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Original article

Responses of the earthworms *Lumbricus terrestris* and *Aporrectodea caliginosa* to wheat straw provision across a range of residue sizes

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ABSTRACT

Earthworm mediated incorporation of soil surface applied crop residues could provide benefits to belowground ecosystem services, such as an increased rate of soil formation and carbon sequestration. In addition, increased soil organic matter within the upper soil profile can increase food availability for other soil fauna and micro-organisms, with potential benefits for soil structure and health. Previous research has assessed the potential mass of surface applied organic matter that can be assimilated by earthworms; however, particle size of material may limit the rate of bioturbation and influence earthworm function and behaviour. The aims of the present study were to investigate the preference and utilisation of wheat (*Triticum aestivum*) straw residues at different particle sizes by two common, temperate earthworm species, *Lumbricus terrestris* and *Aporrectodea caliginosa.* These were addressed within controlled laboratory experiments, where two different scales were tested: Expt 1; with 3 modal straw lengths, as determined from the field post-harvest (40, 20 and 1 cm); and Expt 2; micro particle sizes (1 cm and 1 mm). The effect of straw length on earthworm utilisation was tested by earthworm incubation experiments in plastic bags, where removal from the soil surface was measured over a period of 8 weeks in monocultures and mixed species treatments. Litter removal was investigated by mass depletion over time and depth of incorporation. Choice chambers were used to quantify straw selection and removal at micro particle size. Expt 1 showed straw removal (63 ± 6 %) was significantly higher with a *L. terrestris* monoculture and 1 cm length. The largest masses of straw were incorporated at 0–60 mm depth of soil. There was no evidence to support a facilitation effect of *L. terrestris* on *A. caliginosa*, and increased earthworm mortality was detected in mixed species treatments. The choice chambers of Expt 2 indicated a preference for 1 mm particle size by both earthworm species with a more rapid use by *L. terrestris* than *A. caliginosa*. These experiments highlight how retention of straw residues on the field, linked with tillage practices and further straw management post-harvest could have significant implications for plant protection and earthworm populations.

1. Introduction

Removal of crop residues, such as straw, can have negative impacts on soil properties, by depletion of nutrients from the soil system, leading to a 12–19 % reduction in Soil Organic Matter (SOM) content and enhanced soil erosion [1]. Re-application of crop residues post-harvest to arable soils and the retention of crop stubble can help to mitigate global climate change [2,3]. Straw residues are reapplied to soil using different methods, the most common practices involve incorporation during tillage, where methods differ with tillage depth [4]: deep tillage; where soil is overturned and straw incorporated at 30–40 cm depth, subsoil (non inversion) tillage; where soil is deeply loosened to 35–40 cm depth and straw incorporated, and shallow tillage (shallow non inversion); where straw stubble is retained on the surface and straw incorporated at 5–10 cm depth. Crop residue re-application can increase Soil Organic Carbon (SOC) sequestration [5], reduce nutrient leaching [6] and increase SOM [7], which improves soil physical and chemical properties and increases habitats for microbial and macrofaunal communities [8,9]. However, incorporation of residues with tillage can also pose some challenges, including increasing the risk of residue or stubble-borne diseases through pathogen inoculum [3,10].

No-tillage farming systems can have significant benefits to soil health, by improving soil structure, reducing compaction caused by tillage and improve soil hydraulic properties and reduce soil moisture loss [11,12]. However, when comparing wheat yields in conventional agriculture with no-tillage systems, conventional tends to have higher

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yields in temperate climates [13]. In addition, nutrient management practices require further management to increase yields [14]. Conservation agricultural management, which applies no-tillage with residue retention and crop rotation, could be a solution to this issue, where long-term adoption of these methods can reduce negative yield impacts [15,16]. Mulching of straw on the soil surface can provide a natural layering of soil organic matter, which has direct benefits to soil physical characteristics and biological processes, such as moisture retention, increased bacterial and fungal diversity and provision of a physical layer of organic matter on the surface to further reduce soil erosion [17–19].

Conservation agroecosystems, including reduced tillage, with crop residue applications are likely to significantly increase soil fauna populations [20–22], which in turn may benefit decomposition of surface applied residues and increase pathogen resistance [23,24]. Earthworms represent the largest biomass of soil fauna in terrestrial ecosystems, where their behaviour above and belowground may have a significant effect on decomposition rate and bioturbation of residues in no-tillage systems [25]. The increase of N mineralisation by earthworms can have a critical role in plant production, where they can increase crop yields by 25 % and aboveground biomass by 23 % [26]. Earthworm casting has positive impacts on soil properties, such as an increased aggregate stability [27], available nutrient content [28] and SOC storage [29]. Combining reduced tillage farming with organic matter application can increase the rate of nutrient mineralisation and hydraulic activity in soils by stabilised earthworm burrows and plant root channels [30,31]. Ecological interactions involving earthworms and their movement throughout soil may be important processes to enhance degradation of recalcitrant organic matter, such as cereal straw [32]. Activity of increased earthworm density and species richness under no-tillage management with crop residue applications could mitigate the yield reduction experienced under no-tillage systems [13].

Within no-till agroecosystems, retention of the straw and the particle size of straw can have significant effects on earthworm ecological groups [33–35], their access to the material, its utilisation, and the spatio-temporal effects of its bioturbation [36]. Provision of a litter layer offers a habitat for epigeic species, which may survive in the aboveground layer of decomposing organic matter [25]. Anecic and epi-anecic species utilise organic matter as a food source and it may also form the organic fraction of a midden [37,38], where a midden is a mixed collection of earthworm casts, organic matter (such as straw) and inorganic material around the burrow entrance [25]. Currently, in most temperate agroecosystems, endogeic earthworms, such as *Aporrectodea caliginosa* (Savigny, 1826), are the most abundant ecological group due to their survival capability in soils undergoing tillage [39]. Endogeic species are geophagous, assimilating decomposed organic matter from soil [40] and therefore have better survival under straw applications with both mechanically incorporated organic matter and no-tillage with crop residue surface applications [41]. However, the impact of *A. caliginosa* on early stages of straw decomposition is primarily conducted from surface-casting rather than physical bioturbation [42,43].

Effects of organic matter particle size on earthworm feeding capabilities have been investigated [33,44–47], such that a smaller size may accelerate decomposition [31,45]. Within such laboratory incubation experiments, applications of organic matter are often limited to small particle sizes <1 cm [31,45]. At a field scale, it is unlikely that this particle size is produced, therefore effects on earthworms will likely differ to those recorded in the laboratory. A larger straw particle size (>1 cm) may increase the impact of larger species such as *Lumbricus terrestris* (L. 1758), which can feed upon and use larger particle sizes for midden development [43]. Analysis of residue incorporation of straw lengths found in the field could determine the effect of decomposition by incorporation alongside that through direct feeding.

Survival and population development of epi-anecic species such as *L. terrestris* under no-tillage management could have a significant impact on the incorporation and decomposition rate of cereal residues. Recent field experiments in Finnish soils (classified as Protovertic Luvisol) have indicated a 29–41 % increase in the rate of straw incorporation between a harvest to spring season [43]. An increase in *L. terrestris* populations in this environment could have an impact on other earthworm species through differing burrowing activities and food competition [46–48]. Laboratory experiments have indicated facilitative interactions between *L. terrestris* and juvenile *A. chlorotica* where survival and development were enhanced by adult *L. terrestris* fed with manure [47]. However, inter- and intra-specific competition may significantly impact earthworm population development [49,50]. Further investigation of *L. terrestris* interactions with other earthworm species in temperate agroecosystems, such as *A. caliginosa*, could indicate how they will interact in the field and influence straw decomposition and soil structure.

The aim of this work was to determine how wheat straw collected from the field post-harvest was utilised by two common earthworm species, epi-anecic *L. terrestris* and endogeic *A. caliginosa*. These earthworm species were chosen for this study because they are abundant in wheat fields in European soils [41] and have different bioturbation behaviours [25]. Specific objectives were to (i) measure the effect of straw length (1–40 cm) on earthworm bioturbation behaviour; (ii) determine the effects of earthworm activity on straw incorporation depth; (iii) compare rates of straw removal when provided at a smaller scale (0.1–1 cm); and (iv) investigate any mechanistic interactions between *L. terrestris* and *A. caliginosa*.

These research questions were investigated through two laboratory experiments: (i) A microcosm experiment analysing the effect of earthworm activity on decomposition of surface applied wheat straw at modal particle sizes found on the field (range of 1–40 cm – see Fig. 1) and (ii) choice chamber experiments investigating straw preference of earthworms at a micro-scale particle size (0.1–1 cm).

Based on previous research, it was hypothesized that smaller lengths/particle sizes of straw would be incorporated belowground and decomposed at a more rapid rate. Also, that the presence of epi-anecic *L. terrestris* would have a larger effect on straw decomposition. In addition, micro-scale (milled) straw would be consumed more rapidly than larger cut pieces.

2. Materials and methods

2.1. Preparation for experiments

Earthworms were obtained from two sources. *A. caliginosa* were collected from pasture at Walton Hall Farm, Preston, UK (53.747367, −2.683059), by digging and hand-sorting of soil to 30 cm depth, then taken to the laboratory in field soil. Adult *L. terrestris* were of Canadian origin [51] and purchased from a commercial UK outlet. The latter were utilised to ensure availability of stock adult animals in the same condition, as field collection can be problematic and laboratory production time consuming [52].

Sterilised Kettering loam was selected, as loam-based soils support larger earthworm populations than other soils in temperate climates [53] and this soil has frequently been used in earthworm laboratory culture [52,54,55]. Wheat straw for these experiments was collected post-harvest in October from Brook Lane Farm, Preston, Lancashire (53.718633, −2.681857) and left to air dry at room temperature for 14 days before use. Brook Lane was a conventional arable farm practicing reduced tillage management, where straw stubble was left intact between harvest and spring sowing.

Following earthworm collection, they were acclimated into laboratory conditions prior to experimental start. Monocultures of each species were set up in 750 ml plastic containers, 3/4 filled with Kettering loam soil (24 % clay, 43 % sand, 35 % silt; pH 6.7; 25 % soil moisture) and fed with dried, rewetted wheat straw (*Triticum aestivum L.*) collected from Brook Lane farm at a particle size <1 mm (milled using an analytical mill IKA A11, Oxford and sieved to ensure uniformity), applied at the surface for *L. terrestris* and mixed into the soil for *A. caliginosa*. To regulate

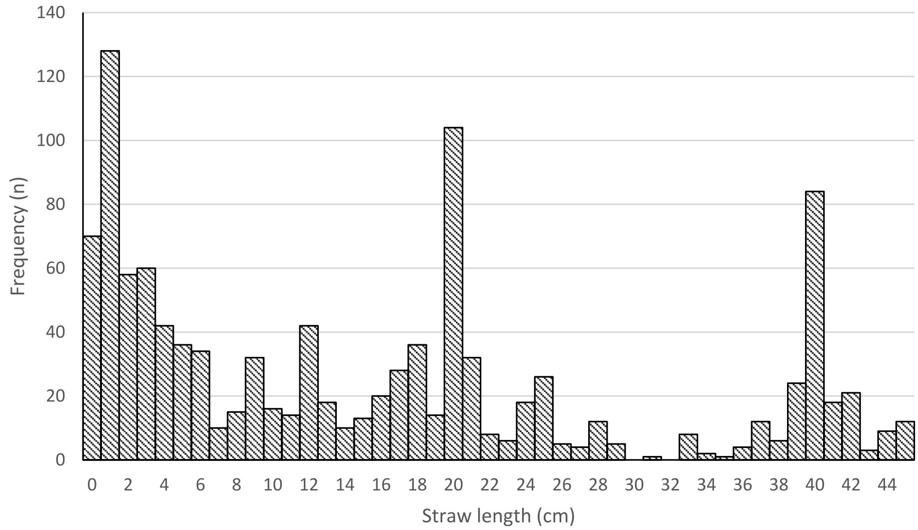

Fig. 1. Distribution of wheat straw residue length (N = 1000) collected post-harvest from Brook Lane Farm, Preston.

airflow, small holes were made with a dissection needle in container lids. Number of earthworms per container was 2 for *L. terrestris* and 6 for *A. caliginosa* [54]. Earthworms were kept in temperature-controlled incubators (LMC, Kent) at 15 ± 1 °C, in 24 h darkness [54]. Earthworm equilibration from field/purchased conditions took place over 28 days before use in experiments [55]. To retain soil moisture, containers were sprayed weekly with water. Earthworms were refed bi-weekly at a rate of 20 g adult^{-1} month^{-1} for *L. terrestris* and 10 g adult^{-1} month^{-1} for *A. caliginosa* [54].

Two experiments were conducted in laboratories at the University of Lancashire. For consistency, all treatments were maintained at the same temperature used for the equilibration periods (15 °C) and in 24 h darkness, to promote maximum earthworm activity [55].

2.2. Experiment 1: use of field-collected straw by earthworms (1, 20, and 40 cm lengths)

This experiment tested straw (mass and depth) incorporation by earthworms, when applied on the surface. Treatment lengths were determined by measuring randomly collected wheat straw residues from the field (length to the nearest cm). A tri-modal distribution was determined and used as the 3 treatments for this experiment (Fig. 1).

The three straw lengths selected as treatments for investigation were therefore 1, 20 and 40 cm. Mapped on to these straw lengths, three earthworm treatments were: (i) *L. terrestris* monoculture (N = 2); (ii) *A. caliginosa* monoculture (N = 3); (iii) Mixed culture (*L. terrestris,* N = 1; *A. caliginosa,* N = 3). Each treatment had 5 replicates. In addition, there were two sets of control treatments applied to this experiment: (1) earthworm control samples, where no straw was applied to soil (earthworms only); (2) straw control samples, where no earthworms were added (straw only). Full experimental design is presented in Supplementary Fig. 1.

The experimental design used polyethylene bags (600 gauge; heavy plastic), 3 L volume for treatments with *L. terrestris* present and 2 L for *A. caliginosa* monoculture. Kettering loam (25 % moisture content) was used, with only mature earthworms in good physical condition selected. Mean masses: *L. terrestris* = 6.44 ± 0.33 g; *A. caliginosa* = 0.65 ± 0.03 g. These were placed on the soil surface and left overnight to burrow into the soil. Thereafter, 10 g of air-dried wheat straw (of the given treatment length) was rewetted and placed on the soil surface of each bag. These were left for 8 weeks but monitored weekly by mass, with moisture added as required.

At experimental end, any straw remaining on the soil surface was removed with forceps and had mass determined after oven drying at 105 °C for 24 h. Any soil attached to straw particles was carefully removed with forceps. This permitted surface straw mass and straw moisture content to be calculated. To enable depth measurement of straw incorporation, soil from within each plastic bag was deconstructed and sampled at specific depths (0–60; 60–120; 120–180 mm for *L. terrestris*-containing samples; 0–60; 60–120 mm for *A. caliginosa*). During soil deconstruction, earthworms were removed from the units and had masses determined. The depth at which each earthworm was located was recorded and soil was searched for cocoons by wet sieving (sieve sizes 2 mm and 1 mm). Straw particles found from hand sorting at each depth belowground had particle size and mass determined.

2.3. Experiment 2: Earthworm selection of straw at a small particle scale (1 mm vs. 1 cm)

To assess particle size preference of *L. terrestris* and *A. caliginosa*, for straw at a smaller scale, modified choice chambers, as designed by Rajapaksha et al. [56], were set up under controlled environmental conditions. This soil-mediated system allowed measurement of straw particle removal by earthworms over time, without disturbing the earthworm activity. Circular aluminium foil trays (diameter 160 mm; depth 30 mm) and Eppendorf tubes (diameter 10 mm and depth 40 mm) were used as the basis of the soil chambers. Tubes and their caps were separated, and a 10 mm hole was drilled into the tube cap, to permit the passage of earthworms. Equally spaced holes (approx. 10 mm diameter) were made in the foil tray wall, enabling drilled caps to be affixed to the inner side and tubes to be attached from the outside. Trays were filled with Kettering loam (25 % moisture), a proven substrate for earthworms [51,55].

Food preference of wheat straw particle size was examined with monocultures of adult earthworms: either *L. terrestris* or *A. caliginosa*. The straw particle sizes tested were 1 cm (manually measured and cut using scissors) and 1 mm (milled using an analytical mill: IKA A11, Oxford). The individual mass of each cap-less, labelled tube was recorded empty. These were filled with dry straw particles, which were soaked with water for 2 h, and excess drained through inversion on to absorbent paper. After equilibration, tubes filled with moist straw particles had masses recorded once again. Earthworm number per chamber was based on biomass (*L. terrestris* N = 2: 10 ± 0.2 g; *A. caliginosa* N = 10: 10 ± 0.05 g). For each choice chamber, there were 8 tubes (see Fig. 2), with 4 filled with either 1 cm or 1 mm particles of wheat straw. Tubes were randomly arranged around each tray. Ten replicated trays were set up for each earthworm species. To prevent moisture loss and earthworm escape, trays were covered with a sheet of aluminium foil,

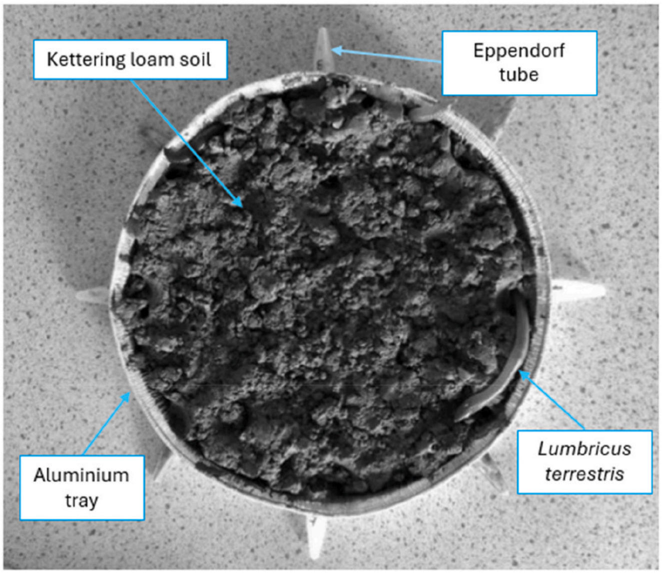

Fig. 2. Choice chamber (with aluminium foil cover removed), viewed from above (tray diameter = 160 mm; tray depth = 30 mm; Eppendorf tube diameter = 10 mm; Eppendorf tube depth = 40 mm). Wheat straw removal from tubes, by here *L. terrestris* (N = 2), supplied with replicated particle sizes of either 1 cm or 1 mm, over 24 days.

held in place with an elastic band. To ensure air circulation, two holes were made in each sheet using a mounted needle. All choice chambers were incubated in darkness at 15 °C with each tube mass (with remaining contents) recorded every 3 days over a period of 24 days. After assessment, each was reaffixed in the same position. Particle size preference was assessed by calculating the mean mass loss of straw from food tubes for each earthworm species.

To monitor moisture variation throughout the experiment, control choice chambers containing no earthworms were prepared and monitored as those in the experiment. The tube mass of controls was measured every 3 days at the same time as the samples. Following tube sampling, each tray was weighed and sprayed with water, as required to maintain soil moisture content compared with the earthworm-free chambers. At experimental end, the number of surviving earthworms, their general condition and masses were recorded.

2.4. Statistical analyses

For both experiments, standard error of the mean (±S.E.) was applied. Statistical analysis was conducted using SPSS v28 software.

Experiment 1. Two statistical models were applied to test the effects of earthworm species and straw length on (i) total straw removal and (ii) straw transportation. Prior to statistical testing, data was tested for normality using a Shapiro-Wilks test ($p > 0.05$) and for homogeneity of variance using a Levene's test.

(i) A General Linear Model was developed to test the effects of earthworm species and straw particle size on mean total straw removal. Post-hoc Tukey Kramer (HSD) testing was used to determine the significance within groups.
(ii) A General Linear Mixed Model was applied to test the effects of straw particle size and earthworm species on straw transportation, with earthworm species and straw length being fixed effects and depth being a random factor.

In addition to the two statistical models, the effects of straw particle size application on earthworm biomass loss, mortality and cocoon production was tested. Prior to statistical testing, data was tested for normality using a Shapiro-Wilks test ($p > 0.05$) and for homogeneity of variance using a Levene's test. There was unequal variance in the data and effects were tested by a Welch one-way ANOVA.

Experiment 2. A General Linear Mixed Model was applied to test the effects of straw particle size and earthworm species on the removal of straw over time. Earthworm species and particle size were fixed effects, and time was a random factor. Prior to statistical testing, data was tested for normality using a Shapiro-Wilks test ($p > 0.05$) and for homogeneity of variance using a Levene's test. Post-hoc Tukey Kramer multiple comparisons tests determined the timing where the differences occurred.

3. Results

3.1. Experiment 1

3.1.1. Total straw removal

Mean total mass of straw removed over the experiment was highest for *L. terrestris* monoculture with 1 cm straw length (6.3 ± 0.6 g) (Table 1). The effect of straw length on total straw removal was significant across all earthworm treatments, where Tukey tests indicated that 1 cm was different to both 20 and 40 cm straw treatments. Although *L. terrestris* incorporated the largest mean mass, *A. caliginosa* removed a mean straw mass ranging from 1.3 to 2.3 g across all straw length treatments, where difference in total straw mass removed was lower (Table 1).

There was a significant difference between the mass of straw removed across earthworm species, where Tukey tests indicated that the mixed species treatment was significantly different to the monoculture groups. Mean straw mass removed with all straw lengths for mixed species treatments was low (<1g).

3.1.2. Depth of incorporation

Mean (±S.E) straw mass (g) incorporated by earthworms from the straw length treatment into 3 soil depths (0–60 mm; 60–120 mm; 120–180 mm) is presented in Fig. 3.

L. terrestris monocultures incorporated straw to the greatest soil depth (160 mm) and straw was recorded at 120–180 mm (Fig. 3A). For all earthworm treatments, the most straw mass was incorporated into the upper soil layer (0–60 mm). *L. terrestris* monocultures displayed differences in straw mass incorporation between straw lengths at all soil depths, with 1 cm length providing the largest mass removed from the soil surface.

A. caliginosa monocultures incorporated lower masses of straw into soil than *L. terrestris* (Fig. 3B). Unlike *L. terrestris*, at each depth of incorporation, there were no significant differences in the mass of straw for straw length treatments. A comparison of straw incorporation into 60–120 mm depth between *A. caliginosa* monocultures (Fig. 3B) and mixed species treatments (Fig. 3C) showed no discernible differences, where mean total mass incorporated was 0.1–0.2 g for all straw lengths.

Although the total mass of straw removed under mixed species was lower than monoculture treatments (Table 1), straw was incorporated into the soil at the greatest depth (120–160 mm) for 1 cm lengths and

Table 1
Total mass of wheat straw removed (g ± S.E.) over 8 weeks by *L. terrestris* (N = 2), *A. caliginosa* (N = 3) and Mixed earthworm species (*L. terrestris* N = 1; *A. caliginosa* N = 3) with 3 straw lengths (1 cm, 20 cm and 40 cm). (Different letters in a column denote differences ($p < 0.05$)).

Straw length (cm)	Mean ± S.E. Straw Removed (g)		
	L. terrestris	*A. caliginosa*	Mixed Species
1	6.37 ± 0.60^{a}	1.27 ± 0.55^{a}	0.88 ± 0.19^{a}
20	0.94 ± 0.13^{b}	1.71 ± 0.17^{a}	0.65 ± 0.56^{ab}
40	0.39 ± 0.39^{c}	2.27 ± 0.12^{b}	0.23 ± 0.37^{b}

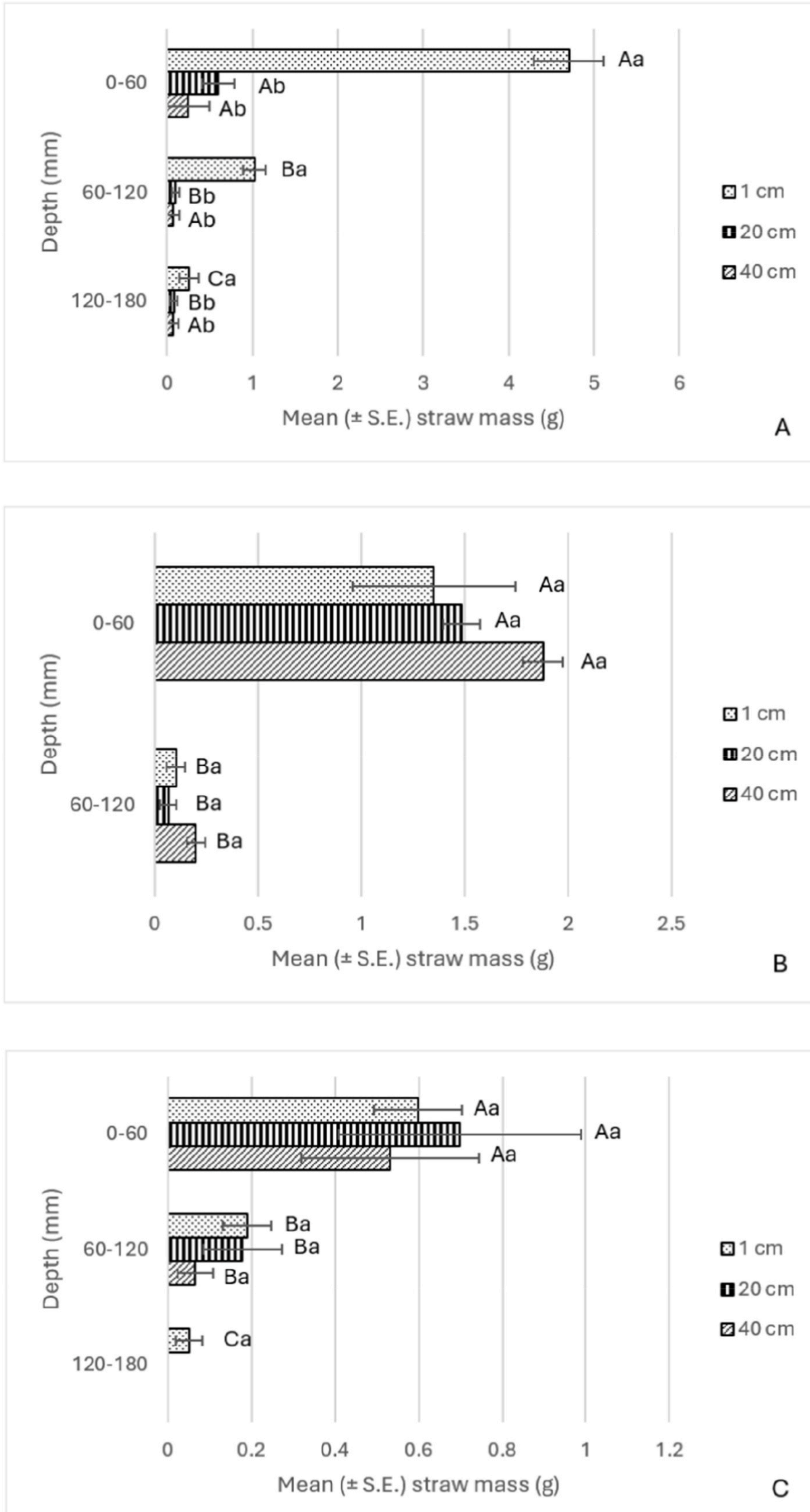

Fig. 3. Mean (±S.E) wheat straw mass (g) incorporated into 3 soil depths (0–60 mm; 60–120 mm; 120–180 mm) after 8 weeks with earthworm treatments (A = *L. terrestris*; B = *A. caliginosa*; C = *L. terrestris* and *A. caliginosa*) with three separate straw lengths (1, 20, 40 cm). Note the different scales of the x-axis (*A. caliginosa* monoculture depth was restricted to 120 mm). N = 5 replicates per treatment. For each earthworm treatment, statistical differences are represented by different letters (Tukey-Kramer, $p < 0.05$). Upper case lettering refers to straw mass at each depth. Lower case lettering refers to straw lengths within each depth.

not the larger modal particle length treatments (Fig. 3C).

3.1.3. Earthworm parameters

At experimental end, a reduction in earthworm mass was recorded within all treatments (Table 2). Loss of biomass in *L. terrestris* monocultures was lower with all straw treatments compared with the straw-free control (Table 2). Full survival (100 %) was recorded for *L. terrestris* monocultures under all straw treatments, with mean mortality of 20 % for the control. Reproduction over the 8-week period was low, but *L. terrestris* monocultures produced cocoons (mean 1.4 ± 0.51 n^{-1}) with the 1 cm straw length treatment.

A mean reduction in biomass for *A. caliginosa* monocultures was similar (29 %) or higher (38–58 %) than the control with no straw addition (Table 2). No cocoons were produced during the experiment and mean mortality rate with straw treatments was 6.7–40 %.

Mean biomass loss in mixed species treatments was high (31–77 %) and mortality increased with increasing straw length (Table 2). The high mean biomass loss at 40 cm straw length (77 %) was mainly due to *L. terrestris*, which has a proportionately higher biomass than *A. caliginosa*. Comparison of the mortality and biomass between *A. caliginosa* monocultures and *A. caliginosa* within mixed species treatments showed no discernible differences. However, there was a higher *L. terrestris* mortality under mixed species treatments.

3.2. Experiment 2

At a micro scale, a preference for milled straw (1 mm particle size) was observed for both earthworm species investigated. *L. terrestris* consumed 1 mm particle straw at a faster rate than *A. caliginosa*, where 87.6 % of the straw mass was consumed by day 6 of the experiment and 100 % was consumed by experimental end (Fig. 4). The rate of removal of 1 cm straw increased with *L. terrestris* following day 9 when most of the 1 mm straw had been removed. The rate of straw consumption by *A. caliginosa* was highest at the start of the experiment (days 0–9) for both particle sizes. From day 9 to experimental end, the rate of straw removal by *A. caliginosa* was higher with 1 mm particle straw, where 89.7 % ± 2.2 was removed. At experimental end, 100 % survival of both species was recorded, with a mean mass loss over the 24 days of 4.8 % for *L. terrestris* and 3.6 % for *A. caliginosa*.

It took *A. caliginosa* 3 days longer to consume 50 % of the straw mass (Fig. 4). At the timepoint of 50 % total removal of straw (Table 3), there was a significant effect of particle size on the remaining straw mass (%) for each earthworm species, where milled straw (1 mm) was removed at a more rapid rate than 1 cm pieces.

4. Discussion

4.1. Straw removal by L. terrestris and A. caliginosa at modal lengths

4.1.1. The effect of modal straw length on earthworm bioturbation behaviour

Of the 3 modal straw lengths, there was a significant increase in the mass of surface straw removed with 1 cm compared with 20 cm and 40 cm in *L. terrestris* monocultures, where it was indicated that 64 % of applied straw was incorporated (Fig. 3). As *A. caliginosa* are geophagus and consume large amounts of soil alongside organic matter [25], a lower removal rate was predicted, where surface straw removal ranged from 12 to 23 % across all lengths, with no recorded effect of particle length on the mass of straw removed (Fig. 3). In no-till agroecosystems, which may benefit *L. terrestris* populations [57], applications of straw at 1 cm length would accelerate bioturbation and decomposition.

Straw removal under mixed culture treatments had negative effects compared with monocultures. Although the total earthworm number per L of soil was within the acceptable range for experimentation [54], there was an increased rate of biomass loss for both earthworm species (Table 2) and a reduction in the rate of straw removal (Fig. 3). It was surprising that there was no recorded effect of particle size on straw removed by *L. terrestris* in a mixed species treatment. This could suggest that *L. terrestris* behaviour differs depending upon earthworm species diversity in the soil, which could impact its ability to incorporate material and feeding behaviour. Further investigation of *L. terrestris* burrowing activity with different species of earthworms common in no-till agroecosystems at differing life stages could provide more information on how species diversity may impact straw removal potential by *L. terrestris* populations.

This experiment was conducted over a relatively short period (8 weeks). As a food offering, 20 cm and 40 cm straw lengths may not be palatable for earthworms, but may have significant impacts on survival in field settings; by offering a habitat for epigeics [32] and providing raw material to form a midden in species such as *L. terrestris* [52]. Additionally, in agricultural practices where straw return is the sole organic matter source, it is unknown whether straw lengths of 20 cm and 40 cm may become accessible at a later period through the process of microbial decomposition. Therefore, larger straw lengths may be useful at later periods in the year, sustaining populations when smaller particle straw has already been utilised. It is evident that *L. terrestris* populations can survive in the field under straw applications [43] however this may cause population collapse if quality of residue is poor, e.g. oat applications have been shown to have a negative effect on *L. terrestris* populations compared with wheat and barley [58,59]. It is suggested that the negative effect of oat on *L. terrestris* population size was caused by a reduction in exogenous C content [58,60], however in these experiments organic matter was applied to the field following tillage treatment, which is also likely to have an increased negative effect on *L. terrestris* [57]. Further analysis of straw residue utilisation by *L. terrestris,* when offered mixed particle sizes over an increased period (e.g. 1 year) could explore impacts on survival and the potential for decomposed straw as a food source to sustain populations.

Earthworm biomass reduced over the period of the experiment (Table 2). *L. terrestris* reduced in biomass at a lower rate than the control under all straw treatments (Fig. 3). In contrast, *A. caliginosa* monoculture biomass reduced at an equal (1 cm and 40 cm straw lengths) or a higher rate (20 cm straw length) than the control (Table 2). This could be for several reasons. The soil surface application of straw was to replicate a no-till management system; however surface application of organic matter is not suited to endogeic species [25]. Kettering loam is low in

Table 2
Mean biomass loss, cocoon production and mortality of earthworm treatments with 3 wheat straw length treatments (1 cm, 20 cm and 40 cm) plus a control with no straw. The difference between straw length treatments for earthworm treatments was tested by one-way ANOVA. Statistical differences in columns are presented by different letters.

Parameter	*L. terrestris*			*A. caliginosa*			*Mixed Species*		
	Biomass loss (%)	Cocoon production (n^{-1})	Mortality (%)	Biomass loss (%)	Cocoon production (n^{-1})	Mortality (%)	Biomass loss (%)	Cocoon production (n^{-1})	Mortality (%)
Control	60.6 ± 10.2[a]	0[a]	20 ± 20[a]	29.5 ± 5.4[a]	0[a]	6.7 ± 6.7[a]	39.0 ± 3.3[a]	0[a]	5 ± 5[a]
1 cm	33.3 ± 3.6[b]	1.4 ± 0.5[b]	0[a]	29.3 ± 10.4[a]	0[a]	6.7 ± 6.7[a]	31.0 ± 3.6[a]	0.2 ± 0.2[a]	5 ± 5[a]
20 cm	37.9 ± 3.5[b]	0[a]	0[a]	58.9 ± 9.9[a]	0[a]	40 ± 12.5[b]	44.6 ± 5.0[b]	0[a]	20 ± 12.25[a]
40 cm	35.2 ± 1.4[b]	0[a]	0[a]	38.9 ± 15.4[a]	0[a]	20 ± 20[a]	77.3 ± 9.5[b]	0[a]	40 ± 15[b]

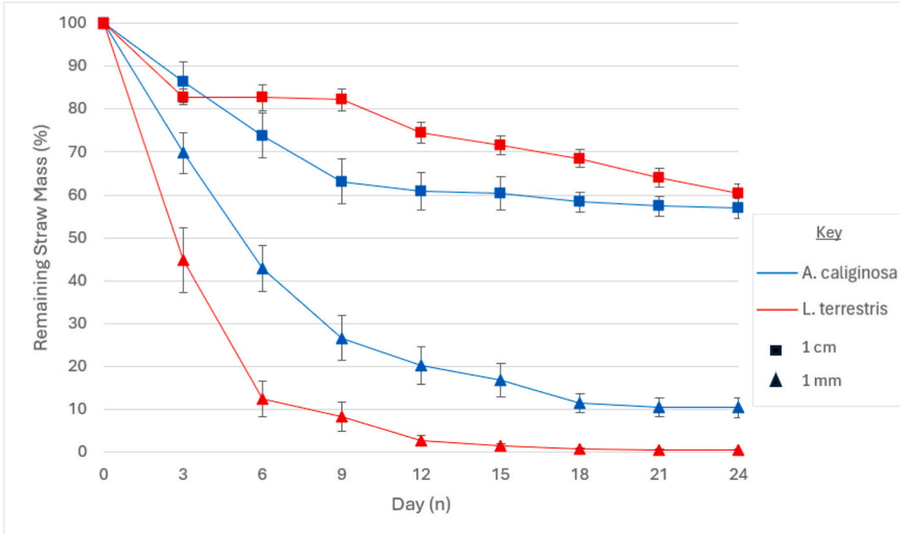

Fig. 4. Removal of wheat straw (mean % ± S.E.) by adult *A. caliginosa* (N = 8) and adult *L. terrestris* (N = 2) over 24 days with either 1 cm or 1 mm particle sizes.

Table 3
Mean (±S.E.) removed wheat straw mass (% of original) in choice chambers of earthworms at 50 % total removal. Different letters in a row indicate significant differences ($p < 0.05$).

Earthworm Species	Days taken to remove 50 % Straw (1 mm)	Straw Particle Size	
		1 cm	1 mm
A. caliginosa	9	26.5 % ± 5.26[a]	63.2 % ± 2.47 [b]
L. terrestris	6	12.4 % ± 4.12[a]	82.7 % ± 1.68 [b]

organic matter content, and the application of fresh straw is unlikely to be degraded enough for *A. caliginosa* to assimilate. In addition to this, movement to the surface to access food requires further energy expenditure, which might be why some earthworm treatments reduced in biomass further over the experimental period. The shortest straw length applied (1 cm) could be too large for *A. caliginosa* to utilise as food due to their mouthpart size [61]. Most laboratory experiments testing *A. caliginosa* use organic matter <1 mm particle size [55]. Regardless of biomass reduction, 1–2 g straw was incorporated by *A. caliginosa* during the experiment with all straw length treatments. This experiment supports findings by Capowiez et al. [62] where x-ray tomography highlighted how *A. caliginosa* adapted their burrowing behaviour to organic matter placement, indicating partial feeding of surface organic matter. Straw length could be a limiting factor to utilisation, particularly when applied fresh. The amount of straw incorporated by *A. caliginosa* at this laboratory scale could amount to a significant level of straw incorporation at a field scale, given the large abundance of *A. caliginosa* within western agroecosystems [9,63].

4.1.2. The effects of earthworm activity on straw incorporation depth

Analysis of straw deposition within 3 subsections of the soil profile identified differences between *A. caliginosa* and *L. terrestris* and the effects of straw length on their bioturbation behaviour. For *L. terrestris* monocultures, the utilisation of straw residues within the upper 6 cm of the soil profile suggests that *L. terrestris* use this material within their midden (Fig. 3A). Microorganism activity and soil aeration is at its highest in the upper soil profile [64], therefore organic matter retained at this level may stimulate decomposition and soil formation further by supporting microbial processes [65]. The effect of straw length on the rate of removal was significant at all straw depths, where 1 cm length had the highest mass of straw removed. The diameter of an adult *L. terrestris* burrow ranges between 7 and 10 mm [25] therefore it is more likely that 1 cm length material will have less physical obstruction with a burrow wall during belowground bioturbation and may result in the rate of removal being higher.

A. caliginosa deposited 90–96 % of straw incorporated within the upper subsection of soil (Fig. 3B) and there were no differences within the mass of straw deposited between particle size at either depth. As *A. caliginosa* make more semi-permanent horizontal burrows, their impact on straw dispersal may be more significant on a spatial scale in the upper soil profile compared with *L. terrestris*, which tend to live within a semi-permanent, vertical burrow throughout its adult life [25, 32]. Maintaining organic matter within the upper soil profile again indicates how increased activity of earthworms in no-till may accelerate decomposition and nutrient mineralisation of surface residues, positively impacting crop growth.

Although the total mass of straw removed under mixed culture treatments was lower than monocultures (Table 1), the straw deposition within depth of soil was like that of *L. terrestris* monoculture (Fig. 3A–C). However, there was no effect of straw length on the mass of straw removed to each soil depth. Small amounts (1 g) of straw residues were recorded with all straw length treatments at lower depths (120–180 mm; Fig. 3) with *L. terrestris*, indicating their bioturbation effects may have some positive influence on carbon sequestration [66]. Earthworm activity is suggested to increase CO_2 emissions from soil and reduce the amount of sequestered C [67,68] because it has a larger effect on stimulating OM nutrient mineralisation, which releases CO_2, rather than stabilizing residue derived C in biogenic aggregates. However, this could be organic matter-dependant [69], where earthworms with composted straw applications increased SOC compared with biochar. Further investigations of the effects of *L. terrestris* bioturbation on C storage in soils is required to determine how they may influence the decomposition of straw at different depths.

4.1.3. Interactions between L. terrestris and A. caliginosa

Although *L. terrestris* and *A. caliginosa* are common earthworm species in temperate soils, there is limited research investigating their behavioural interactions. Facilitation by *L. terrestris* to *A. caliginosa* has been suggested in laboratory analyses of phosphorus transport mediated by earthworm activity, where it was indicated that *A. caliginosa* could access phosphorus from litter incorporated into a *L. terrestris* burrow [70]. However, this could be limited by incorporation depth, where soil organic matter distribution analysis of *A. caliginosa* indicated that they are mainly active in the upper 3 cm of soil [71]. Field investigations of

A. caliginosa and *L. terrestris* populations have indicated that *A. caliginosa* may gain from organic matter obtained within *L. terrestris* middens [47,72], however, this could be at certain life stages (such as juvenile *A. caliginosa* feeding on decomposed OM in a midden) and it is uncertain how adult *A. caliginosa* and adult *L. terrestris* co-habit, even though they are often identified together in field soil samples. In this experiment, *L. terrestris* increased the amount of straw within the soil at lower depths in monoculture (Fig. 3). This was predicted to increase food availability for endogeics, but recorded negative effects on *A. caliginosa* in mixed culture.

Comparisons of *A. caliginosa* survival rates between monocultures and mixed culture treatments with *L. terrestris* were conducted to determine whether *L. terrestris* bioturbation effects increased *A. caliginosa* survival. It was hypothesized that *A. caliginosa* survival may increase with *L. terrestris* populations because they can be facilitated through the presence of an *L. terrestris* midden [47,72]. The mortality rate of *A. caliginosa* ranged from 6.7 to 40 % in monoculture treatments (Table 1) and 6.7–27 % in mixed culture (when removing *L. terrestris* mortality from sample mortality rate). Both the control and 1 cm straw treatments had *A. caliginosa* mortality rates of 6.7 % with increasing mortality rates at the larger straw lengths. There is no evidence in this experiment to suggest that adult *A. caliginosa* benefitted from the bioturbation activity of *L. terrestris*. Observations at experimental end indicated evidence of midden development by *L. terrestris*, however, the material within the midden might not have been decomposed sufficiently for *A. caliginosa* to utilise. Further experiments over longer time periods could explore this further.

Further observations at experimental end indicated that *L. terrestris* were located on the soil surface within the surface straw; it is possible that *L. terrestris* was attempting to disperse away from *A. caliginosa*. There have been limited numbers of laboratory investigations researching interspecific effects of *L. terrestris* and *A. caliginosa*. Le Bayon and Binet [73] investigated the effects of these two species on phosphorus availability with two organic matter types (sewage sludge and ryegrass). Juveniles were tested and a positive effect of organic matter on growth was determined in mixed culture. Applications of organic matter were *ad libitum* over an 8-week period. Further research by Eriksen-Hamel et al., [74] indicated that competitive interactions occur between *L. terrestris* and *A. caliginosa* in laboratory cultures with a population size of *A. caliginosa* of N = 10 and greater. *A. caliginosa* density was much lower in the current experiment to remove potential negative laboratory-induced inter-specific interactions, where niche separation and migration are not possible [74]. Field investigations of the spatial distribution of *A. caliginosa* and *L. terrestris* burrows have indicated no patterns in burrow distribution over an unploughed field [75]. Although it is suggested that juvenile earthworms of numerous species benefit from the presence of *L. terrestris* middens [47,49,50], the ability for *A. caliginosa* hatchlings to benefit would be determined by, where within the soil profile cocoons are laid, and how easily they can locate a midden once hatched.

4.2. Straw preference by L. terrestris and A. caliginosa at micro particle sizes

Earthworm selection of straw (1 mm or 1 cm) indicated a preference for smaller particle size by both *L. terrestris* and *A. caliginosa* (Fig. 4). The preference was more pronounced with *L. terrestris*, where 100 % of 1 mm straw was removed after 15 days, with 82.7 % of this by day 6 (Table 2). These findings support those of Sizmur et al. [33] that showed milled cereal straw can have positive effects on *L. terrestris* populations. Following 100 % removal of 1 mm straw, *L. terrestris* increased the removal of 1 cm straw (Fig. 4). This highlights that *L. terrestris* can consume 1 cm straw lengths and supports findings from Experiment 1. *L. terrestris* behaviour is limited by resource availability aboveground [36], where it has been determined that in resource poor areas, *L. terrestris* will actively seek out straw deposits. Due to the burrow-midden complex of *L. terrestris*, it is possible that straw utilisation differs dependent upon particle size, where larger particles are used for midden construction and smaller particle sizes for feeding. In resource poor areas, the earthworms may be less selective. To ensure an active and healthy population of *L. terrestris*, it is recommended that a mixture of particle sizes is made available to meet both feeding and behavioural requirements.

A. caliginosa had similar particle size preferences to *L. terrestris*, however removed a lower total mass of straw over the experimental period (Fig. 4). There was a clear difference between the mass of 1 mm particle size straw removed compared with 1 cm (Table 2), however at experimental end, neither material was totally removed. The heterogenous burrowing behaviour of *A. caliginosa* could have made selection of organic matter and determination of preference less conclusive than *L. terrestris*. The lower removal rate observed with *A. caliginosa* compared with an anecic species concurred with observations by Rajapaksha et al., [56], where *A. caliginosa* removed forestry litter at a slower rate than *L. terrestris* but had similar organic matter preferences. This supports previous research that *A. caliginosa* will feed selectively on smaller particle size [35,54], and may disperse in the field towards areas which are more resource rich [76]. However, other factors accounting for *A. caliginosa* populations in agroecosystems are rainfall [73,77] and soil compaction [78]. In no-tillage systems, where the population size of *A. caliginosa* and *L. terrestris* are increased, straw particle size could have a significant impact on organic matter decomposition rate and appropriate management of residue applications could influence nutrient mineralisation within soil.

4.3. Conclusion

This investigation highlights how particle size of surface applied straw residues can have a significant impact on utilisation by earthworms through dispersal and consumption of straw from the soil surface. Surface application of modal lengths of straw found post-harvest indicated that there was a significant benefit to *L. terrestris* of 1 cm particle size compared with 20 and 40 cm lengths. Therefore, a reduction of stubble particle size to 1 cm would increase decomposition and incorporation rate in environments where *L. terrestris* populations are increased, such as no-tillage agroecosystems. *L. terrestris* incorporated most of the straw at this particle size into the upper 60 cm of soil, which could increase microbial activity and nutrient mineralisation of the material, regenerating the soil for the next season. However, consideration should be made to the burrow-midden complex of *L. terrestris* populations and the requirement for larger particle size organic matter at the burrow surface. To sustain *L. terrestris* populations, smaller applications of larger particle sized material (20–40 cm) could be used for longer term organic matter layer provision and for maintenance of a midden. In addition, there was a limited effect of modal straw length on *A. caliginosa* populations, which are the species most present in arable systems. Applications of particle size at a micro-scale indicated a food preference of 1 mm, showing how milling some material could improve food availability for earthworms in arable environments, dependent upon financial viability.

Earthworm responses to wheat straw residues have been shown as mixed. Use appears to be species (ecological group)-specific and depend on dimensions of the residues. Further work may be warranted in this area, and could usefully explore more earthworm species, be developed to a small-scale field setting with more realistic environmental factors and encompass more lengthy time periods.

CRediT authorship contribution statement

Peter Bentley: Writing – original draft, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kevin R. Butt:** Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ejsobi.2025.103799.

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