



Rhizosheath formation and persistence in winter cover crop mixtures in the field

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Abstract

Background and Aims While much research has focused on the benefits of cover crop diversity for crop productivity, there is limited evidence on how root diversity and species selection stabilise soil. Although cover crops can potentially improve on-farm soil and water management, how they bind soil (through rhizosheath development) and whether multi-species cover crops offer additional benefits has attracted little attention. This study aimed to assess rhizosheath persistence in field-grown cover crops and their mixtures to understand the impact of species diversity on soil binding capacity.

Methods *Brassica juncea*, *Secale cereale* and *Vicia faba* were sown as monocultures and mixtures in a winter cover crop field trial near Dundee, Scotland. Soil cores were collected three times during

January–March 2023. Measurements included rhizosheath mass, root length, and root hair length and density.

Results While overall rhizosheath mass decreased by 27% with plant age, *Secale cereale* maintained the largest rhizosheath mass per unit root length (1.75 and 5.60 times greater than *Vicia faba* and *Brassica juncea*, respectively) regardless of time, diversity or species combination. The fibrous rooting system and long, dense root hairs of *Secale cereale* made this cover crop exceptionally effective at binding soil. Root hair length and density partially explained (42%) the variation in rhizosheath mass.

Conclusion This field trial highlights that species selection is more important than diversity per se and indicates that *Secale cereale* is particularly effective at binding soil to the roots, suggesting it might be a particularly valuable cover crop over winter months.

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Introduction

The resilience of agroecosystems to climate stress can be strengthened by planting cover crop mixtures over the winter months. Cover crop root systems can enhance biogeochemical interactions in the rhizosphere (Hallama et al. 2019) that can improve soil health and functioning during a time of the year

where field soils would otherwise be left bare and more vulnerable to the effects of extreme weather conditions. Increasing cover crop diversity has the potential to further improve ecosystem functioning through the complementary use of resources in time and space (Brooker et al. 2021; Homulle et al. 2022).

By binding soil to the roots, rhizosheath formation has the potential to promote soil structure and stabilisation (Mo et al. 2023) by enhancing soil aggregation around root systems (Marasco et al. 2018) that is critical for mitigating soil erosion. Several factors influence rhizosheath formation and its stability such as root traits, microbial activity, soil characteristics and moisture content (Mo et al. 2023). Primarily, rhizodeposition (from root decay and root-derived exudates, including mucilage) and drying-wetting cycles facilitate soil aggregation (Carminati et al. 2010; Aslam et al. 2022; Rahim et al. 2023), and root hairs can expand rhizosheath mass (Brown et al. 2017; Burak et al. 2021). Soil aggregates in the rhizosheath have greater tensile strength than those in the bulk soil (Czarnes et al. 2000). Therefore, investigating the rhizosheath formation capacity of crops used in our agricultural systems is essential to optimise soil structure and stabilisation in our fields.

Rhizosheath formation has been mostly studied in crop species grown under controlled conditions. For example, a comprehensive glasshouse screening study confirmed rhizosheath presence in most angiosperm orders tested, but with varying specific rhizosheath masses, *i.e.* rhizosheath mass per unit of root mass, across species (Brown et al. 2017). The few field trials that exist show that specific rhizosheath weight varied across grassland species in China, becoming larger with increasing nitrogen availability (Mo et al. 2022; Tian et al. 2022). The relative lack of field data highlights the need for additional experiments to verify the factors influencing rhizosheath formation in species with contrasting rooting systems (Hallett et al. 2022; Mo et al. 2023). Since cover crops are planted to protect the soil over the winter months, complementary root traits between cover crop species could lead to synergistic or additive effects on soil binding capacity and soil stabilisation.

Although rhizosheaths can improve soil stability by aggregating soil, their persistence over time is sensitive to environmental conditions. Rhizosheath formation by grasses in a semi-arid savanna was a plastic trait that varied annually depending on

rainfall patterns, where rhizosheath thickness was greater in wetter than drier years, attributed to better growing conditions encouraging exudate production and root hair development (Hartnett et al. 2013). Similarly, Marin et al. (2021) found *Hordeum vulgare* specific rhizosheath mass (rhizosheath mass per unit of root length) decreased during the growing season in an exceptionally dry summer in the UK, whereas research in controlled conditions found that dry soils stimulated rhizosheath formation (Watt et al. 1994; Haling et al. 2014; Liu et al. 2019). Thus, the plasticity of root traits and their dynamic relationship requires further investigation to assess whether the rhizosheath persists in cover crop species over the winter months in temperate climates such as in the UK.

Root hairs, tubular-shaped outgrowths of root epidermal cells, are considered the key root trait for rhizosheath formation as they provide a physical framework to adhere to soil particles and increase the root-soil surface area contact to facilitate rhizosheath formation (Haling et al. 2010). Species without root hairs (*e.g.* *Allium schoenoprasum* and *A. cepa aggregatum*) did not form rhizosheaths (Brown et al. 2017), and although root exudation from root-hairless mutants of *Hordeum vulgare* and *Zea mays* allowed limited rhizosheath formation, soil binding was significantly greater when root hairs were present (Burak et al. 2021). Further, root hairs can promote mucilage production (Galloway et al. 2022; Marasco et al. 2018), enhancing rhizosheath formation. Therefore, understanding the root hair characteristics of cover crop species is important for assessing the soil binding capacity of their root systems.

Longer and denser root hairs can be important for rhizosheath formation, although the literature contains variable results. Tomato rhizosheath mass was positively correlated with root hair length under dry conditions, and with root hair density under well-watered conditions (Karanja et al. 2021). Specific rhizosheath mass and root hair length and density were strongly correlated in *Hordeum vulgare* (Marin et al. 2021), *Triticum aestivum* (Delhaize et al. 2012) and *Vigna unguiculata* (Opoku et al. 2022) while in different *Hordeum vulgare* genotypes (Brown et al. 2017; George et al. 2014; Haling et al. 2010) and sorghum (Adu et al. 2023) they were weakly or not correlated. Shorter root hairs have been found to correlate positively

with specific rhizosheath weight (Brown et al. 2017); with root hairs up to 300 μm long suggested to be the primary driver of rhizosheath formation (Rongsawat et al. 2021). Alternatively, when root hairs are absent or their length is $> 300 \mu\text{m}$, mucilage and other root hair traits (e.g. morphology and density) become dominant. This suggests that factors affecting rhizosheath formation dominate or complement each other depending on species and genotype.

This study investigated rhizosheath persistence in a winter cover crop mixtures field trial, assessing whether root traits such as root length, root hair length and root hair density affected rhizosheath dynamics of different cover crop combinations and whether rhizosheath mass changed over time. We hypothesised that: 1) cover crop diversity will increase rhizosheath mass; 2) rhizosheath mass will change over time; and 3) rhizosheath mass will increase with longer and denser root hairs.

Materials and methods

Field site

A winter cover-crop mixtures field trial was sown on 1st September 2022 at the James Hutton Institute's Balruddery Farm, Dundee, Scotland ($56^{\circ}28'46.6''\text{N}$ $3^{\circ}07'53.1''\text{W}$, Fig. 1). *Secale cereale* (G), *Brassica juncea* (B) and *Vicia faba* (L) were sown individually at a rate of 18.5 g/m^2 , 1.5 g/m^2 , and 20 g/m^2 respectively, and in all possible combinations in equal fractions, i.e. sowing rates for each species were halved or reduced to a third in the mixtures. The rates were recommended by the seed merchant, DLF Seeds A/S. These grass, brassica and legume species were chosen due to their suitability to climatic conditions and their contrasting plant functional groups (Tilman et al. 1997). A total of seven plant treatments were tested: grass (G), brassica (B), legume (L), grass and brassica (GB), grass and legume (GL), brassica and legume (BL), and grass, brassica and legume (GBL).

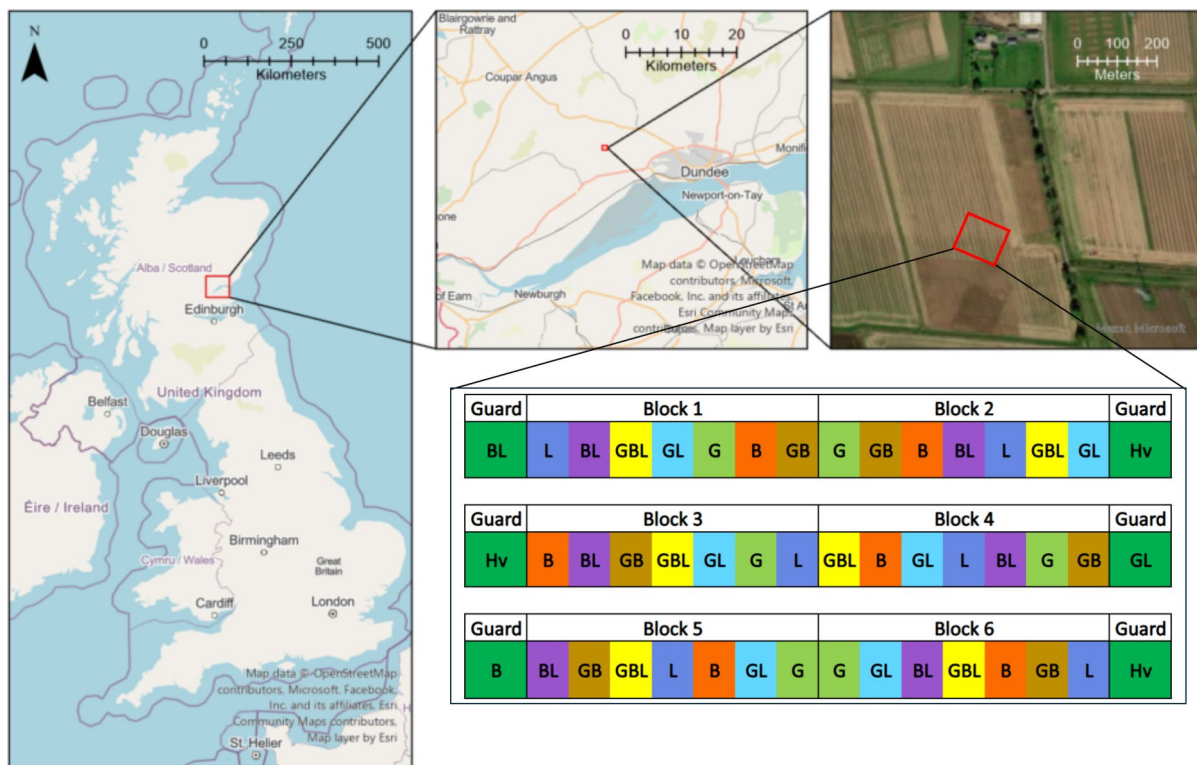


Fig. 1 Layout of field trial at Balruddery Farm, UK, comprising plots of *Secale cereale* (G), *Brassica juncea* (B), *Vicia faba* (L) as single species and in all possible combinations, includ-

ing guard plots composed of BL, *Hordeum vulgare* (Hv), GL, and B (in dark green). Basemaps: Esri, OpenStreetMap and Microsoft

The experimental layout was a randomised design of six blocks. Guard strips of barley (cv. Laureate) were sown at the ends of each block to limit edge effects on outside plots. The experimental plots (2 m long $\times$ 1 m wide) were established on a 5° slope. The soil texture was silt loam (28.47% sand, 51.35% silt, 20.18% clay). The bulk density was 1.14 g cm⁻³.

Field measurements

Plots were sampled three times: in January (30th—31st January), February (14th—15th February) and March (1st—2nd March) 2023. Total rainfall during the sampling period was 32.3 mm, and 514.1 mm between the sowing date and the end of the sampling period. At each time point, three soil moisture measurements were taken at a 7.6 cm depth in a zig-zag shape across each plot during using a FieldScout TDR 350 Soil Moisture Meter.

At each sampling, photographs were taken of a 0.5 m $\times$ 0.5 m quadrat and uploaded to Canopeo (Patrignani and Ochsner 2015) to estimate canopy coverage percentage. On the last sampling time point, the number of plant individuals of each species was recorded to calculate stem density, and aboveground biomass was harvested by cutting at the stem base, then oven-dried at 70 °C for four days and weighed.

One soil core (6.4 cm diameter $\times$ 20 cm height) was taken per plot at each sampling time point. Before taking the core, the number of plants per species present within the cored diameter was recorded, then the plants were harvested by cutting at the stem base and oven-dried at 70 °C for four days after which the dry mass was recorded. Cores were stored in a cold room at 4 °C while they were processed over the next 4–5 days. Rhizosheath development was measured by carefully breaking the core open, removing the roots from the core and gently shaking them by hand until the bulk soil detached. Using deionised water, the rhizosheath of each species was washed off the roots into a pre-weighed aluminium tray. Roots from each species were easily differentiated due to their contrasting root architectures and colouring. Rhizosheath trays were oven-dried at 105 °C overnight and the dry mass was recorded and expressed per unit area.

Roots were stored in 50% ethanol at 4 °C until all were processed together following the last sampling time point. Roots were suspended in water and an image scanned using an Epson Expression 10000XL

scanner (Epson UK, London, UK). Background colour settings were adjusted for the differing root colour of each species *i.e.* a white background for the dark *Vicia faba* roots and a black background for the light *Secale cereale* and *Brassica juncea* roots. Images were analysed for average diameter and root length using WinRHIZO (Regent Instruments, Quebec, Canada), with the latter expressed per unit area.

Root sections were then photographed using a compound light microscope (Leica MZF111, Leica Microsystems, Bannockburn, IL, USA) at 3.2x (for grass) and 5 $\times$ (for brassica and legume) magnification with a Leica DC480 camera attachment (Leica Microsystems (UK) Ltd, Milton Keynes, UK). Photographs were taken of the root hair zones of all species within all treatments and time points. Since brassica tap roots were hairless, images were taken of the finer lateral roots where hairs were present. Representative root hair length of each species within all treatments was estimated by measuring 10 individual root hairs per image using ImageJ software (U.S. National Institutes of Health, Bethesda, Maryland, USA) providing an average value for each sample which was then taken forward for further data analysis. Root hair density was calculated by counting the number of root hairs within a 1 mm² area of root surface using ImageJ. Root hair length and density were multiplied to calculate total root hair length per unit of root length, a single variable to represent the combination of both root traits.

Once the images were taken, roots were oven-dried at 70 °C for four days and the dry mass recorded. Specific rhizosheath mass was calculated by dividing the rhizosheath soil dry mass by the corresponding root length. Total rhizosheath of each species was calculated by estimating the average rhizosheath mass per plant in a core sample and then extrapolating to rhizosheath mass per m² by using the plant density determined from the number of plants in a quadrat.

Data analysis

Statistical analysis was performed in R (R Core Team 2023). To normalise the data, canopy coverage (% ground cover), root hair density (number of hairs mm⁻²), root length (cm m⁻²) and specific rhizosheath mass (g cm⁻¹, rhizosheath dry mass per unit of root length) were square root transformed, while root hair length (μm), rhizosheath dry mass (g m⁻²), total

root hair length per unit of root length, and above-ground plant dry mass (g m^{-2}) were logarithmically transformed.

Factorial repeated measures ANOVAs were performed to assess the main effects and interactions of the factors of soil moisture, sampling time, diversity, species and treatment (*i.e.* species combination) on canopy coverage, aboveground dry mass, root diameter, rhizosheath mass, root length, specific rhizosheath mass, root hair length and density, and total root hair length per unit of root length. Block was set as random factor and plot was included as a nested factor to account for repeated measures on the same plots at different time points. Pairwise comparisons using a post hoc Tukey's HSD test were conducted to identify significant differences within groups following a significant ANOVA result.

Linear regressions were performed to identify relationships between rhizosheath mass and volumetric soil moisture content; and between specific rhizosheath mass and root hair length, root hair density, and total root hair length per unit of root length. A multiple linear regression was performed to assess the combined effect of root hair length and density on specific rhizosheath mass. All results presented are mean $\pm$ standard error and significance is at a 95% confidence level. Packages used were ggplot2, stats, dplyr and emmeans.

Results

Volumetric soil moisture content did not differ ($F(6, 105) = 1.51$, $p = 0.19$) between species treatments, but decreased significantly between sampling times ($F(2, 105) = 76.67$, $p < 0.001$), averaging $22.1 \pm 0.3\%$ at time point 1, $20.8 \pm 0.2\%$ at time point 2, and $16.6 \pm 0.2\%$ at time point 3 ($n = 42$ per time point).

Canopy coverage differed significantly ($F(6, 98) = 6.63$, $p < 0.001$) across species treatments. In the three species mix (GBL) coverage averaged $33 \pm 3\%$ and was significantly greater than coverage in B ($23 \pm 2\%$; $t(98) = 3.92$, $p = 0.005$), GL ($22 \pm 2\%$; $t(98) = 4$, $p = 0.002$) and L ($19 \pm 2\%$; $t(98) = 5.66$, $p < 0.001$). The field bean monoculture coverage was significantly less than in G ($28 \pm 2\%$; $t(98) = 3.74$, $p = 0.005$), GB ($26 \pm 2\%$; $t(98) = 3.21$, $p = 0.02$) and BL ($26 \pm 2\%$; $t(98) = 3.14$, $p = 0.03$). Although not significantly different between time points overall ($F(2,$

$98) = 1.34$, $p = 0.25$), there was an interactive effect between treatments and time ($F(12, 98) = 1.71$, $p = 0.04$). Table 1 shows coverage significantly decreased between time point 2 and 3 for brown mustard (B) and field bean (L) in monocultures, but no other treatments varied significantly over time. At time point 1, field bean monoculture coverage was significantly less than that of the three species mix, but neither differed significantly from other treatments. At time point 2, both GB and GL coverage were significantly less than GBL coverage, and at time point 3, field bean monoculture coverage was significantly less than that of rye monoculture, GB, and GBL coverage. Therefore, the three species mix consistently showed the most coverage and field bean monoculture generally the least.

Aboveground plant dry biomass (g m^{-2}) differed significantly across species ($F(2, 185) = 170.14$, $p < 0.001$), diversity levels ($F(2, 185) = 29.88$, $p < 0.001$) and time ($F(2, 185) = 10.16$, $p < 0.001$) with significant interactions occurring between species and diversity ($F(4, 185) = 8.51$, $p < 0.001$) and species and time ($F(4, 185) = 3.56$, $p = 0.007$). Overall, rye aboveground biomass was approximately 3.5 times greater ($55 \pm 6 \text{ g m}^{-2}$) than brown mustard ($16 \pm 2 \text{ g m}^{-2}$), and brown mustard was 1.5 times greater than field bean ($11 \pm 1 \text{ g m}^{-2}$). Species in monoculture treatments produced significantly more aboveground biomass than when grown in mixes of two ($t(185) = 3.72$, $p < 0.001$) and three species ($t(185) = 7.25$, $p < 0.001$), as well as being greater in mixes of two

Table 1 Coverage (%) and standard error of the mean of all treatments per sample time ($n = 6$)

	T1	T2	T3
Grass (G)	26.5 (± 2.3) ^{ab}	24.6 (± 1.6) ^{ab}	32.0 (± 2.4) ^a
Brassica (B)	22.1 (± 3.0) ^{ab AB}	29.8 (± 1.8) ^{ab A}	19.4 (± 3.9) ^{ab B}
Legume (L)	19.3 (± 2.7) ^{b AB}	24.2 (± 2.2) ^{ab A}	13.5 (± 1.7) ^{b B}
BL	25.3 (± 1.8) ^{ab}	29.1 (± 2.0) ^{ab}	24.1 (± 4.1) ^{ab}
GB	25.8 (± 2.6) ^{ab}	23.6 (± 1.1) ^b	29.6 (± 2.8) ^a
GL	21.1 (± 2.4) ^{ab}	21.6 (± 1.5) ^b	25.9 (± 2.9) ^{ab}
GBL	32.2 (± 4.3) ^a	35.5 (± 5.7) ^a	31.0 (± 4.7) ^a

Values not sharing a letter are significantly different from each other ($p < 0.05$). Significant differences between treatments within each time point (columns) are shown by lower case letters. Significant differences between time point within each treatment (rows) are shown by upper case letters

rather than three species ($t(185) = 4.65$, $p = 0.001$). Field bean followed this decreasing pattern with increasing diversity, while brown mustard decreased from a monoculture to two ($t(185) = 3.47$, $p = 0.01$) and three species mixes ($t(185) = 5.46$, $p < 0.001$), but not between two and three species mixes ($t(185) = 2.88$, $p = 0.09$). Rye aboveground biomass did not differ significantly between diversity levels (Table 2). Overall, aboveground biomass increased significantly from time point 1 to 2 ($t(185) = 4.18$, $p = 0.001$) by 31% and did not significantly change from time point 2 to 3 ($t(185) = 2.2$, $p = 0.07$) or time point 1 to 3 ($t(185) = 0.84$, $p = 0.67$). The increase in mass from time point 1 to 2 was driven largely by an increase in dry mass of brown mustard, specifically when grown in the three species mix (GBL) (Table 2). Thus, rye consistently maintained the greatest aboveground dry mass regardless of species combination and time point, while field bean and brown mustard aboveground dry mass decreased with increasing diversity.

Root diameter was significantly ($F(2, 185) = 525.76$, $p < 0.001$) greater in field bean, averaging 1.12 ± 0.03 mm, whereas rye and brown mustard averaged 0.38 ± 0.01 mm and 0.38 ± 0.01 mm respectively. Average root diameter (mm) did not change significantly with time ($F(2, 185) = 0.65$, $p = 0.52$) or diversity level ($F(2, 185) = 2.4$, $p = 0.09$).

Root length (cm m^{-2}) differed significantly between species ($F(2, 185) = 224.9$, $p < 0.001$). On average, rye roots ($8,807 \pm 345 \text{ cm m}^{-2}$) were longer than those of brown mustard ($3,678 \pm 255 \text{ cm m}^{-2}$), and field bean roots were the shortest ($2,042 \pm 149 \text{ cm m}^{-2}$). Overall root length (cm m^{-2}) was significantly

greater in monocultures than in the two ($t(185) = 3.64$, $p = 0.001$) and three species mixes ($t(185) = 4.67$, $p < 0.001$), but did not differ significantly ($t(185) = 1.8$, $p = 0.17$) between the two and three species mixes. This pattern was found in brown mustard, where root length in a monoculture was greater than in the two ($t(185) = 3.22$, $p = 0.03$) and three species mixes ($t(185) = 3.78$, $p = 0.006$), but similar ($t(185) = 1.2$, $p = 0.95$) between two and three species mixes. Brown mustard root length was greater in a monoculture than in GB ($t(185) = 3.87$, $p = 0.008$) and GBL ($t(185) = 3.89$, $p = 0.007$) but was not significantly different to BL ($t(185) = 1.76$, $p = 0.83$), and the mixes did not differ between each other. Field bean root length in a monoculture was significantly greater than in the three species mix ($t(185) = 4.2$, $p = 0.001$), but was not significantly different between the monoculture and the two ($t(185) = 2.86$, $p = 0.10$) or the two and three species mixes ($t(185) = 2$, $p = 0.54$). Rye root length did not differ significantly between diversity levels (Fig. 2). Although the species with longest roots (rye) maintained its length across diversity levels, growing brown mustard and field bean in mixes decreased their root lengths compared to their growth in monocultures.

Cover crop diversity significantly decreased ($F(2, 185) = 11.09$, $p < 0.001$) total rhizosheath mass (g m^{-2}). Overall, monocultures had a significantly larger rhizosheath mass than two ($t(185) = 2.83$, $p = 0.01$) and three species ($t(185) = 4.57$, $p < 0.001$) mixes, being significantly smaller in the three species than the two species mixes ($t(185) = 2.47$, $p = 0.03$) (Fig. 3).

Table 2 Aboveground plant dry mass (g m^{-2}) and standard error of the mean of all treatments per sample time ($n = 6$)

Values not sharing a letter are significantly different from each other ($p < 0.05$). Significant differences between treatments within each time point (columns) are shown by lower case letters. Significant differences between time point within each treatment (rows) are shown by upper case letters

	T1	T2	T3
Grass (G)	56.62 (± 13.37) ^a	63.11 (± 7.66) ^a	30.48 (± 2.65) ^{abc}
Brassica (B)	14.70 (± 2.73) ^{ab}	26.60 (± 5.00) ^{abc}	37.21 (± 14.37) ^{ab}
Legume (L)	19.21 (± 2.96) ^{ab}	23.37 (± 3.15) ^{abc}	16.27 (± 3.37) ^b
BL—B	11.04 (± 3.67) ^{bcd}	21.76 (± 3.16) ^{abc}	24.36 (± 5.88) ^{abc}
BL—L	12.32 (± 3.54) ^{bc}	13.74 (± 2.26) ^{bcd}	11.91 (± 2.03) ^{cd}
GB—G	50.31 (± 6.69) ^a	72.64 (± 2.63) ^a	56.76 (± 11.18) ^a
GB—B	7.37 (± 2.42) ^{bcd}	11.83 (± 2.63) ^{cd}	7.93 (± 1.89) ^{cd}
GL—G	61.59 (± 20.82) ^a	50.09 (± 7.42) ^{ab}	70.51 (± 14.33) ^a
GL—L	7.51 (± 1.50) ^{bcd}	8.95 (± 2.03) ^{cd}	6.96 (± 1.11) ^{cd}
GBL—G	33.03 (± 4.00) ^a	60.68 (± 8.53) ^a	51.39 (± 6.06) ^{ab}
GBL—B	3.40 (± 1.19) ^{dB}	10.86 (± 1.76) ^{cd A}	10.7 (± 2.08) ^{cd AB}
GBL—L	3.97 (± 1.28) ^{cd}	5.82 (± 2.20) ^d	4.83 (± 1.40) ^d

Fig. 2 Root length (cm m^{-2}) across species treatments distinguishing the species within treatments by colour, where green is *Secale cereale* (G), yellow is *Brassica juncea* (B) and blue is *Vicia faba* (L) ($n = 18$ per boxplot). Boxes indicate the 25 & 75% quartile and lines the median, with smaller points indicating individual samples. Species significantly ($p < 0.05$) differ from each other if they do not share a letter

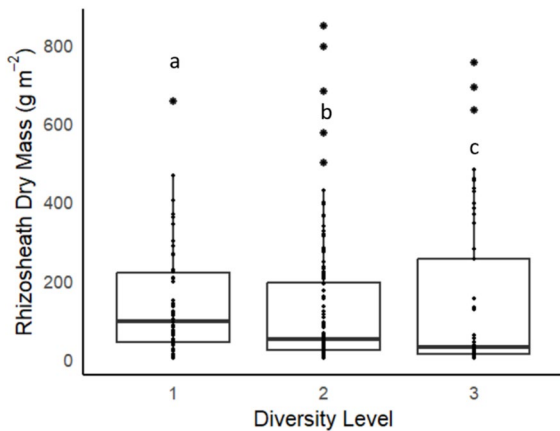
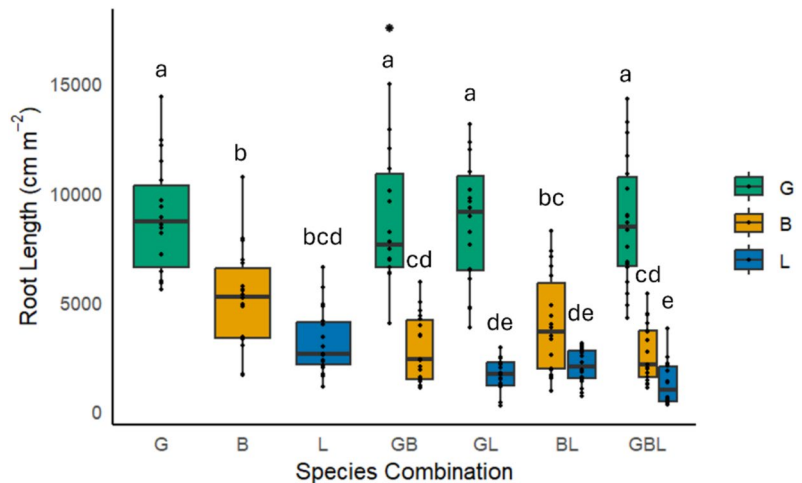


Fig. 3 Rhizosphere dry mass (g m^{-2}) across diversity levels (level 1 $n = 54$; level 2 $n = 108$; level 3 $n = 54$). Boxes indicate the 25 & 75% quartile and lines the median, with smaller points representing individual species per plot. Diversity levels significantly differ ($p < 0.05$) from each other if they do not share a letter

Rhizosphere mass (g m^{-2}) differed significantly ($F(2, 185) = 228.02$, $p < 0.001$) between species. On average, rye bound 7 times more soil ($325.0 \pm 20.3 \text{ g m}^{-2}$) than field bean ($49.0 \pm 4.6 \text{ g m}^{-2}$) and 11 times more than brown mustard ($28.7 \pm 3.2 \text{ g m}^{-2}$). There was a significant interaction ($F(4, 185) = 7.58$, $p < 0.001$) between diversity level and species driven by field bean rhizosphere mass, which was overall significantly larger in a monoculture than in the two species ($t(185) = 3.85$, $p = 0.005$) and the three species mixes ($t(185) = 6.67$, $p < 0.001$), and significantly larger in two than three species mixes ($t(185)$

$= 3.87$, $p = 0.004$). At the treatment level, field bean rhizosphere mass was significantly larger in a monoculture than in GL and in GBL ($t(200) = 3.53$, $p = 0.02$ and $t(200) = 7.09$, $p < 0.001$, respectively), but not significantly different to BL ($t(200) = 3.23$, $p = 0.06$). Brown mustard rhizosphere mass was significantly smaller in GBL than BL ($t(200) = 3.84$, $p = 0.008$), but remained similar across all other treatments. For rye, rhizosphere mass did not differ across diversity levels or treatments. Thus, rye bound the largest amount of soil per m^2 regardless of diversity and species combination, brown mustard bound the least amount of soil regardless of diversity and species combination except when grown in a three species mix (GBL), and field bean bound more soil in a monoculture and when grown with brown mustard (BL) than when grown with rye (GL, GBL) (Fig. 4).

Rhizosphere mass (g m^{-2}) decreased with time ($F(2, 185) = 4.41$, $p = 0.01$), specifically between time point 1 and 3 ($t(185) = 2.62$, $p = 0.02$) by 27% (Fig. 5). Rhizosphere dry mass increased significantly ($F(1, 213) = 4.35$, $p = 0.03$) with soil moisture, although moisture explained little of the variation ($r^2 = 0.01$).

Root length (cm m^{-2}) did not change significantly over time ($F(2, 185) = 0.09$, $p = 0.9$), however specific rhizosphere mass (rhizosphere dry mass per unit of root length) did ($F(2, 185) = 6.71$, $p = 0.01$). Overall, specific rhizosphere mass decreased by 22% from time point 1 to time point 3, and did not change ($F(4, 185) = 0.34$, $p = 0.84$) within species over time (Fig. 6a) but differed between species ($F(2, 185) = 157.33$, $p < 0.001$). Specific rhizosphere mass of

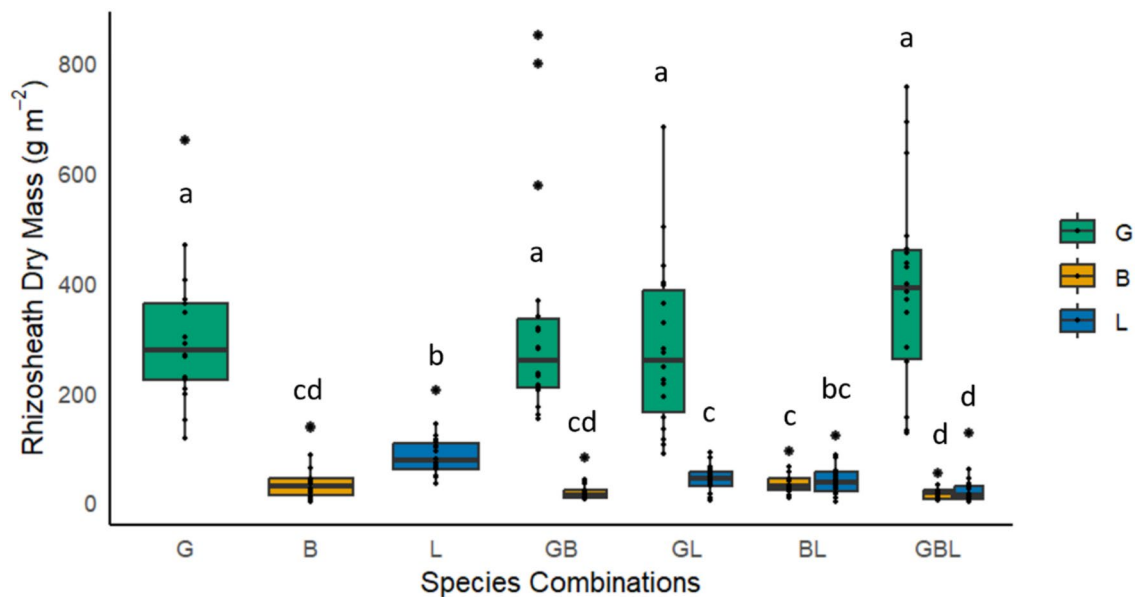


Fig. 4 Rhizosheath dry mass (g m^{-2}) across species treatments distinguishing the species within treatments by colour, where green is *Secale cereale* (G), yellow is *Brassica juncea* (B) and blue is *Vicia faba* (L), ($n = 18$ per boxplot). Boxes

indicate the 25 & 75% quartile and lines the median, with smaller points indicating individual samples. Species significantly ($p < 0.05$) differ from each other if they do not share a letter

rye was 1.75 times greater than field bean and 5.60 times greater than brown mustard, while that of field bean was 3 times greater than brown mustard. Specific rhizosheath mass does not change within species across species combinations (Fig. 6b), and was greater in rye particularly when combined with field bean and brown mustard (GBL).

Across species, specific rhizosheath mass was significantly positively related to root hair length ($F(1, 213) = 155.50$, $p < 0.001$; $r^2 = 0.41$) and density ($F(1, 213) = 75.56$, $p < 0.001$; $r^2 = 0.25$), with both independent variables being correlated with each other ($F(1, 213) =$, $p < 0.001$, $r^2 = 0.57$) and together explaining 42% of specific rhizosheath mass variation (Fig. 7a,b). When total root hair length per unit of root length was calculated, specific rhizosheath mass was also significantly positively related with this variable ($F(1, 213) = 141.1$, $p < 0.001$; $r^2 = 0.39$) (Fig. 7c). However, within each species, specific rhizosheath mass was not significantly related to root hair length, to root hair density, or total root hair length per unit of root length (Table 3). Diversity level did not affect root hair length ($F(2, 185) = 0.33$, $p = 0.71$), density ($F(2, 185) = 1$, $p = 0.36$), or total root hair length per unit of root length ($F(2, 185) = 0.39$, $p = 0.67$), but

all differed significantly between species ($F(2, 185) = 950.61$, $p < 0.001$; $F(2, 185) = 120.43$, $p < 0.001$; and $F(2, 185) = 578.82$, $p < 0.001$, respectively). Brown mustard had the shortest and least dense root hairs, field bean had longer and denser root hairs, and rye had the longest and densest root hairs (Table 4, Fig. 8). Thus, variation in root hair traits affected rhizosheath mass.

Discussion

To our knowledge, this study is the first to assess the persistence of rhizosheath mass in three functionally diverse cover crop species grown in the field. We provide evidence that cover crop species rather than diversity is key for rhizosheath formation, with specific root traits such as those of rye retaining more soil regardless of sowing density. While farmer selection of cover crop species may be determined by their other benefits to cropping systems, species differences in rhizosheath formation suggest opportunities for maximising soil aggregation.

Overall, species grown in monocultures bind more soil per m^2 than when grown in mixtures (Fig. 3), in

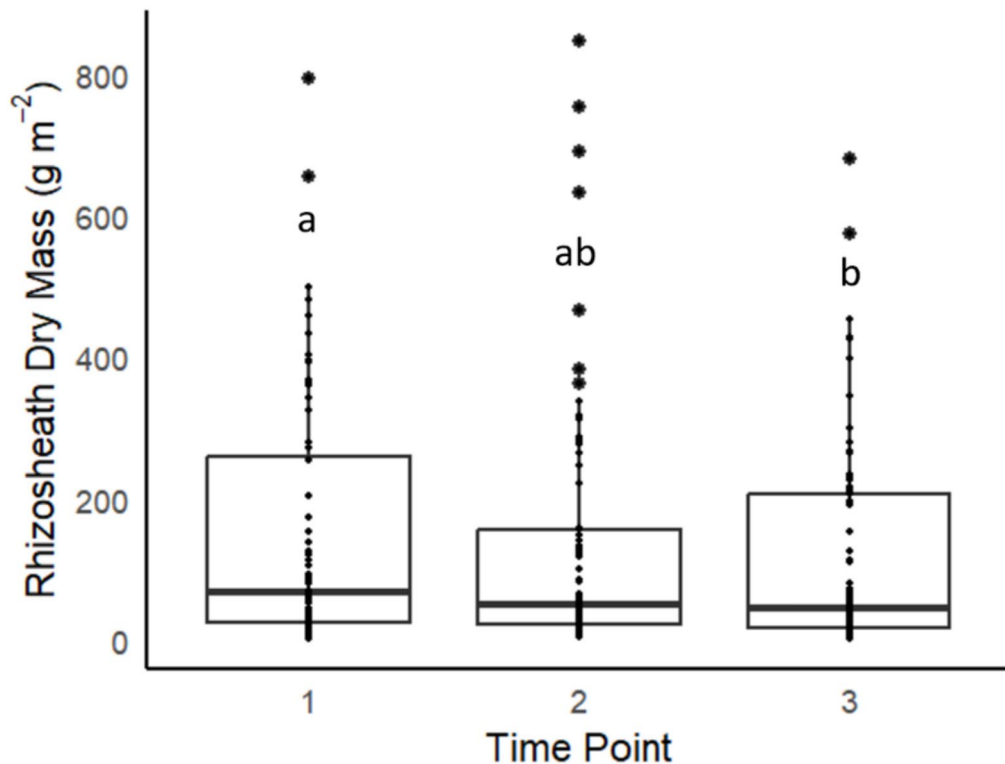


Fig. 5 Rhizosheath dry mass (g m^{-2}) across time points ($n = 72$ per boxplot). Boxes indicate the 25 & 75% quartile and lines the median, with points indicating individual samples.

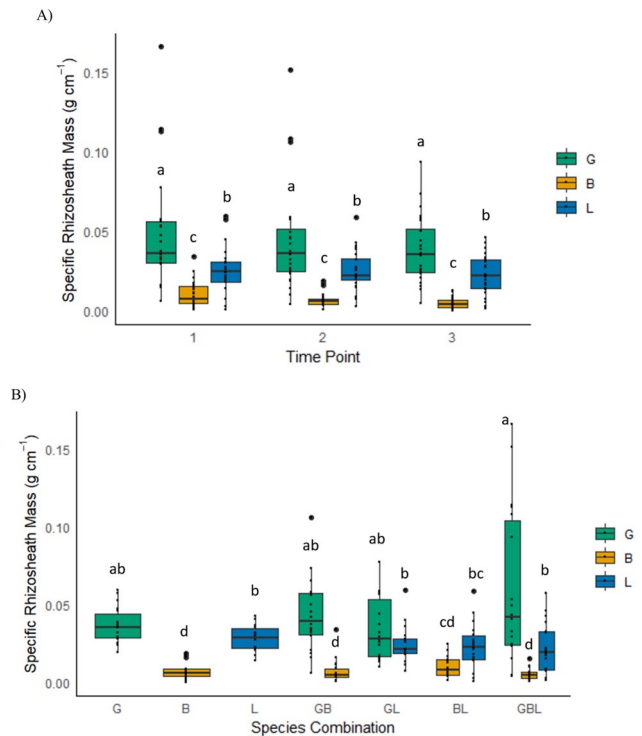
Time points are significantly different ($p < 0.05$) from each other if they do not share a letter

contrast to our hypothesis that cover crop diversity would increase rhizosheath mass. This is partly due to the different soil binding ability of certain species as well as the reduction of plant density with increasing diversity. Sowing rates for each species were halved or reduced to a third in the mixtures, leading to a reduction in rhizosheath mass per m^2 particularly for field bean, probably due to its already low sowing density. However, rye rhizosheath mass per m^2 maintained a large rhizosheath mass irrespective of whether sown at low (mixtures) or high (monoculture) density (Fig. 4), suggesting that it is highly competitive for space both with itself (intraspecific) and with the other two species (interspecific). This result suggests that rye could be sown at a lower monocrop density than recommended by cover crop seed suppliers.

Rye suppressed the soil binding capacity of field bean through competition, as field bean bound more soil per m^2 when combined with brown mustard than when combined with rye. The complementary

relationship between brown mustard and field bean and competitive effect of rye was also observed in the differences in canopy ground coverage (Table 1), aboveground biomass (Table 2), root dry mass (Table S1) and root length (Fig. 2) and specific rhizosheath mass (Fig. 6b) between species and cropping combinations. Rapidly establishing grass species typically dominate in mixed systems, especially over legumes (Hauggaard-Nielsen et al. 2012; Farney et al. 2018). Root interactions determine this competitive effect, as physical barriers in the soil between grass and legume species doubled legume aboveground biomass (Walker and King 2009). Rye's fibrous rooting system extends throughout the topsoil, while the taproots of brown mustard and field bean grow towards the subsoil (Kemper et al. 2020). These differences in root spatial distribution complement each other, leading to positive effects on root development (root length and mass density, specific root length) and nutrient acquisition (Kemper et al. 2022). Although we expected to see niche differentiation

Fig. 6 Specific rhizosheath mass (rhizosheath dry mass per unit of root length, g cm^{-1}) across time points ($n = 24$ per boxplot) (A) and species treatments ($n = 18$ per boxplot) (B) distinguishing the species within time points or treatments by colour, where green is *Secale cereale* (G), yellow is *Brassica juncea* (B) and blue is *Vicia faba* (L), ($n = 24$ per boxplot). Boxes indicate the 25 & 75% quartile and lines the median, with smaller points indicating individual samples. Species significantly ($p < 0.05$) differ from each other if they do not share a letter



allowing each species to develop relatively larger root and rhizosheath masses when grown in mixtures, the root spatial distribution of rye and its ability to extend and fill the available space suppressed the soil binding capacity of other species.

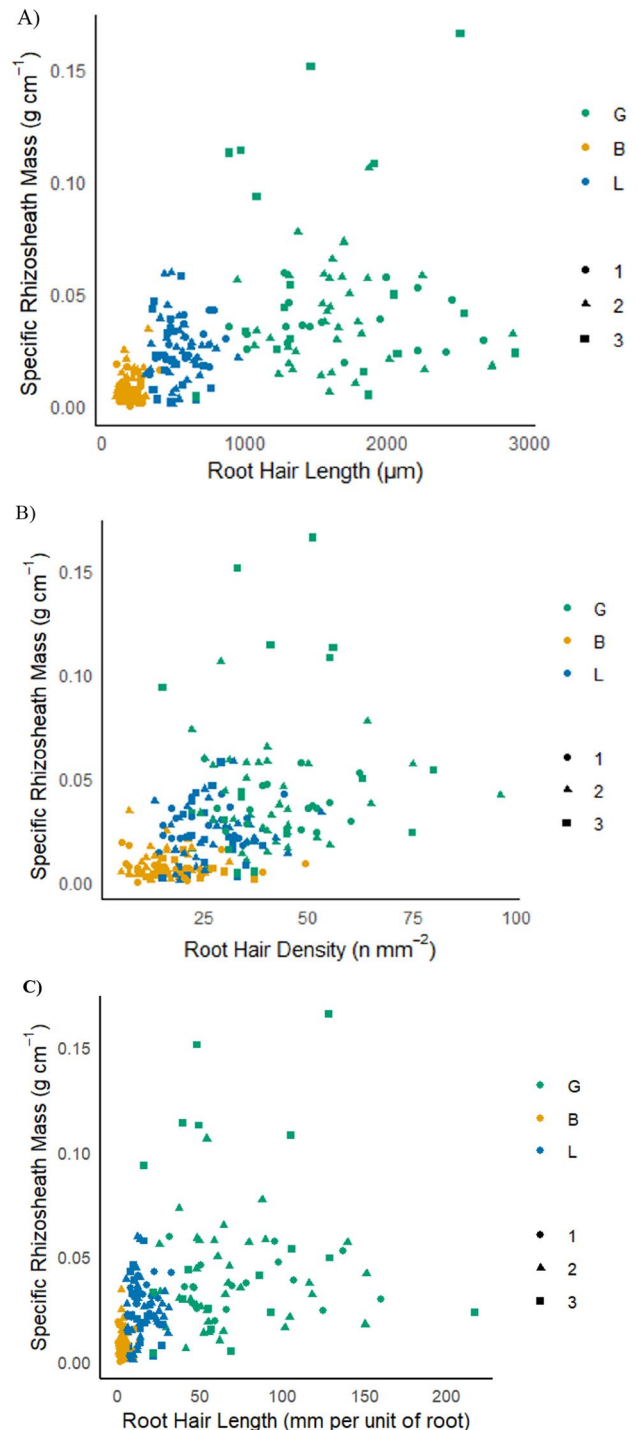
Over time, the cover crops bound less rhizosheath soil, confirming our second hypothesis. Although there was no reduction in root length with time, soil binding capacity (rhizosheath mass per m^2) and specific rhizosheath mass overall decreased by 27% and 22%, respectively, from the start to the end of the trial. Nevertheless, specific rhizosheath mass of each individual species did not statistically change over time (Fig. 6a). Barley rhizosheath mass also decreased with plant age in a field trial of similar duration (George et al. 2014), possibly linked to an increase in rainfall and soil moisture content. Rhizosheath is a plastic trait that changes with soil moisture, with larger maize rhizosheaths (rhizosheath volume) under dry conditions in a controlled environment (Watt et al. 1994), but larger rhizosheaths (rhizosheath thickness) in the field in wetter years due to better growing conditions that encouraged root activity (Hartnett et al. 2013). In this study, soil moisture decreased with time as did rhizosheath mass. However, limited soil drying

between January and March in Scotland (soil moisture ranged from 22.1% to 16.6%) seemed insufficient to encourage soil aggregation and affect rhizosheath formation. Since soil moisture explained little of the variability in rhizosheath mass ($r^2 = 0.01$), other factors were more important in determining rhizosheath mass.

Plant maturity may have diminished rhizosheath formation over time. Younger, actively growing root systems with greater root exudation may stimulate rhizosheath formation, while root hair death and lignification in older roots likely weakened rhizosheath attachment to the roots. Soil retention capacity of ryegrass and alfalfa, with a fibrous and taproot systems respectively, was greater during early growth stages and then gradually decreased as plants aged due to stunted root growth following unfavourable weather conditions (Liu et al. 2024). In the present field trial, the cover crops were sown in September and sampled from January to March, when the winter months constrained growth and temperatures were gradually increasing but not yet reaching favourable temperatures for greater root development.

Root hair length and density contributed to rhizosheath formation, confirming our third hypothesis.

Fig. 7 Specific rhizosheath mass (rhizosheath dry mass per unit of root length, g cm^{-1}) plotted against root hair length (A), root hair density (B) and total root hair length per unit of root length (C) with species distinguished by colour (*Secale cereale* (G) in green, *Brassica juncea* (B) in yellow and *Vicia faba* (L) in blue), and diversity levels distinguished by shape (n in Species B = 72, G = 72 and L = 72; n in diversity level 1 = 54, 2 = 108 and 3 = 54)



Longer root hairs are associated with larger rhizosheaths (Delhaize et al. 2012; Marin et al. 2021; Opoku et al. 2022) as our results show overall (Fig. 7a and Table 3). Rongsawat et al. (2021) suggested root

hair length is the primary driver of rhizosheath formation when root hairs are $<300 \mu\text{m}$, and, beyond $300 \mu\text{m}$, other root hair traits, such as density, become more important. Here, no relationships were found for

Table 3 Relationships between specific rhizosheath mass (g cm^{-1}) and root hair length (RHL, μm) and density (RHD, number mm^{-2}), and total root hair length per unit of root length (RHL mm^{-1} root) for each species, overall, and the overall combined effect of root hair length and density on specific rhizosheath mass with slope, F-value and degrees of freedom, significance ($p < 0.05$) and coefficient of determination (r^2) reported

Species	RHL (μm)	RHD (n mm^{-2})	RHL mm^{-1} root
<i>Brassica juncea</i> (B)	$y = 0.08 - 0.01x$ F (1, 69) = 0.01 $p = 0.99$ $r^2 = -0.01$	$y = 0.1 - 0.003x$ F (1, 70) = 0.71 $p = 0.40$ $r^2 = -0.01$	$y = 0.08 - 0.004x$ F (1, 69) = 0.51 $p = 0.47$ $r^2 = -0.006$
<i>Secale cereale</i> (G)	$y = 0.21 - 0.01x$ F (1, 70) = 0.01 $p = 0.95$ $r^2 = -0.01$	$y = 0.16 - 0.005x$ F (1, 70) = 0.71 $p = 0.48$ $r^2 = -0.01$	$y = 0.17 + 0.004x$ F (1, 70) = 0.09 $p = 0.75$ $r^2 = -0.01$
<i>Vicia faba</i> (L)	$y = 0.46 + 0.05x$ F (1, 70) = 0.16 $p = 0.68$ $r^2 = 0.01$	$y = 0.11 + 0.007x$ F (1, 70) = 1.27 $p = 0.26$ $r^2 = 0.01$	$y = 0.12 + 0.01x$ F (1, 70) = 0.92 $p = 0.33$ $r^2 = -0.001$
Overall	$y = 0.04x - 0.16$ F (1, 213) = 155.50 $p < 0.001$ $r^2 = 0.41$	$y = 0.01 + 0.02x$ F (1, 213) = 75.56 $p < 0.001$ $r^2 = 0.25$	$y = 0.06 + 0.03x$ F (1, 213) = 141.1 $p < 0.001$ $r^2 = 0.39$
Combined effect	$y = -0.16 + 0.04\text{RHL} + 0.002\text{RHD}$ F (2, 212) = 77.63 $p < 0.001$ $r^2 = 0.42$		

Table 4 Average root hair length (RHL, μm), density (RHD, number mm^{-2}) and total root hair length per unit of root length (RHL mm^{-1} root) per species with the standard error of the

mean in brackets. Species are significantly different from each other ($p < 0.001$) if they do not share a letter

Species	n	RHL (μm)	RHD (n mm^{-2})	RHL mm^{-1} root
<i>Brassica juncea</i> L. (B)	72	197 (± 7) ^c	17 (± 1) ^c	3.5 (± 0.3) ^c
<i>Secale cereale</i> L. (G)	72	1,636 (± 59) ^a	42 (± 2) ^a	71.3 (± 4.6) ^a
<i>Vicia faba</i> L. (L)	72	545 (± 16) ^b	26 (± 1) ^b	15.2 (± 0.9) ^b

individual species between root hair length or density and specific rhizosheath mass (Table 3), although the shorter ($< 300 \mu\text{m}$) and sparser root hairs in mustard bound less soil than the longer ($< 300 \mu\text{m}$) and denser root hairs in field bean and rye (Fig. 7a). This suggests hair density is of greater importance in $< 300 \mu\text{m}$ long root hairs than proposed. Across all species that varied in root hair length (197–1636 μm), overall root hair density explained 25% of the variation in rhizosheath similar to sorghum (14%—Adu et al. 2023) and cowpea (20%—Opoku et al. 2022). While root hair length explained more (41%) of the variation of specific rhizosheath mass (increasing to 42% when combined with root hair density), both variables were correlated. When root hair length and density were combined into a single variable (total root hair length per unit of root length), the variation in specific rhizosheath mass accounts for slightly lesser (39%)

variation than average root hair length alone. This suggests that while both traits contribute to rhizosheath development, average root hair length may have a stronger individual influence compared to average root hair density, or that their combined effect does not enhance explanatory power beyond average root hair length alone. Although average root hair length seems the primary driver for rhizosheath formation, other factors such as mucilage (Akhtar et al. 2018; Galloway et al. 2022) are likely to also be important.

Interestingly, rye had the greatest total root hair length per unit of root length *i.e.* both the longest and most dense root hairs of the three species, a combination that allows it to provide the most suitable root structure for rhizosheath expansion and therefore form the largest rhizosheath mass of the three species. However, not all variation in rhizosheath mass was explained by root hair length and density. Although

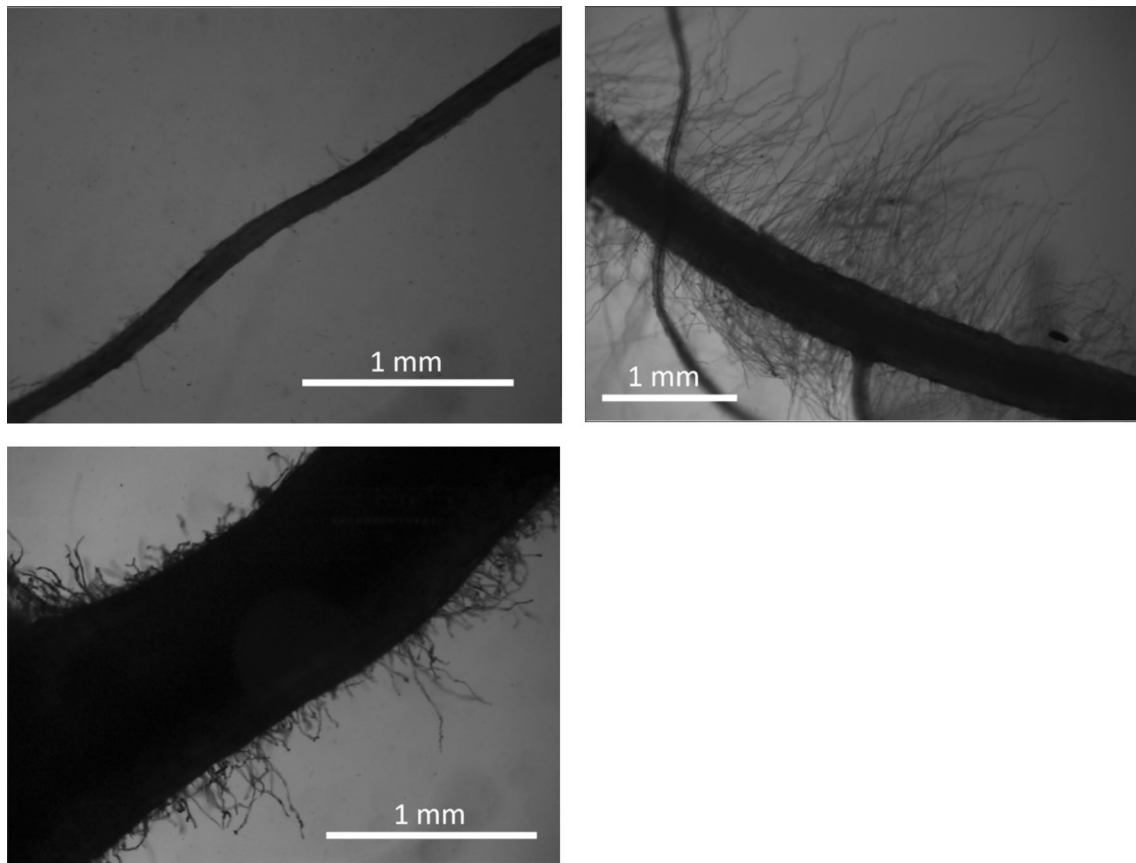


Fig. 8 Example photographs, randomly selected, of root hairs in *Brassica juncea* (top left), *Secale cereale* (top right) and *Vicia faba* (bottom left)

rye is clearly an important species for binding soil compared to field bean and brown mustard, further work is needed to clarify the mechanisms by which these species bind soil and form a rhizosheath, such as through mucilage production.

The greater soil binding capacity of rye, along with other above-ground factors, may have facilitated its dominance over the other species through better access to resources. Root hairs enhance nutrient and water acquisition (Haling et al. 2013; Marin et al. 2021; Duddek et al. 2022) by increasing root-soil contact. The long and dense root hairs of rye coupled with its fibrous rooting system, which can expand and fill the available space, increases the volume of accessible soil, both for resource exploitation and for soil binding and retention. This may result in rye's further expansion and ability to outcompete the other species, binding more soil in the process. Therefore, selecting rye and other cover crop species with similar root

traits will help retain and protect the soil over the winter months.

A key finding here is that the presence of certain species dictates the cover crop mixture's soil binding capacity. This highlights the importance of selecting cover crops for functional diversity rather than species diversity. Mahaut et al. (2020) found that species do not contribute equally to ecosystem functioning suggesting some play a greater role than others in regulating a given function, and in the present study rye could be considered a key species for improving the soil binding capacity of a system. Further, it may be possible to design cover crops mixtures for better soil binding by selecting for root traits such as root hair length and density and root exudation.

The persistence of cover crop rhizosheaths over time, particularly after cover crop termination, remains largely unknown. Since the rhizosheath is a hotspot for plant-soil-microbe interactions, its

potential to influence soil function beyond the lifespan of the cover crop is of significant interest. Rhizosheath-associated bacterial communities could persist in the soil and shape microbial dynamics that could benefit the subsequent cash crop. These microbial legacies may enhance nutrient cycling, soil structure, and ultimately benefit productivity of the subsequent crop. For example, the extent to which arbuscular mycorrhizal associations, which promote soil aggregation and structure formation (Peng et al. 2013), persist after the cover crop and benefit the following crop is unknown. Understanding this legacy effect could inform better cover crop management strategies to optimise long-term soil health.

Beyond beneficial microbial interactions, the role of rhizosheaths in interacting with other soil organisms, such as pathogenic microbes, nematodes, and invertebrate pests, also remains unknown. Cover crops can act as reservoirs for pests and pathogens that impact the following crop (Rand et al. 2022). While rhizosheaths may create favourable conditions for beneficial microbes, they could also influence pest populations or harbour pathogens that impact both the cover crop and subsequent cash crops. Future research should investigate how rhizosheath formation and microbial legacies vary across different cover crop species and species mixtures. Exploring whether certain species combinations enhance beneficial microbial persistence while minimizing pathogen carryover could refine cover crop selection not just to protect soil during the winter months, but also for optimising soil conditions for the following crop. Such insights could contribute to more resilient agroecosystems by leveraging the biological and structural benefits of rhizosheaths beyond the cover crop phase.

In summary, this study contributes novel field data on the mass and persistence of the rhizosheath and the traits associated with its formation in several functionally diverse cover crop species. The presence of certain species rather than diversity *per se* is more important in determining rhizosheath formation. While overall rhizosheath mass decreased with plant age, rye maintained the largest rhizosheath out of the three species regardless of time, diversity level or species combination and outcompeted brown mustard and field bean. Root morphological traits in rye, such as its fibrous rooting system and long, dense root hairs, make this cover crop

potentially highly effective at binding soil. Root hair length and density explained only moderate to weak variation in rhizosheath mass, therefore other factors like mucilage production or composition are likely to be important. The ability of rye to extend and fill the space equally regardless of sowing density coupled with its extensive soil binding capacity, makes this species an excellent choice to include in a cover cropping system for soil retention. Further research on rhizosheath formation mechanisms could enable the design of cover crop mixtures with better soil binding by selecting complementary root traits such as root hair length, density, and exudation, while also considering the competitive nature of the species. Whether the persistence of cover crop rhizosheaths and their associated bacterial and fungal communities influence soil function for the subsequent crop is unknown and may be an important consideration for cover crop selection.

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Authors Contributions Conceptualization, CMS, ICN, JNQ, TSG, AJK; Supervision, ICN, JNQ, TSG, AJK; Data curation, CMS; Formal analysis, CMS; Investigation, CMS; Methodology, CMS, AJK.; Writing—original draft, CMS; Writing—review and Editing, ICN, JNQ, TSG, AJK.

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Data availability Raw data that support this study are available as electronic supplementary material.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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