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Impact of wheat cultivar development on biomass production and carbon input in tillage-eroded soils

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Abstract. Crop biomass, especially from belowground, improves soil health and recovery. However, the effects of cultivar traits and tillage erosion on biomass production, particularly root biomass, remain unclear. We quantified root system characteristics throughout the wheat growing season, considering different cultivars and varying soil erosion gradients. This data informed a model assessing cultivar performance on root biomass production under different soil water and erosion scenarios. Tillage erosion reduced total wheat biomass, leaving 3.2 tons less carbon per hectare annually. Recently developed cultivars produced 70% more grain in depositional soils and 30% more in highly eroded soils than earlier cultivars. However, this increased grain yield came with a trade-off: carbon input into soil decreased by 32% in eroded soils and 43% in depositional soils. Simulations reveal recently developed cultivars are more sensitive to drying soils, which received 12 kg C ha^{-1} less than those with earlier cultivars over the five years.

1 Introduction

The top 0.3 meters of global soils contain approximately 700 Pg of terrestrial organic carbon (OC) (Doetterl et al., 2016). Annually, tillage erosion displaces around 0.5 Pg of this carbon pool (Quinton et al., 2010). Beyond the significant impact of nutrient loss through lateral movement (Alewell et al., 2020; Quinton et al., 2010), tillage erosion disrupts soil structure, altering microbial processes (Hartmann and Six, 2023) and disturbing carbon (C) and nitrogen (N) cycling (Nie et al., 2019). Consequently, tillage erosion has been identified as a key factor in reducing C inputs from crop biomass (Öttl et al., 2021). Additionally, a breeding strategy of crops focused solely on increasing grain yield, often at the expense of biomass production (Fang et al., 2017), not only weakens crop resilience in the face of increasing climate change challenges (Martre et al., 2024; Qiao et al., 2022), but also jeopardizes the recovery of eroded soils and neglects their potential for enhanced C sequestration (Hoffmann et al., 2018).

The drive for greater operational efficiency in crop production has led to machinery innovations that have accelerated the pace of tillage erosion, reducing its timeline from centuries (van der Meij et al., 2019; Quinton et al., 2022) to decades (Borrelli et al., 2023; Wilken et al., 2020). Modern agriculture imposes soil stresses that leads to chronic compaction in root zones and impairing soil function (Keller et al., 2019). This has increased the demand for tillage tools that can break up deeper soil layers (Barbosa, 2020). Consequently, greater tillage depths and speeds increase soil translocation (Kietzer, 2007; Van Oost et al., 2006; Öttl et al., 2022), accelerating the leveling of hummocky landscapes (van der Meij et al., 2019; Poesen, 2018). This process exacerbates soil thinning on convex hilltops and shoulders (Fig. 1a), reducing local water-holding capacity (Quinton et al., 2022). Moreover, it alters the distribution of total organic carbon (OC), primarily through the redistribution of particulate organic matter (POM), which plays a crucial role in microbial activity, increasing within-field variations of soil organic carbon (SOC) and inducing depletions of N (Nie et al., 2019). As a result, tillage erosion has been identified as a key factor negatively impacting biomass production in a range of crops in hummocky landscapes (Öttl et al., 2021).

Crop biomass affects soil environmental function as a C sink and water storage, helping stabilize crop yields under increasing climate variability (Qiao et al., 2022). Grain yield in wheat is closely linked to above-ground biomass (Lichthardt et al., 2020). This relationship has traditionally guided breeding strategies which aimed at boosting productivity by increasing total crop biomass (Sanchez-Garcia et al., 2015). Enhancing canopy light capture through rapid early growth of leaf area or delayed leaf senescence has also been identified as a key strategy for improving yields (Parry et al., 2011). However, wheat shoot is highly sensitive to soil water and nutrient availability, e.g. with growth declining under increased water stress (Jiang et al., 2020). These resources are often limited on hilltops and shoulders eroded by tillage (Quinton et al., 2022), making wheat shoot a reliable indicator for mapping erosional status in hummocky landscapes. In such areas, erosion reduces above-ground biomass (Herbrich et al., 2018), a change that can be detected using the Photosynthetically Active Radiation (Öttl et al., 2021).

Beyond canopy traits, direct selection for root system architecture to achieve greater root length, biomass, density, and lateral root dispersion has been associated with enhanced water and nutrient uptake, leading to higher grain yields (Cormier et al., 2016). Root traits like depth and density are particularly critical for N capture (Holz et al., 2024), further supporting yield improvements (Martre et al., 2024). Moreover, root biomass is vital for maintaining and increasing SOC because it remains in the soil two to three times longer than C from other above ground biomass or manure (Kätterer et al., 2011). This makes it a more durable and effective contributor to long-term soil health. Given the potential of root biomass to enhance SOC sequestration, genotype selection and breeding aiming at increased root biomass offers a promising and easily implementable management option. However, increasing root C inputs could reduce grain yields, challenging food security. Balancing root development with crop productivity is crucial for sustainable agriculture (Heinemann et al., 2023).

Although genetic variation in root system size among wheat cultivars is well-documented, root distribution is heavily influenced by soil characteristics, nutrient availability (Robinson, 2001), and mechanical impedance (Keller et al., 2019). Estimating root development is challenging, as no aboveground traits can serve as reliable proxies, making root quantification in field experiments labor-intensive and difficult to compare across studies (Freschet et al., 2021). As a result, SOC models typically estimate root C inputs based on crop yields using allometric functions specific to crop types (Keel et al., 2017). These functions relate yield to total biomass, including the root-to-shoot ratio (Jacobs et al., 2020). However, due to a lack of data, genotype-specific allometric functions are not available. Literature indicates significant variation in root-to-shoot ratios across wheat genotypes, with earlier developed cultivars showing a ratio of 1.13, compared to 0.61 and 0.8 in modern cultivars (Fang et al., 2017). Consequently, estimates of annual C input based on a constant root-to-shoot ratio introduce considerable uncertainty into projections of SOC dynamics in agriculture. Moreover, experimental and modelling studies considering tillage erosion in C balance analyses are rare and usually focus on areas with significant water erosion and high rainfall, typically in fertile loess soils (Bouchoms et al., 2017; Nadeu et al., 2015).

Heavily eroded soils are more efficient at capturing C due to their higher mineral content with unsaturated surfaces, which stabilize plant-derived C through organo-mineral complexes (Doetterl et al., 2016; Remus et al., 2018). This potential for increased C sequestration in eroded landscapes has been modeled (Berhe et al., 2008) and experimentally confirmed (Hoffmann et al., 2018). However, understanding how soil erosion impacts C inputs from both aboveground and belowground biomass is still a significant gap in existing models (Bouchoms et al., 2019). Improving these estimates requires the consideration of plant cultivars and the soil's erosion status on C contributions from roots and rhizodeposition.

We hypothesize that wheat biomass production, both aboveground and belowground, is shaped by the combined effects of wheat cultivar traits and their interaction with soil erosional status, influencing cultivar performance and, consequently, carbon inputs to the soil. The accumulation of C, particularly from belowground biomass, enhances the crop's ability to support soil health, strengthening the soil's capacity to recover (Barbosa et al., 2020). To address this, our primary objective is to quantify root system characteristics (e.g., biomass, branching, and area along the soil profile) throughout the entire wheat growing season, focusing on different cultivars and varying soil erosion intensities. These measurements will be correlated with above-ground data of different wheat cultivars to develop a model for evaluating the potential impacts of soil water content and eroded soil properties on root biomass production. By shifting our focus from traditional water erosion to regions dominated by tillage erosion in temperate, relatively dry climates—key areas for crop production in the northern hemisphere—we aim to gain new insights into the current and future challenges of tillage erosion and SOC management.

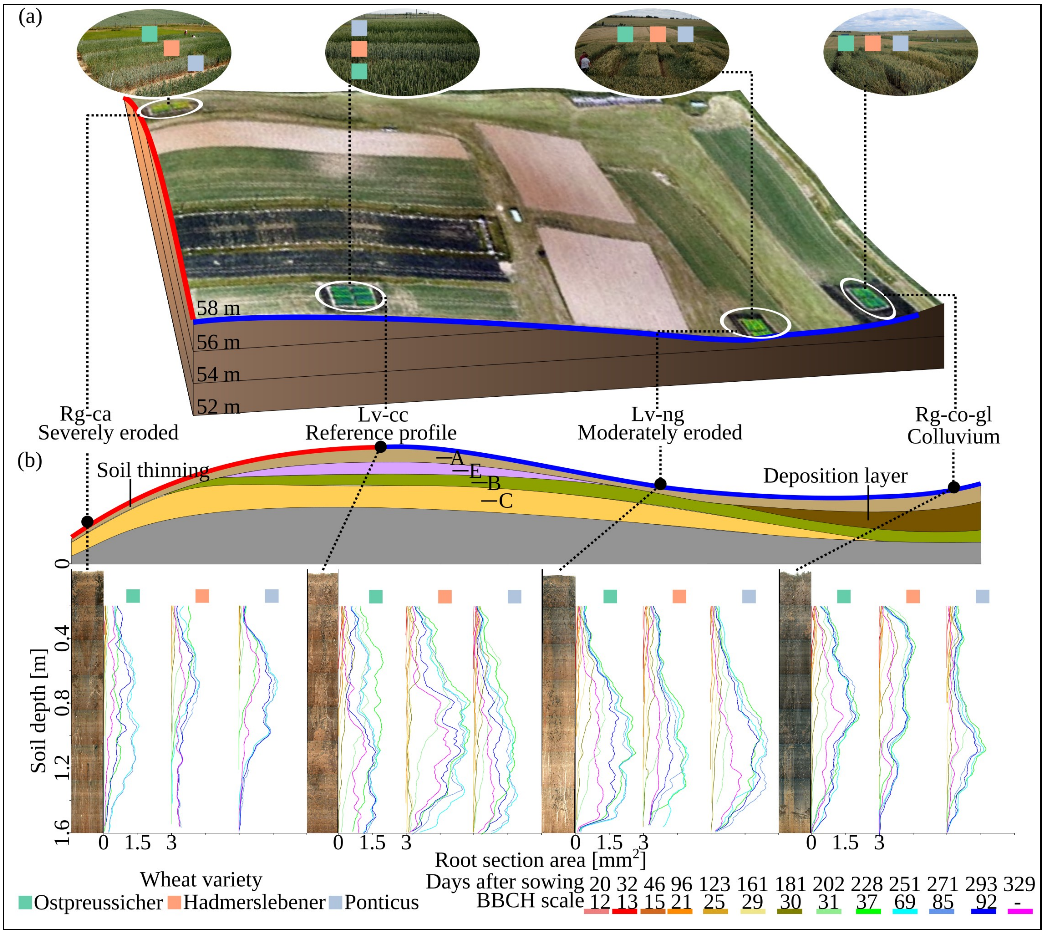

Figure 1: Details of the experimental field. (a) shows the location of the experimental plots (Calcaric Regosol (Rg-ca), Calcic Luvisol (Lv-cc) Nudiargic Luvisol (Lv-ng) and Gleyic-Colluvic Regosols (Rg-co.gl)). (b) Cross section of the experimental field, detailing the process of erosion on soil layers (A, E, B and C), with rhizotron images from each plot, along with the corresponding average root area values measured throughout the soil profile for each wheat cultivar along time.

2 Material and methods

2.1 Experimental configuration

The measurements were performed at the experimental field site CarboZALF (Sommer et al., 2016) located near Prenzlau in North-Eastern Germany (53°23' N, 13°47 E). The four focused soil types were classified as Calacric Regosol (Rg-ca), Nudiargic Luvisol (Lv-ng), Calcic Luvisol (Lv-cc) and Gleyic-Colluvic Regosol (Rg-co.gl) (IUSS, 2015). They are characteristic for the erosion-affected hummocky arable soil landscape evolved from glacial till ground moraine (Sommer et al., 2008).

The soil types can be ordered by their degree of soil erosion, mainly by tillage: an intensively truncated profile at the steep slope (Rg-ca), a less truncated profile at the slight slope (Lv-ng), a relatively intact profile at the plateau position (Lv-cc), and a non-eroded profile with deposited topsoil material and groundwater influence (Rg-co.gl) at a topographic depression (Fig. 1).

Three cultivars of winter wheat, representing a time-related breeding progress, were sown on October, 6th, 2022, (300 grains per m², seed germination October, 17th, preceding crop: summer barley) and harvested on July, 27th, 2023: Ostpreussischer Eppweizen (1910), Hadmerslebener Qualitas (1957), and Ponticus (2015). At the four soil site, the wheat cultivars were sown in each four adjacent plots with parallel stripes of 1.0 m width and 9.3 m length (Fig. 1). Annual precipitation in 2022 and 2023 and annual mean temperatures in 2022 and 2023 are provided in (Figure S1).

2.2 Intercepted Photosynthetically Active Radiation (IPAR)

The canopy analysis system sensor SunScan (SunScan SS1; Delta-T Devices Ltd., Cambridge, UK) combined with its BF5 sensor, capable of measuring incident and transmitted Photosynthetically Active Radiation (PAR), was used to calculate Intercepted Photosynthetically Active Radiation (IPAR) and Leaf Area Index (LAI). These measures were carried out at BBCH 37, 69, 85 and 92 (Fig. 1).

2.3 Above-ground biomass

Above-ground biomasses (total shoot, straw and grain) were determined gravimetrically from wheat plants harvested from 1 m² subplots in four replicates for BBCH 92. Dry mass was measured after drying samples at 60°C for over 24 hours (Herbrich et al., 2018).

2.4 Rhizotron installation and Rhizoscanning

Immediately after the seeding, a soil core of 1.55 m length and 6.3 mm in diameter was drilled at the center of each wheat stripe using a tractor-driven apparatus (Leue et al., 2019). Each wheat cultivar and soil received 4 replicates. A transparent acrylic glass tube of 1.6 m length and 6.2 mm outer diameter (2.0 inch inner diameter) was installed in each drill hole. In sum over four soil sites, four plots per sites, and three wheat cultivars per plot, 48 tubes were installed. The above-ground part of the tubes was covered with black tape in order to minimize light and moisture intrusion and heat exchange (Herbrich et al., 2018).

At 12 dates (BBCH-scale) plus one after harvest (Fig. 1), rhizoscans were taken inside the tubes using the mini-rhizotron imaging system CI 600 (Root Imager CI 600; CID Inc., Camas, USA): October 26th 2022 (BBCH Rg-ca: 11-12, other sites: 12), November 07th (BBCH RG-ca: 13, other sites: 13-15), November 21st (BBCH Rg-ca: 13-15, other sites: 22), January 10th 2023 (BBCH Rg-ca: 20-23, other sites: 21-26), February 06th (BBCH Rg-ca: 20-23, other sites: 21-26), March 21st (BBCH 24-29), April 4th (BBCH 24-29), April 26th (BBCH Rg-ca: 30, other sites: 31), May 22nd (BBCH 37), June 14th (BBCH 69), July 4th (BBCH 85) and July 27th 2023 (BBCH 92).

The rotating scanner yields 360°-images of the tube-soil interface with 215.9 mm height and 195.7 mm width at a resolution of 300 dpi. After each scan, the scanner is pushed perpendicularly downwards in fixed steps. A horizontal overlapping of 1 cm ensured the later merging of the images (Fig. 1). Particular attention was payed to maintaining both the soil and the plant population around the tube undisturbed.

2.5 Root segmentation and image analysis

The raw images from rhizoscan underwent processing in two steps. Firstly, a deep-learning model(Smith et al., 2022) was trained on a dataset comprising varied root shapes, colors, and soil types (background). The training phase involved annotating a region of interest (ROI 700x700 pixels) from 257 raw images using Root Painter (Smith et al., 2022). This process entailed manually selecting roots and distinguishing them from soil or other non-root objects. The root segmentation model was evaluated by comparing the annotated and trained dataset with the predicted results. Accuracy and precision were then measured for each annotated image. Subsequently, the trained model was utilized to segment all 560 images in the dataset. Secondly, the segmented images, disregarding the first 20 cm, underwent filtering and standardization to eliminate non-root objects (such as soil particles, water drops, and straw), after which the root volume and average diameter were quantified using RhizoVisionExplorer (Seethepalli et al., 2021). This involved considering the average diameter and overall length for cylindrical roots. The model used for this considered broken roots, since a continuous image was not always possible and the pixel threshold for non-roots objects as well as root pruning were set to 5. Based on the measured root diameter [mm] and a constant specific root length of 100 mg^{-1} (Herbrich et al., 2018), root tissue density (RTD [g mm^{-3}]) was calculated (Rose, 2017). By combining the measured root volume (mm^3) with RTD, we determined the root mass [g] across all crop development stages. Finally, using root mass per plant and the number of plants harvested per square meter, we converted the root mass to root biomass (RB [g m^{-2}]) for each crop development stage.

The total carbon content was estimated by assuming that aboveground biomass and root biomass contained 45% carbon, excluding root exudates from the calculation (Heinemann et al., 2023).

2.6 Unsupervised and supervised machine learning (ML)

Principal component analysis (PCA) was performed via Scikit-Learn package in Python (Pedregosa et al., 2011). The clustering of data, variable loadings and their relationships were evaluated. Two principal components were selected and the total variance explained by each component (soil density, pH, $CaCO_3$, root diameter, C, N LAI, IPAR, root biomass, soil water) was quantified. Based on this exploration, we defined a set of variables to perform the yield prediction by random forest resemblance algorithm.

Data-driven machine learning technique was employed to analyze the importance of each feature on the output. Therefore, the independent variables (features) were defined as IPAR, soil water, soil plot and wheat cultivar to explain the output measured by root biomass (dependent variable). A total of 30% of the samples were used to train the multiple output regression random forest ensemble learning algorithm (Pedregosa et al., 2011). The trained algorithm was used to predict new data combining variables and output. For the assessment of the regression algorithm (Geron, 2017) the metrics were: 1) coefficient of determination R2-score, which is the proportion of the variance in the output that is predictable from the variable (the best possible score is 1.0) and 2) Mean Absolute Percentage Error (MAPE), which finds all absolute errors (xi – x), adds them all and divide by the number of errors. In random forest regressor, the depth of 100 was used as a decision node in a tree can be used to assess the relative importance of that variable in predicting the output with 1000 estimators. For this calculation, whose values are positive and sum to 1.0, the higher the value, the more important is the contribution of the variable to the prediction function. The mean decrease impurity method available in scikit-learn was applied for each output.

The trained algorithm was employed to estimate the relationship between IPAR (Intercepted Photosynthetically Active Radiation) and root biomass production across various soil erosion gradients (Rg-ca, Lv-ng, Lv-cc, and Rg-co.gl) and soil water content levels (18, 21, 24, 27, and 30 $cm^3\ cm^{-3}$). The estimated maximum root biomass values under each condition were plotted against the corresponding water content. The slope of this linear relationship was then calculated to determine the reduction in root carbon deposition to the soil over the past five years for each erosion gradient, reduced water content scenario, and wheat cultivar. For this, lysimeter data for the Quillow catchment was used (BONARES repository).

2.7 Statistical analyses

All statistical analyses were carried out in the R software package (R Core Team, 2017). Analyses of differences among treatments were performed using a two-way analysis of variance (ANOVA). Differences between data sets were considered significant at $p < 0.01$ and $p < 0.05$ for the feature importance. Tukey's post hoc test was used.

3 Results

3.1 Root biomass

The overall trend shows a greater root cross-sectional area in Luvisols compared to Regosols (Fig. 1). Specifically, the initial development of the root for all wheat cultivars was hindered by Calcaric Regosol (Rg-ca) due to the very dense glacial till (C horizon) starting at 30 cm depth (Table S1 and Fig. 1). The significance of the absolute values for root biomass is illustrated in Fig. 2. At the Rg-ca, root biomass was highest around BBCH 85, with Ostpreussischer Eppweizen showing slightly higher values (200 $g\ m^{-2}$) than the other cultivars. In Nudiargic Luvisol (Lv-ng) soil, all cultivars exhibited higher root biomass around BBCH 69, with Ostpreußischer leading with approximately 400 $g\ m^{-2}$. In Calcic Luvisol (Lv-cc), all cultivars exhibited higher root biomass around BBCH 69, with Hadmerslebener Qualitas leading (550 $g\ m^{-2}$), then declining sharply after BBCH 85. In Gleyic-Colluvic Regosols (Rg-co.gl), root biomass is more evenly distributed between BBCH 37 and 92, with Ostpreußischer again showing higher values overall (200 $g\ m^{-2}$). Between BBCH 37 and 92 is the moment when the most root branches are formed (Figure S2). For the wheat cultivars Ostpreußsicher and Ponticus, an increasing trend in the maximum total root biomass was observed for the sequence of soils: Rg-ca < Rg-co.gl < LV-cc < LV-ng. For the Hadmerslebener wheat the order was: Rg-ca < Rg-co.gl < LV-ng < LV-cc.

Luvisols exhibited the highest root biomass growth rate (approximately 10 $g\ m^{-2}\ day^{-1}$), while the highest rates in Regosols are around 5 $g\ m^{-2}\ day^{-1}$ (Fig. 3). For all soil types, the peak of root growth occured at 228 days after sowing (BBCH 37), except for Rg-ca, where it occurs at 251 days (BBCH 69). Ostpreußischer and Ponticus showed the highest values in Rg-ca and Lv-ng, whereas in Lv-cc and Rg-co.gl, Hadmerslebener and Ostpreußischer, respectively, outperformed the other cultivar. The maximum decomposition rate (negative growth rate) occured around 293-350 days (after BBCH 92) for all soils and wheat cultivars. The highest degradation rate (around 5 $g\ m^{-2}\ day^{-1}$) was observed in Lv-ng and Lv-cc for the Ponticus and Ostpreußischer cultivars, respectively. The greatest root concentration was observed at BBCH 37 and 69 (228 and 251 days after sowing) of the Hadmerslebener at Lv-cc between the soil layers of 0.8 and 1.2m depth followed by Ostpreußischer at Lv-ng at depth between 0.8 and 1.6m (Fig. 1). At Rg-ca, Ostpreußischer presented the greatest homogeneity of root distribution profile along soil depth. The highest root degradation appeared in Rg-ca for the wheat cultivars Ponticus and Ostpreußischer at soil depth of 0.8 and 1.2 m respectively.

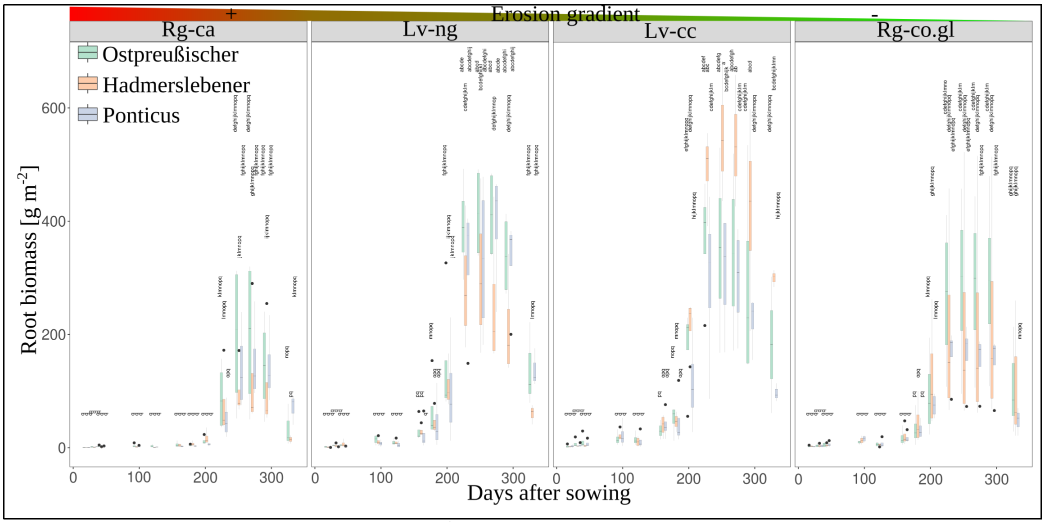

Figure 2: Crop season root biomass (g m^{-2}) evolution for the three wheat cultivars (Ostpreußischer, Hadmerslebener, and Ponticus) under different soil erosional status: Calacric Regosol (RG-ca), Nudiargic Luvisol (LV-ng), Calcic Luvisol (LV-cc) and Gleyic-Colluvic Regosol (RG-co.gl). The letters above the boxplots indicate significant differences in grain yield between treatments ($p < 0.05$), based on post-hoc tests.

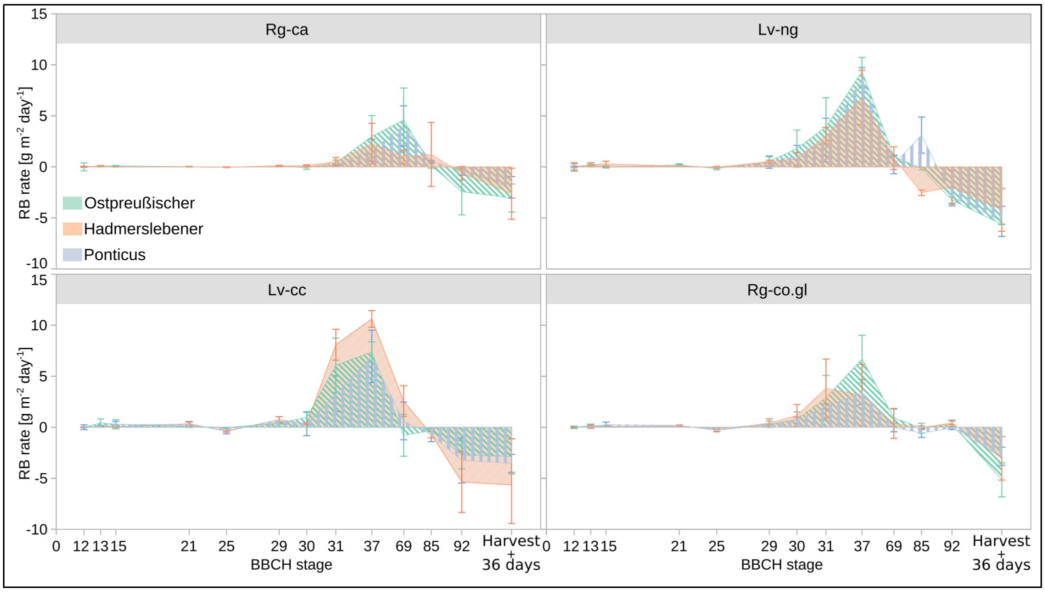

Figure 3: Root biomass rate and standard error for the entire crop season for the three wheat cultivars (Ostpreußischer, Hadmerslebener, and Ponticus) under different soil erosional status: Calacric Regosol (RG-ca), Nudiargic Luvisol (LV-ng), Calcic Luvisol (LV-cc) and Gleyic-Colluvic Regosol (RG-co.gl).

3.2 Shoot biomass

The total shoot biomass decreases with the increase in soil erosion degree (Figure S3), with wheat in Rg-ca at knolls producing 500 g m^{-2} less biomass in comparison to Rg-co.gl at depressions. The more recently developed cultivar

(Ponticus) tend to produce greater shoot biomass than the other cultivars of the study, but without significant differences within soil types. When analysing grain production, it is directly proportional to the age of the wheat cultivars (Figure S4), with a more pronounced effect in soils with lower erosion levels. The earlier developed cultivar (Ostpreussischer) in Rg-ca produced 44% less grain than the Ponticus cultivar in Rg-co.gl. Straw production is also directly proportional to the degree of soil erosion but inversely proportional to the age of the wheat cultivar (Figure S5). In this case, the Ponticus cultivar produced 50% less straw mass than the Ostpreußischer cultivar when comparing the extremes along the erosion-deposition gradient (Rg-ca and Rg-co.gl). This ratio between grain and straw biomass resulted in a nearly constant harvest index (HI) (Fig. 4) across different levels of soil erosion for the more recent wheat cultivars: Ponticus had values close to 0.7, and Hadmerslebener had values around 0.6. However, the earlier developed cultivar (Ostpreußischer) showed a greater dependency of the HI on the degree of soil erosion by a HI reduction of 45% from the most eroded soil (Rg-ca) to the deposition soil (Rg-co.gl).

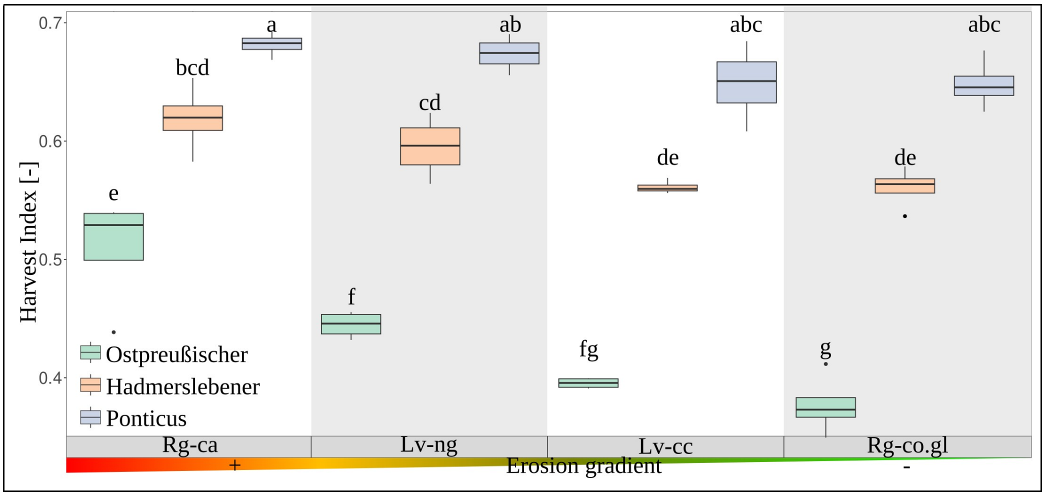

Figure 4: Harvest index (-) of three wheat cultivars (Ostpreußischer, Hadmerslebener, and Ponticus) under different soil erosional status: Calacric Regosol (RG-ca), Nudiargic Luvisol (LV-ng), Calcic Luvisol (LV-cc) and Gleyic-Colluvic Regosol (RG-co.gl). The letters above the boxplots indicate significant differences in grain yield between treatments ($p < 0.05$), based on post-hoc tests.

3.3 Root to shoot ratio

No clear trend can be observed in the root-to-shoot ratio across soil erosion levels and wheat cultivars (Fig. 5). The values for Ostpreußischer fluctuated around 0.28. However, Hadmerslebener presented the lowest value in Rg-ca and the highest value in Lv-cc, with a difference of more than four times. Ponticus presented the highest value in Lv-ng and the lowest value in Rg-co.gl, with a difference of more than two times.

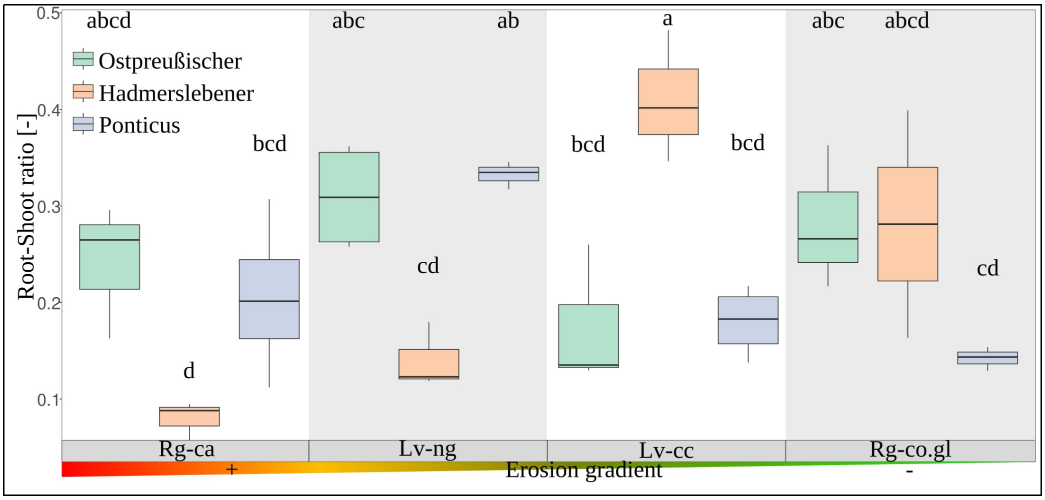

Figure 5: Root-shoot ratio (-) of three wheat cultivars (Ostpreußischer, Hadmerslebener, and Ponticus) under different soil erosional status: Calacric Regosol (RG-ca), Nudiargic Luvisol (LV-ng), Calcic Luvisol (LV-cc) and Gleyic-Colluvic Regosol (RG-co.gl). The letters above the boxplots indicate significant differences in grain yield between treatments ($p < 0.05$), based on post-hoc tests.

3.4 Modeling root biomass production across erosion levels

Principal component 1 (PC1) explains 47.1% of the total variance in the dataset while PC2 explains 22.7%, a total of 69.8% of the variance (Fig. 6a). Colored confidence ellipses representing the clustering of soil types by erosion level indicating that variables like density, pH and Calcium Carbonate ($CaCO_3$) had a stronger negative effect on Rg-ca while SOC and N had stronger and positive effect on Rg-co.gl. Root biomass and soil water are positively correlated and contribute significantly to PC1 and PC2. Root biomass and soil water are closely associated with Lv-cc and Lv-ng soil types. The Intercepted Photosynthetically Active Radiation (IPAR) and Leaf Area Index (LAI) are positively correlated with root biomass, indicating that higher light interception and leaf area are associated with increased root biomass, particularly in Lv-cc and Lv-ng soils.

The supervised machine learning regression achieved a coefficient of determination (R^2) of 0.89, with a Mean Absolute Percentage Error (MAPE) of 26% (Fig. 6b). According to the random forest ensemble algorithm the IPAR was the most important factor for predicting the root biomass values (Fig. 6c). All wheat cultivars in all soil types exhibited a similar asymptotic regression model for the relationship between root biomass and IPAR (Fig. 7). This relationship featured an initial rapid increase in biomass with increasing IPAR, followed by a plateau, indicating a saturation point where additional light absorption no longer significantly boosted root biomass. The plateau values varied based on soil water content, wheat cultivar, and soil erosion degree, as highlighted by the order of importance in Fig. 6c.

At a model-assigned soil water content of 18 $cm^3\ cm^{-3}$, root biomass plateaued at lower levels compared to higher water contents. Among the cultivars, Ostpreußischer generally exhibited the highest biomass across all soil types at this water content. At 24 $cm^3\ cm^{-3}$, the shape of the graphs and the plateau values of root biomass remained consistent with those observed at the lower water content. At 30 $cm^3\ cm^{-3}$, the highest biomass values were recorded across all soil types, showing a more rapid increase in biomass with IPAR. Hadmerslebener outperformed most of the other cultivars under these conditions. Luvisols (Lv-ng and Lv-cc) consistently supported higher root biomass compared to Regosols (Rg-ca and Rg-co.gl) across all wheat cultivars and soil water contents, with differences reaching up to 50% at higher water contents. The maximum observed biomass was 450 $g\ m^{-2}$ for Lv-cc soil with a water content of 30 $cm^3\ cm^{-3}$, achieved by

Hadmerslebener. In contrast, the minimum observed value was 180 g m^{-2} for Ponticus in Rg-ca soil with a water content of 18 cm^3 cm^{-3}.

Simulations revealed that the two more recent wheat cultivars experienced an average root biomass reduction of 4 to 8 g m^{-2} per 1% decrease in volume of soil water content, showing greater sensitivity compared to the 2 g m^{-2} reduction observed in the earlier developed cultivar (Table S2). A five year historical analysis of the Quillow catchment shows that soil water levels have been decreasing by an average of 0.19 cm^3 cm^3 per year (Figure S1a). As a result of soil drying, our simulations estimate that over the past five years, recently developed cultivars contributed 21 to 35 kg C ha^{-1} less C to highly eroded soils, excluding exudates. In contrast, earlier developed cultivars contributed only 9 kg C ha^{-1} less C. This difference was even more pronounced in depositional soils, where recently developed cultivars contributed 41 kg C ha^{-1} less C.

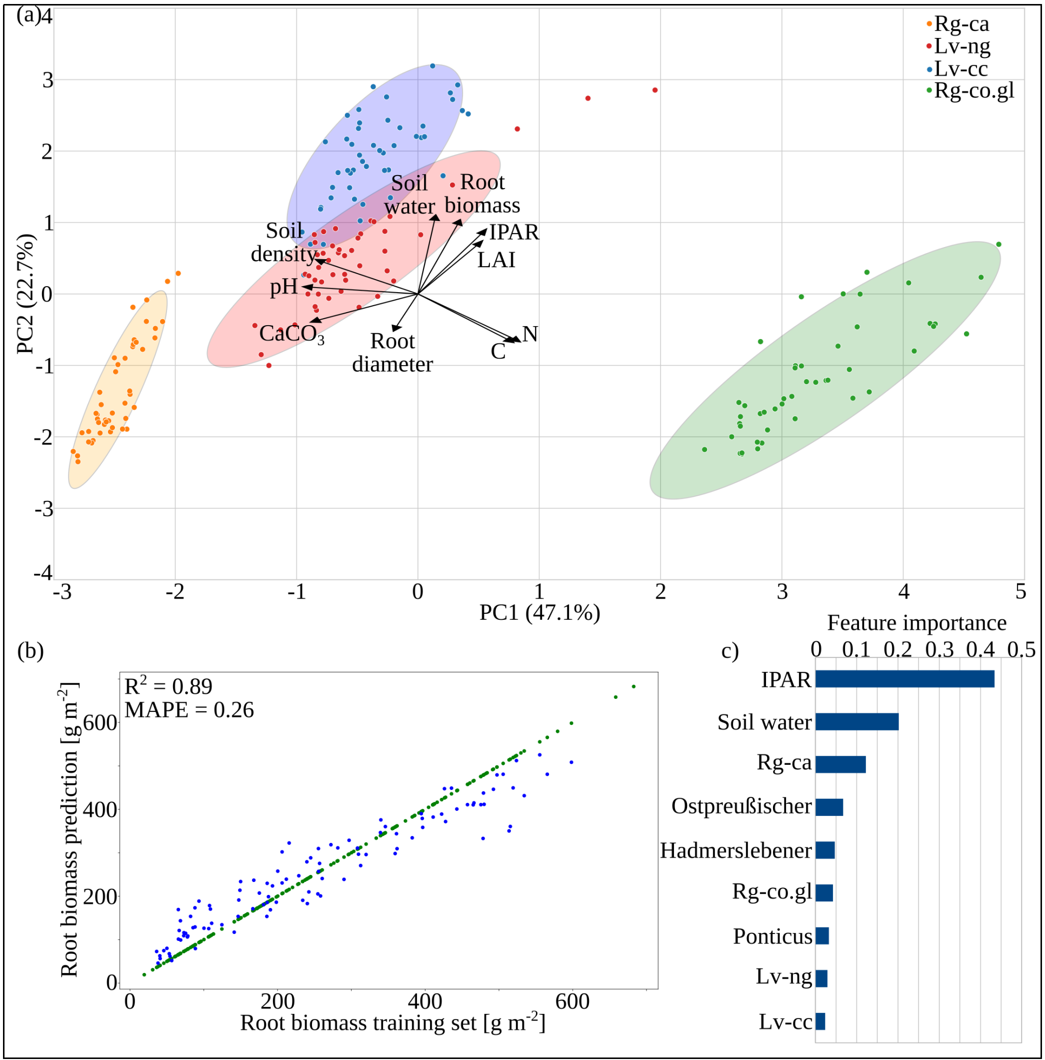

Figure 6: Unsupervised and supervised machine learning. a) Visual representation of the principal component analysis (PCA), showing the relationships between different variables across four groups of soils (Rg-ca, Lv-ng, Lv-cc, and Rg-co.gl). Confidence ellipses: Represent the clustering of different soil types based on the PCA. b)

Evaluation of random forest (RF) meta-estimator metrics (mean absolute percentage error (MAPE)) and c) importance of each feature in the prediction of root biomass.

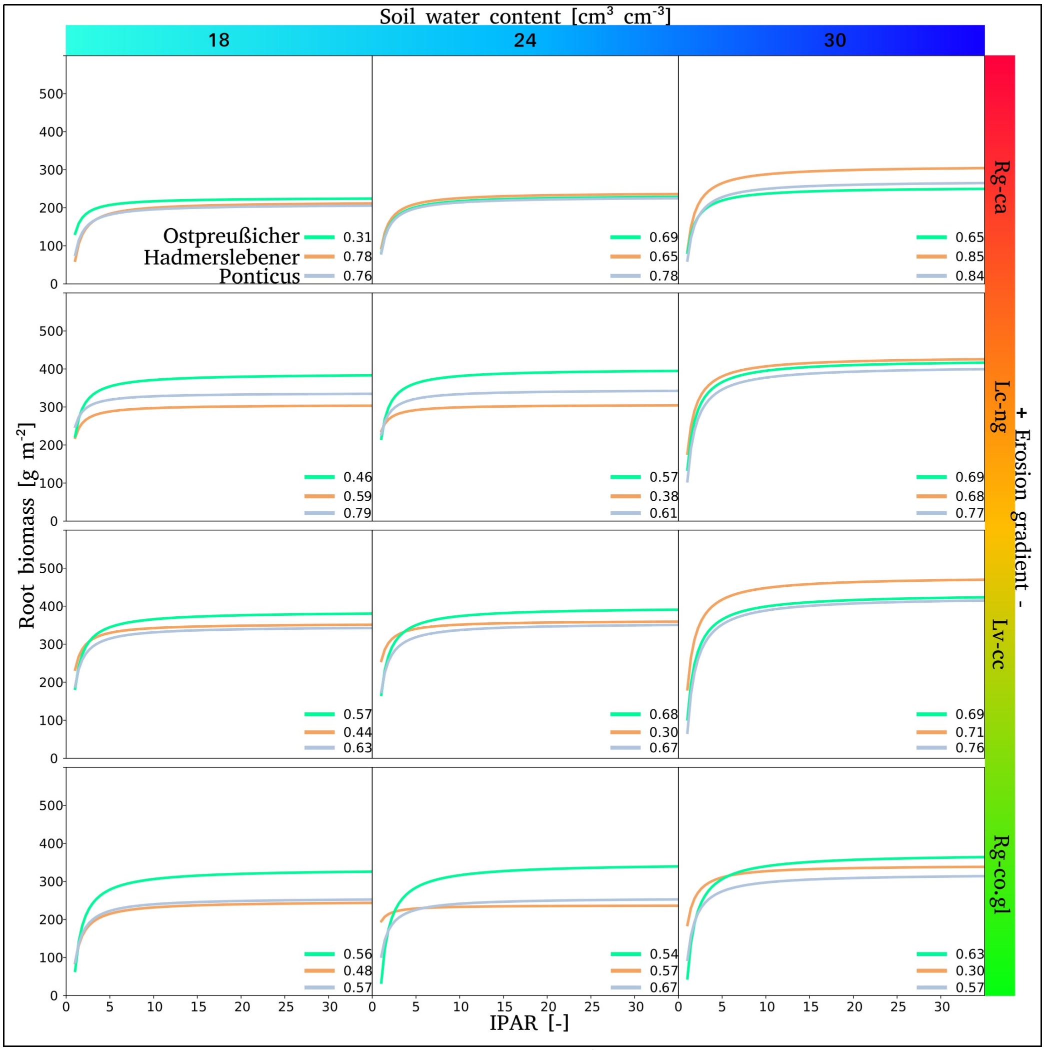

Figure 7: Simulated relationship between root biomass (g m^{-2}) and IPAR (incident photosynthetically active radiation) across four different soil types (Rg-ca, Lv-ng, Lv-cc, and Rg-co.gl) and three different wheat varieties (Ostpreußischer, Hadmerslebener, and Ponticus). Each soil type is represented in a separate column, while each row corresponds to a different level of soil water content (18, 24, and 30 cm³ cm^{-3}).

4 Discussion

Soil erosion can reduce total wheat biomass—both above and below ground—by up to 50%, equivalent to 3.2 tons of C per hectare not deposited into the soil annually. This loss underscores the importance of wheat cultivar selection, as biomass production and allocation strategies vary among cultivars. Earlier cultivars exhibit significant straw biomass reductions in response to erosion, while recently developed cultivars face greater declines in grain yield under eroded soil conditions. Earlier-developed wheat cultivars demonstrate greater resilience in root biomass production, even under conditions of intense erosion and low soil water content. Heavily eroded soils are more efficient at capturing C (Hoffmann et al., 2018) than depositional soils, as they are well below local equilibrium in C cycling. Eroded soils often contain larger quantities of minerals with unsaturated surfaces, where plant-derived C can be stabilized through the formation of organo-mineral complexes (Doetterl et al., 2016). Therefore, it is essential to strategically allocate C inputs to specific sites in order to maximize sequestration potential in these soils, while also minimizing the plant's energy expenditure on biomass production in areas where it is less effective.

Shoot biomass was similar across the wheat cultivars and was only significantly reduced in the most eroded soil (Figure S3). This finding is consistent with previous studies, where tillage erosion plays a key role in driving spatial variability in biomass production, especially in relatively dry arable hummocky landscapes (Öttl et al., 2021). This is evident from the lowest Leaf Area Index values (used as a proxy for above-ground biomass), which are often found on hilltops, where tillage erosion is most severe (Kosmas et al., 2001). The general pattern of lower biomass on eroded hilltops compared to depositional areas is observed across various common crops in Quillow catchment (Öttl et al., 2021). When splitting shoot biomass into grain and straw, the spatial variability is even greater than in total shoot biomass, due to the varying responses of each wheat cultivar to erosion-related soil properties (c.f Figure S4 and 5). Wheat cultivars show different strategies of biomass allocation and resilience to soil erosion. For instance, the two recently-developed cultivars maintain a consistent harvest index (HI) as both grain and straw biomass increase proportionally with decreasing erosion (Fig. 4). In contrast, the oldest cultivar produces more straw than grain as erosion lessens (Figure S5), leading to a lower harvest index (Fig. 4).

The trend in wheat cultivar development in Germany shows an increase in grain production, primarily driven by a higher number of grains per spike (Würschum et al., 2018). However, this does not follow the historical cultivar development approach of boosting productivity by increasing total crop biomass (Lichthardt et al., 2020). Instead, our results show that shoot biomass remains constant across different wheat cultivars, within same soil type (Figure S3). This is notable because recent cultivar development efforts have not focused on increasing plant height or promoting rapid early leaf-area growth to optimize canopy architecture and photosynthetic efficiency (Parry et al., 2011). While the idea that future yield gains could be achieved by increasing shoot biomass without altering the harvest index (HI) has been proposed (Sanchez-Garcia et al., 2015), our findings suggest a different strategy. Recent cultivar developments have prioritized reducing straw biomass (Figure S5), indicating that other mechanisms, such as enhanced photosynthetic capacity and efficiency, may be driving yield improvements (Parry et al., 2011). Consequently, the relationship between IPAR and biomass production or grain yield is not universally fixed, but rather it is specific for each cultivar. Our simulations indicate a logarithmic correlation between IPAR and root biomass; however, this relationship cannot be generalized across all wheat cultivars and soil erosional status. Each cultivar has distinct parameters that are further influenced by erosion and water content, making the interaction between IPAR, biomass production, and grain yield highly context-specific (c.f. Fig. 7). In deposition soil, recently developed wheat cultivars produces nearly 70% more grain compared to earlier developed cultivars in deposition soil. In highly eroded soils, recently developed wheat cultivars produces nearly 30% more grain yield compared to earlier developed cultivars (Figure S4).

However, the increase in grain yield comes with a trade-off: there is 32% less C input into highly eroded soils and 43% less C input into depositional soils (Figure S3 and Fig. 2), during BBCH 69–85. Using above-ground biomass as soil cover, besides being a N source, reduces soil temperature and enhancing water retention, which leads to higher wheat yields during dry periods (Hu et al., 2018). Our results indicate that, after considering IPAR, soil moisture is the most critical factor for root biomass production, showing a direct positive effect (Fig. 6). Although N is recognized as a critical factor in improving global wheat yields under climate change (Martre et al., 2024), our results indicate a minimal or non-existent relationship between root biomass and N (Fig. 6a). Although our study cannot conclusively confirm this, a broader study has observed that simulated N deposition did not affect fine root production (Li et al., 2015). However, N fertilization has been shown to accelerate the timing of maximum root biomass production (Kätterer et al., 1993). The relationship between roots and N remains a significant knowledge gap (Holz et al., 2024), requiring further experimental research to better understand the impact of N fertilization on root biomass production in different soil erosional status.

In agricultural soils, crop roots are a significant source of SOC (Poeplau et al., 2021). Root-derived C is particularly important as it stays in the soil two to three times longer than other crop residues or manure-derived C inputs (Kätterer et al., 2011), making it a key factor in maintaining and enhancing SOC. However, simulations across erosion gradients (Table S2) highlight a concerning trend: root biomass of recently developed wheat cultivars exhibit greater sensitivity to declining soil water levels compared to earlier cultivars. This suggests that advances in cultivar development have not significantly improved climate resilience, particularly for root biomass production. With soil water levels decreasing globally (Qin et al., 2023), the capacity of modern wheat cultivars to sustain root carbon inputs in eroded soils appears limited. Moreover, the presence of dense glacial till near surface typically acts as a limiting factor for root development (Stock et al., 2007), leading to reduced root biomass in the highly eroded soil (Fig. 1, Rg-ca). This soil displays a shallow C horizon with high soil density (Table S1), which also restricts root growth. This finding aligns with previous research (Herbrich et al., 2018). Although our results did not clearly show the influence of soil density on total root biomass production (Fig. 6a), it significantly impacted the distribution of roots within the soil profile (Fig. 1).

Higher soil densities slow root elongation rate and consequently root biomass rate (Fig. 3), requiring more time for roots to penetrate deeper layers (Keller et al., 2019). In both Luvisols, the root system reaches maximum depth around the BBCH 29 growth stage (Fig. 1), whereas, in Regosols, root penetration continues up to the BBCH 37 and 69 stages in the more eroded and depositional soils, respectively (Fig. 1). This delayed root development in highly eroded soils contributes to reduced productivity, underscoring the challenges of managing such degraded landscapes for agricultural use. Important to note, however, that excluding the top 20 cm of the soil increased the accuracy of our method for root quantification, as non-root material interferes with the measurements (e.g. straw). However, this led to an underestimation, as roots in this layer were not accounted for. It has long been understood that the transfer of recently assimilated C from the shoot to the root-soil system varies with different stages of crop development (phenology). This was confirmed by the root biomass rate with the maximum C transfer from the shoot to the root system during the start of stem elongation (BBCH 37). The effect was regardless of soil erosion status (Fig. 3) as also stated by previous work(Hoffmann et al., 2018). Stem elongation is the moment when the most root branches are formed (Figure S2) increasing significantly the root area (Fig. 1).

Beyond the potential for gross C input, restoring soil structural health is critical for reviving its environmental functions. In heavily eroded Rg-ca, where the structure is degraded (Barbosa et al., 2024), root system architecture can enhance soil recovery by promoting hierarchical aggregation at both micro and macro levels (Poirier et al., 2018). Root-induced biopores enrich microbial biomass within the drilosphere, which serves as a biological "hot spot" (Bundt et al., 2001). Elevated microbial activity (Leue et al., 2021) and a higher proportion of OC in these areas promote the production of extracellular polymeric substances (Carrel et al., 2017), significantly affecting water and solute transport within the soil, playing a pivotal role in soil function. The historical development of cultivars with higher root branching and expanded root area throughout the soil profile has been particularly beneficial for optimizing soil water exploration (Aguirrezabal et al., 1993). This root system robustness helps maintain biomass production even under conditions of soil hydric stress (Fig. 7), highlighting the importance of varietal development to achieve higher grain yields based not only in photosynthetic capacity and efficiency but also on crop biomass (Lichthardt et al., 2020), preferably root biomass, to assist soil structural recovery and improve crop resilience and water use efficiency (Qiao et al., 2022).This falls within the context of sustainable agricultural practices (Piñeiro et al., 2020) (e.g. mulching, reduced or no-tillage, and crop rotation) enhancing the benefits of robust root systems by minimizing soil structural disturbance, and preserving SOC.

5 Conclusions

The findings of this study highlight the significant impact of soil erosion gradient and wheat cultivars on biomass production, with reductions of up to 50% in total biomass, both above and below ground. Recently developed cultivars produce 70% more grain in depositional soils and 30% more in highly eroded soils compared to earlier cultivars. However, this increased grain yield comes with a trade-off: carbon input into the soil is reduced by 32% in eroded soils and 43% in depositional soils. These results suggest cultivar selection (or development) should balance grain yield with carbon sequestration potential, especially in eroded areas. Our model shows that earlier-developed cultivars are more efficient at converting intercepted light into root biomass, particularly in eroded soils with limited water availability, demonstrating their adaptability in adverse environments. In contrast, newer cultivars are more sensitive to water and erosion. Long-term experiments on the impact of water scarcity on root biomass in degraded landscapes, particularly in temperate, dry regions affected by tillage-driven erosion—key areas for crop production in the northern hemisphere—are essential for improving food security and soil carbon turnover.

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Author contributions

M.S. conceived of the presented idea. L.A.P.B. structured and took the lead in writing the manuscript. M.S., M.L., and M.W. conceived and planned the experiments. M.L. and M.W. carried out the experiments. L.A.P.B. performed all image analyses, planned and executed the simulations and data analysis. M.S., M.L., M.W., and L.A.P.B. contributed to the interpretation of the results. All authors provided critical feedback and helped shape the research, analysis, and manuscript.

Competing interests

The authors declare no competing interests.

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