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RESEARCH ARTICLE

Variability in maize root biomass distribution under drought can contribute to climate change adaptation

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Abstract

Aims Sustaining agricultural productivity and ensuring food security through adaption to climate change are main challenges in modern agriculture. Leveraging the connection between roots and their growth environment could be an effective approach to addressing these issues. Thus, this study aimed to quantify the root biomass production and depth distribution among different maize varieties under contrasting water regimes and to investigate the influence of variety and water regime on the relationship between the biomass allocation to above- and below-ground biomass.

Methods Root traits (biomass, root distribution, length, diameter) to 100 cm soil depth and yields were assessed in 10 different maize varieties grown at four experimental sites, each with two contrasting water regimes.

Results The average root biomass of maize down to 100 cm was found to be 3.2 ± 1.2 Mg ha^{-1} across all sites and treatments. Well-watered conditions led to 29% higher root biomass in the top soil (0-30 cm) compared to water deficit conditions. In the subsoil (30–100 cm) however, root biomass was 25% higher under water deficit and increased significantly with the number of water stress days. Varieties differed site-specifically by 59 to 71% for root biomass and by 10 to 48% for yield under well-watered conditions.

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Under water deficit conditions varieties differed by 63 to 72% for root biomass and by 20 to 74% for yield.
Conclusions Subsoil roots may play a pivotal role for water acquisition during water stress periods and may contribute more than topsoil roots and above ground biomass to the accrual of soil carbon.

Keywords EJP soil · Yield · Grain maize · Root depth distribution · Root length · Water stress

Introduction

There has been a notable increase in both the frequency and intensity of extreme weather events in the last decades (Field et al. 2012). For instance, Europe has already experienced severe heatwaves in 2003 (Luterbacher et al. 2004), 2018–2019 (Buras et al. 2020; Mitchell et al. 2019) and 2022 (Toreti et al. 2022). Such events have the potential to elevate the risk of multiple crop failures occurring at regional and even global scale (Beillouin et al. 2020). The factors that drive crop development include water, atmospheric temperature, and photosynthetically effective radiation (Qin et al. 2023). Thus, for example, the 2003 European heatwave led to a decrease in European gross primary production, estimated at approximately 30% (Ciais et al. 2005).

In Europe, maize is the second-most cultivated crop after wheat (Eurostat 2025) and future yields are threatened by climate change due to drought stress (Harrison et al. 2014). Maize yields will likely be threatened by heat and water stress at crucial growth stages, such as silking and grain filling (Cairns et al. 2012). Severe water deficits during grain filling are estimated to occur 25% more often by 2050 (Harrison et al. 2014). Subsequently, average maize yields are projected to decrease by 9% for the 2020s to 15% by the 2080s compared to current yields for north and central Europe, while for southern Europe the decrease is expected to be 28% by 2080 compared to current yields (Knox et al. 2016). However, it is possible to mitigate yield losses through adaptation to future climate regimes, e.g. maize yields can potentially be enhanced by up to 7% if crop cycle duration and sowing dates were optimized at farm scale (Parent et al. 2018). Another means for climate change adaptation is direct breeding for adaptation of physiological traits under rainfed and more challenging conditions (Welcker et al. 2022).

Breeding and selecting varieties that show best yields in field trials under drought environments of current climates can allow to develop suitable varieties for projected future climates (Harrison et al. 2014). A new ideotype of maize roots with deep and steep roots that would optimise water and nitrogen from the subsoil was suggested for best performances under drought conditions (Lynch 2013). However, a large root system may be an ineffective use of resources in high-input agriculture where nutrient availability does not limit plant growth (Lynch 2018). An efficient root system was linked to a declining biomass allocation to roots, as well as a more efficient water capture (van Oosterom et al. 2016). However, the reallocation of biomass to roots under water deficit conditions is a known drought adaptation mechanism (Yan et al. 2023). This characteristic differs between maize varieties (Zhao et al. 2018), thereby determining the response of varieties to drought. Herein lies a potential to increase drought tolerance by breeding for these traits. Furthermore, Heinemann et al. (2023) demonstrated in a global review containing 13 experiments that root biomass and yield can be increased simultaneously by selecting the appropriate varieties.

In addition to the function of roots to acquire water and nutrients (Fitter 2002; Hodge et al. 2009), the average contribution of roots to total mean annual organic carbon input into arable soils accounts for 43% (Jacobs et al. 2020). Carbon inputs into arable soils are needed to maintain or enhance soil organic carbon (SOC) stocks (Riggers et al. 2021). SOC is important for soil health (Lal 2016; Bünemann et al. 2018) and food production (Oldfield et al. 2019). A major pathway of SOC formation are C inputs from roots with a higher C retention as compared to aboveground biomass (Rasse et al. 2005; Kätterer et al. 2011). A modeling approach reported that increasing the biomass allocation to roots in maize will result in increased SOC stocks of 0.05 to 0.15 Mg C ha^{-1} per year (Cotrufo et al. 2024). For comparison, by the end of the twenty-first century an average annual SOC loss of between 0.065 and 0.120 Mg ha^{-1} year^{-1} was projected for Germany (Riggers et al. 2021). Increased SOC stocks, in turn, can improve soil functions, such as water retention (Rawls et al. 2003) and soil fertility (Smith et al. 2015) potentially resulting in increased yields (Campos-Cáliz, et al., 2024; Kätterer and Bolinder 2024).

However, the visualisation and quantification of root systems remains challenging, as there is a lack of low-cost, high-throughput phenotyping methods. The manual excavation of roots, the use of rhizotrons and ingrowth cores and soil coring are common methods to study root biomass in the field (Addo-Danso et al. 2016). Root traits are often assessed during seedling stage but rarely close to maturity or at harvest. Consequently, studies that investigate root biomass or root traits of different crops and varieties together with aboveground parameters are scarce. Recent studies showed the need for reliable root data to better understand various ecosystem functions such as C sequestration in soils, resource use efficiency and plant nutrition to allow for projections of C sequestration and yields in future drier climate conditions (Fan et al. 2016; Keel et al. 2017; Ordóñez et al. 2020). Currently, root-derived C inputs are mostly estimated from crop yields using allometric functions in SOC modelling (Keel et al. 2017). These allometric functions are specific to crop type and are yield-dependent (Jacobs et al. 2020; Keel et al. 2017). More recent data and knowledge challenge the concept of yield-dependent allocation functions for arable crops (Taghizadeh-Toosi et al. 2016; Hirte et al. 2018b). However, the evidence is insufficient to establish new and robust allocation functions.

Thus, comprehensive datasets are needed to quantify the variability of root biomass production and distribution in the field under contrasting water regimes. This work is framed from a soil science perspective, with an emphasis on how water availability, maize variety and soil texture drive the variability of C inputs derived from root biomass. By integrating root biomass and depth distribution data with aboveground parameters, we aim to improve our understanding of aforementioned root biomass C inputs under field conditions. The objectives of this study were i) to quantify the root biomass production and depth distribution among different maize varieties under contrasting water regimes, ii) to investigate the influence of variety and water regime on the biomass allocation to roots and shoots, and iii) quantify the effects of variety and water treatment on the variability of root biomass derived C inputs.

Material & methods

Field experiments

A set of ten commercial maize hybrids was used in this study. These varieties were released by different breeders in Europe from 2009 to 2018 and belong to mid-early (FAO 280) to mid-late (FAO 480) maturity classes (Table 1). The set of maize hybrids was grown in four field experiments (defined as combinations of site × water regime) across France in 2022 (Fig. 1, Table 2) as part of the H2020_INVITE project. The experimental designs corresponded to randomised complete block or split block designs, according to national conventionality in variety testing. The sites were Ouzouer-Le-Marché (hereafter referred to as Ouzouer), Le Magneraud, Pusignan and Mauguio. They differed in terms of soil texture, pH, SOC content (Supplementary Table 1) and soil depth (Pusignan 85 cm, Ouzouer, Le Magneraud, Mauguio: >100 cm). The field trials were managed in accordance with regional conventional practices. A maximum of 190 kg N ha^{-1} was applied in order to satisfy the crops' needs. Daily weather data on precipitation and mean temperature are reported in Supplementary Fig. 1.

At each site, two contrasting treatments were applied: well-watered (WW) and water deficit (WD). Soil water potential (SWP) was measured every day with tensiometers at 30 and 60 cm depths, located in plots sown with a reference hybrid. In the WW treatment, the objective was to irrigate optimally and avoid getting SWP lower than −300 hPa at 30 cm

Table 1 The ten maize varieties used, their names and abbreviations in this study, FAO index group, year of release

Variety code	FAO index group	Breeder	Year of release
ARV32	(280—310)	EURALIS	2012
ARV79	(280—310)	RAGT	2014
ARV04	(310—400)	KWS	2018
ARV18	(310—400)	BAYER	2009
ARV20	(310—400)	BAYER	2016
ARV39	(310—400)	RAGT	2012
ARV52	(310—400)	KWS	2018
ARV85	(310—400)	RAGT	2015
ARV72	(400—470)	PIONEER	2014
ARV23	(310—400)	BAYER	2009

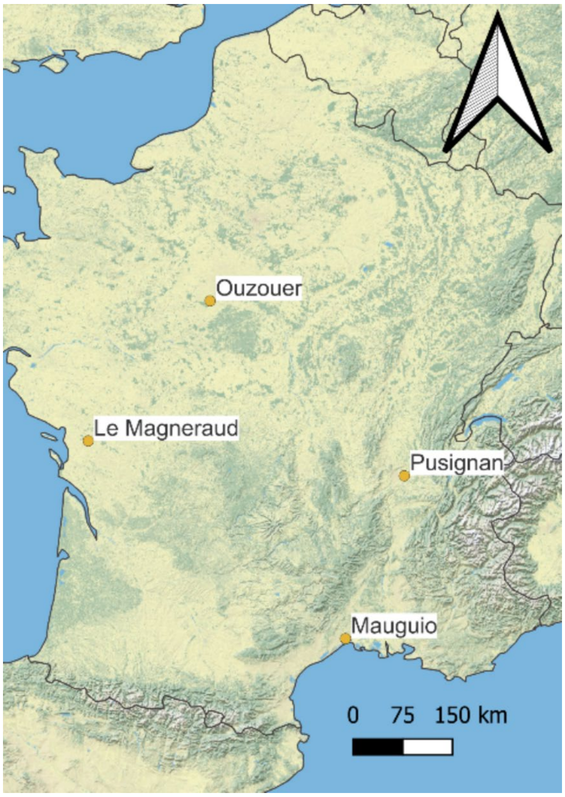

Fig. 1 Maize trial sites of the study in France

depth, to cover maize evaporative demand during the whole crop cycle. In the WD treatment, the objective was to avoid irrigation or rain water supply to plants from 8 leaves stage to grain abortion limit stage. Rainout shelters were used in one site (Ouzouer) for better monitoring water supply in the trial. Each treatment of the experiments had three replicates of four-row plots. Depending on sites, plot size varied between 15.6 m^2 and 22.5 m^2 and plant density between 7.5 and 8.5 plants m^{-2} (Table 2). The two central rows of each plot were harvested mechanically, and grain yield was determined and scaled to 15% moisture content. The WD treatment in Mauguio was considerably damaged by *Ustilago maydis* infestation favoured by water deficit conditions.

The water treatments lead to differences in water availability expressed as SWP (Supplementary Fig. 2). Koehler et al. (2023) reported a critical SWP ranging from −461 hPa to −1268 hPa for 48 maize varieties at which plants decreased transpiration upon soil drying. The mean of the range reported by Koehler et al. (2023) was used to derive a variety unspecific critical SWP which is −864.5 hPa. With this, the water stress days per site and water treatment were calculated to estimate the plants' water stress (Table 2, Supplementary Fig. 3).

Root and soil sampling

Root sampling of the maize hybrids was conducted shortly after harvest in October 2022. Most of maize root biomass is expected to be in the upper 30 cm of soil (Hirte et al. 2018b; Komainda et al. 2018). Thus, six representative plants per plot were selected based on plant density and condition after harvest and excavated with a shovel down to 30 cm. This excavation aimed to extract a soil monolith with the dimensions of 15 × 15 × 30 cm to capture the same size across all sites. The excavated roots were washed directly in the field with tap water, the roots belonging to neighbouring plants were discarded. A multi sprayer attached to a hose was used with low pressure to prevent damaging of the roots. The excavated roots stocks were spread out on a blanket to dry in the sun. Sun dried samples were carefully stored and transported to the lab. Subsequently, root stocks were dried at 55 °C using an oven until the weight remained constant.

In addition, three varieties (ARV18, ARV72, ARV79) were selected where root samples down to 100 cm depth were taken using soil coring. These varieties were selected because they belong to different maturity classes (Table 1). A soil auger with an inner diameter of 6 cm was driven 100 cm into the soil using an electric hammer to extract core samples. Two cores per plot were taken, one directly under a plant and one between crop rows. In total, six cores per variety were taken at each site and water treatment, three under a plant and three between crop rows. Two additional soil cores per site were randomly taken inside the plots for soil analyses. The soil cores were cut into the following depth increments: 0–15, 15–30, 30–50, 50–75 and 75–100 cm. Soil texture was determined on samples from the additional soil cores.

For root biomass determination from the soil cores, roots were extracted from each soil core separately as follows: The soil core was dispersed in a hydro vortex, and roots were separated from the mineral soil fraction through floating and recovered on a 0.5 mm sieve (Smucker et al. 1982) using an

Table 2 Location, weather data (temperature and precipitation) for the periods sowing to harvest, vegetative, flowering and grain filling for the study sites

Site	Le Magneraud	Mauguio	Ouzouer-Le-Marché	Pusignan
Location (decimal degrees)	46.1530 −0.6936	43.6130 3.9790	47.8842 1.5194	45.7135 5.0464
Climate (Köppen Geiger)	Cfb	Csa	Cfb	Cfb
Mean temp (sowing to harvest) [C°]	21.2	24.9	20.9	22.1
Precipitation sum (sowing to harvest) [mm]	269.9	428.0	91.6	539.8
Mean PAR (sowing to harvest) [MJ m^{-2}]	23.0	25.3	22.4	22.7
Water stress days WW treatment (sowing to harvest)	0	0	5	14
Water stress days WD treatment (sowing to harvest)	18	15	31	27
Mean of daily mean temp (vegetative) [C°]	20.3	25.0	19.4	20.6
Precipitation sum (vegetative) [mm]	66.2	8.0	13.0	38.6
Mean of daily mean temp (flowering) [C°]	25.1	27.2	21.0	23.2
Precipitation sum (flowering) [mm]	1.4	1.5	15.0	130.7
Mean of daily mean temp (filling) [C°]	22.9	25.7	22.9	24.0
Precipitation sum (filling) [mm]	26.0	167.1	11.2	68.4
Plot size (m^2)	22.5	22.5	15.6	20.8
Plant density (plants m^{-2})	7.8	7.5	8.5	8.1

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 $39 \pm 3\%$.

Soil analyses were performed on samples from the additional soil cores that were sieved (2 mm) and dried at 40 °C. 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.

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) (Eq. 1, 2). This was done for each depth increment as follows:

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

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

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.

Root biomass from excavated roots down to 30 cm was upscaled to field scale by using the plant density of each established plot:

$$RB_{30cm} = RB_{plant} * PD \tag{3}$$

where RB_{plant} is the root biomass per plant down to 30 cm (g plant^{-1}) and PD is the plant density (plants m^{-2}).

R:S ratios were calculated here as the ratio of root biomass to aboveground biomass (Eq. (4). The harvest index (HI) was used to estimate the total aboveground biomass from grain yield. The HI of 0.5 was derived from Jacobs et al. (2020).

$$R : Sratio = \frac{RB_{extra}}{\frac{Yield*0.85}{HI}} \tag{4}$$

Statistics

The root biomass data is slightly right skewed; thus, the median was used to describe average values. 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 and different sources of variability. A random intercept model was used to assess the variability in non-transformed aboveground data and log-transformed root biomass and R:S data to meet the assumption of homogeneous distribution of the residuals. The log-transformation of root biomass and R:S were used for the next calculation steps. The variety differences were tested for yield, root biomass and R:S ratio across water treatments (Eq. 5) and with a split data set per water treatment (Eq. 6).

$$\text{dependent variable } \sim Variety + stressdays * watertreament + 1|Site|Replicate \tag{5}$$

$$\text{dependent variable } \sim Variety + stressdays + 1|Site|Replicate \tag{6}$$

The effects of environmental indices like soil texture on root biomass, R:S and yield were tested using mixed-effects models with an interaction term of variety and index

$$\text{dependent variable } \sim Variety * index + watertreatment + 1|Site|Replicate \tag{7}$$

The relationship between root biomass and yield was tested as follows:

$$\text{yield } \sim rootbiomass * watertreatment * stressdays + 1|Site|Replicate \tag{8}$$

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.

Software

All analyses were performed with R, version 4.4.2 (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) and ggpubr (Kassambara 2023) for visualisation. The root scans were analysed using RhizoVision Explorer v2.0.3 (Seethepalli and York 2020; Seethepalli et al. 2021).

Results

Root biomass production and distribution

The average root biomass of maize at a depth of 0–100 cm was found to be 3.2 ± 1.2 Mg ha^{-1} across all sites and water treatments. 90.1% of the total root biomass was found in 0- 15 cm of the soil and only 9.9% in 15–100 cm depth. Under WD conditions, 86.5% of the total plant root biomass was located in the 0–15 cm increment. However, under WW conditions, this proportion increased to 92.9% of the total plant root biomass. Thus, root biomass in 0–15 cm decreased from 2.3 ± 1.5 Mg ha^{-1} under WW condition to 1.6 ± 0.8 Mg ha^{-1} under WD conditions.

The contrasting water treatments resulted in significantly different root biomass within a soil layer, irrespective of site and variety (Fig. 2). WW conditions led to 29% higher root biomass in the topsoil (0–30 cm) compared to WD conditions. In the subsoil (30–100 cm) in contrast to the topsoil (0–30 cm), root biomass was 25% lower under WW conditions than under WD conditions (Fig. 2). There was a significant increase of root biomass in the subsoil with increasing number of stress days but no significant interaction with variety. Total root biomass was negatively related to the number of stress days ($p < 0.001$).

For the root biomass across the total sampling depth as well as for the top soil root biomass the SWP in 30 and 60 cm depth exhibited a significant positive correlation during the vegetative and the flowering

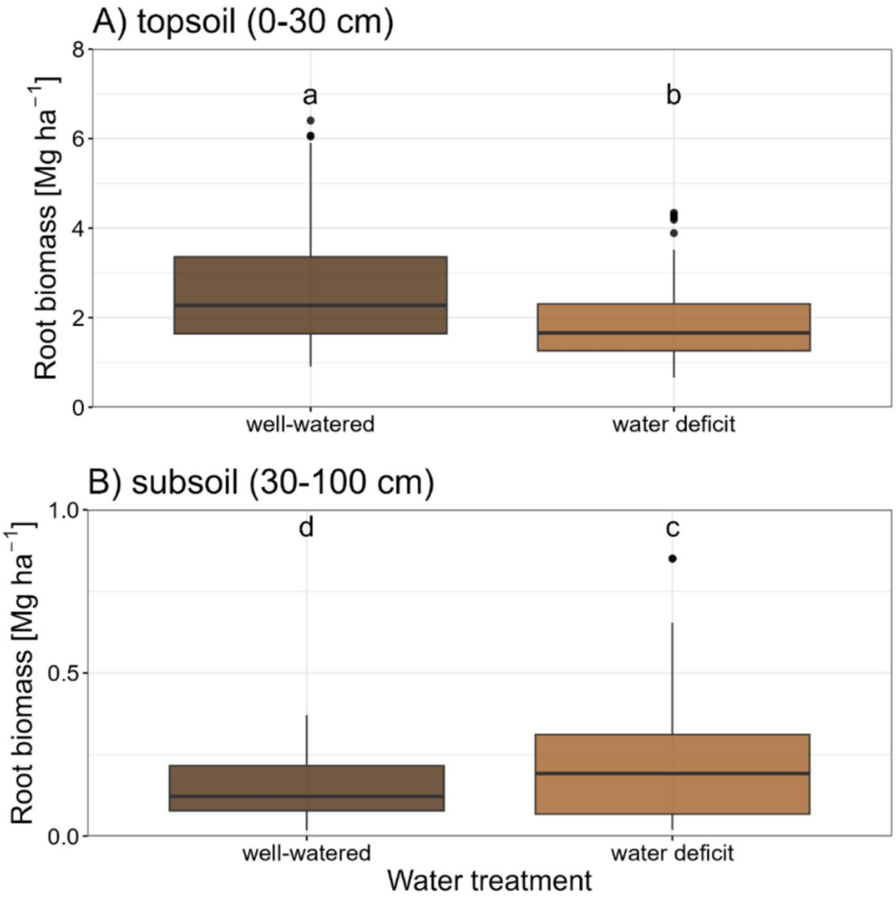

Fig. 2 Comparison of root biomass [Mg ha^{-1}] of water treatments in top- (0–30 cm) and subsoil (30–100 cm). Statistical grouping via a comparison of estimated marginal means per water treatment and soil layer is indicated by letters

Table 3 Significance of correlation coefficients for main effects of climatic variables for root biomass in the total sampling depth of 0–100 cm, root biomass in the topsoil (0–30 cm) and subsoil (30–100 cm) based on linear mixed models

		Root biomass (total sampling depth) [Mg ha^{-1}]	Root biomass topsoil [Mg ha^{-1}]	Root biomass subsoil [Mg ha^{-1}]
Vegetative	SWP 30 [MPa]	**0.003 (+)**	**0.049 (+)**	0.056
	SWP 60 [MPa]	**0.01 (+)**	0.23	0.26
	SWP mean [MPa]	**0.003 (+)**	0.071	0.08
	Mean Temp [°C]	0.964	0.895	0.727
	Max Temp [°C]	0.661	0.81	0.619
	Min Temp [°C]	0.766	0.947	0.193
	Rain sum [mm]	**0.001 (-)**	0.925	0.319
Flowering	SWP 30 [MPa]	**0.001 (+)**	**0.022 (+)**	0.057
	SWP 60 [MPa]	**0.001 (+)**	**0.031 (+)**	0.054
	SWP mean [MPa]	**0.001 (+)**	**0.022 (+)**	0.055
	Mean Temp [°C]	0.75	0.813	0.917
	Max Temp [°C]	0.865	0.733	0.886
	Min Temp [°C]	0.513	0.883	0.254
	Rain sum [mm]	0.641	0.497	0.056
Grain filling	SWP 30 [MPa]	**0.041 (+)**	0.138	0.187
	SWP 60 [MPa]	0.349	0.479	0.3
	SWP mean [MPa]	0.124	0.265	0.226
	Mean Temp [°C]	0.123	0.767	0.305
	Max Temp [°C]	**< 0.001 (+)**	0.571	0.617
	Min Temp [°C]	0.87	0.938	0.233
	Rain sum [mm]	0.582	0.912	0.422

SWP: Soil water potential at 30 cm, 60 cm or the mean of both, Temp: daily mean temperature or mean of daily maximum/minimum temperatures.

Table 4 Comparison of average total root biomass [Mg ha^{-1}] per site separated in well-watered (WW) and water-deficit (WD) treatments with the relative difference (in %) between WW to WD

Site	WW median root biomass [Mg ha^{-1}]	WD median root biomass [Mg ha^{-1}]	Relative difference
Le Magneraud	$2.3^{b} \pm 1.3$	$2.1^{a} \pm 0.7$	−8.8
Mauguio	$3.2^{a} \pm 1.9$	$1.5^{b} \pm 0.9$	−52.5
Ouzouer	$2.3^{b} \pm 0.9$	$1.8^{ab} \pm 0.6$	−22.4
Pusignan	$2.3^{b} \pm 1.1$	$2.0^{a} \pm 0.7$	−12.4

Statistical differences via a comparison of estimated marginal means per water treatment and site indicated by letters. SD indicates standard deviation.

stage (Table 3). Thus, the drier the soil the fewer root biomass was found. For the subsoil, this correlation was barely not significant. However, it is worth to note that the effect had been reversed. Accordingly, in dry conditions there would be more roots in the subsoil.

Statistical analysis of the data revealed significant variations in root biomass among the sites, with Mauguio exhibiting the highest values among all four sites with 3.2 ± 1.9 Mg ha^{-1} in WW conditions (Table 4). However, under WD conditions, the highest total root biomass was observed in Le Magneraud (2.1 ± 0.7 Mg ha^{-1}) and Pusignan (2.0 ± 0.7 Mg ha^{-1}). Mauguio showed the highest relative difference (−52.5%) between WW and WD conditions and Le Magneraud the smallest (−8.8%). Data on the depth distribution of root biomass at the four sites showed that Ouzouer exhibited higher absolute root biomass in the subsoil in comparison to the other three sites for both water treatments. In Ouzouer the average root biomass below 30 cm under WW conditions was 0.3 Mg ha^{-1} and increased to 0.5 Mg ha^{-1} under WD conditions. This corresponded to 6% of the total root biomass below 30 cm depth under WW conditions and 16% below 30 cm depth under WD conditions (Supplementary Fig. 4). Ouzouer also showed the highest number of water stress days under WD conditions and concurrently demonstrating the most prominent difference (26 stress days) in water stress days between the two water treatments (Table 2). Consequently, at sites where water treatments did not result in substantial differences in water stress, there was minimal change in the root biomass proportion in the subsoil. In Le Magneraud, the proportion of

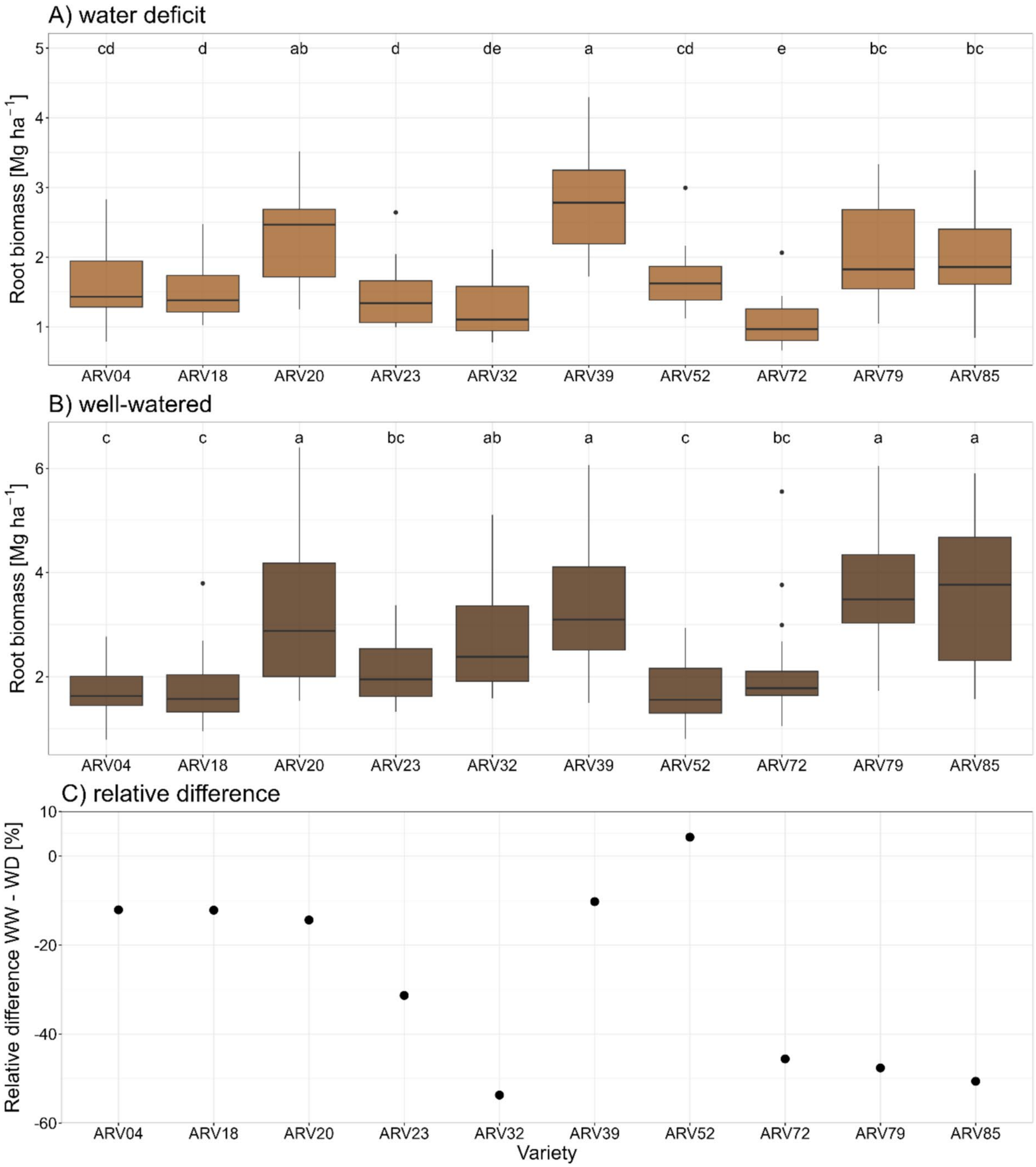

Fig. 3 Root biomass in the top soil (0–30 cm) by variety for water deficit (**A**) and well-watered conditions (**B**) and the relative difference of medians per variety between the two water treatments (**C**). Statistical grouping via a comparison of estimated marginal means per variety is indicated by letters

root biomass below 30 cm increased from 4% under WW to 7% under WD conditions (18 stress days difference).

Total root biomass differed significantly ($p < 0.05$) between maize varieties across both water treatments (Supplementary Table 2) ranging from 1.6 to 3.7 Mg root biomass ha^{-1} in the WW treatment and from 0.9 to 2.8 Mg ha^{-1} in the WD treatment. Thus, variety selection could site-specifically increase root biomass by 59 to 71% in the WW treatment and by 63 to 72% in the WD treatment considering the lowest and best performing variety.

The relative variety differences for total root biomass became apparent once the water conditions were considered separately (Fig. 3). In general, a loss of total root biomass by on average −27% under WD conditions compared to WW conditions was found for almost all varieties, where ARV52 was the exception. In contrast, for ARV52 the average root biomass actually increased slightly by 4%. Under WW conditions, the difference between the best performing and the worst performing variety was 2.2 Mg ha^{-1} or 59% in relative terms. Under WD conditions this difference was 1.8 Mg ha^{-1} or 65%. A significant interaction of variety and water stress days was found for the root biomass in the topsoil. Root biomass always declined with increasing number of stress days but the slope depended on variety (Supplementary Fig. 5).

In the subsoil (30–100 cm), there were no differences of root biomass for the three varieties that were additionally sampled with coring. Subsoil root biomass accounted for 3% of the total root biomass among the three varieties in the WW treatment. Irrespective of variety and water treatment, a significant positive correlation was identified between the soils' silt content and total root biomass ($p < 0.001$). In line with this, sand content exhibited a negative correlation with root biomass ($p < 0.001$). However, clay content did not show a significant correlation with root biomass ($p = 0.62$).

Classified by FAO maturity groups no distinct differences were observed for the root biomass. The mid-early varieties (FAO 280–310) ARV32 and ARV79 as well as the later variety (FAO 400–470) ARV72 and ARV85 showed the highest differences between root biomass under WW and WD conditions with up to 40% less root biomass (Fig. 3). Three varieties from the intermediate maturity group (ARV04, ARV39 and ARV18) exhibited the lowest differences between water treatments (max. 14%) but also showed generally low root biomass independently of the water treatment.

Root architecture

The mean root diameter exhibited a depth-dependent variation, with a significantly higher mean diameter observed in the topsoil (0–30 cm) compared to the subsoil (30–100 cm). Furthermore, water treatments have been observed to result in varying diameters, with higher diameters being attained under WW conditions. The diameters exhibited by the varieties did not demonstrate a significant difference. The root diameter exhibited a significant correlation with the texture. Silt exhibited a significant negative influence on root diameter ($p = 0.02$), whereas clay demonstrated a significantly positive influence ($p = 0.04$).

A significant variation in root length was observed among the different varieties, with ARV72 exhibiting the highest root length across all sites and both water treatments. However, the WD treatment resulted in a significantly higher total root length than the WW treatment across sites. However, the root length for the total sampling depth exhibited a negative correlation with SWP in 30 and the mean SWP during the vegetative stage (Supplementary Table 3). The data revealed a negative correlation between the root length and the SWP (30 cm and 60 cm), as well as the mean SWP during the flowering and grain-filling stages. In contrast, a positive correlation was observed between the mean diameter and the SWP at 30 and 60 cm depth for all three developmental stages. The total precipitation during the vegetative stage exhibited a positive correlation with the root length in the topsoil. The precipitation during the flowering period had a positive effect on the mean diameter throughout the entire sampling depth, as well as in both the topsoil and subsoil layers.

Yield

Average yield across all sites and varieties was 12.3 ± 3.1 Mg ha^{-1}. Over both water treatments, the yield varied significantly between varieties (Supplementary Table 4). The yield ranged in the WW

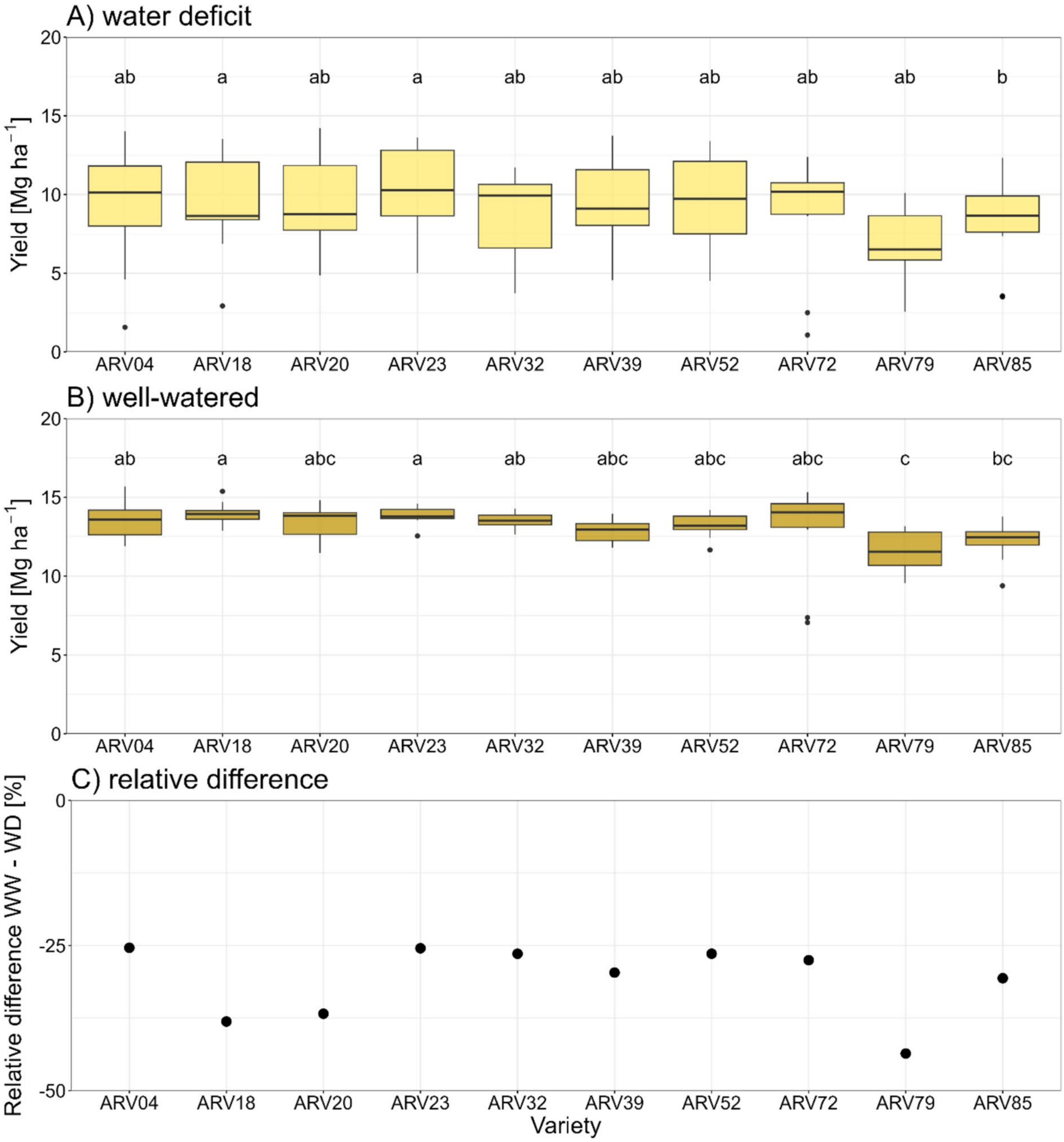

Fig. 4 Yields by variety for water deficit (**A**) and well-watered conditions (**B**) and the relative difference of medians per variety between the two water treatments (**C**). Statistical grouping via a comparison of estimated marginal means per variety is indicated by letters

treatment from 11.6 to 14 Mg ha^{-1} and in the WD treatment from 6.5 to 10.3 Mg ha^{-1}. The average yield was significantly higher (+32%) under WW conditions (13.4 ± 1.4 Mg ha^{-1}) than under WD conditions (9.0 ± 3.1 Mg ha^{-1}). There was a significant decrease of yield with increasing water stress days but no interaction with variety. At both water treatments, the yield varied significantly between varieties with a site-specific increase in yield by 10 to 48% in the WW treatment and 20 to 74% in the water deficit treatment when the lowest performing variety is compared to the best.

The varieties ARV79, ARV18 and ARV20 showed the highest relative yield difference between water treatments (44% decline under WD). Under WW conditions, the difference between the best performing and the worst performing variety was 2.4 Mg ha^{-1} or 17.1%. Under WD conditions this difference increased to 3.8 Mg ha^{-1} or 36.7%. The variability of yield between sites was lower at well-watered conditions with an average coefficient of variation (CV) of 11% as compared to water deficit conditions (34%) (Fig. 4). No maturity group specific trend was found.

Biomass allocation

The median R:S ratio across varieties, sites and water treatments was 0.16 ± 0.07. R:S ratios were significantly lower under WW conditions (0.15 ± 0.06) than under WD conditions (0.17 ± 0.07). Over both water treatments, the R:S ratio varied significantly between varieties (Supplementary Table 5) ranging from 0.06 to 0.30 under WW conditions and from 0.07 to 0.22 under WD conditions (Fig. 5). No maturity group specific trend was found.

Water deficit effects on the R:S ratios depended on the variety (Fig. 5). For varieties ARV18 and ARV72 the water deficit did not result in changed R:S ratio. In contrast, ARV79 showed higher R:S ration under WD than WW conditions.

The root biomass difference due to water deficit ranged from −87% to 27% depending on the variety, while the yield loss ranged from −2% to −75% (Fig. 6). This indicated a higher impact of WD on root biomass than on yield. A positive root biomass difference indicated that the average root biomass was higher under WD conditions than under WW conditions and was found for variety ARV18

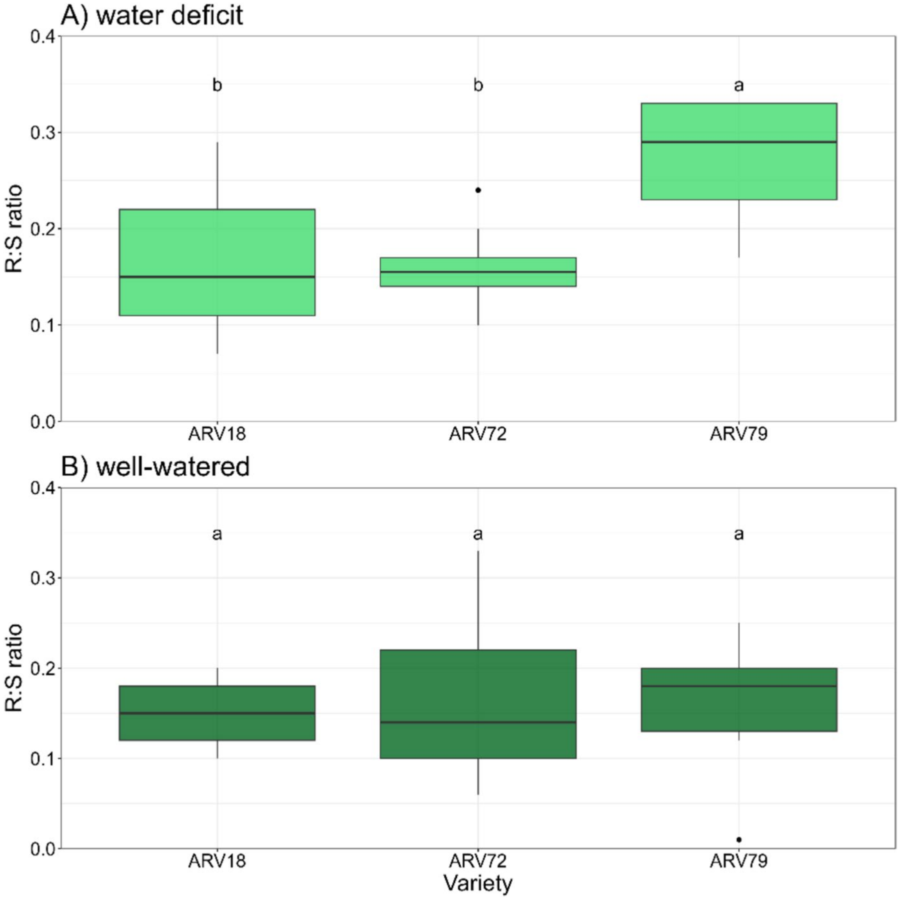

Fig. 5 R:S (root to shoot) ratio by variety for water deficit (**A**) and well-watered conditions (**B**). Statistical grouping via a comparison of estimated marginal means per variety for each water treatment is indicated by letters

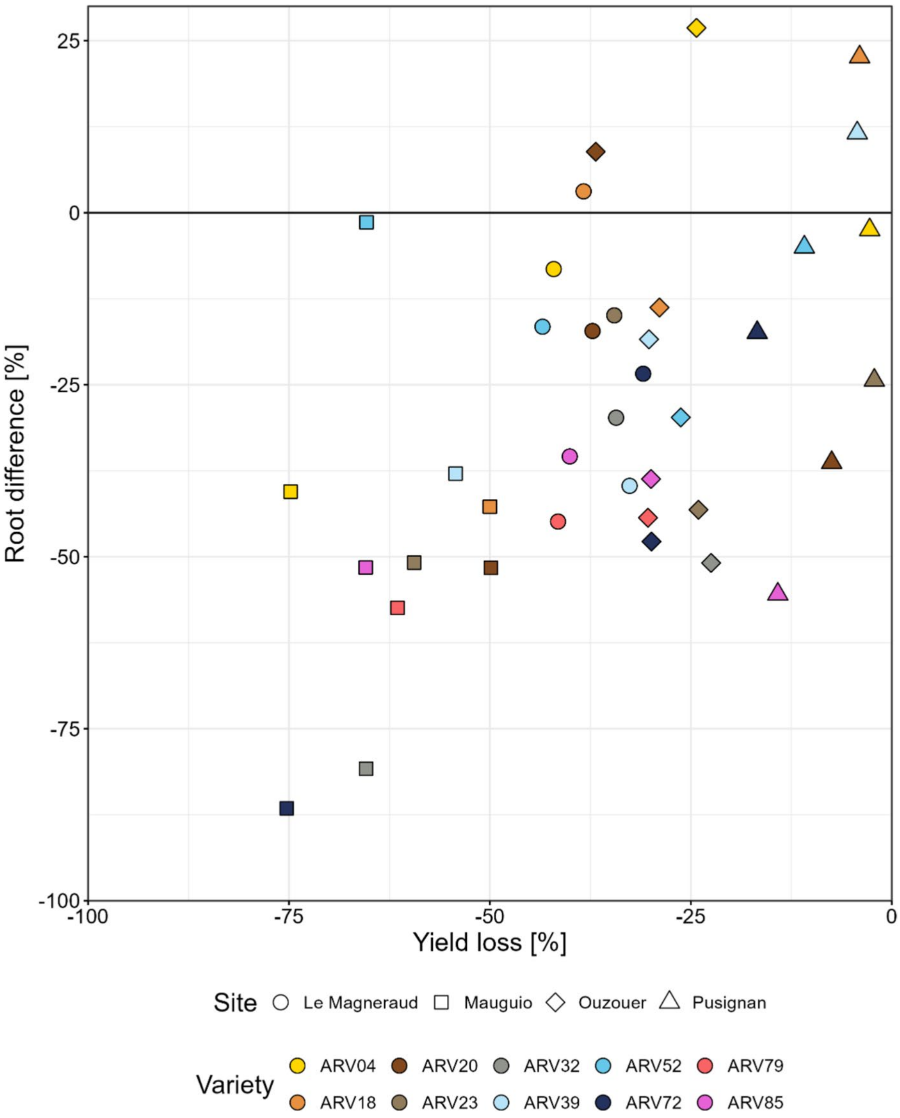

Fig. 6 Relative root difference between well-watered conditions and water deficit conditions and relative yield loss from well-watered conditions to water deficit conditions averaged per site and variety

at Pusignan and Le Magneraud, for ARV39 at Pusignan, for ARV20 at Ouzouer and for ARV04 at Ouzouer. A positive yield difference was not observed showing always less yield under WD conditions. Thus, yield always declined from WW to WD conditions for all varieties (Fig. 6).

Per site and water treatment, trends of yield with increasing root biomass C were mostly negative but not significant (Fig. 7). Significant negative trends were found at Ouzouer WW ($p = 0.04$) and Ouzouer WD ($p = 0.005$). A nonsignificant positive trend for yield with increasing root biomass was found at Pusignan WD ($p = 0.9$).

Discussion

Drought impact on root biomass production and distribution depends on variety

The root biomass of maize (0–100 cm) found in this study are in the upper end of reported values ranging from 1.8 Mg ha^{-1} to 3.4 Mg ha^{-1} derived by differing sampling methods and depths between 0-210 cm (Hirte et al. 2018a; Komainda et al. 2018; Ordóñez et al. 2020; Xu et al. 2020). Xu et al. (2020) sampled 0–30 cm with a monolith method and reported a maximum of 1.8 Mg ha^{-1}. Hirte et al. (2018a) combined a

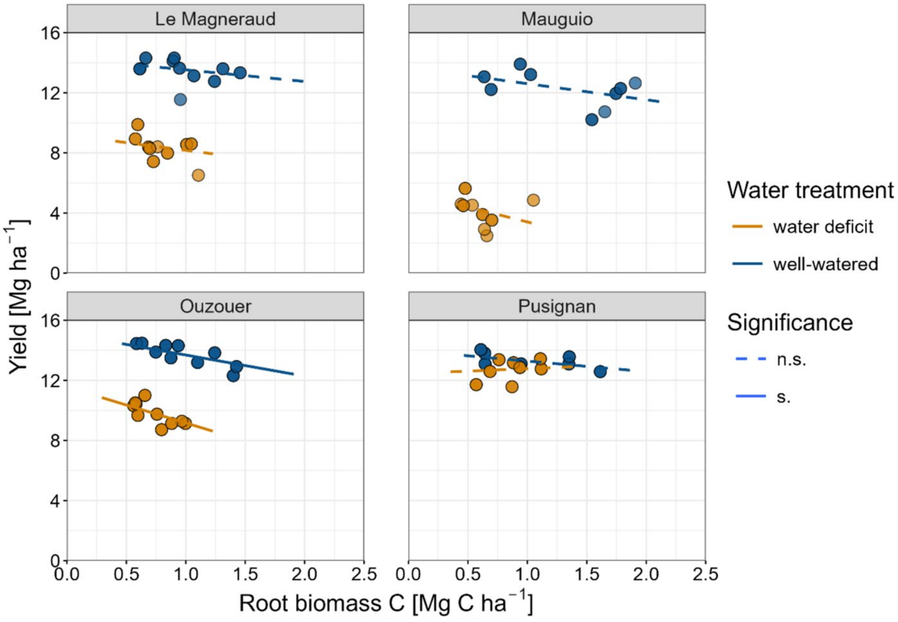

Fig. 7 Relationship between yield (Mg ha^{-1}) and root biomass C (Mg C ha^{-1}) per water treatment (WW: well-watered, WD: water deficit) and site. The trends were based on a linear mixed effect model. Dots represent the mean values per variety at each site and water treatment. Significant (p-value ≤ 0.05) correlations are represented by solid lines, while non-significant correlations are represented by dashed lines

monolith and an auger approach and found not more than approximately 2 Mg ha^{-1} in 0-75 cm. Komainda et al. (2018) reported up to 3.4 Mg ha^{-1} for a combined method of ingrowth core and soil auger to a depth of 60 cm. Ordóñez et al. (2020) sampled down to 210 cm and reported root biomass of maximum 2.8 Mg ha^{-1}. The sampling method, position and depth has a significant impact on the estimated root biomass (Ordóñez et al. 2018). Our sampling design was chosen to be cost and time efficient as only a very limited time period after harvest was available for sampling due to agricultural management following harvest at the four sampling sites.

Differences between varieties were found for root biomass which was unclear before as literature showed conflicting evidence (Shao et al. 2019; Xu et al. 2020; Taube et al. 2020). Significant variety differences in root biomass of maize were reported by Shao et al. (2019) for eight varieties under three different planting densities with up to 50% increase between the variety with the lowest to the variety with the highest root biomass. We found higher differences of root biomass between the variety with the lowest to the variety with the highest root biomass by 59 to 71% in the WW treatment and by 63 to 72% in the WD treatment. In contrast, Xu et al. (2020) did not find significant variety differences for root biomass in a Belgian field experiment. Still, the difference between the variety with the lowest root biomass and the variety with the highest root biomass ranged between 29 and 45% at the three Belgian sampling sites. One could argue that the varieties were genetically too similar to show significant differences but the varieties differed in their photosynthetic capacity (Swanckaert et al. 2017). However, Taube et al. (2020) constructed a timeline of the breeding progress in silage maize in Germany from 1970 to 2012 with ten varieties released in this period. Genetic variability was present and the analysis also showed a non-significant increase in root biomass of 13% from the 1970 variety to the 2012 variety. Insignificance could have been caused by a high variability of root biomass data. However, this raises the question of how these findings should be interpreted in relation to the C input from root biomass to the soil in the context of SOC modelling. Root derived C inputs also vary significantly depending on the variety, and show great variability between water treatments. Within the limited range of varieties included in this study, the variation in root biomass and, consequently, the root-derived C inputs between varieties can reach up to 72%. For SOC models, this entails a high degree of uncertainty.

In the subsoil (30–100 cm), we found no differences in root biomass for the three sampled varieties (ARV72, ARV18, ARV79). This contrasts findings by

Hund et al. (2009) where differences in rooting depth were found among four different varieties (Ac7643, Ac7729/TZSRW, CML444, SC-Malawi). However, in that study, the proportion of deep roots was increased by a limited water availability irrespective of variety (Hund et al. 2009). This is supported by the present study where the root biomass in the subsoil was enhanced by 25% by WD conditions compared to WW conditions. The variability of root biomass in the subsoil is subsequently important vor the SOC build up below the plough horizon. Approximately 20% of agricultural management's impact on SOC occurs in subsoil layers, underscoring the importance of deep soil C dynamics for C sequestration (Skadell et al. 2023).

Biomass allocation

The average R:S ratio across the three varieties, sites and water treatments was 0.16 ± 0.07. Even though data for shoot biomass was not available in this study and had to be estimated based on the yield, the R:S ratios fit to earlier reported R:S values for maize of 0.05—0.19 under various pedo-climatic conditions (Heinemann et al. 2023). Komainda et al. (2018) reported R:S ratios between 0.17 to 0.22 for two maize varieties at harvest averaged over years and two different N treatments in northern Germany. R:S ratios of 0.04 to 0.13 with an average of 0.09 ± 0.02 were found for maize across 10 locations, three years and multiple cropping systems in Iowa, USA (Ordóñez et al. 2020). In our study, R:S ratios varied significantly between varieties for both water treatments. Earlier findings did not report significant differences in R:S ratios of maize (Komainda et al. 2018; Xu et al. 2020). Komainda et al. (2018) included only two genotypes in their study which limits the ability to find significant variety differences. Another factor for insignificant variety differences might be a high variability in the data or a method that was not suitable. Xu et al. (2020) chose a soil monolith approach. To avoid collecting roots from neighbouring plants, they set the width only to 10 cm. It is possible that this sampling approach did not allow to capture variety differences.

Previous research indicated that limited water availability had a greater impact on shoot growth (dry weight −75%) than on root growth (root surface area −51%) (Hund et al. 2009) leading to increased R:S ratios with water stress which is in line with our findings (Fig. 5). This was also supported by Yan et al. (2023) reporting an increase in R:S ratios from 0.11 under moderate drought to 0.20 under light drought conditions in a field experiment in China. Another factor that plays a role in the biomass allocation under drought conditions is the timing of drought. Yield can be reduced by 75% due to drought during flowering and by 40% by drought during grain filling stage compared to a continuous water supply (Barron et al. 2003). In our study, yield was reduced by 32% due to WD conditions across four sampling sites. The WD conditions in our experiments occurred also during flowering and grain filling. The differences between the two water treatments however was not as big as expected following Barron et al. (2003). This might be the case because WW conditions were not optimal, plants grown under these conditions experienced also water limitations during crucial growth stages (Supplementary Figs. 2 and 3). This could have resulted in a reduction of the yield in both water treatments, thereby lowering the observed difference.

The timing of drought is expected to alter the yields of maize varieties classified into different maturity groups. Early-maturing varieties are able to avoid droughts in the late season; however, if water stress conditions start mid-season, these varieties perform worse than mid- and late-maturing varieties (Cairns et al. 2012; Grewer et al. 2024). In our study, ARV32 and ARV79 can be assigned to an earlier and ARV72 and ARV23 to a later maturity group, other varieties belong to an intermediate maturity group (Table 1). However, it was not possible to assign any distinguishable behaviours to the groups in this study.

Irrespective of maturity group, our results indicated that plants invested more resources into roots to adapt to drought conditions. Generally, above- and belowground biomass production declined from WW to WD conditions. Figure 6 showed that the reactions of root biomass to water deficit were greater than those of the yield. Returning to the root-derived C inputs to the soil this finding poses the question of whether yield-dependent allocation functions, as currently employed to calculate C inputs from underground biomass based on yield data, are truly suitable. Hirte et al. (2018b) also found a disconnect between above and belowground C dynamics in two Swiss field trials under different farming systems but the evidence is insufficient to determine whether this is the case for arable crops at large. Thus, yield-independent allocation functions for estimating belowground C might be more suited to generated reliable data.

Benefit of roots under drought stress

There seems to be a fine line between a beneficial (for yield and yield stability) root system and an unfavourable (investment without return) root system under current, common climate conditions (Lynch 2018; White et al. 2013). Roots are especially valuable under extreme conditions such as drought, heat or limited nutrient availability (Comas et al. 2013). However, it was stated that plants with low root biomasss in the topsoil should be adapted to drougth conditions (Bolaños et al. 1993).

When talking about the benefits of roots under water stress root biomass might not be the best measure to evaluate it. The root system architecture and the plasticity of the root system are equally important to discuss. The root anatomical and architectural responses to drought are complex phenomena that vary among cultivars and root classes, as well as along root axes (Hazman and Kabil 2022). Hund et al. (2009) reported higher transpiration, stomatal conductance and shoot biomass for maize varieties with increased rooting depth. An improved drought tolerance through increased rooting depth and water acquisition from subsoil was reported from a field experiment in Pennsylvania, USA for eight varieties of maize (Gao and Lynch 2016). This enhancement was attributed to a reduced number of crown roots. Furthermore, the best performing varieties in a root phenotyping study grew at steeper root angles when exposed to drought stress (Klein et al. 2020). Generally, with increased stress days and lower SWP we found more root biomass in the subsoil. However, with lower SWP the root length generally increased and the root diameter decreased (Supplementary Table 3). This can be attributed to a drought adaption mechanism of plants whereby roots are thinned during water deficit conditions. The root thinning occurs as a means to reduce the consumption of photosynthetic resources, leading to a reduction in root biomass (Yan et al. 2022).

Another factor that needs to be included in this discussion is the soil texture. Soil texture has significant effects on how maize responds to drought stress, influencing both root development and water uptake mechanisms. It was shown that sandy soils lead to higher root diameters and root length densities in maize compared to a loamy substrate (Vetterlein et al. 2022). Cai et al. (2021) were able to quantify the variation in soil–plant hydraulic conductance and root length of maize in response to soil conditions, including water limitations and soil texture differences. Both studies point out that soil texture strongly influences root trait plasticity in maize and consequently the drought response.

The metabolic costs of roots can account for more than 50% of the daily photosynthesis (Lambers et al. 2003). Thus, an overinvestment in root biomass can be expected to limit aboveground biomass and thus yield if higher root biomass does not lead to increased resource acquisition. However, for the aim of C sequestration in soils a high root biomass and therefore root derived C inputs are favourable. As illustrated in Fig. 7, it appears that a trade-off exists between grain yield and root biomass C. It seems that, either high yields can be achieved or high levels of root biomass C inputs to the soil can be achieved. Based on a systematic review and a comprehensive field study one might expect that high yields and root biomass C inputs can be achieved simultaneously (Heinemann et al. 2023, 2025). However, it is important to bear in mind that site conditions have a strong influence on root biomass. For instance, soil depth influences the distribution and production of root biomass (see Pusignan, Supplementary Fig. 4). Moreover, the root architecture exhibits a high degree of plasticity with regard to texture (Vetterlein et al. 2022). Furthermore, diseases such as the infection by *Ustilago maydis* in Mauguio have the potential to further alter the correlation between yield and root mass. This again poses the question of whether yield-dependent allocation functions are truly suitable for calculation root-derived C inputs to soils.

Conclusions

Root biomass in the top soil (0–30 cm) was 29% higher under WW conditions compared to WD conditions. In the subsoil (30–100 cm) however, root biomass was 25% higher under WD conditions and increased significantly with the number of water stress days. Only a small root fraction of 3.4 to 6.6% was located in the subsoil. Still, these roots may play a pivotal role for water acquisition during water stress periods and may contribute more than topsoil roots and above ground biomass to the accrual of soil C. Under the pressure of more frequent extreme weather events due to climate change this could be a way to prevent from crop failures and may contribute to climate mitigation via C sequestration in the soil. However, the calculation of root derived C inputs into soils via C allocation functions might introduce high variability into SOC modelling as the experimental data showed that root biomass C of maize cannot be directly estimated from aboveground biomass data.

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Author contribution H. Heinemann: data curation, formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing.

F. Seidel: methodology, data curation, project administration, funding acquisition, conceptualization, writing – review and editing.

J. Hirte: project administration, funding acquisition, methodology, validation, conceptualization, writing – review and editing.

C. Welcker: funding acquisition, conceptualization, project administration, resources, writing – review and editing.

R. Chapuis: management of field platform experiment, data curation, writing – review and editing.

C. Gelot: management of field experiment, data curation, writing – review and editing.

K. Beauchêne: management of field platform experiment, data curation, writing – review and editing.

N. Luchaire: data curation, writing – review and editing.

J. Bouidghaghen: data curation, writing – review and editing.

A. Don: conceptualization, data curation, validation, project administration, funding acquisition, methodology, supervision, writing – review and editing.

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Data availability The dataset generated during the current study are available in the Zenodo repository, https://doi.org/10.5281/zenodo.14229689.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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