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Full Length Article

Field-based Drought Tolerance Assessment of Carrot Germplasm from Diverse Geographical Origins

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Abstract

Drought stress is becoming increasingly frequent and severe under climate variability, adversely affecting carrot root length, weight, and diameter. This study tested the hypothesis that drought stress differentially affects taproot traits in cultivated and wild carrot accessions originating from diverse geographical regions. The drought tolerance responses of 110 (64 cultivated and 46 wild) carrot accessions were evaluated for three years. Length, weight, and diameter of carrot roots were noted under well-watered conditions and drought stress field conditions; absolute decreases due to drought (AD), growth inhibition index (GI), relative drought tolerance (RDT), and drought tolerance index (DTI) of these three traits were also calculated. Of the 110 carrot accessions, 27 were classified as tolerant, 30 as moderately tolerant, 27 as moderately susceptible, and 26 as susceptible. Pearson's correlation coefficient analysis revealed that root weight and diameter were positively and significantly correlated ($P < 0.001$; $r = 0.81$) under drought stress. Principal component analysis (PCA) revealed five principal components, of which the first two captured 59 percent variation. Based on the contribution percentage towards overall variation, indices of root weight and diameter were prominent in PC1 and PC2, respectively, highlighting their importance. Hence, these findings suggest that root weight is a reliable trait to be considered for future drought stress tolerance studies of carrot germplasms. This study identified drought-tolerant carrot accessions of various colors as a novel genetic resource from different geographical origins.

Keywords: Carrot; Drought stress; Root weight; Field study; Tolerance index

Introduction

Carrot (*Daucus carota* L.) is a globally significant root vegetable that is rich in carotenoids (provitamin A), dietary fiber and a variety of bioactive compounds of importance. Since the organ harvested is the taproot, water scarcity during root initiation and root filling has an overproportionate effect on yield and root quality (*e.g*., size, texture and marketability). Climate change is increasing the frequency and severity of drought stress events which reduces carrot productivity, especially in the areas where irrigation water is limited or unreliable (Zhang *et al.* 2021; Kowalczyk and Kubo 2022).

Carrots, which are rich in vitamins, minerals, carbohydrates, proteins, fibers, carotenoids, and phenolic pigments, improve human resistance to a variety of viral and cardiovascular disorders (Jahanbakhsh and Jahanbakhsh 2018; Singh *et al*. 2021; Altun and Arslan 2022). Owing to its functional properties, carrot consumption and demand are increasing in both domestic and foreign markets. As a root crop, carrot requires proper irrigation schedules, including adequate water delivery, particularly during the sensitive stages of root growth and development. Carrot farming requires a water supply of 6000-9000 m^3 ha^{-1}, with an average pan evaporation rate of 6-7 mmd^{-1} (Quezada *et al*. 2011). Recent studies have also investigated the effects of drought stress on carrot seed production (Ali *et al.* 2022; Jagosz *et al*. 2025). Low moisture availability, particularly during the sensitive stages of growth, has a negative impact on carrot biomass and quality (Subba *et al*. 2016; Razzaq *et al*. 2017; Bashir *et al*. 2021). Agro-molecular details of carrot gene pool also explored genetic diversity (Mudihal *et al*. 2025) as well as morpho-physiological variation among carrot genotypes has also been evaluated under field conditions (Hossain *et al.* 2026). Recent advances in carrot genetics have also been comprehensively reviewed (Rahma *et al.* 2024; Siqueira *et al.* 2025).

Although significant progress has been made in drought biology of carrot over the last few years (Seleiman *et al.* 2021), the evidence base, the evidence base is still fragmented

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by experimental scale, developmental window, and germplasm set. Most of the work so far has been based on small panels of commercial cultivars or contrasting breeding lines, and has focused on the physiological, biochemical and transcriptomic responses, including the effects of drought on taproot development, carotenoid metabolism and stress signalling pathways (Zhang *et al.* 2021; Oztürk-Gökçe *et al.* 2022). More recent work has extended to tissue-specific hormonal and metabolic regulation, albeit within a single cultivar (Geem *et al.* 2025); responses to reproductive stages across 18 accessions under controlled conditions (Jagosz *et al.* 2025); and morphological and physiological variation among 66 genotypes over one field season (Hossain *et al.* 2026). Brainard *et al.* (2022) established that root size and shape are strongly polygenic traits of clear agricultural relevance, but this work was carried out without drought stress and confined to cultivated material. What is still missing, then, is multi-year field evidence on how simple, readily scorable taproot traits behave across a geographically broad panel spanning both cultivated and wild carrot. Two questions in particular remain open: which trait - root length, weight, or diameter - most reliably separates drought-tolerant from drought-sensitive germplasm, and whether that response tracks domestication status, root color, or geographic origin.

We addressed these gaps by evaluating 110 carrot accessions (64 cultivated, 46 wild) from 26 countries under well-watered and drought-stressed field conditions across three consecutive years. The design is, to our knowledge, novel in combining a globally diverse cultivated-wild panel with repeated multi-year field testing, simultaneous scoring of root length, weight, and diameter, and four complementary drought-response indices - absolute decrease, growth inhibition index, relative drought tolerance, and drought tolerance index. Mixed-effects modelling, correlation analysis, principal component analysis and agglomerative hierarchical clustering were used to partition genetic, environmental and germplasm-linked sources of variation. The aims of this study were to: (i) quantify the effects of drought imposed in the field on major taproot traits, (ii) identify which root trait and drought-response index best discriminated between tolerant and susceptible accessions, (iii) classify accessions into drought-tolerant, moderately drought-tolerant, moderately drought-susceptible, and drought-susceptible groups and (iv) determine whether domestication status, root color and geographic origin explained variation in drought response. This is one of the largest multi-year drought field tests of carrot ever reported, and provides a useful phenotypic approach to select breeding material for maintaining storage-root productivity under water-limited conditions.

Materials and Methods

Germplasm detail

A total of 110 carrot accessions (64 cultivated and 46 wild; Supplementary Table S1) with five root colors and five geographical regions (Asia, Europe, Africa and North/South America) were obtained from the USDA germplasm collections (University of Wisconsin–Madison, USA) and the National Plant Genome Source collections of plant introductions. All accessions were evaluated at the taproot developmental stage.

Field experimentation

The field trials were conducted at Nur-Pur-Thul, District Khushab, Pakistan (71.90°E, 31.88°N) for three consecutive seasons. Each seasonal experiment followed a randomized complete block design (RCBD) with three replicates. The 110 accessions were randomized independently within each replicate under each water regime. Carrot was sown in November and harvested during the second week of March in each growing season. Each accession was sown in a single 6 ft. row with 3 ft. inter-row spacing in two parallel experiments: a well-watered control and a drought-stress treatment. The experimental soil was classified as sandy loam. Detailed meteorological data for each growing season are provided in Supplementary Fig. S1. Agronomic management (land preparation, weeding, and pest control) was identical across treatments.

Irrigation management and drought-stress protocol

Both the well-watered and drought-stress experiments received irrigation after sowing to promote uniform germination and seedling establishment. Five irrigations were applied to the well-watered experiment during the crop-growing period. Drought stress was imposed by withholding irrigation 15 days after germination. Thereafter, the drought-stress plots received water only from natural rainfall until harvest. This protocol was consistent with the field drought-screening procedure previously used for carrot germplasm at Nur-Pur-Thal (Simon 2021; Simon *et al.* 2021; Zhu *et al.* 2021).

Phenotyping of root traits

At harvest (second week of March), five representative plants were sampled per plot. Root length (RL) was measured from the tip to the reduced stem using a ruler (cm). Fresh root weight (RW) was recorded using a digital balance (g). Because carrot thickness is not uniform along the root, the taproot diameter (RD) was measured at the widest portion of the root approximately 2 cm below the crown using a vernier caliper. Two perpendicular measurements were taken and averaged to minimize irregularity effects. Root diameter was expressed in centimeters (cm).

Drought response indices

For each accession and root trait, the mean values under well-watered and drought-stress conditions were used to calculate four drought-response indices. Let X_C represent the trait value of an accession under the well-watered condition and X_S represent its value under drought stress. $\bar{X}_C$ represent the overall mean of all accessions under the well-watered condition.

The absolute decrease caused by drought was calculated as:

$$AD = X_C - X_S \quad (1)$$

The growth inhibition index was calculated as:

$$GI(\%) = \left(\frac{X_C - X_S}{X_C}\right) \times 100 \quad (2)$$

Relative drought tolerance was calculated as:

$$RDT = \frac{X_S}{X_C} \quad (3)$$

The drought tolerance index was calculated as:

$$DTI = \frac{X_C \times X_S}{(\bar{X}_C)^2} \quad (4)$$

In total, 18 parameters were analyzed. Of these, six: control (C), stress (S), absolute decrease due to drought (AD), growth inhibition index (GI), relative drought tolerance (RDT), and drought tolerance index (DTI) were assessed for root length (RL), root weight (RW) and root diameter (RD).

Classification of accessions based on root-weight DTI

Based on predefined DTI_{RW} thresholds, the 110 accessions were separated into four drought-tolerance classes. Accessions with DTI_{RW} > 0.40 were classified as tolerant (T), those with values of 0.20–0.40 as moderately tolerant (MT). Accessions with values of 0.10 ≤ DTI_RW < 0.20 were classified as moderately susceptible (MS), and those with values < 0.10 as susceptible (S) (Fig. 2d). The mean DTI_{RW} differed significantly among the four classes ($P < 0.001$, $R^2 = 0.91$); Tukey's HSD at the 5% level of significance was 0.09, and all four groups differed significantly from one another.

Statistical analysis

Mixed linear model (MLM) was used in which genotypes, domestication (wild, or cultivated), color, origin, treatment, were taken as fixed effects while years and replicates were assumed as random effects. The model was expressed as:

$$y = X\beta + Zu + \varepsilon \quad (5)$$

Where, y = vector of phenotypic observations, X = design matrix for fixed effects, β = vector of fixed effects (genotypes, domestication, color, origin, treatment), Z = design matrix for random effects, u = vector of random effects (year, replicate), with $u \sim N(0, G)$, ε = vector of residual errors, with $\varepsilon \sim N(0, R)$. The model parameters were estimated using restricted maximum likelihood (REML) as implemented in the lme4 R package (Bates *et al.* 2018; R Core Team 2018) specifying the model; Y ~ genotypes + domestication + color + origin + treatment + (1 | year) + (1 | replicate).

Mean comparison analysis based on the geographic origin, domestication status, and color of roots for the traits were calculated using the least significant difference (LSD) test function in the agricolae package with a 5% level of significance (Mendiburu 2023). Pearson's correlation (r) analysis was performed using corrplot package v. 0.92 (Wei and Simko 2021) in R software. Principal component analysis (PCA) was performed on 110 accessions in rows and 18 parameters in columns to classify the accessions and parameters using RStudio (R Core Team 2018).

Results

Composition of the carrot germplasm

The panel comprised 110 carrot accessions representing five primary root colors and five geographic regions. White- and orange-rooted accessions were the most abundant, comprising 48 and 43 accessions, respectively, whereas the remaining accessions included nine yellow, six pure-colored and four red-rooted accessions (Table S1; Fig. 1a). Europe contributed the largest number of accessions, followed by Asia and North America (Fig. 1b). The accessions originated from 26 countries, with Turkey, France and the USA contributing 23, 18 and 12 accessions, respectively (Fig. 1c).

Effects of drought stress and classification of accessions

Drought stress significantly reduced root length, root weight and root diameter relative to the well-watered treatment (Fig. 2a–c). The treatment comparisons produced test statistics of t = 10.33 for root length, t = 12.90 for root weight and t = 14.00 for root diameter with $P < 0.001$ for all three traits. Mean root length decreased from 33.94 cm under well-watered conditions to 12.82 cm under drought stress, representing a 62.2% reduction. Root weight declined from 63.73 to 12.92 g under stress, representing a 79.73% reduction in RW. Root diameter reduced from 2.48 to 0.14 cm, which shows a 94.36% reduction in RD under drought stress. Root diameter exhibited the largest proportional reduction among the three measured traits.

Root weight was selected for DTI-based classification on the basis of its multivariate discriminatory performance rather than the visual appearance of its boxplot or the magnitude of its treatment statistic alone. Root-weight-derived indices were the three largest contributors to PC1, each accounting for approximately 13% of the variation represented by that component (Fig. 5b1). Moreover, root weight under drought was strongly and positively correlated with root diameter under drought (r = 0.81, $P < 0.001$; Fig. 4). These observations support the use of root weight as the primary trait for DTI-based classification.

Table 1: Mean separation for root length on the basis of region, domestication status and primary root color

	Category	Count	Root length control	Root length stress	Absolute decrease	Inhibition index	Relative tolerance	Tolerance index
Region	Asia	29	39.09 ± 1.77 A	12.89 ± 0.46 AB	26.19 A	56.63 A	0.43 BC	0.43 BC
	Europe	60	34.24 ± 1.22 AB	12.71 ± 0.29 AB	21.53 AB	49.50 AB	0.50 BC	0.50AB
	Africa	8	21.64 ± 2.68 BC	10.55 ± 0.46 B	11.09 BC	39.23 BC	0.61 A	0.57 AB
	South America	1	24.17 ± 0.58 BC	13.92 ± 0.99 AB	10.25 BC	42.33 BC	0.58 AB	0.58 A
	North America	12	29.04 ± 1.52 B	14.63 ± 1.03 A	14.41 BC	42.41 BC	0.58AB	0.58 A
Status	Wild	46	35.37 ± 1.10 BC	13.24 ±0.30AB	22.13 AB	52.31 BC	0.48 AB	0.47 AB
	Cultivated	64	31.96 ± 1.40 BC	12.24 ± 0.37CD	19.72BC	46.29 BC	0.54 A	0.54 A
Color	Orange	43	31.19 ± 1.24 BC	13.52 ± 0.39 A	17.67BC	47.36 BC	0.53 AB	0.51 AB
	Pure	6	49.21 ± 3.53 A	13.22 ± 0.95AB	35.99 A	63.36 A	0.37 BC	0.36 BC
	Red	4	42.72 ± 3.98AB	13.05 ± 0.96AB	29.67AB	62.12 AB	0.38 BC	0.38 BC
	White	48	32.03 ± 1.34 BC	12.15 ± 0.36CD	19.88BC	47.25 BC	0.53 AB	0.53 AB
	Yellow	9	43.20 ± 3.45 AB	12.70 ± 0.60CD	30.51AB	60.50 AB	0.40 BC	0.40 BC

Means written next to the same letters are not significantly different using Fisher's least significant difference test at alpha = *0.05*

Table 2: Mean separation for root weight on the basis of region, domestication status and primary root color

	Category	Count	Root weight control	Root weight stress	Absolute decrease	Inhibition index	Relative tolerance	Tolerance index
Region	Asia	29	80.04 ± 3.2AB	11.82 ± 0.82BC	68.22 BC	80.04 AB	0.20 BC	0.20 BC
	Europe	60	55.19 ± 2BC	13.71 ± 0.80BC	41.48 EF	66.59 BC	0.33 A	0.34 A
	Africa	8	82.23 ± 8.6AB	10.60 ± 1.61BC	71.63BC	79.94 AB	0.20 BC	0.22 BC
	South America	1	103.81 ± 1.2A	17.26 ± 2.37A	86.54A	83.35 A	0.17 BC	0.17 BC
	North America	12	51.37 ± 2.9BC	12.79 ± 1.3BC	38.58 EF	71.15 AB	0.29 AB	0.30 AB
Status	Wild	46	84.17 ± 2.11 AB	11.51 ± 0.58 AB	72.66 AB	82.83 AB	0.17 CD	0.17 EF
	Cultivated	64	35.30 ± 1.36 BC	14.88 ± 0.95 A	20.42 BC	56.35 CD	0.44 A	0.45 A
Color	Orange	43	90.75 ± 2.72 A	11.88 ± 0.64 AB	78.87 A	83.01 AB	0.17 CD	0.17 EF
	Pure	6	53.29 ± 4.88 BC	13.73 ± 3.13 AB	39.56 B	73.22 BC	0.27 BC	0.29 CD
	Red	4	65.32 ± 5.77 B	8.15 ± 1.50 B	57.18 AB	83.60 AB	0.16 CD	0.16 EF
	White	48	36.92 ± 1.52 BC	14.43 ± 0.92 AB	22.49 BC	57.90CD	0.42 AB	0.43 AB
	Yellow	9	83.86 ± 3.22 AB	11.39 ± 1.58 AB	72.47 AB	85.67 A	0.14CD	0.14 EF

Means written next to the same letters are not significantly different using Fisher's least significant difference test at alpha = *0.05*

Table 3: Mean separation for root diameter on the basis of region, domestication status and primary root color

	Category	Count	Root diameter control	Root diameter stress	Absolute decrease	Inhibition index	Relative tolerance	Tolerance index
Region	Asia	29	3.37 ± 0.19 A	0.14 ± 0.01 AB	3.23 A	94.20A	0.06 B	0.06 B
	Europe	60	2.06 ± 0.07 B	0.14 ± 0.00 AB	1.92 B	90.84 B	0.09 A	0.09 A
	Africa	8	1.86 ± 0.10 BC	0.13 ± 0.01 B	1.73 BC	92.36 AB	0.08 AB	0.08 AB
	South America	1	2.56 ± 0.01 AB	0.19 ± 0.01 A	2.37 AB	92.55 AB	0.07 AB	0.07 AB
	North America	12	2.81 ± 0.17 AB	0.14 ± 0.01 AB	2.67 AB	94.13 AB	0.06 B	0.06 B
Status	Wild	46	2.92 ± 0.10 AB	0.13 ± 0.00 AB	2.79 AB	94.16 AB	0.06 B	0.06 AB
	Cultivated	64	1.86 ± 0.07 CD	0.14 ± 0.00 A	1.71 BC	89.50 DE	0.11 A	0.10 A
Color	Orange	43	3.35 ± 0.14 A	0.14 ± 0.00 A	3.22 A	94.68 A	0.05 BC	0.05 AB
	Pure	6	2.15 ± 0.11 BC	0.14 ± 0.01 A	2.01 BC	93.14 BC	0.07 AB	0.07 AB
	Red	4	2.26 ± 0.27 BC	0.11 ± 0.01 B	2.15 BC	93.76 BC	0.06 B	0.06 AB
	White	48	1.85 ± 0.06 CD	0.14 ± 0.00 A	1.70 BC	89.66 DE	0.10 AB	0.10 A
	Yellow	9	1.98 ± 0.09 CD	0.12 ± 0.01 AB	1.85 BC	92.75 BC	0.07 AB	0.07 AB

Means written next to the same letters are not significantly different using Fisher's least significant difference test at 5% level of significance

Accessions were classified using predefined thresholds for the drought tolerance index calculated from root weight. Accessions with DTI_{RW} > 0.40 were classified as tolerant and those with 0.20 ≤ DTI_{RW} ≤ 0.40 as moderately tolerant. Accessions with 0.10 ≤ DTI_{RW} < 0.20 were classified as moderately susceptible while those with DTI_{RW} < 0.10 were classified as susceptible. Accordingly, 27 accessions were classified as tolerant, 30 as moderately tolerant, 27 as moderately susceptible and 26 as susceptible (Figure 2d). The overall mean DTI_{RW} was 0.287. Mean DTI_{RW} differed significantly among the four tolerance classes, with a mean square of 1.732, residual mean square of 0.0045, $P < 0.0001$, R^2 = 0.91 and an HSD value of 0.09 at the 5% level of significance. All four tolerance classes differed significantly from one another.

Effect of region, domestication and color on studied traits

The mixed-model analysis indicated significant accession-associated variation in all 18 measured and derived variables ($P < 0.001$; Fig. 3). Under well-watered conditions, Asian and European accessions exhibited the greatest mean root lengths (39.09 ± 1.77 and 34.24 ± 1.22 cm, respectively). North American accessions had the greatest mean root length (14.63 ± 1.03 cm) under drought stress conditions. Root-length DTI was highest for South and North American accessions (0.58) followed by African accessions (0.57) (Table 1; Fig. 3).

Wild accessions had substantially greater root weight under well-watered conditions than cultivated accessions

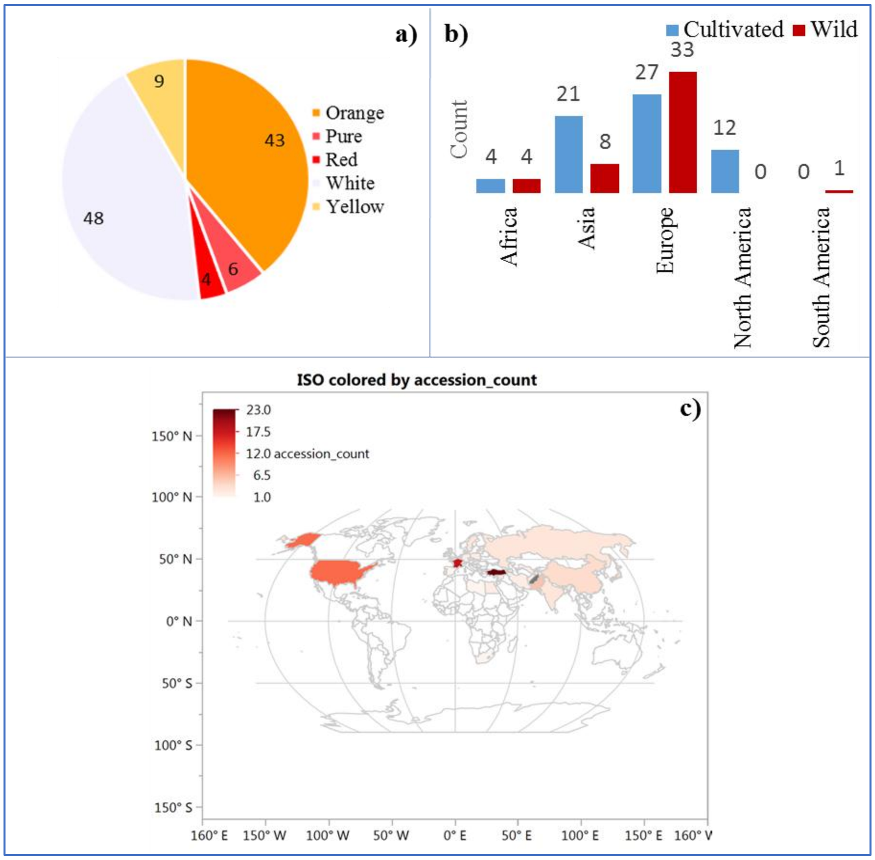

Fig. 1: Distribution according to color (**a**), continents (**b**) and geographic-quantile view of 110 carrot-accessions (**c**) collected from 26 countries of the world

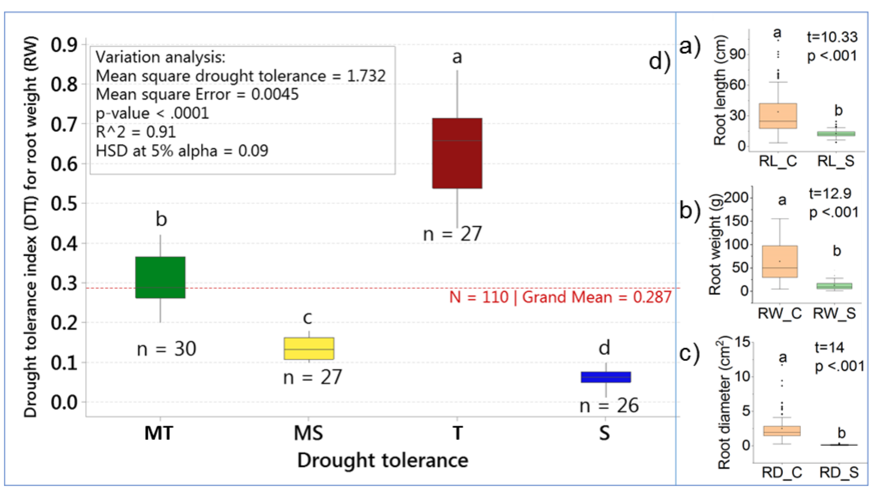

Fig. 2: Effect of drought stress (C: control; S: drought stress) at three traits (**a**, **b**, **c**) and classification of same 110 accessions into tolerant (T), moderately tolerant (MT), moderately susceptible (MS) and susceptible (S) on the basis of drought tolerance index (**d**)

(84.17 ± 2.11 versus 35.30 ± 1.36 g). Under drought stress, however, cultivated accessions maintained a greater mean root weight than wild accessions (14.88 ± 0.95 versus 11.51 ± 0.58 g). This difference was also reflected in the root-weight tolerance indices: cultivated accessions had mean RDT and DTI values of 0.44 and 0.45, respectively, compared with 0.17 for both indices in wild accessions (Table 2).

Among the color groups, orange-rooted accessions had the greatest root weight under the control treatment (90.75 ± 2.72 g). White-rooted accessions maintained the greatest mean root weight under drought stress (14.43 ± 0.92 g).

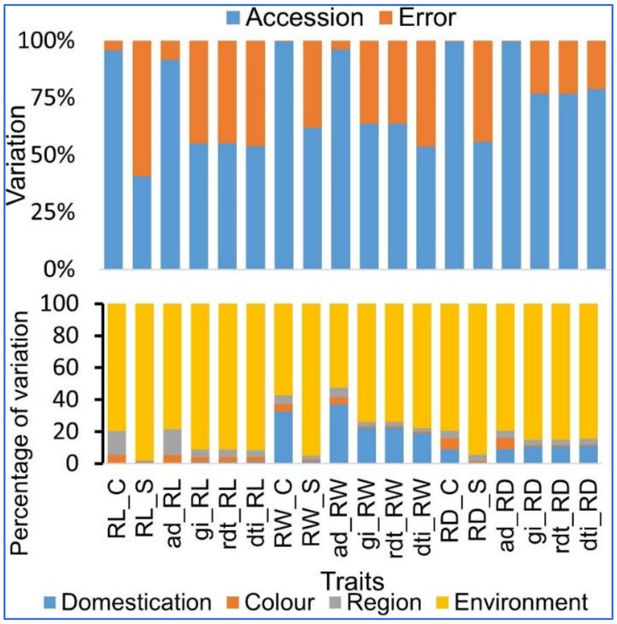

Fig. 3: Variation pattern of eighteen studied attributes in 110 carrot accessions (upper graph), due to (lower graph) domestication status (wild, cultivated; df = 01), color (df = 4), region (4) and environment (df = 650). RL_C: root length (cm) in control; RL_S: Root length (cm) under drought stress; RW: root weight (g), RD: root diameter (cm); ad_RL: absolute decrease in root length due to drought; gi: growth-inhibition index, rdt: relative drought tolerance and dti: drought tolerance index calculated separately for root length (RL), root weight (RW) and root diameter

White-rooted accessions also had the highest root-weight DTI (0.43) followed by pure-colored accessions (0.29), as compared to other three groups. Orange and yellow accessions showed greater inhibition of root weight with GI values of 83.01% and 85.67%, respectively, compared with 57.90% for white-rooted accessions.

Wild accessions had a greater root diameter (2.92 ± 0.10 cm) under well-watered conditions than cultivated accessions (1.86 ± 0.07 cm), but the corresponding drought-stress means were similar (0.13 ± 0.00 and 0.14 ± 0.00 cm, respectively; Table 3). Diameter-based DTI was higher in cultivated accessions (0.10) than wild accessions (0.06). Orange-rooted accessions had the greatest control root diameter (3.35 ± 0.14 cm), but white-rooted accessions had the highest diameter-based DTI (0.10).

Correlations and hierarchical clustering of root traits

Pearson's correlation analysis was performed using data from 110 accessions and 18 variables. The absolute critical r-value, as depicted in Fig. 4, was determined to be 0.158 at the 5% level of significance. Agglomerative hierarchical clustering grouped the 18 variables into three major clusters. Parameters associated with root length, such as the drought tolerance index (dti_RL), relative drought tolerance (rdt_RL), and root length under stress (RL_S), were positively correlated and were classified into the third group. Meanwhile, the GI of root weight and diameter, along with root weight under control conditions and the absolute decrease due to drought, displayed positive correlations and were grouped together as the second diagonal rectangle in the middle of Fig. 4. In the first rectangle, the remaining nine parameters showed significant positive correlations ($P < 0.05$). It is noteworthy that following the determination of the critical r-value at 0.158, correlations below -0.158 and above 0.158 in the matrix (Fig. 4) were considered statistically significant.

Principal component analysis and clustering of accessions

Principal component analysis (PCA) was performed on the same data matrix with the dimensions (110 varieties in rows and 18 parameters in columns) mentioned above. This revealed five principal components with eigenvalues higher than one (Fig. 5a). Overall, 59% of the variation was explained by the first two principal components (PCs). Root weight and related parameters were grouped in PC1, and the percentage contribution was above the threshold (dotted line, Fig. 5b1). The average contribution of all traits to PC1 was taken as the threshold contribution. The maximum percentage of trait contribution in PC2 was up to 20%, and five traits related to root weight and diameter contribution to the PC2 above threshold level (Fig 5b2). Four clusters of 110 genotypes obtained through AHC were also incorporated, and are shown in the score plot (Fig. 5c). When dispersed in a two-dimensional space, these four clusters authenticated the AHC grouping and showed a specific pattern of color-wise clusters. The cluster-1 contained 33 genotypes including 25 orange-colored accessions. Cluster-2 contained 33 genotypes, of which 27 were white (Supplementary Table S1). The eigenvalues of each genotype according to which these are scattered in Fig. 5c are shown in Supplementary table S1. The most important variable in the dataset was root weight because it contributed the highest percentage toward PC1 (Fig. 5d).

Accessions with high positive PC2 scores were more closely associated with greater control root length and root-length reduction, whereas those with negative PC2 scores were associated with higher root-length tolerance indices. The partial concentration of orange- and white-rooted accessions in different clusters indicates that root-color groups coincided with differences in root morphology and drought response, although the overlap among clusters shows that root color did not independently determine tolerance.

Discussion

Drought markedly restricted taproot development across the evaluated carrot germplasm which confirms that storage-root

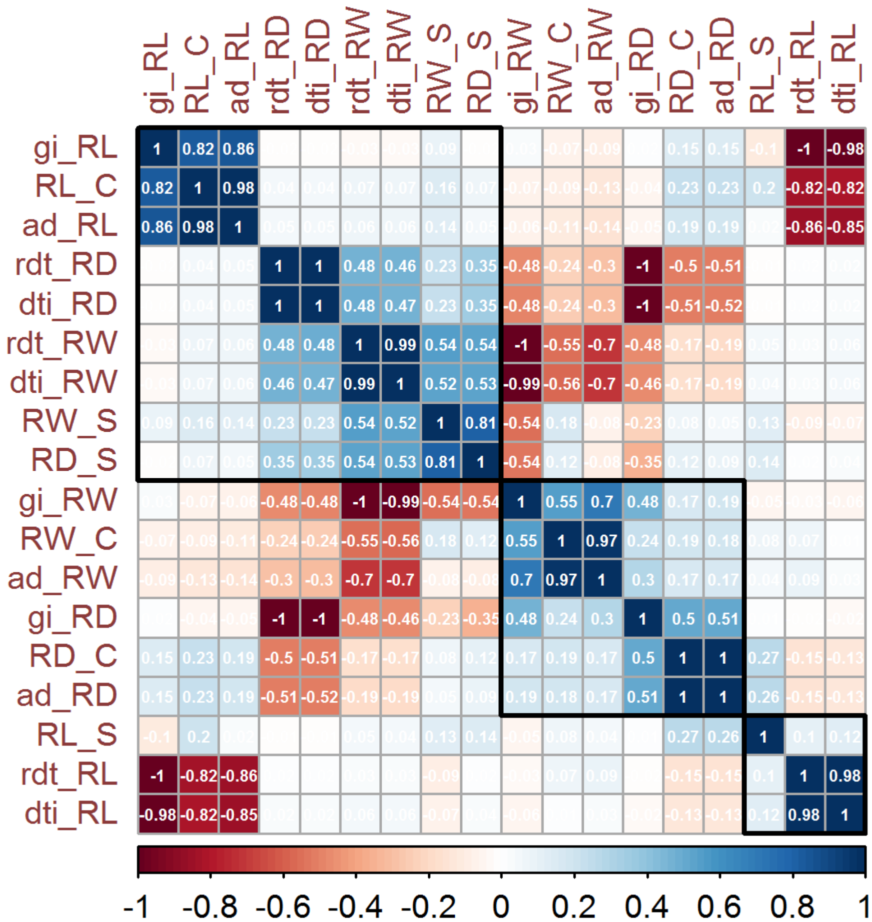

Fig. 4: Pearson's Correlation coefficient (r) among 18 studied traits. Variables have been ordered by agglomerative hierarchical clustering (AHC) method and the absolute r-value ± 0.158 has been calculated as significant at 5% alpha for 110 carrot accessions (degree of freedom = 108). Three rectangle boxes at the diagonal indicate the related clusters of 18 traits

formation is highly sensitive to limited water availability (Devi and Sinclair 2013). Similar reduction in all three taproot traits was reported by Junaid *et al.* (2023), who observed cultivar-dependent losses after drought was imposed during taproot formation. More recently, Hossain *et al.* (2026) also reported significant drought-induced reductions in carrot root length, diameter, fresh weight and marketable yield under field conditions. Root weight exhibited one of the strongest drought responses and showed high discriminatory power for classifying drought tolerance. This classification approach has previously been validated in sugar beet under such conditions (Fotouhi *et al.* 2017). The extent of root weight suppression indicates the dual dependence of taproot filling on carbon assimilation as well as on water availability. Hence, this may serve as a meaningful selection criterion for drought tolerance screens (Zhang *et al.* 2021). The reduction in root weight is consistent with the known effects of drought on sink activity, cambial cell expansion, and assimilate transport (Junaid *et al.* 2023).

The effects associated with geographic origin, domestication status, root color, and treatment environment indicate that carrot drought response is influenced by both germplasm background and growing conditions. Accessions from Asia and Europe produced significantly longer roots than those from Africa, North America, and South America, a pattern consistent with deeper rooting as an adaptation to soils where water retreats below the surface during dry periods (Comas *et al.* 2013; Wang and Qin 2017). Farwan *et al.* (2023) reported a root length range of 14.5–21.0 cm among Asiatic carrot genotypes evaluated across multiple environments. Root length exhibited high heritability and moderate genetic advance, indicating predominantly additive gene action and suggesting that this trait is amenable to selection for improved drought tolerance (Thabet *et al.* 2018). Wild accessions and orange-colored genotypes yielded greater root weight and diameter than their cultivated and non-orange counterparts, respectively. Wild relatives of crop plants frequently retain drought-adaptive variation that selective breeding has eroded from elite cultivars, and the present results suggest that orange-pigmented germplasm may co-inherit root mass traits favorable under water deficit (Awad *et al.* 2017; Rehman *et al.* 2019; Klein *et al.* 2020). Region- and color-associated variation in these traits therefore constitutes actionable phenotypic targets for introgression into elite breeding pools.

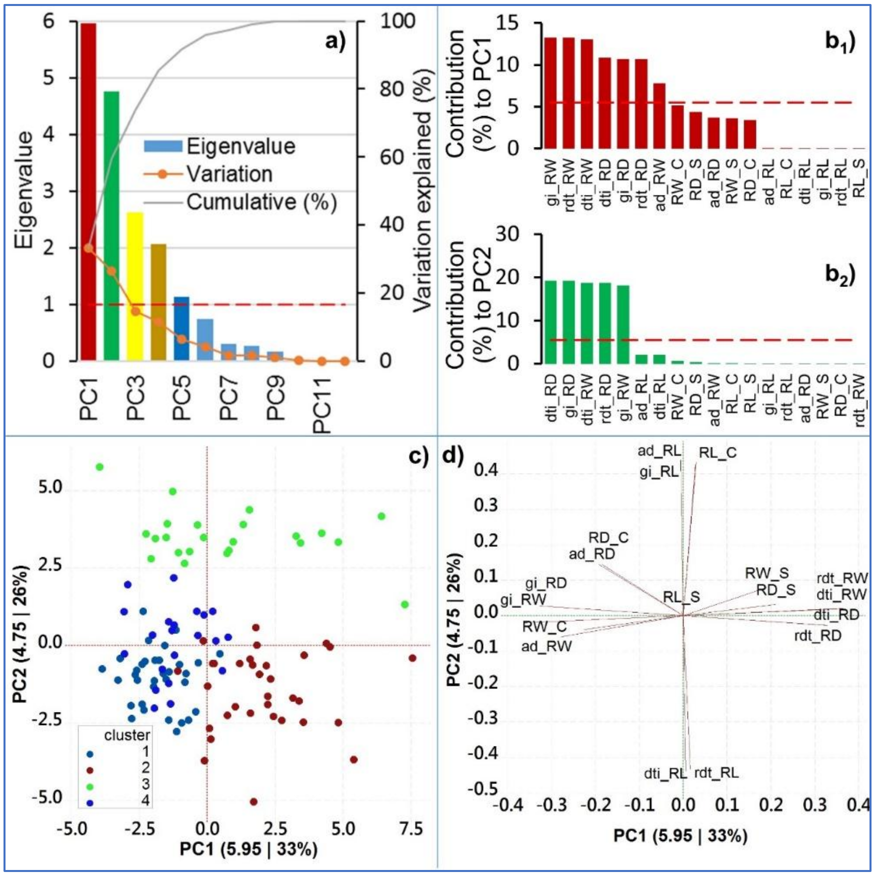

Fig. 5: Principal component analysis (PCA) of eighteen studied traits of 110 carrot accessions reveals five potential principal components (PCs) with eigenvalue greater than one (**a**), percentage contribution of eighteen traits to first two PCs (**b$_1$** and **b$_2$**), score plot of clustered 110 genotypes (**c**) and loading plot of 18 traits (**d**) with eigenvalue and variation percentage explained by PC1 (x-axis) and PC2 (y-axis)

Pearson's correlation analysis and agglomerative hierarchical clustering (AHC) partitioned the 18 parameters into three coherent groups. Root-length-based drought indices (dti_RL, rdt_RL, RL_S) clustered together, reflecting the coordinated suppression of taproot elongation under stress. Growth inhibition indices for root weight and diameter, root weight under control conditions, and absolute decrease in root weight formed a second cluster, indicating that genetic capacity for high root biomass production in the absence of stress coincides with pronounced absolute loss under deficit - a pattern expected when high-yielding genotypes have greater tissue mass at risk. The remaining nine parameters, primarily associated with stress-state values and tolerance ratios, formed a third positively correlated group (Ghimire *et al.* 2020). The multivariate prominence of root-weight- and root-diameter-related variables indicates that biomass retention and radial root growth represent major dimensions of carrot response to drought. Their contributions to different components further suggest that these traits provide complementary rather than entirely redundant information. The partial concentration of orange- and white-rooted accessions in different multivariate groups suggests that pigmentation classes may share genetic backgrounds associated with root morphology. However, the overlap among groups indicates that root color alone is insufficient for predicting drought response, and the possible association requires molecular validation (Rehman *et al.* 2019).

Root weight exhibited the highest loading on PC1 and the most significant univariate discriminator of drought sensitivity, highlighting its dual role of relevance to agronomic performance and stress tolerance. Fresh root mass directly relates to commercial yield and is positively correlated with carotenoid and fiber content, dry matter, and overall nutritional density - qualities driving market value (Raviteja *et al.* 2021). The storage root which serves as a main carbon sink in response to drought requires sustained phloem loading and expansion driven by turgor which is compromised by water scarcity. The higher root weight retained with stress in accessions may possess superior osmotic adjustment or more efficient water acquisition mechanisms (Comas *et al.* 2013; Hanum and Meirani 2020; Klein *et al.* 2020). The positive association between root weight and diameter indicates that maintenance of radial root expansion contributes substantially to biomass retention under drought. Integrating these traits with root length in a multi-trait selection framework may provide a more comprehensive assessment of drought response than reliance on a single root characteristic (Klein *et al.* 2020; Silva *et al.* 2020).

Retention of root weight during drought is probably due to a combination of water conservation, osmotic adjustment, hormonal regulation, antioxidant protection, and continued supply of assimilates to the storage root. Previous studies suggest that ABA-mediated signaling contributes to stomatal closure and lower transpiration water loss, while auxin-induced changes in lateral-root development may help to better access residual soil moisture; interestingly, Geem *et al.* (2025) showed increased expression of ABA- and auxin-related genes in carrot storage roots and lateral-root growth under water deficit. Accumulation of compatible osmolytes has been reported to contribute to sustain the turgor of the cells, stabilize membranes and proteins, and serve as metabolic substrates to support further root elongation (Geem *et al.* 2025). Drought-induced oxidative damage may also be mitigated by the genotype-dependent activation of antioxidant enzymes such as catalase, guaiacol peroxidase, and glutathione reductase, which helps to maintain photosynthetic tissues and carbon assimilation and translocation to the storage root (Jagosz *et al.* 2025). In this regard, Junaid *et al.* (2023) demonstrated that cultivars with higher relative water content, dry matter and photosynthetic pigments performed better for both root yield and quality under drought conditions. Accessions with higher root-weight DTI in the present study may possess greater capacity for water uptake, osmotic regulation, redox homeostasis, and assimilate partitioning; however, this has not been measured directly and should be confirmed by specific physiological and biochemical studies.

The genetic diversity captured in this panel spanning cultivated varieties, wild accessions, and geographically distinct landraces represents a substantive resource for drought-resilience breeding in carrot. Wild relatives in particular may harbor drought-adaptive alleles absent from elite gene pools, as has been demonstrated in closely related root crops (Bolton and Simon 2019; Wiśniewska *et al.* 2019). However, drought tolerance in carrot is polygenic; the phenotypic variation quantified here through DTI, RDT, and GI is the net product of multiple physiological mechanisms whose genetic architecture remains largely uncharacterized (Sallam *et al.* 2019; Oztürk-Gökçe *et al.* 2022). Translating the trait associations established in this field study into molecular breeding tools will require genome-wide association studies or quantitative trait locus mapping to identify markers linked to root weight maintenance under stress - an area where progress in other root crops has shown that marker-assisted selection can substantially accelerate variety development (Wang and Qin 2017). A further consideration is that field-imposed drought at the establishment stage, as applied here, may not fully recapitulate stress responses at the critical root-filling period; targeted validation of the tolerant accessions under defined phenological-stage drought is warranted to confirm that DTI-based rankings are stable across growth stages (Comas *et al.* 2013; Awad *et al.* 2017).

Taken together, these findings establish root weight as one of the most informative traits for field-based drought tolerance screening in carrot germplasm. DTI calculated for root weight provided a stable classification framework, partitioning 110 diverse accessions into four tolerance categories and identifying 27 tolerant accessions spanning multiple colors and geographical origins. The co-variation of root weight with root diameter, their joint prominence in PCA, and their consistent response across domestication classes and regions collectively support their utility as a trait-based selection framework. Wild accessions and orange-colored genotypes stand out as priority material for further characterization. Integrating DTI-based phenotypic pre-screening with genome-enabled approaches will be essential to dissect the genetic architecture of these traits and develop drought-tolerant carrot varieties capable of maintaining productivity under the increasingly water-limited conditions projected for carrot-growing regions (Devi and Sinclair 2013; Fotouhi *et al.* 2017; Rehman *et al.* 2019; Wiśniewska *et al.* 2019).

Conclusion

This analysis of 110 carrot accessions emphasizes the importance of root weight as one of the main selection criteria for identifying drought-tolerant germplasm, which is essential in increasing the crop resilience under the water-limited conditions. The trait which is most likely to respond to drought stress is root weight, which has a significant impact on nutrient storage, yield, and market quality, making it a cornerstone trait in carrot breeding programs. The arrangement of accessions into tolerant, moderately tolerant, moderately susceptible and susceptible groups based on the drought tolerance index of root weight provided a solid basis for selecting better accessions. Regional and color-specific differences, particularly among wild and orange carrots, reveal genetic variation that could be exploited in breeding programs. Root weight can be combined with other traits such as root length and diameter to improve the selection of drought-tolerant varieties. Multivariate analyses support the value of these traits for breeding carrots that can perform better under future climate change scenarios.

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Authors' Contributions

Saba Manzoor: Performed field work, data collection and write-up. Naima Huma Naveed: Reviewed, edited and validated the overall write up. Nasim Ahmad Yasin:

Investigated the results. Muhammad Jamil: Performed the data analysis and write-up. Yasmeen Saleem reviewed and edited. Aamir Ali: Supervised and designed the research as a team leader.

Conflict of Interest

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

Data Availability

The data reported in this paper have been deposited as supplementary tables in the Excel format that are publicly accessible.

Declaration of Generative AI Use

No generative AI tools were used in the preparation of this manuscript, including for content generation, language improvement, editing, or translation. The authors take full responsibility for the content, accuracy, originality, and integrity of the manuscript.

Ethics Approval

This study did not involve human or animal subjects; therefore, ethical approval was not required.

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Supplementary Table S1: Detail of carrot germplasm regarding their domestication, root color, geographical origin (continents and country), accession, tolerance, principal component score and cluster membership.

Dom	RC	Continent	Country	SN	Acc	DT	PC1	PC2	Cluster
Cultivated	Orange	Africa	South Africa	1	PI 502245	MS	-2.80464	-2.3588	1
Cultivated	Orange	Asia	China	2	PI432901	MS	-1.10139	-0.82443	2
Cultivated	Orange	Asia	China	3	PI 432898	R	2.42165	-2.29185	2
Cultivated	Orange	Asia	Iran	4	PI226464	MS	-3.98024	5.76237	3
Cultivated	Orange	Asia	Japan	5	PI294079	S	-1.44089	0.77005	4
Cultivated	Orange	Asia	Japan	6	PI294080	MR	0.74847	0.26381	4
Cultivated	Orange	Asia	Japan	7	PI 294082	MS	-1.43336	-1.21848	4
Cultivated	Orange	Asia	Russia	8	PI325993	MR	-0.00643	-1.31823	2
Cultivated	Orange	Asia	Russia	9	PI458859	MS	-0.35766	0.31883	4
Cultivated	Orange	Asia	Russia	10	PI458860	MR	-1.64003	-0.90926	1
Cultivated	Orange	Asia	South Korea	11	PI508473	MS	-2.4184	-1.89776	1
Cultivated	Orange	Asia	South Korea	12	PI537093	MS	-0.70508	-2.40543	1
Cultivated	Orange	Europe	France	13	PI261783	MR	-2.08535	2.80115	3
Cultivated	Orange	Europe	France	14	PI341204	S	-3.08532	1.09203	4
Cultivated	Orange	Europe	France	15	PI341207	R	2.16219	-0.64768	2
Cultivated	Orange	Europe	France	16	PI341208	MR	-1.31469	0.49023	4
Cultivated	Orange	Europe	France	17	PI643119	MS	-2.18054	0.16556	1
Cultivated	Orange	Europe	France	18	PI 264238	MR	-1.48722	3.92886	3
Cultivated	Orange	Europe	Germany	19	PI502915	MS	-1.03105	-0.61451	1
Cultivated	Orange	Europe	Germany	20	PI 502919	S	-3.30857	-1.11574	1
Cultivated	Orange	Europe	Hungary	21	PI515990	S	-2.42024	-0.59992	1
Cultivated	Orange	Europe	Hungary	22	PI515992	MR	-0.3524	-0.56234	1
Cultivated	Orange	Europe	Hungary	23	PI 531326	MS	-1.94637	-0.4744	1
Cultivated	Orange	Europe	Lithuania	24	PI 503345	S	-2.82595	-1.93699	1

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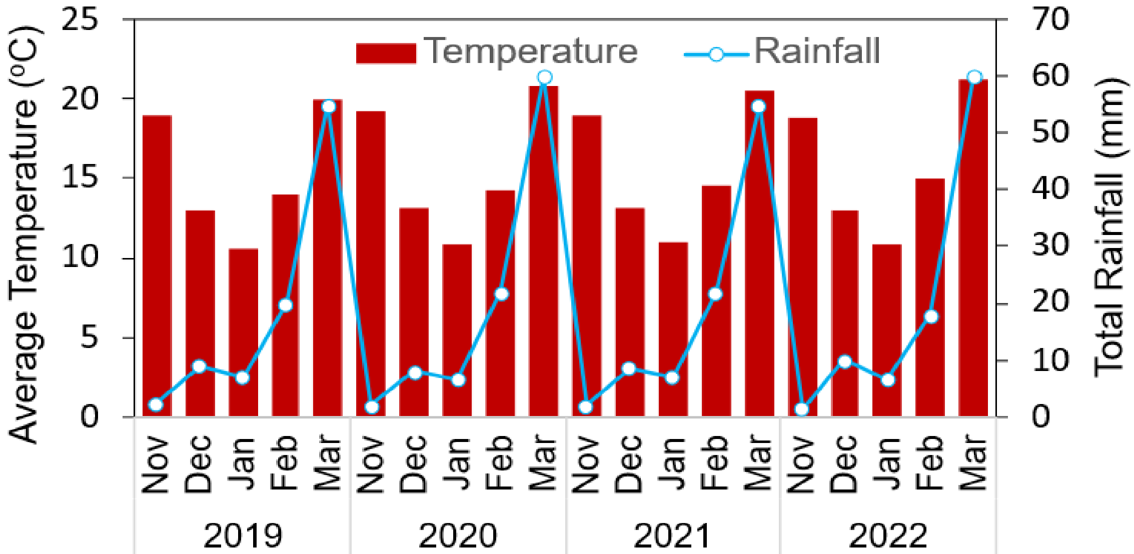
Cultivated	Orange	Europe	Netherlands	25	PI632389	S	-2.35159	-2.07557	1
Cultivated	Orange	Europe	Netherlands	26	PI642756	S	-3.22036	-0.42326	1
Cultivated	Orange	Europe	Netherlands	27	PI 632391	MS	-1.14827	-2.77567	1
Cultivated	Orange	Europe	Poland	28	PI285613	MS	-1.23139	0.65759	4
Cultivated	Orange	Europe	Poland	29	PI535887	S	-3.89613	-0.75216	1
Cultivated	Orange	Europe	Sweden	30	PI269322	MR	-1.92172	3.45146	3
Cultivated	Orange	Europe	Sweden	31	PI 269316	MR	-0.37323	3.88689	3
Cultivated	Orange	Europe	Sweden	32	PI 269319	S	-1.52438	3.48656	3
Cultivated	Orange	Europe	Turkey	33	PI652400	R	3.14355	-1.69851	2
Cultivated	Orange	North America	USA	34	PI632393	S	-1.4212	-0.85368	1
Cultivated	Orange	North America	USA	35	PI642761	MS	-2.38138	1.1051	1
Cultivated	Orange	North America	USA	36	PI 632382	MS	-0.79982	-0.91294	1
Cultivated	Orange	North America	USA	37	PI 632383	S	-2.66296	-0.94048	1
Cultivated	Orange	North America	USA	38	PI 632384	S	-1.99004	-1.32887	1
Cultivated	Orange	North America	USA	39	PI 632385	S	-2.6112	-0.79776	1
Cultivated	Orange	North America	USA	40	PI 632386	MS	-0.83651	-1.18787	1
Cultivated	Orange	North America	USA	41	PI 634653	MS	-0.96322	-2.49554	1
Cultivated	Orange	North America	USA	42	PI 634654	S	-2.58665	-1.12017	1
Cultivated	Orange	North America	USA	43	PI 634655	S	-1.5876	-0.00622	1
Cultivated	Pure	Africa	Egypt	44	PI279776	MS	-0.85329	2.65162	3
Cultivated	Pure	Africa	Syria	45	PI652304	S	-2.30963	-0.51703	1
Cultivated	Pure	Asia	Afghanistan	46	PI 256066	MR	0.93308	3.34101	3
Cultivated	Pure	Asia	China	47	PI432899	R	1.5797	-2.18038	2
Cultivated	Pure	Asia	Iran	48	PI254234	MR	1.30891	3.89859	3
Cultivated	Pure	Europe	Turkey	49	PI509433	MR	-0.14056	0.98624	4
Cultivated	Red	Asia	India	50	Ames25740	MS	-0.40193	1.1049	4
Cultivated	Red	Asia	India	51	PI652253	S	-1.42932	-2.40105	1
Cultivated	Red	Asia	Japan	52	PI 264543	R	0.78237	3.07004	3
Cultivated	Red	Europe	Turkey	53	PI509434	S	-2.95156	1.9643	4
Cultivated	White	Europe	Spain	54	PI295862	S	-1.25353	2.18443	4
Cultivated	White	North America	USA	55	PI643114	S	-1.78714	-0.47733	1

Cultivated	Yellow	Africa	Egypt	56	PI279777	MS	-1.0708	2.99371	3
Cultivated	Yellow	Asia	Afghanistan	57	PI 390887	MS	-2.03835	0.33401	4
Cultivated	Yellow	Asia	Afghanistan	58	PI 430534	S	-3.06643	-0.26569	4
Cultivated	Yellow	Asia	India	59	PI652242	MS	-1.17033	0.50331	1
Cultivated	Yellow	Asia	Pakistan	60	PI 163235	MR	1.54279	4.37556	3
Cultivated	Yellow	Asia	Pakistan	61	PI 269486	S	-2.26777	3.59977	3
Cultivated	Yellow	Europe	Netherlands	62	PI451759	MS	-1.5346	-1.09477	1
Cultivated	Yellow	Europe	Turkey	63	PI 652243	MS	0.44205	-0.27292	1
Cultivated	Yellow	Europe	Turkey	64	PI 652374	S	-0.44434	-2.13452	1
Cultivated	Yellow	North America	USA	65	PI634652	S	-1.97021	-1.1395	1
Wild	white	Asia	Pakistan	66	PI274297	R	3.42141	3.30769	3
Wild	White	Africa	Libya	67	PI279764	R	4.81684	3.33573	3
Wild	White	Africa	Syria	68	PI 652338	MR	0.2388	-0.57743	2
Wild	White	Africa	Tunisia	69	Ames29111	R	5.38678	-3.6844	2
Wild	White	Africa	Tunisia	70	Ames30198	R	7.54413	-0.41189	2
Wild	White	Asia	China	71	PI478369	S	-1.67302	-0.76663	4
Wild	White	Asia	Pakistan	72	PI 269485	MR	-0.15269	3.48215	3
Wild	White	Asia	Pakistan	73	PI 269487	MR	-0.6685	3.03052	3
Wild	White	Asia	Pakistan	74	PI 274298	R	3.26246	3.52736	3
Wild	White	Asia	Syria	75	Ames25732	MR	7.26105	1.3277	3
Wild	White	Asia	Uzbekistan	76	Ames27396	R	4.51266	-0.04759	2
Wild	White	Asia	Uzbekistan	77	Ames27397	MR	0.18464	1.10154	4
Wild	White	Europe	France	78	Ames31193	R	6.40612	4.16495	3
Wild	White	Europe	France	79	PI478861	R	1.81039	0.00601	2
Wild	White	Europe	France	80	PI478865	MR	-0.12361	-3.71454	2
Wild	White	Europe	France	81	PI478868	MR	0.30591	0.15113	4
Wild	White	Europe	France	82	PI478879	MS	-1.90774	-1.44138	4
Wild	White	Europe	France	83	PI478883	R	-0.16834	0.14453	2
Wild	White	Europe	France	84	PI478884	MR	1.91075	-0.92711	2
Wild	White	Europe	France	85	PI 478863	S	-1.96116	-2.02368	4
Wild	White	Europe	France	86	PI 478866	MS	-1.36309	-1.88429	4

Wild	White	Europe	France	87	PI 478874	R	2.21811	-1.90406	2
Wild	White	Europe	France	88	PI 478876	R	1.56482	-0.44628	2
Wild	White	Europe	France	89	PI 478881	MR	-1.22332	-0.31725	4
Wild	White	Europe	Portugal	90	Ames26381	R	4.81882	-2.48706	2
Wild	White	Europe	Portugal	91	Ames26383	MS	1.01562	-1.97013	2
Wild	White	Europe	Turkey	92	PI652351	R	1.76942	0.57409	2
Wild	White	Europe	Turkey	93	PI652352	MR	0.05971	-2.66969	2
Wild	White	Europe	Turkey	94	PI652391	MR	1.69493	-5.04476	2
Wild	White	Europe	Turkey	95	PI652392	MR	0.72617	-2.25909	2
Wild	White	Europe	Turkey	96	PI652393	R	1.65148	-0.63382	2
Wild	White	Europe	Turkey	97	PI652394	R	3.52497	-2.47456	2
Wild	White	Europe	Turkey	98	PI652396	MR	1.18116	-0.58573	2
Wild	White	Europe	Turkey	99	PI652398	MR	0.12276	-3.02493	2
Wild	White	Europe	Turkey	100	PI652399	MR	0.18479	-0.58725	2
Wild	White	Europe	Turkey	101	PI 652348	MR	0.71827	2.97654	3
Wild	White	Europe	Turkey	102	PI 652354	R	3.54705	-0.31452	2
Wild	White	Europe	Turkey	103	PI 652356	R	4.37488	0.0665	2
Wild	White	Europe	Turkey	104	PI 652359	R	4.19776	3.6178	3
Wild	White	Europe	Turkey	105	PI 652360	R	2.73061	-2.41696	2
Wild	White	Europe	Turkey	106	PI 652370	MR	0.5377	-0.8178	4
Wild	White	Europe	Turkey	107	PI 652373	R	3.36653	-1.78651	2
Wild	White	Europe	Turkey	108	PI 652379	R	2.21204	-1.64401	2
Wild	White	Europe	Turkey	109	PI 652382	R	2.31492	-1.07974	2
Wild	White	South America	Chile	110	PI 280706	MS	-1.29451	4.96855	3

Code	Detail	
Continent=	Geographical origin	RC = Root color
Dom =	Domestication	SN = Serial Number

Acc: Accession #	**DT: Degree of Tolerance**	**PC1: Principal Component 1**	**PC2: Principal Component 2**	**Cluster**



Supplementary Fig. S1: Temperature and rainfall (at 71.90°E, 31.88°N) during the carrot growing season