



Soil Texture Rather Than Water Potential Determines the Root:Shoot Ratio in Ryegrass and Alfalfa

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Abstract

Backgrounds A fixed root:shoot ratio is widely used to estimate the underground biomass in the carbon (C) cycle in grassland ecosystems, although edaphic and climatic factors may influence the root:shoot ratio. Our current understanding of the effects of the soil texture and water potential on the root:shoot ratio is rather poor.

Methods Thus, we conducted a pot experiment where we measured the dry weights of the roots and shoots to investigate the responses of ryegrass (*Lolium perenne*, L.) and alfalfa (*Medicago sativa*, L.) in terms of C allocation to different soil textures and water potentials.

Results The root:shoot ratios in ryegrass and alfalfa were significantly affected by the soil texture, but not by the soil water potential (−400 kPa to −40 kPa). Integrated analysis of previous studies indicated a significant average negative correlation between the root:shoot ratio and clay content according to a linear mixed model ($k = -0.0045$). This correlation might be related to the hydraulic properties of the root-soil contact zone.

Conclusions We assume that the soil water potential in our experiment was insufficient to affect root hydraulic conductivity, but further evidence is required. Our findings could be useful for future estimates of ecosystem C stocks.

Keywords Alfalfa · Root:shoot ratio · Ryegrass · Soil texture · Soil water potential

1 Introduction

The root biomass is the core link in the soil organic matter allocation and process (Tsegay and Meng 2021). Huang et al. (2021) suggested that the stabilization efficiency of root-derived carbon (C) in the soil is two times greater than that of aboveground residues. However, compared with the aboveground biomass, measuring the root biomass is more challenging due to the difficulty of accurately collecting the root biomass (Tian et al. 2018).

The root:shoot ratio is generally used to estimate the root biomass (Mokany et al. 2006). Fixed allocation coefficients are widely applied although the root:shoot ratio

is known to be affected by biotic and abiotic factors (Qi et al. 2019), including the plant species (Warren et al. 2015), stand condition (Costa et al. 2014; Zhang et al. 2022), climate (Reich et al. 2014), and nutrition (Martin et al. 2022). Previous studies (Khan et al. 2012; Moore and Lawrence 2013) demonstrated that the root:shoot ratio is influenced by the soil physical properties, particularly by the differences in the bulk density and thus the penetration resistance, as well as differences in the water-holding capacity and availability of nutrients. Studies have indicated that the soil texture is the main factor that affects the root:shoot ratio (Zhang et al. 2015; Moore and Lawrence 2013). The soil bulk density and shear strength are both related to the soil texture, and they can considerably affect root growth due to mechanical constraints (Barbosa et al 2018; Cai et al. 2021; Nunes et al. 2021). Poeplau and Katterer (2017) found that the soil texture rather than nutrient availability was the most important factor that affected root growth in spring barley, and they also hypothesized that this correlation was due to texture-related differences in water availability. Our current understanding of the effect of soil water on

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the root:shoot ratio is unclear. In particular, Ma and Fang (2006) reported that the soil water content had no significant effect on the root:shoot ratio. By contrast, Mrak et al. (2019) reported that soil water deficit increased the root:shoot ratio because more roots were needed to absorb water. These different results might be explained by differences in the soil types, indexes analyzed, and plant species used in their studies. The distributions of the soil texture and rainfall usually exhibit some zonality at a regional scale. Therefore, it is important to understand the effects of the soil texture and soil water on the root:shoot ratio to obtain more precise estimates of root-derived C inputs. The soil water potential is determined by the soil texture and water content, and our current understanding of the effect of the soil water potential on plant C allocation is rather poor. It has been shown that the soil water potential is particularly useful for understanding the movement of water from the soil to plants (Kutlu et al. 2018). However, further research is required to determine whether the soil water potential can be used to obtain better prediction of the root:shoot ratio.

In general, the effects of the soil texture and water potential on the root:shoot ratio are not considered adequately when estimating belowground C inputs. Thus, in the present study, we conducted a pot experiment to determine whether the soil texture or water potential is a better predictor of the root:shoot ratio. The plants used in this study were ryegrass and alfalfa, which are major perennial herbaceous plants on the Loess Plateau in China.

Table 1 Physicochemical properties and hydraulic parameters for soil samples

Parameter	Sandy soil	Silty clay loam soil
Sand (%)	90.47	6.51
Silt (%)	6.17	61.18
Clay (%)	3.36	32.31
Bulk density (g cm^{-3})	1.60	1.40
Total N ($\mu\text{g g}^{-1}$)	20	102
$\text{NH}_4\text{-N}$ ($\mu\text{g g}^{-1}$)	7.30	8.10
Total P ($\mu\text{g g}^{-1}$)	270	700
Plant-available P ($\mu\text{g g}^{-1}$)	2.60	6.80

Plant-available P concentrations were determined by bicarbonate extraction

Table 2 Soil water content and hydraulic conductivity under different water potentials

Water potential (kPa)	Water content ($\text{cm}^3 \text{cm}^{-3}$)			Hydraulic conductivity (cm d^{-1})		
	Sandy soil	Mixture	Silty clay loam soil	Sandy soil	Mixture	Silty clay loam soil
-40	0.07	0.17	0.25	7.67×10^{-3}	1.03×10^{-3}	6.04×10^{-3}
-100	0.05	0.14	0.21	5.88×10^{-6}	1.27×10^{-4}	1.01×10^{-3}
-400	0.04	0.12	0.17	3.56×10^{-8}	2.03×10^{-5}	8.08×10^{-5}

2 Materials and Methods

2.1 Soil Samples

Sandy soil and silty clay loam soil samples were collected from the towns of Shenmu ($109^{\circ}30'34.3''\text{E}$, $38^{\circ}48'22.6''\text{N}$) and Yangling ($108^{\circ}02'6.4''\text{E}$, $34^{\circ}16'46.7''\text{N}$), respectively, in Shaanxi province, China. The sandy soil and silty clay loam soil samples were air dried and passed through a 2-mm sieve. Selected properties of the two soil samples are listed in Table 1. The soil texture was analyzed by laser diffraction using a Mastersizer 2000 (MS-2000, Malvern, UK). The bulk densities of both soil types were measured by using the core sampling method at the beginning and end of the experiment, and they did not vary greatly during the experiment (sandy soil, 1.60 g cm^{-3} ; silty clay loam soil, 1.40 g cm^{-3} ; and equal mixture of sandy soil and silty clay loam soil, 1.50 g cm^{-3}). Total nitrogen (N) was measured using the Kjeldahl method (Guo et al. 2019). The $\text{NH}_4^+\text{-N}$ contents were measured using a Seal Auto Analyzer. Total phosphorus (P) was determined by melt-molybdenum, antimony, and scandium colorimetry. The plant-available P was extracted with bicarbonate, and the concentration was determined with a molybdenum blue colorimetric method using ultraviolet-photometry.

2.2 Soil Characteristics

The sandy soil and silty clay loam soil samples were characterized by clay fractions of 3.36% and 32.31%, respectively, and sand fractions of 90.47% and 6.51% (Table 1). The N and P contents were low in both samples (Table 1). Thus, external N and P were fully supplied.

The relationships between the soil water content and three soil water potentials (-40 kPa, -100 kPa, and -400 kPa) were determined at 20 °C for the sieved soils during drying down using the centrifuge method (Nimmo and Akstin 1988) with a high speed centrifuge (CR21G, Japan). As shown in Table 2, the soil water content increased as the water potential increased in the same soil type. The soil water content of the silty clay loam soil was higher than those of the mixture and sandy soil at the same water potential. At a soil water potential of -40 kPa, the soil water content of the silty clay loam soil was 3.6 times higher and 1.5 times higher than those of the sandy soil and mixture, respectively. At a soil

water potential of -400 kPa, the soil water content of the silty clay loam soil was 4.3 times higher and 1.4 times higher than those of the sandy soil and mixture, respectively.

The relationships between the soil water content and hydraulic conductivity were determined by using a retention curve (RETc) computer model (Peters et al. 2021). As shown in Table 2, the hydraulic conductivity increased as the water potential increased in the same soil type. The hydraulic conductivity of the sandy soil was lowest at a soil water potential of -40 kPa.

2.3 Pot Experiment

The sieved soil was packed into prepared pots with a diameter of 15 cm and height of 20 cm. Each treatment was replicated four times, with a total of 36 pots (three soil textures \times three soil water potentials \times four pots). External N and P were supplied as carbamide and calcium superphosphate,

respectively, at approximate rates of 150 and $120 \mu\text{g g}^{-1}$ dry soil. The fertilizer was weighed and mixed with the soil samples before packing. No other fertilizer was supplied throughout the experiment. All of the soil substrates were incubated for 60 days before sowing the ryegrass and alfalfa seeds. Thirty seeds were sown in each pot, and the seedlings were thinned to 20 plants per pot at 2 weeks after emergence. The target water content was maintained in each pot by irrigation according to Table 2, and the contents were verified by weighing every 3 days. The pot experiment based on the growth of ryegrass and alfalfa under different soil textures and water potentials is illustrated in Fig. 1, and the amounts of water applied are shown in Fig. 2. The shoots were cut off in the ryegrass and alfalfa flowering periods. The roots were then carefully separated from the soil by washing and sieving in a water tub. The shoots and roots were dried in an oven at 60°C for 48 h and weighed separately. The 64-day experiment was conducted from June to August during 2019

Fig. 1 Images showing the pot experiments conducted with ryegrass (a) and alfalfa (b) before cutting

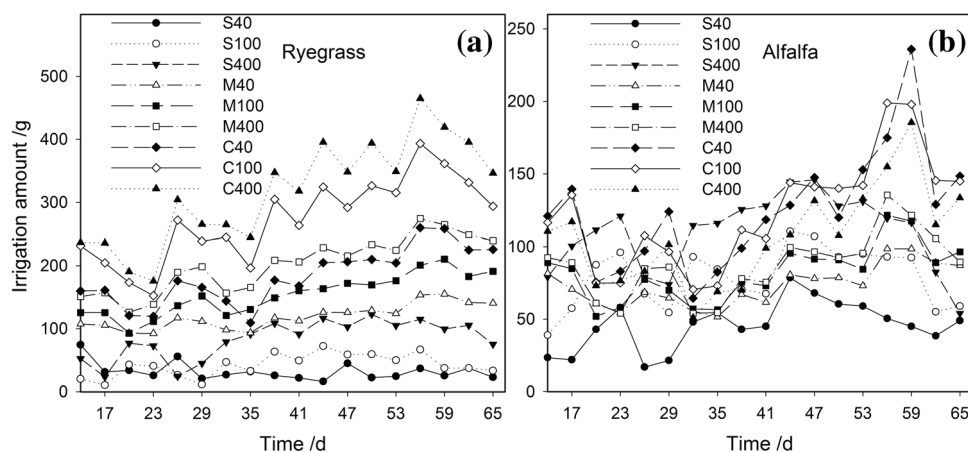
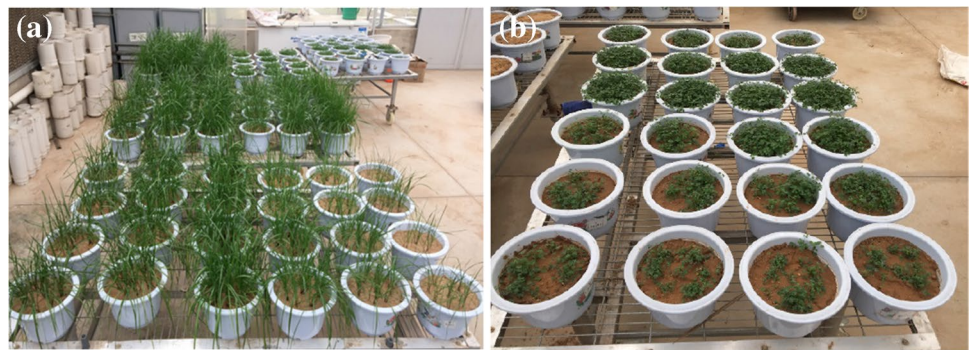


Fig. 2 Amounts of irrigation water applied to ryegrass (a) and alfalfa (b) over time. S40, sandy soil at a soil water potential of -40 kPa; S100, sandy soil at a soil water potential of -100 kPa; S400, sandy soil at a soil water potential of -400 kPa; M40, mixture at a soil water potential of -40 kPa; M100, mixture at a soil water potential of

-100 kPa; M400, mixture at a soil water potential of -400 kPa; C40, silty clay loam soil at a soil water potential of -40 kPa; C100, silty clay loam soil at a soil water potential of -100 kPa; C400, silty clay loam soil at a soil water potential of -400 kPa

in a glasshouse at the Institute of Soil and Water Conservation, Yangling, Shaanxi, China. The temperature in the greenhouse was kept between 20 and 30 °C, with no supplemental lighting or other additional conditions.

2.4 Statistical Analysis

The effects of the soil texture, water potential, and their interactions on the shoot biomass, root biomass, and root:shoot ratio were determined by two-way analysis of variance, followed by the least significant difference test. We also compared our results with data obtained in previous studies to assess their generality and representativeness. In particular, eight previous studies that investigated the effects of the soil texture on the root:shoot ratio in different crops (Table 4) were selected. A linear mixed effect model was used to test the effects of different soil textures on the root:shoot ratio, and the continuous clay content variable was treated as a fixed effect. All statistical analyses were conducted using IBM SPSS 20 software. Statistically significant differences were accepted at the 5% significance level.

3 Results

3.1 Biomass Production

The ryegrass and alfalfa shoot biomasses under different soil textures and water potentials are shown in Fig. 3. The highest shoot biomasses in ryegrass ($10.48 \pm 0.87 \text{ g pot}^{-1}$) and alfalfa ($3.50 \pm 0.03 \text{ g pot}^{-1}$) occurred in silty clay loam soil at a soil water potential of -40 kPa . The lowest shoot biomasses in ryegrass ($1.16 \pm 0.32 \text{ g pot}^{-1}$) and alfalfa ($0.72 \pm 0.05 \text{ g pot}^{-1}$) occurred in sandy soil at a soil water potential of -400 kPa . The shoot biomass increased as the soil water potential increased (Fig. 3). At the same water potential, the shoot biomass was higher in silty clay loam

soil than the mixture and sandy soil. Table 3 shows that the water potential and soil texture had significant ($P < 0.001$) effects on the shoot biomass in ryegrass and alfalfa.

Figure 4 shows the ryegrass and alfalfa root biomasses under different soil textures and water potentials. The highest root biomasses in ryegrass ($3.02 \pm 0.28 \text{ g pot}^{-1}$) and alfalfa ($1.80 \pm 0.19 \text{ g pot}^{-1}$) occurred in silty clay loam soil at a soil water potential of -40 kPa . The lowest root biomass in ryegrass ($0.63 \pm 0.21 \text{ g pot}^{-1}$) and alfalfa ($0.46 \pm 0.05 \text{ g pot}^{-1}$) occurred in sandy soil at a soil water potential of -400 kPa . The changes in the shoot biomass were similar to those in the root biomass. Figure 4 and Table 3 show that the water potential and soil texture had significant ($P < 0.001$) effects on the root biomass in ryegrass and alfalfa.

3.2 Root:shoot ratio

Figure 5 shows that the root:shoot ratio was higher in sandy soil than the mixture and silty clay loam soil. The highest root:shoot ratios in ryegrass ($0.54 \pm 0.03 \text{ g pot}^{-1}$) and alfalfa ($0.64 \pm 0.08 \text{ g pot}^{-1}$) occurred in sandy soil at a soil water potential of -400 kPa . The lowest root:shoot ratio in ryegrass ($0.25 \pm 0.02 \text{ g pot}^{-1}$) occurred in silty clay loam soil at a soil water potential of -400 kPa . The lowest root:shoot ratio in alfalfa ($0.50 \pm 0.02 \text{ g pot}^{-1}$) occurred in silty clay loam soil at a soil water potential of -400 kPa . The average root:shoot ratios for ryegrass were 0.51 in sandy soil, 0.33 in the mixture, and 0.27 in silty clay loam soil, and those for alfalfa were 0.61 in sandy soil, 0.52 in the mixture, and 0.51 in silty clay loam soil. Table 3 shows that the soil textures had significant effects on the root:shoot ratios in ryegrass ($P < 0.001$) and alfalfa ($P = 0.036$). A linear function ($Y = aX + b$) was applied to describe the relationship between the shoot/root biomass (Y) and clay content (X). Average positive slopes of 25.11 (shoot biomass and soil texture) and 5.25 (root biomass and soil texture) were obtained for ryegrass and average

Fig. 3 Shoot biomasses in ryegrass (a) and alfalfa (b) under each treatment. Different uppercase letters (A, B, and C) indicate significant differences in means ($P < 0.05$) between different soil textures under a specific soil water potential. Different lowercase letters (a, b, and c) indicate significant differences in means ($P < 0.05$) between different soil water potentials under a specific soil texture

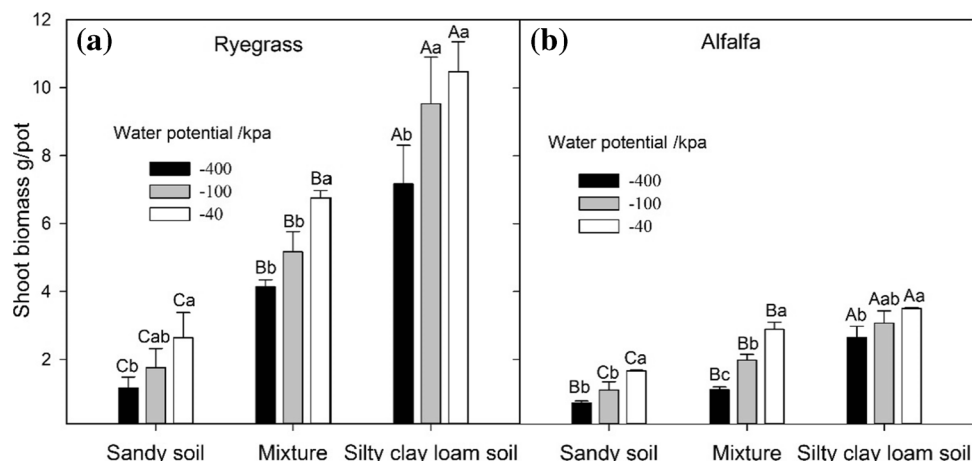


Table 3 Summary of analysis of variance results to determine the effects of soil texture, water potential, and their interaction on the shoot and root biomasses and root:shoot ratio in ryegrass and alfalfa

	Dependent variable	Source	Sum of squares	df	Mean square	F	P
Ryegrass	Shoot biomass	Texture	256.307	2	128.154	191.908	<0.001
		Water potential	28.628	2	14.314	21.435	<0.001
		Texture*Water potential	3.868	4	0.967	1.448	0.255
		Residual	13.356	20	0.668		
		Total	302.159	28	144.103		
	Root biomass	Texture	11.179	2	5.589	78.610	<0.001
		Water potential	5.151	2	2.575	36.220	<0.001
		Texture*Water potential	0.315	4	0.079	1.108	0.380
		Residual	1.422	20	0.071		
		Total	18.067	28	8.315		
	Root:shoot	Texture	0.310	2	0.155	274.894	<0.001
		Water potential	0.003	2	0.001	2.531	0.105
		Texture*Water potential	0.011	4	0.003	5.022	0.060
		Residual	0.011	20	0.001		
		Total	0.335	28	0.160		
Alfalfa	Shoot biomass	Texture	4.480	2	6.599	138.786	<0.001
		Water potential	13.199	2	2.240	47.106	<0.001
		Texture*Water potential	0.554	4	0.138	2.911	0.068
		Residual	0.571	21	0.027		
		Total	18.804	29	9.004		
	Root biomass	Texture	2.814	2	1.407	46.519	<0.001
		Water potential	1.385	2	0.693	22.900	<0.001
		Texture*Water potential	0.170	4	0.042	1.405	0.291
		Residual	0.363	21	0.017		
		Total	4.732	29	2.159		
	Root:shoot	Texture	0.042	2	0.021	4.448	0.036
		Water potential	0.002	2	0.001	0.160	0.854
		Texture*Water potential	0.005	4	0.001	0.261	0.897
		Residual	0.057	21	0.003		
		Total	0.106	29	0.026		

df, degrees of freedom

Fig. 4 Root biomasses in ryegrass (a) and alfalfa (b) under each treatment. Different uppercase letters (A, B, and C) indicate significant differences in means ($P < 0.05$) between different soil textures under a specific soil water potential. Different lowercase letters (a, b, and c) indicate significant differences in means ($P < 0.05$) between different soil water potentials under a specific soil texture

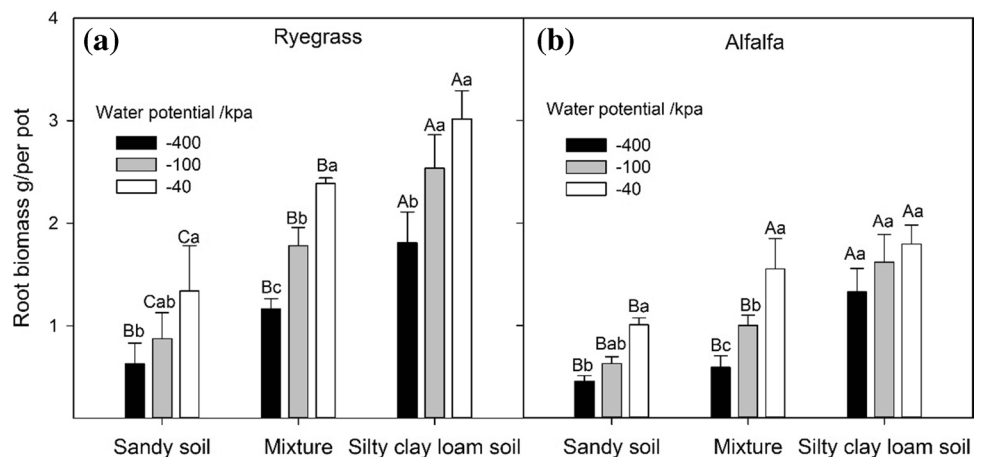


Fig. 5 Root:shoot ratios in ryegrass (a) and alfalfa (b) under each treatment. Different uppercase letters (A, B, and C) indicate significant differences in means ($P < 0.05$) between different soil textures under a specific soil water potential. Different lowercase letters (a, b, and c) indicate significant differences in means ($P < 0.05$) between different soil water potentials under a specific soil texture

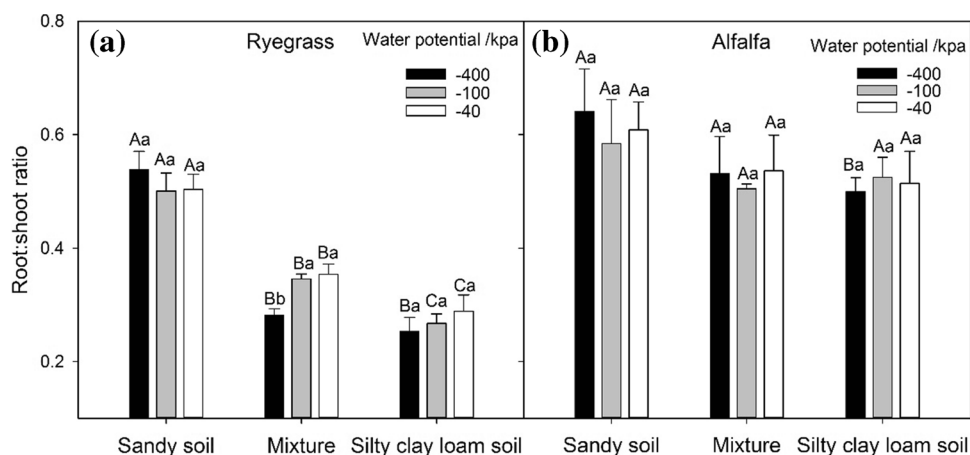


Table 4 Regression equations between root:shoot (R/S) ratio and clay content (X)

Number of pairs	Regression equation	R^2	Plant species	References
4	$R/S = -0.0032x + 0.1528$	0.9747	Wheat	Al-Khafaf et al. 1989
4	$R/S = -0.0010x + 0.3117$	0.2296	Switchgrass	Evers and Parsons 2003
3	$R/S = -0.0114x + 0.7699$	0.9034	Maize	Wakeel et al. 2005
3	$R/S = -0.0041x + 0.1992$	0.9847	Cotton	Li et al. 2005
2	$R/S = -0.0012x + 0.0797$	1.0000	Wheat	Khan et al. 2012
6	$R/S = -0.0064x + 0.9591$	0.3320	Cotton	Moore and Lawrence 2013
3	$R/S = -0.0059x + 0.2647$	0.9480	Cereals	Poeplau and Katterer 2017
3	$R/S = -0.0276x + 0.5272$	0.9792	Alfalfa	Jia et al. 2019
3	$R/S = -0.0084x + 0.5024$	0.9138	Ryegrass	This study
3	$R/S = -0.0034x + 0.6098$	0.8355	Alfalfa	This study

positive slopes of 6.67 (shoot biomass and soil texture) and 3.07 (root biomass and soil texture) for alfalfa. Therefore, the significant effect of soil texture on the root:shoot ratio was due to a sharp increase in the shoot biomass and a slow increase in the root biomass as the soil texture changed from coarse to fine-textured soil (Fig. 3, Fig. 4, Table 3). However, the water potential had no significant effects on the root:shoot ratios in ryegrass ($P = 0.105$) and alfalfa ($P = 0.854$).

3.3 Integration of Previous Studies

Effects of different soil textures on the root:shoot ratio have been demonstrated in some previous studies. Thus, we collected and analyzed eight previous studies that investigated the relationship between the clay content and root:shoot ratio (Al-Khafaf et al. 1989; Evers and Parsons 2003; Wakeel et al. 2005; Li et al. 2005; Khan et al. 2012; Moore and Lawrence 2013; Poeplau and Katterer 2017; Jia et al. 2019). The linear regression equations and R^2 values calculated between the root:shoot ratio are shown in Table 4. A fixed effects linear mixed model was applied to

Table 5 Summary statistics for the fixed effects in the linear mixed model applied to investigate the effect of the clay content on the root:shoot ratio, with estimated coefficients (B), standard error of the coefficients (SE), and F and P values

Fixed effect	B	SE	F	P
Intercept	0.4067	0.0813	25.002	0.001
Clay content	-0.0045	0.0012	15.001	0.001

investigate the effect of the clay content on the root:shoot ratio and a significant ($P < 0.001$) average negative slope of -0.0045 ± 0.0012 (standard error; Table 5) was obtained for the different plant species.

4 Discussion

The root and shoot biomasses in ryegrass and alfalfa increased significantly as the clay content increased. In addition, the root:shoot ratios in ryegrass and alfalfa decreased significantly as the clay content increased. These changes were due to a sharp increase in the shoot biomass and a slow increase in the root biomass

as the soil texture changed from coarse to fine-textured soil. Eight previous studies (Table 4) showed that the root:shoot ratio was affected by the soil texture, thereby agreeing with the results obtained in the present study, despite the different plant species investigated. Similarly, Poeplau and Katterer (2017) reported that the soil texture is a major factor that controls the root:shoot ratio in cereals. In addition, Herkelrath et al. (1977) suggested that roots in coarse soil are partly exposed to large air-filled pores, which create a physical discontinuity to hinder the movement of water from the soil to the roots, thereby forcing the plant to increase the root surface area. The physical discontinuity between the root surface and soil particles was experimentally confirmed using the thin-section technique (Kooistra et al. 1992). North and Nobel (1997) investigated and confirmed the extent and size of the root-soil contacts that developed during soil drying. Li et al. (2005) provided evidence that root-soil contact is related directly to the hydraulic conductance at the soil:root interface. The root-soil contact increased as the aggregate or soil particle size decreased according to estimates based on three-dimensional X-ray microtomographs (Schmidt et al. 2012). Cai et al. (2021) suggested that the soil texture is the main factor that determines the uptake of water and soil-plant hydraulics under drought. Therefore, the observed effect of the soil texture on the root:shoot ratio was probably due to differences in the direct root:soil interface and texture-related differences in water availability (Saha et al. 2020), thereby resulting in greater plant C allocation to the underground organs to promote hydraulic conductivity in the coarse-textured soil.

The root and shoot biomasses in ryegrass and alfalfa increased significantly as the soil water potential increased. The soil water potential reflects the availability of soil water to plants, which might influence plant growth (Vogel et al. 2016). A higher soil water potential is more beneficial for the absorption and utilization of soil water by plants, thereby promoting plant growth (Cai et al. 2018). However, the soil water potential had no clear effect on the root:shoot ratio in the present study because of the similar responses by the shoot biomass and root biomass. Liu et al. (2015) reported the occurrence of progressively greater root shrinkage, loss of root-soil contact, and increased resistance to water flow at the soil:root interface as the soil water potential decreased. In addition, Cai et al. (2021) suggested that the soil hydraulic conductivity dropped by several orders of magnitude and became even lower than the root hydraulic conductivity at more negative soil water potentials. However, further studies are needed to determine how the soil hydraulic conductivity changes the root hydraulic conductivity under different soil textures, which might help explain the relationship between the soil water potential and root:shoot ratio.

The results obtained in this study highlight the importance of considering the soil texture for accurately estimating the underground biomass and root-derived C inputs. A 5% increase in the clay content would decrease the annual root-derived carbon input by $0.07 \text{ Mg ha}^{-1} \text{ year}^{-1}$ when an average coefficient of -0.0045 is applied. This demonstrates that considerable errors might occur when constant root:shoot ratio values are used to estimate root-derived C inputs.

5 Conclusions

In the present study, we determined whether the soil texture or water potential is a better predictor of the root:shoot ratio. Experimental observations demonstrated that the root:shoot ratios in ryegrass and alfalfa decreased significantly as the clay content increased, whereas the soil water potential had no clear effect on the root:shoot ratio. Integrated analysis of previous studies also showed that effects of different soil textures on the root:shoot ratio were observed in several other crop types. These effects might be attributable to the weaker root-soil contacts in coarse-textured soil leading to the production of a greater root area to increase the hydraulic conductance. Thus, estimating root-derived carbon inputs by assuming a constant root:shoot ratio for a given soil may lead to considerable errors if the soil texture is not considered, and it is independent of the water potential over a medium range. Understanding root biomass dynamics is essential for improving our knowledge of carbon allocation and storage in terrestrial ecosystems. According to our novel findings, the incorporation of plant-specific root:shoot ratios under different soil textures in models could substantially improve the accuracy of root biomass estimates for applications such as carbon accounting and studies of ecosystem dynamics. Thus, the novel results obtained in the present study might help to improve the accuracy of fine-scale ecosystem carbon stock estimates on local or global scales, which could clearly deviate greatly from the estimates utilized widely for policy and strategy development. Furthermore, more accurate root biomass estimates may facilitate better predictions of local and global carbon cycles under future conditions, particularly under ongoing climate change.

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Author Contribution All authors contributed to the study conception, design, data collection, analyses, and writing and revising the manuscript. All authors read and approved the final manuscript.

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Data Availability The data used to support the findings of this study are available from the corresponding author upon request.

Declarations

Competing Interests The authors declare no competing interests.

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