Comparative assessment of ecosystem C exchange in Miscanthus and reed canary grass during early establishment

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Abstract

Land-use change to bioenergy crop production can contribute towards addressing the dual challenges of greenhouse gas mitigation and energy security. Realisation of the mitigation potential of bioenergy crops is, however, dependent on suitable crop selection and full assessment of the carbon (C) emissions associated with land conversion. Using eddy covariance-based estimates, ecosystem C exchange was studied during the early-establishment phase of two perennial crops, C3 reed canary grass (RCG) and C4 Miscanthus, planted on former grassland in Ireland. Crop development was the main determinant of net carbon exchange in the Miscanthus crop, restricting significant net C uptake during the first 2 years of establishment. The Miscanthus ecosystem switched from being a net C source in the conversion year to a strong net C sink (−411 ± 65 g C m−2) in the third year, driven by significant above-ground growth and leaf expansion. For RCG, early establishment and rapid canopy development facilitated a net C sink in the first 2 years of growth (−319 ± 57 (post-planting) and −397 ± 114 g C m−2, respectively). Peak seasonal C uptake occurred three months earlier in RCG (May) than Miscanthus (August), however Miscanthus sustained net C uptake longer into the autumn and was close to C-neutral in winter. Leaf longevity is therefore a key advantage of C4 Miscanthus in temperate climates. Further increases in productivity are projected as Miscanthus reaches maturity and are likely to further enhance the C sink potential of Miscanthus relative to RCG.

Keywords: bioenergy crops, C4 photosynthesis, carbon balance, eddy covariance, grassland, land-use change, leaf longevity, perennial rhizomatous grasses, Phalaris arundinacea, reed canary grass

Received 2 October 2015; revised version received 24 December 2015 and accepted 29 December 2015

Introduction

Global concerns surrounding the impact of anthropogenic greenhouse gas (GHG) emissions on our climate allied with challenges to global energy security are driving interest in renewable energy, including bioenergy. In the European Union, member states have committed to increasing the contribution of renewable energy to 20% of total energy consumption by 2020 (EU, 2009). Furthermore, limitations identified in first-generation liquid biofuels have engendered an increased focus on second-generation alternatives produced from ligno-cellulosic plant materials (Sims et al., 2010). Realisation of the potential of bioenergy in the EU will, however, require significant agricultural land area, estimated at between 18 and 21 million hectares (Özdemir et al., 2009).

Perennial rhizomatous grasses (PRGs), such as Miscanthus × giganteus and reed canary grass (RCG), confer many advantages as potential nonfood bioenergy crops and have received increasing attention in Europe and the USA in recent decades (Landström et al., 1996; Lewandowski et al., 2003). Miscanthus, a C4 plant originating from East Asia, can be highly productive, yielding 10–25 t dry matter ha−1 y−1 in central and northern Europe (Lewandowski et al., 2000; Finnan & Burke, 2014), while yields of RCG, a C3 perennial grass indigenous to temperate regions of Europe, Asia and North America, ranged from 5 to 12 t dry matter ha−1 y−1 in trials in northern Europe (Landström et al., 1996; Saijonkari-Pakhala, 2001; Lewandowski et al., 2003; Kandel et al., 2013). As perennial species, both Miscanthus and RCG invest significant resources below ground, thus building reserves for more rapid canopy development in the spring compared with annual crops (Beale & Long, 1995; McLaughlin & Walsh, 1998).
High productivity in *Miscanthus* has historically been attributed to the superior light-, water- and nitrogen-use efficiency afforded by the C₄ photosynthetic pathway (Long, 1983). For example, the maximum efficiency of solar energy conversion in C₄ crops has been estimated to be 40% higher than that of C₃ species (Monteith, 1978). Furthermore, studies have highlighted the crop’s exceptional ability to maintain high photosynthetic productivity even in cool temperate climates (Beale & Long, 1995). This is most likely achieved through a combination of reduced susceptibility to photoinhibition and decreased sensitivity to chilling temperatures (Beale *et al.*, 1996; Naidu & Long, 2004; Wang *et al.*, 2008).

More recent studies have, however, identified extended leaf longevity and high leaf area as the driving factors contributing to greater productivity in *Miscanthus*. In a side-by-side comparison of field-scale stands of *Miscanthus* and C₄ maize (*Zea mays*) in the USA, Dohleman & Long (2009) showed that the efficiency of captured sunlight-to-biomass conversion was almost identical in both crops averaged over two growing seasons. However, light interception efficiency was 61% higher in *Miscanthus*, which developed a closed canopy a month earlier than maize and maintained it a month longer in the autumn. This resulted in substantial net carbon gains for the cold-tolerant *Miscanthus* crop due to enhanced leaf area duration (Dohleman & Long, 2009).

The question remains, however, as to whether *Miscanthus* can out-perform native C₃ bioenergy crop candidates in temperate regions in terms of productivity, leaf longevity and net C sequestration. RCG, in particular, grows vigorously after seed establishment and easily out-competes weeds after the first year of establishment (Lewandowski *et al.*, 2003). Indeed, its competitive advantages have allowed RCG to become an invasive species in certain wetland areas of the mid-western and north-western USA (Wrobel *et al.*, 2009). To date, no direct comparisons of *Miscanthus* and RCG under the same environmental conditions have been made to understand the relative dynamics of crop development and C assimilation in these ecosystems. This information would: (1) provide focus for exploiting favourable plant traits and developing superior genotypes for bioenergy production, (2) highlight the relative merits of *Miscanthus* and RCG in different climatic zones with varying growing seasons and (3) reveal the C balance implications of land-use change (LUC) to these crops.

Additional factors, such as the previous land use and the magnitude of LUC-related emissions, will significantly impact the long-term C balance of established bioenergy crops. The initial transition phase of LUC can be associated with substantially increased GHG emissions (Guo & Gifford, 2002; Fargione *et al.*, 2008; Donnelly *et al.*, 2011; Poeplau *et al.*, 2011; Houghton *et al.*, 2012), particularly if bioenergy crop yields are low (Don *et al.*, 2012). The time taken for the crop to achieve maximum productivity is also likely to be a significant determinant of the early establishment C balance.

In mature *Miscanthus* crops, soil C sequestration rates of 0.4–0.66 Mg ha⁻¹ y⁻¹ have been reported for plantations established on former croplands (Don *et al.*, 2012; Zimmermann *et al.*, 2012; Poeplau & Don, 2014). Less information is available on grasslands converted to *Miscanthus*, but limited meta-analysis data has shown an annual carbon sequestration rate close to zero (no positive or negative effect) (Don *et al.*, 2012; McCalmont *et al.*, 2016; Qin *et al.*, 2016). Measurements of carbon exchange in RCG plantations have provided evidence of net C uptake in these ecosystems (Shurpali *et al.*, 2009; Mander *et al.*, 2012; Lind *et al.*, 2015); however, these studies were largely confined to drained peat extraction areas and there is little information on the carbon balance of RCG crop plantations established on mineral soils.

This study presents the first side-by-side field-scale comparison of *Miscanthus* and RCG to investigate comparative differences in crop development, leaf longevity and ecosystem-scale C fluxes from initial establishment to near maturity. The bioenergy crops were established on land previously under permanent grass. Conversion of grassland to bioenergy crops is of particular relevance in Ireland and in the wider European continent as over 90% and 35% of utilised agricultural area in Ireland and the EU-27, respectively, is currently used for grass production (Central Statistics Office, 2014; Huyghe *et al.*, 2014). The specific aim of the study was to address the following questions: (1) what are the C emissions associated with the initial LUC from grassland, which we define as the ‘transitional phase’? (2) What are the longer term C balance implications of establishing *Miscanthus* and RCG crops on permanent grasslands (the ‘post-establishment phase’)? (3) How does leaf longevity in *Miscanthus* compare to that of an indigenous C₃ bioenergy crop and does it result in higher net C uptake?

**Materials & Methods**

**Site description & management**

The study was carried out from late April 2009 to the end of December 2011 at the Teagasc Environmental Research Centre, Johnstown Castle, Co. Wexford in the south-east of Ireland (52.3°N, 6.5°W, 67 m above sea level). This region has a maritime temperate climate with a mean annual rainfall of 1038 mm distributed evenly across the year and a mean annual air temperature of 10.4 °C. The seasonal range in temperature is narrow (Fig. 1), with an average summer air temperature of
14.9 °C and an average winter air temperature of 6.3 °C. The prevailing wind direction is south-westerly.

The Miscanthus and RCG crops were established on two former grassland sites (2 ha and 1 ha in area, respectively) (Fig. 2). Most of the experimental area had been maintained as grassland for at least 37 years and was managed organically for beef production since 2006. The Miscanthus site had been conventionally tilled and reseeded with perennial ryegrass in 2000 and surface seeded with white clover in 2005. The RCG site had been conventionally tilled and reseeded with perennial ryegrass and red clover in 2005. Otherwise, historical land management activities were comparable at both sites. The swards received organic fertiliser in the form of cattle slurry and farmyard manure. Grazing took place every 3–4 weeks until October 2008. Soils in this area are variable and are classified as imperfectly drained Gleys (FAO classification: Gleyic Cambisol) or moderately to well-drained Brown Earth soils (Cambisol). Selected soil physical and chemical properties of the Miscanthus, RCG and adjacent reference grassland sites are summarised in Table 1. The wilting point, field capacity and water content at saturation were calculated using a hydraulic properties model (http://hydrolab.arusda.gov/soilwater/ Index.htm) as 0.17, 0.32 and 0.59, respectively, for all sites.

On the 1st April 2009, both sites were sprayed with glyphosate to eradicate the extant vegetation. The soil was conventionally tilled using a mouldboard plough to a depth of 20 cm on the 27th April 2009 (approximately one tenth of the Miscanthus site) and completed on the 29th April 2009, followed by power-harrowing on the 1st and 5th June 2009. Miscanthus rhizomes were planted on one site on the 9th and 10th June 2009 and the soil was consolidated using a heavy roller 1 week later. Additional herbicides were applied to the Miscanthus site in the early establishment phase to reduce competition from grass and broad-leaf weeds. The selective herbicide MCPA was sprayed to control broad-leaf species (13th August 2009 and 27th July 2010) while glyphosate was applied soon after harvesting (5th March 2010 and 8th March 2011) to control grass weeds. The crop was cut with a conditioner mower on the 4th March 2010 and 4th March 2011 but the limited biomass material that was cut was left on the ground.

The second site lay fallow until April 2010 when RCG was established. For this, the site was power-harrowed and seeded with RCG (Phalaris arundinacea L.) at a rate of 30 kg ha$^{-1}$ on the 15th April 2010, and then consolidated with a heavy roller 1 day later. MCPA was applied on the 29th June 2010 to reduce competition from broad-leaf species. The RCG crop was harvested once during the study period, on the 12th October 2010, while harvesting of the 2011 crop was delayed until spring 2012, which is the preferred time for harvesting. No fertilisers were applied over the duration of the study.

**Micrometeorological measurements**

Ecosystem-scale CO$_2$ fluxes were measured using an open-path eddy covariance (EC) system commencing on the 28th April 2009 and 15th April 2010 at the Miscanthus and RCG sites, respectively. The instrumentation was identical at both sites and consisted of an open-path infrared gas analyser (IRGA) (LI-7500, LI-COR Biosciences, Lincoln, NE, USA) coupled with a 3D sonic anemometer (CSAT3, Campbell Scientific, Logan, UT, USA). EC data were collected at a frequency of 10 Hz and averaged over 30-minute intervals. The flux tower was located in the north-eastern corner of the fields to maximise the fetch in the direction of the prevailing south-westerly wind (Fig. 2). Tower height was increased during periods of active growth to maintain its position above the canopy while restricting the flux footprint to the experimental area for as much time as possible. The maximum tower height was 4 m and 3 m at the Miscanthus and RCG sites, respectively, while the minimum sensor to canopy height ratios were 1.47 (Miscanthus) and 1.52 (RCG).

Ancillary biometric sensors included an air temperature and relative humidity probe (HMP45C, Campbell Scientific, Logan, UT, USA), a net radiation sensor (NR-Lite, Kipp & Zonnen, Delft, The Netherlands) and a down-welling quantum sensor (SKP 215, Skye Instruments Ltd., Llandrindod Wells, UK). Two self-calibrating soil heat flux plates were installed at 8 cm soil depth (HFP01SC, Hukseflux, Delft, The Netherlands) and averaging soil temperature probes were installed at 2 cm and 6 cm depth above the soil heat flux plates. Time domain reflectometers (CS616, Campbell Scientific, Logan, UT, USA) measured soil volumetric water content (VWC) in the upper 15 cm of soil. Daily meteorological data (mean air temperature, total rainfall and global solar radiation) were obtained from a Met Éireann synoptic weather station located 1.7 km from the field site.

**Quality assurance and flux analysis**

Data quality control procedures included spike removal (Vickers & Mahrt, 1997), time lag compensation using a covariance maximisation procedure and compensation for air density fluctuations using the WPL term (Webb et al., 1980). The double rotation method (Kaimal & Finnigan, 1994) was used to correct for sonic anemometer tilt as the alternative planar fit method requires several weeks of measurement with constant instrumental set-up and is often not recommended for measurements over canopies with dynamic height variation (Moureaux et al., 2012). Spectral attenuation effects were corrected following the analytical methods of Moncrieff et al. (1997). Tests on developed turbulence and stationarity were applied to the calculated fluxes (Table 13, Mauder & Foken, 2004) and data of questionable quality (QC-flag = 2) were removed, while data of moderate quality (QC-flag = 1) were retained but not included in the regression analysis performed in the gap-filling procedure. Data screening based on the results of these tests has been shown to result in a less systematic distribution of data gaps compared to the removal of fluxes below a derived friction velocity (u*) threshold (Ruppert et al., 2006). Plausible limits were also applied to net ecosystem exchange (NEE) ($-$50 < NEE < 30 μmol CO$_2$ m$^{-2}$ s$^{-1}$), latent heat ($-$20 < LE < 600 W m$^{-2}$) and sensible heat ($-$100 < H < 300 W m$^{-2}$) fluxes. The peak location of the flux footprint, $x_{2σ_{max}}$, and the distance from the flux tower which includes 90% of the source area contributing to the measured flux, $x_{2σ_{50}}$, were estimated for the prevailing south-westerly wind direction using the Kljun et al. (2004) model as 35 m and 95 m, respectively, for the Miscanthus site and 32 m and 87 m, respectively, for the
RCG site. Owing to the relatively constrained field sizes, detailed footprint analysis was conducted on half-hourly fluxes based on the analytical Kormann & Meixner (2001) footprint model. Since analytical models tend to overestimate flux footprints in comparison to more complex Lagrangian stochastic models due to the neglect of along-wind velocity fluctuation (Kljun et al., 2003), this approach is likely to be conservative. Sample flux footprints for the two towers at their maximum height under unstable conditions are shown in Fig. 2. At the maximum height, the footprint of the Mis-
canthus tower was well conserved within the Miscanthus field while close to 90% of the flux footprint from the RCG tower was derived from the RCG field. At lower heights (April 2009 to August 2011 for the Miscanthus tower and April 2010 to June 2011 for the RCG tower), the flux footprints were better confined to the experimental areas. Half-hourly data were rejected if less than 70% of the derived footprint originated from the respective experimental areas, similar to previous studies (Ammann et al., 2007; Baum et al., 2008; Davis et al., 2010; Vanderborght et al., 2010). This resulted in 17.4% and 14.9% of fluxes being rejected overall for the Miscanthus and RCG sites, respectively.

The positioning of the EC sensors in relation to the inertial boundary layer was also monitored due to the relatively low measurement heights. The thickness of the inertial boundary layer, calculated according to equation 5 of Munro & Oke (1975), reached maximum values of 4.9 m, 4.9 m and 7.0 m in 2009, 2010 and 2011, respectively, for Miscanthus and values of 2.8 m and 3.7 m in 2010 and 2011, respectively, for RCG. The lower limit of the inertial boundary layer was estimated to occur between \((z-d) = 5z_0\) and \((z-d) = 10z_0\) (Garratt, 1992), where \(z\) is the height above ground, \(d\) is the zero-plane displacement height and \(z_0\) is the roughness length of the crop surface. This yielded maximum values in the range 1.1–1.6 m, 1.1–1.5 m and 3.0–4.2 m in 2009, 2010 and 2011, respectively, for Miscanthus and RCG sites, respectively. These estimates suggested that the sensors were within the appropriate inertial boundary layer for the vast majority of the experiment.

The quality of the CO2 flux estimates was assessed by examining energy balance closure (EBC) at the site. This routine provides an independent check of the degree to which turbulent

### Table 1

Physical and chemical characteristics of the soils at the Miscanthus, RCG and adjacent reference grassland sites in autumn 2011. Bulk density (BD), texture, pH and total nitrogen (TN) are reported for 0–15 cm soil depth. The soils at all sites are classified as loam. Total carbon (TC) and total organic carbon (TOC) are shown for three depths: 0–15 cm (A), 15–30 cm (B) and 30–45 cm (C).

|          | BD (g cm\(^{-3}\)) | Sand (%) | Silt (%) | Clay (%) | pH | TN (%) | TC (%) A | TC (%) B | TC (%) C | TOC (%) A | TOC (%) B | TOC (%) C |
|----------|-------------------|----------|----------|----------|----|--------|--------|--------|--------|--------|--------|--------|
| Miscanthus | 0.98              | 50       | 32       | 18       | 6.4| 0.3    | 3.2    | 2.9    | 1.5    | 2.4    | 2.2    | 1.1    |
| Grassland reference | 0.99              | 51       | 32       | 18       | 6.5| 0.3    | 2.9    | 2.9    | 2.1    | 2.2    | 2.2    | 1.5    |
| RCG       | 0.97              | 48       | 33       | 19       | 6.7| 0.3    | 2.8    | 2.5    | 1.9    | 2.2    | 1.9    | 1.4    |
| Grassland reference | 0.88              | 52       | 30       | 19       | 6.2| 0.3    | 2.7    | 2.5    | 2.1    | 2.0    | 1.8    | 1.5    |

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fluxes are captured in the boundary layer and may highlight significant bias in measurements (Twine et al., 2000). Energy balance closure was tested by comparing half-hourly and daily sums of net radiation with the sum of good quality (QC-flag = 0, 1) LE and H fluxes and energy storage terms using the equation

\[ R_n = LE + H + G + S_s + S_p \]  \hspace{1cm} (1)

where \( R_n \) is net radiation, LE is the latent heat flux, H is the sensible heat flux, G is the soil heat flux, \( S_s \) is soil heat storage above the heat flux plates and \( S_p \) is the energy stored in photosynthate. Heat storage in the soil surface layer (of depth \( \Delta z \)) was calculated as

\[ S_s = \frac{\Delta T (\theta_v \rho_w c_w + \rho_s c_s) \Delta z}{\Delta t} \]  \hspace{1cm} (2)

where \( \Delta T \) is the change in average soil temperature above the heat flux plates over the time interval \( \Delta t \), \( \theta_v \) is the soil volumetric water content, \( \rho_w \) is the density of water, \( c_w \) is the specific heat capacity of water, \( \rho_s \) is the soil bulk density and \( c_s \) is the specific heat capacity of soil [a value of 837 J kg\(^{-1}\) K\(^{-1}\)] was used for \( c_s \) (Scott, 2000). The energy captured during photosynthesis and stored in biomass, \( S_p \), was computed by equating photosynthetic fixation of 2.5 mg CO\(_2\) m\(^{-2}\) s\(^{-1}\) to an energy flux of 28 W m\(^{-2}\) (Meyers & Hollinger, 2004). For this calculation, photosynthetic rates were based on gross primary productivity (GPP) estimates calculated by subtracting modelled total ecosystem respiration (TER) from measured NEE. Heat storage in plant biomass and canopy air was not measured and considered minor relative to the other terms in equation 1, particularly in the case of Miscanthus which had a sparse, open canopy for much of the study.

The regression analysis of half-hourly energy fluxes yielded a slope of 0.945 ± 0.004 [95% confidence interval (CI)] and intercept of 5.2 W m\(^{-2}\) for the Miscanthus site and a slope of 0.905 ± 0.004 and intercept of 6.3 W m\(^{-2}\) for the RCG site (Fig. 3). Calculating daily sums of energy fluxes resulted in a small increase in the slope for Miscanthus to 0.963 ± 0.013 and a larger increase in the slope for RCG to 0.964 ± 0.016 (Fig. 3). This suggests that there was a small contribution from additional nonestimated storage terms, such as heat storage in plant biomass or canopy air, to the energy balance of these ecosystems. These contributions tend to be negligible on a daily scale (Oncley et al., 2007). Although these slopes were significantly different from one, they compare well with

\[ y = 0.95x + 5.24, \ R^2 = 0.96 \text{ for Miscanthus (half-hourly); } y = 0.91x + 6.3, \ R^2 = 0.96 \text{ for RCG (half-hourly); } y = 0.96x + 0.2, \ R^2 = 0.99 \text{ for Miscanthus (daily); } y = 0.96x + 0.04, \ R^2 = 0.97 \text{ for RCG (daily)} \]

The solid black lines indicate a 1 : 1 relationship. Daily sums were calculated using the available data in a 24-h period.

Fig. 3  Energy balance closure on a half-hourly timescale for Miscanthus (a) and RCG (b) and a daily timescale for Miscanthus (c) and RCG (d) in 2011. The dashed black lines represent the regression lines [\( y = 0.95x + 5.24, \ R^2 = 0.96 \text{ for Miscanthus (half-hourly); } y = 0.91x + 6.3, \ R^2 = 0.96 \text{ for RCG (half-hourly); } y = 0.96x + 0.2, \ R^2 = 0.99 \text{ for Miscanthus (daily); } y = 0.96x + 0.04, \ R^2 = 0.97 \text{ for RCG (daily)} \]. The solid black lines indicate a 1 : 1 relationship. Daily sums were calculated using the available data in a 24-h period.
reported ranges of EBC of 0.53–0.99 (Wilson et al., 2002) and 0.70–0.94 (Stoy et al., 2013) and suggest that the vast majority of the available energy was accounted for. Consequently, turbulent energy exchange was satisfactorily resolved by the EC measurement system.

In addition, cospectral analysis of the high frequency data was performed to assess the frequency response of the EC system. Fast Fourier transforms were applied to the 10 Hz data to yield full cospectra, which were subsequently reduced into exponentially spaced frequency bins and ensemble-averaged. Normalised, ensemble-averaged and frequency-weighted cospectra for both sites are presented in Fig. 4 for unstable conditions and compared with the universal theoretical Kaimal cospectral function (Moncrieff et al., 1997). The shapes of the measured cospectra are generally consistent with the Kaimal curve, except for small deviations from the theoretical −4/3 slope in the inertial subrange. This result is indicative of some small-scale dampening of the high frequency signal, however, the flux postprocessing routines employed included a correction for high frequency losses. The CO2 spectral correction factor (SCF) for Miscanthus had a median of 1.17 and mean ± 95% CI of 1.19 ± 0.001. For RCG, the median was 1.15 and the mean was 1.16 ± 0.002. These values fall in the expected range of CO2 correction factors (1.04–1.25; Aubinet et al., 2001) and compare well with an SCF of 1.12 for a similar open-path system (Haslwanter et al., 2001).

Gaps in the flux data created by measurement failures and data quality analysis procedures were filled using semiempirical gap-filling techniques. TER was modelled by relating soil temperature to nocturnal measured NEE using the exponential Lloyd & Taylor (1994) equation

\[ \text{TER} = R_{10}e^{E_0(1/(283.15-T_0)-1/(T-T_0))} \]  

(3)

where \( R_{10} \) is ecosystem base respiration at a reference temperature of 10 °C, \( E_0 \) is an activity energy parameter, \( T_0 \) was set to 227.13 K as in the original study and \( T \) is soil temperature (K). Significant seasonality has been demonstrated in the \( E_0 \) param-
An assessment of the uncertainty associated with annual CO_{2} flux estimates was performed in a similar way to Black et al. (2007). Firstly, the contribution of uniform systematic errors to the measured fluxes was evaluated following Goulden et al. (1996). Assuming spectral similarity between latent heat, sensible heat and CO_{2} flux, the imbalance between available energy and measured latent and sensible heat, as calculated in the long-term energy balance, was used as an approximation of the underestimation of ecosystem exchange by the EC measurement system. Secondly, sampling uncertainty errors, associated with the imputation of half-hourly missing data during gap-filling procedures, were assessed in a similar way to Falge et al. (2001). Artificial datasets were created with 10, 25, 35 and 45% of the data replaced by gaps and gap-filling procedures were followed to fill the artificial gaps. The mean bias error was calculated as the mean difference between measured and calculated values for the complete data series. The final uncertainty estimate was computed for each measured or gap-filled half-hourly flux based on either the uniform systematic error derived from the energy balance closure, expressed as a percentage, or the mean bias error arising from sampling uncertainty (gap-filling).

**Soil respiration**

Soil respiration was monitored using a closed dynamic chamber coupled with a portable infrared gas analyser (Environmental Gas Monitor EGM-4, PP Systems, Hitchin, UK). Chamber measurements were made on bare soil at 10 sampling points in the Miscanthus and RCG sites, yielding an estimate of the flux of CO_{2} from the soil surface which combines contributions from autotrophic (plant root) and heterotrophic (microbes and soil fauna) components. Measurements were carried out from early June 2010 to early September 2011 at approximately weekly intervals during the growing season and monthly intervals during the winter. Soil temperature and VWC (0–7 cm) were recorded at each sampling point using a WET sensor (Delta-T Devices, Cambridge, UK).

**Crop analysis**

Above-ground Miscanthus biomass was calculated as the product of average shoot density and total dry biomass (leaf + stem) per shoot sampled prior to harvesting and at least monthly during the growing seasons of 2010 and 2011. Shoot density estimates (shoots m^{-2}) were based on the number of shoots counted in a quadrat of area 2.1 m^{2} at 10 random locations in the Miscanthus plantation. Total dry biomass per shoot was measured by cutting a minimum of 35 random shoots at ground level during each sampling event and drying the leaf and stem biomass at 70 °C to constant weight. Below-ground biomass was sampled on three occasions (February 2010, January 2011 and September 2011) by excavating all below-ground plant material associated with three randomly located Miscanthus plants to a depth of 40 cm. Roots, live rhizomes and dead rhizomes were separated, washed free of soil over a 2 mm sieve and dried to constant weight at 70 °C. Below-ground biomass was up-scaled from the plant scale to a per unit area (m^{-2}) basis using calculated above- to below-ground ratios and average above-ground biomass on each individual sampling date. The contribution of understory vegetation was assessed by clipping all above-ground material in quadrats of area 0.25 m^{2} placed inside the large Miscanthus quadrats with subsequent determination of dry matter yields after oven drying at 70 °C.

Above-ground RCG biomass was assessed by cutting all vegetation at ground level in quadrats of area 0.25 m^{2} randomly positioned at five locations within the crop. Sampling was carried out in September 2010, prior to harvest in October 2010 and in June and September 2011. A root auger of volume 750 cm^{3} (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands) was used to sample below-ground biomass to a depth of 45 cm in January and October 2011 at 4 random locations in the crop. The intact soil cores were mixed with water in the laboratory, washed over a 0.2 mm sieve and dried at 70 °C to constant weight.

**Results**

**Environmental conditions**

Mean annual air temperatures were close to the 30-year mean temperature in 2009 (10.0 °C) and 2011 (10.4 °C) but dipped in 2010 to 9.3 °C. Two prolonged periods of cold weather were experienced during these years (December 2009 to February 2010 and November 2010 to January 2011) (Fig. 1). In addition, summer mean
temperature was 7% lower than the long-term mean in 2011. Rainfall totals were highly variable, with higher than average rainfall in 2009 (1427 mm), close to the average in 2010 (972 mm) and below average in 2011 (839 mm). Exceptionally wet summer months characterised 2009, with atypically high rainfall also occurring in November. The mean monthly soil VWC at the Miscanthus site was high for much of the study, only reducing below field capacity (0.32 m\(^3\) m\(^{-3}\)) in August 2010 and August and September 2011. Soil VWC in the RCG site was below field capacity from May to August of each year but remained above field capacity (0.32 m\(^3\) m\(^{-3}\)) outside of the peak growth period. In general, soil VWC was higher in Miscanthus than RCG, most obviously from May to July 2011. Vapour pressure deficit (VPD) was always low, ranging from a monthly average of 0.06 kPa in February 2011 to a maximum monthly average of 0.37 kPa in June 2009 and August 2010 (Fig. 1).

**Crop development**

Establishment and growth of the Miscanthus crop was slow in the first 2 years after planting. Prior to the first harvest in March 2010, above-ground dry biomass totalled just 10 ± 4.0 (standard error of the mean, SEM) g m\(^{-2}\) while below-ground biomass stocks were estimated at 13.8 ± 7.1 g m\(^{-2}\) (Table 2). Following the growing season of 2010, above-ground biomass reached a seasonal maximum of over 100 ± 20.2 g m\(^{-2}\) in September and a maximum GLAI of 0.55 ± 0.05 m\(^2\) m\(^{-2}\) was recorded in October (Fig. 5). The contribution of understory vegetation to ecosystem productivity was substantial at this time. Above-ground biomass stocks of understory vegetation, dominated mostly by grass species (Agrostis stolonifera, Poa trivialis and Alopecurus geniculatus), totalled 110 ± 21.7 g m\(^{-2}\) in September 2010, with an associated GLAI of 3.56 ± 0.70 m\(^2\) m\(^{-2}\).

**Table 2** Above- and below-ground biomass stocks in the Miscanthus and RCG crops in g (dry matter) m\(^{-2}\). Total above- and below-ground stocks in Miscanthus are divided into their constituent pools. Values in parentheses represent the standard error of the mean.

| Date          | Above-ground (g m\(^{-2}\)) | Below-ground (g m\(^{-2}\)) |
|---------------|-----------------------------|----------------------------|
|               | Stem | Leaf | Total | Live Rhizome | Dead Rhizome | Root | Total   |
| **Miscanthus**|      |      |       |              |              |       |         |
| February 2010 | 8.2  | 1.6  | 9.9   | 10.7         | 0            | 3.0  | 13.8    |
| September 2010| 63.9 | 36.6 | 100.5 | 73.6         | 9.3          | 22.3 | 105.2   |
| January 2011  | 33.1 | 6.5  | 39.6  | 73.6         | 9.3          | 22.3 | 105.2   |
| March 2011    | 53.3 | 4.9  | 58.2  | 83.8         | 16.0         | 63.7 | 410.8   |
| June 2011     | 52.3 | 31.5 | 83.8  | 83.8         | 16.0         | 63.7 | 410.8   |
| September 2011| 1001.6 | 308.9 | 1310.5 | 1310.5      | 16.0         | 63.7 | 410.8   |
| **Reed Canary Grass** |     |      |       |              |              |       |         |
| September 2010|      |     |       |              |              | 653.0 | (76.4) |
| October 2010  |      |     |       |              |              | 589.3 | (28.5) |
| January 2011  |      |     | 675.4 | (93.9)      |              | 489.0 | (46.3) |
| June 2011     |      |     | 706.4 | (61.2)      |              | 834.5 | (72.5) |

**Fig. 5** Temporal pattern of green leaf area index (GLAI) in Miscanthus and leaf area index (LAI) in RCG during the 2010 and 2011 growing seasons. Vertical bars represent the standard error of the mean.
Following initial slow development in 2011, growth rates increased exponentially towards the end of the summer, yielding 1311 ± 465 g m⁻² in late September 2011. GLAI increased steadily over this time (Fig. 5, Table 2). Above-ground crop expansion was facilitated by a four-fold increase in below-ground biomass between January and late September 2011 when total below-ground Miscanthus biomass was 410.8 ± 166.4 g m⁻², comprising 80.6% live rhizome, 3.9% dead rhizome and 15.5% root (Table 2). Correspondingly, stocks of understory vegetation declined, associated with herbicide application in spring 2011 and increased competition from Miscanthus plants. Estimated above-ground biomass from weeds was 5.8 ± 2.2 g m⁻² and 14.5 ± 6.3 g m⁻² in late June and late September 2011, respectively, while their GLAI was calculated as 0.19 ± 0.07 m² m⁻² and 0.47 ± 0.20 m² m⁻² at the same times, representing significant reductions from 2010 values.

In contrast with the slow establishment of Miscanthus, rapid growth was observed in the new RCG plantation after sowing in mid-April 2010. A dense green canopy developed early in the first growing season resulting in a seasonal maximum LAI of 8.8 ± 0.4 m² m⁻² at the start of August 2010 (Fig. 5). A reduction in LAI was then observed as the crop senesced. At the time of the first harvest in October 2010, 589 ± 29 g m⁻² had accumulated in above-ground biomass and the LAI was 6.5 ± 0.4 m² m⁻². In the second year of establishment, above-ground growth began earlier than in the conversion year and, by early June 2011, a growing season maximum LAI of 5.1 ± 0.2 m² m⁻² was recorded and above-ground biomass totalled 675 ± 94 g m⁻². Flowering and senescence occurred earlier in 2011 than in 2010 with the result that, by August 2011, the crop had completely senesced. Significant below-ground biomass stocks were recorded in the RCG crop in the second year of establishment (Table 2), with the maximum below-ground stock in September 2011 (835 ± 73 g m⁻²) exceeding above-ground biomass estimates. Understory vegetation made a minor contribution to above-ground biomass in the RCG ecosystem, accounting for just 3.4% and 0.5% of total above-ground biomass in June and late September 2011, respectively.

Carbon fluxes

Flux measurements at the Miscanthus site began 1 day before the majority of the grassland field was tilled. Ecosystem exchange of carbon was dominated by respiratory fluxes in the first month post-disturbance. Half-hourly NEE fluxes ± SEM averaged 4.0 ± 0.1, 3.3 ± 0.1, 3.3 ± 0.1 and 2.7 ± 0.1 μmol CO₂ m⁻² s⁻¹ in the first

Fig. 6  Diurnal course of half-hourly fluxes of net ecosystem carbon exchange in μmol CO₂ m⁻² s⁻¹ in the Miscanthus ecosystem during 2009 (beginning in late April) (a), 2010 (b) and 2011 (c) and in the RCG ecosystem during 2010 (beginning in mid-April) (d) and 2011 (e). Dashed vertical dark blue lines mark the ‘break-even point’ at which cumulative NEE becomes negative (net C uptake). Dashed vertical red lines indicate the timing of the end of net C uptake.
4 weeks following tillage, respectively, with positive fluxes indicating a net release of C to the atmosphere. Monthly cumulative NEE ± uncertainty amounted to 104.7 ± 3.1, 62.7 ± 2.7 and −12.1 ± 3.1 g C m⁻² in the first 3 months, respectively, post-tillage, representing significant initial net losses of carbon from the ecosystem.

A small recovery in photosynthetic activity was apparent in subsequent months, concurrent with the slow development of the newly-established Miscanthus crop and the emergence of understory vegetative species prompted by a flush of germination after the initial soil disturbance. However, seasonal maximum rates of instantaneous net C assimilation, recorded in mid-October 2009, were no greater than −15 μmol CO₂ m⁻² s⁻¹ (Fig. 6). The magnitude of photosynthetic uptake was similarly modest in 2010, peaking at −17 μmol CO₂ m⁻² s⁻¹ in late September. The seasonal pattern of NEE changed dramatically in 2011, however, concomitant with significant increases in above-ground Miscanthus biomass, large-scale leaf expansion and higher GLAI. Maximum instantaneous rates of net C assimilation were −30 to −35 μmol CO₂ m⁻² s⁻¹ between mid-August and late September 2011.

Measurements of NEE in the RCG crop began the same day the site was harrowed and seeded in mid-April 2010. Early half-hourly fluxes of NEE were dominated by ecosystem respiration but C uptake became evident from mid-May onwards (Fig. 6). Weekly-averaged NEE was 2.6 ± 0.1, 1.7 ± 0.1, 0.8 ± 0.1 and −0.2 ± 0.1 μmol CO₂ m⁻² s⁻¹ in the first 4 weeks following planting, respectively. As a result, the ecosystem represented a net source of carbon over the first month (cumulative NEE was 33.3 ± 2.4 g C m⁻²) but switched to a net sink during the second (−88.0 ± 4.8 g C m⁻²) and third month (−127.3 ± 13.9 g C m⁻²).

Rapid establishment and extensive early canopy development in the RCG crop accompanied strong photosynthetic activity early in the first growing season. Just over 2 months after planting (late June 2010), a seasonal maximum NEE of −35 μmol CO₂ m⁻² s⁻¹ was recorded. Net C uptake continued until late September 2010 at a decreasing rate (Fig. 6). Winter NEE fluxes were small as a result of the exceptionally cold temperatures recorded from November 2010 to January 2011. However, photosynthetic activity resumed when daily mean temperatures began to exceed about 5 °C in February 2011. Net ecosystem C accumulation continued until a seasonal maximum NEE of −38 μmol CO₂ m⁻² s⁻¹ was recorded in mid-May 2011, after which rates of C uptake declined.

Daily fluxes of TER and GPP are shown in Fig. 7. Maximal daily values of GPP in the Miscanthus crop increased from −7.3 and −9.2 g C m⁻² d⁻¹ in September 2009 and June 2010, respectively, to −14.1 g C m⁻² d⁻¹ in August 2011. Maximal daily TER was 10.0, 9.5 and 7.4 g C m⁻² d⁻¹ in September 2009, June 2010 and July 2011, respectively for Miscanthus. In the RCG crop, maximal daily GPP values of −17.6 and −16.3 g C m⁻² d⁻¹ were recorded in late June 2010 and
mid-May 2011, respectively, while maximal daily TER values of 9.2 and 7.6 g C m\(^{-2}\) d\(^{-1}\) were observed in mid-July 2010 and 2011, respectively. Higher TER values were generally associated with warmer soil temperatures and higher ecosystem productivity.

The cumulative effect of the measured NEE fluxes over the course of the study is also shown in Fig. 7. In the Miscanthus crop, cumulative NEE was 183 ± 28 g C m\(^{-2}\) from late April to the end of December 2009, 13 ± 45 g C m\(^{-2}\) in 2010 and −411 ± 65 g C m\(^{-2}\) in 2011 (Table 3). GPP increased from −797 g C m\(^{-2}\) in 2009 to −1684 g C m\(^{-2}\) in 2011. Cumulative TER peaked in 2010 (1514 g C m\(^{-2}\)) and decreased in 2011 to 1273 g C m\(^{-2}\), concomitant with below average summer temperatures. In the RCG crop, cumulative NEE values were −319 ± 57 g C m\(^{-2}\) from mid-April to the end of December 2010 and −397 ± 114 g C m\(^{-2}\) during 2011. An increase in GPP was observed from the conversion year (−1430 g C m\(^{-2}\), 8½-month period) to the second year of establishment (−1708 g C m\(^{-2}\)), while TER also increased over this period from 1112 to 1311 g C m\(^{-2}\).

The ‘break-even’ point at which cumulative NEE became negative (net C uptake) occurred in early October in 2010 and late June in 2011 for Miscanthus (Fig. 6). For RCG, the ‘break-even’ point occurred much earlier in the year than for Miscanthus: in early June in the conversion year (2010) and late February in 2011. With regard to winter fluxes, net C uptake did not cease in Miscanthus until mid-October and mid-November in 2010 and 2011, respectively, and the Miscanthus ecosystem subsequently remained relatively C-neutral until year end. In contrast, net C loss was observed from late October onwards in the conversion year for RCG and at a higher rate in 2011 from late September onwards.

The net rate of long-term C accumulation in an ecosystem is better described by the NECB. Since no removal of C through harvesting occurred during the Miscanthus experiment, the cumulative NEE values quoted for 2009, 2010 and 2011 are representative of the NECB of this ecosystem. For the RCG crop, the NECB was calculated as 66 ± 58 g C m\(^{-2}\) (a net C sink), while the NECB for the second year of RCG establishment was 397 ± 114 g C m\(^{-2}\), as no biomass was harvested in this year. These values assume that contributions from leaching, methane, VOC, carbon monoxide and particulate carbon were negligible.

Leaching of dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) are likely to be the most significant of these nonestimated fluxes (Osborne et al., 2010; Smith et al., 2010). Kindler et al. (2011) reported average DOC and biogenic DIC losses from European croplands of 4.1 ± 1.3 and 14.6 ± 4.8 g C m\(^{-2}\) y\(^{-1}\), respectively. This study included an Irish cropland (Carlow) with well-drained, sandy loam soil which lost 2.6 ± 0.5 and 15.2 ± 4.1 g C m\(^{-2}\) y\(^{-1}\) as DOC and biogenic DIC, respectively. Following tillage disturbance of a grassland lysimeter at Johnstown Castle with comparable soil to the Miscanthus and RCG sites (low to medium drainage capacity), DOC leaching amounted to 1.6 g C m\(^{-2}\) over a 33-week period (Ó Ni Chonchubhair, B. Osborne, K. Richards and G. Lanigan, unpublished results). While such C losses comprise a small fraction of the annual NEE estimates for Miscanthus and RCG in 2011, their significance for the long-term NECB is far greater.

Based on chamber measurements, soil respiration (below-ground autotrophic and heterotrophic respiration) accounted for the majority of TER, with small contributions from leaf and stem respiration (Fig. 7). This was particularly evident in 2011 when significant below-ground biomass had developed in both crops. Soil respiration in Miscanthus varied from 1.3 ± 0.1 (SEM) g C m\(^{-2}\) d\(^{-1}\) in December 2010 to 7.7 ±

### Table 3

|                  | GPP   | TER   | NEE ± uncertainty | NECB† ± uncertainty |
|------------------|-------|-------|-------------------|---------------------|
| **Miscanthus**   |       |       |                   |                     |
| 28th Apr 2009 – | −797  | 979   | 183 ± 28          | −183 ± 28           |
| 31st Dec 2009    | (Ploughing – year end) | | | |
| 2010             | −1501 | 1514  | 13 ± 45           | −13 ± 45            |
| 2011             | −1684 | 1273  | −411 ± 63         | 411 ± 63            |
| **RCG**          |       |       |                   |                     |
| 15th Apr 2010 –  | −1430 | 1112  | −319 ± 57         | 66 ± 58             |
| 31st Dec 2010    | (Harrowing/planting – year end) | | | |
| 2011             | −1708 | 1311  | −397 ± 114        | 397 ± 114           |

*Positive NEE values represent a net release of C to the atmosphere, negative values a net uptake of C by the ecosystem.
†NECB = −ΣNEE – C\(_{\text{harvest}}\) where C\(_{\text{harvest}}\) is the carbon removed from the ecosystem at harvest.

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In RCG, fluxes ranged from 0.9 ± 0.1 in January 2011 to 8.7 ± 1.0 g C m⁻² d⁻¹ in July 2011. During intervals of active RCG growth and slow Miscanthus development, soil respiration in RCG exceeded that of Miscanthus, most notably in autumn 2010 and in April and May 2011. Outside of these periods, soil respiration fluxes were comparable in both ecosystems.

Controls on ecosystem carbon fluxes

Net assimilation of carbon by the Miscanthus ecosystem was closely related to crop development during the growing season, as shown in Fig. 8(a). When Miscanthus GLAI values were 0.5 m² m⁻² or lower, gross photosynthesis was cancelled out by a comparable ecosystem respiration rate and monthly sums of NEE fluctuated around zero. As leaf expansion progressed and a greater fraction of incident light was intercepted by the Miscanthus crop, large increases in monthly NEE were recorded, reaching a peak of ~161.8 g C m⁻² during August 2011.

A strong positive relationship was observed between monthly sums of TER and GPP for much of 2009 and 2010 and the winter months of 2011 (Fig. 8b). Notable deviations from a 1 : 1 linear relationship in May and June 2009 correspond to significant reductions in photosynthetic capacity after conventional inversion tillage. Monthly TER also exceeded monthly GPP in September 2009. This month was characterised by a 3-week period when rainfall was significantly reduced (total 1.2 mm) after a summer of exceptionally wet weather. In addition, respiration outweighed photosynthesis in March and April 2010 and in April 2011 following systemic herbicide application. However, the largest departures from slopes close to unity were observed in the growing season of 2011, when GPP was approximately 1.5 times greater than TER.

The relationship between monthly sums of TER and GPP in the RCG ecosystem is shown in Fig. 9(a) for 2010 and 2011. A strong positive association was observed between the two variables in both years, with respiratory fluxes representing roughly 50% of GPP across the full measurement period. The only months when TER exceeded GPP were April 2010 (after planting), November – December 2010 and October – December 2011. The impact of soil VWC on monthly TER fluxes in the RCG crop can be seen in Fig. 9(b). A negative relationship was evident in 2010 as VWC increased and reached values in excess of 0.4 m³ m⁻³, presumably due to oxygen-limitation. Monthly sums of TER in 2011 (drier year) were comparable to 2010 values at high moisture contents, but when soil VWC decreased below a mid-range level (~0.26 m³ m⁻³), a positive relationship was observed between TER and VWC.

Discussion

In the discussion below, we address the three questions posed, relating to (1) the transitional-phase C fluxes, (2) the postestablishment phase C fluxes associated with the Miscanthus and RCG crops and (3) the role of leaf longevity in regulating net C exchange. We discuss how our results compare with previous studies involving land-use transitions and examine the implications of our findings for bioenergy crop selection.

Fig. 8  Monthly sums of net ecosystem exchange (NEE) in the Miscanthus ecosystem are plotted against green leaf area index (GLAI) for 2010 and 2011 in (a). Panel (b) shows the correlation for the Miscanthus ecosystem of monthly sums of total ecosystem respiration (TER) with monthly sums of gross primary productivity (GPP), plotted in absolute values (|GPP|) to facilitate the comparison. The black solid line indicates a 1 : 1 relationship while the dashed lines represent regression lines: 2009 (black line) y = 0.78x + 39.6, R² = 0.58; 2010 (dark grey line) y = 0.93x + 9.6, R² = 0.97; 2011 (light grey line) y = 0.40x + 49.3, R² = 0.85. Months showing deviations from the 1 : 1 line are marked with their respective month number in the calendar year.

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Carbon fluxes during land-use transition to bioenergy crops

Significant carbon emissions and changes in SOC have been attributed to land-use transitions such as deforestation and conversion to cropland (Davidson & Ackerman, 1993; Houghton et al., 2012; Poeplau & Don, 2013). Net C losses in the early stage of LUC can arise as a result of diminished photosynthetic capacity following herbicide application, enhanced mineralisation after tillage as well as reduced C uptake while the new crop develops to full maturity.

Table 4 summarises findings from previous research on C fluxes during land-use transitions. In a reseeding experiment in Johnstown Castle, cumulative TER from a grass sward with similar soil type to the bioenergy crop sites was 278\,g\,C\,m^{-2} in the month following herbicide application (Chonchubhair, B. Osborne, K. Richards and G. Lanigan, unpublished results). Including photosynthetic uptake (albeit at a diminishing rate) would reduce this value significantly. For example, Zenone et al. (2011) recorded a cumulative NEE of 19–46 g\,C\,m^{-2} in the month after herbicide application to long-term grassland. However, further variable net C losses occur in the posttillage period, dependent on the former land use, environmental conditions and tillage intensity. Cumulative NEE in the first 3 months posttillage in the Miscanthus ecosystem was 155.4 ± 8.9 g\,C\,m^{-2} and falls in the mid-range of estimated short-term tillage-induced emissions. These losses were primarily driven by minimal photosynthetic activity and slow above-ground development of the rhizome-propagated plants. This slow establishment is typical of Irish and many northern European trials where 3–5 years is generally required for full establishment (Lewandowski et al., 2000; Clifton-Brown et al., 2007).

Following RCG planting in April, net C losses of 33.3 ± 2.4 g\,C\,m^{-2} were recorded in the first month. However, the ecosystem became a strong net C sink after this. A number of factors may have contributed to this result. Firstly, the RCG site had been ploughed 1 year previous to crop establishment. Therefore, any increased mineralisation of SOC made available by tillage is most likely to have occurred in the months following the initial soil disturbance (Vellinga et al., 2004; Willems et al., 2011). Secondly, a high seeding rate was employed to guarantee successful establishment. Thirdly, RCG is considered a highly competitive plant that grows rapidly and pre-empts the development of other vegetation early in the growing season (Lavergne & Molofsky, 2004). For example, Adams & Galatowitsch (2005) highlighted a shift from a low root:shoot ratio (<1) in the first 4 months of development to a higher ratio (>2) in the remainder of the 2-year study, which enabled RCG to initially monopolise above-ground space and later to spread vegetatively below ground.

Rapid early colonisation and crop development can therefore reduce the early transitional C losses associated with land-use change. However, our results suggest that significant net ecosystem C losses can be generated as a result of reduced photosynthetic assimilation and enhanced decomposition rates, particularly in C-rich grasslands. This loss represents a short-term land conversion carbon debt that must be overcome before net C sequestration is attained in the newly established bioenergy crop.
C balance implications post-establishment

The Miscanthus ecosystem switched from a net C source of $183 \pm 28 \text{ g C m}^{-2}$ in the conversion year (8-month period) to C-neutral in the second year and a strong C sink in the third year ($-411 \pm 63 \text{ g C m}^{-2}$). In contrast, rapid and early development of the RCG crop resulted in the ecosystem being a net C sink both during the conversion year ($-319 \pm 57 \text{ g C m}^{-2}$, 8½-month period post-planting) and in the second year of establishment ($-397 \pm 114 \text{ g C m}^{-2}$). Previous assessments of C fluxes in the conversion year show highly variable results (Table 4), with cumulative NEE ranging from $-58$ to $+312 \text{ g C m}^{-2}$ depending on crop type and establishment technique, location and duration of measurements. Only a limited number of studies revealed small C sinks in the conversion year, similar to RCG in this study. Even after harvested biomass losses were

Table 4  Transitional-phase and post-establishment phase C fluxes associated with different land-use transitions. Annual fluxes from permanent grasslands are included for comparison. Cumulative fluxes refer to net ecosystem exchange (NEE), total ecosystem respiration (TER) or soil respiration (SR). For transitional-phase fluxes, the time period refers to the sampling duration in months (M). For long-term fluxes, the length of establishment is given in years (Y), where Y1 is the conversion year.

| Original land use | New land use | Location | Time period | Cumulative NEE$^A$, TER$^B$ or SR$^C$ (g C m$^{-2}$) | Research note | Reference |
|-------------------|--------------|----------|-------------|-------------------------------------------------|--------------|-----------|
| Grass             | Grass        | Ireland  | 1 M         | $278 \pm 29^B$                                  | Summer reseeding | Unpublished results* |
| Grass             | Soybean      | USA      | 1 M         | $19-46^A$                                       |              | Zenone et al. (2011) |
| Grass             | Miscanthus   | Ireland  | 3 M         | $155 \pm 9^A$                                  |              | This study |
| Wheat             | Wheat        | USA      | 2 M         | $29-41^C$                                       |              | Dao, 1998 |
| Grass             | Spring barley| Denmark  | 3 M         | $260^C$                                         |              | Eriksen & Jensen (2001) |
| Grass             | Miscanthus   | Ireland  | 8 M         | $183 \pm 28^A$                                  | From tillage | This study |
| Arable            | Miscanthus   | USA      | 7 M         | $-58^A$                                         | From planting | Zeri et al. (2011) |
| Grass             | RCG          | Ireland  | 8.5 M       | $-397 \pm 57^A$                                 | From planting | This study |
| Grass/Arable      | RCG          | Finland  | 5.3 M       | $-57^A$                                         | From 1.5M post-planting | Lind et al. (2015) |
| Grass/Arable      | Poplar       | Belgium  | 7 M         | $75 \pm 4.4^A$                                  | From 2M post-planting | Zenone et al. (2015) |
| Arable            | Poplar       | Canada   | 12 M        | $312^A$                                         | From 4M post-tillage | Cai et al. (2011) |
| Grass/Wheat       | Switchgrass  | USA      | 12 M        | $-31^A$                                         | From 4M post-planting | Skinner & Adler (2010) |
| Grass             | Soybean      | USA      | 12 M        | $205-262^A$                                     | No-till      | Zenone et al. (2013) |
| Grass             | Miscanthus   | Ireland  | Y2          | $13 \pm 45^A$                                   |              | This study |
| Grass             | Miscanthus   | Ireland  | Y3          | $-411 \pm 63^A$                                 |              | This study |
| Arable            | Miscanthus   | USA      | Y3          | $-554 \pm 20^A$                                 |              | Zeri et al. (2011) |
| Grass             | RCG          | Ireland  | Y2          | $-397 \pm 114^A$                                |              | This study |
| Grass/Arable      | RCG          | Finland  | Y2, 3†      | $-259^A$                                        | Fertilised   | Lind et al. (2015) |
| Drained peat      | RCG          | Finland  | Y4-7        | $-9 \text{ to } -211^A$                         |              | Shurpali et al. (2009) |
| Arable            | Switchgrass  | USA      | Y3          | $-485 \pm 20^A$                                 |              | Zeri et al. (2011) |
| NA                | Switchgrass  | USA      | Y3, 4†      | $-448^A$                                        | Growing season only | Wagle et al., 2015; |
| Grass/Arable      | Poplar       | Belgium  | Y2          | $-96 \pm 15^A$                                  |              | Zona et al. (2013) |
| Arable            | Poplar       | Canada   | Y5          | $-1^A$                                          |              | Cai et al. (2011) |
| Grass             | Ireland      | Annual   |             | $-200 \text{ to } -385^A$                      | Johnstown Castle; similar soil | Peichl et al. (2012) |
| Grass             | Ireland      | Annual   |             | $-193 \text{ to } -258^A$                      | South-west region | Jaksic et al. (2006) |
| Grass             | Europe       | Annual   |             | $-240 \pm 70^A$                                 | 9 sites      | Soussana et al. (2007) |

NA, not available.

*Órlaith Ni Choncubhair, Bruce Osborne, Karl Richards, Gary Lanigan.
†Mean value given for these years.
‡Chamber measurements.

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incorporated, the NECB of this RCG ecosystem post-
planting was still positive, indicating a net C sink of
66 ± 58 g C m⁻² in the conversion year.

Net C fluxes in 2011 compare favourably with long-
term fluxes from previous studies (Table 4), which
range from close to C-neutral for poplar and RCG in
certain years to in excess of −450 g C m⁻² y⁻¹ for Mis-
canthus and switchgrass. Good agreement exists
between our results and the studies on Miscanthus in
the USA (−554 ± 20 g C m⁻² y⁻¹, Zeri et al., 2011) and
RCG on mineral soil in Finland (−259 g C m⁻² y⁻¹,
Lind et al., 2015), taking account of location and com-
parative differences in season length and environmental
controls. Studies focussed on the LUC transition from
permanent grassland to Miscanthus or RCG are severely
lacking, however, despite the fact that almost one-third
of utilised agricultural land in Europe is grassland (Fis-
cher et al., 2010).

In this study, the key driver of ecosystem C fluxes in
Miscanthus was crop development, constraining
monthly-cumulated NEE in the first 2 years close to
zero as primary production was counterbalanced by
ecosystem respiration. In addition to the inherent
limitations of slow establishment in northern Europe,
varying other factors may have contributed to the poor
agronomic performance observed including relatively
late planting, possible rhizome failure and competition
from understory grass species. However, in the third
growing season, exponential above-ground growth and
leaf expansion was accompanied by a 4-fold increase in
below-ground biomass, resulting in strong net C
uptake from June to October of that year.

In the case of RCG, environmental conditions and
crop phenology were the main drivers of ecosystem C
exchange. Since crop establishment was rapid and early
canopy development was uninhibited by competition
from other species, physiological activity was dictated
by soil temperature, moisture and incident radiation.
Net C uptake of −35 µmol CO₂ m⁻² s⁻¹ was observed
just over two months after planting, culminating in a
strong net C sink of −319 ± 57 g C m⁻² in the conver-
sion year and an increased net sink in the second year
(−397 ± 114 g C m⁻²). Furthermore, below-ground bio-
mass represented a significant C stock of 3.4 t C ha⁻¹,
similar to the results of Xiong & Kätterer (2010).

During periods when RCG productivity exceeded
that of Miscanthus (autumn of the conversion year and
early in its second year), higher soil respiration (below-
ground autotrophic and heterotrophic) was recorded in
RCG than Miscanthus. This may indicate that there was
a larger contribution from the autotrophic component
to total below-ground respiration in RCG at these times.
Soil respiration fluxes were similar in both crops outside
of these periods. In a Finnish RCG crop which had 70%
In contrast with RCG which exhibited early season leaf development, significant increases in leaf area did not occur until June for Miscanthus. As a result, the ‘break-even’ point of net C uptake did not occur until late June in 2011. However, Miscanthus maintained growth and substantial leaf area late into the autumn and sustained net ecosystem C accumulation until mid-November. After this, the crop remained C-neutral until the end of the year, similar to the findings of Zeri et al. (2011). Indeed, strong coupling of TER and GPP was observed during much of the current study, which meant that significant C losses did not occur.

Dohleman & Long (2009) demonstrated a 59% longer growing season in Miscanthus (199 days on average) than C₄ maize (126 days on average). Our results show that the longevity of photosynthetically active leaves in Miscanthus is comparable even to native C₃ crops. Indeed, the number of recorded days with net C uptake in 2011 was almost identical for both crops (215 and 212 days for Miscanthus and RCG, respectively). This result compares very favourably with an average cropping season length of 149 days in Irish spring barley (Davis et al., 2010) and 212 days of net C uptake (six-year average) in an Irish grassland (Peichl et al., 2011). This further highlights the exceptional performance of C₄ Miscanthus in cool temperate climates where C₄ metabolism should be temperature-limited and implies that Miscanthus may confer an advantage as a bioenergy crop in the long term. If leaf photosynthetic capacity and longevity is comparable to native C₃ crops and C emissions outside of the growing season are close to zero, the net C balance of Miscanthus is likely to be favourable.

Implications of the study

Bioenergy crop cultivation in northern Europe may focus more on grassland conversion to avoid a reduction in the area of croplands dedicated to food and feed production. However, permanent grasslands in northern Europe show strong annual net C uptake, with NEE values ranging from −193 to −385 g C m⁻² y⁻¹ (Table 4). This highlights the potential negative impacts associated with disturbing grasslands that are highly productive and supply substantial amounts of stabilised C to the soil (Jackson et al., 1996; Jones & Donnelly, 2004; Poeplau et al., 2011). Our study demonstrated that a significant C debt can be associated with the early-establishment phase of these bioenergy crops but highlighted the future potential of Miscanthus to surpass RCG and possibly long-term grasslands in terms of its C sink strength. Additional measurements of other associated GHGs, such as N₂O and CH₄, will be necessary, however, to assess the full GHG implications of land-use change to this crop.

Furthermore, the duration of the full crop production cycle must be considered. In the case of Miscanthus, productive yields may be achievable for up to 15 years or more (Clifton-Brown et al., 2007; Christian et al., 2008; Arundale et al., 2014) but this is likely to be much shorter for RCG (approximately 7–10 years; Saijonkari-Pahkala, 2001; Finnan, 2007). Therefore, more cultivation and replanting will be required in long-term RCG plantations and this has associated C balance implications due to more regular soil disturbance and consequent reductions in productivity.

Although the theoretical light-use efficiency benefits afforded by the C₄ photosynthetic pathway are often highlighted, the empirical results of this work suggest that high biomass productivity will be controlled more by leaf- or canopy-related factors, both genetic and environmentally derived, rather than the photosynthetic characteristics of individual leaves. Further to this, the distinct difference in the timing of peak C uptake between the two crops is significant and provides information on the suitability of these crops in different climatic zones. While the late season performance of Miscanthus may constrain its productivity in regions with a short growing season, RCG may be a better candidate in these regions due to its early emergence in spring and subsequent rapid development. Growing Miscanthus under a clear, plastic film, as is common practice for maize production in parts of northern Europe, may also be a valuable tool to encourage earlier emergence in spring and enhance further the duration of net C uptake in the crop (Clifton-Brown et al., 2011).

A final point worth noting is the relative allocation of biomass above and below ground in these two bioenergy crops. At the time of peak biomass yield in 2011, more than 50% of total RCG biomass was below ground compared with 24% in Miscanthus and above-ground biomass in Miscanthus was almost double that recorded in RCG. Greater investment of resources below ground could enhance long-term C sequestration; however, lower above-ground yields have significant implications for the economic viability and C-offsetting potential of the RCG crop.

Acknowledgements

This research was funded by the Department of Agriculture, Food and the Marine Research Stimulus Fund (Project Ref. 07 527). The authors also gratefully acknowledge the technical assistance of Brendan Swan, Kevin McNamara, Vincent Staples, Carmel O’Connor and Teresa Cowman in Johnstown Castle.
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