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Unraveling root and rhizosphere traits in temperate maize landraces and modern cultivars: Implications for soil resource acquisition and drought adaptation

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Abstract

A holistic understanding of plant strategies to acquire soil resources is pivotal in achieving sustainable food security. However, we lack knowledge about variety-specific root and rhizosphere traits for resource acquisition, their plasticity and adaptation to drought. We conducted a greenhouse experiment to phenotype root and rhizosphere traits (mean root diameter [Root D], specific root length [SRL], root tissue density, root nitrogen content, specific rhizosheath mass [SRM], arbuscular mycorrhizal fungi [AMF] colonization) of 16 landraces and 22 modern cultivars of temperate maize (*Zea mays* L.). Our results demonstrate that landraces and modern cultivars diverge in their root and rhizosphere traits. Although landraces follow a 'do-it-yourself' strategy with high SRLs, modern cultivars exhibit an 'outsourcing' strategy with increased mean Root Ds and a tendency towards increased root colonization by AMF. We further identified that SRM indicates an 'outsourcing'

strategy. Additionally, landraces were more drought-responsive compared to modern cultivars based on multitrait response indices. We suggest that breeding leads to distinct resource acquisition strategies between temperate maize varieties. Future breeding efforts should increasingly target root and rhizosphere economics, with SRM serving as a valuable proxy for identifying varieties employing an outsourcing resource acquisition strategy.

KEYWORDS

arbuscular mycorrhizal fungi, Index for Adaptive Responses, phenotypic plasticity, rhizosheath, root diameter, root economics space, specific root length

1 | INTRODUCTION

In the future, sustainable agroecosystems must cope with and mitigate the consequences of extreme changes in the Earth's climate system. The threat of increasing droughts in many regions of the world, including Central Europe (Lehner et al., 2017; Li et al., 2009), poses serious challenges for agriculture (IPCC, 2019; Malhi et al., 2021; Olesen et al., 2011; Wiebe et al., 2019). Over the last 50 years, drought events in Europe have increased by 1% yr^{-1} and their impact on cereal yield losses has tripled (Brás et al., 2021). In addition, refined global climate and crop models predict that yield quantity and quality losses in cropping systems will likely perpetuate in the future. Yield losses are expected to be particularly noticeable in C_4 crops such as maize, which benefit less from higher atmospheric CO_2 concentrations (Jägermeyr et al., 2021). In light of more intense and unpredictable droughts, modern agriculture must be adapted to erratic weather conditions (Anderson et al., 2020; Olesen et al., 2011). Consequently, the breeding and selection of cultivars that can tolerate adverse future conditions become imperative (Zhao et al., 2022).

A key to improving the adaptation of crop cultivars to future climate conditions may lie in functional root traits and interactions among roots, microorganisms, and soil particles, which in concert shape rhizosphere traits. The term 'rhizosphere' generally refers to the soil volume around living roots that is predominantly controlled by root activity and is of a highly dynamic nature (Hinsinger et al., 2009; York et al., 2016). This concept needs to be distinguished from 'rhizosheath', which is a component of the rhizosphere and comprises soil particles that strongly adhere to roots on excavation (Aslam et al., 2022; York et al., 2016). Although there is substantial work on water and nutrient acquisition under drought that addresses above- and belowground plant traits such as shoot and stomata traits or rooting depth (e.g., Henry et al., 2012; Lynch, 2013; Richards & Passioura, 1989; Varshney et al., 2021), the soil around the roots has received less attention so far. This is even though, in general, functional root and rhizosphere traits are essential for water and nutrient uptake, hydraulic conductivity and root–soil contact, and investments in these traits become increasingly important under drought (Carminati & Vetterlein, 2013; Comas et al., 2013). Important

rhizosphere traits comprise root associations with arbuscular mycorrhizal fungi (AMF) and specific rhizosheath mass (SRM). In particular, SRM can be considered an integral proxy for root and rhizosphere processes such as the formation of root hairs, root exudation and the promotion of exopolysaccharide-producing microbes (for review, see Aslam et al., 2022; Ndour et al., 2020). Importantly, SRM with presumably high heritability (de la Fuente Cantó et al., 2022; Ndour et al., 2020) and high consistency between laboratory and field experiments (George et al., 2014) is proposed as a promising breeding target with positive effects on resource acquisition (e.g., Brown et al., 2012; George et al., 2014; Ma et al., 2011), especially under drought (Ndour et al., 2020).

In recent years, considerable progress has been made in root and rhizosphere economics, that is, in conceptually linking root and rhizosphere traits relevant to water and nutrient uptake to soil resource acquisition strategies. According to the leaf and root economics spectrum, plant species can generally be classified along a gradient from 'fast' to 'slow' acquirers (conservation gradient), representing a trade-off between fast and slow resource return on investment (for review, see Weemstra et al., 2016; Weigelt et al., 2021). Key traits of the root economics spectrum are root tissue density (RTD) and root nitrogen content (Root N), reflecting costs for root construction and the level of metabolic activity, respectively (Weemstra et al., 2016). Recent findings suggest that an additional classification of plant species along a collaboration gradient is advisable (Bergmann et al., 2020). In this extended root economics space (RES), the collaboration gradient is independent of the fast-slow growing gradient. Instead, it depends on the degree of association with fungal species (e.g., AMF) or whether root-economic carbon investment is confined to the plant's own root structures. In particular, thicker roots (i.e., larger fine root diameter; Root D) are usually associated with greater AMF colonization in many terrestrial plants (Galindo-Castañeda et al., 2019; Ma et al., 2018; Wen et al., 2019). This association is presumed to occur because increased root cortex may be linked to an expanded AMF habitat, suggesting an 'outsourcing' strategy (Bergmann et al., 2020). In contrast, reduced mycorrhizal colonization and the formation of long and thin roots (i.e., high specific root length [SRL]), indicate a 'do-it-yourself' (DIY) resource acquisition strategy (Bergmann et al., 2020)
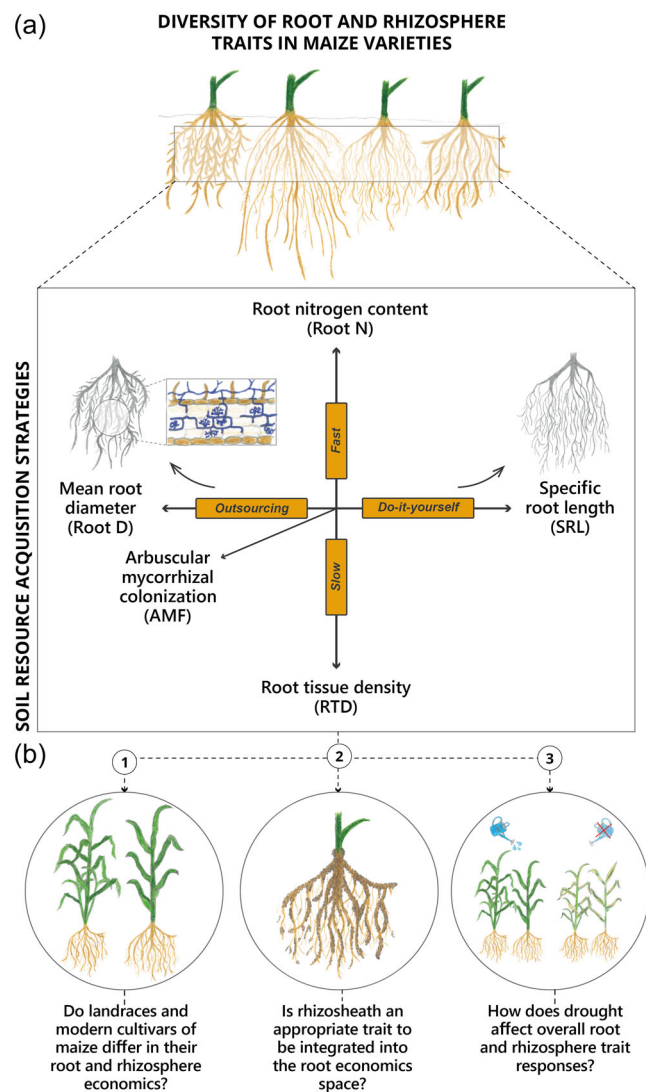
(a)

DIVERSITY OF ROOT AND RHIZOSPHERE TRAITS IN MAIZE VARIETIES

SOIL RESOURCE ACQUISITION STRATEGIES

Root nitrogen content (Root N)

Fast

Slow

Mean root diameter (Root D)

Outsourcing — Do-it-yourself

Specific root length (SRL)

Arbuscular mycorrhizal colonization (AMF)

Root tissue density (RTD)

(b)

① Do landraces and modern cultivars of maize differ in their root and rhizosphere economics?

② Is rhizosheath an appropriate trait to be integrated into the root economics space?

③ How does drought affect overall root and rhizosphere trait responses?

FIGURE 1 Conceptual framework and resulting main research questions. (a) The rationale is based on a large intraspecific diversity of root and rhizosphere traits and aims to utilize this variation for the requirements of sustainable agroecosystems. The conceptual basis is the 'root economics space', which combines root and rhizosphere traits relevant to water and nutrient uptake to soil resource acquisition strategies. (b) This root and rhizosphere economics may differ between maize varieties, particularly between landraces and modern cultivars (indicating breeding effects), may be improved with information about the soil around the roots, and may be affected by drought.

(Figure 1a). In addition to root and mycorrhizal traits, root exudation traits were suggested to be included in a root-economic consideration (Wen et al., 2022). In contrast, the role of many other actors of the whole rhizomicrobiome, such as bacteria or saprotrophic fungi, remains unconsidered within plant economics concepts. Certain combinations of relevant root and rhizosphere traits in the RES reveal different strategies of resource acquisition between plant species. Although substantial intraspecific variation exists in functional root and rhizosphere traits across numerous plant species

(e.g., An et al., 2010; Corneo et al., 2017; Lemoine et al., 2023; Wen et al., 2020), the extent to which conceptual RES strategies differ within plant species, particularly among members of the Poaceae family, remains underexplored.

In addition to the strategies employed by a plant species or variety to acquire soil resources, high trait plasticity and thus the ability to rapidly adapt to changing growth environments may be critical to plant resilience, which in turn implies yield stability (Nimmo et al., 2023; Schneider & Lynch, 2020). During drought, future cultivars should exhibit sufficient trait plasticity to respond to severe fluctuations in water and nutrient availability (Comas et al., 2013; Fromm, 2019). High trait plasticity also seems particularly promising in low-input cropping systems with high spatiotemporal resource heterogeneity (Schneider & Lynch, 2020), and at the root–rhizosphere interface during drought, when drying soil should remain in contact with the roots (Carminati & Vetterlein, 2013; Fromm, 2019). In general, root and rhizosphere traits show remarkable plasticity under drought (Comas et al., 2013; Gao & Lynch, 2016; Koevoets et al., 2016), although large intraspecific differences exist (Kano et al., 2011; Melino et al., 2015). However, whether a trait´s plasticity has an adaptive rather than a maladaptive or neutral effect on plant fitness is uncertain (Schneider, 2022). To date, however, how a specific resource acquisition strategy may alter to drought and thus to water and nutrient limitations is still poorly understood (but see studies on legumes, Ho et al., 2005; Sharma et al., 2021).

Breeding and parallel changes in growth environments, such as higher and more homogeneous nutrient availability, may have led to changes in ecophysiological adaptation strategies (for review, see Schmidt et al., 2016), which include a coherently functioning plant-soil system (e.g., adapted symbiotic interactions with the rhizomicrobiome, nutrient mineralization pathways, and trait plasticity). The objective of this study is to investigate whether root and rhizosphere traits of temperate maize varieties (*Zea mays* L.), their soil resource acquisition strategies and trait plasticity have changed significantly over time, especially in the last 80 years (Schmidt et al., 2016; York et al., 2015). First, our aim was to investigate whether there are distinct strategies for acquiring soil resources between maize varieties. Second, we aimed to test whether incorporating rhizosheath into the RES could lead to improved identification of distinct acquisition strategies, given its significance as an indicator integrating rhizosphere processes. And third, we sought to explore the trait responses to drought by applying indices of plasticity and drought-adaptive response (Figure 1b). This allows us to assess the impact of drought on the root and rhizosphere economics.

Landraces are characterized by their local adaptation to spatially and temporally heterogeneous soil environments and higher inter-specific competition in earlier growth environments, which implies less intensive agriculture. Therefore, we hypothesize that landraces exhibit diverse soil resource acquisition strategies and increased multitrait drought response indices compared to modern cultivars. The driving forces for such a progression could be intensified breeding efforts specifically targeting aboveground traits under

changing modern cultivation practices (Paez-Garcia et al., 2015; Wissuwa et al., 2009). We, therefore, assessed key root and rhizosphere traits across 38 Central European landraces and modern cultivars of maize in a greenhouse phenotyping experiment under both well-watered and drought-stressed conditions.

2 | MATERIALS AND METHODS

2.1 | Experimental setup

We conducted a greenhouse mesocosm experiment at the Bavarian State Research Center for Agriculture from October to December 2020. Using a high-throughput phenotyping facility (LemnaTec Scananalyzer 3D, LemnaTec GmbH), we investigated root and rhizosphere traits of landraces and modern cultivars of maize (*Zea mays* L.) under well-watered and drought-stressed conditions. The total number of 38 varieties comprised 16 landraces (i.e., year of release: pre-1945), 16 hybrid cultivars, and six open-pollinated varieties (OPVs) selected based on a wide range of genetic backgrounds from various breeders, cultivation types, and origins mainly from German, Swiss, Italian and Austrian regions in Central Europe (Supporting Information S1: Table S1). Hereafter, hybrid cultivars and OPV are considered modern cultivars, since in both cases intensive breeding has taken place in recent decades under rapidly changing cultivation practices. The soil for the experiment was obtained from an agricultural field (topsoil material) of the TU Munich research farm in Duernast (48°24′23.7″N, 11°41′24.4″E). Before filling the cuboid mesocosms, the soil was air-dried, sieved (<2 mm), homogenized and had a 'clay loam' texture (WRB, 2022) with 33.2% sand, 39.5% silt, 27.3% clay, OC and N contents of 13.9 and 1.4 mg g^{-1}, δ^{13}C and δ^{15}N of −25.5‰ and 5.3‰, and a pH of 6.3. The phosphorus availability was 9.2 mg 100 g soil^{-1} (determination with calcium lactate/acetate method). Each mesocosm (37 × 27 × 31 cm) was filled with 9.9 kg of soil and two maize plants of the same variety were grown. The plants were separated by a foil-wrapped polystyrene block (20 × 25 × 27.5 cm) to meet the weight restrictions of the facility, but hydraulically connected with thin soil layers at the top and bottom. For more information on the soil's hydraulic properties, see Koehler et al. (2023). A total of 310 mesocosms were established (38 varieties × 2 treatments × 4 replicates + 6 bare soil controls) and randomly positioned in the greenhouse.

Germination was initiated on 6 October 2020 by sowing three seeds per mesocosm side in the pre-irrigated soil. Eight days after sowing (DAS), mesocosms were thinned to one plant per side. During the experiment, the average temperature in the greenhouse was 20.8°C (daytime) and 18.9°C (nighttime) with a photoperiod of 14 h, while the relative humidity ranged between 52.1% and 56.1%. Both greenhouse temperature and humidity were automatically recorded and logged (Pt1000, temperature and humidity sensor, RAM GmbH Mess- und Regeltechnik). Furthermore, mesocosms were weight-based irrigated from the top and automatically rotated daily to avoid greenhouse effects on the position of the mesocosm. Plants were fertilized three times: 12, 18 and 25 DAS using KNO$_3$, NH$_4$NO$_3$ and MgSO$_4$*7H$_2$O, respectively, in increasing concentrations (Supporting Information S1: Methods S1). Before the drought treatment was applied, all mesocosms were covered with meshes and layers of plastic beads to minimize evaporation from the soil. Soil drying was initiated 37 DAS by withholding irrigation for the drought-stressed mesocosms at a time when comparably developed plants were in the leaf development growth stage (BBCH-scale 15-16). Up to this point and continuing for the well-watered mesocosms, plants were kept under optimal water conditions at a mean water potential of −60 hPa/pF 1.7. During the experiment, the soil water status was determined regularly (Supporting Information S1: Methods S2). Irrigation was accompanied by weighing so that daily transpiration could be calculated as the difference in weight of each mesocosm from one to another day. For more information on the calculation of the normalized transpiration ratio, see Koehler et al. (2023).

2.2 | Sampling procedure

Sampling started 64 DAS with plants still in the vegetative stem elongation growth stage, after the last drought-stressed mesocosm experienced a decrease in transpiration of at least 50% (Koehler et al., 2023). The soil water potentials of well-watered and drought-stressed mesocosms can be found in Supporting Information S1: Figure S1. Sampling lasted 10 days and included sampling of the aboveground biomass (Supporting Information S1: Methods S3), the root system, as well as rhizosheath. The root systems of both plants in each mesocosm were excavated separately as gently and intact as possible (Freschet et al., 2021). To obtain the rhizosheath, the root system with adhering soil was shaken for 15 s with a custom-made device capable of uniform vibration, followed by careful removal of larger soil fragments (>3 cm) by hand if necessary. The operationally defined rhizosheath which remained attached was carefully stripped by hand. Additionally, broken roots were collected from the soil for 5 min, shaken manually and also used for rhizosheath collection. The excavated and collected broken roots were subsequently soaked in water and washed, while one of the two mesocosm root systems was randomly selected and stored in ethanol (70%) for analyses of AMF and root morphology, whereas the other root system was directly dried and used for chemical analyses (Freschet et al., 2021). In addition, a subsample of remaining bulk soil was taken (~10 wt%) for each mesocosm side separately. Roots therein were washed and likewise either stored in 70% ethanol or dried to later extrapolate to the entire root system. Sampling the root system with these three consecutive techniques (i.e., excavation of root system, 5 min search of broken roots, and subsampling of remaining roots not used for rhizosheath collection) allowed an unbiased comparison of the varieties. Furthermore, by keeping those roots from the subsample from which no rhizosheath was taken separate, air-dry rhizosheath mass could be normalized to root length.

2.3 | Root and rhizosheath analyses

All roots (i.e., the excavated root system, collected broken and subsample roots) were scanned using a flatbed scanner (Epson Perfection V800 Photo together with Epson Scan 3.9.3) and 20 × 25 cm acrylic scanning trays. For this, roots were cut and evenly distributed in scanning trays with deionized water to avoid overlapping. The image resolution was set to 600 DPI. RhizoVision Explorer v2.0.2 was used for image analysis (Seethepalli & York, 2020). A detailed description of the integrated algorithms can be found in Seethepalli et al. (2021). The settings for image preprocessing included a threshold level of 200, a filter for 'non-root objects' (maximum size 0.5 mm^2) and a setting for feature extraction by enabling 'root pruning' (threshold at 5).

To obtain root biomass, scanned roots were dried at 40°C for 3 days to constant weight. In addition, a subsample was taken which was further dried at 105°C. The total dry root biomass at 105°C was calculated as follows:

$$RB_{105} = RB_{40} \times DMR,$$

where RB_{105} is the upscaled total dry root biomass dried at 105°C, RB_{40} is the total root biomass dried at 40°C and DMR is the dry matter ratio, which is calculated as follows:

$$DMR = \frac{RB_{105S}}{RB_{40S}}.$$

Here, RB_{105S} is the root biomass of the subsample dried at 105°C and RB_{40S} the root biomass of the subsample dried at 40°C.

Using root imaging analyses, we obtained mean Root D, SRL (root length per RB_{105}) and RTD (root volume per RB_{105}). The nitrogen content of the roots (Root N) was measured using an elemental analyser (EA: Flash IRMS, Thermo Scientific) coupled to an isotope ratio mass spectrometer. The calibration was done with acetanilide STD C_8H_9NO (Thermo Scientific).

The total air-dried rhizosheath mass was calculated from an air-dried portion and its water loss over the total fresh rhizosheath mass. Furthermore, total air-dried rhizosheath mass was normalized by the total root length to SRM (total air-dried rhizosheath mass per root length).

2.4 | AMF colonization

A subsample of fine roots stored in ethanol was used for microscopic quantification of AMF colonization (% of root length colonized) using slight modifications of the ink–vinegar method (Vierheilig et al., 1998). For this analysis, 12 contrasting varieties were selected based on a positive correlation between an index of biomass and water use efficiency (Supporting Information S1: Figure S2). In general, 10–15 fragments with a 2–3 cm length were cleared in 10% KOH for 24 h at room temperature and then rinsed in acidified tap water. For staining, roots were heated for 3 min in an ink–vinegar solution (5% ink in 5% vinegar) at 85°C and subsequently rinsed again in acidified tap water.

The stained root fragments were mounted on microscope slides with lactoglycerol and examined with a compound microscope at ×100 magnification (Motic BA210, Motic Instruments Inc.). The magnified intersections method was used to quantify AMF structures (McGonigle et al., 1990). For each sample, at least 150 intersections (i.e., field of views with centred crosshair position) were examined and checked for the presence of arbuscules, vesicles, and hyaline and unseptate AMF hyphae. Intersections without any AMF structures were also noted (I_n). AMF colonization was thereafter calculated using the percentage ratio of non-negative intersections to the total number of intersections (I_t) examined according to the following equation:

$$AMF\ colonization\,[\%] = \frac{I_t - I_n}{I_t} \times 100.$$

2.5 | Statistical evaluation of root and rhizosphere traits

All data were *analyzed* in R v. 4.2.2 (R Core Team, 2022). Unless otherwise stated, observations refer to a single, randomly selected plant of the two plants per mesocosm, which is considered a replicate. All four replicates per variety and treatment were used except for the analyses for AMF colonization, which refers to three replicates per variety and treatment. To examine the alignment of varieties in the RES under optimal growth conditions, principal component analyses (PCA) were performed with samples from the well-watered group for root and rhizosphere traits (i.e., Root D, SRL, RTD, Root N, SRM and AMF colonization). In addition, relationships between traits were calculated with Pearson's correlation analyses. Furthermore, two-way analyses of variance with variety as random effect were performed for most root and rhizosphere traits using linear mixed-effects models (package 'lme4', version 1.1.35.1). Models were validated by testing the residuals for normality using a combination of the Shapiro–Wilk test and visual inspection (Q–Q plot). Levene's test was used to check for variance homogeneity. For proportional AMF colonization data, a binomial generalized linear mixed-effects model was employed. In general, a *p*-value < 0.05 was considered statistically significant. If a significant interaction between 'Treatment' (i.e., well-watered or drought-stressed) and 'Age' (i.e., landraces or modern cultivars) was found, the Tukey honest significance difference posthoc test with Holm's method for *p*-adjustment for multiple comparisons was used (package 'emmeans', version 1.8.8). In addition, Cohen's *d* as a measure of the effect size was determined for better interpretation of the results (Cohen, 2013). The variety-specific percentage trait response of each landrace and modern cultivar to drought was calculated by the proportion of the mean value under drought relative to the mean value of the well-watered control.

2.6 | Plasticity and drought-adaptive response index

To assess the overall potential of the plants to alter their traits in response to a stressor (i.e., drought), we used a multitrait plasticity

index (PI). The multitrait plasticity is defined as the absolute deviation in trait values between well-watered and drought-stressed treatments for each plant separately. However, the PI only provides information on the range of potential variation in trait values. To investigate the specific response to drought and to approximate effective adaptation, we additionally used the Index for Adaptive Responses (InARes), hereafter also referred to as drought-adaptive response index.

The PI and InARes were computed with the R package 'InARes v. 1.0' (Kiene et al., 2023). The indices are based on data transformation methods that normalize and standardize observations to a control (in our case the well-watered control). This allows the combination of multiple functional root and rhizosphere traits to one index value. To account for the different root-rhizosphere systems, a distinction was made between landraces and modern cultivars by defining landraces and modern cultivars as separate groups with independent controls.

According to the InARes framework (Kiene et al., 2023), for calculating index values, root and rhizosphere trait data (i.e., Root D, SRL, RTD, Root N and SRM) for both PI and InARes were first transformed to obtain standardized and normalized relative trait expressions. For the PI, the transformation of individual observations ($cex_{i,k}$) was calculated as follows:

$$cex_{i,k} = \frac{x_i - \mu_c}{\max(\overrightarrow{x_{ct}}) - \mu_c},$$

where $cex_{i,k}$ is the transformed (centred to control mean) value of the kth trait of the ith individual. It is calculated for each trait and individual separately. The untransformed individuals' trait value is x_i, μ_c is the mean value of the control, $\max(\overrightarrow{x_{ct}})$ are the maximum trait values across the well-watered and drought-stressed treatment. For the InARes, values were transformed slightly differently:

$$rex_{i,k} = \frac{x_i - \mu_c}{\max(\overrightarrow{x_{ct}}) - \min(\overrightarrow{x_{ct}})},$$

where $rex_{i,k}$ is the relative trait expression of the kth trait of the ith individual. By using the span of the trait expressions in the denominator, the InARes takes into account that even small trait alterations due to drought can make a strong contribution to the InARes index value; vice versa for large trait alterations with a large span.

The calculation of PI values across all root and rhizosphere traits was thereafter conducted as follows:

$$PI_i = \frac{\sum_k^{n_{traits}} cex_{i,k}}{n_{traits}},$$

where PI_i is the individuals' mean absolute value of all traits. As before, it is calculated at the individual level, which allows the uncertainty (i.e., standard deviation) of this value to be estimated. The number of traits included in PI corresponds to n_{traits}, $cex_{i,k}$ is the value of the kth trait of the ith individual that is included. The InARes, in contrast, is calculated as follows:

$$InARes_i = \frac{\sum_k^{n_{traits}} \frac{rex_{i,k}}{\max(\|\overrightarrow{rex_{i,k(ct)}}\|_\infty) \cdot sgn(median(\overrightarrow{rex_{i,k(t)}}))}}{n_{traits}},$$

where $InARes_i$ is the individuals' weighted mean value of all traits. The InARes is also computed at the individual level to better estimate uncertainties (i.e., standard deviation). $\overrightarrow{rex_{i,k(ct)}}$ is the vector of all rex values of the kth trait of the well-watered and drought-stressed treatment, and $\overrightarrow{rex_{i,k(t)}}$ is the vector of all rex values of the kth trait of the drought-stressed treatment. The signum function ($sgn(median(\overrightarrow{rex_{i,k,t}}))$) assesses the sign of the median of $\overrightarrow{rex_{i,k(t)}}$. The full weighing term corresponds to $\max(\|\overrightarrow{rex_{i,k(ct)}}\|_\infty) \cdot sgn(median(\overrightarrow{rex_{i,k(t)}}))$. The InARes is based on the assumption that the predominant drought response reflects the direction of adaptation to a stressor. Although this is not necessarily applicable in all cases, it is a common assumption in ecological studies that allows us to approximate whether an individual trait alteration is adaptive or maladaptive. Thus, each trait is weighted according to its magnitude of divergence from the control mean reflecting the implicit importance of a change in the respective trait towards the prevailing population response to drought for the individual plant. The resulting InARes value therefore reflects the population's response to drought, taking into account estimated maladaptation. However, it is calculated at an individual level to estimate uncertainties.

The index values of PI were compared between landraces and modern cultivars using linear mixed-effects models with varieties as random effects (package 'lme4'). The InARes values were fitted using a weighted linear mixed-effects model with varieties as random effects (package 'nlme', version 3.1.163) to account for nonhomogeneity of variances within the 'Age' (i.e., landraces vs. modern cultivars) variable. The models were validated as described in Section 2.5. Effect sizes, specifically Cohen's d, were calculated to quantify the magnitude of observed effects.

3 | RESULTS

3.1 | Variety-specific variation of maize in the RES

The alignment of 38 maize varieties in the RES showed wide variation of varieties along the PC1 and PC2 axes (Figure 2). Overall, the first PCA axis (PC1) explained 49% of all variations in root traits and SRM, and a combined explanatory power (PC1 + PC2) of 70% can be reported. Along the PC1 gradient ('collaboration gradient'), landraces clustered on the 'SRL side' with longer and thinner roots, while modern cultivars were clustered towards the 'Root D side' with shorter and thicker roots and higher SRM (for further comparison of landraces and modern cultivars under optimal water conditions, see Table 1). Landraces and modern cultivars further dispersed along the PC2 ('conservation gradient'), with a tendency of enhanced RTD for landraces and higher Root N for modern cultivars. The two root traits Root D and SRL had a high negative correlation ($r = -0.61$, $p < 0.001$), as did Root D and RTD ($r = -0.45$, $p < 0.001$). SRM was positively correlated with Root D

($r = 0.52$, $p < 0.001$) and negatively with SRL ($r = -0.34$, $p < 0.001$), whereas there was no correlation of the addressed traits with Root N, nor between RTD and either SRL or SRM.

When comparing landraces and modern cultivars grown under optimal water conditions, Root D in landraces ($M = 327.8$ μm, SD = 32.3) was significantly smaller than Root D in modern cultivars ($M = 365.4$ μm, SD = 37.5), with an average difference of 37.6 μm ($p < 0.001$, Cohen's $d = 1.30$) (Table 1 and Supporting Information S1: Table S2). A significant difference with large effect size between landraces and modern cultivars was also obtained for SRL (average difference of 28.1 m g^{-1}, $p < 0.001$, $d = 1.57$). With significance and medium effect size, RTD (7.0 mg cm^{-3}, $p = 0.043$, $d = 0.43$) and SRM (1.02 mg cm^{-1}, $p = 0.002$, $d = 0.66$) differed between landraces and modern cultivars under well-watered conditions. No significant difference and no effect between landraces and modern cultivars were found for Root N ($p = 0.689$, $d = 0.16$).

A second PCA was done for a subset of 12 maize varieties with additional information on AMF colonization (Figure 3). The selected landraces and modern cultivars showed similar alignment in the RES as for the complete data set (cf. Figure 2). The correlation between Root D and SRL was negative ($r = -0.58$, $p < 0.001$), as was the relationship between Root D and RTD ($r = -0.47$, $p = 0.004$) (Figure 3). Notably, SRM showed a trend towards positive correlation with AMF colonization ($r = 0.31$, $p = 0.067$). Although landraces and modern cultivars exhibited comparable levels of root colonization by AMF under well-watered conditions, hybrid cultivars (i.e., a subgroup of modern cultivars) showed significantly higher AMF colonization compared to landraces ($p = 0.001$, $d = 0.40$) (Table 1 and Supporting Information S1: Table S2).
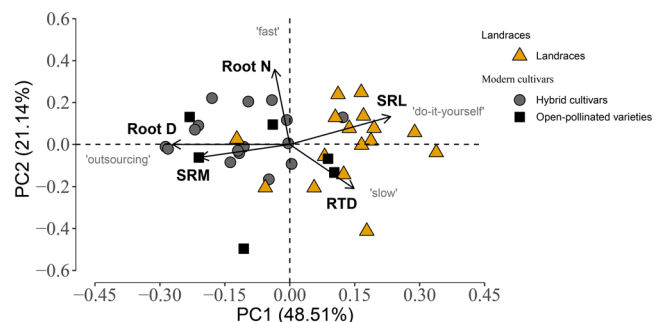

FIGURE 2 Principal component analysis with traits of the root economics space (RES) concept and specific rhizosheath mass (SRM) of 38 maize varieties grown under optimal water conditions. Shaded in grey are the two gradients of the RES concerning resource acquisition strategies, from 'outsourcing' to 'do-it-yourself' and 'fast' to 'slow'. Here, the mean values of the varieties are given; a principal component analysis (PCA) at the individual plant level can be found in Supporting Information S1: Figure S3. Root D, mean root diameter; Root N, root nitrogen content; RTD, root tissue density; SRL, specific root length. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Summary two-way ANOVA table with mean values (M), SD, p values and χ^2 statistics.

		Well-watered		Drought-stressed					
		Landraces	Modern cultivars	Landraces	Modern cultivars		Treatment	Age	Treatment × Age
Root D (μm)	M	327.8$_b$	365.4$_a$	309.4$_c$	324.3$_{b,c}$	p	<0.001	<0.001	<0.001
	SD	32.3	37.5	31.2	28.4	χ^2	89.62	18.51	11.39
SRL (m g^{-1})	M	122.6	94.5	115.1	92.9	p	0.048	<0.001	0.156
	SD	28.0	18.4	19.5	16.1	χ^2	3.91	42.02	2.02
RTD (mg cm^{-3})	M	69.2$_b$	62.2$_c$	82.8$_a$	85.5$_a$	p	<0.001	0.363	0.010
	SD	13.7	11.9	11.6	24.1	χ^2	106.58	0.83	6.73
Root N (mg N g^{-1})	M	21.2	21.7	17.9	18.0	p	<0.001	0.689	0.629
	SD	4.2	4.0	3.4	3.2	χ^2	100.33	0.16	0.23
SRM (mg cm^{-1})	M	3.72$_b$	4.74$_a$	1.09$_c$	1.22$_c$	p	<0.001	0.012	0.013
	SD	1.80	2.40	0.52	0.85	χ^2	317.45	6.24	6.16
AMF (%)	M	56.6	60.3	49.1	53.3	p	<0.001	0.171	0.959
	SD	9.6	10.4	8.8	12.3	χ^2	55.23	1.88	0.96

Note: Summary two-way ANOVA table with mean values (M), SD, p values and χ^2 statistics of each root and rhizosphere trait model comparing landraces and modern cultivars of maize ('Age') grown under well-watered and drought-stressed conditions ('Treatment'). In case of significant interaction 'Treatment × Age', Tukey's HSD posthoc test with Holm's method for p-adjustment was used: means in the same row not sharing subscripts are significantly different from each other. A detailed summary of the Tukey HSD posthoc test with p values and effect sizes (Cohen's d) can be found in Supporting Information S1: Table S2.

Abbreviations: AMF, root colonization of arbuscular mycorrhizal fungi; ANOVA, analysis of variance; HSD, honest significance difference; Root D, mean root diameter; RTD, root tissue density; Root N, root nitrogen content; SRL, specific root length; SRM, specific rhizosheath mass.
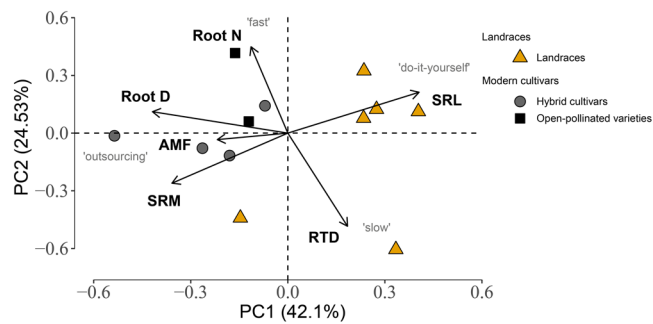
FIGURE 3 Principal component analysis with core traits of the root economics space (RES), specific rhizosheath mass (SRM) and arbuscular mycorrhizal fungi (AMF) colonization of six landraces and six modern cultivars grown under optimal water conditions. Shaded in grey are the two gradients of the RES concerning resource acquisition strategies, from 'outsourcing' to 'do-it-yourself' and 'fast' to 'slow'. Here, the mean values of the varieties are given; a principal component analysis (PCA) at the individual plant level can be found in Supporting Information S1: Figure S3. Root D, mean root diameter; Root N, root nitrogen content; RTD, root tissue density; SRL, specific root length. [Color figure can be viewed at wileyonlinelibrary.com]

3.2 | Responses of root and rhizosphere traits to drought

In general, all root and rhizosphere traits showed a significant treatment effect (Table 1). Drought had a strong effect on Root D with smaller diameters in both landraces ($p = 0.001$, $d = 0.64$) and modern cultivars ($p < 0.001$, $d = 1.42$) (Table 1 and Supporting Information S1: Table S2). The SRL was significantly reduced under drought-stressed conditions ($p = 0.048$, Table 1). Similarly, the effect of drought on RTD was significant with denser roots in response to drought in both landraces ($p < 0.001$, $d = 0.84$) and modern cultivars ($p < 0.001$, $d = 1.44$) (Supporting Information S1: Table S2). However, RTD of landraces and modern cultivars showed no significant differences under drought ($p = 0.358$, $d = 0.17$, Supporting Information S1: Table S2). Furthermore, Root N, SRM and AMF colonization exhibited a clear treatment effect ($p < 0.001$, Table 1), each with lower values under drought, whereas no significant differences between landraces and modern cultivars were observed for any of the three root and rhizosphere traits. However, hybrid cultivars in particular showed significantly higher AMF colonization under drought compared to landraces (Supporting Information S1: Table S2).

Examination of percentage trait response to drought at variety level revealed that the majority of varieties responded similarly in Root D, RTD, Root N, SRM and AMF colonization (Figure 4). Only few varieties displayed no response or response in the opposite direction to the majority. For SRL, a clear direction of drought response could not be identified. Although there was a tendency towards lower SRL values under drought, both comparatively strong increases and decreases of SRL values under drought could be observed in some varieties.

3.3 | Multitrait plasticity and drought-adaptive response

More detailed analyses of phenotypic adaptation of key root and rhizosphere traits to drought were performed using an individual-level multitrait approach employing the PI and InARes. Using PI, a significant difference with a large effect size was found between landraces and modern cultivars in phenotypic plasticity ($p < 0.001$, $d = 0.93$; Figure 5a). On average, landraces ($M = 0.32$, $SD = 0.09$) showed a 28% increased phenotypic plasticity of core RES traits and SRM compared to modern cultivars ($M = 0.25$, $SD = 0.07$). Whereas phenotypic plasticity describes how morphologically variable varieties respond to drought, InARes includes in the calculation whether the trait adaptation to drought conforms with the change in the overall population. In other words, the higher the InARes values, the more an individual responds differently across all traits to the population mean in homologous direction to the population change. In general, a similar trend as for PI could be observed (Figure 5b). Landraces showed an average 25% higher drought-adaptive response than modern cultivars ($p = 0.007$) with a medium effect size ($d = 0.59$). Noteworthy was a clear clustering within modern cultivars, with OPV showing both a tendency of increased phenotypic plasticity ($p = 0.056$, $d = 0.82$; Figure 5c) and a significantly increased drought-adaptive response ($p = 0.016$, $d = 0.86$; Figure 5d) compared to hybrid cultivars, whereas OPV showed no differences to landraces in plasticity and drought-adaptive response ($p = 0.358$, $d = 0.29$; $p = 0.968$, $d = 0.01$).

4 | DISCUSSION

4.1 | Landraces and modern cultivars diverge in their root and rhizosphere economics

Sole focus on aboveground breeding objectives over the last 80 years, combined with major changes in agricultural growth environments (e.g., intensified mineral fertilization), may have significantly altered soil resource acquisition strategies in modern cultivars of maize compared to landraces (Schmidt et al., 2016; York et al., 2015). Our results provide evidence that landraces and modern cultivars diverge in the RES (Figure 2). We show that landraces are predominantly DIY strategists, while modern cultivars are classified as outsourcing strategists with a tendency towards fast belowground growth.

In general, domestication of many crops has led to a decrease in Root D and an increase in SRL when comparing wild relatives with domesticated crops (for review, see Isaac et al., 2021; but see Martín-Robles et al., 2019). In contrast, our data suggest that later intensive breeding has reversed this shift in traits, as we observed higher Root D and lower SRL in modern cultivars compared to landraces. This is consistent with data on landraces and modern cultivars of *Triticum aestivum* L. (Nimmo et al., 2023; Siddique et al., 1990), *Triticum durum* Desf. (Bochicchio et al., 2022) and maize (Ning et al., 2014). High SRL
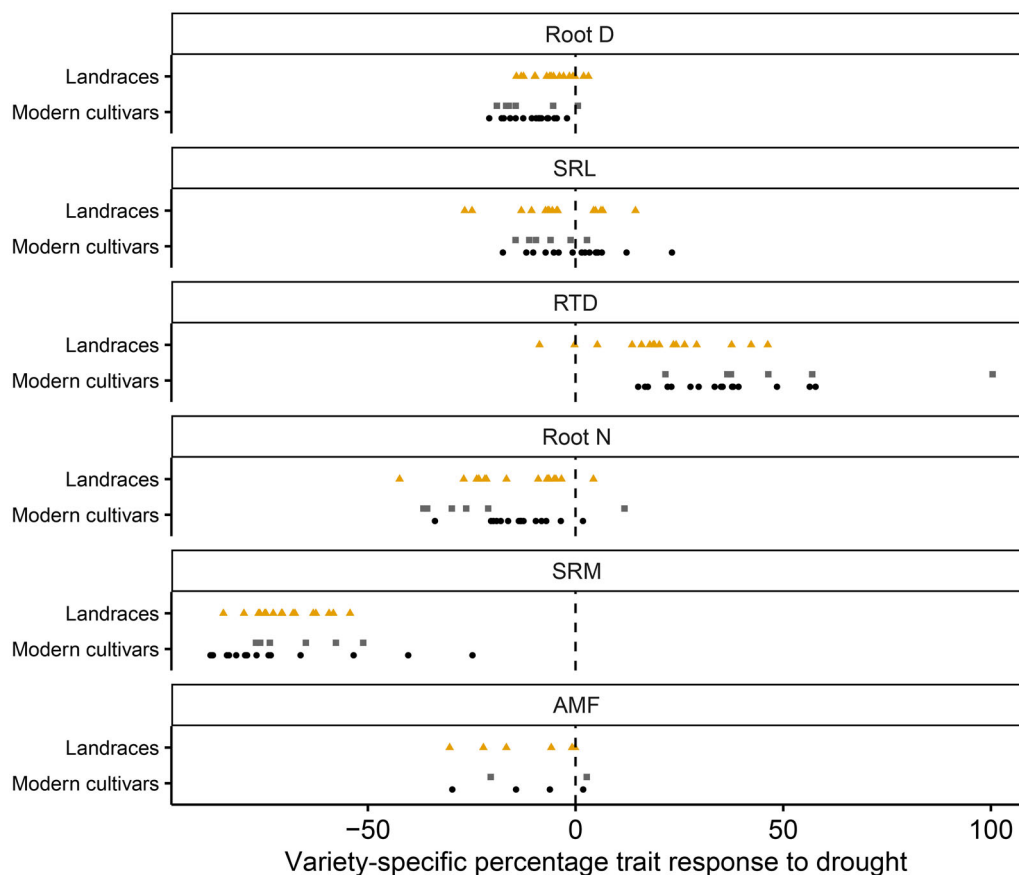
FIGURE 4 Percentage trait responses of each landrace and modern cultivar of maize to drought. Positive values indicate an increase in variety mean values under drought stress compared to the well-watered control; negative values vice versa. Black circles stand for hybrid cultivars, grey squares for open-pollinated varieties (OPV). Hybrid cultivars and OPV are considered modern cultivars. AMF, root colonization of arbuscular mycorrhizal fungi; Root D, mean root diameter; Root N, root nitrogen content; RTD, root tissue density; SRL, specific root length; SRM, specific rhizosheath mass. [Color figure can be viewed at wileyonlinelibrary.com]

and low Root D, as exhibited by landraces in our study, are commonly linked with an increased root surface area and the potential to access a larger soil volume at a comparatively low cost (Comas et al., 2013). Moreover, high SRL may be particularly important in P-limited soils (Sharma et al., 2021; Wen et al., 2019) and under conditions where, for example, increased weed pressure and thus interspecific competition for nutrients and water occurs (Schmidt et al., 2016). With sufficient P supply and low interspecific competition, modern cultivars may afford to sacrifice benefits of high SRL. This effect could occur if traits in the rhizosphere have a functional redundancy to high SRL, such as enhanced AMF colonization or rhizosheath formation (see also Wen et al., 2019), possibly encouraging an outsourcing resource acquisition strategy.

Indeed, AMF colonization was significantly higher in hybrid cultivars compared to landraces. However, a well-established hypothesis is that intensified breeding under high P conditions reduces the association of modern crops with AMF (Martín-Robles et al., 2018; Porter & Sachs, 2020; Tawaraya, 2003). This cannot be demonstrated in our study nor substantially confirmed in the literature. For example, a comparison of 76 maize landraces, 141 inbred lines, and 38 hybrid cultivars showed that hybrid cultivars had

significantly higher and never lower AMF colonization compared to landraces and inbred lines (An et al., 2010). In other studies, although using a smaller number of landraces and modern cultivars of maize, the authors showed context-dependencies, for example, the dependence of the plant-AMF association on the Glomeromycotina species involved (Londoño et al., 2019; Wang et al., 2019). Although the actual plant-AMF association strongly depends on host-fungus interactions and edaphic properties such as nutrient availability or soil texture (Bennett & Groten, 2022), the general potential for AMF association could be derived from Root D, a trait that may explain genotypic variation. We found that Root D was significantly larger in modern cultivars compared to landraces by 37.6 µm, twice as much as the mean cortical cell diameter of about 20 µm reported for maize (Chimungu et al., 2014). A larger Root D is usually positively correlated with AMF colonization in the roots of many terrestrial plants, including crops, presumably because more root cortex provides more AMF habitat (Galindo-Castañeda et al., 2019; Ma et al., 2018; Wen et al., 2019), unless this is at the expense of root cortical aerenchyma formation (Galindo-Castañeda et al., 2019). Interestingly, however, root cortical aerenchyma was also shown to positively correlate with the colonization of AMF for hybrid maize
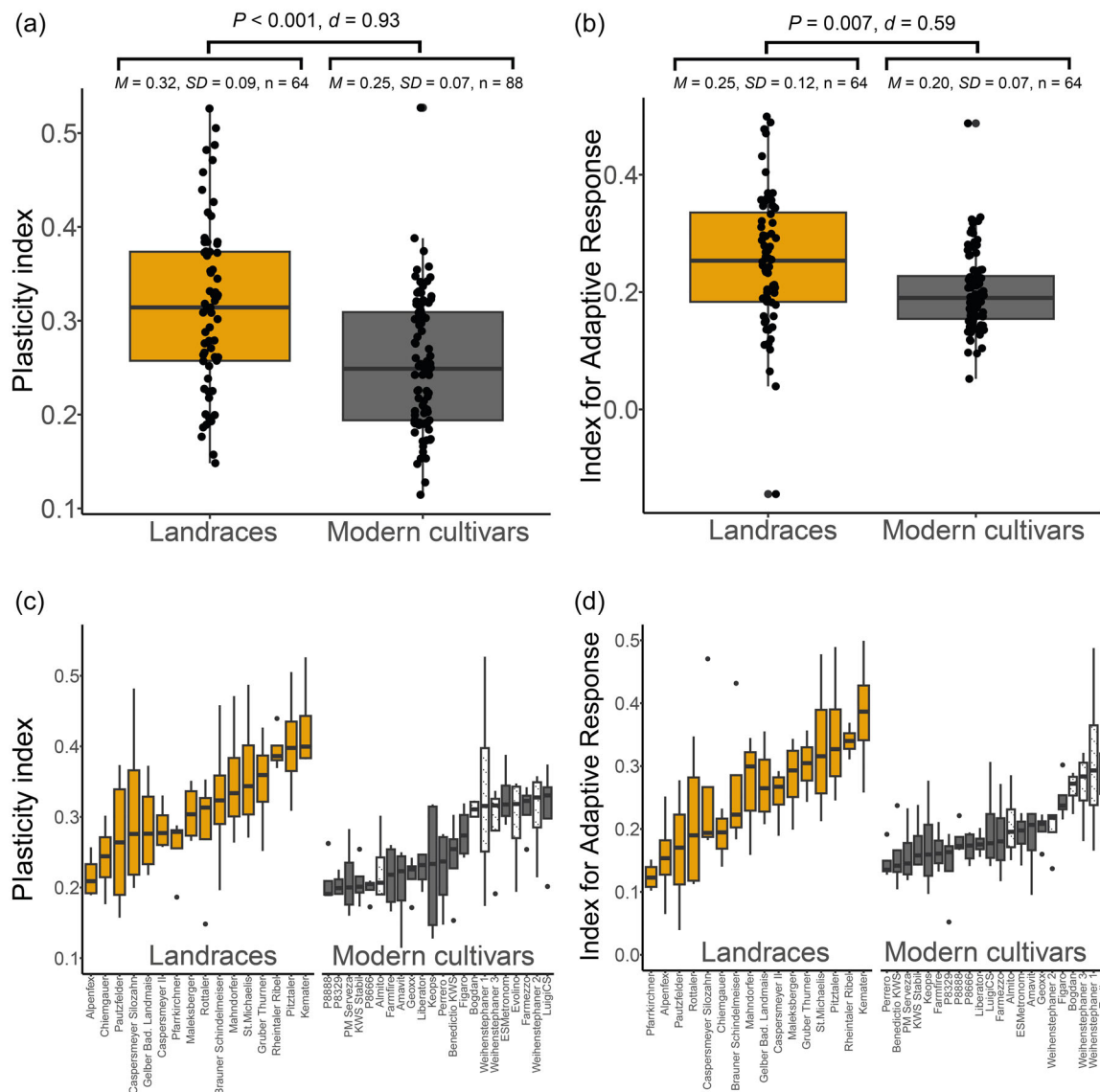
FIGURE 5 Multitrait drought response analyses of landraces and modern cultivars of maize using two indices. (a) plasticity index (PI); (b) Index for Adaptive Responses (InARes) as a drought-adaptive response index to approximate effective adaptation; (c) PI for each variety; (d) InARes for each variety. Open-pollinated varieties (OPV), among modern cultivars, are dotted. p values were derived from underlying linear mixed-effects models, d corresponds to Cohen's d effect size. [Color figure can be viewed at wileyonlinelibrary.com]

cultivars with the largest Root Ds (Galindo-Castañeda et al., 2019). Increased aerenchyma formation in the root cortex, which in turn is linked to reduced RTD, does therefore not necessarily restrict the suitability of roots as a habitat for AMF.

The categorization of varieties into slow and fast growth along the conservation gradient was weak and mainly influenced by RTD rather than Root N. Landraces exhibited high RTD, which is usually associated with resource conservation and possibly reflecting nutrient-poor soils in earlier growth environments (Milla et al., 2015). Lower RTD in modern cultivars, on the other hand, may be associated with more nutrient-rich breeding environments and thus improved nutrient availability through increased mineral fertilization (Milla et al., 2015). The input of plant-available N sources has increased considerably and steadily since 1945, as also indicated by the N

surplus in many agricultural systems (Batool et al., 2022). However, regarding Root N, we could not observe any differences between landraces and modern cultivars under well-watered conditions. This indicates that the efficiency of nitrogen uptake either reached comparable levels or that landraces and modern cultivars performed a similar N translocation into the aboveground plant tissue during the experiment until shortly before flowering with steadily increasing N demand. The findings conform to a recent study where no specific effects on N acquisition processes were found when comparing maize hybrids released between 1936 and 2015 (Schmidt et al., 2020). In contrast, Emmett et al. (2018) indicated significant improvements in N acquisition, especially in maize hybrids with high N demand, possibly as a result of intensified breeding under altered cultivation practices.

Overall, this study is the first to show a clear differentiation of soil resource acquisition strategies based on the RES within varieties of a single species. Root morphological and mycorrhizal traits suggest that maize landraces follow a DIY strategy, while modern cultivars are outsourcing strategists with a tendency to fast belowground growth.

4.2 | Enhanced SRM is an indicator of an outsourcing resource acquisition strategy

Using SRM, we integrated a proxy for various rhizosphere processes into the RES (Figure 2). Irrespective of the complexity of the root-rhizosphere system, we hypothesize that increased formation of rhizosheath can approximate important traits related to an outsourcing resource acquisition strategy.

In our study, we observed significantly enhanced SRM in modern cultivars compared to landraces. This is in line with a study by Adu et al. (2017), which also compared maize landraces and modern cultivars, albeit focusing on the seedling stage. Traits relevant for rhizosheath formation primarily include root hairs (e.g., Adu et al., 2017; Burak et al., 2021; George et al., 2014; Holz et al., 2018) and specific rhizodeposits (i.e., predominately polysaccharide-rich exudates; Burak et al., 2021; Galloway et al., 2020), which act as binding agents adhering soil particles together or as substrate for microbes triggering a cascade of further rhizosheath-promoting effects (Naseem et al., 2018; Ndour et al., 2020; Vidal et al., 2018). Besides, AMF can alter the soil structure and thus increase SRM by intertwining soil particles (Leifheit et al., 2014; Rillig & Mummey, 2006). Fungal hyphae have been demonstrated to have remarkable effects on the formation of soil aggregates and microstructure (Leifheit et al., 2014; Vidal et al., 2018). In our study, SRM showed only a weak positive correlation with AMF colonization ($r = 0.31$, $p = 0.067$), which could be addressed through more direct trait linkages in future studies, e.g. by using extraradical AMF traits (see Moreno-Espíndola et al., 2007). However, we observed a positive correlation between SRM and Root D. Interestingly, Mwafulirwa et al. (2021) showed that larger diameters in maize roots were associated with greater soil organic matter (SOM) mineralization (i.e., positive priming). According to the authors, this may be due to enhanced assimilate transport capacity of larger Root Ds and possibly associated with greater amounts of rhizodeposits. This is supported by a recent study showing that root exudation correlates positively with Root D and negatively with RTD (Williams et al., 2022). Hence, the positive correlation between SRM and Root D, likely caused by enhanced exudation, further supports the idea of including SRM in the RES as an indicator for the outsourcing strategy.

Taken together, we identified SRM indicative of an outsourcing strategy as a promising trait for breeding purposes. A high SRM by enhanced rhizodeposition together with increased AMF association may offset the benefits of resource acquisition through high SRL and foster an outsourcing resource acquisition strategy in modern cultivars.

4.3 | Landraces exhibit higher plasticity and drought-adaptive responses compared to modern cultivars

Drought generally resulted in significant trait responses in both landraces and modern cultivars, but with large variety-specific variation (Figure 4). Root D was reduced under drought compared to the well-watered plants, while SRL remained constant. Moreover, RTD significantly increased under drought, whereas Root N decreased.

An increase in RTD and decrease in Root N under drought may indicate an expansion of the conservative slow-acquisition strategy with increased investment in root construction (e.g., cell wall stabilization poor in N) and a slowdown in nutrient cycling and dynamics with a concomitant increase in root longevity (Bergmann et al., 2020; Kramer-Walter et al., 2016; Wen et al., 2022). Drought generally slows down the microbial mineralization of SOM as well as N diffusivity and mass flow (He & Dijkstra, 2014). Under field conditions and in the long term, plants can adapt to access water and N reserves in the subsoil (Lynch, 2018) or interact positively with the rhizomicrobiome via rhizodeposits (R. Wang et al., 2021) and overcome the negative interactions between water scarcity and N availability, emphasizing the importance of rooting depth to be considered in plant economic considerations (Weigelt et al., 2021).

In addition, along the collaboration gradient in the RES, root morphological adaptation under drought with reduced Root D and increased SRL can generally be considered a drought adaptation (Comas et al., 2013). The rationale behind is an increase in hydraulic conductivity by reducing apoplastic barriers to water transport into the xylem in thinner roots and a larger soil volume explored by roots with high SRL, which is critical under drought (Comas et al., 2013; Lozano et al., 2020). This is potentially accompanied by an accentuation of DIY resource acquisition with comparatively low C investment. In contrast, however, a meta-analysis on how drought affects root traits and responses in plants showed that Root D and RTD in grasses are usually increased under drought, while SRL is decreased (Zhou et al., 2018). Thicker roots under drought could be adaptive in three ways: (1) increased soil penetration resistance (Colombi et al., 2018), (2) enhanced capacity for AMF association and (3) improved osmoregulation due to the potential storage of nonstructural carbohydrates (Lozano et al., 2020; Zhou et al., 2018). The inconsistency of these described adaptation responses suggests that there is no uniform adaptation strategy for drought (Lozano et al., 2020).

Moreover, the colonization of AMF significantly decreased in both landraces and modern cultivars under drought. Recent studies also revealed negative (Begum et al., 2019) or no effects (Hu et al., 2020; Quiroga et al., 2018, 2019) of drought on AMF colonization. In theory, maintaining high AMF colonization under drought could be a beneficial plant strategy, as hyphae access water films in smaller soil pores that are inaccessible to plant roots, thus enhancing the soil and root hydraulic conductance (Abdalla & Ahmed, 2021; Abdalla et al., 2023; Chareesri et al., 2020). This is

likely to be of particular importance for varieties tending towards an outsourcing resource acquisition strategy, with limited capability of root morphological compensations. Furthermore, from a plant perspective, it may be crucial to maintain root-soil contact under drought, especially at root segments destined to remain hydraulically connected to the soil (e.g., root tips; Carminati & Vetterlein, 2013). Besides AMF, a stable rhizosheath, in particular, is likely to be an important factor in this regard (Brown et al., 2017). In our study, SRM was significantly reduced under drought compared to the well-watered plants. However, this was surprising as other studies have shown that rhizosheath is enhanced in dry soils (Watt et al., 1994; Liu et al., 2019), mainly explained by increased adhesiveness of mucilage and plastic elongation of root hairs under drought conditions (Watt et al., 1994).

To the best of our knowledge, there are no studies to date that display any particular specificity of varieties in drought response in the respective root and rhizosphere traits. In general, with few exceptions, the varieties used in this study responded similarly to drought, but with differences in their intensity of expression. However, a variety-specific trait response with contrasting tendencies was found in SRL, where some varieties responded with a strongly increased, and others with a strongly reduced SRL.

If maize individuals were considered separately and multitrait drought-response indices were used, landraces seem to conceal an increased potential in many traits to respond to environmental changes with higher plasticity and in a more drought-adaptive manner (see PI and InARes, Figure 5). However, the variation between the varieties was considerable large, and InARes only helps us to approximate effective adaptation (see Supporting Information S1: Figures S4 and S5). The consideration of larger sample sizes per variety and the evaluation of fitness parameters (e.g., grain yield) in future studies could improve the estimation of adaptation with InARes and contribute to a better understanding of variety-specific strategies. The usefulness of increased plasticity in landraces may be contextualized with their earlier growth environments (Schneider, 2022), underlining the importance of the local origin of landraces (Berger et al., 2011). Thus, environments characterized by increased interspecific competition and more heterogeneous soil resources may call for plasticity, whereas high plasticity in modern cultivars under high-input cropping systems may even be considered detrimental, as phenotypic plasticity comes with costs (Schneider, 2022).

5 | CONCLUSIONS

In summary, we showed that temperate landraces and modern cultivars of maize diverge in their soil resource acquisition strategies. We found important evidence of breeding effects on root and rhizosphere economics within a single plant species. Further, SRM was found to be indicative of an outsourcing strategy. As a result, we suggest considering SRM as a proxy in plant breeding targeting varieties with an outsourcing resource acquisition strategy. Since the

measurement of root and rhizosphere traits, such as AMF colonization, root hairs or root exudation, makes large-scale phenotyping for breeding difficult, an alternative examination of SRM seems more promising. However, the advantages and disadvantages of different soil resource acquisition strategies for plant performance remain elusive. Further breeding objectives can be derived from the findings that landraces have increased multitrait plasticity and drought-adaptive responses compared to modern cultivars. To shed more light on the entire root-rhizosphere system, future studies on root and rhizosphere traits and multitrait drought responses should consider cost–benefit trade-offs of resource acquisition strategies under various drought intensities as well as soil properties and farming practices. We encourage further research to gain a more comprehensive understanding of the root-rhizosphere system, its plasticity and its ability to adapt to variable future growth conditions. Integrating this understanding into practical applications is pivotal for improving food security through stabilized agroecosystems.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The complete dataset on root and rhizosphere traits is available from the BonaRes Repository at Leibniz Centre for Agricultural Landscape Research (ZALF), Germany at doi:10.20387/bonares-9fa5-72a2. Aboveground biomass data will be linked to this dataset after an embargo no later than 12 months from the date of publication.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.