



Root-To-Shoot Ratios of Flood-Tolerant Perennial Grasses Depend on Harvest and Fertilization Management: Implications for Quantification of Soil Carbon Input

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Quantifying soil organic carbon stocks (SOC) is a critical task in decision support related to climate and land management. Carbon inputs in soils are affected by development of belowground (BGB) and aboveground (AGB) biomass. However, uncertain fixed values of root:shoot ratios (R/S) are widely used for calculating SOC inputs in agroecosystems. In this study, we 1) assessed the effect of harvest frequency (zero, one, two, and five times annually) on the root and shoot development of the perennial grasses *Phalaris arundinacea* (RCG), *Festuca arundinacea* (TF), and *Festulolium* (FL); 2) determined the effect of management on the carbon and nitrogen content in AGB and BGB; and 3) assessed the implications of R/S for SOC quantification. We found the highest yields of BGB in zero-cut treatments with 59% (FL)–70% (RCG) of total biomass. AGB yield was highest in the five-cut treatments with 54% (RCG)–60% (FL), resulting in a decreasing R/S with frequent management, ranging from 1.6–2.3 (zero cut) to 0.6–0.8 (five cuts). No differences in R/S between species were observed. Total carbon yield ranged between 5.5 (FL, one cut) and 18.9 t ha⁻¹ year⁻¹ (FL, zero cut), with a higher carbon content in AGB (45%) than BGB (40%). We showed that the input of total organic carbon into soil was highest in the zero-cut treatments, ranging between 6.6 and 7.6 t C ha⁻¹ year⁻¹, although, in the context of agricultural management the two-cut treatments showed the highest potential for carbon input (3.4–5.4 t C ha⁻¹ year⁻¹). Our results highlighted that using default values for R/S resulted in inaccurate modeling estimations of the soil carbon input, as compared to a management-specific application of R/S. We conclude that an increasing number of annual cuts significantly lowered the R/S for all grasses. Given the critical role of BGB carbon input, our study highlights the need for comprehensive long-term experiments regarding the development of perennial grass root systems under AGB manipulation by harvest. In conclusion, we indicated the importance of using more accurate R/S for perennial grasses depending on management to avoid over- and underestimation of the carbon sink functioning of grassland ecosystems.

Keywords: root:shoot ratio, perennial grass, peatland, soil organic carbon, paludiculture, wetland, carbon sink

INTRODUCTION

Undisturbed mires are wetland biomes where peat accumulates, typically at rates of $\sim 1 \text{ mm year}^{-1}$ over centuries (Parish et al., 2008), making these ecosystems one of the largest global organic carbon (C) reserves with substantial impact on atmospheric carbon dioxide (CO_2) concentrations (Moomaw et al., 2018). In Denmark, wetlands with $>6\%$ organic C cover about 291,000 ha, of which 59% are used for agriculture (Greve et al., 2021). The massive losses of C from these agroecosystems are controlled by the balance between current net C inputs and peat mineralization, which is substantial and largely depends on the drainage conditions (Straková et al., 2012). National emission factors for drained organic agricultural soils in Denmark were established by empirical gas flux measurements in 2008–2009 and averaged $35 \text{ Mg CO}_2 \text{ ha}^{-1} \text{ year}^{-1}$ across eight sites in crop rotation and with permanent grass (Elsgaard et al., 2012). Climate change mitigation by rewetting of agricultural soils with $>6\%$ organic C is currently supported by national governmental incentives. Following this, it is envisaged that an area of 88,500 ha potentially can be rewetted and converted to permanent natural grassland (Ministry of Food, Agriculture and Fisheries of Denmark, 2021). Whereas reductions in CO_2 emissions from slower peat mineralization are well documented in relation to increasing groundwater tables (Renou-Wilson et al., 2014), there is an unmet challenge in documenting the net C sequestration from new plant biomass on wet organic soils. This is in particular true for wetlands with $>12\%$ organic C and cultivated with perennial grasses, also known as paludiculture, which may contribute to greenhouse gas (GHG) mitigation (Tanneberger et al., 2020) and nutrient retention (Giannini et al., 2017; Vroom et al., 2018).

The input and cycling of organic C in soil ecosystems is highly affected by plant mechanisms regulating the development of aboveground (AGB) and belowground (BGB) biomass (i.e., shoots and roots, respectively) and consequently the quantity of litter input (Kumar et al., 2017), while decomposition of soil organic matter (SOM) is affected by soil nutrient stoichiometry (Kumar et al., 2021). Factors controlling AGB production of perennial grasses are well studied, but little is known about BGB, in particular for flood-tolerant perennial grasses. Roots play a significant role in the soil C cycle (Puget and Drinkwater, 2001; Moore et al., 2019; Dijkstra et al., 2020), indicate productivity (Thakur et al., 2021) and are crucial for the buildup of SOM on both mineral soils and peatlands (Klingensfuß et al., 2014; Leifeld et al., 2020). Not only root biomass but also in particular root exudates, secretions, lysates, cap cells, and mucilages (Carminati and Vetterlein, 2013; van Veelen et al., 2018) are important C inputs affecting the soil status of being either a source or a sink of C. For the estimation and modeling of changes in soil C stocks, a fixed default root:shoot ratio (R/S) is widely used to account for total biomass C. However, R/S is known to vary as a result of multiple environmental and climatic factors as well as management (Kibet et al., 2016; Sainju et al., 2017a; Hu et al., 2018). The optimal partitioning theory (OPT) of plant biomass allocation between AGB and BGB proposes that environmental factors will force plants to allocate new biomass to

those parts needed to secure the most deficient resources for optimal plant growth (Fraser et al., 2015; Yang et al., 2018). In contrast, the isometric allocation hypothesis (IA) states that BGB scales linearly with AGB, independent of abiotic factors. Further, it has been stated that defoliation of AGB by harvest or grazing will decrease total BGB (Reid et al., 2015). However, due to the high on-site variability and the challenge of root extraction, in particular for perennial grasses, accurate estimations of R/S under different conditions are rare (Bolinder et al., 2002). Instead, and notably for grassland ecosystems, the allometric approach, using a fixed R/S (Bolinder et al., 2007), is used for modeling of BGB soil C inputs. Nevertheless, recent research highlighted the potential overestimation as well as uncertainty of this modeling approach (e.g., Mokany et al., 2006; Taghizadeh-Toosi et al., 2016; Keel et al., 2017).

While currently an effort is made to review R/S for different biomes and climate zones (e.g., Qi et al., 2019), an assessment of the R/S of grasses under different harvest frequencies is still lacking. This is particularly true for flood-tolerant grass species, which are increasingly introduced on both wetland and upland soils for both climate change mitigation and added-value products, such as grass protein as a substitute for soy (Nielsen et al., 2021). Hence, there is a need for consolidated estimates of R/S for commonly used paludiculture crops under different harvest frequencies (Karki et al., 2014). In the present study, we addressed this need in an annual trial and hypothesized that different R/S would be observed in flood-tolerant perennial grasses by manipulating the harvest frequency during the growth season under provision of adequate nutrient availability. The specific aims of the study were 1) to determine the effect of harvest frequency on the root and shoot development in the first year of cultivation of the perennial grasses reed canary grass (RCG; *Phalaris arundinacea* L.), tall fescue (TF; *Festuca arundinacea* Schreb.) and festulolium (FL; *Festuca* spp. \times *Lolium* spp.), 2) to assess species-specific differences in R/S biomass ratios, 3) to determine the effect of harvest frequency on the C and nitrogen content in above- and belowground biomass, and 4) to assess the implications of R/S for soil C modeling.

MATERIALS AND METHODS

Site Description and Experimental Design

The experiment was performed at the outdoor semi-field facilities of Aarhus University Foulum, Denmark. The average air temperature in the 8-month study period from March to November 2019, representing the annual growth period of grasses, ranged between 5.0°C and 16.8°C , with August as the warmest month. Monthly average precipitation ranged between 12 and 122 mm, with April as the driest and October as the wettest month. Global and net radiation was highest in June, with 20 and 8 MJ m^{-2} , respectively (Figure 1).

The perennial grasses RCG (cultivar: Lipaula), TF (cultivar: Kora), and FL (cultivar: Hykor) were grown in polyvinyl carbonate (PVC) cylinders (diameter 15 cm, depth 50 cm) that were placed in three trenches at the semi-field facility. The PVC

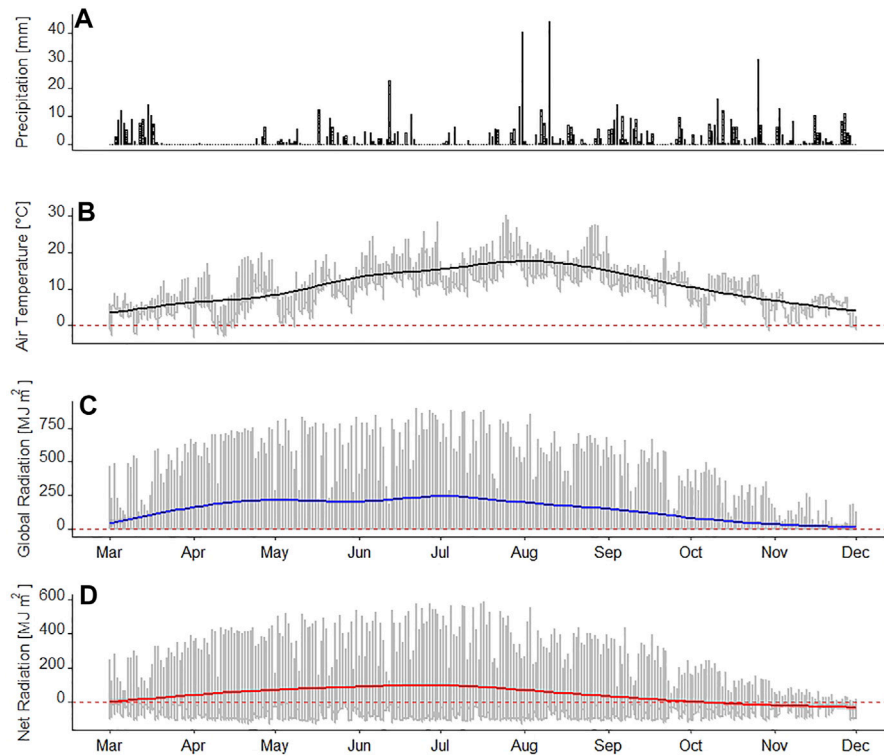


FIGURE 1 | Environmental data for the year 2019 showing **(A)** precipitation (in mm), **(B)** temperature in Celsius, **(C)** global radiation (MJ m^{-2}), and **(D)** net radiation (MJ m^{-2}). Bold lines for temperature and radiation indicate the daily means, while dashed red lines indicate zero.

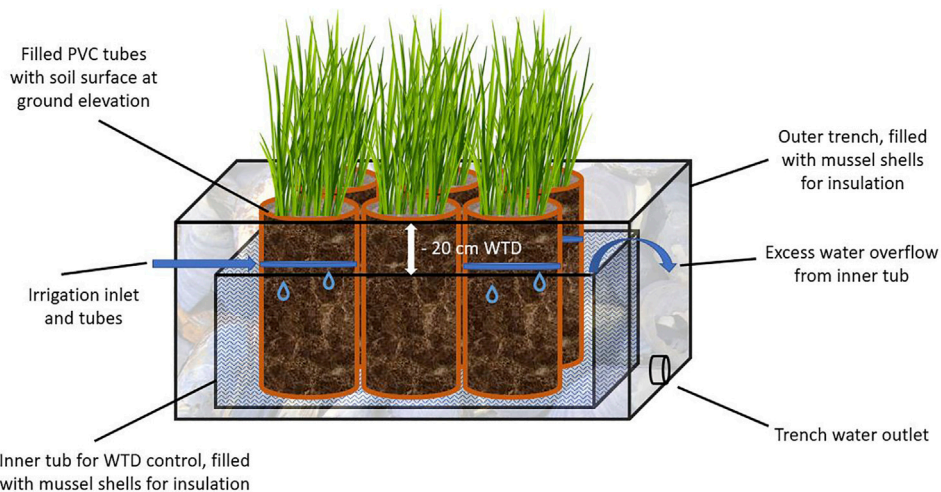


FIGURE 2 | Schematic sketch of the experimental setup representing water table depth (WTD) control of the polyvinyl carbonate (PVC) cylinders, filled with soil and cultivated with the various grass species.

cores were filled with coarse sandy soil (1.5% total organic C, $17.5 \text{ kg NH}_4\text{-N ha}^{-1}$, $35.0 \text{ kg NO}_3\text{-N ha}^{-1}$, pH 5.8) and maintained at a controlled water table depth (WTD) of -20 cm. This setup was chosen to simplify root washing as

compared to peat soil where separation of new and old plant remains is unfeasible. The WTD control was ensured by placing the PVC tubes in tubs ($78.5 \text{ cm} \times 48.5 \text{ cm} \times 30 \text{ cm}$) with the soil surface at ground elevation. The tubs allowed for overflow of excess

TABLE 1 | Dates and amounts of fertilizer application, calendar weeks of aboveground biomass harvest occurrences, and dates for root extraction following the final biomass harvest for the various treatments as indicated by number of cuts.

Number of cuts	Fertilizer application	Fertilizer date (week no.)	Biomass harvest (week no.)	Root extraction (week no.)
Zero	40 kg N and K ha ⁻¹ year ⁻¹	12	45	45
One	1 × 100 kg N and K ha ⁻¹	12	31	31
Two	2 × 100 kg N and K ha ⁻¹	12, 26	25, 37	37
Five	5 × 40 kg N and K ha ⁻¹	12, 22, 26, 31, 38	21, 25, 31, 37, 44	44

water and were automatically filled twice daily with demineralized water to maintain a stable WTD (Figure 2). Sowing of seeds (25 kg ha⁻¹) was performed by hand on March 14, 2019 (week 11). The cylinders ($n = 20$) in each cultivar group were randomly assigned to four harvest and fertilization treatments, including zero, one, two, and five annual cuts with five replicates each (Table 1). The treatment with one annual biomass harvest was chosen to determine BGB development in the first half of the growing period. Initial fertilization of all treatments was applied on March 19, 2019. The setup was exposed to natural changes in temperature and precipitation.

Above and Belowground Biomass and Net Primary Productivity

AGB was harvested at a stubble height of 5 cm in calendar weeks 21, 25, 31, 37, and 44, depending on treatment regarding harvest frequency (Table 1). Stubble and BGB were separated and determined following the last AGB harvest. Roots were extracted from the soil by fine washing: two rinsing cycles using a soft spray nozzle with demineralized water and a 20-cm-diameter soil sieve with 2-mm mesh size, followed by three rinsing cycles and a 250- μ m mesh size sieve. Total biomass dry matter (DM) for each cut and plant fraction was determined after oven-drying at 60°C to constant weight. Following drying, all samples were milled (Retsch SM 200, Retsch GmbH, Haan, Germany) and analyzed for total nitrogen (TN) and total organic carbon (TC) concentrations using a vario MAX CN (Elementar Analysensysteme GmbH, Hanau, Germany). Recovered roots were considered as BGB, and harvested yields and stubble were considered as AGB. Root:shoot ratios and NPP were calculated as

$$\text{Root: shoot ratio (R/S)} = \text{BGB/AGB} \quad (1)$$

$$\text{Net primary production (NPP)} = \text{BGB} + \text{AGB} \quad (2)$$

The calculation of NPP has been chosen to be simplified, in our study excluding the, unquantified contribution of, e.g., root secretions and exudates to NPP. The amount of C in AGB and BGB plant parts was calculated by multiplying the biomass (t DM) and the TC concentration in biomass (Mg C t⁻¹ DM).

Extrapolation of Results for Calculation of Soil Carbon Input

We calculated the soil carbon input from biomass for each treatment under the following observations and assumptions of 1) observed yields of AGB and BGB, 2) the determined R/S, and

3) the various individual concentrations of TC in AGB and BGB as well as the stubble fraction of AGB. The method has been adapted from Kätterer et al. (2011) and Poeplau (2016) under the modification to account for specific TC concentrations in the stubble fraction, and BGB. Hence, we calculated the TC input into soil using the following assumptions and equations: ANPP is the aboveground NPP, which was calculated by multiplying the AGB yield by the carbon concentration in AGB as derived by biomass analyses for the various treatments (Eq. 3).

$$\text{ANPP} = \text{AGB Yield} * \text{C in AGB} \quad (3)$$

BNPP is the belowground NPP, calculated as the harvested AGB yield multiplied with the derived R/S for the various treatments and multiplied with the carbon concentration in BGB as derived by biomass analyses for the various treatments (Eq. 4).

$$\text{BNPP} = (\text{AGB Yield} * \text{R/S}) * \text{C in BGB} \quad (4)$$

AC_{in} (t C ha⁻¹ year⁻¹), the TC input into the soil from AGB, was calculated as the yield of the not harvested stubbles multiplied by the carbon concentration in those, divided by two. This was a conservative estimate, based on the assumption that only approximately 50% of the stubble biomass (S) fraction becomes available as structural soil carbon input according to Schneider et al. (2006) (Eq. 5).

$$\text{AC}_{in} = \frac{(\text{Stubble Yield} * \text{C in Stubble biomass})}{2} \quad (5)$$

BC_{in}, the TC input into soil (t C ha⁻¹ year⁻¹) for a depth of 50 cm, as equivalent to the length of the used PVC tubes, was calculated according to Equation 6. This is in detail described by Poeplau (2016), where d is the sampling depth (in cm), d_r is the assumed maximum rooting depth for a flooded soil, and d_{50} is the depth of 50% of BNPP distribution. In our calculations, d was set to 50 cm as the depth of the PVC tubes, d_r to 70 cm, since the maximum rooting depth under high WTDs is not likely to significantly exceed the sampling depth (Kohzu et al., 2003; Fan et al., 2017; D'Imperio et al., 2018), and d_{50} to 15 cm, according to average observations from this study across treatments. This was multiplied by 0.65 according to a conservative root turnover estimation for temperate wetlands with similar mean annual average temperature and precipitation values as our study site (Gill and Jackson, 2000; DuPont et al., 2014; Leifeld et al., 2015).

$$BC_{in} = \left(\frac{d^*(d_{50} + d_r)}{d_r*(d_{50} + d)} * BNPP \right) * 0.65 \quad (6)$$

This resulted in the final TC input into soil ($t\ C\ ha^{-1}\ year^{-1}$), which was calculated as the sum of AC_{in} and BC_{in} (Eq. 7).

$$TC_{in} = AC_{in} + BC_{in} \quad (7)$$

Scenarios of Soil Carbon Input Based on Default R/S

Two commonly used R/S were applied for default calculation of soil carbon input: first, an R/S of 0.8 as stated by Bolinder et al. (2007) for grass species in eastern and western Canada. This ratio is based on a literature review on 35 publications. Second, we used the R/S of 2.8, which is derived from semi-arid grassland data, but used as a default expansion factor by the IPCC (2006) and applied in Denmark's National Inventory Report (2020). These R/S values were applied to averaged total AGB yields and the commonly used average of 45% TC within biomass (Kätterer et al., 2011).

In addition, the carbon input into soil for RCG treatments was exemplarily calculated identical to the R/S scenarios, assuming identical biomass yields, for better comparability.

Statistical Analyses

Observations were averaged and summed up to yields over the entire growing period. Standard error was reported to present the distribution of data. Two-way analyses of variance were performed using linear mixed models with the function *lmer* of the package *lme4* (Bates et al. (2015), Version 1.1–23, 2020) in the statistical software R (R Core Team (2020) Version 4.0.2—“Taking Off Again”), in which the following model was used:

$$Y_{ijk} = \mu + s_i + t_j + st_{ij} + \epsilon_{ijk}$$

where Y_{ijk} is the observed dependent variable, μ is the overall mean, s_i is the fixed effect of species, t_j is the fixed effect of combined harvest frequency and fertilization treatment, st_{ij} is the species by treatment interaction, and ϵ_{ijk} is the experimental error. The model residuals were inspected for normality and homoscedasticity, and variables were log-transformed in order to stabilize the variance and normal distribution. A Tukey's HSD test at the 95% confidence level was used to test for significance of differences between treatment means. Correlation effects between the observed R/S and the various biomass treatments were determined by multiple linear regression using Pearson's correlation.

RESULTS

Root and Shoot Measurements Cumulated Biomass Yield

Cumulated DM plant biomass at the end of the growing season ranged between $16.8\ t\ ha^{-1}\ year^{-1}$ (FL, five cuts) and $46.2\ t\ ha^{-1}\ year^{-1}$ (FL, zero cuts) across all treatments (Table 2) and were

affected by the annual harvest strategy [$\chi^2(3) = 110.4, p < 0.001$]. Generally, and for all species, the highest yields were found in the zero-cut treatments, ranging between 39.4 (TF) and 46.2 (FL) $t\ ha^{-1}\ year^{-1}$. There was a consistent decrease of BGB and cumulative biomass yield with increasing number of annual cuts, with the one-cut treatment being an exception due to the different timing of harvest, presumably in combination with lesser N availability. However, while for RCG and TF there was no difference of total yields between the one- to five-cut treatments, there was, for FL, a significant ($p < 0.001$) increase of both AGB and BGB development, when comparing the one- and two-cut treatments. Species alone did not affect total biomass yield despite the observation of high overall yields for the FL two-cut treatment, close to three-fold as compared to the FL five-cut treatment. For all species, there was a significant difference ($p < 0.001$) between yields of the zero-cut treatment and all other treatments. Overall and across treatments, RCG and TF yields were near identical.

Root:shoot Ratio

The ratio between AGB and BGB (R/S) varied between 0.6 (FL, five cuts) to 2.3 (RCG, zero-cuts), significantly ($p < 0.001$) affected by the annual harvest strategy (Table 2). The smallest contribution of BGB to total biomass was observed for the five-cut treatments, ranging between 38% (FL) and 45% (RCG). In the zero-cut treatments, BGB contributed with 61% (FL) to 70% (RCG) of total biomass. For all species, the R/S of the zero-cut treatment was significantly ($p < 0.001$) higher than for the other treatments [$\chi^2(2) = 46.8, p < 0.001$], while no differences in R/S were observed for the one- to five-cut treatments. There was no significant ($p > 0.5$) difference of R/S in between species across the various treatments. The differences between one and two annual cuts and between two and five annual cuts were non-significant (Figure 3). However, the Pearson correlation identified strong positive correlations between AGB and BGB based on yield results combined for treatment but differentiated for species (minimum $R > 0.61$), combined for species but differentiated for treatment (minimum $R > 0.76$), and differentiated for both species and treatment (minimum $R > 0.71$) (Figures 4A–C).

Total Carbon

The mean content of TC across all species and treatments was 45% for aboveground grass biomass, 44% for stubble biomass, and 40% for belowground biomass. A decreasing trend of TC content within AGB was observed with increasing number of cuts for all species (Table 3). TC yield ($t\ TC\ ha^{-1}\ year^{-1}$) within biomass generally followed the pattern of total DM biomass yield, with an increasing aboveground TC yield with increasing number of annual cuts and an increasing belowground TC yield with fewer annual cuts. The highest total plant TC yield was found in the FL zero-cut treatment ($18.9\ t\ ha^{-1}\ year^{-1}$) and the lowest in FL one-cut ($5.5\ t\ ha^{-1}\ year^{-1}$). There were no significant differences for TC yields between the zero- and five-cut treatments in AGB. Generally, TC yield was highly affected by management [$\chi^2(15) = 80.9, p < 0.001$].

TABLE 2 | Yields of dry matter (DM) of aboveground (AGB), belowground (BGB), and stubble (S) biomass for the various species and treatments. Total yields for above- and belowground plant fractions are indicated as sums. The root to shoot (R/S) ratio indicates the ratio of belowground to combined aboveground and stubble biomass. Letters indicate differences between treatments, where treatments with the same letters are not significantly different. Standard error is given in brackets ($n = 5$).

Treatment	DM ($\text{t ha}^{-1} \text{ year}^{-1}$)				R/S
	AGB	BGB	S	Sum	
Festulolium					
0 Cut	14.0 (± 2.8)ab	28.1 (± 4.3)a	4.2 (± 0.7)a	46.2 (± 7.7)a	1.6 (± 0.1)a
1 Cut	5.6 (± 0.8)c	6.3 (± 1.6)c	1.3 (± 0.3)b	13.2 (± 2.7)b	0.9 (± 0.1)b
2 Cuts	18.1 (± 2.1)a	18.9 (± 3.1)b	3.9 (± 0.8)a	41.0 (± 6.0)a	0.8 (± 0.1)b
5 Cuts	9.6 (± 1.5)bc	6.4 (± 1.1)c	0.8 (± 0.2)b	16.8 (± 2.8)b	0.6 (± 0.0)b
Reed canary grass					
0 Cut	11.2 (± 1.5)a	28.0 (± 3.7)a	1.1 (± 0.1)b	40.3 (± 5.3)a	2.3 (± 0.1)a
1 Cut	6.7 (± 0.9)b	9.5 (± 0.9)b	1.3 (± 0.2)ab	17.4 (± 2.0)b	1.2 (± 0.1)b
2 Cuts	9.4 (± 1.7)ab	13.5 (± 2.8)b	1.9 (± 0.5)a	24.8 (± 5.0)b	1.2 (± 0.3)b
5 Cuts	11.2 (± 1.4)a	10.0 (± 0.7)b	0.8 (± 0.1)b	22.0 (± 2.2)b	0.8 (± 0.0)b
Tall fescue					
0 cut	11.1 (± 1.4)a	25.1 (± 3.0)a	3.1 (± 0.6)a	39.4 (± 5.1)a	1.8 (± 0.1)a
1 cut	6.4 (± 0.7)b	9.9 (± 1.4)b	2.2 (± 0.5)ab	18.5 (± 2.5)b	1.2 (± 0.1)b
2 cuts	8.5 (± 2.2)ab	10.5 (± 2.0)b	2.9 (± 0.5)a	21.9 (± 4.7)b	1.0 (± 0.1)b
5 cuts	11.0 (± 2.0)a	9.5 (± 1.0)b	1.2 (± 0.2)b	21.7 (± 3.2)b	0.8 (± 0.1)b

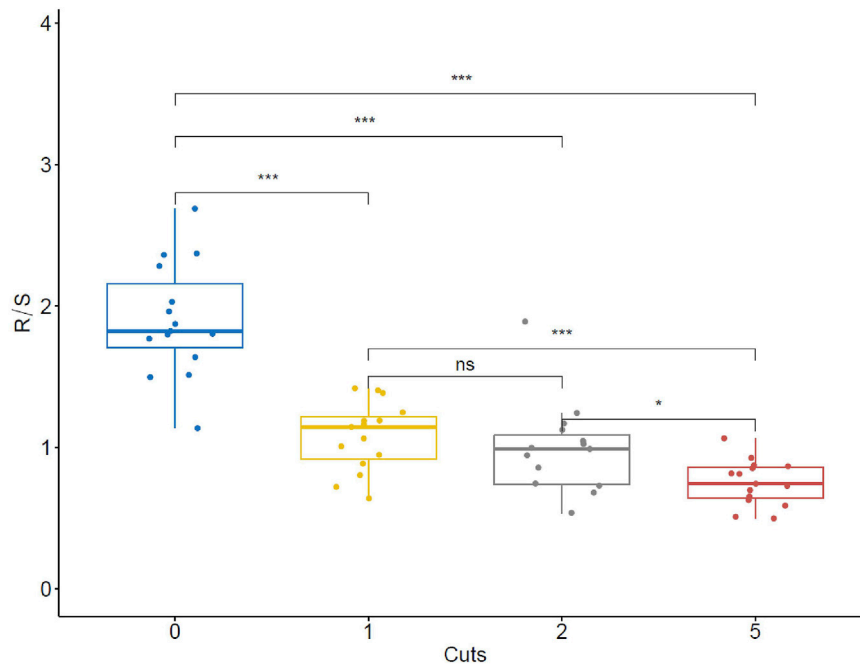
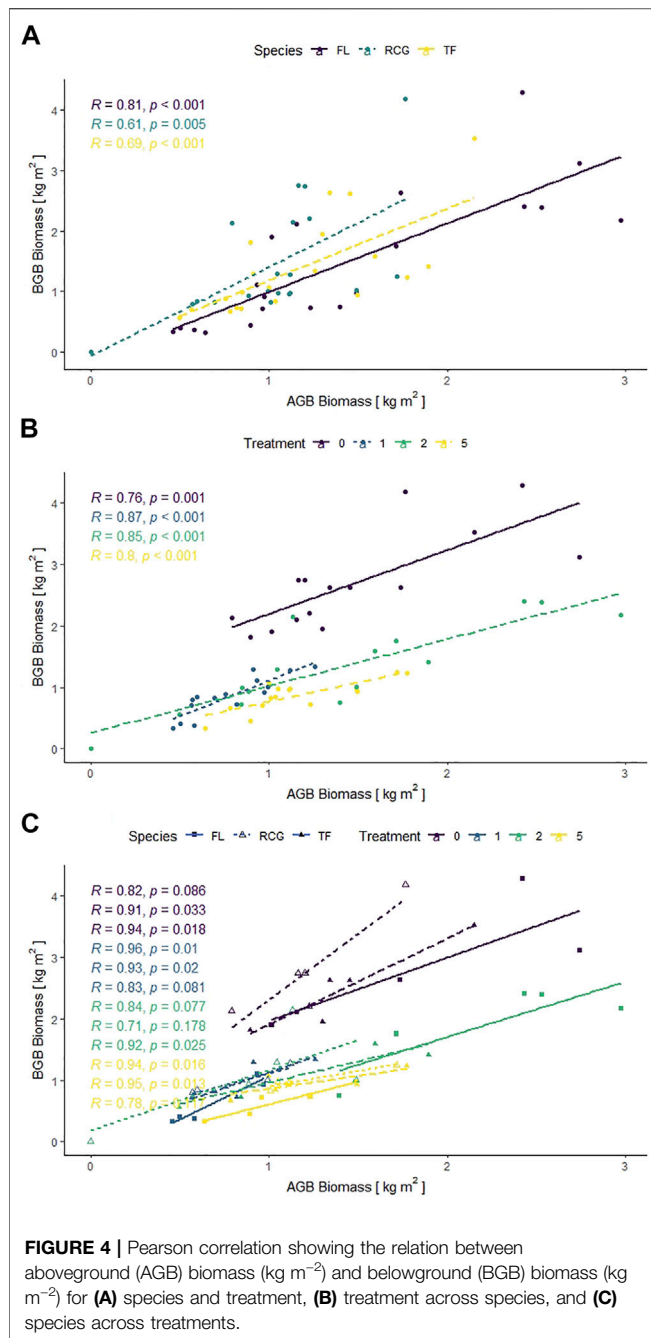


FIGURE 3 | Differences of root:shoot ratios (R/S) for the various treatments of zero, one, two, and five annual cuts across species. Stars denote statistical significances between treatments according to p -values with ns indicating non-significance.

Total Nitrogen

TN in biomass was significantly affected by treatment [$\chi^2(3) = 53.2, p < 0.001$]. For all species and treatments, the content of TN was higher in AGB than in BGB and stubble biomass. Averaged across species, TN content in AGB increased from 1.4% in the

zero-cut treatment to 4.0% in the five-cut treatments (Table 3). This is also depicted in TN yields, where more TN was harvested in the five-cut treatments ($26.4\text{--}34.4 \text{ g N m}^{-2} \text{ year}^{-1}$) as compared to the zero-cut treatments ($13.6\text{--}17.8 \text{ g N m}^{-2} \text{ year}^{-1}$), despite similar or lower AGB yields. In contrast to AGB, the TN content



in BGB was not affected by increasing harvest and fertilization frequencies ($p < 0.5$). On a cumulative basis, the highest plant TN yield was found in the zero-cut treatment for RCG ($51.1 \text{ g m}^{-2} \text{ year}^{-1}$) and TF ($41.6 \text{ g m}^{-2} \text{ year}^{-1}$), while for FL, most TN ($51.1 \text{ g m}^{-2} \text{ year}^{-1}$) was found in the two-cut treatment.

Carbon-to-Nitrogen Ratio

We found that for all three grass species, the carbon-to-nitrogen (C/N) ratio within AGB, as well as in the combined AGB and S (AGB + S) biomass, decreased significantly ($p < 0.001$) with increasing number of annual cuts. For instance, in AGB + S, the

C/N decreased from 32.1 (RCG)–39.3 (FL) for the zero-cut treatment to 15.4 (RCG)–19.0 (TF) for the treatment with five annual cuts (Table 4). Regarding S biomass, the C/N was for all treatments higher as compared to the C/N of AGB, with significant ($p < 0.001$) differences for the one-to five-cut treatments. For BGB, no significant difference of the C/N ratio between the various treatments was observed, except for FL. However, cumulative across all plant parts, the C/N ratio followed the pattern of the C/N in AGB + S, showing significant ($p < 0.001$) differences between the treatments with zero and five annual cuts, with one- and two-cut treatments ranging in between.

Scenarios of Soil Carbon Input

The input of TC into soil was for all species highest in the zero-cut treatments, ranging between $6.6 \text{ t C ha}^{-1} \text{ year}^{-1}$ (TF) and $7.6 \text{ t C ha}^{-1} \text{ year}^{-1}$ (FL). A gradient of lesser TC input with increasing number of cuts was observed for all species, with the five-cut treatment being significantly lower than the treatment with zero harvests (Table 5). The one-cut treatment, harvested in August, was not significantly different to the five-cut treatment. Generally, TC_{in} was significantly ($p < 0.001$) affected by the random effect of harvest and fertilization treatment. When theoretically assuming equal AGB yields for all treatments on the example of RCG and the two literature-derived R/S scenarios (Table 6), TC_{in} ranged between $2.8 \text{ t C ha}^{-1} \text{ year}^{-1}$ (five cuts) and $7.3 \text{ t C ha}^{-1} \text{ year}^{-1}$ (zero cuts) for RCG. TC_{in} using the R/S from Bolinder (2007) and the IPCC (2006) was 3.1 and $9.6 \text{ t C ha}^{-1} \text{ year}^{-1}$, respectively. For all treatments and scenarios, TC_{in} was significantly affected by the R/S [$X^2(1) = 56.4, p < 0.001$].

DISCUSSION

In this study, we highlight that AGB and BGB as well as R/S differed greatly among the various harvest frequencies, with frequent cuts resulting in reduced BGB yields and lower R/S for all assessed species. However, while the effects of water saturation and nutrient availability on biomass development and the R/S are relatively well known (e.g. Guo et al., 2016), there are only little comparable data available regarding R/S for RCG, TF, and FL under various annual cuts within the first year of establishment. Mander et al. (2012) reported an R/S of 0.91 (unfertilized) and 0.67 (fertilized) for RCG on an abandoned peat extraction site in Estonia without harvest, while Klimesová (1994) found a R/S of between 1.9 and 2.1 for RCG in a pot experiment under similar soil and water conditions and for the same timeframe as in this study. The latter values are similar to the R/S of 2.3 for the RCG treatment without harvest in our study. Bolinder et al. (2002) reported for RCG and TF in the second year after cultivation R/S values of 1.0 and 0.6 for a treatment with two annual cuts. These values, 0.2 and 0.4 lower than the corresponding R/S from RCG and TF under two annual cuts observed in our study, are within a similar range. However, the higher R/S observed in our study probably results from a younger sward age, indicating the plant's need for optimal biomass allocation under the establishing growth period. Cougnon

TABLE 3 | Yields of total carbon (TC) and total nitrogen (TN), as well as TC and TN content in percentages, of aboveground (AGB), belowground (BGB), and stubble (S) biomass for the various species and treatments. Total yields for above- and belowground plant fractions are indicated as sums. Letters indicate differences between treatments, where treatments with the same letters are not significantly different. Standard error is given in brackets (n = 5).

Treatment	TC (t ha ⁻¹ year ⁻¹)				TN (g m ⁻² year ⁻¹)				TC %			TN %		
	AGB	BGB	S	Sum	AGB	BGB	S	Sum	AGB	BGB	S	AGB	BGB	S
Festulolium														
0 cut	6.4 (±1.3) ab	10.7 (±1.8)a	1.9 (±0.3)a	18.9 (±3.5)a	16.1 (±2.5)b	27.2 (±3.4)a	4.5 (±0.6)a	47.8 (±6.6)ab	45.6 (±0.32)a	37.6 (±1.00)b	44.6 (±0.41)a	1.2 (±0.15)d	1.0 (±0.06)b	1.1 (±0.16) ab
1 cut	2.4 (±0.4)c	2.6 (±0.7)b	0.6 (±0.1)b	5.5 (±1.2)b	13.8 (±2.8)b	9.8 (±2.8)b	2.2 (±0.8) bc	25.8 (±6.5)c	42.3 (±0.66)c	41.4 (±0.97)a	43.1 (±0.61) ab	2.4 (±0.24)c	1.5 (±0.08)a	1.5 (±0.19)a
2 cuts	8.2 (±1.0)a	8.0 (±1.3)a	1.7 (±0.4)a	17.9 (±2.6)a	27.6 (±2.1)a	20.3 (±3.0)a	3.3 (±0.5) ab	51.1 (±5.6)a	44.3 (±0.12)b	42.3 (±0.54)a	43.9 (±0.14) ab	3.2 (±0.11)b	1.1 (±0.05)b	0.9 (±0.11)b
5 cuts	4.2 (±0.7) bc	2.4 (±0.4)b	0.3 (±0.1)b	7.0 (±1.1)b	26.4 (±3.4)a	7.2 (±0.8)b	1.1 (±0.2)c	34.6 (±4.4)bc	43.6 (±0.30)b	38.5 (±0.92)b	42.6 (±1.08)b	3.9 (±0.20)a	1.2 (±0.10) ab	1.4 (±0.21)a
Reed canary grass														
0 cut	5.3 (±0.7)a	11.6 (±1.6)a	0.5 (±0.1)b	17.4 (±2.4)a	17.8 (±4.0)a	32.0 (±7.0)a	1.3 (±0.2)a	51.1 (±11.2)a	47.1 (±0.11)a	41.3 (±0.46) ab	41.4 (±1.68)b	1.5 (±0.15)c	1.1 (±0.08)a	1.2 (±0.16)b
1 cut	3.1 (±0.4)b	3.7 (±0.2)b	0.6 (±0.1) ab	7.3 (±0.7)b	13.1 (±3.1)a	10.9 (±1.5)b	1.3 (±0.4)a	25.3 (±5.0)b	46.1 (±0.07)b	39.2 (±1.67)b	44.6 (±0.16)a	1.9 (±0.19)c	1.1 (±0.04)a	0.9 (±0.15)b
2 cuts	4.4 (±0.8) ab	5.8 (±1.2)b	0.9 (±0.2)a	11.1 (±2.2)b	20.7 (±5.0)a	17.1 (±6.3)b	2.2 (±0.8)a	40.1 (±12.1) ab	45.4 (±0.17)c	43.5 (±0.25)a	45.4 (±0.25)a	3.1 (±0.31)b	1.2 (±0.19)a	1.1 (±0.13)b
5 cuts	5.1 (±0.7)a	4.0 (±0.4)b	0.4 (±0.0)b	9.5 (±1.1)b	34.4 (±7.2)b	11.9 (±1.3)b	1.7 (±0.2)a	47.9 (±8.7)a	44.5 (±0.33)d	40.0 (±1.10)b	43.8 (±0.94) ab	4.7 (±0.30)a	1.2 (±0.05)a	2.1 (±0.23)a
Tall fescue														
0 cut	5.1 (±0.7)a	9.6 (±1.2)a	1.4 (±0.3)a	16.1 (±2.1)a	13.6 (±1.5)b	24.6 (±2.0)a	3.4 (±0.6)a	41.6 (±4.1)a	45.4 (±0.10)a	38.4 (±0.60) ab	44.1 (±0.48)a	1.3 (±0.16)c	1.0 (±0.12)a	1.2 (±0.24)a
1 cut	2.9 (±0.3)b	3.7 (±0.4)b	0.9 (±0.2) ab	7.5 (±0.9)b	15.9 (±4.2) ab	13.3 (±3.3)b	3.6 (±1.6)a	32.9 (±9.2)a	44.4 (±0.15)b	38.2 (±1.50) ab	42.9 (±0.08)b	2.4 (±0.35)b	1.3 (±0.17)a	1.4 (±0.31)a
2 cuts	3.8 (±1.0) ab	4.1 (±0.7)b	1.3 (±0.2)a	9.2 (±1.9)b	18.3 (±7.3)a	10.7 (±2.1)b	3.1 (±0.8)a	32.1 (±10.2)a	44.4 (±0.28)b	40.0 (±1.36)a	44.0 (±0.26)a	3.1 (±0.29)a	1.0 (±0.10)a	1.0 (±0.16)a
5 cuts	4.9 (±0.9)a	3.5 (±0.4)b	0.5 (±0.1)b	9.0 (±1.4)b	27.4 (±5.5) ab	9.3 (±1.3)b	1.4 (±0.1)b	38.2 (±7.0)a	44.1 (±0.19)b	37.1 (±0.67)b	42.9 (±0.40)b	3.6 (±0.19)a	1.0 (±0.11)a	1.3 (±0.18)a

et al. (2013) reported 1 kg DM m⁻² more BGB for TF with five annual cuts than in our experiment for an already established sward, receiving 100 kg N ha⁻¹ and 100 kg K ha⁻¹ more than in this study, and 300 (FL)–700 (TF) g DM m⁻² more BGB in 3-year-old swards with five annual cuts, receiving similar fertilization amounts as in our study (Cougnon et al., 2017). We also found such differences in R/S for treatments without any harvest. For instance, Xiong et al. (2009) determined an R/S of 6.5 for RCG after a full year of growth, which differs significantly to our observed value of 2.3 after 210 days. Since the water table has been permanently controlled to –20 cm, a depth indicated as optimal for AGB development of flooding-tolerant perennial

grasses (Miller and Zedler, 2003; Ustak et al., 2019), and adequate nutrients were provided, we interpret the observed differences in R/S for all species regarding harvest frequencies as a response of the plant's biomass allocation. This is in accordance with the OPT (Kobe et al., 2010), where, as a consequence of more frequent harvest and removal of biomass involved in light energy capturing, more biomass is allocated to AGB organs in order to maximize photosynthesis. Further, the IA was supported by significant linear relationships between AGB and BGB, which is in line with other studies for temperate grasslands (e.g., Wang et al., 2010; Yang et al., 2018), indicating a coexistence of the OPT and IA theories. However,

TABLE 4 | Carbon-to-nitrogen (C/N) ratios in aboveground biomass (AGB), stubble biomass (S), combined aboveground and stubble biomass (AGB + S), and belowground biomass (BGB), as well as across all plant parts (cum) for the various treatments and species. Letters indicate differences between treatments, where treatments with the same letters are not significantly different.

Treatment	C/N AGB	C/N S	C/N AGB + S	C/N BGB	C/N Cum
Festulolium					
0 cut	38.8 (±4.3)a	42.0 (±5.5)ab	39.3 (±4.4)a	38.6 (±2.9)a	38.9 (±3.5)a
1 cut	18.0 (±1.6)b	30.3 (±2.9)b	19.4 (±1.6)b	27.0 (±1.0)b	22.2 (±1.3)b
2 cuts	29.5 (±2.3)a	52.5 (±5.7)a	31.9 (±2.7)a	39.2 (±1.7)a	34.6 (±2.0)a
5 cuts	15.9 (±1.1)b	32.6 (±4.6)b	16.6 (±1.2)b	33.0 (±2.5)ab	20.0 (±1.4)b
Reed canary grass					
0 cut	31.6 (±3.0)a	38.6 (±5.4)ab	32.1 (±3.1)a	38.0 (±2.4)a	35.7 (±2.6)a
1 cut	25.1 (±2.0)ab	54.5 (±7.3)a	27.4 (±2.3)a	34.8 (±2.4)ab	30.7 (±2.4)ab
2 cuts	21.8 (±2.1)ab	43.4 (±5.1)ab	23.8 (±2.3)ab	39.6 (±6.0)a	29.6 (±3.5)ab
5 cuts	15.0 (±1.3)b	22.3 (±2.3)b	15.4 (±1.3)b	34.1 (±0.7)a	19.7 (±1.5)b
Tall fescue					
0 cut	38.0 (±4.6)a	42.9 (±7.6)a	39.0 (±5.2)a	39.6 (±4.3)a	39.4 (±4.6)a
1 cut	20.1 (±2.1)b	36.1 (±6.2)a	22.2 (±2.4)b	30.9 (±3.0)a	25.8 (±2.7)ab
2 cuts	24.9 (±3.8)ab	47.5 (±7.2)a	28.3 (±4.3)ab	41.0 (±3.9)a	32.5 (±4.0)ab
5 cuts	18.2 (±1.5)b	34.9 (±5.1)a	19.0 (±1.6)b	39.8 (±4.8)a	23.9 (±2.0)b

TABLE 5 | Total annual harvested biomass yields in t dry matter (DM) ha⁻¹ year⁻¹ of the three perennial grasses under the various treatments, the content of total carbon (TC) in aboveground (AGB), stubble (S), and belowground (BGB) biomass and the determined root:shoot ratio (R/S), used for the calculation of aboveground net primary productivity (ANPP), stubble net primary productivity (SNPP), and belowground net primary productivity (BNPP), the input of carbon into soil from aboveground biomass residues (AC_{in}) and belowground biomass (BC_{in}), resulting in the total carbon input (TC_{in}) over a rooting depth of 50 cm. Letters indicate differences between treatments, where treatments with the same letters are not significantly different.

t DM ha ⁻¹ year ⁻¹		%				t TC ha ⁻¹ year ⁻¹						
AGB yield	S Yield	TC in AGB	TC in S	TC in BGB	R/S	ANPP	SNPP	BNPP	AC _{in}	BC _{in}	TC _{in}	
Festulolium												
0 cut	14.0	4.2	46	45	38	1.6	6.4	1.9	11.0	0.9 a	6.7 a	7.6 a
1 cut	5.6	1.3	42	43	41	0.9	2.3	0.6	2.5	0.3 b	1.5 c	1.8 c
2 cuts	18.1	3.9	44	44	42	0.8	8.0	1.7	7.4	0.9 a	4.5 b	5.4 b
5 cuts	9.6	0.8	44	43	39	0.6	4.2	0.4	2.4	0.2 b	1.5 c	1.7 c
Reed canary grass												
0 cut	11.2	1.1	47	41	41	2.3	5.3	0.5	11.6	0.2 a	7.0 a	7.3 a
1 cut	6.7	1.3	46	45	39	1.2	3.1	0.6	3.7	0.3 a	2.3 b	2.5 b
2 cuts	9.4	1.9	45	45	44	1.2	4.3	0.9	6.0	0.4 a	3.6 b	4.1 b
5 cuts	11.2	0.8	45	44	40	0.8	5.0	0.4	3.8	0.2 a	2.3 b	2.5 b
Tall fescue												
0 cut	11.1	3.1	45	44	38	1.8	5.1	1.4	9.8	0.7 a	5.9 a	6.6 a
1 cut	6.4	2.2	44	43	38	1.2	2.9	0.9	3.9	0.5 b	2.4 b	2.9 b
2 cuts	8.5	2.9	44	44	40	1.0	3.8	1.3	4.5	0.6 a	2.8 b	3.4 b
5 cuts	11.0	1.2	44	43	37	0.8	4.9	0.5	3.6	0.2 c	2.2 b	2.4 b

even though we were able to confirm our hypothesis, that different ratios between AGB and BGB will be observed in flood-tolerant perennial grasses under different harvest frequencies during the growth season under provision of adequate nutrient availability, there might remain a limitation of our observation for wet organic soils: that the R/S analysis was not performed on samples grown on peat soil cores. However, since R/S is rather affected by nutrient availability than soil types

(Lambert et al., 2014; Pinno et al., 2014; Lehtonen et al., 2016), we assume a reliable validity of the indicated R/S for similar growth conditions, including fertilizer management, also on peat soils. This is supported by other research, comparing differences in R/S for certain species and treatments between cultivation on mineral and organic soil types. Xiong et al. (2009) for example found similar R/S for RCG under different fertilization rates on both mineral and organic soils. Björk et al. (2007) reported similar

TABLE 6 | Calculation of the total carbon input into soil using averaged biomass yields on the example of reed canary grass and two literature-derived scenarios, applying different root to shoot (R/S) ratios. The contents of total carbon (TC) in aboveground (AGB), stubble (S), and belowground (BGB) biomass and the determined R/S were used for the calculation of aboveground net primary productivity (ANPP), stubble net primary productivity (SNPP), and belowground net primary productivity (BNPP), the input of carbon into soil from aboveground biomass residues (AC_{in}), and belowground biomass (BC_{in}), resulting in the total carbon input (TC_{in}) over a rooting depth of 50 cm. Yields are indicated in t dry matter (DM) ha⁻¹ year⁻¹.

t DM ha ⁻¹ year ⁻¹		%			t TC ha ⁻¹ year ⁻¹							
AGB yield	S yield	TC in AGB	TC in S	TC in BGB	R/S	ANPP	SNPP	BNPP	AC _{in}	BC _{in}	TC _{in}	
Reed canary grass scenario												
0 cut	10.0	2.0	47	41	41	2.3	4.7	0.8	11.3	0.4	6.9	7.3
1 cut	10.0	2.0	46	45	39	1.2	4.6	0.9	5.6	0.4	3.4	3.9
2 cuts	10.0	2.0	45	45	44	1.2	4.5	0.9	6.3	0.5	3.8	4.3
5 cuts	10.0	2.0	45	44	40	0.8	4.5	0.9	3.8	0.4	2.3	2.8
Scenarios												
Bolinder	10.0	2.0	45	45	45	0.8	4.5	0.9	4.3	0.5	2.6	3.1
IPCC	10.0	2.0	45	45	45	2.8	4.5	0.9	15.1	0.5	9.2	9.6

findings for root mass in Swedish heath and meadow tundra ecosystems, and Lambert et al. (2014) stated that R/S of *Arundo donax* was stable across soil types. Nonetheless, we propose that future research not only has to emphasize an assessment of cultivation treatments on R/S on mineral and organic soils but also needs to monitor TC and TN in AGB and BGB, as well as their development with increasing production years, due to expected variations (Sainju et al., 2017b). The C/N ratio can aid as an indicator for litter quality, with easier decomposable substrates having low C/N ratios (Rydin and Jeglum, 2013). Recalcitrant plant litter, indicated by high C/N ratios (Poirier et al., 2018), hence has the potential to increase soil C input—either directly to the pool of particulate organic matter (POM) or as microbial necromass following decomposition by microorganisms in the acrotelm (Worrall et al., 2017; Rossi et al., 2020). The potential for long-term C storage in the POM pool is in particular high for wet organic soils due to anoxic conditions in the catotelm, indicated by higher contents of lignin with increasing peat depth (Williams and Yavitt, 2003). Further, in soils with <12% SOC, additional C storage through the POM pool has the potential to overcome soil C saturation (Cotrufo et al., 2019). However, for drained soils where microbial activity is found in deeper layers, there is no consensus whether the C/N in BGB can be used as a predictor for the decomposability of root litter, and hence the C storage potential, as indicated by interspecific variation (Bonanomi et al., 2021). However, while R/S and C in biomass have been assessed for RCG on mineral and organic soils (Xiong et al., 2009; Xiong and Kätterer, 2010), this study was to our knowledge among the first to, besides R/S, also assess C/N in AGB and BGB parts.

The input of carbon into soil is a critical component of the global C cycle, thus significantly contributing to various aspects of ecosystem functioning. Modeling existing and changing soil organic carbon (SOC) stocks hence is a critical task in decision support related to optimal climate and land management (Taghizadeh-Toosi et al., 2016). However, while it is recognized that C allocation in belowground plant organs depends on vegetation type (Keller and Phillips, 2019), growing conditions (Whitehead, 2020), and plant development stages and

management (Pausch and Kuzyakov, 2018), only few of these complex relationships (Cheng et al., 2014) are set into context with soil geochemistry and accounted for during SOC modeling (Finke et al., 2019). For instance, previously reported R/S for perennial grasses showed a broad distribution of median values, which has been shown in reviews by Bolinder et al. (2007) and Pausch and Kuzyakov (2018). Given the critical role of BGB carbon input, our study highlights the importance of acquiring more extensive knowledge regarding the development of perennial grass root systems depending on AGB manipulation by harvest. We only found marginally significant differences in R/S for the various treatments and species, apart for the, in agriculturally used grasslands, uncommon zero-cut strategy, which could indicate that a fixed R/S for perennial grasses might be reasonable to use if accurately defined.

However, our calculation of soil C input for perennial grasses under different harvest frequencies revealed significant differences for the various management options and applied R/S. This highlighted a potential risk for over- and underestimation of the C sink functioning of wetlands and grassland ecosystems. While, for instance, using the IPCC default R/S of 2.8 resulted in an estimated annual carbon input into soil of 9.6 t C ha⁻¹ year⁻¹ for a RCG yield of 10 t DM ha⁻¹ year⁻¹, our results ranged between 2.8 and 7.3 t C ha⁻¹ year⁻¹ for the same AGB yield, depending on annual harvest frequencies. Since, for instance, the default IPCC (2006) estimate of R/S of 2.8 is applied in the Danish National Inventory Report (2020), the discrepancy of TC input from BGB resulting from varying R/S might have far-reaching consequences for policymaking. For instance, depending on whether management measures are extensive, e.g., designated nature areas without any biomass manipulation, or intensive, e.g., biomass harvest up to five times annually, the choice of R/S for the quantification of an organic soil C sink function must be made carefully and adapted to the ecosystem in question. This is in particular true for the designation of rewetting measures on wetland areas, including the choice of land use and land cover, for climate considerations. In the context of optimum grassland management for agricultural production, we showed that a strategy with two annual cuts has the highest potential to contribute to SOC

buildup. We hence advocate an inclusion of more accurate R/S for modeling, taking differences resulting from grass management, as well as site-specific climatic and biogeochemical conditions (Sahoo et al., 2021), into consideration to reduce uncertainties for policymaking on agroecosystems.

However, a limitation of this study is the assessment of harvest frequency on R/S during the establishment year only, which emphasizes the need for more long-term data on root growth of managed and unmanaged perennial grasses in wet environments. Hence, we suggest a future multi-annual study, with at least 2 years of trial, to increase the validity of results by accounting for the plants long-term response to management, taking interannual climatic variability into consideration. Previous studies demonstrated that R/S varies with ley age (Bolinder et al., 2002; Acharya et al., 2012; Huang et al., 2021), the associated interannual climatic variability (Poorter et al., 2012; Li et al., 2021), and nutrient availability (Cong et al., 2019); hence, further years of experimental analysis have to determine whether our findings regarding the effect of harvest frequency on R/S and the associated implications of management for SOC input are applicable on the long term. Further, it is yet unclear how the determined R/S for the assessed grasses can be applied in the evaluation of SOC input by plant biomass in wet or rewetted agricultural wetlands. For wet organic soils and in the context of paludiculture, we suggest that not only root growth but also rooting depth and specific root turnover rates have to be assessed. Only few studies assessed the maximum potential rooting depth by flood-tolerant perennial grasses in correlation with the WTD profile on organic soils, as compiled by Fan et al. (2017). Houde et al. (2020) highlighted the significance of turnover of perennial grass roots for the C storage potential, and Schwiieger et al. (2020) emphasized the significance of roots as the main peat-forming component in grass-covered fen peatlands. However, while wetland ecosystems potentially have the second-highest root turnover rates of all ecosystems (Gill and Jackson, 2000), the complexity between rooting depth, WTD, C/N, and litter recalcitrance (Shurpali et al., 2010; Straková et al., 2012; Leifeld et al., 2015; D'Imperio et al., 2018) as well as AGB manipulation and root turnover rates for soil C input still needs to be defined.

With an increasing policy focus on wetland restoration, including paludiculture, for GHG mitigation and nutrient retention, as well as the concomitant need to point out sites with the highest mitigation potential, not only assessments of GHG emissions and optimum management (e.g., Geurts et al., 2019; Tanneberger et al., 2020; Nielsen et al., 2021) but also site- and plant community-specific BGB NPP should be taken into consideration for an accurate evaluation of the C sink potential.

CONCLUSION

While it is known that C inputs in soils are affected by development of AGB and BGB, as well as a variety of biotic and abiotic factors, little has been known so far on the effect of harvest frequency on the R/S of perennial grasses. In conclusion, this study found significant differences in the R/S for the flood-tolerant perennial grasses *Phalaris ar.*, *Festuca ar.*, and *Festuca* × *Lolium*, affected by annual harvest frequencies of AGB, with less biomass allocated to

belowground parts with increasing number of cuts. No species-specific differences in the ratio were observed for any treatments. In addition, our results showed that both the OPT of plant biomass allocation and the IA hypothesis seemed to coexisted. Further, we demonstrated the importance to accurately define R/S for the calculation of carbon input into soils to avoid significant over- or underestimation. Our results showed that there are significant differences regarding the annual carbon input into soils, depending on the R/S applied. We found that using the IPCC default factor for R/S of 2.8, applied for both managed and unmanaged grasslands, resulted in 55%–71% higher carbon input rates as compared to our scenarios with two and five annual cuts, commonly applied in agricultural systems. This discrepancy indicates a significant inaccuracy for modeling and quantification of the C sink or source function of wet organic grassland areas, which might have far-reaching consequences for policymaking and carbon accounting. Further, we not only demonstrated how measurements of AGB and BGB provided a more accurate baseline for estimation of soil carbon input but also indicated the need for further assessment of R/S and C/N of perennial grasses, particularly for those cultivated on wet organic soils, to define the soil C sink capacity.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

CN developed and performed the study design and experimental work, the analysis of the data, and the writing of the manuscript. All authors contributed to the study design and the writing and reading of the manuscript and approved the final manuscript.

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