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Soil organic matter stabilization and carbon-cycling enzyme activity are affected by land management

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Abstract. Increasing carbon (C) storage in soil is a key aspect of climate change mitigation strategies and requires an understanding of the impacts of land management on soil C cycling. The primary aim of this study is to investigate how land management impacts key soil organic matter stabilization and cycling processes affecting soil C storage. Soil sampling was undertaken across seven transects crossing the boundary between agriculture and forestry. The transects covered 3 pasture (AP) and 4 arable (AA) fields combined with 3 young secondary woodlands (50-60 years old - WY) and 4 mature/ancient semi-natural woodlands (110 to >400 years old - WM). Physical fractionation of soil organic matter pools was performed, together with pH, carbon and nitrogen content, as well as activity of four enzymes associated with C transformation in the soil. Woodland soils were associated with significantly higher content of light fraction C and greater enzyme activity in comparison to agricultural soils. Enzyme activity and soil organic C decreased with soil depth regardless of land-use type. We did not, however, observe any effect of the distance from the land use boundary on either enzyme activity and soil C pools. Our results indicate that analysis of soil organic matter (SOM) fractions can act as an indicator of decomposition rates of SOM in forest and agricultural ecosystems.
Keywords: enzyme activity, soil carbon accumulation, soil organic matter fraction, forest, agriculture

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Introduction

Recent evidence clearly shows that, in order to avoid severe global warming, humans must not only limit emissions but also develop strategies for the removal of CO_2 from the atmosphere (Mathieu et al. 2015, Balesdent et al. 2018). One promising strategy is to increase storage of carbon in soils and in plant biomass of managed ecosystems (Lal 2002, 2004a, 2004b, Zomet et al. 2017). Overall, around twice as much carbon (C) is stored in soils than in the atmosphere, and the global soil C stock has been estimated at 2500 Pg C (Lal 2010) – although this may underestimate deeper soil C pools (Harper & Tibbett 2013). Most of soil C is present in the plant rooting zone, commonly referred to as the topsoil, to around 40 cm depth (Buchholz et al. 2014). This soil layer contains C-based compounds with the highest turnover, deeper horizons are often considered to contain more stable C not responsive to management or environmental change. In a review of available soils data, Harrison et al. (2011) showed that the top 20 cm of soil can contain from one to three quarters of the total soil organic C. Since land use change predominantly impacts the topsoil layer, it could act as the most important factor controlling SOC stabilization (Wiesmeier et al. 2019).

A majority of soils in the UK have developed under forest cover, from the period of post-glaciation forest expansion until the start of forest clearance (Kirby & Watkins 2015). Currently, 74% of total UK forest carbon is located in the soil down to 1m depth. Carbon storage in forest soils differ depending on soil depth, type of soil and forest characteristics with 30-70% of the carbon stock in the profile accumulated at the surface soil horizons (0-20 cm) (Vanguelova et al. 2013). The accumulation of C compounds in topsoils results from the natural stratification of organic matter deposition and activity of soil dwelling organisms (Phillips & Marion 2004). Agricultural soils, on the other hand, have undergone significant changes due to the removal of the dominant form of vegetation and repeated disturbance of topsoil strata (Stockfisch et al. 1999). One of the consequences of converting forest soils to agricultural use is loss of C in the form of CO_2 emission (Van der Werf et al. 2009). In fact, UK forest soils have significantly higher C stocks than similar soils in agricultural systems, particularly those in intensively managed arable systems (Vanguelova et al. 2013). It is clear that soil organic matter (SOM) content depends on plant biomass production and on input of dead organic matter to provide energy and nutrition to soil organisms (Hairiah et al. 2006). The abundance and composition of microorganisms depends on litter and root inputs from trees (Muys et al. 1992, Scheu et al. 2003, Ushio et al. 2008, Ladygina & Hedlund 2010, Błońska et al. 2016, Lladó et al. 2017). The chemical composition of organic matter generated by the tree component differs from crop residues, and this difference impacts soil physical, chemical and biological quality (Baldrian & Šnajdr 2011, Kotroczó et al. 2014).

Most studies reporting on soil C sequestration focus on measurements of total soil organic carbon (SOC), but the quality of SOM can also significantly influence the lifetime of carbon storage in the soil (Wang et al. 2009, Bellamy et al. 2005, Lal 2005). Carbon sequestration must be considered as a process of C stabilization and not just a simple accumulation of organic matter in the soil. The binding of organic matter by oxides and clay minerals leads to stabilization of SOM and inhibits its decomposition (Jandl et al. 2007). SOM transformation results from the activity of soil microorganisms and their enzymes (Błońska et

al. 2018, Pająk et al. 2018). Enzymes represent the fundamental apparatus that enables microorganisms to decompose organic matter, and thus may inform on soil C sequestration potential and its nutrient cycling capacity (Allison et al. 2007). Extracellular enzyme activity reflects the biogeochemical cycles of basic nutrients in soil (Adamczyk et al. 2014). Several common hydrolytic enzymes contribute to the C cycle (β-D-cellobiosidase, β-Glucosidase, β-Xylosidase) and N cycle (N-acetyl- β-Glucominidase), their main functions are the degradation of cellulose, hemicelluloses and chitin (Parvin et al. 2018). Substrate availability and nutrient limitation are two strong drivers of enzyme activities in soil and consequently of C, N and P cycles (Stock et al. 2019). Since microbial growth in soil is typically limited by energy, high enzyme activity generally occurs in soil with intensive C input (Wei et al. 2019). The primary objectives of this study were to investigate effects of land use on SOM stabilization processes in the soil along with C transformation enzyme activities as key mechanisms affecting soil C storage. We made use of existing and well-established boundaries between woodlands and agricultural fields to assess long-term effects of land management on soil enzymatic activity.

In this study, we were interested in the strength of the spill-over effect of SOM stabilisation from undisturbed forest soil to managed agricultural soil. We hypothesised that: (i) the C in agricultural soil has smaller proportion of stable C than forest soil, (ii) C cycling enzyme activities differed between agricultural and forest soils and (iii) land management effects on biogeochemical processes will change the vertical stratification of soil carbon processes and enzyme activity.

Materials and methods

Study sites

All sites sampled in this study are part of the Woodland Creation and Ecological Networks project (WrEN; www.wren-project.com), a "natural" chronosequence experiment, which provides a unique opportunity to study soil development and changes over large spatial and temporal scales (Watts et al., 2016). Seven transects were sampled, consisting of 3 pasture (AP) and 4 arable (AA) plots combined with 3 young secondary woodlands (50-60 years old - WY) and 4 mature/ancient semi-natural woodlands (110 to >400 years old - WM). All sites were located within the English Midlands (Fig. 1); an area characterised by surface water gleysols as the dominant soil type (WRB 2014). The texture of this soil type is described as silt loam, with 7% sand, 80% silt and 13% clay. This soil type is known to have very little spatial variability of soil carbon content (Vanguelova et al. 2013, Vanguelova et al. 2016). To further reduce site variability, woodland sites were of similar size (a range of 2 to 5 ha) (Ashwood et al. 2019). All woodland sites were unmanaged broadleaf woodlands, with a canopy dominated by *Quercus robur*, *Fraxinus excelsior*, *Betula pendula*, *Prunus avium*, *Acer pseudoplatanus*, *Salix* sp. and *Populus* sp. The wider Midlands area receives approx. 1460 h sunshine and 741 mm rainfall per annum, and a mean daily maximum temperature of 14.1 °C (Met Office 2018).

Within each site, a transect was marked out between the centre of the woodland and an adjacent agricultural field. Four sampling points were located at approx. 15 metre intervals on either side of the agro-forest boundary, as shown in Figure 1. At each sampling point, three soil samples were taken from the following depths: organic horizon (only in the forest), minerals soils of 0-20 cm and 20-40 cm depth. Altogether, 140 soil samples were taken for the purpose of this analysis. See Watts et al. (2016) and Ashwood et al. (2019) for more information about WrEN sites and the wider soil sampling campaign.

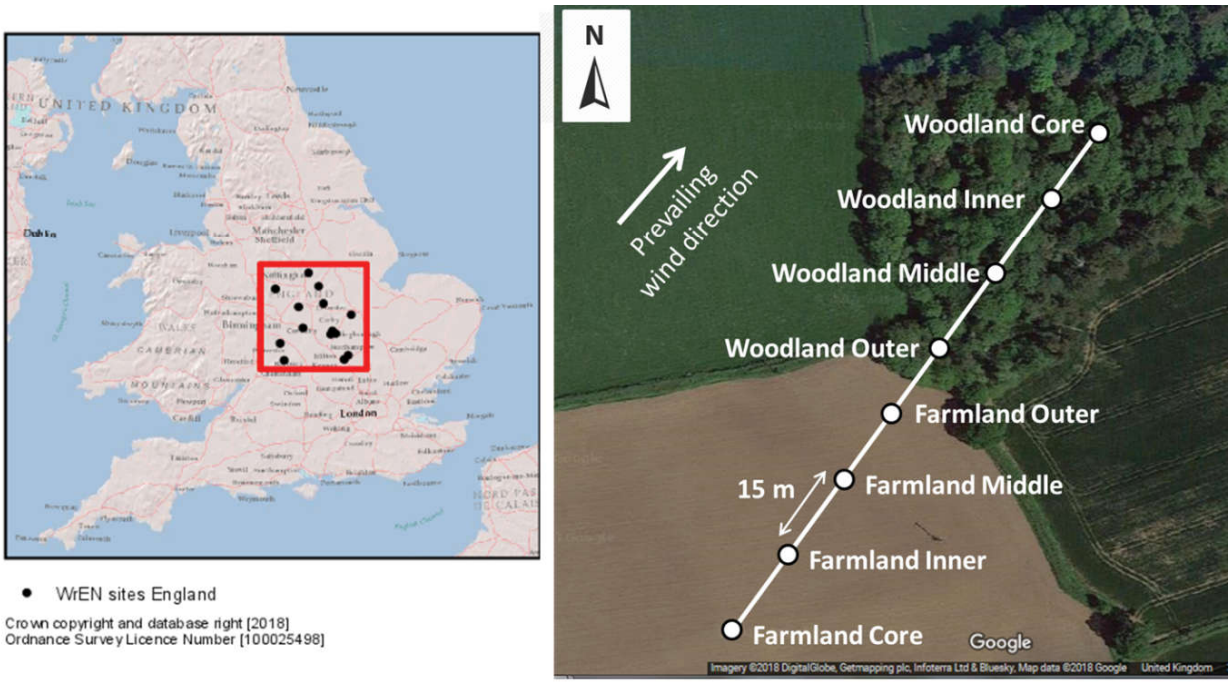

Figure 1 Map showing the locations of WrEN sites in England, and the layout of a transect between the agricultural and forest parts of the site. The location and labelling of sampling locations is also shown.

Soil description

Soil samples obtained in the field were dried and sieved through 2.0-mm mesh and analyzed for pH, C and N content by Forest Research laboratory services at Alice Holt Lodge, Farnham, UK. Total C and N concentrations were determined by a C-N Elemental Analyzer (Carlo Erba (THERMO), FLASH EA 1112 Series). Soil pH was measured in water suspension (soil: water ratio 1:2.5). Particle-size distribution was determined using laser diffraction (Analysette 22, Fritsch, Idar-Oberstein, Germany).

Physical separation of SOM fractions

Physical separation of soil organic matter fractions was performed using the method described by Sohi et al. (2001). A 15 g of soil was centrifuged with 90 ml of NaI (1.7 g cm^{-3}). The free light fraction (fLF) was separated. The remaining soil pellet was mixed with fresh 90 mL of NaI and subjected to sonication (60 watts for 200 s) to destroy aggregates. After repeat centrifugation, the occluded light fraction (oLF) was collected. The remaining fraction was constitued of mineral associated fraction (MAF) of SOM. After drying (40°C for 2 days), C fractions were weighed and analysed for $C_{fLF,}$ C_{oLF}, C_{MAF} and $N_{fLF,}$ N_{oLF}, N_{MAF}, respectively using an LECO CNS True Mac Analyzer (Leco, St. Joseph, MI, USA).

Enzyme activities

Carbon transformation enzyme activities were determined using fluorogenically labeled substrates (Pritsch et al. 2004, Sanaullah et al. 2016). Four fluorogenic enzyme substrates based on 4-methylumbelliferone (MUB) were used: MUB-β-D-cellobioside for β-D-cellobiosidase (CB), MUB-β-D-xylopyranoside for xylanase (XYL), MUB-N-acetyl-β-D-glucosaminide for N-acetyl-β-D-glucosaminidase (NAG), MUB-β-Dglucopyranoside for β-glucosidase (BG) (Turner, 2010). We mixed 2.75 g of soil with 92 ml universal buffer (pH 6.0).

Soil suspension was then pipetted into wells on a microwell plate (800 µl), containing the substrate (200 µl) and modified universal buffer (pH 6.5). Fluorescence was measured by incubations of soil suspension (for 1.5 h at 35 °C) in 96-well microplates (Puregrade Germany) and the fluorescence determined immediately on a multidetection plate reader (SpetroMax), with excitation at 355 nm and emission at 460 nm wavelength. Enzyme activity was expressed in nmol MUB in 1 gram of dry soil in 1 hours (nmol MUB $\cdot g^{-1}$ d.s. h^{-1}).

Statistical analysis

General linear models (GLMs) were used to investigate the effect of the type of land management, transect point and soil depth on soil properties and enzyme activity. Edge effects were evaluated by fitting linear regressions to separate agricultural and forest soil transect data, the slopes of fitted lines were tested for difference from 0.0 by extra sum-of-squares *F* test to indicate significance of observed trends. Principal component analysis (PCA) was used to evaluate the relationships between soil properties (enzyme activity, carbon of soil organic matter fractions) and land-use type. Pearson correlation coefficients between soil properties were also calculated. Properties of different land management types were compared using a parametric Honestly Significant Difference (HSD) test. Differences with alpha at $p < 0.05$ were considered statistically significant. All analyses were performed with Statistica 12 software (StatSoft 2012).

Results

The key chemical properties of study soils are given in Table S1, Supporting Information. Organic horizons were present only in the forested part of each site, and those in young woodlands were characterized by higher but more variable C content in the light fraction (95.1 g $\cdot kg^{-1}$) than those in mature woodlands (42.8 g $\cdot kg^{-1}$, Table S2, Supp. Info.). Mineral topsoil (0-20cm) of both woodland age types contained significantly more C_{fLF} compared to arable soils. Deeper soil (20-40 cm) in the WM and WY plots also had a significantly higher C_{fLF} content compared to the soils of both AP and AA. The only significant trend along the transects was the significant decrease of C_{oLf}, from the forest boundary towards the core of the forest ($p = 0.025$, Fig. 2). The highest content of occluded fraction C was found in the mineral topsoil (0-20 cm) of young woodlands, the lowest in mature woodlands and arable agriculture soils. In deeper soil (20-40 cm), there were no significant differences in the C_{oLF} content in any land use types. Small amounts of C_{MAF} were found in the organic horizons of young and mature woodland soils. In the mineral soil (0-20 and 20-40 cm), C_{MAF} content was similar across all land uses and soil depths. In the transects, there was a trend to reduced C_{MAF} content in the organic horizons of both woodland types towards the field-forest boundary (Table S2, Supp. Info.).

Organic horizons of young woodlands were characterized by a higher content of N_{fLF}. Both shallow (0-20 cm) and deeper (20-40cm) mineral soil in either woodland type contained significantly more N_{fLF} compared to arable soils (Table S3, Supp. Info.). Mineral soil N_{fLF} content along the transects showed no trend towards the field-forest boundary. The highest N_{oLF} content was recorded in the organic horizons of young and mature woodlands. In the mineral soil (0-20 cm) of young woodland and pasture plots, there were more N_{oLF} recorded than in arable soils. Low N_{MAF} content was found both in organic horizons and mineral soils of all investigated plots (Table S3, Supp. Info.).

The highest CB activity was recorded in organic horizons in forest soils (Fig. 3, Table S4, Supp. Info.). There was no statistically significant difference in CB activity of soils due to land use or as a function of distance from the

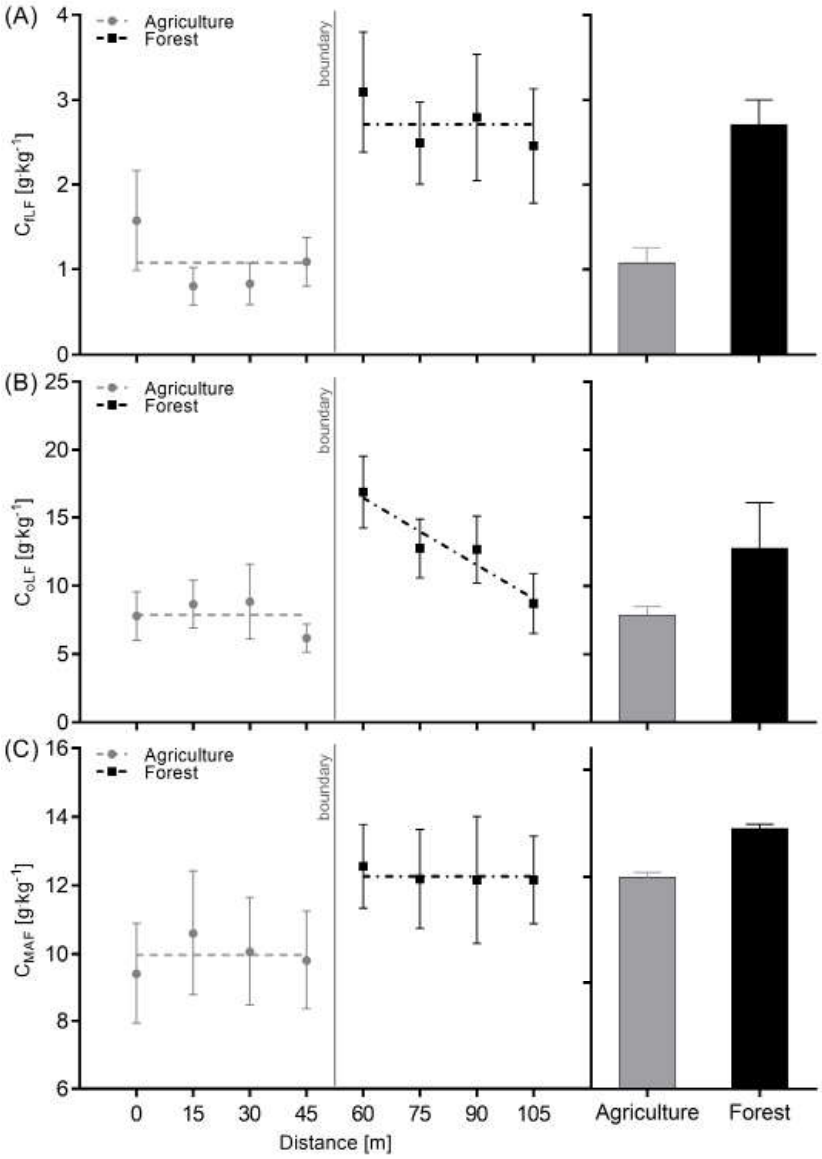

Figure 2 Carbon transformation enzyme activity in mineral soil 0-40 cm depth along a transect crossing a boundary between agricultural and forest land use. CB - β-D-cellobiosidase activity, XYL - xylanase activity, NAG - N-acetyl-β-D-glucosaminidase activity, BG - β-glucosidase activity. Symbols represent mean value for individual transect points from 7 separate sites in England, columns are overall mean, all error bars ± SEM. Dotted lines are linear fits, no slopes were different from zero (P = 0.14-0.96).

boundary. The highest BG activity was recorded in organic horizons of woodland soils (WM and WY, 138.92 nmol MUB · g^{-1} d.s. h^{-1} and 154.25 nmol MUB · g^{-1} d.s. h^{-1} respectively). In mineral topsoil (0-20 cm), significantly higher BG activity was found in woodland soils in WM land type compared to arable soils (AA). The organic horizons of the studied soils were characterized by the highest NAG activity. In mineral topsoil, at the depth of 0-20 cm, the highest NAG activity was recorded in the soils of young woodlands (mean 41.51 nmol MUB · g^{-1} d.s. h^{-1}), the lowest in the soils of the arable land (mean 9.19 nmol MUB · g^{-1} d.s. h^{-1}). In deeper mineral soil (20-40 cm), there were no differences in NAG activity. Significantly higher XYL activity was recorded in the topsoils (0-20cm) of young woodlands (mean 36.81 nmol MUB · g^{-1} d.s. h^{-1}), in comparison to mature woodland and arable land. In deeper soil (20-40cm), there was a similar pattern as in topsoil (0-20cm).

The GLM analysis (Table 1) shows that land use type influenced the differentiation of XYL activity. In the case of CB, BG and NAG activity, the soil depth was the most significant. For the C content in soil organic matter fraction, the GLM analysis indicates the influence of management type and soil depth (Table 2). Enzyme activity and carbon in the soil organic matter fraction were also driven by the sample position within a transect, albeit to a lesser extent. Enzyme activity was significantly correlated with pH, N and C content (Table 3). More specifically, CB, BG and NAG activity correlated with C and N of the light fractions and XYL activity cor-

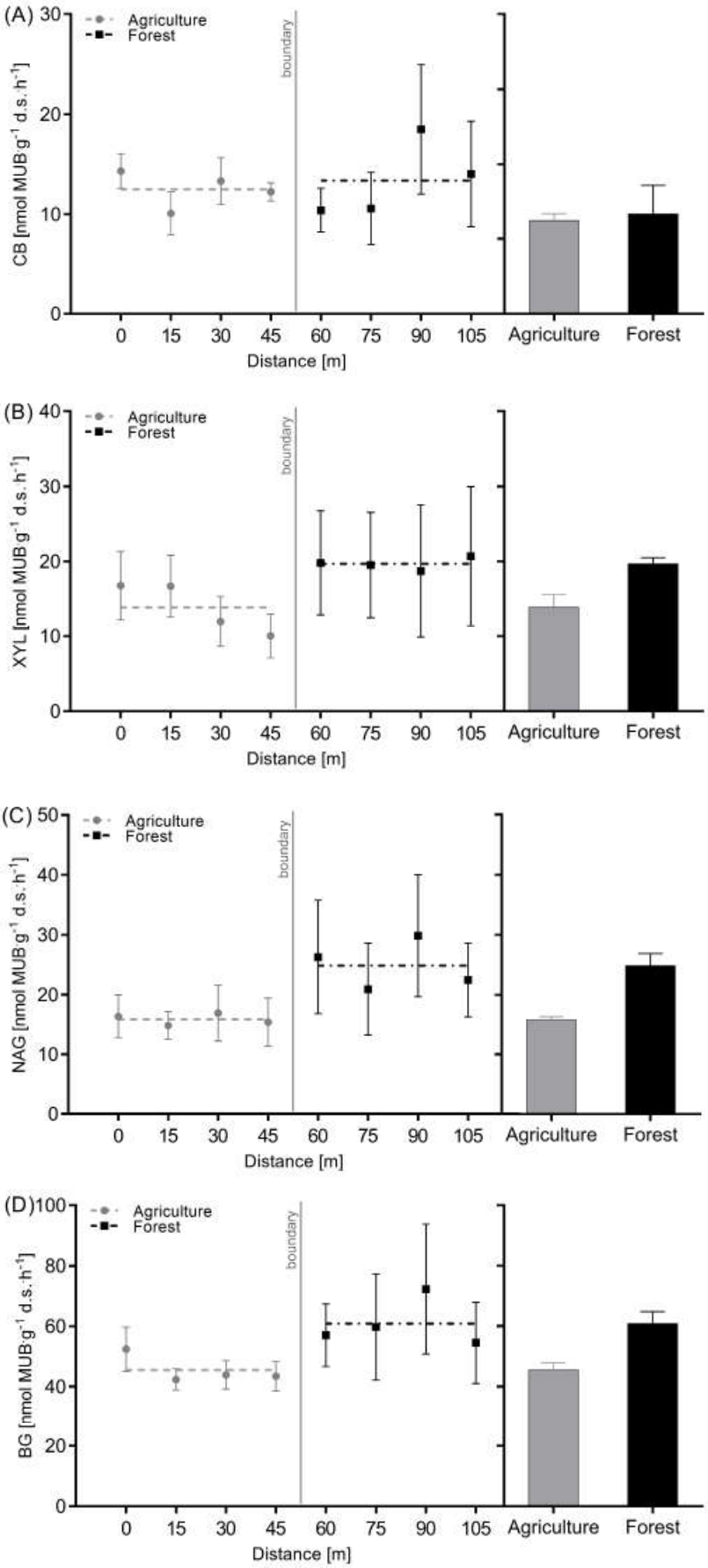

Figure 3

Carbon transformation enzyme activity in mineral soil 0-40cm depth along a transect crossing a boundary between agricultural and forest land use. CB - β-D-cellobiosidase activity, XYL – xylanase activity, NAG - N-acetyl-β-D-glucosaminidase activity, BG - β-glucosidase activity. Symbols represent mean value for individual transect points from 7 separate sites in England, columns are overall mean, all error bars ± SEM. Dotted lines are linear fits, no slopes were different from zero (P = 0.14-0.96).

Table 1 Results of multivariate analysis of variance based on the general linear model (GLM) for the enzymes activity, including the management type, transect point and soil depth (significance effect, $p < 0.05$, are show in bold)

	CB		BG		NAG		XYL	
	F	*p*-value	*F*	*p*-value	*F*	*p*-value	*F*	*p*-value
Management type (MT)	2.07	0.153	0.26	0.612	2.38	0.126	**13.59**	**0.000**
Transect point	0.33	0.802	0.10	0.960	0.77	0.515	0.45	0.720
Soil depth (D)	**6.45**	**0.012**	**4.78**	**0.031**	**6.59**	**0.012**	2.40	0.124
MT x Transect point	0.99	0.449	0.90	0.527	0.50	0.868	0.76	0.654
MT x D	0.72	0.580	1.18	0.321	1.03	0.397	2.14	0.080
Transect point x D	0.34	0.916	0.60	0.730	0.48	0.822	0.06	0.999

Note. Abbreviations: CB - β-D-cellobiosidase activity, XYL – xylanase activity, NAG - N-acetyl-β-D-glucosaminidase activity, BG - β-glucosidase activity.

Table 2 Results of multivariate analysis of variance based on the general linear model (GLM) for the carbon in organic matter fraction, including the management type, transect point and soil depth (significance effect, $p < 0.05$, are show in bold)

	C_{LF}		C_{oLF}		C_{MAF}	
	F	*p*-value	*F*	*p*-value	*F*	*p*-value
Management type (MT)	**11.31**	**0.001**	1.48	0.226	0.21	0.645
Transect point	0.56	0.643	1.64	0.184	0.50	0.681
Soil depth (D)	0.13	0.721	**5.10**	**0.026**	0.86	0.356
MT x Transect point	0.07	1.000	0.53	0.852	0.58	0.811
MT x D	**5.52**	**0.000**	2.41	0.053	**3.38**	**0.012**
Transect point x D	0.42	0.867	1.62	0.148	0.59	0.738

Table 3 Correlations between enzymes activity and physic-chemical properties of soils

	CB	BG	NAG	XYL
pH H_2O	**-0.293**	**-0.270**	**-0.270**	**-0.494**
Total N	**0.501**	**0.660**	**0.518**	**0.357**
TOC	**0.471**	**0.681**	**0.502**	**0.286**
C_{LF}	**0.392**	**0.626**	**0.432**	0.139
N_{LF}	**0.379**	**0.611**	**0.417**	0.130
C_{oLF}	**0.311**	**0.275**	**0.362**	**0.282**
N_{oLF}	**0.379**	**0.296**	**0.428**	**0.392**
C_{MAF}	0.128	0.008	0.113	**0.282**
N_{MAF}	0.140	-0.015	0.109	**0.331**
sand	0.117	**0.279**	**0.286**	**0.194**
silt	-0.151	**-0.211**	**-0.215**	-0.147
clay	0.010	-0.178	-0.180	-0.118

Note. Abbreviations: CB - β-D-cellobiosidase activity, XYL – xylanase activity, NAG - N-acetyl-β-D-glucosaminidase activity, BG - β-glucosidase activity, TOC – total organic carbon, CfLF – carbon of free light fraction, CoLF – carbon of occluded light fraction, CMAF – carbon of mineral associated fraction, NfLF – nitrogen of free light fraction, NoLF – nitrogen of occluded light fraction, NMAF – nitrogen of mineral associated fraction

related with C and N of oLF and MAF fractions. Additionally, positive correlation between sand content and BG, NAG and XYL activity was noted. The effect of land management on the fractional composition and enzymes activity was also confirmed by the PCA. Depending on the horizon (0-20 cm and 20-40 cm), two main factors had a significant total impact on the variance, increasing it from 40.58% to 57.85%. For both horizons, plots of woodlands were related to higher enzymes activity (BG, CB, NAG and XYL). Additionally, forest soils were characterised by higher content of C in soil organic matter fraction (Fig. 4a,b). The soils studied at the agricultural plots differed in the C contents of the individual soil organic matter fractions. Factor 1 was related to the carbon of soil organic matter fractions and enzymes activity. Factor 2 was associated with type of land management (Fig. 4a,b).

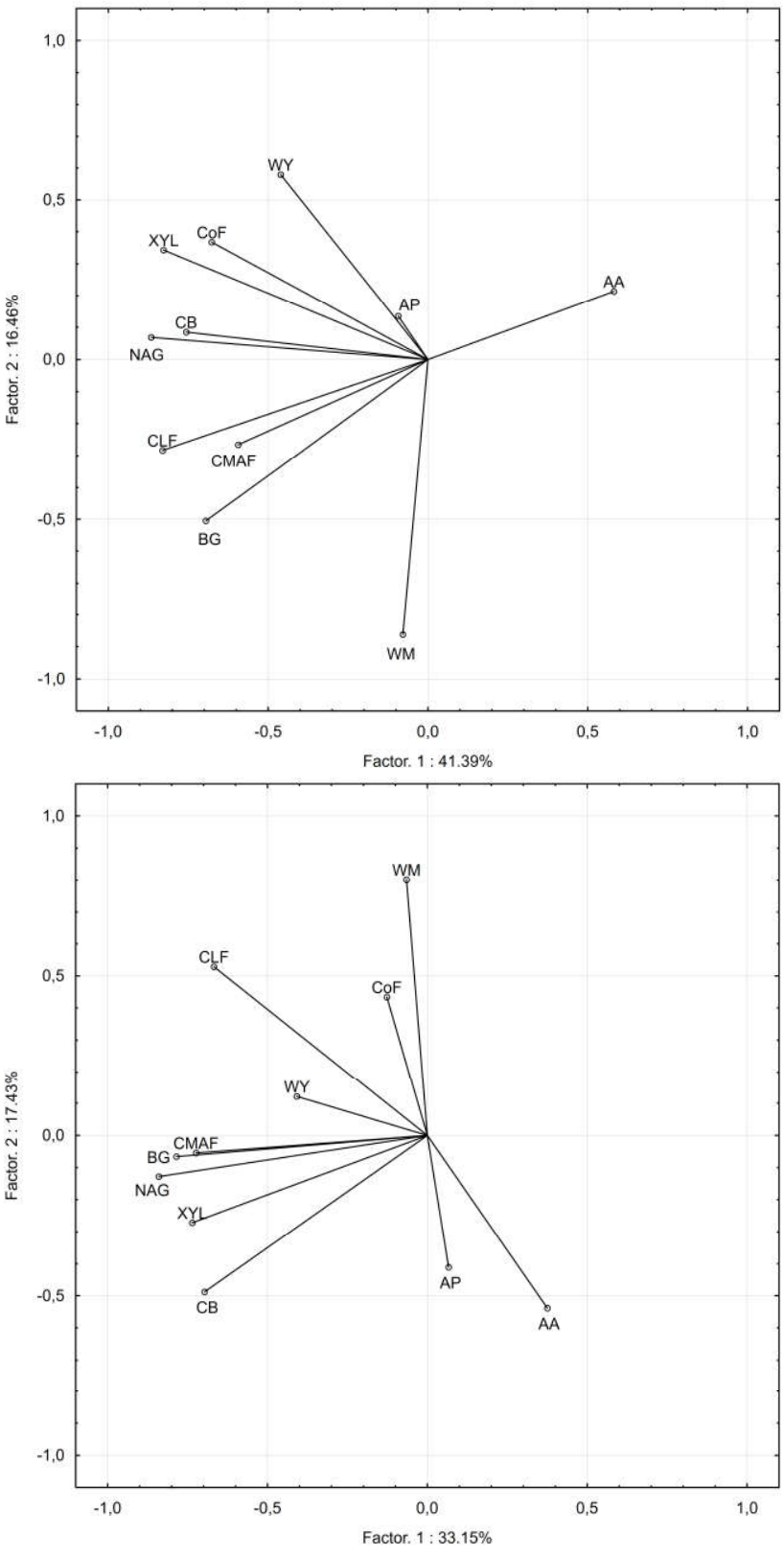

Figure 4

Diagram of PCA with projection of variables on a plane of the first and second for soil, a – diagram for 0-20 cm horizons, b – diagram for 20-40 cm horizons (CB - β-D-cellobiosidase activity, XYL – xylanase activity, NAG - N-acetyl-β-D-glucosaminidase activity, BG - β-glucosidase activity, AP – pasture, AA – arable, WY - young woodlands, WM - mature woodlands, CfLF – carbon of free light fraction, CoLF – carbon of occluded light fraction, CMAF – carbon of mineral associated fraction)

Discussion

Land use type and soil carbon pools

Forest ecosystems have been shown to hold more C below ground due to foliage and root litter inputs, especially when compared to intensively managed arable systems (Vanguelova et al. 2013, Błońska et al. 2017). This was confirmed at the WrEN sites, with significantly higher soil carbon stocks under mature forest compared to neighbouring arable plots (Ashwood et al. 2019). Elsewhere, forest soils have been found with a greater accumulation of free light fraction carbon (Błońska et al. 2017). In our study, the topsoil mineral C_{fLF} content was significantly higher in forest (WM and WY) plots compared to arable plots (AA), but not different to pastures (AP). Pasture topsoil C content is frequently found to be similar to that of forest topsoil, due to the dense root systems semi-permanently colonising the soil and the low-intensity soil disturbance compared to arable fields (Sparling et al. 2000, Gregory et al. 2016). Net primary productivity, a proxy for OM input to soils, has also been shown to differ between contrasting vegetation types; with the greatest OM input to soils found in forests and the lowest under agricultural crops (Houghton et al. 1983).

Forest ecosystem development mimicking secondary succession can also significantly influence above and belowground carbon dynamics (Benham et al. 2012, George et al. 2010). Forest development was shown to increase total topsoil carbon storage with age in a long-term oak chronosequence on the same soil type as the WrEN sites (Benham et al. 2012). In this study, the average labile C_{fLF} content in the mineral topsoil in young forest (WY) plots was double that of mature woodland (WM) plots. One of the reasons for this observation may be higher labile carbon availability due to the disturbance during land preparation and forest planting, coupled with the fact that young forests typically have microclimatic environments which support faster OM decomposition and turnover before forest canopy closure (Benham et al. 2012).

Focusing on the more stable SOM, we did not find any difference in the C_{MAF} soil fraction due to land use. The concentration of C_{MAF}, as a stable carbon fraction, is highly dependent on soil type and the availability of clay minerals for the formation of stable carbon complexes, which are highly resistant to microbiological decomposition. The residence time of C_{MAF} has been estimated to be between 100 and 1000 years (Parton et al. 1987, Schimel et al. 1994). Despite higher intermediate C_{fLF} and C_{oLF} presence in the soils of forest when compared to agricultural plots, in our study soil C_{MAF} is very similar across all land uses. This suggests that the clay in these soils has reached its capacity for carbon accumulation and it is carbon saturated.

Land use type and enzyme activity

We saw clear differences in enzymatic activity between woodland soils and agricultural soils, with the former characterized by higher enzymatic activity in the organic horizon and topsoil. The results show the importance of land use in shaping enzymatic activity of soils, an observation consistent with other studies (Acosta-Martinez et al. 2007, Li et al. 2014). Differences in enzymatic activity are likely driven by changes in the quantity and quality of SOM (Błońska et al. 2016, Błońska et al. 2017), an assertion supported by the strong relationship between CB, BG and NAG activity with C and N light fraction (fLF and oLF). The light fraction of SOM contains easily decomposable compounds and is therefore quickly transformed (von Lützow et al. 2007, Schnecker et al. 2016), so is regarded as highly labile and reported to be a major N and C source (Boone 1994).

Among the enzymes considered in this study, β-glucosidase activity showed the greatest variability in soils. Extracellular enzymes,

especially β-glucosidase, are primarily secreted by ectomycorrhizal fungi, the activity of these enzymes is lower in soil directly influenced by arbuscular and ericoid mycorrhizas (Gianfreda 2015). Higher β-glucosidase activity in the topsoil of our forest soils, compared to arable soils, may then be explained by the fact that ectomycorrhizae are the dominant type of symbiotic fungi in forests (Kałucka & Jagodziński 2016). In addition, strong mineral fertilization and chemical plant protection agents (especially fungicides) in arable soils reduce the prevalence of mycorrhiza; possibly contributing to a reduction of extracellular enzyme activity.

Soil depth and soil carbon pools

In cropped soils, SOC is usually less vertically stratified than in soils under natural ecosystems (Yang et al. 2007). Our research confirmed the decreasing trend of soil organic carbon content with increasing soil depth, in both woodland and agricultural soils. Additionally, in our study we noted a decrease in enzyme activity in deeper soil. Soil depth influences the abundance, composition and functions of soil microbial communities (Kramer & Gleixner 2008, Stone et al. 2014). Observed decreases in CB enzyme activity at depth was much less pronounced in the forest centre, compared to the middle and outer part of forest transects (e.g. closer to the open agricultural field). The rhizosphere is characterized by higher enzymatic activity as a result of released exudates stimulating the activity of microorganisms (Kotroczó et al. 2014). The concentration of plant-derived cellulosic compounds usually declines with increasing depth, and root biomass is mostly concentrated in the upper mineral soil (Rumpel & Kögel-Knabner 2011). Greater root presence in topsoil therefore leads to increased carbon transformation capacity of soil enzymes in shallow horizons. In our study, we found greater content of C_{fLF} in surface horizons, regardless of land use. Reduction of enzymatic activity with depth was more pronounced in woodland soils, surface horizons of forest soil are enriched with tree litter and fine roots with faster turnover rate (Brunner et al. 2013).

Edge effects of tree-crop boundary

In our observation of C content of woodland soil transects, we expected to see a trend of increasing accumulation of the free light C fraction from the woodland centre towards its edges. The observed increase in C_{oLF} can be explained by a more diversified structure of the stand close to the edge, and greater richness and diversity of vegetation (Williams-Linera 1990, Harper et al. 2005, Kahana et al. 2015) – a situation akin to the structure of the forest. A strong edge effect with increased nitrogen deposition, faster tree growth and higher soil C stocks at the forest edge compared to forest interior was found in forests neighbouring intensive agricultural fields in the East of England (Vanguelova and Pitman,. 2019). A more pronounced edge effect was observed in the oldest forest plots (WM), than in the younger plots in this study as more time is likely needed for such effect to become pronounced.

The forest edge habitat was previously characterized by higher air temperature, higher soil moisture and pH and higher enzyme activity (Bogyó et al. 2015) – the latter confirmed by our study. Similarly, vegetation NPP and diversity near the edge has the potential to increase litter fall and thus soil C deposition (Ruwanza 2018). Soil temperature and moisture affect soil microbial processes (Vágó et al. 2006), plus differences in the chemistry of detritus inputs influence decomposition rates and shift enzyme activity (Weintraub et al. 2012). We did not find any evidence of any of these processes affecting enzyme activity across the boundary, all of these effects appear in the soil under each land use type in this study.

Conclusions

The results of our study confirm the importance of land use and management type in shaping the enzymatic activity of soils and soil carbon, transformation, accumulation and sequestration. We found strong differences in soil parameters critical to C storage; soils under tree cover had significantly higher C content and higher activity of C transformation enzymes than agricultural soils. Our results indicate that analysis of SOM fractions can be used to assess the stability and circulation of total SOC in different ecosystems. The increased input of plant residues into forest soil eventually leads to a high organic matter content as well as high SOC in the unprotected fractions, while the mineral clay soil might have reached its capacity for more stable carbon accumulation. Additionally, our study shows that long-term forest creation and management is crucial for increasing SOC sequestration. These results show that land use clearly affects SOM fractions, which are important drivers of soil microbial community composition and its enzyme activity.

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Supporting Information

The online version of this article includes supporting information:

Table S1 Key properties of soils across land uses, transect position and soil depth

Table S2 Carbon of organic matter fraction (g · kg^{-1}) of soils in different variant of study plots

Table S3 Nitrogen of organic matter fraction (g · kg^{-1}) of soils in different variant of study plots

Table S4 Enzyme activites (nmol MUB · g^{-1} d.s. h^{-1}) of soils in different variant of study plots