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Soil Use and Management

DOI:
[10.1111/sum.12517](https://doi.org/10.1111/sum.12517)

Published: 31/12/2019

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):
Ford, H., Healey, J. R., Webb, B., Pagella, T. F., & Smith, A. R. (2019). How do hedgerows influence soil organic carbon stock in livestock-grazed pasture? *Soil Use and Management*, 35(4), 576-584. <https://doi.org/10.1111/sum.12517>

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1 **How do hedgerows influence soil organic carbon stock in livestock-grazed pasture?**

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5 **Running head title:** Hedgerows and soil organic carbon

6 **Abstract**

7 Hedgerows have the potential to influence ecosystem function in livestock-grazed pasture.
8 Despite this, they are often ignored when quantifying farmland ecosystem service delivery. In
9 this study, we assess the contribution of hedgerows to the ecosystem function of carbon (C)
10 storage, with a particular emphasis on soil organic carbon (SOC). We measured SOC stock (kg
11 C m⁻²), on an equivalent soil mass basis, at 0-0.15 m depth in pasture adjacent to 38
12 hedgerows (biotic) and 16 stone walls or fences (abiotic controls) across ten farms in the
13 county of Conwy, Wales, UK. Pasture SOC stock (~7 kg C m⁻²) was similar adjacent to biotic
14 and abiotic field boundaries, positively associated with soil moisture and negatively with soil
15 bulk density (BD). For biotic boundaries two further variables were significantly associated
16 with SOC stock, distance from hedgerow (decrease in SOC stock) and slope orientation
17 (upslope SOC stock greater than downslope). For pasture adjacent to hedgerows a model
18 combining the aforementioned variables (BD, soil moisture, distance from hedgerow, slope
19 orientation) explained 78% of variation in SOC stock. This study demonstrates that, whilst
20 hedgerows do have subtle positive effects on SOC stock in adjacent pasture, SOC storage
21 adjacent to field boundaries is influenced more by soil moisture content and BD than field
22 boundary type.

23 **Keywords:** Agriculture; Agroforestry; Ecosystem function; Grassland; Soil carbon; Woody
24 linear feature

25 **Introduction**

26 The importance of hedgerows for provision of regulatory ecosystem services, including water
27 quality, flood risk reduction, soil erosion prevention, shelter provision (livestock) and climate
28 change mitigation (via carbon (C) storage), has been increasingly recognised over the past
29 decade (Wolton *et al.*, 2014; Scholefield *et al.*, 2016). Despite this, the contribution of
30 hedgerows, lines of trees and shrubs typically managed by regular cutting (Baudry, Bunce &
31 Burel, 2000) and other woody linear features (e.g. lines of trees or riparian strips), are
32 generally not properly accounted for when quantifying ecosystem services (Scholefield *et al.*,
33 2016; Cardinael *et al.*, 2018) due to a paucity of data on extent and condition.

34 The store of soil organic carbon (SOC) is usually dominated by soil organic matter (SOM), a
35 complex combination of plant- or animal-derived organic residues (e.g. leaf litter, root
36 biomass and exudates, microbial biomass, animal faeces) in various states of decomposition
37 (Baah-Acheamfour *et al.*, 2015). During the process of decomposition, C within SOM is either
38 incorporated into the soil matrix as SOC, released to the atmosphere as carbon dioxide or
39 methane, or transferred to ground water through leaching (Benham *et al.*, 2012). Dissolved
40 organic C inputs, from exudation and plant-derived decomposition products of high molecular
41 weight compounds, are thought to be the main source of SOC with a long residence time in
42 terrestrial ecosystems (Sokol & Bradford, 2019). Labile C inputs from root and hyphal turnover
43 directly influence microbial resource use efficiency (Lange *et al.*, 2015), with microbial
44 necromass forming a major part of the slow-cycling SOM/SOC pool in deeper soils.

45 Grassland SOC stocks are greatest in temperate moist-cool climates (Abdalla *et al.*, 2018),
46 where seasonally water-logged soils reduce the availability of oxygen, limiting the breakdown
47 of SOM. Soil type is also important, with SOC positively correlated with clay content (Jobbagy
48 & Jackson, 2000), as SOM is physically protected from microbial decomposition by adsorption
49 onto clay minerals within the soil. The effects of livestock grazing on SOC are dependent on
50 several factors including the physical properties of soil, precipitation levels, responsiveness of
51 the plant community to grazing and depth of soil sampling (Bardgett & Wardle, 2010).
52 Livestock grazing is often associated with increased allocation of plant resources below-
53 ground, with enhanced below-ground biomass and root turnover leading to SOC
54 accumulation (Kemp & Michalk, 2007). Negative impacts on SOC are largely seen where over-
55 grazing leads to sparse vegetation cover and soil erosion (Golluscio *et al.*, 2009). There is
56 general consensus that livestock-grazed pastures in temperate zones, particularly where
57 rainfall is plentiful, are a net C sink (Ostle *et al.*, 2009; Soussana *et al.*, 2010) with SOC stock
58 broadly comparable between semi-natural grassland and woodland (Bullock *et al.*, 2011).

59 Detailed study of spatial variation in SOC (content and stock) has shown it to be greater close
60 to hedgerows in both grassland and arable systems (Holden *et al.*, 2019), the effect decreasing
61 with distance from the hedge boundary, for up to 4 m into neighbouring fields (Follain *et al.*,
62 2007; D'Acunto *et al.*, 2014; Van Vooren *et al.*, 2017). Hedgerow woody plant root
63 architecture and depth can influence SOC storage, with deeper-rooted species associated
64 with greater SOC (Crossland, 2015). Position relative to hedgerows is also important, with SOC
65 greater upslope of contour-planted hedgerows, where the hedgerow acts as a physical barrier
66 reducing soil erosion and increasing A-horizon depth (Follain *et al.*, 2007). Regular hedgerow
67 management (via cutting with a tractor-mounted flail) increases the amount of surface litter
68 adjacent to the hedgerow (Axe *et al.*, 2017) potentially increasing inputs to soil. Regular

69 cutting also decreases the shoot-to-root ratio, which can influence fine root turnover and
70 either increase (Peter & Lehmann, 2000) or decrease (Crossland, 2015) SOC storage. Even
71 though hedgerow age (years since planting) is highly likely to influence SOC dynamics, due to
72 change in the quality and rate of C inputs via root and hyphal turnover, exudation, and leaf
73 litter over time as hedgerow plants grow, to our knowledge this aspect has not been studied
74 previously.

75 In this study, we focused on the contribution of hedgerows to the ecosystem function of C
76 storage in livestock-grazed pasture, with a particular emphasis on SOC. To do this we
77 measured SOC stock (kg C m⁻² of land area), expressed on an equivalent soil mass (ESM) basis
78 (Cardinael et al., 2018), in pasture adjacent to 38 hedgerows (biotic) and 16 stone walls or
79 fences (abiotic controls). We hypothesised that SOC stock would: i) increase with hedgerow
80 age (years since planting); ii) decrease with distance from hedgerow and iii) be greater
81 upslope of hedgerows than downslope.

82 **Materials and methods**

83 *Study area and sampling design*

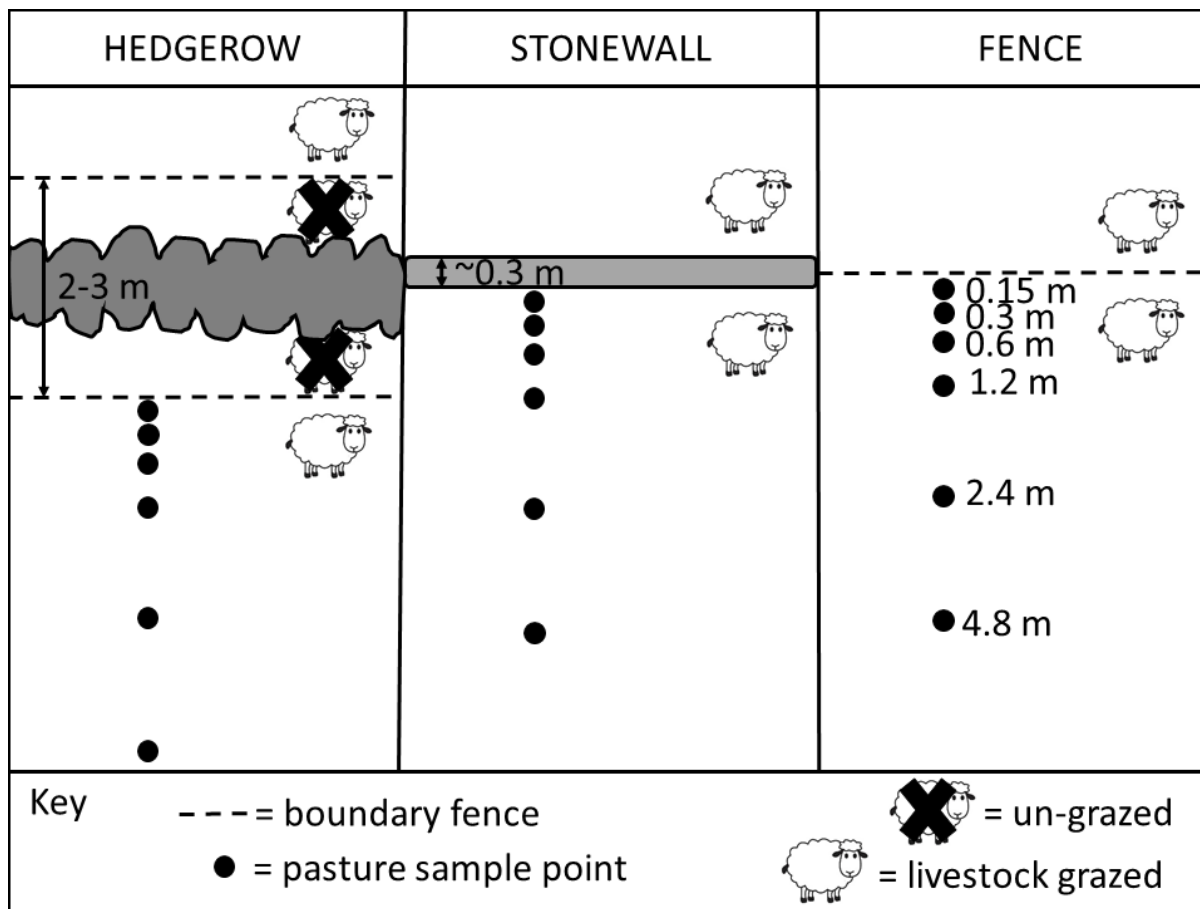
84 The study area (centred on 53.04° N, 3.71° W) encompassed ten tenant farms located within
85 the county of Conwy, Wales, UK close to the village of Ysbyty Ifan, all within the same River
86 Conwy catchment. All the farms were managed as mixed livestock, primarily Welsh mountain
87 sheep, with some beef cattle. All fields were permanent pasture with no arable crops grown.
88 Pasture type was predominantly grassland that had been semi-improved with a mixture of
89 productive grass species, in most cases mixed with clover (*Trifolium* spp., N-fixing), forbs and
90 mosses. Certain fields were cut each year for silage. Soils were classified as either stagnogleys
91 (slowly permeable, seasonally wet, acid loam or clay soil) or brown earth (freely draining,

92 slightly acid loam soil) (Hallett *et al.*, 2017). The study area was categorised as poor (grade 4
93 or 5) agricultural land (Agricultural Land Classification of England and Wales, 2018), with
94 elevation 175-335 m asl. Mean annual precipitation is approximately 2,500 mm, with mean
95 monthly maximum and minimum temperatures of 12 and 6 °C.

96 Before study-site selection, all field boundaries across the ten farms were verified by the
97 tenant farmer as being in the place indicated on a satellite-derived image. Each hedgerow
98 was marked on the image and its age since planting, reported by the farmer, recorded in
99 years. All other field boundaries were assumed to be a fence or stone wall. The study design
100 allowed more than one side of the same field (typically 3-5 straight-sided polygons) to be
101 considered as an independent boundary. For example, a single field could have two abiotic
102 boundaries (stone wall and fence) and two hedgerows of different ages, giving four
103 independent boundaries. In total, 82 hedgerows were recorded and stratified into each of
104 five age-since-planting categories (1-5, 6-10, 11-15, 16-20 or ≥ 40 years). Eight replicates of
105 each age-since-planting category were randomly selected for data collection. Abiotic
106 boundaries were also randomly selected and subject to site-visit verification to ensure that
107 eight stone walls and eight fences were sampled. This approach ensured that all ten farms,
108 typically each located in one landscape unit characterised by altitude, soil type and
109 management style, were represented in the sampling structure. All hedgerows, apart from
110 the ≥ 40 years category, were planted under the regulations of previous government agri-
111 environment schemes: double-fencing with 2-3 m total width to exclude livestock and
112 planting with a tree/shrub species mix of pre-dominantly *Crataegus monogyna*, *Prunus*
113 *spinosa* and *Corylus avellana*. Some of the selected ≥ 40 years hedgerows were, unavoidably,
114 single-fenced with a road on the opposite side to the pasture. The age of the stone walls was

115 uncertain although, from local knowledge, it is assumed they have been in position for > 100
116 years.

117 For each of the 56 selected boundaries, the exact position of a sampling transect (one per
118 boundary) was decided by ground conditions [specifically, avoidance of ditches, drains or
119 tracks, and avoidance of stone or rush (*Juncus* spp.) covered ground]. The position of each
120 sampling transect was located at least 5 m away from the end of each linear boundary, with
121 the exact position judged visually to be representative of the whole boundary. Each sampling
122 transect was set up perpendicular to the boundary line starting at the boundary edge (for
123 hedgerows this was defined as the fence line, ca. 1.5 m away from the centre of the hedge)
124 and ending 4.8 m into the adjacent grazed pasture (Figure 1). Sampling transects were only
125 set up in one direction for each boundary. As ground conditions were not assessed until each
126 farm visit, it was difficult to ensure an equal representation of slope orientations of transects
127 in advance. The following information was recorded for each transect: i) latitude, longitude
128 and elevation above sea level logged using a Garmin etrex 20x GPS; ii) slope orientation
129 relative to field boundary (downslope, flat or variable, upslope, across slope; from now on
130 referred to as “slope orientation”); iii) presence or absence of tree standards along the
131 boundary within 5 m of transect origin; iv) soil texture, classified from a sample of fresh soil
132 ~0.05 m deep using the hand texturing method (Natural England, 2008). For hedgerow
133 boundaries only, two additional variables were recorded: v) dominant species of woody plant
134 in the adjacent section of hedgerow (*C. monogyna*, *P. spinosa* or *C. avellana*); vi) management
135 of hedgerow [simplified into three categories a) regularly cut (typically annually with a tractor-
136 mounted flail); b) un-managed (no active management for 5 years, often with tall and thin
137 shoots and/or long horizontal shoots); c) too young for management to be appropriate]. All
138 field work was carried out October-December 2017.



140

141 **Figure 1** Pasture soil sampling transect schematic for biotic (hedgerow) and abiotic (stone wall
 142 and fence) boundaries.

143

144 *Soil samples*

145 Soil samples were taken at six distances along each transect (0.15, 0.3, 0.6, 1.2, 2.4 and 4.8 m
 146 from the origin), with the 4.8 m sample assumed to be indicative of the wider pasture away
 147 from the boundary line (Figure 1). Two soil samples were taken at each distance, one at ~0.05
 148 m depth for pH analysis using 10 g fresh mass of soil with 25 ml of distilled water in a 1:2.5
 149 dilution method (Rowell, 1994) to determine pH (Hanna Instruments pH meter 209, Leighton

150 Buzzard, England). The second was an intact core (0.15 m deep, 0.05 m diameter), for
151 assessment of BD, field soil moisture content, soil organic matter content, and SOC stock.
152 Where stones prevented a full-length soil core being taken, the soil sample volume was
153 adjusted. Stones and woody roots (coarse roots > 2 mm diameter) were removed from each
154 soil sample and their volume recorded. Fine roots were not removed. The soil sample was
155 then dried at 105 °C for 72 hours for measurement of field soil moisture content (%) and BD
156 (g cm^{-3}). Each dried sample was then ground (pestle and mortar) and sieved through 2 mm to
157 remove any fine roots or small stones (not previously removed). SOM (% of dry soil) was
158 measured from a sub-sample of ~10 g using the loss-on-ignition method (375 °C for 16 hours;
159 Ball, 1964). SOC concentration (g kg^{-1} of dry soil mass) was calculated using the conversion
160 factor of 0.55 of SOM mass (Emmett *et al.*, 2010) with SOC stock (kg C m^{-2}) of 0-0.15 m depth
161 re-calculated on an ESM basis, a layer of 0-1000 t ha^{-1} as in Lee *et al.* (2009). Most methods
162 of calculating SOC stock involve multiplying SOC concentration by BD to a fixed soil depth,
163 however this can lead to misleading results as soil compaction enhances SOC stock. The ESM
164 method used here allows SOC stock to be compared uncoupled from the influence of
165 livestock-compaction. Data for two hedgerows (one in the 6-10 and one in the 11-15 years'-
166 old category) were excluded due to high SOM content (>25%) indicating peat soil (Natural
167 England, 2008). Peat soils were excluded as they are associated with very low BD values, likely
168 to skew results. In addition to calculating SOM content in the standard way (% of dry soil mass
169 after stones removed), SOM content was also calculated with stones included (% of dry soil
170 with stones included) to provide an indication of the SOM content in the field conditions.

171

172 *Statistical analysis*

173 All statistical analyses were carried out in R v3.4.3 (R Core Team, 2018). Linear mixed effects
174 models were used to compare soil characteristics (at six distances 0.15, 0.3, 0.6, 1.2, 2.4 and
175 4.8 m along each transect) of the livestock-grazed pasture [SOC stock, SOM content (stones
176 removed), SOM content (stones included), BD, moisture content, stone content, woody root
177 content, pH] adjacent to three field boundary types: i) hedgerows (n = 38); ii) stone walls (n =
178 8) and iii) fences (n=8). Linear mixed-effects models were also used to predict SOC stock
179 adjacent to biotic and abiotic field boundaries from the sampled and measured variables. For
180 hedgerows the following potential explanatory variables were tested: i) age-since-planting
181 category of hedgerow; ii) absolute hedgerow age since planting in years; iii) perpendicular
182 distance from hedgerow boundary; iv) soil type as identified by soil maps (Hallett et al., 2017);
183 v) pasture routinely (once a year) cut for silage (*Boolean*); vi) slope orientation (simplified into
184 three categories: 'upslope', 'flat or variable' and 'downslope' with 'across slope' excluded due
185 to lack of replication); vii) management (regularly cut/not cut/too young); viii) dominant
186 hedgerow woody species; ix) standard trees present or absent (*Boolean*); x) soil pH; xi) soil
187 woody root content (% by volume of intact core, before stones removed); xii) soil moisture
188 (% of dry soil mass); xiii) soil BD. Field soil texture was not used as all soils were assessed as
189 broadly silty-clay loam. Predictive models of SOC stock, for fence and stone-wall boundaries,
190 tested the same explanatory variables but with i), ii) and vii) excluded.

191 Linear mixed-effects models, with 'transect' nested within 'farm' (indicative of one landscape
192 unit characterised by altitude, soil type and management style) identified as the true level of
193 replication [e.g. lme (SOC ~ BD + Moisture + Distance, random = ~1|Farm/Transect)] were
194 used. Best fit models were selected on the basis of lowest Akaike Information Criterion (AIC)

195 value (Zuur et al., 2009), with variables excluded if non-significant (one exception was made
196 where a non-significant variable decreased the AIC value relative to the model including only
197 significant variables). Likelihood-ratio-based pseudo-R-squared values were calculated for
198 each model (Grömping, 2006) with results presented using the ANOVA output of the mixed
199 effects models.

200 Linear mixed effects models were also used to compare soil characteristics [SOC stock, SOM
201 content (stones removed), BD, moisture content, stone content, woody root content, pH]
202 adjacent to and more distant from field boundaries. Adjacent samples were located at 0.15,
203 0.3, 0.6 and 1.2 m distance from the boundary edge (based on estimated zone of influence of
204 hedgerow on SOC stock as ~2 m perpendicular to the boundary edge, Figure 2c). Distant
205 samples were located at 2.4 and 4.8 m from the boundary edge and were assumed to be more
206 indicative of the wider pasture.

207 **Results**

208 *Boundary type and pasture soil characteristics*

209 There were no significant differences in SOC stock or SOM content with stones removed (0-
210 0.15 m depth) in adjacent pasture between hedges, stone walls and fences (Table 1).
211 However, when SOM content was adjusted to include stone content of field soil it was
212 significantly greater adjacent to fences (~11%) than stone walls (~10%). Woody root content
213 was greater adjacent to hedgerows than either abiotic field boundary.

214 *SOC stock adjacent to field boundaries*

215 In pasture soil adjacent to biotic (hedgerow) boundaries SOC stock was significantly: i)
216 positively associated with soil moisture content; ii) negatively associated with BD; iii)

217 negatively associated with distance from hedgerow; and iv) greater upslope than downslope
218 of the boundary (Figure 2). In pasture soil adjacent to abiotic boundaries SOC stock was
219 positively associated with soil moisture content for both walls and fences (Table 2) and
220 negatively associated with BD adjacent to fences.

221 In pasture soil adjacent to hedgerow boundaries, SOC stock was not associated with: i) age
222 since planting (category or years) ($P \geq 0.65$); ii) hedgerow management ($P \geq 0.32$); iii) mapped
223 soil type, stagnogleys versus brown earth ($P \geq 0.54$); or iv) the hedgerow's dominant woody
224 plant species (*C. monogyna*, *P. spinosa* or *C. avellana*) ($P \geq 0.46$).

225 *Boundary effects on soil characteristics*

226 For biotic (hedgerow) boundaries, SOM content, SOC stock, stone content and woody root
227 volume were significantly greater, but soil BD and pH significantly lower, adjacent to the
228 boundary than distant from it in the pasture (Table 3). Soil moisture content was not
229 significantly different between the two zones. In contrast, for abiotic boundaries (stone walls
230 and fences combined) stone content was significantly greater adjacent to the boundary than
231 distant from it, whereas all other variables did not differ significantly between the two zones
232 (Table 3).

233

234 **Table 1** Soil characteristics of livestock-grazed pasture, adjacent to biotic (hedgerow) and
 235 abiotic (stone wall and fence) field boundaries. Means and standard errors of the mean are
 236 presented alongside the significance of differences between boundary types.

237

Variable	Hedge (n = 38) ^d	Wall (n = 8) ^d	Fence (n = 8) ^d	Sig. ^c
SOC stock (kg C m ⁻²)	6.62 ± 0.09	7.24 ± 0.25	7.02 ± 0.28	<i>ns</i>
SOM content (% dry soil mass; stones removed)	12.0 ± 0.16	13.2 ± 0.45	12.8 ± 0.51	<i>ns</i>
SOM content (% dry soil mass; stones included)	10.7 ± 0.19 ^{ab}	10.2 ± 0.49 ^b	11.2 ± 0.59 ^a	***
Stone content (% by volume of core)	10.3 ± 1.19 ^b	21.4 ± 3.26 ^a	11.7 ± 2.55 ^b	***
BD (g cm ⁻³)	0.79 ± 0.01 ^{ab}	0.84 ± 0.02 ^a	0.77 ± 0.02 ^b	***
Moisture content (% of dry soil mass)	40.4 ± 0.39 ^{ab}	37.9 ± 0.80 ^b	44.6 ± 0.98 ^a	***
Woody root content (% by volume of core)	1.17 ± 0.18 ^b	0.17 ± 0.09 ^a	0.00 ± 0.00 ^a	**
pH	5.37 ± 0.03 ^b	5.20 ± 0.07 ^b	5.75 ± 0.05 ^a	***

238 ^{ab}Superscript letters (a, b) denote significant differences between groups

239 ^cSignificance: ** $P < 0.01$; *** $P < 0.001$; *ns* not significant

240 ^dSamples located at 0.15, 0.3, 0.6, 1.2, 2.4, 4.8 m from boundary edge

241

242

243 **Table 2** Best fit models of soil organic carbon stock (kg C m⁻²), expressed on an equivalent soil
 244 mass (ESM) basis, for livestock-grazed pasture adjacent to abiotic (fence and stone wall) field
 245 boundaries.

Explanatory variable	F-value	d.f. ^d	Significance ^c	Effect on response variable
ESM soil organic carbon stock model: Stone walls (AIC = 158.6, r ² = 0.59) ^{ab}				
Soil moisture	31.5	39	***	Positive association
ESM soil organic carbon stock: Fences (AIC = 150.1, r ² = 0.74) ^{ab}				
Soil moisture	27.1	38	***	Positive association
Bulk density	53.8	38	***	Negative association

246 ^aANOVA output of linear mixed effects models presented with explanatory variable information

247 ^bSamples located at 0.15, 0.3, 0.6, 1.2, 2.4, 4.8 m from boundary edge

248 ^cSignificance of differences are indicated by *** $P < 0.001$

249 ^dDegrees of freedom for ANOVA term

250

251 **Table 3** Soil of livestock-grazed pasture, adjacent to and more distant from field boundaries.
 252 Means and standard errors of the mean are presented alongside the significance of
 253 differences between boundary types. Biotic (hedgerow) and abiotic (fence and stone wall)
 254 boundaries were analysed separately.

Variable	Hedgerows (n = 38)			Fences and stone walls (n = 16)		
	Adjacent ^a	Distant ^b	Sig. ^{cde}	Adjacent ^a	Distant ^b	Sig. ^{cde}
SOM content (% dry soil mass; stones removed)	12.4 ± 0.20	11.3 ± 0.23	↑ ***	12.9 ± 0.46	13.0 ± 0.46	ns
SOC stock (kg C m ⁻²)	6.82 ± 0.11	6.21 ± 0.13	↑ ***	7.12 ± 0.25	7.15 ± 0.25	ns
BD (g cm ⁻³)	0.78 ± 0.01	0.81 ± 0.01	↓ **	0.81 ± 0.02	0.78 ± 0.02	ns
Moisture content (% of dry soil mass)	40.5 ± 0.78	40.3 ± 0.57	ns	41.0 ± 0.93	41.9 ± 1.09	ns
Stone content (% by volume of core)	12.5 ± 1.6	6.03 ± 1.50	↑ **	20.31 ± 2.81	8.88 ± 2.54	↑ **
Woody root content (% by volume of core)	1.55 ± 0.25	0.41 ± 0.17	↑ **	0.13 ± 0.00	0.06 ± 0.00	ns
pH	5.33 ± 0.03	5.43 ± 0.06	↓ *	5.48 ± 0.06	5.46 ± 0.09	ns

255 ^aAdjacent samples located at 0.15, 0.3, 0.6 and 1.2 m from boundary edge (based on zone of influence of
 256 hedgerow, figure 2)

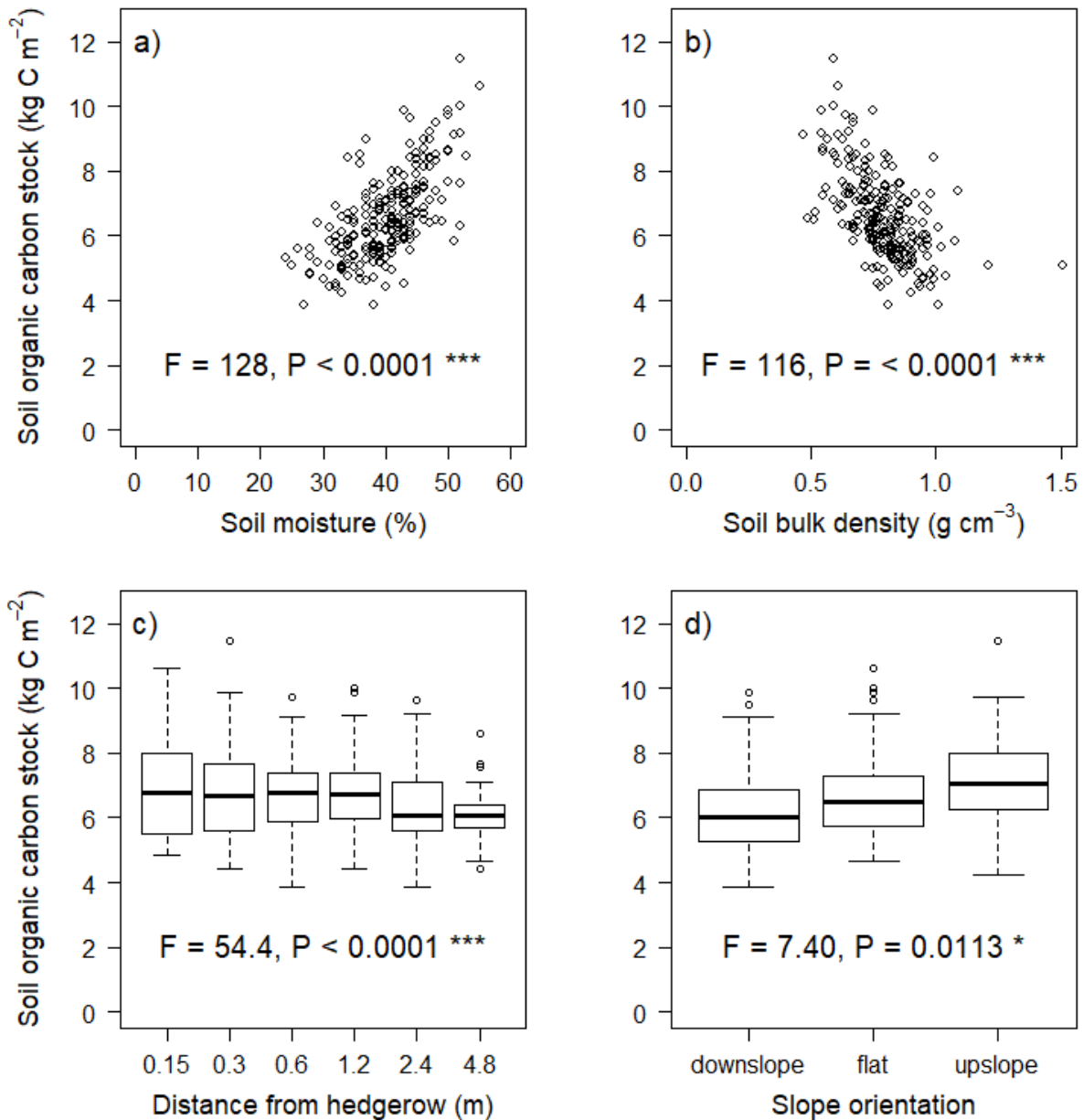
257 ^bDistant samples located at 2.4 and 4.8 m from boundary edge, assumed to be representative of the wider
 258 pasture away from the zone of influence of the boundary

259 ^cSignificance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns not significant)

260 ^d↑ indicates that the variable is significantly higher in the adjacent zone than the distant zone

261 ^e↓ indicates that the variable is significantly lower in the adjacent zone

262



263

264 **Figure 2** Best fit multi-variable model ($r^2 = 0.74$) of soil organic carbon stock (kg C m⁻²; top
 265 0.15 m of soil), expressed on an equivalent soil mass basis, for livestock-grazed pasture
 266 adjacent to biotic (hedgerow) field boundaries consisting of four significant explanatory
 267 variables: a) gravimetric soil moisture content; b) soil bulk density; c) distance from
 268 hedgerow, d) slope orientation (in relation to hedgerow). ANOVA output of linear mixed-
 269 effects models (selected on the basis of lowest AIC value) are presented with F statistics and
 270 P values (n = 228).

271 Discussion

272 *Hedgerow age*

273 We found no evidence of a relationship between SOC stock and either hedgerow age category
274 or exact time since planting (from 1 year to ≥ 40 years). One explanation for this is that the
275 majority of hedgerows identified by farmers as being 1-5 years since planting contained either
276 standard trees or other remnants of a previously-removed hedgerow. The management
277 practice (incentivised by agri-environment payment schemes) had been for farmers to replant
278 hedgerows in the position where hedgerows had previously existed (where the soil may have
279 contained a legacy of past hedgerow effects). Another legacy of the previous hedgerows was
280 high abundance of bracken (*Pteridium aquilinum*) in the land enclosed by the boundary
281 fences of recently (re-)planted hedgerows. Bracken is a perennial fern with an extensively
282 branched rhizome system and is associated with higher levels of SOM and SOC content than
283 adjacent grassland (Marrs *et al.*, 2007). Therefore, analysis of the effects of hedgerow age on
284 adjacent soil needs to take account of the longer-term land use history. One manifestation of
285 this is that adjacent soil may be affected not only by the woody plants forming the hedgerow
286 itself, but also the other vegetation that develops in the hedgerow zone, thus forming a more
287 integrated 'biotic' linear habitat feature.

288 *Hedgerow zone of influence*

289 In this study SOC stock of adjacent pasture was broadly comparable (~ 7 kg C m⁻²) between
290 biotic and abiotic field boundaries. However, a much greater effect of proximity to boundary
291 was shown for hedgerows than for abiotic boundaries. SOC stock was greatest close to
292 hedgerow boundaries, decreasing with perpendicular distance from the hedgerow, in line
293 with findings from other grassland and arable systems (Follain *et al.*, 2007; D'Acunto *et al.*,

294 2014). SOC stock reduced markedly between 1.2 and 2.4 m from the fenced hedgerow
295 boundary (equivalent to ca. 2.2 and 3.4 m from the base of the hedgerow itself, indicating a
296 slightly narrower range of influence of the hedgerow on SOC storage dynamics than the ~4 m
297 previously identified (D'Acunto *et al.*, 2014; Van Vooren *et al.*, 2017). In contrast, there was
298 no evidence of greater SOC stock adjacent to abiotic boundaries than in more distant pasture.

299 In this study soil BD was lower adjacent to fences than stone walls, with hedgerows
300 intermediate between the two. This can be attributed to two contrasting mechanisms. The
301 increase in organic matter inputs associated with hedgerows may reduce soil BD, by
302 increasing soil porosity and aggregate structures, or diluting the mineral soil component
303 (Holland, 2004). However, where landscape features including hedgerows or walls (but not
304 fences) provide shelter and encourage livestock to congregate during adverse weather
305 conditions this is expected to increase soil BD (Abdalla *et al.*, 2018), albeit asymmetrically with
306 greater compaction on the leeward side.

307 *Hedgerows and topography*

308 The effect of contour hedgerows on reducing soil erosion is well established, leading to
309 accumulation of eroded soil upslope of hedgerows, whereas the land immediately downslope
310 of hedgerows is often a zone of net erosive soil loss (Follain *et al.*, 2007). As this eroded soil
311 is generally topsoil it can have a high SOC stock, and this may enhance the SOC content of soil
312 left *in situ*, measured at 0-0.15 m depth in the present study, relative to soil downslope of the
313 hedgerow. It is also possible that the roots of hedgerow woody plants grow preferentially
314 upslope (Caubel-Forget *et al.*, 2001) to increase plant stability, access soil enriched by run-off
315 and sediment, and avoid water-logged or compacted soil (Jackson *et al.*, 2000), which would

316 lead to higher rates of fine-root turnover and associated SOC storage upslope than downslope
317 of contour-planted hedgerows.

318 *Relationship between SOC and multiple variables*

319 Two environmental variables, soil moisture and soil BD, were clearly associated with SOC
320 stock for pasture adjacent to both biotic and abiotic boundaries, in combination explaining
321 more than half of the variation in SOC stock, with these relationships likely to extend across
322 the whole pasture. A positive association between SOC and soil moisture is well recognised,
323 particularly in clay-rich grasslands (Jobbagy & Jackson, 2000) and a negative relationship
324 between SOC content (or SOC stock in this study as expressed on an equivalent soil mass
325 basis) and BD is well established and recently confirmed in a silvopastoral setting (Upson *et*
326 *al.*, 2016). In our study, three quarters of the variation in SOC stock in pasture adjacent to
327 hedgerows was explained by a model that combined four variables [distance from hedgerow,
328 slope orientation (relative to hedgerow), soil moisture and BD], with no evidence of a
329 relationship between SOC stock and other measured variables (i.e. hedgerow age,
330 management, dominant woody plant species or mapped soil type). One possible explanation,
331 for the quarter of variation in SOC stock unaccounted for, is the effect of the functional
332 composition of hedgerow woody plants and associated herbaceous plants (especially *P.*
333 *aquilinum*), and pasture grasses and forbs, not measured directly in this study.

334 **Conclusions**

335 This study aimed to quantify the influence of hedgerows on SOC storage in adjacent pasture,
336 and is of particular relevance to upland farming systems in Wales. SOC stock in adjacent
337 pasture was comparable ($\sim 7 \text{ kg C m}^{-2}$) between hedgerow and abiotic field boundaries. Our
338 first hypothesis, that SOC stock in pasture adjacent to hedgerows would increase with age

339 (years since planting) was rejected, largely due to the effect of management legacy on
340 boundary location. Our second hypothesis, that SOC stock would decrease with distance from
341 hedgerow was accepted with pasture SOC stock (to 0.15 m depth) 15% greater within 2 m of
342 the hedgerow boundary than further into the pasture, with no such effect for abiotic
343 boundaries. Our third hypothesis, that SOC stock would be greater upslope of hedgerows than
344 downslope was also accepted. However, this multi-farm study demonstrated that the
345 influence of hedgerows on the ecosystem function of SOC storage in livestock-grazed pasture
346 is still small in comparison with the dominant influence of BD and soil moisture.

347 **Acknowledgements**

348 All authors acknowledge the financial support provided by the Welsh Government and Higher
349 Education Funding Council for Wales through the Sêr Cymru National Research Network for
350 Low Carbon, Energy and Environment. Thanks are also due to the National Trust and the
351 Fferm Ifan group that allowed access to their land.

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