

Research Article

The Assimilation and Retention of Carbon in Upland Heath Plant Communities Typical of Contrasting Management Regimes: A ^{13}C Tracer Study

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Upland heath is an extensive habitat in the UK and is currently managed for a range of objectives: agricultural grazing, sporting interests, and biodiversity conservation. Increasingly land management will also have to address the provision of the ecosystem service of carbon sequestration (transfer of CO_2 from the atmosphere into long-lived pools for storage). This study investigates carbon sequestration in *Calluna*- and *Nardus*-dominated upland heath vegetation communities in NE Scotland, which typically occurs as a result of low and high intensity management (grazing and burning) regimes, respectively. A $^{13}\text{CO}_2$ tracer experiment compared the rate of carbon assimilation and the retention of assimilated carbon over six weeks during the growing season between these two communities. There was no difference in $^{13}\text{CO}_2$ uptake between *Calluna*- or *Nardus*-dominated vegetation communities and they both retained over 40% of the assimilated ^{13}C after six weeks. The ^{13}C retained was mostly held in *Calluna* leaf and stem tissue in the *Calluna*-dominated community and in graminoid leaves in the *Nardus*-dominated community. Consideration of the strategies of the dominant species and the attributes of the tissues in which ^{13}C was retained suggests that *Calluna*-dominated vegetation may be of greater benefit to carbon sequestration in the longer term.

1. Introduction

The management of ecosystems for carbon (C) sequestration, defined as the transfer of CO_2 from the atmosphere into long-lived C pools for storage [1], has become a national and an international objective [2–4]. C stocks within different ecosystems in the UK are fairly well quantified [5], but estimating changes in stocks in response to land management is more difficult [6, 7].

There are 1.2 million hectares of upland heath within the UK, the majority in Scotland [8]. Upland heath in “favourable condition,” is dominated by dwarf shrubs (>25% cover), typically the evergreen ericoid *Calluna vulgaris* (hereafter referred to as *Calluna*), with graminoids and mosses

interspersed. This habitat is predominantly underlain by organomineral and organic soils, with organic matter up to c. 0.5 m deep. The average upland heath soil C density is 89.9 t ha^{-1} in the top 15 cm of the soil [9], representing a national C stock of 108 M tonnes and significantly more if total soil depth is accounted for. Given the importance of this habitat as a C store, we need to understand the consequences of different land management practices for C sequestration and storage.

Upland heath is traditionally managed by low intensity grazing and rotational burning, creating a mosaic of different aged *Calluna* stands, providing young, nutritious plants for all-year round forage and older, larger plants as cover for wildlife, notably important bird species [10]. Upland heath

has suffered significant decline and although its total extent has stabilised in recent years, its condition remains variable [8, 11]. Much is currently in “unfavourable condition,” characterised by the replacement of dwarf shrubs with graminoids, typically as a result of over grazing and/or poor burning practice [12]. One graminoid which commonly becomes dominant is *Nardus stricta* (hereafter referred to as *Nardus*), a tussock-forming perennial grass of low nutritional value which is less preferred than *Calluna* by grazing animals [13, 14]. The dominance of *Nardus* over large areas is thus of less benefit to agriculture and biodiversity conservation than a *Calluna* sward.

Change in plant species composition can influence ecosystem C dynamics [15–20]. *Calluna*, an evergreen shrub, exhibits a slow growth rate [21] and produces long-lived leaves, with low N content and high concentrations of phenolics [22, 23] and lignified woody stem material. Thus, *Calluna* litter is recalcitrant, resisting decomposition and reducing soil respiration. Graminoids exhibit contrasting traits, with faster growth enabling rapid C assimilation but also resulting in greater C loss through plant respiration [16]. Faster growing species also tend to produce leaves with shorter lifespan and higher N content, thus, generating large amounts of litter and increasing rates of decomposition and subsequently soil respiration [23, 24]. Shifts in abundance of subdominant functional groups following change in dominant species may also influence C dynamics; metabolically active herb species have labile plant litter which is easily decomposable, whereas moss species are slow growing and produce recalcitrant litter [25]. Thus, a shift between *Calluna* and *Nardus* dominance of upland heath could alter the C balance of the system; it would be predicted that a *Calluna*-dominated system would be a stronger carbon sink than a *Nardus*-dominated sward.

This study employs an *in situ* $^{13}\text{CO}_2$ pulse labelling experiment to compare C assimilation and retention in upland heath plant communities dominated by *Calluna* and by *Nardus*. We investigate which plant fractions are most important for CO_2 uptake and which most strongly retain assimilate over six weeks during the growing season. Due to differences in relative growth rate and rate of decomposition, we hypothesise that there will be higher assimilation of $^{13}\text{CO}_2$, but also a faster turnover and subsequent lower retention of assimilate in the *Nardus*-compared to the *Calluna*-dominated communities.

2. Materials and Methods

2.1. Site Description. Experimental work was carried out at Glensaugh Research Farm, SE Grampian Highlands, Scotland (56°54' N, 2°34' W). The site is at 365–390 m altitude with a mean annual temperature of 7.5°C and precipitation of 1131 mm [31]. The soil is a podzol with an organic horizon of 30–60 cm depth. The experimental site is lightly grazed all year round by sheep (1.1 ewes ha⁻¹) and by cattle during the summer (0.25 cattle ha⁻¹). The main plant community is *Calluna-Vaccinium myrtillus* (hereafter, *Vaccinium*) heath (NVC H12) [32]. The *Calluna* sward is approximately eight years old and in the building phase of its growth cycle [10].

At this site, the *Calluna*-dominated vegetation forms a mosaic with graminoid-dominated vegetation, characterised as *Nardus-Galium saxatile* grassland (NVC U5) [33]. The moss, *Hypnum jutlandicum*, was abundant in both vegetation communities.

2.2. Experimental Design. In May 2009, five blocks were established within an area of approximately 80 × 80 m, with blocks being >10 m apart. Paired plots (40 cm diameter, >5 m apart) of representative *Calluna*-dominated and *Nardus*-dominated vegetation communities were established within each block. At each plot, a stainless steel collar was driven into the soil (to ~3 cm) to create a small trench, allowing for placement of a collar during labelling.

2.3. In Situ $^{13}\text{CO}_2$ Pulse Labelling. At three of the blocks stainless steel collars (40 cm diameter, 12 cm height) were slotted into the trenches around each plot. A transparent bell-shaped chamber (BELL060101, Haxnicks; 36 cm height, 40 cm diameter, and 28 l volume) was placed onto a rubber seal (to ensure a closed headspace) on top of each collar. Each chamber was equipped with a pair of 12 V DC fans (Sunon, 1.1 W) to ensure adequate mixing of headspace gas and two suba-seals at opposite sides of the chamber for injection of $^{13}\text{CO}_2$.

Labelling took place during 10.00–17.00 h on the 3rd of June 2009. A few drops of 1 M HCl were injected into 1.25 g of 99% ^{13}C -enriched sodium bicarbonate ($\text{NaH}^{13}\text{CO}_3$) in a gas tight jar. 5 cm³ of the $^{13}\text{CO}_2$ evolved was injected into each side of the chamber, creating a CO_2 concentration of 1–2 times ambient. This was repeated approximately every 30 min for a total of 12 additions. To avoid overheating, chambers were removed just prior to each addition to enable mixing with ambient air. During labelling, temperature within the chambers remained between 22 and 30°C for 80% of the time, and photosynthetic active radiation ranged from 470 to 1900 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

2.4. CO_2 Flux Measurements. CO_2 flux was measured on the two nonlabelled adjacent blocks during labelling and on all three labelled blocks 6 days after labelling. Measurements were made with a dynamic open system (air flow 50 l min⁻¹) comprising custom built transparent chambers (28 l, 40 cm diameter) attached to EGM-4 infrared gas analyser (PP Systems, Hansatech, UK). Net ecosystem exchange (NEE) and total ecosystem respiration (R_{TOT}) (using a blackout hood) were measured over 30 minutes each, recording 2 minute averages, and gross primary production (GPP) was calculated as the difference between NEE and R_{TOT} (e.g., [20]). In data presentation, CO_2 assimilated is shown as negative, and CO_2 emitted is shown as positive.

2.5. Sampling and Harvesting. Shoot and root biomass were sampled from each plot immediately after labelling on day 0 (initial allocation) and on days 15 and 42. Above- and below-ground plant materials were collected away from the labelled plots for the determination of ^{13}C natural abundance. On

days 0 and 15, four young stems of ericaceous shrubs (*Calluna* and *Vaccinium*) were sampled from each *Calluna*-dominated plot and split into leaf and stem (3-4 year old) tissues. Older *Calluna* stems (>4 years, comprising 30% of total stem biomass) were not sampled to avoid damaging the remaining plant. Small samples of moss (*Hypnum jutlandicum*) and graminoid leaves (mainly *Nardus*) were also taken from these plots. From the *Nardus*-dominated plots, graminoid leaves, moss, and herbs (*Galium saxatile* and *Potentilla erecta*) were sampled. Two soil cores (2.1 cm diameter, 10.5 cm depth) were taken from each plot for root samples. After 42 days, all above-ground vegetation and further four soil cores were taken from each plot.

2.6. Growth Assumptions. To determine the amount of ^{13}C initially taken up in each plot and subsequently retained, back calculations were made from final biomass (day 42) to estimate biomass of each component of the vegetation at day 0 (= final mass - 42 * daily production estimate) and day 15 (= final mass - 27 * daily production estimate). Production estimates for ericaceous shrubs, herbs, and roots were obtained from the literature (Table 1). Due to the warm, dry weather, moss growth was assumed to be negligible over the 6-week experiment [34]. Production estimates for graminoids were obtained from field measurements. Graminoid shoots ($n = 60$) in both *Calluna*- and *Nardus*-dominated areas were tagged and their length was measured on days 0, 15, and 42. Mean initial : final length ratio provided an estimate of growth rate.

2.7. ^{13}C Analysis. Samples were divided into the following plant fractions: *Calluna* leaf, *Calluna* stem (up to c. 4 years), *Vaccinium* leaf, *Vaccinium* stem, moss, graminoid leaf, herbs, and roots. Leaf samples were taken from current year's growth. Roots were extracted from soil cores by washing and sieving (2 mm sieve). Samples were dried at 80°C for 48 hours, weighed, and finely ground in a ball mill. Subsamples (2–5 mg) were analysed for ^{13}C on an elemental analyser linked to a mass spectrometer. Samples from day 0, day 15, and natural abundance were analysed on an ANCA GSL prep unit connected to a Europa Scientific 20-20 stable isotope analyser (Sercon, Crewe, UK); day 42 samples were analysed on a Flash EA 1112 Series Elemental Analyser connected via a Conflo III to a Delta^{Plus} XP isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany). Appropriate cross-calibration was undertaken to ensure comparability of data.

2.8. Stable Isotope Calculations and Data Analysis. The ^{13}C signatures of the natural abundance samples were within the expected range for a C3 plant assemblage [35]. To calculate the ^{13}C atom % excess of the labelled samples, the natural abundance values were subtracted from the enriched values. The amount of ^{13}C was calculated as biomass multiplied by percent C, multiplied by the atom % excess.

2.9. Statistical Analysis. Biomass data were analysed using ANOVA. CO_2 flux data were analysed using linear mixed

TABLE 1: Production estimates used for back calculating initial biomass from final biomass. Data are derived from annual production estimates from the literature with the exception of *Calluna*. For *Calluna*, the June and July production proportions [26] were applied to an annual estimate of production [27]. All data have been converted to $\text{g m}^{-2} \text{day}^{-1}$.

Plant tissue	Production $\text{g m}^{-2} \text{day}^{-1}$	Reference
<i>Calluna</i> leaf	1.6720	[26, 27]
<i>Calluna</i> stem	0.1270	[28]
<i>Vaccinium</i> leaf and stem	0.0007	[29]
Root (graminoid)	0.7400	[30]
Root (<i>Calluna</i>)	0.5010	[28]
Herb	0.0140	[30]
Graminoid leaf	Applied initial : final biomass ratio	Measured
Moss	0	Assumption

models with flux (NEE , R_{TOT} , and GPP) as fixed and plot nested within block, as random variables. Flux data from the two sampling days were combined as there was no significant difference between days. The analysis of ^{13}C data (both enrichment and content) was performed separately for photosynthetic tissues (*Calluna* leaf, *Vaccinium* leaf and stem, graminoid leaf, moss and herb) and nonphotosynthetic tissues (*Calluna* stem and roots). Linear mixed models, with repeated measures, were used to analyse the effect of time since $^{13}\text{CO}_2$ pulse and plant fraction on ^{13}C enrichment. Vegetation community was added in the analysis of ^{13}C enrichment of plant fractions common to both communities and in comparison of ^{13}C pools between communities. Time was used as a fixed repeated (autoregression 1) factor, with plot the subject of the repeated factor. Plot was also nested within block and used as a random factor. Type 1 sum of squares was used in all models. The residuals of linear mixed models were checked for normality. Post hoc testing was performed using LSD pairwise comparisons based on a significant main effect. All data were analysed using statistical package IBM SPSS statistics (version 19). Due to the *in situ* nature of our experiment, the number of species and thus number of C pools and fluxes between pools within the system, our data did not enable modelling as in Street et al. [36].

3. Results

3.1. CO_2 Fluxes. The measurements made during and 6 days after labelling showed that there is no difference in NEE ($F_{1,6} = 0.380$, $P = 0.560$), R_{TOT} ($F_{1,6} = 2.067$, $P = 0.201$), or GPP ($F_{1,6} = 2.425$, $P = 0.170$) between *Calluna*- and *Nardus*-dominated vegetation communities (Figure 1).

3.2. Biomass. *Calluna*-dominated plots tended to contain greater plant biomass than *Nardus*-dominated plots with 2079.7 ± 367.3 (SE) and 1269.9 ± 282.1 g m^{-2} , respectively,

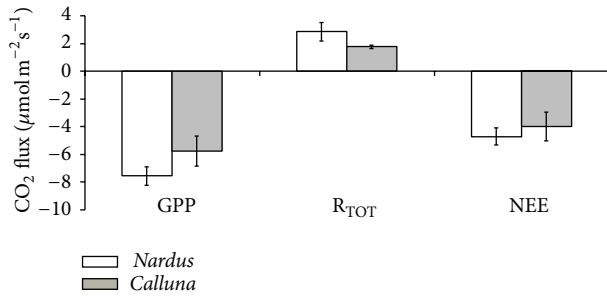


FIGURE 1: CO₂ fluxes of *Calluna*-dominated and *Nardus*-dominated vegetation communities: GPP: gross primary production, R_{TOT}: total respiration, and NEE: net ecosystem exchange. Mean ($n = 5$) \pm 1 S.E.

but this was not significantly different ($F_{1,4} = 3.1$, $P = 0.155$) (Table 2). The two communities had similar amounts of photosynthetic biomass (380.2 and 310.7 g m⁻² in *Calluna*- and *Nardus*-dominated vegetation communities), and root material formed the largest single biomass fraction (57% in *Calluna* plots, 75% in *Nardus* plots) (Table 2).

3.3. ¹³C Enrichment in Plant Fractions. In the *Calluna*-dominated community, the graminoid and dwarf shrub leaves were the most ¹³C-enriched photosynthetic tissues, and their enrichment declined substantially over 42 days (Figure 2(a), Table 3). *Vaccinium* stem and moss were least enriched, but both increased in enrichment over 15 days before declining further after 42 days (Figure 2(a), Table 3). The effects on ¹³C enrichment of time since ¹³CO₂ pulse, plant fraction, and their interaction were all significant ($F_{2,18} = 24.7$, $P < 0.001$; $F_{4,18} = 41.5$, $P < 0.001$; and $F_{8,18} = 3.5$, $P = 0.007$ resp.). These factors also influenced enrichment of nonphotosynthetic tissues (sampling day, $F_{2,9} = 17.2$, $P = 0.001$; plant fraction, $F_{1,9} = 98.3$, $P < 0.001$; and interaction, $F_{2,9} = 17.7$, $P = 0.001$). *Calluna* stem was initially more enriched than root material, with the latter showing increased enrichment over 15 days before decreasing to below detection by 42 days (Figure 2(b), Table 3). There was an apparent tendency towards an increase in enrichment of the *Calluna* stem after 15 days which was maintained at the end of the experiment (Figure 2(b), Table 3).

In the *Nardus*-dominated plant community, ¹³C enrichment differed between sampling day ($F_{2,12} = 8.2$, $P = 0.004$) and photosynthetic plant fraction ($F_{2,12} = 25.4$, $P < 0.001$) with no interaction ($F_{4,12} = 1.3$, $P = 0.327$). The graminoid and herb leaves were more highly enriched than the moss and remained so throughout; even though leaf enrichment declined substantially (Figure 2(c), Table 3). There was a tendency towards an increase in enrichment after 15 days in the moss tissue (Table 3). Enrichment of roots also appeared to increase after 15 days, but there was no significant influence of sampling day ($F_{2,6} = 2.3$, $P = 0.213$) (Figure 2(d)).

Those plant fractions that occurred in both *Calluna*- and in *Nardus*-dominated plots (graminoid leaf, moss, and roots) showed similar ¹³C enrichment in both (photosynthetic,

TABLE 2: Dry biomass of photosynthetic (white) and nonphotosynthetic (bold) plant fractions within *Calluna*- and *Nardus*-dominated communities. Mean ($n = 3$) \pm 1 S.E.

	Plant biomass, g m ⁻²	
	<i>Calluna</i> -dominated community	<i>Nardus</i> -dominated community
<i>Calluna</i> leaf	223.7 \pm 38.4	
Graminoid leaf	18.9 \pm 13.0	204.7 \pm 56.5
<i>Vaccinium</i> leaf	4.1 \pm 0.8	
<i>Vaccinium</i> stem	34.5 \pm 7.9	
Moss	99.1 \pm 6.5	94.4 \pm 30.5
Herb		11.6 \pm 2.8
<i>Calluna</i> stem	507.7 \pm 74.6	
Root	1191.8 \pm 266.2	959.2 \pm 217.2

TABLE 3: Change in ¹³C enrichment after 15 and 42 days (as % of initial enrichment, day 0), in photosynthetic (white) and nonphotosynthetic (bold) plant fractions within *Calluna*- and *Nardus*-dominated communities. Mean ($n = 3$) \pm 1 S.E.

Tissue	Days after labelling			
	15		42	
	% change	\pm S.E.	% change	\pm S.E.
<i>Calluna</i> -dominated community				
<i>Calluna</i> leaf	-53.7	3.0	-78.7	1.9
Graminoid leaf	-63.4	1.9	-85.8	0.8
<i>Vaccinium</i> leaf	-66.3	2.8	-71.1	2.0
<i>Vaccinium</i> stem	+36.3	39.4	-59.3	26.3
Moss	+60.0	39.0	-100.0	0.0
<i>Calluna</i> stem	+59.1	62.5	+34.7	58.4
Root	+3.9	58.7	-100.0	0.0
<i>Nardus</i> -dominated community				
Graminoid leaf	-62.2	1.8	-84.5	2.0
Moss	+12.8	17.2	-84.9	9.4
Herb	-67.8	8.6	-82.2	3.0
Root	+63.2	20.7	-55.8	37.4

$F_{1,15} = 3.6$, $P = 0.072$; nonphotosynthetic, $F_{1,9} = 4.8$, $P = 0.094$).

3.4. ¹³C Content of *Calluna*- and *Nardus*-Dominated Plant Communities. The *Calluna*-dominated vegetation assimilated an average of 103.9 \pm 21.8 mg ¹³C m⁻², with 78% and 22% initially allocated to photosynthetic (mostly in *Calluna* leaves) and nonphotosynthetic tissues, respectively (Figure 3). Plant fraction ($F_{4,18} = 37.3$, $P < 0.001$), time since ¹³CO₂ pulse ($F_{2,18} = 5.7$, $P = 0.009$), and their interaction ($F_{8,18} = 4.1$, $P = 0.002$) all influenced photosynthetic tissue ¹³C content. After six weeks, 34% of the ¹³C initially held in photosynthetic plant parts were retained, with the majority still held in the *Calluna* leaves (Figure 3). *Calluna*

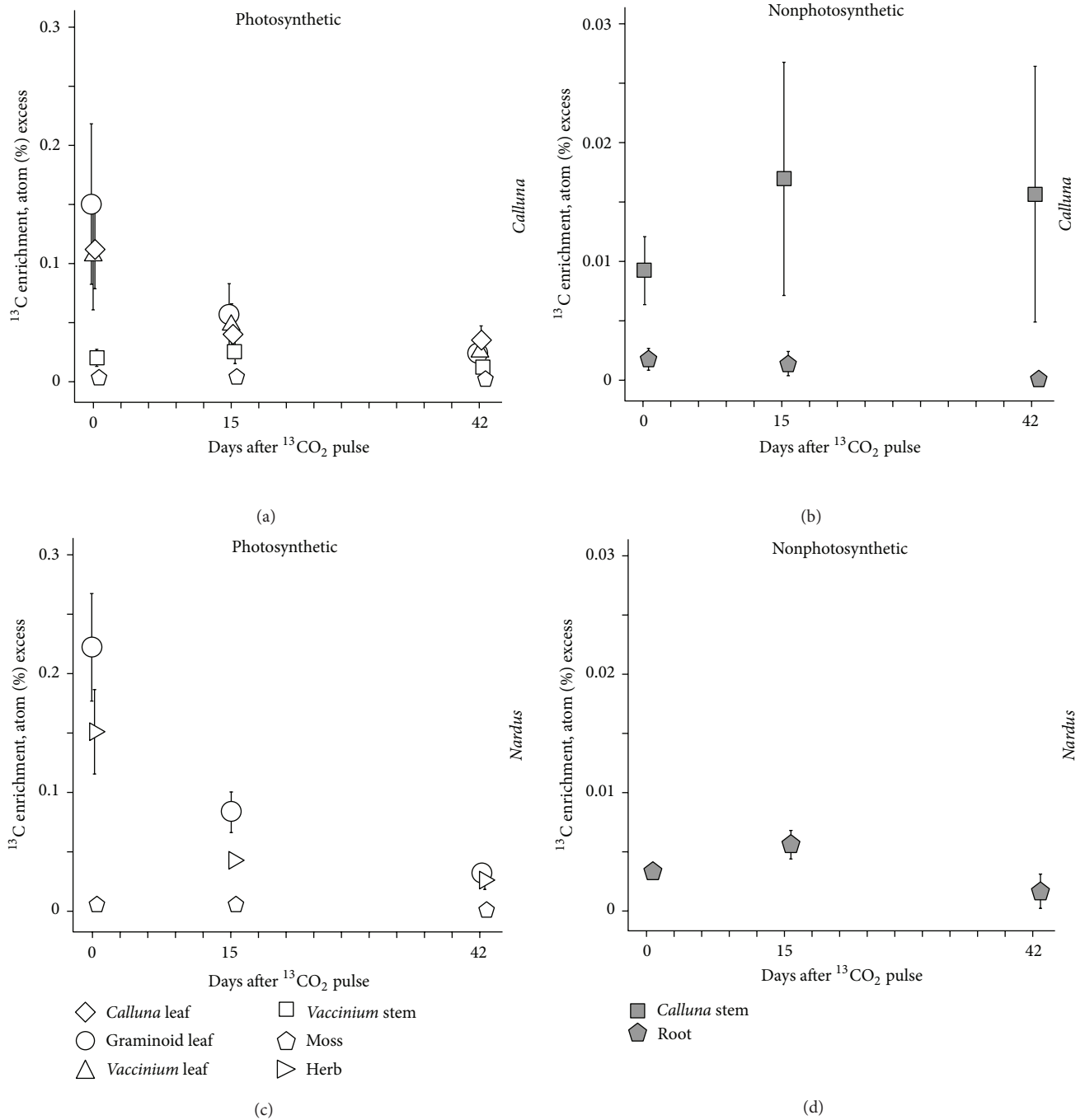


FIGURE 2: Time-course of ^{13}C enrichment (atom % excess) in (a, c) photosynthetic and (b, d) nonphotosynthetic plant fractions from (a, b) *Calluna*-dominated and (c, d) *Nardus*-dominated vegetation communities. Mean ($n = 3$) \pm 1 S.E.

and *Vaccinium* leaves retained c. 30% of their initial ^{13}C pool, whilst graminoid leaves and *Vaccinium* stem retained c. 50%. Movement of ^{13}C assimilate within the vegetation was reflected in the slight increase in ^{13}C within the *Vaccinium* stem and moss and a doubling of ^{13}C in the *Calluna* stem over the first 15 days; this pattern was not observed in the roots. Of the ^{13}C initially allocated to nonphotosynthetic tissues, 89% remained at the end of six weeks, all of this

being in *Calluna* stems which accumulated ^{13}C , whilst roots lost all enrichment (Figure 3; plant fraction, $F_{1,9} = 8.2$, $P = 0.017$; time since $^{13}\text{CO}_2$ pulse, $F_{1,9} = 0.3$, $P = 0.758$; and interaction, $F_{2,9} = 0.9$, $P = 0.455$). In total, 46% of the originally assimilated ^{13}C was retained in the *Calluna*-dominated community after 6 weeks, with 57% and 43% of the remaining ^{13}C allocated to photosynthetic and nonphotosynthetic tissues, respectively.

	^{13}C pool (mg m^{-2})			Initial ^{13}C pool retained after 6 weeks (%)
	0 days	15 days	42 days	
<i>Calluna</i> leaf	68.6 ± 18.2	36.5 ± 8.5	21.9 ± 7.5	31.9%
Graminoid leaf	5.9 ± 5.5	4.4 ± 4	2.9 ± 2.7	49.2%
<i>Vaccinium</i> leaf	2.4 ± 1.2	0.8 ± 0.4	0.7 ± 0.4	29.2%
<i>Vaccinium</i> stem	3.2 ± 1.4	3.8 ± 1.8	1.7 ± 1.6	53.1%
Moss	0.6 ± 0.3	0.9 ± 0.5	0	0%
<i>Calluna</i> stem	14.2 ± 1.8	24.2 ± 11.1	20.5 ± 11.7	144.4%
Root	8.9 ± 4.9	5.6 ± 3.2	0	0%

FIGURE 3: ^{13}C content (mg m^{-2}) at three time points after $^{13}\text{CO}_2$ pulse labelling and ^{13}C retention (as % of initial pool) after six weeks within photosynthetic (white) and nonphotosynthetic (shaded) plant fractions of a *Calluna*-dominated community. Mean ($n = 3$) ± 1 S.E.

Nardus-dominated vegetation assimilated $76.7 \pm 3.7 \text{ mg } ^{13}\text{C m}^{-2}$, of which 82% was initially allocated to photosynthetic tissue, with most (85%) held in graminoid leaves (Figure 4). The only nonphotosynthetic tissue, the roots, initially accounted 18% of the assimilated ^{13}C . Plant fraction ($F_{2,12} = 136.1$, $P < 0.001$), time since $^{13}\text{CO}_2$ pulse ($F_{2,12} = 9.7$, $P = 0.001$), and their interaction ($F_{4,12} = 4.5$, $P = 0.011$) influenced the ^{13}C content of photosynthetic tissues in this community. ^{13}C content decreased over time, with photosynthetic tissues retaining 70% and 45% after 15 days and six weeks, respectively. Graminoid leaves remained the biggest ^{13}C pool after six weeks, retaining c. 50% of their initial content compared to 16% in moss and herbs. ^{13}C content of the nonphotosynthetic plant fraction, the roots, almost doubled after 15 days and subsequently dropped to 35% of initial pool size (time since pulse label, $F_{2,6} = 8.7$, $P = 0.017$) (Figure 4). In total, the *Nardus*-dominated community retained 43% of the assimilated ^{13}C over 6 weeks, with 85% and 15% of the remaining ^{13}C allocated to photosynthetic and nonphotosynthetic tissues, respectively.

3.5. Comparison of ^{13}C Dynamics in the Two Vegetation Communities. There was no difference between the two vegetation communities in the amount of ^{13}C initially assimilated or in the amount retained after six weeks (vegetation community, $F_{1,9} = 0.5$, $P = 0.506$; time since pulse label, $F_{2,9} = 51.9$, $P < 0.001$; and interaction, $F_{2,9} = 1.5$, $P = 0.270$). Graminoids were responsible for a much greater part of total C dynamics in the graminoid community, due to their dominance, but their leaves exhibited similar ^{13}C enrichment and retention in both communities. Moss also behaved similarly in both communities, representing a tiny fraction of C assimilation and retention despite its substantial biomass. The dynamics of ^{13}C in the roots differed between the two communities (vegetation community, $F_{1,9} = 11.4$, $P = 0.006$; time since $^{13}\text{CO}_2$ pulse, $F_{2,9} = 7.2$, $P = 0.009$; interaction $F_{2,9} = 2.1$, $P = 0.165$). Initially, the roots accounted for 22% of the assimilate in the graminoid community and half this proportion (11%) in the *Calluna* vegetation. The graminoid

roots continued to accumulate ^{13}C over 15 days and after six weeks still retained approximately one-third of their initial ^{13}C content, whilst the *Calluna* community roots lost ^{13}C over the entire period and did not retain any after six weeks. A clear difference between the communities is the presence in the *Calluna* community of woody stem tissue which accumulated ^{13}C during the experiment and accounted for 43% of the ^{13}C remaining after 6 weeks.

4. Discussion

The use of $^{13}\text{CO}_2$ pulse labelling within an upland heath demonstrated that, contrary to our hypothesis, there were no significant differences between *Calluna*- and *Nardus*-dominated communities in the amount of $^{13}\text{CO}_2$ assimilated or the proportion of ^{13}C retained over six weeks. Whilst this study represents a short snapshot in time, it nevertheless provides a useful comparison of ^{13}C assimilate dynamics in these two contrasting plant communities.

4.1. C fluxes in *Calluna*- and Graminoid-Dominated Communities. Graminoid-dominated vegetation has been previously shown to have greater gross CO_2 fluxes and $^{13}\text{CO}_2$ uptake than dwarf shrub vegetation [20, 37, 38]. In contrast to these studies, we observed no difference in measured CO_2 fluxes between the graminoid- and *Calluna*-dominated communities during the growing season. The graminoid-dominated community was mostly composed of *Nardus*, which has a lower growth rate than other grasses, it associates with, for example, *Agrostis canina* and *Holcus lanatus*, but a higher relative growth rate than *Calluna* [21]. However, the *Calluna* was in the “building phase” of its life cycling and so exhibiting high productivity which could explain their similarity in CO_2 cycling [10]. The age of the *Calluna* studied by Ward et al. [20] and Trinder et al. [38] is unknown, but this is likely to influence C assimilation. Furthermore, these studies were in deep peat ecosystems with different dominant graminoids (e.g., *Eriophorum* species) to those commonly associated with changes in upland heath management practices. In our study, both photosynthetic biomass and CO_2 fluxes were similar

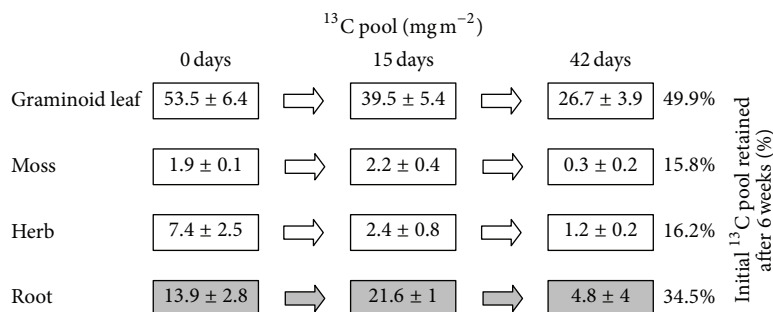


FIGURE 4: ^{13}C content (mg m^{-2}) at three time points after $^{13}\text{CO}_2$ pulse labelling and ^{13}C retention (as % of initial pool) after six weeks within photosynthetic (white) and nonphotosynthetic (shaded) plant fractions of a *Nardus*-dominated community. Mean ($n = 3$) \pm 1 S.E.

in the two communities, hence their similarity in $^{13}\text{CO}_2$ assimilation in early summer.

4.2. Assimilation and Translocation of $^{13}\text{CO}_2$. In the *Calluna*-dominated community, graminoid and dwarf shrub leaves had a similar $^{13}\text{CO}_2$ assimilation rate (reflected in initial enrichment), which was much greater than that of the moss and the photosynthetic stems of *Vaccinium*. Other studies have shown higher $^{13}\text{CO}_2$ uptake by graminoids than by ericaceous shrubs [20, 38, 39], although these may have included some stem material in shoot samples which could have diluted the shrub ^{13}C signature. In the *Nardus*-dominated community, the graminoids and herbs assimilated ^{13}C most rapidly, and the mosses again had very low assimilation rate. Graminoid and moss assimilation rates were similar in the two plant communities showing that *Calluna* was not creating more shading effect than the graminoid canopy, as has been noted previously [20].

There was a sharp decline in ^{13}C enrichment in the photosynthetically active tissues of the vascular plants over 15 days (by 56% on average) with a more gradual decline over the following 27 days (79% decline over the whole 42 days). The rate of decrease in enrichment is similar to recent peatland tracer studies in which graminoid and dwarf shrub shoots lost 68% and 63% of enrichment, respectively, over 21 days [20], and *Calluna* shoots lost 60% of enrichment over 30 days [38]. This decline can be attributed to shoot respiration, to rapid allocation of ^{13}C below-ground to roots (as was most evident in the *Nardus*-dominated community) and microbial biomass [40, 41], and to translocation of assimilate to other plant parts such as *Calluna* stem.

Nonphotosynthetic tissues, that is, *Calluna* stems and, to a much lesser extent, the roots of both vegetation communities were ^{13}C enriched immediately after labelling, showing evidence of rapid translocation of assimilate. Rapid allocation of fixed C to the roots has also been shown in an upland grassland tracer study only after 4 hours of labelling [42] with maximum enrichment 21–48 h after labelling [41, 42]. The timing of our sampling meant that we may have missed the enrichment peak in the roots, but we did detect an

increase after 15 days. *Calluna* stem enrichment was also increased after 15 days and maintained thereafter as ^{13}C was transported from the leaves to this carbohydrate store [43].

In both vegetation communities, the moss had minimal initial ^{13}C enrichment but showed a slight increase after 15 days before losing most of the tracer again. Similar low enrichment has been observed in moss in *Calluna*-dominated vegetation [20] and may be explained by the lower photosynthetic rates of mosses than vascular plants and their shaded position at the bottom of the canopy. Much higher enrichment and subsequent retention has been achieved when $^{13}\text{CO}_2$ has been applied to moss in the absence of vascular plants in peatland and arctic tundra communities in which mosses dominate [36, 44, 45]. A large proportion of the CO_2 fixed by mosses originates from soil respiration [46], which could be the source of the ^{13}C acquired by the moss in the heathland after 15 days.

4.3. Retention of ^{13}C in the Vegetation. Both immediately after labelling and six weeks later, when over 40% of the ^{13}C was still retained by both vegetation communities, the majority of the label was contained in the photosynthetically active tissues of the dominant plant groups. Although similar amounts of ^{13}C were both assimilated and retained in both communities, the pool of ^{13}C within each plant fraction, and hence community, may differ in its residence time. For example, the *Calluna* stems accumulated ^{13}C over two weeks and retained it thereafter such that they contained a significant proportion of the total ^{13}C pool after 6 weeks. This ^{13}C may have been incorporated into lignin or lignin-like compounds which are recalcitrant and thus exhibit a longer residence time in the soil [47]. C will be retained longer in *Calluna* leaves, which survive several years [48], than in *Nardus* leaves which senesce (at least partially) each autumn [49]. *Calluna* leaves also contain higher concentrations of recalcitrant C-based secondary metabolites than heathland grasses and so will decompose more slowly [50, 51]. Thus, although the *Nardus*- and *Calluna*-dominated vegetation communities studied had similar C sequestration rate and

retention of assimilate over 6 weeks, it is likely that the residence of assimilated C will be longer in the *Calluna* community.

The roots in both vegetation types contained rather a small proportion of the ^{13}C that remained six weeks after labeling, but, of the remaining ^{13}C , there was a higher allocation to roots in the *Nardus*- than in the *Calluna*-dominated communities. This may reflect the one-year lifespan of *Nardus* roots [52] and hence a greater requirement to allocate C to root growth than in *Calluna* which has a slower root turnover [53, 54].

5. Conclusion

This study has shown similar C assimilation and retention over six weeks by a *Calluna*-dominated community, typical of traditional low intensity management, and graminoid-dominated vegetation such as typically results from heavy grazing and/or overfrequent burning. *Calluna*- and *Nardus*-dominated communities assimilated 103.9 ± 21.8 and $76.7 \pm 3.7 \text{ mg } ^{13}\text{C m}^{-2}$, respectively, after six weeks with 46% and 43% retained, respectively, over the period. However, consideration of the strategies of the dominant species and the attributes of the tissues in which ^{13}C was retained has suggested that *Calluna*-dominated vegetation may be of greater benefit to carbon sequestration in the longer term.

5.1. Application. The current trend in upland management is for a decrease, or even removal, of livestock grazing [55] which reduces a strong driver of the transition from *Calluna*- to graminoid-dominated heath and, where *Calluna* has persisted within the graminoid plant community, may result in recovery of shrub cover (e.g., [56]). In the light of our findings, this trend may represent positive management for C sequestration by upland heath.

Conflict of Interests

The authors do not have a direct financial relation with the commercial identity mentioned in the present paper.

Acknowledgments

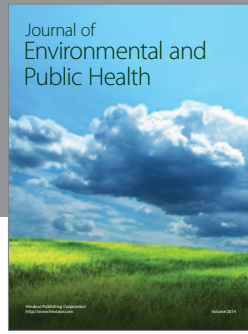
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