

Salinity stress and drought stress differentially affect biomass allocation, leaf orientation and performance of two sesame (*Sesamum indicum* L.) cultivars

Taha Mohamed El-Katony

tmsoliman2000@yahoo.co.uk

Damietta University

Nemat Mohamed Hassan

Damietta University

Samia Helmy

Damietta University

Shaimaa Nassim Abdelfatah

Damietta University

Research Article

Keywords: Drought. Salinity. Sesame genotypes. Gas exchange. Carbohydrate fractions. Leaf orientation

Posted Date: December 15th, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-7362732/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Additional Declarations: No competing interests reported.

Abstract

Drought and salinity stresses are major threats to crop productivity in the arid lands. This work investigates the differential impact of salinity and drought on growth and performance of two sesame cultivars: Soh9 and Shnd at water potentials of 0, -100, -250 and -450 kPa with the same nutrient supply in a hydroponic sand culture. Under no stress, leaves of Soh9 exhibited vertical orientation with higher pigment and soluble sugar contents but lower polysaccharide content relative to leaves of Shnd. Salinity and drought differentially affect leaf orientation only in Soh9, where drought induced horizontal leaf position but salinity led to the opposite effect. Whereas drought induced stronger reduction in foliage biomass than did salinity, with enhancement of root biomass, salinity reduced foliage and root biomass with favored allocation of plant biomass to root. Salinity reduced leaf pigment content, particularly in Soh9 but drought either increased it or was without effect. Both drought and salinity, post a threshold of -100 kPa, reduced rates of photosynthesis and transpiration as well as stomatal conductance, with stronger impact of salinity than drought. The lowering in carbohydrate content under stress, being more aggressive under salinity than drought, was associated with increasing proportion of pectin at the expense of starch and variable changes in soluble sugar proportions.

1 Introduction

In natural habitats, plants may experience combined stresses simultaneously such as the combined stress of high temperature, water deficit and high irradiance in the hot dry summer of arid habitats [1]. Among the different abiotic stresses affecting plants, salinity stress and water stress are particularly serious and mostly interrelated. Mostly, saline soils are abundant in semiarid and arid regions where rainfall is insufficient for leaching of excessive soluble salts out of the rhizosphere [2]. In turn, irrigation with poor quality water, a practice common in the arid developing countries, can induce secondary salinization. Soil is considered saline when electrical conductivity of its saturation extract exceeds 4 dS m^{-1} (equivalent to 40 mM NaCl) with an exchangeable sodium percentage lower than 15 [3].

Although the majority of crop plants are glycophytes, few species are salt-tolerant and can even benefit from mild salinity. Justification of crop salt response relies upon two criteria: the threshold salinity and the slope of the salinity-growth response line beyond the threshold. Differences in salt tolerance can occur among different species and cultivars as well as for the different plant developmental stages [4, 5]. Similarly, drought stress represents a major challenge to plant productivity and land use, particularly in the arid regions. Even in the tropical rain forests, land plants can experience different degrees of transient water stress when water absorption lags behind evapotranspiration [6]. The witnessed global warming will further aggravate the threat of drought to plant productivity. Intrinsically, plants have low water use efficiency, with < 1% of the absorbed water being invested in the biomass versus > 90% of the absorbed mineral nutrients [1]. Water is translocated within the plant down a gradient of 1) water potential (Ψ_w) across membranes from the soil to the root and throughout the root, 2) hydrostatic pressure in the xylem vessels and 3) water vapor gradient from the leaf to air.

Under the impact of salinity, plants suffer from several hazards including osmotic stress, ion toxicity, nutrient imbalance and oxidative stress; the relative effect of either factor depends on the level, duration and mode of exposure to salt stress as well as the plant developmental stage. For example, long-term salinity stress leads mainly to ion toxicity in the older leaves but to water deficit and shortage of carbohydrates in the younger leaves [7]. Salinity and drought cause morphological, physiological, biochemical and molecular changes in the plant. To cope with stress, the plant has to expend additional energy for ion exclusion or compartmentalization (salinity stress) as well as for osmotic adjustment and detoxification of reactive oxygen species (salinity and drought stresses), which will slow down plant growth [8]. As a rule, shoot growth is more depressed by salinity and drought than root growth, partially because of favored biomass allocation to roots at the expense of shoots [9].

In addition to the direct toxicity of high levels of Na^+ and Cl^- to the cytoplasm, salt toxicity may also be attributed to interference with respiration, photosynthesis and protein synthesis. Salinity can cause insufficient cellular K^+ concentrations for enzyme activation, protein synthesis, photosynthesis and stomatal movement [10]. Hence, the ability of plants to protect enzymes from the adverse effects of Na^+ or Cl^- can be attributed to the synthesis of compatible solutes such as sugars and amino acids (e.g. proline) that can stabilize the structure of membranes and macromolecules [11]. The role of compatible

solute in plant protection is also evident under drought stress, where plant cells adjust Ψ_w by accumulating inorganic ions and organic acids in the vacuoles, with the synthesis of compatible solutes such as glycine betaine, sorbitol, and proline in the cytoplasm. The salinity-induced reduction in photosynthesis can be attributed to the reductions in leaf area (a capacity factor) and net CO₂ fixation per unit leaf area (an efficiency factor) in addition to the decreased demand of sink tissues for assimilates [12]. Further, the effect of salinity on photosynthetic efficiency includes both stomatal and nonstomatal limitations. Stomatal limitations are manifested as lowered intercellular CO₂ concentration while nonstomatal factors include the decrease in quantum efficiency and inhibited Ribisco activity [13]. Stomatal closure and the lowered stomatal conductance represent a way to prevent excessive dehydration of the leaves as a feedforward response to anticipate water deficit before the development of severe drought.

Sesame (*Sesamum indicum* L.), a Pedaliaceae member and one of the most valuable oil cash crops in Africa and Asia [14], is a robust crop with wide niche and marked drought tolerance. The high oil content of sesame seeds (up to 63%) is characterized with high proportion of unsaturated fatty acids, particularly omega 3 and γ -tocopherol [15]. Sesame seeds are also rich in human-compatible proteins, vitamins, dietary fibers and dietary minerals, particularly Ca²⁺ [16, 17]. Furthermore, sesame seeds contain bioactive components such as polyphenols, lignans, phytosterols, quinones and triterpenoids [18]. The present work investigates the differential impact of NaCl salinity and water-withholding drought, at the same Ψ_w , on growth and performance of two Egyptian sesame cultivars: Sohag 1 (Sohg) and Shandaweel 3 (Shnd). Partitioning of biomass, photosynthetic pigments and carbohydrate fractionations have been integrated with photosynthetic efficiency to achieve a plausible explanation of plant tolerance to abiotic stress.

2 Materials and Methods

2.1 Plant material

Seeds of cultivars Sohag 1 (Sohg) and Shandaweel 3 (Shnd) of sesame (*Sesamum indicum* L.) were obtained from the Agricultural Research Center (ARC), Egypt. The two experimental sesame cultivars are national cultivars, produced and released by Oil Crops Research Department, Field Crops Research Institute (FCRI), Agricultural Research Center (ARC), Ministry of Agricultural and Land Reclamation, Egypt according to The International Union for the Protection of New Varieties of Plants (UPOV) guideline (Egypt is a member of UPOV) and the Intellectual Property Rights (IPR) national law. The acquired names "Sohag 1" and "Shandaweel 3" are given by the breeder program of ARC and are related to national districts of Egypt.

2.2 Effect of salinity and drought on sesame growth and performance

Seeds were selected for homogeneity, surface-sterilized in 10% (v/v) Clorox for 20 minutes, washed thoroughly with tap water and sown on plastic pots of 15 cm diameter and 20 cm height full of 1.1 kg of water-washed sand, five seeds per pot. Seeds were watered with 0.2 mM CaSO₄ for 7 days; thereafter, seedlings were successively thinned to one per pot and received the nutrient solution in a successive manner. First, seedlings were watered with a one-tenth strength nutrient solution for three days, followed by half-strength solution for six days and finally the full-strength solution for 13 days. The full-strength nutrient solution had the following composition:

Macronutrients (mM): N (as NO₃⁻) 16, K 7.5, P 1.5, Ca 5, Mg 1.5 and S 1.5.

Micronutrients (μM): Fe 50, Mn 5, Cu 0.5, Zn 0.5, B 25, Mo 0.25 and Na 50.

After 13 days of irrigation with the full nutrient solution, plants of 31 days-old and eight true leaves were subjected to stress at four ψ_w : 0, -100, -250 and -450 kPa, induced either as NaCl stress or drought stress. The experimental water potentials corresponded to 0, 25, 61 and 110 mM NaCl, respectively for salinity stress and 100%, 23.6%, 14.1% and 10.2% field capacity, respectively or 20, 4.71, 2.83, 2.04 g water/100 g sand, respectively for drought stress. The water holding capacity of the sand used as growth medium was estimated as 20% (w/w). To achieve the required ψ_w of salinity and drought stresses, the formula of [19] and the ψ_w -water content curves of [20], respectively were consulted.

To ensure homogenous supply of water and nutrients, irrigation was dispended over four evenly-spaced daily intervals, with the same dose of nutrients throughout. This implied proportional increase in strength of the nutrient solution as the supply of water decreased in drought stress. The nutrient solution was prepared as a stock solution so as 1 ml of which will provide the nutrient supply for one pot per day. The scheduled supply of nutrient solution, water (for drought stress) and NaCl (for salt stress) is shown in Table 1.

Plants were grown in the greenhouse at the Faculty of Science, Damietta University during the period from July to August 2023. Irradiance ranged from 1500 to 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ from natural sunlight, with a temperature of 38/25°C in a 14/10 h light/dark period and relative humidity of about 75% in average. Plants were harvested six days after application of stress, when they were 37 days old. Just before harvest, measurements of leaf angle, leaf dimensions, photosynthetic pigments and gas exchange were carried out in the third youngest leaf pair. Plants were thoroughly washed from sand, separated into leaves, stem and root, blotted gently and fresh weights were recorded. An aliquot of fresh leaves was kept frozen at -80°C for estimation of photosynthetic pigments and carbohydrate fractions. Dry weights were recorded after drying of the fresh plant material at 80°C for 48 h and were corrected for the leaf portions kept frozen.

Table 1
Supply of nutrients, water and NaCl solution to the sand culture to obtain the experimental water potentials with the same dose of nutrients under the impact of salinity stress and drought stress

	kPa			
	0.00	-100	-250	-450
Salinity stress				
mM NaCl	0	25	61	110
ml water before addition of stocks	200	200	200	200
ml stock NS per pot per day	1.0	1.0	1.0	1.0
ml NaCl (2 M) per pot per day	0	2.75	6.71	12.1
Final volume (ml)	220	220	220	220
ml working solution per pot per 6 h	55	55	55	55
Drought stress				
Water content of sand (% DW)	20	4.71	2.83	2.04
Water content (% field capacity)	100	23.6	14.1	10.2
Stock N.S. (ml) per pot per day	1.0	1.0	1.0	1.0
Water (up to ml) per pot per day	220	51.92	31.02	22.44
ml working solution per pot per 6 h	55	12.98	7.76	5.61

2.3 Plant analysis

2.3.1 Estimation of photosynthetic pigments

Photosynthetic pigments were determined according to the method described by [21]. Frozen leaf discs were macerated in 80% acetone using cold mortar and pestle in dim light with a pinch of magnesium carbonate to neutralize the plant acids. The slurry was centrifuged and the clear extract was brought up to volume with 80% acetone where the absorbance was read at 470, 646 and 663 nm using a UNICO 7200 series spectrophotometer. The concentrations of chlorophyll a (Chl a), chlorophyll b (Chl b) and carotenoids (Carot) were calculated ($\mu\text{g ml}^{-1}$) according to the following equations:

$$\text{Chl a} = 12.21 E_{663} - 2.81 E_{646}$$

$$\text{Chl b} = 20.13 E_{646} - 5.03 E_{663}$$

$$\text{Carot} = \frac{(1000 E_{470} - 3.27 \text{ Chl a} - 104 \text{ Chl b})}{229}$$

Concentrations were presented as $\mu\text{mol pigment g}^{-1}$ leaf FW.

2.3.2 Estimation of gas exchange parameters

Photosynthesis rate (A), stomatal conductance to CO_2 (G_s), substomatal CO_2 concentration (C_i) and transpiration rate (E) of the third youngest leaf pair were measured at 10:00 a.m. using an LCA-4 portable gas exchange system (Analytical Development Company Ltd, England). Measurements were conducted with leaf area of 6.25 cm^2 , leaf chamber CO_2 concentration of 390 ppm at chamber temperature of 44°C and photosynthetic photon flux density of $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$.

2.3.3 Estimation of carbohydrate fractions

Soluble sugars, starch, hemicellulose and pectic substances were sequentially assayed in the leaves. For extraction of soluble sugars, a known weight of the frozen leaf material was grinded to a fine powder in liquid nitrogen, then thoroughly extracted in 1.2 ml of 80% ethanol and kept at -4°C overnight [22]. The mixture was centrifuged at $8000 \times g$ for 10 minutes; the supernatant was quantitatively transferred to clean Eppendorf tubes, evaporated to dryness at 70°C and re-dissolved in distilled water for determination of soluble sugars. An aliquot of the soluble carbohydrate extract was completed to 1 ml with distilled water, then carefully mixed with 3 ml of the anthrone reagent and heated at 80°C for 10 min in a water bath. The mixture was cooled for 30 min in an ice bath and absorbance was recorded at 623 nm against the reagent blank.

The plant debris left after ethanolic extraction was used for determination of the insoluble carbohydrate fractions. For estimation of starch, the debris remained after extraction of soluble sugars was re-suspended in 1.5 ml of 3% HCl with boiling for 3 hours and the mixture was centrifuged at $8000 \times g$ for 10 min [23]. The liberated glucose units were estimated by the anthrone method as mentioned above, and starch content was expressed as μg glucose equivalents (Gluc. eq.). For estimation of hemicellulose, the residue left after extraction of starch was re-suspended in 1.2 ml of 5% H_2SO_4 , boiled for 2.5 hours and then centrifuged at $8000 \times g$ for 10 min. The supernatant was quantitatively transferred to clean Eppendorf tubes, and the liberated glucose units were estimated by the anthrone method [24]. For estimation of pectic substances, the residue left after extraction of hemicellulose was re-suspended in 1 ml of 72% H_2SO_4 at 4°C for 24 hours, then centrifuged at $8000 \times g$ for 10 min. The supernatant was quantitatively transferred to clean Eppendorf tubes, and the liberated glucose units were estimated by the anthrone method [24]. The anthrone reagent was prepared by dissolving 1.67 g anthrone in 1 l of 80% H_2SO_4 (v/v) for 8.6 mM anthrone. The different carbohydrate fractions were estimated with reference to a glucose calibration curve in the range of 0–100 $\mu\text{g/ml}$.

2.4 Definitions and calculations

The photosynthetic water use efficiency was defined as the photosynthesis rate (A)/transpiration rate (E) ratio [1]. RWR, StWR and LWR refer to the proportions of the plant dry matter allocated to root, stem and leaves respectively. Similarly, Chl a ratio, Chl b ratio and Carot ratio refer to the proportions of Chl a, Chl b and carotenoids, respectively in the total leaf pigment content.

2.5 Experimental design and statistical analysis

The experiment was factorial with three factors and three replications in a completely randomized design. The main factors were: 1) sesame cultivar with two levels: Sohg and Shnd, 2) type of abiotic stress with two levels: salinity and drought and 3) severity of stress in terms of Ψ_w of sand with four levels: 0, -100, -250 and -450 kPa. Data were subjected to three-way ANOVA using SPSS version 22, and the effects of the main factors and their interactions were assessed. Mean separation was

performed using the Duncan's multiple range test at $P < 0.05$. The correlations between plant growth and physiology were depicted in terms of the significant Pearson correlation coefficients.

3 Results

3.1 Plant growth

The most affected growth attributes, justified by the magnitude of the F ratio, was the leaf angle, while the least affected one was leaf dimensions (Table 2). In absence of stress, Shnd exhibited horizontal leaf position relative to Sohng. The effect of stress on leaf angle was observed only in Sohng, which experienced 39% reduction by salt stress versus 52% increase by drought stress across the whole range of ψ_w ; this in contrast to non-significant decrease and increase, respectively in Shnd (Fig. 1a). Lowering ψ_w of sand from 0 to -450 kPa led to progressive decrease in leaf length and width by 27% and 20%, respectively as an average for the two types of stress in Sohng but to non-significant reductions in Shnd (Fig. 1b, c). Consequently, stress led to progressive mild increase in the leaf width/length ratio in Sohng but to a transient top at moderate stress, followed by a decrease at severe stress in Shnd (Fig. 1d).

Whereas the dry weights of root and leaves were comparable in the two cultivars irrespective of the stress regime, stem dry weight was higher in Sohng than Shnd in absence of stress but the reverse was true under stress. Lowering ψ_w from 0 to -450 kPa reduced leaf dry weight of Sohng and Shnd by an average of 44% under salinity stress post a beneficial threshold salinity of -100 kPa, but drought stress led to a progressive average reduction of 42% for the two cultivars (Fig. 2a). However, progression of salinity and drought stress from 0 to -450 kPa reduced stem dry weight by an average of 64% and 20% for Sohng and Shnd, respectively (Fig. 2b). The lesser impact of salinity than drought on foliage biomass was manifested as the emergence of -100 kPa beneficial threshold salinity, along with less-aggressive reduction under moderate stress. Lowering ψ_w from 0 to -450 kPa reduced root dry weight of Sohng and Shnd by an average of 65% post a threshold of -100 kPa under salinity stress but led to progressive increases of 38% and 75% in Sohng and Shnd, respectively under drought stress (Fig. 2c).

Shoot water content was non-significantly affected by genotype and stress except for the significant reduction only in Shnd under severe salinity. By contrast, the genotypic difference emerged in water content of root, with higher values in Sohng than Shnd particularly under stress, and stronger reduction under drought than salinity (Table 3).

The differential impact of stress on dry weights of plant organs resulted in alteration of biomass partitioning among leaves, stem and root. Under salinity stress, Sohng increased allocation of biomass to leaves at the expense of stem and root; whereas Shnd increased allocation to stem at the expense of root with marginal increase in leaf proportion. By contrast, under drought stress both cultivars increased allocation of biomass to root at the expense of foliage (stem and leaves) (Fig. 3).

Table 2

Three-way ANOVA showing the effect of the main factors: sesame cultivar (Cv), type of stress (Stress) and water potential of the medium (kPa) and their interactions on leaf dimensions, biomass and biomass partitioning and water content of plant organs

Source of variation	df	Leaf angle		Leaf length		Leaf width		Leaf W/L ratio		Root water		Shoot water	
		F	P	F	P	F	P	F	P	F	P	F	P
Cv	1	83.55	0.000	0.611	0.440	0.361	0.552	3.121	0.087	7.651	0.009	0.378	0.543
Stress	1	10.16	0.003	0.126	0.725	0.361	0.552	0.269	0.608	39.24	0.000	0.499	0.485
kPa	3	0.709	0.554	11.16	0.000	3.252	0.034	3.003	0.045	11.18	0.000	4.894	0.007
Cv × Stress	1	5.491	0.025	1.823	0.186	2.373	0.133	0.488	0.490	1.574	0.219	1.775	0.192
Cv × kPa	3	0.919	0.443	1.715	0.184	1.053	0.383	1.291	0.294	2.576	0.071	3.063	0.042
Stress × kPa	3	5.133	0.005	0.423	0.738	0.065	0.978	0.430	0.733	20.02	0.000	1.536	0.224
Cv × Stress × kPa	3	2.150	0.113	0.880	0.462	0.627	0.603	0.375	0.772	1.297	0.293	2.771	0.058
		Root dry weight		Stem dry weight		Leaf dry weight		RWR		StWR		LWR	
		F	P	F	P	F	P	F	P	F	P	F	P
Cv	1	0.498	0.486	0.827	0.370	0.691	0.412	1.360	0.252	4.987	0.033	1.043	0.315
Stress	1	96.52	0.000	21.73	0.000	48.02	0.000	272.2	0.000	25.20	0.000	69.17	0.000
kPa	3	1.368	0.270	21.99	0.000	30.42	0.000	10.45	0.000	4.264	0.012	0.683	0.569
Cv × Stress	1	0.778	0.384	0.282	0.599	0.036	0.851	0.002	0.963	0.643	0.428	0.428	0.518
Cv × kPa	3	1.610	0.206	8.508	0.000	1.172	0.336	1.358	0.273	5.591	0.003	1.950	0.141
Stress × kPa	3	41.62	0.000	7.303	0.001	14.22	0.000	48.01	0.000	4.181	0.013	13.78	0.000
Cv × Stress × kPa	3	0.167	0.918	0.442	0.724	0.371	0.775	0.016	0.997	1.086	0.369	0.945	0.431

Table 3
Effect of salt stress and drought stress on water content of shoot and root of cvs Sohg and Shnd of sesame. Each value is the mean of three replicates $\pm$ SE. Means with common letters are not significantly different at $p \leq 0.05$

Stress and water potential (kPa)	Shoot water (% FW)	Root water (% FW)
Sohg		
Salt stress		
0	86.02 $\pm$ 0.10 ^a	91.17 $\pm$ 0.86 ^{ab}
-100	87.22 $\pm$ 0.16 ^a	91.81 $\pm$ 0.87 ^{ab}
-250	86.37 $\pm$ 0.39 ^a	92.03 $\pm$ 0.30 ^{ab}
-450	86.63 $\pm$ 1.60 ^a	94.02 $\pm$ 1.26 ^a
Drought stress		
0	86.02 $\pm$ 0.10 ^a	91.17 $\pm$ 0.86 ^{ab}
-100	87.40 $\pm$ 0.49 ^a	93.89 $\pm$ 0.09 ^a
-250	86.02 $\pm$ 0.29 ^a	89.65 $\pm$ 1.30 ^{bc}
-450	85.49 $\pm$ 0.27 ^a	84.79 $\pm$ 1.57 ^d
Shnd		
Salt stress		
0	86.69 $\pm$ 0.42 ^a	91.86 $\pm$ 0.56 ^{ab}
-100	86.84 $\pm$ 0.44 ^a	92.40 $\pm$ 0.70 ^{ab}
-250	88.17 $\pm$ 0.20 ^a	91.08 $\pm$ 0.89 ^{abc}
-450	80.50 $\pm$ 3.44 ^b	91.35 $\pm$ 1.11 ^{ab}
Drought stress		
0	86.69 $\pm$ 0.42 ^a	91.86 $\pm$ 0.56 ^{ab}
-100	87.43 $\pm$ 0.16 ^a	89.74 $\pm$ 0.31 ^{bc}
-250	86.51 $\pm$ 0.64 ^a	88.02 $\pm$ 2.48 ^c
-450	85.80 $\pm$ 1.08 ^a	81.62 $\pm$ 0.84 ^e

3.2 Photosynthetic pigments

The contents of Chl a, Chl b and carotenoids were significantly higher in Sohg than Shnd; the genotypic difference was either most evident under mild stress (Chl a and Chl b) or was maintained under all levels of stress (carotenoids). The impact of salinity on photosynthetic pigments was more aggressive than that of drought, which exerted beneficial effect in Shnd. Increasing salinity from 0 to -450 kPa reduced the contents of Chl a, Chl b and carotenoids by 45%, 35% and 35%, respectively as averages for Sohg and Shnd; but whereas the reductions were progressive in Sohg, they occurred post a threshold of -100

kPa in Shnd (Fig. 4). Meanwhile, drought stress non-significantly affected pigment content of Sohg but led to 55% and 78% increases in Chla and Chl b contents, respectively in Shnd, without effect on carotenoid content (Fig. 4). Partitioning of photosynthetic pigments among Chl a, Chl b and carotenoids showed mild response to treatments, except for: 1) salinized Sohg—where carotenoid proportion was increased at the expense of Chl a, and 2) droughted Shnd—where chlorophyll proportion was increased at the expense of carotenoids (Fig. 5).

3.3 Gas exchange

Table 4 reveals that the most affected gas exchange parameters were the rate of photosynthesis (A), followed by stomatal conductance (Gs) and transpiration rate (E) while the least affected parameter was substomatal CO₂ concentration (Ci). In contrast to the increased Ci by stress, E, Gs and A were lowered. The increases in Ci, across the whole range of ψ_w , amounted to 54% and 39% in Sohg and Shnd, respectively (with -100 kPa threshold under salinity stress) but were progressive with lower magnitude (33% and 14% in Sohg and Shnd, respectively) under drought stress (Fig. 6a). By contrast, the reduction in E amounted to 77.5% under salinity stress and 47.5% under drought stress as an average for the two cultivars post a threshold of -100 kPa (Fig. 6b). The genotypic gap in G_s and A was marked, in favor of Sohg, in absence of stress but were narrowed under stress. Lowering ψ_w from 0 to -450 kPa reduced Gs and A by an average of 85% under salinity stress and 57% under drought stress in the two cultivars post a threshold of -100 kPa (Fig. 6c, d).

The genotypic difference in water use efficiency (WUE) was marked, in absence of stress and under severe drought stress, in favor of Sohg. Increasing salinity from 0 to -450 kPa reduced WUE by an average of 47% for the two cultivars, either progressively in Sohg or post -100 kPa threshold in Shnd. Meanwhile, the decrease in WUE across the whole range of ψ_w under drought stress amounted to 3% in Sohg and 38% in Shnd post a threshold of -250 kPa (Fig. 6e).

3.4 Sugar fractions

ANOVA revealed that among the assayed sugar fractions, the most affected component was hemicelluloses followed by soluble sugars, whereas pectic substances were the least affected one (Tables 5). Soluble sugar (SS) content of leaves was markedly higher in Sohg than Shnd in absence of stress and under drought stress but turned in favor of Shnd under salinity stress. SS content of Sohg leaves experienced 58% and 38% reductions under salinity stress and drought stress, respectively upon lowering of ψ_w from 0 to -450 kPa. Meanwhile, SS content of Shnd leaves experienced overall non-significant changes under stress, although approaching a minimum at -250 kPa (Fig. 7a).

In contrast to SS, the leaf content of polysaccharides (starch, hemicellulose and pectic substances) was higher in Shnd than Sohg in absence of stress; but the genotypic difference was either diminished or turned in favor of Sohg under stress. In Sohg, lowering ψ_w post a threshold of -100 kPa down to -450 kPa reduced starch content of leaves by 51% as an average for salinity stress and drought stress; but in Shnd, the reduction was progressive across the whole range of ψ_w , with stronger magnitude under salinity (72%) than under drought (56%) (Fig. 7b). The low hemicellulose content of Sohg leaves was subjected to moderate changes under stress (either a reduction under salinity or an increase under drought). By contrast, the high hemicellulose content of Shnd leaves experienced 70% average reduction across the whole range of ψ_w ; either progressively under drought or post a transient increase at -100 kPa under salinity (Fig. 7c). Across the whole range of ψ_w , salinity stress (on Sohg) as well as salinity and drought stress (on Shnd) led to an average 20% reduction in the leaf pectic substances; only drought stress led to non-significant increase in Sohg (Fig. 7d).

Starch constituted the greatest carbohydrate fraction of sesame leaves (> 50%), followed by soluble sugars and pectic substances (about 20% each), with minor hemicellulose component. In Sohg, mild salinity and drought stresses lowered SS ratio in favor of starch, but severe stresses led to the opposite effect; meanwhile the fraction of pectic substances or that of pectic substances and hemicellulose were progressively increase (Fig. 8a, b). In Shnd, stress—particularly salinity—led to progressive increase in the ratios of SS and pectic substances at the expense of starch and hemicellulose (Fig. 8c, d).

Table 4

Three-way ANOVA showing the effect of the main factors: sesame cultivar (Cv), type of stress (Stress) and water potential of the medium (kPa) and their interactions on the content of photosynthetic pigments and gas exchange of sesame leaves

Source of variation	df	Chl a		Chl b		Carot		Chl a ratio		Chl b ratio		Carot ratio	
		F	P	F	P	F	P	F	P	F	P	F	P
Cv	1	26.05	0.000	15.66	0.000	29.73	0.000	2.662	0.113	1.854	0.183	5.011	0.032
Stress	1	16.14	0.000	12.02	0.002	16.45	0.000	0.109	0.744	2.567	0.119	1.335	0.256
kPa	3	0.807	0.499	1.077	0.373	5.003	0.006	1.682	0.190	3.960	0.017	3.096	0.041
Cv × Stress	1	2.142	0.153	0.104	0.750	7.180	0.012	0.487	0.490	6.970	0.013	0.569	0.456
Cv × kPa	3	1.835	0.161	1.332	0.281	0.281	0.839	2.580	0.071	2.882	0.051	5.485	0.004
Stress × kPa	3	6.889	0.001	2.257	0.101	5.215	0.005	3.792	0.020	1.553	0.220	1.793	0.168
Cv × Stress × kPa	3	0.699	0.560	0.422	0.738	1.059	0.380	0.383	0.766	1.096	0.365	0.686	0.567
		Substomatal CO ₂ (Ci)		Transpiration rate (E)		Stomatal conductance (Gs)		Photosynthesis rate (A)		A/E ratio			
		F	P	F	P	F	P	F	P	F	P		
Cv	1	0.071	0.791	2.307	0.139	11.19	0.002	13.54	0.001	6.306	0.017		
Stress	1	0.089	0.768	10.68	0.003	7.701	0.009	17.55	0.000	10.10	0.003		
kPa	3	17.43	0.000	61.65	0.000	61.56	0.000	96.24	0.000	10.02	0.000		
Cv × Stress	1	0.077	0.783	0.749	0.393	6.509	0.016	1.068	0.309	0.824	0.371		
Cv × kPa	3	1.247	0.309	0.504	0.682	1.016	0.398	2.866	0.052	2.452	0.081		
Stress × kPa	3	1.836	0.161	3.583	0.024	1.688	0.189	8.000	0.000	5.336	0.004		
Cv × Stress × kPa	3	0.016	0.997	0.567	0.641	2.361	0.090	0.353	0.787	1.070	0.376		

4 Discussion

Understanding of the mechanisms, the plant can adopt to withstand drought and salinity stress is crucial for maintenance of crop productivity under unfavorable conditions. Stress effects on plant growth and performance are genotype-dependent but also depend on the severity and type of stress. Sesame, a moderately salt- and drought-tolerant crop [25, 26] is often cultivated under arid and semi-arid conditions.

Salinity and drought differentially affected shoot and root growth of sesame with more stress tolerance of cv. Shnd than Sohg. The less aggressive impact of salinity than drought on foliage growth of sesame can be viewed in light of the hypothesis that the accumulating salt ions can aid in lowering of water potential of plant tissues and hence allowing efficient water absorption under stress [27]. The beneficial effect of mild salinity to foliage growth and the lesser dehydrating effect of salinity

Table 5

Three-way ANOVA showing the effect of the main factors: sesame cultivar (Cv), type of stress (Stress) and osmotic potential of the medium (kPa) and their interactions on the content of carbohydrate fractions of sesame leaves

Source of variation	df	Soluble sugars		Starch		Hemicellulose		Pectic substances	
		F	P	F	P	F	P	F	P
Cv	1	31.48	0.000	0.243	0.625	181.9	0.000	2.811	0.103
Stress	1	0.642	0.429	0.513	0.479	4.795	0.036	6.783	0.014
kPa	3	27.92	0.000	79.90	0.000	58.64	0.000	11.74	0.000
Cv × Stress	1	4.540	0.041	4.050	0.053	64.88	0.000	1.715	0.200
Cv × kPa	3	13.18	0.000	13.63	0.000	64.70	0.000	7.530	0.001
Stress × kPa	3	0.216	0.885	3.138	0.039	4.750	0.008	3.307	0.032
Cv × Stress × kPa	3	2.298	0.096	1.709	0.185	8.668	0.000	0.699	0.559
		Soluble sugars ratio		Starch ratio		Hemicellulose ratio		Pectic substances ratio	
		F	P	F	P	F	P	F	P
Cv	1	31.18	0.000	0.995	0.326	165.1	0.000	0.202	0.656
Stress	1	2.344	0.136	0.016	0.902	1.868	0.181	0.136	0.715
kPa	3	41.88	0.000	31.97	0.000	10.81	0.000	28.13	0.000
Cv × Stress	1	16.97	0.000	36.93	0.000	81.70	0.000	0.747	0.394
Cv × kPa	3	47.87	0.000	10.61	0.000	28.92	0.000	0.942	0.432
Stress × kPa	3	3.677	0.022	1.468	0.242	0.968	0.420	0.465	0.709
Cv × Stress × kPa	3	6.934	0.001	7.246	0.001	12.54	0.000	0.552	0.651

than drought on root is in line with this hypothesis. However, the stronger dehydrating effect of salinity than drought on shoot suggests different patterns of osmotic susceptibility between shoot and root. In contrast to its more aggressive effect on foliage biomass, drought improved root biomass of sesame. However, decreased root volume and root hydraulic conductivity of three wheat varieties by PEG-drought stress and NaCl-salinity stress has been reported [28]. The reduction in root volume along with increased root density by drought reported by [29] implies either less severe impact of drought on root biomass than on root volume or even enhanced root biomass production by drought.

A functional equilibrium is always achieved by plants to balance their biomass allocation between root and shoot [1]. Accordingly, it is expected that plants invest more biomass in the root at the expense of foliage under water deficit to optimize acquisition of water and nutrients and to restrict transpirational water loss. The signaling processes regulating this balance may involve sugars, phytohormones and small RNAs [30]. The present work suggests that salinity favors allocation of plant biomass to the foliage at the expense of root while drought led to the opposite effect. However, this pattern was subjected to genotypic intervention; whereas the favored allocation of plant biomass to the shoot under salinity occurred in favor of either leaves (Sohg) or stem (Shnd), the favored biomass allocation to root under drought occurred at the expense of either stem and leaves (Sohg) or only leaves (Shnd). Drought has been claimed to increase root to shoot biomass ratio of plants [31] and specifically to favor allocation of plant biomass to root and stem at the expense of leaves [32]. By contrast, it has been claimed that root growth is less salt-sensitive than shoot growth, thus leading to increased root/shoot ratio of salinized plants, as has been reported by [33] and [34]. Hence, it seems that the effect of stress on biomass allocation is controversial and

depends on the experimental conditions and genotype [35]. Leaf weight ratio has been reported to decrease in *Medicago sativa* [36] but to increase in *Setaria viridis* [37] by drought.

In contrast to the inherent horizontal leaf orientation of Shnd with marginal effect of stress, the vertical leaf orientation of Sohg was differentially affected by salinity and drought; being more vertical under salinity but less vertical under drought. This fact lends support to the observation of preferred conservation of leaf biomass by Sohg and of stem biomass by Shnd under stress. The positive correlations (under salinity stress) and the negative correlations (under drought stress) between leaf angle and the rates of photosynthesis and transpiration observed only in Sohg (Fig. 9) implies that, in the stress-sensitive Sohg, horizontal leaf orientation can improve gas exchange under salinity stress but vertical leaf orientation is appropriate under drought stress. Leaf orientation is an important factor in regulation of plant carbon–water–energy nexus to optimize photosynthesis and light interception under the impact of abiotic stress. However, it has been claimed that, in general, leaves are vertical in hot dry environments but more horizontal in mesic and light-limited environments [38]. Unfavorable environmental conditions can evoke leaf movements, such as reversible epinastic responses [39], which can aid in plant adaption to stress conditions via protecting the leaves from photo-inhibition by reducing the leaf area exposed to solar irradiation [40].

The differential effect of salt stress and drought stress on photosynthetic pigments of sesame leaves was manifested as stronger negative impact of salinity on Sohg than Shnd, versus a mild reduction (Sohg) or even improvement (Shnd) by drought. The increased photosynthetic pigments of *Cynanchum acutum* leaves under drought was attributed to drought-induced P deprivation [32]. Furthermore, abiotic stress can minimize the genotypic gap in chlorophyll content between sesame cultivars that is approximating the less green Shnd to the greener Sohg. The symptoms of salt stress on plants include chlorosis and scorching of leaves [41]. Chlorophyll content of leaves was decreased under both salinity and drought stress in *Robinia pseudoacacia* [42] and under drought in wheat [43], canola [44] and barley [45]. However, the effect of salinity on chlorophyll content of wheat leaves was genotype-dependent, being promotive in salt-tolerant genotypes but inhibitory in salt-sensitive genotypes [46]. The effect of stress on partitioning of photosynthetic pigments among Chl a, Chl b and carotenoids was particularly evident in Shnd, in which stress, can increase Chl a proportion at the expense of carotenoids. In accordance with the present findings, Chl a and Chl b contents were subjected to differential impact of salinity in rice leaves [47] and of drought in wheat [43].

The present findings suggest stronger impact of salinity than drought on gas exchange of sesame leaves, a pattern that contradicts the response of foliage growth. Photosynthesis rate (A), transpiration rate (E) and stomatal conductance (Gs) are positively related to water potential of the medium [48]. Lowered photosynthesis under stress is usually linked to stomatal closure but can also result from impaired biochemical and photochemical constraints [49]. The intimate association between the patterns of retardation in A, E and Gs under the impact of salinity and drought indicates that the reduced photosynthetic activity under stress can be attributed to the stress-induced stomatal closure and lowering of stomatal conductance (Fig. 9). The fact that A, E and Gs are positively correlated with each other but negatively correlated with Ci, along with the coincidence of minimal Ci with maximal A and Gs at mild salinity (Fig. 6) implies that stress can inhibit photosynthetic efficiency

without effect on or even enhancement of respiration but mild salinity can enhance photosynthetic efficiency through increasing stomatal conductance. In agreement with the present findings, drought stress has been found to induce stomatal closure with consequent severe inhibition in photosynthesis along with mild inhibition or even promotion in respiration [50, 32].

Stomatal movement under stress can control photosynthesis and transpiration in a way to increase water use efficiency. The present findings suggest that cv. Sohg with high photosynthesis potential exhibited marked drought robustness; in contrast to cv. Shnd of low photosynthesis potential, which although benefited from mild stress experienced more susceptibility to severe drought. Transpiration rate, in accordance with Gs, benefited from mild salinity in Shnd and mild drought in Sohg but was reduced under severe stress, with stronger impact of salinity than drought. According to the present finding, abiotic stress seems to reduce the water use efficiency (A/E ratio) of sesame with stronger impact of salinity on Sohg and of drought on Shnd. It has been reported that water-use efficiency was increased in *Robinia pseudoacacia* under salinity and drought stress [42] and in *Vicia faba* [34] under salinity stress. The lowered water use efficiency of sesame under severe drought, observed in

the present work, can be attributed either to greater sensitivity of the photosynthetic machinery than transpiration to water deficit or to progression of water loss despite of stomatal closure, probably via cuticular transpiration as proposed by [51]. Stomatal closure is a physiological adaptation to water deficit to avoid desiccation arising from transpirational water loss [52]; but the closed stomata will certainly inhibit photosynthesis by cutting down the influx of CO₂ to the mesophyll with the probability of continuation of water loss via alternative avenues such as the cuticular transpiration.

It has been claimed that abiotic stress affects cell wall composition and production of compatible solutes [53]. The inhibited photosynthesis, concomitant with the unaffected or favored respiration under abiotic stress results in lowering of carbohydrate reserves of sesame leaves, which can be assigned to the decline in the major carbohydrate fraction (starch), followed by soluble sugars with marginal changes in pectic substances. However, the two sesame cultivars adopted different patterns of carbohydrate fractionation in response to stress. In Sohg, abiotic stress induced reductions in proportions soluble sugars and starch in favor of either pectic substances (salinity) or pectic substances and hemicellulose (drought). By contrast, in Shnd, abiotic stress increased the proportions of soluble sugars and pectic substances at the expense of starch and hemicellulose. Thus, the shared stress-induced response, irrespective of the genotype and type of stress, is the reduced proportion of starch in favor of pectic substances. The increased proportions of soluble sugars and pectic substances in Shnd under the impact of drought stress can aid in drought tolerance by contributing either to osmotic adjustment (soluble sugars) or by increasing cell wall elasticity (pectic substances). Osmotic and elastic adjustment are alternative strategies for a species to acclimate to water stress. Cells with highly elastic walls contain more water at full turgor; hence, their volume can decrease more before the turgor-loss point is reached. Elasticity of the cell wall depends on the chemical interactions between cell wall components [1]. It has been proposed that pectins, the major polyanionic polysaccharide in the walls of growing cells, play a critical role in cell wall expansion [54]. However, the role of soluble sugars in osmotic adjustment under stress is evident only in Shnd, despite the stronger impact of salinity and drought on leaf carbohydrate content of Shnd than Sohg.

Conclusions

The difference in stress-resistance was marked between the two sesame cultivars, with stronger aggressive impact of drought than salinity on foliage growth, which points to the role of salt ions in facilitating water absorption via lowering of water potential of foliage. Salinity shifted allocation of plant biomass to the foliage (specifically leaves of Sohg and stem of Shnd) at the expense of root; meanwhile, drought favors allocation of plant biomass to the root at the expense of stem of Sohg and leaf of Shnd. Thus, despite the contrasting effect of salinity and drought on rootage, Sohg seems to conserve leaves under stress but Shnd conserves stem. In a way to improve gas exchange, the sensitive Sohg adopts horizontal leaf orientation under salinity stress but vertical leaf orientation under drought stress. Abiotic stress narrowed the genotypic gap in chlorophyll content between sesame cultivars that is approximating the less green Shnd to the greener Sohg. In contrast to the influence on foliage growth, the impact of salinity on gas exchange of leaves was stronger than that of drought. The reduced photosynthetic activity under stress is related to stomatal closure and was accompanied with either no effect on or enhancement of respiration; however, mild salinity can enhance photosynthesis through increasing stomatal conductance. The photosynthetically less efficient genotype (Shnd) was more impacted by drought but at the same time, benefited from mild stress. Both E and Gs, benefited from mild salinity in Shnd and mild drought in Sohg but were subjected to stronger impact of salinity than drought. Stress reduced water use efficiency of sesame with stronger impact of salinity on Sohg and of drought on Shnd. The lowered water use efficiency can be attributed either to greater sensitivity of the photosynthetic machinery than transpiration to water deficit or to progression of water loss despite of stomatal closure, probably via cuticular transpiration. The stress-induced lowering in leaf carbohydrate reserves can be assigned to the decline in starch, either along with soluble sugars in favor of pectic substances (in Sohg) or of starch in favor of soluble sugars and pectic substances (in Shnd). The increased proportions of soluble sugars and pectic substances in Shnd under drought can aid in drought tolerance by contributing either to osmotic adjustment (soluble sugars) or to increased cell wall elasticity (pectic substances).

Declarations

Acknowledgments

The authors acknowledge the Oil Crops Research Department, Field Crops Research Institute (FCRI), Agricultural Research Center at Giza, Egypt for providing seeds of the two sesame cultivars.

Funding

This work was supported by a research grant from Damietta University, Egypt as a part of M.Sc. program (Grant No. 1259/11/2021).

Open access funding provided by The Science, Technology & Innovation Funding Authority (STDF) in cooperation with The Egyptian Knowledge Bank (EKB).

Author contributions

Conceptualization: TME; Methodology: SNA, SHA; Formal analysis and investigation: SNA, NMH; Writing - original draft preparation: SNA, TME; Writing - review and editing: TME, NMH; Funding acquisition: SHA; Resources: SNA; Supervision: TME, NMH. All authors read and approved the final manuscript.

Declaration of competing interest

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

Data availability

All data of this study are cited within the paper; raw data and calculations will be available on request.

Permission to collect the seeds

The manuscript is a purely eco-physiological study on performance of two sesame (*Sesamum indicum* L.) cultivars and does not include any human participants, groups of humans or animal subjects.

Seeds of cultivars Sohag 1 (Sohg) and Shandaweel 3 (Shnd) of sesame (*Sesamum indicum* L.) were obtained from the Agricultural Research Center (ARC), Egypt. The two experimental sesame cultivars are national cultivars, produced and released by Oil Crops Research Department, Field Crops Research Institute (FCRI), Agricultural Research Center (ARC), Ministry of Agricultural and Land Reclamation, Egypt according to The International Union for the Protection of New Varieties of Plants (UPOV) guideline (Egypt is a member of UPOV) and the Intellectual Property Rights (IPR) national law. The acquired names "Sohag 1" and "Shandaweel 3" are given by the breeder program of ARC and are related to national districts of Egypt.

Ethics declaration: not applicable.

Consent to publish declaration: not applicable.

Consent to participate declaration: not applicable.

Clinical Trial Number: not applicable.

References

1. Lambers H, Oliveira RS. Plant water relations. In: Lambers H, Oliveira RS, editors. Plant Physiological Ecology. Cham, Switzerland: Springer International Publishing; 2019. pp. 187–263.
2. Bahmani K, Noori SAS, Darbandi AI, Akbari A. Molecular mechanisms of plant salinity tolerance: a review. Aust J Crop Sci. 2015;9:321–36.
3. George E, Horst WJ, Neumann E. (2012). Adaptation of plants to adverse chemical soil conditions. In: Marschner P, editor. Marschner's Mineral Nutrition of Higher Plants, 3rd edn. Academic Press; 2012. pp. 409–472.

4. Ismail AM, Heuer S, Thomson MJ, Wissuwa M. Genetic and genomic approaches to develop rice germplasm for problem soils. *Plant Mol Biol.* 2007;65:547–70.
5. El-Katony TM, Deyab MA, El-Adl MF, Ward FME. The aqueous extract and powder of the brown alga *Dictyota dichotoma* (Hudson) differentially alleviate the impact of abiotic stress on rice (*Oryza sativa* L). *Physiol Mol Biology Plants.* 2020;26:1155–71. <https://doi.org/10.1007/s12298-020-00805-2>.
6. Le TS, Harper R, Dell B. Application of remote sensing in detecting and monitoring water stress in forests. *Remote Sens.* 2023;15:3360.
7. Singh P, Choudhary KK, Chaudhary N, Gupta S, Sahu M, Tejaswini B, Sarkar S. Salt stress resilience in plants mediated through osmolyte accumulation and its crosstalk mechanism with phytohormones. *Front Plant Sci.* 2022;13:1006617.
8. Munns R, Gilliam M. Salinity tolerance of crops—what is the cost? *New Phytol.* 2015;208:668–73.
9. Bernstein N, Eshel A, Beeckman T. Effects of Salinity on Root Growth. *Plant Roots: The Hidden Half.* Tylor Frances. 2013;848. <https://doi.org/10.1201/b14550>.
10. Wang M, Zheng Q, Shen Q, Guo S. The critical role of potassium in plant stress response. *Int J Mol Sci.* 2013;14:7370–90.
11. Yancey PH. (1994). Compatible and counteracting solutes. In: Strange K ed. *Cellular and Molecular Physiology of Cell Volume Regulation.* Boca Raton, FL: CRC Press; 1994. Pp. 81–109.
12. Kumari A, Sharma B, Singh BN, Hidangmayum A, Jatav HS, Chandra K, Singhal RK, Sathyanarayana E, Patra A, Mohapatra KK. Physiological mechanisms and adaptation strategies of plants under nutrient deficiency and toxicity conditions. In: Aftab T, Roychoudhury A, editors. *Plant perspectives to global climate changes.* London: Elsevier; 2022. pp. 173–94.
13. Pan T, Liu M, Kreslavski VD, Zharmukhamedov SK, Nie C, Yu M, Kuznetsov VV, Allakhverdiev SI, Shabala S. Non-stomatal limitation of photosynthesis by soil salinity. *Crit Rev Environ Sci Technol.* 2020;51:791–825. <https://doi.org/10.1080/10643389.2020.1735231>.
14. Tesfaye T, Tesfaye K, Keneni G, Ziyomo C, Alemu T. Genetic diversity of sesame (*Sesamum indicum* L.) using high throughput diversity array technology. *J Crop Sci Biotechnol.* 2022;25:359–71.
15. Rout K, Yadav BG, Yadava SK, Mukhopadhyay A, Gupta V, Pental D, Pradhan AK. QTL landscape for oil content in *Brassica juncea*: analysis in multiple bi-parental populations in high and 0 erucic background. *Front Plant Sci.* 2018;9:1448. <https://doi.org/10.3389/fpls.2018.01448>.
16. Liu HM, He MK, Yao YG, Qin Z, Cai XS, Wang XD. Pectic polysaccharides extracted from sesame seed hull: Physicochemical and functional properties. *Int J Biol Macromol.* 2021;192:1075–83. <https://doi.org/10.1016/j.ijbiomac.2021.10.077>.
17. Morris JB, Wang ML, Tonniss BD. Variability for oil, protein, lignan, tocopherol, and fatty acid concentrations in eight sesame (*Sesamum indicum* L.) genotypes. *Ind Crops Prod.* 2021;164:113355. <https://doi.org/10.1016/j.indcrop.2021.113355>.
18. Majdalawieh AF, Massri M, Nasrallah GK. A comprehensive review on the anti-cancer properties and mechanisms of action of sesamin, a lignan in sesame seeds (*Sesamum indicum*). *Eur J Pharmacol.* 2017;815:512–21. <https://doi.org/10.1016/j.ejphar.2017.10.020>.
19. Money NP. Osmotic pressure of aqueous polyethylene glycols: Relationship between molecular weight and vapor pressure deficit. *Plant Physiol.* 1989;91:766–9. <https://doi.org/10.1104/pp.91.2.766>.
20. Slatver RO, McIlroy IC. *Practical Microclimatology.* C.S.I.R.O., Melbourne; 1961. 310 pp.
21. Wellburn AR, Lichtenthaler H. (1984). Formulae and program to determine total carotenoids and chlorophylls a and b of leaf extracts in different solvents. In: Sybesma C, editor. *Advances in photosynthesis research*, Vol. II, Martinus Nijhoff/Dr W. Junk Publ. The Hague – Boston – Lancaster; 1984. pp. 9–12.
22. Chow PS, Landhäusser SM. A method for routine measurements of total sugar and starch content in woody plant tissues. *Tree Physiol.* 2004;24:1129–36.
23. Buysse JAN, Merckx R. An improved colorimetric method to quantify sugar content of plant tissue. *J Exp Bot.* 1993;44:1627–9.

24. Southgate DAT. Determination of carbohydrates in foods II. —Unavailable carbohydrates. J Sci Food Agric. 1969;20:331–5.
25. El Harfi M, Hanine H, Rizki H, Latrache H, Nabloussi A. Effect of drought and salt stresses on germination and early seedling growth of different color-seeds of sesame (*Sesamum indicum*). Int J Agric Biol. 2016;18:1088–94. <https://doi.org/10.17957/IJAB/15.0145>.
26. Hussaini A, Usman M, Falgore JY, Sani SS, Zakari Y, Muktar HD. A search for suitable growing environment for sesame production in Nigeria. Asian J Agricultural Ext Econ Sociol. 2020;38:18–33.
27. Zhang H, Irving LJ, McGill C, Matthew C, Zhou D, Kemp P. The effects of salinity and osmotic stress on barley germination rate: sodium as an osmotic regulator. Ann Bot. 2010;106:1027–35. 10.1093/aob/mcq204. Epub 2010 Oct 7. PMID: 20929898; PMCID: PMC2990672.
28. Fu Y, Li P, Hamani AKM, Wan S, Gao Y, Wang X. Effects of single and combined drought and salinity stress on the root morphological characteristics and root hydraulic conductivity of different winter wheat varieties. Plants. 2023;12(14):2694.
29. Sun Y, Robert CA, Thakur MP. Drought intensity and duration effects on morphological root traits vary across trait type and plant functional groups: a meta-analysis. BMC Ecol Evol. 2024;24. <https://doi.org/10.1186/s12862-024-02275-6>.
30. Dastborhan S, Kalisz A, Kordi S, Lajayer BA, Pessarakli M. Morphological, physiological, and biochemical responses of plants to drought and oxidative stresses. In: Pessarakli M, editor. Handbook of Plant and Crop Physiology. 4th ed. CRC; 2021. pp. 517–41.
31. Zhou G, Zhou X, Nie Y, Bai SH, Zhou L, Shao J, Cheng W, Wang J, Hu F, Fu Y. Drought-induced changes in root biomass largely result from altered root morphological traits: Evidence from a synthesis of global field trials. Plant Cell Environ. 2018;41:2589–99.
32. El-Katony TM, Khedr AA, Mergeb SO. Drought stress affects gas exchange and uptake and partitioning of minerals in swallowwort (*Cynanchum acutum* L). Rend Lincei Scienze Fis e Naturali. 2018;29:23–34.
33. Lovelli S, Scopa A, Perniola M, Di Tommaso T, Sofo A. Absciscic acid root and leaf concentration in relation to biomass partitioning in salinized tomato plants. J Plant Physiol. 2021;169:226–33.
34. El-Katony TM, El-Fatah A. Genotypic differences in photosynthesis and partitioning of biomass and ions in salinized faba bean. Russ J Plant Physiol. 2021;68(6):1161–72.
35. Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. New Phytol. 2012;193:30–50. <https://doi.org/10.1111/j.1469-8137.2011.03952.x>.
36. Erice G, Louahlia S, Jose Irigoyen J, Sanchez-Diaz M, Avice JC. Biomass partitioning, morphology and water status of four alfalfa genotypes submitted to progressive drought and subsequent recovery. J Plant Physiol. 2010;167:114–20. <https://doi.org/10.1016/j.jplph.2009.07.016>.
37. Mao W, Allington G, Li YL, Zhang TH, Zhao XY, Wang SK. Life history strategy influences biomass allocation in response to limiting nutrients and water in an arid system. Pol J Ecol. 2012;60:545–57.
38. Yang X, Li R, Jablonski A, Stovall A, Kim J, Yi K, Ma Y, Beverly D, Phillips R, Novick K, Xu X, Lerdau M. Leaf angle as a leaf and canopy trait: Rejuvenating its role in ecology with new technology. Ecol Lett. 2023;26:1005–20.
39. Geldhof B, Pattyn J, Eyland D, Carpentier S, Van de Poel B. A digital sensor to measure real-time leaf movements and detect abiotic stress in plants. Plant Physiol. 2021;187:1131–48.
40. Van Geest G, Van Ieperen W, Post AG, Schoutsen CGLM. Leaf epinasty in chrysanthemum: enabling breeding against an adverse trait by physiological research. Acta Hort. 2012;953:345–50.
41. Muhammad M, Waheed A, Wahab A, Majeed M, Nazim M, Liu YH, Li L, Li WJ. Soil salinity and drought tolerance: An evaluation of plant growth, productivity, microbial diversity, and amelioration strategies. Plant Stress. 2023;11:100319.
42. Fan Y, Wang J, Yan M, Wang X, Du G, Li H, Li M, Si B. Salt addition mitigate mortality risk and prolong survival of *Robinia pseudoacacia* subjected to drought stress. Agronomy. 2024; 14: 439. <https://doi.org/10.3390/agronomy14030439>.

43. Ahmad M, Waraich EA, Shahid H, Ahmad Z, Zulfiqar U, Mahmood N, Al-Ashkar I, Ditta A, El Sabagh A. Exogenously applied potassium enhanced morpho-physiological growth and drought tolerance of wheat by alleviating osmotic imbalance and oxidative damage. *Pol J Environ Stud.* 2023;32:4447–59.
44. Dawood MG, Sadak MS. Physiological role of glycinebetaine in alleviating the deleterious effects of drought stress on canola plants (*Brassica napus* L). *Middle East J Agric Res.* 2014;3:943–54.
45. Bouhraoua S, Ferioun M, Nassira S, Boussakouran A, Akhazzane M, Belahcen D, Hammani K, Louahlia S. Biomass partitioning and physiological responses of four Moroccan barley varieties subjected to salt stress in a hydroponic system. *J Plant Biotechnol.* 2023;50:115–26.
46. El-Hendawy SE, Hu Y, Schmidhalter U. Growth, ion content, gas exchange, and water relations of wheat genotypes differing in salt tolerances. *Aust J Agric Res.* 2005;56:123–34.
47. Amirjani MR. Effect of salinity stress on growth, sugar content, pigments, and enzyme activity of rice. *Int J Bot Stud.* 2011;7:73–81.
48. Meyer E, Aspinwall MJ, Lowry DB, Palacio-Mejía JD, Logan TL, Fay PA, Juenger TE. Integrating transcriptional, metabolomics and physiological responses to drought stress and recovery in switchgrass (*Panicum virgatum* L). *BMC Genomics.* 2014;15:527–42.
49. Pinheiro C, Chaves MM. Photosynthesis and drought: can we make metabolic connections from available data? *J Exp Bot.* 2011;62:869–82.
50. Jorge TF, Rodrigues JA, Caldana C, Schmidt R, Van Dongen J, Thomas-Oates J, Antonio C. Mass spectrometry-based plant metabolomics: metabolite responses to abiotic stress. *Mass Spectrom Rev.* 2016;35:620–49.
51. Kosma DK, Bourdenx B, Bernard A, Parsons EP, Lu S, Joubes J, Jenks MA. The impact of water deficiency on leaf cuticle lipids of Arabidopsis. *Plant Physiol.* 2009;151:1918–29.
52. Nilson SE, Assmann SM. The control of transpiration. Insights from Arabidopsis. *Plant Physiol.* 2007;143:19–27.
53. Dos Santos TB, Ribas AF, De Souza SGH, Budzinski IGF, Domingues DS. Physiological responses to drought, salinity, and heat stress in plants: A review. *Stresses.* 2022;2:113–35.
54. Siemianowski O, Rongpipi S, Del Mundo JT, Freychet G, Zhernenkov M, Gomez ED, Anderson CT. Flexible pectin nanopatterning drives cell wall organization in plants. *JACS Au.* 2024;4:177–88.

Figures

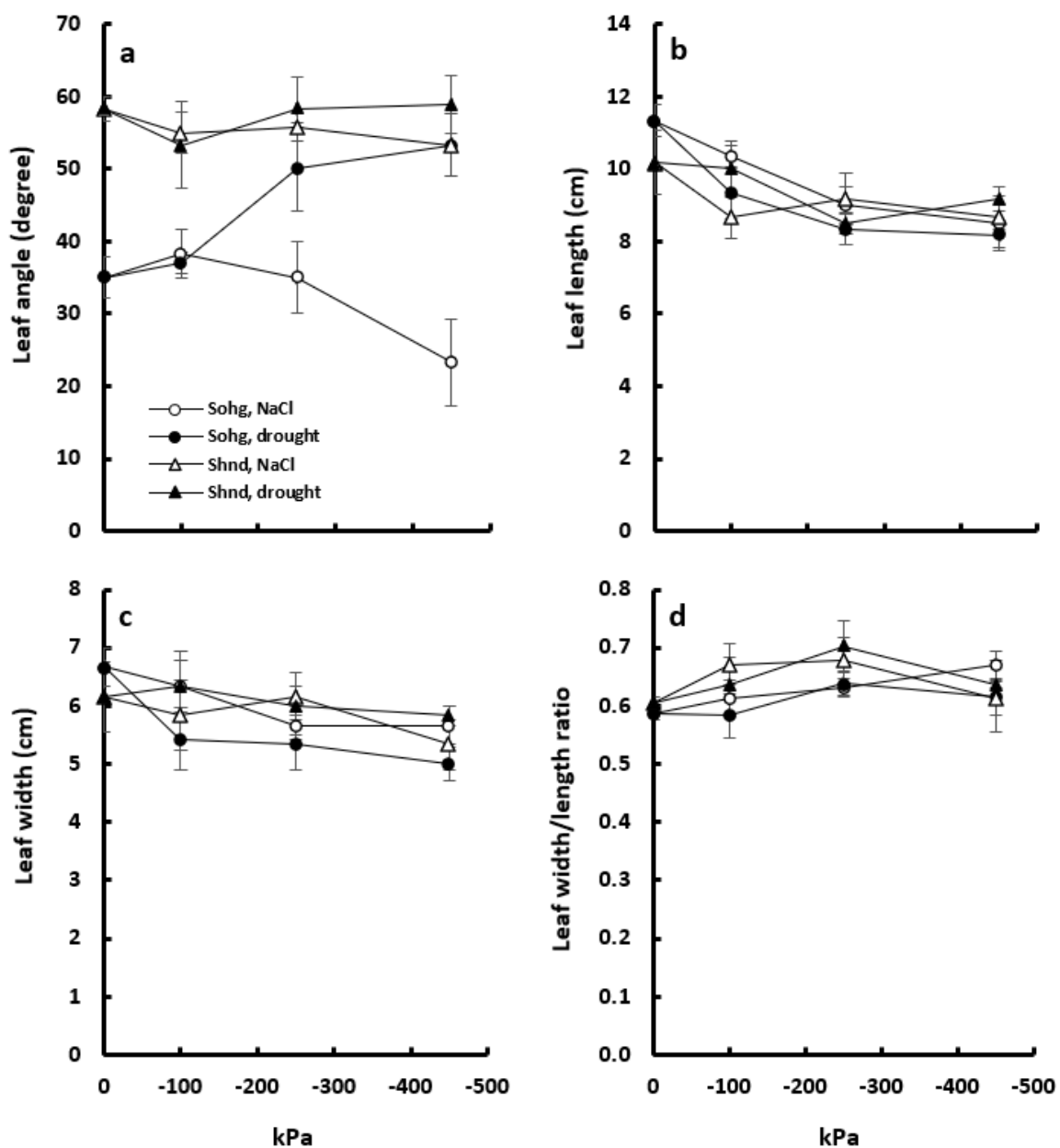


Figure 1

Effect of salt stress and drought stress on leaf angle (a), leaf length (b), leaf width (c) and leaf width/length ratio (d) of cvs Sohg and Shnd of sesame. Each value is the mean of three replicates $\pm$ SE

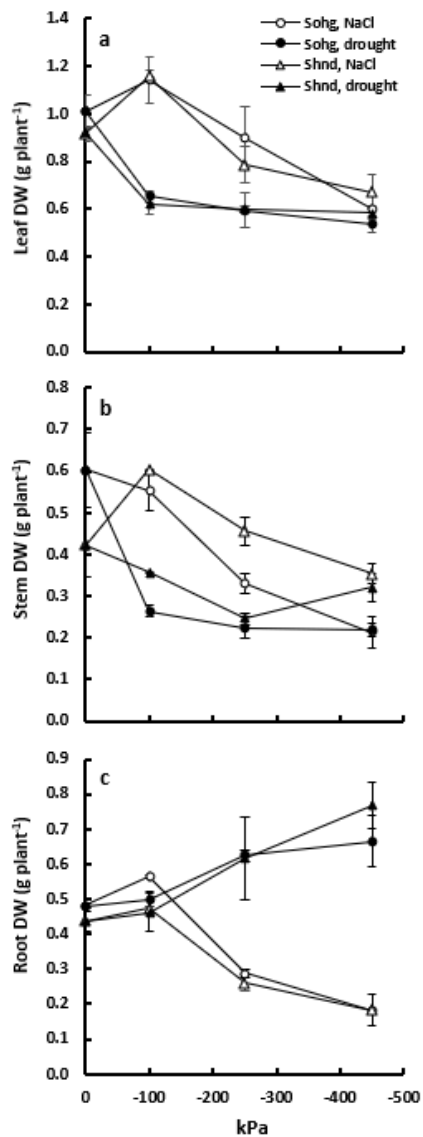


Figure 2

Effect of salt stress and drought stress on dry weight of leaves (a), stem (b) and root (c) of cvs Sohg and Shnd of sesame. Each value is the mean of three replicates $\pm$ SE

Table 3 Effect of salt stress and drought stress on water content of shoot and root of cvs Sohg and Shnd of sesame. Each value is the mean of three replicates $\pm$ SE. Means with common letters are not significantly different at $p \leq 0.05$

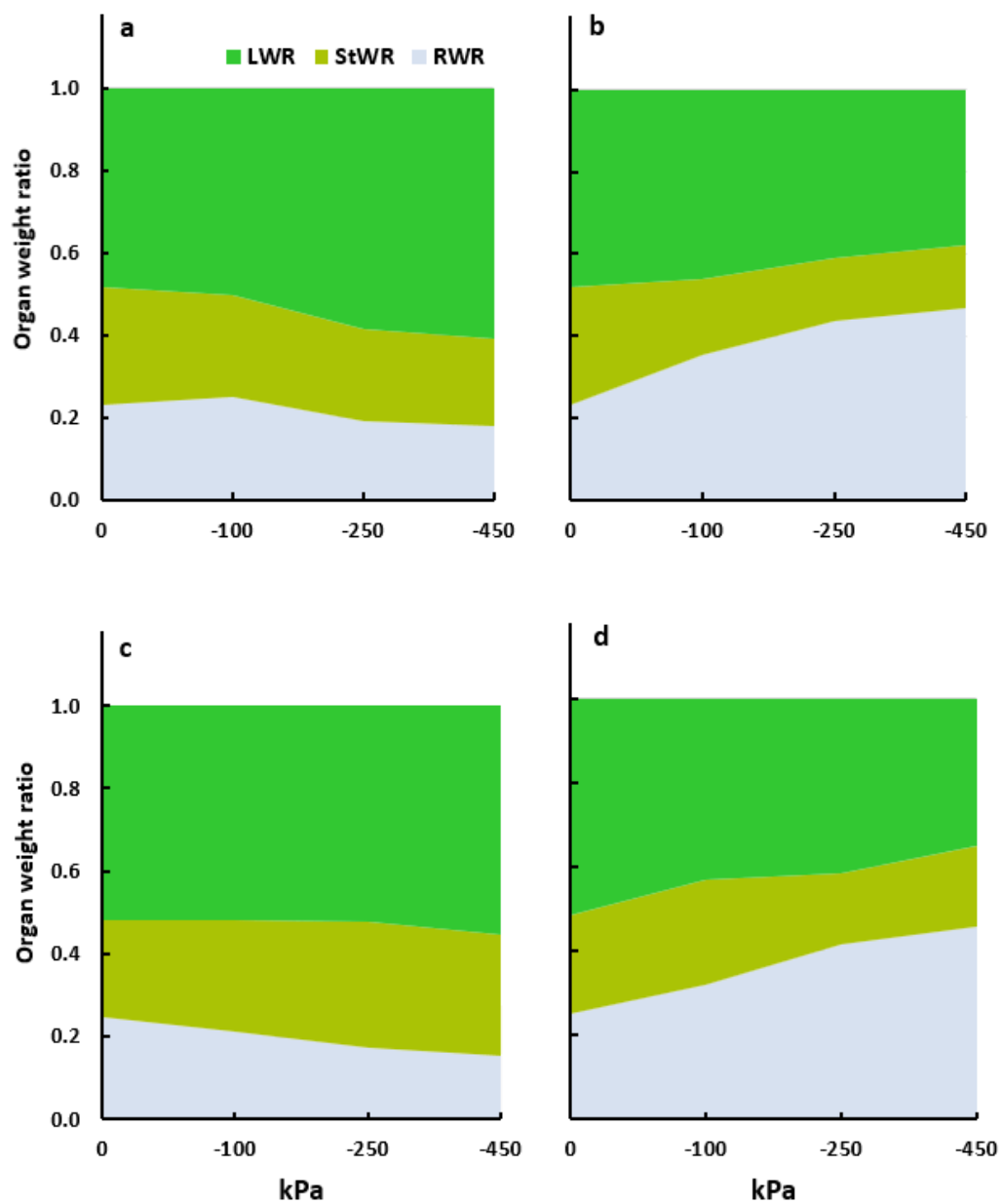


Figure 3

Effect of salt stress and drought stress on biomass partitioning among leaves, stem and root of Sohg NaCl (a), Sohg drought (b), Shnd NaCl (c) and Shnd drought (d) of sesame. Each value is the mean of three replicates

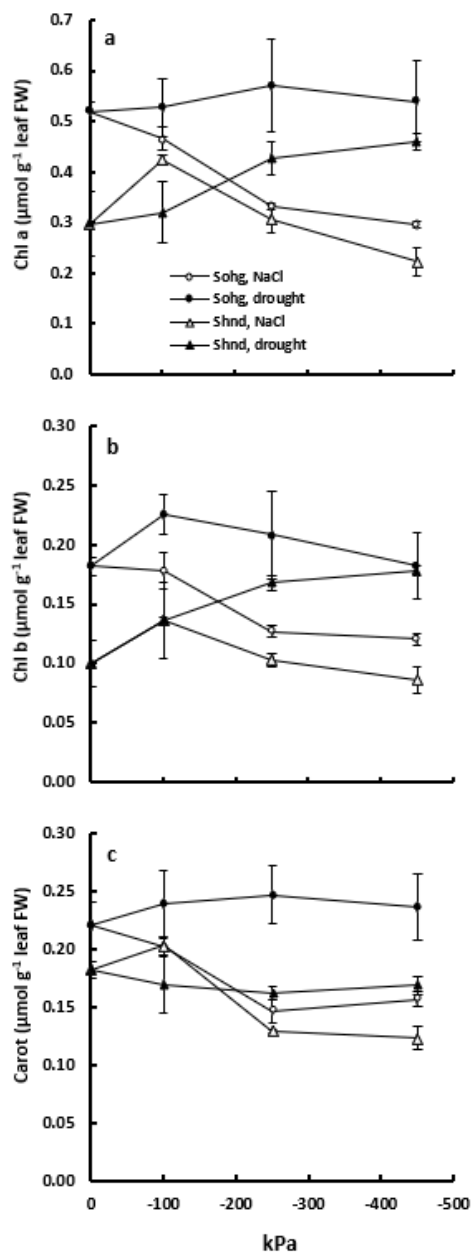


Figure 4

Effect of salt stress and drought stress on the content of Chl a (a), Chl b (b) and Carot (c) of cvs Sohg and Shnd of sesame leaves. Each value is the mean of three replicates $\pm$ SE

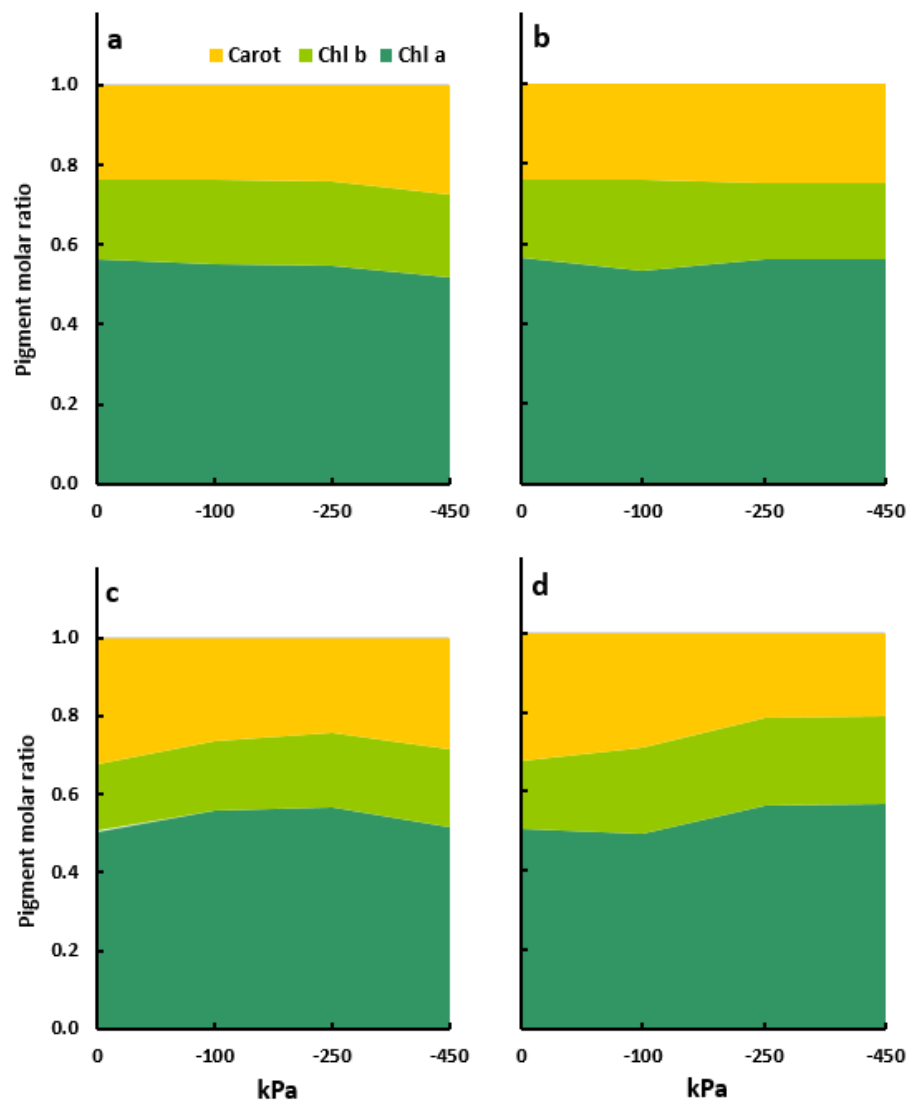


Figure 5

Effect of salt stress and drought stress on pigment partitioning among Chl a, Chl b and Carot of Sohg NaCl (a), Sohg drought (b), Shnd NaCl (c) and Shnd drought (d) of sesame. Each value is the mean of three replicates

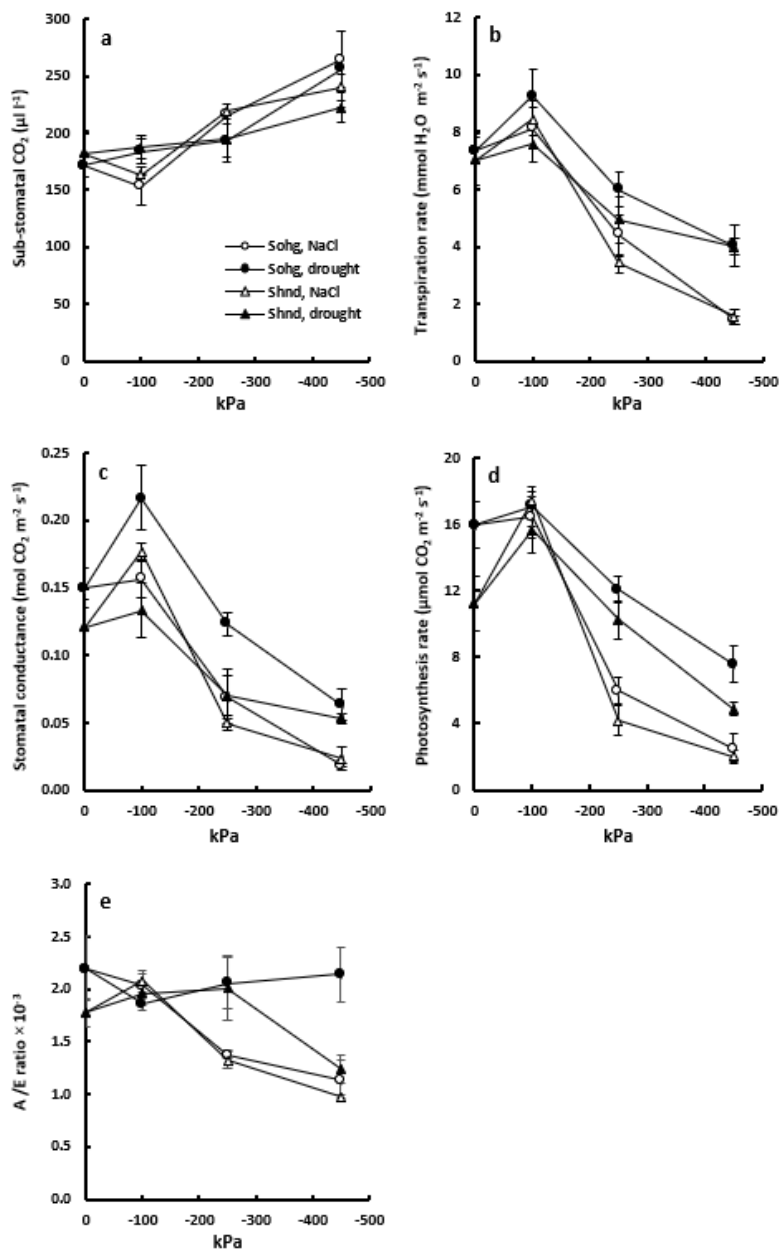


Figure 6

Effect of salt stress and drought stress on substomatal [CO₂] (a), transpiration rate (b), stomatal conductance (c), photosynthesis rate (d) and water use efficiency in terms of the A/E ratio (e) of cvs Sohg and Shnd of sesame. Each value is the mean of three replicates ± SE

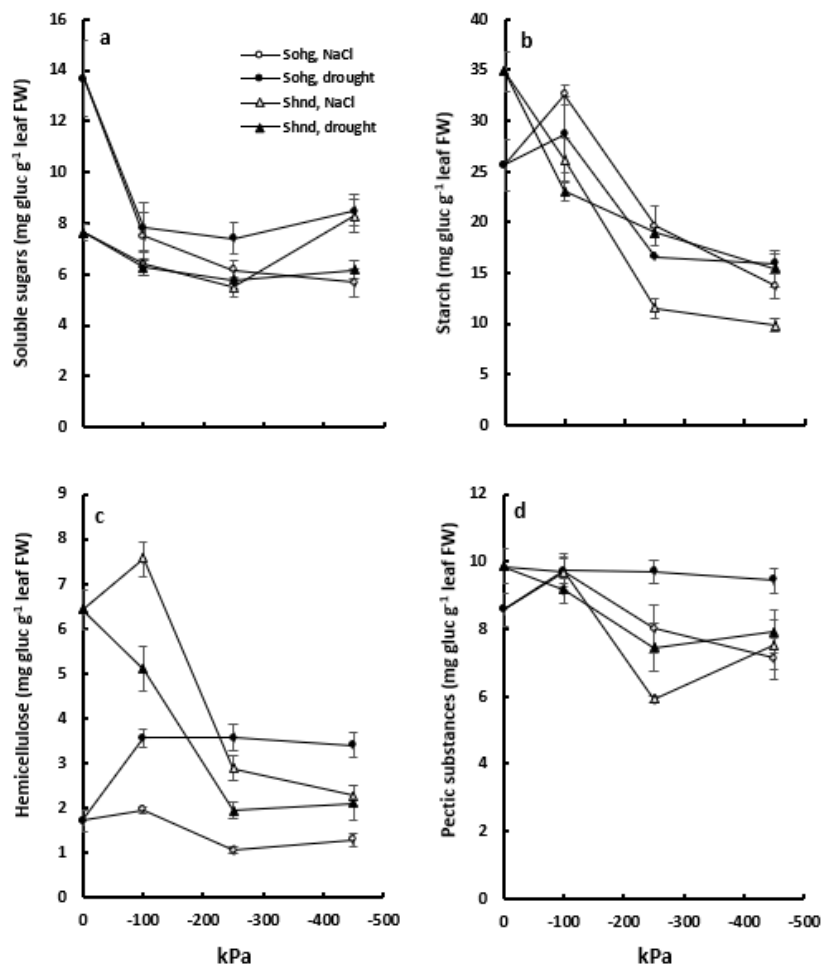


Figure 7

Effect of salt stress and drought stress on the content of soluble sugars (a), starch (b), hemicellulose (c) and pectic substances (d) in the leaves of cvs Sohg and Shnd of sesame. Each value is the mean of three replicates $\pm$ SE

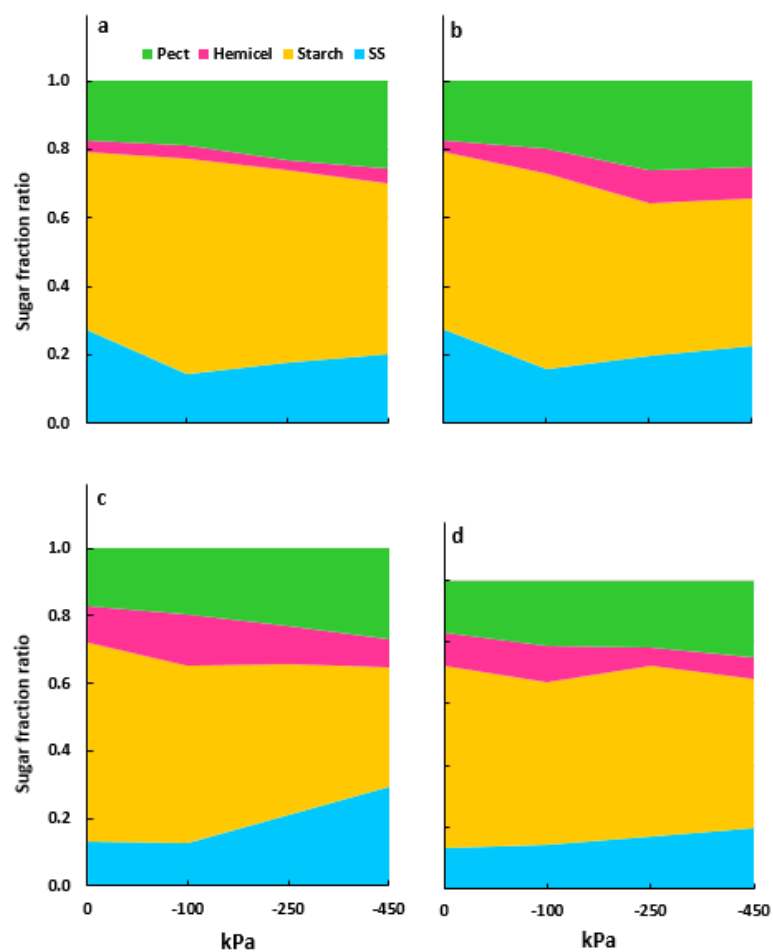


Figure 8

Effect of salt stress and drought stress on carbohydrate partitioning among soluble sugars, starch, hemicellulose and pectic substances in the leaves of Sohgh NaCl (A), Sohgh drought (B), Shnd NaCl (C) and Shnd drought (D) of sesame. Each value is the mean of three replicates

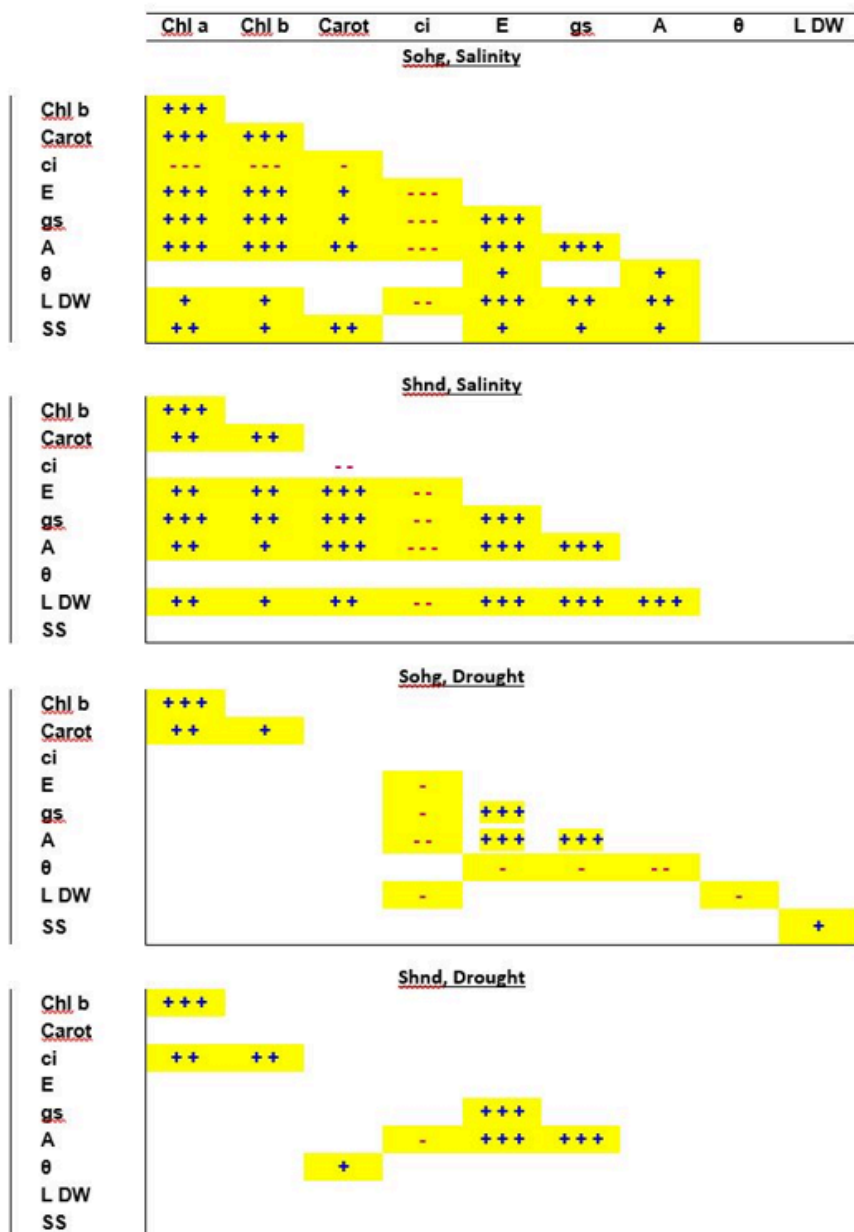


Figure 9

Correlation analysis showing the relationships between gas exchange measurements, leaf angle (θ) and leaf biomass of cvs. Sohg and Shnd of sesame under salinity stress and drought stress. +++ and --- denote very highly significant ($P < 0.001$) positive and negative correlation, respectively; ++ and -- highly significant ($P < 0.01$) correlation, + and - just significant ($P < 0.05$) correlation