Enhanced root carbon allocation through organic farming is restricted to topsoils

Running title: Drivers of root biomass in farming systems

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Abstract

Soils store significant amounts of carbon (C) and thus can play a critical role for mitigating climate change. Crop roots represent the main C source in agricultural soils and are particularly important for long-term C storage in agroecosystems. To evaluate the potential of different farming systems to contribute to soil C sequestration and thus climate change mitigation, it is of great importance to gain a better understanding of the factors influencing root C allocation and distribution. So far, it is still unclear how root C allocation varies among farming systems and whether the choice of management practices can help to enhance root C inputs. In this study, we compared root C allocation in three main arable farming systems, namely organic, no-till, and conventional farming. We assessed root biomass, vertical root distribution to 0.75 m soil depth, and root-shoot ratios in 24 winter wheat fields. We further evaluated the relative importance of the farming system compared to site conditions and quantified the contribution of individual management practices and pedoclimatic drivers. Farming system explained one third of the variation in topsoil root biomass and root-shoot ratios, both being strongly positively related to weed biomass and soil organic C content and negatively to mineral nitrogen fertilization intensity. Root C allocation was significantly higher in organic farming as illustrated by an increase in root biomass (+40%) and root-shoot ratios (+60%) compared to conventional farming. By contrast, the overall impact of no-till was low. The importance of pedoclimatic conditions increased substantially with soil depth and deep root biomass was largely controlled by precipitation and soil texture, while the impact of management was close to zero. Our findings highlight the potential of organic farming in promoting root C inputs to topsoils and thereby contributing to soil organic matter build-up and improved soil quality in agroecosystems.

Keywords

root carbon inputs; farming system; agricultural management; on-farm study; root biomass distribution; subsoil

1. Introduction

Soils play a prominent role in the global carbon (C) cycle as they contain substantially more C than the atmosphere and land vegetation combined (Lehmann and Kleber, 2015). Increasing soil organic C therefore holds great promise for mitigating climate change. Agricultural soils could be a key in this effort because 34% of the land surface is currently under agricultural use (Ritchie and Roser, 2020) and management substantially influences soil organic C storage by altering inputs and decomposition rates (Janzen, 2015; Paustian *et al.*, 2016).

Root C is one of the most important contributors to soil organic C and constitutes up to 90% of all C inputs to arable soils (Kätterer *et al.*, 2011). Due to its resistant chemical composition (Rasse *et al.*, 2005) and preferential incorporation into more stable fractions (Ghafoor *et al.*, 2017), root C has a longer residence time in soil than C derived from above ground crop residues and manure (Kätterer *et al.*, 2011; Menichetti *et al.*, 2015; Zhang *et al.*, 2015). Particularly, root C inputs to deep soil have been linked to long-term C storage (Russell *et al.*, 2009; Fan *et al.*, 2019) due to the low decomposer abundance and high storage capacity of deep unsaturated layers (Rasse *et al.*, 2005; Rumpel *et al.*, 2012; Sanaullah *et al.*, 2016). Hence, the promotion of more and deeper roots has been proposed as a strategy to mitigate climate change with an estimated potential to remove atmospheric CO_2 of about 1 Pg yr^{-1} (Lynch and Wojciechowski, 2015; Paustian *et al.*, 2016; Pierret *et al.*, 2016). Thus, it is crucial to understand how management can promote root C inputs to agricultural soils in order to sequester C in the long-term, but also to stimulate C dynamics, thereby enhancing the manifold benefits of soil organic matter for agricultural soils (Janzen, 2015; Paustian *et al.*, 2016).

Agricultural management affects root biomass allocation in various ways by its impact on crop nutrition and soil properties through e.g. type and amount of fertilization, crop rotation, or soil tillage (Malhi and Lemke, 2007; Chirinda *et al.*, 2012; Qin *et al.*, 2018). For instance, in organic farming, the application of synthetic nutrient inputs is prohibited, which often leads to reduced mineral nitrogen (N) availability (Lorenz and Lal, 2016). It is expected that this increases biomass allocation below ground as crops need to cope with primarily growth-limiting resources (Lynch *et al.*, 2012; Poorter *et al.*, 2012). No-till farming is another alternative to conventional farming and is characterised by reduced or zero soil disturbance through tillage. Hence, it often results in accumulation of organic matter and nutrients but also increased bulk density in the topsoil (Huggins and Reganold, 2008; Powlson *et al.*, 2014). This may lead to a shift in biomass allocation and increased superficial root proliferation (Qin *et al.*, 2018; Mondal *et al.*, 2020), thereby altering vertical root distribution (Dwyer *et al.*, 1996; Ball-Coelho *et al.*, 1998; Barzegar *et al.*, 2004). So far, the influence of different farming systems on root C allocation has still not been clearly established and current knowledge is based on controlled field studies conducted at a small number of sites. In organic farming, both similar (Steingrobe *et al.*, 2001; Lazicki *et al.*, 2016; Hirte *et al.*, 2018a) and higher (Chirinda *et al.*, 2012; Hu *et al.*, 2018) root biomass compared to conventional farming has been reported for cereals. No-till was even found to influence root biomass in any direction for cereals or rapeseed, i.e. tillage effects were negative, absent, or positive (Plaza-Bonilla *et al.*, 2014; Li *et al.*, 2017; Sarker *et al.*, 2017).

The unclear picture of how agricultural management influences root C allocation may be linked to the impact of soil and climate characteristics that often overlay management effects. Soil properties such as mechanical impedance or nutrient availability as well as climatic conditions such as precipitation or temperature affect root growth to a large extent and complex interactions of stimuli often obliterate root response to individual drivers (reviewed by Rich and Watt, 2013). Consequently, biomass allocation to roots and shoots can vary by a factor of 10 across environments (Enquist and Niklas, 2002; Poorter *et al.*, 2012). In order to unravel the potential of agricultural management to enhance root C inputs to soil (Paustian *et al.*, 2016; Dignac *et al.*, 2017), management effects need to be assessed over a wide range of pedoclimatic conditions. On-farm measurements over multiple locations can not only provide practice-related, generalizable results but could also allow for quantitative comparisons of the effects of specific management practices on crop parameters beyond classified farming systems (Nkurunziza *et al.*, 2017; Büchi *et al.*, 2019).

We therefore established a network of 24 farms classified as conventional, no-till, or organic in Switzerland and investigated root biomass in the top and subsoil in winter wheat fields. In addition, we collected detailed information on management practices and soil and climate conditions for each field. Our objectives were (i) to assess the impact of organic, conventional and no-till farming on root biomass and plant biomass allocation and (ii) to evaluate the relative importance of management- and site-related variables for root and shoot biomass, root-shoot ratios, and vertical root distribution.

2. Methods

2.1. Farming systems and sites

The study was conducted in 2016 on 24 commercial farms in the northern part of Switzerland, which were categorized as conventional with tillage (conventional), conventional without tillage (no-till), or organic with tillage (organic) according to the farm structure census 2015 (Supplementary table 1; FSO, 2017; Büchi *et al.*, 2019). No-till soil management implied that not more than 25% of the soil surface could be disturbed at sowing (Swiss Federal Council, 2013). All farms were managed according to the certification scheme Proof of Ecological Performance PEP (Swiss Federal Council, 2013), the guidelines of the Swiss Farmer Association for Integrated Production IP-Suisse (IP-SUISSE, 2019), or the regulations of the Federation of Swiss Organic Farmers BIO-Suisse (Swiss Federal Council, 1997). The farms were located at eight sites spread over a distance of roughly 100 km arranged in farming system triplets of one conventional, no-till, and organic farm each (Supplementary figure 1). The nearest weather stations operated by the Federal Office of Meteorology and Climatology with recorded long-term precipitation data were chosen as reference points for the sites (Supplementary table 2). Annual temperature and precipitation (1981–2010) for Zurich-Affoltern (08°31’04”, 47°25’40”), which is centrally located within the study area, are 9.4 °C and 1054 mm, respectively.

2.2. Growth conditions of winter wheat

On each farm, one field was selected for plant and soil analyses. Winter wheat (*Triticum aestivum,* L.) was sown between 2 and 26 October 2015 and harvested between 18 July and 4 August 2016. Varieties, type of fertilization, weed and pathogen control, and use of growth retardants differed between farms (Supplementary table 1). Organic fertilizers were applied as cattle or pig slurry using an injector or as cattle manure, compost, humus acid suspension, or granulated organic N fertilizer (Büchi et al., 2019).

2.3. Root and shoot sampling

Root and shoot biomass of wheat and weeds was sampled at wheat flowering between 14 and 23 June 2016. A circular area with a radius of 10 m and a distance of at least 20 m to the nearest edge of the field was defined as sampling area and divided into four quarters (Supplementary figure 2). Within each quarter, shoot samples were taken directly above the ground on one randomly selected sampling plot covering four wheat rows of 0.5 m length with electric grass clippers and separated into wheat and weed shoot biomass. On the same sampling plots, root samples were collected by taking two soil cores, one within and one half-way between wheat rows, to a depth of 0.75 m by means of a metal sampling rod (inner diameter: 60 mm; lined with polyethylene film) driven into soil with an electric breaker (EH50, Wacker, Germany) and extracted with a 3-cylinder-lifting unit (ZGM-9E ECO, Nordmeyer Geotool GmbH, Germany). The cores were separated into three layers of 0.25 m length (top: 0–0.25 m, intermediate: 0.25–0.5 m, deep: 0.5–0.75 m) and stored in polyethylene film at 4 °C for a maximum of three weeks until further processing.

2.4. Biomass determination

Roots were extracted from each soil core separately using an automated root washer (Hydropneumatic Elutriation System GVF 13000, Gillison`s Variety Fabrication Inc., USA). The field-fresh soil was dispersed for 10 minutes in a high-energy hydrovortex at a water pressure of approximately 350 kPa and roots were separated from the mineral fraction by flotation and recovered on a 0.5 mm mesh (Smucker et al., 1982). The thus retained root samples were transferred to aluminium dishes and extraneous organic matter was visually identified based on shape, structure, colour, and elasticity of particles and removed from the samples using tweezers (Schuurman and Goedewaagen, 1971; Hirte et al., 2017). Identifiable weed roots, e.g. tap or rhizomatous roots, were removed from the root samples. However, a certain proportion of weed roots could not be distinguished from wheat roots by eye and remained in the samples. All plant material was dried at 55 °C until constant weight (shoots: 72 h; roots: 48 h) and dry weight was recorded.

2.5. Management and pedoclimatic variables

The following variables and their importance for root biomass and distribution were investigated: mineral N fertilization intensity, sowing density, above ground weed biomass, soil bulk density, soil texture, soil organic C, total N and available P in soil, and precipitation (Supplementary table 3). Mineral N fertilization intensity and sowing density were derived from questionnaires returned by the farmers (Büchi et al., 2019). Mineral N fertilization intensity was calculated from fertilizer-N input (total N in mineral fertilizers and ammonium-N in organic fertilizers as estimated by Büchi *et al.*, 2019) in the wheat season 2015/2016 as the amount of applied N (kg ha^{-1} season^{-1}) relative to the recommended amount of available N (kg ha^{-1} season^{-1}) for wheat according to the Principles of Agricultural Crop Fertilisation in Switzerland (Richner and Sinaj, 2017). Although wheat variety was an important aspect of management, this categorical information could not be accounted for due to the great diversity of 15 different genotypes and, thus, the lack of replications across fields (Supplementary table 1).

Soil was sampled on each farm between 20 April and 27 May 2016 for determination of soil texture, organic C, total N, available P, and bulk density. Except for bulk density, 15–20 samples were taken in five soil layers (0–0.05 m, 0.05–0.2 m, 0.2–0.25 m, 0.25–0.5 m, 0.5–0.75 m) on transect lines that ran in 45° angles to the seedling rows and divided the quarters for root and shoot biomass sampling. Composite samples per layer were dried and soil texture (sedimentation), organic C (oxidation with potassium dichromate), and available P (CO_2-saturated water extraction and colorimetry) were determined on 2-mm sieved fine soil according to the Swiss reference methods (Agroscope, 1996). Total soil N was measured after dry oxidation according to the Dumas method (Bremner, 1965). For soil bulk density measurements, undisturbed samples of 100 ml volume and 50 mm height were taken in the middle of each layer except the 0.5–0.75 m layer and oven-dried at 105°C for at least 72 h (Colombi *et al.*, 2019). Bulk density values of the 0.25–0.5 m layer were used for the 0.5–0.75 m layer. The weighted averages of variables measured on samples from the upper three layers (0–0.05 m, 0.05–0.2 m, 0.2–0.25 m) served as composite values for the 0–0.25 m layer for further analyses.

Precipitation during the wheat growing season (October 2015 to June 2016) was retrieved from the nearest local weather station to each farm operated by either MeteoSwiss, the Federal Roads Office, the Cantons of Lucerne, Thurgovia, or Zurich, or MeteoGroup Switzerland. Due to clustering of farms within sites and limited spatial distribution of local weather stations, 12 data sets for the total of 24 farms were available. We tested the effect of cumulative precipitation during several time periods on the investigated response variables and found the strongest effect for precipitation between March and mid-June, i.e. between tillering and flowering, corresponding to the main part of the vegetative growth phase. From here on, we refer to this time period when we report values and the effect of precipitation.

2.6. Calculations and statistics

To extrapolate to field scale, root biomass sampled within and between rows was weighted with respect to row width for each layer individually (adapted from Frasier et al., 2016):

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

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

where RB_{within} and $RB_{between}$ are root biomass (g m^{-2}) within and between rows, respectively, M_{within} and $M_{between}$ are the dry weights of roots (g) extracted from the soil cores taken within and between rows, respectively, D is the inner diameter of the sampling rod (m), and s is the distance between rows (m). Root biomass was obtained by summing RB_{within} and $RB_{between}$. Root-shoot ratios were calculated for each subplot from averaged total root (0–0.75 m) and shoot biomass and were ln-transformed prior to statistical analysis (Poorter and Sack, 2012). Unless otherwise stated, root-shoot ratios relate to wheat shoot biomass (excluding weed) but were also analysed for wheat plus weed shoot biomass.

A few data points (12 out of 576) needed to be eliminated when problems with sampling or sample processing occurred (e.g. sieve clogging and root loss in the root washer). Consequently, root biomass could not be estimated for those instances and only 3 out of 4 field replications were used. Root and shoot biomass and root-shoot ratios of individual subplots on each farm were treated as lower-level replicates for statistical analysis and were averaged per farm for data presentation. Mean data for farming systems and sites are presented as averages of farming system/site and farm and standard errors of farming system/site.

We analysed the data in a three-step procedure and thereby investigated the following response variables: root biomass and the proportion of root biomass in the individual layers (0–0.25 m, 0.25–0.5 m, 0.5–0.75 m) and total root biomass (0–0.75 m) of wheat and weeds, wheat shoot biomass, and root-shoot ratio. (i) To test for differences in response variables between farming systems and sites, we fitted the data to mixed effects models (fixed factors: farming system and site; random factor: farm) and determined differences between group means by ANOVA and subsequent simultaneous multiple comparison of estimated marginal means of group pairs with Tukey-adjustment of p-values. (ii) To further evaluate the effects of the management and pedoclimatic variables on the response variables, we used mixed effects models (fixed factor: management or pedoclimatic variable; random factor: farm) in univariate analyses and ANOVA. (iii) To determine the relative importance of (a) farming system and site and (b) management and pedoclimatic variables for the response variables, we conducted multivariate linear regressions without prior variable selection and calculated variance decomposition metrics: (a) LMG metrics for uncorrelated categorical regressors (Lindeman Merenda Gold; Lindeman, 1980) and (b) CAR scores for correlated numerical regressors (Correlation-Adjusted coRrelation; Zuber and Strimmer, 2011). While LMG metrics are unweighted averages over orderings of sequential contributions of explanatory variables to models of different sizes (Grömping, 2015), CAR scores are based on simultaneous orthogonalization of correlated explanatory variables and subsequent estimation of marginal correlations between response and decorrelated explanatory variables (Zuber and Strimmer, 2011). Shoot biomass and root-shoot ratios were related to soil variables in the top layer. We considered a significance level of $p < 0.05$.

We used the software R version 3.4.2 (R Core Team, 2019) and the R packages lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017), pbkrtest (Halekoh and Højsgaard, 2014), emmeans (Lenth, 2018), and relaimpo (Grömping and Lehrkamp, 2018) for statistical analyses and the R packages ggplot2 (Wickham, 2016), GGally (Schloerke et al., 2018), gridExtra (Auguie, 2017), and lemon (Edwards, 2019) for data visualization.

3. Results

We analysed total root biomass, vertical root distribution, wheat shoot biomass, and root shoot ratios from 24 farms arranged in farming system triplets (conventional, no-till, organic) that were located at eight sites in Switzerland. The sites spread over a distance of just 100 km, yet pedoclimatic characteristics varied considerably among farms (Supplementary table 3). Total root biomass in the 0–0.75 m soil profile ranged among individual farms from 87–274 g m^{-2}. Root biomass varied between

55–178 g m^{-2} in the top layer, 12–53 g m^{-2} in the intermediate layer, and 7–43 g m^{-2} in the deep layer, corresponding to 55–78%, 10–28%, and 8–22% in the respective layers of total root biomass. Wheat shoot biomass ranged among farms from 909–1692 g m^{-2} and root-shoot ratios from 0.07–0.22.

3.1. Differences in root parameters between farming systems

Total root biomass was 132 g m^{-2} in conventional, 156 g m^{-2} in no-till, and 182 g m^{-2} in organic farming and was significantly higher in organic than conventional ($p = 0.018$) and intermediate in no-till farming (Figure 1). Differences between farming systems were limited to the top layer, where root biomass was 87, 101, and 132 g m^{-2} in conventional, no-till, and organic farming, respectively, and significantly higher in organic compared to both conventional ($p = 0.003$) and no-till farming ($p = 0.032$; Figure 1). The proportion of topsoil root biomass was highest in organic (73%), lowest in no-till (64%; $p = 0.017$), and intermediate in conventional farming (66%; Supplementary figure 2). In the intermediate and deep layer, respectively, root biomass and its proportion were similar among farming systems, averaging 27 g m^{-2} (18%) and 23 g m^{-2} (14%; Figure 1; Supplementary figure 2).

Wheat shoot biomass at flowering was similar among farming systems and averaged 1311 g m^{-2} (Figure 1). Consequently, root-shoot ratios were significantly higher in organic farming than in both conventional and no-till farming, irrespective of whether shoot biomass referred to wheat shoot biomass only (organic 0.15; conventional 0.09, $p < 0.001$; no-till 0.11, $p = 0.002$) or wheat plus weed shoot biomass (organic 0.14; conventional 0.09, $p < 0.001$; no-till 0.10, $p = 0.005$; Figure 1).

3.2. Variation in root parameters among sites

Total root biomass ranged from 105–221 g m^{-2} among the eight farming system triplets and differed significantly between sites ($p = 0.011$). In addition to the large variation in topsoil root biomass (75–151 g m^{-2}; $p = 0.015$), significant differences between sites also occurred in deep root biomass (11–35 g m^{-2}; $p = 0.014$), while root biomass was similar in the intermediate layer (27 g m^{-2}). Vertical root distribution was not significantly affected by site conditions as the proportion of root biomass was similar among sites in all layers (top: 68%, intermediate: 18%, deep: 15%). Similar to the farming system comparison, wheat shoot biomass at flowering was similar among sites (1311 g m^{-2}) but root-shoot ratios differed significantly (0.07–0.18; $p < 0.001$; Supplementary table 4).

3.3. Differences in management and pedoclimatic variables between farming systems and sites

Compared to conventional and no-till farming, organic farming involved lower N fertilization intensity ($p = 0.003$ and 0.025, respectively) but higher weed biomass ($p = 0.011$ and 0.009, respectively; Supplementary table 3). Topsoil bulk density was higher in no-till than in conventional and organic farming ($p < 0.001$ each). All other variables were similar among farming systems except for organic C and total N in the intermediate layer, which were higher in organic than in no-till ($p = 0.009$ and 0.017, respectively) and intermediate in conventional farming (Supplementary table 3). The sites differed in mineral N fertilization intensity, topsoil bulk density, precipitation, soil organic C, total soil N, sand, silt, and clay content in the top and intermediate layer (see Supplementary table 3 for p-values). In the deep layer, all soil variables were similar among both farming systems and sites (data not shown).

3.4. Explained variation in root and shoot biomass and root-shoot ratio

Farming system and site

Farming system and site as explanatory variables accounted for 19 and 54%, respectively, of the variation in total root biomass. In the top, intermediate, and deep layer, respectively, the variation in root biomass was by 32, 11, and <1% explained by farming system and by 44, 39, and 66% by site (Figure 2a). The variation in the proportion of root biomass was by 37, 26, and 20% explained by farming system and 22, 12, and 46% by site in the three soil layers (Figure 2b). Farming system and site, respectively, accounted for 15 and 40% of the variation in shoot biomass (Figure 2c) and 28 and 57% of the variation in root-shoot ratios (Figure 2d).

Management and pedoclimatic variables

The outcomes of the two evaluation methods (univariate and multivariate analyses) were largely in agreement, i.e. explanatory variables with high relative importance were also significantly related to the respective response variable, with few exceptions. Relative importance metrics and relations of all variables are shown in Figures 3 and 4 and corresponding p-values in Supplementary table 5. Here, we focus on concordant results for both evaluation methods.

In the top, intermediate, and deep layer, respectively, the investigated management and pedoclimatic variables explained together 78, 74, and 72% of the variation in root biomass and 68, 51, and 70% of the variation in the proportion of root biomass (Figure 3). In the top layer, root biomass and the proportion of root biomass were strongest related to weed biomass (positive) and mineral N fertilization intensity (negative; Figure 3). High importance for root biomass was also assigned to soil organic C (positive) and for the proportion of root biomass to soil bulk density (negative; Figure 3). In the intermediate layer, sowing density explained the largest part of the variation in root biomass and its proportion (positive), while root biomass was additionally strongly related to silt content (negative) and the proportion of root biomass to mineral N fertilization intensity (positive; Figure 3). In the deep layer, precipitation had the highest importance for root biomass and a strong positive effect, while the proportion of root biomass was not significantly related to any variable (Figure 3).

The investigated management and pedoclimatic variables explained 53 and 88% of the variation in shoot biomass and root-shoot ratios, respectively (Figure 4). Available soil P was the only variable with a significant relation (positive) to shoot biomass with high importance, while large parts of the variation in root-shoot ratios were explained by mineral N fertilization intensity (negative) and weed biomass (positive; Figure 4).

4. **Discussion**

4.1. Management effects on root biomass allocation to agricultural soils

In this comprehensive on-farm study, we found 40% higher total root biomass under organic compared to conventional farming. This is to our knowledge the first study highlighting this substantial farming system effect on root biomass allocation in an on-farm setting characterized by a wide range of management and pedoclimatic conditions across fields. The results thus allow particularly robust conclusions on farming system effects on root biomass allocation. Moreover, conventional agriculture in Switzerland relies to a high degree on cultivation practices that are also typical of organic farming such as long and diverse crop rotations, inclusion of cover crops, and frequent organic fertilization (Nitsch and Osterburg, 2005). A comparison of more divergent systems (e.g. mono-cropping with sole mineral fertilization vs. long crop rotations with sole organic fertilization) might reveal even more pronounced farming system effects. Hence, the here presented results constitute rather conservative estimates for enhanced root C allocation through organic farming in agroecosystems.

This study therefore provides supportive evidence for higher root C inputs into organic compared to conventional soils, which has also been found by Chirinda *et al.* (2012) and Hu *et al.* (2018) at several long-term field sites in Denmark. Those and our findings suggest an effect size of plus 20–40% root biomass in organic compared to conventional systems and thereby oppose the currently prevailing view that organic farming reduces root C inputs along with yields (Lorenz and Lal, 2016). In our study, shoot biomass at flowering showed only a small, non-significant difference among organic and conventional farming and grain yield at harvest was even about 30% lower on the organic than conventional fields (Büchi *et al.*, 2019). Consequently, biomass allocation below and above ground follows different patterns in organic and conventional systems.

The farming system effect on total root biomass was mainly a composite of effects of three management-related factors on root biomass in the topsoil. Among the most important drivers was weed biomass, which was an order of magnitude higher in organic (56 g m^{-2}) than conventional farming (5 g m^{-2}). Weed roots can trigger over-proliferation of crop roots (Depuydt, 2014) when crops and weeds compete for the same below ground resources (Kiær et al., 2013). However, information on root biomass of weeds would be inevitable to clearly disentangle physiological and methodological causes. As fibrous roots of weeds and crops are often not distinguishable by eye, precise classification requires elaborate methods (Watt et al., 2008; Hirte et al., 2017). As we could remove only clearly identifiable weed roots from the root samples, we assume that weed roots have partly altered sample weight. As a conservative estimate from our weed shoot biomass data and published root-shoot ratios of weeds that correspond to total weed root biomass (Blackshaw *et al.*, 2003; Moreau *et al.*, 2017; Hu *et al.*, 2018), we consider weed root biomass in the organically managed soils to be at most 25 g m^{-2}, thus potentially accounting for up to 50% of the surplus root biomass in organic compared to conventional farming. The presence of weeds, however, is an important aspect of management and contributes in real terms to root biomass and thus organic C inputs to soil.

Similarly important for topsoil root biomass was mineral N fertilization intensity, which was 40% lower on the organic than conventional farms. Low mineral N availability in soil has previously been found as the main reason for higher root biomass in organic compared to conventional farming (Chirinda et al., 2012; Hu et al., 2018). In mineral N limited systems, crops invest a larger proportion of assimilates in below ground organs in order to increase plant interception of soil-borne resources (Lynch *et al.*, 2012). By contrast, total soil N was not related to root biomass in our study, indicating that this variable, unlike mineral N fertilization intensity, did not represent available soil N fractions adequately. The importance of available soil P for root biomass was similarly low despite its strong positive effect on shoot biomass. Phosphorus supply influences rooting characteristics predominantly by altering topsoil root proliferation, whereas root biomass is only affected under severe P shortage (Hermans *et al.*, 2006). This highlights the outstanding role of N nutrition in the studied farming systems.

Soil organic C was the third factor that was prominently related to topsoil root biomass. Although it differed more strongly among sites than farming systems, it was elevated in the organic compared to the conventional soils. This difference proved to be significant in the extended farm network which also included the farms from this study (Colombi *et al.*, 2019). Higher soil organic C can be a consequence of higher root biomass or *vice versa* as the underlying processes can be bi-directional. On the one hand, continuously increased root biomass enhances soil organic C in the long-term (Lajtha *et al.*, 2014) due to its strong influence on soil organic matter formation (Rasse *et al.*, 2005; Kätterer *et al.*, 2011; Menichetti *et al.*, 2015). On the other hand, higher soil organic C can improve soil aeration and thus stimulate root growth (Colombi *et al.*, 2019). Methodological aspects of sample processing can also entail spurious relationships between soil organic C and root biomass when root samples contain large amounts of extraneous organic matter due to e.g. frequent organic fertilization (Hirte *et al.*, 2017). However, as C inputs to soil by crop residues and organic fertilizers were not substantially increased on the organic compared to the conventional farms (Colombi *et al.*, 2019), we assume a causal relationship between higher root C inputs and increased organic C content in the organically managed soils.

Root biomass in no-till soils was intermediate and not significantly different from that in conventionally and organically managed soils. Interestingly, it was markedly elevated by data from one farm (274 g m^{-2}) that used a seed mix of two wheat varieties. Knowledge on root traits in mixed wheat stands is scarce but findings for other crops suggest that competition between genotypes in mixed stands increases biomass allocation below ground compared to single stands (Ninkovic, 2003; Lin et al., 2014). As revealed by the medians, root biomass in no-till farming (138 g m^{-2}) was actually much closer to that in conventional (118 g m^{-2}) than that in organic farming (178 g m^{-2}). This lack of tillage effects on root biomass and, consequently, root-shoot ratios supports previous findings (Anderson, 1988; Williams *et al.*, 2013; Plaza-Bonilla *et al.*, 2014). However, several studies have reported a shift in vertical root distribution due to no-till (Dwyer *et al.*, 1996; Ball-Coelho *et al.*, 1998; Barzegar *et al.*, 2004), which we did not observe. Despite a clear relation to soil bulk density in the top layer, the proportion of topsoil root biomass differed by only 2% between no-till and conventional farming in our study. Instead, weed biomass and mineral N fertilization intensity were the main drivers of vertical root distribution and accounted for the increased proportion of topsoil root biomass by 8% in the organically managed soils.

4.2. Pedoclimatic drivers of root biomass

Management effects on total root biomass resulted solely from the large differences in root biomass between organic and conventional fields in the topsoil, where farming system explained 32% of the variation. This decreased to basically zero in the subsoil, reflecting the lack of differences in root biomass between farming systems below 0.25 m depth. In contrast to farming system, site governed root biomass not only in the top layer but most prominently in the deep layer, where it accounted for 66 and 46% of the variation in root biomass and the proportion of root biomass, respectively. Although the sites spread over a distance of just 100 km, their edaphic characteristics varied strongly, representing the diversity of European soils (Ballabio *et al.*, 2016; Ballabio *et al.*, 2019).

Below 0.25 m soil depth, spring precipitation became increasingly important for root biomass and explained even 40% of its variation in the deep layer. We infer that water was not limiting at any of the studied fields as rainfall was 150 mm (50%) higher than mean annual precipitation (30-year climate norm) from April to June 2016. The particularly moist spring conditions even caused below-average yields (Büchi *et al.*, 2019), which was possibly linked to fewer sunshine hours, higher pest and disease pressure, and fewer opportunities for farmers to perform mechanical soil cultivation for e.g. weeding. Instead, since rainfall is one of the most important driving forces of nitrate leaching in agroecosystems (Goulding *et al.*, 2000; Jabloun *et al.*, 2015), the strong positive relation between precipitation and deep root biomass could be an indication of root response to relocation of N.

Subsoil root biomass was also prominently linked to soil texture, in particular silt content in the intermediate layer and sand content in the deep layer, which ranged between sites from 29 to 40% and

31 to 54%, respectively. Their respective negative and positive effects on subsoil root biomass support findings of greater rooting depth in coarse- than medium-textured soils in temperate climate (Schenk and Jackson, 2005). The unfavourable capacity of sandy soils to hold plant-available water and nutrients forces plants to root deeper in order to meet their demand for those resources. In our study, higher nutrient availability in silty soils was likely to result in lower investment of wheat in root growth below the topsoil, which has also been reported from two Swiss long-term field trials (Hirte *et al.*, 2018a).

Sowing density, which was the only driver of root biomass entirely independent of farming system and site, had a strong positive impact in the intermediate soil layer. While it has previously been shown that root biomass in the topsoil increases with sowing density, no effects have so far been found in the subsoil (Marcinkevičienė *et al.*, 2013; Hecht *et al.*, 2016). We assume that fertilization and weed control were the main drivers of root response in the topsoil and overlaid the potential influence of sowing density on topsoil root biomass in our study. Our results indicate that effects of sowing density are not confined to topsoils but might easily be masked by concurring drivers, which will need to be addressed in detail in future research.

This on-farm study drew on a clustered design with a range of varying cultivation measures to reflect standard agricultural practice. Hence, unexplored management practices constitute an additional source of variation in root biomass, both between and beyond farming systems. For instance, our data were obtained from 15 wheat genotypes, which differed distinctly among and within farming systems. Most genotypes cultivated in organic farming, such as the variety “Wiwa”, are long-stalked and thus superior in weed suppression (Dierauer and Klaiss, 2020), but their rooting patterns have yet to be investigated in detail. Wheat genotypes can vary by a factor of five in root biomass (Mathew *et al.*, 2019), suggesting that the genotype–environment–management triad that profoundly governs above ground crop parameters (Hillel and Rosenzweig, 2013; Hatfield and Walthall, 2015), also plays a significant role in below ground biomass allocation. We therefore argue that a major part of the 30% variation in root biomass, which remained unexplained in our study, may be assigned to genetic drivers. Thus, future research employing multidimensional networks with completely crossed designs of genotype x environment x management can allow to disentangle the complex interactions of farming system and variety in biomass allocation.

4.3. Implications for soil C dynamics, soil C modelling, and climate change mitigation

Higher root biomass in organic than conventional topsoils implies considerably larger total below ground C inputs via root biomass and rhizodeposition. The surplus of roughly 25 g m^{-2} wheat root biomass (excluding weeds) in organic farming can be extrapolated to 25 g m^{-2} total below ground C inputs that are additionally allocated to soil by organic compared to conventional wheat in Swiss agricultural practice (C concentration in wheat roots: 44%; rhizodeposition-root ratio: 1.3; Hirte *et al.*, 2018a; Hirte *et al.*, 2018b). On top of that, weeds provide an extra source of substantial C inputs to organically managed soils. This stimulates soil organic matter dynamics profoundly, thereby releasing plant nutrients, providing energy for soil microbes, and contributing to soil organic matter build-up (Janzen, 2015; Lorenz and Lal, 2016). Hence, by increased topsoil root C inputs, organic farming fosters soil chemical, biological, and physical processes that enhance soil quality and sustainability of this agroecosystem.

As a consequence of higher root-shoot ratios in organic farming, the well-established approach in soil C modelling of deriving root biomass from shoot biomass at harvest and plant C allocation coefficients usually inferred at flowering (Bolinder et al., 1997) may therefore not be suitable for different farming systems. This is supported by recent studies reporting only poor agreement between estimated and actually measured root biomass in organic farming (Taghizadeh-Toosi et al., 2016; Hirte et al., 2018b; Hu et al., 2018). While it has previously been suggested that the major source of this mismatch is the higher shoot biomass in conventional than organic systems at harvest (Hirte *et al.*, 2018b; Hu *et al.*, 2018), our findings provide evidence that it is further amplified by management-induced differences in root biomass at flowering. The current use of plant C allocation coefficients in soil C modelling therefore needs to be revisited, both with regard to farming systems and plant ontogeny.

Among the proposed strategies to mitigate climate change through increased C inputs to agricultural soils (Smith *et al.*, 2014; Paustian *et al.*, 2016), an increase in deep root C is least susceptible to rapid reversal and therefore of particular importance for long-term C sequestration (Kell, 2012). This study provides the first robust data on the potential of agricultural management practices to alter deep root C inputs in the most prevalent arable farming systems in Europe. We give evidence that pedoclimatic drivers substantially govern root biomass below 0.5 m depth, where the impact of farming system is close to zero. Yet, more than one-third of the variation in subsoil root biomass remains unexplained, leaving room for prospects to control crop root C inputs to deep layers. We expect that insights into genetic diversity will contribute to fill this gap and that multidimensional genotype–environment–management networks should become a central part of future research on soil C management.

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Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Tables and figures

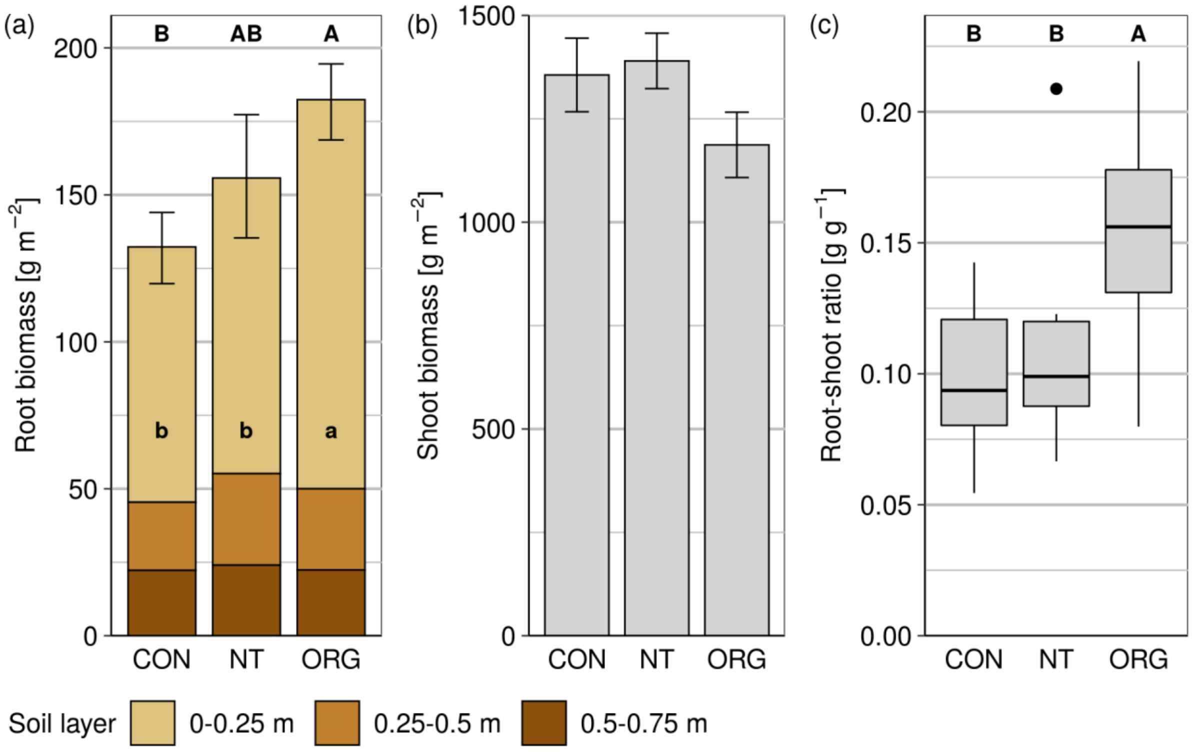

Figure 1: Root biomass in the top (0–0.25 m), intermediate (0.25–0.5 m), and deep (0.5–0.75 m) soil layers, wheat shoot biomass, and root-shoot ratios in conventional (CON), no-till (NT), and organic (ORG) winter wheat fields at flowering in Switzerland (n = 8 sites; average of 4 field replications each). Error bars refer to standard errors of total root (0–0.75 m) and shoot biomass of 8 sites. Different letters denote significant differences between estimated marginal means of root biomass in the individual soil layers (lower case letters) and total root biomass and root-shoot ratios (upper case letters) at p <0.05 (Tukey HSD).

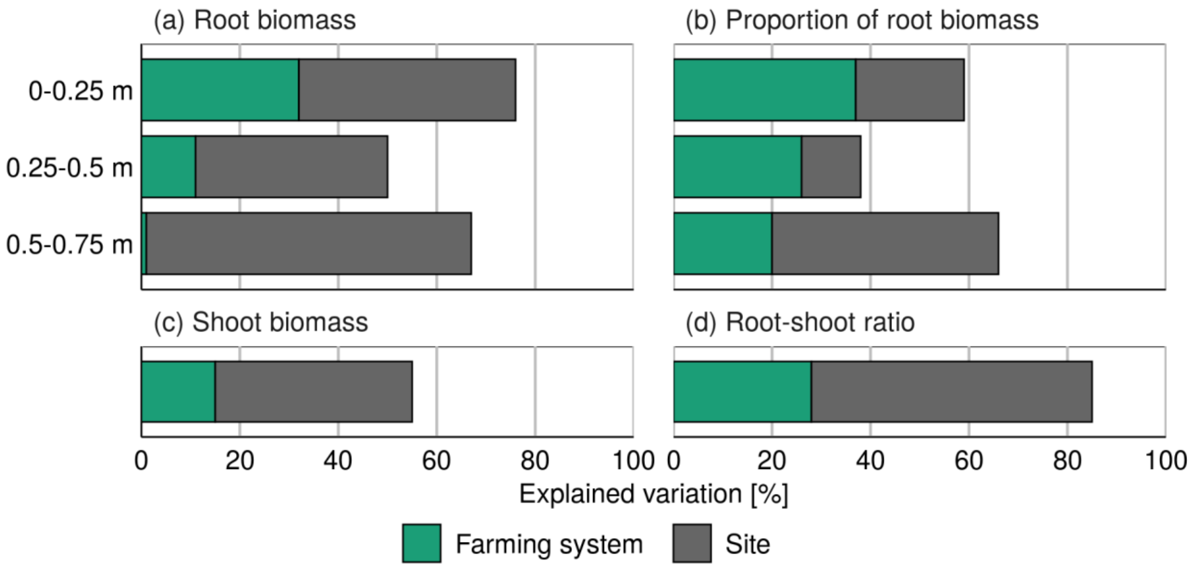

Figure 2: Explained variation ($R^2 * 100$) by farming system and site in (a) root biomass and (b) the proportion of root biomass in the top (0–0.25 m), intermediate (0.25–0.5 m), and deep (0.5–0.75 m) soil layer, respectively, (c) wheat shoot biomass, and (d) root-shoot ratios in 24 winter wheat fields in Switzerland. R^2 decomposition method: LMG metrics.

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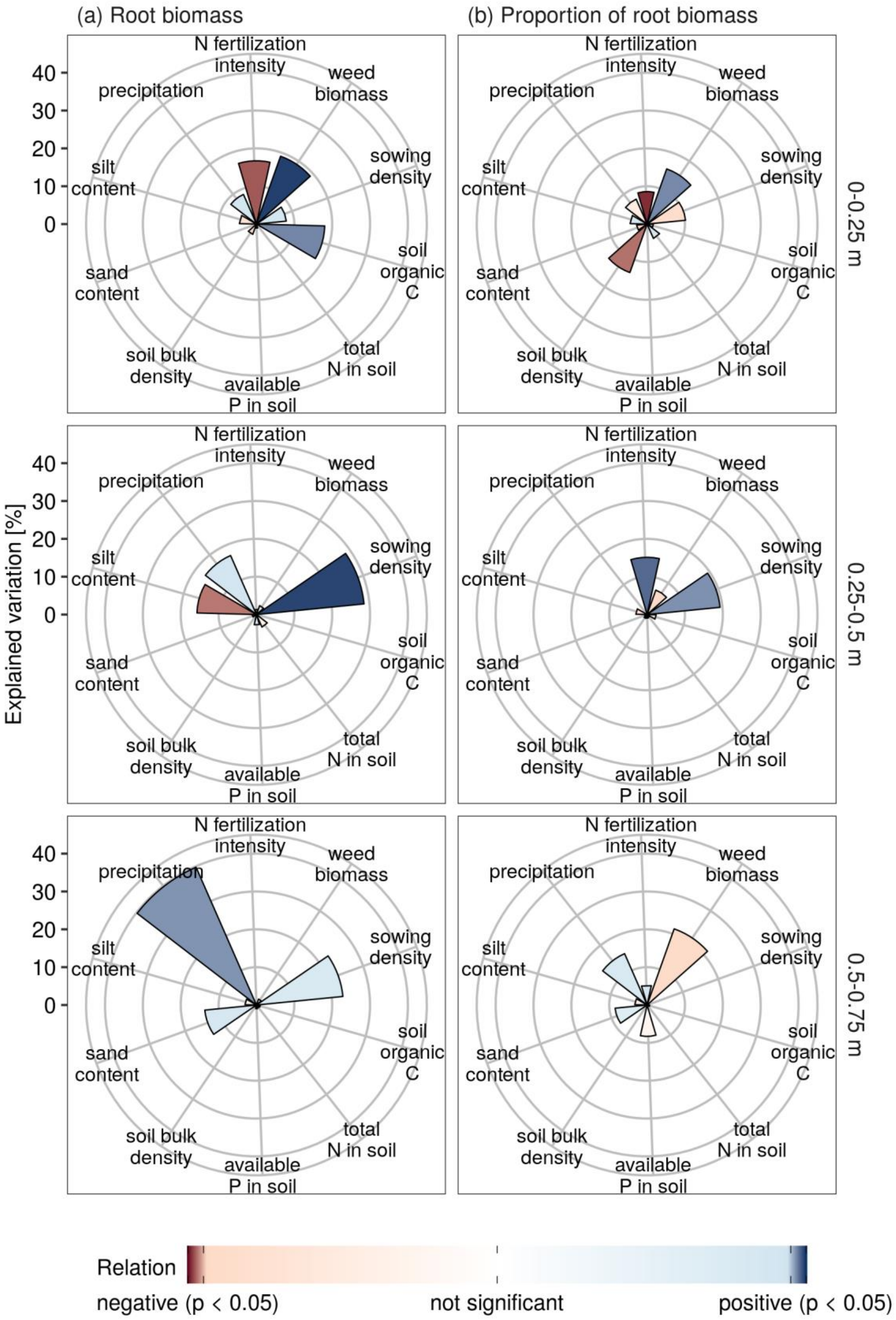

*Figure 3: Explained variation (R^2 * 100) by management and pedoclimatic variables in (a) root biomass and (b) the proportion of root biomass in the top (0–0.25 m), intermediate (0.25–0.5 m), and deep (0.5–0.75 m) soil layer, respectively, in 24 winter wheat fields in Switzerland. R^2 decomposition method: CAR*

scores. Negative / positive relations refer to univariate relations between each management and pedoclimatic variable and root biomass (see Supplementary table 5 for p-values).

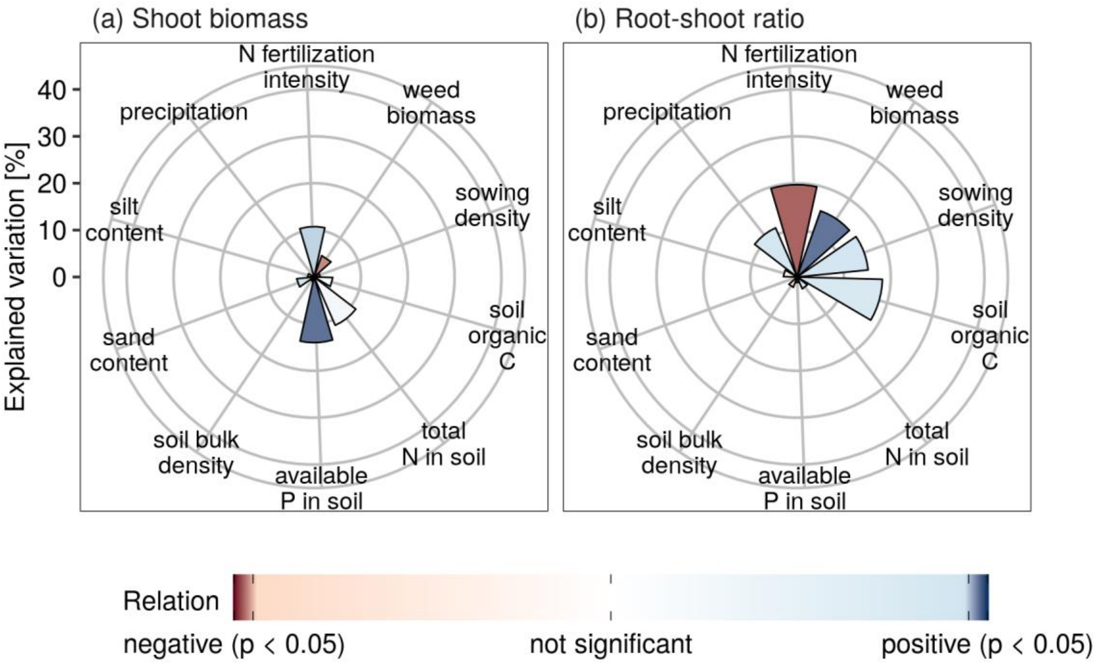

*Figure 4: Explained variation (R^2 * 100) by management and pedoclimatic variables in (a) shoot biomass and (b) root-shoot ratios in 24 winter wheat fields in Switzerland (soil variables: top layer). R^2 decomposition method: CAR scores. Negative / positive relations refer to univariate relations between each management and pedoclimatic variable and shoot biomass or root-shoot ratio (see Supplementary table 5 for p-values).*

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