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

Hilary Ford*, John R. Healey, Bid Webb, Tim F. Pagella, Andrew. R. Smith

School of Natural Sciences, Bangor University, Bangor, LL57 2DG, UK.

*Corresponding author. *Email address*: hilary.ford@bangor.ac.uk (H. Ford).

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Abstract

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

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

Introduction

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

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

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

Detailed study of spatial variation in SOC (content and stock) has shown it to be greater close to hedgerows in both grassland and arable systems (Holden *et al*., 2019), the effect decreasing with distance from the hedge boundary, for up to 4 m into neighbouring fields (Follain *et al*., 2007; D'Acunto *et al*., 2014; Van Vooren *et al*., 2017). Hedgerow woody plant root architecture and depth can influence SOC storage, with deeper-rooted species associated with greater SOC (Crossland, 2015). Position relative to hedgerows is also important, with SOC greater upslope of contour-planted hedgerows, where the hedgerow acts as a physical barrier reducing soil erosion and increasing A-horizon depth (Follain *et al*., 2007). Regular hedgerow management (via cutting with a tractor-mounted flail) increases the amount of surface litter adjacent to the hedgerow (Axe et al., 2017) potentially increasing inputs to soil. Regular cutting also decreases the shoot-to-root ratio, which can influence fine root turnover and either increase (Peter & Lehmann, 2000) or decrease (Crossland, 2015) SOC storage. Even though hedgerow age (years since planting) is highly likely to influence SOC dynamics, due to change in the quality and rate of C inputs via root and hyphal turnover, exudation, and leaf litter over time as hedgerow plants grow, to our knowledge this aspect has not been studied previously.

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

Materials and methods

Study area and sampling design

The study area (centred on 53.04° N, 3.71° W) encompassed ten tenant farms located within the county of Conwy, Wales, UK close to the village of Ysbyty Ifan, all within the same River Conwy catchment. All the farms were managed as mixed livestock, primarily Welsh mountain sheep, with some beef cattle. All fields were permanent pasture with no arable crops grown. Pasture type was predominantly grassland that had been semi-improved with a mixture of productive grass species, in most cases mixed with clover (*Trifolium* spp., N-fixing), forbs and mosses. Certain fields were cut each year for silage. Soils were classified as either stagnogleys (slowly permeable, seasonally wet, acid loam or clay soil) or brown earth (freely draining, slightly acid loam soil) (Hallett *et al*., 2017). The study area was categorised as poor (grade 4 or 5) agricultural land (Agricultural Land Classification of England and Wales, 2018), with elevation 175-335 m asl. Mean annual precipitation is approximately 2,500 mm, with mean monthly maximum and minimum temperatures of 12 and 6 °C.

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

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

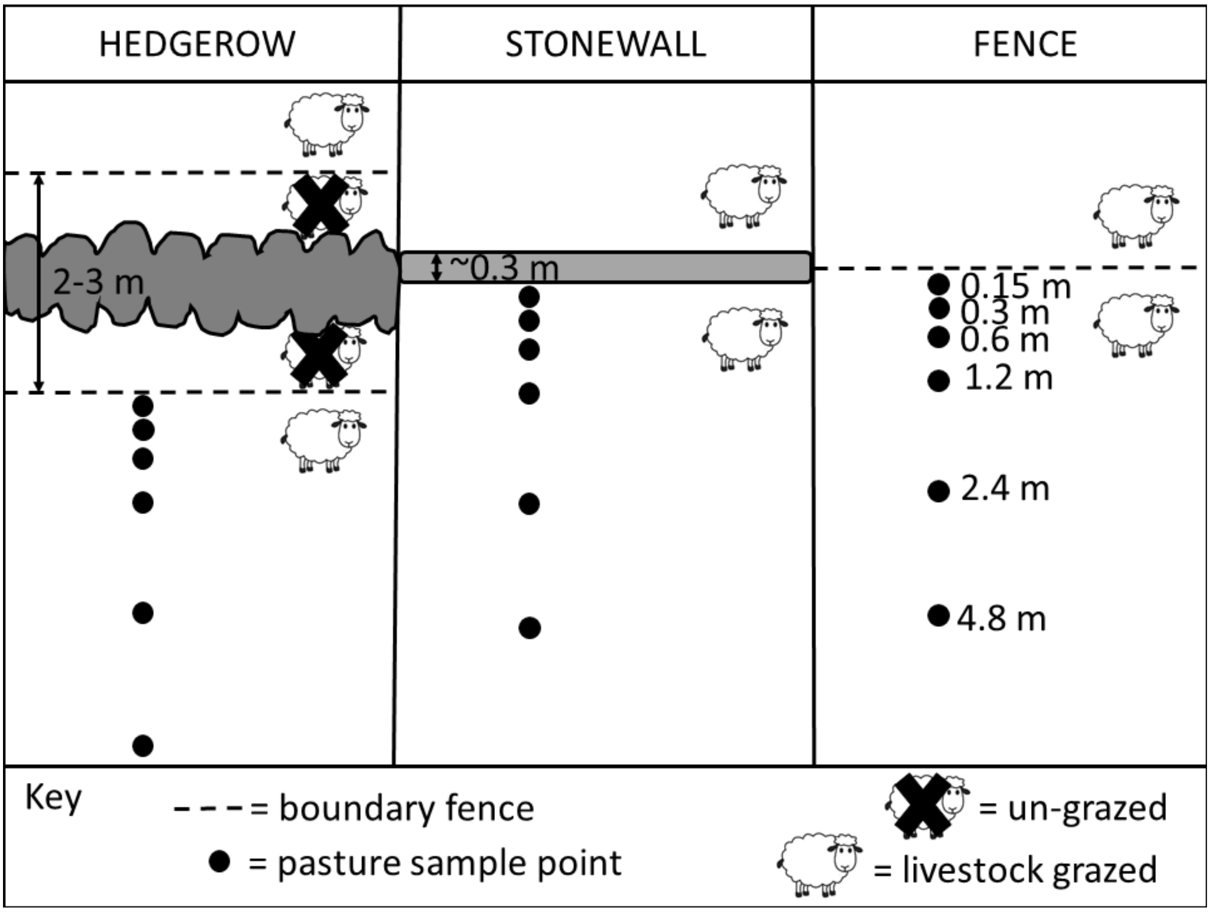

Figure 1 Pasture soil sampling transect schematic for biotic (hedgerow) and abiotic (stone wall and fence) boundaries.

Soil samples

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

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

Statistical analysis

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

Linear mixed-effects models, with ‘transect’ nested within ‘farm’ (indicative of one landscape unit characterised by altitude, soil type and management style) identified as the true level of replication [e.g. lme (SOC ~ BD + Moisture + Distance, random = ~1|Farm/Transect)] were used. Best fit models were selected on the basis of lowest Akaike Information Criterion (AIC) value (Zuur et al., 2009), with variables excluded if non-significant (one exception was made where a non-significant variable decreased the AIC value relative to the model including only significant variables). Likelihood-ratio-based pseudo-R-squared values were calculated for each model (Grömping, 2006) with results presented using the ANOVA output of the mixed effects models.

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

Results

Boundary type and pasture soil characteristics

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

SOC stock adjacent to field boundaries

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

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

Boundary effects on soil characteristics

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

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

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	*ns*
SOM content (% dry soil mass; stones removed)	12.0 ± 0.16	13.2 ± 0.45	12.8 ± 0.51	*ns*
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}	***

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

[c] Significance: ** $P < 0.01$; *** $P < 0.001$; *ns* not significant

[d] Samples located at 0.15, 0.3, 0.6, 1.2, 2.4, 4.8 m from boundary edge

Table 2 Best fit models of soil organic carbon stock (kg C m^{-2}), expressed on an equivalent soil mass (ESM) basis, for livestock-grazed pasture adjacent to abiotic (fence and stone wall) field 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

[a] ANOVA output of linear mixed effects models presented with explanatory variable information

[b] Samples located at 0.15, 0.3, 0.6, 1.2, 2.4, 4.8 m from boundary edge

[c] Significance of differences are indicated by *** $P < 0.001$

[d] Degrees of freedom for ANOVA term

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

Variable	Hedgerows (n = 38)			Fences and stone walls (n = 16)		
Proximity to boundary	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*

[a] Adjacent samples located at 0.15, 0.3, 0.6 and 1.2 m from boundary edge (based on zone of influence of hedgerow, figure 2)

[b] Distant samples located at 2.4 and 4.8 m from boundary edge, assumed to be representative of the wider pasture away from the zone of influence of the boundary

[c] Significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; *ns* not significant)

[d] ↑ indicates that the variable is significantly higher in the adjacent zone than the distant zone

[e] ↓ indicates that the variable is significantly lower in the adjacent zone

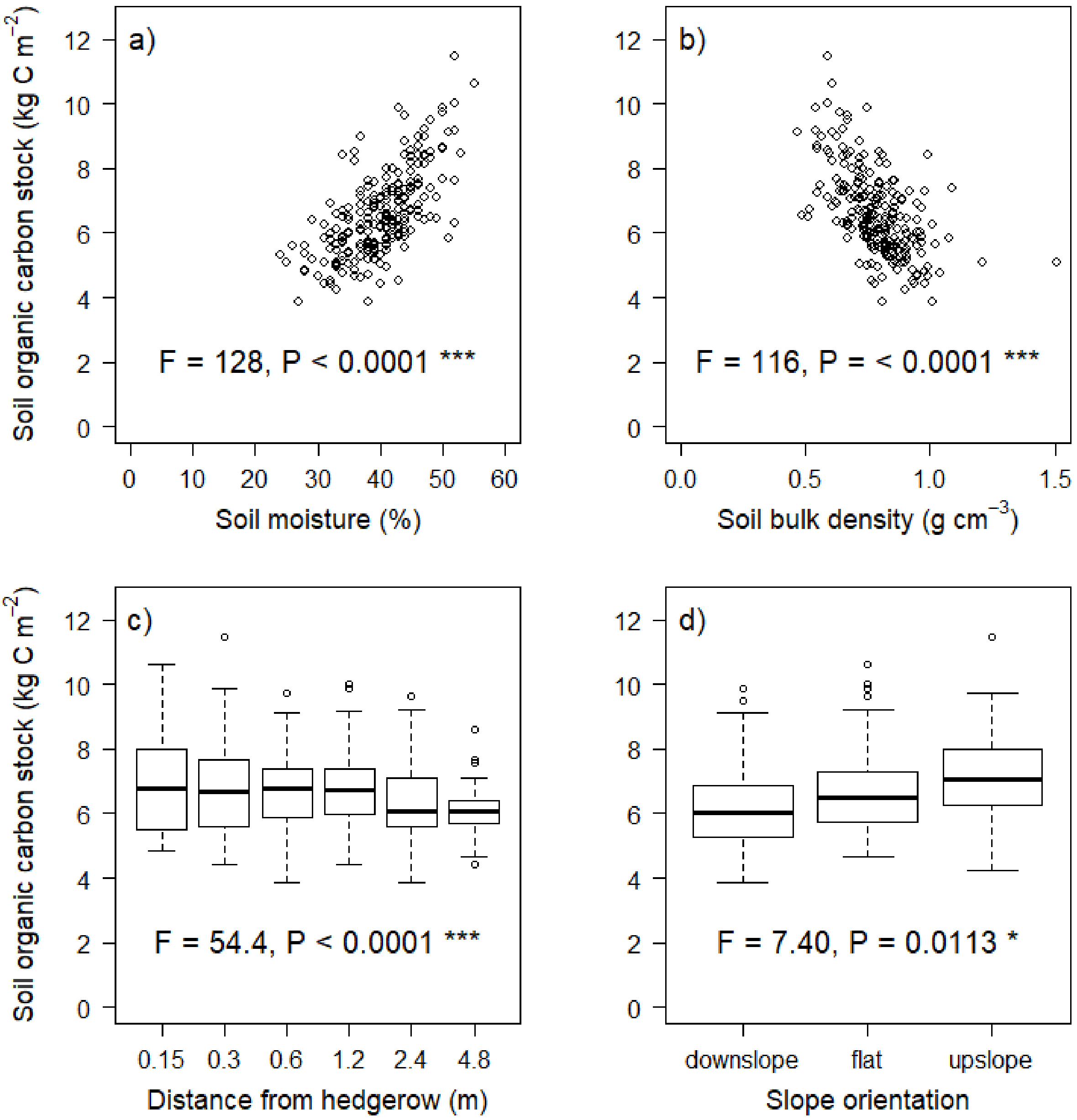

Figure 2 Best fit multi-variable model ($r^2 = 0.74$) of soil organic carbon stock (kg C m^{-2}; top 0.15 m of soil), expressed on an equivalent soil mass basis, for livestock-grazed pasture adjacent to biotic (hedgerow) field boundaries consisting of four significant explanatory variables: a) gravimetric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

Discussion

Hedgerow age

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

Hedgerow zone of influence

In this study SOC stock of adjacent pasture was broadly comparable (~7 kg C m^{-2}) between biotic and abiotic field boundaries. However, a much greater effect of proximity to boundary was shown for hedgerows than for abiotic boundaries. SOC stock was greatest close to hedgerow boundaries, decreasing with perpendicular distance from the hedgerow, in line with findings from other grassland and arable systems (Follain *et al*., 2007; D’Acunto *et al*., 2014). SOC stock reduced markedly between 1.2 and 2.4 m from the fenced hedgerow boundary (equivalent to ca. 2.2 and 3.4 m from the base of the hedgerow itself, indicating a slightly narrower range of influence of the hedgerow on SOC storage dynamics than the ~4 m previously identified (D'Acunto *et al*., 2014; Van Vooren *et al*., 2017). In contrast, there was no evidence of greater SOC stock adjacent to abiotic boundaries than in more distant pasture.

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

Hedgerows and topography

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

Relationship between SOC and multiple variables

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

Conclusions

This study aimed to quantify the influence of hedgerows on SOC storage in adjacent pasture, and is of particular relevance to upland farming systems in Wales. SOC stock in adjacent pasture was comparable (~7 kg C m^{-2}) between hedgerow and abiotic field boundaries. Our first hypothesis, that SOC stock in pasture adjacent to hedgerows would increase with age (years since planting) was rejected, largely due to the effect of management legacy on boundary location. Our second hypothesis, that SOC stock would decrease with distance from hedgerow was accepted with pasture SOC stock (to 0.15 m depth) 15% greater within 2 m of the hedgerow boundary than further into the pasture, with no such effect for abiotic boundaries. Our third hypothesis, that SOC stock would be greater upslope of hedgerows than downslope was also accepted. However, this multi-farm study demonstrated that the influence of hedgerows on the ecosystem function of SOC storage in livestock-grazed pasture is still small in comparison with the dominant influence of BD and soil moisture.

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