Turkish Journal of Botany

http://journals.tubitak.gov.tr/botany/

Research Article

Turk J Bot
(2023) 47: 111-126
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doi:10.55730/1300-008X.2750

Drought stress effects on morphophysiological and quality characteristics of commercial carrot cultivars

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Received: 19.09.2022 • **Accepted/Published Online:** 17.01.2023 • **Final Version:** 23.03.2023

Abstract: The effects of drought stress on plant growth and development are getting more pronounced due to increasing influence of climate change on environmental stresses. Current study was devised to explore the drought effects on eight commercial carrot cultivars, having different root colors as a base for further studies to understand the response of carrot. Drought stress for 10 days was applied to carrot plants at taproot formation stage in semicontrolled greenhouse. The results revealed that orange and yellow colored carrot cultivars exhibited the least decline in physiological functioning (relative water contents and dry matter) that assisted in maintaining higher yield and quality attributes in contrast to purple and black carrot cultivars. However, anthocyanin contents in nonpurple cultivars Tendersweet and Solar Yellow showed 72% decrease, whereas in purple carrot cultivars 3-fold increase was observed in Eregli Black and Cosmic Purple. Beta-carotene contents showed 59% decrease in cultivar Eregli Black under drought; however, it was increased in cultivars Solar Yellow and Coral Orange by 17% and 3%, respectively. Sugar accumulation exhibited variable response of carrot cultivars; minimal sucrose contents in cultivars Cosmic Purple, Solar Yellow and Tendersweet were detected after they were subjected to drought. Overall, the results showed that cultivars Atomic Red and Coral Orange performed well under water scarce condition. We believe this study may help the researchers to move forward in understanding the drought effects for the selection of promising cultivars to be used in development of tolerant varieties with breeding strategies.

Key words: Anthocyanins, drought stress, reducing sugars, HPLC, photosynthetic pigments, yield attributes

1. Introduction

Carrot (*Daucus carota* L.) is a cross-pollinated, biennial root vegetable crop which belongs to the family Apiaceae. This family comprises 466 genera including famous crops like coriander, cumin dill, fennel, parsley, and caraway (Clarkson et al., 2021). Carrot germplasm is rich, and it consists of a variety of colors, including purple, red, orange, yellow, and white (Xu et al., 2020). Moreover, it is a cool climate crop grown in temperate and subtropical regions for edible purposes (Selvakumar and Kalia, 2019). Carrot is a versatile crop and has tremendous nutrition value among root vegetables (Uncu and Uncu, 2020). It is among the top 10 vegetables, based on global production records of primary vegetables, after tomatoes, onions, cabbage, cucumbers, and eggplant (FAO, 2021).

Carrot root consists of carotenoids, dietary fibers, carbohydrates, antioxidants, minerals, and nutrients (Que et al., 2019). These characteristics also make it a good source of healthy nutrition for humans. Carrot plants are rich sources of beta-carotene, which is precursor of vitamin A; moreover, beta-carotene plays a key role in protection of phytochemical processes in plants (Terletskaya et al., 2021). Beta-carotene quenches triplet chlorophyll which halts singlet oxygen formation and protects plant against stress damage (Farooq et al., 2009). Investigation of carotenoid accumulation in carrot root is relatively easy due to the large accumulation in root and the high diversity of root color (Clotault et al., 2012). Carrot plant consists of soluble sugars including fructose, glucose, and sucrose; moreover, during maturity cycle of plant growth, there is more sucrose accumulation in carrot root. Additionally, sugars in carrot along with terpenes determine the taste and flavor of carrot root. Soil moisture plays an important role for the synthesis of sugar contents of carrot root (Ombódi et al., 2015). Anthocyanins exist in nature in wide range of colors and different plant species. Especially, purple carrots are unique due to highly nutritious value as it contains higher anthocyanins (Blando et al., 2021). Anthocyanins are significant in plant stress response; moreover, they are key regulators of drought tolerance (Cirillo et al., 2021). They accumulate in plants under abiotic stress conditions

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(Landi et al., 2015) and their significant increase in carrot plants under drought stress was also reported (Öztürk Gökçe et al., 2022). Additionally, anthocyanins are also considered biologically active compounds, and act as phenolic antioxidants in plants.

Climate change has adversely affected humans' natural ecosystem and humankind is already observing its influence on our environment in the form of altered precipitations, droughts, floods, and high temperatures. Climate change, low precipitation, decreased water table are some of the main factors which result in drought stress (Vadez et al., 2012; Wang et al., 2022). Decline in precipitations and glaciers has threatened plant growth as they affect general agricultural production all over the world; carrot production has also been affected by climate change (Ren et al., 2021; Zhang et al., 2021; Kowalczyk and Kuboń, 2022).

Drought is one of the major abiotic stress factors that severely influence plant growth (Duan et al., 2021; Zhu et al., 2021). Carrot is susceptible to abiotic stress; drought stress has severe effects on the production and quality of carrots (Razzaq et al., 2017). Inadequate soil water availability during carrot root growth period negatively affects the taproot production (Öztürk Gökçe et al., 2022). Drought stress adversely affects carrot quality and chemical composition; moreover, dry matter concentration in carrot increases under water scarcity (Seleiman et al., 2021), and cultivars with higher dry matter content are more tolerant to drought stress (Abid et al., 2018). Intense drought inhibits photosynthesis by dismantling photosynthetic apparatus resultantly affecting chlorophyll components of plant (Wang et al., 2018). Reduction of chlorophyll contents in plants is mainly caused by reactive oxygen species (ROS) which negatively interferes with chloroplast functioning (Qi et al., 2018).

Under drought condition, plants undergo various morphological and physiological changes to survive stress (Farooq et al., 2009). Several studies summarizing morphophysiological responses of major crops and main vegetables such as tomato and potato to drought are available in the literature. Interestingly, studies on carrot, a frequently used vegetable all over the world, are noticeably limited. There is minimal information available on drought sensitivity of different growth stages of carrot plant and it is scarcely explored (Zhang et al., 2021; Bashir et al., 2021). Moreover, to the best of our knowledge, there are no studies comparing several carrot cultivars under drought stress at the taproot formation stage to explore differences in their tolerance levels. To ensure food security, it is important to address issues related to drought stress and factors initiating it. Moreover, it is needed to develop cultivars which can withstand abiotic stress conditions. As taproot is the primary organ which is affected by and senses drought stress at first, the current study was hypothesized to estimate the impact of drought stress on taproot traits along with other morphophysiological and quality traits of different commercial carrot cultivars. The study findings suggest the differential behavior of carrot cultivars in response to drought stress. Moreover, this study provides the basis for the adaptation of resilient cultivars to ensure food security.

2. Materials and methods

2.1. Plant material and growth conditions

Eight commercial carrot cultivars having different root colors were selected including Atomic Red (scarlet root color), Coral Orange (bright orange root color), Cosmic Purple (deep purple skin fading to a bright orange root center), Eregli Black (intense purple root color), Salkim Orange (bright orange root color), Scarlet Nantes (bright orange red root color), Solar Yellow (yellow root color), and Tendersweet (Figure S1). Carrot materials were planted in semicontrolled greenhouse conditions of Agricultural Genetic Engineering Department of Niğde Ömer Halisdemir University. The temperature was set at 25 °C (day) and 15 °C (night). Humidity was controlled between 40% and 70% and there was no artificial lighting. The daytime/photoperiod at germination was 10 h and it was 14 h at harvest.

Pots (90 L) were filled with peat and perlite in 3:1 ratio, in two groups (control and drought stress). The experiment was conducted by following the completely randomized design (CRD). Ten carrot plants were maintained in each pot; until taproot formation stage (60 days), the plants were watered adequately every 3 days. At taproot initiation stage, the plants were exposed to two different moisture regimes; the plants were deprived of water for drought stress (DS) application for 10 days and when the plants showed leaf bending, stress application was terminated and data was collected. The control plants, on the other hand, were maintained at 100% field water capacity. All the measurements were taken in three replications.

2.2. Morphological measurements

All the morphological measurements were taken from three plants from each pot. Plant height and number of leaves of carrot plants were measured with meter rod and leaves were counted manually.

2.2.1 Root traits measurement

Carrot root traits including root diameter, root length, and root weight were measured using a measuring scale in three replications instantly after harvest.

2.3. Physiological measurements

Physiological traits were measured from the control and drought groups from three randomly selected plants in three replications from each group. All physiological measurements were taken during 10:00–13:00.

2.3.1. Relative water content

The relative water content (RWC) of carrot leaves in three replications was measured as carrot leaf chunks of about 1–2 g (fresh leaves) were collected from the control and drought groups in triplicates. Next, fresh weight of carrot leaves was measured; the leaves were placed in distilled water overnight. Turgid weight was then measured, and the leaves were oven-dried at 100 °C for 2 h to determine their dry weight. RWC values of plants were calculated according to the following equation:

$$RWC(\%) = \left[\frac{fw - dw}{tw - dw}\right] \times 100$$

Fresh weight = *fw*,
Dry weight = *dw*,
Turgid weight = *tw*.

2.3.2. Leaf temperature

Leaf temperature was measured using IRT instrument (MASTECH BM380) Laser Temperature Measuring Instrument) with three replications from each pot and the averages of these values were further used for analysis.

2.3.3. Gravimetric soil moisture (GSM)

For GSM measurement soil samples (40–50 g) were collected from both treatment group pots from 10 cm deep in three replications and then weighed. Soon after, all samples were dried as they were placed in oven at 105 °C for 24 h until there was no remaining moisture and the samples were weighed again. The moisture content was expressed as mass of water per mass of dry soil. Determination of GSM was done by using the following calculation:

$$GSM = (fw\ (s) - dw(s)/dw(s))$$

Gravimetric soil moisture = *GSM*,
Fresh weight = *fw*,
Dry weight = *dw*,
Soil = *s*.

2.3.4. Dry matter contents

In oven-dry method, 3–5 carrot roots (randomly selected) from the control and drought groups were harvested and chopped; subsequently, fresh weight was measured using an electronic weigh balance. Later, the samples were oven dried at 100 °C for 3 h. Dry roots were then weighed again and TDM% was calculated by the following formula:

$$DM\% = \frac{dw\ (o)}{fw\ (i)} \times 100$$

Dry matter percentage = *DM %*,
Oven dry weight = *dw (o)*,
Initial fresh weight = *fw (i)*.

2.4. Photosynthetic pigments

2.4.1. Chlorophyll and carotenoids measurements

Chlorophyll *a*, *b* and carotenoids contents in carrot fresh leaves were investigated by using fresh carrot leaf samples (0.5 g); they were extracted with 80% acetone (10 mL) and kept overnight in dark. The extracted mixture was centrifuged at 10,000 rpm for 5 min at 4 °C. The optical density of the supernatant was recorded by using UV-Vis spectrophotometer (UV-1800, Shimadzu) at 470 nm, 646 nm, and 663 nm.

Calculations were done by using the following formulas:

$$Chl\ a\ \left(\frac{mg}{g}\right) = 12.7(A663) - 2.69(A645)$$

$$Chl\ b\ \left(\frac{mg}{g}\right) = 22.9(A645) - 4.68(A663)$$

$$Chl\ b\ \left(\frac{mg}{g}\right) = 22.9(A645) - 4.68(A663)$$

Chlorophyll a (mg/g) = *Chl a*,
Chlorophyll b (mg/g) = *Chl b*,
Total chlorophyll (mg/g) = *Chl t*.

2.5. Quality traits

2.5.1. Anthocyanins

Extraction of anthocyanins from the dried roots was done by suspending the samples in 10 mL of acidified methanol (methanol: water: HCl, 79: 20: 1, v/ v) and extracting at 0 °C for 72 h in dark with continuous shaking. The extracts were then centrifuged for 10 min at 5000 rpm and absorbance was measured at 530 and 657 nm for each supernatant (Mirecki and Teramura, 1984). Readings from absorbance at wavelength 530 nm as corrected for scattering using the absorbance readings at 657 nm using Rayleigh's formula as follows:

$$Corrected\ A530 = A530 - \frac{1}{3}\ A567$$

2.5.2. Beta-carotene

Beta-carotene was measured using a UV-Vis spectrophotometer as performed by Biswas et al. (2011). Freeze-dried carrot root samples (1 g) were weighed in 15-mL falcon tubes. Next, 5 mL of acetone was added to the falcon tubes (chilled) and the tubes were shaken for 15 min in a shaker at 4 ± 1 °C. Next, for 10 min, the mixture was vortexed and centrifugation at 1370 × *g* for 10 min was performed. Filtering of supernatant with Whatman filter paper No. 42 was done. The extract absorbance was measured at 449 nm using a UV-Vis spectrophotometer. All solutions were protected from light by covering them with aluminum foil and kept at 4 °C. The equation for the standard calibration curve is as follows:

$$y = 4.1374x + 0.2989\ (R2 = 0.9956)$$

Concentration in µg/mL = y,

Optical density value= x.

2.5.3. Sugar contents

Sample preparation for sugar measurements

The reducing sugars in carrot roots were measured according to the method described by Plata-Guerrero et al. (2009) with few modifications. Exactly 3–5 g of lyophilized freeze-dried carrot root powder was put in a 50-mL falcon tube and 25 mL of bidistilled H_2O was added and the solution was vortexed for 5 min. Next, 2 mL of each Carrez 1 and Carrez 2 solutions ((250 mM zinc sulfate and 85 mM potassium hexacyanoferrate (II) trihydrate) were added to the falcon tubes. The tubes were then filled with bidistilled water up to 50 mL. Homogenization of all samples in the tubes was done for 5 min and they were centrifuged at 14,000 × g for 10 min. The supernatant was subjected to purification twice, firstly with Whatman filter paper No. 42 and then again with 0.45-µm nylon membrane. The filtered completely purified solution was then transferred to 1.5-mL vial for HPLC (Shimadzu Prominence Series) measurement.

The standards (≥99.9% pure) fructose, glucose, and sucrose were purchased from Merck and Sigma Aldrich; 0.25 g of each fructose, glucose, and sucrose were weighed on sensitive electronic balance and mixed in 50 mL of ultrapure water to prepare a stock solution of 5000 ppm (5 mg/mL). The dilutions were done with ultrapure water, these 8 standard solutions of reducing sugars and sucrose with a final volume of 1.5 mL were used to calculate the standard calibration curve in HPLC (Table S1). Area under the detected peaks of carrot taproot samples (reducing sugars and sucrose) at their respective retention times was determined according to the calibration curve.

HPLC conditions for sugar measuremens

Acetonitrile and dd$H_2$0 was used as a mobile phase/eluent in 80%:20% (w/w) precisely 628.8 g: 199.6 g. The flow rate was 0.9 mL/min with isocratic flow, 20 µL of sample was injected in NH2 inertsil column (GL Sciences). The temperature of column was 40 °C, and detection was done with the help of refractive index (RI) detector.

2.6. Statistical analysis

Treatment dataset comprising stress and control groups was analyzed by analysis of variance (ANOVA). The least significant difference (LSD) was used at $p \leq 0.05$ for the comparison of treatment means by Statistical package Statistix 8.1 (Tallahassee Florida, USA). Principal components analysis (PCA) was done by using Origin 2020.

3. Results

3.1. Number of leaves and plant height

Drought decreased the number of leaves in all the cultivars in this study, 35% reduction was recorded in Cosmic cultivar, whereas 33% reduction was observed in Eregli Black cultivar. Solar Yellow and Coral Orange cultivars were the least affected as only 13% and 14% decrease was recorded, respectively. Figure 1a represents the decrease in the number of leaves in all the cultivars. Pairwise comparison showed that there were nonsignificant differences between Cosmic, Atomic Red, Eregli Black, and Scarlet Nantes in terms of leaf number. Furthermore, Salkim Orange and Tendersweet cultivars showed significant differences ($p < 0.05$) compared to all cultivars under study.

The drought stress also resulted in stunted plant height of all the cultivars except 'Tendersweet', which showed increased plant height (13%) under drought. There were nonsignificant ($p > 0.05$) differences among Cosmic, Solar Yellow, Scarlet Nantes, Eregli Black, and Atomic Red cultivars in terms of plant height in response to drought. Furthermore, highest plant height was observed in cultivar Coral Orange (Figure 1b).

3.2. Root traits

Though drought negatively affected the root weight of all cultivars under study, maximum reduction was observed in cultivars Tendersweet (77%), Atomic Red (70%), and Solar Yellow (68%) (Figure 2a). Cultivars Coral Orange and Salkim Orange expressed tolerance regarding root weight, minimum decreases of 23% and 27% were observed in these cultivars. Pairwise comparison test showed that under drought, cultivars Scarlet Nantes and Cosmic exhibited nonsignificant ($p > 0.05$) differences between them. However, for root weight trait, all the other cultivars were significantly different from each other.

Root diameters of cultivars Coral Orange and Solar Yellow were the least affected under drought whereas, cultivars Cosmic Purple and Tendersweet showed 35% and 38% decrease, respectively, compared to their control group plants (Figure 2b). Statistically, nonsignificant ($p > 0.05$) differences for root diameter were found between cultivars Salkim Orange, Scarlet Nantes, Eregli Black, and Tendersweet. However, cultivars Solar Yellow and Coral Orange were significantly ($p < 0.05$) different from all the other cultivars under this study and nonsignificant ($p > 0.05$) differences were found between them.

Water deficit influenced adversely on root length of all the cultivars in the study, cultivars Eregli Black (4%) and Solar Yellow (9%) showed minimum decrease in root length under drought as compared to their control group. Water deficit drastically affected root length of cultivars Cosmic Purple and Tendersweet compared to their control group (Figure 2c). There were nonsignificant ($p > 0.05$) differences between cultivars Salkim Orange and Solar Yellow under drought. Moreover, cultivars Eregli Black and Atomic Red showed significant ($p < 0.05$) differences compared to other cultivars under this study but there were nonsignificant ($p > 0.05$) differences between these cultivars under drought. All carrot cultivars taproot pictures under drought and control condition are presented (Figure S1).

3.3. Physiological traits

3.3.1. Relative water content (RWC)

Drought negatively influenced relative water content of all the cultivars under this study, Scarlet Nantes exhibited highest reduction (41%) in RWC under drought. Furthermore, cultivars Salkim Orange, Tendersweet, and Cosmic Purple also showed reduction of 35%, 32%, and 29% under drought in RWC, respectively (Figure 3a). Cultivar Solar Yellow showed tolerance to DS with 9% decrease in RWC as compared to other cultivars. Highest RWC under drought was observed in cultivar Solar Yellow with mean value of 61.35%. ANOVA indicated that the behavior of all cultivars to drought was significantly ($p < 0.05$) different. Cultivars Tendersweet, Salkim Orange, and Scarlet Nantes showed the lowest RWC mean values, and according to pairwise comparison test, they showed similar response to drought.

3.3.2. Dry matter content

Maximum increase in dry matter percentage under drought was observed in cultivar Coral Orange, whereas 24% decrease was observed in cultivar Cosmic Purple (Figure 3b). Cultivar Solar Yellow showed significant ($p < 0.05$) differences for dry matter compared to other cultivars under drought. Salkim Orange and Scarlet Nantes showed nonsignificant ($p > 0.05$) differences between each other, whereas it exhibited significant differences ($p < 0.05$) with other cultivars under study.

3.3.3. Leaf temperature

The highest increase in leaf temperature under drought was observed in cultivar Solar Yellow with 45% increase compared to its control group. The lowest increase was

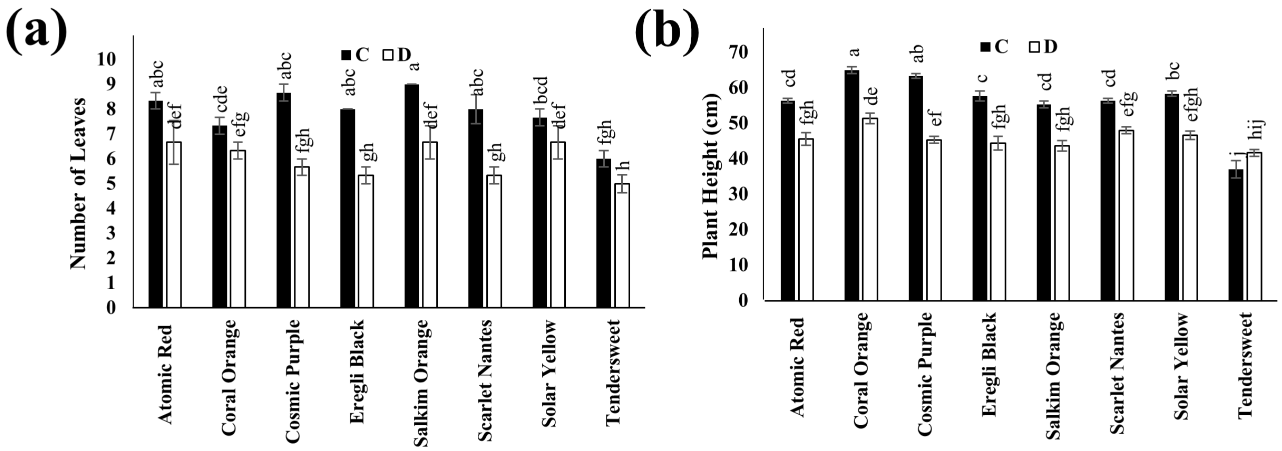

Figure 1. Effect of drought stress on number of leaves (a) and plant height (b) of eight carrot cultivars. C is control, whereas D is drought stress group. Vertical bars represent standard deviation, letters show significant differences ($p < 0.05$), bars sharing the same letters are not significantly different from each other.

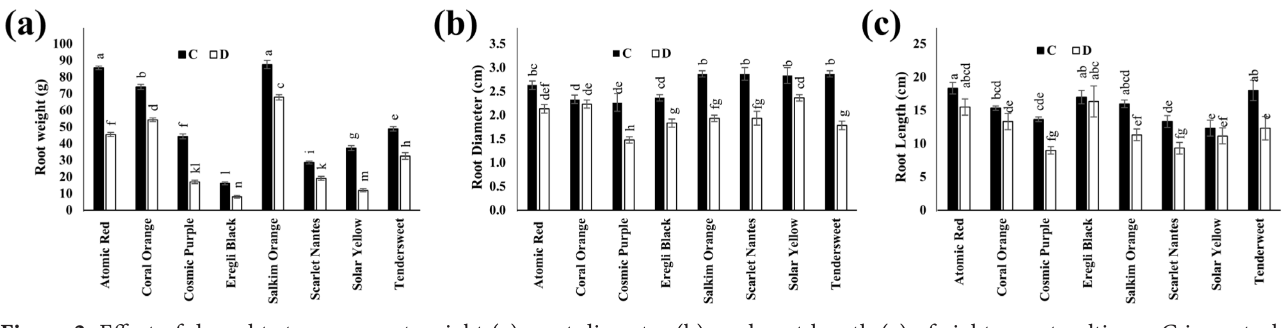

Figure 2. Effect of drought stress on root weight (a), root diameter (b), and root length (c) of eight carrot cultivars. C is control, whereas D is drought stress group. Vertical bars represent stan dard deviation, letters show significant differences ($p < 0.05$), bars sharing the same letters are not significantly different from each other.

recorded in cultivars Coral Orange (7%) and Tendersweet (10%). Cultivar Solar Yellow showed susceptibility to drought for leaf temperature and significantly ($p < 0.05$) different response compared to other cultivars, whereas cultivars Atomic Red, Salkim Orange, and Eregli Black showed nonsignificant ($p > 0.05$) differences between each other for leaf temperature. The effect of drought on leaf temperature of all cultivars in this study is shown in Figure 3c.

3.3.4. Gravimetric soil moisture (GSM)

Cultivars Scarlet Nantes, Eregli Black, and Salkim Orange showed the lowest GSM value, which showed that under drought these cultivars required the highest amount of water (Figure 3d). Statistically, there were nonsignificant ($p > 0.05$) differences among these varieties. Cultivar Solar Yellow absorbed less amount of water, which shows its tolerance to drought. Collectively, it was observed that drought increased the requirement of moisture for susceptible plants and as a result there was low GSM% recorded from drought-subjected plants as compared to the control group plants. Along with cultivar Solar Yellow, Tendersweet also exhibited low requirement of moisture under drought; 50% increased GSM difference was observed as compared to the control group plants.

3.4. Photosynthetic pigments

3.4.1 Chlorophyll and carotenoids contents

Chlorophyll contents of all carrot cultivars under study were negatively affected by drought. When drought was applied, the highest reduction (55%) in the chlorophyll 'a' content was seen in cultivar Solar yellow. Cultivars Scarlet Nantes, Salkim Orange, and Eregli Black showed similar response to drought and exhibited decrease in chlorophyll 'a' content by 27%, 24%, and 27%, respectively. The lowest reduction was seen in cultivars

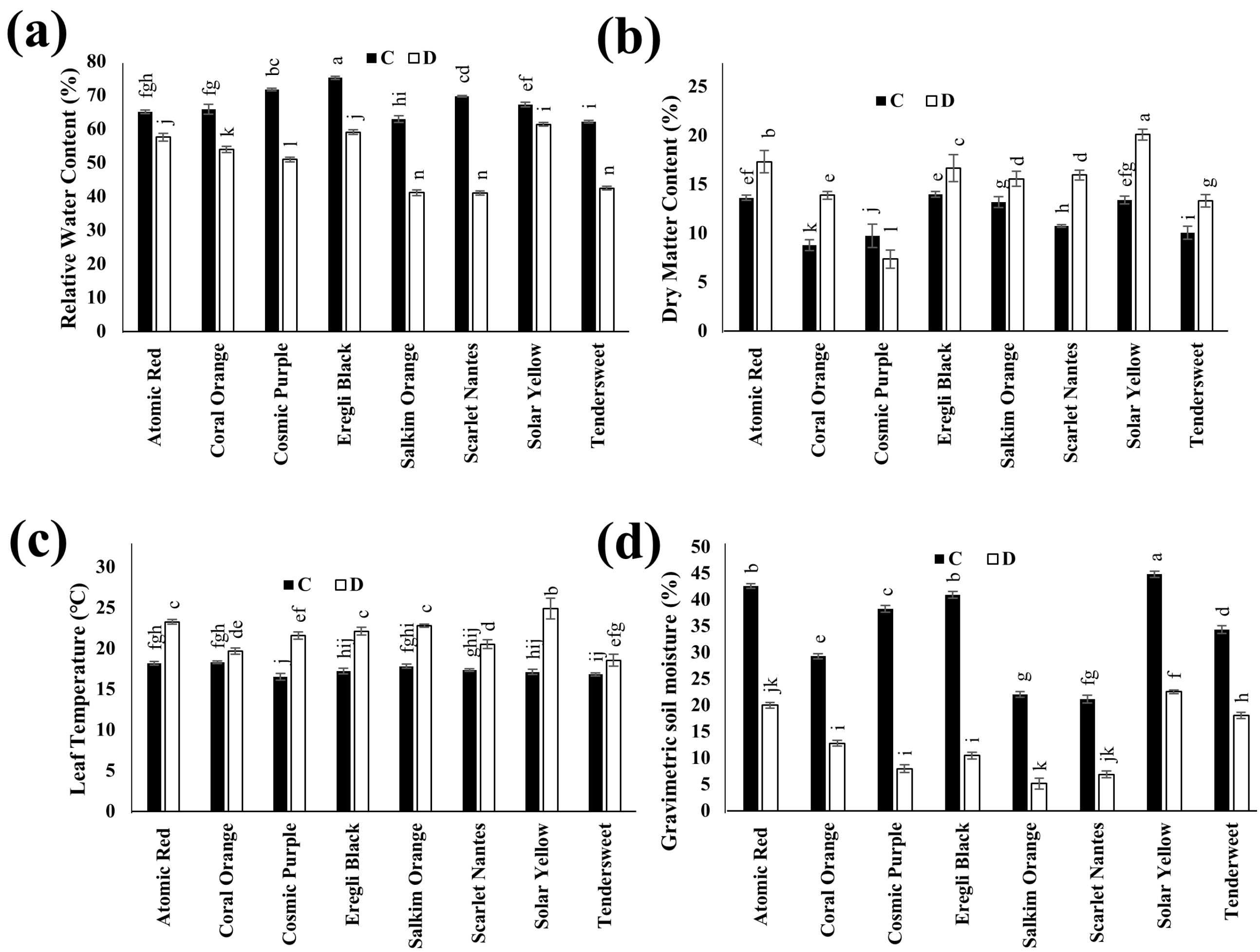

Figure 3. Effect of drought stress on relative water content (a), dry matter content (b), leaf temperature (c), and gravimetric soil moisture (d) of eight carrot cultivars. C is control, whereas D is drought stress group. Vertical bars represent standard deviation, letters show significant differences ($p < 0.05$), bars sharing the same letters are not significantly different from each other.

Atomic Red and Cosmic Purple with only 4% and 3% decrease under drought as compared to the control group plants (Figure 4a) and there were nonsignificant ($p > 0.05$) differences among them. Cultivars Scarlet Nantes and Eregli black also showed nonsignificant ($p > 0.05$) differences between them.

ANOVA for chlorophyll 'b' content showed that cultivar Atomic Red showed significant differences ($p < 0.05$) with all the other cultivars under drought. It also showed the highest mean value (10.28) for chlorophyll 'b', whereas the lowest mean value under drought was recorded for Cosmic Purple (7.172 mg/g) cultivar. There was 48% decrease in cultivar Solar Yellow under drought followed by cultivar Cosmic Purple (39%). Three cultivars Atomic Red, Coral Orange, and Scarlet Nantes showed tolerance to drought, only 4%, 9%, and 5% decrease in chlorophyll 'b' was observed respectively (Figure 4b).

Drought substantially decreased carotenoids content in Solar Yellow cultivar, whereas Coral Orange cultivar showed tolerance to water deficit with an increase of 30% and Scarlet Nantes cultivar showed 4% increase in carotenoids content (Figure 4c). According to pairwise comparisons test cultivars Atomic Red, Salkim Orange, and Eregli Black showed nonsignificant ($p > 0.05$) differences between each other while Coral Orange showed significant ($p < 0.05$) differences under drought compared to all the other cultivars.

3.5 Quality traits

3.5.1 Anthocyanins

Except cultivars Tendersweet, Solar Yellow, and Coral Orange, all carrot cultivars in the study showed increased anthocyanin contents under drought. Significant ($p \leq 0.05$) decrease in cultivars Tendersweet and Solar Yellow was observed under drought. Maximum increase under drought was observed in cultivar Cosmic Purple followed by cultivar Eregli Black. However, all the other cultivars showed stability in their anthocyanin contents under drought (Figure 5a).

3.5.2 Beta-carotenes

All carrot cultivars except Coral Orange and Solar Yellow showed decrease in beta-carotene contents when exposed to drought. Cultivar Eregli Black showed the highest decrease (60%) in beta-carotene contents (27 µg/DW) under drought compared to its control (C) group plants (70 µg/DW) (Figure 5b). Moreover, there were no significant ($p \geq 0.05$) differences observed in beta-carotene contents of other carrot cultivars which were subjected to drought.

3.5.3 Reducing sugars and sucrose measurement

Variable response of carrot cultivars for sugar contents (fructose, glucose, and sucrose) under the influence of drought was observed. Cultivars Atomic Red (6520 ppm), Coral Orange (6027 ppm), and Tendersweet (4108 ppm) showed increase in fructose contents under drought condition (Figure 6a). However, cultivars Cosmic Purple, Solar Yellow, and Eregli Black showed decline in fructose contents under drought condition. No change in fructose contents in cultivar Scarlet Nantes (5186 ppm) was observed, at drought and C condition. Cultivars Coral Orange, Scarlet Nantes, and Eregli Black showed increase in their glucose levels under drought condition (Figure 6b). However, in cultivars Cosmic Purple, Solar Yellow, and Tendersweet, significant change was observed when they were exposed to drought condition. In cultivar Atomic Red, stable glucose contents were noted (5542 ppm) at drought and control conditions. The retention peaks during HPLC analysis (Figures S2–S4) revealed that cultivars Atomic Red and Scarlet Nantes showed increase in their sucrose contents under drought compared to their C group plants (Figure 6c); moreover, cultivar Coral Orange showed stability in sucrose contents (6080 ppm) under drought and C conditions. The distribution of quality traits using pie charts is represented in Figure 7 in carrot cultivars used in this study. Interestingly, there was no sucrose detected via HPLC in cultivars Solar Yellow and Tendersweet under drought condition, this

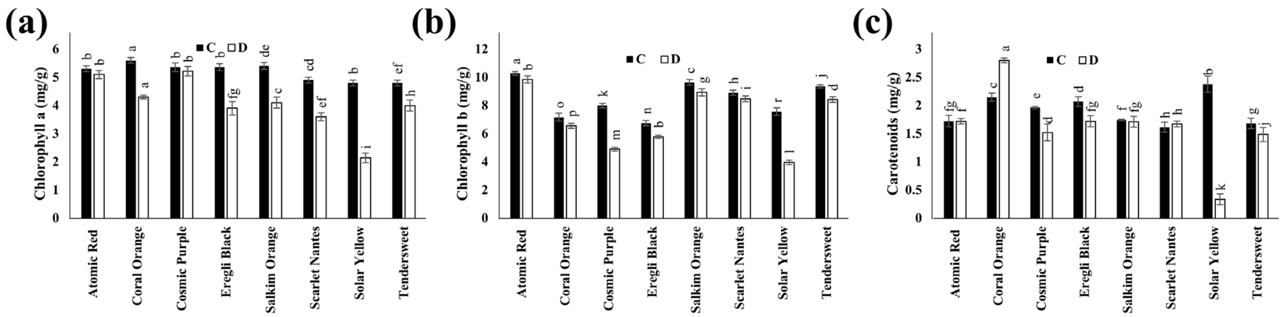

Figure 4. Effect of drought stress on chlorophyll 'a' (a), chlorophyll 'b' (b), and carotenoids contents (c) of eight carrot cultivars. C is control, whereas D is drought stress group. Vertical bars represent standard deviation, letters show significant differences ($p < 0.05$), bars sharing the same letters are not significantly different from each other.

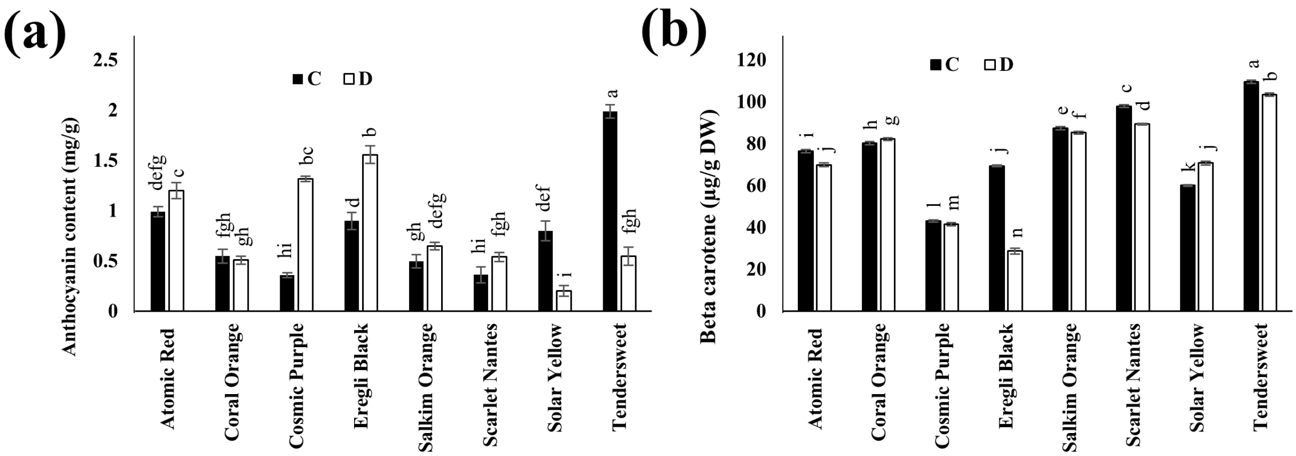

Figure 5. (a) Effect of drought stress on anthocyanin contents and (b) beta-carotene contents of eight carrot cultivars. C is control, whereas D is drought stress group. Vertical bars represent standard deviation, letters show significant differences ($p < 0.05$), bars sharing the same letters are not significantly different from each other.

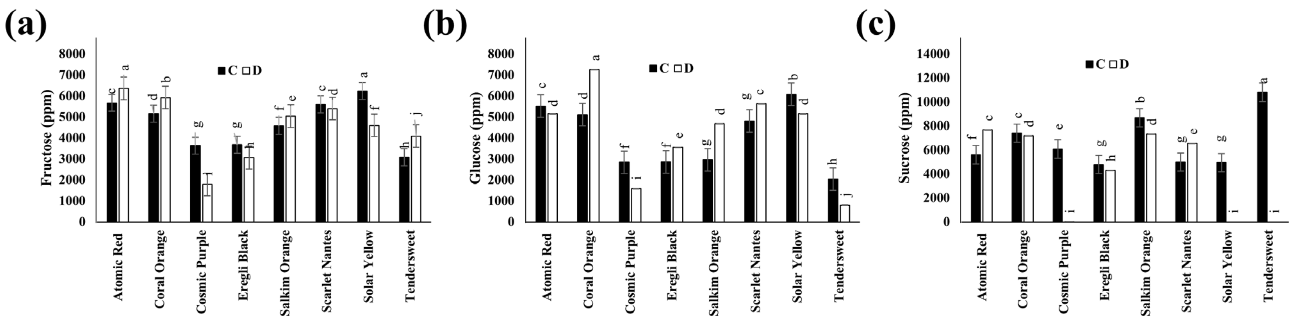

Figure 6. Effect of drought stress on sugar contents of carrots (a) fructose, (b) glucose, and (c) sucrose. C control, whereas D is drought stress group. Vertical bars represent standard deviation, letters show significant differences ($p < 0.05$), bars sharing the same letters are not significantly different from each other.

might suggest a breakdown in sucrose pathway or its degradation under drought.

3.8. PCA analysis

PCA analysis was performed to study the quality trait and drought relationship of all eight carrot cultivars, it revealed that under C condition (Figure 8), fructose and glucose contents were lower in cultivars Atomic Red, Solar Yellow, and Scarlet Nantes, whereas Beta-carotenes, anthocyanins, and sucrose contents in cultivar Tendersweet were maximum. At drought condition, cultivar Eregli Black showed the highest anthocyanin contents, and sugar contents including sucrose, fructose, and glucose were higher in cultivars Atomic Red, Coral Orange, and Salkim Orange. In cultivars Atomic Red and Coral Orange, sugar contents showed positive correlation with drought. From biplot results, we assumed that these genotypes exhibited differentially genotypic specific response to drought. Overall response of carrot cultivars to drought with respect to its quality and physiological attributes is shown (Figure 9).

4. Discussion

Water scarcity or inadequate availability of soil moisture negatively affects plant growth, but there is scarce knowledge available on carrot plant's behavior to drought stress (Zhang et al., 2021). Water scarcity is one of the major constraint, obstructing growth, yield, deteriorated quality, and decreasing plant production (Farooq et al., 2009). Therefore, in this study eight commercial carrot cultivars having different root colors were subjected to drought. All carrot cultivars showed differential response in their quality traits in response to drought.

Leaf number and plant height except for Tendersweet cultivar significantly decreased in all the cultivars in this study under the influence of drought (Figures 1a and 1b). Reduction in leaf number and height might be attributed to drought which causes stomatal closure, CO_2 reduction, Calvin cycle inhibition, electron transfer disturbance, and production of ROS (Chavoushi et al., 2020). Water deficit decreases plant height and stem length in many plant genotypes (Anjum et al., 2017).

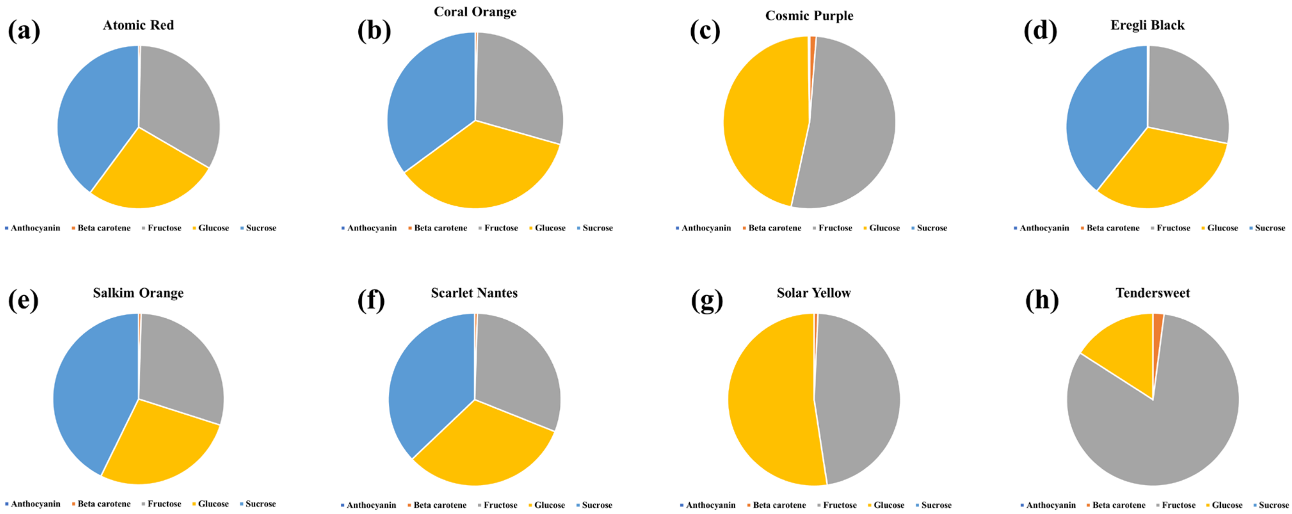

Figure 7. The pie chart represents the distribution of quality traits under DS in carrot cultivars. (a) Atomic Red, (b) Coral Orange, (c) Cosmic Purple, (d) Eregli Black, (e) Salkim Orange, (f) Scarlet Nantes, (g) Solar Yellow, and (h) Tendersweet. Dark blue color: Sucrose contents, Orange color: Beta-carotene contents, Grey color: Fructose contents, Light blue color: Anthocyanin contents and Yellow color: Glucose contents.

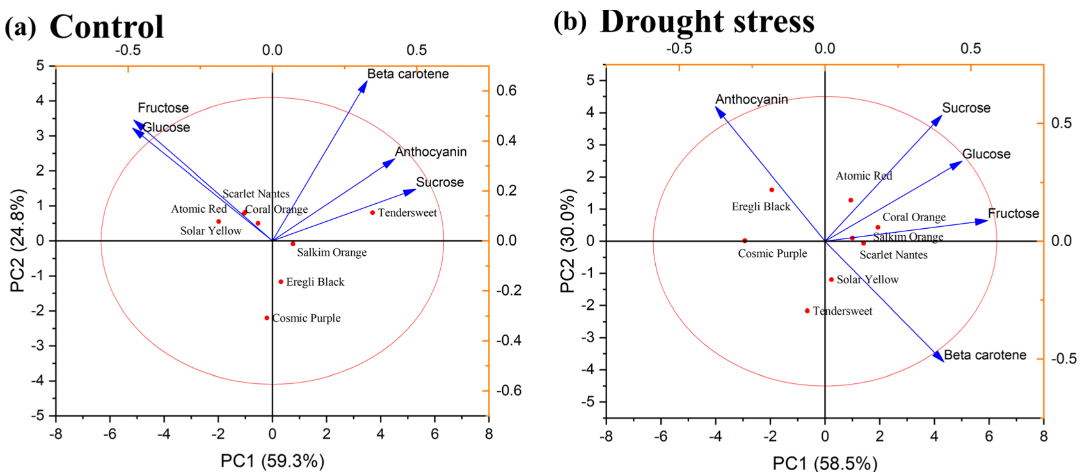

Figure 8. PCA analysis of selected carrot cultivars. (a) control group, adequate moisture available, (b) drought group plants.

Cultivar Tendersweet exhibited resilience by regulating its physiological machinery under drought, it showed stable yield, which might be due to activation of molecular and physiological cascades under stress which triggered response at physiological and metabolic level (dos Santos et al., 2022). Other carrot cultivars showed limited growth to reduce water loss and expand root length to absorb more soil water (Shahzad et al., 2016). In another study on coriander, it was described that when exposed to drought, plants showed variation in leaf characteristics (Jamali, 2013).

Plants fulfill their water need with absorption of soil moisture via their root system. Plant roots play an important role in nutrient uptake from soil and are crucial organs in sensing drought; plants are unable to uptake adequate water under drought (Farooq et al., 2009). Root weight decline of eight cultivars under the influence of drought compared to their control group is presented in Figure 2a). Maximum root weight was observed in cultivar Salkim Orange under drought influence, which showed its ability to tolerate drought. We concluded that this cultivar exhibited high ability to maintain relatively higher root weight which indicated its ability in minimizing conductance and moisture loss; moreover, it sufficiently uptakes CO_2 for necessary photosynthesis activity and root growth. These results are

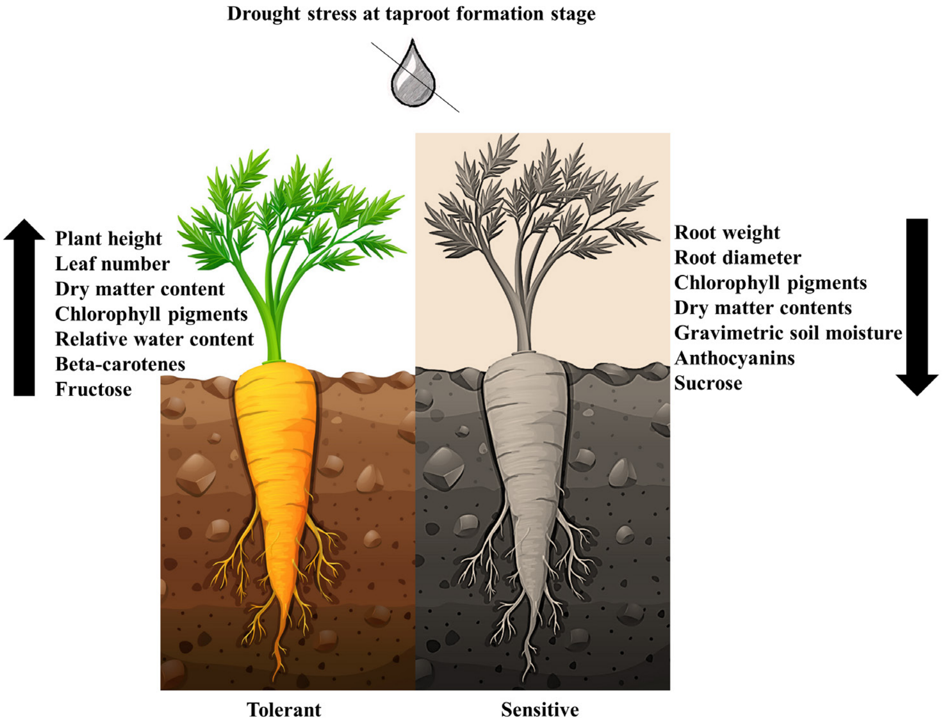

Figure 9. Pictorial representation interpreting the drought effect on carrot cultivars grown in controlled and drought stress environments. The drought stress inhibited the plant growth traits in this study. Downward arrow represents the traits which were decreased in sensitive carrot cultivars (Cosmic Purple, Salkim Orange, and Solar Yellow), whereas upward arrow shows the traits which were increased in tolerant carrot cultivars (Atomic Red and Coral Orange).

in accordance with a previous study (Becker et al., 2016). Moreover, increased stomatal conductance gave rise to more water supply via plant roots (Kano et al., 2011).

Water deficit forces decline in plant root diameter, which assists in increased root length for absorption of soil water for plant survival (Kulkarni and Phalke, 2009). The present study showed that root diameter and root length were reduced under drought, but overall reduction in root diameter was much higher compared to root length reduction (Figures 2b and 2c). We concluded that drought stress associates with root colonization and causes taproot xylem vessels to shrink, which led to declined root diameter and length in this study (Kim et al., 2020). Furthermore, reduction might also be associated with root parenchyma which controls lignin accumulation in roots (Wang et al., 2017). Increased root diameter in cultivar Coral Orange might be contributed by increased stomatal conductance, which gave rise to higher root biomass due to increased moisture supply via plant roots (Kano et al., 2011)

Present results are in accordance with a recent study where the reduction of 28.67% in root length was recorded in carrot plants when exposed to drought (Razzaq et al., 2017). In susceptible carrot genotypes, it was observed that soil moisture deficiency caused detrimental effect on carrot roots (Bashir et al., 2021). Previously, it was reported that overall plant growth hindered with the occurrence of drought during final root development, drought also negatively affected marketable and nutritional quality of carrots (Sørensen et al., 1997).

Drought stress causes lower relative water content which leads to yield losses; it also results in low leaf water potential (Álvarez et al., 2009). Similarly, the present results exhibited reduced RWC in all carrot cultivars under drought (Figure 3a). Scarlet Nantes cultivar showed susceptibility for RWC under drought by reducing its leaf relative water content by 41% and its root weight reduced compared to other cultivars under study. Growth and yield significantly declines when RWC is decreased (Hayatu et al., 2014), we assume that current findings are attributed to changes in leaf water potential and osmotic adjustment of carrot cultivars under drought. Moreover, RWC is an effective trait to select drought tolerant genotypes, indirect association of RWC contents with leaf traits and enzyme activity was found in amaranth (Slabbert and Krüger, 2014).

In this study, enhanced dry matter % was observed in all cultivars except cultivar Cosmic Purple (Figure 3b).

It might be due to inhibition of biomolecules and their concentration in susceptible carrot cultivars (Tsuchihashi and Goto, 2004). Moreover, according to Dragland (1979), increased dry matter concentration occurs under late season drought. All cultivars except Cosmic Purple showed increase in dry matter % at harvest. Decrease in dry matter % is also credited with inability of cultivar Cosmic purple in dry matter partitioning in different parts of its root (Polania et al., 2016).

When exposed to drought, leaf temperature in plants is considered an indicator of stress tolerance (Naveed et al., 2014). In the current study, Coral Orange and Tendersweet cultivars showed the lowest increase in leaf temperature, whereas Cosmic Purple exhibited the highest leaf temperature under drought (Figure 3c). Increase in leaf temperature is attributed to decreased transpiration rate which caused stomatal closure in plants under drought compared to adequately watered plants (O'Neill et al., 2006). Cultivars which exhibited high leaf temperature might not be able to regulate their transpiration rate and stomatal conductance under drought because leaf temperature decreases with the increase in stomatal conductance (Fauset et al., 2019). Moreover, the differences in leaf temperature of different genotypes occur because of genotypical carbon exchange rate of their canopy (Reynolds et al., 1994). GSM % explains the amount of water absorbed or used by the plant. To achieve effective growth, different plants tend to meet different soil moisture contents. It is an efficient parameter to be measured to analyze the water use of selected genotypes (Dong et al., 2011; Koskei et al., 2021). Cultivars Salkim Orange, Eregli Black, and Cosmic Purple were susceptible and showed the lowest GSM %, which means that they require higher availability of soil moisture than other cultivars (Figure 3d). In our recent study, it was also observed that cultivar Cosmic Purple exhibited sensitivity to drought regarding its gene regulation and biochemical traits (Junaid et al., 2022).

In this study, water deficit negatively affected chlorophyll 'a' and chlorophyll 'b' contents in all the carrot cultivars under study (Figures 4a and 4b). These pigments play a key role in plant growth and development; moreover, it was reported that under water scarce conditions, these pigments tend to decline and the plant becomes vulnerable (Astorga and Melendez, 2010). Reduction in photosynthetic pigments in the present study was observed in all carrot cultivars irrespective of their color (Figure 4). Furthermore, Ebadollahi-Natanzi and Arab-Rahmatipour (2020) described that under low moisture climatic conditions, reduced chlorophyll and carotenoids contents were observed in carrot plants. Some plants show drought tolerance and maintain their chlorophyll content under stress; it has also been reported previously in soyabean and potato cultivars (Guzzo et al., 2021). This might be the reason that Atomic Red, Coral Orange, and Scarlet Nantes cultivars showed tolerance to drought in this study by exhibiting higher photosynthetic pigments under water scarcity, whereas the ability of maintaining chlorophyll contents may differ with genotype, time span, and ferocity of stress. That is why we observed differential responses between cultivars. According to Li et al. (2006), plants which maintain relatively higher chlorophyll contents under drought can productively use light energy, and this is also attributed to drought tolerance. Solar Yellow cultivar showed the lowest chlorophyll and carotenoids contents under drought (Figure 4), it can be due to that drought susceptible genotypes exhibit low light harvesting ability. As it is known that ROS production is operated when there is adequate energy absorption during photosynthesis, this might be the reason that plants degrade their absorbing pigments to avoid it (Herbinger et al., 2002). Furthermore, decline in chlorophyll contents is also attributed to active oxygen species which negatively influence chloroplast functioning (Qi et al., 2018).

Anthocyanins are the most common form of flavonoids, which are bioactive dietary constituents and enhance human health and prevent chronic diseases (Birt and Jeffery, 2013). Physiologically, they are also part of defense mechanism in plants and involved in carrot root color and considered a major goal for carrot breeding (Simon, 2020). Many plants produce anthocyanins in response to abiotic stress as their defense mechanism (Delgado-Vargas et al., 2000). Increase in anthocyanin contents is considered a stress tolerance indicator in plants. The present results showed that when exposed to drought, the cultivars Tendersweet and Solar Yellow showed sharp decline in anthocyanin contents (Figure 5a). We assumed that this may be part of their defensive mechanism to decrease anthocyanin contents; moreover, the root color of these two cultivars (Orange and Yellow) might also be the reason of lower anthocyanin concentration; it was previously reported in purple carrots that the genes involved in anthocyanin accumulation show higher transcript levels (Yildiz et al., 2013). Anthocyanin accumulation in carrot roots is controlled by *P1* gene (Cavagnaro et al., 2014); maybe, high regulation of flavonoid pathway genes in purple carrots under drought was the reason of sharp increase in roots of cultivars Eregli Black and Cosmic Purple (Xu et al., 2017). From the present results, we speculated that increase in anthocyanin concentrations in purple carrot cultivars is highly attributed to drought occurrence.

Carotenoids are a vast group of isoprenoid molecules, which are produced by all photosynthetic and many nonphotosynthetic organisms (Simkin et al., 2008).

Beta-carotene is a broadly studied carotenoid which is an important part of human diet (Bakan et al., 2014). However, there is limited knowledge available on the effects of drought on carotene contents of the carrot plant. It is known that carrot roots differ in carotenoid contents depending on location of growth and availability of moisture in soil (Ombódi et al., 2015). The current study showed variation in beta-carotene contents in different colored carrot cultivars, which may be attributed to the presence of different carotene (lycopene etc.) compounds in carrot taproots (Just et al., 2009). The present study showed significant decline in beta-carotene contents of cultivar Salkim Orange; however, the increase in cultivars Solar Yellow and Coral Orange (Figure 5b), although the increase was minimal, represents resilience to drought in both cultivars. The results suggested the susceptible nature of cultivar Salkim Orange under the influence of drought because recent studies suggest that accumulation of beta-carotenes helps in drought and salt tolerance in carrot and potato respectively (Kim et al., 2012). Another study also explained that increase in beta-carotene contents in a genotype may be an indicator of drought tolerance (Chávez, 2008). This is due to their antioxidant activity, when exposed to drought, they play an important role in drought tolerance in plants (Zhang et al., 2021). The decline in beta-carotene contents in cultivar Salkim orange may be due to specific molecular response of this cultivar; recently, it is speculated that upregulation of *DcLCYB* gene in carrot is responsible for increase in beta-carotene under drought (Zhang et al., 2021). Silencing or absence of *DcLCYB* gene in this cultivar might be the reason for lower beta carotene. Difference in beta-carotene contents in carrot cultivars can also be genotypic specific response to drought, genetic polymorphism (Jourdan et al., 2015), cultivar specific cell organization, and it may be attributed to their gene expression (Perrin et al., 2017). In cultivars Solar Yellow and Coral Orange, significant increase in beta carotene under drought suggests their resilient behavior, it might be attributed to higher transcription of responsible genes in beta-carotene synthesis (Öztürk Gökçe et al., 2022).

Sugars in carrot root mainly comprise fructose, glucose, and sucrose; they are mainly constituted by free sugars (95%) and carbohydrates (40%–60%) (Alabran and Mabrouk, 1973). Sucrose is a major contributor globally in human sugar uptake (Gibson et al., 2013). During abiotic stress, sucrose is predominant carbohydrate which is mobilized from starch. Sucrose is the main product of photosynthesis in plants. The effect of drought on plants may affect carbon availability in the form of sucrose (O'Hara et al., 2013). Sucrose mobilization in plants is directly dependent on phloem transport system of plant (Ruan, 2012). HPLC analysis illustrated that in cultivars Cosmic Purple, Solar Yellow, and Tendersweet, there were no sucrose contents detected under drought. However, there was reasonably good amount of sucrose present in their control well-watered plant roots. This suggested negative effect of drought on sucrose contents of these cultivars. A study suggested decrease in sucrose contents after harvesting (Phan et al., 1973), or it might be due to sucrose breakdown into fructose contents as increase in fructose content was observed in cultivar Tendersweet under drought. This might explain that sucrose contents break down into fructose under drought (Figure 6); moreover, it can be a genotypic effect that has main influence on sugar contents in carrot apart from environmental factors. Lower or no sucrose content in carrot cultivars under drought can be also attributed to the utilization of sucrose in carrot cytoplasm under effect of abiotic stimuli (Cavagnaro, 2019). Restricted sucrose accumulation might contribute to physiological constraint due to ions and compatible solute accumulation (Hoffmann, 2010). Moreover, the sucrose contents under drought response also depend upon the enzymatic cleavage activity. In cultivars Atomic Red and Scarlet Nantes, increase in sucrose contents may also be attributed to higher enzymatic activity. Sucrose hydrolyzation phenomenon occurs to form fructose and glucose under certain conditions (Krause et al., 1998). We speculate from these results that sucrose contents in carrot cultivars under drought also have genotypic specific response.

Reducing sugars (fructose and glucose) revealed that cultivars Cosmic Purple and Solar Yellow showed sharp decline in fructose contents when exposed to drought. However, there was no significant change observed in other cultivars in this study (Figure 6a). It was reported that sucrose disintegrates to form reducing sugars (Rodríguez et al., 2010). This might be the reason of declined sucrose accumulation in response to drought. Moreover, glucose contents in cultivars Cosmic Purple, Solar Yellow, and Tendersweet were also significantly reduced under drought (Figure 6b). Sucrose phosphate synthase is associated with hydrolyzing sucrose into fructose, and drought may have influenced the enzymatic sucrose phosphate synthase which caused decrease in fructose and glucose contents in carrot cultivars (Liu et al., 2018). However, in other studies, it is also reported that drought affects accumulation of reducing sugars, which plays a positive role in osmoregulation under drought (Ozturk et al., 2021). Additionally, sugar contents play an indirect role in carbohydrate mobilization under drought (Li et al., 2020). Fructose and sucrose may play an important role in osmotic protection against abiotic stresses by cell membrane protection that scavenge ROS (Kapoor et al., 2019). This suggested that cultivars

Coral Orange and Atomic Red were resilient against drought for reducing sugars or they might have different physiological and molecular functioning for reducing sugars synthesis. From earlier literature, we assumed that carrot cultivars showed differential genotypic responses for sugar accumulation under drought. Pictorial representation interpreting the drought effects on quality and physiological attributes of carrot cultivars is shown (Figure 9).

5. Conclusion

We have uncovered the contrasting behavior of different colored commercial carrot cultivars based on their morphophysiological and quality characteristics. Results obtained in the study provide an insight into the different mechanisms associated with quality traits in carrot genotypes with their response to drought. It was concluded that drought negatively affected yield characteristics of all carrot cultivars. Orange and Yellow colored carrot cultivars showed the least decline in physiological functioning that assisted in maintaining higher yield and quality attributes in contrast to purple and black carrot cultivars. The study revealed that purple carrot cultivars sharply increase their anthocyanin contents when exposed to drought. However, orange colored carrot cultivars exhibited higher beta-carotene accumulation under drought. Sugar accumulation exhibited variable response in carrot cultivars, as no sucrose contents in cultivars Cosmic Purple, Solar Yellow, and Tendersweet were detected under drought, which indicated sucrose breakdown into reducing sugars under drought. Overall, cultivars Atomic Red and Cosmic Purple exhibited cultivar-specific resilience to drought for morphophysiological and quality traits. Different physiological responses of these cultivars under drought might be attributed to their different genetic background, and their interaction with external stimuli (drought). The current study provided new information regarding influence of drought on various characteristics of different colored carrot cultivars, albeit there is significant research gap to associate drought effects with morphology, physiology, and quality traits of carrot, so further physiological and molecular mechanisms involved need to be studied to improve drought tolerance in carrot.

Acknowledgement

We acknowledge the Scientific Research Projects Unit (BAP) of Niğde Ömer Halisdemir University, Niğde, Türkiye for providing funds for this study under the Project No. TGT 2020/14-BAGEP. This study was part of the PhD. thesis work of Muhammad Daniyal Junaid. He also acknowledges the Ayhan Şahenk Foundation for providing fellowship during his doctoral study.

Conflict of interest

Authors declare no conflicts of interest.

Ethical approval

Not applicable.

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Supplementary

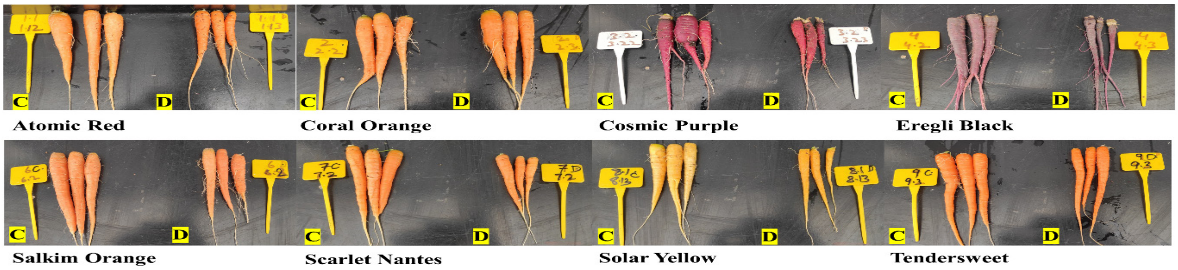

Figure S1. Drought stress effects on carrot taproot growth in eight cultivars. ‘C’ represents control group whereas, ‘D’ represents drought group.

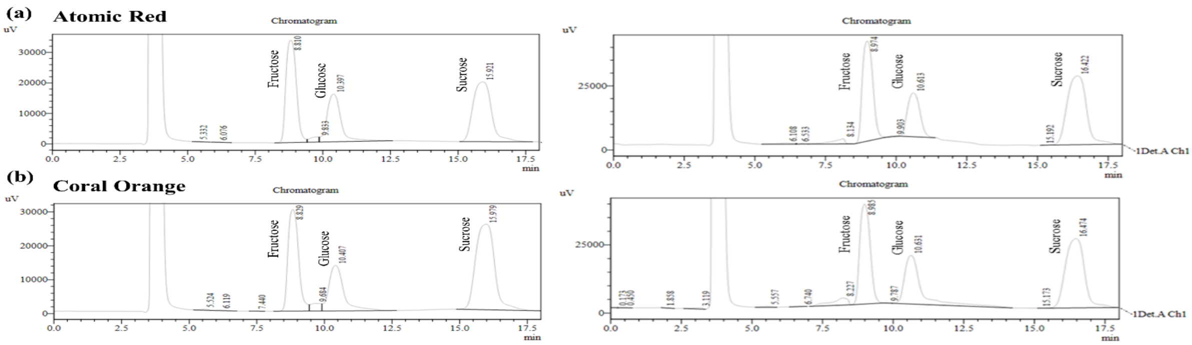

Figure S2. HPLC chromatograms representing fructose, glucose, and sucrose retention time of cultivars (a) Atomic red and (b) Coral Orange under control (left) and drought stress (right).

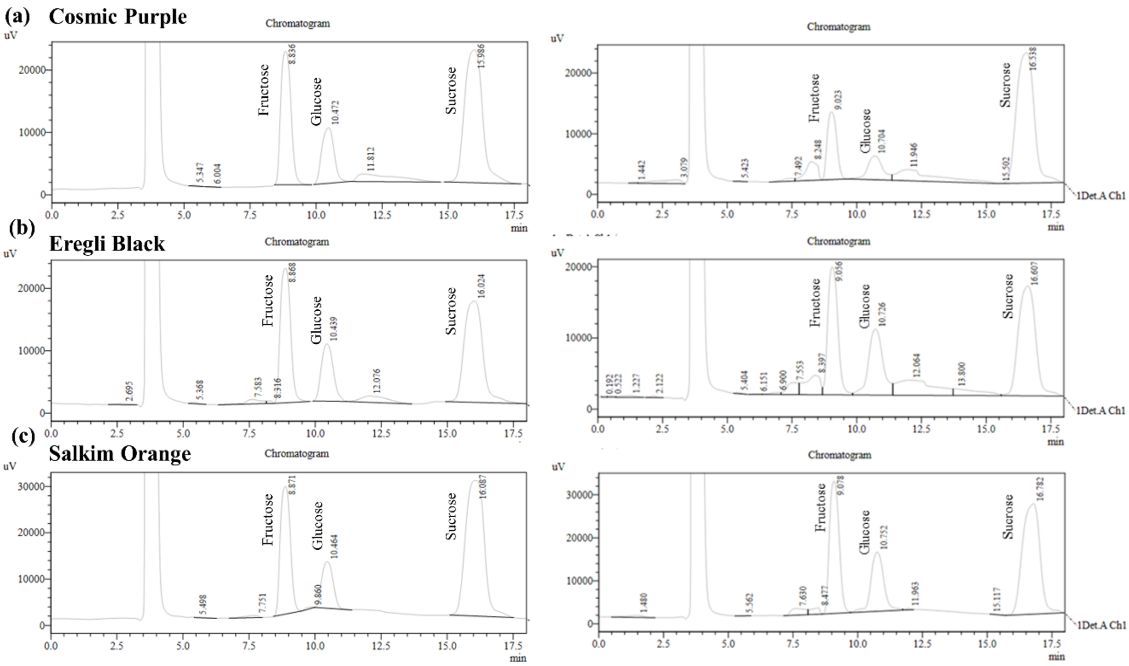

Figure S3. HPLC chromatograms representing fructose, glucose, and sucrose retention time of cultivars (a) Cosmic Purple, (b) Eregli Black, and (c) Salkim Orange under control (left) and drought stress (right).

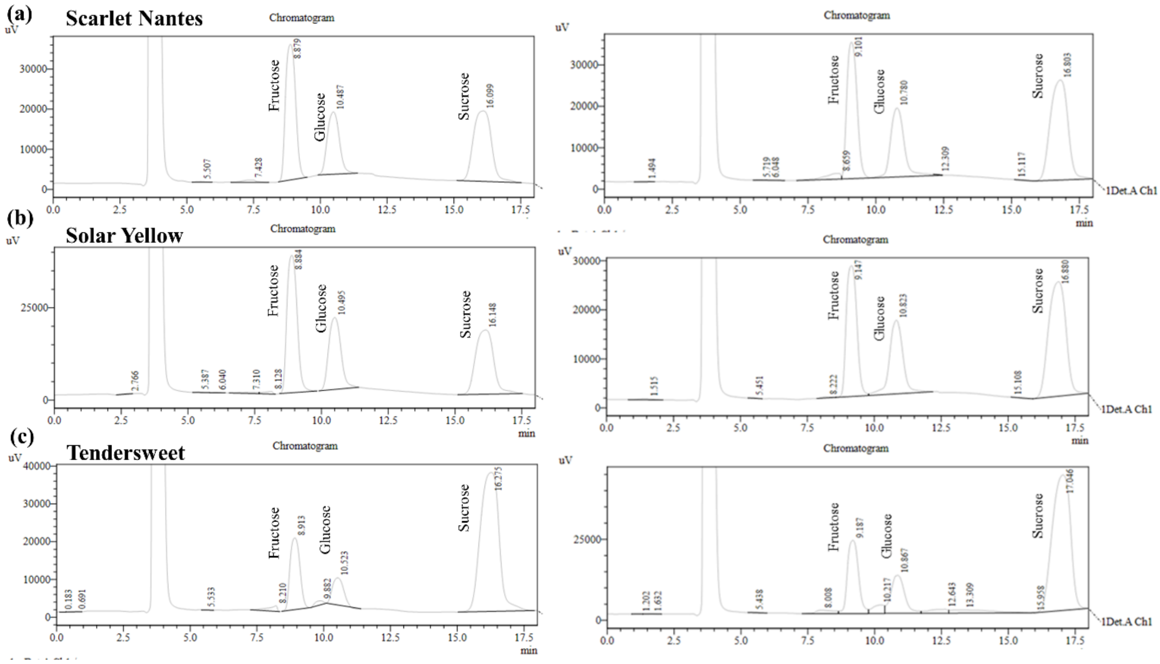

Figure S4. HPLC chromatograms representing fructose, glucose, and sucrose retention time of cultivars (a) Scarlet Nantes, (b) Solar Yellow, and (c) Tendersweet under control (left) and drought stress (right).

Table S1. Preparation of standard solution for sugars measurements via HPLC.

Stock solution	**ddH$_2$0 concentration**	**Final volume**
1.5 mL	0 µl ddH20	5000 ppm
750 µL	750 µl ddH20	2500 ppm
375 µL	1125 µl ddH20	1250 ppm
300 µL	1200 µl ddH20	1000 ppm
150 µL	1350 µl ddH20	500 ppm
75 µL	1425 µl ddH20	250 ppm
30 µL	1470 µl ddH20	100 ppm
15 µL	1485 µl ddH20	50 ppm