributed to shorter regeneration times between treatments (i.e. vegetation at different successional stage). Irrespective, the results observed here provide an overview of biomass dynamics and accumulation patterns for similar moorlands.

Grazing effects on above-ground biomass and height

In contrast to our expectation (Hypothesis 2), sheep grazing had no effect on any above-ground biomass variables (Total, *Calluna*, litter and bryophytes) or vegetation height. Therefore, grazing does not reduce ecosystem production neither interacts with fire, thus Hypothesis 2 is rejected. These results were not at all unexpected because the summer-only sheep grazing intensity was very low in the 1960s (0.1-0.3 sheep ha^{-1}, Rawes and Welch, 1969), and this has been reduced as part of a conservation management plan twice over the course of this study. The actual grazing pressure on a given spot on the site is a function of both the absolute numbers on the reserve and the movements of sheep between vegetation types to find more productive grassland communities (Rawes and Welch, 1969). In any case, this study adds weight to the evidence that grazing removal in slow growing high-altitude moorlands produce a dwarf shrub species dominance, especially *Calluna* (Hartley and Mitchell, 2005).

Calluna height and biomass accumulation patterns through time

After prescribed burning the ecosystem recovers from a combination of resprouting by *Calluna* and bryophytes (e.g. biomass and height increases) and the colonization of new species including *Calluna* from seedlings and bryophytes from propagules (Lee et al., 2013b). This is effectively known as the "reorganization and aggrading phases" for moorlands as described by Bormann and Likens (1979) for forest. In this study, our results for *Calluna* biomass and vegetation height showed these patterns since the absolute growth rates were increasing over the first 8 and 4 years, respectively (maximum rates of 76.08 g m^{-2} $year^{-1}$ for biomass and 4.61 cm $year^{-1}$ for height). This is transformed into a rapid post-fire accumulation of *Calluna* biomass and vegetation height. It is interesting to mention that the AGR values might help to determine what kind of management is optimal in view of the pasture availability based on growth. In this case, the greater biomass production will be produced by burning rotations lower than 10-12 years, i.e. when AGR for biomass is maintained at maximum values.

The main increase in total biomass resulted only from *Calluna* growth, with all other components (biomass of litter, bryophytes, graminoids and other vascular plants group) contributing in a very variable manner. Graminoids and other vascular plants constituted a trivial component of the total biomass, whereas litter and bryophyte biomass stayed constant over time since last burning. This result may be due to the practice of "cool burns" (discussed at Harris et al., 2011a), as a consequence of high rainfall and the relatively moist vegetation at Moor House, this produced relatively little damage to the underlying moss and litter layers, or even some *Calluna* stems. However, further research is needed to confirm this hypothesis through estimates of pre- and post-fire biomass.

The vegetation at Moor House achieved a modelled asymptote at 20 years for *Calluna* biomass and 15 years for vegetation height, suggesting that after 20 years more or less equilibrium conditions are reached. Essentially this is evidence to support the view that the system was approaching to "steady-state" (Bormann and Likens, 1979). In this "steady-state" any growth in the above-ground vegetation must be compensated either by respiration or transfer into the peat. This is an interesting result since the time needed to reach the biomass asymptote at Moor House (20 years) is much lower than more productive lowland heaths where asymptotes are reached at more than 36-40 years (Chapman and Webb, 1978; Miller, 1979), or even in similar low-productive moorlands at Kerloch where an asymptote was estimated at 25 years (Miller, 1979). It seems that if the management of this moorland is focused on optimizing C fixation by means of biomass accumulation the fire rotational interval should be around 20 years. Irrespective, the differences in biomass asymptotes between these contrasting moorlands indicate the difficulties of managing sites using simple prescriptions, instead of develop site-specific management plans.

Management implications

The present work demonstrates that burning rotations lower than 20 years reduced the above-ground biomass and vegetation height on this moorland compared to stands unburned for more than 50 years. The modelled outputs suggest that an asymptote in *Calluna* growth and vegetation height occurs at 20 and 15 years after fire, respectively. In the case of *Calluna* biomass the asymptote is produced simultaneously as the longest rotation interval for this moorland (long-rotation of 20 years). In contrast, no grazing effect was detected on biomass or vegetation height in this plant community. Therefore, in order to maximize the C fixation in similar moorlands, fire-return intervals should be around the *Calluna* accumulation asymptote, i.e. 20 years since last fire. However, this return-interval could reduce the component of some important peat-forming species such as *Sphagnum* and *Eryophorum* (Lee et al., 2013a), which are favoured in 10-years rotation intervals.

Finally, the analogous accumulation curves for *Calluna* biomass and vegetation height (same response to burning treatments) are an interesting result to assist in heathlands management. Land managers usually use moorlands age or *Calluna* biomass to identify the optimal time to burn (Harris et al., 2011a). However, since here *Calluna* biomass and vegetation height were similar, the use of vegetation height could be a new faster way to assess the optimal time to burn since it is more reliable and faster to measure by land managers in the field. This approach was suggested by Harris et al. (2012) for Peak District moorlands and they suggested using 25 cm height as a yardstick to determine when prescribed burning should be applied to maintain diversity and an upper value of 40 cm as the maximum that should be allowed otherwise there would be a predicted loss of species diversity. The asymptote at Moor House was within this range (36 cm) suggesting that vegetation height might be a useful tool for guiding when to implement prescribed burning.

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Table 1. Details of experimental treatments within each of the four replicate blocks for the Moor House study site, where post-fires biomass accumulation patterns were studied over each sub-plot (n=28). The treatment history of experimental plots description is included. Key to burning treatments: S=short-rotation; L=long-rotation; N=no-rotation post 1954/5, R=reference plots, unburned for at least 87 years.

Main-plot treatments	Sub-plot treatments			
Grazed/Enclosed	Burning rotation	No of burns since 1954	Year of last burn	Years between sampling (2011) and last burn
Enclosed	N	1	1954/55	56/57
Enclosed	S	6	2006	5
Enclosed	L	3	1995	16
Grazed	N	1	1954/55	56/57
Grazed	S	6	2006	5
Grazed	L	3	1995	16
Grazed	R	0	1924?	Minimum 87

Table 2. Effects of time since last burn on above-ground vegetation biomass (g m^{-2}) and vegetation height (cm) in the Hard Hill grazing and burning experiment at Moor House; the data presented are derived from a Mixed-effects modelling: The treatments were three burning rotations within the formal experiment, 5 years after last burn-short (S), 16 years since last burn-long (L) rotations plus no-burn after 1954/5 (N) compared to the reference plots (R) as intercept. Arithmetic means (±SE, n=4 plots, each with three sub-samples/plot) are presented along with the statistical estimates from the analyses.

Variables	Mean±SE	Estimate±SE	t-value	p-value
Total Biomass (g m^{-2})				
R(~90)	2223±201	2223.17±218.06	10.20	<0.001
N(56/57)	2079±144	-143.92±02.80	-0.71	0.496
L(16)	1593±119	-629.79±02.80	-3.11	0.013
S(5)	1198±165	-1024.83±02.80	-5.05	<0.001
Calluna vulgaris (g m^{-2})				
R(~90)	705±73	704.95±82.61	8.53	<0.001
N(56/57)	808±80	103.13±104.02	0.99	0.347
L(16)	672±39	-33.30±104.02	-0.32	0.756
S(5)	60±16	-645.33±104.02	-6.23	<0.001
Litter (g m^{-2})				
R(~90)	993±107	993.11±131.55	7.55	<0.001
N(56/57)	758±91	-235.59±156.64	-1.50	0.167
L(16)	801±105	-191.86±156.64	-1.22	0.252
S(5)	811±110	-181.68±156.64	-1.16	0.276
Bryophytes (g m^{-2})				
R(~90)	522±98	522.54±137.05	3.81	<0.001
N(56/57)	513±183	-9.98±171.65	-0.06	0.955
L(16)	120±56	-402.78±171.65	-2.35	0.043
S(5)	319±73	-203.47±171.65	-1.19	0.266
Height (cm)				
R(~90)	37.3±1.2	37.25±2.04	18.30	<0.001
N(56/57)	37.4±1.2	0.17±2.88	0.06	0.955
L(16)	35.0±1.3	-2.25±2.88	-0.78	0.455
S(5)	23.0±2.2	-14.25±2.88	-4.95	<0.001

Table 3. Parameters for the non-linear mixed models trough time since last burning for *Calluna* biomass (g m^{-2}) and vegetation height (cm) accumulation curves in the Hard Hill grazing and burning experiment at Moor House.

Variable	Model selected		Estimate±SE	t-value	p-value
Calluna biomass (g m^{-2})	Gompertz	Asym	795.87±80	10.08	<0.001
		b_2	8.07±3.55	2.28	0.035
		b_3	0.78±0.04	20.12	<0.001
Height (cm)	Logistic	Asym	36.31±0.84	43.11	<0.001
		xmid	4.09±1.64	2.49	0.015
		scal	1.97±3.65	0.54	0.591

Table 4. Comparison of total above-ground biomass data (g m^{-2}) from Moor House with literature values; np = information not presented.

Location	Site	Elevation (m)	Stand Age (years)	Biomass (g m^{-2})	Reference
Peak District	Bamford	300-420	3-14	163±37-2138±72	Harris et al. (2011a)
			38	5364±569-8019±270	
Peak District	Broomhead	300-460	2-15	132±17-2279±190	
			40-50	6540±844-7114±701	
Peak District	Howden	272-540	2-15	267±9-2262±60	
			50	5577±470-6401±596	
Peak District	Midhope	270-480	3-15	334±11-2673±90	
			40	5241±660-10024±337	
Peak District	Snailsden	350-470	3-16	517±39-2375±185	
			40	5250±662-6507±549	
Moor House	Hard Hill Burning Experiment	600-632	90	2223±201	This study
Moor House	Hard Hill Burning Experiment	600-632	56/57	2079±144	This study
Hexham	Blanchard moor	305	10	1920	Robertson and Davies (1965)
Kincardineshire	North Cairn o' Mount	274	15	2930	Robertson and Davies (1965)
Kincardineshire	Kerloch Moor	140-280	25	1840	Kayll (1966)
Teesdale	np	290-850	6	600	Bellamy and Holland (1966)
Teesdale	np	290-850	14	2000	Bellamy and Holland (1966)
Dorset	Poole Basin	90	?	1820	Chapman (1967)
Dartmoor		320-340	?	2000	Chapman (1967)

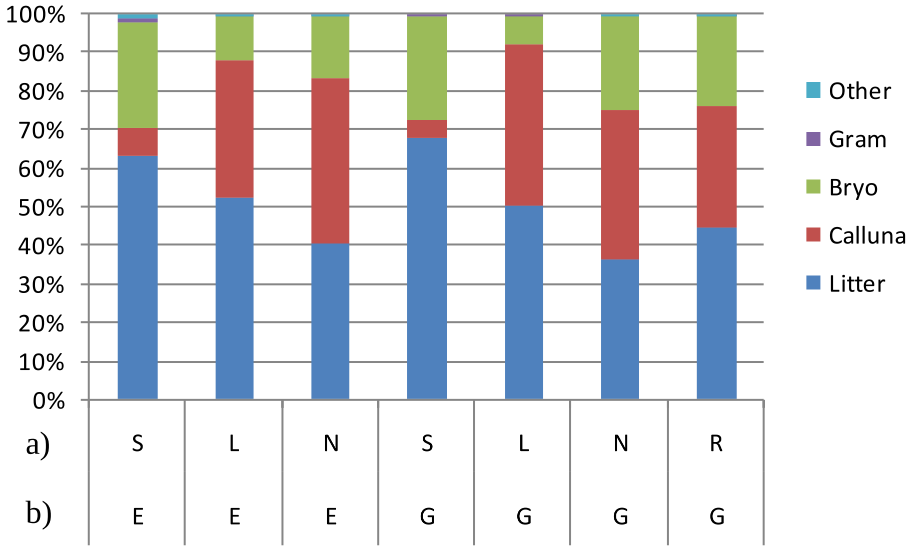

Fig. 1. Distribution of the five main fractions of biomass (%) in the Hard Hill grazing and burning experiment at Moor House. The treatments were: a) burning treatments: short-rotation (S), long-rotation (L), no-burn after 1954/5 (N) and reference plots (R); b) grazing treatments: enclosed (E) and grazed (G). The colour codes were: blue=Litter, red=*Calluna*, green=Bryophytes, purple=Graminoids and sky-blue=Other vascular plants.

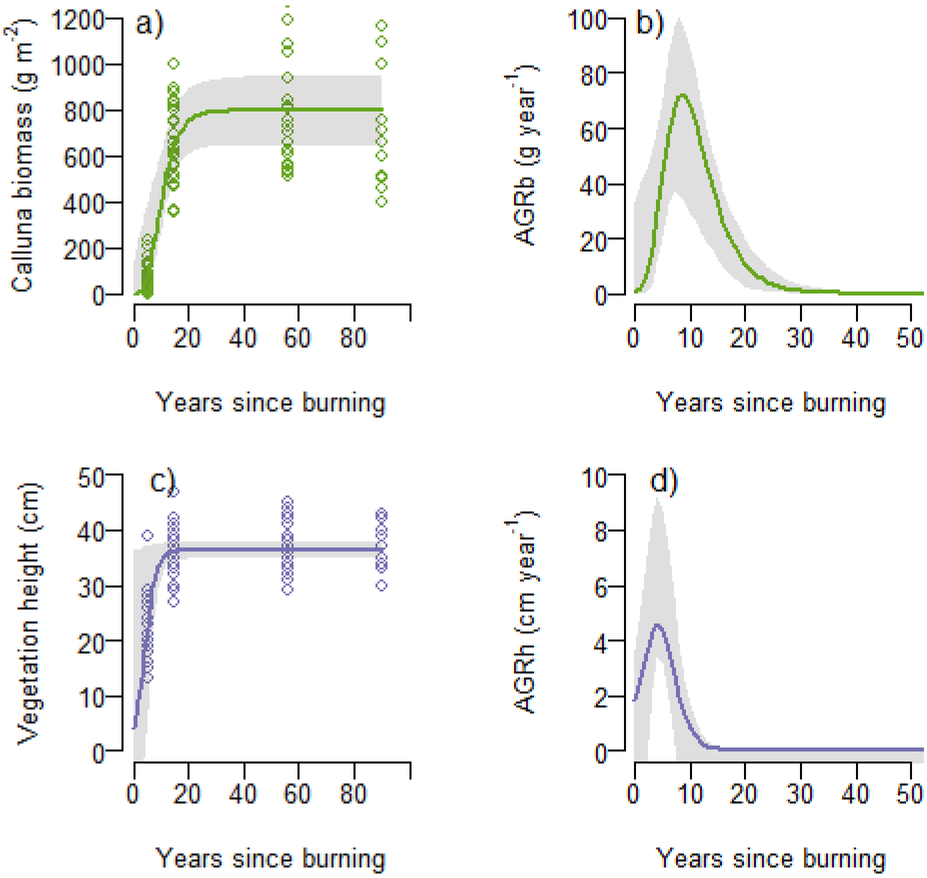

Fig. 2. Observed and predicted values from non-linear mixed effects models through years since last burning in the Hard Hill Grazing and Burning experiment at Moor House. Relationship between (a) *Calluna* biomass and years since burning modelled by a Gompertz model, (b) absolute growth rate (AGRb) on a time basis for *Calluna* biomass, (c) vegetation height and years since the last burning modelled by a logistic model, and (d) absolute growth rate (AGRh) on a time basis for vegetation height. Grey bands indicate 95% confidence intervals.