GCB Bioenergy

WILEY

Global Change Biology Bioenergy
BIOPRODUCTS FOR A SUSTAINABLE BIOECONOMY

RESEARCH ARTICLE OPEN ACCESS

Genotypic Differences in Soil Carbon Stocks Under *Miscanthus*: Implications for Carbon Sequestration and Plant Breeding

Amanda J. Holder[1] | Rebecca Wilson[1] | Jeanette Whitaker[2] | Paul Robson[1]

[1]IBERS, Aberystwyth University, Plas Gogerddan, Aberystwyth, Ceredigion, UK | [2]UK Centre for Ecology & Hydrology, Lancaster Environment Centre, Lancaster, UK

Correspondence: Paul Robson (ppr@aber.ac.uk)

Received: 8 April 2025 | **Revised:** 12 August 2025 | **Accepted:** 13 August 2025

Funding: This work was supported by the Perennial Biomass Crops for Greenhouse Gas Removal project (BBSRC grant BB/V011553/1) and the strategic programme for Resilient Crops (BBSRC grant BB/X011062/1).

Keywords: biomass | *miscanthus* traits | plant breeding | roots | soil organic carbon | soil–plant interactions

ABSTRACT

Biomass crops provide renewable material for bioproducts and energy generation with the potential for negative greenhouse gas emissions through bioenergy with carbon capture and storage. *Miscanthus* spp. is a perennial crop with rapid biomass production and low inputs. However, uncertainty exists over impacts on soil organic carbon (SOC) stocks in conversion from agricultural grasslands, and the interaction between divergent *Miscanthus* species and SOC sequestration. As a C_4 plant (in contrast to C_3 temperate grassland species) the fate of *Miscanthus* derived carbon can be traced in the soil through its isotopic signature. Taking advantage of this, we use soil cores (pre and post conversion) to investigate species groupings and genotypic effect on SOC stocks in a rare long-term field trial located in the UK. Results show that 10 years after conversion from a managed grass pasture to *Miscanthus*, expected SOC losses due to cultivation were recovered (*Miscanthus* spp. mean of 82 Mg C ha^{-1} compared to pre-conversion stocks of 79 Mg C ha^{-1}, 0–30 cm soil depth) but significant variation in SOC between genotypes was observed (a difference of 32 Mg C ha^{-1} between the highest and lowest). Of the plant traits investigated, a large rhizome mass was correlated with C_4 carbon, and leaf litter was associated with increased SOC. As well as providing empirical data for the impact on SOC in a likely land use conversion, our findings show a genotypic influence on SOC sequestration processes, revealing the potential of *Miscanthus* selection to maximise climate mitigation benefits. With only 2 of the 13 genotypes identified as sequestering lower SOC compared to the others, there remains a wide genotypic base to select from. Yield is a primary breeding target (commercially and for increased CO_2 uptake); we demonstrate that high yield need not be at the expense of low soil carbon.

1 | Introduction

The impact of crop choice and land management decisions on soil carbon (C) is a prominent consideration in the formation of agricultural and land use policy, especially with increases in soil organic carbon (SOC) stocks seen as part of achieving greenhouse gas (GHG) reductions and NetZero ambitions (IPCC 2019; EC (European Commission) 2021; DESNZ (Department for Energy Security and Net Zero) 2023a). The challenge of achieving NetZero will require a portfolio of technologies, including emissions removal, because some sectors of economic activity are particularly difficult to decarbonise. Biomass crops are currently unique in allowing widespread removal of contemporaneous C plus long-term storage if embedded in products not designed for combustion or geologically stored through C capture and storage (CCS). Therefore, biomass crops are integral to

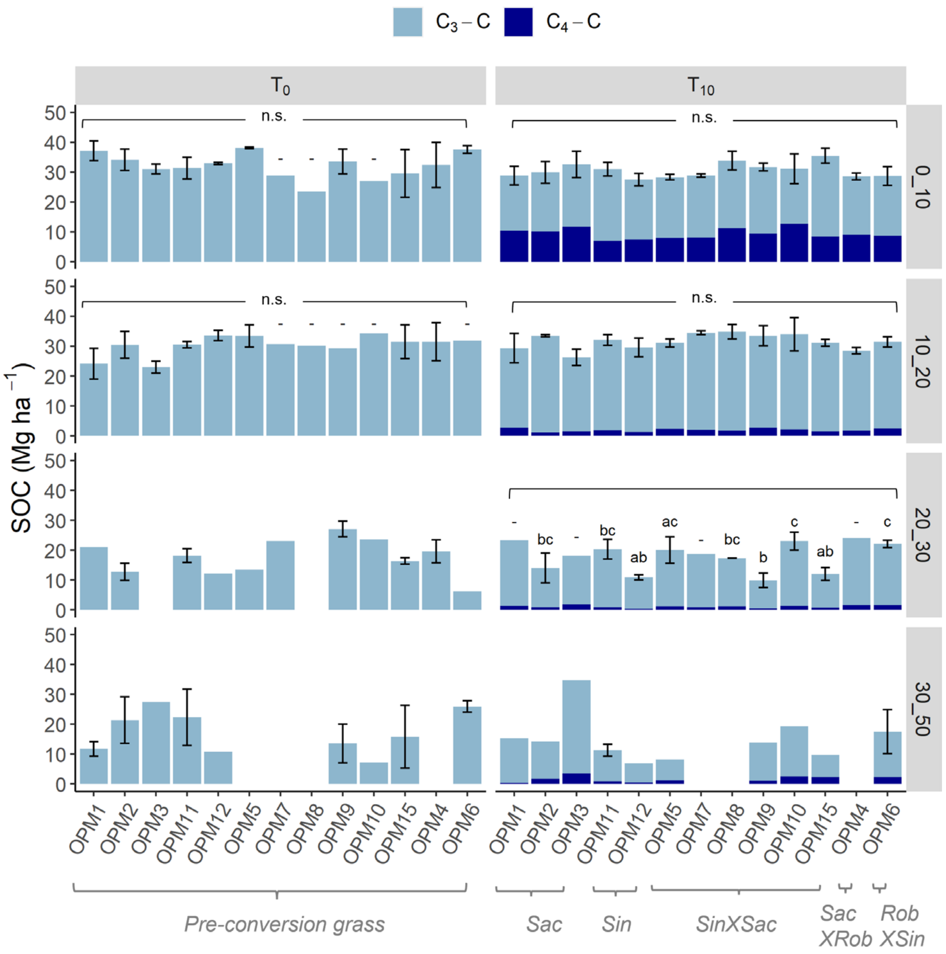

FIGURE 1 | Effects of *Miscanthus* genotype and grouping on SOC stocks (Mg ha^{-1}, fixed depth) within four soil depth increments. The first column shows pre-conversion (T_0) stocks (the genotype ID at T_0 corresponds to the genotype subsequently planted) and the second column the stocks 10 years post-conversion (T_{10}) with the *Miscanthus* groupings shown below. Shadings represent C_3 or C_4 derived C. Error bars represent the SEM. Statistical difference was explored within T_0 (depths 0–10 cm and 10–20 cm) and within T_{10} (depths 0–10 cm, 10–20 cm, 20–30 cm) where different letters denote significance, following Tukey post hoc tests (genotypes with only one rep in the depth increment were excluded and are marked with a dash).

the required mix of renewable energy forms, with increases in supply needed to meet expected future demand (EC (European Commission) 2019; DESNZ (Department for Energy Security and Net Zero) 2023b). Biomass crops have the potential to deliver negative emissions and ensuring that their cultivation does not contribute significantly to climate change through in-field GHG emissions or SOC loss is essential to maximise their climate mitigation benefits. A united approach is therefore required to identify plant traits promoting SOC sequestration processes that can be targeted in breeding programmes, thereby releasing the potential to enhance yield and increase soil C stocks to deliver greater C savings (Jansson et al. 2021; Poffenbarger et al. 2023).

Miscanthus is a perennial biomass crop with a lifecycle of up to 20 years and efficient C_4 photosynthesis promoting rapid biomass growth (Winkler et al. 2020). *Miscanthus* has been identified as suitable for bioenergy production and as a biomass crop for a number of other diverse end uses from building material to animal bedding (Lewandowski et al. 2018). The planting of *Miscanthus* is likely to increase due to its suitability for different climatic regions (Kalinina et al. 2017) along with low requirements for agricultural inputs (e.g., fertiliser) over its lifetime. This is combined with the ability to be grown on lower grade agricultural land (Quinn et al. 2015) and predicted global SOC benefits (Shepherd et al. 2020). Many areas of *Miscanthus* production are estimated to achieve C intensities of production that are low and even negative without CCS due to C sequestration into soil in combination with high yields increasing uptake of atmospheric carbon dioxide (CO_2) and other characteristics of the crop (Robson et al. 2019; Figure 1). Soil disturbance (e.g., ploughing) can lead to the loss of soil C stocks (Balesdent et al. 2000) but as a perennial crop *Miscanthus* has the potential to increase SOC because repeated soil disturbances from annual cultivation are not required, and minimal soil intervention is expected during the crop lifetime (Keiser et al. 2025). In land use change from permanent grasslands where there are generally higher initial C stocks than other land cover types, SOC loss may occur due to the *Miscanthus* cultivation event, but there is also the potential for these losses to be recovered over the crop lifetime. Currently, less is known about the fate of C stocks due to soil disturbance in future reversions after the crop lifetime, but losses and gains of SOC have been reported in comparisons to arable sites (Abraha et al. 2019; Dufossé et al. 2014; Rowe et al. 2020; Martani et al. 2023).

Currently, the majority of *Miscanthus* planted is the sterile clone *Miscanthus* × *giganteus* (Greef and Deuter 1993), a natural hybrid of *Miscanthus sacchariflorus* and *Miscanthus sinensis* (Lewandowski et al. 2000), but breeding programmes are producing and trialling novel genotypes crossing a range of *Miscanthus* species (*M. sinensis, M. floridulus and M. sacchariflorus*) and subspecies (e.g., *M. robustus* and *lutarioriparius*, subspecies of *M. sacchariflorus*) to improve climate resilience and productivity (Clifton-Brown et al. 2019).

Research to date suggests that land conversion to *Miscanthus* can be broadly beneficial to SOC stocks depending on the type of land converted. Empirical evidence shows that in land use change from arable to *M.* × *giganteus* after 5–10 years there is generally a positive impact increasing SOC in the region of 7%–23% compared to pre-conversion or paired site stocks (Qin et al. 2016; Rowe et al. 2016). Whereas grassland to *M.* × *giganteus* conversions are either neutral or negative with reductions of −16 to increases of +10% reported compared to pre-conversion or paired site stocks (Qin et al. 2016; Rowe et al. 2016). Recent longer-term studies have found no significant differences in SOC stocks after ~20 years since conversion for *Miscanthus* plantations compared to nearby agricultural grasslands (Zang et al. 2018; Leifeld et al. 2021), with another reporting higher SOC in the upper soil profile (0–40 cm) (Hu et al. 2018). However, variations with land management, soil type, climate and depth of sampling can all affect results. Therefore, there is a need for more long-term field studies covering the lifetime of the crop to provide data to improve model predictions of where and how the greatest C benefits can be achieved (Whitaker et al. 2018; Shepherd et al. 2021).

The main plant-C input pathways to SOC from *Miscanthus* are through leaf fall, root and rhizome turnover and root exudation (Carvalho et al. 2017). As plant-C enters the soil and is decomposed, a significant proportion of the C is released to the atmosphere as respiration, but some is assimilated by microbes and stabilised through organo-mineral associations and aggregation (Dynarski et al. 2020). *Miscanthus* is a C_4 plant that allows the fate of *Miscanthus-derived* C to be traced through the plant–soil–atmosphere using its isotopic signature (Balesdent et al. 1987). New plant C inputs can either displace existing C_3–C, leading to no change (Robertson et al. 2017), or via priming effects, which increase the mineralisation of existing C_3-C (Kuzyakov et al. 2000) lead to reduced SOC stocks.

Senesced leaves and harvest residues provide substrate for decomposers and a soil covering that influences biological activity and the subsequent incorporation of C into the soil (Lemus and Lal 2005; Agostini et al. 2015). In European climates, leaf fall normally occurs between late October and February, which is before a typical late winter/early spring harvest, meaning that the majority of senesced leaves remain in the field (Nunn et al. 2017). Within this period, the timing of leaf fall can vary depending on environmental conditions and genotypic differences (Nunn et al. 2017). For *Miscanthus*, it has been suggested that the largest contribution to SOC comes from below-ground biomass as opposed to above-ground residues (Rasse et al. 2005; Carvalho et al. 2017). *Miscanthus* has a substantial root and rhizome system providing the potential for roots and rhizomes to contribute extensively to SOC stocks.

In an established plantation, below ground biomass is an important part of the C stock within the soil profile, albeit with a shorter residence time (decades) compared to other SOC pools (10 to 100+ years) (Christensen et al. 2016; Martani et al. 2021). *M.* × *giganteus* planted onto marginal land types (i.e., not highly productive agricultural land) has been shown to increase soil microbial diversity, biomass and C use efficiency, resulting in the enhancement of soil C cycling and increases in SOC (Kane et al. 2023) but it is uncertain as to whether these benefits remain true for all *Miscanthus* species. *Miscanthus* species groupings and genotypes differ in above and below ground morphology, physiology and biomass accumulation, and breeding programmes are currently exploiting this diversity by aiming to produce improvements in yield and resilience to environmental challenges (Clifton-Brown et al. 2019; Awty-Carroll et al. 2023). However, this same genotypic diversity also has the potential to be harnessed to deliver increased SOC (Poirier et al. 2018). In other grass species and grassland communities, genotypic variations in C inputs to the soil have been shown to arise from differences in: below ground root architectural traits such as rooting mass, depth and spread (Bardgett et al. 2014); varying quantities of leaf litter (Xu et al. 2013); and differences in plant growth interacting with other traits such as root exudation (Semchenko et al. 2021).

The majority of *Miscanthus* below-ground biomass is found in the upper soil layer (0–20 cm) with root mass reducing with increasing soil depth (Martani et al. 2021) but *Miscanthus* roots have been found to depths of ~2 m (Neukirchen et al. 1999). *M. sinensis* types are mostly tussock-forming and have numerous thin stems and rhizomes that form dense clumps. In contrast, *M. sacchariflorus* is often taller (> 2 m) with fewer, thicker stems and laterally spreading rhizomes (Robson et al. 2013; Chae et al. 2014). *M. sinensis* types tend to have a greater root length density throughout the soil profile than *M.* × *giganteus* (Gregory et al. 2018). *M. sinensis* has also been found, during a pulse-labelled $^{13}CO_2$ study, to allocate more photoassimilates to below-ground biomass than *M.* × *giganteus* and *M. lutarioriparius*, thereby providing increased potential for C to be transferred to the soil (Briones et al. 2023). The presence of deep roots can promote C sequestration to stable SOC pools in lower soil horizons (Rehbein et al. 2015) and being below typical plough depths, SOC sequestered deeper in the soil is likely to be less affected by future agricultural land use changes (Martani et al. 2022).

Some *Miscanthus* species differences in SOC have previously been observed. Higher SOC stocks have been reported under *M. sinensis* compared to *M.* × *giganteus* (Gregory et al. 2018) possibly due to a greater allocation of C to below ground biomass (Briones et al. 2023) and differences in root length density. Although no difference between their SOC stocks has also been found (Ouattara et al. 2021). Using the natural abundance of C_3 and C_4 soil C isotopes in soil, Richter et al. (2015) found *M. sacchariflorus* provided the lowest C_4-C contribution to SOC with the greatest retention of existing C_3-C in the upper soil layer compared to *M. sinensis* and *M.* × *giganteus* after 14 years. In contrast, they found *M.* × *giganteus* was associated with the largest accumulation of C_4-C but the highest loss of C_3-C, leading to overall SOC remaining similar for the different species. The *M. sacchariflorus* rhizome tends to spread more than *M.* × *giganteus*, which, along with morphological differences in above ground biomass (Robson et al. 2013), may be factors in the soil C differences observed. In a comparison of five *Miscanthus* hybrids, it was reported that SOC stocks under one hybrid were significantly less, suggesting that genotypic differences could be important as well as broader species differences (Holder et al. 2019).

Above ground harvest yield is currently a key breeding target (Clifton-Brown et al. 2019; Chupakhin et al. 2021) both commercially and to improve uptake of atmospheric CO_2. To maximise the overall negative emissions potential, it is important to capitalise on the C benefits of both yield and SOC sequestration. But the extent to which genotypic differences are important is not known, or which traits are the most significant contributors to SOC. Identifying species or genotypic traits that can be linked to SOC sequestration would inform breeding strategies and help to evaluate breeding targets so that at the very least beneficial traits are not lost in the process. Care is also needed to ensure that the typically higher SOC stocks of improved and semi-improved grasslands (compared to arable land) that are likely to be targeted for bioenergy production are not depleted by the land use change to *Miscanthus*.

In this study we utilise a rare long-term field trial planted with diverse *Miscanthus* genotypes to investigate SOC stock change following land use conversion from an agricultural grassland. Soil samples taken pre-conversion and again after 10 years of *Miscanthus* growth enable the interaction between 13 promising *Miscanthus* genotypes (covering five species groupings) and SOC sequestration to be evaluated. Using the soil $\delta\ ^{13}C$ isotopic signature differences in the contribution to below ground C in terms of soil C_4-C as well as below ground biomass (rhizome and root) of the *Miscanthus* genotypes and species groupings are investigated. Combined with this, the potential relationships of plant traits likely to interact with SOC and that can be exploited in breeding programmes (rhizome and root mass, harvest yield and ripening loss) are explored. Using the empirical data collected we examine the following research questions:

- Do *Miscanthus* genotypes or species groupings differentially affect SOC stocks following 10 years of cultivation on grassland?
- Are genotypic differences in the proportion or amount of *Miscanthus*-derived C with soil depth determined by root or rhizome traits?
- Is there a trade-off between yield and SOC sequestration across a range of *Miscanthus* genotypes?

2 | Materials and Methods

2.1 | Site Description

The *Miscanthus* genotype trial was established in 2012 as part of a wider European plant trial (Kalinina et al. 2017) and was located near Aberystwyth, UK. The site is representative of marginal agricultural land due to shallow soils with a high soil stone content and a predominantly wet and cool climate (Lewandowski et al. 2018). Soil and climate characteristics are shown in Tables 1, 2. Air temperature and precipitation at the start and during the trial period were within the 30-year average for the location (Met Office, n.d.).

TABLE 1 | Location details of the experimental site and soil characteristics from soil samples taken pre-conversion to *Miscanthus*.

Location and soil characteristics	Value
Latitude (decimal degrees)	52.43
Longitude (decimal degrees)	−4.01
Altitude (m)	39
Agricultural land classification (ALC)[a]	3b
Soil texture	Sandy loam
Clay (%)	10
Silt (%)	30
Sand (%)	60
Stone fraction	0.35
England and Wales soil series classification[b]	Denbigh
WRB classification[c]	Eutric Endoleptic Cambisols
pH in water	5.3
Total K ($kg\,ha^{-1}$)	126
Total P ($kg\,ha^{-1}$)	46
Total N mineralised ($kg\,ha^{-1}$)	31
C:N ratio	9.1
Bulk density ($kg\,m^{-3}$), 0–10-cm soil depth	0.61
Bulk density ($kg\,m^{-3}$), 10–20-cm soil depth	0.98
Bulk density ($kg\,m^{-3}$), 20–30-cm soil depth	1.17
Bulk density ($kg\,m^{-3}$), 30–50-cm soil depth	1.41

[a] Welsh Government (2023).
[b] Cranfield University (2025).
[c] IUSS Working Group WRB (2022).

The experiment comprised a randomised block trial with three replicates of 15 *Miscanthus* genotypes established into an area of extensively grazed semi-improved long-term pasture with a perennial ryegrass (*Lolium perenne*) sward not reseeded for at least 5 years prior to planting (historic farm data suggests this was permanent pasture). Each plot (5 × 5 m) contained a single *Miscanthus* genotype (49 plants at a density of 1.96 plants m^{-2}) (Figures S1.1 and S1.2). Plots were separated by 3 m wide grass (*Lolium perenne*) paths on all sides. Prior to planting, the existing uniform grass sward was sprayed off with glyphosate at a rate of $4\,L\,ha^{-1}$ and the plots were ploughed to an approximate 25 cm depth. During the establishment year, fertiliser was applied once at rates of 44 and $110\,kg\,ha^{-1}\,year^{-1}$ of P (phosphorus) and K (potassium), respectively. In year two, fertiliser was added in spring at a rate of $140\,kg\,ha^{-1}$ K, $100\,kg\,ha^{-1}$ P and $60\,kg\,ha^{-1}$ N (nitrogen). No further fertiliser was added. The 13 genotypes sampled for this experiment provide a range of *M. sacchariflorus* , *M. sinensis*, and hybrid types with differing senescence timing (Table 3). *M. sacchariflorus* (genotype ID OPM1 to OPM4) has a more spreading rhizome compared to the other species (Nunn et al. 2017).

TABLE 2 | Climate conditions for site covering the period 2012–2022. The mean of total monthly precipitation and 24h maximum and minimum air temperatures along with the standard error of the mean. Climate data covering the experimental period were taken from a meteorological station within 1km of the experimental site.

Month	Air temperature (Max)°C	Air temperature (Min)°C	Precipitation mm
Jan	8.6 ± 0.3	3.1 ± 0.3	120.8 ± 13.9
Feb	9.0 ± 0.5	2.9 ± 0.5	94.6 ± 12.6
Mar	10.7 ± 0.5	3.3 ± 0.5	74.0 ± 11.8
Apr	13.1 ± 0.5	4.5 ± 0.4	52.0 ± 9.6
May	15.8 ± 0.5	7.5 ± 0.3	70.5 ± 13.3
Jun	18.6 ± 0.4	10.5 ± 0.3	90.0 ± 18.3
Jul	20.3 ± 0.6	12.5 ± 0.1	79.8 ± 12.5
Aug	19.6 ± 0.4	12.6 ± 0.2	93.7 ± 8.3
Sep	17.9 ± 0.4	10.2 ± 0.4	120.4 ± 15.7
Oct	14.9 ± 0.3	8.4 ± 0.5	122.5 ± 13.6
Nov	11.5 ± 0.4	4.8 ± 0.5	126.1 ± 13.7
Dec	10.0 ± 0.4	4.2 ± 0.6	15.4 ± 14.7

2.2 | Soil Cores

Intact and uncompressed soil cores were taken using an 8.5cm diameter, 1m long, cylinder auger (Eijkelkamp, Giesbeek, The Netherlands) pushed in and extracted with a telehandler (John Deere and New Holland TH6.32). At time zero (T_0, May 2012) after the grass sward was sprayed but before ploughing, one core was taken per plot. In May 2022 (T_{10}) three soil cores (one at plant centre, C, taken at the original planting position; one at the plant edge, E; and one in the inter-row, I) were taken in each plot to account for the differences in below-ground biomass and soil C due to the spacing and spread of the *Miscanthus* plants, according to the method in Zatta et al. (2014) (Figure S2.1).

On both sampling occasions, soil cores were taken to a maximum depth of 60cm, with the first 30cm split into 10cm depth increments. In addition, at T_{10} core depth increments (to 30cm) were split longitudinally, with one half dried and used for bulk density, pH, root mass and soil C analysis, and the remaining fresh soil used for soil hand texture (AHDB 2017). The 30–60cm segments were not split. Due to the shallowness of soils, not all soil cores achieved the maximum desired depth.

All soil samples except those used for soil texture were oven dried (40°C) and sieved (2mm) prior to analysis. Root and rhizome were hand sorted from the stone fraction remaining on the sieve (≥2mm). The mean density of a subset of stone and rhizome segments was taken using water displacement to provide a dry bulk density (Table S2.1) adjusted for stone and rhizome volume (Poeplau et al. 2017). Mean pH was measured using dried soil in pure water (Jenway 3010 pH meter).

2.3 | CN and Isotope Analysis

Below ground biomass was pre-milled (Pulverisette 15, Fritsch) and both sieved soil and below ground biomass were then ball

TABLE 3 | *Miscanthus* genotypes, species grouping, and senescence characteristics. Senescence timing is based on senescence scores observed at the Aberystwyth site in year 3 (Nunn et al. 2017): Early, 80%–100% brown at first frost; Mid, 60%–80% brown at first frost; and Late, ≤60% brown at first frost.

Genotype ID	Species	Grouping	Senescence
OPM1	*M. sacchariflorus*	*Sac*	Late
OPM2	*M. sacchariflorus*	*Sac*	Late
OPM3	*M. sacchariflorus*	*Sac*	Late
OPM4	*M. sacchariflorus × M. sacchariflorus (Robustus)* [a]	*Sac×Rob Hyb*	Late
OPM5	*M. sinensis × M. sacchariflorus*	*Sin×Sac Hyb*	Mid
OPM6	*M. sacchariflorus (Robustus)* [a] *× M. sinensis*	*Rob×Sin Hyb*	Early
OPM7	*M. sinensis × M. sacchariflorus*	*Sin×Sac Hyb*	Early
OPM8	*M. sinensis × M. sacchariflorus*	*Sin×Sac Hyb*	Early
OPM9	*M. sinensis × M. sacchariflorus (M. × giganteus)*	*Sin×Sac Hyb*	Mid
OPM10	*M. sinensis × M. sacchariflorus*	*Sin×Sac Hyb*	Early
OPM11	*M. sinensis (Goliath)*	*Sin*	Late
OPM12	*M. sinensis*	*Sin*	Late
OPM15	*M. sinensis × M. sacchariflorus × open M. sinensis* [b]	*Sin×Sac Hyb*	Mid

[a] Robustus is a *M. sacchariflorus* subtype.
[b] Open-pollinated hybrid with dominating *M. sinensis* phenotype.

milled (Labman automated preparation system) in preparation for C and N, and C isotope analysis (ANCA-SL elemental analyser linked to a PDZ Europa 20/20 Isotope Ratio Mass Spectrometry). Total C values are reported as representative of the SOC due to the acid soils with low presence of inorganic C in the area (Rudeforth 1970; Rawlins et al. 2011; Kristl et al. 2016).

SOC stocks were calculated to a fixed depth of 30 or 50 cm depending on core sample length and using individual sample bulk density. Soil C stocks and below ground biomass at T_{10} were scaled up to Mg ha^{-1} using the percentages relating to the representative area covered by each core location (plant centre 10%; plant edge 31%; and inter-row 59%) providing one value per plot. SOC stocks calculated as Equivalent Soil Mass values (ESM) are contained in Table S2.2.

The *Miscanthus* derived soil C (C_4-C) percentage was calculated using Equation (1):

$$\textit{Miscanthus}\ C\,\% = \left(\delta_n - \delta_0\right) / \left(\delta_r - \delta_0\right) \tag{1}$$

where δ_0 is the soil C isotope abundance at T_0, δ_n is the abundance at T_{10} and δ_r is the isotope abundance of the below ground biomass at T_{10} (Balesdent et al. 1987). C_4-C stocks (Mg ha^{-1}) were calculated as a percentage of SOC stocks (Mg ha^{-1}) using the percentage C_4-C calculated in equation (1).

2.4 | Yield and Ripening Loss

Plots were harvested after senescence from year one to seven. Leaf litter and stubble remained on the field and harvested biomass stalks were removed from the site. Due to disruptions to field work arising from the COVID-19 pandemic, the plots were not cut back from years 8–10 (2020–2022). In the spring of year 11, the dry matter harvest yield was taken following the same protocol as used in year four (Nunn et al. 2017). The percentage ripening loss (primarily leaf litter drop) for each genotype was calculated from the difference between the year three estimated autumn and spring yields, taken from serial harvest cuts as detailed in Nunn et al. (2017). This percentage was used with the year 11 spring harvest yield to provide a value for ripening loss in Mg ha^{-1}.

2.5 | Statistical Analysis

Data analysis was completed using R (version 4.2.3, R Core Team 2023) and model residuals and plots were checked for the appropriateness of each model. All linear mixed models (package 'nlme', Pinheiro et al. 2023) were used with the random effect of replicate and maximum likelihood (ML) estimation. Post hoc tests for significant factors were carried out using Tukey HSD (package 'multcomp', Hothorn et al. 2008).

2.6 | Analysis of SOC Change Pre and 10 Years After Land Use Conversion

For the analysis of SOC change after 10 years of the *Miscanthus* crop, linear models were used. A complete set of soil samples from all plots and depths was not available from T_0. Therefore, where sufficient samples existed to make relevant statistical comparisons (0–10 cm and 10–20 cm depths) plots at T_0 corresponding to the *Miscanthus* genotype subsequently planted were compared to explore the variability of SOC (Mg ha^{-1}) stocks prior to conversion to *Miscanthus*. To examine the variance at T_{10} the fixed effect of genotype was used with separate models for each depth increment (genotypes with only one replicate for the depth increment were removed). Mean change in SOC stocks (Mg ha^{-1}) in the 0–30 cm and 0–50 cm depths was investigated using separate models including the fixed factors of land use type (T_0 grassland and T_{10} *Miscanthus*), genotypes and grouping (*Sac*, *Sin*, *Sin*×*Sac*, *Sac*×*Rob* and *Rob*×*Sin*).

2.7 | Analysis of *Miscanthus* Derived Below Ground C Stock

To determine the effects of genotype and grouping on *Miscanthus* derived SOC (percentage C_4-C) a general linear mixed model (package 'glmmTMB', Brooks et al. 2017) was used with genotype and grouping as fixed factors (separate models), the random factor of replicate and a beta distribution. Effects of genotype and grouping on root and rhizome mass (Mg ha^{-1}) were explored using separate linear mixed models for each depth increment (genotypes with only one replicate were removed). Tests were performed on log transformed data where normality of the residuals was not initially achieved. Similarly, to investigate the effects of genotype and grouping on total *Miscanthus* derived C stock (Mg C ha^{-1}), i.e., the total of below ground biomass C (root and rhizome) and soil C_4-C, separate linear mixed models for each depth increment were used. Genotypes with only one replicate within the depth increment were removed.

2.8 | Analysis of *Miscanthus* Traits and Soil C Relationships

To explore the potential relationships of *Miscanthus* traits with SOC and C_4-C, Akaike's information criterion (AIC) was used for the selection of the best fit linear models with fixed factors of: sample depth increment (0–10, 10–20 and 20–30 cm); year 11 harvest yield (dry matter, Mg ha^{-1}); ripening loss (Mg ha^{-1}); and rhizome and root mass (dry matter, Mg ha^{-1}) (R packages 'nlme' (Pinheiro et al. 2023) and 'MuMIn' (Barton 2023)). Linear mixed models were used to explore genotypic and grouping differences in yield, and general linear mixed models with a beta distribution were used for percentage ripening loss.

3 | Results

3.1 | SOC Stock Variation and Change

The average SOC stock of the experimental area prior to conversion to *Miscanthus* (T_0) was 97.8 Mg ha^{-1} ± 6 (0–50 cm) (Table 4) with no significant differences found between samples at this time point (Figure 1). After 10 years of cultivation (T_{10}) mean SOC stock including all *Miscanthus* spp. was 97.7 Mg ha^{-1} ± 3.7 (0–50 cm, Table 4). SOC stocks under the *Miscanthus* genotypes ranged from 80.2 to 120.6 Mg ha^{-1}

TABLE 4 | Total soil organic carbon (SOC, Mg ha^{-1}) pre-conversion and 10 years post-conversion to a range of *Miscanthus* genotypes. SOC is calculated to a fixed depth of 30 cm and 50 cm. The ± values indicate the standard error of the mean (SEM).

Grouping	SOC (0–30)	SOC (0–50)
T_0	79.4 ± 3.9	97.8 ± 6.0
T_{10} *All genotypes*	81.7 ± 1.9	97.7 ± 3.7
T_{10} *Sin×Sac Hyb*	83.3 ± 2.4	96.2 ± 6.7
OPM5	79.4 ± 6.0	81.5
OPM7	82.4	nd
OPM8	86.0 ± 4.4	nd
OPM9	78.9 ± 5.6	98.4
OPM10	97.3 ± 3.3	113.3
OPM15	78.6 ± 2.1	91.7
T_{10} *Sac*	82.6 ± 6.2	109.1 ± 7.9
OPM1	97.2	112.6
OPM2	73.6 ± 6.2	94.1
OPM3	86.0	120.6
T_{10} *Rob×Sin Hyb*	82.3 ± 5.5	94.4 ± 5.6
OPM6	82.3 ± 5.5	94.4 ± 5.6
T_{10} *Sac×Rob Hyb*	81.3	nd
OPM4	81.3	
T_{10} *Sin (2)*	74.8 ± 6.8	90.7 ± 6.4
OPM11	84.6 ± 4.5	95.9 ± 6.5
OPM12	65.1 ± 8.1	80.2

Note: nd, Maximum sample depth was 30 cm.

(0–50 cm) and from 65.1 Mg ha^{-1} ± 8.1 to 97.3 Mg ha^{-1} ± 3.3 (0–30 cm). For the 0–30 cm soil depth, three genotypes had significantly smaller SOC stocks (Mg ha^{-1}: 65.1 ± 8.1 OPM12; 73.6 ± 6.2 OPM2; 78.6 ± 2.1 OPM15) compared to OPM10 which had the highest SOC stock (97.3 Mg ha^{-1} ± 3.3 OPM10). OPM12 was also significantly lower than the eight genotypes with SOC stocks above 80 Mg ha^{-1} ($p < 0.001$) (Table 4). SOC stock was higher in the 0–20 cm depth increment compared to the lower depths, but the greatest variation in SOC stocks was observed in the 20–30-cm depth increment. Lower SOC stocks in the 20–30 cm depth for OPM9, OPM12 and OPM15 compared to most of the other genotypes ($p < 0.001$) were reflected in their low values for the 0–30 cm depth (Figure 1). Samples from 30 to 50 cm were not accessible for sufficient replicates to make meaningful statistical comparisons at this depth increment. However, the greatest value (34.7 Mg ha^{-1}) was recorded for OPM3 (30–50 cm) (Figure 1) which contributed to its high overall value (120.6 Mg ha^{-1}) for the 0–50 cm soil depth. Comparing SOC stocks between *Miscanthus* species groupings (*Sac*, *Sin*, *Sin×Sac*, *Sac×Rob* and *Rob×Sin*) no significant differences were found (for the full 0–50-cm depth, and when split by depth increments).

Comparing the SOC stocks for the 0–30-cm and 0–50-cm depth increments between T_0 and T_{10} revealed no significant differences between T_0 and the *Miscanthus* genotypes, their grouping, or *Miscanthus* overall (mean of all genotypes). When the data was split by depth increment, at 0–10 cm OPM5 was significantly less than the corresponding T_0 plots ($p < 0.01$) (28.3 ± 0.9 vs. 38.1 ± 0.3 Mg ha^{-1}, respectively) (Figure 1) and at 20–30 cm OPM9 was significantly reduced at T_{10} compared to T_0 ($p < 0.05$) (9.9 ± 2.4 vs. 27.1 ± 2.6 Mg ha^{-1}, respectively) (Figure 1).

3.2 | *Miscanthus* Derived Below Ground C Stock

The largest proportion of *Miscanthus* derived C_4-C was found at the 0–10 cm depth increment where OPM10 had a significantly higher percentage of C_4-C than OPM11, OPM12 and OPM15 ($p < 0.01$) (Figure 2). *Miscanthus*-derived soil C was also present at 30–50 cm although this lowest depth was not sampled across sufficient replicates to allow for statistical analysis by genotype. There was no significant difference in the proportion of *Miscanthus* derived C_4-C in the soil C pool between species groupings at any depth.

Miscanthus rhizome mass ranged from 3.8 to 26.2 Mg ha^{-1} for the 0–30 cm depth increment, with the majority located at 0–10 cm where large variations between replicates were observed (Figure 3). There was no significant difference between species grouping or genotype for rhizome mass in the 0–10-cm depth. However, at 10–20 cm OPM4 (*Sac×Rob*) (8.9 Mg ha^{-1} ± 2.7) was higher than most other genotypes (excluding OPM2, OPM3 and OPM9) and groupings ($p < 0.001$). Most genotypes followed a similar trend of reduced rhizome mass moving from the plant centre to the inter-row. The greatest concentration of rhizome for the *Sin* grouping was found at the plant centre with none in the inter-row position. In contrast, two of the *Sac* grouping (OPM1, OPM3) and one of the *Sin×Sac* grouping (OPM8) had less rhizome mass at the plant centre compared to the plant edge and inter-row positions (Figure S3.1).

Coarse root mass was more evenly spread across the centre, edge and inter-row sampling positions (Figure S3.2) and ranged from 2.5 to 12.6 Mg ha^{-1} (0–30 cm). Only small amounts of root mass were found in the 30–50 cm depth (Figure 4). At 10–20 cm, root mass from OPM1 (5.7 Mg ha^{-1} ± 1.8) was significantly higher than OPM6 (1.3 Mg ha^{-1} ± 0.3) ($p < 0.05$); but no other significant differences existed between genotypes or species groupings.

When considering the total below ground C stock attributable to *Miscanthus* (i.e., the C in *Miscanthus* below ground biomass and soil C_4-C combined) no genotypic statistical differences were observed. In the 10–20-cm depth increment, the *Sac×Rob* grouping had significantly higher total *Miscanthus* derived C stock (7.5 Mg ha^{-1} ± 1.5 Mg ha^{-1}) than the lowest grouping (*Sin*, 2.7 Mg ha^{-1} ± 0.6) (Figure 5). No other significant differences were found in the *Miscanthus* derived C stocks. At the 0–10-cm depth increment, total *Miscanthus* derived C was similar to C_3-C stocks for three of the genotypes (OPM1, OPM3 and OPM8) (Figure 5).

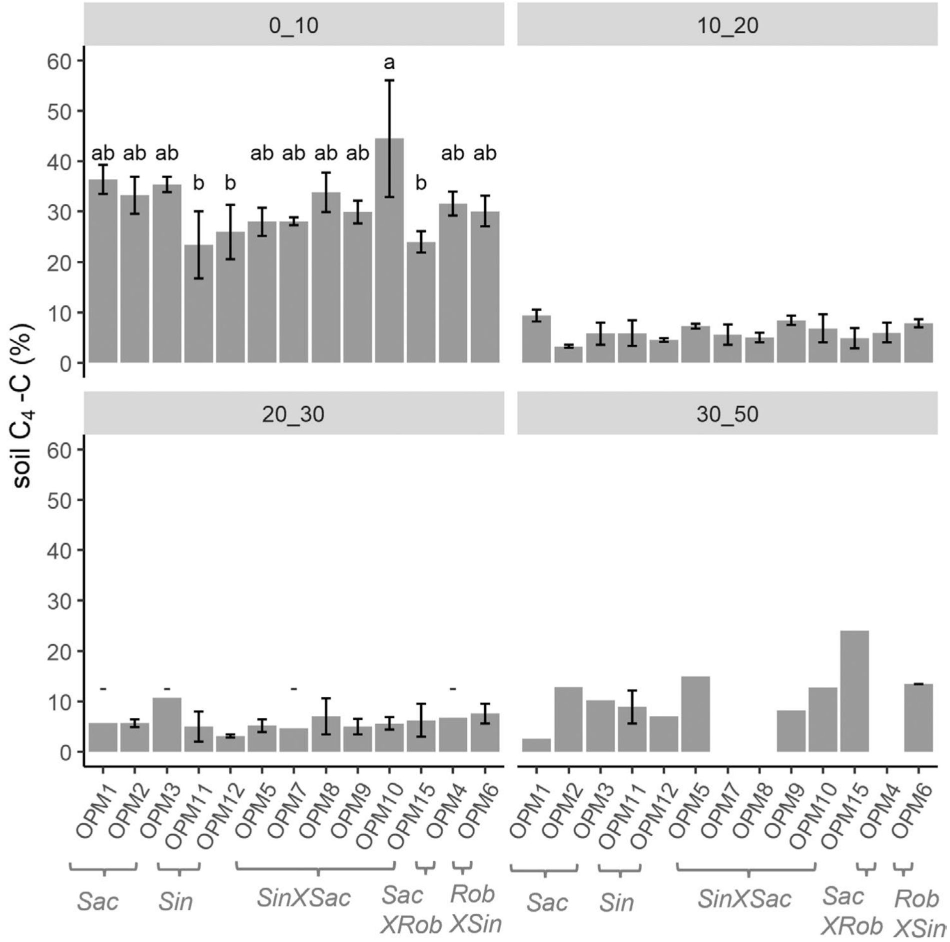

FIGURE 2 | Comparison of *Miscanthus* derived soil C (% C_4-C) between *Miscanthus* genotypes after 10 years of cultivation, for each depth increment (0–10, 10–20, 20–30 and 30–50 cm). *Miscanthus* species groupings are shown below the brackets. Error bars show the SEM. Statistical genotypic differences were explored for the 0–10, 10–20 and 20–30 cm depths; different letters denote significance following Tukey post hoc tests (genotypes with only one rep in the depth increment were excluded and are marked with a dash).

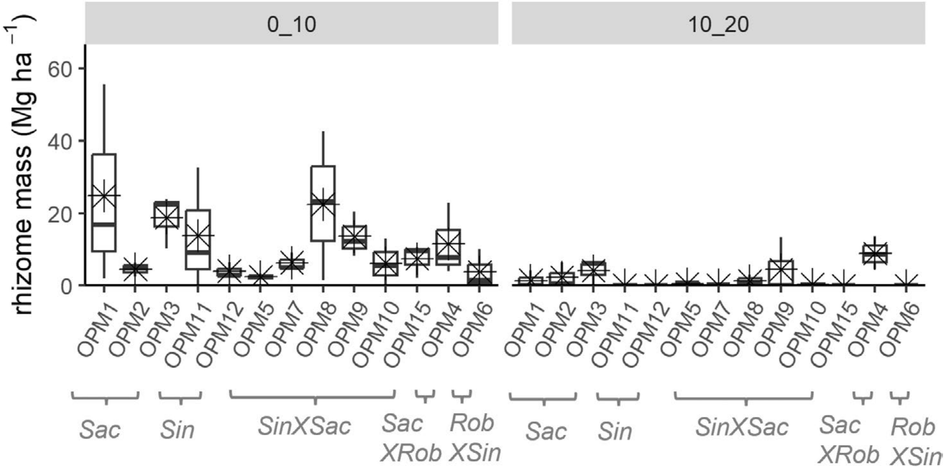

FIGURE 3 | Comparison of rhizome mass between *Miscanthus* genotypes after 10 years of cultivation, for the 0–10 and 10–20 cm depth increments. *Miscanthus* groupings are shown below the brackets.

3.3 | *Miscanthus* Traits and Soil C Relationships

In contrast to the small genotypic differences found for root and rhizome mass, harvest yield for the *Sac* species was significantly higher than most of the other groupings (excluding *Sac*×*Rob*) ($p < 0.001$). Yield for OPM9 (35 ± 3 Mg ha^{-1}), along with the three *Sac* species, was significantly higher than the seven lowest yielding genotypes ($p < 0.001$) (Table 5). The highest ripening

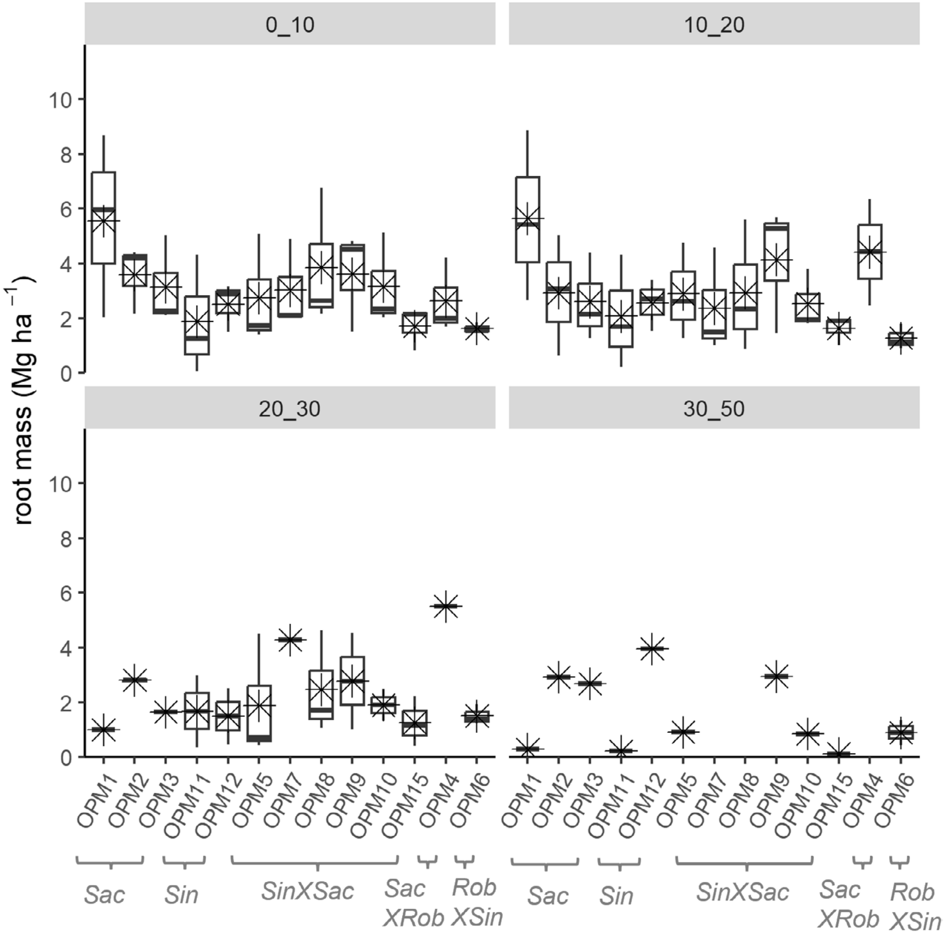

FIGURE 4 | Comparison of root mass between *Miscanthus* genotypes after 10 years of cultivation, for each depth increment (0–10, 10–20, 20–30 and 30–50 cm). *Miscanthu* groupings are shown below the brackets.

loss of 13 ± 8 Mg ha^{-1} for OPM9 was significantly higher than the ripening loss for OPM6, OPM10, OPM7 and OPM15 ($p < 0.05$) (Table 5).

As traits with the potential to influence SOC and C_4-C stocks, ripening loss and yield were included with rhizome and root mass in best fit model selection. Using data from all the *Miscanthus* genotypes, the combination of fixed factors achieving the closest fit suggests that rhizome mass and soil depth increment had a strong association with soil C_4-C (R^2 0.86) (Figure 6). This was not the same for SOC, where instead ripening loss and depth increment had a positive but weaker relationship (R^2 0.62) (Figure 6). Yield and root mass were not found to be important predictive factors.

In analysis by individual genotype, it was found that yield was also the least important factor (not improving model fit for OPM1, OPM2, OPM7 and OPM10) with the inclusion of a mix of depth increment, below-ground biomass and ripening loss giving the best results for predictions of C_4-C. For SOC, yield was not a good predictor for genotypes OPM3, OPM4, OPM7 and OPM10, but, as found for C_4-C, the combination of all factors achieved the best results for each genotype.

4 | Discussion

Biomass crops are acknowledged to be an important part of global ambitions to achieve GHG reductions and NetZero (CCC (Committee on Climate Change) 2018; DESNZ (Department for Energy Security and Net Zero) 2023b). It is therefore important to maximise the C benefits, both yield and sequestration, of growing *Miscanthus* and to ensure that cultivation does not create SOC loss that may partially negate the wider benefits derived from the crop. *Miscanthus* can have a productive lifetime of ~20 years (Winkler et al. 2020) but long-term field trials tracking SOC change in crop conversion from pasture to *Miscanthus* are rare, with the majority reflecting crops of 5 years old or less (Qin et al. 2016). In this study, we have provided further empirical data demonstrating that a conversion from long-term managed pasture to *Miscanthus* had no significant effect on soil C. SOC of 98 Mg ha^{-1} (0–50 cm) at both pre-conversion (T_0) and after 10 years of *Miscanthus* cultivation (T_{10}) implies that any losses expected during land use change cultivation were recouped. It is assumed that soil C stocks were at a steady state at T_0 but it is also possible that if the land remained as pasture, the stocks could have increased or decreased depending on several factors including pasture

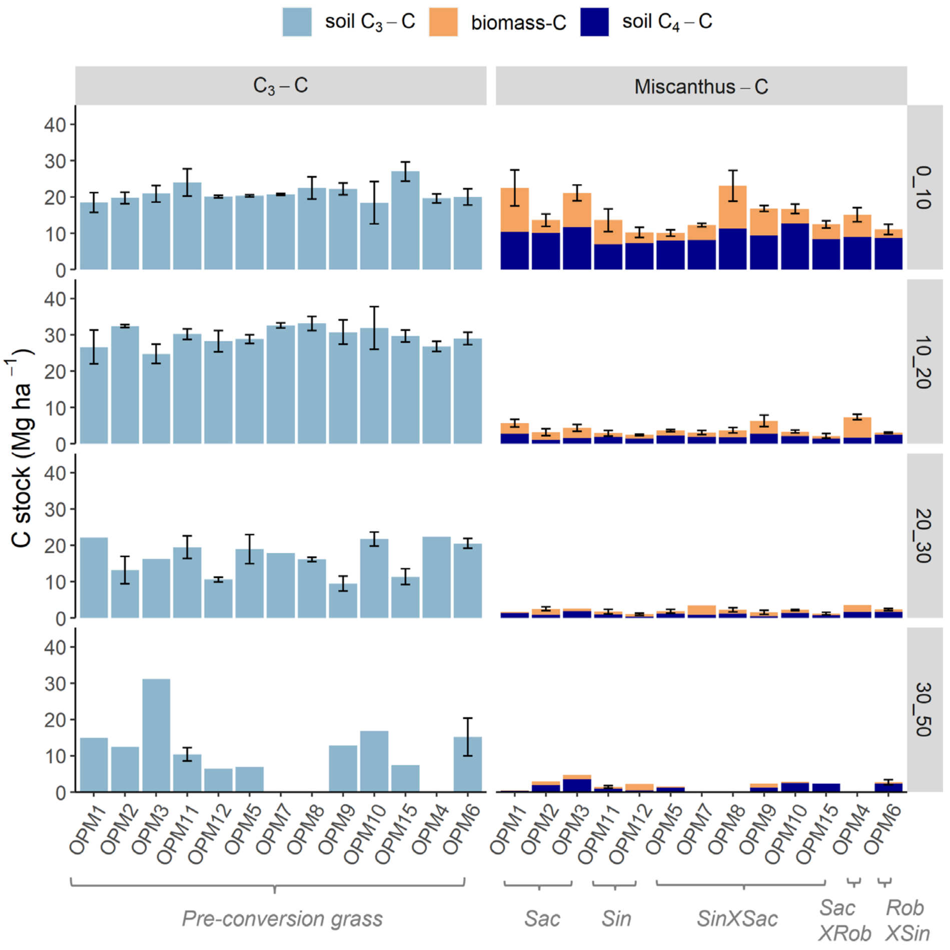

FIGURE 5 | Total *Miscanthus* derived C stock after 10 years of cultivation: Below ground biomass (root and rhizome) and soil C_4-C compared to the C_3-C stock (Mg C ha^{-1}) for each soil depth (0–10, 10–20, 20–30 and 30–50 cm) and genotype. *Miscanthus* species groupings are shown below the brackets. Error bars show the SEM.

TABLE 5 | Mean above-ground *Miscanthus* harvest yield at year 11 and percentage ripening loss (difference between the year three autumn and spring yields) for each genotype. SEM is indicated by the ± values.

Species grouping	Genotype ID	Year 11 yield (Mg ha^{-1})	Ripening loss (%)	Year 11 ripening loss (Mg ha^{-1})
Sac	OPM1	27 ± 5	12 ± 7	4 ± 3
	OPM2	26 ± 4	11 ± 6	4 ± 2
	OPM3	32 ± 2	29 ± 17	10 ± 6
Sin	OPM11	7 ± 1	55 ± 32	4 ± 2
	OPM12	18 ± 3	29 ± 17	4 ± 3
Sac×Rob	OPM4	17 ± 3	27 ± 16	5 ± 3
Rob×Sin	OPM6	9 ± 2	23 ± 13	2 ± 1
Sin×Sac	OPM10	8 ± 1	23 ± 13	2 ± 1
	OPM15	9 ± 2	19 ± 11	1 ± 1
	OPM5	13 ± 4	24 ± 14	3 ± 2
	OPM7	6 ± 1	26 ± 15	2 ± 1
	OPM8	10 ± 3	41 ± 24	4 ± 2
	OPM9	35 ± 3	35 ± 20	13 ± 8

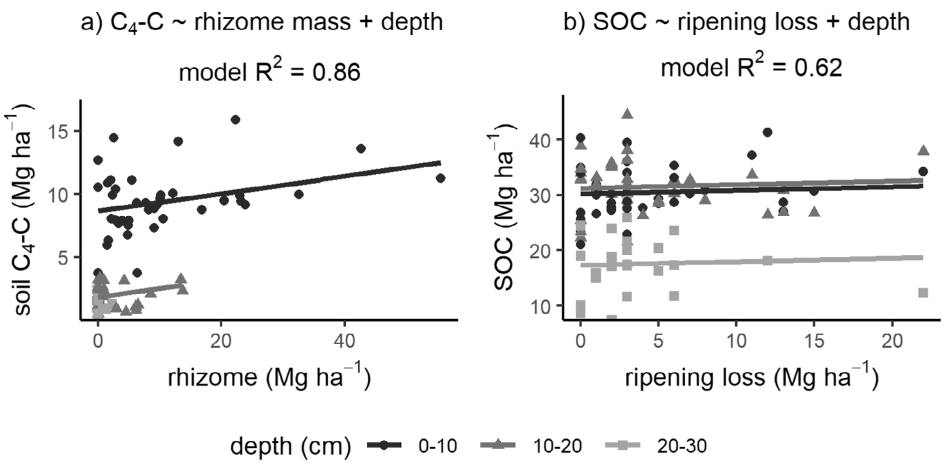

FIGURE 6 | Best fit models following model selection based on AIC (from fixed factors of yield, ripening loss, root and rhizome mass, and depth increment): (a) rhizome mass and soil C_4-C stock; and (b) ripening loss and SOC. Trend lines reflect the linear model predictions.

management (Soussana et al. 2004). Estimated grassland sequestration rates are between 0 to 0.5 Mg C ha^{-1} year^{-1} covering a range of management practices (Conant et al. 2001; Lal 2018). Soil C sequestration rates in land use transitions from grassland to *Miscanthus* are estimated to be in the range of 0 to 2 Mg C ha^{-1} year^{-1} (Qin et al. 2016; Leifeld et al. 2021) which is similar to the results of this study. Little is known about the effect of *Miscanthus* species or genotypic differences on SOC stocks, or how variations in above- and below-ground plant traits interact with soil C. The results of this study therefore provide valuable data addressing this question.

4.1 | Effect of *Miscanthus* Genotype and Species Grouping on SOC Sequestration

Our results show the differential effect of *Miscanthus* genotype, but not species grouping, on SOC sequestration after 10 years of cultivation on a previously managed long-term grass pasture. Work to date has suggested that *M. sinensis* types may be more beneficial to soil C sequestration compared to *M. sacchariflorus* and *M.* × *giganteus* (Richter et al. 2015; Gregory et al. 2018; Briones et al. 2023). But contrary to this, and more aligned with Ouattara et al. (2021), we found no significant differences between the *Miscanthus* species groupings examined. However, the importance of considering *Miscanthus* genotypic differences in maintaining or improving SOC stocks was shown at T_{10}, with the lowest SOC stocks for the 0–30 cm soil depth approximately a third lower than the highest (65 vs. 97 Mg ha^{-1}). The difference of 0.6 Mg C_4-C ha^{-1} year^{-1} (0–20 cm soil depth) between the lowest and highest recorded C_4-C value could mean the difference between neutral or positive soil C stocks following land use change to *Miscanthus* and equates to an estimated total of 12 Mg C_4-C ha^{-1} over a 20-year crop lifetime.

Encouragingly, from a breeding point of view, only two genotypes (OPM12 *Sin* and OPM15 *Sin*×*Sac Hyb*) had significantly lower C stocks (0–30-cm soil depth) and were also identified as contributing lower amounts of C_4-C compared to the other genotypes. With only modest differences between the remaining 11 genotypes studied, this still provides a wide genotypic base to select from.

Of the two commercially available genotypes included (OPM9 *M.* × *giganteus* and OPM11 *Goliath*) neither had SOC stocks lower than T_0 (0–30-cm soil depth). OPM11 was amongst the lowest in recorded percentage C_4-C contribution (0–10-cm depth increment) but overall C stocks for both genotypes were not significantly different to the other genotypes. Despite returning to pre-conversion SOC stocks, OPM9 appeared to have lost existing C_3-C between T_0 and T_{10} in the 20–30 cm depth increment. This agrees with the findings of Richter et al. (2015) who also found *M.* × *giganteus* to be associated with losses of existing soil C.

4.2 | Interaction of *Miscanthus* Root and Rhizome With SOC and Soil Depth

Although no significant difference was found for rhizome or root mass between the *Miscanthus* genotypes, rhizome mass was found to be a trait of interest related to the accumulation of *Miscanthus-derived* soil C (C_4-C) with increasing rhizome mass increasing C_4-C. *M. sacchariflorus* types tend to have greater rhizome mass than *M. sinensis* . Although we did not see this clear divide in the genotypes examined, a greater number of experimental replicates may have produced a stronger trend, which was diluted here by variation in rhizome mass recorded over the three replicates.

The sampling strategy did not allow for complete recovery of root mass from the soil samples, with only coarser roots being extracted. Therefore, the impact of fine root mass has not been included in this study but could well play a role in SOC sequestration, particularly in lower soil depths.

Due to differences in biochemical quality, *Miscanthus* rhizome is more rapidly mineralised than *Miscanthus* roots (Beuch et al. 2000; Ferrarini et al. 2022) which may be a factor in the correlation found between C_4-C and rhizome and not root mass. The non-living portion of *M.* × *giganteus* rhizome is estimated to represent around 1%–7% of the total rhizome mass (3–7 year old plants) (Beuch et al. 2000; Kahle et al. 2001; Amougou et al. 2011). But the in-field turnover dynamics for *Miscanthus* rhizome grown in an agricultural setting, and how this may change with plantation age, are largely unknown.

Total below ground biomass was previously found to be positively correlated with *Miscanthus* derived soil C (Zatta et al. 2014) and in this study, we found rhizome mass to be correlated with C_4-C in a similar way. However, in this study, we did not find the negative (or any) relationship of below ground biomass with SOC that has been observed elsewhere (Zatta et al. 2014; Martani et al. 2021). These negative associations are likely to be connected to soil priming effects (Kuzyakov et al. 2000; Zatta et al. 2014; Martani et al. 2021). For the genotypes used in this study, we found that C_4-C additions displaced older C_3-C in all the genotypes except OPM9. After 10 years of *Miscanthus* growth at the experimental site in this study, it is possible that the SOC was at, or close to, steady state.

The majority of SOC was accumulated in the 0–20-cm soil depth, but the greatest variation was seen below this. The input of SOC at lower depths is valuable not only to overall SOC stocks but also to its resident time (Rehbein et al. 2015). Three genotypes (OPM9, 12 and 15), including the two poorest performing in terms of SOC sequestration, had significantly lower SOC below 20 cm compared to most of the others, showing the importance of SOC accrual at depth even in shallow soils of this type. Of note is that *Miscanthus* derived soil C and root biomass were found in the lowest 30–50-cm depth increment for all genotypes (where sampling to this depth was possible). Although sufficient samples were not obtained for statistical analysis, this C store could promote longer-term SOC sequestration due to physical distance from zones of higher microbial activity (Lal 2018) and land management activities. In this grassland transition, initial soil C stocks were higher than would be expected in arable land, and it is not known whether variations in genotypic ability to sequester C may be clearer in different types of land conversions. Certainly, further work on deeper soil profiles is needed to quantify the influence of genotypes at depth.

The value of below ground biomass to C stocks has been noted previously (Martani et al. 2021); we found that at the 0–10-cm depth, total *Miscanthus* derived C (C_4-C and biomass C) was similar to the C_3-C stocks for three of the genotypes. The range of 2 to 12 Mg C ha^{-1} (0–10 cm) for the *Miscanthus* biomass C stock compares favourably with an estimated ~5 Mg C ha^{-1} observed for a 3-year-old grass pasture root C stock (Gregory et al. 2022). The C stock held in *Miscanthus* below ground biomass is not a long-term store but is still a valuable C pool within the soil profile (Christensen et al. 2016; Martani et al. 2021). In the case of rhizome mass, this C pool is likely to remain in place for the crop lifetime (Poeplau et al. 2019). The majority of mineralised below ground biomass is likely to enter the particulate SOC pool (short term, but able to continue to accumulate), but some also enters the mineral-associated SOC pool, which generally has longer-term storage but can reach saturation (Ridgeway et al. 2022; Xu et al. 2024). In future conversions of *Miscanthus* plantations to other uses, depending on the tillage method used, portions of below ground biomass are likely to exist beyond the land use change and will continue to play a role in SOC cycling. Emerging evidence suggests that when linked with paired arable sites, this could lead to SOC gains in the first years during reversion (Dufossé et al. 2014; Martani et al. 2023) then a stabilisation of SOC stocks to near pre-conversion levels. But there is also the possibility of SOC loss. For example, Rowe et al. (2020) found a 20% loss in paired arable sites compared to a *Miscanthus* crop reverted 3 years previously. However, there are many site-specific (e.g., climate) and agronomic factors (e.g., method of crop removal and subsequent tillage regime) in these types of long-term crop rotations that make it difficult to estimate future effects; results are likely to differ depending on the counterfactual used.

4.3 | Yield and Ripening Loss Interactions With SOC Sequestration

Although the *Sac* species grouping (along with hybrid OPM9) produced the highest yields in year 11, harvest yield was not correlated with soil C. Furthermore, yield was not found to be a good predictor of either SOC or C_4-C and, across the 13 genotypes sampled, the two genotypes with the lowest soil C were also not high yielding. Given the importance of maintaining high above-ground yield as a breeding target, our results show that increased yield need not be at the expense of low soil C sequestration. Links between yield and SOC are not clear and are subject to interacting variables. In a number of studies exploring links between increased SOC and yield (for a variety of crops) findings varied from negative to neutral to positive associations (Moinet et al. 2023). *Miscanthus* yield, as with most crops, is highly impacted by yearly climate and soil moisture conditions (Nunn et al. 2017) but competition for N between plants and soil microbes is also a factor affecting both plant growth and SOC. For example, plant nutrient resource acquisition and allocation (e.g., root exudation rate and composition) can have contrasting effects in soil C cycles (Wen et al. 2022), can impact and be impacted by plant growth (Terrer et al. 2021; Pantigoso et al. 2022), and are in turn influenced by biotic and abiotic factors (Ahlawat et al. 2024). One reason *Miscanthus* is suitable for poor-quality land is due to its ability to translocate N to rhizomes during senescence that supports the following year's growth (Magenau et al. 2022) which may reduce competition for soil N resources. Our results show that increased rhizome mass was associated with increased SOC, but also that high below-ground biomass did not equal low above-ground harvest yields.

Ripening loss (primarily leaf litter drop) was identified as a useful factor in predicting SOC, although interestingly not C_4-C. *Miscanthus* leaf litter forms an important C input to soil (Amougou et al. 2012) but C from above ground litter has also been shown to be lost through respiration to a greater extent than below ground litter (Ridgeway et al. 2022). In the analysis of the individual genotypes, ripening loss was just one of the mix of factors required to improve model fit for predictions of C_4-C. These experimental plots were not harvested in years 8, 9 and 10, and this may therefore have impacted the composition (due to weed growth) and quantity of above ground litter inputs. By year 8, the *Miscanthus* plots were fully mature with a closed canopy and a litter layer that shaded out the majority of weed competition, apart from isolated patches of brambles (*Rubus fruticosus*) beginning to take hold in some plots. The soil core samples, being taken from plants away from the plot edges, were not taken from these patches. Although an annual harvest of a *Miscanthus* crop is generally carried out after most of the senesced leaves have fallen, harvesting also creates additional harvest residues (such as portions of stalk) which would not have been there for the last 3 years of the experimental period, reducing above ground C_4 inputs to soil organic matter.

5 | Conclusion

Over the long-term timescale of this study, any losses of soil C during the establishment of *Miscanthus* were recouped. There was no division among species, revealing that genotypic differences are of more importance. Whilst two *Miscanthus* genotypes were identified with low contributions to soil C, none of the genotypes studied were significantly different to T_o SOC stocks. However, teasing out the traits responsible for the differences in soil C cycling remains elusive and of interest for further research. Of the traits considered here, the value of a high rhizome mass stood out, along with an influence of litter drop. In deeper soil profiles, the variations in root morphology could potentially affect SOC sequestration ability. Yield is a primary target of breeding programmes, and of the genotypes examined, we found that high harvest yield was not at the expense of low soil C.

Author Contributions

Amanda J. Holder: formal analysis, investigation, methodology, writing – original draft. **Rebecca Wilson:** investigation, methodology, writing – review and editing. **Jeanette Whitaker:** writing – review and editing. **Paul Robson:** conceptualization, funding acquisition, writing – review and editing.

Acknowledgements

This work was supported by the Perennial Biomass Crops for Greenhouse Gas Removal project (BBSRC grant BB/V011553/1) and the strategic programme for Resilient Crops (BBSRC grant BB/X011062/1). Thanks are also expressed to Aberystwyth University staff Chris Ashman, Chris Glover and Joe Sharple for taking the soil cores and year 11 yield and to Debbie Allen for performing the carbon isotope analysis.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in "Pure" at https://doi.org/10.20391/f29c2b88-54ae-47c5-a959-48c967bac1e9, "Soil core and Miscanthus trait data from OPTIMISC trial, 2022".

References

Abraha, M., I. Gelfand, S. K. Hamilton, J. Chen, and G. P. Robertson. 2019. "Carbon Debt of Field-Scale Conservation Reserve Program Grasslands Converted to Annual and Perennial Bioenergy Crops." *Environmental Research Letters* 14, no. 2: 024019. https://doi.org/10.1088/1748-9326/aafc10.

Agostini, F., A. S. Gregory, and G. M. Richter. 2015. "Carbon Sequestration by Perennial Energy Crops: Is the Jury Still out?" *Bioenergy Research* 8: 1057–1080. https://doi.org/10.1007/s12155-014-9571-0.

AHDB. 2017. "Nutrient Management Guide (RB209)." In *Section 1 Principles of Nutrient Management and Fertiliser Use*. Agriculture & Horticulture Development Board.

Ahlawat, O. P., D. Yadav, N. Walia, P. L. Kashyap, P. Sharma, and R. Tiwari. 2024. "Root Exudates and Their Significance in Abiotic Stress Amelioration in Plants: A Review." *Journal of Plant Growth Regulation* 43: 1736–1761. https://doi.org/10.1007/s00344-024-11237-7.

Amougou, N., I. Betrand, S. Cadoux, and S. Recous. 2012. "*Miscanthus × Giganteus* Leaf Senescence, Decomposition and C and N Inputs to Soil." *GCB Bioenergy* 4: 698–707. https://doi.org/10.1111/j.1757-1707.2012.01192.x.

Amougou, N., I. Betrand, J.-M. Machet, and S. Recous. 2011. "Quality and Decomposition in Soil of Rhizome, Root and Senescent Leaf From *Miscanthus × Giganteus*, as Affected by Harvest Date and N Fertilization." *Plant and Soil* 338: 83–97. https://doi.org/10.1007/s11104-010-0443-x.

Awty-Carroll, D., E. Magenau, M. Al Hassan, et al. 2023. "Yield Performance of 14 Novel Inter- and Intra-Species *Miscanthus* Hybrids Across Europe." *GCB Bioenergy* 15, no. 4: 399–423. https://doi.org/10.1111/gcbb.13026.

Balesdent, J., C. Chenu, and M. Balabane. 2000. "Relationship of Soil Organic Matter Dynamics to Physical Protection and Tillage." *Soil & Tillage Research* 53, no. 3–4: 215–230. https://doi.org/10.1016/S0167-1987(99)00107-5.

Balesdent, J., A. Mariotti, and B. Guillet. 1987. "Natural 13C Abundance as a Tracer for Studies of Soil Organic Matter Dynamics." *Soil Biology and Biochemistry* 19, no. 1: 25–30. https://doi.org/10.1016/0038-0717(87)90120-9.

Bardgett, R. D., L. Mommer, and F. T. De Vries. 2014. "Going Underground: Root Traits as Drivers of Ecosystem Processes." *Trends in Ecology & Evolution* 29, no. 12: 692–699. https://doi.org/10.1016/j.tree.2014.10.006.

Barton, K. 2023. "MuMIn: Multi-Model Inference. R Package Version 1.47.5." https://CRAN.R-project.org/package=MuMIn.

Beuch, S., B. Boelcke, and L. Belau. 2000. "Effect of the Organic Residues of *Miscanthus × Giganteus* on the Soil Organic Matter Level of Arable Soils." *Journal of Agronomy and Crop Science* 183: 111–119.

Briones, M. J., A. Massey, D. M. Elias, et al. 2023. "Species Selection Determines Carbon Allocation and Turnover in *Miscanthus* Crops: Implications for Biomass Production and C Sequestration." *Science of the Total Environment* 887: 164003. https://doi.org/10.1016/j.scitotenv.2023.164003.

Brooks, M. E., K. Kristensen, K. J. van Benthem, et al. 2017. "glmmTMB Balances Speed and Flexibility Among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *R Journal* 9, no. 2: 378–400. https://doi.org/10.32614/RJ-2017-066.

Carvalho, J. L., T. W. Hudiburg, H. C. Franco, and E. H. DeLucia. 2017. "Contribution of Above-and Belowground Bioenergy Crop Residues to Soil Carbon." *GCB Bioenergy* 9, no. 8: 1333–1343. https://doi.org/10.1111/gcbb.12411.

CCC (Committee on Climate Change). 2018. *Biomass in a Low-Carbon Economy*, 162.

Chae, W. B., S. J. Hong, J. M. Gifford, A. L. Rayburn, E. J. Sacks, and J. A. Juvik. 2014. "Plant Morphology, Genome Size, and SSR Markers Differentiate Five Distinct Taxonomic Groups Among Accessions in the Genus *Miscanthus*." *GCB Bioenergy* 6: 646–660. https://doi.org/10.1111/gcbb.12101.

Christensen, B. T., P. E. Lærke, U. Jørgensen, T. P. Kandel, and I. K. Thomsen. 2016. "Storage of *Miscanthus*-Derived Carbon in Rhizomes, Roots, and Soil." *Canadian Journal of Soil Science* 96, no. 4: 354–360. https://doi.org/10.1139/cjss-2015-0135.

Chupakhin, E., O. Babich, S. Sukhikh, et al. 2021. "Methods of Increasing *Miscanthus* Biomass Yield for Biofuel Production." *Energies* 14: 8368. https://doi.org/10.3390/en14248368.

Clifton-Brown, J., K.-U. Schwarz, D. Awty-Carroll, et al. 2019. "Breeding Strategies to Improve *Miscanthus* as a Sustainable Source of Biomass for Bioenergy and Biorenewable Products." *Agronomy* 9: 673. https://doi.org/10.1111/gcbb.12566.

Conant, R. T., K. Paustian, and E. T. Elliott. 2001. "Grassland Management and Conversion Into Grassland: Effects on Soil Carbon." *Ecological Applications* 11, no. 2: 343–355. https://doi.org/10.1890/1051-0761(2001)011[0343:GMACIG]2.0.CO;2.

Cranfield University. 2025. "Land Information System (LandIS) Soils Guide." http://dream-cdt.ac.uk/landis/soilsguide/index.cfm.

DESNZ (Department for Energy Security and Net Zero). 2023a. "Carbon Budget Delivery Plan, HC 1269." UK Government Policy Paper. https://www.gov.uk/official-documents.

DESNZ (Department for Energy Security and Net Zero). 2023b. *Biomass Strategy* UK Government Policy Paper. https://www.gov.uk/government/publications/biomass-strategy.

Dufossé, K., J. Drewer, B. Gabrielle, and J.-L. Drouet. 2014. "Effects of a 20-Year Old *Miscanthus*×*Giganteus* Stand and Its Removal on Soil Characteristics and Greenhouse Gas Emissions." *Biomass and Bioenergy* 69: 198–210. https://doi.org/10.1016/j.biombioe.2014.07.003.

Dynarski, K. A., D. A. Bossio, and K. M. Scow. 2020. "Dynamic Stability of Soil Carbon: Reassessing the "Permanence" of Soil Carbon Sequestration." *Frontiers in Environmental Science* 8: 514701. https://doi.org/10.3389/fenvs.2020.514701.

EC (European Commission Joint Research Centre). 2019. *Brief on Biomass for Energy in the European Union*. Publications Office. https://doi.org/10.2760/546943.

EC (European Commission). 2021. "Reaping the Benefits of Healthy Soils for People, Food, Nature and Climate." Communication From the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A52021DC0699.

Ferrarini, A., E. Martani, C. Mondini, F. Fornasier, and S. Amaducci. 2022. "Short-Term Mineralization of Belowground Biomass of Perennial Biomass Crops After Reversion to Arable Land." *Agronomy* 12: 485. https://doi.org/10.3390/agronomy12020485.

Greef, J. M., and M. Deuter. 1993. "Syntaxonomy of *Miscanthus* × *Giganteus* Greef et Deu." *Angewandte Botanik* 67, no. 3–4: 87–90.

Gregory, A. S., J. A. Dungait, I. F. Shield, et al. 2018. "Species and Genotype Effects of Bioenergy Crops on Root Production, Carbon and Nitrogen in Temperate Agricultural Soil." *Bioenergy Research* 11: 382–397. https://doi.org/10.1007/s12155-018-9903-6.

Gregory, A. S., A. Joynes, E. R. Dixon, et al. 2022. "High-Yielding Forage Grass Cultivars Increase Root Biomass and Soil Organic Carbon Stocks Compared With Mixed-Species Permanent Pasture in Temperate Soil." *European Journal of Soil Science* 73, no. 1: e13160. https://doi.org/10.1111/ejss.13160.

Holder, A. J., J. Clifton-Brown, R. Rowe, et al. 2019. "Measured and Modelled Effect of Land-Use Change From Temperate Grassland to *Miscanthus* on Soil Carbon Stocks After 12 Years." *GCB Bioenergy* 11, no. 10: 1173–1186. https://doi.org/10.1111/gcbb.12624.

Hothorn, T., F. Bretz, and P. Westfall. 2008. "Simultaneous Inference in General Parametric Models." *Biometrical Journal* 50, no. 3: 346–363.

Hu, Y., G. Schäfer, J. Duplay, and N. J. Kuhn. 2018. "Bioenergy Crop Induced Changes in Soil Properties: A Case Study on *Miscanthus* Fields in the Upper Rhine Region." *PLoS One* 13, no. 7: e0200901. https://doi.org/10.1371/journal.pone.0200901.

IPCC. 2019. "Summary for Policymakers." In *Climate Change and Land: An IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fluxes in Terrestrial Ecosystems*, edited by P. R. Shukla, J. Skea, E. Calvo Buendia, et al. In Press.

IUSS Working Group WRB. 2022. "World Reference Base for Soil Resources." In *International Soil Classification System for Naming Soils and Creating Legends for Soil Maps*, 4th ed. International Union of Soil Sciences. (IUSS).

Jansson, C., C. Faiola, A. Wingler, et al. 2021. "Crops for Carbon Farming." *Frontiers in Plant Science* 12: 636709. https://doi.org/10.3389/fpls.2021.636709.

Kahle, P., S. Beuch, B. Boelcke, P. Leinweber, and H.-R. Schulten. 2001. "Cropping of *Miscanthus* in Central Europe: Biomass Production and Influence on Nutrients and Soil Organic Matter." *European Journal of Agronomy* 15: 171–184.

Kalinina, O., C. Nunn, R. Sanderson, et al. 2017. "Extending *Miscanthus* Cultivation With Novel Germplasm at Six Contrasting Sites." *Plant Science* 8: 563. https://doi.org/10.3389/fpls.2017.00563.

Kane, J. L., R. G. Schartiger, N. K. Daniels, et al. 2023. "Bioenergy Crop *Miscanthus* x Giganteus Acts as an Ecosystem Engineer to Increase Bacterial Diversity and Soil Organic Matter on Marginal Land." *Soil Biology and Biochemistry* 186: 109178. https://doi.org/10.1016/j.soilbio.2023.109178.

Keiser, A. D., E. Heaton, A. VanLoocke, J. Studt, and M. D. McDaniel. 2025. "Historical Land Management Alters New Soil Carbon Inputs by Annual and Perennial Bioenergy Crops." *GCB Bioenergy* 17, no. 8: e70052. https://doi.org/10.1111/gcbb.70052.

Kristl, M., M. Muršec, V. Šuštar, and J. Kristl. 2016. "Application of Thermogravimetric Analysis for the Evaluation of Organic and Inorganic Carbon Contents in Agricultural Soils." *Journal of Thermal Analysis and Calorimetry* 123: 2139–2147. https://doi.org/10.1007/s10973-015-4844-1.

Kuzyakov, Y., J. K. Friedel, and K. Stahr. 2000. "Review of Mechanisms and Quantification of Priming Effects." *Soil Biology and Biochemistry* 32: 1485–1498.

Lal, R. 2018. "Digging Deeper: A Holistic Perspective of Factors Affecting Soil Organic Carbon Sequestration in Agroecosystems." *Global Change Biology* 24, no. 8: 3285–3301. https://doi.org/10.1111/gcb.14054.

Leifeld, J., C. Alewell, and S. M. Paul. 2021. "Accumulation of C4-Carbon From *Miscanthus* in Organic-Matter-Rich Soils." *GCB Bioenergy* 13, no. 8: 1319–1328. https://doi.org/10.1111/gcbb.12861.

Lemus, R., and R. Lal. 2005. "Bioenergy Crops and Carbon Sequestration." *Critical Reviews in Plant Sciences* 24: 1–21. https://doi.org/10.1080/07352680590910393.

Lewandowski, I., J. Clifton-Brown, A. Kiesel, A. Hastings, and Y. Iqbal. 2018. "2-*Miscanthus*." In *Perennial Grasses for Bioenergy and Bioproducts*, edited by E. Alexopoulou. Academic Press. https://doi.org/10.1016/B978-0-12-812900-5.00002-3.

Lewandowski, I., J. C. Clifton-Brown, J. M. O. Scurlock, and W. Huisman. 2000. "*Miscanthus*: European Experience With a Novel Energy Crop." *Biomass and Bioenergy* 19: 209–227. https://doi.org/10.1016/S0961-9534(00)00032-5.

Magenau, E., J. Clifton-Brown, D. Awty-Carroll, et al. 2022. "Site Impacts Nutrient Translocation Efficiency in Intraspecies and Interspecies Miscanthus Hybrids on Marginal Lands." *GCB Bioenergy* 14, no. 9: 1035–1054. https://doi.org/10.1111/gcbb.12985.

Martani, E., A. Ferrarini, and S. Amaducci. 2022. "Reversion of Perennial Biomass Crops to Conserve C and N: A Meta-Analysis." *Agronomy* 12: 232. https://doi.org/10.3390/agronomy12020232.

Martani, E., A. Ferrarini, A. Hastings, and S. Amaducci. 2023. "Soil Organic Carbon Significantly Increases When Perennial Biomass Plantations Are Reverted Back to Annual Arable Crops." *Agronomy* 13, no. 2: 447. https://doi.org/10.3390/agronomy13020447.

Martani, E., A. Ferrarini, P. Serra, M. Pilla, A. Marcone, and S. Amaducci. 2021. "Belowground Biomass C Outweighs Soil Organic C of Perennial Energy Crops: Insights From a Long-Term Multispecies

Trial." *GCB Bioenergy* 13, no. 3: 459–472. https://doi.org/10.1111/gcbb.12785.

Met Office. n.d. "Location Specific Long Term Averages: Gogerddan Station 1991–2020." https://www.metoffice.gov.uk/research/climate/maps-and-data/location-specific-long-term-averages/gcm44vmfs.

Moinet, G. Y., R. Hijbeek, D. P. van Vuuren, and K. E. Giller. 2023. "Carbon for Soils, Not Soils for Carbon." *Global Change Biology* 29, no. 9: 2384–2398. https://doi.org/10.1111/gcb.16570.

Neukirchen, D., M. Himken, J. Lammel, U. Czypionka-Krause, and H.-W. Olfs. 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.

Nunn, C., A. F. S. J. Hastings, O. Kalinina, et al. 2017. "Environmental Influences on the Growing Season Duration and Ripening of Diverse *Miscanthus* Germplasm Grown in Six Countries." *Frontiers in Plant Science* 8: 907. https://doi.org/10.3389/fpls.2017.00907.

Ouattara, M. S., A. Laurent, F. Ferchaud, et al. 2021. "Evolution of Soil Carbon Stocks Under *Miscanthus* × *Giganteus* and *Miscanthus sinensis* Across Contrasting Environmental Conditions." *GCB Bioenergy* 13, no. 1: 161–174. https://doi.org/10.1111/gcbb.12760.

Pantigoso, H. A., D. Newberger, and J. M. Vivanco. 2022. "The Rhizosphere Microbiome: Plant–Microbial Interactions for Resource Acquisition." *Journal of Applied Microbiology* 133, no. 5: 2864–2876. https://doi.org/10.1111/jam.15686.

Pinheiro, J., D. Bates, and R Core Team. 2023. "Nlme: Linear and Nonlinear Mixed Effects Models, R Package Version 3.1–162." https://CRAN.R-project.org/package=nlme.

Poeplau, C., K. Germer, and K.-U. Schwarz. 2019. "Seasonal Dynamics and Depth Distribution of Belowground Biomass Carbon and Nitrogen of Extensive Grassland and a *Miscanthus* Plantation." *Plant and Soil* 440: 119–133. https://doi.org/10.1007/s11104-019-04074-1.

Poeplau, C., C. Vos, and A. Don. 2017. "Soil Organic Carbon Stocks Are Systematically Overestimated by Misuse of the Parameters Bulk Density and Rock Fragment Content." *Soil* 3: 61–66. https://doi.org/10.5194/soil-3-61-2017.

Poffenbarger, H., M. Castellano, D. Egli, A. Jaconi, and V. Moore. 2023. "Contributions of Plant Breeding to Soil Carbon Storage: Retrospect and Prospects." *Crop Science* 63: 990–1018. https://doi.org/10.1002/csc2.20920.

Poirier, V., C. Roumet, and A. D. Munson. 2018. "The Root of the Matter: Linking Root Traits and Soil Organic Matter Stabilization Processes." *Soil Biology and Biochemistry* 120: 246–259. https://doi.org/10.1016/j.soilbio.2018.02.016.

Qin, Z., J. B. Dunn, H. Kwon, S. Mueller, and M. M. Wander. 2016. "Soil Carbon Sequestration and Land Use Change Associated With Biofuel Production: Empirical Evidence." *GCB Bioenergy* 8, no. 1: 66–80. https://doi.org/10.1111/gcbb.12237.

Quinn, L. D., K. C. Straker, J. Guo, et al. 2015. "Stress-Tolerant Feedstocks for Sustainable Bioenergy Production on Marginal Land." *Bioenergy Research* 8: 1081–1100. https://doi.org/10.1007/s12155-014-9557-y.

R Core Team. 2023. "R: A Language and Environment for Statistical Computing." R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rasse, D. P., C. Rumpel, and M.-F. Dignac. 2005. "Is Soil Carbon Mostly Root Carbon? Mechanisms for a Specific Stabilisation." *Plant and Soil* 269: 341–356. https://doi.org/10.1007/s11104-004-0907-y.

Rawlins, B. G., P. Henrys, N. Breward, D. A. Robinson, A. M. Keith, and M. Garcia-Bajo. 2011. "The Importance of Inorganic Carbon in Soil Carbon Databases and Stock Estimates: A Case Study From England." *Soil Use and Management* 27: 312–320. https://doi.org/10.1111/j.1475-2743.2011.00348.x.

Rehbein, K., A. Sandhage-Hofmann, and W. Amelung. 2015. "Soil Carbon Accrual in Particle-Size Fractions Under *Miscanthus* × *Giganteus* Cultivation." *Biomass and Bioenergy* 78: 80–91. https://doi.org/10.1016/j.biombioe.2015.04.006.

Richter, G. M., F. Agostini, M. Redmile-Gordon, R. White, and K. W. Goulding. 2015. "Sequestration of C in Soils Under *Miscanthus* Can Be Marginal and Is Affected by Genotype-Specific Root Distribution." *Agriculture, Ecosystems & Environment* 200: 169–177. https://doi.org/10.1016/j.agee.2014.11.011.

Ridgeway, J. R., E. M. Morrissey, and E. R. Brzostek. 2022. "Plant Litter Traits Control Microbial Decomposition and Drive Soil Carbon Stabilization." *Soil Biology and Biochemistry* 175: 108857. https://doi.org/10.1016/j.soilbio.2022.108857.

Robertson, A. D., C. A. Davies, P. Smith, A. W. Stott, E. L. Clark, and N. P. McNamara. 2017. "Carbon Inputs From *Miscanthus* Displace Older Soil Organic Carbon Without Inducing Priming." *Bioenergy Research* 10: 86–101. https://doi.org/10.1007/s12155-016-9772-9.

Robson, P., E. Jensen, S. Hawkins, et al. 2013. "Accelerating the Domestication of a Bioenergy Crop: Identifying and Modelling Morphological Targets for Sustainable Yield Increase in *Miscanthus*." *Journal of Experimental Botany* 64: 4143–4155. https://doi.org/10.1093/jxb/ert225.

Robson, P. R. H., A. Hastings, J. C. Clifton-Brown, and J. P. McAlmont. 2019. "Chapter 7 Sustainable Use of Miscanthus for Biofuel." In *Achieving Carbon-Negative Bioenergy Systems From Plant Materials*, edited by C. Saffron. Burleigh Dodds Science Publishing 9781786762528. www.bdspublishing.com.

Rowe, R. L., A. M. Keith, D. Elias, et al. 2016. "Initial Soil C and Land-Use History Determine Soil C Sequestration Under Perennial Bioenergy Crops." *GCB Bioenergy* 8, no. 6: 1046–1060. https://doi.org/10.1111/gcbb.12311.

Rowe, R. L., A. M. Keith, D. M. O. Elias, and N. P. McNamara. 2020. "Soil Carbon Stock Impacts Following Reversion of *Miscanthus* × *Giganteus* and Short Rotation Coppice Willow Commercial Plantations Into Arable Cropping." *Global Change Biology. Bioenergy* 12, no. 9: 680–693. https://doi.org/10.1111/gcbb.12718.

Rudeforth, C. 1970. *Soils of North Cardiganshire [Sheets 163 and 178]*. Agricultural Research Council.

Semchenko, M., P. Xue, and T. Leigh. 2021. "Functional Diversity and Identity of Plant Genotypes Regulate Rhizodeposition and Soil Microbial Activity." *New Phytologist* 232, no. 2: 776–787. https://doi.org/10.1111/nph.17604.

Shepherd, A., E. Littleton, J. Clifton-Brown, M. Martin, and A. Hastings. 2020. "Projections of Global and UK Bioenergy Potential From *Miscanthus*× Giganteus—Feedstock Yield, Carbon Cycling and Electricity Generation in the 21st Century." *GCB Bioenergy* 12, no. 4: 287–305. https://doi.org/10.1111/gcbb.12671.

Shepherd, A., M. Martin, and A. Hastings. 2021. "Uncertainty of Modelled Bioenergy With Carbon Capture and Storage due to Variability of Input Data." *GCB Bioenergy* 13, no. 4: 691–707. https://doi.org/10.1111/gcbb.12803.

Soussana, J. F., P. Loiseau, N. Vuichard, et al. 2004. "Carbon Cycling and Sequestration Opportunities in Temperate Grasslands." *Soil Use and Management* 20, no. 2: 219–230. https://doi.org/10.1111/j.1475-2743.2004.tb00362.x.

Terrer, C., R. P. Phillips, B. A. Hungate, et al. 2021. "A Trade-Off Between Plant and Soil Carbon Storage Under Elevated CO_2." *Nature* 591: 599–603. https://doi.org/10.1038/s41586-021-03306-8.

Welsh Government. 2023. "Agricultural Land Classification: Predictive Map." https://www.gov.wales/agricultural-land-classification-predictive-map.

Wen, T., G. H. Yu, W. D. Hong, et al. 2022. "Root Exudate Chemistry Affects Soil Carbon Mobilization via Microbial Community Reassembly."

Fundamental Research 2, no. 5: 697–707. https://doi.org/10.1016/j.fmre.2021.12.016.

Whitaker, J., J. L. Field, C. J. Bernacchi, et al. 2018. "Consensus, Uncertainties and Challenges for Perennial Bioenergy Crops and Land Use." *GCB Bioenergy* 10, no. 3: 150–164. https://doi.org/10.1111/gcbb.12488.

Winkler, B., A. Mangold, M. von Cossel, et al. 2020. "Implementing *Miscanthus* Into Farming Systems: A Review of Agronomic Practices, Capital and Labour Demand." *Renewable and Sustainable Energy Reviews* 132: 110053. https://doi.org/10.1016/j.rser.2020.110053.

Xu, S., L. L. Liu, and E. J. Sayer. 2013. "Variability of Above-Ground Litter Inputs Alters Soil Physicochemical and Biological Processes: A Meta-Analysis of Litterfall-Manipulation Experiments." *Biogeosciences* 10, no. 11: 7423–7433. https://doi.org/10.5194/bg-10-7423-2013.

Xu, Y., X. Duan, Y. Wu, et al. 2024. "The Efficiency and Stability of Soil Organic Carbon Sequestration by Perennial Energy Crops Cultivation on Marginal Land Depended on Root Traits." *Soil and Tillage Research* 235: 105909. https://doi.org/10.1016/j.still.2023.105909.

Zang, H., E. Blagodatskaya, Y. Wen, X. Xu, J. Dyckmans, and Y. Kuzyakov. 2018. "Carbon Sequestration and Turnover in Soil Under the Energy Crop *Miscanthus*: Repeated 13C Natural Abundance Approach and Literature Synthesis." *GCB Bioenergy* 10, no. 4: 262–271. https://doi.org/10.1111/gcbb.12485.

Zatta, A., J. Clifton-Brown, P. Robson, A. Hastings, and A. Monti. 2014. "Land Use Change From C3 Grassland to C4 *Miscanthus*: Effects on Soil Carbon Content and Estimated Mitigation Benefit After Six Years." *GCB Bioenergy* 6, no. 4: 360–370. https://doi.org/10.1111/gcbb.12054.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** gcbb70076-sup-0001-FigureS1-S3-TableS2-S2.docx.