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Optimising Root and Grain Yield Through Variety Selection in Winter Wheat Across a European Climate Gradient

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ABSTRACT

Ensuring food security through sustainable practices while reducing greenhouse gas emissions are key challenges in modern agriculture. Utilising genetic variability within a crop species to identify varieties with higher root biomass carbon (C) could help address these challenges. It is thus crucial to quantify and understand intra-specific above- and belowground performance under varying environmental conditions. The study objectives were to: (a) quantify root biomass and depth distribution in different winter wheat varieties under various pedoclimatic conditions, (b) investigate the influence of variety and pedoclimatic conditions on the relationship between above- and belowground biomass production, and (c) assess whether optimised winter wheat variety selection can lead to both greater root biomass C and yield, boosting C accrual. Root biomass, root distribution to 1 m soil depth and root-to-shoot ratios were assessed in 10 different winter wheat varieties grown at 11 experimental sites covering a European climatic gradient from Spain to Norway. Median root biomass down to 1 m depth was $1.4 \pm 0.7 \, \text{Mg ha}^{-1}$. The primary explanatory factor was site, accounting for 60% of the variation in root biomass production, while the genetic diversity between wheat varieties explained 9.5%. Precipitation had a significantly negative effect on total root biomass, especially in subsoil. Significant differences were also observed between varieties in root-to-shoot ratios and grain yield. The difference between the variety with the lowest root biomass and the one with the highest across sites was on average $0.9 \, \text{Mg ha}^{-1}$ which is an increase of 45%. Pedoclimatic conditions had a greater influence than variety, and determined the relationship's direction between root biomass and grain yield. A site-specific approach is, therefore, needed to realise the full potential for increased root biomass and yield offered by optimised variety selection.

Summary

- The variability in root biomass among 10 winter wheat varieties was quantified in field trials.
- Root biomass differs significantly between varieties, but is mainly driven by site conditions.
- Root-to-shoot ratios decreased with increasing precipitation.
- Root biomass was 45% higher in the best performing variety compared to the worst performing one.

1 | Introduction

Climate change is negatively impacting the natural resources that are essential to agriculture. Long-term changes in temperature and precipitation since 1989 have reduced wheat and barley yields across Europe by 2.5% and 3.8%, respectively (Moore and Lobell 2015). The increasing frequency and intensity of extreme weather events (Field et al. 2012) can increase the risk of multiple simultaneous crop failures within regions or even globally (Beillouin et al. 2020). At the same time, global demand for food is expected to grow by 35%–56% between 2010 and 2050 (Dijk et al. 2021). Consequently, agriculture is facing two challenges: (1) fulfilling food demands (Smith et al. 2013; Lal et al. 2015) and (2) reducing greenhouse gas emissions to mitigate climate change effects (Minasny et al. 2017; IPCC 2021). These two challenges are difficult to address simultaneously as reduced emissions often lead to reduced productivity (Frank et al. 2017).

Soils are a major component in the global carbon (C) cycle as they contain significantly more C than the atmosphere and terrestrial vegetation combined (Lehmann and Kleber 2015). Plants fix atmospheric CO_2 through photosynthesis and incorporate the assimilated C into their biomass. Plant residues and rhizodeposition are therefore major pathways for C to enter soil (Lehmann and Kleber 2015; Sokol et al. 2019). Increasing soil C stocks in managed ecosystems is promoted as a climate change mitigation measure that could be the answer to both abovementioned challenges (Lal et al. 2015; Rumpel et al. 2020). Increased organic C inputs from plants to arable soils are needed to build up soil organic carbon (SOC) and increase C stocks (Lal et al. 2015; Griscom et al. 2017). Increased SOC improves soil functions such as water retention (Rawls et al. 2003), potentially leading to increased yields (Campos-Cáliz et al. 2024; Oldfield et al. 2019; Kätterer and Bolinder 2024).

The belowground C allocation represents a significant source of SOC, with roots contributing on average 25% of the total mean annual organic C inputs into arable soils (Jacobs et al. 2020), and roots have shown to be three times more efficient for building up SOC than shoot biomass (Rasse et al. 2005). Owing to the key role played by root systems in building up soil C stocks, it has been hypothesised that promoting plants with enhanced root systems further reinforces this effect (Heinemann et al. 2023). Among root traits, root depth appears to be the most important factor for C stabilisation in deeper soil layers (Poirier et al. 2018). By targeting deeper root systems, more C may be allocated to subsoils, promoting additional C accrual (Button et al. 2022). Deeper root systems can also enhance water and

nutrient acquisition (Lynch and Wojciechowski 2015; Paustian et al. 2016; Mathew et al. 2019). Enhanced water acquisition is a benefit for crops grown in rain-fed agriculture as drought events can occur more often due to climate change. For example, in wheat, rooting depth was positively correlated with yield under terminal or intermittent drought in a Mexican field experiment (Lopes and Reynolds 2011). In general, an increased rooting depth is likely to enhance yields (Kell 2011, 2012; Lilley and Kirkegaard 2011; Odone et al. 2024). Another potential advantage of deeper roots is that they can take up nitrate from deeper soil layers. Nitrate leaching below the rooting zone is a source of emissions in high-input agricultural systems, and deeper roots can help mitigate this (Saengwilai et al. 2014; Lynch and Wojciechowski 2015). Thus, deeper roots have the potential to stabilise or increase yields while simultaneously contributing to an increase in belowground C inputs. However, this may only be the case in circumstances where topsoil resources are inadequate to satisfy the plant's requirements.

The allocation of biomass and hence the allocation of C between roots and shoots, expressed as the root-to-shoot ratio (R:S ratio), varies greatly between plant species (Bolinder et al. 2007; Mathew et al. 2020) and within plant species (Siddique et al. 1990; Narayanan et al. 2014; Fang et al. 2014; Mathew et al. 2019). Thus, there may be potential to increase soil C inputs by choosing a variety that produces more root biomass and builds a deeper root system. As the R:S ratio range varies greatly even within one crop and there are insufficient data on the belowground biomass of commercially used crops (Odone et al. 2024), the size of this potential remains unknown. Previous reported R:S ratios of winter wheat vary considerably at between 0.03 and 3.04 (Siddique et al. 1990; Fang et al. 2014; Mathew et al. 2019). However, several studies have identified negative correlations between R:S ratio and grain yield in cereals (Siddique et al. 1990; Fang et al. 2017). This suggests that root biomass might come at the expense of crop productivity. Nevertheless, positive correlations between R:S ratio and grain yield have also been reported (Mathew et al. 2019). These studies show that there is no consensus in the literature; comprehensive studies on different varieties are urgently needed to quantify the relationship between roots and yield. An explanatory factor for the variability in R:S ratios could be the effect of droughts. However, there have been contrasting reports on the direction of this effect as well. Water stress is known to decrease dry weight in both shoots and roots, with a greater decline in the shoot system, resulting in an increase in the R:S ratio (Friedli et al. 2019). This contradicts Kou et al. (2022) who reported reduced R:S ratios. The observed inconsistency in results may well be attributable to differences in the timing and intensity of water stress and in the varieties.

These contrasting findings indicate that root biomass and its relationship to the aboveground biomass of wheat varieties depend on the pedoclimatic conditions. To quantify these effects and obtain detailed insights, a comprehensive field study was conducted with 10 varieties of winter wheat grown at 11 sites covering a European climatic gradient from Spain to Norway. The objectives of this study were: (a) to quantify the root biomass and depth distribution among different winter wheat varieties under various pedoclimatic conditions, (b) to investigate the influence of variety and pedoclimatic conditions on the

relationship between aboveground and belowground biomass production, and (c) to assess whether an optimised winter wheat variety selection can simultaneously lead to increased root biomass C and yield, increasing C accrual.

TABLE 1 | The 10 winter wheat varieties used, their abbreviations in this study and their year of release.

Variety	Variety abbreviation	Year of release[a]
Altigo	Al	2011
Aurelius	Au	2016
Bernstein	Be	2015
Dagmar	Da	2012
Julie	Ju	2014
Montalbano	Mo	2014
MV Nador	Na	2012
Nogal	No	2013
RGT Reform	Re	2014
Tenor	Te	2017

[a]European plant variety protection EUPVP—Common Catalogue Information System (2024).

2 | Methods

2.1 | Field Experiments

In a pan-European coordinated field trial, 10 winter wheat varieties (Table 1) were grown at 11 sites across Europe in the 2021/2022 season. The sites represent a broad gradient of pedoclimatic conditions (Figure 1, Table 2). The selected varieties are currently used in Europe and differ in crop productivity, based on the yield of the previous year in the same trial. The selected varieties and their year of release are given in Table 1. All 10 varieties were grown at all sites with the following exceptions: the varieties Altigo and Tenor were not seeded in Freising, Germany (DE-Fr), while Aurelius was not seeded in Ås, Norway (NO-As).

Daily climate data were gathered from nearby weather stations (AT-Gn (GeoSphere Austria Data Hub 2024), BE-Ge (Weather Belgium—RMI 2024), CH-Ca (Climate diagrams and normals per station—MeteoSwiss 2024), CH-Es (Agrometeo 2024), DE-Fr (Bayerisches Landesamt für Umwelt 2024), DE-No (Agrarmeteorologisches Messnetz Sachsen 2023), LT-Do (Lithuanian Hydrometeorological Service under the Ministry of Environment 2022) CZ-Cr, ES-Le, HU-Sz and NO-As: data retrieved from on-site weather stations). The aridity index (AI) was used to further describe the dryness of the climate at the sites. Mean annual temperature and precipitation and mean temperature

Site ID	Country	Site
AT-Gn	Austria	Grossnondorf
BE-Ge	Belgium	Gembloux
CH-Ca	Switzerland	Changins
CH-Es	Switzerland	Eschikon
CZ-Cr	Czech Republic	Chrlice
DE-Fr	Germany	Freising
DE-No	Germany	Nossen
ES-Le	Spain	Sucs
HU-Sz	Hungary	Székkutas
LT-Do	Lithuania	Dotnuva
NO-As	Norway	As

FIGURE 1 | Winter wheat trial sites. Red dots represent the sites and are labelled with a site-specific identifier.

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TABLE 2 | Location, mean annual precipitation (MAP) and mean annual temperature (MAT) for the period 1991–2020, yearly aridity index (AI) for the period of 1970–2000, and weather data (temperature and precipitation) for the period 01.09.21–31.08.22 for the sampling sites.

Country	Site/nearest town	Site-specific identifier	Coordinates	MAT [°C]	Mean temperature (01.09.21–31.08.22) [°C]	MAP [mm]	Mean precipitation (01.09.21–31.08.22) [mm]	AI (Zomer et al. 2022)
Austria	Grossnondorf/Hollabrunn	AT-Gn	48°37′47.9″N 15°58′48.1″E	10.2	11.2	650	422	0.54
Belgium	Gembloux	BE-Ge	50°35′52.0″N 4°41′24.5″E	10.2	11.2	793	554	0.97
Switzerland	Changins/Nyon	CH-Ca	46°24′03.6″N 6°13′55.1″E	10.7	12.4	995	692	1.11
Switzerland	Eschikon/Lindau	CH-Es	47°27′02.3″N 8°40′56.4″E	9.2	10.9	1175	797	1.23
Czech Republic	Chrlice/Brno	CZ-Cr	49°7′28.99″N 16°38′03.0″E	9.0	11.6	451	436	0.49
Germany	Dürnast/Freising	DE-Fr	48°24′25.4″N 11°41′39.1″E	9.8	9.8	960	650	0.96
Germany	Nossen	DE-No	51°3′20.02″N 13°16′31.7″E	9.2	10.5	645	474	0.76
Spain	Sucs/Lleida	ES-Le	41°41′44.7″N 0°25′35.1″E	15.5	13.3[1]	450	156[a]	0.26
Hungary	Székkutas/Hódmezővásárhely	HU-Sz	46°30′45.3″N 20°31′15.3″E	12.2	11.2	635	483	0.47
Lithuania	Akademija/Dotnuva	LT-Do	55°23′28.6″N 23°51′49.8″E	7.8	8.0	705	686	0.78
Norway	Ås	NO-As	59°39′50.0″N 10°45′34.9″E	6.4	7.4	876	603	1.00

[a]Data only available from 1.12.2021 to 31.8.2022.

and sum of precipitation for the period 09/2021–08/2022 were calculated for general site characterisation (Table 2). The mean temperature and sum of precipitation for the specified time periods, namely 1 week before sowing until harvest (season), 1 week before sowing until emergence (emergence), emergence until flowering (flowering) and flowering until harvest (harvest), were calculated to characterise the specific weather conditions during the wheat growing season for each site individually (Figure S1).

At each site, the field experiments had three replicates. In CH-Es, the trial was only replicated twice due to space limitations. The experimental designs corresponded to randomised complete block, lattice, split block or latinised alpha designs, according to national conventionality in variety testing. Plot size varied between 4 and 18.5 m² among the sites (Table S1). The trial fields were managed according to regional, conventional practice except in Belgium, where the trial was managed without fungicide and growth regulators (Table S1). The grain was harvested at all sites with combine harvesters, and grain yield was determined and reported at 15% moisture at plot scale to make the sites comparable. Straw biomass was collected during the harvest and weighed afterwards. The remaining stubble biomass was quantified for a subplot manually by cutting the remaining stubble (0.25×0.25 m).

2.2 | Root and Soil Sampling

Root sampling was conducted within 1 week after harvest in July and August 2022. A soil auger with an inner diameter of 6 cm was driven 1 m into the soil using an electric hammer to extract core samples. Due to the technical equipment and expertise required for the sampling of root biomass, only two teams were able to carry out the task. Consequently, the sampling design had to be carefully balanced between achieving a high accuracy and maintaining practical feasibility. Two cores per plot were taken, one directly under a plant and one between crop rows. The soil cores were extracted and cut into the following depth increments: 0–15, 15–30, 30–50, 50–75 and 75–100 cm. In total, six cores per variety were taken at each site. In CH-Es, the first replicate was sampled twice; these samples were considered as pseudo-replicates. Two additional soil cores per site were randomly selected and taken for soil analyses.

In addition to the soil cores, one 25×25×15 cm soil monolith per plot was excavated to examine root biomass in the upper 15 cm with an additional approach. A metal frame was placed at least one crop row away from the edge of each plot; it was driven into the soil and the entire soil volume was retrieved. One frame per field replicate was taken where two crop rows had to be inside of the frame to generate data on root biomass in and between the rows. Soil from the frame was collected in a plastic box and all rootstocks and other visible coarse roots were sampled. To determine fine root content, a composite sample of 500 g of the remaining soil was taken. In total, three soil monoliths per variety were taken at each site.

2.3 | Root and Soil Analysis

For biomass determination, roots were extracted from each soil core separately. In the first step, the soil was sieved to ≤ 2 mm. This fine soil was dispersed in a hydro vortex, and roots were separated from the mineral fraction by floating and recovered on a 0.5 mm sieve (Smucker et al. 1982) using an automated root washer (Gillison's Variety Fabrication Inc.). The root samples were subsequently transferred to aluminium dishes where extraneous organic matter was visually identified and removed using tweezers (Hirte et al. 2021). Finally, washed roots were dried at 55°C using an oven until the weight remained constant. The C content (%) of dried roots was measured by dry combustion on subsamples using an elemental analyser (LECO, TruMac, St. Joseph, MI, USA). The average C content of roots was 41 ± 3%.

Soil analyses were performed on samples from the additional soil cores that were sieved (2 mm) and dried at 40°C. Water content, rock fragment content (> 2 mm) and bulk density of the fine soil and total soil were assessed by drying and weighing the samples (Poeplau et al. 2017). Soil pH was measured in 0.1 M $CaCl_2$ solution at a ratio of 1:2.5, and total C and N were measured by dry combustion (LECO, TruMac, St. Joseph, MI, USA). Organic C was determined as the difference between total C and inorganic C. To determine inorganic C, aliquots were combusted for 16 h in a muffle furnace at 400°C. The remaining C fraction was defined as total inorganic C and was subsequently measured again with the elemental analyser. Available soil phosphorus was measured by Olsen extraction and colorimetry (Olsen 1954). Phosphorus, calcium, magnesium and potassium were measured to determine plant-available nutrients (Table S2).

2.4 | Calculations

Root biomass collected by soil coring was extrapolated to field scale by weighting with respect to row width, adapted from Frasier et al. (2016) by Hirte et al. (2021) (Equations (1) and (2)). This was done for each depth increment:

$$RB_{within} = \frac{M_{within}}{\pi * \left(\frac{D}{2}\right)^2} * \frac{D}{S} \tag{1}$$

$$RB_{between} = \frac{M_{between}}{\pi * \left(\frac{D}{2}\right)^2} * \frac{S-D}{S} \tag{2}$$

where RB_{within} and $RB_{between}$ represent root biomass (g m⁻²) within and between rows, M_{within} and $M_{between}$ are the dry weights of roots (g) extracted from the soil cores, D is the inner diameter of the soil corer (m) and S is the distance between rows (m). The total root biomass for the whole sampling depth was calculated by summing up the area-related biomass per depth increment. R:S ratios were calculated from the area-related total root biomass and the total aboveground biomass.

Root biomass collected from monolith excavation was calculated according to Hirte et al. (2018) as follows:

$$RB_{crown} = d * BD * DW_{crown} * 10 \tag{3}$$

$$RB_{fine} = d * BD * DW_{fine} * 10 \tag{4}$$

where RB_{crown} and RB_{fine} are the area-related root biomass ($g\,m^{-2}$) of root stocks and fine roots, DW_{crown} and DW_{fine} are the mass-related dry weights ($g\,kg^{-1}$) of root stocks and fine roots, d is the depth (m) to which the soil monolith was excavated and BD is the bulk density ($g\,m^{-3}$) of the soil monolith. Topsoil root biomass was obtained by summing up RB_{crown} and RB_{fine}. By multiplying the area-related root biomass ($g\,m^{-2}$) and mean C content of roots ($mg\,C\,g^{-1}$ root), the C input of root biomass ($g\,C\,m^{-2}$) was calculated and upscaled to $Mg\,C\,ha^{-1}$.

The root samples from site ES-Le contained noticeable high residues of the preceding crop alfalfa in all soil depths, which could not be properly separated from wheat roots. Thus, a way to ensure that the wheat root biomass could be determined without additional error from extraneous root material was needed. By analysis of the nitrogen concentration, a correction factor was derived to correct total root biomass in the samples to account for the proportion of alfalfa roots and allow the determination of wheat root biomass. Different correction factors for the topsoil fine roots (median = 0.516; SD = 0.069) and subsoil fine roots (median = 0.392; SD = 0.097) were derived as these differed significantly from one other.

2.5 | Statistics

Differences in the dependent variables root biomass, R:S and grain yield between varieties were evaluated by means of linear mixed-effects models to account for the prominent hierarchical data structure (nested design) and different sources of variability (Equation (5)). A random intercept model was used to assess the variability in non-transformed data and log-transformed root biomass and R:S data to meet the assumption of homogeneous distribution of the residuals (Equations (6–8)). The log-transformation of root biomass and R:S were used for the next calculation steps.

$$Dependent\ variable \sim Variety + 1\,|\,Site\,|\,Replicate \qquad (5)$$

$$Yield \sim 1 + 1|Variety + 1|Site + 1\,|\,Replicate \qquad (6)$$

$$\log(R{:}S) \sim 1 + 1|Variety + 1|Site + 1\,|\,Replicate \qquad (7)$$

$$\log(root\ biomass) \sim 1 + 1|Variety + 1|Site + 1\,|\,Replicate \quad (8)$$

The effects of pedoclimatic variables (temperature and precipitation during the developmental stages, clay content, bulk density, total inorganic carbon and soil organic carbon, soil N, pH, phosphorus and potassium contents) on root biomass, R:S and yield were tested using mixed-effects models with an interaction term of variety and pedoclimatic variables. For soil characteristics, depth was also used as an explanatory variable:

$$Dependent\ variable \sim Variety * climate\ variable + 1\,|\,Site \quad (9)$$

$$Dependent\ variable \sim Variety * soil\ variable + depth + 1\,|\,Site \quad (10)$$

The effect of total root biomass on yield was tested as follows:

$$Yield \sim root\ biomass * variety + 1\,|\,Site\,|\,Replicate \qquad (11)$$

The models were checked for influential cases by computing Cook's distance and for heteroscedasticity by performing Levene's test. Overall, model performances were checked by pseudo-R^2 (marginal and conditional R^2) for generalised mixed models and the normality of the residuals (QQ-plots). Statistical differences were assigned at group level based on analysis of variance (ANOVA) and subsequent multiple pairwise comparison of estimated marginal means. Differences in slopes for root biomass, R:S and yield between varieties were tested by multiple pairwise comparisons of estimated marginal trends. For all multiple comparisons, a Šidák adjustment of p-values was applied and a significance level of alpha = 0.05 was used.

2.6 | Software

All analyses were performed with R, version 4.4.0 (R Core Team 2023), with the R packages tidyverse (Wickham et al. 2019) and openxlsx (Schauberger and Walker 2023) for data management, emmeans (Lenth 2023), multcomp (Hothorn et al. 2008) and predictmeans (Luo et al. 2023) for statistical analysis, nlme (Pinheiro et al. 2023) and lme4 (Bates et al. 2015) for model fitting, and ggplot2 (Wickham 2016), ggbiplot (Vu 2011) and ggpubr (Kassambara 2023) for visualisation.

3 | Results

3.1 | Wheat Root Biomass Production and Distribution

Median root biomass across all sites and varieties was $1.4 \pm 0.7\,Mg\,ha^{-1}$ (Table S3) and differed significantly between varieties (Figure 2). The highest median root biomass was recorded for the variety Bernstein in DE-No ($3.4 \pm 0.7\,Mg\,ha^{-1}$), the lowest for Altigo in LT-Do ($0.6 \pm 0.1\,Mg\,ha^{-1}$). Across all sites, a mean difference of $0.9\,Mg\,ha^{-1}$ between the variety with the lowest root biomass and the one with the highest was observed, which corresponded to an increase of 45%.

On average, 78% of the total root biomass was found in the upper 30 cm across all sites and varieties. Root biomass in the upper 15 cm was significantly higher than root biomass in the depth intervals below 15 cm. The distribution of total root biomass to topsoil (0–30 cm) and subsoil (30–100 cm) was comparable between varieties. However, within depth classes there was a considerable variation in total root biomass between varieties. Montalbano, MV Nador, RGT Reform and Bernstein displayed the highest root biomass in both depth classes (Table S4).

A random intercept model with linear combinations of variety and site as random effects showed that site was the primary explanatory factor, accounting for 60% of the variation in root biomass, while variety explained only 9.5% and the replication 3.8%. The residual covered 27.3%, indicating that the chosen model covered the main sources of variance. The total root biomass showed significant site differences irrespective of variety (Figure 3). The highest mean root biomass was observed in DE-No, with a mean of $2.67\,Mg\,ha^{-1}$ across all varieties. The variability between varieties at one site differed from one site
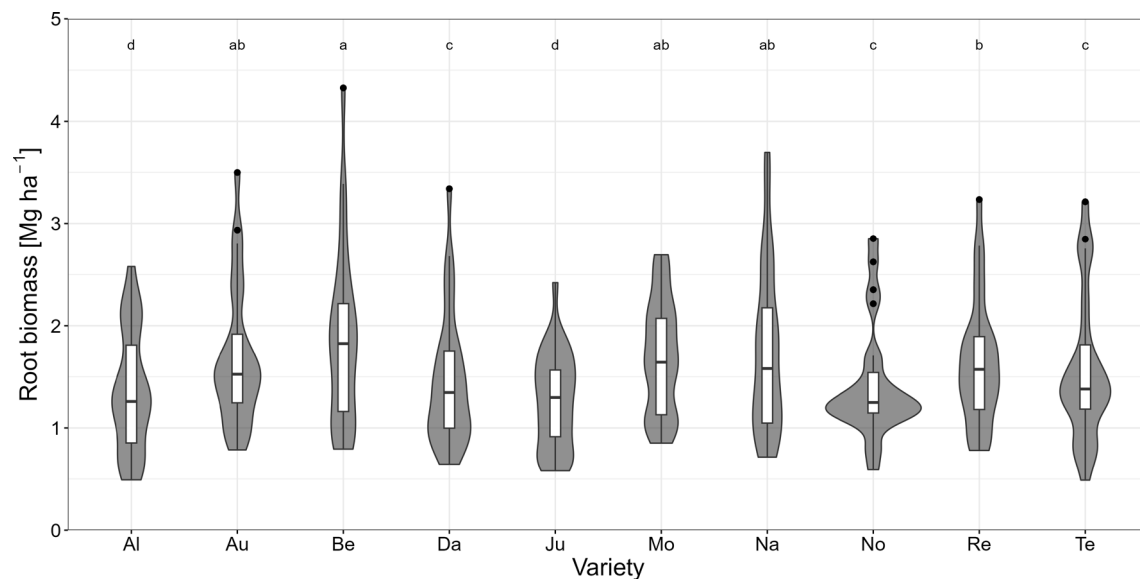
FIGURE 2 | Violin plots of total root biomass [Mg ha^{-1}] in depth 0–100 cm per variety across sites. Letters indicate statistical grouping via a comparison of estimated marginal means per variety.

to another. The highest difference between the variety with the lowest root biomass and the one with the highest was 1.8 Mg ha^{-1} in CH-Es. The lowest root biomass was found in CH-Ca (0.86 Mg ha^{-1}). The smallest difference between the variety with the lowest root biomass and the one with the highest was 0.46 Mg ha^{-1} in LT-Do.

The effects of pedological variables were significant for the total root biomass. Irrespective of variety, root biomass was positively related to total inorganic C, phosphorus and potassium contents. A negative relation with root biomass was found for clay content, bulk density and SOC and soil N contents (Table 3).

Root biomass and root biomass distribution differed significantly between sites. Sites with the highest root biomass in the topsoil did not necessarily show a high root biomass in the subsoil, and vice versa. HU-Sz had the lowest biomass (0.63 Mg ha^{-1}) in the depth increment 0–15 cm, but the highest root biomass (0.21 Mg ha^{-1}) in the depth increment 75–100 cm. With regard to climatic variables, total root biomass was negatively related to rainfall throughout the season, regardless of the timing of the rainfall. This relation was only significant in the subsoil, not in the topsoil. In topsoil, however, precipitation between flowering and harvest was negatively related to root biomass. Temperature throughout the season was not significantly related to total root biomass or the root biomass in either depth class (Table 4).

3.2 | Influence of Soil and Climate Variables on the Relationship Between Aboveground and Belowground Biomass Production

The median R:S ratio was 0.15 ± 0.08 across all sites and varieties. The highest R:S ratio was recorded for the variety Bernstein in ES-Le (0.59), the lowest for Tenor in CH-Es (0.03). R:S ratios differed significantly between varieties with Bernstein, Montalbano and Nador being the varieties with the highest root

biomass per shoot biomass (Figure 4). A random intercept model with linear combinations of variety and site as random effects showed that site was the primary explanatory factor, accounting for 69.8% of the variation in R:S ratios, while variety explained only 6.7% and the replication 2.1%.

The temperature throughout the season had a significant positive effect on R:S ratios, while precipitation exhibited a negative effect. A higher temperature between emergence and flowering resulted in a significantly higher R:S ratio (Table 3). Potassium content and pH, however, had a significantly negative effect on R:S ratio (Table 5).

3.3 | Relationship Between Grain Yield and Root Biomass C

Grain yields differed significantly between varieties (Figure 5). Across all sites, Tenor was the highest-yielding variety, followed by Julie, Aurelius, Dagmar and RGT Reform together with Altigo. The lowest-yielding varieties were Bernstein and Nogal, followed by Montalbano and MV Nador. There was a significant positive correlation across all sites between root biomass C and grain yield for each variety except MV Nador, where the correlation was not significant.

High-yielding varieties were not necessarily the same as those with high root biomass (Figures 2 and 5, Table S5). By comparing the coefficients of variation (CV) per site for yield and root biomass, it became clear that root biomass was more variable between sites than yield (Table S6). CH-Es, DE-Fr and NO-As showed the highest CVs for root biomass. NO-As, BE-Ge and CH-Ca had the highest CV for yield. The CV for root biomass across all 11 sites (44%) was higher than the CV for yield across all 11 sites (37%).

In this dataset, site did not have a consistent effect on the relationship between yield and root biomass (Figure 5). The sites can be classified into three clusters, according to statistical
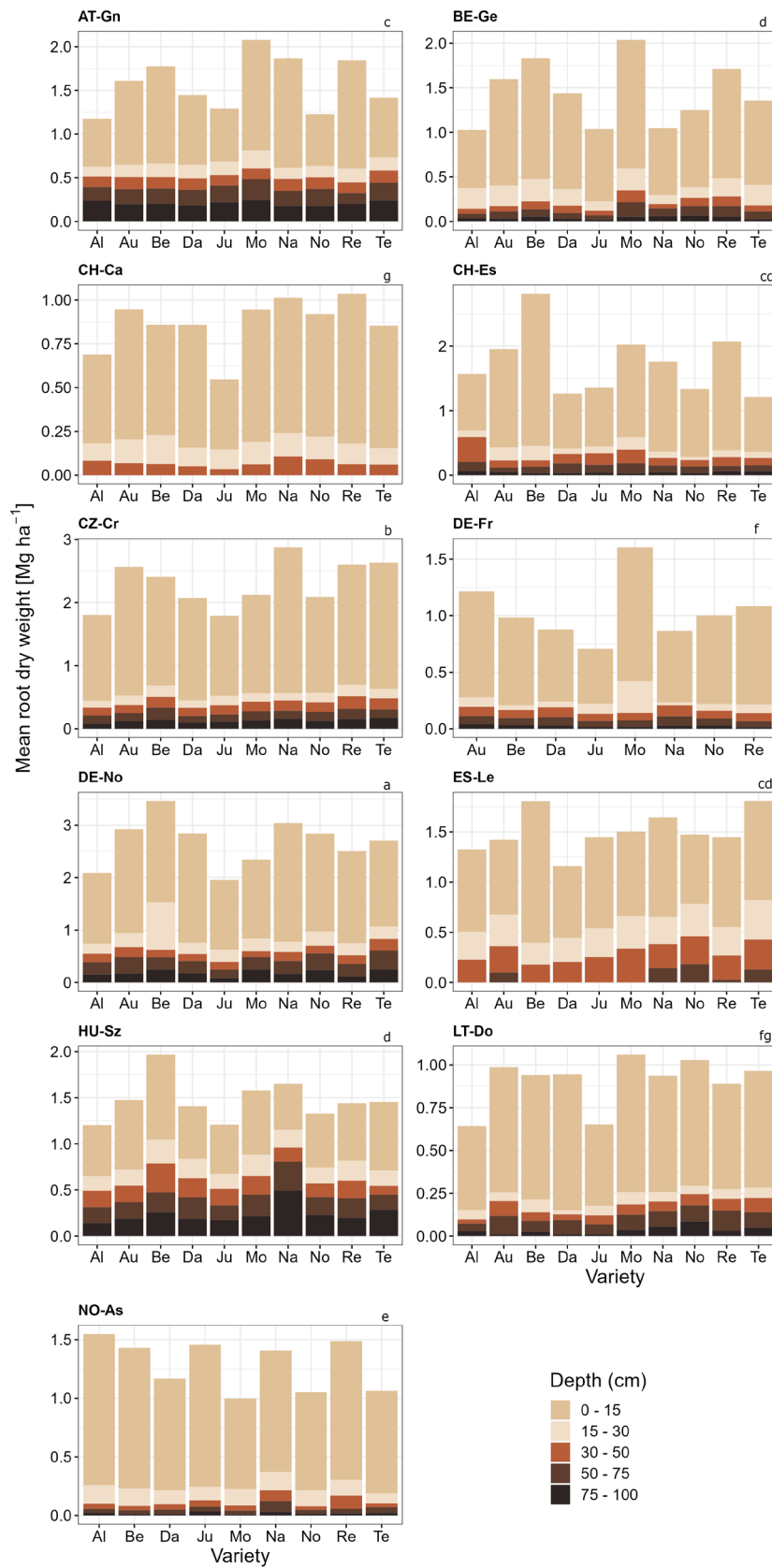
FIGURE 3 | Mean root dry weight [Mg ha^{-1}] per variety at each sampling site distinguished by depth increments. Scales differ between sites to improve readability. An absence of depth segments indicates that rooting depth was limited at that site. Lowercase letters in the top right corner indicate statistical groupings via a comparison of estimated marginal means per site.

grouping of grain yield and linear trends: (1) low-yielding sites without any effect of root biomass (ES-Le, HU-Sz and CH-Ca), (2) mid-yielding sites with a significantly positive correlation between root biomass and grain yield (NO-As, DE-Fr, LT-Do and BE-Ge), and (3) high-yielding sites with a significantly negative correlation between root biomass and grain yield (CZ-Cr, CH-Es, AT-Gn). DE-No is at the same yield level as the high-yielding sites, but shows a non-significant negative trend (Figure 6).

4 | Discussion

4.1 | Root Biomass Production Is Driven by Plant Genetics

In this study, total root biomass differed significantly between wheat varieties (Figure 2) which is in line with earlier findings, that also reported genetic differences in root biomass production (Waines and Ehdaie 2007; Fang et al. 2014; Akman et al. 2017; Mathew et al. 2019; Heinemann et al. 2023). However, the ranges in root biomass that were found in this study's data set (0.3–4.3 Mg ha^{-1}) were lower than ranges reported elsewhere.

TABLE 3 | Significance of the correlation coefficients for the effects of pedological variables on total root biomass based on linear mixed models. p-values < 0.05 are highlighted in bold. The direction of significant effects is indicated in brackets: Positive (+), negative (−).

Variable	Total root biomass
Clay [%]	**< 0.001 (−)**
BD [g cm^{-3}]	**0.006 (−)**
TIC [%]	**< 0.001 (+)**
SOC [%]	**< 0.001 (−)**
Soil N [%]	**< 0.001 (−)**
pH [−]	0.167
Phosphorus [mg kg^{-1}]	**0.002 (+)**
Potassium	**< 0.001 (+)**

Waines and Ehdaie (2007) reported higher values from 0.97 to 11.76 Mg ha^{-1} with wheat plants grown in greenhouses, while Mathew et al. (2019) reported an even higher range from 0.26 to 16.22 Mg ha^{-1} in a wheat field trial with contrasting water regimes. Both studies covered larger genetic differences than is the case in the present study, but did not include different pedoclimatic conditions. Waines and Ehdaie (2007) considered landraces and modern bread wheat varieties. Mathew et al. (2019) investigated 100 wheat genotypes including Triticale under drought-stressed and non-stressed conditions, which could also have induced a greater variability in root biomass. In this study, the difference between the variety with the lowest root biomass and the one with the highest across sites was on average 0.9 Mg ha^{-1} which is an increase of 45%. This highlights the potential of wheat variety selection towards higher root biomass growth, and confirms that root growth is driven by plant genetics.

According to the optimal partitioning theory, plants allocate more biomass to the organ that can capture the most limiting resources to optimise performance (Gedroc et al. 1996; McCarthy and Enquist 2007; Thornley 1972). For example, more root biomass is produced when nutrients are a limiting factor (Gedroc et al. 1996). Therefore, it is assumed that plants allocate more biomass belowground than aboveground at lower levels of soil nutrient or water availability (Freschet et al. 2015). Thus, a higher root biomass was expected at sites such as HU-Sz, ES-Le and CZ-Cr with low precipitation, high temperatures and aridity indices below 0.5 (Table 2). In fact, no significantly higher root biomass was found at the sites with less favourable conditions (Figure 5). This could be the case because insufficient resources were available to develop greater root biomass. Nevertheless, precipitation throughout the growing season was found to exhibit negative effects on root biomass. Bakhshandeh et al. (2019) also reported drought stress leading to +21% higher root biomass compared with high water availability. Deep roots have been identified as a very effective means of facilitating the utilisation of subsoil water in the absence of topsoil water during periods of drought (Lopes and Reynolds 2011; Lynch 2018; Shoaib et al. 2022). In contrast, more roots in the topsoil are beneficial in soils with high water availability. This is due to the higher water uptake rates of shallow roots compared with deep roots (Müllers et al. 2022).
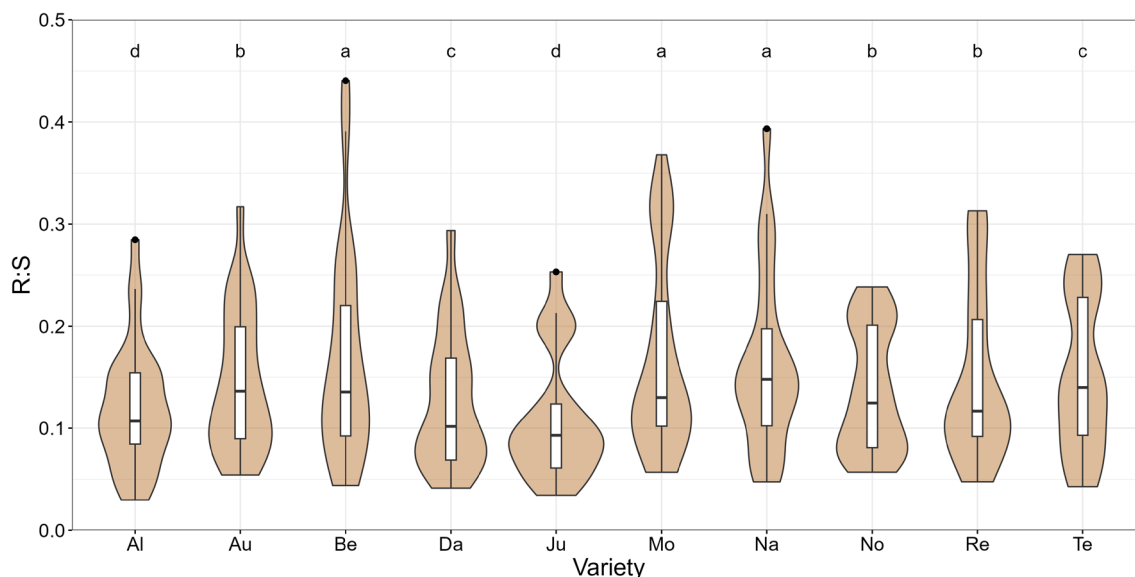
TABLE 4 | Significance of the correlation coefficients for the main effects of climatic variables on total root biomass (0–100 cm), root biomass in topsoil (0–30 cm) and subsoil (30–100 cm) based on linear mixed models. p-values < 0.05 are highlighted in bold. The direction of significant effects is indicated in brackets: Positive (+), negative (−).

Variable	Total root biomass in 0–100 cm depth	Root biomass in topsoil	Root biomass in subsoil
Temp. season [°C]	0.316	0.181	0.443
Prec. season [mm]	**0.042 (−)**	0.126	**0.023 (−)**
Temp. emergence [°C]	0.713	0.271	0.385
Prec. emergence [mm]	0.834	0.410	0.455
Temp. flowering [°C]	0.272	0.284	0.287
Prec. flowering [mm]	0.110	0.495	**0.012 (−)**
Temp. harvest [°C]	0.687	0.706	0.360
Prec. harvest [mm]	0.115	**0.035 (−)**	0.825

FIGURE 4 | Violin plots of root-to-shoot (R:S) ratios per variety across sites. Letters indicate a statistical grouping via a comparison of estimated marginal means.

TABLE 5 | Significance of the correlation coefficients for the effects of pedoclimatic variables on root-to-shoot (R:S) ratios based on linear mixed models. *p*-values <0.05 are highlighted in bold. The direction of significant effects is indicated in brackets: Positive (+), negative (−).

Variable	R:S ratios
Temp. season [°C]	**0.047 (+)**
Prec. season [mm]	**0.012 (−)**
Temp. emergence [°C]	0.132
Prec. emergence [mm]	0.968
Temp. flowering [°C]	**0.004 (+)**
Prec. flowering [mm]	0.057
Temp. harvest [°C]	0.077
Prec. harvest [mm]	0.050
Clay [%]	0.884
BD [g cm^{-3}]	0.538
TIC [%]	0.681
SOC [%]	0.614
Soil N [%]	0.890
pH [−]	**<0.001 (−)**
Phosphorus [mg kg^{-1}]	0.502
Potassium	**0.028 (−)**

4.2 | R:S Ratios Are Elastic

The difference in root biomass was reflected in the R:S ratio, which expresses biomass allocation between roots and shoots. This varied significantly between the 10 varieties, ranging from 0.09 to 0.15 across sites. These values are similar to previously reported R:S ratios. Other field experiments have reported R:S ratios from 0.09 to 0.15 (Hirte et al. 2021), 0.03 to 3.04 (Mathew et al. 2019) or even 1.00 to 1.36 (Fang et al. 2014). Under drought stress, R:S ratios can be up to 60% higher than without drought stress (Bakhshandeh et al. 2019). Genetic differences that affect photosynthesis uptake and C storage in plant organs could explain different R:S ratios within species (Bakhshandeh et al. 2019; Fang et al. 2017). Consequently, less heat-tolerant wheat varieties would be unable to complete growth cycles, which would lead to a reduced capacity to regulate biomass allocation due to drought (Gupta et al. 2020). It is not only water availability that influences the R:S ratio. No significant effects of soil texture on R:S ratios were found in the present study although this has been observed in previous research. Poeplau and Kätterer (2017) observed a higher R:S in sandy soil compared with a clay loam. Junchao et al. (2023) reported a negative correlation between R:S ratio and clay content. This could have been the case in this study because differences between soil textures were not big enough. Other research indicates that plants are generally able to modify their belowground phenotypes more easily than their aboveground ones (Tolley and Mohammadi 2020).

The reported findings contrast with the simple approaches to estimating the belowground C allocation of plants, for example, for soil carbon modelling (Riggers et al. 2019). Soil C inputs from plants are estimated from measured agricultural yields using allometric equations that often assume a fixed harvest index per crop type. This method leads to substantial uncertainties in estimating and modelling plant-derived soil C inputs (Keel et al. 2017). There are no genotype-specific allometric functions due to an absence of data, and R:S ratios are assumed to be constant across environments. To ensure these large uncertainties can be reduced, a method needs to be developed to deal with the reported genetic ranges of R:S ratios, together with the effect of various environmental factors influencing them, when estimating plant-derived C inputs to the soil. The development of distinct functions for commercial
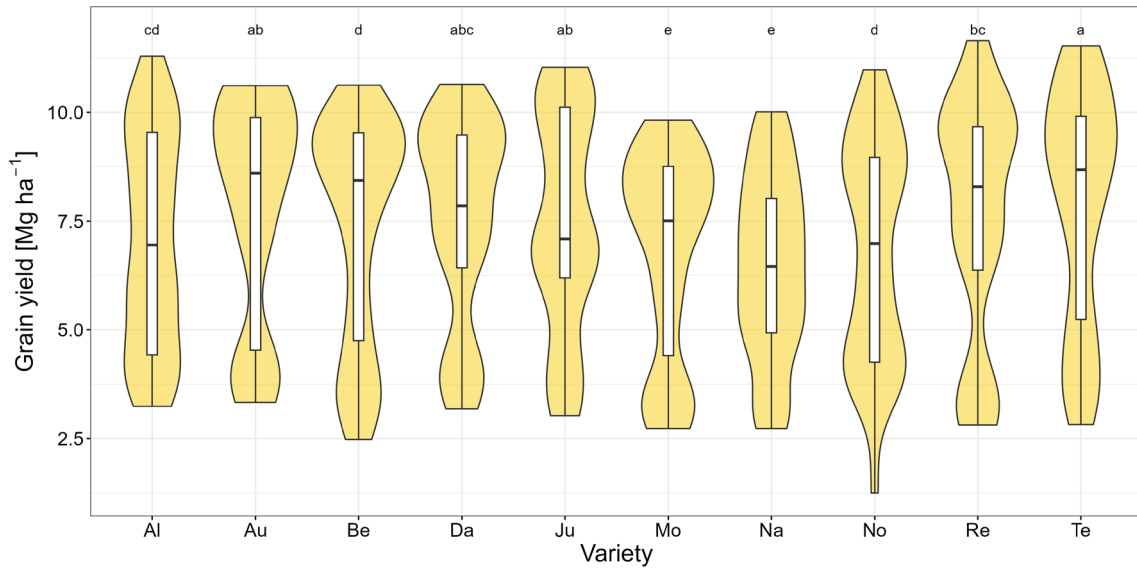
FIGURE 5 | Violin plot of grain yield at 15% moisture [Mg ha^{-1}] per variety across sites. Letters indicate a statistical grouping via a comparison of estimated marginal means.
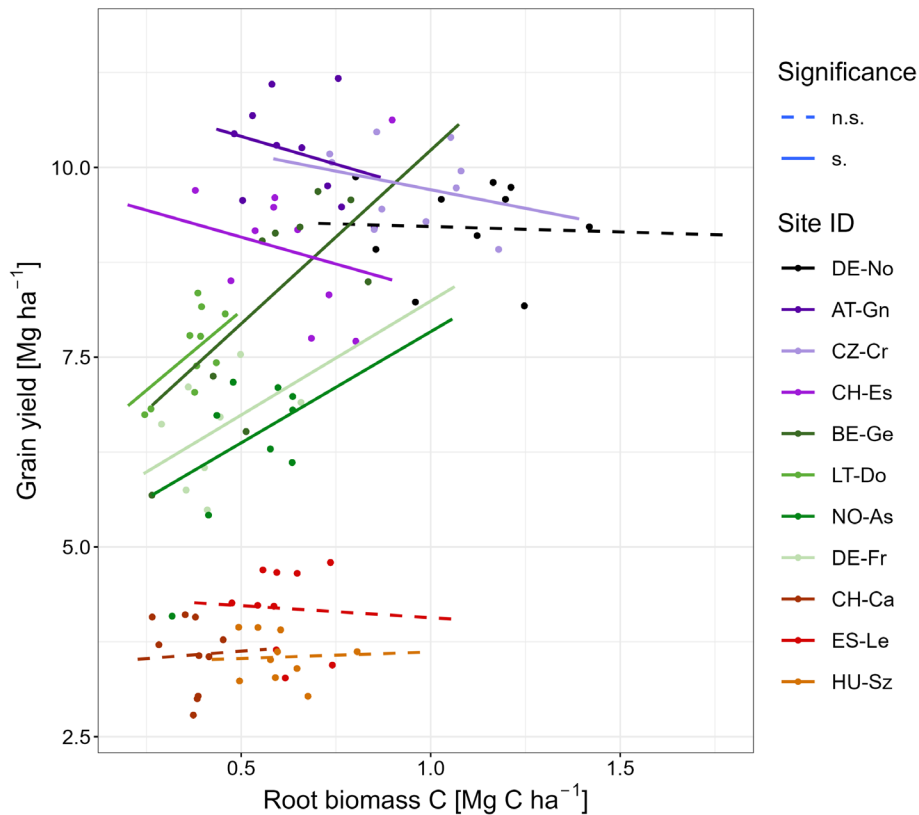

FIGURE 6 | Relationship between grain yield (Mg ha^{-1}) and root biomass C (Mg C ha^{-1}) per site. Dots represent the mean values per variety at each site. Significant (p-value ≤ 0.05) correlations are represented by solid lines, while non-significant correlations are represented by dashed lines.

varieties appears to be a highly ambitious undertaking given the workload that is associated with root research. However, functions for the different quality grades may be a more pragmatic proposition. In order to implement such an approach, it might be necessary that variety testers also assess the plant's belowground part.

4.3 | The Impact of Increased Root Biomass on Yield Is Site-Specific

Recent findings suggest that root traits have a significant impact on grain yield and its components (Fang et al. 2017; Mathew et al. 2019; Severini et al. 2020). There are two possible

contrasting consequences of higher root biomass on aboveground biomass production in general, and on yield in particular. Either a higher root biomass can support the plant through better resource acquisition, resulting in higher yields (Waines and Ehdaie 2005; Mathew et al. 2019; Severini et al. 2020; Tolley and Mohammadi 2020), or a higher root biomass can be achieved at the expense of aboveground biomass, resulting in lower yields (Feng et al. 2023; Vain et al. 2023). Instead of agreeing with one of these opposing possibilities, the present study's dataset demonstrated that it is the site-specific pedoclimatic conditions that determine how higher root biomass affects yields: High-yielding sites showed a negative relationship between yield and root biomass whereas mid-yielding sites showed positive relations between yield and root biomass (Figure 5). This highlights, that there is a potential to optimise both yield and root biomass simultaneously.

As drought periods become more severe and frequent (Alencar and Paton 2024), the aridity index (AI) as an indicator of dryness is increasingly important because dryness can have an influence on the relationship between the root mass fraction and yield, as shown by Chai et al. (2023). The root mass fraction proposed by Chai et al. (2023) is calculated in the same way as the R:S ratio. Thus, for the sake of simplicity, the term R:S ratio is used below, rather than root mass fraction. According to Chai et al. (2023), an elevated R:S ratio did not result in significant yield changes in arid regions with an AI < 0.44. When the R:S ratio exceeded a limit of 0.2, Chai et al. (2023) found that the yield declined strongly with an increasing proportion of root biomass, but with R:S ratios below this limit no significant effect was observed. As shown in Table 2, site ES-Le is below the AI threshold of 0.44, while two other sites are close to it (HU-Sz, CZ-Cr) and are characterised as semi-arid. In line with the results of Chai et al. (2023), a significant negative effect of higher R:S ratio was found for ES-Le, but the R:S ratio threshold of 0.2 could not be detected. This indicates that under the pedoclimatic conditions found in ES-Le, increased allocation of biomass to roots had no benefit and thus came at the expense of yield (Maire et al. 2013; Chai et al. 2023). For more humid regions with AI ≥ 0.44, an increase in yield was observed by Chai et al. (2023) when the R:S ratio was below 0.08, while a decrease was noted when the ratio exceeded this value. The present study's dataset did not support these findings; instead, a higher allocation of biomass to the roots was beneficial, resulting in advantages in nutrient acquisition and higher grain yields, as also reported by Akman et al. (2017) and Mathew et al. (2019), for example.

The results of this study stress that no unique conclusions about the complex pedoclimatic conditions can be drawn. Instead, a site-specific approach is needed to identify both the potential and limitations of variety selection for simultaneously increasing root biomass and yield. The grouping of the experimental site according to stress level, thereby reducing their complexity, is not the optimal solution for resolving the coherences. Nevertheless, it provides a comprehensive overview of the relationships and their directions. When pedoclimatic conditions are too severe (see ES-Le, HU-Sz, CH-Ca), more root biomass will not result in higher grain yields (Figure 5). When conditions are favourable, for example, there are no water or nutrient limitations, more root biomass will instead come at the expense

of grain yield (Figure 5: At-Gn, CZ-Cr, CH-Es). Only if sites show moderate conditions will increased root biomass stimulate grain yield, such as at BE-Ge, De-Fr, LT-Do, NO-As (Figure 5). This shows, that there is a potential to optimise both yield and root biomass simultaneously. However, this potential is greatest under moderate stress conditions.

In addition to pedoclimatic conditions, genetics play a major role in determining variety yield performance. MV Nador, for example, is known to be drought tolerant (Cseresnyés et al. 2021), while Nogal is susceptible to water stress (Raya-Sereno et al. 2023) and RGT Reform is known to be most productive under wetter conditions (de Lima et al. 2021). In general, cultivars from central/northern Europe are the most productive under temperate and wet conditions, while southern European cultivars are less productive under these conditions (de Lima et al. 2021). It has been suggested that the diverse adaptation to climatic conditions is achieved by the selection of more suitable aboveground traits, which may simultaneously lead to a reduced root diversity (Voss-Fels et al. 2017). However, these findings could not be confirmed by this dataset with regard to root biomass. The contrasting behaviour of MV Nador and Nogal could also be attributed to the effects of root system architecture traits.

4.4 | Applicability of Variety Selection for C Allocation Belowground

The potential of variety selection to have a significant impact on climate change mitigation without negatively affecting yields has already been highlighted by other authors. Nasiri et al. (2024) showed in a greenhouse pot experiment with 12 varieties and three soil types that SOC was significantly influenced by wheat variety and that SOC showed a positive correlation with root dry weight. Coucheney et al. (2024) demonstrated through a modelling approach that by introducing a winter wheat ideal phenotype with greater root production, root biomass could be increased by 26% in the topsoil and by 16% in the subsoil, while simultaneously exerting a minimal influence on aboveground biomass production and grain yield.

Nevertheless, the findings of the present study indicate that the potential to increase root biomass without compromising yield is not uniform across all regions. It has been suggested that certain soils can support both high grain yield and C storage, especially those with a substantial rooting depth, a neutral pH and a fine texture (Rouch et al. 2023). This is in line with the present findings where a higher root biomass was present at sites where roots can reach deeper soil layers.

C derived from root biomass is not the only C that is allocated belowground by plants. It has been reported that 20%–50% of the total photosynthetic C is transferred to the roots, with between 27% and 50% of this transferred C being rhizodeposits (Kuzyakov and Domanski 2000). Rhizodeposition, like root biomass C, is driven by site characteristics and genetics. It is challenging and costly to measure rhizodeposition, yet it needs to be considered when estimating the full potential of variety selection for enhancing C inputs into the soil. Varieties with higher R:S ratios and thicker roots might allocate more C belowground via rhizodeposition at the expense of grain yield (Bakhshandeh

et al. 2019), but rhizodeposition does not always differ between varieties (van de Broek et al. 2020).

5 | Conclusions

Not one variety simultaneously achieved the highest grain yields and highest root biomass production across the extensive European climatic gradient studied here. The varieties producing high root biomass C are not the varieties that lead to high grain yield regardless of location. However, considering a specific site, there is potential to optimise both yield and root biomass simultaneously. Thus, a site-specific approach is required in order to achieve the potential of variety selection for both larger root biomass and higher yields. The potential of variety selection to boost C accrual and potentially increase soil C stocks is greatest under moderate pedoclimatic conditions when varieties are selected that best fit the conditions.

Author Contributions

H. Heinemann: data curation, formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing. **F. Durand-Maniclas:** investigation, data curation, methodology, writing – review and editing. **F. Seidel:** methodology, data curation, project administration, funding acquisition, conceptualization, writing – review and editing. **F. Ciulla:** data curation, methodology, writing – review and editing. **T. G. Bárcena:** funding acquisition, writing – review and editing. **M. Camenzind:** writing – review and editing, data curation. **S. Corrado:** data curation, writing – review and editing. **Z. Csűrös:** funding acquisition, resources, writing – review and editing. **Zs. Czakó:** data curation, writing – review and editing. **D. Eylenbosch:** funding acquisition, data curation, resources, writing – review and editing. **A. Ficke:** data curation, writing – review and editing. **C. Flamm:** funding acquisition, resources, writing – review and editing. **J. M. Herrera:** methodology, funding acquisition, conceptualization, project administration, resources, writing – review and editing. **V. Horáková:** funding acquisition, data curation, resources, writing – review and editing. **A. Hund:** resources, writing – review and editing. **F. Lüddeke:** funding acquisition, resources, writing – review and editing. **F. Platz:** resources, data curation, writing – review and editing. **B. Poós:** resources, funding acquisition, writing – review and editing. **D. Rasse:** funding acquisition, resources, validation, writing – review and editing. **M. da Silva-Lopes:** funding acquisition, resources, writing – review and editing. **M. Toleikiene:** funding acquisition, data curation, resources, writing – review and editing. **A. Veršulienė:** data curation, writing – review and editing. **M. Visse-Mansiaux:** methodology, data curation, writing – review and editing. **K. Yu:** resources, writing – review and editing. **J. Hirte:** project administration, funding acquisition, methodology, validation, conceptualization, writing – review and editing. **A. Don:** conceptualization, data curation, validation, project administration, funding acquisition, methodology, supervision, writing – review and editing.

Data Availability Statement

The data that support the findings will be available in Zenodo at https://doi.org/10.5281/zenodo.14011616 following a 12 month embargo from the date of publication. After this period of time, the data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.