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Estimating root: shoot ratio and soil carbon inputs in temperate grasslands with the RothC model

Christopher Poeplau

Abstract

Background and aims Carbon inputs to soil are mostly site- and management-nonspecific estimates based on measured yield. However, in grasslands most carbon input is root-derived and plant carbon allocation patterns are known to vary strongly across sites and management regimes. The aim here was to estimate carbon inputs by fitting the RothC model to time series of soil organic carbon (SOC) data from field sites and to explain the observed variability in root: shoot ratio (R:S).
Methods Time series of SOC stocks in 15 different temperate grasslands were simulated using eight different literature-derived R:S values, which were compared to the optimised, site-specific R:S. The model-derived root inputs were validated with literature-derived root biomass data.
Results A single, static R:S for yield-based carbon input estimation for all grasslands was not appropriate. Nitrogen fertilisation ($R^2 = 0.57$) significantly reduced the optimised R:S, which can be explained by the higher investment of plants in roots for nitrogen acquisition under nitrogen deficiency. The average R:S derived was 5.9 ± 1.9 for unfertilised soils and 2.4 ± 1.5 for fertilised soils.
Conclusions The results enable distinction of unfertilised and fertilised temperate grasslands

regarding carbon input parameterisation for the RothC model and highlight the importance of nutrient regime for the carbon cycle.

Introduction

Grassland ecosystems can be considered particularly important for the global carbon (C) cycle for three reasons: 1) Grassland soils have high soil organic carbon (SOC) stocks, due to high belowground productivity, e.g. Bolinder et al. (2012) found four-fold more roots under leys than under cereal crops; 2) grasslands occupy 68 % of global agricultural area (Leifeld et al. 2015).; and 3) compared with forests, which are ecosystems with similarly high SOC stocks (Poeplau and Don 2013), human interventions in grasslands are far more frequent, leading to a higher impact of management on carbon fluxes (Soussana et al. 2004). In total, grassland soils are estimated to store 295 GT of carbon (Bolin et al. 2000).

For reliable predictions of carbon fluxes and SOC stocks in grasslands under climate change or other alterations in environmental conditions or management, precise understanding of the processes and process rates involved is needed. Carbon turnover models such as RothC (Coleman and Jenkinson 1996), ICBM (Andrén and Kätterer 1997), C-TOOL (Taghizadeh-Toosi et al. 2014) and CANDY (Franko et al. 1997), are widely

C. Poeplau (✉)
Thuenen Institute of Climate-Smart Agriculture, Bundesallee 50, 38116 Braunschweig, Germany
e-mail: christopher.poeplau@thuenen.de

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used for regional- to continental-scale SOC stock projection (Andrén et al. 2008; Borgen et al. 2012; Gottschalk et al. 2012). The advantage of such simple models over more complex process models such as CENTURY (Parton et al. 1988), DNDC (Li et al. 1997) or DAISY (Svendsen et al. 1995) is the relatively small number of required input parameters, which most closely reflects the availability of parameters on larger scales. As a simplification, constant model parameters, often obtained only from a single calibration site (RothC, ICBM), are modified by site-specific properties. For instance, the decomposition rate constants of different model pools are modified by soil temperature, based on the temperature-dependency of microbial activity (Zak et al. 1999). Soil moisture and texture are also important drivers of SOC decomposition and are integrated into the majority of SOC models in different ways; although it is well established that SOC stocks are strongly input-driven (Christopher and Lal 2007; Kätterer et al. 2012), it is mostly only the carbon output (decomposition) that is well parameterised in those models.

Plant litter-derived carbon input, in contrast to decomposition rate, is treated as a static parameter estimated with yield-based allocation functions (Bolinder et al. 2007), although it has been shown that plant carbon allocation patterns, especially the partitioning of carbon assimilates into above- and belowground organs, are highly sensitive to environmental constraints and management. Soil moisture, nutrient availability, bulk density, soil shear strength, soil texture, salinity and, in grasslands, also cutting/grazing regime and species composition, have been found to influence rooting pattern and thus carbon inputs to the soil (Ericsson 1995; Jones 1983; Mueller et al. 2013; Munns 2002). It is therefore an oversimplification to use a static, constant root: shoot ratio (R:S) for the wide range of grassland management regimes and environmental conditions that exist world-wide. Scanning the literature reveals possible R:S values in grassland ranging from >10 (Fiala 2010) to 0.8 (Kuzyakov and Domanski 2000). In a large survey on the Tibetan plateau (112 sites), Yang et al. (2009) found a median R:S value of 5.8, but a range of 0.8–13. This illustrates the magnitude of the uncertainty in a single, static R:S, as usually used to estimate carbon input in carbon models.

Root-derived carbon (root biomass and rhizodeposits) is the major source of SOC and may be the main reason why grasslands store more SOC than arable land (Bolinder et al. 2012; Franzluebbers 2012). Rasse et al. (2005) suggested that SOC in general is mainly root-derived. In managed grasslands, the majority of the above-ground biomass is removed by cutting or grazing, so the majority of the total carbon input is root-derived. However, the actual amount of root-derived carbon is difficult to assess experimentally, since it comprises root exudates and rhizodeposits with high turnover (Hertel and Leuschner 2002). Thus, root-derived carbon input data are rarely available as model input and hence values have to be estimated using allocation functions. Each model uses specific allocation functions derived from sources ranging from regional datasets (Bolinder et al. 2007) to pot experiments (Kuzyakov and Domanski 2000). However, to our knowledge, none of the models listed, with the exception of C-TOOL, has calibrated or tested the given allocation function for grasslands. This might be attributable to the lack of well-documented, globally representative long-term grassland experiments needed for model calibration (Debreczeni and Körschens 2003). A further difficulty in perennial systems compared with annual cropland is that measured root biomass stocks do not correspond to root litter input as annual carbon input to the soil. Instead, only a certain part of the total root biomass is turned over annually. In a global meta-analysis, Gill and Jackson (2000) found root turnover in grasslands to be temperature-dependent, with an average root turnover of 0.5 yr.$^{-1}$ for grasslands in the temperate climate zone, which is in line with the range of 2–3 years for complete turnover of grassland roots derived from a global compilation of 45 sites (Fiala 2010).

In the RothC model, plant-derived carbon input estimation is solved analytically, by calculating the annual input needed to obtain the given SOC stock under steady-state conditions. However, this approach cannot be used when: i) SOC stock is not in steady state or ii) the model application is to determine whether the SOC stock of a specific site or region is in steady state or not. Thus, in all projections for which the actual SOC level is known but historical land use and management is unknown, carbon inputs have to be estimated (Wiesmeier et al. 2015). However, it is not documented which input estimation should be used to best fit the RothC parameterisation. The aims of this study were thus to identify: i) the most appropriate carbon input estimation function for temperate grasslands in the RothC model and ii) site-specific optimum allocation coefficients and

explain them with pedo-climatic or management variables. To examine the importance of carbon input for model output, the hypothesis that the model is more sensitive to variation in R: S than to similar relative variation in any decomposition rate modifier was also tested.

Material and methods

Concept and carbon input estimation

We fitted the RothC model with the standard parameterisation to time series of SOC data (at least three points in time) for permanent grasslands for which climate, basic soil characteristics, yield and management data were available. The only unknown was thus the total annual carbon input, which we optimised to fit the model to the observed data. RothC was thus used inversely with the goals of: i) estimating the actual R:S for each specific site and ii) identifying the most appropriate allocation function (for each site and on average) based on measured data that could be used as a default coefficient in the RothC model in future SOC projections. To do so, we derived the total carbon input by applying a range of different allocation functions or R: S values found in the literature to the reported amount of harvested biomass. We selected studies that are already used in carbon models (Bolinder et al. 2007; Kuzyakov and Domanski 2000) or reviews that comprehensively synthesise R:S values for a large number of grasslands (Fiala 2010; Jackson et al. 1996) and might thus have the potential to be included in carbon models. Based on the selected R: S values, which ranged from 0.81 to 8 (Table 1), eight different total annual carbon input values were calculated for each site (seven different R:S plus the average of all). Since the amount of above-ground biomass was crucial in this approach, pastures (grasslands grazed by animals) were excluded and only meadows (mown grasslands) in which the harvested biomass was actually measured were used. Total carbon input was calculated using the following eqs. And assumptions:

$$\text{ANPP} = \frac{HB}{0.7} \times 0.45 \tag{1}$$

where ANPP is aboveground net primary production [Mg C ha^{-1} yr.$^{-1}$] and HB is harvested biomass [Mg

DM ha^{-1} yr.$^{-1}$]. It was assumed that HB accounted for 70 % of total ANPP (Christensen et al. 2009), since: i) a certain fraction of biomass accrual occurs after the last cut and is turned over in winter, ii) some of the cut material is not harvested and weighed and iii) a certain fraction remains as standing live biomass. The grass biomass was assumed to contain a carbon concentration of 45 % (Kätterer et al. 2011). When organic fertiliser was applied (manure or slurry), German default values for dry matter content and carbon concentration were used to calculate the total fertiliser-derived carbon input (FC_{in}) [Mg ha^{-1} yr.$^{-1}$]. The total aboveground carbon input (AC$_{in}$) [Mg ha^{-1} yr.$^{-1}$] was successively calculated as:

$$AC_{in} = \frac{\text{ANPP} \times 0.3}{2} + FC_{in} \tag{2}$$

where $ANPP \times 0.3$ is the part of ANPP that is not harvested. It was further assumed that only 50 % of that fraction is turned over annually and becomes available for soil organic matter formation (Schneider et al. 2006). The total belowground net primary production (BNPP) [Mg C ha^{-1} yr.$^{-1}$] was calculated as:

$$\text{BNPP} = \text{ANPP} \times R : S_i \tag{3}$$

where $R : S_i$ is the individual R:S as listed in Table 1. In this study, R: S thus refers to ANPP:BNPP. According to the well-constrained annual root turnover of 50 % in the temperate zone (Gill and Jackson 2000), the total annual belowground carbon input (BC_{in}) [Mg ha^{-1} yr.$^{-1}$] was calculated as:

$$BC_{in} = \frac{\text{BNPP}}{2} \tag{4}$$

In long-term experiments or soil monitoring sites, SOC concentrations are mostly only determined in the topsoil to a maximum depth of 30 cm. Although the majority of the root biomass is located in the topsoil, most plant roots extend to much greater depth. To determine the fraction of total BNPP that is distributed to a certain sampling depth d [cm], the Michaelis-Menten-type function as described by Kätterer et al. (2011) was used:

$$BNPP_d = \frac{d \times (d_{50} + d_r)}{d_r \times (d_{50} + d)} \tag{5}$$

where d_r is maximum rooting depth and d_{50} is the depth to which 50 % of the total BNPP is distributed. The d_{50}

Table 1 Reported average root:shoot ratio (R:S) values included in the analysis with their source (Reference), a description of the study (species, grassland type, origin of the included data), whether rhizodeposition is included in the estimate and the model in which the respective ratio is officially implemented

Reference	R:S	Species/ grassland type/ origin	Rhizodep.	Model
Fiala 2010	8	Calamagrostis villosa, unmanaged	yes	
Jackson et al. 1996	3.7	Global temperate grasslands	no	
Bolinder et al. 2007 (1)	3.34	Grassland/pasture (mainly Northern America)	yes	ICBM new
Luo	2.03	Chinese steppe grass species	no	
Bolinder et al. 2007 (2)	1.27	Different grass species (mainly Northern America)	yes	ICBM new
Kuzyakov and Domanski 2000	0.96	Different grass species (pot/field experiments)	yes	ICBM old
Christensen et al. 2009	0.81	Ryegrass, meadow fescue, timothy ley mix	yes	C-TOOL
Average of All	2.87			

was set to 15 cm and d_r to 150 cm, to fit the observed average grassland root distribution in a global meta-analysis (Jackson et al. 1996), where 44 % of the total root biomass was found in the upper 10 cm.

Finally, the total carbon input (TC_{in}) [Mg ha^{-1} yr.$^{-1}$] to a certain depth d was calculated as:

$$TC_{ind} = BC_{in_d} + AC_{in} \qquad (6)$$

Study sites and model initialisation

A total number of 15 temperate grasslands at 13 different sites (Europe and USA) were modelled (Table 2) to estimate R:S. Monthly average values for temperature, precipitation and potential evaporation were obtained from publications, data holders or the weather data grid of the German Meteorological survey (DWD). The grasslands used varied strongly in soil texture (1–70 % clay), climate parameters (4.1–11.5 °C mean annual temperature (MAT), 392–969 mm mean annual precipitation (MAP), 551–785 mm potential evaporation), fertilisation regime (0–460 kg N ha yr.$^{-1}$) and cutting frequency (0–3.5 cuts per year) (Table 3).

Modelling was performed in the R environment, using the package SoilR, in which the RothC model is implemented (Sierra et al. 2012). The RothC model consists of five different pools with the following decomposition rate constants, k, in a first-order decay: depleted plant material (DPM, k = 10), resistant plant material (RPM, k = 0.3), microbial biomass (BIO, k = 0.66), humified organic matter (HUM, k = 0.02) and inert organic matter (IOM, k = 0). Initial pool distribution was estimated based on total SOC stock and clay content, using the pedotransfer-functions

described by Weihermueller et al. (2013) (active pools) and Falloon et al. (1998) for IOM. The DPM/RPM ratio for plant material was set to 1.44 in fertilised grasslands and 0.69 in unfertilised. Carbon inputs from manure were split in the DPM/RPM/HUM ratio of 49/49/2, as described in the RothC documentation, which can be downloaded at www.rothamsted.ac.uk/sustainable-soils-and-grassland-systems/rothamsted-carbon-model-rothc.

Statistics and validation

Root mean square error (RMSE) was used to evaluate the model performance with each of the individual R:S values. In addition, RMSE was minimised by manually optimising the R:S. This was done by approximating the local minimum to the second decimal place. The site-specific region of the local minimum in RMSE was thereby derived from the model runs with the eight individual R:S values (Table 1). To avoid overrepresentation of sites with high variation in SOC content over time, each individual RMSE ($RMSE_i$) was normalised by the optimised RMSE ($RMSE_{opt}$) of each grassland modelled:

$$RMSE_{norm} = RMSE_i - RMSE_{opt} \qquad (7)$$

The performance of each R:S considered compared with the best fit possible, not compared with the data points directly, was thus evaluated. Linear mixed effect models (lme in the R package nlme) (Pinheiro et al. 2009) were used to explain the variability in modelled optimised R:S with site-specific pedo-climatic (clay content, MAT, MAP, potential evaporation) and management variables

Table 2 List of grassland sites included in the analysis with identification number (ID), country, reference, duration [years], number of soil organic carbon measurements available (SOC) and sampling depth (Depth) [cm]

ID	Site	Country	Reference	Duration	SOC	Depth
1	Rothamsted Park Grass unfertilised	UK	original data	160	9	23
2	Rothamsted Park Grass 96 kg N	UK	original data	158	5	23
3	Rothamsted Park Grass Manure	UK	original data	160	5	23
4	Schleswig Holstein soil monitoring site 8	Germany	original data	18	6	10
5	Schleswig Holstein soil monitoring site 26	Germany	original data	18	6	10
6	Schleswig Holstein soil monitoring site 28	Germany	original data	18	6	10
7	Schleswig Holstein soil monitoring site 35	Germany	original data	6	3	10
8	Schleswig Holstein soil monitoring site 38	Germany	original data	6	3	10
9	Baden-Württemberg soil monitoring site 31	Germany	original data	19	3	40
10	Fischweier	Germany	Werth et al. 2005	27	8	8
11	Hepsisau	Germany	Werth et al. 2005	27	8	8
12	Melchingen	Germany	Werth et al. 2005	27	8	8
13	St. Johan	Germany	Werth et al. 2005	27	8	8
14	Askov	Denmark	Christensen et al. 2009	5	6	20
15	Swift Current	USA	Campbell et al. 2000	10	4	15

(cutting frequency, total N input). Therefore, site was used as a random effect, to account for the fact

Table 3 General site description for the grassland sites included in the analysis with site identification number (ID), clay content [%], mean annual temperature (MAT) [°C], mean annual precipitation (MAP) [mm], potential evaporation [mm], amount of annual nitrogen (N) input (organic and inorganic combined) [kg N ha^{-1} yr.$^{-1}$] and annual cutting frequency (Cuts)

ID	Clay	Cuts	N	MAT	MAP	Evaporation
1	23	2	0	9.2	704	599
2	23	2	96	9.2	704	599
3	23	2	76*	9.2	704	599
4	13	3	409	8.3	840	564
5	4.5	3.5	195	8.5	802	575
6	9.5	5	460	8.7	765	580
7	12	2.5	NA	8.3	788	564
8	1	1	122	8.6	742	573
9	60	2	130	7.3	954	551
10	9	0	0	11.5	794	615
11	51	0	0	7.6	969	551
12	70	0	0	7.6	969	551
13	52	0	0	7.6	969	551
14	11	3.5	225	7.7	862	543
15	25	2	41	4.1	393	785

*96 kg N ha^{-1} yr.$^{-1}$ 1856–1904; 76 kg N ha^{-1} yr.$^{-1}$ 1905 onwards

that grasslands located at the same site were not independent observations. The goal was to derive a response function with one or several of those variables that could be used to estimate R:S in future modelling efforts. Interactions between variables were not considered to avoid overfitting and to keep a potential model interpretable. Residual qq-plots were used to test normal distribution of the residues, whereby N input and number of cuts were log-transformed to ensure approximate normal distribution of the residues. The Akaike Information Criterion (AIC) was used to select the best model. Finally, four different datasets were considered to validate the model-derived optimised R:S (and a potential response function) by estimating total root biomass of independent grassland sites. The selection criteria for validation datasets were: i) reported belowground biomass to a certain depth and ii) reported yield or above-ground biomass. The selected studies investigate gradients in fertilisation (Sochorová et al. 2016), species richness in unfertilised natural grasslands (Fornara and Tilman 2008), species for intensive forage production (Bolinder et al. 2002) and a pasture experiment with contrasting stocking rates and N-fertilisation (unfertilised vs. 210 kg N ha^{-1} yr.$^{-1}$). Gradients were thus present across studies and within studies. Measured root biomass was chosen for validation, in

order to test, whether the R:S estimation as embedded in the other assumptions made (equations 1 and 5) would be able to predict realistic root biomass values. The reported yields were used to calculate root biomass using Eq. 1, 3, 4 and 5 and the R:S values that were subject to validation. This calculated root biomass was then compared to the measured root biomass, using the modelling efficiency (EF) to evaluate the performance of the model approach. Thereby an EF of 0 indicates that the model prediction is better than the simple average of all observed values and an EF of 1 indicates a perfect match between modelled and measured values (Loague and Green 1991). All statistics and calculations were performed in R. Errors given in the text are standard deviations.

Sensitivity analysis

The derivation of total annual carbon input described above involved several assumptions (Eq. 1–6). To test how sensitive the RothC model was to each of the assumptions and to test the hypothesis that the model is more sensitive to variation in R:S than to variation in decomposition rate modifiers, a model sensitivity analysis was conducted. For this analysis, we used all 15 sites available. The average of all R:S values (2.87; Table 1) and the following assumed or measured parameters were increased by 50 %: Annual yield, amount of non-harvested biomass (NPP yield), proportions of living and dead aboveground biomass turned over each year (Aboveground input), proportion of total BNPP in the top 15 cm soil layer, maximum rooting depth, annual root turnover, DPM/RPM ratio, temperature, precipitation, evaporation, clay content, PM/HUM ratio. The first seven parameters were grouped as input-related, the latter five as output-related parameters or decomposition rate modifiers. DPM/RPM ratio, which determines the flow of plant-derived carbon into the DPM and RPM pools, was classified as a mixture of both input- and output-related. The PM/HUM ratio (PM = DPM + RPM) was modified to assess the model sensitivity to initial pool distribution, whereby the PM/HUM ratio at steady state is around 0.17. The model was run for 100 years and the deviation in SOC stock change between the unchanged reference scenario (ref) and the modified scenario (mod) was calculated for each site and modified parameter. It should be noted that a 50 % variation in temperature might not be very meaningful, since temperature is not

a mass and its variation depends on the unit chosen (°C). However, it was used as a proxy here to ensure variation of a similar degree in all parameters.

Results

Root: shoot ratio estimation

The average optimised R: S for all experiments was 3.6 ± 2.4, while minimum and maximum optimised R:S were 0.72 and 8.8 respectively (Table 4). The maximum R:S was thus 12-fold the minimum R:S. Among the literature-derived ratios tested, the average of all had the lowest $RMSE_{norm}$ (3.3 ± 4.8 Mg C ha^{-1}). However, the high range of predicted R:S ratios indicates that a single value is not appropriate for carbon input calculation.

A significant negative effect of nitrogen fertilisation and number of cuts on the optimised R:S was found (Fig. 1A, B). Due to the high inter-correlation between both variables (nitrogen fertilisation and number of cuts) ($R^2 = 0.71$, data not shown), inclusion of both variables in one regression model did not add explanatory power. Furthermore, it was not possible to test the effect of cutting frequency without the covariance in nitrogen fertilisation, since no experiment with varying cutting frequency but constant nitrogen fertilisation was available (conversely the Rothamsted Park Grass Experiment had a fertilisation gradient but a constant number of cuts). In that experiment, for which gapless yields for 137 years and relatively frequent SOC measurements were available, a very pronounced difference in predicted R:S ratio was found for the unfertilised (6.96) and 96 kg N ha^{-1} yr.$^{-1}$ fertilised (2.87) meadows. This is well in line with the observed overall trend. Figure 2 illustrates the potential misfit of the RothC model that might occur if the same R:S value (here the average R:S, 2.87) were applied to both treatments. In that case, the model would have underestimated the SOC stock in the unfertilised meadow by 35 Mg ha^{-1} or 40 %. Assuming that all other parameters in the model were generally unaffected by the fertilisation treatment, an equal R:S ratio in the unfertilised and fertilised meadows is unrealistic. Nitrogen fertilisation was thus determined to be the main driver for R:S in grasslands. Due to the fact that: i) the correlation was mainly driven by the unfertilised grasslands

Table 4 Normalised root mean square error (RMSE$_{norm}$) [Mg SOC ha^{-1}] for each R:S ratio in each experiment, with average value and standard deviation (SD) and the optimised R:S ratio with average value and standard deviation for each experiment. The root:shoot ratios in columns are in decreasing order (Table 1)

ID	Fiala	Jackson	Bolinder1	Average	Luo	Bolinder2	Kuzyakov	Christensen	Optimised
1	66.1	9.1	4.3	0.2	9.3	19.4	23.5	25.5	2.8
2	6.6	12.8	15.0	17.9	23.1	27.9	29.8	30.7	6.3
3	19.3	4.3	5.9	8.3	14.8	20.6	23.0	24.1	4.8
4	16.1	4.8	3.9	2.6	0.5	0.0	0.0	0.0	0.8
5	15.0	5.6	4.9	3.9	2.0	0.4	0.2	0.1	0.7
6	21.7	8.1	7.0	5.5	2.9	0.6	0.1	0.0	0.9
7	7.4	2.0	1.5	0.9	0.0	0.4	0.8	1.0	2.0
8	4.5	0.1	0.0	0.1	0.4	0.6	0.7	0.8	3.3
9	19.9	0.1	0.5	1.0	1.9	2.7	4.3	5.0	4.0
10	0.1	0.7	0.8	1.0	1.3	1.6	1.7	1.8	8.8
11	7.6	0.0	0.3	1.0	2.2	3.5	4.1	4.3	3.7
12	0.5	0.6	0.3	0.7	1.8	2.9	3.4	3.6	5.2
13	2.7	2.8	3.6	4.5	6.2	7.8	8.4	8.7	5.6
14	14.3	0.2	0.1	0.8	3.6	6.1	7.1	7.6	3.5
15	8.2	2.7	2.2	1.6	0.5	0.0	0.1	0.3	1.3
Average	**14.0**	**3.6**	**3.4**	**3.3**	**4.7**	**6.3**	**7.1**	**7.6**	3.6
SD	16.1	3.9	3.9	4.7	6.5	8.9	9.9	10.4	2.3

(non-significant when unfertilised grasslands were excluded) and ii) the total amount of nitrogen fertilisation is, or should be, a function of potential NPP of a specific pedo-climate region, it was decided to use two different R:S values, one for fertilised and one for unfertilised grasslands, instead of a function describing the relationship between nitrogen input and R:S. Thus, the unfertilised grasslands had an average R:S of 5.9 ± 1.9 and the more intensively managed, fertilised and cut meadows had an average R:S of 2.4 ± 1.5. Assuming all other assumptions made in Eqs. 1, 2, 4 and 5 apply to temperate grasslands soils, the coefficient for directly converting harvested carbon to annual carbon inputs (C$_{input}$:C$_{harvest}$ ratio) to a certain soil depth for unfertilised and fertilised grasslands can be extracted from Fig. 3. The associated uncertainty concerning R:S (coefficient of variation for the experiments included) was 32 % for the unfertilised and 59 % for the fertilised grasslands. None of the other variables considered significantly improved the regression model, and thus a large part of the observed variation remained unexplained.

Validation

The R: S values for unfertilised and fertilised grasslands were validated with four datasets of measured root biomass to a certain depth, all of which included several treatments. Two of these datasets included different fertilisation treatments, one was obtained from an unfertilised experiment testing the effect of species richness and one dataset was obtained from a fertilised experiment testing different perennial ley species. The total number of 20 observations was predicted with high precision (EF = 0.84, Fig. 4), which indicates that both the distinction between unfertilised and fertilised grasslands and the assumptions used to estimate total belowground production in a certain soil layer performed well. Sochorová et al. (2016) found a similar difference in R:S between fertilised and unfertilised meadows in the Rengen experiment. Therefore the measured root biomass was predicted with high precision using the two R:S values derived. Species richness in the Cedar Creek experiment (Fornara and Tilman 2008), as one of the additional drivers of R:S considered, did not have an influence on R:S, despite a strong influence on total NPP. Only the scatter observed between different ley species in the study by Bolinder et al. (2002) was not captured accurately by the modelling approach.

Model sensitivity to input- and output-related parameters

The RothC model was found to be equally sensitive to climate variables and the input-related parameters yield, R:S and root turnover (Fig. 5), with 50 % variation causing deviations from the reference model prediction of up to 35–45 Mg ha^{-1} after 100 years. Furthermore, the proportion of aboveground non-harvested biomass (NPP yield) and the proportion of roots in the upper 15 cm were revealed to be important parameters, with a variation in
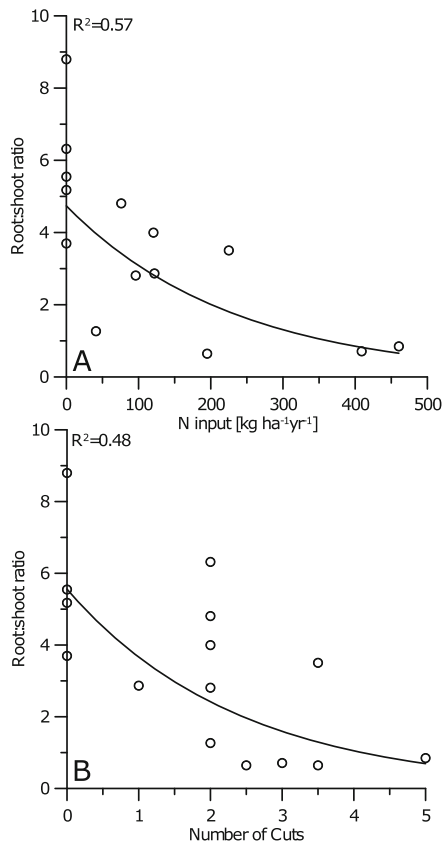
Fig. 1 Model-optimised root:shoot ratio in the experiments included in this analysis as a function of A) nitrogen (N) fertilisation [kg ha^{-1} yr.$^{-1}$] and B) annual cutting frequency

final SOC stock of up to 15 Mg ha^{-1} after 100 years. The influence of the latter decreased with increasing sampling depth, but the average sampling depth of the 15 grasslands was relatively shallow (15.1 cm), which explains the relatively high sensitivity of the model to the root distribution
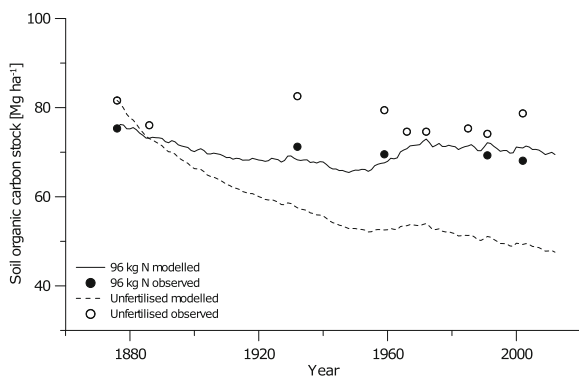

Fig. 2 RothC-modelled trend in soil organic carbon (SOC) stocks for the unfertilised and fertilised treatments in the Rothamsted Park Grass Experiment, calculated using the average of all R:S (2.87) for both treatments and measured SOC stocks over time
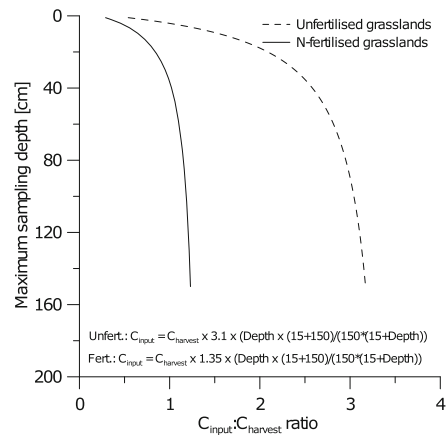
Fig. 3 Ratio of soil carbon input to carbon offtake at harvest (C$_{input}$:C$_{harvest}$) as a function of considered soil depth for unfertilised and fertilised grasslands (without organic amendments) based on Eqs. 1–6 and the estimated average R:S ratio for both grassland types. Those functions can be used to convert harvested carbon directly to annual C input in a modelling context

parameter. All other parameters, including clay content and the initial pool distribution (PM/HUM), were of minor importance (<5 Mg ha^{-1} in 100 years).

Discussion

Inverse estimation of root: shoot ratio and annual carbon inputs

Root carbon input is the most important (Rasse et al. 2005), yet most uncertain, component of SOC
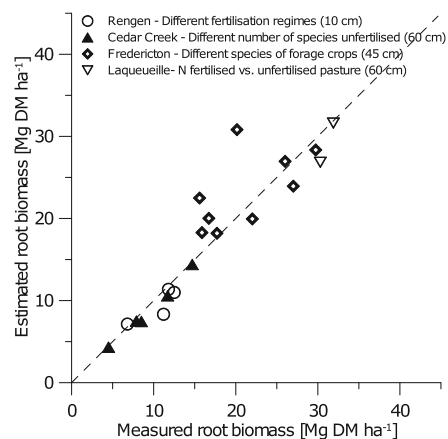

Fig. 4 Estimated root biomass (using the two model-derived root:shoot ratios for unfertilised and fertilised grasslands) plotted against measured root biomass from four independent experiments (Bolinder et al. 2002; Fornara and Tilman 2008; Sochorová et al. 2016). Dotted line indicates 1:1 relationship
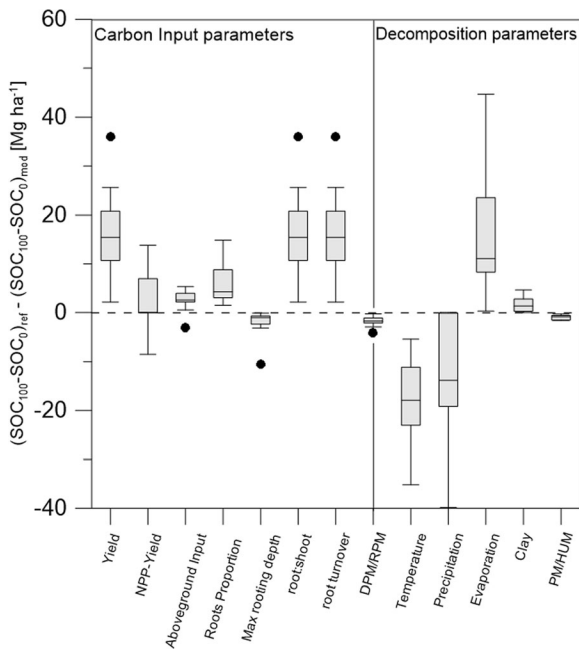
Fig. 5 Boxplot indicating the sensitivity of the RothC model to 50 % variation in different parameters, expressed as the absolute soil organic carbon (SOC) stock difference between the unmodified reference scenario (ref) and the modified scenario (mod) after 100 years. Parameters were divided into carbon input parameters (external parameters as introduced in Eqs. 1–6) and decomposition parameters (internal). DPM/RPM ratio was considered as being on the exact border between input- and output-related parameters. The dashed line indicates the modelled final SOC stock under "business as usual", using the optimised R: S (2.87) and the available soil and climate data

reproduction. In this study, the RothC model was used to inversely estimate R:S ratio for various long-term grassland experiments. The average optimised R: S of 3.68 was equal to the global average R:S ratio of 3.7 for grasslands found by Jackson et al. (1996). Furthermore, the range of R:S ratios obtained was well in line with that reported in the literature (Yang et al. 2009). Finally, the validation of the estimated R:S ratios revealed that they were realistic in absolute terms and in specific soil depth increments. It can thus be concluded that the concept of inverse estimation of R:S and total annual carbon inputs using well documented long-term grassland experiments was successful. However, the results of this study also indicate that it is not appropriate to use a fixed, static R:S to estimate total carbon inputs, as performed by most carbon balance models.

A significant part of the observed variability in R: S was explained by nitrogen fertilisation regime. It has been observed previously that nutrient availability

drives carbon allocation in plants. When experiencing deficiency of major nutrients (N, P, K), plants generally invest more in belowground organs to maximise nutrient acquisition from the soil (Ericsson 1995; Wilson 1988). For cereals, R:S is reported to increase by 15–50 % under nitrogen deficiency (Hansson et al. 1987; Welbank et al. 1973). For grassland, this shift may be higher, since cereals are bred for yield optimisation and thus for high carbon allocation to grains. Indeed, in a German long-term grassland fertilisation experiment, Sochorová et al. (2016) reported an almost threefold R:S ratio in the unfertilised control compared with the CaN-fertilised treatment, which is well in line with the difference in R:S determined in the present study. Furthermore, at the French site Laqueueille, which was used as validation dataset (original data), 1.9 higher R:S was found in unfertilised pasture compared with N-fertilised pasture.

It might be somewhat one-dimensional to optimise only R:S to obtain the best model fit to observed SOC stocks. However, the effect of nitrogen availability on SOC decomposition is highly uncertain (Neff et al. 2002) and numerous studies in recent years have indicated that nitrogen deficiency leads to nitrogen mining and thus higher decomposition of SOC and lower stabilisation of fresh carbon input (Ammann et al. 2007; Craine et al. 2007; Kirkby et al. 2014). Implementing such a mechanism in carbon balance models has been suggested (Reed et al. 2011), but in the present case would have led to an even more pronounced difference in R:S between unfertilised and fertilised grasslands. The opposite, i.e. decelerated turnover of SOC under nitrogen deficiency, has also been reported (Allen and Schlesinger 2004) and implemented in RothC by the different DPM/RPM ratio for "unimproved pastures and shrublands" (0.69 compared with 1.44 for improved pastures and croplands). This shift in carbon input partitioning into the most active SOC pools was applied in this study.

Cutting frequency was also found to significantly affect R:S, with lower R:S in more often cut grasslands. However, it is less clear whether direct causality exists, since cutting frequency was highly correlated to nitrogen fertilisation. It can be speculated that higher cutting frequency leads to higher competition for light, so that more carbon is allocated to aboveground organs. However, there is no clear evidence of such an effect in the literature. Vinther (2006) investigated the effect of cutting frequency (3–4 times compared with 7–12

times) on R:S in a Danish ryegrass-clover sward. A slight, but non-significant decrease in R:S with increasing cutting frequency was found (for both plants), while the interannual variability in R:S was much higher, leading the author to conclude that the sensitivity of R:S to weather conditions might be more important than its sensitivity to management interventions. After 19 years of contrasting number of cuts but constant nitrogen fertilisation, Kramberger et al. (2015) did not find an effect of cutting frequency on SOC stocks, but observed a decrease in yield with increasing cutting frequency (from 12-weekly to 2-weekly intervals). This might indicate that the opposite, i.e. increasing R:S with increasing cutting frequency, had actually occurred. Finally, (Seiger and Merchant 1997) found a significant decrease in R:S with increasing cutting frequency of Japanese knotweed in pot experiments. In addition to nitrogen fertilisation, cutting frequency might thus play a certain role for plant carbon allocation.

Importance of input estimation and major uncertainties

The sensitivity analysis revealed that SOC simulation in grasslands is highly sensitive to carbon input estimation. Although the hypothesis that the RothC model is more sensitive to variation in R:S than to variation in any decomposition rate modifier had to be rejected, it was shown that R:S variation has a similarly high impact as the degree of variation in climate variables. However, there was a notable difference in uncertainty for the two types of data. Even if climate data are not available for a specific site, they can be estimated with much higher precision than the 50 % variation assumed here. In contrast, 50 % variation in R:S is highly precise, compared with the possible range of R:S for grasslands found in the literature. This illustrates the high importance of accurate carbon input estimation, as highlighted previously by Ludwig et al. (2007). Self-evidently, the model sensitivity to yield (or ANPP estimation in general) and root turnover was clearly as high as the sensitivity to R:S estimation. However, the global pattern of root turnover (Gill and Jackson 2000) shows well constrained temperature dependency of root turnover, with less than 50 % variation for studies conducted in the temperate zone. Measuring root turnover is complicated and costly and the total number of available datasets is limited. The same is true for rhizodeposits. The good fit of the estimated belowground input with the measured root biomass data suggests that either: i)

the RothC model was calibrated without considering rhizodeposits at all or that ii) the role of rhizodeposits in SOC reproduction may be overestimated (in models). As an example, Bolinder et al. (2007) calculated total root-derived carbon input by multiplying root biomass by 1.65. In fact, rhizodeposits are thus entirely treated as root biomass. However, root exudates are also known to: i) be very labile substances with presumably short residence time and ii) to cause priming, i.e. enhanced decomposition of native SOC (Kuzyakov 2002). Keiluweit et al. (2015) pointed out that increasing root exudates might even cause net loss of SOC. It is thus very likely that rhizodeposits are not comparable to root biomass regarding SOC formation. Moreover, it remains an open question how important reliable estimates of rhizodeposits, their turnover and potential priming effects are to improve the performance of carbon balance models.

Finally, the model sensitivity to ANPP, on which the total carbon input calculation is based, is very problematic. This is especially true for grassland ecosystems, in which the exported biomass is rarely quantified. In this study, only sites for which yield data were available to parameterise belowground carbon inputs were selected. However, when those are not present and ANPP has to be estimated, the final uncertainty of the derived carbon input will strongly increase. There are a large number of models available for NPP prediction, often based on temperature, precipitation and radiation. However, when applied in specific regions, the prediction of these models is scarcely comparable (Lin and Zhang 2013). Furthermore, the effects of soil fertility, species composition, grazing intensity, cutting frequency and fertilisation on ANPP are only captured (to a certain extent) in complex growth models such as PASIM (Calanca et al. 2007). To overcome the lack of reliable biomass data in grasslands, it should be comprehensively tested how well ecosystem models such as CENTURY are able to predict SOC dynamics without calculating input data from measured yields. For live biomass and SOC dynamics separately, Parton et al. (1993) were able to show reasonably well fits to observed data of a global set of differently managed grasslands.

Compared with carbon input and climate variables, the model sensitivity to other parameters such as initial pool distribution or even clay content was negligible. Similarly, Senapati et al. (2013) found no significant influence of different initialisation methods on RothC-

projected SOC stock changes in Australian grasslands. In addition, the uncertainty in clay content is small, since soil texture is a basic soil parameter and is mostly measured or data are available from soil maps. Due to the much higher proportion of belowground carbon inputs in grasslands compared with cropland (Bolinder et al. 2012) and the wider range of possible management regimes, it can be concluded that, particularly in grasslands the current degree of simplification in carbon balance models concerning carbon inputs is not acceptable.

This study provides RothC-derived coefficients for yield-based estimation of carbon inputs in temperate grasslands that can be used for carbon modelling. The results showed that plant carbon allocation to above- and belowground organs is highly variable. This variability has to be accounted for, since the sensitivity of the model to carbon inputs is just as high as its sensitivity to climate data, although these are most often available. Nitrogen fertilisation was identified as an important driver for R:S in grasslands, but further investigations should follow to explain more of the observed variability and to disentangle the complexity below ground (Rumpel et al. 2015). Interactions with the phosphorus cycle and the role of mycorrhiza and root exudates for long-term carbon storage are other carbon input-related topics on which further understanding is necessary (Poeplau et al. 2016; Rumpel et al. 2015; Sochorová et al. 2016). Using the derived R:S values for unfertilised and fertilised grasslands in future applications of the RothC model will improve model performance in temperate grasslands. It has been decided to use two fixed values for unfertilised and fertilised grasslands, since across sites, the balance of plant N demand and N availability is not directly reflected in the amount of N applied. Soil mineral nitrogen concentration might be a better indicator for a potential response function. Furthermore, it remains to be tested, i) how other carbon models perform with the derived ratios, ii) if the results are applicable to grasslands in other climate zones and iii) if similar mechanisms can be found in croplands or forests.

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