

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 https://centaur.reading.ac.uk/54179/

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

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 End User Agreement.

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading



Reading's research outputs online

Legacy effects of grassland management on soil carbon to depth 1

2 Running header: Management and deep soil carbon

3

- Susan E.Ward^{1*}, Simon M.Smart², Helen Ouirk¹, Jerry R.B Tallowin³, Simon R. Mortimer⁴, 4
- Robert S. Shiel⁵, Andy Wilby¹, Richard D. Bardgett⁶ 5

6

- ¹Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ. UK. 7
- 8 ²Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue,
- 9 Bailrigg, Lancaster, LA1 4AP, UK.
- ³Rothamsted Research, North Wyke, Okehampton, Devon, EX20 2SB, UK. 10
- ⁴Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, 11
- 12 The University of Reading, Earley Gate, PO Box 237, Reading, RG6 6AR, UK.
- 13 ⁵School of Agriculture, Food and Rural Development, University of Newcastle, Newcastle
- 14 upon Tyne, NE1 7RU, UK.
- ⁶ Faculty of Life Sciences, Michael Smith Building, The University of Manchester, Oxford 15
- 16 Road, Manchester M13 9PT, UK.
- *Corresponding Author. E-mail: s.e.ward@lancaster.ac.uk. Tel: +44 (0)1524 510531 17

18

- **Keywords**: soil carbon, soil depth, grassland, management intensity, soil carbon stocks, 19
- 20 legacy effect, carbon inventory
- 21
- **Type of paper:** Primary Research Article

Abstract

22

23

24

25

26

27

28

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

The importance of managing land to optimise carbon sequestration for climate change mitigation is widely recognised, with grasslands being identified as having the potential to sequester additional carbon. However, most soil carbon inventories only consider surface soils, and most large scale surveys group ecosystems into broad habitats without considering management intensity. Consequently, little is known about the quantity of deep soil carbon and its sensitivity to management. From a nationwide survey of grassland soils to 1 m depth, we show that carbon in grasslands soils is vulnerable to management and that these management effects can be detected to considerable depth down the soil profile, albeit at decreasing significance with depth. Carbon concentrations in soil decreased as management intensity increased, but greatest soil carbon stocks (accounting for bulk density differences), were at intermediate levels of management. Our study also highlights the considerable amounts of carbon in sub-surface soil below 30cm, which is missed by standard carbon 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 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 findings highlight the existence of substantial carbon stocks at depth in grassland soils that are sensitive to management. This is of high relevance globally, given the extent of land cover and large stocks of carbon held in temperate managed grasslands. Our findings have implications for the future management of grasslands for carbon storage and climate mitigation, and for global carbon models which do not currently account for changes in soil carbon to depth with management.

46

47

48

49

50

51

52

53

54

55

56

57

58

59

60

61

62

63

64

65

66

67

68

69

Introduction

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

71 McLauchlan 2006, Smith 2014).

72

73

74

75

76

77

78

79

80

81

82

83

84

85

86

87

88

89

90

91

92

93

70

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

94

Another factor contributing to uncertainty over legacy effects of management and land use change is that most studies on soil carbon stocks are on more easily sampled surface soils. Even the IPCC recommend soil carbon accounting for the surface 30 cm of soil only (IPCC 2006), and although they advocate sampling beyond 30cm, this is rarely done. As a result, soil carbon stocks at depth are largely ignored (Fontaine et al. 2007, Chapman et al. 2013), and little is known about the quantity of soil carbon at depth and how it responds to land management and associated vegetation change in grasslands (Jobbagy and Jackson 2000, Soussana et al. 2004, Fontaine et al. 2007). Given the substantial quantities of carbon in grassland soils, and the fact that grasslands worldwide are subject to increasing intensification of management, this represents a major gap in knowledge.

The overarching aim of our study was to quantify the distribution of soil carbon across

English grasslands to depth (1 metre), and the relationship of surface and deep soil carbon to
grassland management at a national scale. To do this, we carried out a nationwide survey of
English grasslands. This included all the main grassland habitats found in Great Britain,
namely acid, calcareous, mesotrophic and wet grassland, sampled across the broad range of
soil and climatic conditions (de Vries et al. 2012, Manning et al. 2015), thereby
encompassing a wide range of variation across a representative spatial domain (Smart et al.
2012). Cumulative soil carbon stocks and mean depths from the survey were then used in
conjunction with land cover data for matching grassland broad habitats from the Countryside
Survey (Carey et al. 2008) to estimate total grassland soil carbon stocks in Great Britain to a
depth of 1m, and to make comparisons with existing estimates of grassland soil carbon
storage. Using two abundance-weighted leaf traits known to be indicators of soil fertility and
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 functional composition than deeper carbon.

121

119

120

122

123

124

125

126

127

128

129

130

131

132

133

134

135

136

137

138

139

140

141

142

143

Methods

Field sampling.

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

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
148	status, typically received less than 25 kg N ha ⁻¹ yr ⁻¹ and, have been managed in a traditional,
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 leys and related
152	grasslands) communities (Rodwell 1992). These intensively managed grasslands typically
153	receive >100 kg N ha ⁻¹ yr ⁻¹ , and have been subjected to standard intensive management
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 $\sim 2550\ kg\ N$
158	ha ⁻¹ yr ⁻¹ , and intermediate levels of plant diversity, grazing and cutting (Table 1).
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.

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

random effects of region and location included plus a fixed effect of soil depth. Estimates of cumulative soil carbon stocks were summarised by the posterior distribution of values estimated for each soil depth and each level of management intensity, with the clustering of samples within locations accounted for in the mixed effects model. Abundance-weighted means for plant traits SLA and LDMC were calculated for sample plots using plant species data, derived from field surveys carried out in 2005 to help classify management intensity classifications, and paired with soil carbon measurements at each soil depth. Plant trait information was derived from the LEDA database based on UK values reported for each species (Kleyer et al. 2008). We modelled the between-location variation in total soil carbon at each depth increment in terms of the abundance weighted plant traits, testing linear and quadratic models at each depth; region and location were introduced as random effects.

Upscaling

Cumulative soil carbon stocks and soil depths from our survey were combined with the UK Countryside Survey land cover data (Carey et al. 2008) to estimate total grassland soil carbon in Great Britain to a depth of 1m. Grassland types and management categories from our survey were matched with the UK Countryside Survey (CS) broad habitat classifications of improved, neutral, calcareous and acid grasslands (Emmett et al. 2010). Our 'intensively managed' grassland category mapped to the CS category 'improved grasslands'; our '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 estimate from CS to a depth of 15cm with our modelled cumulative carbon stocks (see Fig. 3). Cumulative soil carbon stocks for each management category were multiplied by the land cover area, and adjusted to account for the fact that not all grasslands surveyed had soil to the

219	full 1m depth, to give an estimate of total grassland soil carbon stocks (supporting
220	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	
240	Soil bulk density increased with depth down the soil profile ($F_{4,2011} = 57.5$, $P < 0.0001$), and
241	was also influenced by grassland management ($F_{4,2011} = 25.9$, $P < 0.0001$) (Table 3, Table
242	S3.1). The strongest effects of management were in the top 20 cm of the profile, where bulk
243	density was lowest in extensively managed and greatest in intensively managed grasslands,

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

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

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

Plant traits and soil carbon at varying depth

Of 20 model tests (linear and quadratic fits attempted for two traits at five depths) only two significant relationships were found. These were for a unimodal and linear model between abundance-weighted SLA and soil carbon at 40 and 60cm depth, respectively. Consequently there was little evidence for consistent relationships with the plant traits SLA and LDMC and their systematic change down the soil profile.

Discussion

The aim of this study was to investigate the amount of soil carbon in grasslands to 1 m depth, and the sensitivity of soil carbon to management intensity at depth increments to 1 m. Our study was carried out at a national scale across a broad range of grasslands and soil conditions, thus extending knowledge from past studies into land management and deep carbon at the field scale. We reveal two key findings. First, we show that long-term changes in grassland management intensity have strongly influenced soil carbon, and that this effect is seen to considerable depths down the soil profile, albeit at decreasing significance with depth. Second, we show that considerable stocks of carbon are contained in sub-surface grassland 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 management change.

Management intensity

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

We suggest that both biological and physical mechanisms contributed to the greater cumulative carbon stocks observed at intermediate levels of grassland management. Soil carbon sequestration is dictated by processes controlling the balance of carbon inputs and carbon outputs. Carbon inputs are derived from primary productivity through photosynthetic uptake of carbon, input to soil in the form of root exudates and litter; plus additional inputs from animal manure. Carbon losses are through a range of biological and physical processes including respiration, decomposition, erosion, leaching and removal of biomass by harvesting or grazing animals. Because we measured total rather than organic soil carbon, it is possible that differences in total soil carbon are due, in part, to variations in inorganic carbon, from liming or the influence of parent bedrock, particularly in calcareous soils. It is also possible 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
325	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
328	et al. 2008, Manning et al. 2015). We did not directly measure plant productivity,
329	decomposition, or other processes involved in carbon cycling. However, it has been shown
330	in other studies that extensive grassland management can reduce soil carbon accumulation
331	over time as plant productivity declines in response to nutrient limitation (Allard et al. 2007),
332	and that intensive management involving the application of large amounts of fertiliser can be
333	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
335	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
337	decomposition, although, as pointed out, the effect of other concomitant management factors
338	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,

345

346

347

348

349

350

351

352

353

354

355

356

357

358

359

360

361

362

363

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

364

365

366

367

368

Differences in carbon stocks between management levels were also strongly influenced by variations in soil bulk density, which increased as management intensified and with depth.

This increase in bulk density with more intensive management is likely largely explained by soil compaction from a greater use of machinery and trampling from grazing animals

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

Carbon stocks at depth

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409

410

411

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

412

413

414

415

416

417

418

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

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

Conclusion

management intensification.

In conclusion, the findings of our national-scale study, which encompassed a broad range of
grasslands and environmental conditions, show that carbon in grasslands soils is vulnerable to
management, and that the legacy of long-term grassland management impacts on soil carbon
to considerable depth down the profile. Moreover, we highlight the presence of substantial
stocks of carbon in sub-surface soil in grasslands, which are not accounted for by the majority
of standard carbon inventories (IPCC 2006, Emmett et al. 2010, Sanderman et al. 2011),
indicating that large stocks of unaccounted for soil carbon are sensitive to changes in land
management intensity. Our finding suggest potential future benefits for soil carbon
sequestration alongside biodiversity through extensification of the most highly managed and
fertilised grasslands, given that soil carbon concentrations decrease with management
intensity, and that cumulative stocks of soil carbon to depth when bulk density was accounted
for were greatest in grasslands managed at intermediate levels of intensity and plant diversity.
Given the global extent of managed grasslands, these findings not only have implications for
their future management for soil carbon storage and climate mitigation, that would benefit
future global carbon targets (United Nations FCCC 2015), but also for global carbon models
which need to take account of deep soil carbon stocks, and changes in this soil carbon at
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, 499 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 501 decomposition 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 515 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 http://www.fao.org/home/en/. 523 Fontaine, S., S. Barot, P. Barre, N. Bdioui, B. Mary, and C. Rumpel. 2007. Stability of 524 organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450:277-525 U210. 526 Fornara, D. A., R. Bardgett, S. Steinbeiss, D. R. Zak, G. Gleixner, and D. Tilman. 2011. Plant 527 effects on soil N mineralization are mediated by the composition of multiple soil 528 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. 534 Gibson, D. J. 2008. Grasses and Grassland Ecology. Oxford University Press, Oxford. 535 Gifford, R. M. and M. L. Roderick. 2003. Soil carbon stocks and bulk density: spatial or 536 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 JC. 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.

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 Layorel, 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.
592	McLauchlan, K. 2006. The Nature and Longevity of Agricultural Impacts on Soil Carbon and
593	Nutrients: A Review. Ecosystems 9:1364-1382.
594	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
602	den Akker, M. Billet, B. Emmett, C. Evans, M. Lindner, T. Palosuo, P. Bellamy, R.
603	Jandl, and R. Hiederer. 2008. Review of existing information on the interrelations
604	between 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.
606	Large losses of soil C and N from soil profiles under pasture in New Zealand during
607	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.
611	Smith, P. 2014. Do grasslands act as a perpetual sink for carbon? Global Change Biology
612	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
619	procedure for isolating soil organic matter fractions suitable for modeling. Soil
620	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.
624	Soussana, J. F., P. Loiseau, N. Vuichard, E. Ceschia, J. Balesdent, T. Chevallier, and D.
625	Arrouays. 2004. (Carbon cycling and sequestration opportunities in temperate
626	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.
628	Agricultural Management and Soil Carbon Storage in Surface vs. Deep Layers. Soil
629	Science Society of America Journal 75:92-101.
630	Tallowin, J. R. B. and R. G. Jefferson. 1999. Hay production from lowland semi-natural
631	grasslands: a review of implications for ruminant livestock systems. Grass and Forage
632	Science 54 :99-115.
633	Tallowin, J. R. B., R. E. N. Smith, J. Goodyear, and J. A. Vickery. 2005. Spatial and
634	structural uniformity of lowland agricultural grassland in England: a context for low
635	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.
638	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.
642	

643	Supportin	g Inform	ation
-----	-----------	----------	-------

- S1. Methods for modelling cumulative soil carbon.
- 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.
- S5. BUGS code for modelling cumulative soil carbon stocks.

649

Tables

650

651

652

653

Table 1. Typical values for grassland management practices, including fertiliser use, grazing management (LU -= livestock units), cutting regimes, and plant species diversity for the three levels of management intensity.

	Extensive	Intermediate	Intensive
Fertiliser application rate	< 25 kg N ha ⁻¹ yr ⁻¹	25 – 50 kg N ha ⁻¹ yr ⁻¹	> 100 kg N ha ⁻¹ 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 to 1.5 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)

654

655 Data 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 656 657 and (b) C content of soil fractions in surface soils.

Soil de	pth (cm)	(n)	Extensively managed	Intermediate management	Intensively managed	
(a) Bulk soil	carbon conce	entration	(%C)			
Depth (cm)	0 - 7.5	(515)	$11.53 (\pm 0.54)^{a}$	$10.60 (\pm 0.54)^{b}$	$8.59 (\pm 0.44)^{\text{c}}$	**
	7.5 - 20	(499)	$8.18 (\pm 0.59)^{a}$	$7.77 (\pm 0.53)^{a}$	$6.13 (\pm 0.47)^{b}$	**
	20 - 40	(446)	$6.48 (\pm 0.84)^{ab}$	$6.34 (\pm 0.74)^{a}$	$5.59 (\pm 0.72)^{b}$	**
	40 - 60	(359)	$6.85 (\pm 1.28)$	6.51 (± 1.12)	$5.35 (\pm 0.96)$	*
	60 - 100	(277)	9.76 (± 1.66)	7.25 (± 1.43)	$7.55 (\pm 1.37)$	
(b) Carbon c	ontent of soil	fraction	s in surface soils (0-	-7.5 cm) (g C kg ⁻¹ soil _,)	
Free SOM	1		$43.9 (\pm 9.1)^a$	$34.3 (\pm 8.9)^{b}$	$23.6 (\pm 7.9)^{c}$	**
Intra-aggregate 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)	

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

⁽*P*<0.10), with letters denoting differences between the 3 levels of management. 659

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

661

662

663

Soil depth (cm)	(n)	Extensively managed	Intermediate management	Intensively managed	
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)	$1.05 (\pm 0.04)$	$1.06 (\pm 0.04)$	$1.13 (\pm 0.03)$	**
60 - 100	(300)	$1.02 (\pm 0.05)$	$1.05 (\pm 0.04)$	$1.09 (\pm 0.04)$	**

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

666

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)

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

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

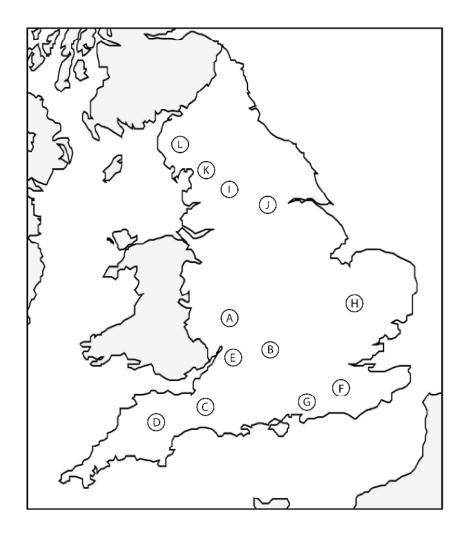


Figure 1 209x234mm (300 x 300 DPI)

