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Bioenergy driven land use change impacts on soil greenhouse gas regulation under Short Rotation Forestry

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Abstract

Second-generation bioenergy crops, including Short Rotation Forestry (SRF), have the potential to contribute to greenhouse gas (GHG) emissions savings through reduced soil GHG fluxes and greater soil C sequestration. If we are to predict the magnitude of any such GHG benefits a better understanding is needed of the effect of land use change (LUC) on the underlying factors which regulate GHG fluxes. Under controlled conditions we measured soil GHG flux potentials, and associated soil physico-chemical and microbial community characteristics for a range of LUC transitions from grassland land uses to SRF. These involved ten broadleaved and seven coniferous transitions. Differences in GHGs and microbial community composition assessed by phospholipid fatty acids (PLFA) profiles were detected between land uses, with distinctions between broadleaved and coniferous tree species. Compared to grassland controls, CO_2 flux, total PLFAs and fungal PLFAs (on a mass of C basis), were lower under coniferous species but unaffected under broadleaved tree species. There were no significant differences in N_2O and CH_4 flux rates between grassland, broadleaved and coniferous land uses, though both CH_4 and N_2O tended to have greater uptake under broadleaved species in the upper soil layer. Effect sizes of CO_2 flux across LUC transitions were positively related with effect sizes of soil pH, total PLFA and fungal PLFA. These relationships between fluxes and microbial community suggest that LUC to SRF may drive change in soil respiration by altering the composition of the soil microbial community. These findings support that LUC to SRF for bioenergy can contribute towards C savings and GHG mitigation.

Keywords: land use change, short rotation forestry, greenhouse gases, soil respiration, bioenergy, Phospholipid Fatty Acids

1. Introduction

The greatest contributors to global greenhouse gases (GHGs) are emissions from fossil fuel use and land use change (LUC) [1]. Land use patterns have changed in response to human needs over time [2], and now in order to meet renewable energy and GHG emissions reduction targets, LUC to bioenergy crops is under serious consideration [3,4,5]. Estimates suggest that 13-22 % of the world's global energy demands by 2050 could be met through biomass [6]. In Europe, bioenergy currently accounts for almost two-thirds of the total renewable energy and much of this comes from energy crops [7] and, furthermore, the European Union has committed to increase the proportion of renewable energy from 9 % in 2010 to 20 % of total energy consumption by 2020 [8]. Although there are competing land demands from activities such as food production, infrastructure, recreation and biodiversity [9], the rationale remains for converting certain land to bioenergy crop production [10]. For a bioenergy crop to be considered as a viable and sustainable option in the future it must provide GHG savings in comparison to the use of fossil fuels [11,12]. Impacts of LUC on GHG emission reduction are dependent on the land uses involved, but LUC to bioenergy has the potential to deliver GHG emissions savings through soil C sequestration, with the greatest potential following LUC from arable crops to forestry [13,14]. In addition, and linked to changes in soil C, LUC can also influence GHG fluxes between the soil and the atmosphere [15].

Together with other dedicated bioenergy crops, Short Rotation Forestry (SRF) could contribute to biomass requirements for renewable energy targets [16,17]. Short Rotation Forestry is defined as high density plantations of fast-growing tree species, grown on short rotational lengths (greater than 10 years) and harvested at breast height of 10–20 cm for biomass [16,17]. Although not currently widely practised in the UK commercially, a suite of species is under consideration for SRF, including coniferous and broadleaved species types [16,17,18]. Tree species can influence soil organic carbon (SOC) sequestration and GHG fluxes due to varying rates of rhizodeposition [19], differences in above and below-ground C partitioning [20] and differences in litter inputs and decomposition rates [21].

Litter decomposition rates are generally distinct between coniferous and broadleaved species, with litter decomposition most rapid for deciduous broadleaved species [22,23,24]. Litter decomposition rates are strongly related to litter qualities including, litter N and lignin content, C/N ratio, and leaf area [21,23,25,26] and these can vary greatly between tree species. Litter quality can also affect soil pH, which in turn can alter soil microbial activity affecting decomposition of soil organic matter [24]. Roots also directly add organic material to the soil through exudation (rhizodeposition), fine root turnover and through coarse root shedding [24]. Root-derived inputs (rhizodeposits) are chemically diverse and range in complexity from labile exudates to senescent material released as a consequence of tissue turnover [27]. These compounds provide a diverse source of substrate to soil microbial communities and are responsible for the stimulation of microbial biomass and activity in the rhizosphere [27]. Soil microbial community composition can be measured by analysis of phospholipid fatty acids (PLFAs). PLFA analysis has become widely used to study soil microbial communities [28,29] and quantifies total soil microbial biomass and the proportions of bacteria and fungi. Total PLFA is well-correlated with other methods for microbial biomass estimation and readily discriminate land use, soil type and land management practises (e.g. Bardgett et al. [30]).

Around half of soil respiration is derived from plant root respiration; the remaining respiration is associated with the decomposition of organic matter by the microbial community [24,27]. In the absence of root respiration, the rate of heterotrophic respiration (the CO_2 mainly derived from soil microbial activity) is largely a function of microbial community composition and organic matter quality, and ultimately organic matter quality is regulated by plant inputs [31,32]. Examining this component of respiration following LUC to SRF may give an indication of how changes in organic matter quality, or differences between species types, influence CO_2 fluxes. As emissions of methane (CH_4) and nitrous oxide (N_2O) contribute to climate change they must also be considered in LUC to forestry [24]. CH_4 has a global warming potential (GWP) 25 times greater than CO_2 [1]. CH_4 is produced under anaerobic conditions and therefore emissions are more likely in wet soils [33]. CH_4 is consumed in aerobic conditions [33] and because of this net CH_4 emissions in any soil depend on both production and consumption rates. It is generally accepted that forests are strong sinks for CH_4 [34]. N_2O is a powerful

GHG and has a global warming potential (GWP) 298 times that of CO_2 [1]. Unlike CH_4 and CO_2, N_2O can be produced under both aerobic and anaerobic conditions and can be consumed in wet, nitrogen-poor soils [35]. Recent studies indicate a tendency towards higher N_2O emissions from deciduous than coniferous forest soils [36,37] due to differences in tree litter quality and soil moisture [24].

Our previous work examining changes in soil C stock following the establishment of different SRF species has shown greater litter accumulation, and an overall increase in soil C stock in coniferous soils (relative to agricultural controls) compared to broadleaved soils [38]. Despite broadleaved species having no overall effect on soil C stock, the response was more variable suggesting that individual species influence soil C accumulation differently. When combined with estimates of C stocks in aboveground biomass the likelihood of C accumulation under conifers was further strengthened [38]. In addition to these findings on soil C, knowledge on GHG fluxes under SRF is needed to contribute to a better understanding of sustainability of this bioenergy land use. Therefore, we examined potential soil GHG fluxes, under standardised conditions, from LUC transitions, and the associated changes in soil physico-chemical and soil microbial community characteristics. The gas flux measurements also yield additional information on the potential for the biological consumption and production of GHGs such as N_2O and CH_4. Specifically, we tested for 1) differences in GHG potential fluxes, soil physico-chemical (pH, C concentration) and microbial community characteristics between land uses (controls and different SRF species types), and 2) whether changes in soil physico-chemical (pH, C concentration) and microbial community characteristics could explain changes in CO_2 flux.

2. Materials and Methods

2.1. Site selection and sampling strategy

Sampling was undertaken at six sites across the UK from replicated experimental and commercial SRF sites. A paired plots approach was used where SRF species and adjacent land continuing in former land use could be identified at each location. To confirm that the soil for the control land use was comparable

to the transitional SRF land use, data on management history and soil type had been collected and examined (Table. 1). Following soil sampling, texture analysis was carried out and was used to confirm similarity in soil type between control land use and transitional land use at each site (Table. 1). Expert advice and current literature on potential SRF tree species was also used to make an informed decision regarding suitable site selection [17,18,39]. The tree species chosen for this study, which have been broadly classified as coniferous (7 transitions) and broadleaved (10 transitions), included Alder (*Alnus glutinosa*), Ash (*Fraxinus excelsior*), Downy birch (*Betula pubescens*), Hybrid larch (*Larix x eurolepis*), Poplar (*Populus spp.*), Scots pine (*Pinus sylvestris*), Silver birch (*Betula pendula*), Sitka spruce (*Picea sitchensis*), and Sycamore (*Acer pseudoplatanus*). All sites with the exception of the site in North-West England (20 years into its second rotation; Table. 1) are in their first rotation ranging in age from 12 to 24 years.

A hierarchical sampling design was used to capture spatial variability [38]. Five sampling locations were randomly selected within each paired plot (transition) (i.e. control or tree species) using an overlain grid. At each randomly selected sampling location, soil cores were taken from three positions, resulting in 15 spatially nested samples per transition.

Three soil cores (30 cm x 4.8 cm) were taken at each sampling location using a split-tube soil corer (Eijkelkamp Agrisearch Equipment BV, Giesbeek, The Netherlands), at the grid intersect and then at distances of 1 m and 1.5 m in random compass directions. Prior to soil sampling, the litter (L) and fermentation layers (L_f) were removed. Soil cores were divided into 0–15 cm and 15–30 cm sections in the field, bagged, and returned immediately to the laboratory where they were stored at 4 °C.

Insert Table 1 here.

2.2. Laboratory processing

Soil core sections were quartered lengthways, with quarters being allocated for different subsequent analyses; one quarter was used to derive soil C concentration and pH, and others allocated for microbial analysis and to the controlled GHG potentials laboratory incubation experiment. For further details on the soil processing methods see Keith et al. [38].

Soil C concentration and pH analysis

Sieved (<2 mm) oven-dried subsamples of soil were ball-milled using a Fritsch Planetary Mill (Fritsch, Idar-Oberstein, Germany) to a fine powder, and then a 100 mg sub-sample was used for the assessment of C concentration using a LECO Truspec total CN analyser (Leco, St.Joseph, MI, USA). Fresh, bulked samples were sieved to 2 mm to remove stones and roots. 10 g of bulk soil was then mixed well with 25 cm^3 of deionised water and allowed to stand for 30 minutes, before the pH of the liquid layer was recorded using a Hanna pH 210 Benchtop Meter (Hanna Instruments, RI, USA).

Phospholipid fatty acid (PLFA) analysis

Subsamples of frozen soil were bulked at plot level (i.e. cores within plots bulked with 0–15 cm and 15–30 cm depths kept separate) and then freeze-dried prior to PLFA analysis. PLFAs were extracted using a modified Bligh-Dyer extraction [40]. Total microbial biomass was estimated as the sum of all extracted PLFAs [41]. Bacterial biomass was estimated from the total concentration of the markers i-15:0, a-15:0, 15:0, i-16:0, 16:1ω7c, 16:1ω7t, i-17:0, a-17:0, cy-17:0, 18:1ω7c and 7,8,cy-19:0 [42]. Fungal biomass was estimated from the concentration of the marker 18:2ω6 [42] and 18:9ω1 [43]. For more detailed methods of PLFA extraction and analysis see Appendix.

Soil incubations (soil GHG potentials)

Fresh soil samples were used for laboratory incubations. Samples were bulked at plot level and homogenized, resulting in five samples per transition for each of the two depths (0–15 cm and 15–30 cm).

Bulk soil samples were sieved (<2 mm) and 5 g dry soil weight equivalent weighed into 160 ml glass Wheaton bottles (Wheaton Science Products, USA). These were pre-incubated in the dark for 72 hours at 10 °C and 20 °C (target incubation temperatures for experiment) to allow equilibration [44,45]. To maintain controlled moisture across all soils, water holding capacity (WHC) was adjusted to 60 % using a WHC method adapted from Ohlinger [46] where 100 % saturation is calculated as the amount of water remaining in the soil after being saturated and left to drain for 12 h in a fully humid airspace. A water holding capacity of 60% was chosen as being approximate to field capacity [47] and optimum for microbial respiration [48,49]. Following equilibration all bottles were flushed with standard compressed air for 1 minute and crimp-sealed with gas-tight septa. To compensate for gas sampling over the enclosure period, 15 ml of air was added to each bottle following closure. Bottles were then incubated at two temperatures (10 °C and 20 °C) for 7 days with headspace gas samples (5 ml) taken at 0, 24, 48 and 168 hours. Gas samples were stored in 3 ml evacuated exetainers (Labco, Lampeter, UK) for up to 2 weeks prior to analysis.

Gas samples were analysed for CO_2, CH_4 and N_2O concentrations on a PerkinElmer Autosystem XL Gas Chromatograph (GC) (PerkinElmer, Waltham, MA, USA) with flame ionization detector and electron capture detector equipped with a poropack Q column operated at 60 °C with an argon carrier gas. Certified gas standards (Air Products, Crewe, UK) within the range of the samples being analysed were used to calibrate the GC. Gas fluxes (CO_2, CH_4 and N_2O) were calculated using the approach of Holland et al. [50] by plotting the linear accumulation of each gas over the seven day enclosure period. For CO_2, CH_4 and N_2O data to be included as results a linear response ($R^2 > 0.95$) in CO_2 concentrations with time was required. Where N_2O and CH_4 were non-linear they were still considered in the analysis as concentration changes were often negligible e.g. no flux, resulting in a low R^2 value. The CO_2 fluxes were also expressed on a mass of C basis, in addition to being expressing by dry soil mass, in order to standardise fluxes for potential differences in soil C across land use types and transitions.

2.3. Statistical methods

205 The influence of SRF transitions on soil C, soil pH, microbial community variables, GHG fluxes and
206 GHG temperature response ratios was tested using linear mixed effect models with the *nlme* package
207 in the R statistical program [51,52]. The significance of these models was examined using the *anova.lme*
208 function. The effect of the different land uses (control and SRF types) was tested, with a fixed effect
209 containing levels for Control, Coniferous, and Broadleaved transitions. The effect of depth and its
210 interaction with SRF types was included in each model. To meet model assumptions, CH_4 and N_2O data
211 were transformed prior to analysis, with data made positive by addition of the lowest value + 1 before
212 log-transformation. For CH_4, variance was not heterogeneous across treatments and therefore data were
213 weighted by treatment using the *varIdent* function. Data on all CO_2 fluxes and temperature response
214 ratios were also log-transformed prior to testing.
215
216 Standardised effect sizes (Cohens' D) of change across LUC transitions were also calculated for CO_2
217 fluxes (on a mass of C basis), soil pH, total PLFA and fungal PLFA. Linear regressions between the
218 LUC effect sizes for CO_2 flux and, effect sizes of soil pH, total PLFA and fungal PLFA were then
219 undertaken to assess whether changes in soil characteristics were related to changes in CO_2 flux across
220 transitions.
221
222 **3. Results**
223
224 ***3.1 Land use change to broadleaved and coniferous SRF***

225 *Soil C concentration and pH*
226 Soil C concentration responded significantly to land use type ($F_{2,207} = 15.96$, $p < 0.001$) with higher soil
227 C concentration in the coniferous soils compared to the grassland controls or the broadleaved soils (Fig.
228 1A). Although the magnitude of differences in soil C concentration varied with depth the pattern
229 remained the same, leading to no interaction between land use and depth ($F_{2,207} = 2.78$, $p = 0.064$, Fig.
230 1A).
231

Land use type had a significant effect on soil pH ($F_{2,207}$ = 13.53, $p < 0.001$) with, as expected, the most notable differences between the coniferous soils and both the grassland and broadleaved soils (Fig. 1B), and more acidic conditions measured under the coniferous land use. Little difference was observed between pH in the grassland control and broadleaved soils (Fig. 1B). . There was also a significant effect of depth on soil pH ($F_{1,207}$ = 24.85, $p < 0.001$) where, across all land use types, pH was slightly higher at 15–30 cm compared to 0–15cm depth but with no interaction between land use type and depth ($F_{2,207}$ = 1.22, p = 0.297, Fig. 1B).

Microbial community (PLFAs)

Considering total PLFA data on a soil mass basis there was an effect of land use type ($F_{2,205}$ = 18.64, $p < 0.001$) and depth ($F_{1,205}$ = 413.05, $p < 0.001$), and an interaction between land use type and depth ($F_{2,205}$ = 10.54, $p < 0.001$) (Fig. 1C). At 0–15 cm total PLFA in the control (105.70 ± 9.27 μg g^{-1} soil) was similar to the coniferous soils (101.26 ± 11.18 μg g^{-1} soil), but noticeably lower in the broadleaved soils (66.35 ± 3.22 μg g^{-1} soil). However, when considering total PLFA on a mass of carbon basis the pattern changes to reflect that of CO_2 on a mass of C basis with lower total PLFA present in the coniferous soils compared to the grassland controls or broadleaved soils (Fig 1D). The effect of land use type ($F_{2,205}$ = 18.64, $p < 0.001$) and depth ($F_{1,205}$ = 413.05, $p < 0.001$) were still significant but not their interaction ($F_{2,205}$ = 10.54, p = 0.193) (Fig. 1D).

On a soil mass basis there was also an interaction between land use type and depth in the fungal PLFA data ($F_{2,205}$ = 4.36, p = 0.014), with higher fungal PLFA in the coniferous soil at 0–15 cm compared to the other land use types, but no differences apparent between the land use types in the 15–30 cm soils (Fig. 1E). Fungal PLFA concentration was lower in the 15–30 cm soils than in the 0–15 cm soils in all land uses ($F_{1,205}$ = 198.14, $p < 0.001$) but most noticeably in the coniferous soils. As with the total PLFA, considering fungal PLFA on a mass of C basis resulted in a switch, with lower concentrations of fungal PLFA measured in the coniferous soils compared to other land uses, although this was not significant (Fig. 1F). Depth was also significant ($F_{1,205}$ = 198.14, $p < 0.001$) but not the interaction between land use and depth ($F_{2,205}$ = 4.36, p = 0.364) (Fig 1F). Bacterial PLFAs followed the same pattern as total

PLFA with differences between the land uses ($F_{2,205}$ = 10.79, $p < 0.001$) decreasing from control > coniferous > broadleaved at 0–15 cm depth, and from control > broadleaved > coniferous at 15–30 cm depth (data not shown).

Insert Fig. 1 here

GHG Fluxes

An effect of land use type ($F_{2,207}$ = 15.41 , $p < 0.001$) on CO_2 flux on a soil mass basis was found where fluxes were lower in broadleaved soil than in either coniferous land uses or grassland control. There was little difference in soil CO_2 flux between control and coniferous land use and no interaction between land use and depth, although fluxes were lower in the 15–30 cm layer than in the 0–15 cm layer ($p < 0.001$, Fig. 2A). However, when considering soil CO_2 flux on a mass of C basis the output is considerably different. Although the effects of land use type ($p = 0.028$), depth ($p < 0.001$) and the interaction between land use and depth ($p = 0.136$) were consistent, CO_2 fluxes are now considerably lower in coniferous soils compared to the grassland control and broadleaved land use. The CO_2 flux was similar between grassland control and broadleaved land uses at 0–15 cm when accounting for soil C concentration (Fig. 2B).

The temperature response ratio of soil CO_2 flux was greater under coniferous than under broadleaved or grassland land uses at both depths, though not significantly so. The coniferous and grassland land uses demonstrated a trend towards higher temperature responses ratios at 15–30 cm depth compared to 0–15 cm, this was not the case for the broadleaved land use where the temperature response ratio was slightly lower at 15–30 cm compared to 0–15 cm. The temperature responses followed the same pattern across land use types on a soil mass and mass of C basis (Table. 2).

CH_4 fluxes ranged from -0.58 to 0.20 ng CH_4-C g^{-1} h^{-1} across land uses and depths, indicating that CH_4 was being consumed under all species (Fig. 2C). Although greatest consumption was measured from broadleaved soils and the lowest in coniferous soil, there was no significant effect of land use on CH_4 flux ($F_{1,207}$ = 0.148, $p = 0.862$). There was an effect of depth on CH_4 flux ($F_{1,207}$ = 18.46, $p < 0.001$) with

lower uptake measured at 15–30 cm depth across all land uses but no interaction between land use and depth ($F_{2,207}$ = 1.78 , p = 0.171).

Soil N_2O flux rates were also very low, ranging from -0.16 – 0.05 ng N_2O-N g^{-1} h^{-1}, and there was no difference between the land uses (Fig. 2D). There was a depth effect ($F_{1,207}$ = 22.72 , p < 0.001) and higher flux rates were measured in the 0–15 cm soils but there was no interaction between land use and depth ($F_{2,207}$ = 2.62, p = 0.075).

Insert Fig. 2 here.

Insert Table 2 here.

3.2 Effect sizes across land use transitions

Linear regressions were performed on effect sizes of soil characteristics and CO_2 fluxes on a mass of C basis across grassland to SRF transitions to determine the variables in which changes were most strongly related. There were positive relationships between LUC effect sizes of soil pH and CO_2 flux (0–15 cm: F = 4.0, p = 0.067, R^2 = 0.176; Both depths: F = 4.8, p = 0.038, R^2 = 0.115; Fig. 3A). Stronger positive relationships, however, were shown between LUC effect sizes of both total and fungal PLFA, and CO_2 flux. Total PLFA effect sizes had a significant relationship with CO_2 flux effect sizes considering only 0–15 cm samples (F = 117.2, p < 0.001, R^2 = 0.893) and both depths (F = 220.2, p < 0.001, R^2 = 0.887), with the slope of the relationship virtually identical (Fig. 3B). Likewise, fungal PLFA effect sizes also had a significant relationship with CO_2 flux effect sizes considering only 0–15 cm samples (F = 8.9, P < 0.001, R^2 = 0.378) and both the 0–15 cm and 15–30 cm depths (F = 12.8, p < 0.001, R^2 = 0.312), with similar slopes (Fig. 3C).

Insert Fig. 3 here.

4. Discussion

311 Utilising laboratory soil incubations under standardised temperature and moisture conditions, we
312 examined potential GHG fluxes in soils from LUC transitions to SRF. This study demonstrated clear
313 differences in CO_2 flux but not N_2O or CH_4 fluxes between grassland and SRF land uses and, in line
314 with a previous study at these sites looking at soil C stocks [47], distinctions between transitions to
315 broadleaved and coniferous tree species were also observed. Such laboratory approaches are important
316 to disentangle different factors influencing soil respiration and C turnover and they allow exploration
317 of the direction and magnitude of relationships [52]. However, they are not without their limitations
318 due to the unnatural and standardised conditions. Short-term incubations, such as those carried out in
319 this study, only measure the initial response of soil GHG processes to changes in temperature and
320 therefore may not reflect the effect of long-term changes in temperature [53]. Soil is also disturbed
321 during sample preparation as a result of sieving, homogenising and removing roots, and this may alter
322 the soil structure and environment resulting in artificial aeration of soils which can affect soil
323 atmosphere GHG exchange [54,47]. Nonetheless, where reductionist laboratory experiments are
324 required, using fresh sieved soils has been recommended as having the least impact on microbial
325 communities and C cycling processes [55].
326
327 ***4.1. Differences between transitions to broadleaved and coniferous species***
328
329 Soil GHG fluxes are influenced by many natural and anthropogenic factors such as soil type, pH,
330 nutrient status, forest type, stand age and land management [24], and therefore measurements are
331 generally very variable reflecting the diversity of these factors. In this study, there were differences in
332 CO_2 flux expressed by soil mass between coniferous and broadleaved soils, with no apparent change
333 under coniferous tree species. However, once CO_2 flux had been expressed on a mass of C basis to
334 account for differences in soil C between land use type and across transitions, LUC from grassland to
335 coniferous SRF resulted in greatly reduced CO_2 fluxes while in the broadleaf SRF CO_2 fluxes were
336 generally unchanged. A reduction in CO_2 flux may be expected to be associated with lower
337 decomposition rates and hence increased soil C concentration and, indeed, the reduced CO_2 fluxes in
338 transitions from grassland to conifers (this study) and increased soil C concentration and C stocks [38]

suggest that there is good potential for enhanced C storage under coniferous SRF as a bioenergy crop. The similar CO_2 fluxes and soil C concentration under grassland controls and broadleaved SRF suggests that, while there is less potential for soil C storage under this type of SRF, its overall effect will not be negative. This is supported by previous analysis of soil C in the same SRF transitions which showed that broadleaved species contained similar stocks of soil C to controls [38].

Other studies have also found mixed outcomes with respect to differences between conifer and broadleaved species. Brüggemann et al. [56] found a similar pattern in a laboratory experiment measuring soil respiration from under different tree species with highest rates being measured from spruce soils in both the organic layers and A_h horizons compared to four deciduous species. In contrast to the results of this study and those of Brüggemann et al. [56] soil respiration rates were found to be ~10 % lower in coniferous stands compared to adjacent deciduous stands in a review by Raich and Tufekcioglu [57]. Results of some studies have been variable, for example Schaufler et al. [47] looked at the effect of land use on soil GHG emissions under controlled laboratory conditions and discovered that tree species had variable effects on GHG flux rates, with CO_2 flux declining in the order of beech > pine > oak > spruce. Others have found no differences in CO_2 fluxes/respiration rates between coniferous and deciduous species types [58,59,60,61]. These variable findings suggest that how CO_2 flux is expressed may be important to the outcome determining whether there are broad differences between coniferous and broadleaved tree species.

In this study the temperature sensitivity of CO_2 flux (for both soil mass and mass of C basis) was higher, though non-significant, in the coniferous soils at both depths, and lowest in broadleaved soils (Table. 2). In the grassland and coniferous soils the temperature response of respiration also increased at depth. C-rich coniferous soils are formed from high volumes of lignin-rich recalcitrant needle litter which decomposes slowly, leading to the formation of a thick C-rich humic layer [24]. Mixed findings exist regarding the response of recalcitrant C to increased temperature [62] but generally it is thought that temperature sensitivity increases with recalcitrance of a substrate [63] as more energy is required for the enzymatic decomposition of recalcitrant substances than more labile substances [64].

Differences in N_2O fluxes were not significant but values suggested a potential for N_2O consumption in the broadleaved compared to N_2O production in the other land uses. The trend of higher emissions under coniferous compared to broadleaved species may in part be attributed to soil N availability, though this was not measured. Soil N availability is a key driver of soil N_2O emissions and it is known that coniferous stands receive more N via deposition than adjacent deciduous stands [65, 66]. However, other studies indicate there may be higher N_2O production from broadleaved than coniferous forest soils [36,37,67,68] which highlights the complexity surrounding the multiple interacting drivers of soil N_2O production and consumption [69]. CH_4 was consumed under all land uses in this study but there were no significant differences in consumption rates. This is consistent with the knowledge that aerobic forest soils and grasslands are important terrestrial sinks for CH_4 [70, 71]. There was a trend towards greater methane consumption in broadleaved soils which follows the work of others. Our results showed that CH_4 oxidation rates were higher in the surface 0–15 cm soils which supports the notion that methanotrophy in forests has a sub-surface maximum in the upper soil layers [72, 73].

Soil physico-chemical properties and soil microbial community characteristics were also found to differ between coniferous and broadleaved land uses following conversion to SRF. As expected soil acidity increased in the coniferous soils, but there was no change in pH between the control grassland and broadleaved soils. It is well known that growing conifers affects soil pH, by creating more acidic soil conditions due to the poorer quality of their litter inputs [22,23,24]. These acidic conditions created under coniferous tree species can inhibit microbial activity and reduce decomposition rates leading to potential increases in soil C [24]. In this study, greater C concentrations were measured in the coniferous soils compared to the grassland control and broadleaved soils and, once PLFAs had been normalised on a mass of carbon in the soil basis, a reduction in total PLFA was observed. However biomass is not necessarily a direct measure of activity but related to a range of other factors including microbial community composition [30]. Differences in microbial composition were also observed with higher fungal PLFA concentrations on a mass of C basis in broadleaved soils compared to both grassland control and coniferous soils. Other authors have observed greater fungal PLFA under coniferous species

compared to broadleaved species [74]. In contrast Priha et al. [75] measured higher total PLFA and fungal PLFA in birch soil compared to pine or spruce soils. Nevertheless, these differences in soil physico-chemical and microbial characteristics may be important drivers of the GHG fluxes observed in this study.

4.2 Links between respiration and microbes across LUC transitions

In order to assess which variables were most strongly related to changes in CO_2 flux across LUC transitions in this study, effect sizes were assessed to determine whether changes in CO_2 flux were related to changes in soil pH and microbial community characteristics. While the effect sizes of soil pH significantly related to effect sizes of CO_2 flux, R-squared values were relatively low. In contrast, the positive relationships found between PLFA effect sizes and CO_2 effect sizes were stronger. In particular, reductions in CO_2 flux were strongly associated with reductions in total PLFA across transitions. These data suggest that shifts in microbial communities across these LUC transitions have a greater impact than the direct effect of changes in soil pH.

Changes in the microbial communities observed due to LUC to SRF may be linked to impacts on microclimate and/or litter and root inputs [76]. A study by Vesterdal et al. [61] found different soil C turnover rates among six tree species (beech, lime, spruce, maple, ash, oak) despite having similar quantities of aboveground litterfall; the authors suggest that tree species have the greatest impact on soil C stocks via the indirect effects of litter quality on microbial activity and decomposition rates. The quality of tree inputs from litter and rhizodeposition also vary due to differences in plant chemistry between coniferous and broadleaf species which in turn influences soil microbial composition and more specifically the relative abundance of fungi and bacteria. Clear differences in the abundance of soil fungal and bacterial PLFAs were observed in this study between land uses, with higher concentrations (on a mass of C basis) of both measured in the broadleaved compared to the coniferous soils. Fungi are considered to promote slower decomposition cycles with increased nutrient retention [31] and are important for degrading more complex substrates compared to bacteria [77]. As in this case, differences

in the composition of the microbial communities (e.g. the relative abundance of fungi and bacteria) have been shown to influence CO_2 fluxes from soil in other studies [78,79].

5. Conclusions

SRF is a growing bioenergy land use in temperate climates which has the potential for reduced GHG emissions and increased C storage but understanding of its effects on these factors is limited. Comprehensive data on C changes associated with LUC to bioenergy crops are essential to be able to assess their sustainability. This study provides evidence that LUC to SRF for bioenergy could lead to GHG savings through reduced C loss via soil respiration. These findings strongly suggest that careful consideration should be given to the selection of SRF species in order to optimise soil C storage and GHG reduction.

Changes in land use and management has significant impacts on the microbial community, and there is a challenge to better understand the effect of LUC to bioenergy on GHG fluxes and their relationship with the soil microbial community. Here, lower CO_2 fluxes under SRF appeared to be associated with reductions in microbial biomass and changes in broad community composition (i.e. bacteria and fungi). Consequently, both direct and indirect effects of planting SRF on the soil microbial community may be important mechanisms by which GHG emissions are reduced.

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Figure captions

Figure 1. Measured (A) Soil carbon concentration (g kg^{-1}), (B) Soil pH, (C) Total PLFA (μg g^{-1} soil), (D) Total PLFA (μg g^{-1} C), (E) Fungal PLFA (μg g^{-1} soil) and (F) Fungal PLFA (μg g^{-1} C) from soils under different land uses (control, broadleaved and coniferous) and different depths. Data in (C) and (E) are based on soil dry weight. Note scales are not consistent; error bars represent standard error.

Figure 2. Potential fluxes of (A) CO_2 (μg g^{-1} soil hr^{-1}), (B) CO_2 (μg g^{-1} C hr^{-1}), (C) CH_4 (ng g^{-1} soil hr^{-1}), and (D) N_2O (ng g^{-1} soil hr^{-1}) from soils under different land uses (control, coniferous and broadleaved) and different depths. Fluxes in (A), (C) and (D) are based on soil dry weight. Note scales are not consistent; error bars represent standard error.

Figure 3. The relationship between Land Use Change (LUC) transition effects on soil CO_2 (on a mass of C basis) potential flux, pH and soil microbial community measures. Effect sizes of (A) pH and CO_2 potential flux, (B) Total PLFA and CO_2 potential flux and (C) Fungal PLFA and CO_2 potential flux. The effect of LUC transitions measured as standardised effect sizes, Cohen's D. Black and grey symbols represent samples from 0–15 cm and 15–30 cm, respectively; dashed and dotted lines represent significant relationship between effect sizes for 0–15 cm samples only and both depths, respectively.

Table 1. Details and soil characteristics of sampling locations used to examine the effects of Short Rotation Forestry on soil greenhouse gas regulation in GB. Land uses in bold represent control land use. Management terms; Pasture = grazed grassland, Rough Pasture = seasonally or un-grazed grassland, F = fertilised, NF = No Fertiliser applied. Soil type based on the Avery soil classification; texture class derived based on the Soil Survey of England & Wales texture classes. C stock values represent means ± SD; n = 15. Table adapted from Keith et al. (2015).

Region	Lat.	Long.	Land use transition	Established	Management	Soil type	Texture class	C stock (0–30 cm) t C ha^{-1}	Sampling Date
Powys, Wales	52.0	-3.6	**Grassland**	Pre 1988	Pasture. F: '98 -'09 160kg N ha^{-1}	Brown earth	Silt loam	76.2 ± 9.0	10 /02/2012
			H. Larch	1988	N F	Brown earth	Silt loam	76.3 ± 8.4	10 /02/2012
			Sycamore	1988	N F	Brown earth	Silt loam	65.1 ± 7.3	10 /02/2012
Moray, Scotland	57.6	-3.2	**Grassland**	Pre 1988	Rough Pasture. N F	Podzol	Sandy loam	94.8 ± 22.4	14/03/2011
			D. Birch	1998	N F	Podzol	Sandy loam	111.5 ± 31.4	15/03/2011
			S. Birch	1998	N F	Podzol	Sandy loam	81.5 ± 21.3	14/03/2011
			Sitka	1999	N F	Podzol	Sandy loam	136.9 ± 44.5	15/03/2011
Moray, Scotland	57.7	-3.3	**Grassland**	1994	Pasture. N F	Ground-water gley	Loamy sand	39.3 ± 8.5	17/03/2011
			Poplar	1994	N F	Ground-water gley	Loamy sand	35.2 ± 6.2	17/03/2011
			Alder	1996	N F	Ground-water gley	Loamy sand	38.8 ± 8.5	18/03/2011
			Ash	1996	N F	Ground-water gley	Loamy sand	35.6 ± 6.6	18/03/2011
North-West, England	54.0	-2.4	**Grassland**	Pre 1956	Rough Pasture. N F	Surface-water gley	Sandy silt loam	117.2 ± 46.3	18/10/2011
			Alder	1956 (1991)	N F	Surface-water gley	Sandy silt loam	122.3 ± 25.7	18/10/2011
			Scots pine	1956 (1991)	N F	Surface-water gley	Sandy silt loam	146.8 ± 45.7	18/10/2011
			Sitka	1991	N F	Surface-water gley	Sandy silt loam	143.4 ± 43.7	18/10/2011
Aberdeenshire, Scotland	56.9	-2.6	**Grassland**	1988	Pasture. F: '02 -'09 0.97 t N ha^{-1}	Podzol	Sandy silt loam	80.6 ±9.9	26/10/2011
			Sycamore	1988	N F	Podzol	Sandy silt loam	83.1 ± 14.5	26 /10/2011
			Scots pine	1988	N F	Podzol	Sandy silt loam	76.2 ±20.9	25/10/2011
			H. Larch	1988	N F	Podzol	Sandy silt loam	74.5 ± 13.1	19/03/2012
North Lanarkshire, Scotland	55.8	-3.8	**Grassland**	Pre 1990	Pasture. F: Unknown	Surface-water gley	Sandy silt loam	122.9 ± 24.1	24/11/2011
			Alder	1990	F: Unknown	Surface-water gley	Sandy silt loam	100.8 ± 25.0	23/11/2011
			Poplar	1990	F: Unknown	Surface-water gley	Sandy silt loam	92.0 ±10.7	24/11/2011
			Sitka	1990	F: Unknown	Surface-water gley	Sandy silt loam	140.9 ± 27.8	23/11/2011

Table 2. Soil CO_2 flux temperature response ratio's (ratio between CO_2 flux at 10 °C and 20 °C) and summary statistics from linear mixed effect models on the effect of land use type (grassland control, coniferous and broadleaved), depth and their interaction on CO_2 fluxes in soils. CO_2 (µg g^{-1} soil h^{-1}) data are based on soil dry weight. Values represent means ± standard error.

Land Use/Depth	**CO_2** (µg g^{-1} soil h^{-1})	**CO_2** (µg g^{-1} C h^{-1})
Grassland 0-15 cm	2.88 (± 0.35)	2.83 (± 0.32)
Grassland 15-30 cm	3.28 (± 0.36)	3.40 (± 0.45)
Coniferous 0-15 cm	3.27 (± 0.46)	3.21 (± 0.43)
Coniferous 15-30 cm	3.57 (± 0.51)	3.70 (± 0.63)
Broadleaved 0-15 cm	2.72 (± 0.86)	2.75 (± 0.09)
Broadleaved 15-30 cm	2.61 (± 0.96)	2.57 (± 0.08)
Mixed model fixed effect		
Land Use	P = 0.874	P = 0.862
Depth	P = 0.719	P = 0.790
LU: Depth Interaction	P = 0.131	P = 0.066

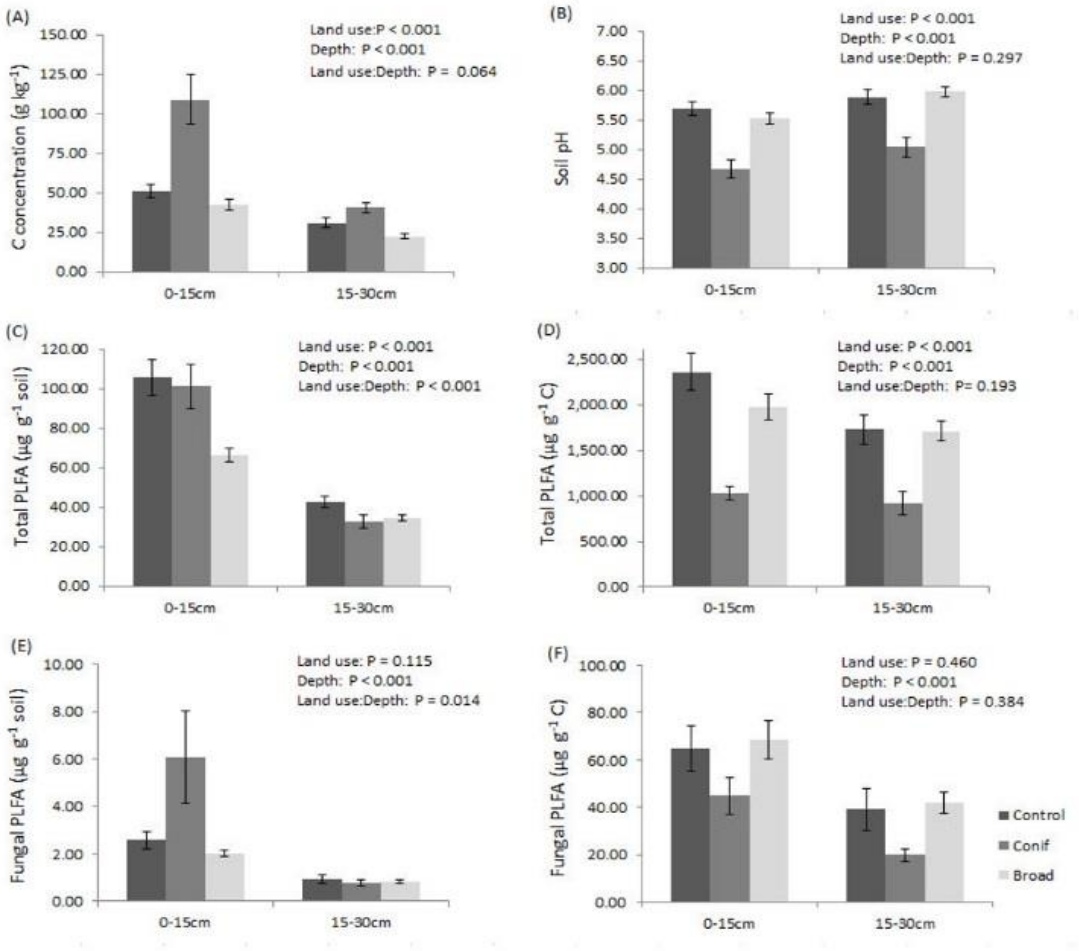
(A)
C concentration (g kg-1)
Land use:P < 0.001
Depth: P < 0.001
Land use:Depth: P = 0.064
0-15cm
15-30cm
(B)
Soil pH
Land use: P < 0.001
Depth: P < 0.001
Land use:Depth: P = 0.297
(C)
Total PLFA (µg g-1 soil)
Land use: P < 0.001
Depth: P < 0.001
Land use:Depth: P < 0.001
(D)
Total PLFA (µg g-1 C)
Land use: P < 0.001
Depth: P < 0.001
Land use:Depth: P= 0.193
(E)
Fungal PLFA (µg g-1 soil)
Land use: P = 0.115
Depth: P < 0.001
Land use:Depth: P = 0.014
(F)
Fungal PLFA (µg g-1 C)
Land use: P = 0.460
Depth: P < 0.001
Land use:Depth: P = 0.384
Control
Conif
Broad

Figure 1.

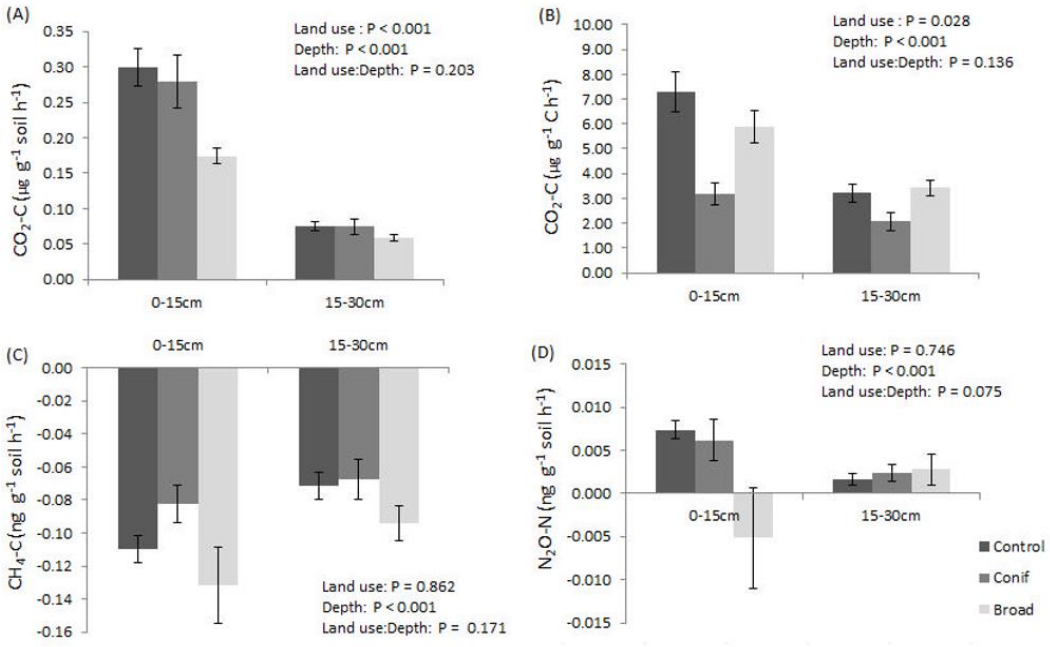
(A)
Land use : P < 0.001
Depth: P < 0.001
Land use:Depth: P = 0.203
CO_2-C (µg g^{-1} soil h^{-1})
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0-15cm
15-30cm
(B)
Land use : P = 0.028
Depth: P < 0.001
Land use:Depth: P = 0.136
CO_2-C (µg g^{-1} C h^{-1})
10.00
9.00
8.00
7.00
6.00
5.00
4.00
3.00
2.00
1.00
0.00
0-15cm
15-30cm
(C)
0-15cm
15-30cm
CH_4-C (ng g^{-1} soil h^{-1})
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
-0.14
-0.16
Land use: P = 0.862
Depth: P < 0.001
Land use:Depth: P = 0.171
(D)
Land use: P = 0.746
Depth: P < 0.001
Land use:Depth: P = 0.075
N_2O-N (ng g^{-1} soil h^{-1})
0.015
0.010
0.005
0.000
-0.005
-0.010
-0.015
0-15cm
15-30cm
Control
Conif
Broad

Figure 2.

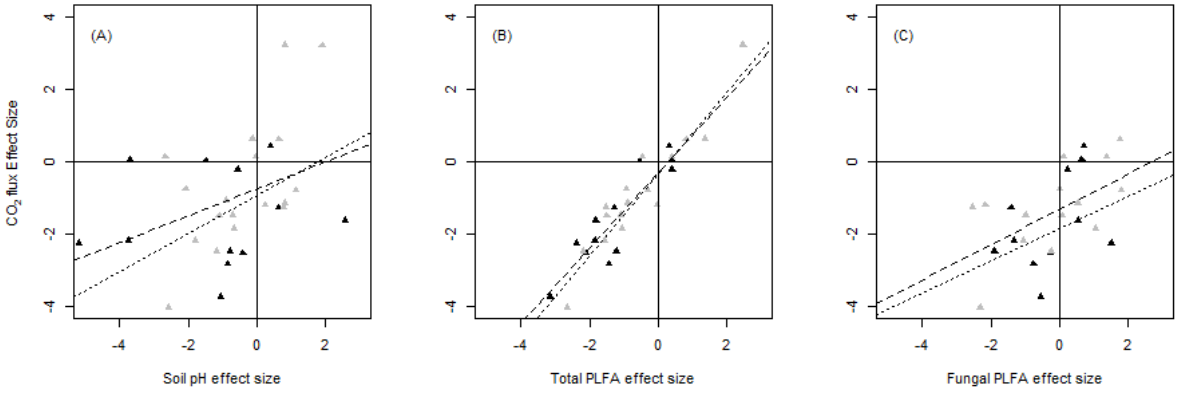
(A)
(B)
(C)
CO_2 flux Effect Size
Soil pH effect size
Total PLFA effect size
Fungal PLFA effect size
-4
-2
0
2
4

Figure 3.