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Evaluation and selection of sesame mutants (*Sesamum indicum* L.) for optimal nutritional profiles in seeds under field drought conditions☆

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Abstract – Sesame (*Sesamum indicum* L.) is a crucial oilseed crop, valued for its nutritional qualities and resilience to environmental stress. However, as drought and global temperatures increase, sesame cultivation is increasingly threatened. While sesame seeds are widely consumed in African and Asian countries, a few studies explore the drought impact on seed nutritional composition, focusing instead on sesame oil. This study addresses this gap by evaluating the nutritional profiles of seeds from 11 M_4 mutants and their wild-type parents, cultivated under field water deficit conditions (50 % of control irrigation) at two distinct locations, Taoujdate and Afourare, in Morocco, in 2021. Targeted traits include seed moisture, ash content, oil content, total polyphenols, anthocyanins, flavonoids, total amino acids, and antioxidant activity. Data analysis revealed that specific mutants responded favorably to water deficit, with increased levels of polyphenols, anthocyanins, antioxidant activity, oil content, and moisture. Notably, mutant ML2-68 showed high ash content (9.53 %) and stability, ideal for diverse environments. ML2-72 maintained high oil content (49.05 %), total amino acids (14.46 mg GlyE/g), anthocyanins (4.51 mg/g), and moisture (5.08 %), while US2-6 excelled in phenolic compound (25.13 mg/g) accumulation and free radical scavenging (96.09 %), suggesting health benefits. These results position genotypes ML2-68, ML2-72, US2-7, and US2-6 as promising for enhancing sesame crop nutrition and stability in challenging environments, supporting efforts to develop drought-resilient varieties.

Keywords: Drought stress / mutant / nutritional profile / resilience / sesame seeds

Résumé – Sélection de mutants de sésame (Sesamum indicum L.) pour des profils nutritionnels optimaux des graines en conditions de sécheresse au champ. Le sésame (*Sesamum indicum* L.) est une culture oléagineuse essentielle, réputée pour ses qualités nutritionnelles et sa résilience aux stress environnementaux. Avec l'augmentation de l'aridité et des températures mondiales, la culture du sésame est de plus en plus menacée par la sécheresse. Malgré la consommation répandue des graines de sésame dans les pays africains et asiatiques, les recherches portant sur l'impact de la sécheresse sur leur composition nutritionnelle sont rares, en comparaison aux études sur l'huile de sésame. Cette étude vise à combler cette lacune en évaluant les profils nutritionnels des graines de sésame issues de 11 mutants M_4 et de leurs parents de type sauvage, conduits au champ dans des conditions de déficit hydrique (irrigation réduite à 50 % du témoin) dans deux localités distinctes, Taoujdate et Afourare, au Maroc, en 2021. Les caractères ciblés incluent la teneur en humidité, la teneur en cendres, la teneur en huile, les polyphénols totaux, les

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☆ Contribution to the Topical Issue "Adapting to climate change / Adaptation au changement climatique".

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anthocyanines, les flavonoïdes, les acides aminés totaux et l'activité antioxydante des graines. L'analyse des données a montré que certains mutants réagissaient positivement au déficit hydrique, avec des augmentations des niveaux de polyphénols, anthocyanines, activité antioxydante, teneur en huile et humidité des graines. Parmi eux, le mutant ML2-68 s'est révélé particulièrement robuste, présentant la teneur en cendres la plus élevée (9,53 %) et une grande stabilité, le rendant bien adapté à la culture dans divers environnements. ML2-72 s'est distingué par le maintien de niveaux élevés en teneur en huile (49,05 %), acides aminés totaux (14,46 mg GlyE/g), anthocyanines (4,51 mg/g) et humidité (5,08 %). US2-6 s'est démarqué par son accumulation significative de composés phénoliques (25,13 mg/g) et sa capacité supérieure de piégeage des radicaux libres (96,09 %), soulignant ses potentiels bienfaits pour la santé. Ces résultats indiquent que les génotypes tels que ML2-68, ML2-72, US2-7 et US2-6 sont prometteurs pour l'amélioration de la valeur nutritionnelle et de la stabilité de la culture du sésame dans divers environnements, notamment les milieux difficiles. Cette recherche ouvre de nouvelles perspectives pour l'amélioration de la qualité nutritionnelle des cultures de sésame, en mettant en avant l'importance de poursuivre les efforts pour développer des variétés résistantes à la sécheresse.

Mots-clés : Graines de sésame / mutant / profil nutritionnel / résilience / sécheresse

Highlights

- Identification of sesame mutants with enhanced nutritional profiles under drought conditions.
- The mutant line ML2-72 shows high oil, amino acids, anthocyanins, and moisture content, making it ideal for varied environments.
- ML2-68, US2-7, and US2-6 mutants demonstrate stability and potential health benefits through high flavonoid and phenolic content.
- These genotypes provide promising germplasm for the development of drought-tolerant and nutrient-rich sesame cultivars.

1 Introduction

Sesame is a time-honored oilseed crop, extensively cultivated in various regions, including arid and semi-arid areas. It is renowned for its high and diversified oil content (Zahran *et al.,* 2020), ranging from 38 % to 60 %, which is rich in unsaturated essential fatty acids and low in saturated fatty acids (Chen *et al.,* 2023). Additionally, sesame seeds are a valuable source of protein (20–32 %), carbohydrates (20–27 %), fiber (9–11 %), and antioxidants such as sesamin and sesamol (Dravie *et al.,* 2020). The seeds are widely used in culinary applications, including cooking oil, cakes, sweets, pastes, and flour, owing to their rich nutritional profile, which includes essential minerals, amino acids (*e.g.*, valine, methionine, tryptophan), lignans, vitamins, niacin, and a distinctive roasted flavor (Dravie *et al.,* 2020). Beyond their culinary uses, sesame seeds have a long history of medicinal use, particularly in oriental cultures (Wang *et al.,* 2023).

Water scarcity is a critical environmental stressor that affects plant growth and development, often limiting crop production. Although sesame is more resilient to water scarcity than many other oilseed crops, it experiences significant declines in productivity and quality under severe drought conditions (Ebrahimian *et al.*, 2019). Drought stress has been shown to significantly impact the oil content, protein levels, sesamin, sesamolin, polyphenols, and antioxidant capacity of sesame seeds (Hoyos *et al.*, 2024). However, some studies, such as that by Ozkan and Kulak (2013), suggest that drought may not influence the oil yield and mineral contents (Ca, Mg, K, Na) of sesame seeds. Studies indicate that drought stress can lead to reductions in oil content and fatty acids such as linoleic, linolenic, and palmitic acids (Ozkan and Kulak, 2013; Dossa *et al.*, 2017; Ebrahimian *et al.*, 2019; Mahdavi *et al.*, 2020; Qureshi *et al.*, 2023). On the other hand, drought conditions have been found to increase flavonoid content, antioxidant activity, and other polyphenolic components. Changes in the nutritional profile of sesame seeds have been reported, including a reduction in oil percentage associated with an increase in protein percentage under drought conditions (Eskandari *et al.*, 2009).

As global water scarcity intensifies, there is increasing interest in drought-tolerant crops rich in natural antioxidants due to their unique properties and potential health benefits. Sesame, with its robust profile of bioactive compounds, emerges as a promising candidate. Although sesame seeds are more widely consumed than oils in many African and Asian countries (Abbas *et al.*, 2022), little research into their nutritional profiles under drought conditions has been carried out (Eskandari *et al.*, 2009; Ozkan and Kulak, 2013; Wei *et al.*, 2022; Hoyos *et al.*, 2024). Mutagenesis breeding has shown promise in developing drought-tolerant sesame mutants (Kouighat *et al.*, 2020). Notably, four sesame mutants, namely ML2-5, ML2-10, ML2-37, and ML2-72, have demonstrated drought tolerance during germination and flowering stages (Kouighat *et al.*, 2021, 2023, 2024).

Building on previous research, the present study aims to assess and compare the nutritional profiles of seeds from these sesame mutant lines grown under drought conditions in two contrasting environments, Afourare and Taoujdate. These sites were selected as they represent the two key areas of sesame production in Morocco, namely Tadla and Sais, respectively (Kouighat *et al.,* 2022a). By investigating their antioxidant activity and key bioactive compounds, we seek to identify and select promising mutant lines with optimal nutritional profiles for the future development of resilient and high-quality sesame cultivars.

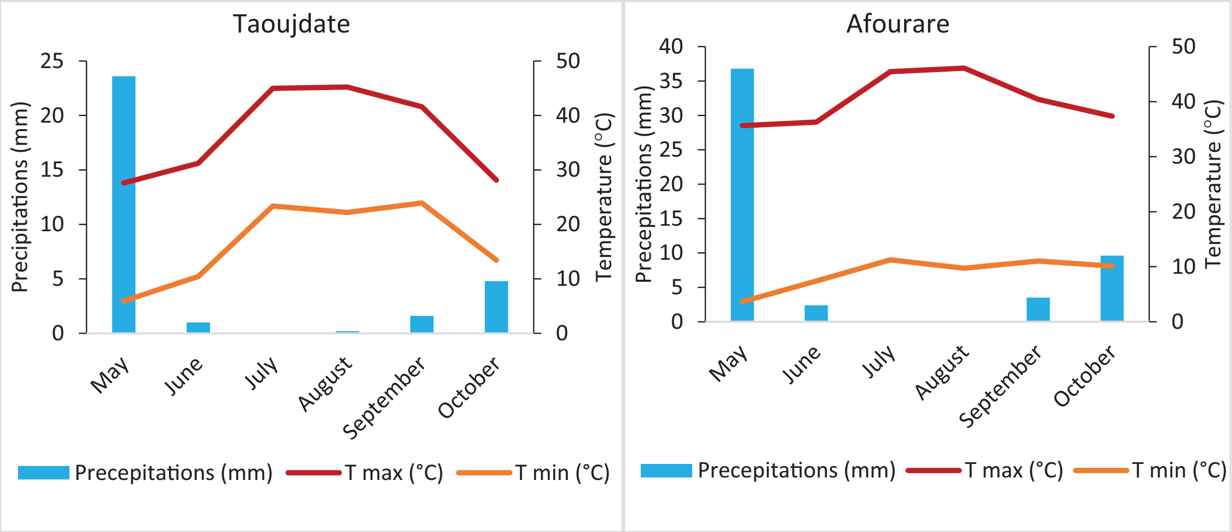

Fig. 1. Climatological data from both environments during the study period.

2 Materials and methods

2.1 Study site

The research was conducted at two distinct experimental stations of the Institut National de la Recherche Agronomique (INRA) in Morocco: Taoujdate and Afourare. Taoujdate, belonging to El Hajeb province, is located 550 meters above sea level and experiences a continental climate (2°13’00" N 6°30’00" W). Its soil is characterized as clayey, brown calcareous, and alluvial. On the other hand, Afourare, located in Beni-Mellal province, is 446 meters above sea level, has chronic luvisol soil, and a semi-arid climate (33°55’59" N 5°16’28" W). Both sites provided climate data during the experiment period *via* automated weather stations, which are shown in Figure 1.

2.2 Plant material

The plant material contains 13 sesame genotypes (Tab. 1) derived from a mutagenesis breeding program (Kouighat *et al.*, 2020, 2022a, 2022b). This program involved two wild-type parents: the Moroccan cultivar ML13 and the foreign accession US06 (PI561704). Seeds of these cultivars were treated with 0.5 % and 1 % ethyl methane sulfonate (EMS) for five hours to induce mutations. The treated seeds were then sown to develop the M_1 generation, from which desirable mutants were selected in subsequent generations. From these efforts, 11 promising mutant lines were chosen for this study (Kouighat *et al.*, 2021, 2022c, 2023, 2024). These included five mutants M_4 from ML13 (ML2-10, ML2-37, ML2-5, ML2-68, and ML2-72) and six M_4 from US06 (US1-2, US1-3, US2-6, US2-7, US1-DL, and US2-1).

2.3 Experimental design and application of drought stress

The factorial experiment employed a randomized complete block design (RCBD) with three replications. Seeds of each genotype were sown at both the experimental stations (Taoujdate and Afourare) on April 22nd, 2021, in plots consisting of two rows, each 2 meters long, with 60 cm spacing between rows and 15 cm between plants within each row. The cultural practices followed Langham’s (2008) recommendations for sesame production.

Water deficit was applied from the apparition of four pairs of leaves to physiological maturity. Two irrigation regimes were applied: full irrigation (FI) and deficit irrigation (restricted irrigation, RI). RI received 50 % of the water supplied to FI. A drip irrigation system was used to manage water delivery, consisting of 16 mm diameter polyethylene pipes with drippers delivering 2 L/h. For the FI regime, two pipes with two drippers per plant were used, while the RI regime used one pipe with one dripper per plant, as described by Kouighat *et al.* (2023). The drippers in the field maintained an average flow rate of 1.6 L/h over a continuous two-hour period, demonstrating a calculated uniformity coefficient (UC) of 92.81 %. The total water application for FI was determined based on a survey among Moroccan sesame farmers (Kouighat *et al.*, 2023) and the findings of Boureima and Diouf (2011) on sesame water requirements in arid African regions. The cumulative water application for FI amounted to 510 mm. This setup provided a comprehensive comparison of the growth and yield performance of different sesame genotypes under varying water availability.

2.4 Methods and seed quality traits measured

Moisture content (%) was determined following the method outlined by Rao *et al.* (2002), where 0.5 g of seeds were weighed and then dried in an oven at 103 °C for 3 h. Ash content (%) was measured using the dry ash method: 2 g of the sample was placed in a crucible and heated at 550°C in an oven until the sample turned gray, indicating complete combustion. Oil content was estimated using a Soxhlet extractor (SER 148/6, Velp Scientifica, Italy) with 150 ml of pure N-hexane as the solvent, from 20 g of powdered seeds.

Table 1. Origin and main phenotypic characteristics of the sesame genotypes studied.

Genotype	Origin	Characteristics
ML13	Local cultivar from Morocco	Parent (check cultivar), tall plant, low number of small capsules per plant, beige seeds, high carbohydrate content, small capsules, moderate drought-tolerance during germination
ML2-10	Developed by EMS-mutagenesis from ML13	Tall plant, high branching, small capsules, brown seeds, high protein content, tolerant to severe drought during germination
ML2-37		Tall plant, high branching, brown seeds, high phenol content, tolerant to severe drought during germination and flowering stages
ML2-5		Tall plant, high branching, small capsules, brown seeds, high protein content, tolerant to severe drought during germination
ML2-68		Tall plant, high branching, late maturity, grey seeds, low total phenol content, high protein content
ML2-72		Short plant, low branching, late flowering, brown seeds, low carbohydrate content, tolerant to severe drought during flowering stage
US06	Accession from USA	Parent (check cultivar), short plant, unbranched, large capsules, white seeds, high protein content, drought-sensitive during germination
US1-2	Developed by mutagenesis from US06	Short plant, unbranched, high number of capsules per plant, white seeds, high flavonoids, and anthocyanins content
US1-3		Short plant, unbranched, large capsules, low number of capsules per plant, early maturity, white seeds
US1-DL		Tall plant, high branching, late flowering, white seeds, high ash, sugars, and carbohydrate content
US2-1		Short plant, high number of capsules per plant, early maturity, white seeds, high flavonoid content
US2-6		Short plant, unbranched, early flowering and maturity, black seeds, high phenols and lignans content, drought-sensitive
US2-7		Short plant, low branching, high number of capsules per plant, white seeds, high crude fiber, and flavonoid content

Biochemical analyses were conducted on the seeds. For each genotype at each site, 5 g of seed powder was weighed and ground using a mechanical grinder. The sample was then mixed with 30 mL of 80 % ethanol and allowed to stand for 24 h, followed by centrifugation at 3000 rpm for 10 min. Total amino acid content (mg GlyE/g) was measured by colorimetry using the method of Yemm *et al*. (1955), with glycine as the standard. The total phenolic content was determined using the Folin-Ciocalteu method as described by Tohidi *et al*. (2017), and results were expressed in milligrams of gallic acid equivalents per gram (mg GAE/g) of the dry sample. The total flavonoid content was measured in milligrams of quercetin equivalents per gram (mg QE/g) according to Khan *et al*. (2019), using a dosage method based on aluminum chloride, sodium nitrite, and NaOH. Total anthocyanin content was determined in milligrams of cyanidin-3-O-glucoside equivalents per gram of sesame seed (mg/g), following the differential pH method outlined by Abdel-Aal and Hucl (1999). The free radical scavenging activity (%) of the seed extracts was assessed using the method of Suja *et al.* (2004), employing the stable free radical 2,2-diphenyl-1-picrylhydrazyl (DPPH), which loses its purple color when reacting with antioxidants.

2.5 Statistical analyses

The data gathered underwent analysis of variance (ANOVA) to assess the significance of differences among the 13 sesame genotypes studied under drought conditions in two contrasting environments, Afourare and Taoujdate, representing the sesame-growing regions of Morocco. The three factors studied, genotype (13 levels), water regime (two levels), and environment (two levels) were considered fixed. In case of significant differences, Tukey's post hoc test was then employed to compare means and discern distinct groups of genotypes. Also, a Wilcoxon test is used to compare paired samples between the two sites for each genotype. Furthermore, Pearson's correlation and Principal Component Analysis (PCA) were performed to identify the association between the traits studied and those characterizing each group of genotypes. The statistical analyses were done using SPSS (version 28) and XLSTAT (version 23) software programs.

3 Results and discussion

3.1 Analysis of variance

The results of the analysis of variance showed a significant effect of environment, water regime, genotype, and their interactions on the seven phytochemical parameters studied (Tab. 2). This indicates there is a genetic diversity among the 13 sesame genotypes that also responded differently to the environment (Afourare/Taoujdate) and to the level of irrigation (FI/RI) under which they grow. These findings suggest the opportunity to select high-performing lines that exhibit high nutritional quality for each water supply and each environmental condition.

Table 2. Results of the analysis of variance (means squares and level of significance) of 13 sesame genotypes evaluated under two water regimes across two contrasting environments.

Source of variation	Df	Moisture	Ash	Oil	TAA	TPC	TFC	TAC	FRSA
Environment (E)	1	0.071**	15.8***	19.2***	6.2***	509.5***	9.1***	0.3***	599.1***
Water regime (WR)	1	0.1**	5.7***	412.2***	125.2***	69.8***	35.7***	50.1***	2.2*
Genotype (G)	12	0.5***	8.5***	19.6***	36.8***	183.9***	32.6***	9.6***	72.4***
G × WR	12	0.3***	6.9***	12.0***	18.3***	62.6***	6.7***	3.4***	48.1***
E × G	12	0.4***	9.5***	30.1***	30.2***	93.9***	8.8***	8.2***	55.2***
E × G × WR	12	0.6***	2.4***	20.2**	16.3***	30.2***	7.3***	7.9***	27.4***
Error	104	0.013	0.009	10.995	0.324	0.037	0.118	0.007	0.464

Df, degree of freedom; TAA, total amino acid content; TPC, total phenolic content; TFC, total flavonoid content; TAC, total anthocyanin content; FRSA, free radical scavenging activity. *, **, *** Significant differences at the probability level of 5%, 1%, and 1‰, respectively.

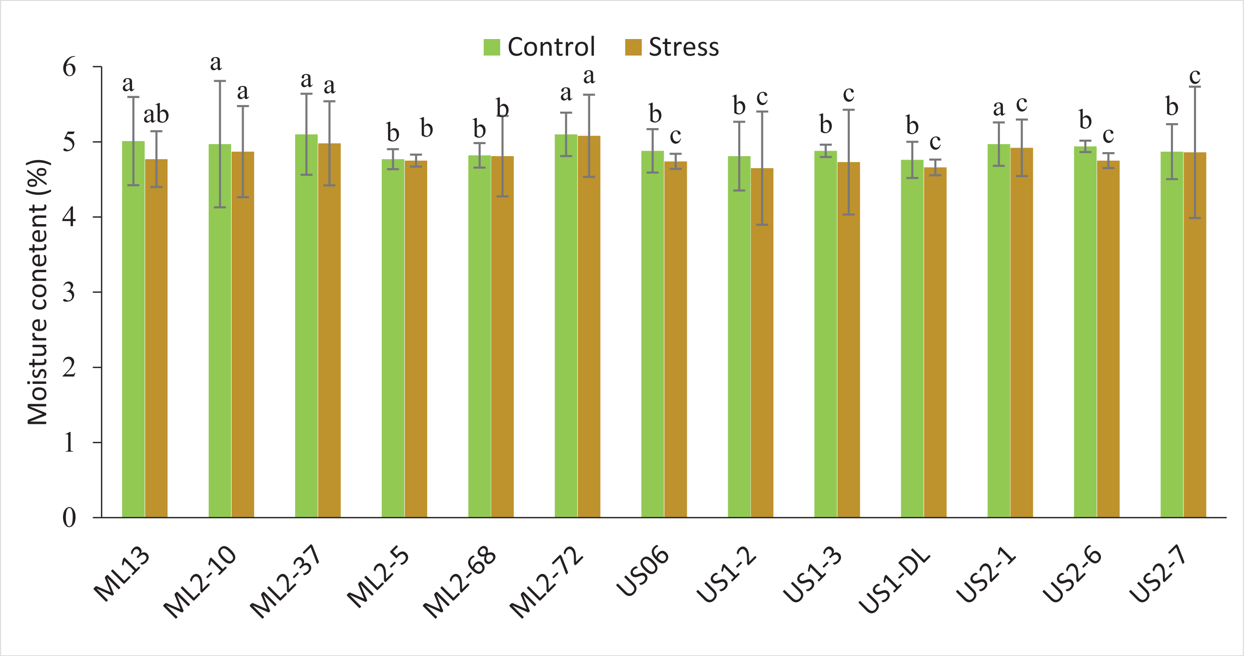

Fig. 2. Average moisture content in sesame seeds under two distinct conditions, full irrigation (control) and restricted irrigation (drought stress). The alphabets on the error bar represent Tukey's post hoc groups. Genotypes with the same letters, for each water regime, are not significantly different.

3.2 Seeds' moisture content

All the sesame genotypes demonstrated a decrease in moisture content when subjected to drought conditions (Fig. 2). However, the magnitude of this reduction varied significantly among the different genotypes, ranging from 0.25 % in ML2-68 to 4.68 % in ML13 Notably, genotypes ML13, US1-2, and US1-3 displayed particularly pronounced reductions in moisture content, with percentages of 4.68 %, 3.24 %, and 3.09 %, respectively. Conversely, certain genotypes such as ML2-68, US2-7, and ML2-5 exhibited minimal reductions, each less than 0.36 %, indicating potential resilience to drought-induced stress. Maintaining elevated moisture levels in the seed, under drought, could potentially be attributed to an adaptive plant response to this stress through mechanisms like accumulation of osmoprotective compounds (Akula and Ravishankar, 2011). While high-moisture sesame seeds are beneficial for culinary purposes, enhancing dishes with better taste and texture (Zhang *et al.*, 2023), it's crucial to maintain proper storage conditions to prevent spoilage (Berhe *et al.*, 2023). Notably, the moisture content significantly influenced aroma compounds, color intensity, and sensory properties of sesame seeds (Yang *et al.*, 2024), with moisture levels between 5 and 10 % correlating with heightened roasted sesame and nutty odors. Interestingly, across both control and stress conditions, seeds from the mutants ML2-72 and ML2-37 consistently retained the highest moisture levels, averaging 5.09 % and 5.04 %, respectively. This highlights their remarkable resilience in maintaining superior nutritional quality in the seeds.

Table 3. Wilcoxon test results for paired samples between the two sites for each genotype

	Moisture		Ash		Oil		TAA		TPC		TFC		TAC		RSA	
Genotype	Statistic	p-value	Statistic	p-value	Statistic	p-value	Statistic	p-value	Statistic	p-value	Statistic	p-value	Statistic	p-value	Statistic	p-value
ML13	0.5	0.01	0.1	0.04	0.1	0.04	0.1	0.04	0.2	0.02	0.1	0.0	0.2	0.02	0.1	0.04
ML2-10	0.6	0.00	0.2	0.03	0.3	0.02	0.2	0.02	0.3	0.02	0.3	0.02	0.3	0.01	0.2	0.02
ML2-37	0.4	0.01	0.2	0.03	0.2	0.02	0.3	0.02	0.4	0.01	0.4	0.01	0.4	0.02	0.3	0.02
ML2-5	0	1	0.1	0.05	0.4	0.01	0	1	0.1	0.04	0.1	0.04	0.1	0.04	0	1
ML2-68	0	1	0	1	0	1	0.1	0.04	0	1	0	1	0	1	0.1	0.05
ML2-72	0	1	0.4	0.02	0.5	0.01	0.4	0.01	0.5	0.01	0.5	0.01	0.5	0.00	0.4	0.01
US06	0.1	0.02	0	1	0	1	0.3	0.01	0.1	0.03	0.1	0.04	0.1	0.03	0.3	0.02
US1-2	0.3	0.01	0.3	0.02	0.1	0.04	0.2	0.02	0.3	0.02	0.3	0.02	0.3	0.02	0.2	0.02
US1-3	0.2	0.02	0	1	0	1	0.1	0.05	0	1	0	1	0	1	0.1	0.04
US1-DL	0.1	0.03	0	1	0	1	0	1	0.2	0.02	0.2	0.02	0.2	0.03	0	1
US2-1	0.5	0.01	0.3	0.01	0.2	0.03	0.3	0.01	0.3	0.01	0.3	0.01	0.3	0.01	0.3	0.01
US2-6	0.3	0.02	0.1	0.03	0.1	0.04	0.1	0.03	0.4	0.01	0.4	0.01	0.4	0.01	0.1	0.03
US2-7	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1

TAA, total amino acid content; TPC, total phenolic content; TFC, total flavonoid content; TAC, total anthocyanin content; FRSA, free radical scavenging activity.

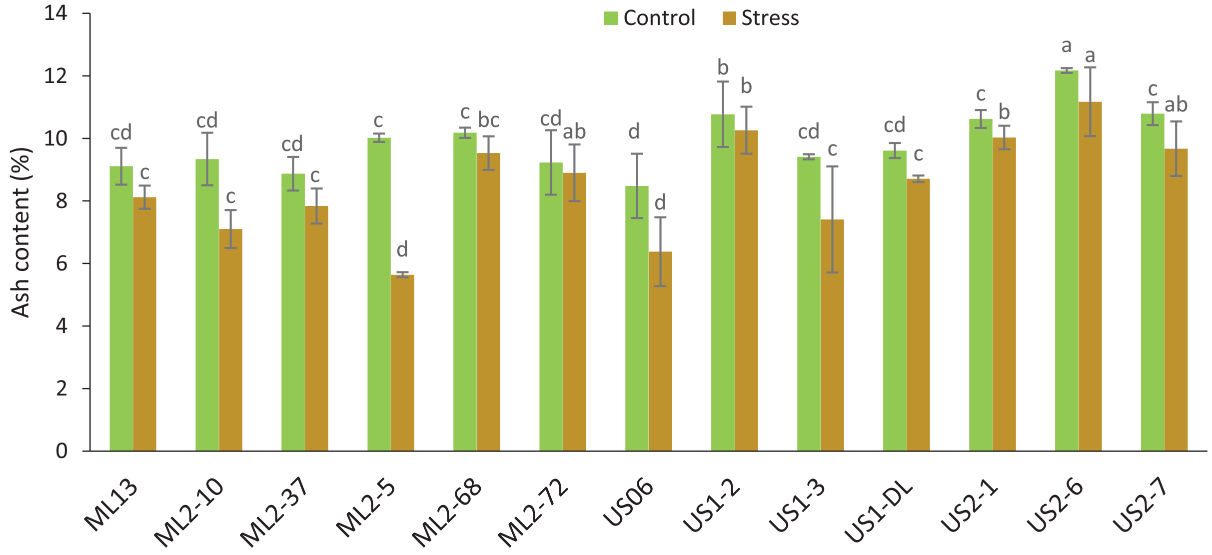

Fig. 3. Average ash content in sesame seeds under two distinct conditions, full irrigation (control) and restricted irrigation (drought stress). The alphabets on the error bar represent Tukey's post hoc groups. Genotypes with the same letters, for each water condition, are not significantly different.

Environmental effects on moisture content were also notable; some genotypes were more stable than others in maintaining average moisture content between the two environments. Genotypes ML2-5, ML2-68, and ML2-72 exhibited genetic stability ($p > 0.05$) (Tab. 3), with minimal variations of less than 0.3 % in seed moisture levels between the two sites. The stability and high moisture content of mutant ML2-72 across different environments, combined with its strong agronomic and physiological performance under water deficit conditions (Kouighat *et al.,* 2023), highlight its potential as a robust genotype for sesame cultivation under variable climatic conditions. This stability is particularly important for ensuring consistent seed quality and nutritional value, which are critical factors for both agricultural production and consumer satisfaction.

3.3 Seeds' ash contents

The genotypes studied experienced a reduction in ash content when subjected to drought stress, with a rate ranging from 3.58 % in ML2-72 to 43.71 % in ML2-5 (Fig. 3). The average ash content varied from 8.87 (US06) to 12.17 % (US2-6) under non-stressful conditions (FI), and from 5.63 (ML2-5) to 11.17 % (US2-6) under stressful conditions (RI). Drought stress has the potential to influence the bioavailability and mobility of minerals, as well as the interplay among

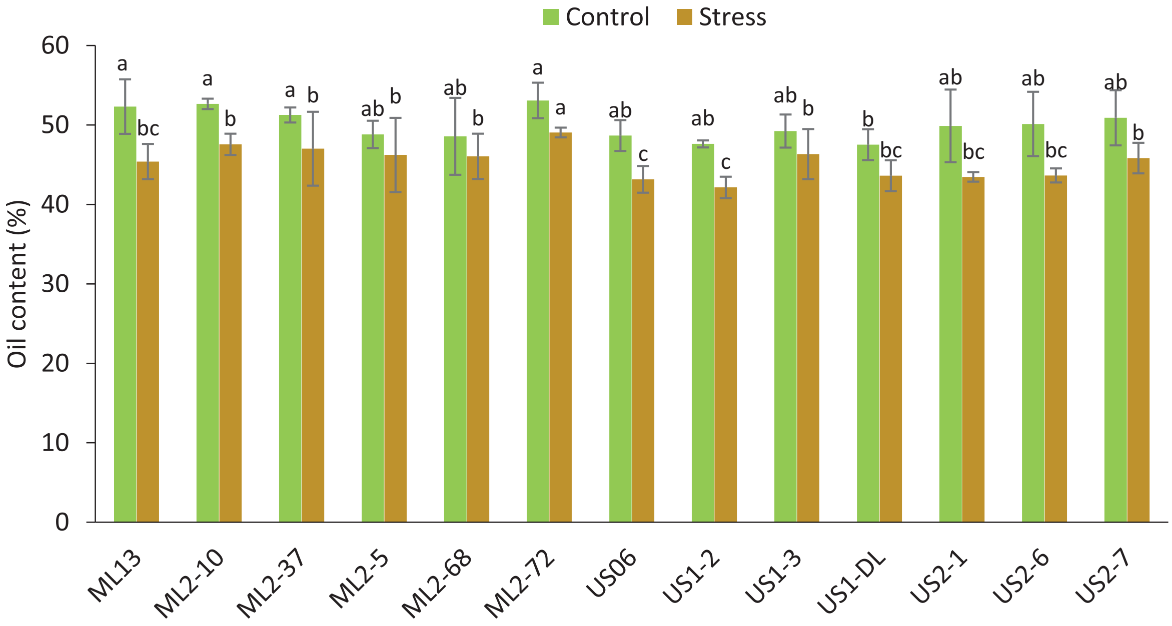

Fig. 4. Average oil content in sesame seeds under two distinct conditions, full irrigation (control) and restricted irrigation (drought stress). The alphabets on the error bar represent Tukey's post hoc groups. Genotypes with the same letters, for each water condition, are not significantly different.

mineral nutrients in plants (Etienne *et al.*, 2018). On average, the highest average ash content (11.67 %) was recorded in the mutant line US2-6, while the lowest one (7.42 %) was registered in its wild-type parent US06. According to the literature, ash content in sesame seeds varied between 2.0 % and 11.05 % (Mi *et al.*, 2022), which indicates that the mutant US2-6 has an average ash content higher than those found in sesame genotypes existing so far. Other mutant lines, such as US1-2, US2-1, ML2-68, and ML2-72, have also exhibited an average ash content significantly higher than those of the two wild-type parents US06 and ML13 (Fig. 3). Higher ash content suggests a richer mineral profile in seeds of those lines, potentially offering greater nutritional benefits (Saeed *et al.*, 2015). Incorporating sesame seeds into one's diet can be particularly beneficial for individuals looking to boost their mineral intake, especially if they have dietary restrictions or preferences that limit their consumption of other mineral-rich foods.

Several genotypes exhibited significant differences between Afourare and Taoujdate environments ($p < 0.05$) (Tab. 3). However, the genotypes ML2-68, US06, US1-3, US1-DL, and US2-7 demonstrated remarkable stability ($p = 1$), indicating a strong intrinsic adaptation to varying environmental conditions. Looking at the overall mean ash content, regardless of water regime, and the stability across both environments, the mutant genotype ML2-68 was found to be the richest, emphasizing its potential suitability for cultivation in both contrasting environments.

3.4 Seed oil content

When subjected to drought stress conditions, there is a consistent decrease in seed oil content across all the genotypes (Fig. 4). This decrease can be attributed to reduced photosynthetic activity caused by stomatal closure, which limits carbon dioxide uptake and reduces the availability of carbon skeletons necessary for fatty acid and oil biosynthesis (Chada *et al.*, 2023). Additionally, plants prioritize the synthesis of stress-defense compounds such as osmoprotectants and antioxidants over storage compounds like oils under water deficit conditions (Baghery *et al.*, 2023). In the absence of drought stress, oil content ranged from 47.52 % (US1-DL) to 53.08 % (ML2-72), indicating genetic variability among these genotypes. However, under stress conditions, this content decreased remarkably, with a notable variation from 42.14 % (US1-2) to 49.0 % (ML2-72). The local cultivar ML13 showed a substantial reduction of 13.22 %, decreasing from 52.31 %, under FI, to 45.39 %, under RI. Conversely, the mutants ML2-68, ML2-5, and US1-3 exhibited lower reductions, all below 6 %. These results are more interesting than those reported by Najafabadi and Ehsanzadeh (2017) who observed a reduction of 19 % in sesame seed oil content as a result of 70 % irrigation of available soil water (ASW). Under the two contrasting water conditions, the ML2-72 mutant exhibited the highest oil content, with an average reaching 51.06 %. Moreover, in a previous study by Kouighat *et al.* (2023), ML2-72 showed, under drought conditions, the lowest reduction (32 %) in seed yield, with a yield of 0.58 t/ha, and the highest average stability index (YSI > 0.51). This highlights its significant potential for improving sesame-based oil production.

Under varying environmental conditions, significant differences were observed among the different genotypes. However, certain genotypes, including ML2-68, US06, US1-3, US1-DL, and US2-7, exhibited high stability ($p > 0.05$) (Tab. 3). Notably, ML2-68 and US1-3 showed minimal reductions in oil content under drought stress while maintaining stability across different environments. These mutants demonstrated a remarkable ability to preserve seed oil quantity despite environmental fluctuations, making them especially valuable for cultivation in diverse growing conditions.

3.5 Bioactive compounds

Drought stress led to an overall increase in total amino acid content (TAA) across genotypes, although the magnitude of this increase varied (Fig. 5). The genotypes US1-DL, ML2-37, and US2-6 exhibited the most significant rises of 50 %, 36 %, and 33 %, respectively. Conversely, ML2-72 displayed the smallest increase at only 4 %, yet consistently maintained the highest average TAA across both stressed and non-stressed conditions, highlighting its potential for superior nutritional value. The observed increase in TAA under stress conditions can be attributed to the involvement of amino acids such as proline, glutamate, and serine in stress mitigation mechanisms, as reported by Rai *et al.* (2012).

Total phenolic content (TPC) also showed a marked increase under stress, with an average of 21.39 mg/g compared to 15.95 mg/g under non-stress conditions (Fig. 5). Genotypes US1-DL, US06, and US2-1 demonstrated the most substantial increases in TPC under drought stress, with rises of 82 %, 53 %, and 60 %, respectively. The line US2-6, however, had the smallest increase at 8 %, though it maintained the highest overall phenolic content at 24.085 mg/g, while ML2-68 had the lowest at 9.535 mg/g. These findings exceed those of previous studies which have indicated that phenolic content tends to increase under stress by 23 to 48 % Hoyos *et al.*, 2024). Additionally, the higher TPC production observed in dark-colored seeds like those of US2-6 supports the conclusion of Shahidi *et al.* (2006) that dark seeds generally accumulate more phenolics under stress.

Total flavonoid content (TFC) also increased under drought stress, with values ranging from 12.60 mg/g (ML2-5) to 17.27 mg/g (US2-7) under normal conditions, and from 12.92 mg/g (ML2-5) to 19.34 mg/g (US2-6) under stress (Fig. 5). The greatest increase in TFC was observed in the mutant ML2-10 at 22.87 %, while ML2-5 exhibited the smallest increase at 2.5 %. These results are consistent with previous findings by Kermani *et al.* (2019) who noted a general rise in flavonoid content under drought conditions. The mutant US2-7 consistently displayed the highest average flavonoid content (18.17 mg/g) across all conditions, making it a prime candidate for nutritional applications due to its superior flavonoid levels.

Total anthocyanin content (TAC) also rose significantly under stress, ranging from 0.35 mg/g (US1-DL) to 2.42 mg/g (US2-7) under normal conditions, and from 1.07 mg/g (ML2-10) to 4.54 mg/g (US2-6) under stress (Fig. 5). Genotypes such as US1-DL, US1-3, and ML13 showed particularly high increases in TAC, with increments of 79.16 %, 78.22 %, and 77.99 %, respectively. The consistent accumulation of anthocyanins in genotypes like ML2-72, US2-7, and ML2-68 across both conditions highlights their potential nutritional significance, supported by the antioxidative and antimicrobial properties of anthocyanins (Khoo *et al.*, 2017).

Free radical scavenging activity (FRSA) also increased under stress, ranging from 85.94 % (ML2-68) to 95.08 % (US2-6) under normal conditions, and from 90.33 % (ML2-68) to 98.2 % (US1-2) under drought stress (Fig. 5). Noteworthy increases were observed in ML13 (9.36 %) and ML2-37 (8.08 %) due to stress, while US06 and US2-6 showed minimal increases of 0.31 % and 0.6 %, respectively. The high FRSA observed in black seeds of US2-6 (95.58 %) compared to white seeds of ML2-68 (88.13 %) aligns with findings by Shahidi *et al.* (2006) regarding the greater antioxidant activity in black sesame seeds. The robust antioxidant capacity of US2-6 can be attributed to its high levels of phenolic compounds, anthocyanins, and flavonoids, which is in agreement with the findings of Dravie *et al.* (2020). Additionally, the presence of antioxidant peptides, as suggested by Shao *et al.* (2020), may further enhance the FRSA of these seeds, indicating their potential health benefits.

Environmental factors significantly influenced the variation in bioactive compounds, as reported in studies on other species (Bor *et al.*, 2009; Curtis *et al.*, 2009; Moura *et al.*, 2013; Cappelaere *et al.*, 2021). Genotypes such as ML2-5, ML2-68, US1-3, US1-DL, and US2-7 exhibited stability ($p > 0.05$) across different locations, maintaining seed quality despite environmental variations (Tab. 3). This stability suggests that these genotypes may offer better nutritional performance in fluctuating environments, while those with significant variation may require more controlled cultivation conditions to maximize their potential.

3.6 Pearson's correlation

Correlation matrix analysis revealed several significant associations among the different parameters studied (Fig. 6). TAA showed a significant positive correlation with TAC ($r = 0.846$***) and a moderate correlation with FRSA ($r = 0.574$*) as well as TPC ($r = 0.532$*), and TFC ($r = 0.529$*). The strong positive correlation between the TAA and TAC suggests a possible joint regulation of the biosynthesis of these two types of compounds. In fact, anthocyanin synthesis involves several metabolic pathways in which amino acids can play a role as precursors or cofactors (Sunil and Shetty, 2022). Regarding the moderate correlation with FRSA as well as TPC and TFC, this suggests that amino acids may contribute to the antioxidant capacity of the sample. Polyphenols, flavonoids, and anthocyanins are all compounds with well-known antioxidant activities. Amino acids could therefore potentially act in synergy with these compounds to neutralize free radicals and thus protect cells against oxidative stress (Aklakur, 2018). Furthermore, FRSA showed a positive correlation with TPC ($r = 0.631$**), indicating that these two parameters may be influenced by similar biochemical mechanisms. These results imply the collective and synergistic contribution of total phenolic compounds to the overall antioxidant activity (Hoyos *et al.*, 2024). In contrast, oil content showed significant negative correlations with FRSA ($r = -0.623$**) and TPC ($r = -0.538$*), suggesting an inverse relationship between these compounds and the seed oil concentration. Oils, especially those rich in unsaturated fatty acids, can be oxidized by free radicals, reducing their ability to neutralize these radicals (Prisacaru, 2016). Therefore, high oil content may indirectly decrease the overall antioxidant activity of the sample. Thus, high oil content could potentially lead to a

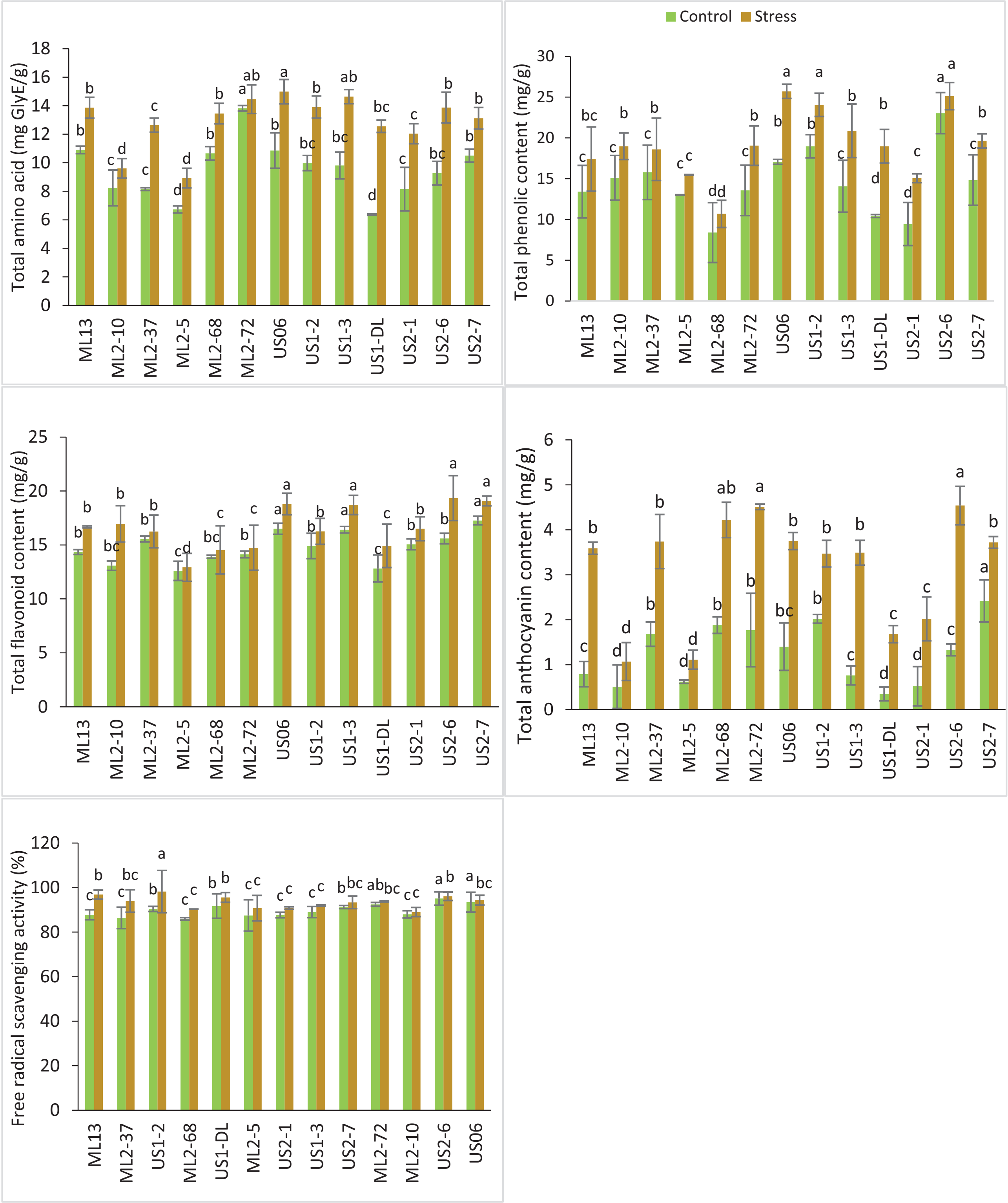

Fig. 5. Average of bioactive compounds in sesame seeds under two distinct conditions, full irrigation (control) and restricted irrigation (drought stress). The alphabets on the error bar represent Tukey's post hoc groups. Genotypes with the same letters, for each water condition, are not significantly different.

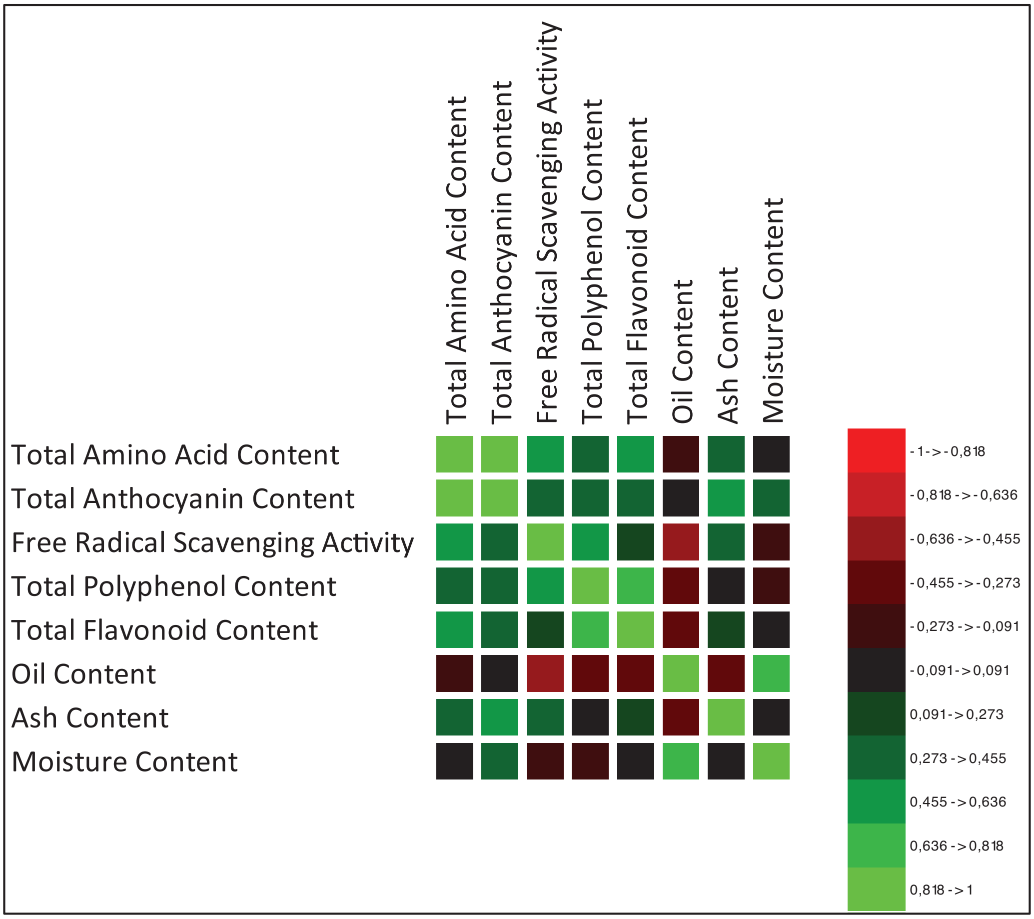

Fig. 6. Correlation matrix based on Pearson's correlation coefficient for nutritional compounds in sesame seeds.

reduction in the availability of phenolic compounds in the sample, which could explain the observed negative correlation between oil content and total phenolic content. Furthermore, oil content is negatively correlated with ash content ($r = –0.553$*). This often happens because storing energy-rich compounds like oils can limit the space or capacity for mineral accumulation in plant cells, leading to a trade-off between the two components (Deamer, 2017). Finally, moisture content has a positive correlation with oil content ($r = 0.647$**). During growth, moisture levels are often higher, and a certain moisture content might even facilitate oil biosynthesis by maintaining the enzymatic activity and metabolic processes necessary for oil accumulation (Gupta *et al.*, 2002).

3.7 Principal component analysis

The results of the principal component analysis (PCA) are depicted in Figure 7. Under normal conditions, the principal components F1 and F2 collectively account for 81.28 % of the total variance in the dataset. Among the variables contributing to F1, one could note total amino acids, polyphenol content, flavonoid content, and anthocyanin content. For F2, significant contributors are oil, ash, and moisture. Upon analyzing the PCA carte, ML2-72, ML13, and ML2-37 share similar traits, exhibiting elevated moisture, oil content, and total amino acids. Conversely, the group comprising US2-6, US06, US1-2, and US2-7 displayed higher levels of ash content, polyphenols, anthocyanins, flavonoids, and free radical scavenging activity. Other genotypes exhibit a diverse array of characteristics.

Under stress conditions, F1 and F2 collectively account for 66.84 % of the total variance. Primary contributors to F1 include total amino acids, flavonoids, phenolic content, ash content, and free radical scavenging activity, while for F2, seed moisture and oil content play significant roles. Genotypes ML2-68, ML2-37, and ML2-72 stand out relatively high moisture levels and oil content. Conversely, the group comprising US2-6, US06, and US1-2 showcases relatively high phenolic content, flavonoids, and free radical scavenging activity. The two mutants ML2-72 and ML2-37 maintained, under both drought and normal irrigation conditions, high oil and moisture contents in the seeds suggesting their tolerance to drought, which confirms the findings of our previous studies (Kouighat *et al.*, 2021, 2023, 2024). On the other hand, the mutants US2-6 and US1-2 stand out for their high levels of phenolic compounds and flavonoids that contribute to strong antioxidant activity.

4 Conclusion

This study highlights the diverse nutritional profiles in various sesame mutant lines under both well-watered and water-stress conditions. Notably, the ML2-72 mutant, which

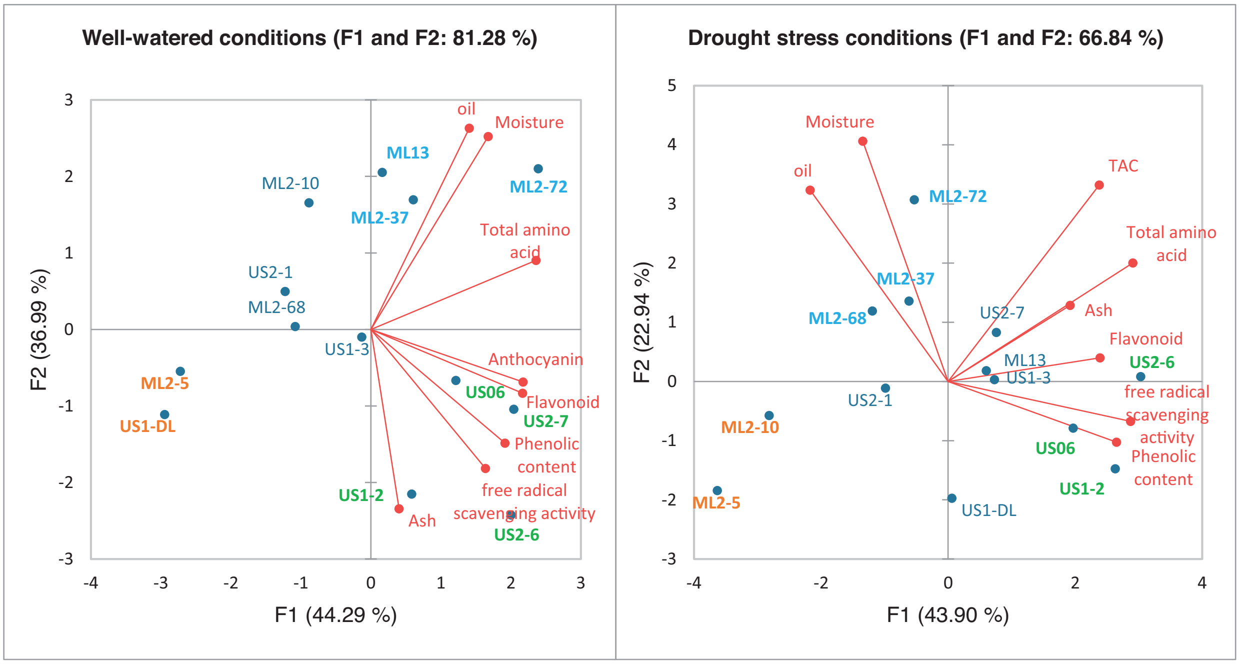

Fig. 7. Box plot of Principal Component Analysis of sesame seeds under two water regime conditions, full irrigation (normal conditions) and restricted irrigation (drought stress).

has demonstrated strong drought tolerance at different life cycle stages, in previous studies, managed to maintain high levels of oil content, total amino acids, anthocyanins, and moisture content, positioning it as an excellent candidate for cultivation in the main sesame-growing areas in Morocco, particularly under deficit water conditions. Additionally, ML2-68 exhibited the highest ash content, while US2-7 consistently demonstrated superior flavonoid levels. The significant accumulation of phenolic compounds in US2-6, along with its impressive free radical scavenging activity, emphasizes the potential health benefits associated with this genotype.

These findings indicate that genotypes such as ML2-68, ML2-72, US2-7, and US2-6 hold substantial promise for enhancing both the nutritional value and stability of sesame crop in challenging environments. These genetic materials represent valuable germplasm with improved nutritional profiles and drought tolerance. The insights derived from this study provide crucial guidance for genetic improvement initiatives aimed at developing more nutritious and stress-resilient sesame varieties, ultimately contributing to global food security and the sustainability of sesame cultivation.

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Conflicts of interest

The authors declare that they have no conflict of interest in relation to current paper.

Author contribution statement

Mohamed kouighat: Conceptualization, investigation, data Curation, writing original draft**. Fatima Ezzahra Moussaoui:** Investigation, data curation, formal analysis**. Atman Adiba:** Resources, formal analysis**. Azzedine Hafid:** formal analysis**. Abdelghani Bouchyoua:** formal analysis**. Mohamed El Fechtali:** Investigation**. Abdelghani Nabloussi:** Conceptualization, supervision, review & editing.

All authors have read and approved the final manuscript.

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