

Legacy effects of grassland management on soil carbon to depth

Article

Accepted Version

Ward, S. E., Smart, S. M., Quirk, H., Tallowin, J. R. B., Mortimer, S. R., Shiel, R. S., Wilby, A. and Bardgett, R. D. (2016) Legacy effects of grassland management on soil carbon to depth. Global Change Biology, 22 (8). pp. 2929-2938. ISSN 1365-2486 doi: https://doi.org/10.1111/gcb.13246 Available at http://centaur.reading.ac.uk/54179/

It is advisable to refer to the publisher's version if you intend to cite from the work.

To link to this article DOI: http://dx.doi.org/10.1111/gcb.13246

Publisher: Wiley-Blackwell

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the <u>End User Agreement</u>.

www.reading.ac.uk/centaur

CentAUR



Central Archive at the University of Reading

Reading's research outputs online

Management and deep soil carbon

1	Legacy effects of grassland management on soil carbon to depth
2	Running header: Management and deep soil carbon
3	
4	Susan E.Ward ^{1*} , Simon M.Smart ² , Helen Quirk ¹ , Jerry R.B Tallowin ³ , Simon R. Mortimer ⁴ ,
5	Robert S. Shiel ⁵ , Andy Wilby ¹ , Richard D. Bardgett ⁶
6	
7	¹ Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ. UK.
8	² Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue,
9	Bailrigg, Lancaster, LA1 4AP, UK.
10	³ Rothamsted Research, North Wyke, Okehampton, Devon, EX20 2SB, UK.
11	⁴ Centre for Agri-Environmental Research, School of Agriculture, Policy and Development,
12	The University of Reading, Earley Gate, PO Box 237, Reading, RG6 6AR, UK.
13	⁵ School of Agriculture, Food and Rural Development, University of Newcastle, Newcastle
14	upon Tyne, NE1 7RU, UK.
15	⁶ Faculty of Life Sciences, Michael Smith Building, The University of Manchester, Oxford
16	Road, Manchester M13 9PT, UK.
17	*Corresponding Author. E-mail: s.e.ward@lancaster.ac.uk. Tel: +44 (0)1524 510531
18	
19	Keywords: soil carbon, soil depth, grassland, management intensity, soil carbon stocks,
20	legacy effect, carbon inventory
21	Type of paper: Primary Research Article

22 Abstract

23 The importance of managing land to optimise carbon sequestration for climate change 24 mitigation is widely recognised, with grasslands being identified as having the potential to 25 sequester additional carbon. However, most soil carbon inventories only consider surface 26 soils, and most large scale surveys group ecosystems into broad habitats without considering 27 management intensity. Consequently, little is known about the quantity of deep soil carbon 28 and its sensitivity to management. From a nationwide survey of grassland soils to 1 m depth, 29 we show that carbon in grasslands soils is vulnerable to management and that these 30 management effects can be detected to considerable depth down the soil profile, albeit at 31 decreasing significance with depth. Carbon concentrations in soil decreased as management 32 intensity increased, but greatest soil carbon stocks (accounting for bulk density differences), 33 were at intermediate levels of management. Our study also highlights the considerable 34 amounts of carbon in sub-surface soil below 30cm, which is missed by standard carbon 35 inventories. We estimate grassland soil carbon in Great Britain to be 2097 Tg C to a depth of 1 m, with ~60% of this carbon being below 30cm. Total stocks of soil carbon (t ha⁻¹) to 1 m 36 37 depth were 10.7% greater at intermediate relative to intensive management, which equates to 10.1 t ha⁻¹ in surface soils (0-30 cm), and 13.7 t ha⁻¹ in soils from 30-100 cm depth. Our 38 39 findings highlight the existence of substantial carbon stocks at depth in grassland soils that 40 are sensitive to management. This is of high relevance globally, given the extent of land 41 cover and large stocks of carbon held in temperate managed grasslands. Our findings have 42 implications for the future management of grasslands for carbon storage and climate 43 mitigation, and for global carbon models which do not currently account for changes in soil 44 carbon to depth with management.

45 Introduction

69

46 Permanent grasslands are found extensively across the temperate zone where they form the 47 backbone of agricultural systems. Global land cover estimates for grasslands range between 48 20-40% of the Earth (FAO 2015), and for the UK, constitute the largest category of land use 49 at 36% of land cover (Carey et al. 2008). The multiple values of grassland ecosystems to 50 mankind has long been recognised, ranging from direct benefits of agricultural production, to 51 indirect ecosystem services such as the regulation of climate and water quality, and 52 pollination services (Heidenreich 2009). As such, grasslands are arguably one of the most 53 valuable biomes for ecosystem service provision, but also are among the most threatened by 54 anthropogenic activities (Gibson 2008). Threats include increasing pressures to meet the 55 food demands of more affluent and larger global populations, and to deliver concomitant 56 multiple ecosystem services demanded by the sustainable intensification agenda (Garnett et 57 al. 2013). Of the multiple ecosystem services provided by grasslands, climate regulation via 58 soil carbon storage and sequestration, is highly valued (Heidenreich 2009). 59 60 In terms of terrestrial carbon storage, soils contain the largest global pool of terrestrial 61 carbon, storing more carbon than is present in plant biomass and the atmosphere combined 62 (Batjes 1996, Jobbagy and Jackson 2000). Temperate grasslands are the third largest global 63 store of carbon in soils and vegetation (after wetlands and boreal forests), storing an 64 estimated 304 Pg C, or 12.3% of global carbon (Royal Society 2001), most of which is in 65 soil. Such carbon stocks are known to be vulnerable to changes in land use and 66 intensification of agricultural management, with the conversion of croplands to permanent 67 grassland generally increasing soil carbon, and the reverse change from grassland to 68 croplands reducing soil carbon stocks (Guo and Gifford 2002, Smith et al. 2008). Moreover,

3

such changes in land use can have a long lasting legacy effect on soil carbon, on a scale of

decades to several hundreds of years, which is often slow to reverse (Dupouey et al. 2002,
McLauchlan 2006, Smith 2014).

72

73 Grassland soil carbon has been shown to respond to changes in management intensity, with 74 agricultural practices such as fertiliser application, irrigation, and livestock grazing affecting 75 soil carbon stocks (Soussana et al. 2004, Smith et al. 2008, van Wesemael et al. 2010). In 76 many parts of Europe, the intensity of grassland management has substantially increased 77 since the 1950's. This has been driven largely by agri-environmental policy and farm 78 subsidies, combined with technological innovations, leading to widespread legacy effects of 79 long-term management on soils and vegetation. In addition to the documented effects of 80 management on soil carbon (Guo and Gifford 2002, Smith et al. 2008), intensification of 81 farming practices has led to widespread reductions in botanical diversity and loss of species-82 rich, traditionally managed grasslands, which now cover less than 3% of the area they did in 83 the 1950's (Gamble et al. 2012). Furthermore, management intensification has caused major 84 changes in plant functional composition, with intensively managed grasslands typically being 85 dominated by fast-growing exploitative species, characterized by high specific leaf area 86 (SLA) and leaf nitrogen concentration (LNC). This compares with less fertile, extensively 87 managed grasslands that are dominated by slower-growing, conservative species of high leaf 88 dry matter content (LDMC) and low leaf N content (Lavorel and Garnier 2002, de Vries et al. 89 2012). Such shifts in plant functional composition are known to have important effects on 90 soil nutrient cycling and carbon dynamics (de Vries et al. 2012, Grigulis et al. 2013, Manning 91 et al. 2015), and LDMC has been correlated with soil fertility (Hodgson et al. 2011, Duru et 92 al. 2012). However, there is a lack of knowledge on the relationship between soil carbon and 93 management intensity with depth linked to the legacy of vegetation change.

94

Management and deep soil carbon

95	Another factor contributing to uncertainty over legacy effects of management and land use
96	change is that most studies on soil carbon stocks are on more easily sampled surface soils.
97	Even the IPCC recommend soil carbon accounting for the surface 30 cm of soil only (IPCC
98	2006), and although they advocate sampling beyond 30cm, this is rarely done. As a result,
99	soil carbon stocks at depth are largely ignored (Fontaine et al. 2007, Chapman et al. 2013),
100	and little is known about the quantity of soil carbon at depth and how it responds to land
101	management and associated vegetation change in grasslands (Jobbagy and Jackson 2000,
102	Soussana et al. 2004, Fontaine et al. 2007). Given the substantial quantities of carbon in
103	grassland soils, and the fact that grasslands worldwide are subject to increasing
104	intensification of management, this represents a major gap in knowledge.
105	
106	The overarching aim of our study was to quantify the distribution of soil carbon across
107	English grasslands to depth (1 metre), and the relationship of surface and deep soil carbon to
108	grassland management at a national scale. To do this, we carried out a nationwide survey of
109	English grasslands. This included all the main grassland habitats found in Great Britain,
110	namely acid, calcareous, mesotrophic and wet grassland, sampled across the broad range of
111	soil and climatic conditions (de Vries et al. 2012, Manning et al. 2015), thereby
112	encompassing a wide range of variation across a representative spatial domain (Smart et al.
113	2012). Cumulative soil carbon stocks and mean depths from the survey were then used in
114	conjunction with land cover data for matching grassland broad habitats from the Countryside
115	Survey (Carey et al. 2008) to estimate total grassland soil carbon stocks in Great Britain to a
116	depth of 1m, and to make comparisons with existing estimates of grassland soil carbon
117	storage. Using two abundance-weighted leaf traits known to be indicators of soil fertility and
118	management intensity (i.e., SLA and LDMC) (Hodgson et al. 2011; Grigulis et al. 2013), we

- also sought to test whether surface carbon stocks are more related to current plant functionalcomposition than deeper carbon.
- 121
- 122
- 123 Methods
- 124 *Field sampling.*

125 A survey of 180 permanent grasslands was conducted in summer 2010 from a range of acid, 126 calcareous, mesotrophic and wet grasslands, using a network of sites located throughout 127 England (Fig. 1) (de Vries et al. 2012, Manning et al. 2015). Sampling sites were in 60 128 different geographical locations, from 12 broad regions of England. At each of the 60 129 locations, three different fields were selected to give a gradient of management intensity of 130 extensive, intermediate and intensive management. These triplicate sets of fields were sited 131 on the same soil type, with similar topography and edaphic characteristics, and all three fields 132 at the same location were sampled on the same day. The three management intensity 133 classifications were based on expert judgement using information from consultations with 134 farmers and land owners, and from vegetation surveys (de Vries et al. 2012, Manning et al. 135 2015), and follow broad classifications that reflect dominant grassland systems in the UK and 136 Europe (Tallowin and Jefferson 1999, Tallowin et al. 2005, Manning et al. 2015) (Table 1). 137 There are clearly many different factors involved in the intensification of grassland 138 management, including increased use of fertilisers, increased disturbance through greater 139 cutting and grazing intensities, and changes in the amount and diversity of plant-derived 140 organic matter inputs to soil due to vegetation change. Given that it is not possible to 141 disentangle the individual effects of these factors on soil carbon stocks at the national scale of 142 sampling done here, we therefore compared grasslands subject to broadly defined levels of 143 agricultural intensification; this approach has been used widely to identify broad-scale trends

Management and deep soil carbon

144	in, and relationships between, vegetation and soil properties along gradients of management
145	intensity (Bardgett and McAlister 1999, Grayston et al. 2004, Allan et al. 2015).

146

147 The extensively managed grasslands had relatively high plant diversity and high conservation status, typically received less than 25 kg N ha⁻¹ yr⁻¹ and, have been managed in a traditional, 148 149 low intensity manner for many decades, with light grazing and annual cutting for hay. The 150 intensively managed agriculturally improved grasslands had low plant diversity of mainly 151 MG6 (Lolium perenne – Cynosurus cristatus) and MG7 (Lolium perenne levs and related 152 grasslands) communities (Rodwell 1992). These intensively managed grasslands typically receive $>100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, and have been subjected to standard intensive management 153 154 practices since the 1950's, with higher grazing pressures and more frequent cutting for silage 155 than the extensively managed grasslands (Tallowin and Jefferson 1999, Tallowin et al. 2005, 156 Critchley et al. 2007). The third category of grasslands is that of intermediate management 157 intensity, which falls between the two other categories, having typical inputs of $\sim 25-50 \text{ kg N}$ ha⁻¹ yr⁻¹, and intermediate levels of plant diversity, grazing and cutting (Table 1). 158 159 160 Soil cores (3.5 cm diameter) were taken from three random areas in each field, to 1 m depth 161 (where possible) using an Eldeman auger, and divided into five depth increments: 0–7.5 cm, 162 7.5-20 cm, 20-40 cm, 40-60 cm and 60-100 cm. A soil pit was dug at one location in each 163 field and three bulk density cores (6 cm length x 6.3 cm diameter) were taken horizontally for 164 each depth increment, from three different faces of the pit. This methodology builds on 165 information from the previous sampling campaign at these locations, where soil was collected 166 from the surface 7.5 cm only (de Vries et al. 2012, Manning et al. 2015). 167

168 Soil Analyses.

169	Soils were sieved (4 mm), oven dried at 60°C, ground using a ball mill, and analysed for total
170	carbon by combustion and gas chromatography (Elementar Vario EL CN analyser). Total
171	soil carbon (organic and inorganic) stocks per unit area (g C cm ³) were calculated from
172	carbon concentrations (%C) and bulk density measures (g cm ⁻³) for all depth increments. A
173	further sample of the three surface soils $(0 - 7.5 \text{ cm})$ collected from each field were pooled in
174	equal proportions for separation into soil organic matter (SOM) fractions (n=180). SOM
175	fractionation was by the flotation and sedimentation method using a sodium iodide (NaI)
176	solution (Sohi et al. 2001, Sohi et al. 2005). This fractionation method distinguishes
177	between: (a) a free SOM fraction (FR-SOM) at density < 1.80 g cm ⁻³ which represents
178	discrete free organic particles located between stable soil aggregates; (b) an intra-aggregate
179	SOM fraction (IA-SOM) at density < 1.80 g cm ⁻³ which represents discrete organic particles
180	located within stable soil aggregates; and (c) a residual heavy organo-mineral fraction at
181	densities > 1.80 g cm ⁻³ . Briefly, 7.5 g (dry wt) soil was added to 90 ml NaI at a density of
182	1.80 g cm ⁻³ , centrifuged for 30 minutes and the first floating FR-SOM fraction removed by
183	suction. The remaining centrifuge pellet was then re-mixed with the NaI, sonicated for 195
184	seconds, re-centrifuged for 30 minutes, and the second floating IA-SOM fraction removed by
185	suction. The remaining pellet, thoroughly rinsed in water, forms the organo-mineral fraction.
186	All soil fractions were dried, then ground in a ball mill and analysed for total C and N as
187	above.
188	
189	Data analysis.

Effects of depth and management on soil carbon concentration, bulk density and soil carbon
stocks were tested by ANOVA using generalised linear models (SAS Enterprise Guide 4.3),
with grassland type and region as factors. Cumulative soil carbon stocks to depth were
estimated by a Bayesian mixed modelling approach (supporting information S1), with

Management and deep soil carbon

194	random effects of region and location included plus a fixed effect of soil depth. Estimates of
195	cumulative soil carbon stocks were summarised by the posterior distribution of values
196	estimated for each soil depth and each level of management intensity, with the clustering of
197	samples within locations accounted for in the mixed effects model. Abundance-weighted
198	means for plant traits SLA and LDMC were calculated for sample plots using plant species
199	data, derived from field surveys carried out in 2005 to help classify management intensity
200	classifications, and paired with soil carbon measurements at each soil depth. Plant trait
201	information was derived from the LEDA database based on UK values reported for each
202	species (Kleyer et al. 2008). We modelled the between-location variation in total soil carbon
203	at each depth increment in terms of the abundance weighted plant traits, testing linear and
204	quadratic models at each depth; region and location were introduced as random effects.
205	
206	Upscaling
207	Cumulative soil carbon stocks and soil depths from our survey were combined with the UK
208	Countryside Survey land cover data (Carey et al. 2008) to estimate total grassland soil carbon
209	in Great Britain to a depth of 1m. Grassland types and management categories from our
210	survey were matched with the UK Countryside Survey (CS) broad habitat classifications of
211	improved, neutral, calcareous and acid grasslands (Emmett et al. 2010). Our 'intensively
212	
	managed' grassland category mapped to the CS category 'improved grasslands'; our
213	managed' grassland category mapped to the CS category 'improved grasslands'; our 'intermediate' grasslands mapped to CS 'neutral' grasslands; and, our 'extensive' grassland
213 214	
	'intermediate' grasslands mapped to CS 'neutral' grasslands; and, our 'extensive' grassland
214	'intermediate' grasslands mapped to CS 'neutral' grasslands; and, our 'extensive' grassland category mapped with the CS 'acid' and 'calcareous' grassland categories. These
214 215	'intermediate' grasslands mapped to CS 'neutral' grasslands; and, our 'extensive' grassland category mapped with the CS 'acid' and 'calcareous' grassland categories. These assumptions were successfully validated by comparing the total grassland soil carbon storage

full 1m depth, to give an estimate of total grassland soil carbon stocks (supporting

information S2).

221

222

223 Results

224 Field survey

225 Across all sites, the greatest concentrations of total carbon (% total C) were in surface soils to 226 7.5 cm depth ($F_{4,2096} = 288, P < 0.0001$) (Table 2). Soil carbon concentration decreased with 227 increasing management intensity ($F_{2,2096} = 10.9$, P < 0.0001), with significantly lower carbon 228 in the most intensive relative to intermediate and extensively managed grasslands, based on 229 all soils at all depths sampled (Table 2). Management effects were strongest in the surface 230 7.5 cm soil (supporting information S3), where total carbon concentration decreased with 231 intensification, being 19% and 25% lower in intensively managed than intermediate and 232 extensively managed grasslands respectively (Table 2). The effects of management intensity 233 on total % carbon decreased with depth, but were still significant to 40cm depth (P < 0.05) 234 and weakly significant (P < 0.10) at 60 cm depth. 70% of fields contained soils to 60cm 235 depth, and 55% of all fields had soils to the full 1 m depth; therefore, the number of samples 236 analysed decreased down the profile (Table 2). Those with deeper soils tended to be from 237 more carbon rich mesotrophic and wet grasslands, hence the observed trend for increased 238 mean carbon concentration at the 60-100 cm depth (Table 2).

239

Soil bulk density increased with depth down the soil profile ($F_{4,2011} = 57.5$, P < 0.0001), and was also influenced by grassland management ($F_{4,2011} = 25.9$, P < 0.0001) (Table 3, Table S3.1). The strongest effects of management were in the top 20 cm of the profile, where bulk density was lowest in extensively managed and greatest in intensively managed grasslands,

Management and deep soil carbon

244	and a trend for greater bulk density in intensively managed grasslands continued to 1 m
245	depth. Total soil carbon stocks per unit area (g C cm ⁻³), calculated from both the soil carbon
246	concentration and bulk density, were also strongly influenced by depth, with greatest mean
247	carbon stocks per unit area in the top 7.5 cm of the profile ($F_{4,1965} = 228, P < 0.0001$), and by
248	management intensity ($F_{2,2096} = 3.1$, $P = 0.05$) (Fig. 2). Specifically, for all soils analysed,
249	total soil C stocks (g C cm ⁻³), were significantly greater in grasslands of intermediate
250	management intensity relative to both the extensive and intensive managed grasslands (Fig.
251	2.). When analysed by depth increments, soils from grasslands at intermediate levels of
252	management had greater soil carbon stocks relative to extensive grasslands at 7.5 cm, and
253	relative to intensive grasslands at 7.5 to 20cm depth ($P < 0.05$), with a trend for greatest C
254	stocks at intermediate levels of management detected to 60 cm depth ($P = 0.1$) (supporting
255	information S3). We estimated cumulative soil carbon storage per m^2 , at 5 depth increments
256	to 1 m depth (Table 4) using a Bayesian mixed effects model (supporting information S1).
257	Uncertainties in carbon stock estimates increased with depth (Table 4), reflecting greater
258	incremental size categories and smaller sample numbers because fewer profiles reached the
259	full 1 m depth. This is a pattern commonly encountered with soil carbon measurements at
260	depth (Syswerda et al. 2011), and in our sites, soils with samples present at 1m depth also
261	tended to be those with greater carbon concentrations. Cumulative stocks of carbon to 1 m
262	depth in grasslands with intermediate levels of management were 10.7 and 7.8% greater than
263	for grasslands with intensive and extensive management respectively (Table 4). This
264	unimodal relationship between soil carbon stocks and management is less apparent in other
265	studies where bulk density has not been taken into account.
266	
267	Although we measured total carbon in bulk soils, fractionation of surface soils (7.5 cm depth)

Although we measured total carbon in bulk soils, fractionation of surface soils (7.5 cm depth)showed that it was only the relatively labile soil organic matter (SOM) fractions that

269	responded to management (Table 2). More specifically, the amount of carbon (g C kg ⁻¹ soil)
270	in the free SOM, which represents $\sim 15\%$ of soil mass (mean of all samples), reduced with
271	increasing management intensity. The amount of carbon in the intra-aggregate SOM
272	fractions (~2% of soil mass) was also lower in the intensive compared with the other two
273	levels of management intensity. In contrast, the amount of carbon present in the recalcitrant
274	organo-mineral fraction, which accounted for the largest remaining proportion of soil mass,
275	did not respond to management intensity.
276	

277 *Plant traits and soil carbon at varying depth*

278 Of 20 model tests (linear and quadratic fits attempted for two traits at five depths) only two

279 significant relationships were found. These were for a unimodal and linear model between

280 abundance-weighted SLA and soil carbon at 40 and 60cm depth, respectively. Consequently

281 there was little evidence for consistent relationships with the plant traits SLA and LDMC and

282 their systematic change down the soil profile.

283

284 Discussion

285 The aim of this study was to investigate the amount of soil carbon in grasslands to 1 m depth,

286 and the sensitivity of soil carbon to management intensity at depth increments to 1 m. Our

287 study was carried out at a national scale across a broad range of grasslands and soil

288 conditions, thus extending knowledge from past studies into land management and deep

289 carbon at the field scale. We reveal two key findings. First, we show that long-term changes

290 in grassland management intensity have strongly influenced soil carbon, and that this effect is

- 291 seen to considerable depths down the soil profile, albeit at decreasing significance with depth.
- 292 Second, we show that considerable stocks of carbon are contained in sub-surface grassland
- 293 soils, below the standard carbon inventory default depth of 30cm under tier 1 of the IPCC

- (2006), suggesting that large stocks of unaccounted for carbon are sensitive to managementchange.
- 296

297 *Management intensity*

298 Our data show that intensive management has reduced the concentration of carbon in soil (% 299 total C), and that soil carbon stocks per m² are greatest at intermediate levels of grassland 300 management intensity. This sensitivity of soil carbon to management has been found in other 301 grassland studies for surface soils in Europe (Soussana et al. 2004, Allard et al. 2007). 302 However, by sampling to 1 m depth from a large number of sites across a broad range of 303 grassland and soil types, our study extends the knowledge of grassland management effects 304 on soil carbon by demonstrating that, although management effects on soil carbon were 305 strongest in surface soils, they are still observed to considerable depth down the soil profile, 306 indicating that extensive stocks of soil carbon at depth are sensitive to management change.

307

308 We suggest that both biological and physical mechanisms contributed to the greater 309 cumulative carbon stocks observed at intermediate levels of grassland management. Soil 310 carbon sequestration is dictated by processes controlling the balance of carbon inputs and 311 carbon outputs. Carbon inputs are derived from primary productivity through photosynthetic 312 uptake of carbon, input to soil in the form of root exudates and litter; plus additional inputs 313 from animal manure. Carbon losses are through a range of biological and physical processes 314 including respiration, decomposition, erosion, leaching and removal of biomass by harvesting 315 or grazing animals. Because we measured total rather than organic soil carbon, it is possible 316 that differences in total soil carbon are due, in part, to variations in inorganic carbon, from 317 liming or the influence of parent bedrock, particularly in calcareous soils. It is also possible 318 that black carbon (charcoal) made up a small proportion of the total carbon observed

319	(Manning et al. 2015). However, by sampling triplicate groups of fields from the same
320	bedrock across a management intensity gradient, we suggest that these effects would be
321	minimal.
322	
323	There are clearly many factors involved in the intensification of grassland management, such

324 as fertiliser addition, the intensity of grazing and biomass removal, and compaction

associated with livestock and machinery, and it is difficult to separate out the effects of each

326 of these in terms of their influence on soil carbon. Such management factors also impact on

327 plant community composition, which is known to influence soil carbon dynamics (De Deyn

et al. 2008, Manning et al. 2015). We did not directly measure plant productivity,

decomposition, or other processes involved in carbon cycling. However, it has been shown

in other studies that extensive grassland management can reduce soil carbon accumulation

over time as plant productivity declines in response to nutrient limitation (Allard et al. 2007),

and that intensive management involving the application of large amounts of fertiliser can be

detrimental to soil carbon (Mack et al. 2004, Soussana et al. 2004, Schipper et al. 2007).

334 Conversely, the application of fertiliser in modest amounts in intermediate grasslands has

been shown to enhance soil carbon (Conant et al. 2011, Leifeld et al. 2011, Smith 2014),

336 which is likely related to an increase in primary productivity without over-stimulating

decomposition, although, as pointed out, the effect of other concomitant management factors

cannot be ruled out.

339

340 In addition to changes in bulk soil carbon, we also found that different fractions of carbon in

341 surface soils to 7.5 cm depth varied in their sensitivity to management. In particular, both the

- 342 labile free SOM and intra-aggregate SOM fractions were reduced by management
- 343 intensification. While these two SOM fractions make up less than a quarter of total soil mass,

Management and deep soil carbon

344	they are of vital importance to soil carbon storage as they contain a greater concentration of
345	carbon than the recalcitrant organo-mineral fraction and account for 31% of soil carbon in
346	intensively managed soils, rising to 37% and 44% of soil carbon in intermediate and
347	extensively managed grassland soils respectively. We found no evidence of a systematic
348	relationship between total soil carbon at varying depth and community weighted values of
349	two key leaf traits (i.e. SLA and LDMC) that are known to be responsive to grassland
350	intensification and to mediate effects on carbon storage via differences in the
351	decomposability of plant material (De Deyn et al. 2008). We expected that the relationship
352	between leaf traits and soil carbon would be strongest at the soil surface and decline in
353	strength with soil depth, reflecting historic plant traits prior to intensification in the last 60
354	years. Using the same network of grassland sites, Manning et al (2015) investigated
355	relationships between plant traits and soil carbon fractions in surface soil (7.5 cm soil depth)
356	and found that only the labile carbon fraction was partially explained by community weighted
357	SLA, with soil carbon stocks being greatest under vegetation with thick and/or dense leaves.
358	In contrast, the less active fractions, which make up the bulk of the carbon pool, were better
359	explained by abiotic factors, including pH and climate (Manning et al. 2015). Our results
360	indicate that the lack of correlation between leaf traits and soil carbon propagates down the
361	soil profile, suggesting that the mediating effect of current plant trait variation on soil carbon
362	is weaker than the long-term effect of other environmental controls on the production and
363	storage of carbon at depth.

364

365 Differences in carbon stocks between management levels were also strongly influenced by
366 variations in soil bulk density, which increased as management intensified and with depth.
367 This increase in bulk density with more intensive management is likely largely explained by
368 soil compaction from a greater use of machinery and trampling from grazing animals

369 (Gifford and Roderick 2003, Batey 2009), but also the greater proportion of higher density 370 soil fractions in fertilised soils (Fornara et al. 2011). The combination of low carbon 371 concentration with high bulk density in intensive grasslands, and high carbon concentration 372 with low bulk density in extensive grasslands, contributed to the equivalence of carbon stocks 373 observed at high and low levels of management intensity, and their lower levels relative to 374 intermediate intensity. This highlights a dilemma in comparing soil carbon stocks both 375 spatially and temporally, in that soil carbon stocks calculated per unit area could be increased 376 by simple physical compaction without a change in soil carbon concentration, particularly if 377 measured at shallow sampling depths. Gifford and Roderick (2003) propose an alternative 378 way of calculating soil carbon based on soil mass rather than volume to avoid this problem of 379 bulk density change associated with land use. For comparison, we estimated cumulative 380 carbon stocks on a soil mass rather than volume basis, using approximated soil mass values 381 (supporting information). On this approximated soil mass basis, differences in cumulative 382 carbon stocks between intermediate and extensive grasslands were reduced, whereas the 383 difference in cumulative carbon stocks for intensive relative to both intermediate and 384 extensive grasslands increased, to an estimated 15% less carbon in intensively managed 385 grasslands (supporting information). This differs from our findings on a bulk density basis, 386 where soil carbon stocks were greatest under intermediate compared with both intensive and 387 extensive intensity of management, but highlights the strong detrimental effect of intensive 388 management on grassland soil carbon stocks. However, these results need to be treated with 389 caution as calculations were made retrospectively on approximated soil mass values without 390 following the recommended protocol (Gifford and Roderick 2003), and did not meet the 391 requirement for samples to be taken from adjacent positions (Chapman et al. 2013). 392

393 *Carbon stocks at depth*

Management and deep soil carbon

394	Our study revealed that considerable stocks of soil carbon are contained in sub-surface
395	grassland soils below the standard carbon inventory default depth of 30cm (IPCC 2006).
396	Using Great Britain as a case study, we combined our model of cumulative soil carbon stocks
397	across a range of grasslands and management intensities with land cover data (Carey et al.
398	2008) for comparable grassland categories, to estimate total grassland soil carbon storage to 1
399	m depth. Cumulative soil carbon stocks were adjusted for depth, based on our survey results
400	of a decreasing proportion of grasslands having soil to the full sampling depth, with 55% of
401	all fields having soil to the full 1 m depth (Table 4). From this, we estimate a total carbon
402	stock in British grassland soils of 2097 Tg C to a depth of 1 m (Fig. 3). This is over three
403	times the amount for soil organic carbon estimated by the latest Countryside Survey to 15 cm
404	depth (660 Tg), and more than double the amount when extrapolated to the standard IPCC
405	recommended carbon accounting depth of 30 cm (estimated at 880 Pg, Fig. 3). Of this figure
406	of 2097 Tg C for grassland carbon storage to 1 m depth, the greatest proportion of grassland
407	soil carbon stocks (1130 Tg C) were in improved grasslands, which account for the largest
408	land cover of all grasslands in Great Britain (Carey et al. 2008) and are most likely to contain
409	soil to 1 m depth. Total stocks of soil carbon to 1 m depth (Table S2.2) were 10.7% greater
410	at intermediate relative to intensive management, which equates to 10.1 t ha ⁻¹ in surface soils
411	to 30 cm depth, and an additional 13.7 t ha ⁻¹ in soils from 30-100 cm depth.
440	

412

At shallower soil depths, our soil carbon values of 76 and 97 t ha⁻¹ at 15 and 30 cm depths
respectively, are in line with those reported elsewhere for the UK, of 48-90 t ha⁻¹ at 15 cm
and 100 t ha⁻¹ at 30 cm depth (Bradley et al. 2005, Emmett et al. 2010, Chapman et al. 2013).
However, our estimation of grassland soil carbon stocks of 2097 Tg C to 1 m depth is
considerably greater than that of Bradley et al. (2005), estimated at 1345 Tg C for UK
pasture, and of Chapman (2013), who reported 138 t ha⁻¹ for improved and 185 t ha⁻¹ for

419	semi-natural grasslands, compared with our value of at 229 t ha ⁻¹ at 1 m depth. This suggests
420	that grassland carbon stocks at depth may be greater than previously thought. However,
421	extrapolation of data needs to be treated with caution, due to the high variability of carbon
422	stocks at depth and regional differences between management and grassland types (Maskell
423	et al. 2013), and our modelling results explicitly quantify the uncertainty associated with our
424	estimates and how the uncertainty increases with depth (Table 4). Differences in soil carbon
425	accounting at depth between studies are likely due to increased uncertainties caused by lower
426	sample numbers and greater incremental size categories (Syswerda et al. 2011), and
427	differences between land use classifications; for example, Bradley et al (2005) estimate a
428	further 2015 Tg C to 1m depth in their semi natural category. Our data also show that around
429	60% of the total grassland soil carbon stocks to 1 m depth are found in sub-surface soils
430	below 30 cm depth. Previous estimates, albeit for organic not total carbon, commonly quote
431	a 50/50 split between surface and sub-surface (30-100 cm) soil carbon (Batjes 1996, Jobbagy
432	and Jackson 2000, Schils et al. 2008), although 60% sub-surface organic carbon has been
433	previously estimated for some grassland soils (Hiederer 2009).
434	
435	Our data clearly reveal an important stock of carbon in grassland soil at depth, which is
436	unrecognised in current surface soil carbon accounting (IPCC 2006, Emmett et al. 2010).
437	Despite the tier 1 default soil sampling depth being 30 cm, the IPCC advocate sampling
438	beyond 30 cm depth, although in likelihood this is rarely done. Our findings provide clear
439	support for the IPCC recommendation of the need for deeper C sampling, not only to improve
440	soil C inventories, but also to take into account changes in soil carbon at depth due to
441	management intensification.
442	

442

443 *Conclusion*

Management and deep soil carbon

444	In conclusion, the findings of our national-scale study, which encompassed a broad range of
445	grasslands and environmental conditions, show that carbon in grasslands soils is vulnerable to
446	management, and that the legacy of long-term grassland management impacts on soil carbon
447	to considerable depth down the profile. Moreover, we highlight the presence of substantial
448	stocks of carbon in sub-surface soil in grasslands, which are not accounted for by the majority
449	of standard carbon inventories (IPCC 2006, Emmett et al. 2010, Sanderman et al. 2011),
450	indicating that large stocks of unaccounted for soil carbon are sensitive to changes in land
451	management intensity. Our finding suggest potential future benefits for soil carbon
452	sequestration alongside biodiversity through extensification of the most highly managed and
453	fertilised grasslands, given that soil carbon concentrations decrease with management
454	intensity, and that cumulative stocks of soil carbon to depth when bulk density was accounted
455	for were greatest in grasslands managed at intermediate levels of intensity and plant diversity.
456	Given the global extent of managed grasslands, these findings not only have implications for
457	their future management for soil carbon storage and climate mitigation, that would benefit
458	future global carbon targets (United Nations FCCC 2015), but also for global carbon models
459	which need to take account of deep soil carbon stocks, and changes in this soil carbon at
460	depth due to management.

461 Acknowledgements

- 462 This research was supported by DEFRA, project number BD5003, which was initiated and
- 463 led by RDB. We thank all landowners and farmers for land access; V. van Velzen, F. de
- 464 Vries, N. Thompson, P. Bentley, E. McCahill, L. Andrew, D. Beaumont, E. Pilgrim, D.
- 465 Senepathi, A. Stone, D. Hogan, O. Tallowin, O. Byrne, E. Mattison and E. Bottoms for help
- 466 in collecting and processing soil samples. We also thank Ed Tipping and 3 anonymous
- 467 reviewers for comments on the manuscript.

468	References
469	Allan, E., P. Manning, F. Alt, J. Binkenstein, S. Blaser, N. Bluethgen, S. Boehm, F. Grassein,
470	N. Hoelzel, V. H. Klaus, T. Kleinebecker, E. K. Morris, Y. Oelmann, D. Prati, S. C.
471	Renner, M. C. Rillig, M. Schaefer, M. Schloter, B. Schmitt, I. Schoening, M.
472	Schrumpf, E. Solly, E. Sorkau, J. Steckel, I. Steffen-Dewenter, B. Stempfhuber, M.
473	Tschapka, C. N. Weiner, W. W. Weisser, M. Werner, C. Westphal, W. Wilcke, and
474	M. Fischer. 2015. Land use intensification alters ecosystem multifunctionality via loss
475	of biodiversity and changes to functional composition. Ecology Letters 18:834-843.
476	Allard, V., J. F. Soussana, R. Falcimagne, P. Berbigier, J. M. Bonnefond, E. Ceschia, P.
477	D'Hour, C. Henault, P. Laville, C. Martin, and C. Pinares-Patino. 2007. The role of
478	grazing management for the net biome productivity and greenhouse gas budget (CO ₂ ,
479	N ₂ O and CH ₄) of semi-natural grassland. Agriculture Ecosystems & Environment
480	121 :47-58.
481	Bardgett, R. D. and E. McAlister. 1999. The measurement of soil fungal : bacterial biomass
482	ratios as an indicator of ecosystem self-regulation in temperate meadow grasslands.
483	Biology and Fertility of Soils 29 :282-290.
484	Batey, T. 2009. Soil compaction and soil management - a review. Soil Use and Management
485	25 :335-345.
486	Batjes, N. H. 1996. Total carbon and nitrogen in the soils of the world. European Journal of
487	Soil Science 47 :151-163.
488	Bradley, R. I., R. Milne, J. Bell, A. Lilly, C. Jordan, and A. Higgins. 2005. A soil carbon and
489	land use database for the United Kingdom. Soil Use and Management 21:363-369.
490	Carey, P. D., S. Wallis, P. M. Chamberlain, A. Cooper, B. A. Emmett, L. C. Maskell, T.
491	McCann, J. Murphy, L. R. Norton, B. Reynolds, W. A. Scott, I. C. Simpson, S. M.

- 492 Smart, and J. M. Ullyett. 2008. Countryside Survey: UK Results from 2007.
- 493 NERC/Centre for Ecology & Hydrology.
- 494 Chapman, S. J., J. S. Bell, C. D. Campbell, G. Hudson, A. Lilly, A. J. Nolan, A. H. J.
- 495 Robertson, J. M. Potts, and W. Towers. 2013. Comparison of soil carbon stocks in
- 496 Scottish soils between 1978 and 2009. European Journal of Soil Science **64**:455-465.
- 497 Conant, R. T., M. G. Ryan, G. I. Agren, H. E. Birge, E. A. Davidson, P. E. Eliasson, S. E.
- 498 Evans, S. D. Frey, C. P. Giardina, F. M. Hopkins, R. Hyvonen, M. U. F. Kirschbaum,
- J. M. Lavallee, J. Leifeld, W. J. Parton, J. M. Steinweg, M. D. Wallenstein, J. A. M.
- 500 Wetterstedt, and M. A. Bradford. 2011. Temperature and soil organic matter
- 501decomposition rates synthesis of current knowledge and a way forward. Global
- 502 Change Biology 17:3392-3404.
- 503 Critchley, C. N. R., J. A. Fowbert, and B. Wright. 2007. Dynamics of species-rich upland hay
- 504 meadows over 15 years and their relation with agricultural management practices.
- 505 Applied Vegetation Science **10**:307-314.
- 506 De Deyn, G. B., J. H. C. Cornelissen, and R. D. Bardgett. 2008. Plant functional traits and
 507 soil carbon sequestration in contrasting biomes. Ecology Letters 11:516-531.
- 508 de Vries, F. T., P. Manning, J. R. B. Tallowin, S. R. Mortimer, E. S. Pilgrim, K. A. Harrison,
- 509 P. J. Hobbs, H. Quirk, B. Shipley, J. H. C. Cornelissen, J. Kattge, and R. D. Bardgett.
- 510 2012. Abiotic drivers and plant traits explain landscape-scale patterns in soil
- 511 microbial communities. Ecology Letters **15**:1230-1239.
- 512 Dupouey, J. L., E. Dambrine, J. D. Laffite, and C. Moares. 2002. Irreversible impact of past
 513 land use on forest soils and biodiversity. Ecology 83:2978-2984.
- 514 Duru, M., J. P. Theau, and P. Cruz. 2012. Functional diversity of species-rich managed
- grasslands in response to fertility, defoliation and temperature. Basic and Applied
- 516 Ecology **13**:20-31.

- 517 Emmett, B. A., B. Reynolds, P. M. Chamberlain, E. Rowe, D. Spurgeon, S. A. Brittain, Z.
- 518 Frogbrook, S. Hughes, A. J. Lawlor, J. Poskitt, E. Potter, D. A. Robinson, A. Scott, C.
- 519 Wood, and C. Woods. 2010. Countryside Survey: Soils Report from 2007. Page 230,
- 520 NERC/Centre for Ecology & Hydrology
- 521 FAO. 2015. Food and Agriculture Organisation of the United Nations
- 522 <u>http://www.fao.org/home/en/.</u>
- Fontaine, S., S. Barot, P. Barre, N. Bdioui, B. Mary, and C. Rumpel. 2007. Stability of
 organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450:277-
- 525 U210.
- Fornara, D. A., R. Bardgett, S. Steinbeiss, D. R. Zak, G. Gleixner, and D. Tilman. 2011. Plant
 effects on soil N mineralization are mediated by the composition of multiple soil
 organic fractions. Ecological Research 26:201-208.
- 529 Gamble, D., C. Perry, and T. St Pierre. 2012. Hay Time Final Report. Clapham, UK.
- 530 Garnett, T., M. C. Appleby, A. Balmford, I. J. Bateman, T. G. Benton, P. Bloomer, B.
- 531 Burlingame, M. Dawkins, L. Dolan, D. Fraser, M. Herrero, I. Hoffmann, P. Smith, P.
- 532 K. Thornton, C. Toulmin, S. J. Vermeulen, and H. C. J. Godfray. 2013. Sustainable
- 533 Intensification in Agriculture: Premises and Policies. Science **341**:33-34.
- Gibson, D. J. 2008. Grasses and Grassland Ecology. Oxford University Press, Oxford.
- Gifford, R. M. and M. L. Roderick. 2003. Soil carbon stocks and bulk density: spatial or
 cumulative mass coordinates as a basis of expression? Global Change Biology
- **537 9**:1507-1514.
- 538 Grayston, S. J., C. D. Campbell, R. D. Bardgett, J. L. Mawdsley, C. D. Clegg, K. Ritz, B. S.
- 539 Griffiths, J. S. Rodwell, S. J. Edwards, W. J. Davies, D. J. Elston, and P. Millard.
- 540 2004. Assessing shifts in microbial community structure across a range of grasslands

541 of differing management intensity using CLPP, PLFA and community DNA 542 techniques. Applied Soil Ecology 25:63-84. 543 Grigulis, K., S. Lavorel, U. Krainer, N. Legay, C. Baxendale, M. Dumont, E. Kastl, C. 544 Arnoldi, R. D. Bardgett, F. Poly, T. Pommier, M. Schloter, U. Tappeiner, M. Bahn, 545 and J.-C. Clement. 2013. Relative contributions of plant traits and soil microbial 546 properties to mountain grassland ecosystem services. Journal of Ecology 101:47-57. 547 Guo, L. B. and R. M. Gifford. 2002. Soil carbon stocks and land use change: a meta-analysis. 548 Glob. Change Biol. 8:345-360. 549 Heidenreich, B. 2009. What are global temperate grasslands worth? A case for their 550 protection., Temperate Grasslands Conservation Initiative, Vancouver, British 551 Columbia, Canada. 552 Hiederer, R. 2009. Distribution of organic carbon in soil profile data. EUR 23980 EN., 553 European Commission Joint Research Centre, Luxembourg: Office for official 554 publications of the European Communities. 555 Hodgson, J. G., G. Montserrat-Marti, M. Charles, G. Jones, P. Wilson, B. Shipley, M. 556 Sharafi, B. E. L. Cerabolini, J. H. C. Cornelissen, S. R. Band, A. Bogard, P. Castro-557 Diez, J. Guerrero-Campo, C. Palmer, M. C. Perez-Rontome, G. Carter, A. Hynd, A. 558 Romo-Diez, L. de Torres Espuny, and F. Royo Pla. 2011. Is leaf dry matter content a 559 better predictor of soil fertility than specific leaf area? Annals of Botany 108:1337-560 1345. 561 IPCC. 2006. 2006 IPCC Guidelines for National Greenhouse Gas Inventories. Prepared by 562 the National Greenhouse Gas Inventories Programme, Eggleston H.S., Buendia L., 563 Miwa K., Ngara T. and Tanabe K. (eds). IGES, Japan. 564 Jobbagy, E. G. and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and 565 its relation to climate and vegetation. Ecol. Appl. 10:423-436.

Management and deep soil carbon

566	Kleyer, M., R. M. Bekker, I. C. Knevel, J. P. Bakker, K. Thompson, M. Sonnenschein, P.
567	Poschlod, J. M. van Groenendael, L. Klimes, J. Klimesova, S. Klotz, G. M. Rusch, M.
568	Hermy, D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L.
569	Goetzenberger, J. G. Hodgson, A. K. Jackel, I. Kuehn, D. Kunzmann, W. A. Ozinga,
570	C. Roemermann, M. Stadler, J. Schlegelmilch, H. J. Steendam, O. Tackenberg, B.
571	Wilmann, J. H. C. Cornelissen, O. Eriksson, E. Garnier, and B. Peco. 2008. The
572	LEDA Traitbase: a database of life-history traits of the Northwest European flora.
573	Journal of Ecology 96 :1266-1274.
574	Lavorel, S. and E. Garnier. 2002. Predicting changes in community composition and
575	ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology
576	16 :545-556.
577	Leifeld, J., C. Ammann, A. Neftel, and J. Fuhrer. 2011. A comparison of repeated soil
578	inventory and carbon flux budget to detect soil carbon stock changes after conversion
579	from cropland to grasslands. Global Change Biology 17:3366-3375.
580	Mack, M. C., E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin. 2004.
581	Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization.
582	Nature 431 :440-443.
583	Manning, P., F. T. de Vries, J. R. B. Tallowin, R. Smith, S. R. Mortimer, E. S. Pilgrim, K. A.
584	Harrison, D. G. Wright, H. Quirk, J. Benson, B. Shipley, J. H. C. Cornelissen, J.
585	Kattge, G. Bönisch, C. Wirth, and R. D. Bardgett. 2015. Simple measures of climate,
586	soil properties and plant traits predict national-scale grassland soil carbon stocks.
587	Journal of Applied Ecology 52 :1188-1196.
588	Maskell, L. C., A. Crowe, M. J. Dunbar, B. Emmett, P. Henrys, A. M. Keith, L. R. Norton, P.
589	Scholefield, D. B. Clark, I. C. Simpson, and S. M. Smart. 2013. Exploring the

- 590 ecological constraints to multiple ecosystem service delivery and biodiversity. Journal
 591 of Applied Ecology 50:561-571.
- McLauchlan, K. 2006. The Nature and Longevity of Agricultural Impacts on Soil Carbon and
 Nutrients: A Review. Ecosystems 9:1364-1382.
- Rodwell, J. S. 1992. British plant communities. Vol 3. Grasslands and montane

595 communities. Cambridge University Press, Cambridge.

- 596 Royal Society. 2001. The role of land carbon sinks in mitigating global climate change.597 Policy document 10/01.
- 598 Sanderman, J., J. Baldock, B. Hawke, L. Macdonal, A. Massis-Puccini, and S. Szarvas. 2011.

599 National soil carbon research programme: field and laboratory methodologies.

600 CSIRO, Urrbrae, South Australia.

- 601 Schils, R., P. Kuikman, J. Liski, M. van Oijen, P. Smith, J. Webb, J. Alm, Z. Somogyi, J. van
- den Akker, M. Billet, B. Emmett, C. Evans, M. Lindner, T. Palosuo, P. Bellamy, R.
- Jandl, and R. Hiederer. 2008. Review of existing information on the interrelationsbetween soil and climate change. European Commission, Brussels.
- 605 Schipper, L. A., W. T. Baisden, R. L. Parfitt, C. Ross, J. J. Claydon, and G. Arnold. 2007.
- Large losses of soil C and N from soil profiles under pasture in New Zealand during
 the past 20 years. Global Change Biology 13:1138-1144.
- 608 Smart, S. M., P. A. Henrys, B. V. Purse, J. M. Murphy, M. J. Bailey, and R. H. Marrs. 2012.
- 609 Clarity or confusion? Problems in attributing large-scale ecological changes to
 610 anthropogenic drivers. Ecological Indicators 20:51-56.
- Smith, P. 2014. Do grasslands act as a perpetual sink for carbon? Global Change Biology
 20:2708-2711.
- 613 Smith, P., D. Martino, Z. Cai, D. Gwary, H. Janzen, P. Kumar, B. McCarl, S. Ogle, F.
- 614 O'Mara, C. Rice, B. Scholes, O. Sirotenko, M. Howden, T. McAllister, G. Pan, V.

- 615 Romanenkov, U. Schneider, S. Towprayoon, M. Wattenbach, and J. Smith. 2008.
- 616 Greenhouse gas mitigation in agriculture. Philosophical Transactions of the Royal
- 617 Society B-Biological Sciences **363**:789-813.
- 618 Sohi, S. P., N. Mahieu, J. R. M. Arah, D. S. Powlson, B. Madari, and J. L. Gaunt. 2001. A
- procedure for isolating soil organic matter fractions suitable for modeling. Soil
 Science Society of America Journal 65:1121-1128.
- 621 Sohi, S. P., N. Mahieu, D. S. Powlson, B. Madari, R. H. Smittenberg, and J. L. Gaunt. 2005.
- 622 Investigating the chemical characteristics of soil organic matter fractions suitable for
 623 modeling. Soil Science Society of America Journal 69:1248-1255.
- Soussana, J. F., P. Loiseau, N. Vuichard, E. Ceschia, J. Balesdent, T. Chevallier, and D.
 Arrouays. 2004. (Carbon cycling and sequestration opportunities in temperate
- grasslands. Soil Use and Management **20**:219-230.
- 627 Syswerda, S. P., A. T. Corbin, D. L. Mokma, A. N. Kravchenko, and G. P. Robertson. 2011.
- Agricultural Management and Soil Carbon Storage in Surface vs. Deep Layers. Soil
 Science Society of America Journal 75:92-101.
- Tallowin, J. R. B. and R. G. Jefferson. 1999. Hay production from lowland semi-natural
- grasslands: a review of implications for ruminant livestock systems. Grass and Forage
 Science 54:99-115.
- Tallowin, J. R. B., R. E. N. Smith, J. Goodyear, and J. A. Vickery. 2005. Spatial and
- structural uniformity of lowland agricultural grassland in England: a context for low
 biodiversity. Grass and Forage Science 60:225-236.
- 636 United Nations FCCC. 2015. United Nations Framework Convention on Climate Change
 637 FCCC/CP/2015/L.9/Rev.1. United Nations, Paris.
- van Wesemael, B., K. Paustian, J. Meersmans, E. Goidts, G. Barancikova, and M. Easter.
- 639 2010. Agricultural management explains historic changes in regional soil carbon

- 640 stocks. Proceedings of the National Academy of Sciences of the United States of
- 641 America **107**:14926-14930.

643 Supporting Information

- 644 S1. Methods for modelling cumulative soil carbon.
- 645 S2. Upscaling cumulative soil carbon to the whole of Great Britain.
- 646 S3. Statistical effects for soil carbon and bulk density.
- 647 S4. Estimating soil C stocks on soil mass basis.
- 648 S5. BUGS code for modelling cumulative soil carbon stocks.

650 Tables

654

Table 1. Typical values for grassland management practices, including fertiliser use, grazing

652 management (LU -= livestock units), cutting regimes, and plant species diversity for the three

653 levels of management intensity.

	Extensive	Intermediate	Intensive
Fertiliser application rate	$< 25 \text{ kg N ha}^{-1} \text{ yr}^{-1}$	$25 - 50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$	$> 100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$
Grazing	Set stocking or continuous grazing at stocking rates generally below 1.0 LU ha ⁻¹	Set stocking or continuous grazing at stocking rates up to1.5 LU ha ⁻¹	Rotational/paddock grazing commonly used with stocking rates of 2.0 -3.5+LU ha ⁻¹
Cutting	Generally one cut in mid – late summer for hay or haylage. Regrowth generally grazed in late summer/autumn	Generally one cut in mid- summer for silage or haylage. Regrowth generally grazed in late summer/autumn	Two – three silage cuts per year (May, July, September/October)
¹ Plant diversity	High diversity (Mean 21 sp. m ⁻²)	Intermediate Diversity (Mean 15 sp. m ⁻²)	Low Diversity (Mean 10 sp. m ⁻²)

¹Data on plant species diversity are derived from De Vries et al. (2012).

Table 2. Effects of management intensity on soil carbon, measured as (a) % C of bulk soil

and (b) C content of soil fractions in surface soils.

Soil de	epth (cm)	(n)	Extensively managed	Intermediate management	Intensively managed	
(a) Bulk soil	carbon conce	entration	e (%C)			
Depth (cm)	0-7.5	(515)	$11.53 (\pm 0.54)^{a}$	$10.60 (\pm 0.54)^{b}$	$8.59 (\pm 0.44)^{c}$	**
	7.5 - 20	(499)	$8.18 (\pm 0.59)^{a}$	$7.77 (\pm 0.53)^{a}$	6.13 (± 0.47) ^b	**
	20 - 40	(446)	$6.48 (\pm 0.84)^{ab}$	$6.34 (\pm 0.74)^{a}$	$5.59 (\pm 0.72)^{b}$	**
	40 - 60	(359)	6.85 (± 1.28)	6.51 (± 1.12)	5.35 (± 0.96)	*
	60 - 100	(277)	9.76 (± 1.66)	7.25 (± 1.43)	7.55 (± 1.37)	
(b) Carbon c	ontent of soil	fraction	s in surface soils (0-	-7.5 cm) (g C kg ⁻¹ soil))	
Free SON	А		$43.9 (\pm 9.1)^{a}$	34.3 (± 8.9) ^b	23.6 (± 7.9) ^c	**
Intra-agg	regate SOM		$3.0 (\pm 0.5)^{a}$	$2.6 (\pm 0.3)^{a}$	$1.8 (\pm 0.2)^{b}$	**
Organo-n	nineral		59.9 (± 4.0)	62.3 (± 3.9)	56.7 (± 3.8)	

658 Values are means \pm s.e. Significant management effects shown by ** (P < 0.05) and *

(P < 0.10), with letters denoting differences between the 3 levels of management.

Table 3. Soil bulk density (g cm⁻³), for grassland soils at each of five depth increments

Soil depth Extensively Intermediate Intensively **(n)** managed managed management (cm) 0 - 7.5(486) $0.64 (\pm 0.02)$ $0.73 (\pm 0.02)$ $0.83 (\pm 0.02)$ ** 7.5 - 20(464) $0.85 (\pm 0.02)$ $0.91 (\pm 0.02)$ $0.98 (\pm 0.02)$ ** 20 - 40 (399) $1.06 (\pm 0.03)$ $1.00 (\pm 0.03)$ ** $1.06 (\pm 0.03)$ 40 - 60 (362) $1.05 (\pm 0.04)$ $1.06 (\pm 0.04)$ $1.13 (\pm 0.03)$ ** (300) 60 - 100 $1.02 (\pm 0.05)$ $1.05 (\pm 0.04)$ $1.09 (\pm 0.04)$ **

sampled, by management intensity and depth.

662 Values are means \pm s.e. Significant management effects shown by ** (P < 0.05).

664 **Table 4.** Mean cumulative soil carbon (kg C m^{-2}).

	Extensively managed	Intermediate management	Intensively managed
Surface to 7.5cm depth	6.61 (± 5.26-8.32)	7.14 (± 5.68-8.96)	6.45 (± 5.12-8.11)
Surface to 20 cm depth (97% of samples)	8.47 (± 6.75-10.65)	9.15 (± 7.29-11.47)	8.26 (± 6.56-10.37)
Surface to 40 cm depth (87% of samples)	12.59 (± 10.04-15.82)	13.60 (± 10.83-17.02)	12.28 (± 9.76-15.40)
Surface to 60 cm depth (70% of samples)	18.71 (± 14.90-23.54)	20.21 (± 16.07-25.36)	18.24 (± 14.53-22.92)
Surface to 100 cm depth (55% of samples)	41.38 (± 32.65-52.33)	44.62 (± 35.20-56.47)	40.30 (± 31.84-50.98)

665 Values are best estimates of the mean carbon stock where soil samples were present, with

lower and upper credible intervals (2.5 and 97.5% tiles of the posterior distribution from a

667 Bayesian mixed effects model).

668 Figure captions

669

670	Figure 1. Sampling locations in England (DeVries et al. 2012). Five farms were selected in
671	each of the 12 regions, and three fields in each farm were sampled: one extensively managed,
672	one of intermediate management and one intensively managed. Regions are: (a) Worcester,
673	(b) Upper Thames, (c) Somerset, (d) Devon, (e) Cotswolds, (f) High Weald, (g) South
674	Downs, (h) Breckland, (i) Dales meadows, (j) Yorkshire Ings, (k) Yorkshire Dales/South
675	Lake District, (l) Lake District.
676	
677	Figure 2. Total carbon per unit area in grassland soils (g C cm ⁻³ soil). Shown for each of five
678	depth increments sampled, with management intensity indicated by coloured bars: white for
679	extensively managed, grey for intermediate management and black for intensively managed
680	soils. Values are means +/- s.e.
681	
682	Figure 3. Estimated cumulative total soil carbon stocks for grasslands in Great Britain (Tg
683	C), adjusted for the availability of soil at depth. Shown in depth increments to 1 m, with
684	management intensity indicated by colour: white for extensively managed, grey for
685	intermediate management and black for intensively managed soils. The solid black circle
686	shows the current GB estimate of soil carbon at 15 cm depth. Dashed lines indicate

recommended soil sampling depths (GB Countryside Survey 15cm, IPCC at 30cm).

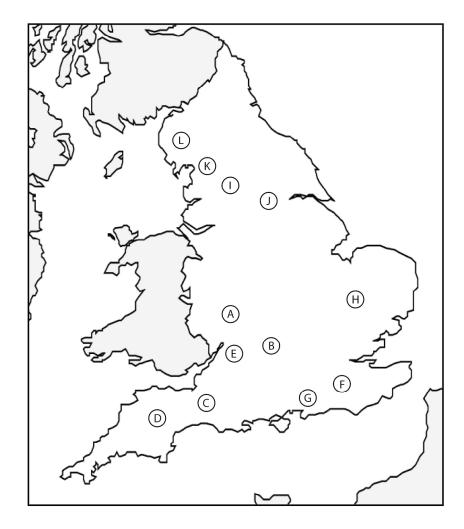
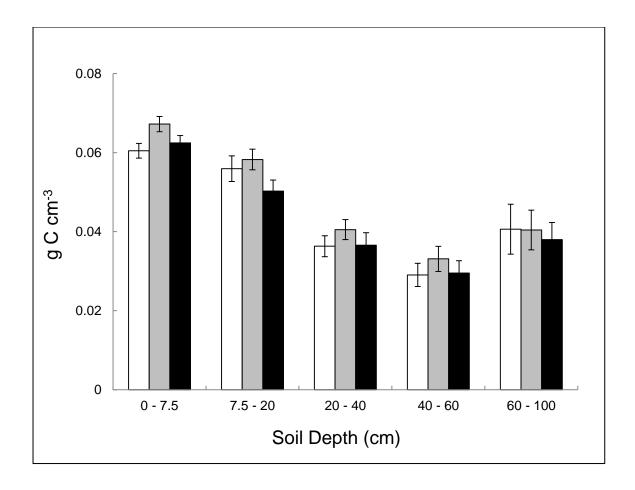
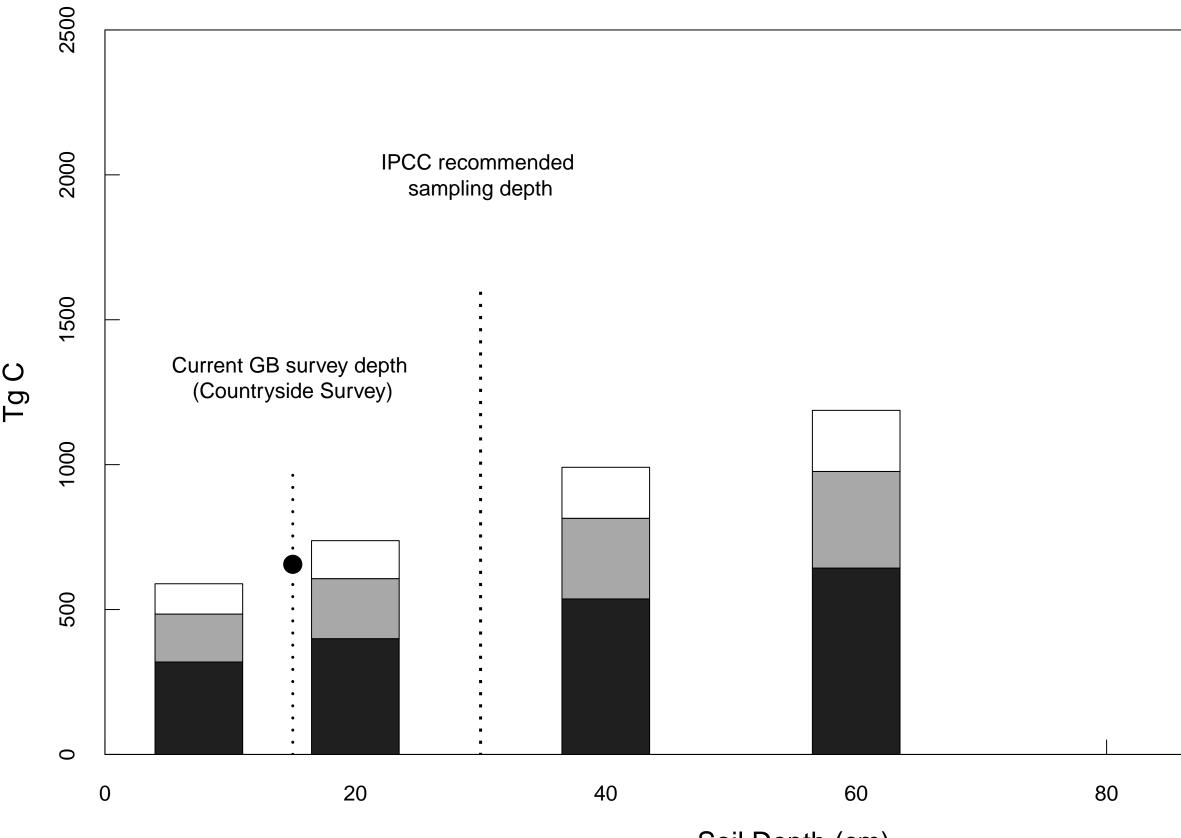


Figure 1 209x234mm (300 x 300 DPI)





Soil Depth (cm)

