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Changes in soil organic carbon under biofuel crops

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Abstract

One potentially significant impact of growing biofuel crops will be the sequestration or release of carbon (C) in soil. Soil organic carbon (SOC) represents an important C sink in the lifecycle C balances of biofuels and strongly influences soil quality. We assembled and analyzed published estimates of SOC change following conversion of natural or agricultural land to biofuel crops of corn with residue harvest, sugarcane, *Miscanthus x giganteus*, switchgrass, or restored prairie. We estimated SOC losses associated with land conversion and rates of change in SOC over time by regressing net change in SOC relative to a control against age since establishment year. Conversion of uncultivated land to biofuel agriculture resulted in significant SOC losses – an effect that was most pronounced when native land was converted to sugarcane agriculture. Corn residue harvest (at 25–100% removal) consistently resulted in SOC losses averaging 3–8 Mg ha^{-1} in the top 30 cm, whereas SOC accumulated under all four perennial grasses, with SOC accumulation rates averaging $<$1 Mg ha^{-1} yr^{-1} in the top 30 cm. More intensive harvests led to decreased C gains or increased C losses – an effect that was particularly clear for residue harvest in corn. Direct or indirect conversion of previously uncultivated land for biofuel agriculture will result in SOC losses that counteract the benefits of fossil fuel displacement. Additionally, SOC losses under corn residue harvest imply that its potential to offset C emissions may be overestimated, whereas SOC sequestration under perennial grasses represents an additional benefit that has rarely been accounted for in life cycle analyses of biofuels.

Keywords: bioenergy, cellulosic ethanol, conservation reserve program (CRP), corn residue, land conversion, *Miscanthus*, prairie, sugarcane, switchgrass

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Introduction

As biofuel production expands globally, it is critical to understand the environmental consequences of cultivating biofuel crops (Renewable Fuels Agency, 2008). One potential impact of biofuel deployment is the storage or release of soil organic carbon (SOC). SOC sequestration is an important component in the life cycle of biofuel production (Ney & Schnoor, 2002; Adler *et al*., 2007) and may be key in determining the greenhouse gas (GHG) reduction potential of biofuels relative to fossil fuels. Additionally, increases in SOC produce a host of other advantages including increased productivity and crop quality, improved water and nutrient retention, decreased runoff of both sediment and pollutants, and increased soil biodiversity (Lal, 2004). Thus, an understanding of changes in SOC under biofuel crops is essential for thorough cost–benefit analyses of biofuels.

SOC contributes substantially to the global carbon (C) cycle, with global storage in the top meter estimated at 1500–1600 Pg C (Jobbágy & Jackson, 2000; Lal, 2004), which is more than two times the amount stored in either vegetation or the atmosphere. The capacity of soils to store organic C is influenced by several variables. Because the rate of decomposition relative to production is low in cold and wet climates (Austin, 2002; Allen *et al*., 2005), SOC storage tends to be greatest

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there (Trumbore, 1997; Jobbágy & Jackson, 2000; Fissore *et al.*, 2008). SOC also is correlated with soil clay content because clay minerals protect organic matter from microbial oxidation through the formation of organo-mineral complexes (Jobbágy & Jackson, 2000). Maintenance of soil structure in any soil type strongly influences soil C residence times, and thus management and disturbance can lead to substantial losses of soil C. Frequent disturbance to the soil (i.e., tillage) exposes protected organic matter and increases the rate of decomposition, resulting in lower steady-state SOC storage (e.g., Grandy & Robertson, 2007; David *et al.*, in press). Vegetation type and root architecture contribute to soil C maintenance as well (Jobbágy & Jackson, 2000; De Deyn *et al.*, 2008; Fissore *et al.*, 2008). SOC concentration generally decreases as a power function of depth, and its vertical distribution is affected by factors such as climate, soil texture, and vegetation type – with generally deeper distribution of SOC in grasslands than in forests (Jobbágy & Jackson, 2000).

Changes in SOC, which are of primary interest because of their potential to sequester or release CO_2 (e.g., Trumbore, 1997), occur as a result of changes in any of the above variables. There is considerable concern that increasing global temperatures will stimulate decomposition and release soil C (e.g., Davidson & Janssens, 2006; Friedlingstein *et al.*, 2006); however, land use changes have more immediate potential to affect global SOC storage (Trumbore, 1997). Conversion of native ecosystems to crops causes substantial losses of SOC (averaging about 30%), which is most rapid immediately following land conversion (Davidson & Ackerman, 1993; Guo & Gifford, 2002; Murty *et al.*, 2002; West *et al.*, 2004; Zinn *et al.*, 2005; De Deyn *et al.*, 2008; David *et al.*, in press), probably stabilizing within the first several decades of cultivation (David *et al.*, in press). Overall, approximately 55–78 Gt C have been released from soil as a result of land conversion during the postindustrial era (Lal, 2004). Conversely, SOC accumulates upon conversion of cultivated land to secondary forest, grassland, or pasture (Potter *et al.*, 1999; Knops & Tilman, 2000; Guo & Gifford, 2002; West *et al.*, 2004; Grandy & Robertson, 2007). Because grasslands tend to have high SOC, conversion of native ecosystems to pasture generally does not release SOC, and sometimes results in modest SOC sequestration (Fisher *et al.*, 1994; Guo & Gifford, 2002; Murty *et al.*, 2002; Osher *et al.*, 2003; Zinn *et al.*, 2005).

While many studies have quantified changes in SOC under potential biofuel crops, results are variable and have yet to be synthesized into a coherent picture. Here, we review changes in SOC under five biofuel cropping systems with potential for widespread, long-term deployment: (1) corn (*Zea mays* L.) with residue harvest, which is touted in the United States as a potential source of cellulosic feedstock for biofuel production (Kadam & McMillan, 2003; Sheehan *et al.*, 2003); (2) sugarcane (*Saccharum* spp. L.), a perennial grass that may be harvested several years in a row without replanting and has been used extensively for ethanol production in Brazil since the 1970s; (3) Miscanthus [*Miscanthus* x *giganteus* Greef et Deu ex. Hodkinson et Renvoize (Hodkinson & Renvoize, 2001)], a large and productive perennial grass used as an energy crop in Europe (Lewandowski *et al.*, 2000); (4) switchgrass (*Panicum virgatum* L.), a large perennial grass native to North America selected by the US Department of Energy as a model energy crop (McLaughlin & Adams Kszos, 2005); and (5) restored native grasslands (North America), which have been promoted for their low input requirements and environmental benefits (Tilman *et al.*, 2006). We employ a paradigm in which controls (adjacent land of the previous land use type) do not necessarily reflect baseline SOC; rather, we allow for the possibility of a land conversion effect (Fig. 1), as an initial loss frequently occurs upon conversion of forest or grassland to agriculture (Davidson & Ackerman, 1993; West *et al.*, 2004). If SOC accumulates following this loss, positive net changes in SOC will occur only after this loss is repaid ('SOC payback time'). Here, we attempt to quantify the land conversion effect, SOC accumulation rate, and SOC payback time (when applicable) for the five above-mentioned crops.

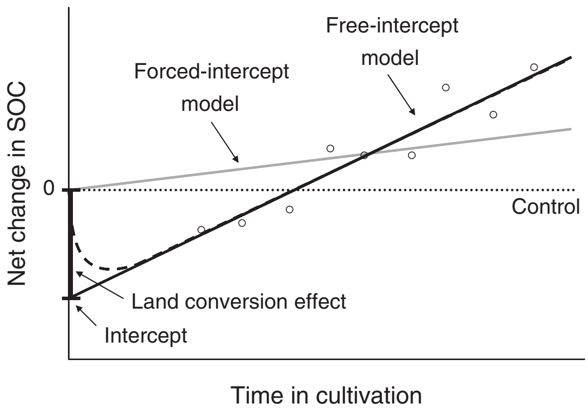

Fig. 1 Schematic diagram of the models used to analyze net changes in soil organic carbon (SOC) relative to controls. The forced-intercept model, which assumes that the control represents the baseline from which changes in SOC deviate, represents the most common method of calculating rates of change in SOC. We focus instead on the free-intercept model, which allows for the possibility of a land conversion loss followed by SOC accumulation. This model uses a regression of net change in SOC relative to the control as a function of time to calculate a SOC accumulation rate and an intercept, which differs from the control when there is a land conversion effect.

Methods

In the spring of 2008, we searched the literature (any publication date) using ISI Web of Science for studies quantifying the change in soil C following crop establishment (Tables 1 and A1). We selected studies according to the following criteria: (1) SOC was measured in fields of at least two known ages, one of which was a control – either a pre-establishment measurement or nearby land whose land use matched the pre-establishment land use; (2) following removal of roots from the soil, total SOC was measured by either dry combustion or dichromate oxidation; (3) SOC was expressed as a concentration (SOC_c; e.g., $g\,C\,kg^{-1}$ soil, %) for a known depth increment or on an area basis (SOC_a; e.g., Mg C ha^{-1}, $g\,m^{-2}$) to a given depth. For each profile, we summed changes in SOC_a from each depth increment to yield a single value representing the entire depth profile sampled. Bulk density values were used to convert between concentration- and area-based estimates of SOC. When bulk density (ρ_b) was not reported, it was calculated using the following adaptation of the Adams–Stewart model (Adams, 1973; Tranter *et al.*, 2007)

$$\rho_b = \frac{100}{\%OM/\rho_{OM} + 100 - \%OM/\rho_m} \quad (1)$$

Here, %OM is the percent organic matter, organic matter bulk density (ρ_{OM}) is assumed to be 0.224 g cm^{-1} (Rawls *et al.*, 2004), and mineral bulk density (ρ_m) is estimated as a function of sand content (%) and depth (cm; Tranter *et al.*, 2007):

$$\rho_m = 1.35 + 0.0045 \cdot \text{sand} - 0.00006 \cdot (44.7\text{sand})^2 + 0.06 \cdot \log(\text{depth}). \quad (2)$$

Because the model requires SOC concentration as an input variable [Eqn (1)], bulk density could not be calculated for studies that reported SOC on an area basis only.

Data were analyzed in two ways. First, we calculated SOC_a accumulation rates and land conversion effects for each site separately (treatments separated). Rates of change in SOC_a were calculated using two models, which we term 'forced-intercept' and 'free-intercept' (Fig. 1). Forced-intercept models represent the most common method of calculating rates of change in SOC; the rate is simply the difference in SOC between a crop of given age and a control divided by the crop age (or, when multiple ages are measured, rate is the slope of a linear regression that includes the control). This forced-intercept model assumes a linear change in SOC through time, and therefore will underestimate rates of SOC change if there is a land conversion loss (Fig. 1). The advantage of this model, however, is that it requires only a control and a crop of one age – which are by far the most commonly available data (Table 1). For the subset of sites with more than one age (Table 1), we applied the free-intercept model, which allowed the intercept of the SOC–time relationship to differ from the control (Fig. 1). Specifically, the rate of change in SOC_a was calculated as the slope of a linear regression between SOC_a and age. We then compared the intercept of this relationship with the control. A one-sided *t*-test was used to assess whether this ratio was <1, indicating that a land conversion loss occurred. Additionally, we compared rates calculated using the forced- and free-intercept models.

Second, combining data from all sites, we used ANOVA models (type III SS) to describe both percentage change in SOC_c (% change relative to the control) and net changes in SOC_a (Mg C ha^{-1}) as a function of age (years). As the intercept was allowed to differ from

Table 1 Data set characteristics by crop

	n	No. of sites	No. of studies	Previous land uses	Age (years): range (median)	Profile depth (cm): max (median)	% harvested	% fertilized	% clay: median
Corn w/residue removal	15	5	3	Agriculture	2.5–11 (2.5)	60 (10)	100	100	20
Sites with multiple ages	0	0	0	na	na	na	na	na	na
Sugarcane	20	15	9	Native (forest, grass)	2–90 (35)	100 (25)	100	45–85	50
Sites with multiple ages	5	5	4	Native (forest, grass)	2–50	70 (15)	100	80–100	51
Miscanthus	10	8	6	Grass	4–18 (9)	100 (25)	100	70–100	13
Sites with multiple ages	5	5	2	Grass	4–16	60 (25)	100	100	65
Switchgrass	87	21	9	Crop, grass, fallow	0.6–14 (4)	360 (30)	93	91	22
Sites with multiple ages	3	3	2	Grass, fallow	0.6–3	90 (30)	100	100	15
Mixed native	42	40	17	Crop	1–68 (7)	120 (20)	0	5	22
Sites with multiple ages	7	7	6	Crop	1–60	120 (83)	0	0	15

zero, this is a free-intercept model (Fig. 1). Other variables included were log(depth; cm), the amount of biomass removal, and soil clay content (%). We tested for interactions between depth and biomass removal with age, but not for other interactions, as the data sets were not sufficiently large. For SOC_c, depth was expressed as the geometric mean of the upper and lower sampling intervals, which is appropriate because SOC distribution is more accurately described as a function of log(depth) than of depth (Jobbágy & Jackson, 2000). For SOC_a, depth was the lowest sampling depth, above which all depth increments were summed to give a single value representing the entire depth profile. Biomass removal was measured as a continuous variable for corn (% residue removal) and as a categorical variable for other crops (e.g., not harvested, regularly harvested, or infrequently grazed/burned). When not reported, clay was estimated based on the categorical texture description. As vertical profiles in soil texture were rarely described, this variable represents the surface texture. Previous vegetation type (crop, grass, or fallow) was included as a categorical variable for switchgrass. Because some of the factors tested did not have a significant effect on SOC and weakened the predictive power of the full model, we also ran reduced models which included only age, log(depth), and % residue removal for corn. Inordinately influential data – as determined by Cook's D, which combines datum residual and leverage – were removed from the statistical models.

Results

We found 46 studies representing 164 site–treatment combinations that matched the criteria outlined above (Tables 1 and A1). Previous land uses, soil types, management practices, and ages and depths sampled varied among crops (Tables 1 and A1).

In corn, change in management from grain harvest to grain and residue harvest (note that no land conversion occurs in this case) consistently resulted in a loss of SOC, with negative changes for all depth increments of all treatments. This loss appears to be most rapid (up to $4.2\,Mg\,C\,ha^{-1}\,yr^{-1}$ to 30 cm) immediately following the change in residue management, as indicated by the negative intercepts and nonsignificant effects of age for both SOC_c (Fig. 2a, Table B1) and SOC_a models (Fig. 3, Table B2) [While the coefficient for the intercept is positive in the SOC_a model, addition of the effects of residue removal and depth made the intercept negative for $\geq$25% residue removal at depths $\geq$18 cm (Table B2).]. The loss was proportionally greatest at shallow depths (Fig. 2a; $P \leq 0.02$ for both full and reduced models; Table B1). The rate of loss increased significantly with percentage residue removal in all models

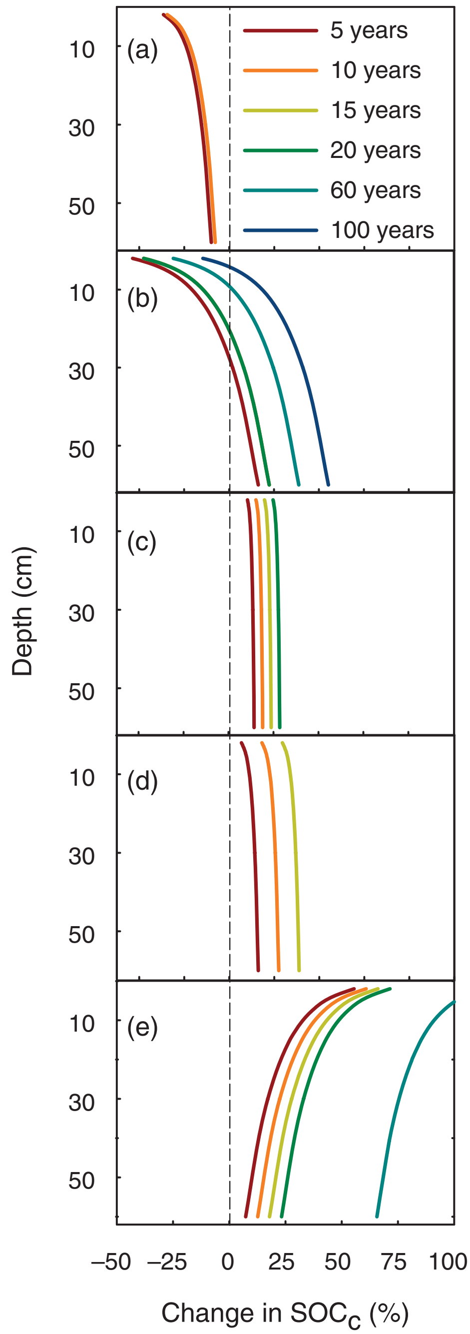

Fig. 2 Projected percentage change in SOC_c ($g\,C\,kg^{-1}$ soil) as a function of depth and time under biofuel crops: (a) corn with 100% residue removal, (b) sugarcane, (c) Miscanthus, (d) switchgrass, and (e) mixed native communities. Estimates are based on the reduced ANOVA models (Table B1). Ages plotted are those represented in our data set (Table 1).

($P \leq 0.02$; Fig. 3; Tables B1 and B2). Specifically, SOC loss increased by approximately 0.2% for every 1% increase in residue removal (Table B1), or by about $0.06–0.09\,Mg\,C\,ha^{-1}$ per 1% increase in residue removal (Table B2). Soils with higher clay content had reduced

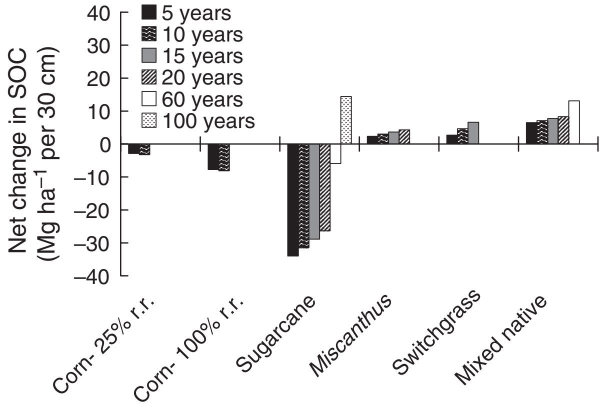

Fig. 3 Projected net changes in SOC_a (Mg C ha^{-1}) in the top 30 cm of soil under biofuel crops of various ages. Estimates are based on the reduced ANOVA model for SOC_a (Table B2). Ages plotted are those represented in our data set (Table 1).

rates of SOC loss in both models (SOC_a: $P = 0.002$, Table B1; SOC_a: $P = 0.30$, Table B2). Overall, our statistical model (Table B2) predicted that 10 years of maize biomass removal resulted in losses of $\sim$3 Mg C ha^{-1} per 30 cm at 25% residue removal and $\sim$8 Mg C ha^{-1} per 30 cm at 100% residue removal (Fig. 3).

Conversion of native ecosystems (forest or grassland) to sugarcane resulted in a large initial loss of SOC followed by recovery. The land conversion loss was roughly 22% or 20 Mg C ha^{-1} (to a median depth of 15 cm) based on comparison of controls and intercepts ($n = 5$, $P = 0.04$), but these estimates varied widely depending on ages and depths measured. Our ANOVA models (Tables B1 & B2) projected slightly higher initial losses of up to $\sim$50% near the surface (Fig. 2b) or $\sim$34 Mg C ha^{-1} in the top 30 cm (Fig. 3). As a result of this initial loss, the forced-intercept model gave negative rates of change in SOC_a (-0.67 Mg C ha^{-1} yr^{-1}, SE = 0.36, $n = 18$; Fig. 4a), indicating a net loss of SOC for the majority of sites (median age = 35; Table 1). However, the free-intercept model indicated that SOC began to rebuild following an initial loss ($dSOC_a/dt = 0.29$ Mg C ha^{-1} yr^{-1}, SE = 0.31, $n = 5$; Fig. 4a). Likewise, the ANOVA models indicated SOC accumulation rates of about 0.33% yr^{-1} (SOC_c reduced model: $P = 0.10$; Fig. 2b) or 0.51 Mg C ha^{-1} yr^{-1} (SOC_a reduced model: $P = 0.006$; Fig. 3). The land conversion loss appears to be repaid within a century (Figs 3 and 4a); however, this SOC payback time is difficult to quantify given the limited sample size ($n = 5$). SOC accumulation was proportionally greater at greater depths (Fig. 2b; $P < 0.0001$ in SOC_c reduced model). Retention of harvest residues on the fields increased the rate of SOC recovery ($P \leq 0.04$ for SOC_c and SOC_a full models; Tables B1 and B2). Soil clay content did not significantly affect changes in SOC under sugarcane (SOC_c: $P = 0.15$, SOC_a: $P = 0.84$).

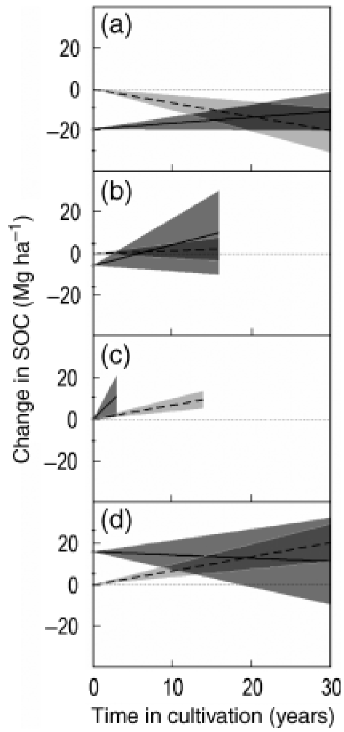

Fig. 4 Projected changes in SOC_a based on forced-intercept (pale gray) and free-intercept (darker gray) models (see text for details) in (a) sugarcane replacing native ecosystems, (b) Miscanthus replacing grassland, (c) switchgrass replacing cropland or grassland, (d) mixed native communities replacing former cropland. Lines and shaded areas are projections of the mean rate of change in SOC_a and the standard error of this mean, respectively. For free-intercept models, the y-intercept is the average difference between controls and intercepts, and error bars represent the standard error of this mean. This figure demonstrates how differing methodologies may lead to widely different projections of changes in SOC.

Conversion of grassland to Miscanthus generally resulted in modest C losses followed by SOC accumulation. The average land conversion loss was approximately 11% or 5.8 Mg C ha^{-1} ($n = 5$; Fig. 4b); however, the ratio of the intercept to the control was not significantly <1 ($P = 0.16$), indicating that this loss was not significant. Free-intercept calculations of SOC accumulation rate averaged 1.0 Mg ha^{-1} yr^{-1} ($n = 5$) and were greater than both paired forced-intercept calculations (exact Wilcoxon's signed-rank test; SOC_c: $P = 0.03$, SOC_a: $P = 0.30$) and the average of all forced-intercept calculations (0.14 ± 0.35 Mg C ha^{-1} yr^{-1}, $n = 8$; Fig. 4b). The tendency for there to be a land conversion loss followed by SOC accumulation was not statistically significant because of the effects of one site where SOC was lost following the establishment of Miscanthus (Kahle *et al.*, 2001). The statistical models did not capture the initial SOC loss (Figs 2c and 3; Tables B1 and B2), and may have thereby underestimated the effects of age ($0.13 \pm 0.48\,\mathrm{Mg\,ha^{-1}\,yr^{-1}}$ in SOC_a reduced model), which were positive (below 24 cm in SOC_c full model) but not significant in any models (all $P > 0.20$; Tables B1 and B2). Depth and clay also did not affect changes in SOC, with the exception of negative effects of clay in the full SOC_a model (Tables B1 and B2). The failure of these statistical models to describe significant effects can be attributed to substantial variation (rates of change in SOC ranging from -3.3 to $3.3\,\mathrm{Mg\,C\,ha^{-1}}$ for the top 30 cm) and a small number of sites ($n = 8$).

Switchgrass studied in the literature typically was planted on cropland, fallow land, or grassland (Table 1). Land conversion effect could not be reliably assessed, as only three sites had data for more than one age, and none of these exceeded 3 years in age (Table 1). In our ANOVA models, the intercept tended to be negative, but never significantly so (all $P > 0.05$; Tables B1 and B2). SOC tended to accumulate over time (Figs 2–4); percentage change in SOC_c increased with age by $1.8\%\,\mathrm{yr^{-1}}$ (Fig. 2d; $P \leq 0.04$ for reduced and full models; Table B1) and SOC_a increased with age at a rate of $\sim 0.4\,\mathrm{Mg\,ha^{-1}\,yr^{-1}}$ according to the ANOVA models (Fig. 3; $P > 0.3$ for reduced and full models; Table B2), or $0.68\,\mathrm{Mg\,ha^{-1}\,yr^{-1}}$ according to the forced-intercept model (SE = 0.30, $n = 87$; Fig. 2c). Percentage change in SOC_c tended to increase with depth, but not significantly so (Fig. 2d, $P = 0.17$). Likewise, change in SOC_a tended to increase with sampling depth, but the relationship was not significant (reduced model: $P = 0.39$). The intercept for switchgrass planted on former grassland was always lower than that of switchgrass planted on cropland, but not significantly so ($P > 0.2$ for both SOC_c and SOC_a models). When biomass was harvested, SOC accumulation tended to be less rapid (SOC_c: $P = 0.05$, SOC_a: $P = 0.66$; Tables B1 and B2), but this was partially offset by higher intercepts (SOC_c: $P = 0.07$; SOC_a: $P = 0.72$; Tables B1 and B2).

Restored prairie or conservation reserve program (CRP) land planted with one or more native prairie species on former cropland were labeled 'mixed native sites.' These were not managed as biofuel crops; none of the fields were harvested and only 5% were fertilized (Table 1). The land conversion effect was positive (Figs 3 and 4d); intercepts were $\sim 68\%$ or $16\,\mathrm{Mg\,C\,ha^{-1}}$ greater than the controls; and the ratios of the intercept to the control was significantly >1 (one-sample *t*-test; $P = 0.02$). Likewise, the intercept was positive in both SOC_c and SOC_a reduced models ($P < 0.0001$ and $P = 0.09$, respectively). This positive intercept may be the result of faster SOC accumulation in young sites than in old sites (Kucharik, 2007), which, in a linear model would be approximated by a positive intercept and an intermediate rate (slope). As a result of the positive intercept, the average free-intercept rate ($-0.15 \pm 0.70\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$, $n = 7$) was less than the average forced-intercept rate ($0.92 \pm 0.47\,\mathrm{Mg\,C\,ha^{-1}\,yr^{-1}}$, $n = 7$; Fig. 4d). In our statistical models, SOC increased with age by approximately $1\%\,\mathrm{yr^{-1}}$ or $0.1\,\mathrm{Mg\,ha^{-1}\,yr^{-1}}$ ($P \leq 0.04$ for both SOC_c and SOC_a reduced models; Fig. 3; Tables B1 and B2). The percentage change in SOC_c decreased strongly with depth (Fig. 2e; Table B1), which was modeled statistically as an age $\times$ depth interaction in the full model ($P < 0.0001$) or as a pure function of depth in the reduced model ($P < 0.0001$). Change in SOC_a increased with sampling depth (reduced model; $P = 0.002$). The effects of clay content were opposite in the SOC_c (negative effect; $P = 0.008$) and SOC_a models (positive effect; $P = 0.0003$). Change in SOC was lower in sites that were burned or grazed than in those that had not been harvested (SOC_c model: $P = 0.05$; SOC_a model: $P = 0.40$), but there were no significant effects of this treatment on the *rate* of change in SOC (age $\times$ treatment interaction; SOC_c model: $P = 0.49$; SOC_a model: $P = 0.50$).

Discussion

Whereas soil C is depleted under corn residue harvest, it accumulates under cultivation of perennial grasses. The harvest of corn residue – even as little as 25% – consistently reduced SOC by $3–8\,\mathrm{Mg\,ha^{-1}}$ in the top 30 cm within the first few years (Figs 2a and 3), with losses increasing linearly with percent residue removal (see also Blanco-Canqui & Lal, 2007). Conversion of native land (grassland or forest) to sugarcane agriculture triggered a large initial loss of SOC (Figs 3 and 4a); however, SOC rebuilds at rates of $\sim 0.3–0.5\,\mathrm{Mg\,ha^{-1}\,yr^{-1}}$ in the top 30 cm following this initial loss (Figs 2–4; Silva *et al.*, 2007), such that the initial C loss may be repaid within a century (Figs 3 and 4a). Cultivation of temperate-zone perennial grasses – Miscanthus, switchgrass, or native mixes – increased SOC by an average of $\sim 0.1–1\,\mathrm{Mg\,ha^{-1}\,yr^{-1}}$ in the top 30 cm (Figs 2–4; see also e.g., Potter *et al.*, 1999; Ma *et al.*, 2000; Kahle *et al.*, 2001; Lemus & Lal, 2005; Liebig *et al.*, 2008). These changes can be explained in light of three principles that govern the C balance of biofuel crops, which we discuss in detail below: (1) conversion of uncultivated land to biofuel crops entails a soil C loss; (2) crops differ in their ability to sequester SOC, with perennial grasses outperforming corn; and (3) there appears to be a trade-off between biomass harvest and SOC sequestration.

Clearing uncultivated land triggered a SOC loss (Figs 1, 3 and 4). This may be attributed to the effects of tillage, which stimulates a release of C from soil (e.g., Reicosky *et al.*, 1997) or to a deficiency of organic inputs relative to decomposition early in crop establishment (Paul *et al.*, 2002). In our analysis, the land conversion loss was most pronounced for sugarcane agriculture (Figs 3 and 4a), as the majority of sites sustained native ecosystems before cultivation (Tables 1, A1). There also was some indication that clearing grassland for cultivation of *Miscanthus* caused modest land conversion losses (Fig. 4b). These losses should be attributed more to the disturbance of native or restored ecosystems, which consistently reduces SOC (Davidson & Ackerman, 1993; Guo & Gifford, 2002; Murty *et al*., 2002; West *et al*., 2004; Zinn *et al*., 2005), than to the cultivation of any specific crop. While crop type and agronomic practices may influence the magnitude of the land conversion loss, these effects cannot be reasonably assessed without side-by-side trials. We emphasize that failure to consider land conversion losses separately from crop-induced SOC changes can severely bias estimates of crop performance (e.g., Figs 1 and 4).

There are substantial differences between crops in the ability to sequester SOC; whereas SOC was lost under corn with residue harvest, all four perennial grasses – sugarcane, Miscanthus, switchgrass, and mixed native grasses – sequestered SOC (Figs 2–4). Change in SOC is an integration of the entire C cycle, and several components thereof may differ between crops. First, crop productivity represents the total C that is potentially available for incorporation into soil organic matter. Aboveground productivity estimates are $\sim$15.6 Mg ha^{-1} yr^{-1} for corn (Graham *et al*., 2007; Petrolia, 2008; World Agricultural Outlook Board, 2008), 50–120 Mg ha^{-1} yr^{-1} for sugarcane (Cheeseman, 2004), 10–61 Mg ha^{-1} yr^{-1} for Miscanthus (Lewandowski *et al*., 2000; Heaton *et al*., 2008), 9–26 Mg ha^{-1} yr^{-1} for switchgrass (McLaughlin & Adams Kszos, 2005; Heaton *et al*., 2008) and 0.5–9 Mg ha^{-1} yr^{-1} for restored prairie (Knapp *et al*., 1993; Briggs & Knapp, 1995; Brye *et al*., 2002; Tilman *et al*., 2006). As corn productivity is within the range of the perennial grasses, differences in productivity cannot explain the SOC loss in corn in contrast to the gain by perennial grasses.

Second, plant strategies – the partitioning of C within the plant and through time – influence how much C becomes harvestable biomass and how much enters the soil. As roots and rhizomes are a primary source of C to the soil in biofuel crops (Garten & Wullschleger, 2000; Wilhelm *et al*., 2004; Lemus & Lal, 2005), belowground allocation of C stands to play a critical role in driving changes in SOC. Allocation of C to root biomass is dramatically lower in traditional annual crops than in temperate grasslands, with globally averaged root : shoot ratios of 0.1 and 3.7, respectively (Jackson *et al*., 1996). The biofuel crops considered here match this pattern; observed root : shoot ratios are $\sim$0.3 for fertilized corn (Bonifas *et al*., 2005), $\sim$0.15 for sugarcane in nonfield conditions (Ebrahim *et al*., 1998; Smith *et al*., 2005), $\sim$1 for Miscanthus (Neukirchen *et al*., 1999), 1.8–6.1 for switchgrass (Ma *et al*., 2001), and 2–8 for North American prairies (Wilson, 1993; Ojima *et al*., 1994). Thus, the temperate perennial grasses introduce far more C to the soil than corn, potentially explaining the difference between corn and these grasses. However, C allocation to roots – if estimated reliably in nonfield conditions – does not explain the apparent C sequestration under sugarcane, which occurs primarily at depths below $\sim$30 cm (Fig. 2b; Skjemstad *et al*., 1999; Rhoades *et al*., 2000; Cheeseman, 2004) and has been attributed to the deep root system of sugarcane (Cheeseman, 2004; Smith *et al*., 2005) or redistribution of topsoil C through leaching and/or tillage (Skjemstad *et al*., 1999; Cheeseman, 2004).

Third, characteristics of crops and their litter influence the rate at which organic matter decomposes. The protective cover of canopies or litter layers affects the microclimate, reducing evaporation rates and dampening temperature fluctuations (Wilhelm *et al*., 2004). As the rate of soil organic matter mineralization generally responds positively to increased soil moisture but negatively to decreased temperature (Leirós *et al*., 1999), it is not clear how differences in cover among crops affect SOC losses. Additionally, decomposition is influenced by litter quality; high lignin content of litter extends the residence time of C in the soil (McClaugherty *et al*., 1985). Development of corn to maximize energy allocation to grain may reduce the complexity of tissues that eventually become litter (Gifford *et al*., 1984), making its tissues readily degradable. Further research on the C cycling of biofuel crops will be necessary to fully understand the functional drivers of differences in the SOC balance between crops.

Harvesting biomass appears to reduce SOC or to slow its rate of accumulation. This result is to be expected based on the principle that SOC equilibrates at higher levels with higher organic matter inputs (Mann *et al*., 2002). The effect of biomass removal is particularly pronounced in the case of corn residue harvest; our results (Fig. 3, Tables B1 and B2) and previous research (Larson *et al*., 1972; Mann *et al*., 2002; Blanco-Canqui & Lal, 2007) demonstrate that SOC loss consistently increases with percentage residue harvest. Losses were proportionally greater at shallow depths (Fig. 2a), reinforcing the conclusion that the loss is caused more by reduced residue inputs than by reduced belowground C inputs. In the case of sugarcane, fields burned before harvest have lower SOC than unburned fields where the harvest residue is retained on the fields (Blair *et al*., 1998; Graham *et al*., 2002), and our models likewise revealed that retention of harvest residue resulted in faster SOC accumulation (Tables B1 and B2).

The effects of biomass harvest on North American grasses are less clear, partially because few studies have provided side-by-side comparisons of different practices. For switchgrass, harvested fields tended to accumulate SOC less rapidly than fields that have not been harvested, but this effect was partially offset by higher intercepts for harvested fields (Tables B1 and 2), which is more likely a statistical artifact than a biological reality. Individual studies shed little light on the question; 4–6 years studies have detected no effects of harvest frequency (Ma *et al.*, 2000; Thomason *et al.*, 2005), while a shift in switchgrass management from CRP (unharvested, unfertilized) to harvesting and fertilizing increased SOC (Lee *et al.*, 2007). In the case of native grasslands, fields that were burned or grazed tended to have lower SOC than those that were not burned (Tables B1and B2); however, the effects of grazing on SOC are mixed (Holt, 1997; Frank *et al.*, 1995; De Deyn *et al.*, 2008; Ingram *et al.*, 2008). Harvesting may also affect the depth distribution of new C inputs; the proportionally greater C accumulation at shallow depths in prairie (Fig. 2e) – which contrasts with the depth-independence of percentage change in C concentration of Miscanthus and switchgrass (Fig. 2c and d) – may be attributable to the fact that prairie sites were not harvested (Table 1). More research will be required to assess the effects of harvest on SOC accumulation under temperate perennial grasses.

Tillage practices also influence SOC. Tillage releases SOC and was probably largely responsible for the observed land conversion losses (Fig. 4). Conversely, reduced tillage results in soil C sequestration (e.g., West & Post, 2002; Bernacchi *et al.*, 2005; Grandy & Robertson, 2007), and SOC accumulation under perennial grasses grown on former cropland may be partially attributable to the cessation of tillage. However, the observed contrast between SOC losses under corn with residue harvest and gains under perennial grasses cannot be explained as an effect of tillage, as 13 of the 15 corn treatments were under no-till practices (Table A1). In the case of corn, we note that a switch from conventional tillage to no-till concurrent with initiation of residue harvest may offset the negative effects of residue harvest (Clapp *et al.*, 2000; Adler *et al.*, 2007).

Soil type, fertilization, and climate also may affect the C balance of biofuel crops. Soil type affects both the input of C to the soil by affecting plant productivity (Epstein *et al.*, 1997) and the decomposition of organic matter (Sorensen, 1981; Paul, 1984; Jobbágy & Jackson, 2000). In our analysis, clay content tended to reduce the net change in SOC, moderating both losses in corn and gains in perennial grasses (Tables B1-2). Additionally, both fertilization and climate have been found to influence SOC. While our dataset lacked the statistical power to reasonably evaluate their effects, we note that several studies included in our data set have detected their impact. Fertilization – which boosts productivity but decreases belowground C allocation (Ma *et al.*, 2001; Bonifas *et al.*, 2005) and may increase soil respiration (Bauhus & Khanna, 1994) – consistently increased SOC gains or decrease SOC losses in perennial grasses, although its effects often were not significant (Ma *et al.*, 2000; Graham *et al.*, 2002; Thomason *et al.*, 2005; Lee *et al.*, 2007). Both productivity and decomposition increase with mean annual temperature such that SOC turnover should be fastest in warm climates (Schimel *et al.*, 1994) and any proportional difference between the input of new organic material and decomposition of the old will tend to translate into faster rates of SOC loss or gain (Post & Kwon, 2000; Paul *et al.*, 2002). However, the differential responses of productivity and decomposition to temperature (Allen *et al.*, 2005) imply that the magnitude and direction of changes in SOC may vary along temperature gradients. In switchgrass crops planted across a temperature gradient in North America, SOC turnover rate, the proportion of switchgrass-derived SOC, and net change in SOC all increased with temperature (Garten & Wullschleger, 2000). Both production and decomposition increase with precipitation, but the relative advantage appears to switch from decomposition at low precipitation to production at high precipitation (Austin, 2002). This suggests that SOC accumulation may tend to increase with precipitation (Paul *et al.*, 2002). For sugarcane fields converted from native forest in Hawaii, sites with rainfalls of $2500\,\mathrm{mm\,yr^{-1}}$ and $4000\,\mathrm{mm\,yr^{-1}}$ had lost similar amounts of forest C, but sites receiving more rainfall had accumulated cane-derived C at a higher rate (Osher *et al.*, 2003).

Our analysis is subject to several limitations. First, our analysis assumes that controls are at steady-state with respect to SOC (Fig. 1), which may not be true of some controls (e.g., fallows, young grasslands). As changes in SOC of controls would bias estimates of rate or land conversion effect, our findings are most properly interpreted as describing the change in SOC relative to what would occur if the land remained under the same land use as the control. In addition, changes in SOC are inherently difficult to measure. SOC is spatially variable, making it difficult to match treatments with controls (Ellert *et al.*, 2000) and to detect change in SOC (Garten & Wullschleger, 1999) – a problem that increases the variability within our data set. Additionally, changes in bulk density may bias calculations of change in SOC_a by changing the total mass of soil within the depth increment. As a result, change in SOC_a is artificially high (tending toward gains) in situations where bulk density has increased and artificially low (tending toward losses) in situations where it has decreased (Ellert *et al.*, 2000). Assuming that bulk density increases with decreased SOC and *vice versa* (Adams, 1973), both losses and gains of SOC_a may be underestimated. For sugarcane, this would imply underestimates of both the land conversion loss and the rate of SOC_a accumulation. It is also noteworthy that our data comes from multiple studies with differing research designs, such that there is substantial within-and between-crop variation in factors such as number of samples, previous land uses, ages and depths sampled, management practices, soil types, and climate (Tables 1, A1). As a result, estimated coefficients should be interpreted with caution; for example, direct numerical comparisons of SOC accumulation rates among crop types would be inappropriate; rather, side-by-side comparisons of perennial grasses will be necessary to rank their SOC accumulation rates. Finally, data sets for some crops are limited in size (e.g., Miscanthus) or representation of certain variables (e.g., old fields with corn residue harvest, harvested mixed native systems; Table 1), which reduces the potential to detect changes and accurately estimate effects.

Changes in SOC will significantly affect efforts to mitigate GHG emissions (Ney & Schnoor, 2002; Adler *et al*., 2007) and impact a host of other ecosystem services (Lal, 2004). Our results therefore have implications for the sustainability of biofuel crops. Removal of corn residue is detrimental with regard to SOC; our analysis indicates that SOC is lost under any level of residue removal (Fig. 3; Mann *et al*., 2002; Blanco-Canqui & Lal, 2007). Previous studies estimated that 20–30% residue removal in the Midwest would be sustainable (Wilhelm *et al*., 2004; Graham *et al*., 2007; but see Mann *et al*., 2002); however, the need to maintain soil C was not considered in these analyses (Graham *et al*., 2007). SOC losses of the magnitude observed here have not been included in life cycle analyses of biofuel production from corn residue (Sheehan *et al*., 2003; Powers, 2005; Spatari *et al*., 2005; Adler *et al*., 2007), which implies that the sustainability and net benefits of biofuel production from residue have been overestimated. Our findings reinforce the argument that – at least in most situations – residue is better left on the fields for the maintenance of soil quality and, thereby, crop production (Lal, 2008). In the case of sugarcane, clearing of native ecosystems resulted in a large land conversion loss of SOC that counteracts the benefits of fossil fuel displacement (Fargione *et al*., 2008); however, the subsequent sequestration of SOC makes the C balance of sugarcane bioenergy more favorable, especially in the long term. Changes in SOC are not typically included in sugarcane life cycle analyses (Mohee & Beeharry, 1999; Beeharry, 2001; Botha & von Blottnitz, 2006), but could have a substantial impact on their outcomes. SOC sequestration by the temperate perennial grasses (i.e., Miscanthus, switchgrass, and North American native mixtures), as observed here and elsewhere (e.g., Potter *et al*., 1999; Ma *et al*., 2000; Kahle *et al*., 2001; Lemus & Lal, 2005; Liebig *et al*., 2005, 2008), would augment the benefits of fossil fuel displacement. Unfortunately, these net benefits are only rarely included in life cycle analyses (McLaughlin & Walsh, 1998; Lettens *et al*., 2003; Lemus & Lal, 2005). We note that – due to their recent inception – there is a lack of information about long-term soil C patterns under switchgrass and Miscanthus crops (Table 1) and that cultivation practices are actively being modified. Advancements in harvest efficiency, reduced allocation to roots through genetic modifications or changes in cultivation practices (e.g., fertilization), or genetic modifications that yield more decomposable plants (Ragauskas *et al*., 2006) could reduce – or possibly even reverse – SOC sequestration.

Land conversion losses will play a major role in determining the C balance of biofuel crops (Fargione *et al*., 2008). Clearing and tillage of natural ecosystems or pastures for the purpose of biofuel cultivation incurs a SOC loss that will offset SOC sequestration by the crop until the new C accumulation reaches a level that restores the initial loss following crop planting (Fig. 1). Land conversion losses must be assessed in the context of the land use that the biofuel crops would replace and should be related to the whole chain of production that contributes to fuel C balances (Fargione *et al*., 2008; Renewable Fuels Agency, 2008; Searchinger *et al*., 2008; Davis *et al*., 2009). Whereas growing perennial grasses on C-depleted soil (e.g., agricultural land) provides an immediate SOC-sequestration benefit, replacing uncultivated land with biofuel crops – either directly or indirectly (Gurgel *et al*., 2007; Searchinger *et al*., 2008) – may not provide any SOC sequestration benefits for decades or even centuries. Therefore, direct or indirect replacement of native ecosystems with biofuel crops should be avoided, and, if biofuels are to be cultivated on land that has not been recently tilled, management practices should seek to minimize SOC losses upon conversion (Renewable Fuels Agency, 2008). In conclusion, with regards to soil C balance, growing perennial grasses on C-depleted soil – without triggering cultivation of native land elsewhere in the world – is preferable to harvesting corn residue or to replacing uncultivated land with biofuel crops. In such cases, the soil C sequestration benefits would augment the GHG reduction associated with fossil fuel displacement.

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References

Adams WA (1973) The effect of organic matter on the bulk and true densities of some uncultivated podzolic soils. *European Journal of Soil Science*, **24**, 10–17.

Adler PR, Del Grosso SJ, Parton WJ (2007) Life-cycle assessment of net greenhouse-gas flux for bioenergy cropping systems. *Ecological Applications*, **17**, 675–691.

Allen AP, Gillooly JF, Brown JH (2005) Linking the global carbon cycle to individual metabolism. *Functional Ecology*, **19**, 202–213.

Austin AT (2002) Differential effects of precipitation on production and decomposition along a rainfall gradient in Hawaii. *Ecology*, **83**, 328–338.

Bauhus J, Khanna P (1994) Carbon and nitrogen turnover in two acid forest soils of southeast Australia as affected by phosphorus addition and drying and rewetting cycles. *Biology and Fertility of Soils*, **17**, 212–218.

Beeharry RP (2001) Carbon balance of sugarcane bioenergy systems. *Biomass and Bioenergy*, **20**, 361–370.

Bernacchi CJ, Hollinger SE, Meyers T (2005) The conversion of the corn/soybean ecosystem to no-till agriculture may result in a carbon sink. *Global Change Biology*, **11**, 1867–1872.

Blair GJ, Chapman L, Whitbread AM, Ball-Coelho B, Larsen P, Tiessen H (1998) Soil carbon changes resulting from sugarcane trash management at two locations in Queensland, Australia, and in North-East Brazil. *Australian Journal of Soil Research*, **36**, 873–882.

Bonifas KD, Walters DT, Cassman KG, Lindquist JL (2005) Nitrogen supply affects root: hoot ratio in corn and velvetleaf. *Weed Science*, **53**, 670–675.

Botha T, von Blottnitz H (2006) A comparison of the environmental benefits of bagasse-derived electricity and fuel ethanol on a life-cycle basis. *Energy Policy*, **34**, 2654–2661.

Briggs JM, Knapp AK (1995) Interannual Variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany*, **82**, 1024.

Brye KR, Gowest ST, Norman JM, Bundy LG (2002) Carbon budgets for a prairie and agroecosystems: effects of land use interannual variability. *Ecological Applications*, **12**, 962–979.

Cheeseman O (2004) *Environmental Impacts of Sugar Production*. CABI Publishing, Wallingford, UK.

Clapp CE, Allmaras RR, Layese MF, Linden DR, Dowdy RH (2000) Soil organic carbon and 13C abundance as related to tillage, crop residue, and nitrogen fertilization under continuous corn management in Minnesota. *Soil and Tillage Research*, **55**, 127.

David MB, McIsaac GF, Darmody RG, Omonode RA (2009) Long-term changes in Mollisol organic carbon and nitrogen. *Journal of Environmental Quality*, **38**, 200–211.

Davidson E, Janssens I (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165–173.

Davidson EA, Ackerman IL (1993) Changes in soil carbon inventories following cultivation of previously untilled soils. *Biogeochemistry*, **20**, 161–193.

Davis SC, Anderson-Teixeira KJ, DeLucia EH (2009) Life-cycle analysis and the ecology of biofuels. *Trends in Plant Science*, **14**.

De Deyn GB, Cornelissen JHC, Bardgett RD (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, **11**, 516–531.

Ebrahim MK, Zingsheim O, El-Shourbagy MN, Moore PH, Komor E (1998) Growth and sugar storage in sugarcane grown at temperatures below and above optimum. *Journal of Plant Physiology*, **153**, 593–602.

Ellert BH, Janzen H, McCockney B (2000) Measuring and comparing soil carbon storage. In: *Assessment methods for soil carbon* (eds Lal R, Kimble JM), Lewis imprint of the CRC Press, Boca Raton, FL.

Epstein HE, Lauenroth WK, Burke IC (1997) Effects of temperature and soil texture on ANPP in the US. Great Plains. *Ecology*, **78**, 2628–2631.

Fargione J, Hill J, Tilman D, Polasky S, Hawthorne P (2008) Land clearing and the biofuel carbon debt. *Science*, **319**, 1235–1238.

Fisher MJ, Rao IM, Ayarza MA, Lascano CE, Sanz JI, Thomas RJ, Vera RR (1994) Carbon storage by introduced deep-rooted grasses in the South American savannas. *Nature*, **371**, 236–238.

Fissore C, Giardina CP, Kolka RK *et al*. (2008) Temperature and vegetation effects on soil organic carbon quality along a forested mean annual temperature gradient in North America. *Global Change Biology*, **14**, 193–205.

Frank AB, Tanaka DL, Hofmann L, Follett RF (1995) Soil carbon and nitrogen of Northern Great Plains grasslands as influenced by long-term grazing. *Journal of Range Management*, **48**, 470–474.

Friedlingstein P, Cox P, Betts R *et al*. (2006) Climate-carbon cycle feedback analysis: results from the C4MIP model intercomparison. *Journal of Climate*, **19**, 3337–3353.

Garten CT Jr, Wullschleger SD (1999) Soil carbon inventories under a bioenergy crop (switchgrass): measurement limitations. *Journal of Environmental Quality*, **28**, 1359–1365.

Garten CT Jr, Wullschleger SD (2000) Soil carbon dynamics beneath switchgrass as indicated by stable isotope analysis. *Journal of Environmental Quality*, **29**, 645–653.

Gifford RM, Thorne JH, Hitz WD, Giaquinta RT (1984) Crop productivity and photoassimilate partitioning. *Science*, **225**, 801–808.

Graham MH, Haynes RJ, Meyer JH (2002) Soil organic matter content and quality: effects of fertilizer applications, burning and trash retention on a long-term sugarcane experiment in South Africa. *Soil Biology and Biochemistry*, **34**, 93–102.

Graham RL, Nelson R, Sheehan J, Perlack RD, Wright LL (2007) Current and potential US corn stover supplies. *Agronomy Journal*, **99**, 1–11.

Grandy AS, Robertson GP (2007) Land-use intensity effects on soil organic carbon accumulation rates and mechanisms. *Ecosystems*, **10**, 58–73.

Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: a meta analysis. *Global Change Biology*, **8**, 345–360.

Gurgel A, Reilly JM, Paltsev S (2007) Potential land use implications of a global biofuels industry. *Journal of Agricultural and Food Industrial Organization*, **5** article 9.

Heaton EA, Dohleman FG, Long SP (2008) Meeting US biofuel goals with less land: the potential of Miscanthus. *Global Change Biology*, **14**, 2000–2014.

Hodkinson TR, Renvoize SA (2001) Nomenclature of *Miscanthus_giganteus* (Poaceae). *Kew Bulletin*, **56**, 759–760.

Holt JA (1997) Grazing pressure and soil carbon, microbial biomass and enzyme activities in semi-arid northeastern Australia. *Applied Soil Ecology*, **5**, 143–149.

Ingram LJ, Stahl PD, Schuman GE *et al*. (2008) Grazing impacts on soil carbon and microbial communities in a mixed-grass ecosystem. *Soil Science Society of America Journal*, **72**, 939–948.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia*, **108**, 389–411.

Jobbágy EG, Jackson RB (2000) Global controls of forest line elevation in the northern and southern hemispheres. *Global Ecology and Biogeography*, **9**, 253–268.

Kadam KL, McMillan JD (2003) Availability of corn stover as a sustainable feedstock for bioethanol production. *Bioresource Technology*, **88**, 17–25.

Kahle P, Beuch S, Boelcke B, Leinweber P, Schulten H-R (2001) Cropping of Miscanthus in Central Europe: biomass production and influence on nutrients and soil organic matter. *European Journal of Agronomy*, **15**, 171–184.

Knapp AK, Fahnestock JT, Hamburg SP, Statland LB, Seastedt TR, Schimel DS (1993) Landscape patterns in soil-plant water relations and primary production in tallgrass prairie. *Ecology*, **74**, 549–560.

Kucharik CJ (2007) Impact of prairie age and soil order on carbon and nitrogen sequestration. *Soil Science Society of America Journal*, **71**, 430–441.

Lal R (2004) Soil carbon sequestration impacts on global climate change and food security. *Science*, **304**, 1623–1627.

Lal R (2008) Crop residues as soil amendments and feedstock for bioethanol production. *Waste Management*, **28**, 747–758.

Lee DK, Owens VN, Doolittle JJ (2007) Switchgrass and soil carbon sequestration response to ammonium nitrate, Manure, and harvest frequency on Conservation Reserve Program land. *Agronomy Journal*, **99**, 462–468.

Leirós MC, Trasar-Cepeda C, Seoane S, Gil-Sotres F (1999) Dependence of mineralization of soil organic matter on temperature and moisture. *Soil Biology and Biochemistry*, **31**, 327–335.

Lemus R, Lal R (2005) Bioenergy Crops and Carbon Sequestration. *Critical Reviews in Plant Sciences*, **24**, 1.

Lettens S, Muys B, Ceulemans R, Moons E, Garcia J, Coppin P (2003) Energy budget and greeenhouse gas balance evalution of sustainable coppice systems for electricity production. *Biomass and Bioenergy*, **24**, 179–197.

Lewandowski I, Clifton-Brown JC, Scurlock JMO, Huisman W (2000) Miscanthus: European experience with a novel energy crop. *Biomass and Bioenergy*, **19**, 209–227.

Liebig MA, Johnson HA, Hanson JD, Frank AB (2005) Soil carbon under switchgrass stands and cultivated cropland. *Biomass and Bioenergy*, **28**, 347–354.

Liebig MA, Schmer MR, Vogel KP, Mitchell RB (2008) Soil carbon storage by switchgrass grown for bioenergy. *Bioenergy Research*, **1**, 215–222.

Ma Z, Wood CW, Bransby DI (2000) Soil management impacts on soil carbon sequestration by switchgrass. *Biomass and Bioenergy*, **18**, 469–477.

Ma Z, Wood CW, Bransby DI (2001) Impact of row spacing, nitrogen rate, and time on carbon partitioning of switchgrass. *Biomass and Bioenergy*, **20**, 413–419.

Mann L, Tolbert V, Cushman J (2002) Potential environmental effects of corn (*Zea mays* L.) stover removal with emphasis on soil organic matter and erosion. *Agriculture, Ecosystems and Environment*, **89**, 149–166.

McClaugherty CA, Pastor J, Aber JD, Melillo JM (1985) Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology*, **66**, 266–275.

McLaughlin SB, Adams Kszos L (2005) Development of switchgrass (*Panicum virgatum*) as a bioenergy feedstock in the United States. *Biomass and Bioenergy*, **28**, 515–535.

McLaughlin SB, Walsh ME (1998) Evaluating environmental consequences of producting herbaceous crops for bioenergy. *Biomass and Bioenergy*, **17**, 73–83.

Mohee R, Beeharry RP (1999) Life cycle analysis of compost incorporated sugarcane bioenergy systems in Mauritius. *Biomass and Bioenergy*, **17**, 73–83.

Murty D, Kirschbaum MUF, Mcmurtrie RE, Mcgilvray H (2002) Does conversion of forest to agricultural land change soil carbon and nitrogen? a review of the literature. *Global Change Biology*, **8**, 105–123.

Neukirchen D, Himken M, Lammel J, Czypionka-Krause U, Olfs HW (1999) Spatial and temporal distribution of the root system and root nutrient content of an established *Miscanthus* crop. *European Journal of Agronomy*, **11**, 301–309.

Ney RA, Schnoor JL (2002) Incremental life cycle analysis: using uncertainty analysis to frame greenhouse gas balances from bioenergy systems for emission trading. *Biomass and Bioenergy*, **22**, 257–269.

Ojima DS, Schimel DS, Parton WJ, Owensby CE (1994) Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry*, **24**, 67–84.

Osher LJ, Matson PA, Amundson R (2003) Effect of land use change on soil carbon in Hawaii. *Biogeochemistry*, **65**, 213–232.

Paul EA (1984) Dynamics of organic matter in soils. *Plant and Soil*, **76**, 275–285.

Paul KI, Polglase PJ, Nyakuengama JG, Khanna PK (2002) Change in soil carbon following afforestation. *Forest Ecology and Management*, **168**, 241–257.

Petrolia DR (2008) The economics of harvesting and transporting corn stover for conversion to fuel ethanol: A case study for Minnesota. *Biomass and Bioenergy*, **32**, 603–612.

Post WM, Kwon KC (2000) Soil carbon sequestration and land-use change: processes and potential. *Global Change Biology*, **6**, 317–327.

Potter KN, Torbert HA, Johnson HB, Tischler CR (1999) Carbon storage after long-term grass establishment on degraded soils. *Soil Science*, **164**, 718–725.

Powers SE (2005) *Quantifying Cradle-to-farm Gate Life-Cycle Impacts Associated with Fertilizer Used for Corn, Soybean, and Stover Production*. U.S. Department of Energy. Available at: http://www1.eere.energy.gov/biomass/pdfs/37500.pdf (last accessed 5 February 2009).

Ragauskas AJ, Nagy M, Kim DH, Eckert CA, Hallett JP, Liotta CL (2006) From wood to fuels: Integrating biofuels and pulp production. *Industrial Biotechnology*, **2**, 55–65.

Rawls WJ, Nemes A, Pachepsky YA (2004) Effect of soil organic carbon on soil hydraulic propteries. In: *Development of; Pedotransfer Fucntions in Soil Hydrology* (eds Pachepsky YA, Rawls WJ), pp. 95–115. Elsevier, Amsterdam.

Reicosky DC, Dugus WA, Torbert HA (1997) Tillage-induced soil carbon dioxide loss from different cropping systems. *Soil and Tillage Research*, **41**, 105–118.

Renewable Fuels Agency (2008) *The Gallagher Review of the Indirect Effects of Biofuels Production*. Renewable Fuels Agency, East Sussex, UK.

Rhoades CC, Eckert GE, Coleman DC (2000) Soil carbon differences among forest, agriculture, and secondary vegetation in lower montane Ecuador. *Ecological Applications*, **10**, 497–505.

Schimel DS, Holland EA, McKeown R (1994) Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles*, **8**, 279–293.

Searchinger T, Heimlich R, Houghton RA *et al*. (2008) Use of US croplands for biofuels increases greenhouse gases through emissions from land-use change. *Science*, **319**, 1238–1240.

Sheehan J, Aden A, Paustian K, Killian K, Brenner J, Walsh M, Nelson R (2003) Energy and environmental aspects of using corn stover for fuel ethanol. *Journal of Industrial Ecology*, **7**, 117–146.

Silva AJN, Ribeiro MR, Carvalho FG, Silva VN, Silva LESF (2007) Impact of sugarcane cultivation on soil carbon fractions, consistence limits and aggregate stability of a Yellow Latosol in Northeast Brazil. *Soil and Tillage Research*, **94**, 420–424.

Skjemstad JO, Taylor JA, Janik LJ, Marvanek SP (1999) Soil organic carbon dynamics under long-term sugarcane monoculture. *Australian Journal of Soil Research*, **37**, 151–164.

Smith DM, Inman-Bamber NG, Thorburn PJ (2005) Growth and function of the sugarcane root system. *Field Crops Research*, **92**, 169–183.

Sorensen LH (1981) Carbon-nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. *Soil Biology and Biochemistry*, **13**, 313–321.

Spatari S, Zhang Y, MacLean H (2005) Life cycle assessment of switchgrass- and corn stover-derived ethanol-fueled automobiles. *Environmental Science and Technology*, **39**, 9750–9758.

Thomason WE, Raun WR, Johnson GV, Taliaferro CM, Freeman KW, Wynn KJ, Mullen RW (2005) Switchgrass response to harvest frequency and time and rate of applied nitrogen. *Journal of Plant Nutrition*, **28**, 1199–1226.

Tilman D, Hill J, Lehman C (2006) Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science*, **314**, 1598–1600.

Tranter G, Minasny B, McBratney AB, Murphy B, McKenzie NJ, Grundy M, Brough D (2007) Building and testing conceptual and empirical models for predicting soil bulk density. *Soil Use and Management*, **23**, 437–443.

Trumbore SE (1997) Potential responses of soil organic carbon to global environmental change. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 8284–8291.

West TO, Marland G, King AW, Post WM, Jain AK, Andrasko K (2004) Carbon management response curves: estimates of temporal soil carbon dynamics. *Environmental Management*, **33**, 507–518.

West TO, Post WM (2002) Soil Organic Carbon Sequestration Rates by Tillage and Crop Rotation: A Global Data Analysis. *Soil Science Society of America Journal*, **66**, 1930–1946.

Wilhelm WW, Johnson JMF, Hatfield JL, Voorhees WB, Linden DR (2004) Crop and soil productivity response to corn residue removal: a literature review. *Agronomy Journal*, **96**, 1–17.

Wilson SD (1993) Belowground competition in forest and prairie. *Oikos*, **68**, 146–150.

World Agricultural Outlook Board (2008) World agricultural supply and demand estimates. USDA. 28 October 2008. ISSN:1554-9089.

Zinn YL, Lal R, Resck DVS (2005) Changes in soil organic carbon stocks under agriculture in Brazil. *Soil and Tillage Research*, **84**, 28–40.

APPENDIX A: SOC data sources

Location	Management*	Previous land use/control	Soil texture†	*N*	Treatments	Biomass removal ‡	N fertilization	Tillage	Age(s) (years)	Sampling depth (cm)	Replicates	Reference
Corn with residue removal												
Coshocton, OH, USA	AG	Crop (corn)	SL	4	4 levels residue removal	25%, 50%, 75%, 100%	+	–	2.5	30	3	Blanco-Canqui & Lal (2007)
South Charleston, OH, USA	AG	Crop (corn)	SL	4	4 levels residue removal	25%, 50%, 75%, 100%	+	–	2.5	30	3	Blanco-Canqui & Lal (2007)
Hoytville, Ohio, USA	AG	Crop (corn)	CL	4	4 levels residue removal	25%, 50%, 75%, 100%	+	–	2.5	30	3	Blanco-Canqui & Lal (2007)
Lancaster, WI, USA	AG	Crop (corn)	SL	1	–	100%	+	–	10	60	4	Karlen *et al.* (1994)
Clarinda, IA, USA	AG	Crop (corn)	SCL	2	2 levels residue removal	50%, 100%	+	+	11	15	4	Larson *et al.* (1972)
Sugarcane												
Durban, KwaZulu-Natal, South Africa	AG	Grass	C	6	3 harvest treatments × 2 fertilizer levels	B/Hr, B/Rr, Rr	+, –	+	59	5	4	Graham *et al.* (2002)
Ramu Valley, Madang, Papua New Guinea	AG	Grass	CL	1	–	Rr	+	+	15, 17	15	1	Hartemink (1998)
Ramu Valley, Madang, Papua New Guinea	AG	Grass	C	1	–	Rr	+	+	15, 17	15	1	Hartemink (1998)
Patchacan, Belize (Xaibe soil)	AG	Forest	C	1	–	+	?	?	15	25	1	Hsieh (1996)
Patchacan, Belize (Louisville soil)	AG	Forest	C	1	–	+	?	?	20	15	1	Hsieh (1996)
Hamakua Coast, Hawaii, USA (MAP: 2500 mm yr^{-1})	AG	Forest	U	1	–	+	+	+	90	100	1	Osher *et al.* (2003)
Hamakua Coast, Hawaii, USA (MAP: 4000 mm yr^{-1})	AG	Forest	U	1	–	+	+	+	50	100	1	Osher *et al.* (2003)
W. slope of Andes, Ecuador	AG	Forest	U	1	–	+	?	?	50	100	2	Rhoades *et al.* (2002)
São Miguel dos Campos, Alagoas, Brazil	AG	Forest (?)	SaC	1	–	B	+	+	2, 18, 25	40	3	Silva *et al.* (2007)
Ingham, Queensland, Australia	AG	Forest	LSa (?)	1	–	+	?	+	20	80	3	Skjemstad *et al.* (1999)
Ingham, Queensland, Australia	AG	Grass	U	1	–	+	?	+	90	80	3	Skjemstad *et al.* (1999)
Tully, Queensland, Autralia	AG	Old building	SaCL	1	–	+	?	+	30	80	3	Skjemstad *et al.* (1999)
Ayr, Queensland, Australia	AG	Grass (?)	U	1	–	+	?	+	35	80	3	Skjemstad *et al.* (1999)
Queensland, Australia	AG	Native scrub	C	1	–	+	?	?	20, 35, 45	10	1	Skjemstad *et al.* (1986)

Continued

APPENDIX A (*Contd.*)

Location	Management*	Previous land use/control	Soil texture†	*N*	Treatments	Biomass removal ‡	N fertilization	Tillage	Age(s) (years)	Sampling depth (cm)	Replicates	Reference
Piraciacaba, São Paulo, Brazil	AG	Forest	C	1	–	+	+	?	12, 50	70	1	Vitorello *et al.* (1989)
Miscanthus												
Cashel Co. Tipperary, Ireland	AG	Grass	SaL	1	–	+	+	–	15	30	8	Clifton-Brown *et al.* (2007)
Stuttgart-Hohenheim, Baden-Wurttemberg, Germany	AG	Grass	SL	1	–	+	?	–	11	5	1	Dorodnikov *et al.* (2007)
Hornum, North Jutland, Denmark	AG	Grass	LSa	1	–	+	+	–	11, 18	20	1	Foereid *et al.* (2004)
Hornum, North Jutland, Denmark	AG	Grass	LSa	1	–	+	+	–	9, 16	100		Hansen *et al.* (2004)
Boitzenhagen, Germany	AG	Grass (?)	SaL	1	–	+	+	–	5, 7	25	1	Kahle *et al.* (1999, 2001)
Güntersleben, Germany	AG	Grass (?)	SL	1	–	+	+	–	6, 8	25	4	Kahle *et al.* (1999, 2001)
Güntersleben, Germany	AG	Grass (?)	SaC	1	–	+	+	–	6, 8	25	2	Kahle *et al.* (1999, 2001)
Klein Markow, Germany	AG	Grass (?)	SaL	1	–	+	+	–	4–10 (7)	25	3	Kahle *et al.* (2001, 2002)
Stuttgart-Hohenheim, Baden-Wurttemberg, Germany	AG	Grass	SL	1	–	+	?	–	9	100	1	Schneckenberger & Kuzyakov (2007)
Großbeeren, Germany	AG	Grass (?)	LSa	1	–	+ (5 years), –(7 years)	?	–	12	100	1	Schneckenberger & Kuzyakov (2007)
Switchgrass												
Castana, IA, USA	AG	Crop	SL	1	–	G	+	–	10	30	4	Al-Kaisi & Grote (2007)
Mandan, ND, USA	AG	Fallow	L	1	–	+	+	–	1, 2, 3	90	2	Frank *et al.* (2004)
Jackson, TN, USA	AG	Grass	L	1	–	+	+	–	5	40	4	Garten & Wullschleger (1999, 2000)
Princeton, NJ, USA	AG	Grass	S	1	–	+	+	–	4	40	4	Garten & Wullschleger (1999, 2000)
Knoxville, TN, USA	AG	Grass	L	1	–	+	+	–	5	40	4	Garten & Wullschleger (1999, 2000)
Blacksburg, VA, USA	AG	Grass	C	1	–	+	+	–	5	40	4	Garten & Wullschleger (1999, 2000)
Moody County, SD, USA	AG	Grass	SCL	3	3 fertilizer	1/year, 1/2year (averaged)	+, –	–	4	90	8	Lee *et al.* (2007)
Shorter, AL, USA	AG	Grass	L	3	3 fertilizer levels	?	+, –	–	4	300	8	Ma *et al.* (2000a)
Shorter, AL, USA	AG	Grass	L	3	3 varieties	?	+	–	10	360	4	Ma *et al.* (2000a)
Shorter, AL, USA	AG	Fallow	SaL	2	2 harvest frequencies	1/year, 2/year	+	–	4	330	2	Ma *et al.* (2000a)
Shorter, AL, USA	AG	Grass	L	3	3 row spacings	+	+	–	2	90	4	Ma *et al.* (2000a)
Fairhope, AL, USA	AG	Crop	SaL	2	2 harvest frequencies	1/year, 2/year	+	–	4	240	2	Ma *et al.* (2000a)

Camp Hill, AL, USA	AG	Grass	CL	2	2 harvest frequencies	1/year, 2/year	+	–	4	210	2	Ma *et al*. (2000a)
Camp Hill, AL, USA	AG	Grass	CL	3	3 row spacings	+	+	–	2	90	4	Ma *et al*. (2000a)
Belle Miwa, AL, USA	AG	Crop	SL	2	2 harvest frequencies	1/year, 2/year	+	–	4	270	2	Ma *et al*. (2000a)
Crossille, AL, USA	AG	Grass	SaL	2	2 harvest frequencies	1/year, 2/year	+	–	4	180	2	Ma *et al*. (2000a)
Shorter, AL, USA	AG	Grass	SaL	1	2 harvest frequencies × 3 row spacings (averaged)	1/year, 2/year	+	–	0.6–2.6 (8)	30	4	Ma *et al*. (2000b)
Camp Hill, AL, USA	AG	Grass	CL	1	2 harvest frequencies × 3 row spacings (averaged)	1/year, 2/year	+	–	0.6–2.6 (7)	30	4	Ma *et al*. (2000b)
Montgomery County, IN, USA ('Dunbar')	C	Crop	CL	1	–	–	–	–	6	100	1	Omonode & Vyn (2006)
Montgomery County, IN, USA ('Loop')	C	Crop	CL	1	–	–	–	–	8	100	1	Omonode & Vyn (2006)
Montgomery County, IN, USA	C	Crop	SaL	1	–	–	–	–	6	100	1	Omonode & Vyn (2006)
Montgomery County, IN, USA	C	Crop	SL	1	–	–	–	–	5	100	1	Omonode & Vyn (2006)
Montgomery County, IN, USA	C	Crop	L	1	–	–	–	–	8	100	1	Omonode & Vyn (2006)
Chickasha, OK, USA	AG	Crop (?)	SL	23	5 fertilizer levels × 3 harvest frequencies; 4 fertilizer levels × 2 harvest frequencies	1/year, 2/year, 3/year	+ , –	–	6	15	3	Thomason *et al*. (2005)
Perkins, OK, USA	AG	Crop (?)	SaL	23	5 fertilizer levels × 3 harvest frequencies; 4 fertilizer levels × 2 fertilizer timings × 2 harvest frequencies	1/year, 2/year, 3/year	+ , –	–	4	15	3	Thomason *et al*. (2005)
Normal, AL, USA	AG	Crop	SL	1	–	+	+	–	5	60	5	Tolbert *et al*. (2002)
Montreal, Quebec, Canada	AG	Crop	SaL	2	2 sites	+	+	–	4	60	4	Zan *et al*. (2001)
Mixed Native												
Castana, IA, USA	PA	Crop	SL	1	–	G	–	v	10	30	4	Al-Kaisi & Grote (2007)
Batavia, IL, USA	P	Crop	SCL	1	–	B (?)	–	–	11, 25	10	1	Allison & Jastrow (2006)
Batavia, IL, USA	P	Crop	SCL	1	–	B (?)	–	–	3–25 (9)	5	1	Allison *et al*. (2005)

Continued

APPENDIX A (*Contd.*)

Location	Management*	Previous land use/control	Soil texture†	*N*	Treatments	Biomass removal ‡	N fertilization	Tillage	Age(s) (years)	Sampling depth (cm)	Replicates	Reference
Gage & Saline counties, NB, USA	C	Crop	SCL	1	–	–	–	–	2–12 (6)	20	2–3	Baer *et al.* (2002)
Arlington, WI, USA	P	Crop	SL	1	–	B (3 years)	–	–	5,10,24	100	1–2	Brye & Kucharik (2003)
Baraboo, WI, USA	P	Crop	SaL, Lsa	1	–	B (5 years)	–	–	4–20 (9)	100	1–3	Brye & Kucharik (2003)
Northfield, MN, USA	P	Crop	L	1	–	B (3–4 years)	–	–	1–6 (6)	65	1	Camill *et al.* (2004)
Cedar Creek, MN, USA	P	Crop	Sa	1	16 species treatment	B (1 year)	–	–	6, 10, 12	20,100	28–35	Fornara & Tilman (2008)
Altwood, KS, USA	C	Crop	SL	1	–	–	–	–	5	100	1	Gebhert *et al.* (1994)
Colby, KS, USA	C	Crop	SL	1	–	–	–	–	5	100	1	Gebhert *et al.* (1994)
Big Springs, TX, USA	C	Crop	LSa	1	–	–	–	–	5	100	1	Gebhert *et al.* (1994)
Seminole, TX, USA	C	Crop	LSa	1	–	–	–	–	5	100	1	Gebhert *et al.* (1994)
Valentine, NB, USA	C	Crop	Sa	1	–	–	–	–	5	100	1	Gebhert *et al.* (1994)
Batavia, IL, USA	P	Crop	SCL	1	–	B (?)	–	–	1, 4, 7, 10	15	1	Jastrow (1996)
Cedar Creek, MN, USA	P	Crop	Sa	1	–	–	–	–	1–68 (38)	10	1	Knops & Tilman (2000)
WI, USA	C	Crop	SL, L	13	13 sites	–	–	–	8–14 (13)	5	1	Kucharik *et al.* (2003)
Batavia, IL, USA	P	Crop	SL	1	–	B (2 years)	–	–	1, 4, 8, 26	10	1	Lane & BassiriRad (2005)
Morris, IL, USA	P	Crop	L	1	–	–	–	–	7, 24	5	5	McKinley *et al.* (2005)
W. MN, USA	P	Crop	L (?)	1	–	–	–	–	2–36 (30)	10	1	McLauchlan *et al.* (2006)
Montgomery County, IN, USA	C	Crop	SL	1	–	–	–	–	7	100	1	Omonode & Vyn (2006)
Montgomery County, IN, USA	C	Crop	SL	1	–	–	–	–	7	100	1	Omonode & Vyn (2006)
Montgomery County, IN, USA	C	Crop	CL	1	–	–	–	–	8	100	1	Omonode & Vyn (2006)
Montgomery County, IN, USA	C	Crop	SaL	1	–	–	–	–	6	100	1	Omonode & Vyn (2006)
Montgomery County, IN, USA	C	Crop	SL	1	–	–	–	–	8	100	1	Omonode & Vyn (2006)
Montgomery County, IN, USA	C	Crop	L	1	–	–	–	–	8	100	1	Omonode & Vyn (2006)
Temple & Riesel, TX, USA	P	Crop	C	1	–	–	–	–	6, 26, 60	120	1	Potter *et al.* (1999)
Arvada, WY, USA	C	Crop	CL	2	2 fertilizer levels	–	+ , –	–	5	28	3	Reeder *et al.* (1998)
Keeline, WY, USA	C	Crop	SaL	2	2 fertilizer levels	–	+ , –	–	5	25	3	Reeder *et al.* (1998)

*Mangagemnt: AG, agriculture; C, conservation, including conservation reserve program (CRP); P, native prairie restoration; PA, pasture; O, other.

†Soil texture: C, clay; CL, clay loam; L, loam; LSa, loamy sand; S, silt; SCL, silty clay loam; SL, silt loam; Sa, sand; SaC, sandy clay; SaCL, sandy clay loam; SaL, sandy loam; U, unknown.

‡Biomass removal: B, burn (for prairie, burn cycle in parentheses, if known); Hr, harvest residue (sugarcane); Rr, return residue to fields (sugarcane); G, grazed. For sugarcane, BH indicates a burn immediately followed by a harvest. N, nitrogen.

Appendix B: ANOVA tables

Table B1 Full and reduced ANOVA models for percent change in SOC_c.

	Full model						Reduced model					
	Estimated coefficient (SE)	df	Type III SS	Mean sq.	F	P	Estimated coefficient (SE)	df	Type III SS	Mean sq.	F	P
Corn												
Intercept	−25.7 (6.4)					0.0002	−17.2 (3.2)					<0.0001
Age (years)	0.36 (0.84)	1	11.9	11.9	0.2	0.67	0.35 (0.41)	1	54.0	54.0	0.7	0.40
Log(depth) (cm)	7.86 (3.24)	1	384	384	5.9	0.02	6.25 (1.48)	1	1367.2	1367.2	17.9	<0.0001
Age × log(depth)	−0.12 (0.39)	1	6.5	6.5	0.1	0.44						
Clay (%)	0.33 (0.10)	1	683	683	10.5	0.002						
Residue removal (%)	−0.226 (0.065)	1	783	783	12.1	0.001	−0.18 (0.03)	1	2233	2233	29.3	<0.0001
Age × residue removal	0.006 (0.008)	1	39.1	39.1	0.6	0.44						
Residuals		46	2985	64.9				49	3733	76.1		
Sugarcane												
Intercept	−41.5 (23.28)					0.09	−56.23 (11.6)					<0.0001
Age (years)	1.09 (0.39)	1	3587	3587	7.7	0.01	0.33 (0.02)	1	2098	2098	2.8	0.10
Log(depth) (cm)	9.37 (9.09)	1	492	492	1.1	0.31	16.43 (3.69)	1	14 927	14 927	19.9	<0.0001
Age × log(depth)	−0.19 (0.19)	1	464	464	1.0	0.33						
Clay (%)	−0.42 (0.28)	1	1021	1021	2.2	0.15						
Biomass removal		1	1280	1280	2.8	0.11						
Standard	0											
Residue retention	−16.2 (9.7)					0.11						
Age × residue retention	0.55 (0.26)	1	2099	2099	4.5	0.04						
Residuals		21	9722	463				35	26 317	752		
Miscanthus												
Intercept	−0.18 (2.76)					0.95	3.68 (16.0)					0.82
Age (years)	0.33 (0.26)	1	8.65	8.7	1.6	0.21	0.76 (1.40)	1	253	253	0.3	0.59
Log(depth) (cm)	0.50 (1.22)	1	0.9	0.9	0.2	0.68	0.88 (3.65)	1	50	50	0.06	0.81
Age × log(depth)	−0.11 (0.11)	1	6.2	6.2	1.0	0.3						
Clay (%)	−0.044 (0.041)	1	5.1	5.1	1.0	0.3						
Residuals		40	212	5.3				42	36 297	864		
Switchgrass												
Intercept	−50.1 (27.5)					0.07	−5.18 (6.37)					0.42
Age (years)	10.9 (4.7)	1	6313	6313	5.3	0.02	1.82 (0.88)	1	5104	5104	4.3	0.04
Log(depth) (cm)	3.7 (3.2)	1	1603	1603	1.3	0.25	2.19 (1.57)	1	2296	2296	1.9	0.17
Age × log(depth)	−0.38 (0.65)	1	391	391	0.3	0.57						
Clay (%)	−0.30 (0.27)	1	1398	1398	1.2	0.28						
Biomass removal:		1	3866	3866	3.2	0.07						
None	0											

Continued

Appendix B (*Contd.*)

	Full model						Reduced model					
	Estimated coefficient (SE)	df	Type III SS	Mean sq.	*F*	*P*	Estimated coefficient (SE)	df	Type III SS	Mean sq.	*F*	*P*
Harvest	46.4 (25.8)					0.07						
Age × biomass removal		1	4585	4585	3.9	0.05						
None	0											
Harvest	−8.07 (4.1)					0.05						
Previous land use:		2	2658	1329	1.1	0.33						
Crop	0											
Fallow	1.3 (3.4)					0.70						
Grass	−2.3 (1.8)					0.21						
Residuals		248	29 4973	1189				258	30 6451	1188		
Mixed native												
Intercept	19.3 (33.9)	1				0.57	60.1 (8.6)					<0.0001
Age (years)	3.13 (3.4)	1		1623	0.85	0.36	1.06 (0.21)	1	56 648	56 648	24.5	<0.0001
Log(depth) (cm)	0.12 (3.46)	1		2.4	0.001	0.97	−14.2 (2.6)	1	67 488	67 488	29.2	<0.0001
Age × log(depth)	−0.70 (0.16)	1		34 274	17.9	<0.0001						
Clay (%)	−0.52 (0.19)	1		13 676	7.1	0.008						
Biomass removal		2	7633	3817	2.0	0.14						
None	0											
Burn or graze	−10.1 (5.2)					0.05						
Annual harvest	−14.0 (32.7)											
Age × biomass removal		2	928	464	0.24	0.79						
None	0											
Burn or graze	0.24 (0.35)					0.49						
Annual harvest	0.28 (3.37)					0.93						
Aesiduals		196	375 309	1915				202	466 661	2310		

Table B2 Full and reduced ANOVA models for change in $SOC_a (Mg\,ha^{-1})$

	Full model						Reduced model					
	Estimated coefficient (SE)	df	Type III SS	Mean sq.	F	P	Estimated coefficient (SE)	df	Type III SS	Mean sq.	F	P
Corn												
Intercept	24.0 (9.0)	1				0.03	23.6 (6.5)					0.004
Age (years)	−0.70 (0.63)	1	5.0	5.0	1.2	0.30	−0.06 (0.18)	1	3.2	3.2	0.8	0.40
Log(depth) (cm)	−7.24 (2.19)	1	44.9	44.9	10.9	0.009	−7.22 (1.88)	1	61.0	61.0	14.8	0.003
Age × log(depth)	–	–	–	–	–	–						
Clay (%)	0.05 (0.05)	1	5.0	5.0	1.2	0.30						
Residue removal (%)	−0.087 (0.032)	1	30.7	30.7	7.5	0.02	−0.065 (0.020)	1	44.3	44.3	10.7	0.007
Age × residue removal	0.0065 (0.0072)	1	3.4	3.4	0.8	0.39						
Residuals		9	37.1	4.1				11	45	4.1		
Sugarcane												
Intercept	0.46 (30.9)	1				0.99	−37.1 (7.8)					0.0001
Age (years)	0.21 (0.52)	1	18.8	18.8	0.2	0.70	0.51 (0.17)	1	3092	3092	9.2	0.006
Log(depth) (cm)	−14.2 (9.0)	1	292	292	2.5	0.14	0.16 (0.10)	1	848	848	2.5	0.13
Age × log(depth)	−24.7 (6.2)	1	20.7	20.7	0.18	0.68						
Clay (%)	0.04 (0.19)	1	4.9	4.9	0.04	0.84						
Biomass removal		1	1843	1843	15.7	0.002						
Standard	0											
Residue retention	−24.7 (6.2)					0.002						
Age × residue retention	0.45 (0.15)	1	1050.3	1050.3	9.0	0.01						
Residuals		13	1524	117				24	8071	336		
Miscanthus												
Intercept	81.9 (65.6)					0.23	17.0 (9.5)					0.09
Age (years)	−5.73 (6.5)	1		25.2	0.8	0.39	0.13 (0.48)	1	3.6	3.6	0.1	0.80
Log (depth) (cm)	−22.4 (20.6)	1		38.1	1.2	0.29	−4.5 (2.5)	1	166	166	3.1	0.09
Age × log (depth)	1.81 (2.07)	1		24.6	0.8	0.40						
Clay (%)	−0.42 (0.12)	1		399	12.4	0.003						
Residuals		14	451	32				17	898	53		
Switchgrass												
Intercept	−16.6					–	−1.3 (3.0)					0.67
Age (years)	5.23	1		35.9	0.4	0.55	0.39 (0.40)	1		63.2	0.97	0.32
Log (depth) (cm)	0.32	1		1.2	0.01	0.91	0.60 (0.41)	1		48.3	0.74	0.39
Age × log (depth)	−0.20	1		4.6	0.05	0.83						
Clay (%)	−0.11	1		70.4	0.71	0.40						
Biomass removal		1		13.2	0.13	0.72						
None	0											
Harvest	14.4											
Age × biomass removal		1		19.5	0.20	0.66						

Continued

Table B2 (*Contd.*)

	Full model						Reduced model					
	Estimated coefficient (SE)	df	Type III SS	Mean sq.	*F*	*P*	Estimated coefficient (SE)	df	Type III SS	Mean sq.	*F*	*P*
None	0											
Harvest	−3.17											
Previous land use		2	29.7	14.8	0.15	0.86						
Crop	0											
Fallow	1.12											
Grass	−0.37											
Residuals		52	5163	99				109	7083	65		
Mixed native												
Intercept	−8.0 (4.7)					0.09	2.78 (2.74)					0.31
Age (years)	0.41 (0.24)	1	215.1	215.1	2.97	0.08	0.12 (0.06)	1		356.9	4.4	0.04
Log (depth) (cm)	2.91 (1.20)	1	425.8	425.8	5.9	0.02	0.92 (0.76)	1		119.0	1.5	0.23
Age × log (depth)	−0.12 (0.07)	1	213.8	213.8	3.0	0.09						
Clay (%)	−0.24 (0.07)	1	983.0	983.0	13.6	0.0003						
Biomass removal		1	58.8	58.8	0.8	0.40						
None	0											
Burn or graze	−1.52 (1.69)											
Age × biomass removal		1	32.8	32.8	0.45	0.50						
None	0											
Burn or graze	−0.08 (0.11)											
Residuals		131	9489	72.4				135	11 006	81.5		

References

Al-Kaisi MM, Grote JB (2007) Cropping systems effects on improving soil carbon stocks of exposed subsoil. *Soil Science Society of America Journal*, **71**, 1381–1388.

Allison SD, Jastrow JD (2006) Activities of extracellular enzymes in physically isolated fractions of restored grassland soils. *Soil Biology and Biochemistry*, **38**, 3245–3256.

Allison VJ, Miller RM, Jastrow JD, Matamala R, Zak DR (2005) Changes in soil microbial community structure in a tallgrass prairie chronosequence. *Soil Science Society of America Journal*, **69**, 1412–1421.

Baer SG, Kitchen DJ, Blair JM, Rice CW (2002) Changes in ecosystem structure and function along a chronosequence of restored grasslands. *Ecological Applications*, **12**, 1688–1701

Blanco-Canqui H, Lal R (2007) Soil and crop response to harvesting corn residues for biofuel production. *Geoderma*, **141**, 355–362.

Brye KR, Kucharik CJ (2003) C and N sequestration in two prairie topochronosequences on contrasting soils in southern wisconsin. *American Midland Naturalist*, **149**, 90–103.

Camill P, McKone MJ, Sturges ST *et al*. (2004) Community and ecosystem level changes in a species rich tallgrass prairie restoration. *Ecological Applications*, **14**, 1680–1694.

Clifton-Brown JC, Breuer J, Jones MB (2007) Carbon mitigation by the energy crop, Miscanthus. *Global Change Biology*, **13**, 2296–2307.

Dorodnikov M, Fangmeier A, Kuzyakov Y (2007) Thermal stability of soil organic matter pools and their δ13C values after C3-C4 vegetation change. *Soil Biology and Biochemistry*, **39**, 1173–1180.

Foereid B, de Neergaard A, Hogh-Jensen H (2004) Turnover of organic matter in a Miscanthus field: effect of time in Miscanthus cultivation and inorganic nitrogen supply. *Soil Biology and Biochemistry*, **36**, 1075–1085.

Fornara DA, Tilman D (2008) Plant functional composition influences rates of soil carbon and nitrogen accumulation. *Journal of Ecology*, **96**, 314–322.

Frank AB, Berdahl JD, Hanson JD, Liebig MA, Johnson HA (2004) Biomass and carbon partitioning in switchgrass. *Crop Science*, **44**, 1391–1396.

Garten CT Jr, Wullschleger SD (1999) Soil carbon inventories under a bioenergy crop (switchgrass): measurement limitations. *Journal of Environmental Quality*, **28**, 1359–1365.

Garten CT Jr, Wullschleger SD (2000) Soil carbon dynamics beneath switchgrass as indicated by stable isotope analysis. *Journal of Environmental Quality* **29**, 645–653.

Gebhert DL, Johnson HB, Mayeux HS, Polley HW (1994) The CRP increases soil organic carbon. *Journal of Soil and Water Conservation*, **49**, 488–492.

Graham MH, Haynes RJ, Meyer JH (2002) Soil organic matter content and quality: effects of fertilizer applications, burning and trash retention on a long-term sugarcane experiment in South Africa. *Soil Biology and Biochemistry*, **34**, 93–102.

Hansen EM, Christensen BT, Jensen LS, Kristensen K (2004) Carbon sequestration in soil beneath long-term Miscanthus plantations as determined by 13C abundance. *Biomass and Bioenergy*, **26**, 97–105.

Hartemink AE (1998) Soil chemical and physical properties as indicators of sustainable land management under sugar cane in Papua New Guinea. *Geoderma*, **85**, 283–306.

Hsieh Y-P (1996) Soil organic carbon pools of two tropical soils inferred by carbon signatures. *Soil Science Society of America Journal*, **60**, 1117–1121.

Jastrow JD (1996) Soil aggregate formation and the accrual of particulate and mineral-associated organic matter. *Soil Biology and Biochemistry*, **28**, 665–676.

Kahle P, Belau L, Boelcke B (2002) Auswirkungen eines 10-jährigen Miscanthusanbaus auf ausgewählte Eigenschaften eines Mineralbodens in Nordost-deutschland. *Journal of Agronomy and Crop Science*, **188**, 43–50.

Kahle P, Beuch S, Boelcke B, Leinweber P, Schulten H-R (2001) Cropping of Miscanthus in Central Europe: biomass production and influence on nutrients and soil organic matter. *European Journal of Agronomy*, **15**, 171–184.

Kahle P, Boelcke B, Zacharias S (1999) Auswirkungen des Anbaus von *Miscanthus x giganteus* auf chemische und physikalische Bodeneigenschaften. *Journal of Plant Nutrition and Soil Science*, **162**, 27–32.

Karlen DL, Wollenhaupt NC, Erbach DC, Berry EC, Swan JB, Eash NS, Jordahl JL (1994) Crop residue effects on soil quality following 10 years of no-till corn. *Soil and Tillage Research*, **31**, 149–167.

Knops JMH, Tilman D (2000) Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology*, **81**, 88–98.

Kucharik CJ, Roth JA, Nabielski RT (2003) Statistical assessment of a paired-site approach for verification of carbon and nitrogen sequestration on Wisconsin Conservation Reserve Program land. *Journal of Soil and Water Conservation*, **58**, 58–67.

Lane DR, BassiriRad H (2005) Diminishing spatial heterogeneity in soil organic matter across a prairie restoration chronosequence. *Restoration Ecology*, **13**, 403–412.

Larson WE, Clapp CE, Pierre WH, Morachan YB (1972) Effects of increasing amounts of organic stovers on continuous corn: II. organic carbon, nitrogen, phosphorus, and sulfur. *Agronomy Journal*, **64**, 204–209.

Lee DK, Owens VN, Doolittle JJ (2007) Switchgrass and soil carbon sequestration response to ammonium nitrate, manure, and harvest frequency on Conservation Reserve Program land. *Agronomy Journal*, **99**, 462–468.

Ma Z, Wood CW, Bransby DI (2000a) Carbon dynamics subsequent to establishment of switchgrass. *Biomass and Bioenergy*, **18**, 93–104.

Ma Z, Wood CW, Bransby DI (2000b) Soil management impacts on soil carbon sequestration by switchgrass. *Biomass and Bioenergy*, **18**, 469–477.

McKinley VL, Peacock AD, White DC (2005) Microbial community PLFA and PHB responses to ecosystem restoration in tallgrass prairie soils. *Soil Biology and Biochemistry*, **37**, 1946–1958.

McLauchlan KK, Hobbie SE, Post WM (2006) Conversion from agriculture to grassland builds soil organic matter on decadal timescales. *Ecological Applications*, **16**, 143–153

Omonode RA, Vyn TJ (2006) Vertical distribution of soil organic carbon and nitrogen under warm-season native grasses relative to croplands in west-central Indiana, USA. *Agriculture, Ecosystems and Environment*, **117**, 159–170.

Osher LJ, Matson PA, Amundson R (2003) Effect of land use change on soil carbon in Hawaii. *Biogeochemistry*, **65**, 213–232.

Potter KN, Torbert HA, Johnson HB, Tischler CR (1999) Carbon storage after long-term grass establishment on degraded soils. *Soil Science*, **164**, 718–725.

Reeder JD, Schuman GE, Bowman RA (1998) Soil C and N changes on conservation reserve program lands in the Central Great Plains. *Soil and Tillage Research*, **47**, 339–349.

Rhoades CC, Eckert GE, Coleman DC (2000) Soil carbon differences among forest, agriculture, and secondary vegetation in lower montane Ecuador. *Ecological Applications*, **10**, 497–505.

Schneckenberger K, Kuzyakov Y (2007) Carbon sequestration under *Miscanthus* in sandy and loamy soils estimated by natural ^{13}C abundance. *Journal of Plant Nutrition and Soil Science*, **170**, 538–542.

Silva AJN, Ribeiro MR, Carvalho FG, Silva VN, Silva LESF (2007) Impact of sugarcane cultivation on soil carbon fractions, consistence limits and aggregate stability of a Yellow Latosol in Northeast Brazil. *Soil and Tillage Research*, **94**, 420–424.

Skjemstad JO, Dalal RC, Barron PF (1986) Spectroscopic investigations of cultivation effects on organic matter of vertisols. *Soil Science Society of America Journal* **50**, 354–359.

Skjemstad JO, Taylor JA, Janik LJ, Marvanek SP (1999) Soil organic carbon dynamics under long-term sugarcane monoculture. *Australian Journal of Soil Research* **37**, 151–164.

Thomason WE, Raun WR, Johnson GV, Taliaferro CM, Freeman KW, Wynn KJ, Mullen RW (2005) Switchgrass response to harvest frequency and time and rate of applied nitrogen. *Journal of Plant Nutrition*, **28**, 1199–1226.

Tolbert VR, Todd DE, Mann LK *et al*. (2002) Changes in soil quality and below-ground carbon storage with conversion of traditional agricultural crop lands to bioenergy crop production. *Environmental Pollution*, **116**, S97-S106.

Vitorello VA, Cerri CC, Victoria RL, Andreux F, Feller C (1989) Organic matter and natural carbon-13 distribution in forested and cultivated Oxisols. *Soil Science Society of America Journal*, **53**, 773–778.

Zan CS, Fyles JW, Girouard P, Samson RA (2001) Carbon sequestration in perennial bioenergy, annual corn and uncultivated systems in southern Quebec. *Agriculture, Ecosystems and Environment*, **86**, 135–144.

