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Cover cropping increases the abundance of mycorrhizal and endophytic fungi structures associated with ecosystem functioning

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Abstract

Soil is one of the most complex microbial environments on earth, providing many ecosystem services to benefit humankind. Many of the services associated with soil microorganisms are particularly important to the agricultural industry as these improve crop stress tolerance, nutrition, and yield. However, conventional agricultural practices that use excessive chemical inputs, tillage, and monocropping have diminished the soil biosphere and lessened the ecosystem services that microbes are able to provide. Cover cropping is one of the key principles underpinning conservation agriculture systems. Despite it being relatively well-known that cover cropping has a beneficial impact on the overall abundance and community structure of soil microbes, the effects on specific microbial structures and their functions are vastly under-researched. In fact, some fungal structures investigated in this study have never been examined under cover cropping systems before. Therefore, soil samples were taken from five cover cropped and five conventionally managed fields growing spring bean (*Phaseolus vulgaris*) in Kent, UK, and the abundance of seven key mycorrhizal and endophytic fungal structures were identified. Cover cropping was associated with a significantly higher abundance of hyphae, arbuscules, vesicles, moniliform hyphae, and microsclerotia, but not spores or chlamydospores. Since these structures are known to be associated with nutrient exchange, overwintering and long-term survival, energy storage, and branching and inoculation, cover cropping practices are likely to improve the functioning of mycorrhizal and endophytic fungi.

Plain Language Summary

As the global population grows, demand for food increases, as does the need for sustainable agricultural approaches to meet our current food needs without compromising the ability of future generations to meet theirs. Cover cropping is where a crop is planted between harvests to protect and improve the soil that main crops are grown in. Soil organisms like fungi benefit from cover cropping by increasing in number and

Abbreviations: CC, cover cropping/cover cropped; NCC, non cover cropping/non cover cropped.

diversity. However, we do not yet understand how cover cropping affects the many functions these organisms perform that improve crop health. This study investigated how seven fungal structures—associated with functions like nutrient uptake, long-term survival, and reproduction—are affected by cover cropping. Cover cropping increased abundance of five of the fungal structures studied and did not affect the other two. The results suggest that these soil organisms may be better at performing their beneficial functions under cover cropping than conventional agriculture.

1 | INTRODUCTION

1.1 | Agriculture and soil health

Intensive, monocultural management practices, referred to widely as conventional agriculture, diminish soil health and the ecosystem services that the surrounding biosphere could provide (Finney et al., 2017). However, conservation agriculture is becoming recognized as an important tool to support sustainable food production and buffer productivity under future climate change scenarios (Page et al., 2020). Conservation agriculture is a "system of agronomic practices that includes reduced tillage or no-tillage, permanent organic soil cover by retaining crop residue, and crop rotations such as cover crops" (Palm et al., 2014). It applies modern agricultural technology, improving productivity, while working concurrently to protect and enhance land resources on which production depends (Dumanski et al., 2006). Conservation agriculture can help to ensure that food demands are met by optimizing yield and profit margins and undertaking soil conservation practices, creating a middle ground between conventional agriculture and organic farming (Dumanski et al., 2006).

1.2 | Cover cropping (CC)

CC is central to conservation agriculture, where noncash crops are grown primarily to protect or improve soil, providing permanent surface cover between growing seasons of main crops (Baumhardt & Blanco-Canqui, 2014). There are a multitude of benefits associated with CC, for example, CC can boost crop yields (Chu et al., 2017; Finney et al., 2017; Miguez & Bollero, 2005; Wittwer et al., 2017); improve nutrient cycling (Adetunji et al., 2020; Chu et al., 2017; Finney et al., 2017; Koudahe et al., 2022; Wittwer et al., 2017); increase soil organic matter (Adetunji et al., 2020; Snapp et al., 2005); and enhance soil structure, aggregation, and hydraulic properties (Chu et al., 2017; Kabir, 2005; Koudahe et al., 2022). However, CC can also have a beneficial impact on the overall abundance and community structure of soil microbes (Cardinale et al., 2011; Muhammad et al., 2021). Despite this, the effects of CC on specific microbial structures and their functions are under-researched, and some structures are yet to be examined under CC systems.

1.3 | The role of mycorrhizal and endophytic fungi

The relationship between CC and soil microorganisms is particularly significant for mycorrhizal fungi, which form a symbiotic relationship with 80% of all plant families (Rintoul, 2016), including many important crop species. Symbiotic relationships between mycorrhizal fungi and plant root organs encourage nutrient exchange, develop soil structure and aggregation, improve water relations, protect from pathogens, sequester carbon, reduce heavy metal and salinity stress, and increase crop yields (Rintoul, 2016). Similarly, endophytic fungi occur in almost every plant in the natural environment and, like mycorrhizae, can improve plant growth and reduce plant stress in suboptimal conditions (Domka et al., 2019). Although mycorrhizal fungi are restricted to plant roots, endophytic fungi colonize the roots, flowers, leaves, stems, and seeds of plants (Di Martino et al., 2022; Domka et al., 2019; Petrini, 1991). While considerable research has examined the effects of CC on mycorrhizal abundance and community structure (Muhammad et al., 2021), few studies have considered the changes in abundance of fungal structures, and the consequences for community functioning.

1.4 | Fungal structures

The most researched fungal structures are hyphae and spores. Hyphae are branching, threadlike filaments that expand in upper soil layers, with a diameter of approximately 2–15 μm (Corazon-Guivin et al., 2019; Müller et al., 2017). They allow nutrients to flow between fungi and plants (Bowles et al., 2017; Rintoul, 2016). Conversely, spores are the main reproductive organs of fungi (Huey et al., 2020) as well as being important storage organs (Müller et al., 2017). Spores vary in

size widely (Kivlin, 2020), ranging from a minimum size of 20 to 800 μm (Corazon-Guivin et al., 2019; Deveautour et al., 2020; Paz et al., 2021). Spores are considered the most persistent component of fungal structures (Wright & Upadhyaya, 1998); however, the viability and functioning of spores in soil can be altered by abiotic and biotic stresses (Rintoul, 2016; Xavier & Germida, 2003).

Two other well-researched fungal structures are arbuscules and vesicles. Derived from the Latin *arbusculum*, meaning "little tree" (Hata et al., 2010), arbuscules are branch-like structures found within plant root cells (Rintoul, 2016) responsible for a mutualistic nutrient exchange between the plant host and fungi (Dodd, 2000; Rintoul, 2016). Vesicles are large swellings on the plant root that are similar in size to intraradically formed spores (Corazon-Guivin et al., 2019). They serve as propagules for some fungi species, and act as a storage structure for complex carbon compounds and mineral nutrients between fungal hyphae and host plants (Habte, 2000; Maiti & Ghosh, 2020; Müller et al., 2017).

Other structures that are less well-understood—but potentially equally important—include microsclerotia, moniliform hyphae, and chlamydospores. Microsclerotia and moniliform hyphae are structures associated with endophytic fungi rather than mycorrhizae (Priyadharsini et al., 2012). Moniliform hyphae are "contracted at short, regular intervals like a string of beads" (Grgurinovic, 1996), whereas microsclerotia typically have multiple layers of cells, with colorless cells interwoven with medulla. Microsclerotia are produced for overwintering and spreading infective propagules in soil and are resistant to soil degradation (Ball, 1979; Gould, 2009; Song, 2018). Finally, chlamydospores are specialized resting survival structures with a thick protective outer cell wall of each spore (Samson, 2016). Chlamydospore morphology can vary widely in their shape (Lagopodi & Thanassoulopoulos, 1995) and size, but generally range from 50 to 60 μm (Liu et al., 2020). They act as a source of inoculation, create immunity against infectious diseases, and are a source of energy (Gould, 2009; Lin & Heitman, 2005; Rodrigues et al., 2019). Importantly, chlamydospores are survival structures for unfavorable conditions (Dallemole-Giaretta et al., 2011; Klironomos & Hart, 2002; Oehl et al., 2009).

1.5 | Study aims

This study compares the abundance of mycorrhizal and endophytic fungi structures in plant roots from fields planted with spring bean (*Phaseolus vulgaris*). The samples were taken from CC sites (using mixed cover crops) compared to samples from sites that have not been under a CC regime. Most studies investigating the effects of management practices on fungi have focused on root colonization by hyphae as a measurement of abundance (García-González et al., 2018). However,

Core Ideas

- Cover cropping increased abundance of hyphae, arbuscules, vesicles, moniliform hyphae, and microsclerotia.
- Fungal structures are important for nutrient exchange, overwintering, long-term survival, energy storage, branching, and inoculation.
- Cover cropping may improve the functioning of mycorrhizal and endophytic fungi.

there are several key mycorrhizal and endophytic structures in plant roots, including hyphae, arbuscules, vesicles, microsclerotia, moniliform hyphae, spores, and chlamydospores. These structures have different functions, which can be broadly categorized as (i) involvement in nutrient exchange (i.e., hyphae and arbuscules), (ii) overwintering and long-term survival (i.e., chlamydospores and microsclerotia), (iii) energy storage (i.e., vesicles and chlamydospores), and (iv) branching and inoculation structures (i.e., moniliform hyphae, hyphae, chlamydospores, and spores). Therefore, this study will quantify the presence of hyphae, arbuscules, vesicles, microsclerotia, moniliform hyphae, spores, and chlamydospores on roots of plants from fields under CC with *P. vulgaris* and fields under a conventional system without CC.

2 | MATERIALS AND METHODS

2.1 | Data collection

Ten individual spring bean (*P. vulgaris*) fields across three different farms were selected within an area within west Kent, UK, measuring approximately 10 km by 5 km. Five fields were under conventional agriculture and five fields had mixed cover crops. From the LANDIS Soilscapes Viewer (https://www.landis.org.uk/soilscapes/), all sites had a loamy and clayey texture, were classed as slightly acid, and were either slowly permeable seasonally wet or with impeded drainage. All sites had similar chemical inputs the previous year (i.e., fertilizer, herbicide, and lime). All the cover crop sites had a winter crop grown from late August to early March 2021, reducing competition and creating a clean seedbed before the spring crop was sewn in late March. Conversely, the sites under non cover cropping (NCC) follow the conventional farming methods of heavy tillage, where the soil is barren and inactive for 7 months until the spring crop is sewn in late March. All samples were collected in late August 2021, the day before harvesting of the spring crop occurred. To collect soil samples, each field was systematically divided into

nine equally sized sections. In the center of each section, five soil cores were collected and pooled together to provide a representative sample for each of the nine sections of the field. Therefore, nine samples per field were collected and 90 samples (45 per treatment) were collected in total. Each core was taken to a depth of 30 cm, using a soil corer with a 2.1 cm diameter. The samples were placed in a sealed sample bag and stored at 4°C for 7 days before laboratory analysis.

2.2 | Root staining

After samples had been refrigerated at 4°C for 7 days, soil samples were sieved into a tray using a 2-mm mesh sieve, removing any stones and leaves. All the roots were removed using forceps and placed into a separate bag in the refrigerator at 4°C. The roots were refrigerated for up to a further 7 days and then placed into a 20% KOH solution for 3 days to clear. During clearing, nuclear and cytoplasmic materials were removed from cells in order to facilitate maximal penetration of the stain (Habte & Osorio, 2001). After 3 days, any roots that did not clear were placed in refreshed 20% KOH solution and left for a further 3 days. Once clearing was completed, the roots were added to 1% HCl solution for 1 h, then strained through a fine mesh sieve and washed with distilled water. The acidified roots were placed in a 1:1:1 solution of lactic acid, glycerol, and distilled water with 0.01% weight to volume (w/v) of acid fuchsin powder for histological staining. After 3 days, roots were again strained through a fine mesh sieve, washed with distilled water, then placed in a "de-stain" solution (1:1:1 solution of lactic acid, glycerol, and distilled water, with no acid fuchsin). Samples were left in de-stain solution for 2 days before the roots were mounted onto microscope slides. For each sample, the roots were emptied into a petri dish. Using forceps, approximately eight individual roots were collected at random and then placed across two microscope slides. Using a plastic pipette, 6–7 drops of the de-stain solution were added to each slide before a coverslip was placed on top of the specimen, avoiding air bubbles. Each slide was marked with its according sample number and left to settle for an additional 2 days. Each slide then was sealed using nail varnish for long-term preservation.

2.3 | Root structure classification

The epifluorescent microscope (Olympus IX83 inverted microscope) was turned on, allowing the microscope to warm up for at least 15 min before use. The CELLSENS software was set to the DSRED fluorophore to visualize the pink-red stain. A stained root slide was then placed on the microscope and focused onto a random point on a root at 100x magnification. Identification of any of the seven mycorrhizal and endophytic structures present on the entire area shown on the screen was recorded using a tally system. This was repeated for 20 randomly selected points on roots for every slide and converted to a percentage. Thus, percentages given in Section 3.1 reflect the proportion of root sections analyzed where a given structure was present. The seven root structures were chosen due to their role in nutrient exchange, overwintering and long-term survival, energy storage, and/or branching and inoculation. Identifications were based on descriptions and images of mycorrhizal and endophytic structures from the literature (see Table S1). Furthermore, an example of each structure as seen under an epifluorescent microscope can be seen in Figure 1.

2.4 | Statistical analysis

The data sets were examined for normality using an Anderson–Darling test. Arbuscules were normally distributed ($p > 0.05$), so a parametric *t*-test was used to determine whether there was a significant difference in structure abundance in CC and conventional systems. Hyphae, vesicles, chlamydospore, moniliform hyphae, spores, and microsclerotia were not normally distributed when examining raw data and data with log, square root, reciprocal root, and reciprocal transformations ($p < 0.05$), therefore, nonparametric Mann–Whitney tests were used to examine whether abundance of each structure was significantly different in the two systems. All data were analyzed using Minitab 19 Statistical Software (Minitab, 2019).

3 | RESULTS AND DISCUSSION

3.1 | Results

Only two mycorrhizal and endophytic structures did not show a significant increase in abundance in CC sites: chlamydospores ($U = 2127.00$, $p = 0.326$) and spores ($U = 1917.00$, $p = 0.589$). However, there was a statistically significant increase in all other structures (see Figure 2). Average hyphae colonization was 70.4% in plant roots from the NCC treatment, compared to 98.3% in the CC treatment ($U = 1146.50$, $p = < 0.001$). Average arbuscule formation was roughly double in the CC roots (70.7%) compared to samples from NCC fields (38.1%) ($t = 4.81$, $p = < 0.001$), and there was a 270% increase the average number of vesicles in roots from CC fields (15.8%) compared to NCC (5.8%) ($U = 1564.00$, $p = < 0.001$). Average moniliform hyphae abundance was slightly higher in CC sites (8.8%) than in roots from NCC sites (7.0%) ($U = 2435.00$, $p = < 0.001$), whereas microsclerotia were, on average, over five times as abundant in roots in

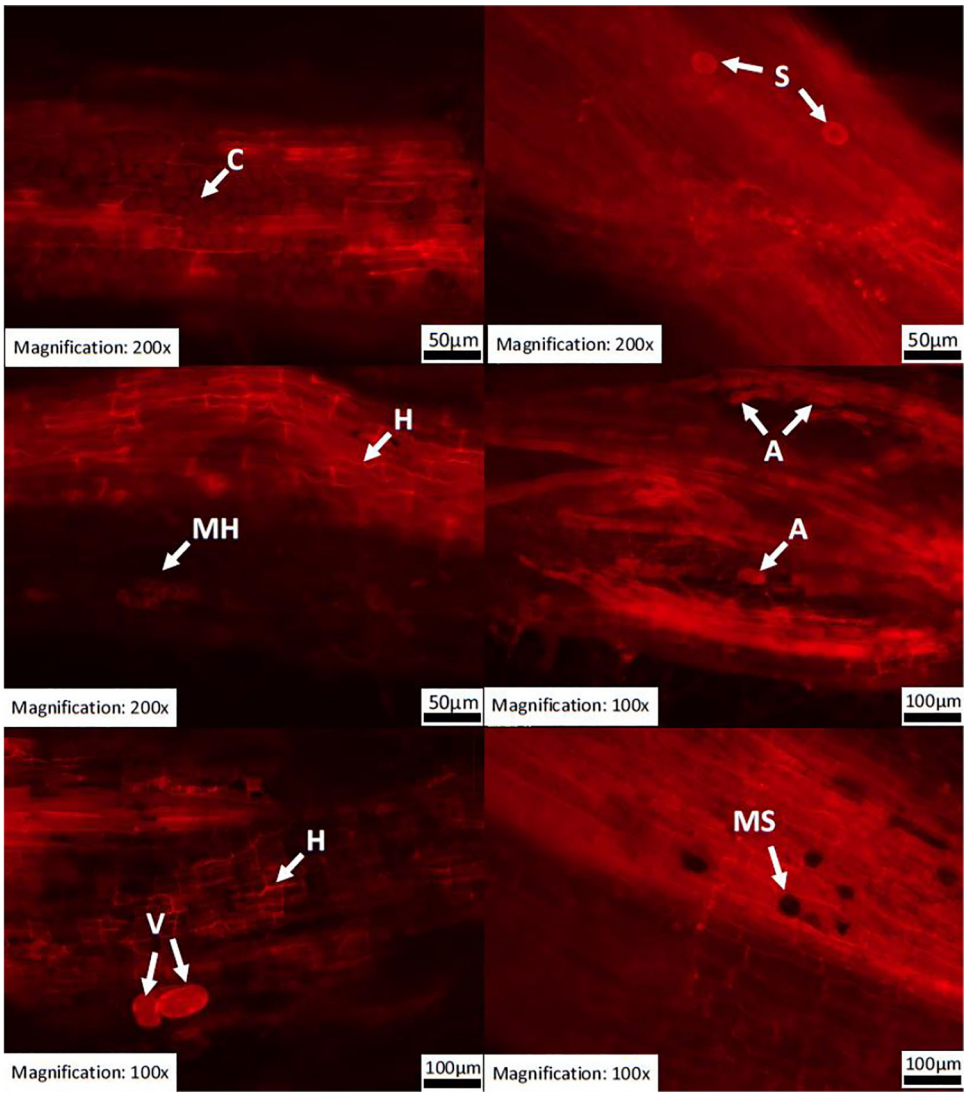

FIGURE 1 Images of legume plant roots stained with acid fuchsin showing arbuscular mycorrhizal and endophytic fungal structures under an epifluorescent microscope. A, arbuscule; C, chlamydospore; H, hyphae; MH, moniliform hyphae; MS, microsclerotia; S, spore; V, vesicle.

CC sites (5.7%) compared to NCC sites (1.1%) ($U = 1742.50$, $p = 0.001$).

3.2 | Effects of CC

3.2.1 | Hyphae

Results indicated a significant difference between CC and NCC techniques, where CC sites had 140% higher hyphae abundance in roots than sites without CC. This is consistent with past research on hyphal colonization, where fields that were CC with only legumes (García-González et al., 2016; Hontoria et al., 2019; Njeru et al., 2014) or a mixture of legumes and other crops (Thapa & Mowrer, 2022) had higher colonization rates than fields without CC that were under no till, conventional tillage, or left fallow. In addition, a meta-analysis of studies investigating CC and tillage regimes found that legume CC resulted in higher fungal colonization than grasses (Bowles et al., 2017), whereas CC with radish (White & Weil, 2010), dandelion (Kabir & Koide (2000), mustard, or vetch (Higo et al., 2020) promoted fungal colonization compared to leaving the field fallow. These results confirm the hypothesis that the undisturbed hyphal network plays an important role in the survival and in root infection of certain fungi species (Jansa et al., 2003) since tillage destroys hyphal networks and the overall hyphal abundance (Higo et al., 2020; Lienhard et al., 2013; Schmidt et al., 2019).

3.2.2 | Spores

There was no significance in spore abundance between roots from CC and NCC sites. Previous research found that the

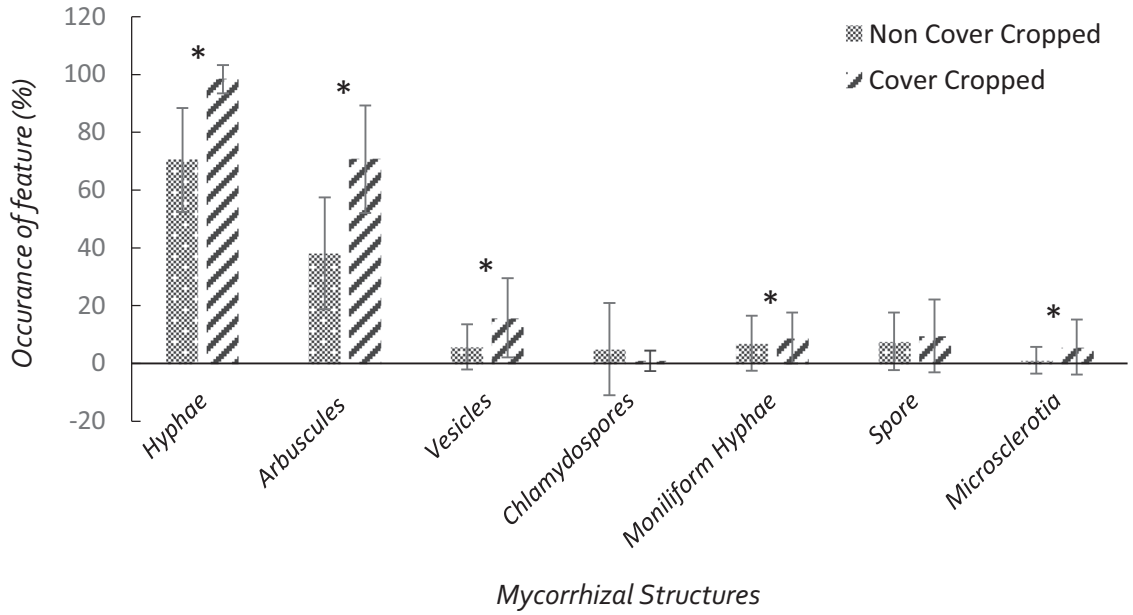

FIGURE 2 Average occurrence of mycorrhizal and endophytic structures found on legume plant roots by treatment ($n = 9$). Error bars represent standard deviation. Statistical significance ($p < 0.001$) is denoted by *.

effect of CC on spore abundance ranges from positive (e.g., García-González et al., 2016; Hontoria et al., 2019) to negligible (Commatteo et al., 2019). However, a meta-analysis of data from 81 studies found that CC significantly increases fungal spore density by 47% on average compared to NCC (Muhammad et al., 2021). This might be due to the increased disturbance in many NCC systems due to the conventional approaches that tend to be applied (tillage, synthetic fertilizers, etc.) as many of these are known to negatively affect fungal spores. Despite this, it has also been noted that the effects differ depending on the cover crop used (Higo et al., 2014; Lehman et al., 2012, 2019; Muhammad et al., 2021), therefore more research should be carried out to address the lack of data available for under-researched cover crops. Similarly, spore species differ in their ability to initiate symbiosis (Klironomos & Hart, 2002), therefore research should ideally determine the species of both the cover crops used and spores identified, although difficulties in identifying fungal spores to species level make this challenging. Previous studies suggest CC supports fungi over winter, thus promoting sporulation, but this is dependent on the cover crop species being used (García-González et al., 2018; Njeru et al., 2015) and may also differ during the growing season, particularly pre- and post-harvest (Njeru et al., 2015).

3.2.3 | Arbuscules

Arbuscule abundance was positively influenced by CC, where CC sites had 185% higher arbuscule abundance in roots compared to NCC sites. Of the little research investigating arbuscule abundance under CC that has been published, Turmel et al. (2011) found that CC using black medic (*Medicago lululina*) had no significant effect on the proportion of fungal arbuscules in roots of flax (*Linum usitatissimum*) or only a trend toward significance (Turmel, 2007) when comparing arbuscules in CC and NCC samples under the same cropping regime. As arbuscules are a key structure for nutrient exchange (Rintoul, 2016), this may suggest changes in nutrient availability/stress in CC sites. However, more research is needed to understand the effects of different CC systems.

3.2.4 | Vesicles

Vesicle abundance was significantly higher in roots from CC fields (approximately 2.7 times more abundant than NCC sites). However, it is difficult to put these results in context as vesicles are infrequently identified or reported in fungal studies and this is the first study examining the effects of CC on vesicles. Some studies mention that vesicles were quantified, but do not provide the data (Lehman et al., 2019; Sweet & Schreiner; 2010). Since the main purpose of vesicles is to store energy, it can be assumed that fungi in CC sites have improved energy storage capacity (Bago et al., 2002), possibly as a stress response.

3.2.5 | Microsclerotia

Within CC fields, microsclerotia abundance in roots was roughly five times greater than in NCC fields. The abundance data for NCC sites (with an average abundance of 1.1%) align

with Priyadharsini et al. (2012), who found that cultivated fields had 0.1%–1.5% abundance. Conversely, Zhao et al. (2016) found that total root colonization consisted mainly of microsclerotia and moniliform cell colonization and Muthuraja and Muthukumar (2019) recorded between 28% and 45% colonization by microsclerotia. Much of the research on microsclerotia has focused on parasitic fungus species, therefore experiments need to consider the importance of microsclerotia structures when examining beneficial effects of fungal associations with crops. Microsclerotia are overwintering and spreading structures and can be found within fungi, soil, or decaying plant material (Ball, 1979; Gould, 2009; Song, 2018). Therefore, the reduction in microsclerotia in sites without cover crops may result in reduced long-term survival and distribution of fungi in those soils. However, since microsclerotia are resistant to soil degradation and can survive for several years—in some cases more than 10 years (Ahmed et al., 2022; Song, 2018)—ideally, studies would use sites that have been managed in a similar way for at least 10 years. In this experiment, sites had been CC for 6–9 years.

3.2.6 | Moniliform hyphae

Moniliform hyphae abundance was significantly higher in roots from CC sites, which had 25% more moniliform hyphae; this is slightly above average compared to previous studies, which found 0.1%–4% abundance (Muthuraja & Muthukumar, 2019; Priyadharsini et al., 2012), although the abundance of moniliform hyphae is considerably higher than this in some cases (Zhao et al., 2016). Of the very limited research examining CC and moniliform hyphae, it was found that CC results in higher root colonization, promoting the growth of branching structures such as moniliform hyphae (Bowles et al., 2017). As with other under-researched structures, more data are needed to understand their importance for plant growth and nutrition, and the effects of different CC systems on their abundance.

3.2.7 | Chlamydospores

Chlamydospore abundance did not differ significantly between the two management regimes. Previous studies suggested that fungal communities will inhabit differently within various managed agroecosystems due to agricultural disturbances imposed by farming practices (Ohel et al., 2009). Previous studies on chlamydospores have tended to focus on the negative associations with fungal pathogens (Lagopodi & Thanassoulopoulos, 1995; Peng et al., 1999; Rodriguez et al., 2021). However, chlamydospores are also important structures for beneficial mycorrhizae and endophytic fungi. For many fungi species, the primary method for overwintering is through chlamydospore formation, both in colonized crops and freely in the soil (Rodriguez et al., 2021). In this first study examining the effects of CC on chlamydospores, no effect of CC has been established. Chlamydospores can maintain viability while dormant and are thought to survive for several years in the soil (Rodriguez et al., 2021), so it may take several years to see effects of CC systems compared to conventional agriculture. In the same vein, it can be assumed that changes to chlamydospore numbers would have implications for fungal abundance in the long term. As they are formed from an existing hyphal cell or conidium (a type of fungal spore) (Samson, 2016), the abundance of these structures could also indicate the past abundance of hyphae and/or spores. So, as with microsclerotia, longer term studies are required to better understand how CC affects their abundance.

3.3 | Implications for mycorrhizal and endophytic functionality

3.3.1 | Involvement in nutrient exchange (i.e., hyphae and arbuscules)

In this study, both hyphae and arbuscules were significantly higher at CC sites than those without cover crops, suggesting that CC is likely to result in better nutrient exchange compared to systems without cover crops. The ability to exchange nutrients from fungi to the host plant is an essential function of fungi (Rintoul, 2016), this function becomes evermore important as access to nutrients via fertilizer becomes more challenging. For example, significant speculation has occurred in recent years about phosphorous reserves: studies suggest this resource could run out within as little as 50 years (Cordell et al., 2009; Daneshgar et al., 2018), although this has been disputed (Cho, 2013). Nutrient relations are likely improved by hyphae not only because it is an essential part of the nutrient exchange process by allowing nutrients to flow between fungi and plants, but also due to its ability to proliferate into areas of soil that are inaccessible to plant roots and link plants and form a "wood wide web" capable of plant–plant nutrient exchange (Rintoul, 2016). These "runner hyphae" allow for the exploration of soil otherwise inaccessible to plants, and for new roots to be colonized (Rillig, 2004). Similarly, arbuscules are the foothold for nutrient exchanges between the plant host and arbuscular mycorrhizal fungi. Simply put, without these structures, no nutrient exchange between fungi and plants would occur, therefore it is unsurprising that studies have demonstrated that where CC increases the abundance of hyphae and/or arbuscules, there is often also evidence of improved nutrition.

3.3.2 | Overwintering and long-term survival (i.e., chlamydospores and microsclerotia)

CC sites had significantly higher microsclerotia abundance than sites without cover crops (five times the abundance on average), but chlamydospore abundance was not significantly different between the two management regimes. Therefore, overwintering and long-term survival may be somewhat better in CC systems than regimes without CC. Spores are associated with the first phase of the fungi life cycle, where spore germination results in hyphae production and proliferation until it finds a host plant root (Denison & Kiers, 2011). In fact, Nara (2009) noted that "fungal spores are functionally analogous to plant seeds in many respects… they are dispersed from mature individuals, germinate in new places and grow into mature individuals." As a result, dormancy periods of these structures have a major influence of fungal survival, although little published work has examined this (Nara, 2009).

The viability and functionality of mycorrhizal and endophytic fungi is not necessarily linked to the plant host lifespan: One study found that fungi could survive for up to 5 months regardless of whether there was a viable host plant (Pepe et al., 2018). Thus, Pepe et al. (2018) argue that conservation of several mycorrhizal and endophytic structures—those in the colonized roots as well as the external mycelium and spores—are essential in preserving fungi in agricultural soils. Similarly, Nguyen et al. (2012) noted that "spores and sclerotia are the main propagules that allow fungi to persist through unfavourable conditions and disperse into new environments." They also mentioned that these propagules "are a means for fungi to escape their current environment, overcome dispersal barriers, and establish in a new favourable habitat" by dispersing through the air or via ingestion of soil or plant matter by animals. However, since spore viability may change over time—one study demonstrated that viability was initially low then increased over a period of several years (Bruns et al., 2009)—the long-term survival rate of spores may be especially important. Therefore, long-term studies (i.e., 10 years or longer) are required to better understand the impact of CC on spores.

It is already well-known that microsclerotia are essential to the long-term survival of pathogenic fungi, where one of the biggest challenges in controlling verticillium wilt diseases is to ensure microsclerotia are removed/destroyed since these are "the most important structures that ensure the survival" of these fungi (Goicoechea et al., 2010). A particular issue is that as plants die, microsclerotia within plant parts such as roots, stems, and leaves will be incorporated in the soil and will start the life cycle again, where germination of microsclerotia occurs as a response to plant root exudation (Goicoechea et al., 2010). However, "despite their importance, very little is known about their longevity and dormancy" of these fungal structures (Nguyen et al., 2012). Since microsclerotia are known to survive for up to 15 years in the soil (Heale & Karapapa, 1999), this could be essential to the survival of mycorrhizal and endophytic fungi in situations where other structures are irreparably damaged. Again, more long-term studies of 10 years or more are required.

3.3.3 | Branching and inoculation structures (i.e., moniliform hyphae, hyphae, chlamydospores, and spores)

In this study, hyphae and moniliform hyphae were significantly higher at CC sites than those without cover crops, but neither chlamydospore or spore abundance was significantly different between the two management regimes. Therefore, some important branching and inoculation functions are likely to be better in CC systems than those without cover crops. Hyphae and spores both have a role in inoculation of plant roots, various external hyphal architectures have been demonstrated to be growing in soil, including runner hyphae, hyphal bridges, absorptive hyphal networks, and infection networks produced by spores, as well as germ tubes and root fragments (Friese & Allen, 1991). However, colonization is "driven by hyphae invasion" (Pot et al., 2022). While hyphae proliferate soil to explore inaccessible sources of nutrients and colonize plants, another function of the mycelial network is to form spores as propagules for dispersal (Rillig, 2004). Since spore germination leads to more hyphae being produced (Denison & Kiers, 2011), these two structures are intricately interlinked. This hyphal network can equate to up to 30 m of hyphae per 1 g of soil (Rintoul, 2016). In fact, fungi are so effective at proliferating through the soil that an individual *Armillaria bulbosa* fungi is famously one of the largest organisms in the world, occupying at least 15 ha of land (Smith et al., 1992). Although microsclerotia and chlamydospores are a source of inoculation and can spread infective propagules, less is known about the mechanisms by which they are involved in fungal branching and inoculation.

3.3.4 | Energy storage (i.e., vesicles and chlamydospores)

Vesicles were significantly more abundant in CC sites (2.7 times higher on average), whereas chlamydospore abundance did not differ significantly between the two management regimes. As a result, some functions associated with energy storage are likely to be better under CC than without cover crops. The main purpose of vesicles is to store lipids as an energy and carbon source, which are then transported as lipid droplets throughout the fungal mycelium (Bago et al., 2002). These lipids represent over half the dry mass of vesicles in arbuscular mycorrhizae and consist of glycolipids, sphingolipids, phospholipids, sterols, and triacylglycerol as a storage lipid (Brands et al., 2018). Similarly, some fungal species are known to store up to 80% of their dry weight as

lipids (Subramaniam et al., 2010). However, little research has been conducted on lipid storage of these two structures for mycorrhizal or endophytic fungi.

3.4 | Implications for land management

Increased fertilizer costs will substantially affect producers globally (Lopez, 2022). However, increased fungi abundance cuts the need for fertilizer inputs as fungi improves nutrient acquisition (Bender & van der Heijden, 2015; Daryanto et al., 2019; García-González et al., 2018; Gosling et al., 2006; Paul, 1984; Sharma et al., 2018). Thus, it is becoming widely accepted that fungi can work alongside or replace phosphorous fertilizers (Roy-Bolduc & Hijri, 2011) and work as a biofertilizer (Sudha & Veeramani, 2021). In addition, CC minimizes inputs—and associated costs—and increases the overall efficiency for the agricultural system. These practices show promise in alleviating global issues, providing cheaper and more sustainable alternatives to fertilizer used in conventional systems (Bergtold et al., 2017) while maintaining soil health for future generations (Jakobsen & Hammer, 2018; Ortas, 2012). Fungi are more sensitive to physical disturbance than other microorganisms (Schmidt et al., 2019). Therefore, it is unsurprising that conservation management practices such as CC promote soil and fungal communities' structure and overall functioning (Schmidt et al., 2019). Subsequently, the increased fungal activity improves crop and soil health (Basu et al., 2018; Higo et al., 2020). Thus, conservation agricultural practices can be more sustainable, improve soil fertility, and reduce input costs. However, it is worth noting that this is not a "one size fits all" solution: A review of several experiments in Europe showed that fungal response to CC (and other agricultural practices) differed depending on the site, soil type, and crops grown (Hannula et al., 2020). There can also be a legacy effect on fungal communities due to historical land uses (Faggioli et al., 2019) or recent CC practices (Detheridge et al., 2016).

4 | CONCLUSION

The health of agroecosystems has been diminished through intensive land management practices. As a result, a paradigm shift is needed to restore farmland and ensure its long-term sustainability. This study demonstrated that CC increases the abundance of several important—and often under-researched—fungal structures. This is likely to lead to improved nutrient exchange to crops, branching and inoculation of host crops, energy storage within fungi and transfer to the plant, and overwintering and long-term survival of fungi. However, there is a lack of research on many of the fungal structures, particularly in the context of the effects of conservation agricultural practices such as CC. Since the effects on some structures may take years to fully materialize, there is also a need for more long-term studies, where the same cropping regimes have been in place for 10 years or more. With a shift in the focus of policy in the UK and elsewhere to soil health and sustainable agriculture in recent years, there is an opportunity to learn how mycorrhizal and endophytic fungi can play a role in sustainable agriculture and promote practices that maintain or increase this valuable natural resource.

AUTHOR CONTRIBUTIONS

P. L. Bromley: Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing—original draft. **N. L. J. Rintoul-Hynes**: Conceptualization; data curation; methodology; project administration; supervision; validation; writing—review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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