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Partitioning of ecosystem respiration of CO_2 released during land-use transition from temperate agricultural grassland to *Miscanthus* × *giganteus*

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Abstract

Conversion of large areas of agricultural grassland is inevitable if European and UK domestic production of biomass is to play a significant role in meeting demand. Understanding the impact of these land-use changes on soil carbon cycling and stocks depends on accurate predictions from well-parameterized models. Key considerations are cultivation disturbance and the effect of autotrophic root input stimulation on soil carbon decomposition under novel biomass crops. This study presents partitioned parameters from the conversion of semiimproved grassland to Miscanthus bioenergy production and compares the contribution of autotrophic and heterotrophic respiration to overall ecosystem respiration of CO₂ in the first and second years of establishment. Repeated measures of respiration from within and without root exclusion collars were used to produce time-series model integrations separating live root inputs from decomposition of grass residues ploughed in with cultivation of the new crop. These parameters were then compared to total ecosystem respiration derived from eddy covariance sensors. Average soil surface respiration was 13.4% higher in the second growing season, increasing from 2.9 to 3.29 g CO₂-C m⁻² day⁻¹. Total ecosystem respiration followed a similar trend, increasing from 4.07 to 5.4 g CO_2 -C m⁻² day⁻¹. Heterotrophic respiration from the root exclusion collars was 32.2% lower in the second growing season at 1.20 g CO₂-C m⁻² day⁻¹ compared to the previous year at 1.77 g CO₂-C m⁻² day⁻¹. Of the total respiration flux over the two-year time period, aboveground autotrophic respiration plus litter decomposition contributed 38.46% to total ecosystem respiration while belowground autotrophic respiration and stimulation by live root inputs contributed 46.44% to soil surface respiration. This figure is notably higher than mean figures for nonforest soils derived from the literature and demonstrates the importance of crop-specific parameterization of respiration models.

Keywords: autotrophic respiration, bioenergy, CO₂ flux, eddy covariance, grassland, heterotrophic respiration, land-use change, *Miscanthus*, modelling

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Introduction

Large-scale production and utilization of biomass is essential if European and UK government targets for decarbonization of energy supplies to mitigate climate change are to be met (Europa 2005; DEFRA 2007; DECC 2012). In 2014, 120 kha of UK agricultural land (2% of total arable land) was being used for the production of bioenergy with 29 kha in England alone being used to produce maize to supply the demands of anaerobic digesters (DEFRA 2015). However, producing highinput, high-effort annual food crops for use in energy production is unsustainable in the long term (Hillier

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et al., 2009; Naik et al., 2010; Felten et al., 2013). Much research effort has been employed in the understanding and development of low-input, high-productivity perennial energy grasses to address some of the environmental issues surrounding large-scale bioenergy production (Lewandowski et al., 2003; Clifton-Brown et al., 2004; Adler et al., 2007; Hastings et al., 2008; Ferchaud et al., 2015). Miscanthus \times giganteus (hereafter Miscanthus) is seen as one of the most promising of these second-generation energy crops to be grown under UK conditions with much research and commercial interest as a result (Clifton-Brown et al., 2007; Heaton et al., 2010; Cadoux et al., 2012; Wang et al., 2012; Zimmermann et al., 2013; Clifton-Brown et al., 2016). Much has been learnt in recent times about the potential environmental costs and benefits of a large-scale roll-out of Miscanthus

© 2016 The Authors. *Global Change Biology Bioenergy* published by John Wiley & Sons Ltd This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited. production (Rowe et al., 2009; McCalmont et al., 2015a; Milner et al., 2015), and it seems clear that, in arable systems particularly, there are significant benefits to be found in utilizing this novel perennial as a long-term break crop in overworked or marginal agricultural soils. What are less clear are the impacts on soil carbon cycling from converting large areas of agricultural grassland into Miscanthus production; as would occur in any large-scale UK roll-out where 65% of utilized agricultural area is grassland of some kind with 1.4 Mha of this being temporary grassland under five years old (DEFRA 2014). There is still some debate surrounding mobilization and loss, through decomposition respiration, of pre-existing soil carbon pools under agricultural grassland following re-cultivation, although the weight of evidence is suggesting that these initial soil carbon losses could be replaced in the short-to-medium term by fresh root and litter inputs from the developing crop (Hansen et al., 2004; Anderson-Teixeira et al., 2009; Zimmermann et al., 2012; McCalmont et al., 2015b).

Accurate parameterization of models of ecosystem respiration (Vellinga et al., 2004; Ryan & Law, 2005; Del Grosso et al., 2005; Agostini et al., 2015; Dondini et al., 2015) is important in understanding the impact of largescale land-use change to bioenergy crop production and any useful contribution it might make to mitigating anthropogenic climate change, particularly where this will involve novel crop species. Studies have shown clear differences between crop species' autotrophic contribution and soil respiration of CO₂ along with increased stimulation of decomposer populations following novel root and litter inputs, demonstrating the need for crop-specific parameterization of respiration models if they are to accurately predict impacts (Hanson et al., 2000; Raich & Tufekciogul, 2000; Van Der Krift et al., 2002; Cheng et al., 2003).

The work presented here was aimed at a better understanding of land-use transition from grassland to Miscanthus cropping; specifically, the relative contribution of individual soil respiration components, auto- and heterotrophic, to overall ecosystem respiration and their distinct responses to changes in environmental conditions. These differing response rates were demonstrated by Wang et al. (2014) who suggest that distinguishing between these two components will be important in long-term prediction of respiration response to global climate warming. Hanson et al. (2000) summarized the partitioning literature with histograms of root input contribution (autotrophic respiration) over a range of vegetation types, emphasizing the importance of this partitioning of soil respiration in model development. Information is also needed when extrapolating to average annual respiration values due to significant differences in root contribution to total respiration between growing and dormant seasons (Edwards, 1991; Rochette & Flanagan, 1997). Something likely to be exacerbated in cultivation cycles of agricultural crops over time, Hanson *et al.* (2000) stress the importance of repeated measurements over the long term to estimate annual and even interannual trends and cycles. For perennial crops particularly, as in the case of *Miscanthus*, these component distinctions are likely to be very different between the cultivation/establishment and maturation years following a land-use change; in these cases, finer scale temporal resolution of these distinctions may be critical.

The destruction of an existing, long-term crop and the cultivation of another can be expected to affect components of soil respiration in several ways and over a range of time scales, particularly if the original crop is first killed with herbicide. Root respiration/exudation and the diffusion gradient of the soil CO2 pool will initially diminish with the dying plants, and subsequent ploughing will result in the release of the remaining pool from soil micro- and macropores (Reicosky et al., 1997; Reicosky & Archer, 2007; Willems et al., 2011). The ploughed input of the dead organic matter to the soil will then provide fresh decomposable material to soil organisms with the newly developing crop also providing new material through root exudates and turnover (Cheng et al., 2003; Kuzyakov, 2010; Hopkins et al., 2013). These fresh inputs might be expected to stimulate decomposer populations; these primed populations can potentially outgrow this new food resource and begin decomposing more stable carbon pools; and soil respiration will also be enhanced by the predation, death and decay of these decomposer populations themselves (Cheng, 2009).

The first of these respiration components, the loss of the soil matrix pore space CO₂ pool following cultivation, has been investigated by several other studies, but none have quantified the total magnitude of the CO₂ loss during this process. Previous studies have captured immediate, short-term flushes of CO₂ following soil disturbance: Ellert & Janzen (1999), studying a spring wheat/fallow rotation on the Canadian Prairies, noted that respiration at least doubled within the first hour after tillage but had returned to an ambient level similar to untilled soil within 24 h. Their sampling rate did not allow enough resolution to pinpoint exactly when respiration had returned to baseline. In a study on Irish grassland Willems et al. (2011) used a higher sampling rate, 20-min intervals for the first three hours, to capture these dynamics. The first sample was taken eight minutes after ploughing of live grass which revealed a brief peak followed by a rapid decline within 45 min. Reicosky & Archer (2007) also

investigated short-term CO_2 release following ploughing, and they noted significantly more CO_2 released with increasing plough depth.

For this study, an experimental approach was employed to attempt to capture this peak flux and return to ambient following extreme soil disturbance and to compare between soils under first healthy grass and subsequently the same grass sprayed with glyphosate in readiness for a crop change. In addition, following cultivation and establishment of the new Miscanthus crop, further components of ecosystem respiration were investigated and quantified. Heterotrophic respiration from the decaying pre-existing grass residue killed by spraying and ploughed in during cultivation was investigated by monitoring respiration using a portable infrared gas analyser (IRGA) from within root exclusion collars which prevented live plant inputs and were kept clear of litter decomposition. Total soil surface respiration within the developing crop, including the autotrophic contribution of live root inputs and the decomposition of organic crop residues, was monitored outside the root exclusion collars from bare soil between plants; in addition, total ecosystem respiration was monitored above the canopy using eddy covariance sensors, further capturing leaf and stem mitochondrial respiration and leaf litter decomposition from the soil surface.

Materials and methods

Site

The study site was a 7.41 ha agricultural grassland site at Aberystwyth in mid-Wales, UK (52°25'17"N 4°04'14"W). Soil type is a sandy loam, dystric cambisol over Denbigh series bedrock with a mean pH of 5.9. Soil depth was typically shallow though extremely variable across the site with a mean of 0.44 m and depths below 0.30 m reaching an underlying gravel layer, baseline soil organic carbon content averaged $78.61 \pm 3.28 \text{ Mg C ha}^{-1}$ in the top 0.30 m. Climate is temperate with 30-year local annual averages of 158 days with rain, 1074.7 mm total rainfall and max/min temperatures of 13.5/ 6.7 °C [Gogerddan 1981-2010 averages (www.metoffice. gov.uk)]. Existing land use at the site was agricultural, semiimproved grassland (silage cut and grazing), which was last resown six years prior to this experiment. The existing grassland was intensively grazed to ground level by sheep which were removed from the site on 20 February 2012, and the land-use change experimental area (central 5.71 ha) was sprayed with glyphosate on 16 March 2012 at 1.5 kg ha⁻¹ to kill off the remaining sward. This area was then ploughed to approximately 20 cm depth on the 4th April before being power-harrowed and planted with Miscanthus × giganteus rhizomes at 16 000 plants ha⁻¹ on the 24th April. For full details of site characteristics, baseline soil analysis and land-use conversion see McCalmont et al. (2015b).

Experimental layout and crop physiological measurements

Figure 1 shows a schematic diagram of the experimental layout of the conversion site with locations of root exclusion collars and plant measurement quadrats. Locations for the eight root exclusion collars (see below for details) were chosen randomly from a 10×10 m grid overlaid within the fetch of the eddy covariance sensors using GIS software (ArcMap 9.3 ESRI, Redlands, CA, USA). Eight plant measurement quadrats were then established 10 m north of these at the beginning of the first growing season (with one exception where this conflicted with a central track which meant this quadrat was located 10 m south instead). Quadrats were re-established 10 m further north during the second growing season (2013) following destructive harvesting of belowground biomass. Quadrats were 2 m long and 1.22 m wide (2.44 m²) capturing two rows of Miscanthus and two inter-rows; in 2012, the number of Miscanthus plants captured in each of these quadrats varied from 5 to 8 (mean 6.75) while in 2013 this was 5 to 7 (mean 6.38). Repeated measures of crop growth parameters, canopy height, leaf area index and stem length (soil surface to top ligule), and density were recorded from these quadrats throughout the growing seasons. For the establishment year, 2012, there were 16 rounds of sampling across the growing season; this was increased to 22 rounds of sampling during the 2013 growing season to better accommodate the faster growing second-year crop. Canopy height was measured by recording the highest point of leaf inflection on each of the plants within a quadrat, the mean of this produced a canopy height estimate for each quadrat; quadrats were then combined to produce a mean canopy height for the site. Results reported below are restricted specifically to respiration parameters, for full results of crop growth and development over the two years see McCalmont et al. (2015b).

CO₂ flux sampling

Definition of terms and component captured

- R_{eco} Total ecosystem respiration. eddy covariance, capturing heterotrophic decomposition of soil organic matter, root/leaf and stems autotrophic respiration and heterotrophic decomposition of litter and crop residues at the surface of the soil.
- R_s Within crop soil surface respiration. Dynamic chamber measurements taken between plant rows on bare soil capturing heterotrophic decomposition of soil organic matter and live root exudates plus live root autotrophic respiration
- $R_{
 m sdecomp}$ Root excluded soil surface respiration. Dynamic chamber measurements taken from within root exclusion collars capturing heterotrophic decomposition of pre-existing crop residues killed with glyphosate and ploughed into the soil during cultivation plus any added decomposition of preexisting soil carbon pools but excluding the autotrophic respiration and heterotrophic decomposition of live root inputs.



Fig. 1 Georeferenced schematic of the experimental layout; total site is 7.41 ha with a central 5.71 ha converted from agricultural grassland to Miscanthus. Open circles indicate locations of the root exclusion collars while open squares show locations of the 2012 plant measurement quadrats. Flags show the location of the two eddy covariance masts (EC1 and EC2), the central meteorological mast and the power supply tower carrying solar and wind chargers.

Total ecosystem respiration (R_{eco})

Total ecosystem respiration was estimated using the eddy covariance technique; the site is instrumented with two replicated open-path eddy covariance masts, one at either end of the site. See McCalmont et al. (2015b) for a more detailed description of instrumentation, data processing and quality control. Briefly, the EC masts were EC150/CSAT3A OPEC systems (Campbell Scientific Inc. (CSI), Logan, UT, USA) with soil moisture and temperature sensors added. In addition, a complementary meteorological sensor mast was set at the centre of the site with replicated soil moisture/temperature at two depths (0.025 and 0.25 m), precipitation, incoming solar radiation and wind speed/direction. Raw eddy covariance data, wind speed/direction and CO₂ concentration, were collected at the EC masts at 20 Hz and integrated into half-hour flux rates using EDDYPRO software (EddyPro® version 4.2.0, LI-COR bioscience, Lincoln, NE, USA) before being further quality controlled. Data gaps, due to power failure, inappropriate wind direction, etc., at EC1 (see Fig. 1) are filled where possible from retained data at EC2. This data set was then further gap-filled and partitioned into GPP and Reco following Reichstein et al. (2005) using the FLUX-NET standard online gapfilling tool: http://www.bgc-jena. mpg.de/bgi/index.php/Services/REddyProcWeb

Soil surface respiration (R_s and $R_{sdecomp}$)

Sampling for R_s and $R_{sdecomp}$ was carried out using an EGM-4 portable infrared gas analyser (IRGA) coupled with an SRC-1 soil respiration chamber, which has a cross sectional area of 0.008 m² and volume of 0.0012 m³ (PP Systems, Amesbury, MA, USA). This equipment does not rely on fixed sample

collars inserted into the soil but can be deployed directly onto the surface of the soil at any location. Sampling monitored CO2 concentration increase within the chamber (μ mol mol⁻¹) at four-second intervals until a rise over ambient of 50 ppm or for two minutes whichever was sooner. Calculations to convert from volumetric concentration increases to flux rates followed standard procedures: linearity of the concentration increases are checked using Pearson product moment correlation before molar measurements of CO2 are converted to mg CO2-C using the ideal gas law with volume to area conversion to produce a surface flux rate over time. Air temperature (°C at +10 cm) and soil temperature (°C to -10 cm) were recorded using a 10 cm temperature probe at each sampling along with three soil volumetric water content measurements $(m^3 m^{-3})$ using a portable soil moisture probe (ML3 ThetaProbe, Delta-T Devices, Cambridge, UK). All $R_{\rm s}$ and $R_{\rm sdecomp}$ sample locations were within the fetch of the eddy covariance sensors.

Immediate CO_2 flush from ploughed soils

Attempting to sample respiration from disturbed soils immediately following commercial-scale ploughing can be challenging (Willems *et al.*, 2011), difficulties arise due to conflicts with machinery passing, poor weather preventing deployment of the IRGA or clumping of heavy soils. To address this, an experimental approach was undertaken prior to cultivation; this was carried out by digging small pits to a representative plough depth, turning over and briefly chopping the soil to mimic ploughing disturbance, and monitoring soil CO_2 flux rates throughout. In addition to estimating the size of the soil CO_2 pool released through ploughing, the difference between concentration gradients under sprayed and healthy grass was also investigated. Sampling was therefore carried out from soil disturbance pits dug into the grassland both before and 18 days after spraying the grass with herbicide in preparation for cultivation; air/soil temperatures and moisture were recorded at each sampling as discussed above.

An initial CO₂ flux reading was first taken from each sample site with the IRGA; this was taken to represent the ambient baseline. A pit 30 cm \times 30 cm \times 20 cm deep was then dug; the soil quickly turned over back into the pit and briefly chopped up with the spade. T₀ sampling was immediate with the IRGA chamber placed at the centre of this soil. Repeat samples were then taken at T₀+5 min; T₀+10 min; T₀+30 min; T₀+60 min; and then at 15 min intervals until the flux rate returned to the ambient. Ambient flux rate might be expected to change slightly during the sampling period; to account for this, samples were taken from the vicinity as the sample flux rate returned to near the initial baseline to check when the two corresponded.

Time-series results of flux rates, in mg CO₂-C m⁻² min⁻¹, are plotted for each sample pit against the time taken from the initial T_0 for the spike in CO₂ flux to return to an ambient rate with linear interpolation between them used to produce a pulse/decay curve; below this was plotted the two data points from the ambient baseline samples, similarly interpolated, to produce a graph with two data series for each soil pit sampled (see Fig. 3).

The integrated area between these two curves represents an estimate of the total mass of carbon (CO₂-C) flushed from the soil as a direct result of the disturbance. Nine randomly distributed pits were sampled in total across the site; four (HG1–HG4) from under healthy grass (HG = healthy grass) three days before spraying and four (SG1–SG4) from under grass 18 days later after herbicide application of glyphosate (SG = sprayed grass), with one extra healthy grass control (HG5) from retained grassland during the sprayed grass sampling.

In addition, the respiration data from the eddy covariance (R_{eco}) data set over the two years were used to investigate the assumption that there would be no significant variability in the ambient flux rate during individual sampling periods. For this, the R_{eco} data were binned into two-hour periods and the mean standard deviation and the percentage that the standard deviation represented of the mean flux rate for all two-hour periods was calculated.

Data handling and integration calculations are carried out using the R statistical language (R Foundation for Statistical Computing, Vienna, Austria).

Auto- and heterotrophic respiration components

Three weeks after final cultivation and planting of *Miscanthus*, eight steel collars 0.55 m diameter by 0.30 m deep were dug into the shallow soil down to the underlying gravel layer (Vogel & Valentine, 2005; Martin & Bolstad, 2009). Care was taken to replace the soil in these root exclusion collars in as consistent a way as possible to the layers in which it had been removed; this was to retain the organic matter and soil horizons resulting from the ploughing in of the grassland residue at depths corresponding to the soils outside the collars.

The soil surface within these collars (see Fig. 2) was maintained free of plant growth or litter input (by weekly hand weeding and clearing of any litter drop) throughout the twoyear study period and prevented encroachment of roots from the newly developing crop. This provided the opportunity to follow soil respiration directly resulting from the decomposition and priming effects of the previous grass crop that was killed and ploughed into the soil (R_{sdecomp}) and gives an insight into the soil carbon decomposition (heterotrophic) component of soil respiration over the land-use change area. Soil surface respiration (R_s) of CO₂ from the bare soil between *Mis*canthus plants (thereby including autotrophic respiration) was monitored using the portable IRGA, weekly where possible, placed at sample points randomly distributed across the site (n = 8) to give a time series of 65 rounds of sampling between the spraying of the grassland in March 2012 and the end of 2013. These random locations were newly chosen for each sampling using a GIS 10×10 m numbered grid overlay with sample points chosen by random number generation and located at the site using GPS.

The root exclusion collars (n = 8) were included from 28 May 2012 which resulted in a further 55 R_{sdecomp} comparisons. The eddy covariance sensors were installed in January 2012 and ran throughout the trial period.

Time-series modelling of soil respiration

A modelling approach was taken to produce continuous timeseries estimations of soil respiration from the intermittent, repeat sampling carried out in the field. This was performed at a daily time step and used environmental data, collected from the meteorological sensors around the field, combined with crop growth parameters. These parameters were used to drive general additive models (GAM) trained on the 65 $R_{\rm s}$ and 55



Fig. 2 Root exclusion collars (*n* = 8) dug into the land-use change areas following the soil disturbance of cultivation and planting.

 R_{sdecomp} mean values measured from 17 March 2012 (the day after spraying out the original grassland) to the end of December 2013. The first step in this process was to convert field measurements taken over a two-hour period, generally between 11:00 and 13:00 h, to a reasonable estimate of a daily mean. This was carried out following Parkin & Kaspar (2003), who used hourly static chamber measurements to demonstrate a near-linear relationship between time of day deviations in air temperature and soil CO₂ flux. They observed that sampling around midday would lead to an overestimation of the daily mean and proposed a Q_{10} -based temperature correction validated on their high-frequency sampling:

Daily average CO₂ flux =
$$R \cdot Q^{\frac{(DAT-T)}{10}}$$
 (1)

where

R = measured CO₂ flux at a specific hour

 $Q = Q_{10}$ factor

DAT = daily average temperature

T = air temperature during measurement.

Parkin & Kaspar (2003) evaluated both soil and air temperatures at Q_{10} factors of 1.25, 1.5 and 2.0 finding that air rather than soil temperature was more effective at correcting time point measurements to their measured daily mean. They found that the most effective Q_{10} factor varied with soil type and was likely to be site specific; conclusions which might be expected following previous work looking at the temperature dependence of soil respiration (Lloyd & Taylor, 1994; Kirschbaum, 1995; Fang & Moncrieff, 2001). Q_{10} factors are here calculated as the relationship between increases in respiration and an increase in temperature of 10 °C using the equation:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10}{(T_2 - T_1)}}$$
(2)

where R_1 and R_2 are respiration rates observed at temperatures T_1 and T_2 .

Initially, Eqn (2) was applied between the highest (22.64 °C) and the lowest (1.67 °C) temperatures recorded during the study period. Next, to better address seasonality in an agricultural system, the measured data were split into growing and dormant season bins (indicated by crop growth monitoring) and Q_{10} factors once again derived. These measured seasonal Q_{10} values were then applied to the similarly binned measured flux rates using Eqn (1) to convert them to mean daily respiration rates. A similar process was applied to the $R_{sdecomp}$ data, also using growing and dormant seasons.

Once the sampling data had been corrected to estimate the mean respiration rates for the day of sampling, meteorological data collected at the sensor masts were averaged across the site and combined with plant growth parameters to investigate significant correlations to these values. Pairwise linear regression plots (not shown) were compared between potential drivers that were found, through stepwise model comparisons, to be most significantly related to the two respiration measures (R_s and $R_{sdecomp}$). As would be expected from the literature, strong correlations were evident between respiration and air and soil temperatures while the close coupling between air and soil temperature suggested that one might be safely excluded from the model. Given literature suggestions that soil surface respiration

is more responsive to rapid changes in air rather than soil temperature (e.g. Parkin & Kaspar, 2003; Reichstein *et al.*, 2005), this was retained as the driving temperature variable for the R_s data and confirmed as appropriate by model substitution checks.

Canopy growth rate ($C_{\rm gr}$) was retained in favour of either stem or leaf growth as increases in both these parameters are captured in the overall canopy height and this combined measure was found to correlate more strongly than the others. These growth rates were simply produced by calculating a mean delta per day over the weekly interval between crop measurements and assuming this mean for each day between those dates.

A soil moisture parameter [vwc ($m^3 H_2O m^{-3}$ soil)] was estimated using a mean figure produced from the continuous monitoring at all three sensor masts across the site. To investigate the impact that the root exclusion collars might have on soil moisture within them and to compare to the site mean figures, localized soil moisture measurements were also taken at each round of respiration sampling using the theta probe inside and outside the exclusion collars.

Both linear and nonlinear correlations between respiration and its drivers were investigated using nonlinear least-squares estimation of residuals and Akaike's information criteria (AIC) values in model comparison. A general additive model (GAM) was derived using penalized maximum likelihood in model fit estimation (Wood, 2006), initially including daily mean air and soil temperature, max/mean and daily extent (number of hours >20 W m⁻²) of global radiation, soil moisture (vwc) and the range of crop growth rates. This modelling was carried out using the MGCV package in R (R Foundation for Statistical Computing, Vienna, Austria).

Results

Immediate CO₂ flush from ploughed soils

Environmental variables. Mean air temperature was slightly higher during the healthy grass (HG) sampling (11.65 \pm 0.5 °C) than during the sprayed grass (SG) sampling (9.47 \pm 0.2 °C) although soil temperatures were broadly the same (HG 9.95 \pm 0.2 °C and SG 10.2 \pm 0.1 °C). Mean soil moisture content was also higher during the HG sampling (HG 0.50 \pm 3.2 m³ m⁻³ and SG 0.38 \pm 3.2 m³ m⁻³), although both of these moisture levels would be expected to be within an optimal range for soil processes at this site and are not believed to be limiting respiration during either sampling.

Variability of ambient flux rates during sample periods

There were a total of 8736 two-hour periods within the two-year eddy covariance data set. Flux rates within these ranged from 0.61 to 10.57 μ mol m⁻² s⁻¹ with the mean standard deviation within each of these two-hour periods being 0.07 μ mol m⁻² s⁻¹. This variability

represented, on average, 2.15% of the mean flux rate in any given period, suggesting that the assumption of a consistent ambient flux rate throughout each sample period was not unreasonable.

Duration of pulse/decay curves

There was a significant difference between the duration of the decay curves of the sprayed and healthy grass sampling (one-way ANOVA, F = 29.67, P < 0.01); the time taken for this spike in CO2 flux to return to ambient averaged 82.5 min under the healthy grass and 18.75 min under the sprayed grass; the healthy grass control sampled during the sprayed grass sampling had still not returned to ambient after 75 min. Figure 3 shows the decay curves over time in minutes for each sample pit with baseline curves plotted below on each chart. Reflecting this difference in pulse/decay times between healthy and sprayed grass, there was a corresponding significant difference in the overall mass of carbon lost from the soil immediately following soil disturbance under the two treatments (One-way ANOVA, F = 18.59, P < 0.01). The maximum observed flux rate was from HG3 at 50.1 mg CO₂-C m⁻² min⁻¹ with a 60min decay to ambient while the maximum rate from under the sprayed grass was 27.08 mg m⁻² min⁻¹ which returned to ambient after 10 min. In total, as a direct result of disturbance, soil from under the healthy grass released an extra 203.31 \pm 27.90 mg CO₂-C m⁻² (\pm SE) while soil from the sprayed grass released only an extra 45.55 \pm 16.22 mg m⁻². The total mass of CO₂-C lost from individual sample pits is given above the curves in each plot in Fig. 3 and shows a relative comparison between the healthy and sprayed grass sampling.

Time-series respiration modelling

Soil moisture/temperature comparison inside and outside root exclusion collars. Soils within the collars ($R_{sdecomp}$) were found to be typically drier than soil outside in the wider crop (R_s) during the first growing and dormant seasons; although R_s soils became drier during the latter half of the second growing season, differences between these moisture contents averaged 12.8 \pm 1.3%. Volumetric water contents over the two years ranged from 16.4 to 67.5% (mean 40.43) for the R_s , while for the $R_{sdecomp}$ this ranged between 12.0 and 73.9 (mean 38.19). Soil temperatures compared between the two treatments were very similar; temperatures ranged between 1.72 and 22.29 °C



Fig. 3 Pulse decay curves for each sample pit, HG1-4 show sampling from under healthy grass and SG1-4 show sampling from under sprayed grass. Upper curve in each chart represents the spike in CO_2 emission following soil disturbance, the lower curve uses flux rates from undisturbed soil at the beginning and end of each sample period to represent an ambient baseline. The integrated area between the two curves is taken to represent the flush of carbon released immediately following disturbance; note significant differences, both in peak flux rates (*y*-axis scales) and their corresponding return times to ambient (*x*-axis scales).

(mean 12.08 °C $R_{\rm s}$ and 12.33 °C $R_{\rm sdecomp}$); over the whole study period, the mean difference between paired measurements inside and outside the root exclusion collars was 0.33 \pm 0.06 °C. See Fig. 4 for a plot of the time series of these soil moisture and temperature measurements.

*Q*₁₀ correction factors

The overall site Q_{10} factor for the R_s component (autotrophic plus heterotrophic respiration measured between plants), calculated across the entire temperature range, was found to be 2.98. After splitting into growing and dormant season bins, Q_{10} factors were derived at 1.96 for the growing season and 3.10 during the colder temperatures of the dormant season. These Q_{10} factors were then applied to growing and dormant season measured CO_2 flux rates (R_s) using Eqn (1) to convert from spot measurements to daily mean respiration rates. The resulting correction factor suggested that midday R_s sampling overestimated the mean daily flux by 23.9 \pm 4.5% (\pm SE) during the dormant season and by $17.3 \pm 2.67\%$ during the growing season, broadly agreeing with Parkin & Kaspar (2003) who found an overestimation during early afternoon sampling of 20 to 40% depending on soil type. The same process was then applied to the $R_{sdecomp}$ (heterotrophic) values measured within the root exclusion collars, Q_{10} factors once again differed between the two seasons, and between the R_s and $R_{sdecomp}$ results; here, the $R_{sdecomp}$ growing season Q_{10} was much higher than the R_s at 2.62 although the dormant season was very similar at 3.15. Corrections were then applied to the measured data in the same way and, in contrast to the R_s data, suggested very similar overestimations between the seasons; dormant at 26.9 \pm 4.76% and growing at 23.8 \pm 4.86%.

GAM model testing and prediction

Within crop soil surface respiration (R_s). The effective degrees of freedom in the model output agreed with the pairs plot in suggesting that both temperature parameters and vwc showed a strong correlation to R_s . While the literature would suggest an exponential relationship might have been typically expected between temperature and respiration, preliminary testing suggested that for this site, within the narrow temperature range seen during the study, a linear fit adequately captured the response. After including air temperature and crop growth parameters in the model, soil temperature and moisture were not found to be adding any significant information (P = 0.96 and 0.71). The R_s model with the



Fig. 4 Plot comparisons between measurements taken inside ($R_{sdecomp}$) and outside (R_s) root exclusion collars at each gas flux sampling; plot (a) shows soil temperature to -10 cm, plot (b) shows soil surface volumetric water content. Error bars show standard error (n = 8), error bars in plot (a) are typically smaller than the plot symbols so are not visible.

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lowest (and therefore best) AIC score and most parsimonious fit was found to be a linear fit of air temperature (T_a) combined with penalized regression spline smoothing of canopy growth rate (C_{gr}) and maximum daily global radiation (R_g); including soil moisture or soil temperature did nothing to improve either its AIC score or the explanation of deviance score which was 83.4%. All three parameters were shown to be highly significant at P < 0.01. Eqn (3) shows the model structure and parameters used.

 $R_{\rm s}$ model:

$$R_{\rm s} \sim T_{\rm a} + s(C_{\rm gr}) + s(R_{\rm gmax}) \tag{3}$$

where

 $R_{\rm s} = {\rm soil} \, {\rm surface} \, {\rm respiration} \, ({\rm auto} + {\rm heterotrophic}) \ ({\rm \mu mol} \, {\rm m}^{-2} \, {\rm s}^{-1})$

 $T_{\rm a}$ = daily mean air temperature (°C)

 $R_{\text{gmax}} = \text{maximum}$ daily incoming solar radiation (W m⁻²)

Soil surface respiration within root exclusion collars $(R_{sdecomp})$

A similar approach was taken with the $R_{sdecomp}$ data; however, as might be expected, the environmental drivers now differed in significance to the R_s data. In this analysis, soil moisture and temperature were now both found to be highly significant while air temperature was not; number of hours in the day where mean global radiation (R_g) exceeded 20 W m⁻² was also highly significant and explained more of the variation than either maximum or mean daily R_g . All three of the above variables were significant at P < 0.001; a further driver that contributed significantly to the model (though far less than for R_s) was, surprisingly, canopy growth rate (C_{gr}) (P < 0.05). See Eqn (4) for a summary of the model structure and parameters used.

R_{sdecomp} model:

 $R_{\text{sdecomp}} \sim \text{VWC}_{\text{mean}} + s(T_{\text{smean}}) + s(R_{\text{ghours}}) + s(C_{\text{gr}})$ (4)

where

 $R_{sdecomp}$ = soil surface respiration within exclusion collars (µmol m⁻² s⁻¹)

 VWC_{mean} = site mean volumetric soil water content (m³ m⁻³)

 $T_{\rm smean}$ = mean soil temperature (°C)

 $C_{\rm gr}$ = canopy growth rate (mm day⁻¹)

 $R_{\text{ghours}} = \text{number of hours solar radiation exceeded}$ 20 W m⁻²)

Figure 5 shows residuals plots for the model fit for R_s ($R_{sdecomp}$ similar) while Fig. 6 shows a modelled time series of daily mean respiration from these two components with measured data from the field sampling overlaid. (Note units for this plot, and the modelling, are

mean flux rates in μ mol CO₂ m⁻² s⁻¹, these are converted to mg CO₂-C m⁻² day⁻¹ for summation into time span totals). The R_s data set, at 65 mean values (n = 8), was too small to split into training and validation data sets for a GAM model approach so testing was limited to in-sample validation through prediction and comparison of measured and modelled data at the same time points. Linear regression between them returned a fit of 0.93, indicating a highly significant correlation between the two with an R^2 value of 0.73 showing low random error with minimal systematic error indicated by an intercept of 0.12 μ mol CO₂ m⁻² s⁻¹. As can be seen in Fig. 6a, model fit for R_s was poorest during the first few months of the cultivation and land-use change; the trend was captured well but predictions are seen to overestimate respiration during the bare soil months between May and July 2012 and then underestimate it during the first two months of strong Miscanthus growth in July and August 2012. Measured vs. modelled R_{sdecomp} comparisons were very similar with a fit of 0.98, R^2 of 0.76 and an intercept at 0.02, though with better approximation than the R_s model at the beginning of 2012 (see Fig. 6b).

Figure 7 shows a time-series line plot of the three respiration components summed to daily carbon mass fluxes (g CO_2 -C m⁻² day⁻¹); the integrated difference in area between the curves represents the contribution of differing factors to overall respiration. The area below $R_{\rm sdecomp}$ reflects the heterotrophic decomposition of soil organic carbon, including decomposition of the ploughed in remains of the original grassland; between $R_{\rm sdecomp}$ and $R_{\rm s}$ indicates the autotrophic contribution from live root inputs and between R_s and R_{eco} the added respiration from surface litter decomposition and leaf/stem respiration, that is the aboveground contribution to total ecosystem respiration. The total ecosystem CO_2 -C respiration flux (R_{eco}), between ploughing on the 4 April 2012 and the end of December 2013, was estimated at 2396.44 g C m⁻²; of this total, the soil surface respiration (R_s) was 1474.76 \pm 30.15 g C m⁻², suggesting that aboveground mitochondrial respiration and surface litter decomposition had contributed 38.46% of the total ecosystem flux. Total $R_{sdecomp}$ for the same period was 789.84 \pm 30.14 g C m⁻², which suggested that autotrophic contribution to soil surface respiration from live root inputs was 46.44%.

Interannual and seasonal variability

There was both seasonal and interannual variation in mean daily respiration rates observed in the three components. Mean daily $R_{\rm s}$ in the 2013 growing season increased 13.4% over 2012, increasing from 2.9 to 3.29 g CO₂-C m⁻² day⁻¹. The dormant season between the



Fig. 5 Residual analysis of model fit [within crop soil surface respiration (R_s)] for the general additive model (GAM). Plots show reasonable normality though some slight deviation at the lower end of the values. Root exclusion collar ($R_{sdecomp}$) respiration residual analysis not shown but similar.

two growing seasons was much lower at 1.16 g CO₂-C m^{-2} day⁻¹. R_{eco} followed a similar pattern but with a larger increase in the second growing season of 32.68%, rising from 4.07 to 5.4 g CO₂-C m⁻² day⁻¹. Again the dormant season flux rate between them was lower at 2.37 g CO₂-C m⁻² day⁻¹. For R_{sdecomp} , the interannual trend was reversed with a reduction in daily mean CO₂ flux between the two growing seasons, 2013 was 32.2% lower at 1.20 g CO₂-C m⁻² day⁻¹ compared to 2012 at 1.77 g CO₂-C m⁻² day⁻¹. The 2012/2013 dormant season $R_{sdecomp}$ respiration reduced to 0.73 g CO₂-C $m^{-2} day^{-1}$ which was in very close agreement with the mean value for the subsequent 2013 dormant season value at 0.74 g CO₂-C m⁻² day⁻¹. Table 1 shows a breakdown into relevant agronomic periods of the respiration values from the individual components and Fig. 7a highlights trends illustrated by moving average smoothing of the model output plots.

Discussion

In this study, we have presented the results of an investigation into the components of ecosystem respiration as affected by a commercially relevant land-use change at a commercial scale; specifically, the impact over the first two years of a crop change of a 6-ha agricultural, semiimproved grassland to a Miscanthus bioenergy crop. The first component to be investigated was the initial flush of soil CO₂ immediately following the disturbance of ploughing, or soil degassing as it is sometimes termed. Results from the experimental approach in this study appear to have captured this initial flush well and have estimated the magnitude of the loss of the soil CO₂ pool under both healthy and sprayed-out grass. Converting to compatible units, the maximum observed flux rate (healthy grass) in this study was 3.01 g CO₂-C m⁻² h⁻¹, which was notably higher than the 1.89 g m⁻² h⁻¹ peak observed in the Willems et al. (2011) study (converted to CO₂-C from their reported CO₂ value of 6.91 g). The flush was greatly reduced under the sprayed grass at 1.62 g m⁻² h⁻¹ suggesting that the soil CO₂ pool had diminished significantly as the grass died off after spraying in preparation for re-cultivation. Unfortunately, Willems et al. (2011) do not report whether their grassland had been sprayed in readiness for ploughing as might be the conventional practice. The total magnitude of the soil CO₂-C pool that was released as a direct result of ploughing was relatively trivial across the site, results suggested that this would be around 2 kg C ha^{-1} ; however, the results do demonstrate well the role

Soil surface respiration (R_s)



Fig. 6 Predicted time series (daily time step) of mean respiration rates, beginning with ploughing at the end of April 2012: (a) daily mean soil surface respiration (R_s) of CO₂ driven by air temperature, canopy growth rate and daily maximum global radiation, (b) daily mean soil carbon decomposition from the root exclusion collars ($R_{sdecomp}$) driven by soil moisture and temperature, day length and a seasonal component captured in canopy growth rate. Grey shading shows standard error of the model fit with the mean of the measured values overlain as solid circles (n = 8) with error bars showing their standard error.

that live plant inputs play in maintaining the diffusion gradient between the soil and the atmosphere, something further quantified in the rest of the study.

The contribution that the Miscanthus crop made to ecosystem respiration was investigated using sampling from inside and outside root exclusion collars and comparing to total ecosystem respiration measured using eddy covariance. This technique for investigating live root contribution to total respiration was directly compared to stable isotope labelling by Rochette et al. (1999) who found very similar results between the two approaches, suggesting both were equally valid; a conclusion supported in other studies (e.g. Hanson et al., 2000; Vogel & Valentine, 2005). The use of these collars has sometimes been criticized for the level of soil disturbance needed to install them, but this is only valid where stable systems are being investigated. In this study, it is the disturbance of land-use change itself that was being investigated making their installation unobtrusive, following as it did the disturbance of

ploughing. Care was taken to replace the soil layers back into the collars as consistently as possible to the way they had been removed meaning the organic matter resulting from the grass residues ploughed in should have remained at reasonably consistent depths to the surrounding soil. It might have been expected that soil moisture would have been higher within these solidwalled collars but, in the first year at least, the results showed this not to be the case. The flat nature of the site meant that lateral soil moisture flow should have been minimal with horizontal drainage through the shallow soils being predominant. It is likely that the bare soil surface within the collars allowed increased surface evaporation compared to the grass weed and plant litter covered soils outside them; particularly during the first growing season with the immature Miscanthus canopy remaining largely open above the collars. These soils outside the collars did, however, became relatively drier than within them in the second growing season as might be expected with the maturing Miscanthus crop



Fig. 7 Time-series plots of daily total respiration of carbon (CO₂-C) from the three modelled components: (solid line) soil organic carbon decomposition ($R_{sdecomp}$), (dashed line) soil surface respiration (R_s), both derived from data sampled with the portable IRGA, and (dotted line) total ecosystem respiration (R_{eco}), derived from flux partitioning of the eddy covariance data. (a) shows smoothed curves using simple moving average to highlight trends while (b) shows original modelled data.

	R _{eco}		R _s		R _{sdecomp}	
Period	Total flux (g CO ₂ -C m ⁻²)	Mean daily flux rate (g CO ₂ -C m ⁻² day ⁻¹)	Total flux (g CO ₂ -C m ⁻²)	Mean daily flux rate (g CO ₂ -C m ⁻² day ⁻¹)	Total flux (g CO ₂ -C m ⁻²)	Mean daily flux rate (g CO ₂ -C m ⁻² day ⁻¹)
Spraying to ploughing (17-Mar-12 to 04-Apr-12	68.53	3.8	72.53 ± 2.04	4.03 ± 0.42	NA	NA
Bare soil (04-Apr-12 to 21-May-12)	129.56	2.7	110.49 ± 7.89	2.30 ± 1.30	As R _s	As $R_{\rm s}$
2012 Growing season (22-May-12 to 24-Oct-12)	634.56	4.07	453.11 ± 0.62	2.9 ± 0.05	276.55 ± 0.47	1.77 ± 0.32
2012/2013 Dormant season (25-Oct-12 to 23-Apr-13)	428.35	2.37	210.14 ± 0.85	1.16 ± 0.06	131.32 ± 0.6	0.73 ± 0.04
2013 Growing season (24-Apr-13 to 24-Oct-13)	993.11	5.4	605.91 ± 0.77	3.29 ± 0.05	221.28 ± 0.50	1.20 ± 0.04
2013 Dormant season (25-Oct-13 to 31-Dec-2013)	210.86	3.1	95.1 ± 0.50	1.39 ± 0.06	50.21 ± 0.34	0.74 ± 0.04

Table 1 Comparison of respiration component sums for agronomic periods during the study

 \pm indicates propagated SE of the model fit.

resulting in increased root to canopy transpiration from which the collars were largely isolated.

For continuous time-series modelling of respiration from the weekly sampling, correction factors agreed well with Parkin & Kaspar (2003) and demonstrate the inadvisability of simple linear interpolation between infrequent sampling, correction and modelling is clearly needed to produce accurate integrated sums. The close agreement between the rates of modelled soil surface respiration (R_s) and the partitioned ecosystem respiration (R_{eco}) from the eddy covariance (see Table 1) during the sprayed dead grass and bare soil

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periods offers good validation of the model and adds confidence to conclusions drawn later in the study period. It is perhaps worth noting the overlap between soil surface (R_s) and total ecosystem (R_{eco}) respiration early in both growing seasons (July) as shown in Fig. 7a. While the $R_{\rm s}$ model fit was poorest at this particular time in the first growing season (July 2012) and this overlap may be exaggerated at this point, the coincidence between soil surface and ecosystem respiration at these early stages of the growing season might be expected as nutrients mobilized from the rhizome, boosting early season emergence and canopy extension, would stimulate autotrophic respiration before increasing summer temperatures begin to drive decomposition of harvest residue and soil surface litter from overwinter leaf drop.

The comparison between the two growing seasons reflected well the increasing influence that the maturing crop, and developing root/rhizome system, had on soil respiration. These live plant influences were more apparent during the growing seasons than dormant seasons as might be expected. The much larger Q_{10} value for R_s (autotrophic plus heterotrophic respiration) during the dormant season (3.10 compared to 1.96 for the growing season) reflected the lack of plant root inputs into this respiration component during this period. With limited root growth/turnover or exudates, overwinter soil respiration is far lower (see Fig. 7) and will consist mainly of existing soil carbon decomposition and incorporation of litter inputs; bacterial or fungal processes dependent on energy input from solar heat flux into the soil. The significance of this growing season root input driver of soil respiration was demonstrated with the comparison of the root excluded R_{sdecomp} component (heterotrophic respiration). For this parameter, the difference between growing and dormant season Q_{10} was much less pronounced (2.62 and 3.15) with both being more in line with the dormant season value from the R_{s} , again demonstrating that the background respiration processes, when removed from plant growth inputs, are primarily temperature driven provided moisture is available within an optimal range. From the respiration model output it appears that, for the R_s component soil moisture (vwc) was likely to have been within this range throughout the study period, including the vwc parameter in the $R_{\rm s}$ model added no significant information to the output once temperature had been included. R_s was more responsive to air temperature than to soil temperature, a result that might be explained by the fact that this component is heavily influenced by soil surface processes such as litter incorporation which would be more immediately responsive to changes in air temperature whereas the deeper soil temperature (-10 cm) would be displaying an

hysteretic response to warming from the air with resulting uncoupling from immediate air temperature changes. The influence of plant growth inputs and autotrophic respiration was demonstrated by the high significance of the canopy growth rate parameter (P < 0.01). $R_{\rm sdecomp}$ (heterotrophic decomposition of existing soil carbon) responded very differently to the range of correlation parameters. This component showed greater significance in responses to soil moisture, soil temperature and to incoming solar radiation rather than air temperature itself. The greater influence of soil rather than air parameters demonstrates that $R_{sdecomp}$ (heterotrophic decomposition of existing soil carbon) is a process occurring deeper in the soil; with no litter inputs at the surface, respiration is less influenced by aboveground air temperature. The much more significant influence of incoming solar radiation rather than air temperature itself is likely demonstrating that it is the direct absorption of solar energy into the darker surface of the exposed soil that drives its temperature increase. This conclusion was reinforced by the number of hours in the day where mean global radiation (R_g) exceeded 20 W $\,m^{-2}$ being more significant than either maximum or mean R_{g} ; that is, time available for the soil to absorb solar radiation being more influential than peaks of incoming energy. A more surprising factor in the $R_{\rm sdecomp}$ model, though, was the influence of canopy growth rate (C_{gr}) on root excluded soil respiration; although its significance was far lower than the other parameters (P < 0.05 compared to P < 0.001), it did add significant information to the model although its direct influence is difficult to explain. Belowground biomass sampling at the end of 2013 revealed that visible root and rhizome mass beneath the establishing Miscanthus extended to <0.15 m while the root exclusion collars went down to 0.30 m and reached a gravel layer beneath the soil so, while it may be possible that the Miscanthus rhizosphere was contributing some priming effect through leaching of soluble carbohydrate or the mobility of stimulated decomposer populations, it is perhaps more likely that C_{gr} is capturing a seasonal trend in the decomposition that has been missed in the other drivers and was not accounted for in the other variables.

The autotrophic contribution of *Miscanthus* root inputs to soil surface respiration over the entire study period was 46.44%, notably higher than the literature average of 36.7% reported by Hanson *et al.* (2000) for nonforest soils measured under field conditions over a range of timescales. This increased contribution of *Miscanthus* cropping to soil carbon cycling agrees well with Anderson-Teixeira *et al.* (2013) who explained net carbon sequestration below perennial energy crops by demonstrating that belowground carbon cycling increased significantly under *Miscanthus* compared to a corn/soya bean rotation. They also showed increased annual duration of higher soil respiration rates, demonstrating that this increased carbon cycling occurred for longer than comparable arable rotations.

When considering studies that reported specifically annual figures for root contribution Hanson et al. (2000) reported a much higher figure of 60% which reflected the very wide range of values that they found in literature studies (from 10% to 90%). This wide range clearly demonstrates not only the importance of crop-specific parameters in ecosystem respiration modelling but also the importance of considering the different levels of this contribution between growing seasons with a maturing crop and at different times of the cultivation cycle, particularly important for process models involving an establishing perennial crop such as Miscanthus. With reference to Table 1, it can be seen that were notable differences in autotrophic and heterotrophic respiration as the crop matured over the two years. The heterotrophic decomposition of the existing soil carbon (primarily the ploughed in remains of the original grassland) had slowed significantly between the two summer seasons, R_{sdecomp} was 32% lower during the second year; however, the winter season flux rates were unchanged between the two years which would reflect well the importance of the temperature driver for decomposition. The decrease in second-year respiration rates likely explained by the availability of material diminishing as the original grassland is decomposed and incorporated into more stable carbon pools.

The total respiration rates, autotrophic and heterotrophic combined (R_s , which includes the $R_{sdecomp}$ component), were rather different in the interyear comparison, dominated as they were by root and litter inputs from the maturing crop. There was an increase in the mean daily flux rate of 13% with a corresponding increase in dormant season respiration rate of 20%. Given the evidence from the root exclusion collars, it would seem likely that this increased respiration at the soil surface was primarily due to the incorporation and decomposition of litter drop and harvest residue from the first year crop that was cut to waste and left in the field along with the weed growth which had been sprayed out with herbicide.

In conclusion, this paper has presented an insight into the variability of soil and ecosystem respiration of CO_2 across the establishment and maturing years of a novel land-use change from agricultural grassland to *Miscanthus* bioenergy. This, along with the broader companion work found in McCalmont *et al.* (2015b), will ideally help to inform crop-specific process models and feed into life cycle assessment conclusions for policymakers.

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