# Seasonal dynamics and depth distribution of belowground biomass carbon and nitrogen of extensive grassland and a *Miscanthus* plantation

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## Abstract

*Background and aims* Belowground carbon (C) inputs are a major source of soil organic carbon (SOC) in terrestrial ecosystems, and substrate C:N ratios drive SOC stabilisation. In perennial systems, quantitative information on seasonal dynamics of belowground biomass is scarce, but necessary, e.g. to improve SOC modelling and representative sampling.
*Methods* Seasonal dynamics and depth distribution of belowground biomass C and N of extensive grassland and *Miscanthus* on sandy soil were estimated. Core samples (1 m depth) were taken six times in 1 year. *Miscanthus*-derived SOC was quantified using $^{13}$C natural abundance.
*Results* Grassland and *Miscanthus* differed strongly in belowground biomass C ($2.5 \pm 0.3$ vs. $7.3 \pm$ 1.1 Mg ha$^{-1}$) and C:N ratios ($28.6 \pm 0.5$ vs. $60 \pm 3.3$). Peak grassland belowground biomass C and N stocks occurred in summer, while those of rhizomatous *Miscanthus* were in winter due to different strategies of resource allocation. Grassland roots showed a strong seasonal pattern of C:N ratios, indicating N remobilisation. *Miscanthus*-derived topsoil SOC was low relative to the high belowground biomass, indicating a slow transfer of rhizome carbon to bulk SOC.
*Conclusions* Representative belowground biomass sampling of perennials should take seasonal dynamics into account, especially in system comparisons. Furthermore, C inputs from rhizome and roots should be estimated separately owing to likely differences in turnover times.

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## Introduction

Plants, and plant roots in particular, are essential soil engineers, shaping the structure and organic matter level of soils in almost all terrestrial ecosystems (Angers and Caron 1998). Roots that penetrate the soil form macropores, which favour fluid transport (Mitchell et al. 1995), and aggregates, which improve the soil structure (Materechera et al. 1992). They are an important food source for soil biota, which induces a further positive effect on soil structure and health (Doran and Zeiss 2000). For soil organic matter formation and thus soil organic carbon (SOC) sequestration, plant roots

have been found to be of major importance due to a much higher stabilisation rate of root-derived carbon (C) as compared to shoot-derived C (Ghafoor et al. 2017; Kätterer et al. 2011; Rasse et al. 2005). There may be various reasons for this, ranging from the relatively high chemical recalcitrance of root biomass as compared to shoot biomass (Fernandez et al. 2003) to greater physicochemical protection of roots in the mineral soil matrix (Balesdent and Balabane 1996).

Higher stabilisation of belowground carbon inputs (BGCI) as compared to aboveground carbon inputs is unassertively incorporated into soil carbon turnover models (Poeplau et al. 2015), while the major uncertainty for modelling soil carbon dynamics remains the quantity of BGCI (Poeplau 2016). A commonly used approach, especially for annual crops, is to estimate BGCI by combining yield data with crop-specific C allocation coefficients (Bolinder et al. 2007). In such an approach, the effects of site, soil, cultivar, weather or management on plant C allocation to aboveground and belowground organs as well as root exudates are neglected. This can cause large over or underestimations, which have been shown to be particularly significant for varying nutrient availability (Taghizadeh-Toosi et al. 2016). This is due to the effect of shifts in plant-internal C allocation to roots and shoots as an adaptation to the prevailing resource limitation (Ericsson 1995; Wilson 1988). It has therefore recently been suggested that BGCI should be estimated independent of crop yield or aboveground net primary production (NPP) (Hirte et al. 2018; Poeplau 2016; Taghizadeh-Toosi et al. 2016). This might be especially important for grasslands and perennial crops, which occur in a much wider range of nutrient inputs and management intensities as compared to croplands. In any case, greater quantitative knowledge and mechanistic understanding about BGCI of different crop and land-cover types is necessary to advance soil carbon modelling.

The most accurate way to parameterise mean annual BGCI at a given site is to measure belowground standing biomass together with root growth and turnover as well as exudation (Pausch and Kuzyakov 2018). However, these measurements are elaborate and costly and can thus only be conducted on a very limited spatial and temporal scale. In essence, such limitations are the major reason for the abundant uncertainties related to BGCI. Among the mentioned methods for accurate, site-specific BGCI quantification, belowground biomass determination via soil cores might be one of the most feasible on any scale exceeding plot scale. However, assessing the average belowground biomass per area at a certain point in time is only a snapshot and might not allow for any extrapolation or for being representative of mean annual root C and N stocks. Especially for perennial plants, knowledge about root phenology and seasonal dynamics of belowground standing biomass is surprisingly scarce (Steinaker and Wilson 2008). It is therefore also unclear whether a belowground biomass value determined at one given point in time can actually be a good estimate for average belowground biomass. Understanding of the seasonal pattern of standing root biomass is also crucial for estimating the annual root turnover, which is often done by dividing annual belowground production by the maximum, or average belowground biomass (Dahlman and Kucera 1965; Yuan and Chen 2012).

Besides quantity of BGCI, also their quality is important. Substrate C:N ratio plays a crucial role in initial litter breakdown (Enríquez et al. 1993), but in microbial anabolism and thus formation of stable SOC (Poeplau et al. 2018b) as well. Soil N availability and plant nutrient demand follow a strong seasonal pattern (Harper 1971; Poudel et al. 2002). Perennial plants, especially those with a rhizome, also remobilise nutrients from belowground biomass to shoots at the start of the vegetation period and translocate nutrients from shoots to roots at the end of the vegetation period. For a rhizomatous *Miscanthus*, N fluxes between aboveground and belowground organs and vice versa have been found to account for up to 100 kg N ha$^{-1}$ yr.$^{-1}$ (Himken et al. 1997). It is thus likely that the C:N ratio of the root biomass is also not constant throughout the season. In non-rhizomateous perennial plants, e.g. grassland plant communities, the seasonal pattern of belowground biomass C:N ratio might however strongly differ: While N remobilisation from and to roots is also observed in grasslands (Louahlia et al. 2000), the total root biomass might follow a strong seasonal pattern at the same time (Bhuyan and Barik 2017). In systems comparisons, e.g. when assessing land-use changes from grassland to the rhizomateous biomass crop *Miscanthus* (Zatta et al. 2014), knowledge on differences in the seasonal dynamic might be necessary to i) select the root sampling date and ii) understand and predict changes in C and N fluxes in the atmosphere-plant-soil continuum. However, to date there is little knowledge on root C:N ratios in general and even less on their intra-annual variation.

Finally, when BGCI are estimated from standing root biomass, assumptions on annual root turnover and rhizodeposition have to be made (Bolinder et al. 2007; Poeplau 2016). Tracing the natural abundance of the stable isotope $^{13}C$ in a C3 soil planted with a C4 plant can be a powerful tool for validating such assumptions (Balesdent et al. 1987) and understanding the transfer of BGCI into bulk SOC. The aim of this study was therefore to follow the intra-annual dynamic of carbon and nitrogen in the belowground biomass of two different perennial land-use types – an extensively managed grassland and an adjacent *Miscanthus* (C4 plant) plantation – to advance understanding of the temporal patterns of belowground plant C and N pools along the soil profile and the fate of root-derived C into the more stable bulk SOC pool.

## Materials and methods

### Study site

The study site is located on the experimental field site of the Julius Kühn Institute, Braunschweig, Germany. The soil was formed on a coarse-textured glacio-fluvial deposit and is classified as an Anthrosol according to the World Reference Base. Average sand, silt and clay contents were 59%, 36% and 5% respectively, and the soil was slightly acidic with an average pH value of 5.4. Mean annual temperature of the site is 8.8 °C and mean annual precipitation is 650 mm (average for the last 30 years). The sampled grassland and *Miscanthus* plantation were located directly next to one another, with the sampling plots being approximately 50 m apart. The *Miscanthus* plantation was initially established on former cropland in May 2009. In 2013, the first plantation was terminated, before a new plantation was established in 2014 on the same field. This adds up to 7 years of *Miscanthus* growth and one fallow year (2013–2014) before the first soil sampling in 2017. The plantation was an active variety trial with several different genotypes of *Miscanthus*. For this study, a *Miscanthus sacchariflorus* (MAXIM.) stand was sampled that was unfertilised and harvested once in April. The grassland was permanent, unfertilised grassland and had not been ploughed for several decades. It was not cut during the study period. The plant community consisted of approximately 60% grasses, mainly ryegrass (*Lolium perenne* L.), 30% herbs, mainly common yarrow (*Achillea millefolium* L.), common dandelion (*Taraxacum officinale*

L.) and narrowleaf plantain (*Plantago lanceolata* L.), and 10% legumes, mainly white clover (*Trifolium repens* L.).

### Belowground biomass and soil sampling and analyses

In the grassland, an area of approximately 8 × 8 m was selected for subsequent root sampling, commencing in April 2017. In the *Miscanthus* plantation, destructive sampling directly in the research plots was not possible. However, the trial was surrounded by an approximately 1 m-wide belt of *Miscanthus* rows, which could be sampled for this study. Between April 2017 and February 2018, the belowground biomass (roots of the grassland and rhizome and roots of *Miscanthus*) of both land-use types was sampled on six different dates, adhering to an approximate sampling interval of 2 months. The exact sampling dates were April 19, June 13, August 1, October 26, December 22 (all 2017) and February 15 (2018).

Belowground biomass samples were obtained in quadruplicate cores 6 cm in diameter to a depth of 100 cm using a machine-driven percussion coring system (Nordmeyer Geotool, Berlin, Germany). Soil cores were split into the following increments: 0–5 cm, 5–15 cm, 15–25 cm, 25–50 cm, 50–75 cm and 75–100 cm.

Moist field samples were stored at 6 °C until they were processed further (usually not longer than 1 week later). A hydropneumatic elutriation system (rootwasher) (GVF, Benzonia, MI, USA) was used to separate the plant parts from the soil (Smucker et al. 1982). This system uses a combination of water and air pressure to gently wash out roots, including the most fragile root structures, as well as other biological materials. After sorting out animals and green plant parts manually, all the samples were oven-dried at 60 °C, weighed, crushed and analysed for C and N by dry combustion in an elemental analyser (LECO TruMac, St. Joseph, MI, USA). The average C content of all belowground biomass samples was 377 g kg$^{-1}$, indicating a relatively low amount of mineral particles left in the samples. Root C and N stocks [Mg ha$^{-1}$] in each depth increment were calculated using the following equation (here for C):

$$C\,Stock_{BB} = \frac{DM_{BB} \times C\,content_{BB}}{Surface_{core} \times 10} \quad (1)$$

where $DM_{BB}$ is the dry belowground biomass [g], $C\,content_{BB}$ is the C content of the respective sample

[g kg$^{-1}$], and *Surface$_{core}$* is the surface area of the soil core used for sampling [cm$^2$].

During the first belowground biomass sampling campaign, soil pits were also dug in a central position in both sampling plots (grassland/*Miscanthus*) for basic soil characterisation. Undisturbed soil samples using sample rings (250 cm$^3$) and pooled disturbed samples were taken in 10 cm, 30 cm and 60 cm depth. Soil bulk density [g cm$^{-3}$] was determined gravimetrically after drying the undisturbed samples at 105 °C. Soil texture was measured using the pipette method based on sedimentation described by Moschrefi ([1983](#)) after sample pretreatment following DIN ISO 11277. Soil pH was measured in 0.01 M CaCl$_2$ solution in a solution-to-soil ratio of 2.5. Basic soil characteristics along the soil profiles are given in Table [1](#).

Stable isotope analysis and soil carbon stock calculation

*Miscanthus* is a C4 plant that discriminates the stable isotope $^{13}$C less than C3 plants during photosynthesis (Balesdent et al. [1987](#); Hatch and Slack [1969](#)). Thus, the difference in the $^{13}$C signature of *Miscanthus* and SOC, which was mainly built up by C3 plants, could be used to track the fate of *Miscanthus*-derived carbon in the soil. To estimate, how much *Miscanthus*-derived carbon entered the bulk SOC pool, the adjacent cropland was used as a reference (end-member). For this analysis, four additional cores were taken on the first sampling date in the *Miscanthus* plantation in proximity to the cores taken for belowground biomass analysis, and another four cores were taken from the adjacent reference cropland. Cores were split into the same depth increments as the belowground biomass cores, dried at 40 °C, sieved to 2 mm, weighed, crushed and analysed for C and N. For stable isotope analysis, the four cores of the adjacent cropland were pooled by depth, while in the *Miscanthus* soil the $^{13}$C signature of each core and depth was measured individually. To determine the $^{13}$C signature of the *Miscanthus* belowground biomass as the second end-member, a pooled biomass sample was used. The $\delta^{13}$C values were measured using an isotope-ratio mass spectrometer (Delta Plus, Thermo Fisher, Waltham, MA, USA) coupled to an elemental analyser (FLASH EA 1122 NA 1500; Wigan, United Kingdom). Resulting $\delta^{13}$C values [‰] were expressed relative to the international standard of Vienna Pee Dee Belemnite (V-PDB). To calculate the fraction [%] of *Miscanthus*-derived SOC ($f_M$) in each individual depth increment of the soil

under *Miscanthus*, the two-pool mixing model, as described by Balesdent et al. ([1987](#)), was used:

$$f_M = \frac{\delta_{MIS} - \delta_{CR}}{\delta_{MR} - \delta_{CR}} \times 100, \qquad (2)$$

where $\delta_{MIS}$ is the $\delta^{13}$C value of the soil under *Miscanthus*, $\delta_{CR}$ is the $\delta^{13}$C value of the cropland soil, and $\delta_{MR}$ is the $\delta^{13}$C value of the *Miscanthus* belowground biomass. The total SOC stock [Mg ha$^{-1}$] of the soil as well as the Miscanthus-derived SOC stock (*SOC Stock$_{MIS}$*) in each depth increment were then calculated as:

$$SOC\ Stock = \frac{mass_{finesoil} \times C\ content_{finesoil}}{Surface_{core} \times 10}, \qquad (3)$$

$$SOC\ Stock_{MIS} = f_M \times SOC\ Stock, \qquad (4)$$

where *mass$_{finesoil}$* is the mass of the soil with a particle size <2 mm [g] and *C content$_{finesoil}$* is the carbon content of the fine soil fraction [g kg$^{-1}$]. The depth distribution of *SOC Stock$_{MIS}$* was compared to the depth distribution of the standing belowground biomass C stock. Due to the unknown contribution of the preceding *Miscanthus* plantation (2009–2013) and the subsequent 1 year fallow phase to the total *SOC Stock$_{MIS}$*, it was not possible to directly estimate rates of BGCI and their stabilisation in the soil. However, correlation of both parameters was used as a proxy for the rate at which *Miscanthus* belowground biomass is transformed into bulk SOC.

Statistical analyses

Effects of land-use type for each sampling depth across all sampling dates as well as the sampling date within each land-use type on belowground biomass carbon and nitrogen stocks and C:N ratios were assessed using one-way (sampling date) and two-way (land-use type x depth) ANOVA. All data, except for the C:N ratios were log-transformed prior to analysis to ensure approximate normal distribution and variance homogeneity across groups. Tukey's HSD test was performed as a post-hoc test. Differences were assessed at a significance level of $p < 0.05$ and are given as letters and asterisks in the figures. Errors given in the text are standard errors. Statistics were performed in R version 3.5.2 (R Development Core Team [2010](#)).

**Table 1** Basic soil parameters of the investigated soils in three sampling depths: bulk density (BD) [g cm$^{-3}$], sand, silt and clay content [%], and pH of $CaCl_2$

| Depth | Grassland | | | | | Miscanthus | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | BD | Sand | Silt | Clay | pH | BD | Sand | Silt | Clay | pH |
| 10 cm | 1.46 | 70 | 22 | 8 | 5.1 | 1.48 | 67 | 26 | 7 | 6.0 |
| 30 cm | 1.72 | 67 | 27 | 6 | 5.4 | 1.70 | 41 | 55 | 4 | 4.3 |
| 60 cm | 1.60 | 70 | 25 | 5 | 6.9 | 1.66 | 70 | 25 | 5 | 4.8 |

## Results

### Average belowground biomass parameters and their depth distribution

In all depth increments, *Miscanthus* belowground biomass C stocks were significantly higher than grassland root C stocks. The average standing C stock of *Miscanthus* to a depth of 100 cm was 7.3 ± 1.1 Mg ha$^{-1}$, while that of grassland was 2.5 ± 0.1 Mg ha$^{-1}$ (Tab. S1). Belowground biomass C stocks declined significantly with increasing sampling depth (Fig. 1, Table 2). In 14 out of 24 grassland soil cores, no root biomass could be detected in 75–100 cm. The average rooting depth of the grassland was thus around 75 cm. For *Miscanthus*, the average root C stock in 75–100 cm depth (0.14 Mg ha$^{-1}$) was even slightly higher

than the average grassland root C stock in 15–25 cm (0.12 Mg ha$^{-1}$). This indicates that the root system of the *Miscanthus* plantation most likely exceeded the sampling depth of one metre. However this was not investigated.

In contrast to C, the belowground biomass N stocks were not significantly different between land-use types in the upper 15 cm of the soil (Fig. 2). In 0–5 cm depth, the average N stock of the grassland roots tended to be higher than that of the *Miscanthus* roots and rhizomes. Only below a sampling depth of 15 cm were significantly higher N stocks found in the *Miscanthus* belowground biomass, which however was only due to higher total belowground biomass, as indicated by the higher C stocks. The total average standing N stocks were 0.08 ± 0.09 Mg ha$^{-1}$ in the grassland and 0.10 ± 0.06 Mg ha$^{-1}$ in the *Miscanthus* plantation. The C:N ratio was generally much wider

**Fig. 1** Boxplots of belowground biomass carbon (C) stocks for grassland and *Miscanthus* by depth increment. Black dots indicate outliers. Grey asterisks indicate a significant difference ($p < 0.05$, log-transformed data) between land-use types
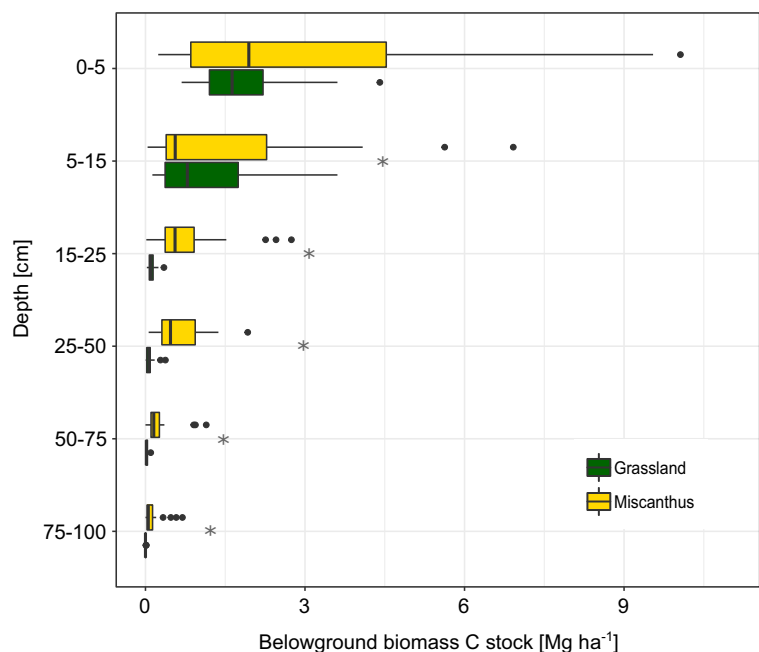
**Table 2** Summary of the analysis of variance to determine the effect of land-use type, depth increment and their interaction on belowground biomass carbon (C), nitrogen (N) and C:N ratio

| Dependent variable | Source | Sum of squares | Mean Square | F value | p value |
|---|---|---|---|---|---|
| Belowground biomass C | Land-use | 111.8 | 111.76 | 132.17 | <0.001 |
| | Depth | 575.2 | 115.03 | 136.04 | <0.001 |
| | Land-use x Depth | 43 | 8.59 | 10.16 | <0.001 |
| Belowground biomass N | Land-use | 0.92 | 0.916 | 5.45 | 0.02 |
| | Depth | 98.13 | 19.625 | 116.85 | <0.001 |
| | Land-use x Depth | 7.48 | 1.49 | 8.91 | <0.001 |
| Belowground biomass C:N | Land-use | 60,866 | 60,866 | 156.07 | <0.001 |
| | Depth | 4171 | 834 | 2.14 | 0.06 |
| | Land-use x Depth | 2988 | 596 | 1.52 | 0.18 |

For C and N, log-transformed data were used

in the *Miscanthus* roots and rhizomes as compared to the grassland roots (Fig. 3). On average across all sampling dates and depth increments, the grassland and *Miscanthus* belowground biomass had a C:N ratio of $28.6 \pm 0.5$ and $59.9 \pm 3.3$ respectively (Tab. S1). In both land-use types, no significant depth dependency of belowground biomass C:N ratios was detected (Fig. 3, Table 2). However, *Miscanthus* C:N ratios tended to be widest in the topsoil layers and outlying high C:N ratios of >100 were only detected in topsoil samples including rhizomes.

Seasonal dynamics of belowground biomass parameters

The grassland belowground biomass peaked in June, with average C and N stocks of $3.7 \pm 0.6$ Mg ha$^{-1}$ and $0.11 \pm 0.02$ Mg ha$^{-1}$ respectively (Figs. 4 and 5). However, due to high variability among the four cores at each sampling date, no significant effect of sampling date on C and N stocks in grassland roots was detected. The *Miscanthus* belowground biomass showed an almost opposite seasonal pattern for C and N stocks. The highest belowground biomass C and N stocks were



**Fig. 2** Boxplots of belowground biomass nitrogen (N) stocks for grassland and *Miscanthus* by depth increment. Black dots indicate outliers. Grey asterisks indicate a significant difference ($p < 0.05$, log-transformed data) between land-use types
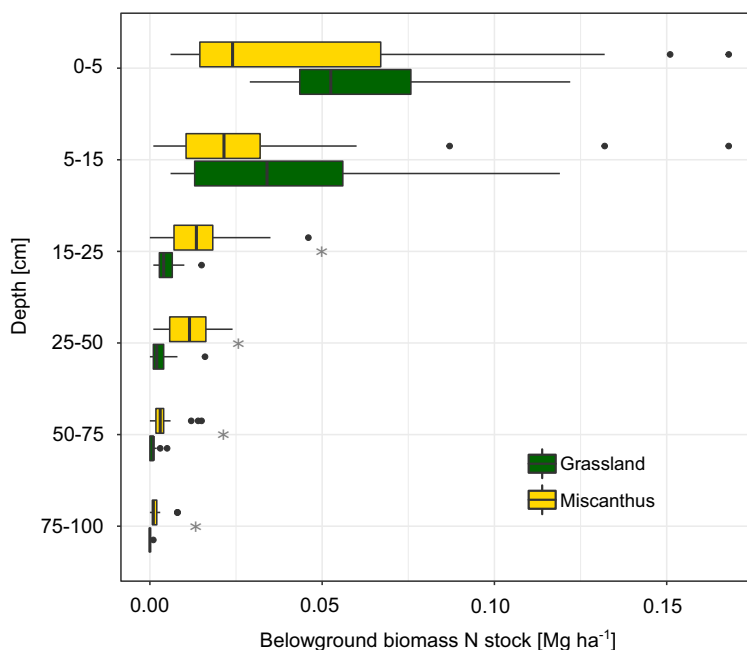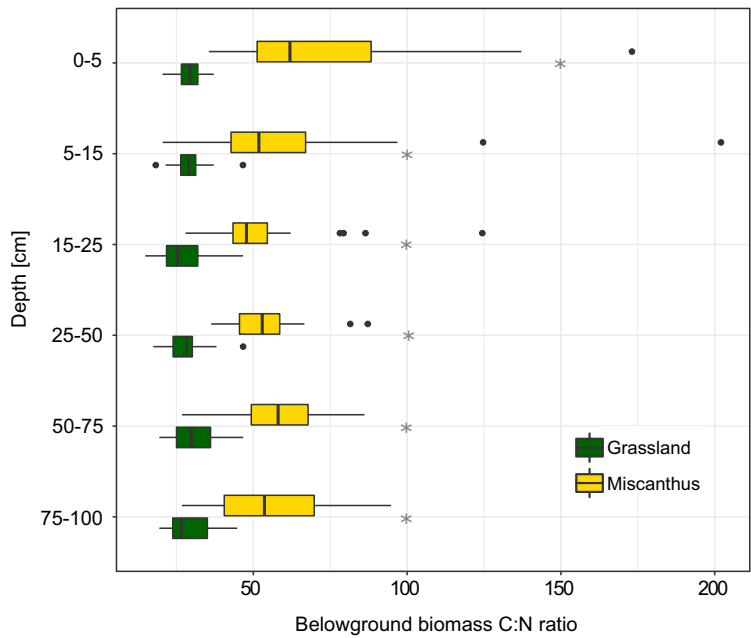
**Fig. 3** Boxplots of belowground biomass carbon-to-nitrogen ratios for grassland and *Miscanthus* by depth increment. Black dots indicate outliers. Grey asterisks indicate a significant difference ($p < 0.05$, log-transformed data) between land-use types



detected in April, i.e. before the previous year's aboveground biomass was harvested, and in February. In February, the C and N stocks of *Miscanthus* belowground biomass were significantly higher than in June (Figs. 4 and 5).

The root C:N ratio of the grassland followed a clear seasonal pattern, with a strong and significant increase in C:N ratio between April and June and a subsequent narrowing afterwards. Grassland roots thus had a significantly narrower C:N ratio in winter as compared to the growing season. For *Miscanthus*, no seasonal pattern in belowground biomass C:N ratio was detected. However, at any sampling date, it was much wider than that of the grassland roots (Fig. 6).

**Fig. 4** Boxplots of belowground biomass carbon (C) stocks as a function of sampling date for grassland and *Miscanthus*. Different letters within one land-use type indicate significant differences between sampling dates ($p < 0.05$, log-transformed data). Black dots indicate outliers. Note the different scales of the y-axes
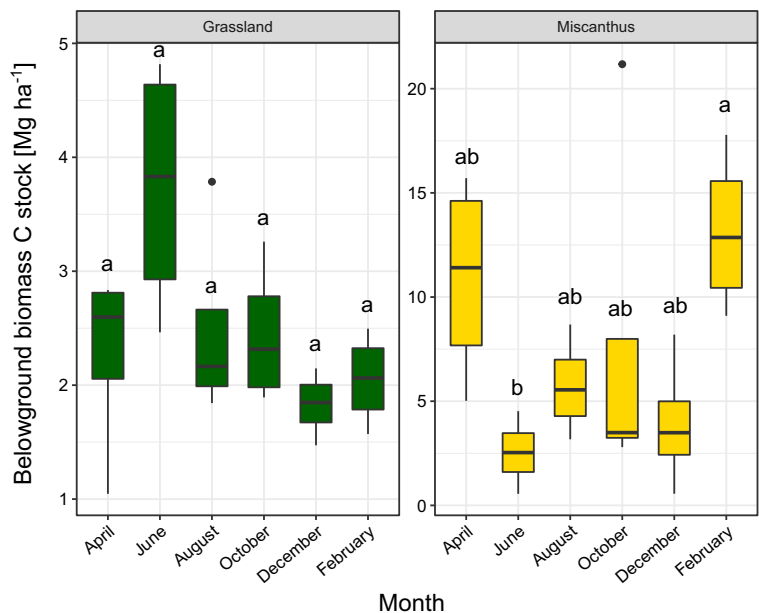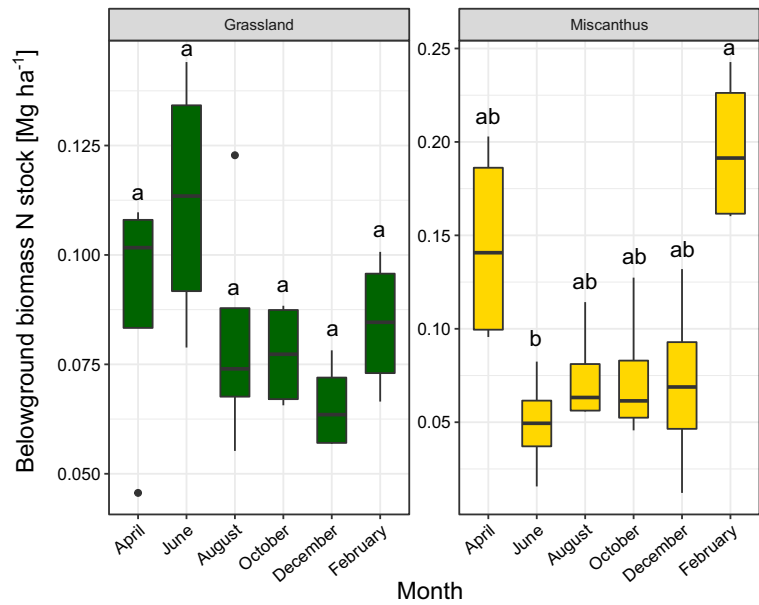
**Fig. 5** Boxplots of belowground biomass nitrogen (N) stocks as a function of sampling date for grassland and *Miscanthus*. Different letters within one land-use type indicate significant differences between sampling dates ($p < 0.05$, log-transformed data). Black dots indicate outliers. Note the different scales of the y-axes



### Fate of Miscanthus-derived carbon into the soil organic carbon pool

The average SOC stock in 0–100 cm under the *Miscanthus* plantation was $70.1 \pm 9.8$ Mg ha$^{-1}$. Of that, a total of $7.69 \pm 1.3$ Mg ha$^{-1}$ or $11 \pm 1.4\%$ was derived from *Miscanthus* inputs within 7 years. Most of these C inputs were located in the top 50 cm, where the

*Miscanthus*-derived SOC fraction ranged from $7 \pm 2\%$ (25–50 cm depth) to $24 \pm 2\%$ (0–5 cm depth) (Table 3). The highest absolute *Miscanthus*-derived SOC stock (SOC$_{MIS}$), however, was detected in the 15–25 cm depth increment and amounted to $3.3 \pm 0.8$ Mg C ha$^{-1}$. This might be a first indication of the fact that the rhizome, which is only located in 0–15 cm, is transformed into SOC at a much lower rate as compared to roots. Figure 7,

**Fig. 6** Boxplots of belowground biomass carbon-to-nitrogen (C:N) ratios as a function of sampling date for grassland and *Miscanthus*. Different letters within one land-use type indicate significant differences between sampling dates ($p < 0.05$, log-transformed data). Black dots indicate outliers. Note the different scales of the y-axes
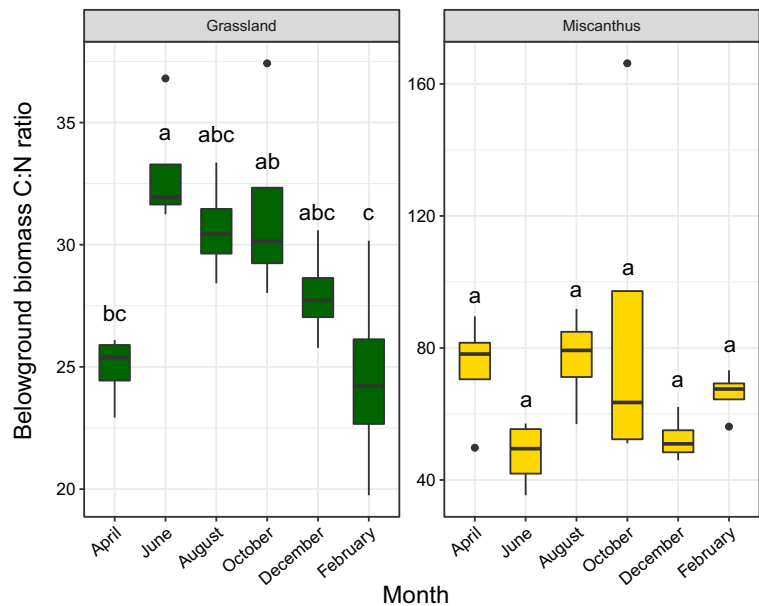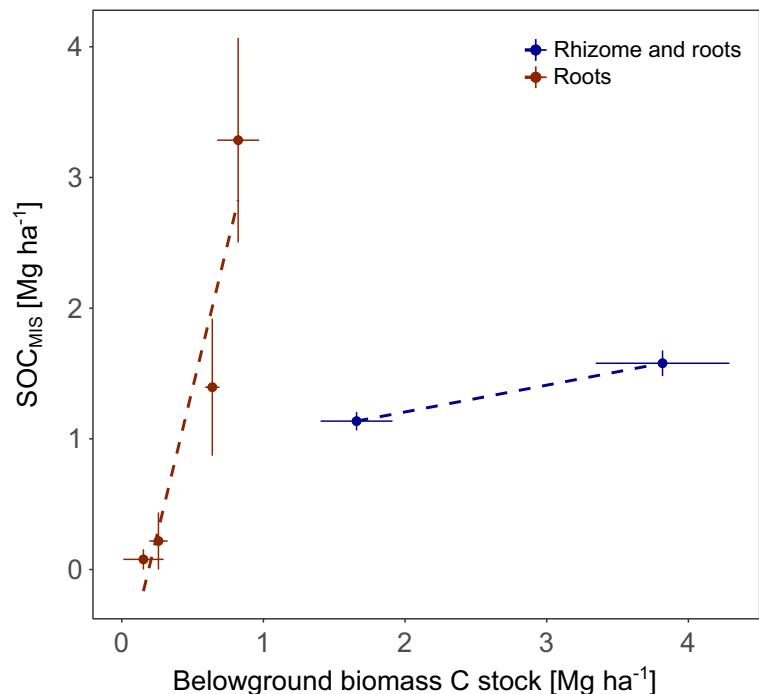
**Table 3** Average $\delta^{13}C$ values of the cropland (CR) and *Miscanthus* (MIS), fraction of *Miscanthus*-derived soil organic carbon ($f_M$) [%] and total *Miscanthus*-derived soil organic carbon stock (SOC$_{MIS}$) [Mg ha$^{-1}$] with standard error of the mean (SE) for all investigated depth increments [cm]

| Depth | $\delta13C_{CR}$ | $\delta13C_{MIS}$ | SE | $f_M$ | SE | SOC$_{MIS}$ | SE |
|---|---|---|---|---|---|---|---|
| 0–5 | −26.61 | −23.31 | 0.29 | 24.12 | 2.12 | 1.58 | 0.09 |
| 5–15 | −26.78 | −24.26 | 0.25 | 18.22 | 1.82 | 1.14 | 0.07 |
| 15–25 | −26.75 | −23.58 | 0.70 | 23.02 | 5.10 | 3.29 | 0.78 |
| 25–50 | −26.06 | −25.09 | 0.26 | 7.42 | 1.99 | 1.40 | 0.52 |
| 50–75 | −25.21 | −25.14 | 0.41 | 2.56 | 2.56 | 0.22 | 0.21 |
| 75–100 | −25.05 | −25.41 | 0.41 | 2.31 | 2.31 | 0.08 | 0.07 |

in which SOC$_{MIS}$ of each depth increment is plotted against the average belowground C stock of each depth increment, underlines this. While a strong positive correlation of SOC$_{MIS}$ and belowground biomass C stock was found for rhizome-free depth increments, the topsoil depth increments (0–15 cm) showed a very distinct pattern: in those increments, the SOC$_{MIS}$ relative to the belowground C stock was much lower than for the rhizome-free increments. Furthermore, SOC$_{MIS}$ did not differ much between 0 and 5 cm and 5–15 cm, while average belowground biomass C stocks were twice as high in 0–5 cm as compared to 5–15 cm (Table 3).

## Discussion

### Belowground biomass carbon and nitrogen stocks, C:N ratios and their depth distribution

The investigated belowground biomass parameters differed strongly between grassland and *Miscanthus*. The total belowground biomass of the *Miscanthus* plantation, as expressed in C stocks in this study, was three times the root biomass of the grassland. The belowground biomass C stocks determined were therefore well in line with values found in the literature: on an



**Fig. 7** *Miscanthus*-derived soil organic carbon (SOC$_{MIS}$) as a function of average belowground biomass carbon (C) stock for those depth increments containing rhizome and roots (0–5 cm > 5–15 cm) as well as depth increments containing only roots (15–25 cm > 25–50 cm > 50–75 cm > 75–100 cm)

Irish *Miscanthus* plantation, Clifton-Brown et al. (2007a) detected a total belowground biomass of 20.7 Mg dry mass ha$^{-1}$, which is similar to the 7.3 ± 1.1 Mg C ha$^{-1}$ found in the present study. Furthermore, the grassland root C stock of 2.5 ± 0.3 measured in this study comes close to the average root C stock of 3.4 ± 1.1 Mg C ha$^{-1}$, as detected by Poeplau et al. (2018c) in seven different temperate grasslands with varying fertilisation regimes. These huge differences in belowground biomass, and thus potentially also in belowground carbon inputs between the two land-use types, should lead to increased SOC stocks following a land-use change from grassland to *Miscanthus*. However, while C sequestration at high rates is often reported for conversions from arable land to *Miscanthus* (Dondini et al. 2009; Poeplau and Don 2013; Zimmermann et al. 2011), no significant effect was found for *Miscanthus* establishment on grassland soils (Zatta et al. 2014; Zimmermann et al. 2011). Zatta et al. (2014) hypothesise that this might be related to a rhizosphere priming effect, i.e. that higher BGCI might catalyse microbial activity and thus increase mineralisation of organic matter (Kuzyakov 2002). Priming is however unlikely to constantly offset increased organic matter inputs. An alternative explanation could be that timespans of 2 to 6 years are simply not long enough to detect changes in SOC stocks after land-use change. A first indication for an increase in SOC content after a land-use change from grassland to *Miscanthus* plantation was found by Poeplau et al. (2018a), who determined C contents in 0–5 cm depth of 15.5 g kg$^{-1}$ under a reference grassland and 18.3 g kg$^{-1}$ under a 22-year-old *Miscanthus* plantation. However, a whole-profile assessment of SOC stock changes after long-term *Miscanthus* cultivation on former grassland soil is lacking. In the present study, a comparison of the two land-use types was not meaningful since the *Miscanthus* was recently converted from a cropland soil, while the grassland had had no change in land-use for a long time.

The total amount of *Miscanthus*-derived SOC was 7.2 ± 1.2 Mg ha$^{-1}$. Thus, averaged over the whole soil profile (0–100 cm depth), SOC consisted of 10% *Miscanthus*-derived SOC. This is well in line with the proportions observed by (Zatta et al. 2014) after 6 years, i.e. up to 18.3% in 0–15 cm and up to 10.6% in 15–30 cm. Interestingly, the *Miscanthus*-derived SOC stock in 0–5 and 5–15 cm was comparable to that in 25–50 cm, despite a much greater belowground biomass C stock in the upper layers (Fig. 7). This can be explained by the fact that a major part of the belowground biomass close to the surface consists of rhizome, which has a much higher lifespan than roots. While roots of grasses in temperate ecosystems are usually turned over completely within 2 to 3 years (Gill and Jackson 2000), parts of the rhizome outlive the whole rotation period of a *Miscanthus* plantation, which is between ten and 20 years (Christian et al. 2009). The isotopic signal of the bulk SOC thus reflects the distinct turnover patterns of the different belowground organs of rhizomatous plants. The slow turnover of the rhizome, which accounts for a large part of the total belowground biomass in the topsoil (Clifton-Brown et al. 2007b), might be an additional explanation for the lack of studies reporting increased SOC stocks after conversion from grassland to *Miscanthus* plantation.

The depth distribution of the belowground biomass in both land-use types followed a Michaelis-Menten type of shape, with a sharp decline with increasing depth in both land-use types (Jackson et al. 1996; Kätterer et al. 2011). However, hardly any grassland roots were detected below 75 cm depth, while the belowground biomass of *Miscanthus* was likely to exceed a depth of one metre. Thus, *Miscanthus* not only produced a higher amount of belowground biomass, but rooting depth was also much greater, indicating that i) the absolute differences in belowground biomass C and N stocks between the two land-use types were even higher than determined, and ii) *Miscanthus* is most likely an efficient crop for improving subsoils, including for increasing subsoil SOC stocks. This is well in line with the observations of Neukirchen et al. (1999), who detected *Miscanthus* roots down to a maximum depth of 250 cm in a sandy loam soil. However, coarse-textured soils are found to have a shallower rooting depth as compared to loamy soils (Madsen 1985). Depending on the particle shape, this might be related to greater soil strength and thus reduced rootability of sandy subsoils (Lipiec et al. 2016), which might also explain the shallow rooting depth of the grassland in the present study as compared to other studies (Jackson et al. 1996; Poeplau et al. 2018c).

Apart from the differences in belowground biomass C stocks between the two land-use types, strong differences were also detected in root C:N ratio. The average C:N ratio in *Miscanthus* belowground biomass (~60) was twice the average C:N ratio in the grassland roots (~28). Extreme values for *Miscanthus* were up to 200, while those C:N ratios >100 were restricted to those

topsoil samples with a very high belowground biomass. Although the rhizome was not separated from the root samples, it was obviously the rhizome that was characterised by such wide C:N ratios. The wide C:N ratios in the rhizome were somewhat unexpected, since it plays a key role in the nutrient economics of *Miscanthus* (Lewandowski et al. 2000). Yet, the generally low nitrogen demand of *Miscanthus*, which has been demonstrated in fertilisation experiments (Amougou et al. 2011; Clifton-Brown et al. 2007b), is reflected in the wide C:N ratio of its biomass. A certain proportion of the measured differences between grassland and *Miscanthus* root C:N ratios might also be explained by the presence of N-fixing legumes in the grassland. However, the observed range in C:N values in the grassland roots of ~25–35 is typically also observed in the roots of other perennial, non-rhizomatous grass species (Herman et al. 1977).

The difference in root C:N ratios between the two land-use types is likely to strongly affect SOC dynamics. Despite a large number of published decomposition experiments related to varying detritus C:N ratios (Enríquez et al. 1993), it is still difficult to predict how this would affect the long-term fate of C in the soil. This is due to opposing effects of substrate C:N ratio on the decomposition rate ($k$), i.e. the time needed to decompose the substrate, and humification rate ($h$), i.e. the transfer rate of C from the labile to the more stabilised SOC pool (Nicolardot et al. 2001). While a strong negative correlation of $k$ and C:N ratio is well established (Enríquez et al. 1993), it has also been shown that increasing N availability leads to greater stabilisation of residues in the soil (Kirkby et al. 2014), which might be explained by greater microbial carbon use efficiency (Manzoni et al. 2017), i.e. a higher proportion of carbon allocated to growth.

## Seasonal pattern of belowground carbon and nitrogen stocks and C:N ratio

For some of the investigated parameters, a clear seasonal pattern was found that differed greatly between land-use types. The grassland tended to have the peak belowground carbon and nitrogen stocks in June, which coincides roughly with the timing of peak aboveground biomass in temperate grasslands (Flanagan and Johnson 2005). During this phaenological phase, the demand for water and nutrients is highest, thus the grassland plant community also invests in additional

roots to maximise the uptake of such resources. Carbon and nitrogen stocks of the grassland belowground biomass tended to be lowest in December and February, which can be explained by the lowest demand for belowground resources during this period. In the grassland, the clearest seasonal pattern was observed for the C:N ratio of the belowground biomass. Between April and June, it increased significantly from 25 to 33, indicating a strong mobilisation of nitrogen from the roots, which could not be seen in the total N stock since new root biomass was simultaneously produced. The strong remobilisation of root nitrogen for shoot and leaf growth, especially at the start of the vegetation period, matches findings of a ^{15}N-labelling study: Ourry et al. (1988) found that after defoliation of ryegrass, the plants relied solely on organic nitrogen remobilisation from roots during the first 6 days of regrowth, and only after this initial phase was additional inorganic nitrogen taken up. Although the grass in the present study was not cut during the year of observation, a similar remobilisation of N from roots after the start of the vegetation period is likely. After the peak in June, C:N ratios of the grassland roots started to decline slightly. Between October and February, i.e. after the end of the growing season, C:N ratios dropped significantly, which points to N translocation from shoots to roots. Certainly, aboveground biomass harvest would have changed the results of the present study, since it has been found to strongly impact C and N allocation to belowground organs (Guitian and Bardgett 2000; Louahlia et al. 2000). An uncut grassland might not reflect the average situation in an agricultural landscape of central Europe. However, this way the comparison between grassland and *Miscanthus* was less confounded from an ecophysiological point of view: during the whole observation period, only the senescent Miscanthus biomass of the preceding year was cut, while no further management intervention occurred between April 2017 and February 2018.

The seasonal pattern of *Miscanthus* belowground biomass parameters differed strongly from that of the grassland. Belowground biomass C and N stocks were highest in February and April and significantly lowest in June. This opposite pattern can most likely be explained by the resource economy of a rhizomatous plant. Not only nitrogen, but carbon as well is translocated to the rhizome and stored there during winter and remobilised during the growing season (Granéli et al. 1992; Price et al. 2002). At the investigated site, the senescent *Miscanthus* was harvested in late April, i.e. after the first

root-sampling event. The strong decline in C and N stocks in the belowground biomass of *Miscanthus* can only be explained by the onset of aboveground growth. Therefore the magnitude of remobilised N (~100 kg) is well in line with the fluxes found in other studies (Himken et al. 1997; Strullu et al. 2011). The very steady belowground C and N stocks between June and December as well as the strong increase between December and February fit the observed pattern at the early regrowth stage. Interestingly, despite these high internal nutrient translocation rates, no seasonal pattern for the belowground biomass C:N ratio was detected. This is most likely due to contrasting and superimposing patterns in the rhizomes and roots of *Miscanthus*. Unfortunately, no distinction was made between these belowground components in this study.

Certainly, aboveground biomass harvest in the grassland would have changed the results of the present study, since it has been found to strongly impact C and N allocation to belowground organs (Guitian and Bardgett 2000; Louahlia et al. 2000). Uncut and unfertilized grassland might not reflect the average situation in an agricultural landscape of central Europe. However, in this way the comparison between grassland and *Miscanthus* was the least confounded from an ecophysiological point of view: during the whole observation period, only the senescent *Miscanthus* biomass of the preceding year was cut in April 2017, while no further management intervention occurred between April 2017 and February 2018. Since the last grassland cut occurred in autumn 2016, both systems had comparable starting conditions with the onset of the vegetation period in 2017 and also comparable conditions thereafter.

Implications for modelling of organic carbon dynamics and root sampling

Large differences were found in total belowground biomass, rooting depth and C:N ratio of the belowground biomass between *Miscanthus* and grassland. Such data is of immense importance for estimating total BGCI and their fate in the soil. It has been suggested that the C:N ratio of substrates is a major quality criterion driving their stabilisation in the soil, and thus important for SOC dynamics in the long term (Manzoni et al. 2017; Wutzler et al. 2017). However there is still limited understanding of the processes involved and the net effect of substrate C:N ratio on SOC build-up, hampering its inclusion in most SOC turnover models. In the likely case that

substrate C:N ratio affects the decomposition rates and humification coefficients at the same time and thus long-term SOC dynamics, the results of the present study suggest that a land-use change from grassland to *Miscanthus* plantation would not be captured correctly if a model ignores such dependencies. For this specific land-use change, however, there is a lack of long-term SOC datasets (>10 years) that could be used to parametrise a substrate C:N ratio dependency. Furthermore, for SOC modelling in *Miscanthus* plantations, it is important to parametrise roots and rhizomes separately due to the presumed differences in turnover rates.

The pronounced and land-use type-specific seasonal pattern of the investigated parameters reveals that belowground biomass characterisation at one specific point in time is problematic. This is especially true when two or more different land-use types are compared: for example, due to opposing seasonal patterns in belowground biomass C and N stocks, a comparison between the two land-use types is highly sensitive to sampling date. For a robust estimate of average standing belowground biomass and associated parameters in perennial plant communities, sampling should be undertaken at least twice. The exact timing might thereby depend on the question and the type of ecosystem. For the two investigated systems, a sampling in summer at peak biomass combined with a sampling in winter should give a good average estimate as well as an indication for possible extremes.

## Conclusions

Knowledge about the quantity, quality and seasonal dynamics of root biomass in perennial systems is scarce. This imposes considerable uncertainty in soil carbon models, which are highly sensitive to carbon input. This study provides important insights into the belowground biomass C and N dynamics of two contrasting perennial land-use types. Furthermore, it has been demonstrated that a representative assessment of belowground biomass parameters, like those of aboveground biomass, requires a consideration of its seasonal dynamic. This is especially crucial when two different land-use types are to be compared. The relatively low *Miscanthus* signal in topsoil SOC suggested a slow turnover of rhizome-derived carbon, which needs to be taken into account when estimating the belowground carbon inputs of rhizomatous plants. Finally, the large differences between

grassland and Miscanthus belowground biomass, especially in deeper soil layers, are likely to lead to SOC sequestration in the long term. Deep rooting plants are also important for soil structure and are more drought resistant than less deep rooting plants. Together with the fact that large amounts of biomass are produced with low fertilizer supply this makes *Miscanthus* an interesting and climate-smart biomass crop, while the current global market is still small.

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