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Functional differences in the microbial processing of recent assimilates under two contrasting perennial bioenergy plantations

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ABSTRACT

Land use change driven alteration of microbial communities can have implications on belowground C cycling and storage, although our understanding of the interactions between plant C inputs and soil microbes is limited. Using phospholipid fatty acids (PLFA's) we profiled the microbial communities under two contrasting UK perennial bioenergy crops, Short Rotation Coppice (SRC) willow and *Miscanthus Giganteus* (miscanthus), and used ^{13}C – pulse labelling to investigate how recent carbon (C) assimilates were transferred through plant tissues to soil microbes. Total PLFA's and fungal to bacterial (F:B) ratios were higher under SRC willow (Total PLFA = 47.70 ± 1.66 SE μg PLFA g^{-1} dry weight soil, F:B = 0.27 ± 0.01 SE) relative to miscanthus (Total PLFA = 30.89 ± 0.73 SE μg PLFA g^{-1} dry weight soil, F:B = 0.17 ± 0.00 SE). Functional differences in microbial communities were highlighted by contrasting processing of labelled C. SRC willow allocated 44% of total ^{13}C detected into fungal PLFA relative to 9% under miscanthus and 380% more ^{13}C was returned to the atmosphere in soil respiration from SRC willow soil compared to miscanthus. Our findings elucidate the roles that bacteria and fungi play in the turnover of recent plant derived C under these two perennial bioenergy crops, and provide important evidence on the impacts of land use change to bioenergy on microbial community composition.

1. Introduction

More carbon (C) is retained within soil than in living vegetation and the atmosphere combined (Jobbagy and Jackson, 2000). At steady state, ecosystem C inputs derived from the photosynthetic assimilation of carbon dioxide (CO_2) are roughly balanced by C losses. C is lost through autotrophic and heterotrophic respiration and to a lesser extent, erosion and leaching of dissolved and particulate C compounds (Davidson and Janssens, 2006). Ecosystem perturbations such as land use change, can alter the magnitude and direction of soil - atmosphere C exchange driving ecosystems towards a new steady state (Anderson-Teixeira et al., 2009; Guo and Gifford, 2002). Alteration of vegetation and associated plant inputs, and a shift in soil abiotic conditions can drive changes in soil microbial community composition, modifying the nature of the interactions between above and below ground ecosystem components (Bronick and Lal, 2005; De Deyn et al., 2008).

Plant taxa vary widely in the rates at which they assimilate C during photosynthesis; partition C to above and below - ground structures, lose C through senescence, root exudation and respiration and drive changes in soil abiotic conditions (Cornwell et al., 2008; De Deyn et al., 2008; Dorrepaal, 2007). In addition to differences in metabolic pathways between taxa, the efficiency with which plants assimilate C is also dependent upon both environmental conditions and the phenological stage (Desalme et al., 2017; Gowik and Westhoff, 2011; Raines, 2011).

Previous isotopic tracer studies have shown a strong coupling between recently fixed plant photosynthates and belowground C allocation to roots, soil microbes and respiratory fluxes (Bahn et al., 2013; Barthel et al., 2014; Carbone et al., 2007; Epron et al., 2011; Hogberg et al., 2008; Jin and Evans, 2010; Sommer et al., 2016;

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Street et al., 2013; Subke et al., 2012; Tavi et al., 2013; Weng et al., 2017). The fate of this C is ultimately controlled by the composition and activity of soil biota, however our understanding of the below ground C flux and its partitioning amongst roots, mycorrhizae and free living soil microbes is still limited (De Deyn et al., 2008; Stuart Chapin et al., 2009). Different microbial groups have however been associated with specific functions; Gram negative bacteria are commonly associated with the rhizosphere and the decomposition of root exudates (Denef et al., 2009; Koranda et al., 2014) whilst Gram positive bacteria are predominant in bulk soil and can decompose older, more complex soil organic matter (SOM) (Bahn et al., 2013). Saprotrophic fungi have wide enzymatic capabilities and predominate in the decomposition of complex organic compounds in plant residues (Baldrian and Valášková, 2008) whilst arbuscular (AMF) and ectomycorrhizal fungi (EMF) are obligate symbionts and exchange C for nutrients with their hosts (Denef et al., 2007; Drigo et al., 2010; Treseder and Allen, 2000). Importantly, soil biota are sensitive to changes in plant diversity with plant community manipulations and changes in land use having been shown to alter microbial communities, rates of soil microbial C turnover, storage and ecosystem functions (Mellado-Vazquez et al., 2016; Steinauer et al., 2015).

In the case of biomass production for bioenergy and biofuels, such changes in microbial C turnover are of particular interest as potential benefits for soil C have been used as a rationale for switching from annual to perennial systems for the production of biomass (Adler et al., 2007). Perennial cropping systems offer the advantage of reduced physical disturbance after crop establishment, with a lack of annual tillage promoting stable soil biotic communities and potentially, minimizing soil carbon loss (Tiemann and Grandy, 2015). However, perennial bioenergy systems represent a significant change in plant taxa, land use and management with the impacts upon soil microbial community structure and function still relatively poorly studied (Cattaneo et al., 2014; Hargreaves and Hofmockel, 2014; Mao et al., 2013). Two of the leading temperate, perennial biomass crops are the hybrid *Miscanthus Giganteus* (miscanthus), a rhizomatous, woody perennial C4 grass native to Asia (Rowe et al., 2009) and short rotation coppice (SRC) willow, a C3 tree native to the United Kingdom which is grown in high density plantations (Hilton, 2002). These have been proposed to be planted across Europe as dedicated bioenergy crops, primarily as a low-carbon substitute for fossil fuels in thermal power generation (Don et al., 2012; Kahle et al., 2001). There remains considerable uncertainty regarding the impact on soil C, of land use change to these bioenergy crops. Walter et al. (2015) reported rates of change of −1.3–1.4 Mg C ha^{-1} yr^{-1} across 21 SRC willow plantations in central Europe. For miscanthus transitions, Poeplau and Don (2014) reported a range of −0.17–1.54 Mg C ha^{-1} yr^{-1} whilst Rowe et al. (2016) reported rates of change of 1.54 ± 0.70 Mg C ha^{-1} yr and −0.93 ± 0.74 Mg C ha^{-1} yr across arable to SRC willow and miscanthus transitions respectively. Much of this variability can be accounted for by the relatively young age of crops, differences in previous land uses and abiotic factors, however an understanding of how biotic processes may control C turnover under these crops is currently lacking. For example, whilst it is suggested that globally, ecosystems dominated by ericoid and EMF can hold more soil C than those dominated by AMF (Averill et al., 2014) no research has considered whether EMF association in SRC Willow processes and sequesters assimilated carbon differently to AMF associating miscanthus.

Utilizing established plantations of miscanthus and SRC willow, which exhibit contrasting photosynthetic pathways, growth rates and environmental tolerances (Larsen et al., 2016; Quinn et al., 2012; Bellarby et al., 2010), we applied ^{13}C - pulse labelling to investigate C assimilation and the transfer, distribution and persistence of plant derived C within microbial communities. ^{13}C - pulse labelling has previously been applied to agricultural systems (Tavi et al., 2013), grasslands (De Deyn et al., 2011; Leake et al., 2006; Ostle et al., 2000), peatlands (Biasi et al., 2012; Fenner et al., 2004; Ward et al., 2009) and forest ecosystems (Epron et al., 2011; Hogberg et al., 2008; Subke et al., 2009). Few tracer studies of this kind have been performed on energy crops (Chaudhary et al., 2012; Horwath et al., 1994; Mikan et al., 2000; Tavi et al., 2013) and none, to our knowledge on miscanthus and SRC willow.

We predicted that miscanthus may have greater carbon use efficiency (CUE) than SRC willow due to its C4 photosynthetic pathway, leading to a reduction in below ground C transport, rhizodeposition and C transfer to microbial communities as measured by ^{13}C − PLFA and soil $^{13}CO_2$ flux. We also hypothesised that C would be transferred below - ground more rapidly under miscanthus relative to SRC willow as previous studies have shown slower transfer rates in trees (Hogberg et al., 2008) relative to tall perennial grasses (Tavi et al., 2013). Finally, we predicted that below - ground C allocation would be greater under SRC Willow due to its association with ectomycorrhizal fungi (EMF), which have been shown previously, to be strong sinks for photosynthates in forest systems (Hogberg et al., 2008).

2. Materials and methods

2.1. Research site

The research sites were two adjacent commercial bioenergy plantations of miscanthus (11.56 Ha) and SRC willow (9.43 Ha) in Lincolnshire, UK. The SRC willow field was planted with six closely related *Salix Viminalis* genotypes although here we targeted the genotype “Bjorn”. Miscanthus and SRC willow were planted in 2006 and 2000 respectively on arable land which was previously managed on a rotation of 1 year oilseed rape followed by 3 years winter wheat. Miscanthus was planted at a density of 10,000 rhizomes ha^{-1} whilst SRC willow was planted at a density of 15,000 stools ha^{-1}. The soil was a fine loam over clay with approximately 53% sand, 32% silt and 15% clay (Case et al., 2012). Mean annual rainfall at the site was 605 mm (Scampton − approximately 3 km away) over 25 years from 1963 to 2004 with a mean annual minimum and maximum temperature of 5.9 °C and 13.1 °C respectively (1971–2000) (Drewer et al., 2012). The experiment was conducted in August 2012 with sampling continuing up to March 2013. In August 2012, rainfall was 67.5 mm with a mean air temperature of 16.28 °C (±3.8 SD). 2012 saw exceptional rainfall across the UK and locally the highest annual rainfall total since records began in 1947 (865.5 mm) (Waddington Met Office Monitoring Station − approximately 14 km away) (Barnes et al., 2017 manuscript in preparation). Both plantations were monitored by eddy covariance throughout the duration of the experiment using Li - Cor LI-7500 A open path IRGA's and Gill R3 Sonic Anemometers. For more detail of site soil parameters, eddy flux instrumentation and site characteristics see (Drewer et al., 2012).

2.2. Pre - pulse measurements

In order to obtain natural abundance $\delta^{13}C$ signatures for each pool, tissue samples of leaves and stems, bulk soil and roots were collected from the 6 × 2.5 m experimental plots described in section 2.3, one week before ^{13}C labelling. 5 plants were sampled in a transect across each plot and pooled into one composite sample of leaves and one of stems per plot. Bulk soil was sampled as described in section 2.7. Briefly, 3 cores were taken from each experimental plot, sectioned into 3 depths (0–10 cm, 10–20 cm and 20–30 cm)