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Research article

Ecological implications of changes in vegetation elemental composition under different heather (*Calluna vulgaris*) managements on British blanket bog

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ABSTRACT

Heather (*Calluna vulgaris*)-dominated peatlands are important biodiversity habitats, often shaped by historical management. In the UK, these habitats were traditionally burnt to rejuvenate vegetation for grazing. Heather burning intensified over the last two centuries for red grouse (*Lagopus lagopus scoticus*) management, creating a mosaic of vegetation composition and ages for shelter, foraging and nesting of many rare upland birds. More recently, burning has been claimed to negatively impact peatlands and associated key ecosystem services, including carbon storage. Regulation has consequently tightened, with burning replaced by cutting or no heather management. However, surprisingly little is known regarding long-term management effects and evidence of negative burning impacts remains contested. Here, we examine how these three management approaches affect elemental composition of two principal food plants, heather and cotton-grass (*Eriophorum* spp.) across three British upland peatlands over ten years. We find that: 1) heather shoot nutrition significantly improved following management (mainly increasing Mn, P, N, Na, Zn, and, for burning only, Fe and K and decreasing Al) compared to no management, 2) management benefits were most pronounced post-burning, and often for longer than post-cutting, 3) impacts were primarily evident in heather shoots and nutrient levels generally realigned over nine years post-management, and 4) cotton-grass, especially flower heads, showed significantly increased Mn on burnt plots. These elemental benefits (Fe, N, Mn, P) are important for carbon uptake, egg formation (K, Zn), avian breeding success and grazing animals (P). This study highlights the value of long-term, holistic monitoring when assessing peatland management strategies.

1. Introduction

Peatlands are commonly considered to be areas consisting of peat deposits more than 30 cm deep, where peat is defined as a soil containing over 30 % organic matter (Joosten and Clarke, 2002). The vast majority of peatlands (80 %) are found in the northern hemisphere, with substantial peat deposits also found in the tropics (Joosten and Clarke, 2002; Limpens et al., 2008). Boreal and sub-arctic peatlands are estimated to store 270–547 Pg (1 Pg = 10^{15} g) of carbon (C), which represents over one third of the world's total soil organic C store (Gorham, 1991; Turunen et al., 1999; Yu et al., 2010). Peat also stores large amounts of water due to the low hydraulic conductivity of the peat matrix, and much of the UK drinking water (around 70 %) originates from peatland areas (Xu et al., 2018).

Blanket bogs, a globally rare peatland habitat, are found across the world (Gallego-Sala and Prentice, 2013), often in upland areas, as cool temperatures and high precipitation are required for their formation (Lindsay, 2010). About 13 % of the world's blanket bog area is found in the UK (Ratcliffe and Thompson, 1988), often with extensive cover of ling heather (*Calluna vulgaris*) and considerable cotton-grass (*Eriophorum* spp.) and *Sphagnum* mosses. Both heather and cotton-grass species are indicators for nutrient-poor upland blanket bog habitat classification

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(JNCC, 2009) and as key 'peat-forming species' contribute to peat formation (JNCC, 2011). Heather is well adapted to burning (Davies et al., 2016) and cotton-grasses can also become temporarily dominant as part of heather management (Whitehead et al., 2021). Heather lives in association with mycorrhizal fungi enabling the breakdown of organic matter and enhancing nutrient uptake in nutrient-poor environments (Read, 1991; Read et al., 2004). Cotton-grasses, such as *E. vaginatum*, are non-mycorrhizal and opportunistic species, which exhibit highly efficient nutrient usage under nutrient-poor conditions and are also effective in uptake under conditions of high nutrient availability (Silvan et al., 2004); *E. angustifolium* is a similar species, often co-occurring on British blanket bogs, but with broader leaves and extensive rhizomes, which are better adapted to permanently flooded areas compared to *E. vaginatum* with dense tussocks and better adaptation to periodically drier conditions (Phillips, 1954; Gebauer et al., 1998). *Sphagnum* mosses are important for supporting peat water holding capacity and enhancing peat-forming conditions (Ashby and Heinemeyer, 2021).

1.1. Heather management

UK heather-dominated uplands are often under vegetation management, including the use of prescribed burning on grouse moors (Davies et al., 2016). Whereas historically burning has been most widely used, increasingly, alternatives such as cutting are being explored and promoted. Whilst no heather management is another option, this limits rejuvenation (Liepert et al., 1993) - older heather has a high rate of evapotranspiration (Worrall et al., 2007) which dries the peat, reduces water tables (Heinemeyer et al., 2023), hinders *Sphagnum* growth (Campeau and Rochefort, 1996) and also cover (Milligan et al., 2018).

Although areas of the English uplands have been subject to periodic burning for many centuries to improve sheep grazing (Simmons, 2003), a rise in the popularity of grouse shooting since the 1800s saw an intensification in heather burning. Depending on site wetness and heather growth rates, burn cycles have usually been on an about 8–25-year rotation (Clay et al., 2015). Controlled burning of vegetation on grouse moor managed blanket bogs tends to encourage heather growth, with dense heather cover providing nesting areas and newly grown shoots being the main food source for red grouse (*Lagopus lagopus scoticus* (Latham)). Low impact burning can promote vegetative regeneration and increase plant nutrient availability (Neary et al., 1999). Regular burning has been advocated and promoted for red grouse management to remove old growth and encourage new shoots of higher nutritious value (Lovat, 1911; Picozzi, 1968), reflecting the recycling of nutrients from ash fertilisation (Allen, 1964). For example, after about 20–30 years, heather stems lignify, turn woody and their growth slows (Gimingham, 1975); repeated burning removes much of this old growth and leaf litter as well as encouraging heather seed germination and regeneration from mature heather root stock (Liepert et al., 1993).

In the UK, heather burning is often presented as a contentious issue and burning has become strongly regulated. However, there is much misinformation about potential impacts of controlled heather burning on peatlands (Ashby and Heinemeyer, 2021; Davies et al., 2016) and it is a historic management tool not only in the UK but also across other countries (Davies et al., 2016). Burning has also been considered to reduce fuel loads and thus likely reduce wildfire risks and severity (Marrs et al., 2019). Importantly, controlled heather burning on UK peatlands should only be done over small areas and during colder months and wetter ground conditions, often referred to as a quick-moving 'cool burn' (Defra, 2007), thus only burning vegetation not peat.

Increasingly, cutting by large machinery is now being promoted as an alternative to burning, avoiding C loss from vegetation combustion, although losses from long-term brash decomposition are considerable (Heinemeyer et al., 2023). Notably, there is even less evidence on the impacts from cutting than from burning (Ashby and Heinemeyer, 2021) and several negative impacts have been reported, including reduced micro-topography (Heinemeyer et al., 2019a; Holmes and Whitehead, 2022), higher carbon loss (i.e., from brash decomposition) and sedge (i.e., cotton-grass) cover with higher methane emissions (Heinemeyer et al., 2023).

1.2. Considerations for grazing and plant growth

Sheep (and less so cattle) tend to graze on heather during the winter months, outside the peak growing season for their main food plants (Holden et al., 2007). Cotton-grass is also important for grazing (Holden et al., 2007), notably during spring (Grant and Armstrong, 1993), when the young flower heads are rich in phosphorus (P) and potassium (K) (Goodman and Perkins, 1959). Cotton-grass shoots are also especially protein-rich (i.e., with a high nitrogen (N) content) in the spring, and may be selectively grazed by female grouse (Moss et al., 1990; Palmer and Bacon, 2001). Both N and P are important nutrients for grouse (Moss, 1969, 1972), particularly for breeding hens (Moss et al., 1975) and chicks (Savory, 1977); there is evidence of selective feeding on heather with high N and P content (Moss, 1972, 1977), especially by chicks (Savory, 1977, 1978). Moreover, grouse are known to also require N, sodium (Na), magnesium (Mg), calcium (Ca) and K for egg laying (Moss, 1977), whilst a lack of manganese (Mn) can cause breeding and development problems in poultry and pheasants (National Research Council, 1994). As grouse prefer to consume younger heather shoots from plants between two and eight years old (Savory, 1978), management is necessary to encourage a constant supply of relatively young heather.

Plant functions also require adequate concentrations of key elements, which vary between vegetation types and habitats (Allen, 1989). Key elements such as iron (Fe), Mn, Mg, N, P are all required for plant growth and C uptake through photosynthesis (e.g., Kumar et al., 2021; Marschner, 2012; Uchida, 2000). However, high atmospheric N depositions in the UK can negatively affect vegetation diversity (Limpens et al., 2003) and C storage (Kivimäki et al., 2013). Therefore, N emission-losses during burning, as reported by Allen (1964), might help reduce potential over fertilisation of blanket bogs.

Whilst there have been studies assessing burning and cutting impacts on C dynamics and vegetation composition (e.g., Heinemeyer et al., 2018; Holmes and Whitehead, 2022; Marrs et al., 2019; Milligan et al., 2018; Whitehead et al., 2021), so far, no experimental study has assessed the potential nutritional impacts of heather management comparing the various management options over a considerable temporal scale. One key study showed nutrient recycling from heather burning in the UK (Allen, 1964), and a recent short-term study for a Polish lowland heathland on mineral soil (Parzych and Piskuła, 2024) also showed considerable benefits to several nutrients (i.e., N, Mn, K, Mg, Zn) in heather shoots immediately after a prescribed fire. However, relatively little is known about the effects of heather cutting on the nutritional value of vegetation for grouse and grazing animals, although there is evidence that heather regeneration after cutting is very similar to that after burning in terms of height and cover (Liepert et al., 1993). Moreover, on blanket bogs, heather and cotton-grass are the two main species of consideration for nutritional food, and overall heather management could affect both species, requiring a detailed analysis, both spatially and temporally.

1.3. Study aims and hypotheses

This study assessed the effects of different types of heather management (i.e., prescribed fire, alternative cutting and no management) on nutrient levels in heather and cotton-grass on blanket bogs. A fully replicated trial at three UK blanket bog sites, including some Before-After Control-Impact (BACI) comparisons in relation to management interventions, assessed nutrient content in vegetation samples taken over a 10-year study period and tested the following three hypotheses.

H1. Heather management increases elemental concentrations in young shoots of heather and cotton-grass compared to those of unmanaged areas.

H2. Elemental concentrations and management impacts are greater in cotton-grass flower heads than leaves.

H3. Elemental concentrations increase more after burning than cutting, regardless of brash removal treatment.

2. Material and methods

2.1. Study sites

This study is part of the long-term Peatland-ES-UK project (https://peatland-es-uk.york.ac.uk/) and samples were collected from three sites in northern England (see Fig. 1), Nidderdale, Mossdale and Whitendale. Each site offers two adjacent (Nidderdale and Mossdale) or closely located (Whitendale) sub-catchments (~10 ha), each of which was allocated either burning or cutting management after an initial pre-management change monitoring period. All sites are classed as blanket bog with poorly drained organic peat (Winter Hill series) with a mean peat depth of about 1.5 m and mostly greater than 50 % heather cover, with some other typical bog vegetation (mainly cotton-grasses and *Sphagnum* or other mosses). All three sites are managed grouse moors with a historic burn rotation (during >100 years, based on estate information and confirmed by charcoal records as outlined in Heinemeyer et al. (2018), indicating an on average 22-year burn rotation since the 1850s). The three sites represent a spectrum of wetness and habitat condition with Nidderdale being the driest and most modified, Mossdale the wettest and least modified and Whitendale the intermediate site. For

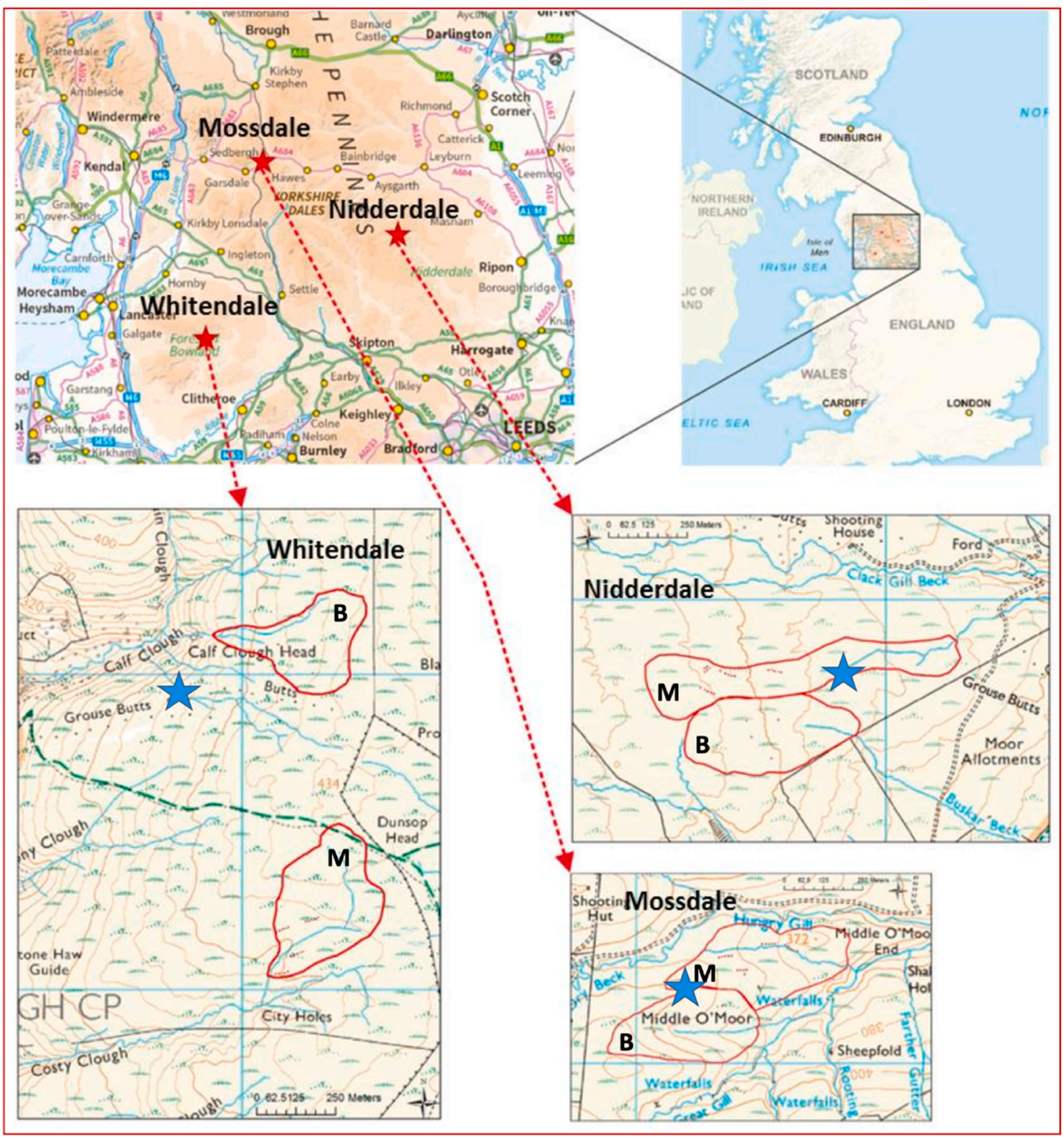

Fig. 1. Location of the three study sites in northern England (**top maps**, red stars). The catchment boundaries (thick red lines) with the burnt (B) and cut/mown (M) catchments are detailed in the **lower maps** for Whitendale, Mossdale and Nidderdale with weather station locations indicated by a blue star. Source: MiniScale® [TIFF geospatial data], Scale 1:1,000,000, Tiles: GB, Updated: December 3, 2015, Ordnance Survey (GB), Using: EDINA Digimap Ordnance Survey Service, http://digimap.edina.ac.uk, Downloaded: 2016-09-09 14:35:01.73. Note the central stream within each sub-catchment (map taken from Heinemeyer et al., 2019b).

more detailed site information in addition to the following section see Heinemeyer et al. (2019b):

Nidderdale is located on the Middlesmoor estate in upper Nidderdale, which lies within the Yorkshire Dales National Park, UK, at 54° 10′ 07″N; 1° 55′ 02″W (UK Grid Ref SE 055747) about 450 m a.s.l. The site showed a mean (± standard deviation during 2012–2021) annual air temperature of 7.4 ± 0.4 °C and annual total precipitation of 1426 ± 277 mm during the ten-year study period, and a mean annual water table depth of −12.5 ± 6.4 cm. The average peat depth is 1.6 ± 0.3 m across the experimental plots with an average slope of 4 ± 3°.

Whitendale is located within the Forest of Bowland (a National Landscape), Lancashire, at 53° 59′ 04″N; 2° 30′ 03″W (UK Grid Ref SD 672543) about 410 m a.s.l. The annual mean (± standard deviation during 2012–2021) air temperature was 7.8 ± 0.4 °C and annual total precipitation was 1795 ± 272 mm during the ten-year study period. The mean annual water table depth was −9.0 ± 6.9 cm. The average peat depth is 1.7 ± 0.4 m at the experimental plots with an average slope of 8 ± 3°.

Mossdale is located in Upper Wensleydale within the Yorkshire Dales National Park at 54° 19 ′01″N; 2° 17 ′18″W (UK Grid Ref SD 813913) about 390 m a.s.l. The site showed a mean (± standard deviation during 2012–2021) annual air temperature of 7.4 ± 0.3 °C and annual total precipitation of 1912 ± 325 mm during the ten-year study period, with mean annual water table depth around −7.7 ± 5.7 cm. The average peat depth is 1.2 ± 0.4 m at the experimental plots with an average slope of 6 ± 3°.

Management (burning and cutting of several patches within each catchment) was done in spring 2013. The site conditions and treatments are shown in Fig. 2. Burnt (**FI**) monitoring plots (5 × 5 m) were located in the burnt catchments, whilst cut monitoring plots, with either brash left (**LB**) or brash removed (**BR**), and unmanaged 'do nothing' (**DN**) monitoring plots were located in the mown catchments. For burnt and cut treatments there were two sets of replicates as a *Sphagnum* pellet addition treatment failed to result in *Sphagnum* growth (at the time a novel management approach to enhance *Sphagnum* moss cover to support rewetting and peatland restoration efforts across the UK, which has since been replaced by planting *Sphagnum* plugs). Therefore, across the three sites, there were 12 DN replicates and 24 replicates each for FI, LB and BR.

Detailed information on vegetation cover and height pre- and post-management is available in a peer-reviewed and published report by Heinemeyer et al. (2023). In summary, cover of heather and cotton-grass on unmanaged plots was about 70 % and 18 %, respectively. For burnt and mown plots heather cover similarly increased from around less than 5 % one year after management to about 40 % in 2021, and cotton-grass cover increased similarly over time since one year after management from about 25 % on mown and 12 % on burnt plots (reflecting pre-management differences) to a peak in 2017–2018 of about 50 % and 35 %, respectively. Cotton-grass cover slightly declined thereafter to about 40 % on mown and 30 % on burnt plots. For cotton-grass, *E. vaginatum* cover was always greater than that of *E. angustifolium*. For unmanaged plots cover of *E. vaginatum* was about 12 % until 2018

Fig. 2. Vegetation cover (**top row**) at the three heather-dominated blanket bog experimental sites taken in 2012 (from left to right: Nidderdale, Mossdale and Whitendale), main managements (**middle row**; from left to right: unmanaged heather area versus managed areas in early spring of 2013 by either burning or cutting with leaving brash, and plot survey pictures (**bottom row**; from left to right: 1 × 1 m pictures for unmanaged 'do nothing', burnt and cut with left brash plots) taken about 6 months after management (2013) at Mossdale. Picture credit A. Heinemeyer.

and thereafter declined to about 6 % whilst *E. angustifolium* slightly increased gradually from 1 % to 2 %. For mown plots cover of *E. vaginatum* increased from 15 % to 30 % in 2018 and thereafter declined to 18 %, whilst *E. angustifolum* cover similarly increased from 1 % to 5 % and then decreased again to 3 %. For burnt plots cotton-grass cover was generally less than on mown plots (as already pre-management), increasing for *E. vaginatum* and *E. angustifolium* from 5 % to 1 % to about 15 % and 7 % in 2018 and subsequently decreasing to 10 % and 4 %, respectively.

2.2. Sampling

Pre-management sampling of heather was conducted during February to April in 2013. Post-management sampling on areas managed in 2013 occurred in August 2015 and subsequently annually during June or July from 2018 to 2021. Five samples of fresh and representative looking heather (the top ~5–10 cm of a green shoot), representing the previous (pre-management samples) and new season's growth (post management samples), were harvested randomly from separate plants across the entire 5 × 5 m monitoring plots from a height relevant to red grouse (i.e., up to 30 cm height). When present, cotton-grass leaves (about 20 cm long) for both species were collected separately, and flower heads irrespective of cotton-grass species (as nearly always only collected from *E. vaginatum*) were collected together during 2019–2021.

2.3. Sample preparation and laboratory analysis

2.3.1. Acid digestion

Oven-dried heather and cotton-grass samples were homogenised into a fine powder using a Retsch MM200l ball mill (Retsch GmbH, Haan, Germany). Approximately 0.5 g of each ground subsample was placed in a Kjeldahl tube with 10 ml of 70 % nitric acid (AnalaR NORMAPUR® grade, VWR International LLC, Radnor, PA, USA). A glass teardrop stopper was placed on top of each tube (SEAL Analytical) and left overnight. For each digestion block (50 tubes), there were two 'blanks' consisting of only nitric acid (i.e., without plant material). Tubes were digested by increasing the temperature by 10 °C every 15 min until 60 °C was reached, left at 60 °C for 3 h and then heated to 110 °C using the same incremental method. After a further 6 h, the tubes were removed from the blocks and left to cool overnight.

A small quantity (5–10 ml) of ultra-pure deionised water was added to each tube and swirled to mix. Each sample was separately filtered through a hardened ashless filter paper (125 mm diameter, No. 540, Whatman, GE Healthcare Life Sciences, Little Chalfont, UK) into a 50 ml volumetric flask. The Kjeldahl tube and teardrop stopper were rinsed onto the filter paper and the filter paper was also then rinsed with ultra-pure water into the volumetric flask (i.e., total sample volume 50 ml). Samples were stored in clean centrifuge tubes at room temperature.

2.3.2. ICP analysis

Elemental composition of the samples was determined using inductively coupled plasma optical emission spectroscopy (ICP-OES; iCAP 7000 Series ICP spectrometer, Thermo Scientific, Waltham, MA, USA). For the instrument and parameter settings, please see Supplementary Table S1 and S2. Prior to analysis, all 10 ml samples were diluted with ultra-pure water by half. Blanks and washes were both nitric acid, which was diluted to the same concentration as that in the samples. Two washes and a standard reference check were run after every 12 samples.

Element concentrations were calibrated using 0.5, 1, 2, 5, 10 and 20 ppm concentrations of a multi-element standard (CertipurR, Merck KGaA, Darmstadt, Germany), containing K, Na, Ca, Mg, Fe, aluminium (Al), Mn, zinc (Zn), copper (Cu), and lead (Pb), which was made up in a nitric acid matrix. P was similarly calibrated using 0.5, 1, 2, 5 and 10 ppm concentrations of a P standard containing H_3PO_4 (CertipurR, Merck KGaA, Darmstadt, Germany). Argon was used as the carrier gas. Nearly all Pb concentrations were below the machine limit of detection. Silicon (Si) was only analysed from 2019 onwards, calibrated using 0.5, 1, 2, 5 and 10 ppm concentrations of a Si standard (Sigma-Aldrich, USA).

All elemental concentrations were converted from ppm to μg g^{-1} dry material or percentage of dry material (whichever was most appropriate for the concentrations) using sample dry weight and dilution concentration. All values which appeared to be produced as a result of machine error (i.e., where negative or apparently devoid of a particular element, like for Pb) were removed. Additionally, some samples were missing due to a lack of plant material and some values were identified as visual outliers, which were remeasured and replaced or excluded if confirmed as outliers (i.e., Cu > 50 μg g^{-1} and Zn > 150 μg g^{-1}). This meant the number of replicates from each group was not the same for all elements.

2.3.3. C:N analysis

Carbon and nitrogen content (C:N) was determined for all heather samples. Approximately 50 mg of each ground, oven-dried 'leafy' subsample was folded into a tin foil cup (Art-No. 05 000 429, Elementar Analysensysteme GmbH, Hanau, Germany) to form a tight ball. The 2013 and 2015 samples were analysed using the "Plant500" method in a C:N analyser (vario Macro, Elementar Analysensysteme GmbH, Hanau, Germany), with glutamic acid standards, and the results were factored according to the standards. The 2018–2021 samples were analysed on a Thermo Flash EA 1112 NC elemental analyser (Thermo Scientific, Waltham, MA, USA), calibrated using a certified reference material (Birch leaf Standard, CatNo. B2166, Elemental Microanalysis Ltd, Okehampton, UK).

2.4. Data analysis

Diagnostic plots, Akaike information criterion (AIC), Likelihood ratio test and deviance scores were consulted to choose appropriate and the most robust statistical models. All analysis was done in R (R Core Team, 2024) and the DHARMa package was used (Hartig, 2024) to create scaled (quantile) residuals for fitted models. Linear mixed modelling (LMM) was used to analyse heather (C, P, K, Na, Mg, Ca), cotton-grass leaves (*E. angustifolium*: K; *E. vaginatum*: P, K, Mg, Ca), and cotton-grass flowers (P). A moderate positive skew was evident in the data and residuals for heather (N, Fe, Al, Mn, Zn and Cu), cotton-grass leaves (*E. angustifolium*: N, P, Na, Mg, Ca, Si, Fe, Al, Mn, Zn, and Cu; *E. vaginatum*: Na, Fe, Al, Mn, Zn, and Cu) and cotton-grass flowers (*E.* spp.: N, K, Na, Mg, Ca, Si, Fe, Al, Mn, Zn, and Cu); consequently, these data were analysed using generalized linear mixed modelling (GLMM), with a Gamma family distribution (glmmTMB package in R; Brooks et al., 2017) using either identity or log-link functions. Cu data still showed some skewed distribution (high values) and were therefore analysed using GLMM with Gamma family distribution and a log link function. Pb concentrations were found to be at or below the detection limit in many samples, resulting in near-zero or negative concentrations. Consequently, Pb was excluded from further analysis.

All elements were analysed using a Before-After Control-Impact (BACI) approach for heather; the only exception was Si, as this was not analysed pre-management. Due to the asymmetric nature of sampling, years were treated as a categorical variable instead of "before vs after," with 2013 the 'control' year (as baseline year) versus the 'impact' years of 2015, 2018, 2019, 2020, 2021. Mixed effect models were used as they handle uneven datasets and missing data points better than ANOVA. "Unmanaged" was the control management (as baseline management), relative to which BACI analyses were performed (e.g., testing for a significant interaction term of year:management for post-management years vs the pre-management baseline by considering any existing pre-management differences), with random effects as (1 | site/block) or (1 | site/plot) or (1 | site/block/plot), which were determined by the likelihood ratio test for model performance (also used to inform about significance and size of site and year effects). Further analysis of the absolute marginal means for paired contrasts between managements were conducted for all years. A BACI analysis for cotton-grass was not possible, as measurements were only taken in 2019, 2020, and 2021 without pre-management baseline sampling. Therefore, a simple control vs impact regression analysis was used for cotton-grass leaves. For cotton-grass further T-tests or Wilcox tests (depending on normality of the data) tested for differences between elemental concentrations in cotton-grass flowers versus leaves across the combined sites and years. In addition to the main statistical output below, more detailed information is provided in the supplementary information for specific paired contrasts, using estimated marginal means (i.e., emmeans; Lenth, 2024) for post-hoc analyses (Table S7 for heather and **S8** for cotton-grass) and overall (for heather Table S9 and for cotton-grass **S10**).

3. Results

Elemental concentrations from vegetation samples were determined for 13 elements. Of these, only 12 were present in sufficient concentrations to be accurately quantified in all samples (Pb not detectable). Detailed results for all elements are available in the supplementary material (Table S3 for heather and **S4** - **S6** for cotton-grass) to facilitate interpretation and to allow comparison to other studies and published literature values.

Elemental concentrations of heather shoots were altered after management implementation compared with before, and the highly significant differences between sites were mostly only of low (<10 %) or medium (<15 %) magnitude apart from for Ca (Table 1A). There were overall statistically significant increases in N, P, Na, Mn and Zn at various points after either management. For several elements the increase was only observed initially (N, P). However, Al decreased in 2015, which was more significant after cutting with leaving brash, but a general decline was also observed in unmanaged plots (Table S3). Moreover, a few elements (K and Fe) only significantly increased after burning (Table 1A) with short-term increases in K (2015) and medium-term increases in Fe (2019–2020). However, N was noticeably lower on burnt than unmanaged plots in 2018 (Fig. 3) and (significantly so in) 2021 (Table 1A). In addition to the BACI results (Table 1A) further paired contrasts between treatments per year (Table 1B) for the key elements shown in Fig. 3 revealed further differences with significantly higher nutrient concentrations for several years (but not in 2013) on burnt versus cut plots, especially for P (2015, 2018–2020) and Fe (2019) and less so for K (2015, 2020) and Mn (2018).

Significant gains in element concentration in heather shoots due to management were primarily, and often for a longer period with higher increases and/or significance levels, observed in burnt versus unmanaged areas, as shown overall for P, K, Fe and Mn (Fig. 3; Table 1A,B) and also at Mossdale (2018–2021) for Na and at Whitendale (2018–2020) for Zn as shown for individual site means (Table S3), compared to those that were cut. Overall significant management impacts (burning and cutting treatments) in heather shoots (Table 1A), when comparing the post-management periods versus the before management (2013), were most strongly (Fig. 3) and significantly ($p < 0.001$) observed for Mn (for Mn four times over the subsequent seven years) and P ($p < 0.01$). However, after eight years post-management, nutrient levels became mostly similar to unmanaged (old) heather (Table 1A; for detailed statistical output see Supplementary Table S9).

Cotton-grass samples (leaves or flower heads) were also analysed combined for all sites, as there were mostly only small or moderate (yet often highly significant) proportions of variance explained by site, which was considerable (i.e., >20 %) only for Mn in (*E. angustifolium*) and Zn (flowers) (Table S10 C,D). Cotton-grasses showed some significant impacts on nutrients (i.e., for Mn, Na, P, K and Fe) from either management (Table 2). All cotton-grass material exhibited a significant ($p < 0.05$) increase in Mn concentrations even six years after management, which was observed across all years and sites on burnt plots and for flowers also on brash removal plots (Table 2A; for detailed statistical output see Supplementary Table S8 and S10). The increase in Mn in cotton-grass material (leaves and flowers) differed more between sites than years (Fig. 4). Moreover, *E. angustifolium* leaves showed overall significantly ($p < 0.05$) higher Fe on brash removal plots but lower P and K on burnt plots compared to unmanaged plots and flowers showed significantly ($p < 0.05$) reduced Fe for brash removal (Table 2A). Na showed an overall significant increase for *E. vaginatum* leaves ($p < 0.01$) and for cotton-grass flowers, which was least significant ($p < 0.05$) on burnt plots (Table 2A). The pair-wise comparisons per year across all sites (Table 2B) also showed significantly lower nutrient content after brash removal (i.e., BR vs LB) for Si ($p < 0.05$) and a marginally significant reduction for Na ($p = 0.099$) but an increase for P ($p = 0.088$) in flowers. Overall, cotton-grass flowers (Table S6) showed noticeably

Table 1A
Statistical output for elemental content (excluding outliers for Zn > 150 and Cu > 50 μg g^{-1}) in heather (*Calluna vulgaris*) samples (young shoots), indicating the direction (upward/downward arrow = increase/decrease) and statistical significance terms (i.e., marginally significant p < 0.1 '.'; p < 0.05*; p < 0.01**; p < 0.001***) for burnt (FI) or cut with either leaving brash (LB) or brash removed (BR) versus unmanaged 'do nothing' (DN: as baseline management) in 2013 (as the baseline year). The overall significances for year, management and their interaction term, site and the percentage of variability explained by site (based on calculating intraclass correlation coefficients from random effects for models with and without site as a factor) are displayed at the top. For further statistical output (p-values and model estimates) see the supplementary table (Table S9) and for detailed model information see section 2.4.

A)	(vs. DN, 2013)	C	N	P	K	Na	Mg	Ca	Fe	Al	Mn	Zn	Cu
	Year	***	***	***	***	***	***	***	***	***	***	***	***
	Management			**		**	.				***	.	
	Year:Management		***	**		.				**	***		
	Site		***	***	***	***	***	***	***	***	***	***	***
	Site % of variability	0	12.5	10.3	0	5.2	12.6	25.7	10.4	14.9	<0.1	6.6	4.8
FI	**2015**		↑ ***	↑ **	↑ *	↑ **				↓ *	↑ ***	↑ *	
	2018					↑ *				↑ *	↑ ***	↑ **	
	2019					↑.			↑ *		↑ **		
	2020					↑ *			↑ *		↑ **	↑ *	↑.
	2021		↓ *			↑ *							
LB	**2015**		↑ ***	↑ **		↑ **				↓ **	↑ ***		
	2018										↑ **	↑ *	
	2019										↑ *	↑.	
	2020										↑ *	↑ *	
	2021					↑.							
BR	**2015**		↑ **	↑ **		↑ **				↓.	↑ ***		
	2018					↑ *					↑ **	↑ *	↑.
	2019										↑.		
	2020										↑.		
	2021		↓ **			↑ *							

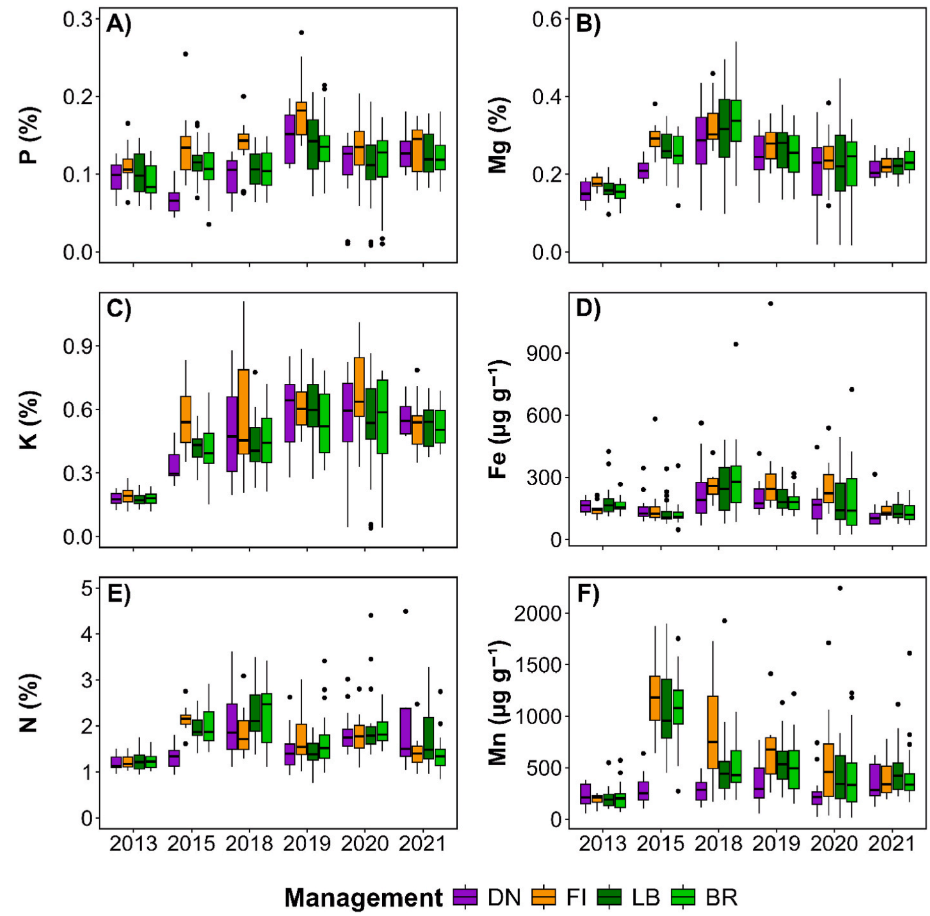

Fig. 3. Elemental content (either as percentage or concentration) in heather shoots combined for all three sites over time for **A)** phosphorus (P), **B)** magnesium (Mg), **C)** potassium (K), **D)** iron (Fe), **E)** nitrogen (N) and **F)** manganese (Mn), for the four management treatments of either unmanaged 'do nothing' (DN), fire 'burnt' (FI) and cut with either left brash (LB) or brash removal (BR). Significant differences are shown in Table 1A,B.

higher overall mean concentrations for six elements compared to leaves (Table 3), which were highly significant ($p < 0.001$) and around two-fold in P, Mg, Cu, Si and Al and of medium significance for Mn ($p = 0.0082$) and of low significance ($p = 0.0122$) for the 1.3-fold higher Zn content. There were no significant differences for slightly lower concentrations for K and Na but three elements showed significantly lower overall mean concentrations (Table 2) in flowers compared to cotton-grass leaves (Table S4 and S5), but whereas Fe showed meaningful (i.e., three-fold) and highly significant ($p < 0.001$) higher concentrations, significances were lower for the very small differences for Ca ($p = 0.0024$) and Zn ($p = 0.0122$).

4. Discussion

This is the first study comparing heather management impacts (burning, cutting or no management) on elemental concentrations on blanket bogs within a long-term BACI study. We could support *hypothesis 1* (*heather management increases elemental concentrations in young shoots of heather and cotton-grass compared to those of unmanaged areas*) by identifying clear heather management benefits across three sites, with increasing content for several elements in heather (Fig. 3; Table 1A,B) and one element (Mn) in cotton-grass (Fig. 4; Table 2), which included elements of key ecological importance for C uptake (in plants via photosynthesis) and nutrition of grazing animals (including red grouse).

Notably, some elements in heather only increased after burning (K and Fe), and more significantly and/or for longer (Na and Mn), whilst others only increased initially or intermittently. Interestingly, the higher nutrient levels after burning compared to cutting could relate to higher concentrations and availability of certain elements in ash (Parzych and Piskuła, 2024), the uptake of which could be supported by rapid microbial community recovery following fire, e.g. via ericoid mycorrhizal fungi (Schellenberg and Bergmeier, 2022). The recent, similar but short-term study by Parzych and Piskuła (2024) on mineral heathland soil also reported considerable benefits in nutrient contents (i.e., N, Mn, K, Mg, Zn) in young heather shoots a few months after burning. Interestingly, as in our study, Mn was the element with the strongest responses. In our study, nutrient content varied over time independently of management as shown in unmanaged samples, likely reflecting seasonal sampling variability (especially for earlier pre-management samples), which outlines that sampling should ideally be done nearer the peak nutrient content period in late spring to early summer. Differences to literature reported values (see Table S3–S5) are thus very likely related to such differences in sampling time. However, our control and management plot sampling each year was done at the same time across all sites to ensure comparability between treatments.

Hypothesis 2 (*elemental concentrations and management impacts are greater in cotton-grass flowers than leaves*) was also supported by overall significantly higher concentrations of around 2-fold (Table 3) for P, Mg, Si, Al, Cu and less so for Mn (although Fe was significantly 3-fold lower, relating to Fe being more concentrated in green leaves) and the observed management related increase in Mn was much more pronounced in cotton-grass flowers (Fig. 4). Finally, the first part of *hypothesis 3* (*elemental concentrations increase more after burning (compared to unmanaged) than cutting and regardless of brash removal treatment*) was partly supported by a periodically higher and/or more significant increase for some elements in heather (Table 1A), only significantly

Table 1B
Additional statistical output for elements shown in Fig. 3 including phosphorus (P), manganese (Mn), nitrogen (N), magnesium (Mg), potassium (K) and iron (Fe) in heather samples between management treatments (i.e., unmanaged ‘do nothing’ (DN), fire ‘burnt’ (FI) and cut with either left brash (LB) or brash removal (BR) within each year (2013, 2015, 2018, 2019, 2020, 2021). Only contrasts with significant (or marginally significant) differences are shown for P, Mg and K from LMM and Mn, N and Fe from GLMM, with significance levels being displayed by asterisks (i.e., marginally significant $p < 0.1$ ‘.’; $p < 0.05$*; $p < 0.01$**; $p < 0.001$***) and arrows indicating direction (upward = increase; comparing 2nd vs 1st management treatments).

Element	Year	Contrast	P value	Significance
P	2015	DN - FI	<0.001	↑***
	2015	DN - LB	<0.001	↑***
	2015	DN - BR	<0.001	↑***
	2015	FI - LB	0.0913	↓.
	2015	FI - BR	0.0137	↓*
	2018	DN - FI	0.0040	↑**
	2018	FI - LB	0.0099	↓**
	2018	FI - BR	0.0077	↓**
	2019	DN - FI	0.0070	↑**
	2019	FI - LB	<0.001	↓***
	2019	FI - BR	<0.001	↓***
	2020	DN - FI	0.0499	↑*
	2020	FI - LB	0.0269	↓*
	2020	FI - BR	0.0465	↓*
Mn	2015	DN - FI	<0.001	↑***
	2015	DN - LB	<0.001	↑***
	2015	DN - BR	<0.001	↑***
	2018	DN - FI	<0.001	↑***
	2018	DN - LB	<0.001	↑**
	2018	DN - BR	<0.001	↑**
	2018	FI - LB	0.0560	↓.
	2018	FI - BR	0.0491	↓*
	2019	DN - FI	0.0068	↑**
	2019	DN - LB	0.0060	↑**
	2019	DN - BR	0.0421	↑*
	2020	DN - FI	0.0045	↑**
	2020	DN - LB	0.0058	↑**
	2020	DN - BR	0.0200	↑*
N	2015	DN - FI	<0.001	↑***
	2015	DN - LB	<0.001	↑***
	2015	DN - BR	<0.001	↑***
	2018	FI - LB	0.0228	↑*
	2018	FI - BR	0.0132	↑*
	2019	FI - LB	0.0296	↓*
	2019	LB - BR	0.0185	↑*
	2021	DN - FI	0.0060	↓**
	2021	DN - BR	<0.001	↓***
	2021	FI - LB	0.0123	↑*
	2021	LB - BR	<0.001	↓***
Mg	2015	DN - FI	0.0588	↑.
	2015	DN - LB	0.0099	↑**
	2015	DN - BR	0.0483	↑*
	2018	DN - BR	0.0211	↑*
K	2015	DN - FI	0.0032	↑**
	2015	DN - LB	0.0611	↑.
	2015	FI - LB	0.0602	↓.
	2015	FI - BR	0.0392	↓*
	2018	FI - LB	0.0551	↓.
	2018	FI - BR	0.0761	↓.
	2020	DN - FI	0.0406	↑*
	2020	FI - LB	0.0199	↓*
	2020	FI - BR	0.0161	↓*
Fe	2015	FI - BR	0.0876	↓.
	2018	DN - BR	0.0628	↑.
	2019	DN - FI	0.0236	↑*
	2019	FI - LB	0.0068	↓**
	2019	FI - BR	0.0031	↓**
	2020	DN - FI	0.0135	↑*
	2020	FI - LB	0.0216	↓*
	2020	FI - BR	0.0507	↓.

Table 2A
Statistical output for elemental content (excluding outliers for Zn > 150 and Cu > 50 μg g^{-1}) in cotton-grass leaves (*Eriophorum angustifolium* and *E. vaginatum*) and flower heads (*Eriophorum* spp.) for combined cotton-grass species samples (2019–2021) indicating the direction (upward arrow = increase) and statistical significance terms (i.e., marginally significant $p < 0.1$ ‘.’; $p < 0.05$*; $p < 0.01$**; $p < 0.001$***) for burnt (FI) or cut with either left brash (LB) or brash removal (BR) versus the unmanaged ‘do nothing’ (DN) treatment. For further statistical output (p-values and model estimates) see the supplementary table (Table S10) and for more detailed model information see section 2.4.

	Leaves: *Eriophorum angustifolium*			Leaves: *E. vaginatum*			Flowers: *E.* spp.		
	FI	LB	BR	FI	LB	BR	FI	LB	BR
P	↓*								
K	↓*		↓.						
Na				↑ **			↑ **	↑ ***	↑*
Mg									
Ca									
Si									↓ **
Fe			↑ *						↓*
Al									
Mn	↑ *		↑.	↑ *	↑.		↑ *	↑.	↑*
Zn									
Cu									↓.

increasing after burning for K in 2015 and 2020, for Fe in 2019 and 2020, Mn showing greater significances throughout and Na showing significances over more years with higher mean values (Table S3) after burning compared to unmanaged heather. P was also significantly higher for burning compared to cutting for paired contrasts in 2018, 2019 and 2020, as was Fe in 2019 and K with less significance in 2020 (and marginal in 2015 and 2018) (Table 1B), without any significant differences between treatments during the pre-management period (2013). For cotton-grass leaves Mn only showed significant increases ($p < 0.05$) several years after burning (Fig. 4 and Table 2A) with site differences for different cotton-grass material showing Mossdale with the highest burn effect and strongly significant lower Mn in cut than burnt *E. vaginatum* leaves (Table S8A) and in 2020 (Table S8B). The overall effect sizes (greater increase in means after burning than cutting) differed between sites for some elements in heather (Table S3), such as for K and Mn (mainly at Whitendale) and P (mainly at Mossdale and Whitendale). Overall, this nutrient benefit (in elemental content) after burning very likely relates to ash fertilisation after fire as previously reported by Pereira et al. (2011) for an oak forest fire and Kelly et al. (2018) for increased levels of P and Ca on upland peat bogs after wildfire. However, there was some small decline in P and K in *E. angustifolium* leaves on burnt plots, but only several years after management. Moreover, the observed (in 2021) lower heather N content in heather on burnt and brash removal plots could relate to reported large N losses during biomass combustion (Allen, 1964) and removal, respectively. The second part of *hypothesis 3*, regarding brash removal, remains unclear with only some indications such as N content of heather in 2021 (Table 1A) and Si and Fe (and marginally Cu) concentrations in cotton-grass flowers showing overall significantly lower values (compared to unmanaged) after brash removal (Table 2A). The only highly significant paired contrast for brash removal (i.e., BR vs LB) per year was for N in heather samples for 2021 (Table 1B) and also significant for Si in cotton-grass flowers (Table 2B). However, these limited reductions in samples taken several years after management could still indicate a potential long-term and cumulative management issue of repeated brash removal causing depletion of some nutrients.

Nutritional requirements of plants are well documented, including macro- and micro-nutrients (Kumar et al., 2021; Marschner, 2012; Uchida, 2000), but also considering particular nutrients affecting plant growth, stomatal controls and photosynthesis, such as Ca (White and Broadley, 2003), N and P (Güsewell, 2004). The observed increase in elemental content, likely linked to photosynthesis and therefore C

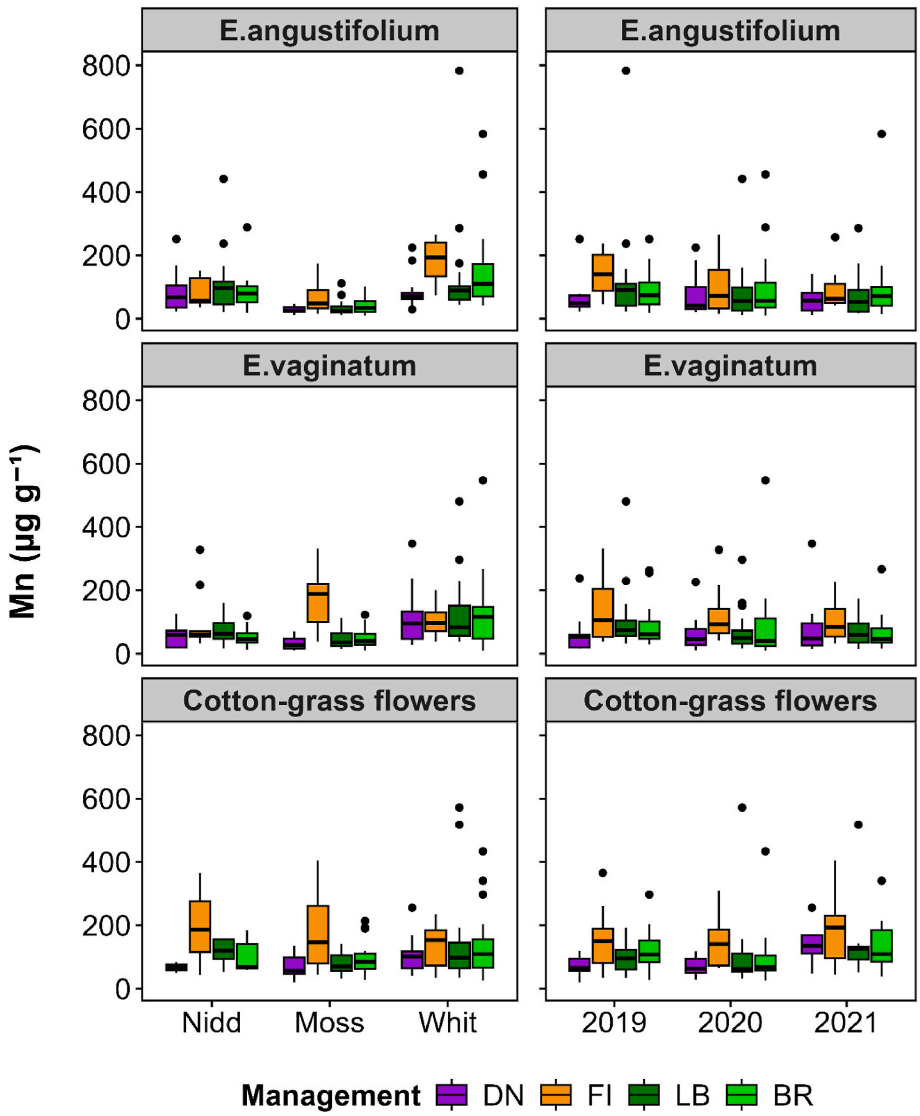

Fig. 4. Elemental concentration of manganese (Mn) in sedge (i.e., cotton-grass; *Eriophorum angustifolium* and *E. vaginatum*) leaves and (*E.* spp.) flowers, either across the three sites for Nidderdale (Nidd), Mossdale (Moss) and Whitendale (Whit), or for different years (2019–2021) for the four management treatments of either unmanaged 'do nothing' (DN), fire 'burnt' (FI) and cut with either left brash (LB) or brash removal (BR). Significant differences are shown in Table 2A,B.

uptake, is of considerable importance as has been discussed recently (Parzych and Piskuła, 2024). Whilst management increased some nutrients in heather only in the short-term (i.e., N, P), others showed long-term increases (i.e., Mn, Na, Zn) compared to unmanaged heather, Fe and K increased only after burning (Table 1A), and P and Fe levels increased more often after burning versus unmanaged and with significantly higher concentrations than either of the cut treatments (Table 1B). Functions of and deficiencies in key plant nutrients are outlined in Marschner (2012); whilst Fe is a crucial co-factor in the chlorophyll enzyme structure for electron transport, Zn is fundamental for the functioning of carboxylase enzyme and thus enabling formation of C bonds after C fixation, Mn activates photosynthetic enzymes and, whilst N is a major component of proteins and therefore plant growth, P is fundamental to energy acquisition and transportation as well as cell growth and metabolism (nucleic acid and nucleotides). Together, the observed increase in these key plant nutrients relates to potentially increased photosynthetic uptake of carbon and most likely also net C storage as indicated by an ongoing study (Heinemeyer et al., 2023).

Management impacts on cotton-grass were less striking and only revealed an overall positive impact on Mn concentrations on burnt plots (Fig. 4). While there was also a noticeable effect for Na, this element is generally not limiting plant growth. However, elemental content in cotton-grass was only assessed in the latter project period, thus missing the likely earlier peak increase (versus unmanaged) as observed for most elements (i.e., 2015) in heather (Fig. 3; Table 1A). Moreover, no BACI analysis could be done for cotton-grass data and future studies would benefit from including pre-management data.

Apart from implications for plants (and likely C uptake), elevated nutrient levels in vegetation on nutrient-poor ombrotrophic blanket bogs (Malmer et al., 1994) are also important for many grazing animals, including sheep and cattle, which graze UK upland areas (e.g., Frazer et al., 2013), but also red grouse (e.g., Moss, 1969). Whilst a diet exclusively of young heather during peak nutrient content (June–July) could sustain a 'dry' sheep (Grant and Armstrong, 1993), heather has lower nutritional value to sheep than alternative grasses, particularly in terms of available protein (Grant and Armstrong, 1993); thus its importance increases during winter, to supplement their diet (Holden et al., 2007).

However, grazing of heather is most important for red grouse, which are often the reason management is carried out. The most striking finding was that, of the eight elements (N, P, Na, Mn, Mg, Zn, K and Al) that showed significant changes in heather shoots following

Table 2B
Statistical output for phosphorus (P), potassium (K), sodium (Na), silicon (Si), iron (Fe) and manganese (Mn), in cotton-grass (*Eriophorum angustifolium, E. vaginatum*) leaves and/or sedge flower samples between management treatments (i.e. unmanaged 'do nothing' (DN), fire 'burnt' (FI) and cut with either left brash (LB) or brash removal (BR) across all years (2019, 2020, 2021)). Contrasts with or with marginally significant differences are shown, with arrows indicating the direction (upward arrow = increase; comparing 2nd vs 1st management treatments) and significance levels (i.e., marginally significant $p < 0.1$'.'; $p < 0.05$*; $p < 0.01$**; $p < 0.001$***).

Element	Vegetation	Contrast	P value	Significance
P	*E. angustifollum leaves*	DN - FI	0.0483	↓*
	Sedge flowers	LB - BR	0.0880	↑.
K	*E. angustifollum leaves*	DN - FI	0.0399	↓*
		DN - BR	0.0512	↓.
Na	*E. vaginatum* leaves	DN - FI	0.0087	↑ **
		FI - LB	<0.001	↓***
		FI - BR	<0.001	↓***
	Sedge flowers	DN - FI	0.0072	↑**
		DN - LB	<0.001	↑***
		DN - BR	0.01754	↑*
		LB - BR	0.0989	↓.
Si	*E. angustifollum leaves*	FI - BR	0.0736	↑.
	Sedge flowers	DN - BR	0.0034	↓ **
		LB - BR	0.0340	↓ *
Fe	*E. angustifollum leaves*	DN - BR	0.0471	↑*
	Sedge flowers	DN - BR	0.0331	↓ *
Mn	*E. angustifollum leaves*	DN - FI	0.0466	↑*
		DN - BR	0.0729	↑.
	E. vaginatum leaves	DN - FI	0.0154	↑*
		DN - LB	0.0549	↑.
		FI - LB	0.0853	↓.
		FI - BR	0.0503	↓.
	Sedge flowers	DN - FI	0.0139	↑*
		DN - LB	0.0555	↑.
		DN - BR	0.0154	↑*

management, all except Al were elevated immediately after management compared to unmanaged heather. Furthermore, all but Mn increased similarly following either burning or cutting compared to unmanaged plots (Table 1A). The significantly higher N, P and Mn content after either management versus DN plots and a decrease after management (Table 1A) also indicates that a mosaic of heather ages is beneficial for providing nutrient-rich vegetation as food for grazing animals (including red grouse) across the landscape (Moss, 1969). The positive management effect of either burning or cutting in a 3-fold increase in Mn content is also of particular importance. A lack of Mn can cause breeding and development problems in poultry and pheasants (National Research Council, 1994), although, as with N and P, it appears that management in general is required to elevate Mn concentrations rather than specifically cutting or burning. Therefore, it may not be advisable to leave heather completely unmanaged if grouse production is a concern, although natural layering of old heather under very wet and mossy conditions (e.g., Mossdale) could rejuvenate stems, leading to a mean stem population age of around 12–15 years as observed at the high elevation and very wet National Nature Reserve (NNR) Moor House (Rawes and Hobbs, 1979) without the need of any management. Additionally, Savory (1978) showed that grouse prefer to eat shoots from between two- and eight-year-old heather and, from the results shown here, either management is more likely to provide this than the unmanaged treatment. Moss (1967) noted that there was no change in chemical composition of heather over six years old, although it did vary seasonally. As seasonal variability is well documented for the three sites (Heinemeyer et al., 2023), this likely explains the differences in heather nutrient content between pre- and post-management DN plots.

One of the elements for which heather differed significantly only between burnt and unmanaged plots was K (Table 1A,B). Estimates of the amount of heather eaten by red grouse range from 63 g d^{-1} for wild cocks to 100 g d^{-1} for wild laying hens (Savory, 1977). Laying hens require high amounts of some elements for egg formation (Jenkins et al., 1965). A wild grouse during egg laying requires up to 160 mg K d^{-1} (Moss, 1977). Therefore, even for the lowest post-management K content on the brash removal plots a hen would only require about 33 g of heather each day to satisfy its K requirements (based on the mean content of 0.49 % shown in Table S3). Even eating heather from pre-management plots, which had significantly lower mean concentrations of only 0.19 %, a hen would only require ~90 g of heather per day, which is still well within the daily intake. Likewise, using the reported daily requirements by a laying hen (assumed to be the maximum amounts required in relation to breeding success; Jenkins et al., 1965) as reported by Moss (1977; cf. Table 3) for N (660 mg), Na (17 mg), Mg (18 mg) and Ca (180 mg), heather from any management would satisfy the hen's requirements. Old heather on pre-management plots had lowest mean concentrations of all these elements (Table S3), which translated into 54 g of heather from these plots to satisfy its N requirements, 19 g for Na, 11 g for Mg and 51 g for Ca. However, for P, with a daily requirement of 86 mg during peak moulting (Moss, 1977; cf. week 3 in Table 1), a hen would require 123 g of heather from pre-management DN plots yet only 38 g of heather would be needed to meet P requirements from the peak P content at Mossdale on burnt plots in 2019. Whilst all these ranges are within the average daily consumption reported by Savory (1978), heather dry matter digestibility is inversely related to the intake above about ~71 g, requiring grouse to select especially nutrient-rich heather (Moss, 1977). This suggests that some form of management is likely required to make it easily available to red grouse, especially for P; it also remains unknown if natural layering on unmanaged areas could provide similarly adequate amounts.

Red grouse selectively consume plants with high N and P contents

Table 3
Statistical output for mean (± standard deviation) elemental content (in percentage for phosphorus (P), potassium (K), sodium (Na), magnesium (Mg), calcium (Ca), silicon (Si) and in μg g^{-1} for iron (Fe), aluminum (Al), manganese (Mn), zinc (Zn) and copper (Cu); excluding outliers for Zn > 150 and Cu > 50 μg g^{-1}) in cotton-grass between flower heads (*Eriophorum* spp.) and leaves (combined *Eriophorum angustifolium* and *E. vaginatum*) for combined sites (Nidderdale, Mossdale and Whitendale) and years (2019–2021) indicating p-values and statistical significance (sign.) terms (i.e., $p < 0.05$*; $p < 0.01$**; $p < 0.001$***) based on either T-tests (T) or Wilcox-tests (W). Arrows indicate the direction of difference for pairs with significant differences, i.e., upwards (bold): flowers > leaves; downwards: flowers < leaves.

Element	Flowers			Leaves			Test		p-value	Sign.
P	0.215	±	0.069	0.152	±	0.065	T	↑	<0.001	***
K	0.728	±	0.303	0.730	±	0.258	T	↓	0.9420	ns
Na	0.041	±	0.026	0.044	±	0.045	W	↓	0.1530	ns
Mg	0.227	±	0.073	0.149	±	0.060	T	↑	<0.001	***
Ca	0.171	±	0.087	0.192	±	0.072	T	↓	0.0024	**
Si	0.018	±	0.018	0.010	±	0.011	W	↑	<0.001	***
Fe	118.28	±	233.47	388.52	±	505.37	W	↓	<0.001	***
Al	44.46	±	58.14	27.68	±	45.06	W	↑	<0.001	***
Mn	117.19	±	89.57	86.88	±	84.46	W	↑	0.0082	**
Zn	117.43	±	36.11	130.45	±	78.86	T	↓	0.0122	*
Cu	42.57	±	36.31	19.37	±	33.07	W	↑	<0.001	***

(Moss, 1972, 1977), which is even more pronounced in chicks than adults (Savory, 1977) with chicks selecting heather with an average of 2.32 % N and 0.25 % P (Savory, 1977). Noticeably, these values are close only to the average values on some burnt plots in this study, especially in 2019 at Mossdale and Whitendale (i.e., 6 years after management). This supports the nutritious benefits from a management mosaic of different ages. Moreover, chicks are likely to only eat the very newest tips (Savory, 1977) and close to the ground; the material in this study included some older growth (away from the growing tip and often higher up the plant) and post-management heather was sampled in late summer, which likely reduced the concentration of some nutrients (Moss, 1967), although it should not have affected the differences between managements within a period. Additionally, both chick and adult red grouse eat other plants and some insects (Savory, 1977). For example, bilberry (*Vaccinium myrtillus*) has a higher P content and tends to start growing earlier in spring than heather (Moss, 1972) and insects like craneflies are an important protein source (Carroll et al., 2015). Unfortunately, few studies on red grouse nutrition have studied moors with high cotton-grass cover, and the nutrient content of cotton-grass was often not considered, although flower buds of cotton-grass represent a high N and P food (Pulliainen and Tunkkari, 1991). For relevant nutrients, our study mainly showed significantly higher levels of Mn compared to unmanaged plots with old heather (Fig. 3) and unmanaged cotton-grass (Fig. 4). Moreover, cotton-grass flowers showed especially high nutrient levels (Table 3 and Table S6) which translated into less daily consumption needs than for heather at an average of 42, 23, 8 g of flower buds for P, K, Mg, respectively, but more for Na with 47 g and 109 g for Ca. However, possible earlier peaks in N and P (but also other elements), as observed for heather (Fig. 3), were likely missed during the delayed post-management cotton-grass sampling. Therefore, considering all aspects of this study and the existing literature, it might be worthwhile for land managers to consider a range of structural ages of key blanket bog species alongside heather when considering management options to benefit grazing animals such as grouse.

5. Conclusions

This study is the first to provide detailed short- and longer-term information on nutritional impacts from different heather management strategies in UK upland peatlands as measured by elemental content of key blanket bog vegetation, namely ling heather and cotton-grass. Several key elements of importance to grazing and photosynthesis (i.e., N, P, Mn, Zn, K) showed significant increases post-management and burning sometimes showed higher enhancement and for longer, which is likely linked to ash fertilisation. However, the magnitude and length of the increased nutrient content varied between elements and was most pronounced for heather shoots in short-term responses in N and P and longer-term responses for Mn, Fe and Zn. For cotton-grass, flower heads showed significantly higher nutrient concentrations than leaves for P, Mg, Mn, Si, Cu and Al with significant management impacts for Na (flowers only) and Mn. However, cotton-grasses were only investigated after several years post-management and the lack of pre-management samples (i.e., no BACI) should be considered in future studies.

Overall, the findings underline the positive impact of heather management on elemental content, especially from burning, in relation to potentially increased carbon uptake from photosynthesis and nutritional benefits for grazing animals, including sheep and cows, but especially for breeding success and egg formation of red grouse. However, for cutting with brash removal, there were some indications of a potential long-term and cumulative management issue of reducing nutrients (N, Si, Fe and K), which should be considered in further studies. Moreover, nutrient levels vary seasonally, which was also reflected in our inter-annual sample variations. Whilst no nutrient levels were found to cause likely limitations in adult grouse nutrition (as shown for laying hens for N, Na, Mg and Ca) or egg formation (K), P was close to peak demand for moulting hens and nutritious requirements for chicks are likely higher but remain unknown and either management certainly improves nutrient provision. However, land managers should clearly consider not only heather, but also other species (e.g., bilberry and cotton-grass) for maximising nutrient availability for grazing and red grouse breeding success. Further research should investigate potential beneficial ecological impacts (e.g., in relation to biodiversity) of N losses from combustion and seasonal changes in elemental contents together with capturing yearly post-management impact on cotton-grass and nutritious demands by grouse chicks.

CRediT authorship contribution statement

Andreas Heinemeyer: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Phoebe A. Morton:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Thomas David:** Writing – review & editing, Visualization, Validation, Formal analysis. **Thomas Holmes:** Writing – review & editing. **Anthony L. Jones:** Writing – review & editing. **Bing Liu:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis.

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Declaration of competing interest

The authors have no specific interests to declare but (since October 2024) AH is a trustee (an unpaid, voluntary role) to The Heather Trust (a registered charity in Scotland, UK), who (alongside many other funders) contributed funding to the elemental analyses (before 2021) but did not influence the study, its findings, their interpretation or writing of the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.126720.

Data availability

Data will be made available on reasonable request.

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