

1 Original article

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3 Linking root length and surface area to yield: variety-specific root plasticity in winter wheat
4 across contrasting European environments

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6 Root traits and yield: variety-specific plasticity in European wheat

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1 Abstract

2 • **Background and aims**

3 Understanding the relationship of root traits and crop performance under varying environmental
4 conditions facilitates the exploitation of root characteristics in breeding and variety testing to
5 maintain crop yields under climate change. Therefore, we (i) evaluated differences in root length
6 and surface area between 10 winter wheat varieties grown at 11 sites in Europe covering a large
7 pedoclimatic gradient, (ii) quantified differences in root response to soil, climate, and management
8 conditions between varieties and (iii) evaluated variety-specific relationships of grain yield and
9 root length and surface area under diverse environmental conditions.

10 • **Methods**

11 At each site, we sampled the roots to 1 m soil depth after harvest and determined various root traits
12 by scanning and image analysis. The impacts of soil, climate, and management on roots and yield
13 of the 10 varieties were analysed by means of multivariate mixed models.

14 • **Key results**

15 Root length averaged 1.4 m root pc⁻¹, 5007 m root m⁻² soil, and 5300 m root m⁻² soil and root
16 surface area 0.039 m² root pc⁻¹, 40 m² root m⁻² soil, and 43 m² root m⁻² soil in 0.00-0.15 m, 0.15-
17 0.50 m, 0.50-1.00 m soil depth, respectively. The variation in both traits was 10 times higher
18 between sites than varieties, the latter ranging by a factor of 2 within sites. Irrespective of variety,
19 temperature was a major driver of subsoil root traits, suggesting that warmer climates promoted
20 root growth in deeper soil layers. Other soil and climate variables affected root length and/or root
21 surface area of individual varieties, highlighting different degrees of root plasticity. The varieties
22 displayed distinctly different relationships between yield and root traits under varying pedoclimatic
23 conditions, highlighting genetic differences in yield response to environmentally driven root
24 plasticity.

• Conclusions

These findings suggest that breeding efforts should target flexible root-yield relationships in the subsoil to maintain crop performance under climate change.

Key words: EJP SOIL, triticum aestivum L., winter wheat, root length, root surface area, heritability, pedoclimatic gradient, root plasticity, deep-rooting, yield, soil, management

1. Introduction

Climate change impacts are stressing agricultural production and increasingly hinder efforts to meet the demands of human nutrition (Nelson et al., 2024). Global warming rates per decade have been consistently higher since 1990 than the baseline from 1973-2022 and precipitation patterns have been shifting, with extreme weather events becoming more common, wetter regions getting wetter and drier regions getting drier (Giorgi et al., 2004; Madsen et al., 2014; Samset et al., 2023). Rising temperatures lead to increased evapotranspiration and thereby increased risk of water shortage (Ajjur & Al-Ghamdi, 2021), while water shortage due to reduced precipitation can lead to increasing temperatures due to less evaporative cooling (Solomon et al., 2007). As a consequence, global maize and wheat production have declined by 3.8% and 5.5%, respectively (Lobell et al., 2011; Moore & Lobell, 2015), and the yields of almost all major crops have stagnated since the mid-1990s in Southern Europe (Agnolucci & De Lipsis, 2020; Brás et al., 2021; Gulino et al., 2023; Le Gouis et al., 2020; Lopes, 2022; Moore & Lobell, 2015). Crops that are adapted to extreme conditions such as drought may better cope with the effects of climate change. An important aspect of climate change adaptation in crops is closely linked to the characteristics of

1 their root system as it facilitates the exploration and uptake of soil resources and thereby sustains
2 vital physiological processes under abiotic stress (Gowda et al., 2011; Lynch, 2013; Lynch, 2018).
3 Root system architecture encompasses the spatial arrangement and attributes of root tissue within
4 the soil profile and is commonly described by length, length density, volume, surface area,
5 diameter, number of tips, branching frequency, and orientation of roots (Khan et al., 2016). Higher
6 root length and greater root surface area in deep soil are beneficial for accessing water in greater
7 soil depths and can therefore better sustain yields during physiologically critical times of water
8 shortage (Li et al., 2019; Lynch, 2013; Maqbool et al., 2022). Deep rooting also promotes organic
9 carbon inputs in the subsoil (Kell, 2011; Lynch & Wojciechowski, 2015), which not only facilitates
10 long-term carbon storage in agroecosystems (Paustian et al., 2016) but also improves growth
11 conditions for deep roots of succeeding crops (Rasse & Smucker, 1998). Understanding the impact
12 of the root system on crop performance could facilitate the exploitation and manipulation of root
13 characteristics to both increase crop yield and optimize agricultural land use (Smith & De Smet,
14 2012). The Food and Agriculture Organization (FAO) has therefore called for the inclusion of root
15 traits in breeding programs (FAO, 2013). However, this requires an understanding of root traits
16 and their relationship to yield under varying environmental conditions (Colombo et al., 2022).
17 The main drivers of root characteristics are attributed to genetics, environment, and management
18 (Hecht et al., 2016; Rogers & Benfey, 2015). Different plant species exhibit distinct types of root
19 systems, most notably tap or fibrous systems, and genotypes of a species develop certain root traits
20 more strongly than others (Akman, 2020; Duan et al., 2023; Fry et al., 2018; Lynch, 1995; Osmont
21 et al., 2007). For instance, total root length was found to vary by factors of two to four among
22 wheat genotypes (Adeleke et al., 2020; Pariyar et al., 2021), and by factors of three to five among
23 maize genotypes (Hund et al., 2007; Sun et al., 2025). Environmental conditions directly affect the
24 root system, as temperature, moisture, and soil physical, chemical, and biological properties

1 influence all root traits (Rich & Watt, 2013), while agricultural management has an indirect effect
2 by altering soil conditions. For example, root length of wheat can vary by a factor of two between
3 sites and root depth by a factor of 1.2 between fertilization treatments on the same site (Svoboda
4 et al., 2020). The extent to which root traits respond to environmental conditions is expressed as
5 root plasticity (Karlova et al., 2021), which differs between crop varieties (Grossman & Rice,
6 2012), resulting in distinct genotype-by-environment (G x E) interactions.

7 Wheat is globally one of the most important staple food crops (Shewry & Hey, 2015) and subject
8 to intensive breeding efforts towards higher and more stable yields by increasing the harvest index
9 (Siddique et al., 1989) or adapting varieties to regionally specific biotic and abiotic stresses
10 (IWGSC et al., 2018). Root system architecture traits are currently not the priority of breeding
11 targets or variety testing programs, presumably due to their inherent hidden nature (Ober et al.,
12 2021), and selecting for those traits using only the shoot phenotype remains challenging (Severini
13 et al., 2020; Uga, 2021). Further, linking root traits to specific genes could enable targeted variety
14 selection (Li et al., 2021) but results between studies are mostly inconsistent (Alahmad et al., 2019;
15 Chen et al., 2022; Xu et al., 2021). Even single traits can be controlled by many different
16 chromosomal regions and genes and even interactions between those (Raffo & Jensen, 2023). Few
17 studies have focused on root trait variability in variety testing panels and their findings were
18 confined to only few growth environments (Fradgley et al., 2020; Mathew et al., 2019).

19 Therefore, the main objective of the present study was to investigate the relationship between yield
20 and root traits of different winter wheat varieties under varying environmental conditions.
21 Specifically, we (i) evaluated differences in root length and surface area between 10 winter wheat
22 varieties grown at 11 pedoclimatically diverse sites in Europe, (ii) quantified differences in root
23 response to pedoclimatic and management conditions between varieties, and (iii) evaluated variety-

1 specific relationships between grain yield and root length and surface area under diverse
2 environmental conditions.

3 2. Materials and methods

4 2.1 Sites and wheat varieties

5 The study was conducted during the 2021/22 winter wheat season as part of a multi-location field
6 experiment established one year earlier. The winter wheat trials were located at 11 sites (Table 1;
7 Supplementary figure 1), which covered all major European pedoclimatic regions from the
8 Mediterranean to the Boreal and from the Atlantic to the Pannonian zone (EEA, 2017). Nine sites
9 had been established within the Horizon 2020 project “INVITE” and were assessed for
10 aboveground crop performance by the INVITE partners in the wheat seasons 2020/21 and 2021/22
11 (Visse-Mansiaux et al., in prep.): Grossnondorf AT (AT-Gn), Gembloux BE (BE-Ge), Changins
12 CH (CH-Ca), Eschikon CH (CH-Es), Chrlice CZ (CZ-Ch), Freising DE (DE-Fr), Nossen DE (DE-
13 No), Lleida ES (ES-Le), and Szekutas HU (HU-Sz). To expand the pedoclimatic gradient to
14 Northern Europe, two sites were added for the Horizon 2020 EJP Soil project “MaxRoot-C” in the
15 exact same set-up as the INVITE sites in the 2021/22 wheat season: Dotnuva LT (LT-Do) and Ås
16 NO (NO-As). The field designs corresponded to either randomized complete block, lattice, split
17 block, or latinized alpha designs according to national conventionality in variety testing. The plot
18 size varied from 8.8 m² to 19.2 m² among sites, except for CH-Es (4 m²). The sites were managed
19 according to local agricultural practices (Table 2) and phenological dates varied based on climatic
20 differences between regions (Supplementary figure 2).

21 Daily climate data were gathered from nearby weather stations (AT-Gn (GeoSphere Austria, 2023),
22 BE-Ge (RMI, 2023), CH-Ca (Federal Office of Meteorology and Climatology MeteoSwiss, 2022),
23 CH-Es (Agrometeo, 2024), DE-Fr (Bayrisches Landesamt für Umwelt, 2023), DE-No
24 (Agrarmeteorologisches Messnetz Sachsen, 2023), LT-Do (Lithuanian Hydrometeorological

1 Service under the Ministry of Environment, 2022), CZ-Cr, ES-Le, HU-Sz, NO-As: data retrieved
2 from on-site weather stations). Mean annual temperature and precipitation and mean temperature
3 and sum of precipitation for the time period 09/2021-08/2022 were calculated for general site
4 characterization (Table 1). Mean temperature and sum of precipitation for the time periods one
5 week before sowing until harvest (season), one week before sowing until emergence (emergence),
6 emergence until flowering (flowering), and flowering until harvest (harvest) were calculated for
7 each site individually to characterize the specific weather conditions during the wheat growing
8 season (Supplementary table 1).

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1 The ten winter wheat varieties chosen for the present study were commercially relevant in large
2 parts of Europe and differed strongly in yield expectation based on their adaptability to certain
3 environmental conditions. The included varieties were *Altigo*, *Aurelius*, *Bernstein*, *Dagmar*, *Julie*,
4 *Montalbano*, *MV Nador*, *Nogal*, *RGT Reform* and *Tenor* (Table 3). At DE-Fr, the varieties *Altigo*
5 and *Tenor* and at NO-As, the varieties *Aurelius* and *Tenor* were not cultivated and therefore not
6 included in our study for those sites.

7 8 2.2 Sampling, sample processing, and measurements

9 2.2.1 Root and soil sampling

10 Root sampling was performed in July and August 2022. The sampling was explicitly conducted
11 after harvest to simultaneously quantify root carbon inputs to soil as net root biomass, which was
12 the main objective of the MaxRoot-C project (Heinemann et al., 2025). At all sites except CH-Es,
13 three field replicates per variety were sampled (30 experimental plots per site). In CH-Es, the 10
14 varieties were part of a variety testing panel with over 100 varieties and two field replicates; two
15 samples were taken from the first field replicate (serving as pseudo-replicates) and one from the
16 second replicate.

17 Two well-established methods were used to quantify root traits (Gregory, 2006), (i) monolith
18 excavation and (ii) soil coring. (i) One 0.25 x 0.25 x 0.15 m (L x W x D) soil monolith per plot
19 comprising two wheat rows was excavated, the entire soil volume was retrieved, and all crown
20 roots were collected. (ii) In addition, two soil cores per plot were taken with a soil auger (inner
21 diameter 6 cm, outer diameter 8 cm), one directly on the crop row and one between crop rows, up
22 to a depth of 1 m. The core was then retrieved from the rod and divided into 5 depth segments of
23 0.00–0.15 m, 0.15–0.30 m, 0.30–0.50 m, 0.50–0.75 m, and 0.75–1.00 m. The core samples from
24 0.00–0.15 m soil depth were not included in this study, as they contained large amounts of

1 extraneous organic matter (roots from preceding crops, above ground crop residues, organic
2 amendments), which could not be differentiated from the recent wheat roots in a precise and
3 efficient manner. From here on, the crown roots from the soil monoliths are referred to as topsoil
4 roots (0.00-0.15 m soil depth) and the roots from the soil cores as subsoil roots (0.15–1.00 m soil
5 depth).

6 Two extra soil cores were sampled from the centre of each field for the determination of soil
7 characteristics. For the sampling period, all samples were stored at ambient temperature for a
8 maximum of ten days and thereafter cooled at 4 °C for a maximum of 60 days or frozen at -18°C
9 for a maximum of 12 months. Detailed information on sampling, sample processing, and
10 measurements are given in SI1.

11

12 2.2.2 Root sample processing and measurements

13 Topsoil root samples were washed manually and subsoil root samples were washed using a root
14 washing machine (Hydropneumatic Elutriation System; Gillison's Variety Fabrication; Smucker
15 et al. (1982)). The washed root samples were expelled into a 500 µm sieve, which might have
16 underestimated root length by 20% compared to a 250 µm sieve (Livesley et al., 1999). Thereafter,
17 the roots had to be further separated from remaining extraneous organic matter by hand. The subsoil
18 root samples of ES-Le had exceptionally high proportions of roots of the preceding crop alfalfa in
19 all soil depths and were therefore not subjected to root measurements by image analysis. Scanning
20 was performed with an Epson perfection v850 flat-bed scanner with a custom-made Plexiglas^(R)
21 tray (York, 2020). The subsoil roots were scanned in a water film, whereas the topsoil roots were
22 scanned without water. To allow for easy 2D scanning, two crown roots per sample were bisected
23 and those four crown root halves were scanned (Supplementary figure 3).

24

2.2.3 Soil sample processing and measurements

Soil analyses were performed on 40 °C-dried and 2 mm-sieved samples. Water content, stone content (> 2mm) and bulk density were assessed by drying and weighing of the samples, particle size distribution (clay < 2 µm, silt 2-50 µm, sand > 50 µm) was measured with a robotic analyzer (Skalar SP2000), soil pH was measured in 0.1 M CaCl₂ solution at a ratio of 1:2.5, total carbon (C) and nitrogen (N) were measured by dry combustion (LECO TruMac CN Macro Determinator), inorganic C was determined by combusting aliquots for 16 h in a muffle furnace at 400 °C, and C and N were measured by elemental analysis. Organic C content was then calculated by subtracting the total inorganic C content from the total C content of these samples. Available soil phosphorus (P) was measured by Olsen-extraction and colorimetry (Olsen, 1954). Data for clay content, bulk density, pH, total N, available P and total inorganic and organic C are presented in Supplementary table 2.

2.2.4 Grain yield and gene sequencing

Grain yield was determined by the site managers and upscaled to Mg ha⁻¹ at 15% moisture (Table 4; more information in Heinemann et al. (2025); Visse-Mansiaux et al. (in prep.)). For genome sequencing, seeds of all ten varieties of three sites (LT-Do, CH-Es, ES-Le), a total of 30 samples, were provided by the site managers and stored in a cool dry place until further analysis. At SGS Institut Fresenius GmbH TraitGenetics Section, plants were grown from the seeds, the DNA was extracted from leaf material, and sequencing was performed with the Illumina Infinium 25K array (Gogna et al., 2022). Based on a cluster file developed for hexaploid wheat, the data was checked for quality and SGS provided a genotype table for the analysed samples.

2.3. Data analyses

2.3.1. Root image analysis

The images (Supplementary figure 3) were analysed using RhizoVision Explorer v2.0.3 (Seethepalli & York, 2021) and the algorithms described by Seethepalli et al. (2021). The specific settings are summarized in Supplementary table 3. Although multiple root parameters were determined, we focused on root length and surface area for further analyses (Supplementary table 4). In the diameter range over 4 mm of the fresh, bisected topsoil roots, which corresponded to the bisected part of the root crown adjoining the stem base, length and surface area were corrected for duplicate measurements.

2.3.2. Handling of missing data and upscaling

Of a total of 330 topsoil root (3 replicates x 10 varieties x 11 sites) and 2640 subsoil root (2 positions x 4 sampling depths x 3 replicates x 10 varieties x 11 sites) samples, 22 topsoil root and 340 subsoil root samples were missing. This concerned the data on the varieties *Altigo* and *Tenor* in DE-Fr and NO-As (not included in the panel), data for 0.15-1.00 m soil depth in ES-Le (contaminated samples), and data for 0.75-1.00 m soil depth and partly for 0.50-0.75 m soil depth in CH-Ca (limited sampling depth). Those were replaced with N/A (not available) for data analyses.

The top- and subsoil root traits were upscaled following two different approaches. Topsoil root traits are reported per plant (pc of crown root), while subsoil root traits are reported per area (m² soil) (see subchapter “Suitability of the study design” for a critical assessment of the two approaches). For the latter, data from soil cores sampled within and between wheat rows were combined using an approach that accounted for the spatial representativeness of the core positions. Given that row widths differed between 10.5 and 15.6 cm across sites (Table 2), the relative proportions of root systems collected between wheat rows likely varied among sites. Root length

1 and surface area of the subsoil roots were therefore upscaled to the soil surface area for each
 2 sampling position and depth segment individually and then summed over positions and depths
 3 (adapted from Frasier et al. (2016) and Hirte et al. (2021) for root biomass):

$$4 \quad \text{root trait}_{\text{row upscaled}} = \frac{\text{root trait}_{\text{row}}}{\pi * \left(\frac{D}{2}\right)^2} * \frac{D}{s} \quad (1)$$

$$\text{root trait}_{\text{inter-row upscaled}} = \frac{\text{root trait}_{\text{inter-row}}}{\pi * \left(\frac{D}{2}\right)^2} * \frac{(s - D)}{s} \quad (2)$$

5 where $\text{root trait}_{\text{row upscaled}}$ and $\text{root trait}_{\text{inter-row upscaled}}$ are area-related root length [m root m⁻² soil]
 6 or surface area [m² root m⁻² soil] within and between rows, respectively, $\text{root trait}_{\text{row}}$ and
 7 $\text{root trait}_{\text{inter-row}}$ are root length [m] or surface area [m²] per soil core within and between rows,
 8 respectively, D is the inner diameter of the sampling rod [m] and s is the distance between rows
 9 [m] (i.e. row width; Table 2). Upscaled subsoil root length and surface area per depth segment were
 10 obtained by summing the respective $\text{root trait}_{\text{row upscaled}}$ and $\text{root trait}_{\text{inter-row upscaled}}$. In addition,
 11 the data for the individual depth segments were summed to two subsoil segments, 0.15-0.50 m and
 12 0.50-1.00 m. For data that was only available for either the row or the inter-row position, the data
 13 point for the missing position was estimated (details in SI2).

15 2.3.3. Statistical analysis of root data

16 First, general variability in non-transformed root trait data among varieties and sites was assessed
 17 by a random intercept model:

$$\begin{cases} Y_{ijk} = \mu + \alpha_i + S_j + R_k + \varepsilon_{ijk} \\ \alpha_i \sim N(0, \sigma_V^2), S_j \sim N(0, \sigma_S^2), R_k \sim N(0, \sigma_R^2), \varepsilon_{ijk} \sim N(0, \sigma^2) \end{cases} \quad (3)$$

1 where Y_{ijk} is the value of the root trait (root length or surface area), α_i is the random effect of variety
 2 i , S_j is the random effect of site j , R_k is the random effect of replicate k , and ε_{ijk} is the error term.
 3 Second, differences in root length and surface area between varieties were evaluated by means of
 4 linear mixed effects models to account for the prominent hierarchical data structure (nested design)
 5 and different sources of variability. Prior to model fitting, root length and surface area were log-
 6 transformed to meet the assumption of homogeneous distribution of the residuals. Separate models
 7 were fitted to the data for the different aggregated soil layers:

$$\begin{cases} \log(Y_{ijk}) = \mu + \alpha_i + S_j + R_{k(j)} + \varepsilon_{ijk} \\ S_i \sim N(0, \sigma_S^2), R_{k(j)} \sim N(0, \sigma_R^2), \varepsilon_{ijk} \sim N(0, \sigma^2) \end{cases} \quad (4)$$

8 where Y_{ijk} is the value of the root trait (root length or surface area), α_i is the fixed effect of variety
 9 i , S_j is the random effect of site j , $R_{k(j)}$ is the random effect of replicate k nested in site j , and ε_{ijk}
 10 is the error term.

11 Third, we tested the effects of the following pedoclimatic and management variables on root length
 12 and surface area using mixed effects models with an interaction term of variety and pedoclimatic
 13 or management variable (Supplementary tables 1-2): *Temp. season* [$^{\circ}\text{C}$], *Temp. emergence* [$^{\circ}\text{C}$],
 14 *Temp. flowering* [$^{\circ}\text{C}$], *Temp. harvest* [$^{\circ}\text{C}$], *Prec. season* [mm], *Prec. emergence* [mm], *Prec.*
 15 *flowering* [mm], *Prec. harvest* [mm], *Soil clay content* [%], *Soil BD* [g cm^{-3}], *Soil pH*, *Soil N* [%],
 16 *Soil P* [mg kg^{-1}], *Sowing density* [grains m^{-2}] and *N fertilization* [kg ha^{-1}]:

$$\begin{cases} \log(Y_{ijkl}) = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} \\ \quad + S_k + R_{l(k)} + \varepsilon_{ijkl} \\ S_k \sim N(0, \sigma_S^2), R_{l(k)} \sim N(0, \sigma_R^2), \varepsilon_{ijkl} \sim N(0, \sigma^2) \end{cases} \quad (5)$$

1 where Y_{ijk} is the value of the root trait (root length or surface area), α_i is the fixed effect of variety
 2 i , β_j is the fixed effect of pedoclimatic variable j , $(\alpha\beta)_{ij}$ is the fixed interaction effect, S_k is the
 3 random effect of site k , $R_{l(k)}$ is the random effect of replicate l nested in site k , and ε_{ijkl} is the error
 4 term. A multivariate Pearson correlation analysis revealed several prominent correlations between
 5 the pedoclimatic and management variables, most importantly between the climate variables
 6 (Supplementary figure 4).

7 The relative importance of all variables for root length and surface area was assessed using a
 8 random forest model (details in SI2).

9 Fourth, the relationships between root length and surface area and yield of individual varieties were
 10 tested using a heteroskedastic mixed effects model (Addy et al., 2022) with an interaction term of
 11 variety and root length or surface area:

$$\begin{cases} Z_{ijkl} = \mu + \alpha_i + \log(Y_j) + (\alpha \log(Y))_{ij} \\ \quad + S_k + R_{l(k)} + \varepsilon_{ijkl} \\ S_k \sim N(0, \sigma_S^2), R_{l(k)} \sim N(0, \sigma_R^2), \varepsilon_{ijkl} \sim N(0, \sigma_i^2) \end{cases} \quad (6)$$

13 where Z_{ijkl} is the yield, α_i is the fixed effect of variety i , $\log(Y)_j$ is the fixed effect of root trait j ,
 14 $(\alpha \log(Y))_{ij}$ is the fixed interaction effect, S_k is the random effect of site k , $R_{l(k)}$ is the random effect
 15 of replicate l nested in site k , and ε_{ijkl} is the error term. The variance function structure grouped

1 by variety allowed for handling the significant heterogeneity of variance in the residuals (Pineiro
2 & Bates, 2006).

3 Fifth, the relationships between root length and surface area and yield of individual varieties under
4 varying pedoclimatic conditions were tested using a heteroskedastic mixed effects model with a 3-
5 way interaction term of variety, root length or surface area, and pedoclimatic variable:

$$\begin{cases}
 Z_{ijklm} = \mu + \alpha_i + \beta_j + \log(Y_k) + (\alpha\beta)_{ij} + (\alpha \log(Y))_{ik} \\
 \quad + (\beta \log(Y))_{jk} + (\alpha\beta \log(Y))_{ijk} \\
 \quad + S_l + R_{m(l)} + \varepsilon_{ijklm} \\
 S_l \sim N(0, \sigma_S^2), R_{m(l)} \sim N(0, \sigma_R^2), \varepsilon_{ijklm} \sim N(0, \sigma_\varepsilon^2)
 \end{cases} \quad (7)$$

7 where Z_{ijkl} is the yield, α_i is the fixed effect of variety i , β_j is the fixed effect of pedoclimatic
8 variable j , $\log(Y)_k$ is the fixed effect of root trait k , $(\alpha\beta)_{ij}$, $(\alpha \log(Y))_{ik}$, $(\beta \log(Y))_{jk}$, $(\alpha\beta \log(Y))_{ijk}$
9 are the fixed 2- and 3-way interaction effects, S_l is the random effect of site l , $R_{m(l)}$ is the random
10 effect of replicate m nested in site l , and ε_{ijklm} is the error term.

11 For the models 4 to 7, outliers were excluded on the basis of the 95% confidence interval (CI) of
12 the standardized residuals in all final models. The models were checked for influential cases by
13 computing Cook's distance and for heteroscedasticity by performing a Levene's test. Overall
14 model performances were checked by pseudo- R^2 (marginal and conditional R^2) for generalized
15 mixed models and the normality of the residuals (QQ-plots). For all models, details on model
16 diagnostics are given in SI2.

17 Differences in root length or surface area between varieties (model 4) were tested by analysis of
18 variance (ANOVA) and subsequent multiple pairwise comparison of estimated marginal means.

19 Differences in slopes for the pedoclimatic and management variables and root length or surface
20 area and yield between varieties (models 5 and 6) were tested by multiple pairwise comparisons of

1 estimated marginal trends. Changes in slopes between root length or surface area and yield with
 2 changing pedoclimatic conditions for every variety were tested by multiple pairwise comparisons
 3 between the slopes of the mean pedoclimatic value ± 1 standard deviation (Aiken, 1991). For all
 4 multiple comparisons, Sidak-adjustment of p-values was applied and a significance level of alpha
 5 = 0.05 was used.

6 Finally, we performed a broad sense heritability analysis (H^2_{piepho}) on root length and surface area
 7 based on a mixed model approach to account for the unbalanced trial design (Piepho & Möhring,
 8 2007). Best Linear Unbiased Estimators (BLUEs) were used for fixed effects and Best Linear
 9 Unbiased Predictors (BLUPs) for random effects:

$$\text{Fixed model} = \begin{cases} Y_{ijk} = \mu + \alpha_i + S_j + (\alpha S)_{ij} + \varepsilon_{ijk} \\ S_i \sim N(0, \sigma_S^2), (\alpha S)_{ij} \sim N(0, \sigma_{VS}^2), \varepsilon_{ijk} \sim N(0, \sigma^2) \end{cases} \quad (8)$$

Random model =

$$\begin{cases} Y_{ijk} = \mu + \alpha_i + S_j + (\alpha S)_{ij} + \varepsilon_{ijk} \\ S_i \sim N(0, \sigma_S^2), \alpha_i \sim N(0, \sigma_V^2), (\alpha S)_{ij} \sim N(0, \sigma_{VS}^2), \varepsilon_{ijk} \sim N(0, \sigma^2) \end{cases} \quad (9)$$

10 where α_i is the fixed effect of variety i in the fixed model and the random effect of variety i in the
 11 random model, S_j is the random effect of site j , $(\alpha S)_{ij}$ is the random interaction effect, and ε_{ijk} is
 12 the error term. Heritability was then calculated according to Piepho and Möhring (2007):
 13

$$H^2_{piepho} = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\bar{v}}{2}} \quad (10)$$

14 where σ_g^2 is the variance of a genotype calculated in formula (8) and \bar{v} is the mean variance of a
 15 difference of two adjusted environment means (BLUE) calculated in formula (9).

1

2 2.3.4. Genetics

3 We prepared the genotype table by translating it from IUPAC-IUB (International Union of Pure
4 and Applied Chemistry-International Union of Biochemistry) code to four bases (A, T, C, G) and
5 determined the major and minor allele for every single nucleotide polymorphism (SNP) by
6 determining the more, respectively less frequently occurring allele in the sample population. The
7 minor allele was coded as 1 and the major allele as 0 (Gauch et al., 2019). The genotype table was
8 further filtered to contain only SNPs with complete observations and was subsequently double-
9 centred (Gauch et al., 2019). Further, we performed double-centred principal component analysis
10 (DC-PCA) and agglomerative hierarchical k-means cluster analysis to estimate the genetic (dis-)
11 similarity among the varieties. For these analyses, only SNPs that varied within the individuals
12 (non-monomorphic) and with no missing observations were used.

13

14 2.3.5. Software

15 All analyses were performed in the R environment, version 4.2.3 (R Core Team, 2023), with the R
16 packages tidyverse (Wickham et al., 2019), readxl (Wickham & Bryan, 2023), reshape (Wickham,
17 2007) and reshape2 (Wickham, 2007) for data management, car (Fox & Weisberg, 2019), grafify
18 (Shenoy, 2021), emmeans (functions emmeans and emtrends) (Lenth, 2023), multcomp (function
19 cld) (Hothorn et al., 2008), MuMIn (function r.squaredGLMM) (Bartoń, 2023), and predictmeans
20 (function residplot) (Luo, 2022) for statistical analysis, DALEX (function explain) (Biecek, 2018),
21 inti (function H2cal) (Lozano-Isla, 2023), nlme (function lme) (Pinheiro, 2023), lme4 (function
22 lmer) (Bates et al., 2015) and randomForest (function randomForest) (Liaw & Wiener, 2002) for
23 model fitting, MLMOI (function moimport) (Hashemi & Schneider, 2020) for genotype data

1 translation, and ggplot2 (Wickham, 2016), ggbiplot (Vu, 2011), ggpubr (Kassambara, 2023), scales
2 (Wickham & Seidel, 2022), sjmisc (Lüdeke, 2018), and sjPlot (Lüdeke, 2023) for visualization.

3

4 3. Results

5 3.1. Genotypic variation in root length and surface area

6 The topsoil roots had on average a root length of 1.4 m root pc⁻¹ and a root surface area of 0.039
7 m² root pc⁻¹ across varieties and sites. In 0.15-0.50 m and 0.50-1.00 m soil depth, respectively, root
8 length averaged 5007 m root m⁻² soil and 5300 m root m⁻² soil and root surface area averaged 40
9 m² root m⁻² soil and 43 m² root m⁻² soil across varieties and sites. The variability in the data was
10 approximately 5 to 15 times higher for the sites than for the varieties (Table 5). The residual SD
11 was about one third of the total SD, indicating that the chosen models covered the sources of
12 variance to a major part (Table 5).

13 The varieties exhibited almost a twofold variation in root length and surface area across individual
14 sites. The topsoil roots ranged between 1.2–1.7 m root pc⁻¹ in root length and 0.031–0.045 m² root
15 pc⁻¹ in root surface area among varieties and differed significantly in both traits (Figure 1).
16 *Montalbano* consistently showed the highest root length and surface area, along with *Bernstein*,
17 *RGT Reform* and *Aurelius* (Figure 1). In contrast *Julie*, *Dagmar* and *Tenor* exhibited the lowest
18 values for both root traits. At a soil depth of 0.15-0.50 m, the root length did not significantly differ
19 among the varieties (average 5007 m root m⁻² soil), but root surface area was highest for *RGT*
20 *Reform* (45 m² root m⁻² soil), lowest for *Altigo* (36 m² root m⁻² soil) and intermediate for all other
21 varieties (Table 5; Figure 1). At a soil depth of 0.50-1.00 m, both root traits varied significantly
22 among the varieties, ranging from 4508 to 5877 m root m⁻² soil in root length and 35 to 49 m² root
23 m⁻² soil in root surface area. *MV Nador* and *Nogal* had the highest values, while *Julie* had the lowest

1 values for both traits (Table 5; Figure 1). Heritability ranged between 0.56–0.63 for both root traits
2 in all soil depths except for root length in 0.15-0.5 m depth ($H^2 = 0.41$) (Table 5).

3

4 3.2. Pedoclimatic and management effects on root length and surface area

5 The main effects of the pedoclimatic and management variables were significant for the root traits
6 in the subsoil only (Table 6). Irrespective of variety, both root length and surface area were
7 positively related to different temperature variables and root surface area was also negatively
8 related to precipitation over the entire season. In 0.50-1.00 m soil depth only, root length and
9 surface area were negatively related to soil bulk density and root surface area was also negatively
10 related to N fertilization. The multivariate random forest model analysis revealed temperature,
11 precipitation, soil clay content, and soil bulk density as most important variables for root length
12 and surface area in the topsoil, while temperature, precipitation, and soil bulk density were most
13 important in 0.15-0.50 m soil depth, and temperature, soil bulk density, and N fertilization in 0.50-
14 1.00 m soil depth (Supplementary figures 5 and 6).

15 For both root traits and all soil depths, significant interactions between variety and pedoclimatic
16 and management variables were observed in multiple instances. However, after Sidak p-value
17 adjustment for multiple pairwise comparison, only a few varieties showed slopes significantly
18 different from zero and from each other. Soil and climate variables, rather than management, were
19 significant drivers of root length and surface area of some varieties (Supplementary figures 7-9).
20 In the topsoil, the root traits were significantly related to soil clay content (negative), soil bulk
21 density (positive), soil pH (negative), temperature before emergence (positive), and temperature
22 before harvest (negative). These effects were most prominent in the varieties *Nogal* and *Aurelius*
23 (Supplementary figure 7). In contrast, all varieties showed significant correlations with one or more
24 pedoclimatic variables in their subsoil root traits, with some varieties responding more strongly

1 than others. An increase in soil pH and temperature before flowering, harvest, and over the season,
2 as well as a decrease in precipitation before emergence and over the season was correlated with an
3 increase in both root traits in 0.15-0.5 m and/or 0.5-1.0 m soil depth (Supplementary figures 8 and
4 9).

6 3.3. Variety-specific relationships between root length and surface area and yield

7 Yields of several varieties across sites were significantly positively correlated with longer roots
8 and greater surface area (Figure 2). The yields of varieties *Aurelius*, *MV Nador* and *RGT Reform*
9 showed significant relationships with root length or surface area in the topsoil only, whereas the
10 yields of varieties *Altigo*, *Julie*, *Montalbano* and *Tenor* showed significant relationships with root
11 length or surface area in the subsoil only. *Nogal* was the only variety with significant relationships
12 of both topsoil and subsoil root traits with yield, while *Bernstein* and *Dagmar* did not show any
13 significant relationships between yield and root traits.

14
15 For all varieties, the relationship between yield and root length and surface area varied significantly
16 with changing pedoclimatic and management conditions, but to very different extents (Figures 3-
17 5). For instance, varieties *Julie*, *MV Nador* and *Nogal* showed a strong positive relationship
18 between grain yield and topsoil root length at high temperatures before harvest, whereas this
19 relationship turned negative at low temperatures before harvest (Figure 3). For *Montalbano*, the
20 relationship between yield and root length and surface area at 0.50-1.00 m soil depth reversed from
21 positive to negative with increasing temperatures over the season (Figure 4). For *Altigo*, the positive
22 relationship of root length and surface area to yield became significantly steeper as temperatures
23 increased (Figure 4).

1 There were notable differences in the interaction between variety and pedoclimatic or management
2 variables between topsoil and subsoil root traits (Figure 5). In the topsoil, *Julie* and *MV Nador*
3 showed the most prominent differences in the relationship between yield and root length and
4 surface area under varying pedoclimatic conditions. In contrast, in the subsoil, *Altigo*, *Julie*,
5 *Montalbano* (0.50-1.00 m soil depth only) and *Nogal* (0.15-0.50 m and 0.50-1.00 m soil depth)
6 showed the most prominent differences, both in terms of number of significant interactions and
7 effect sizes. For the other varieties, changes in the relationship between yield and root traits under
8 changing pedoclimatic and management conditions were generally less pronounced, irrespective
9 of soil depth (particularly for varieties *Bernstein*, *Dagmar* and *Tenor*), or were limited to topsoil
10 root traits only (particularly for varieties *Aurelius* und *RGT Reform*).

11

12 3.4. Genetic similarities of wheat varieties

13 More than 50% of the variance in the SNP data was explained by the first four interaction principal
14 components (IPCs) of the DC-PCA analysis, with a clear decrease for the tenth component
15 (Supplementary figure 10). Two varieties, *MV Nador* and *Nogal*, were prominently separated from
16 the other varieties in the first IPC (17% explained variance) and from each other in the second IPC
17 (14% explained variance). In the third IPC, varieties *Bernstein* and *Dagmar* represented the
18 extremes on both ends and in the fourth IPC, varieties *Altigo* and *Julie* differed strongest from the
19 other varieties (Supplementary figure 10). A similar clustering of genotypes was revealed by
20 agglomerative hierarchical k-means cluster analysis, where *MV Nador* and *Nogal*, *Dagmar* and
21 *Tenor*, *Bernstein* and *Montalbano*, and *Altigo*, *Julie*, *RGT Reform*, and *Aurelius* formed the most
22 prominent clusters (Supplementary figure 11).

1 4. Discussion

2 4.1. Genotypic and environmental influences on root trait variability

3 Both root length and surface area varied strongly, and this variation was about 10 times greater
4 among sites than varieties. In spite of the dominant site effect, we also observed a clear genotypic
5 pattern in root length and surface area irrespective of site. *Bernstein* and *Montalbano* produced
6 longer roots with a larger surface area in the topsoil, whereas *MV Nador* and *Nogal* had greater
7 root length and larger root surface area in deeper soil layers. Although publicly available pedigree
8 information does not indicate any shared breeding history among these 10 varieties, our genetic
9 analysis reveals a higher degree of relatedness between *MV Nador* and *Nogal*, as well as between
10 *Bernstein* and *Montalbano*, than between other pairs of the 10 varieties. This is represented by the
11 proximity of their IPC scores in the DC-PCA and the short vertical distances in the cluster analysis
12 dendrogram (Zhang et al., 2017). Moreover, considering that *MV Nador* (country of origin:
13 Hungary) and *Nogal* (France; registered in Spain) are cultivated more frequently in Southern
14 Europe, while *Bernstein* (Germany) and *Montalbano* (Switzerland) are typical of Central European
15 regions, it is plausible that genetically driven differences in rooting patterns may reflect
16 environmental adaptation. However, further research in larger variety panels would be needed to
17 confirm such associations.

18 The heritability for root length from 0.41 to 0.59 is in line with previous studies, which reported
19 values of 0.62 in soil (Monyo & Whittington, 1970) and 0.48 to 0.70 in hydroponic culture (Xu et
20 al., 2021). High values for traits differing between varieties can be attributed to a significant genetic
21 influence on the phenotypic variance of these traits (Piepho & Möhring, 2007). Conversely, low
22 values for non-significant traits do not necessarily exclude genetic influence but may result from
23 small mean differences and/or large error variances in the phenotype, often caused by high
24 environmental influence (Oldenbroek & van der Waaij, 2015). Heritability for root surface area

1 was generally higher (0.57-0.63) than that for root length, which supports the outcomes of the
2 mixed model approach. In other studies, heritability estimates varied for root traits due to varying
3 stages of growth and environments where genotypes were assessed (Guo et al., 2021; Guo et al.,
4 2020; Timaeus et al., 2021). The variation in heritability values suggests that genotypic expression
5 is influenced by many genes and affected by environmental factors and their interactions. (Mathew
6 & Shimelis, 2022).

7 The significant variation in root traits among sites and the identified genotypic patterns provide
8 deeper insights into how different wheat varieties adapt to varying environmental conditions. The
9 discovery of genotypic subgroups with distinct root traits, such as those favouring topsoil
10 exploration or deeper root proliferation, allows breeders to target specific traits for improvement.
11 For instance, varieties like *MV Nador* and *Nogal*, which seem to be adapted to warm and dry
12 environments with deeper roots, could be further used in new crosses for regions experiencing
13 similar conditions.

14 15 4.2. Pedoclimatic effects on root length and surface area

16 Temperature between emergence and harvest was a major driver of both root length and surface
17 area. In the subsoil, all varieties showed higher root length and surface area with higher
18 temperature, whereas in the topsoil, only individual varieties, most prominently *Nogal* and
19 *Aurelius*, were affected. During the 2021/22 wheat growing season, the natural climate gradient
20 across Europe was intensified, with greater temperature and precipitation anomalies in the south
21 compared to the north (Tripathy & Mishra, 2023). Except for DE-Fr, HU-Sz, and LT-Do,
22 temperatures in 2021/22 were 1-2.5 °C above MAT, and precipitation was on average 30% lower
23 than MAP at all sites. With the lack of rain and higher-than-normal temperatures, it is likely that

1 evaporation also increased (Solomon et al., 2007), potentially inducing drought stress at several
2 sites.

3 Our data suggest that an overall warmer climate stimulates root growth in deeper soil layers
4 irrespective of variety. Plants have an optimal temperature range for root growth and functioning,
5 which ranges between 14 and 18 °C for wheat roots (Porter & Gawith, 1999). In warmer areas,
6 increased temperatures can reduce root development in warmer topsoil layers while promoting root
7 development in the cooler subsoil layers (Calleja Cabrera et al., 2020; Koevoets et al., 2016;
8 Ribeiro et al., 2014). High temperatures affect cell division and differentiation, reducing plant
9 growth and development (Liu et al., 2022; Qi & Zhang, 2020), and alters the stability of
10 membranes, proteins, nucleic acids, and cytoskeleton components (Vu et al., 2019). In contrast,
11 deeper soil layers often provide more favourable conditions for root growth due to lower and more
12 stable temperatures resulting from the natural soil temperature gradient (Lynch & Wojciechowski,
13 2015).

14 Additionally, higher temperatures lead to increased evapotranspiration (Goyal, 2004; Solomon et
15 al., 2007), increasing water uptake from deeper soil layers (Asseng et al., 1998). Deep roots have
16 been considered to be one of the most effective ways to facilitate full utilization of subsoil water
17 when topsoil water is not available under drought conditions (Gowda et al., 2011; Lopes &
18 Reynolds, 2010; Lynch, 2018; Maqbool et al., 2022; Shoaib et al., 2022). This is reflected in the
19 data presented herein, which showed increases in root surface area in deep soil with decreasing
20 precipitation over the entire season. During drought, plants reduce water use by closing stomata,
21 which lowers CO₂ intake and photosynthesis, ultimately reducing biomass production (Chaves et
22 al., 2002). While root growth initially slows, drought avoidance mechanisms soon promote
23 increased primary and secondary root growth, extending into deeper or moister soil layers

1 (Dinneny, 2019). This expansion of root surface area enhances water uptake under limited moisture
2 conditions.

3 Besides temperature, soil bulk density and N fertilization were universal drivers of root length and
4 surface area at a soil depth of 0.50-1.00 m, irrespective of variety. Generally, more compacted soil
5 leads to reduced root length, surface area, and dry matter, but may lead to a larger root diameter
6 (Merotto & Mundstock, 1999; Rich & Watt, 2013), which is consistent with our findings for root
7 length and surface area. Higher bulk density increases mechanical resistance, requiring more
8 energy for root penetration and reducing root elongation (Bengough et al., 2011; Kolb et al., 2017).
9 Compacted soils also have reduced porosity, which limits water infiltration, aeration, and nutrient
10 diffusion (Lipiec et al., 2012). As a result, plants reduce root proliferation in these zones due to
11 poor resource availability (Whalley et al., 2005).

12 Being highly mobile in soils, N is generally the most limiting nutrient in arable farming together
13 with P (Koevoets et al., 2016). The growth of plant roots is locally stimulated by N uptake,
14 although, in total, less photosynthates are allocated to root growth as N availability increases
15 (Rasse, 2002). Hence, low N fertilization appears to stimulate deep root growth as a result of
16 acquiring proportionally more N from deeper soil (Koevoets et al., 2016; Rasse, 2002). This
17 supports previous findings where topsoil root biomass of winter wheat was negatively correlated
18 with N fertilization, while subsoil root biomass was positively correlated with precipitation under
19 wet spring conditions, suggesting that root production followed the leaching of N (Hirte et al.,
20 2018). The universal importance of N for root traits in the subsoil suggests that root foraging for
21 this nutrient is largely independent of climate conditions.

22

1 4.3. Interrelation of root plasticity and grain yield under varying pedoclimatic conditions

2 Grain yield was positively related to an increase in both root length and surface area but whether
3 this link was related to the top- or subsoil was highly dependent on the variety. Among the ten
4 varieties included in our study, three showed a distinct relationship of yield to topsoil root traits,
5 four to subsoil root traits, one to both and two to neither. Several studies have suggested a positive
6 effect of more and deeper roots on grain yield, particularly through increased water and nutrient
7 uptake and consequently higher drought adaptation, which are beneficial for crop yields
8 (Kirkegaard et al., 2007; Maqbool et al., 2022; Odone et al., 2023). Deeper roots are also associated
9 with cooler crop canopies and are correlated with more root biomass, both potentially increasing
10 crop yield (Heinemann et al., 2025; Heinemann et al., 2023; Li et al., 2019; Lopes & Reynolds,
11 2010). These benefits of increased root length in deep soil appear to come at no ‘cost’ to shoot
12 growth or yield and as such should remain a target for breeding (Severini et al., 2020). This
13 encourages the prospect to successfully select wheat varieties with an improved root system to
14 achieve higher yields in warmer environments.

15 Under changing environmental conditions, the relationship between root traits and grain yield
16 changed significantly for some varieties. Across sites, *Altigo*, *Julie*, *Montalbano*, *MV Nador* and
17 *Nogal* demonstrated high root plasticity and the potential to sustain yields under increasingly harsh
18 climatic conditions. This was particularly prominent for *Altigo* and *Julie*, which displayed
19 increased deep root length and surface area with rising temperatures and at the same time
20 proportionally higher yield increases. For *Nogal*, the positive relationship between increased deep
21 root length and surface area and yield was more pronounced at the cooler than the warmer sites.
22 By contrast, *Montalbano* only showed yield increases with increased deep root length and surface
23 area at low temperatures but yield decreases at high temperatures. The importance of root plasticity
24 for sustaining yields under variable conditions has also been proposed for rice under drought and

1 nutrient stresses (Sandhu et al., 2016; Xie et al., 2021), for wheat under soil compaction (Correa et
2 al., 2019), and for maize under different water and nutrient scenarios (Hochholdinger & Tuberosa,
3 2009). Overall, root phenotypic plasticity has been proposed as a breeding target for developing
4 more productive crops in variable environments such as cool, temperate, and warm climates
5 (Schneider & Lynch, 2020).

6 For the varieties without a notable relationship between changes in yield and changes in root length
7 or surface area, physiological processes or root traits not measured in our study might be more
8 important for yield formation than the included traits. Among others, seedling root growth supports
9 early soil exploration, promoting better nutrient and water uptake during establishment (Xie et al.,
10 2017). Root oxidation activity enhances rhizosphere conditions by releasing oxygen, aiding
11 nutrient uptake by roots in waterlogged or anaerobic soils (Yang et al., 2012). A steeper root growth
12 angle promotes deeper rooting, increasing access to subsoil moisture and improving drought
13 resilience and yield stability (Lynch, 2013). These traits or processes also contribute to yield
14 formation, though their relative significance may vary depending on the variety.

15 In summary, the ten varieties can be broadly grouped according to distinct patterns of
16 interrelationships between root plasticity and yield: a consistent relationship where changes in yield
17 are proportional to changes in root traits irrespective of environmental conditions and a varying
18 relationship where changes in yield become more or less pronounced with changes in root traits
19 depending on the environmental conditions. Those strategies might have different advantages in
20 different environments: When the availability of soil resources such as water or nutrients varies
21 frequently, varieties may benefit more from a consistent relationship to ensure a positive yield
22 return on the investment in metabolite allocation to roots. By contrast, when the availability of
23 resources remains stable, irrespective of sufficiency or deficiency for optimal yield, varieties might
24 keep their metabolic costs to a minimum when a positive yield return on the investment in

1 metabolite allocation to roots only occurs under these particular growth conditions. Among the ten
2 varieties, some exhibit both consistent and variable relationships between yield and root length or
3 surface area, particularly in the subsoil, indicating partial agreement rather than a clear separation.
4 Hence, breeding efforts could simultaneously pursue both strategies, leading to varieties suited for
5 both stable and highly variable environments..

6 Given the inherent difficulties in measuring root traits, the lack of cost-effective screening tools,
7 and too little evidence of benefit if selections for specific root traits are made, roots have up to now
8 garnered only little attention in breeding programs. However, through high-throughput
9 phenotyping tools like shovelomics (Trachsel et al., 2011), X-ray computed tomography (Mooney
10 et al., 2012), and minirhizotrons, root trait screening has recently been advanced. Additionally,
11 electromagnetic induction (EMI) surveying offers a non-invasive method to assess spatial soil
12 variability and root–soil interactions in the field (Doolittle & Brevik, 2014; Whalley et al., 2017).
13 These technologies, combined with genomic selection approaches, are making the inclusion of
14 belowground traits in crop improvement more feasible and effective for future studies. Targeting
15 root traits can lead to the development of more resilient wheat varieties capable of maintaining or
16 improving yields under varying and increasingly harsh climatic conditions, such as drought and
17 temperature fluctuations.

18

19 4.4. Suitability of the study design

20 The field design of this study is notable for its scale and consistency: root samples were collected
21 from the same set of 10 wheat varieties on 11 European sites, covering a wide pedoclimatic
22 gradient. This design enabled the collection of over 3,500 root samples as well as diverse
23 pedoclimatic and management data, providing a robust dataset for explorative correlation analyses.
24 Compared to typical root phenotyping field studies, which often use only one or a few sites

1 (Heinemann et al., 2023), our dataset is unusually rich in environmental breadth. This facilitates
2 the assessment of environmental influences using quantitative gradients of soil, climate, and
3 management variables, instead of treating site as nominal variable.

4 However, as data were collected in only one growing season, the geographical climate gradient
5 needed to serve as a proxy for climate variation. Sampling was carried out using a standardized,
6 machine-operated method by two trained teams, minimizing bias from personnel variability. Still,
7 the timing of sampling—conducted after harvest—and the duration of sample transport and storage
8 varied slightly across sites and may have influenced root integrity. Similarly, sample processing
9 was consistent and machine-assisted, but the washing method and sieve size, while standardized,
10 may not have been optimal for capturing full root system architecture (Livesley et al., 1999; Pierret
11 et al., 2005). As a result, we focused on root length and surface area, which are more reliably
12 preserved and measured than other root system architecture traits such as root growth angle or
13 number of root tips under these sample processing conditions.

14 The use of two different upscaling approaches for topsoil and subsoil root traits is another limitation
15 of our study. In the topsoil, upscaling to the area was not appropriate due to the small sample size
16 per field plot (four crown root halves). In contrast, subsoil samples collected by soil coring could
17 not be linked to individual wheat plants and therefore required upscaling to the soil surface area.
18 This inconsistency prevented the calculation of total root length and surface area across the total
19 soil depth of 1 m. As a result, our analysis focuses on the variability of root traits within individual
20 soil depths.

21 Correlation analyses based on linear models are a valuable tool for exploring relationships between
22 variables, but they have key limitations. Data transformations can distort results, especially when
23 linearity is assumed without testing for non-linear patterns. These analyses often overlook
24 interaction effects between predictors and risk overfitting when too many predictors are included.

1 In agriculture, co-linearity among soil, climate, and management variables (Supplementary figure
2 4) can complicate interpretation. To move toward causal understanding, future studies should use
3 multi-year, site-replicated trials, alongside controlled experiments in which one factor is varied at
4 a time.

5 6 Supplementary files

7 Detailed information on sampling, sample processing, and measurements is given in SI1 and
8 information on data analysis is given in SI2. Supplementary tables are presented in SI3 and
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- 1 References
- 2 Addy, J. W. G., Ellis, R. H., MacLaren, C., Macdonald, A. J., Semenov, M. A., & Mead, A.
- 3 (2022). A heteroskedastic model of Park Grass spring hay yields in response to weather
- 4 suggests continuing yield decline with climate change in future decades. *Journal of The*
- 5 *Royal Society Interface*, 19(193), 20220361. <https://doi.org/doi:10.1098/rsif.2022.0361>
- 6 Adeleke, E., Millas, R., McNeal, W., Faris, J., & Taheri, A. (2020). Variation Analysis of Root
- 7 System Development in Wheat Seedlings Using Root Phenotyping System. *Agronomy*,
- 8 10(2), 206. <https://www.mdpi.com/2073-4395/10/2/206>
- 9 Agnolucci, P., & De Lipsis, V. (2020). Long-run trend in agricultural yield and climatic factors in
- 10 Europe. *Climatic Change*, 159(3), 385-405. <https://doi.org/10.1007/s10584-019-02622-3>
- 11 Agrarmeteorologisches Messnetz Sachsen. (2023). *Agrarmeteorologisches Messnetz Sachsen -*
- 12 *Wetterdaten*. <https://www.landwirtschaft.sachsen.de/Wetter09>
- 13 Agrometeo. (2024). <https://www.agrometeo.ch/de>
- 14 Aiken, L. (1991). Multiple regression: Testing and interpreting interactions. *Sage Publications*
- 15 *google schola*, 2, 513-531.
- 16 Ajjur, S. B., & Al-Ghamdi, S. G. (2021). Evapotranspiration and water availability response to
- 17 climate change in the Middle East and North Africa. *Climatic Change*, 166(3), 28.
- 18 <https://doi.org/10.1007/s10584-021-03122-z>
- 19 Akman, H. (2020). Comparison of Field Crops with Tap and Fibrous Root System at Early and
- 20 Late Growth Stages. *Turkish Journal of Agriculture - Food Science and Technology*, 8(5),
- 21 1181-1187. <https://doi.org/10.24925/turjaf.v8i5.1181-1187.3350>
- 22 Alahmad, S., El Hassouni, K., Bassi, F. M., Dinglasan, E., Youssef, C., Quarry, G., Aksoy, A.,
- 23 Mazzucotelli, E., Juhász, A., Able, J. A., Christopher, J., Voss-Fels, K. P., & Hickey, L. T.
- 24 (2019). A Major Root Architecture QTL Responding to Water Limitation in Durum Wheat
- 25 [Original Research]. *Frontiers in Plant Science*, 10.
- 26 <https://doi.org/10.3389/fpls.2019.00436>
- 27 Asseng, S., Ritchie, J. T., Smucker, A. J. M., & Robertson, M. J. (1998). Root growth and water
- 28 uptake during water deficit and recovering in wheat. *Plant and Soil*, 201(2), 265-273.
- 29 <https://doi.org/10.1023/A:1004317523264>
- 30 Bartoń, K. (2023). *_MuMIn: Multi-Model Inference_*. In (Version 1.47.5)
- 31 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models
- 32 Using lme4. *Journal of Statistical Software*, 67(1), 1-48.
- 33 <https://doi.org/10.18637/jss.v067.i01>.
- 34 Bayrisches Landesamt für Umwelt. (2023). *Gewässerkundlicher Dienst Bayern*.
- 35 <https://www.gkd.bayern.de/en/meteo>
- 36 Bengough, A. G., McKenzie, B. M., Hallett, P. D., & Valentine, T. A. (2011). Root elongation,
- 37 water stress, and mechanical impedance: a review of limiting stresses and beneficial root
- 38 tip traits. *Journal of Experimental Botany*, 62(1), 59-68. <https://doi.org/10.1093/jxb/erq350>
- 39 Biecek, P. (2018). DALEX: Explainers for Complex Predictive Models in R. *Journal of Machine*
- 40 *Learning Research*, 19(84), 1-5. <http://jmlr.org/papers/v19/18-416.html>
- 41 Brás, T., Seixas, J., Carvalhais, N., & Jägermeyr, J. (2021). Severity of drought and heatwave
- 42 crop losses tripled over the last five decades in Europe. *Environmental Research Letters*,
- 43 16. <https://doi.org/10.1088/1748-9326/abf004>
- 44 Calleja Cabrera, J., Boter, M., Oñate-Sánchez, L., & Pernas, M. (2020). Root Growth Adaptation
- 45 to Climate Change in Crops. *Frontiers in Plant Science*, 11, 544.
- 46 <https://doi.org/10.3389/fpls.2020.00544>
- 47 Chaves, M. M., Pereira, J. S., Maroco, J., Rodrigues, M. L., Ricardo, C. P., Osório, M. L.,
- 48 Carvalho, I., Faria, T., & Pinheiro, C. (2002). How plants cope with water stress in the
- 49 field. Photosynthesis and growth. *Ann Bot*, 89 Spec No(7), 907-916.
- 50 <https://doi.org/10.1093/aob/mcf105>

- 1 Chen, H., Wei, J., Tian, R., Zeng, Z., Tang, H., Liu, Y., Xu, Q., Deng, M., Jiang, Q., Chen, G.,
2 Liu, Y., Li, W., Qi, P., Jiang, Y., Jiang, Y., Tang, L., Wei, Y., Zheng, Y., Lan, X., & Ma, J.
3 (2022). A major quantitative trait locus for wheat total root length associated with
4 precipitation distribution. *Front Plant Sci*, 13, 995183.
5 <https://doi.org/10.3389/fpls.2022.995183>
- 6 Colombo, M., Roumet, P., Salon, C., Jeudy, C., Lamboeuf, M., Lafarge, S., Dumas, A.-V.,
7 Dubreuil, P., Ngo, W., Derepas, B., Beauchêne, K., Allard, V., Le Gouis, J., & Rincant, R.
8 (2022). Genetic Analysis of Platform-Phenotyped Root System Architecture of Bread and
9 Durum Wheat in Relation to Agronomic Traits [Original Research]. *Frontiers in Plant*
10 *Science, Volume 13 - 2022*. <https://doi.org/10.3389/fpls.2022.853601>
- 11 Correa, J., Postma, J. A., Watt, M., & Wojciechowski, T. (2019). Soil compaction and the
12 architectural plasticity of root systems. *Journal of Experimental Botany*, 70(21), 6019-
13 6034. <https://doi.org/10.1093/jxb/erz383>
- 14 Dinneny, J. R. (2019). Developmental Responses to Water and Salinity in Root Systems. *Annual*
15 *Review of Cell and Developmental Biology*, 35(Volume 35, 2019), 239-257.
16 <https://doi.org/https://doi.org/10.1146/annurev-cellbio-100617-062949>
- 17 Doolittle, J. A., & Brevik, E. C. (2014). The use of electromagnetic induction techniques in soils
18 studies. *Geoderma*, 223-225, 33-45.
19 <https://doi.org/https://doi.org/10.1016/j.geoderma.2014.01.027>
- 20 Duan, D., Feng, X., Wu, N., Tian, Z., Dong, X., Liu, H., Nan, Z., & Chen, T. (2023). Drought
21 Eliminates the Difference in Root Trait Plasticity and Mycorrhizal Responsiveness of Two
22 Semiarid Grassland Species with Contrasting Root System. *Int J Mol Sci*, 24(12).
23 <https://doi.org/10.3390/ijms241210262>
- 24 EEA, E. E. A. (2017). Biogeographical regions in Europe. In
25 BiogeographicalRegionMap2016_2c_ns_insert_v2.eps.75dpi.png (Ed.), (pp. This map
26 reflects the status of the Biogeographical Regions in Europe from 2016 onwards.
27 Changes compared to previous versions are explained in the source dataset.): European
28 Topic Centre on Biological Diversity (ETC/BD).
- 29 EUPVP - Common Catalogue Information System. (2023). *EUPVP - Common Catalogue*
30 *Information System*. Retrieved 06.04. from [https://ec.europa.eu/food/plant-variety-](https://ec.europa.eu/food/plant-variety-portal/index.xhtml?jsessionid=y-tWkVfMm7POADgQyjRRrBaB1FOzeDp2kEcp4HtQHWFJ2r0IQjhZ!1212179126)
31 [portal/index.xhtml?jsessionid=y-](https://ec.europa.eu/food/plant-variety-portal/index.xhtml?jsessionid=y-tWkVfMm7POADgQyjRRrBaB1FOzeDp2kEcp4HtQHWFJ2r0IQjhZ!1212179126)
32 [tWkVfMm7POADgQyjRRrBaB1FOzeDp2kEcp4HtQHWFJ2r0IQjhZ!1212179126](https://ec.europa.eu/food/plant-variety-portal/index.xhtml?jsessionid=y-tWkVfMm7POADgQyjRRrBaB1FOzeDp2kEcp4HtQHWFJ2r0IQjhZ!1212179126)
- 33 FAO. (2013). *Climate-Smart Agriculture Sourcebook*. <https://www.fao.org/3/i3325e/i3325e.pdf>
- 34 Federal Office of Meteorology and Climatology MeteoSwiss. (2022). *Federal Office of*
35 *Meteorology and Climatology MeteoSwiss*. [https://www.meteoswiss.admin.ch/services-](https://www.meteoswiss.admin.ch/services-and-publications/applications/ext/climate-climsheet.html)
36 [and-publications/applications/ext/climate-climsheet.html](https://www.meteoswiss.admin.ch/services-and-publications/applications/ext/climate-climsheet.html)
- 37 Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression*. In (Version 3)
38 <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- 39 Fradgley, N., Evans, G., Biernaskie, J. M., Cockram, J., Marr, E. C., Oliver, A. G., Ober, E., &
40 Jones, H. (2020). Effects of breeding history and crop management on the root
41 architecture of wheat. *Plant and Soil*, 452(1), 587-600. [https://doi.org/10.1007/s11104-](https://doi.org/10.1007/s11104-020-04585-2)
42 [020-04585-2](https://doi.org/10.1007/s11104-020-04585-2)
- 43 Frasier, I., Noellemeyer, E., Fernandez, R., & Quiroga, A. (2016). Direct field method for root
44 biomass quantification in agroecosystems. *MethodsX*, 3, 513-519.
45 <https://doi.org/10.1016/j.mex.2016.08.002>
- 46 Fry, E. L., Evans, A. L., Sturrock, C. J., Bullock, J. M., & Bardgett, R. D. (2018). Root
47 architecture governs plasticity in response to drought. *Plant Soil*, 433(1), 189-200.
48 <https://doi.org/10.1007/s11104-018-3824-1>
- 49 Gauch, H. G. J., Sheng, Q., Hans-Peter, P., Linda, Z., & Rui, C. (2019). Consequences of PCA
50 graphs, SNP codings, and PCA variants for elucidating population structure. *bioRxiv*,
51 393611. <https://doi.org/10.1101/393611>
- 52 GeoSphere Austria. (2023). *Messstationen Tagesdaten v1*. <https://doi.org/10.60669/1dx2-3j91>

- 1 Giorgi, F., Bi, X., & Pal, J. (2004). Mean, interannual variability and trends in a regional climate
2 change experiment over Europe. II: climate change scenarios (2071–2100). *Climate*
3 *Dynamics*, 23(7), 839-858. <https://doi.org/10.1007/s00382-004-0467-0>
- 4 Gogna, A., Schulthess, A. W., Röder, M. S., Ganal, M. W., & Reif, J. C. (2022). Gabi wheat a
5 panel of European elite lines as central stock for wheat genetic research. *Scientific Data*,
6 9(1), 538. <https://doi.org/10.1038/s41597-022-01651-5>
- 7 Gowda, V. R. P., Henry, A., Yamauchi, A., Shashidhar, H. E., & Serraj, R. (2011). Root biology
8 and genetic improvement for drought avoidance in rice. *Field Crops Research*, 122(1), 1-
9 13. <https://doi.org/10.1016/j.fcr.2011.03.001>
- 10 Goyal, R. K. (2004). Sensitivity of evapotranspiration to global warming: a case study of arid
11 zone of Rajasthan (India). *Agricultural Water Management*, 69(1), 1-11.
12 <https://doi.org/10.1016/j.agwat.2004.03.014>
- 13 Gregory, P. J. (2006). Roots and the Architecture of Root Systems. In *Plant Roots* (pp. 18-44).
14 <https://doi.org/https://doi.org/10.1002/9780470995563.ch2>
- 15 Grossman, J. D., & Rice, K. J. (2012). Evolution of root plasticity responses to variation in soil
16 nutrient distribution and concentration. *Evolutionary Applications*, 5(8), 850-857.
17 <https://doi.org/https://doi.org/10.1111/j.1752-4571.2012.00263.x>
- 18 Gulino, D., Sayeras, R., Serra, J., Betbese, J., Doltra, J., Gracia-Romero, A., & Lopes, M. S.
19 (2023). Impact of rising temperatures on historical wheat yield, phenology, and grain size
20 in Catalonia [Original Research]. *Frontiers in Plant Science*, 14.
21 <https://doi.org/10.3389/fpls.2023.1245362>
- 22 Guo, H., Ayalew, H., Seethepalli, A., Dhakal, K., Griffiths, M., Ma, X.-F., & York, L. M. (2021).
23 Functional phenomics and genetics of the root economics space in winter wheat using
24 high-throughput phenotyping of respiration and architecture. *New Phytologist*, 232(1), 98-
25 112. <https://doi.org/https://doi.org/10.1111/nph.17329>
- 26 Guo, X., Svane, S. F., Füchtbauer, W. S., Andersen, J. R., Jensen, J., & Thorup-Kristensen, K.
27 (2020). Genomic prediction of yield and root development in wheat under changing water
28 availability. *Plant Methods*, 16(1), 90. <https://doi.org/10.1186/s13007-020-00634-0>
- 29 Hashemi, M., & Schneider, K. (2020). *MLMOI: Estimating Frequencies, Prevalence and*
30 *Multiplicity of Infection*. In (Version 0.1.1)
- 31 Hecht, V. L., Temperton, V. M., Nagel, K. A., Rascher, U., & Postma, J. A. (2016). Sowing
32 Density: A Neglected Factor Fundamentally Affecting Root Distribution and Biomass
33 Allocation of Field Grown Spring Barley (*Hordeum Vulgare* L.) [Original Research].
34 *Frontiers in Plant Science, Volume 7 - 2016*. <https://doi.org/10.3389/fpls.2016.00944>
- 35 Heinemann, H., Durand-Maniclas, F., Seidel, F., Ciulla, F., Bárcena, T. G., Camenzind, M.,
36 Corrado, S., Csürös, Z., Czako, Z., Eylembosch, D., Ficke, A., Flamm, C., Herrera, J. M.,
37 Horáková, V., Hund, A., Lüddecke, F., Platz, F., Poós, B., Rasse, D., . . . Don, A. (2025).
38 Optimising Root and Grain Yield Through Variety Selection in Winter Wheat Across a
39 European Climate Gradient. *European Journal of Soil Science*, 76(2), e70077.
40 <https://doi.org/https://doi.org/10.1111/ejss.70077>
- 41 Heinemann, H., Hirte, J., Seidel, F., & Don, A. (2023). Increasing root biomass derived carbon
42 input to agricultural soils by genotype selection – a review. *Plant and Soil*.
43 <https://doi.org/10.1007/s11104-023-06068-6>
- 44 Hirte, J., Leifeld, J., Abiven, S., & Mayer, J. (2018). Maize and wheat root biomass, vertical
45 distribution, and size class as affected by fertilization intensity in two long-term field trials.
46 *Field Crops Research*, 216, 197-208. <https://doi.org/10.1016/j.fcr.2017.11.023>
- 47 Hirte, J., Walder, F., Hess, J., Buchi, L., Colombi, T., van der Heijden, M. G., & Mayer, J. (2021).
48 Enhanced root carbon allocation through organic farming is restricted to topsoils. *Sci*
49 *Total Environ*, 755(Pt 2), 143551. <https://doi.org/10.1016/j.scitotenv.2020.143551>
- 50 Hochholdinger, F., & Tuberosa, R. (2009). Genetic and genomic dissection of maize root
51 development and architecture. *Current opinion in plant biology*, 12(2), 172-177.

- 1 Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous Inference in General Parametric
2 Models. *Biometrical Journal*, 50(3), 346-363.
- 3 Hund, A., Richner, W., Soldati, A., Fracheboud, Y., & Stamp, P. (2007). Root morphology and
4 photosynthetic performance of maize inbred lines at low temperature. *European Journal*
5 *of Agronomy*, 27(1), 52-61. <https://doi.org/10.1016/j.eja.2007.01.003>
- 6 IWGSC, T. I. W. G. S. C., Appels, R., Eversole, K., Stein, N., Feuillet, C., Keller, B., Rogers, J.,
7 Pozniak, C. J., Choulet, F., Distelfeld, A., Poland, J., Ronen, G., Sharpe, A. G., Barad,
8 O., Baruch, K., Keeble-Gagnère, G., Mascher, M., Ben-Zvi, G., Josselin, A.-A., . . .
9 Wang, L. (2018). Shifting the limits in wheat research and breeding using a fully
10 annotated reference genome. *Science*, 361(6403), eaar7191.
11 <https://doi.org/doi:10.1126/science.aar7191>
- 12 Karlova, R., Boer, D., Hayes, S., & Testerink, C. (2021). Root plasticity under abiotic stress.
13 *Plant Physiology*, 187(3), 1057-1070. <https://doi.org/10.1093/plphys/kiab392>
- 14 Kassambara, A. (2023). *ggpubr: 'ggplot2' Based Publication Ready Plots*. In (Version 0.6.0)
15 <https://rpkgs.datanovia.com/ggpubr/>
- 16 Kell, D. B. (2011). Breeding crop plants with deep roots: their role in sustainable carbon, nutrient
17 and water sequestration. *Annals of Botany*, 108(3), 407-418.
18 <https://doi.org/10.1093/aob/mcr175>
- 19 Khan, M. A., Gemenet, D. C., & Villordon, A. (2016). Root System Architecture and Abiotic
20 Stress Tolerance: Current Knowledge in Root and Tuber Crops [Review]. *Frontiers in*
21 *Plant Science*, 7. <https://doi.org/10.3389/fpls.2016.01584>
- 22 Kirkegaard, J. A., Lilley, J. M., Howe, G. N., & Graham, J. M. (2007). Impact of subsoil water use
23 on wheat yield. *Australian Journal of Agricultural Research*, 58(4), 303-315.
24 <https://doi.org/10.1071/AR06285>
- 25 Koevoets, I. T., Venema, J. H., Elzenga, J. T. M., & Testerink, C. (2016). Roots Withstanding
26 their Environment: Exploiting Root System Architecture Responses to Abiotic Stress to
27 Improve Crop Tolerance [Review]. *Frontiers in Plant Science*, 7.
28 <https://doi.org/10.3389/fpls.2016.01335>
- 29 Kolb, E., Legué, V., & Bogeat-Triboulot, M.-B. (2017). Physical root–soil interactions. *Physical*
30 *Biology*, 14(6), 065004. <https://doi.org/10.1088/1478-3975/aa90dd>
- 31 Le Gouis, J., Oury, F.-X., & Charmet, G. (2020). How changes in climate and agricultural
32 practices influenced wheat production in Western Europe. *Journal of Cereal Science*, 93,
33 102960. <https://doi.org/10.1016/j.jcs.2020.102960>
- 34 Lenth, R. (2023). *emmeans: Estimated Marginal Means, aka*
35 *Least-Squares Means*. In (Version 1.8.5) <https://github.com/rvlenth/emmeans>
- 36 Li, C., Li, L., Reynolds, M. P., Wang, J., Chang, X., Mao, X., & Jing, R. (2021). Recognizing the
37 hidden half in wheat: root system attributes associated with drought tolerance. *Journal of*
38 *Experimental Botany*, 72(14), 5117-5133. <https://doi.org/10.1093/jxb/erab124>
- 39 Li, X., Ingvordsen, C. H., Weiss, M., Rebetzke, G. J., Condon, A. G., James, R. A., & Richards,
40 R. A. (2019). Deeper roots associated with cooler canopies, higher normalized difference
41 vegetation index, and greater yield in three wheat populations grown on stored soil water.
42 *Journal of Experimental Botany*, 70(18), 4963-4974. <https://doi.org/10.1093/jxb/erz232>
- 43 Liaw, A., & Wiener, M. (2002). Classification and Regression by randomForest. *R News*, 2(3),
44 18-22. <https://CRAN.R-project.org/doc/Rnews/>
- 45 Lipiec, J., Horn, R., Pietrusiewicz, J., & Siczek, A. (2012). Effects of soil compaction on root
46 elongation and anatomy of different cereal plant species. *Soil and Tillage Research*, 121,
47 74-81. <https://doi.org/https://doi.org/10.1016/j.still.2012.01.013>
- 48 Lithuanian Hydrometeorological Service under the Ministry of Environment. (2022).
49 <https://www.meteo.lt/en/other/observation-network/>
- 50 Liu, J., Liu, Y., Wang, S., Cui, Y., & Yan, D. (2022). Heat Stress Reduces Root Meristem Size
51 via Induction of Plasmodesmal Callose Accumulation Inhibiting Phloem Unloading in

- 1 Arabidopsis. *International Journal of Molecular Sciences*, 23(4), 2063.
2 <https://www.mdpi.com/1422-0067/23/4/2063>
- 3 Livesley, S. J., Stacey, C. L., Gregory, P. J., & Buresh, R. J. (1999). Sieve size effects on root
4 length and biomass measurements of maize (*Zea mays*) and *Grevillea robusta*. *Plant*
5 *and Soil*, 207(2), 183-193. <https://doi.org/10.1023/A:1026461107110>
- 6 Lobell, D. B., Schlenker, W., & Costa-Roberts, J. (2011). Climate Trends and Global Crop
7 Production Since 1980. *Science*, 333(6042), 616-620.
8 <https://doi.org/doi:10.1126/science.1204531>
- 9 Lopes, M. S. (2022). Will temperature and rainfall changes prevent yield progress in Europe?
10 *Food and Energy Security*, 11(2), e372. <https://doi.org/10.1002/fes3.372>
- 11 Lopes, M. S., & Reynolds, M. P. (2010). Partitioning of assimilates to deeper roots is associated
12 with cooler canopies and increased yield under drought in wheat. *Functional Plant*
13 *Biology*, 37(2), 147-156. <https://doi.org/10.1071/FP09121>
- 14 Lozano-Isla, F. (2023). *_inti: Tools and Statistical Procedures in Plant Science_*. In (Version
15 0.6.0) <https://CRAN.R-project.org/package=inti>
- 16 Lüdeke, D. (2018). sjmisc: Data and Variable Transformation Functions. *Journal of Open Source*
17 *Software*, 3(26), 754. <https://doi.org/10.21105/joss.00754>
- 18 Lüdeke, D. (2023). *sjPlot: Data Visualization for Statistics in Social Science*. In (Version 2.8.15)
19 <https://CRAN.R-project.org/package=sjPlot>
- 20 Luo, D. G., S; Koolaard, J (2022). *_predictmeans: Predicted Means for Linear and Semi*
21 *Parametric Models_*. In (Version 1.0.8) [https://CRAN.R-](https://CRAN.R-project.org/package=predictmeans)
22 [project.org/package=predictmeans](https://CRAN.R-project.org/package=predictmeans)
- 23 Lynch, J. (1995). Root Architecture and Plant Productivity. *Plant Physiology*, 109(1), 7-13.
24 <https://doi.org/10.1104/pp.109.1.7>
- 25 Lynch, J. P. (2013). Steep, cheap and deep: an ideotype to optimize water and N acquisition by
26 maize root systems. *Annals of Botany*, 112(2), 347-357.
27 <https://doi.org/10.1093/aob/mcs293>
- 28 Lynch, J. P. (2018). Rightsizing root phenotypes for drought resistance. *Journal of Experimental*
29 *Botany*, 69(13), 3279-3292.
- 30 Lynch, J. P., & Wojciechowski, T. (2015). Opportunities and challenges in the subsoil: pathways
31 to deeper rooted crops. *Journal of Experimental Botany*, 66(8), 2199-2210.
32 <https://doi.org/10.1093/jxb/eru508>
- 33 Madsen, H., Lawrence, D., Lang, M., Martinkova, M., & Kjeldsen, T. R. (2014). Review of trend
34 analysis and climate change projections of extreme precipitation and floods in Europe.
35 *Journal of Hydrology*, 519, 3634-3650. <https://doi.org/10.1016/j.jhydrol.2014.11.003>
- 36 Maqbool, S., Hassan, M. A., Xia, X., York, L. M., Rasheed, A., & He, Z. (2022). Root system
37 architecture in cereals: progress, challenges and perspective. *Plant J*, 110(1), 23-42.
38 <https://doi.org/10.1111/tpj.15669>
- 39 Mathew, I., & Shimelis, H. (2022). Genetic analyses of root traits: Implications for environmental
40 adaptation and new variety development: A review. *Plant Breeding*, 141(6), 695-718.
41 <https://doi.org/https://doi.org/10.1111/pbr.13049>
- 42 Mathew, I., Shimelis, H., Shayanowako, A. I. T., Laing, M., & Chaplot, V. (2019). Genome-wide
43 association study of drought tolerance and biomass allocation in wheat. *PLOS ONE*,
44 14(12), e0225383. <https://doi.org/10.1371/journal.pone.0225383>
- 45 Merotto, A. j., & Mundstock, C. M. (1999). Wheat root growth as affected by soil strength. *Revista*
46 *Brasileira de Ciencia do Solo*, 23 (2). <https://doi.org/10.1590/S0100-06831999000200002>
- 47 Monyo, J. H., & Whittington, W. J. (1970). Genetic analysis of root growth in wheat. *The Journal*
48 *of Agricultural Science*, 74(2), 329-338. <https://doi.org/10.1017/S0021859600022954>
- 49 Mooney, S. J., Pridmore, T. P., Helliwell, J., & Bennett, M. J. (2012). Developing X-ray
50 Computed Tomography to non-invasively image 3-D root systems architecture in soil.
51 *Plant and Soil*, 352(1), 1-22. <https://doi.org/10.1007/s1104-011-1039-9>

- 1 Moore, F. C., & Lobell, D. B. (2015). The fingerprint of climate trends on European crop yields.
2 *Proceedings of the National Academy of Sciences*, 112(9), 2670-2675.
3 <https://doi.org/doi:10.1073/pnas.1409606112>
- 4 Müllers, Y., Postma, J. A., Poorter, H., Kochs, J., Pflugfelder, D., Schurr, U., & van Dusschoten,
5 D. (2022). Shallow roots of different crops have greater water uptake rates per unit length
6 than deep roots in well-watered soil. *Plant and Soil*, 481(1), 475-493.
7 <https://doi.org/10.1007/s11104-022-05650-8>
- 8 Nelson, G. C., Cheung, W. W. L., Bezner Kerr, R., Franke, J., Meza, F., Oyinlola, M. A.,
9 Thornton, P., & Zabel, F. (2024). Adaptation to climate change and limits in food
10 production systems: Physics, the chemistry of biology, and human behavior. *Global*
11 *Change Biology*, 30(9), e17489. <https://doi.org/https://doi.org/10.1111/gcb.17489>
- 12 Ober, E. S., Alahmad, S., Cockram, J., Forestan, C., Hickey, L. T., Kant, J., Maccaferri, M., Marr,
13 E., Milner, M., Pinto, F., Rambla, C., Reynolds, M., Salvi, S., Sciara, G., Snowdon, R. J.,
14 Thomelin, P., Tuberosa, R., Uauy, C., Voss-Fels, K. P., . . . Watt, M. (2021). Wheat root
15 systems as a breeding target for climate resilience. *Theoretical and Applied Genetics*,
16 134(6), 1645-1662. <https://doi.org/10.1007/s00122-021-03819-w>
- 17 Odone, A., Popovic, O., & Thorup-Kristensen, K. (2023). Deep roots: implications for nitrogen
18 uptake and drought tolerance among winter wheat cultivars. *Plant and Soil*.
19 <https://doi.org/10.1007/s11104-023-06255-5>
- 20 Oldenbroek, K., & van der Waaij, L. (2015). Textbook animal breeding and genetics for BSc
21 students. *Centre for Genetic Resources, The Netherlands and Animal Breeding and*
22 *Genomics Centre*.
- 23 Olsen, S. R. (1954). *Estimation of available phosphorus in soils by extraction with sodium*
24 *bicarbonate*. US Department of Agriculture.
- 25 Osmont, K. S., Sibout, R., & Hardtke, C. S. (2007). Hidden Branches: Developments in Root
26 System Architecture. *Annual Review of Plant Biology*, 58(Volume 58, 2007), 93-113.
27 <https://doi.org/https://doi.org/10.1146/annurev.arplant.58.032806.104006>
- 28 Pariyar, S. R., Nagel, K. A., Lentz, J., Galinski, A., Wilhelm, J., Putz, A., Adels, S., Heinz, K.,
29 Frohberg, C., & Watt, M. (2021). Variation in Root System Architecture among the
30 Founder Parents of Two 8-way MAGIC Wheat Populations for Selection in Breeding.
31 *Agronomy*, 11(12), 2452. <https://www.mdpi.com/2073-4395/11/12/2452>
- 32 Paustian, K., Lehmann, J., Ogle, S., Reay, D., Robertson, G. P., & Smith, P. (2016). Climate-
33 smart soils. *Nature*, 532(7597), 49-57. <https://doi.org/10.1038/nature17174>
- 34 Piepho, H.-P., & Möhring, J. (2007). Computing Heritability and Selection Response From
35 Unbalanced Plant Breeding Trials. *Genetics*, 177(3), 1881-1888.
36 <https://doi.org/10.1534/genetics.107.074229>
- 37 Piepho, H. P., & Möhring, J. (2007). Computing heritability and selection response from
38 unbalanced plant breeding trials. *Genetics*, 177(3), 1881-1888.
39 <https://doi.org/10.1534/genetics.107.074229>
- 40 Pierret, A., Moran, C. J., & Doussan, C. (2005). Conventional detection methodology is limiting
41 our ability to understand the roles and functions of fine roots. *New Phytologist*, 166(3),
42 967-980. <https://doi.org/https://doi.org/10.1111/j.1469-8137.2005.01389.x>
- 43 Pinheiro, J., & Bates, D. (2006). *Mixed-effects models in S and S-PLUS*. Springer science &
44 business media.
- 45 Pinheiro, J. B., D; R Core Team. (2023). *nlme: Linear and Nonlinear Mixed Effects Models*. In
46 (Version 3.1-162) <https://CRAN.R-project.org/package=nlme>
- 47 Porter, J. R., & Gawith, M. (1999). Temperatures and the growth and development of wheat: a
48 review. *European Journal of Agronomy*, 10(1), 23-36. [https://doi.org/10.1016/S1161-](https://doi.org/10.1016/S1161-0301(98)00047-1)
49 [0301\(98\)00047-1](https://doi.org/10.1016/S1161-0301(98)00047-1)
- 50 Qi, F., & Zhang, F. (2020). Cell Cycle Regulation in the Plant Response to Stress [Mini Review].
51 *Frontiers in Plant Science, Volume 10 - 2019*. <https://doi.org/10.3389/fpls.2019.01765>
- 52 R Core Team. (2023). *R: A language and environment for statistical*

- 1 *computing*. In *R Foundation for Statistical Computing* (Version 4.2.3) R Foundation for
2 Statistical Computing. <https://www.R-project.org/>
- 3 Raffo, M. A., & Jensen, J. (2023). Gene × gene and genotype × environment interactions in
4 wheat. *Crop Science*, 63(4), 1779-1793. <https://doi.org/10.1002/csc2.20986>
- 5 Rasse, D. P. (2002). Nitrogen deposition and atmospheric CO₂ interactions on fine root
6 dynamics in temperate forests: a theoretical model analysis. *Global Change Biology*,
7 8(5), 486-503. <https://doi.org/10.1046/j.1365-2486.2002.00481.x>
- 8 Rasse, D. P., & Smucker, A. J. M. (1998). Root recolonization of previous root channels in corn
9 and alfalfa rotations. *Plant and Soil*, 204(2), 203-212.
10 <https://doi.org/10.1023/A:1004343122448>
- 11 Ribeiro, P. R., Fernandez, L. G., de Castro, R. D., Ligterink, W., & Hilhorst, H. W. M. (2014).
12 Physiological and biochemical responses of *Ricinus communis* seedlings to different
13 temperatures: a metabolomics approach. *BMC Plant Biology*, 14(1), 223.
14 <https://doi.org/10.1186/s12870-014-0223-5>
- 15 Rich, S., & Watt, M. (2013). Soil conditions and cereal root system architecture: Review and
16 considerations for linking Darwin and Weaver. *Journal of Experimental Botany*, 64, 1193-
17 1208. <https://doi.org/10.1093/jxb/ert043>
- 18 RMI, R. M. I. o. B. (2023). *RMI, Royal Meteorological Institute of Belgium*.
19 <https://www.meteo.be/en/belgium>
- 20 Rogers, E. D., & Benfey, P. N. (2015). Regulation of plant root system architecture: implications
21 for crop advancement. *Current Opinion in Biotechnology*, 32, 93-98.
22 <https://doi.org/https://doi.org/10.1016/j.copbio.2014.11.015>
- 23 Samset, B. H., Zhou, C., Fuglestvedt, J. S., Lund, M. T., Marotzke, J., & Zelinka, M. D. (2023).
24 Steady global surface warming from 1973 to 2022 but increased warming rate after 1990.
25 *Communications Earth & Environment*, 4(1), 400. [https://doi.org/10.1038/s43247-023-](https://doi.org/10.1038/s43247-023-01061-4)
26 [01061-4](https://doi.org/10.1038/s43247-023-01061-4)
- 27 Sandhu, N., Raman, K. A., Torres, R. O., Audebert, A., Dardou, A., Kumar, A., & Henry, A.
28 (2016). Rice Root Architectural Plasticity Traits and Genetic Regions for Adaptability to
29 Variable Cultivation and Stress Conditions *Plant Physiology*, 171(4), 2562-2576.
30 <https://doi.org/10.1104/pp.16.00705>
- 31 Schmidt, P., Hartung, J., Rath, J., & Piepho, H.-P. (2019). Estimating Broad-Sense Heritability
32 with Unbalanced Data from Agricultural Cultivar Trials. *Crop Science*, 59(2), 525-536.
33 <https://doi.org/https://doi.org/10.2135/cropsci2018.06.0376>
- 34 Schneider, H. M., & Lynch, J. P. (2020). Should Root Plasticity Be a Crop Breeding Target?
35 [Review]. *Frontiers in Plant Science*, 11. <https://doi.org/10.3389/fpls.2020.00546>
- 36 Seethepalli, A., Dhakal, K., Griffiths, M., Guo, H., Freschet, G. T., & York, L. M. (2021).
37 RhizoVision Explorer: open-source software for root image analysis and measurement
38 standardization. *AoB Plants*, 13(6), plab056. <https://doi.org/10.1093/aobpla/plab056>
- 39 Seethepalli, A., & York, L. M. (2021). *RhizoVision Explorer - Interactive software for generalized*
40 *root image analysis designed for everyone*. In (Version 2.0.3)
- 41 Severini, A. D., Wasson, A. P., Evans, J. R., Richards, R. A., & Watt, M. (2020). Root
42 phenotypes at maturity in diverse wheat and triticale genotypes grown in three field
43 experiments: Relationships to shoot selection, biomass, grain yield, flowering time, and
44 environment. *Field Crops Research*, 255, 107870.
45 <https://doi.org/10.1016/j.fcr.2020.107870>
- 46 Shenoy, A. (2021). *grafify: an R package for easy graphs, ANOVAs and post-hoc comparisons*.
47 In (Version 4.0) <https://doi.org/10.5281/zenodo.5136508>
- 48 Shewry, P. R., & Hey, S. J. (2015). The contribution of wheat to human diet and health. *Food*
49 *and Energy Security*, 4(3), 178-202. <https://doi.org/10.1002/fes3.64>
- 50 Shoaib, M., Banerjee, B. P., Hayden, M., & Kant, S. (2022). Roots' Drought Adaptive Traits in
51 Crop Improvement. *Plants (Basel)*, 11(17). <https://doi.org/10.3390/plants11172256>

- 1 Siddique, K. H. M., Kirby, E. J. M., & Perry, M. W. (1989). Ear: Stem ratio in old and modern
2 wheat varieties; relationship with improvement in number of grains per ear and yield.
3 *Field Crops Research*, 21(1), 59-78. [https://doi.org/10.1016/0378-4290\(89\)90041-5](https://doi.org/10.1016/0378-4290(89)90041-5)
- 4 Smith, S., & De Smet, I. (2012). Root system architecture: insights from Arabidopsis and cereal
5 crops. *Philos Trans R Soc Lond B Biol Sci*, 367(1595), 1441-1452.
6 <https://doi.org/10.1098/rstb.2011.0234>
- 7 Smucker, A. J. M., McBurney, S. L., & Srivastava, A. K. (1982). Quantitative Separation of Roots
8 from Compacted Soil Profiles by the Hydropneumatic Elutriation System. *Agronomy*
9 *Journal*, 74(3), 500-503.
10 <https://doi.org/https://doi.org/10.2134/agronj1982.00021962007400030023x>
- 11 Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., & Miller, H.
12 L. (2007). *IPCC, 2007: Climate Change 2007: The Physical Science Basis. Contribution*
13 *of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on*
14 *Climate Change* (Vol. 4). Cambridge University Press.
- 15 Sun, X., Wang, P., & Mi, G. (2025). Genotypic Differences in Maize Root Morphology in
16 Response to Low-Nitrogen Stress. *Agronomy*, 15(2), 332. [https://www.mdpi.com/2073-](https://www.mdpi.com/2073-4395/15/2/332)
17 [4395/15/2/332](https://www.mdpi.com/2073-4395/15/2/332)
- 18 Svoboda, P., Kurešová, G., Raimanová, I., Kunzová, E., & Haberle, J. (2020). The Effect of
19 Different Fertilization Treatments on Wheat Root Depth and Length Density Distribution
20 in a Long-Term Experiment. *Agronomy*, 10(9), 1355. [https://www.mdpi.com/2073-](https://www.mdpi.com/2073-4395/10/9/1355)
21 [4395/10/9/1355](https://www.mdpi.com/2073-4395/10/9/1355)
- 22 Timaeus, J., Weedon, O. D., & Finckh, M. R. (2021). Combining Genetic Gain and Diversity in
23 Plant Breeding: Heritability of Root Selection in Wheat Populations. *Sustainability*,
24 13(22), 12778. <https://www.mdpi.com/2071-1050/13/22/12778>
- 25 Trachsel, S., Kaeppler, S. M., Brown, K. M., & Lynch, J. P. (2011). Shovelomics: high throughput
26 phenotyping of maize (*Zea mays* L.) root architecture in the field. *Plant and Soil*, 341(1),
27 75-87. <https://doi.org/10.1007/s11104-010-0623-8>
- 28 Tripathy, K. P., & Mishra, A. K. (2023). How Unusual Is the 2022 European Compound Drought
29 and Heatwave Event? *Geophysical Research Letters*, 50(15), e2023GL105453.
30 <https://doi.org/10.1029/2023GL105453>
- 31 Uga, Y. (2021). Challenges to design-oriented breeding of root system architecture adapted to
32 climate change. *Breed Sci*, 71(1), 3-12. <https://doi.org/10.1270/jsbbs.20118>
- 33 Visse-Mansiaux, M., Piepho, H.-P., Horáková, V., Treier, S., Povolný, M., Flamm, C.,
34 Eylesbosch, D., Gouleau, A., Barraïs, S., Csűrös, Z., Poós, B., Pécs, M., Camenzind, M.,
35 Yu, K., Barcena, T., Tolekiene, M., Häner, L. L., Lüddecke, F., Da Silva, M., . . . Herrera,
36 J. M. Towards more efficient evaluation of Value for Cultivation and Use (VCU) in winter
37 wheat: opportunities and challenges that emerged from a pan-European study.
- 38 Vu, L. D., Gevaert, K., & De Smet, I. (2019). Feeling the Heat: Searching for Plant
39 Thermosensors. *Trends in Plant Science*, 24(3), 210-219.
40 <https://doi.org/10.1016/j.tplants.2018.11.004>
- 41 Vu, V. (2011). *_ggbiplot: A ggplot2 based biplot_*. In (Version 0.5.5)
42 <http://github.com/vqv/ggbiplot>
- 43 Whalley, W. R., Binley, A., Watts, C. W., Shanahan, P., Dodd, I. C., Ober, E. S., Ashton, R. W.,
44 Webster, C. P., White, R. P., & Hawkesford, M. J. (2017). Methods to estimate changes
45 in soil water for phenotyping root activity in the field. *Plant and Soil*, 415(1), 407-422.
46 <https://doi.org/10.1007/s11104-016-3161-1>
- 47 Whalley, W. R., Leeds-Harrison, P. B., Clark, L. J., & Gowing, D. J. G. (2005). Use of effective
48 stress to predict the penetrometer resistance of unsaturated agricultural soils. *Soil and*
49 *Tillage Research*, 84(1), 18-27. <https://doi.org/https://doi.org/10.1016/j.still.2004.08.003>
- 50 Wickham, H. (2007). Reshaping Data with the reshape Package. *Journal of Statistical Software*,
51 21(12), 1 - 20. <https://doi.org/10.18637/jss.v021.i12>
- 52 Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. In Springer-Verlag New York.

- 1 Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Golemund, G.,
2 Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K.,
3 Ooms, J., Robinson, D., Seidel, D., Spinu, V., & Yutani, H. (2019). Welcome to the
4 Tidyverse. *Journal of Open Source Software*, 4, 1686.
5 <https://doi.org/10.21105/joss.01686>
- 6 Wickham, H., & Bryan, J. (2023). *_readxl: Read Excel Files_*. In (Version 1.4.2) [https://CRAN.R-](https://CRAN.R-project.org/package=readxl)
7 [project.org/package=readxl](https://CRAN.R-project.org/package=readxl)
- 8 Wickham, H., & Seidel, D. (2022). *_scales: Scale Functions for Visualization_*. In [https://scales.r-](https://scales.r-lib.org)
9 [lib.org](https://scales.r-lib.org)
- 10 WRB, I. W. G. (2014). *World reference base for soil resources 2014. International soil*
11 *classification system for naming soils and creating legends for soil maps* (Vol. 106). FAO.
- 12 WRB, I. W. G. (2022). *World Reference Base for Soil Resources. International soil classification*
13 *system for naming soils and creating legends for soil maps* (Vol. 4). International Union
14 of Soil Sciences (IUSS).
- 15 Xie, Q., Fernando, K. M. C., Mayes, S., & Sparkes, D. L. (2017). Identifying seedling root
16 architectural traits associated with yield and yield components in wheat. *Annals of*
17 *Botany*, 119(7), 1115-1129. <https://doi.org/10.1093/aob/mcx001>
- 18 Xie, X., Quintana, M. R., Sandhu, N., Subedi, S. R., Zou, Y., Rutkoski, J. E., & Henry, A. (2021).
19 Establishment method affects rice root plasticity in response to drought and its
20 relationship with grain yield stability. *Journal of Experimental Botany*, 72(14), 5208-5220.
21 <https://doi.org/10.1093/jxb/erab214>
- 22 Xu, F., Chen, S., Yang, X., Zhou, S., Wang, J., Zhang, Z., Huang, Y., Song, M., Zhang, J., Zhan,
23 K., & He, D. (2021). Genome-Wide Association Study on Root Traits Under Different
24 Growing Environments in Wheat (*Triticum aestivum* L.). *Front Genet*, 12, 646712.
25 <https://doi.org/10.3389/fgene.2021.646712>
- 26 Yang, J.-c., Zhang, H., & Zhang, J.-h. (2012). Root Morphology and Physiology in Relation to the
27 Yield Formation of Rice. *Journal of Integrative Agriculture*, 11(6), 920-926.
28 [https://doi.org/10.1016/S2095-3119\(12\)60082-3](https://doi.org/10.1016/S2095-3119(12)60082-3)
- 29 York, L. M. (2020). Plans for root scanning trays to use on flatbed scanners. *Zenodo*.
30 <https://doi.org/10.5281/zenodo.4122423>
- 31 Zhang, Z., Murtagh, F., Van Poucke, S., Lin, S., & Lan, P. (2017). Hierarchical cluster analysis in
32 clinical research with heterogeneous study population: Highlighting its visualization with
33 R. *Annals of Translational Medicine*, 5, 75. <https://doi.org/10.21037/atm.2017.02.05>

1 Tables

2 *Table 1: Site characteristics: location, soil type, and climate for the 11 sites in Europe.*

| Country (institution ¹) | Site / nearest town | Site abbreviatio n | Coordinates | Soil type ² | Climate (Köppen- Geiger ³) | MAT ⁴ [°C] | Temperatur e 09/2021– 08/2022 [°C] | MAP ⁴ [mm] | Precipitatio n 09/2021– 08/2022 [mm] |
|--|------------------------------|--------------------------|----------------------------------|------------------------|--|-----------------------|--|-----------------------|---|
| Austria (AGES) | Grossnondorf / Hollabrunn | AT-Gn | 48°37'47.9" N 15°58'48.1"E | Calcaric Phaeozem | Dfb | 10.2 | 11.2 | 650 | 422 |
| Belgium (CRAW) | Gembloux | BE-Ge | 50°35'52.0" N 4°41'24.5"E | Hortic luvisol | Cfb | 10.2 | 11.2 | 793 | 554 |
| Switzerland (AGS) | Changins / Nyon | CH-Ca | 46°24'03.6" N 6°13'55.1"E | Calcaric Cambisol | Dfb | 10.7 | 12.4 | 995 | 692 |
| Switzerland (ETH) | Eschikon / Lindau | CH-Es | 47°27'02.3" N 8°40'56.4"E | Gleyic Cambisol | Cfb | 9.2 | 10.9 | 1175 | 797 |
| Czech Republic (UKZUZ) | Chrlice/ Brno | CZ-Cr | 49°7'28.99" N 16°38'03.0"E | Fluvisol | Dfb | 9.0 | 11.6 | 612 | 451 |
| Germany (TUM) | Dürnast / Freising | DE-Fr | 48°24'25.4" N 11°41'39.1"E | Cambisol | Dfb | 9.8 | 9.8 | 960 | 650 |
| Germany (BSA) | Nossen | DE-No | 51°3'20.02" N 13°16'31.7"E | Planosol | Dfb | 9.2 | 10.5 | 645 | 474 |
| Spain (IRT A) | Sucs / Lleida | ES-Le | 41°41'44.7" N 0°25'35.1"E | Gypsisol | Cfb | 15.5 | 13.3 ⁵ | 450 | 156 ⁵ |

| | | | | | | | | | |
|------------------------------|-------------------------------------|-------|----------------------------------|-----------------------------------|-----|------|------|-----|-----|
| Hungary (NEBIH) | Székkutas / Hódmezővásá rhely | HU-Sz | 46°30'45.3" N 20°31'15.3"E | Clayic Chernozem | Dfa | 12.2 | 11.2 | 635 | 483 |
| Lithuania (LAMMC) | Akademija / Dotnuva | LT-Do | 55°23'28.6" N 23°51'49.8"E | Haplic Endocalcaric Luvisol | Dfb | 7.8 | 8.0 | 705 | 686 |
| Norway (NIBIO) | Ås | NO-As | 59°39'50.0" N 10°45'34.9"E | Stagnosol | Dfb | 6.4 | 7.4 | 876 | 603 |

¹ AGES, Austrian Agency for Health and Food Safety; AGS, Agroscope; BSA, Federal Plant Variety Office; CRAW, Walloon Agricultural Research Centre; ETH, Federal Institute of Technology; IRTA, Institute of Agrifood Research and Technology; LAMMC, Lithuanian Research Center for Agriculture and Forestry; NEBIH, National Food Chain Safety Office; NIBIO, Norwegian Institute of Bioeconomy Research; TUM, Technical University Munich; UKZUZ, Central Institute for Supervising and Testing in Agriculture

² Soil type for all sites except NO-As according to WRB (2022), NO-As according to WRB (2014)

³ Cfb, oceanic; Dfa, continental; Dfb, humid continental

⁴ MAP, mean annual precipitation (1991-2020); MAT, mean annual temperature (1991-2020)

⁵ data only available from 1.12.2022 to 31.8.2022

1 *Table 2: Management information for the 11 sites in the growing season 2021/22.*

| Site abbreviation | Sowing density [grains m ⁻²] | Sowing depth [cm] | Row width [cm] | Nitrogen fertilization [kg ha ⁻¹] ¹ | Chemical plant protection | Growth regulators | Preceding crop | Irrigation [mm] |
|-------------------|--|-------------------|----------------|--|---------------------------|-------------------|---------------------------------------|-----------------|
| AT-Gn | 300 | 3 | 12.5 | 130 | yes | no | oil pumpkin | 0 |
| BE-Ge | 275 | 2 | 15.6 | 150 | no | yes | sugar beet | 0 |
| CH-Ca | 350 | 2 | 15.5 | 130 | yes | yes | sunflower | 0 |
| CH-Es | 400 | 2.5 | 12.5 | 130 / 85 ¹ | yes | yes | winter wheat / grass-clover ley | 0 |
| CZ-Cr | 350 | 4 | 12.5 | 130 | yes | no | phacelia | 0 |
| DE-Fr | 350 | 3 | 12.5 | 180 | yes | yes | winter wheat | 0 |
| DE-No | 400 | 3 | 12 | 70 | yes | yes | vicia sativa | 0 |
| ES-Le | 450 | 2 | 15 | 0 | yes | no | alfalfa | 20 ² |
| HU-Sz | 450 | 4.5 | 10.5 | 125 | yes | no | maize | 0 |
| LT-Do | 350 | 3 | 12.5 | 140 | yes | yes | winter wheat | 0 |
| NO-As | 450 | 3 | 12.5 | 136.5 | yes | no | unknown | 0 |

2 ¹ Nitrogen (N) fertilization was calculated according to mineral N content in soil determined in spring. In CH-Es, N fertilization differed
3 between the two field replicates due to differences in pre-crops and soil mineral N contents

4 ² In Es-Le, the wheat received 20 mm of irrigation in spring in order to prevent drought-induced crop failure

1

2 *Table 3: Ten Winter wheat varieties used in this study, their abbreviation, and year of release. Once a variety has been registered in one*3 *EU country or in CH, it can be grown in any other EU country and in CH.*

| Variety | Variety abbreviation | Year of release¹ |
|-------------------|-----------------------------|------------------------------------|
| Altigo | Al | 2011 |
| Aurelius | Au | 2016 |
| Bernstein | Be | 2015 |
| Dagmar | Da | 2012 |
| Julie | Ju | 2014 |
| Montalbano | Mo | 2014 |
| MV Nador | Na | 2012 |
| Nogal | No | 2013 |
| RGT Reform | Re | 2014 |
| Tenor | Te | 2017 |

4 ¹ Source: European plant variety protection EUPVP - Common Catalogue Information System (2023)

5

1 *Table 4: Mean, minimum, and maximum grain yield (15% moisture) of ten winter wheat varieties*
2 *per site in Mg ha⁻¹. Data are averaged across field replications and summarized across the ten*
3 *varieties.*

| Site | AT- Gn | BE- Ge | CH- Ca | CH- Es | CZ-Cr | DE- Fr | DE- No | ES- Le | HU- Sz | LT- Do | NO- As |
|------|-----------|-----------|-----------|-----------|-------|-----------|-----------|-----------|-----------|-----------|-----------|
| Mean | 10.2 | 7.9 | 3.5 | 8.7 | 9.8 | 6.52 | 9.3 | 4.2 | 3.6 | 7.6 | 6.2 |
| Min | 9.2 | 5.0 | 2.8 | 7.7 | 9.2 | 5.49 | 8.2 | 3.3 | 3.0 | 6.7 | 3.1 |
| Max | 11.2 | 9.8 | 4.1 | 9.8 | 10.5 | 7.54 | 10.3 | 4.9 | 3.9 | 8.4 | 7.6 |

4

1 *Table 5: Summary statistics on root length and surface area in the topsoil (0.00-0.15 m, per piece)*
 2 *and subsoil (0.15-0.50 m and 0.50-1.00 m, per area) of ten winter wheat varieties at 11 sites in Europe.*
 3 *Standard deviations (SD) of random effects were derived from a random intercept model with linear*
 4 *combinations of variety and site as random effects. Differences in root traits among varieties were*
 5 *derived from a mixed effects model with variety as fixed effect and site and replicate as nested random*
 6 *effects. The goodness of model fit is indicated by the marginal R^2 for the fixed effects and the*
 7 *conditional R^2 for the whole model. Indication of significance level for differences among varieties*
 8 *based on ANOVA are represented by asterisks ($p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$, n.s. not*
 9 *significant).*

| | Topsoil roots | | Subsoil roots in 0.15-0.50 m | | Subsoil roots in 0.50-1.00 m | |
|----------------------------|---------------------------------|---|--|--|--|--|
| | Length [m pc ⁻¹] | Surface area [m ² pc ⁻¹] | Length [m root m ⁻² soil] | Surface area [m ² root m ⁻² soil] | Length [m root m ⁻² soil] | Surface area [m ² root m ⁻² soil] |
| Summary | | | | | | |
| Mean ¹ | 1.4 | 0.039 | 5007 | 40 | 5300 | 43 |
| Median ¹ | 1.4 | 0.040 | 5031 | 39 | 5387 | 44 |
| Min | 0.4 | 0.011 | 1448 | 13 | 407 | 5 |
| Max | 2.7 | 0.089 | 8841 | 80 | 14'923 | 96 |
| SD of random effects | | | | | | |
| SD ¹ | 0.1 | 0.004 | 384 | 4 | 402 | 5 |
| Variety | 0.1 | 0.003 | 198 | 2.5 | 236 | 3.5 |
| Site | 0.5 | 0.015 | 1720 | 14.5 | 3740 | 25.8 |
| Replicate ² | N/A | N/A | 137 | 0.6 | 615 | 4.3 |
| Residual | 0.4 | 0.013 | 1451 | 12.5 | 1905 | 16.6 |
| Significant differences | | | | | | |
| Variety | *** | *** | n.s. | * | * | * |
| R ² marginal | 0.035 | 0.040 | 0.019 | 0.026 | 0.016 | 0.022 |
| R ² conditional | 0.72 | 0.72 | 0.70 | 0.69 | 0.82 | 0.76 |
| Heritability | | | | | | |
| H ² | 0.56 | 0.63 | 0.41 | 0.57 | 0.59 | 0.62 |

10 ¹ across field replications and varieties

11 ² random intercept model including replicate showed a singular fit for topsoil root traits

12

1 Table 6: Significance of the correlation coefficients for the main effects of pedoclimatic and
 2 management variables for (log-transformed) root length and surface area based on linear mixed
 3 models. *P* values < 0.05 are highlighted in bold font and *p* values > 0.1 are shown as n.s.. The
 4 direction of significant effects is indicated in brackets, +: positive, -: negative.

| Variable | 0.00-0.15 m | | 0.15-0.50 m | | 0.50-1.00 m | |
|--|-------------|--------------|------------------|------------------|------------------|------------------|
| | Length | Surface area | Length | Surface area | Length | Surface area |
| Temp. season [°C] | n.s. | n.s. | 0.059 | 0.073 | 0.069 | 0.046 (+) |
| Temp. emergence [°C] | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. |
| Temp. flowering [°C] | n.s. | n.s. | 0.036 (+) | 0.095 | 0.039 (+) | 0.031 (+) |
| Temp. harvest [°C] | n.s. | n.s. | n.s. | n.s. | 0.002 (+) | 0.008 (+) |
| Prec. season [mm] | n.s. | n.s. | 0.081 | 0.026 (-) | 0.069 | 0.024 (-) |
| Prec. emergence [mm] | n.s. | n.s. | n.s. | n.s. | n.s. | 0.081 |
| Prec. flowering [mm] | n.s. | n.s. | n.s. | 0.086 | n.s. | n.s. |
| Prec. harvest [mm] | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. |
| Soil clay content [%] | n.s. | n.s. | n.s. | n.s. | 0.095 | n.s. |
| Soil bulk density [g cm ⁻³] | n.s. | n.s. | n.s. | n.s. | 0.004 (-) | 0.002 (-) |
| Soil pH [-] | n.s. | n.s. | n.s. | n.s. | n.s. | 0.056 |
| Soil N [%] | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. |
| Soil P [mg kg ⁻¹] | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. |
| Sowing density [grains m ⁻²] | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. |
| N fertilization [kg ha ⁻¹] | n.s. | n.s. | n.s. | n.s. | n.s. | 0.049 (-) |

5

1 Figure legends

2 *Figure 1: Root length and surface area in three soil depths (0.00-0.15 m: per piece; 0.15-0.50 m*
3 *and 0.50-1.00 m: per area) of ten winter wheat varieties at 11 sites in Europe. Bars depict mean*
4 *values of 10 or 11 sites averaged over 3 replications and error bars depict standard errors of 10*
5 *or 11 sites. Groupings according to the outcome of the statistical analysis are indicated by letters*
6 *on top (significant difference if not sharing a letter; comparison of varieties in individual soil*
7 *depths). Missing letters indicate non-significant differences. Please refer to Table 3 for variety*
8 *abbreviations.*

9 *Figure 2: Grain yield of ten winter wheat varieties at 11 sites in Europe as related to root length*
10 *and surface area of the topsoil and subsoil roots. Points are average values per variety and site.*
11 *Significance of trend line is derived from mixed model output with site and replicate as nested*
12 *random effects. Solid line indicates a trend significantly different from zero. Slopes differing*
13 *significantly from each other are indicated in the bottom right of the respective panel. Indication*
14 *of significance level for differences among slopes based on multiple pairwise comparison and*
15 *Sidak-adjustment of p-values are represented by asterisks ($p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$).*
16 *Significance: n.s.: not significant, s.: significant. Please refer to Table 3 for variety abbreviations.*

17 *Figure 3: Relationship between root length in the topsoil and predicted yield of ten winter wheat*
18 *varieties at different values of temperature before harvest. Low, mean, and high scenarios indicate*
19 *mean - 1 SD (18.0 °C), mean (19.6 °C), and mean + 1 SD (21.3 °C) temperature, respectively.*
20 *Please refer to Table 3 for variety abbreviations.*

21 *Figure 4: Relationship between root length and surface area in 0.50-1.00 m soil depth and*
22 *predicted yield of ten winter wheat varieties at different values of temperature over the season.*

1 *Low, mean, and high scenarios indicate mean – 1 SD (7.6°C), mean (8.6°C), and mean + 1 SD*
2 *(9.6°C) temperature, respectively. Please refer to Table 3 for variety abbreviations.*

3 *Figure 5: Indication of significant slope differences of the relationship between yield and root*
4 *length and surface area of ten winter wheat varieties between the low (mean – 1SD) and high*
5 *(mean + 1SD) scenario of a pedoclimatic or management variable. A blue tile indicates a negative*
6 *difference in slopes and a red tile indicates a positive difference, i.e., the relationship between yield*
7 *and root length or surface area becomes less and more pronounced, respectively, with increasing*
8 *values of the pedoclimatic or management variables. Please refer to Table 3 for variety*
9 *abbreviations.*

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ACCEPTED MANUSCRIPT

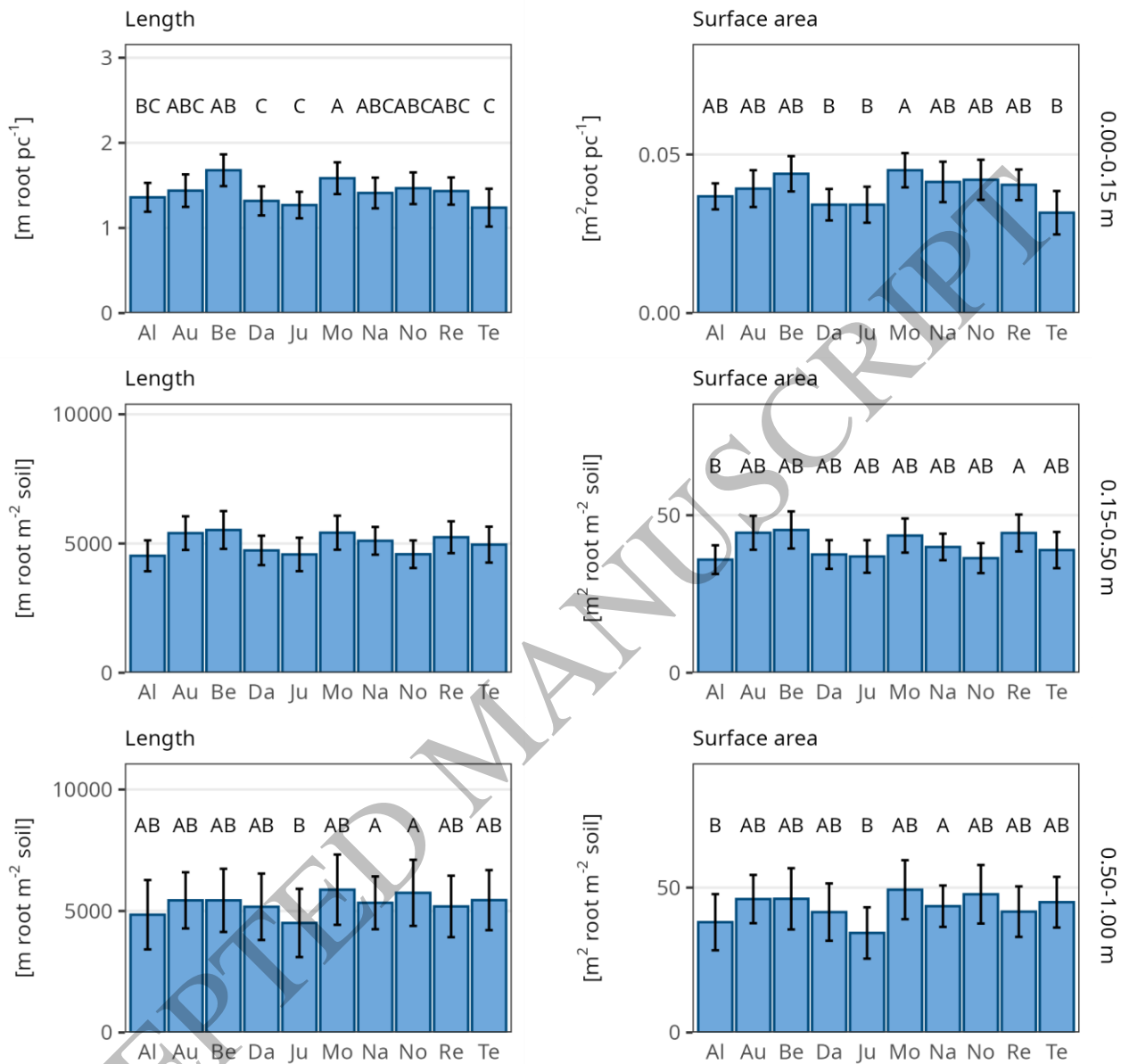


Figure 1
173x160 mm (DPI)

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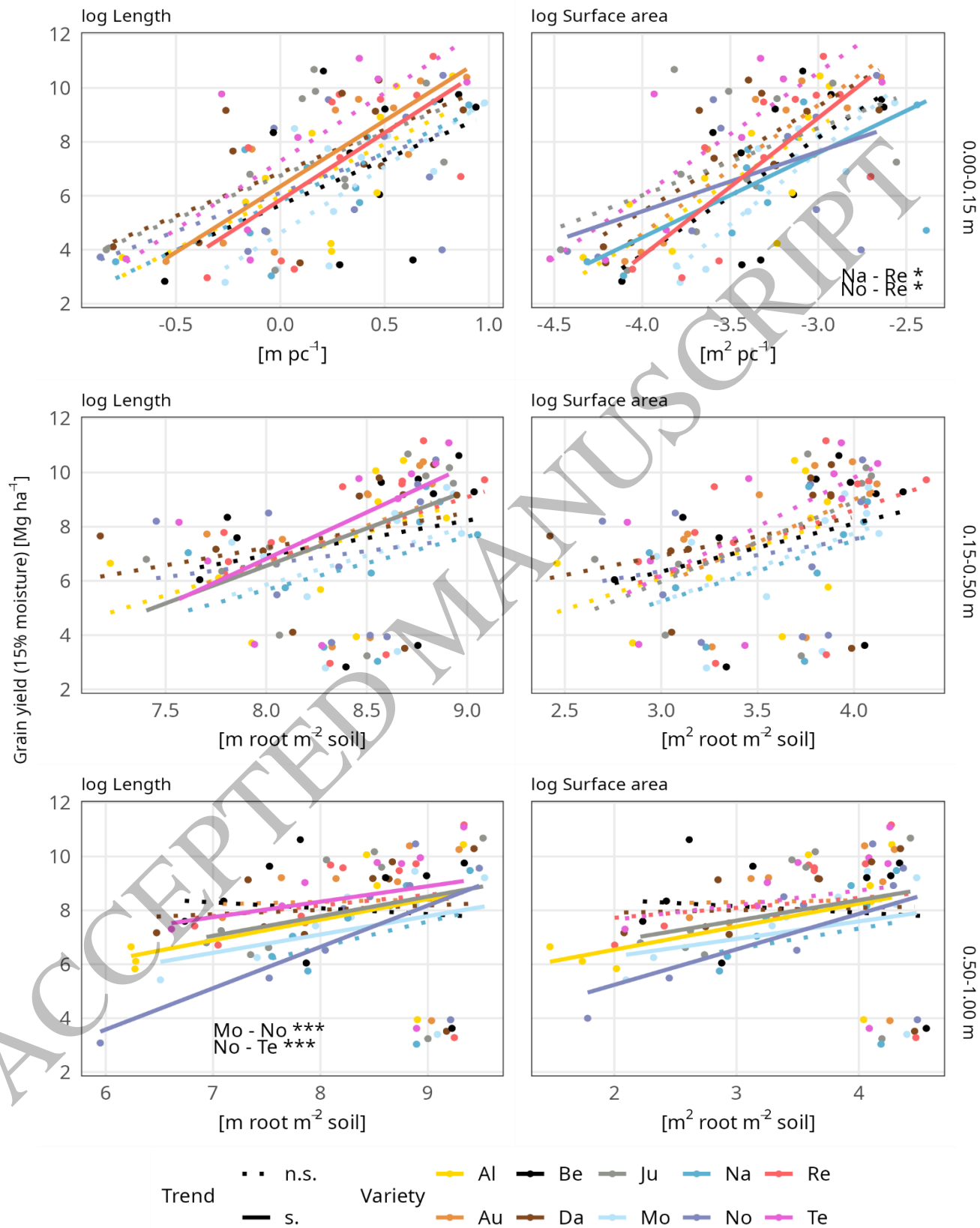


Figure 2
173x230 mm (DPI)

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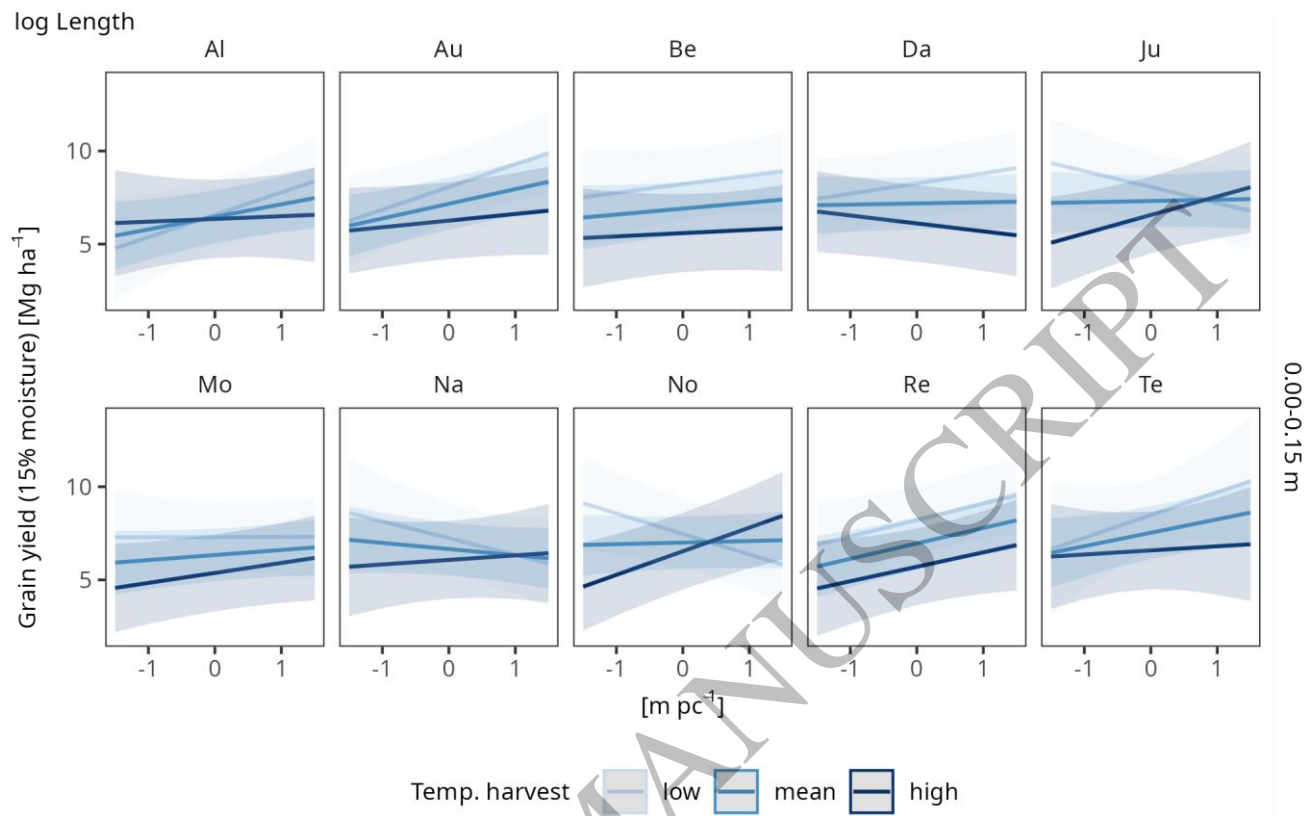


Figure 3
173x110 mm (DPI)

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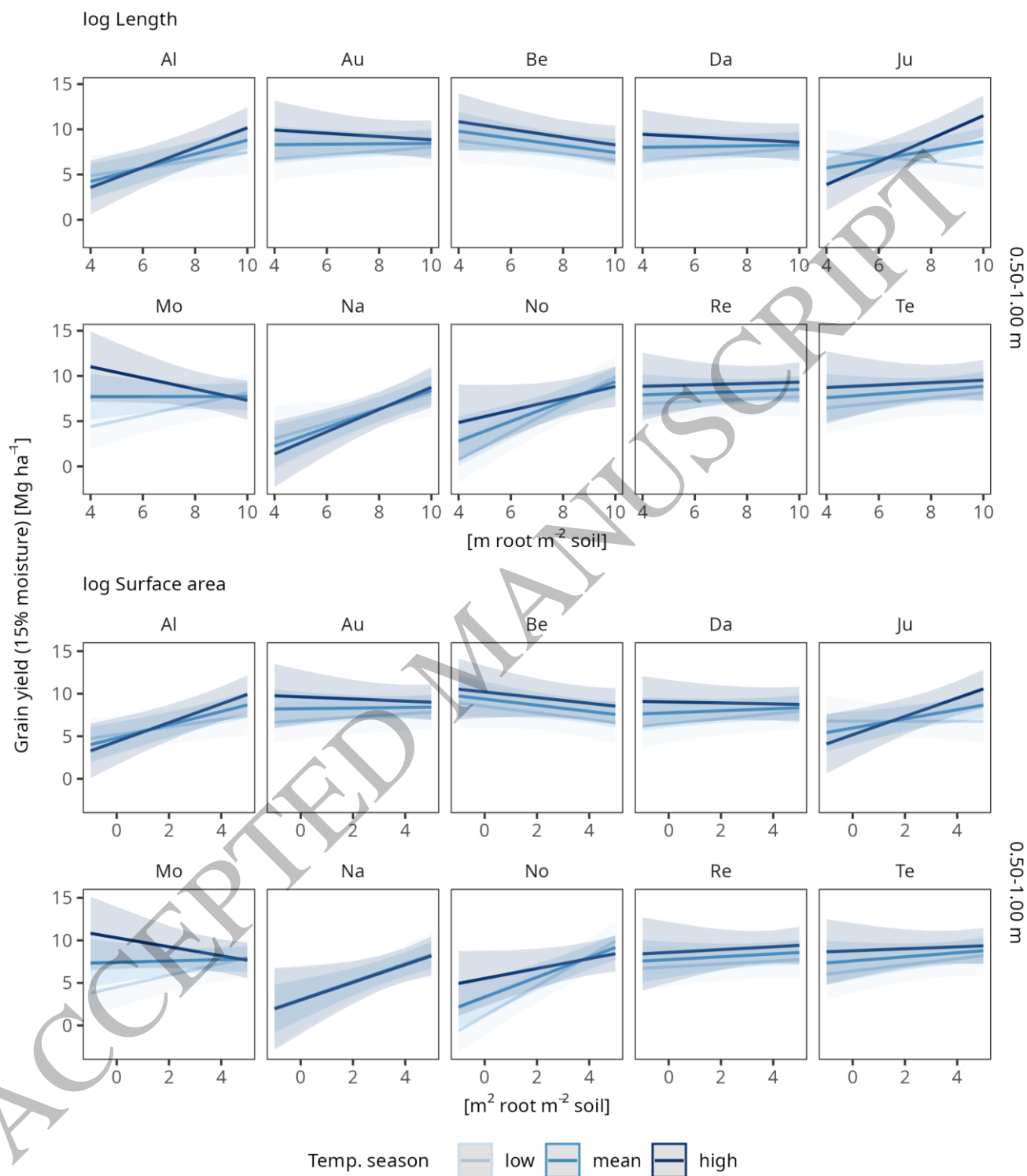


Figure 4
173x200 mm (DPI)

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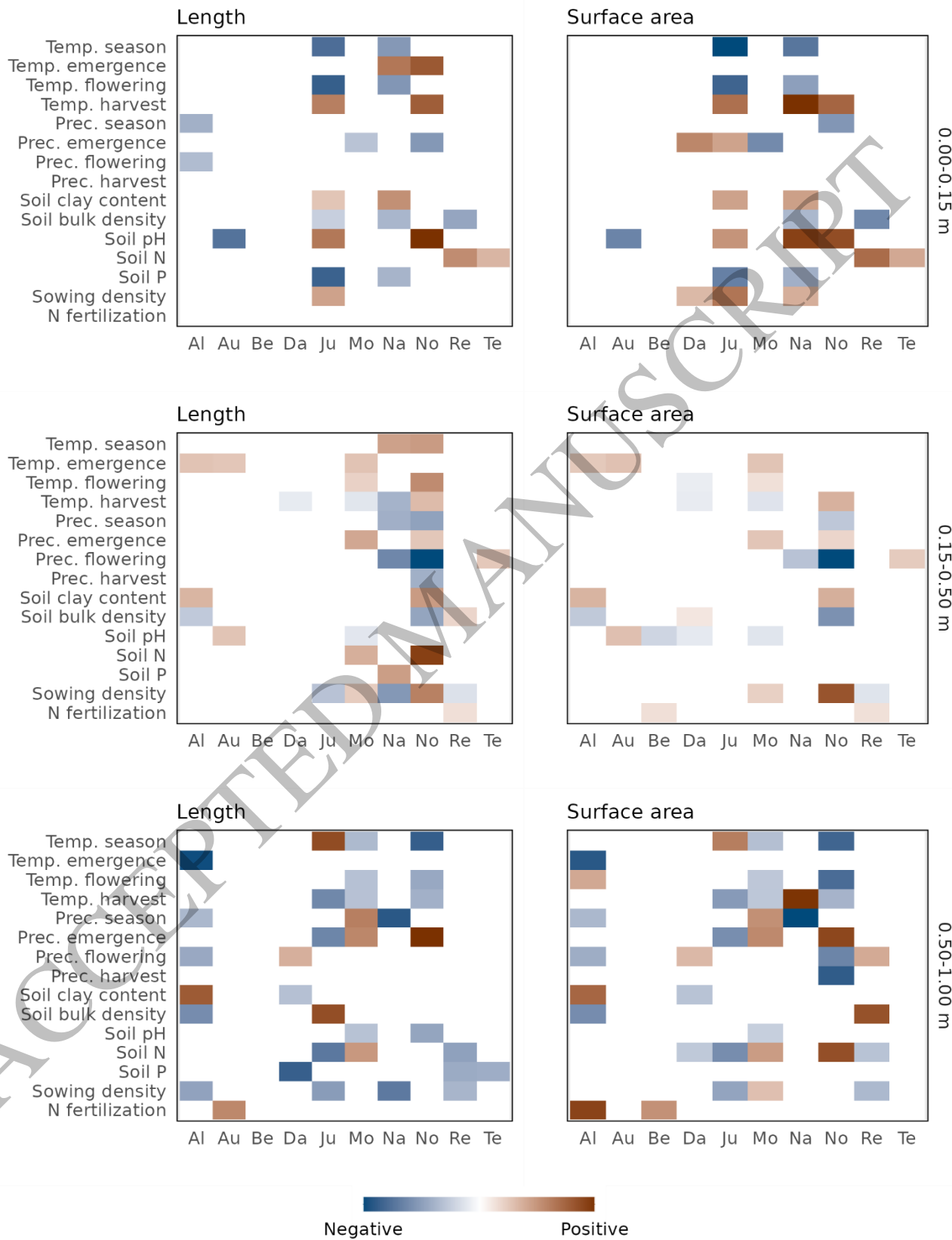


Figure 5
173x220 mm (DPI)

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