




Low water supply differentially affects the growth, yield and mineral profile of kabuli and desi chickpeas (*Cicer arietinum*)

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Funding information

European Commission, Grant/Award Number: 101000622; European Regional Development Fund, Grant/Award Number: NORTE-01-0145-FEDER-000066; Fundação para a Ciência e a Tecnologia, Grant/Award Numbers: UIDB/50016/2020, 2022.01903.CEECIND

Abstract

The climatic events predicted to increase in intensity and frequency in the near future, including drought, may influence the quality and productivity of several important crops for human nutrition, such as legumes. Herein, two chickpea genotypes (*Cicer arietinum*) were analysed for their resilience to low water supply: a commercial white chickpea (kabuli) and a traditional black chickpea (desi) with marginal production in occidental countries. Plants were grown under four levels of water supplies (90%, 75%, 50% and 25% of field capacity) and biometric variables (root, shoot, pods and seeds), proxies of plant fitness (water content and oxidative stress) and the seed nutritional profile (protein and mineral concentrations) were analysed at plant maturity. The results show that the water content in shoots and roots decreased with the decrease in water supplies, with kabuli plants generally having higher water content in shoots and desi in roots. The shoot length was significantly higher in kabuli compared to desi, while the root length increased up to 11% in both species with the decrease in water supplies. The root-to-shoot ratio was higher in kabuli and increased with the decrease in the water supply, being negatively correlated with the number of pods and seeds per plant. Lipid peroxidation also increased with the decrease in the water supply, having slight positive correlations with plant growth parameters while being negatively correlated with plant productivity. No significant effects of plant genotype and water supply were observed on seed K, Ca and protein, but desi was able to sustain higher P, Mg, Zn, Fe, Mn and B concentrations than kabuli, including at lower water supplies. The results suggest that water stress negatively impacts plant growth and productivity and that the two chickpea genotypes have distinct biomass and water allocation strategies to cope with low water supply. These findings may be useful in strategies for improving the productivity and nutritional profile of chickpea crops under water-limited conditions.

Janaina S. Medeiros and Marta Nunes da Silva contributed equally to this work.

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KEYWORDS

drought, genotype by environment interaction, legumes, plant nutrition, water stress

1 | INTRODUCTION

Legumes, such as chickpeas, are a nutrient-rich food option that provides protein, minerals and vitamins, making them an excellent choice for a balanced diet, both as feed and food (Ferreira et al., 2021; Magrini et al., 2016). They also play a crucial role in agriculture and the environment as they form a symbiotic relationship with soil bacteria, reducing atmospheric nitrogen into nitrogenated compounds like ammonia (Roy et al., 2020). This helps to promote plant growth and soil fertility and reduces the reliance on nitrogen-based fertilisers, which are a significant contributor to greenhouse gas emissions in agriculture (Barbieri et al., 2023; Iannetta et al., 2016; White et al., 2022). As such, legumes can be a valuable crop in sustainable agriculture as a cash crop, cover crop or intercropped with other species, including in agroforestry cultivation (Barbieri et al., 2023). Despite their numerous benefits, legumes have been overlooked in developed countries due to insufficient marketing and social awareness, while subsistence agriculture in developing countries heavily relies on them for protein (Magrini et al., 2016; Yadav & Chen, 2007). Even with the incentives and subsidies provided by the European Union to promote the cultivation of these crops, their production has been affected by the co-evolution of crop systems that promote cereals, based on public policies, agrochemical paradigms, market dynamics and food systems that favour public and private investment in cereals over legumes (Balázs et al., 2021). Thus, to promote more sustainable agricultural systems, there is a need for greater innovation in agrotechnology to encourage the cultivation of underutilized crops like legumes to maximise nutritional and ecosystem services.

Chickpeas (*Cicer arietinum*) have gained increasing prominence in recent decades, not only as a mono-crop but also as an intercrop with important cash crops, such as barley, maize and wheat (Latati et al., 2019; Merga & Haji, 2019). This legume is a key staple food in Asia and Africa, which together account for 91.4% of the world's production (FAO, 2020). Chickpeas are divided into two distinct genotypes: kabuli or macrosperm, which has a white tegument and is more prevalent in Europe; and desi, or microsperm, which has darker teguments and is mainly distributed from the eastern Mediterranean to central Asia and the Indian subcontinent, with negligible production in Europe (Rachwa-Rosiak et al., 2015). Chickpeas are nutritionally superior to other legumes due to their high protein content and digestibility, lower content of antinutritional substances (particularly the desi chickpeas), and higher availability of essential minerals such as potassium (K), phosphorus (P), magnesium (Mg), iron (Fe) and manganese (Mn) (Chang et al., 2022; Kaur & Prasad, 2021; Rachwa-Rosiak et al., 2015; Sharma et al., 2018). Recently, chickpea flour was used to produce pasta with significantly higher protein, fibre and essential fatty acids than wheat pasta (Saget et al., 2020), emphasising the importance of enhancing the nutritional quality of legumes like

chickpeas through sustainable agronomic practices and by promoting their inclusion in valuable food products.

Despite their undeniable role in sustainable agroecology and food consumption, several adverse environmental factors, such as drought, salinity and heat, negatively affect the growth, development and productivity of legume plants (Nadeem et al., 2018, 2019; Negrão et al., 2017). Drought is one of the major limiting factors for the development and production of legumes, affecting seed germination, plant photosynthetic capacity, their ability to produce flowers and flowering period, consequently leading to lower pod and grain yields (Chowdhury et al., 2016; Pushpavalli et al., 2015). Chickpeas, in particular, are mainly grown under rainfed conditions in resource-poor, arid and semi-arid regions, being subjected to terminal drought that decreases plant yields by up to 50% (Sabaghpour et al., 2006; Toker et al., 2007). Drought stress impairs key physiological and biochemical processes, whilst irrigated cropping systems, particularly before flowering, resulting in an increase in plant population, dry mass, photosynthetic area, pod filling and water use efficiency (Acharya et al., 2015; Geethanjali et al., 2018; Pendergast et al., 2019). Thus, the limitations imposed by climate change and, in particular, the depletion of water resources in the soil resulting from more frequent and severe drought events will negatively affect the productivity of this crop.

Several chickpea genotypes have demonstrated higher drought tolerance and water use efficiency, enabling them to produce high yields even in regions with low water availability (Khamssi et al., 2011; Parameshwarappa & Salimath, 2010; Shende et al., 2020). While kabuli and desi varieties exhibit similar levels of stress during water shortage, desi is generally more tolerant to drought stress than kabuli (Farooq et al., 2018; Nayyar et al., 2006; Nisa et al., 2020). Although desi plants experience a greater reduction in the vegetative dry matter due to stress, they can accumulate osmoprotectants and maintain higher photosynthetic capacity, productivity and harvest indexes under low water conditions, while kabuli shows decreased starch, protein and mineral, including Ca, P and Fe (Farooq et al., 2018; Nayyar et al., 2006; Nisa et al., 2020). Drought-tolerant chickpea cultivars can accumulate more K, Mg, Mn, calcium (Ca) and boron (B), but the timing of the stress plays a significant role in the extent of growth and mineral accumulation impairment, with early drought stress (pre-anthesis) having less detrimental effects on growth and nutrient uptake than late drought stress (post-anthesis) (Gunes et al., 2006). Furthermore, it has been observed that the method used for water provision can also have an impact on the mineral accumulation in chickpeas, as different studies have reported contrasting results on the concentration of P, Zn and Fe in kabuli chickpeas under water stress (Chandana & Pratinsa, 2013; Gunes et al., 2006). Additionally, most research on the effect of water supply on chickpea morphology, physiology and nutrition has been carried out under rainfed conditions or with water supplied at specific phenological stages, without

considering the water-holding (field) capacity of the soil. This limits the ability to compare results and identify tolerant genotypes that could be useful for crop improvement strategies.

This study aims to investigate the extent to which different chickpea genotypes can cope with low water provision and how this can be leveraged for crop improvement and valorisation. Specifically, a kabuli and a desi chickpea genotype were grown under different water supply conditions (ranging from 90% to 25% of the field capacity) and evaluated for their growth parameters, yield, water content, oxidative stress and nutritional profile. It is hypothesised that there are differences in the abilities of distinct chickpea genotypes to withstand water stress, which can be harnessed for improving crop productivity and nutritional diversity. This study also highlights the need for more data on the nutritional diversity and resilience of traditional chickpea varieties to support their valorisation and promote the sustainability of agroecological systems.

2 | MATERIALS AND METHODS

2.1 | Plant material, germination and crop maintenance

Seeds of two chickpea genotypes (*C. arietinum*) were used: a commercial genotype at the European level, the kabuli (white) chickpea, supplied by Lusosem—Produtos Para Agricultura (Algés, Portugal) and a traditional genotype, poorly exploited in Europe, the desi (black) chickpea, supplied by B-choice (Loures, Portugal). The two chickpea genotypes were germinated and grown in 0.5 L pots, with a universal substrate (COMPO SANA, Compo Group, Germany) and perlite (SIRO, Portugal) (2:1, v:v), in a climate chamber (Fitoclima 5000 EH, Aralab, Rio de Mouro, Portugal) with a 16 h light photoperiod and a light intensity of 200 $\mu\text{mol/s/m}^2$, 22°C during the light period and 20°C during the dark period and relative humidity of 65%. For each genotype, 60 plants were grown and subjected to four water supplies, one plant per pot, arranged in a randomised block design ($n = 15$). For the application of the different water supplies, each pot was weighed and the water volume was adjusted weekly to 90%, 75%, 50% and 25% of the field capacity (FC). The experiment started on 17 January 2022 and ended on 9 May 2022. The application of the different water supplies started 15 days after germination and was maintained until pod maturity.

2.2 | Sampling and morphological evaluation of the plants

At the time of sampling (112 days after germination), plants were carefully removed from the soil, washed and separated into roots, shoots and pods. Shoot and root lengths were recorded using a common ruler, and their fresh weight was evaluated on an analytical scale. Samples were stored separately in paper bags and left to dry for 72 h at 70°C. After this period, the dry weight of the root, shoot and pods

was recorded, and seeds were removed from the pods, counted and weighed.

2.3 | Determination of the water content and root-to-shoot (RS) ratio

Water content in roots and shoots was calculated using the following equation: (fresh weight-dry weight)/(dry weight) $\times 100$ (Jin et al., 2017). The RS ratio was calculated by dividing the root dry weight by the shoot dry weight (Xu et al., 2014).

2.4 | Grain nutritional profile

Grain mineral composition was evaluated by inductively coupled plasma optical emission spectrometry (ICP-OES). Five hundred milligrams of each grain sample were mixed with 10 mL of 65% nitric acid in Teflon reaction vessels and heated in a microwave system (Microwave Digestion System MARS 5, CEM Corporation, USA) according to the manufacturer's instructions. After digestion, the resulting solutions were diluted with ultrapure water to a final sample volume of 50 mL, and the determination of potassium (K), phosphorus (P), magnesium (Mg), calcium (Ca), iron (Fe), zinc (Zn), manganese (Mn) and boron (B) concentration was performed using the ICP-OES Optima 7000 DV (PerkinElmer, USA). Protein concentration was determined through the Bradford methodology (Bradford, 1976) using the Pierce Coomassie Plus Assay Kit (Thermo Fisher Scientific, MA, USA). The kit manufacturer's instructions were adapted for 96-well microplates by adding 5 μL of the sample extract to 280 μL of the Coomassie Plus Reagent.

2.5 | Lipid peroxidation

Measurement of malondialdehyde (MDA), used as a proxy of lipid peroxidation and plant oxidative status, was performed on root and shoot tissues (100 mg), which were homogenised in liquid nitrogen and vigorously mixed with 10 mL of 0.5% thiobarbituric acid in 20% trichloroacetic acid for 30 min. After incubation at 100°C for 30 min, the reaction was terminated by transferring the tubes into ice, after which samples were centrifuged for 10 min at 15000 g. The supernatant was filtered, absorbances were measured at 450, 532 and 600 nm and MDA concentration was estimated as described by You et al. (2022).

2.6 | Statistical analysis

The effects of plant genotype and water supply on plant growth parameters, water content, yield and mineral profile were analysed employing a general linear mixed model, using plant genotype, water supply and their interaction as fixed factors. Data were log-

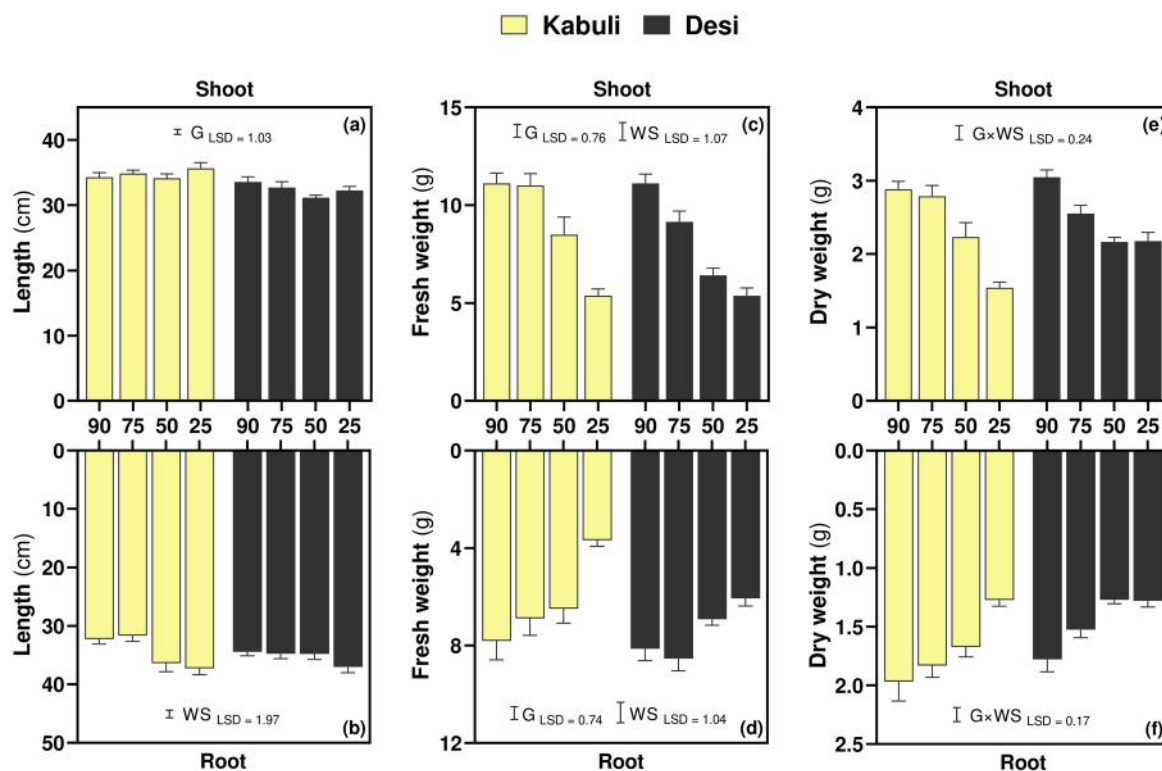


FIGURE 1 Length (a and b), fresh weight (c and d) and dry weight (e and f) of shoots and roots of *Cicer arietinum* kabuli and desi plants grown to grain maturity at different water supplies: 90%, 75%, 50% and 25% of field capacity. Each value represents the mean \pm standard error. Bars represent Fisher's LSD ($p = .05$) for the significant interactions genotype \times water supply and for the independent effects (G, genotype; WS, water supply) when the interaction was not statistically significant.

transformed whenever needed, and residual variance heterogeneity was accepted when this significantly contributed to the model likelihood estimates. Pearson correlation analysis was also performed to explore the relationships between the analysed parameters, and Fisher's least significant difference (LSD) was calculated to separate interaction means. Significance was considered at $p = .05$ using IBM SPSS Statistics v 27.0.1.0 (International Business Machines Corporation, NY, USA).

3 | RESULTS

3.1 | Plant growth and yield

The plant genotype significantly affected the shoot length ($p < .001$, LSD), which was, in general, 7% higher in kabuli than in desi (Table 1, Figure 1a). In turn, the root length was significantly affected by the water supply ($p < .001$, LSD), increasing up to 11% at 25% FC, as compared with 90% FC ($p < .001$, F -test)(Table 1, Figure 1b). Root and shoot fresh weights were significantly affected by the plant genotype and the water supply, while both single effects and their interaction (genotype \times water supply, G \times WS) significantly affected root and shoot dry weights (Table 1, Figure 1c–f). Kabuli generally had a 10% higher shoot fresh weight ($p = .012$, LSD), while the root fresh weight was generally 21% higher in desi ($p = .003$, LSD).

Contrastingly, the root dry weight was generally 13% higher in kabuli ($p = .012$, LSD). At 25% FC, kabuli and desi showed significantly lower root and shoot fresh weight (by 52% and 44%, respectively) and root and shoot dry weight (by 37% and 31%, respectively), as compared with 90% FC ($p < .001$, LSD). Moreover, at 75% and 50% FC, the root dry weight was significantly higher in kabuli (by, respectively, 20%, $p = .0185$ and 32%, $p < .001$, F -test), whereas at 25% FC, desi had a 29% higher shoot dry weight ($p < .001$, F -test). The root length showed a slight increase as shoot fresh and dry weights decreased (Figure 2).

The RS ratio was significantly affected by the plant genotype ($p < .001$, LSD) and water treatment ($p < .016$, LSD) but not by their interaction (Table 1). It was generally higher in kabuli than desi (by 13%) and increased by 15% at 25% FC, as compared with 90% FC (Figure 3a), having a mild negative correlation with the number of pods and seeds per plant (Figure 2). In fact, the number of pods and seeds (Figure 3b,c) of both kabuli and desi significantly decreased (up to 50% and 44%, respectively) with decreasing water supplies (significant water supply effects, $p < .001$, LSD). Nevertheless, kabuli generally had 25% more seeds than desi (significant genotype effect, $p = .011$, LSD). Seed weight per plant was not significantly affected by the plant genotype nor by the water supply (Table 1, SM Figure 1a), but it showed a slight negative correlation with the root length, fresh weight and dry weight (Figure 2).

TABLE 1 Effects of plant genotype (two levels: kabuli and desi) and water supply (four levels: 90%, 75%, 50% and 25% field capacity) on plant growth parameters, water content, yield and mineral profile. F ratios and associated *p* values are shown. Significant *p* values (<0.05) are indicated in bold.

Effects	Genotype		Water supply		Interaction	
	<i>F</i> _{1, 120}	Sig.	<i>F</i> _{3, 120}	Sig.	<i>F</i> _{3, 120}	Sig.
Shoot length	20.092	<.001	1.293	.281	1.383	.253
Root length	1.536	.218	7.327	<.001	2.364	.076
Shoot fresh weight	6.596	.012	45.549	<.001	2.198	.093
Root fresh weight	10.441	.002	14.526	<.001	1.782	.156
Shoot dry weight	2.087	.152	33.465	<.001	4.803	.004
Root dry weight	6.592	.012	12.221	<.001	3.702	.014
Root-to-shoot ratio	18.030	<.001	3.610	.016	1.952	.127
Pods per plant	3.418	.067	15.394	<.001	0.743	.529
Seeds per plant	6.793	.011	8.308	<.001	0.708	.550
Seed weight per plant	1.382	.243	2.610	.056	1.095	.355
Shoot water content	36.314	<.001	13.438	<.001	3.740	.014
Root water content	167.214	<.001	28.190	<.001	9.247	<.001
Shoot MDA	130.275	<.001	0.168	.918	2.954	.036
Root MDA	4.028	.048	1.533	.211	8.635	<.001
Potassium	2.359	.129	0.784	.507	0.108	.955
Phosphorus	15.409	<.001	2.750	.049	0.951	.421
Calcium	0.024	.876	2.162	.100	0.055	.983
Magnesium	17.834	<.001	0.690	.561	1.073	.366
Zinc	11.925	<.001	1.792	.156	0.550	.649
Iron	7.000	.010	1.630	.190	0.247	.863
Manganese	29.119	<.001	2.419	.073	0.137	.937
Boron	22.451	<.001	0.138	.937	0.374	.772
Protein	3.280	.081	0.238	.869	0.152	.927

3.2 | Water content and oxidative stress

With the decrease in water supplies, shoot and root water contents generally decreased up to 11% and 9%, respectively, as compared with 90% FC (significant water supply effect, $p < .001$, Table 1, Figure 4a,b). Nevertheless, water loss occurred differently depending on the plant genotype (significant genotype effect, $p < .001$), with kabuli plants generally having higher water content in shoots (8%) and desi in roots (11%). At 25% FC, the shoot water content was significantly higher in kabuli (14%, $p = .004$, *F*-test), whereas the root water content was higher in desi (20%, $p < .001$, *F*-test). Significant $G \times WS$ effects were observed in shoot and root water contents ($p = .014$ and $p < .001$, respectively). In addition, the root water content showed a moderate negative correlation with the root length and a positive correlation with root and shoot dry weights (Figure 2). Conversely, the shoot water content showed moderate to strong positive correlations with the shoot length, root and shoot fresh weights and root dry weight. The water content in shoots was also positively affected by lipid peroxidation (*viz.* MDA concentration) in both roots and shoots, while the root water content showed a moderate negative correlation with MDA concentration in shoots (Figure 2). In addition, a significant $G \times WS$ interaction was observed in shoot and root MDA ($p < .001$ and

$p = .036$, respectively, Table 1, Figure 4c,d). Compared with 90% FC, at 25% FC, the root MDA content significantly increased by 17% in kabuli ($p = .049$, *F*-test), but decreased by 30% in desi ($p < .001$, *F*-test). In general, MDA concentration in plant tissues showed slight positive correlations with plant growth parameters (root and shoot fresh and dry weights and shoot length), while being negatively correlated with plant productivity (number of pods and seeds per plant and seed weight per plant, Figure 2).

3.3 | Seed nutritional profile

No single or interactive effects of plant genotype and water supply were observed on seed K, Ca and protein concentrations, which averaged $16 \pm 0.77 \text{ mg.g}^{-1}$, $1.7 \pm 0.09 \text{ mg.g}^{-1}$ and $15 \pm 0.99\%$, respectively (Table 1, SM Figure 1). Nevertheless, a slight positive correlation was observed between K concentration and root fresh weight and between Ca and root fresh and dry weights, while the seed protein content was negatively affected by root fresh weight (Figure 2). The protein content also showed moderate negative correlations with shoot length, fresh weight and water content and root dry weight (Figure 2).

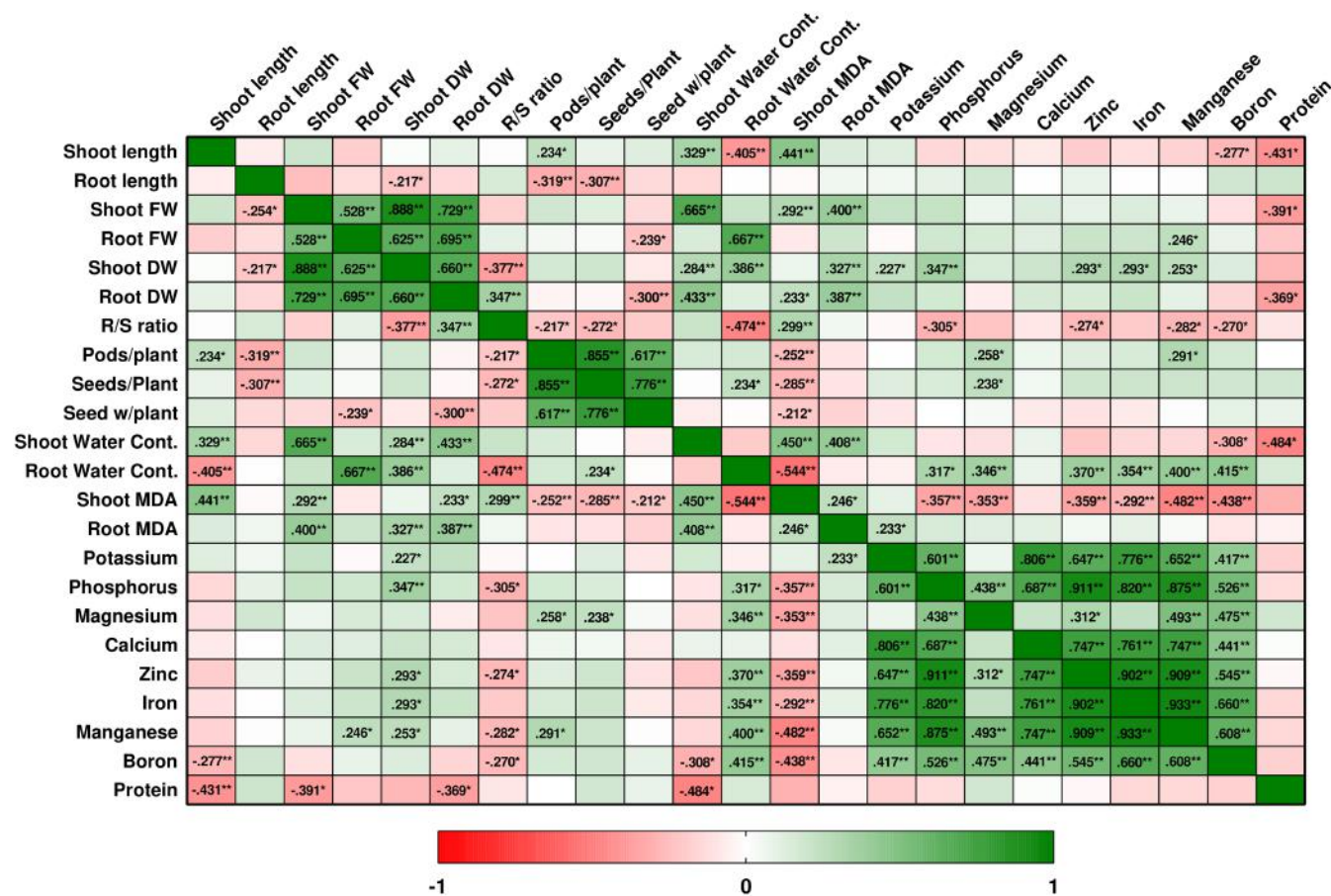


FIGURE 2 Pearson's correlation coefficients between plant growth parameters, yield, water content, oxidative stress and seed nutritional profile. Positive correlations are shown in green and negative correlations in red. Range of correlations: .70–.99—strong relationship; .30–.69—moderate relationship; .20–.29—weak positive relationship; .01–.19—negligible relationship; 0—no relationship. Coefficients of significant correlations are shown (* $p < .05$; ** $p < .01$, 2-tailed). Abbreviations: FW—fresh weight, DW—dry weight; R/S—root/shoot; w—weight; Cont.—content; MDA—malondialdehyde.

Phosphorus (P) was significantly affected by the plant genotype ($p < .001$, LSD) and the water supply ($p = .049$, LSD, Table 1, Figure 5). The average P concentration in kabuli and desi seeds was $4.8 \pm .74$ and 6.9 ± 0.76 $\text{mg} \cdot \text{g}^{-1}$, respectively, being 44% significantly higher in the latter. However, at 50% FC and 25% FC, P concentration was generally lower than at 90% FC (by 29% and 24%, $p = .007$ and $.008$, respectively).

Seed concentration of Mg, Zn, Fe, Mn and B was 43%, 58%, 33%, 55% and 50% higher in desi than in kabuli, but it was not affected by the water supply (significant plant genotype effect, $p = < .001$, $< .001$, $.010$, $< .001$ and $< .001$, respectively, Table 1, Figure 5). The average concentration of Mg, Zn, Fe, Mn and B of desi seeds was: 2.6 ± 0.26 $\text{mg} \cdot \text{g}^{-1}$, 92.9 ± 11.6 $\mu\text{g} \cdot \text{g}^{-1}$, 86.2 ± 11.3 $\mu\text{g} \cdot \text{g}^{-1}$, 45.4 ± 4.13 $\mu\text{g} \cdot \text{g}^{-1}$ and 8.1 ± 0.75 $\mu\text{g} \cdot \text{g}^{-1}$, respectively. The concentration of these minerals was generally positively correlated with the root dry weight and water content but negatively correlated with shoot MDA (Figure 2). A slight positive correlation was also observed between P, Mg and Mn and the number of pods per plant, while B was negatively correlated with the seed weight and Zn with the shoot water content (Figure 2).

4 | DISCUSSION

4.1 | Kabuli and desi chickpeas have distinct morpho-physiological strategies to cope with the low water supply

Recently, there has been an increased focus on the global need to diversify food sources due to the rise in world population and depletion of arable lands (FAO, 2017). To meet the growing demand for food, agricultural productivity must increase by 60% by 2050. However, climate change, particularly water scarcity, poses new challenges to sustainable agricultural productivity (Bourgault et al., 2020). In this context, legumes can play a key role in food security, nutrition and climate change mitigation (Calles et al., 2019; Iannetta et al., 2021). However, water stress affects several stages of chickpea growth, including germination and yield (Azimi et al., 2015; Yücel et al., 2010), and sufficient knowledge of the genotypic differences in resilience to low water availability is still needed to support crop improvement. Concomitantly, the recovery of underutilized varieties such as the black chickpea (desi) may also contribute to the preservation of

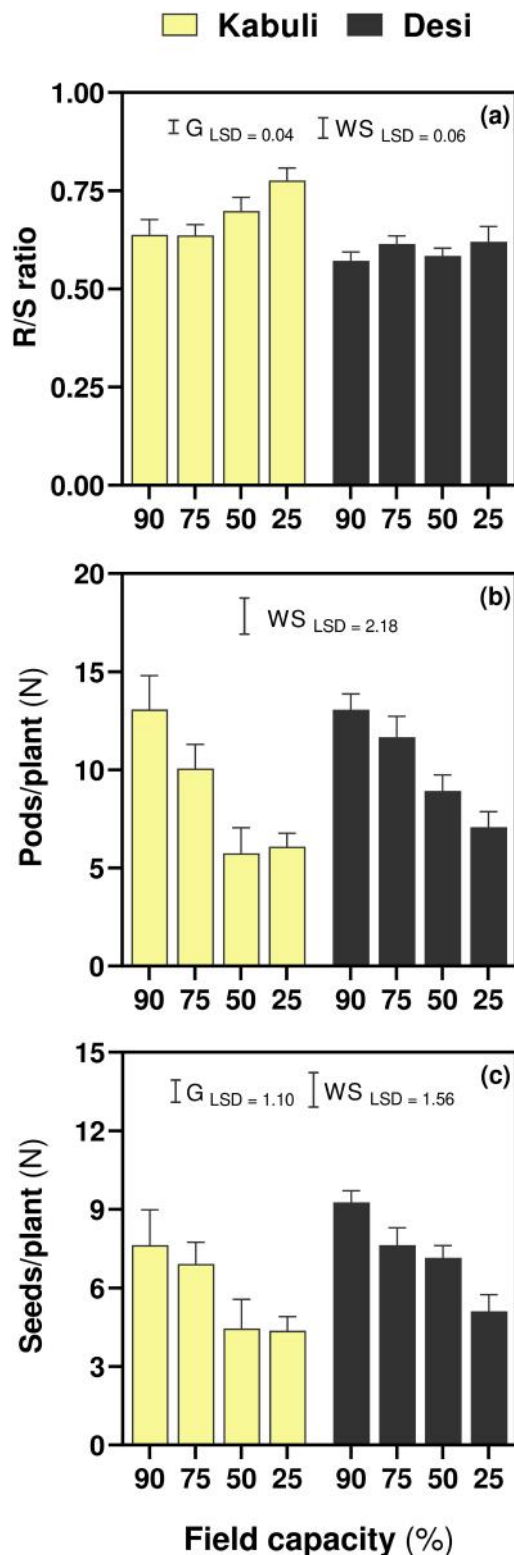


FIGURE 3 Root-to-shoot (R/S) ratio (a), number of pods per plant (b) and number of seeds per plant (c) of *Cicer arietinum* kabuli and desi plants grown to grain maturity at different water supplies: 90%, 75%, 50% and 25% of field capacity. Each value represents the mean \pm standard error. Bars represent Fisher's LSD ($p = .05$) for the significant interactions genotype \times water supply and for the independent effects (G, genotype; WS, water supply) when the interaction was not statistically significant.

biodiversity and promotion of the sustainability of agroecological systems, potentially offering greater genetic variability and resilience to adverse environmental conditions.

Here, water stress was imposed at the young plant stage (15 days after germination) and was maintained until pod maturity, resulting in root elongation in both genotypes (Figure 1b), which was accompanied by the loss of shoot and root water content (Figure 4a,b). Increased chickpea root length represents a coping mechanism against low water availability, which is often observed early in the developmental cycle in water-stressed plants as an attempt to capture more water from the soil (Lakshmi, 2005; Nadeem et al., 2019). Decreased plant height has also been observed in chickpea plants grown under rainfed conditions (Hussain et al., 2015), but here, the shoot height was not affected by the water supply, being generally higher in kabuli than desi (Figure 1b). Nevertheless, low water supply led to decreased shoot and root fresh and dry weights of both kabuli and desi (Figure 1c-f). In plants growing with low water availability, growth is usually retarded, due to the absence of transpiration by closing stomata to prevent water loss from the plant, and apoplastic barriers block the transport of water and solutes into the plant, thus leading to lower biomass accumulation (Basu et al., 2016; Feng et al., 2016). Decreased shoot and root biomass of chickpea plants seem to occur when access to water is restricted at the reproductive stages (germination, flowering and pod initiation), rather than the vegetative stages (Randhawa et al., 2014; Ramamoorthy et al., 2016), and here, we demonstrate that biomass loss starts to become visible at 75%–50% FC (Figure 1c-f). At low water supplies, kabuli had the higher root dry weight, RS ratio (Figure 3a) and shoot water content (Figure 4a) than desi, whereas desi had the higher shoot dry weight and root water content. As a result of root elongation and impaired biomass allocation, chickpeas grown at 25% FC usually show higher RS ratios (Bahavar et al., 2009), resulting from higher investment in root growth as a way to promote water uptake, which directly influences the RS ratio (Hsiao & Xu, 2000; Kuromori et al., 2018; Purushothaman et al., 2016). At 25% FC, the root water content was lower in kabuli, and conversely, the shoot water content was lower in desi (Figure 4). As such, kabuli and desi seem to have distinct biomass and water allocation strategies to adapt to the soil water content and cope with low water supplies, which may be exploited for crop improvement purposes.

Reduced chickpea yield under water stress largely results from pod abortion and impaired pod filling, which seem to occur as soon as water deficits start to develop, regardless of plant phenology (Lepoint et al., 2006; Randhawa et al., 2014). Root traits, such as root length, root biomass and RS ratio, are usually correlated with higher chickpea yield under water stress by facilitating water mining through and minimising transpiration (Kumar et al., 2012; Kashiwagi et al., 2015; Ramamoorthy et al., 2016; Ranjan et al., 2022; Sachdeva et al., 2022). However, this association does not always occur (Serraj et al., 2004; Kashiwagi et al., 2005; Zaman-Allah et al., 2011a), likely due to differences in the experimental setup and plant genotype. Here, the number of pods and seeds per plant showed a negative correlation with the root length and RS ratio, with the seed

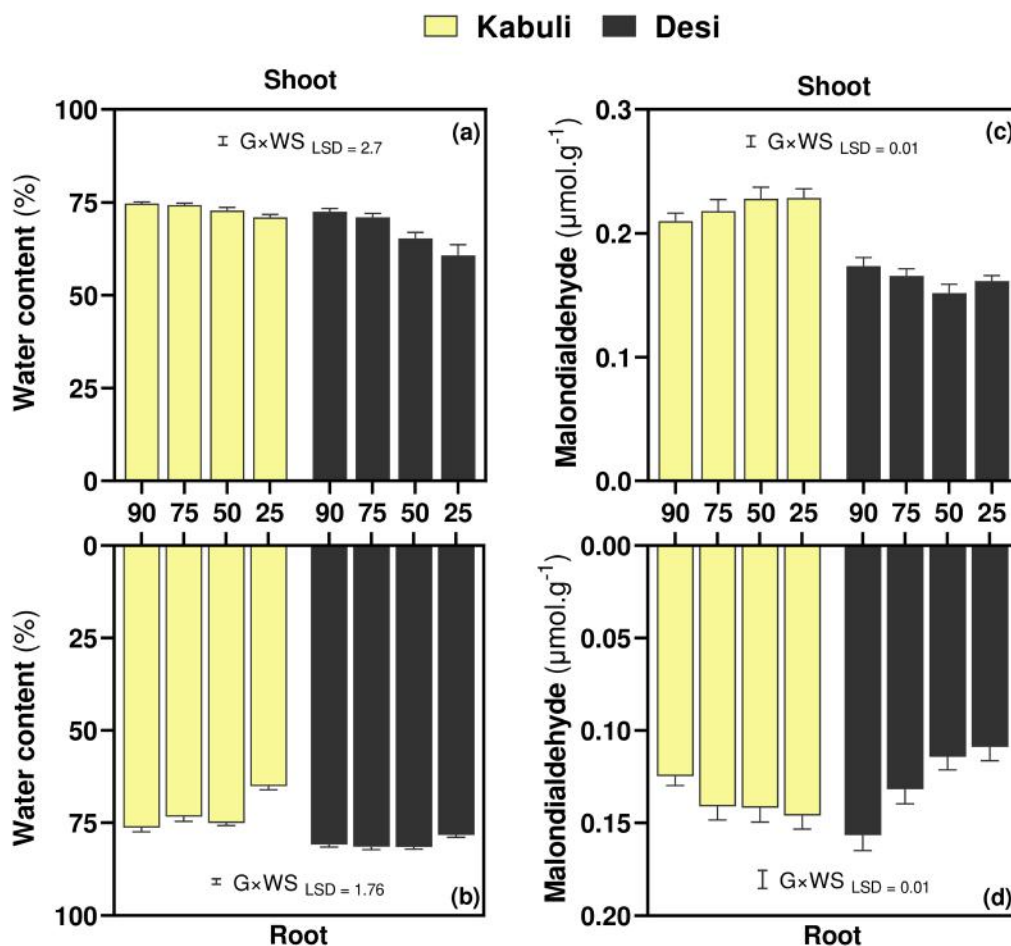


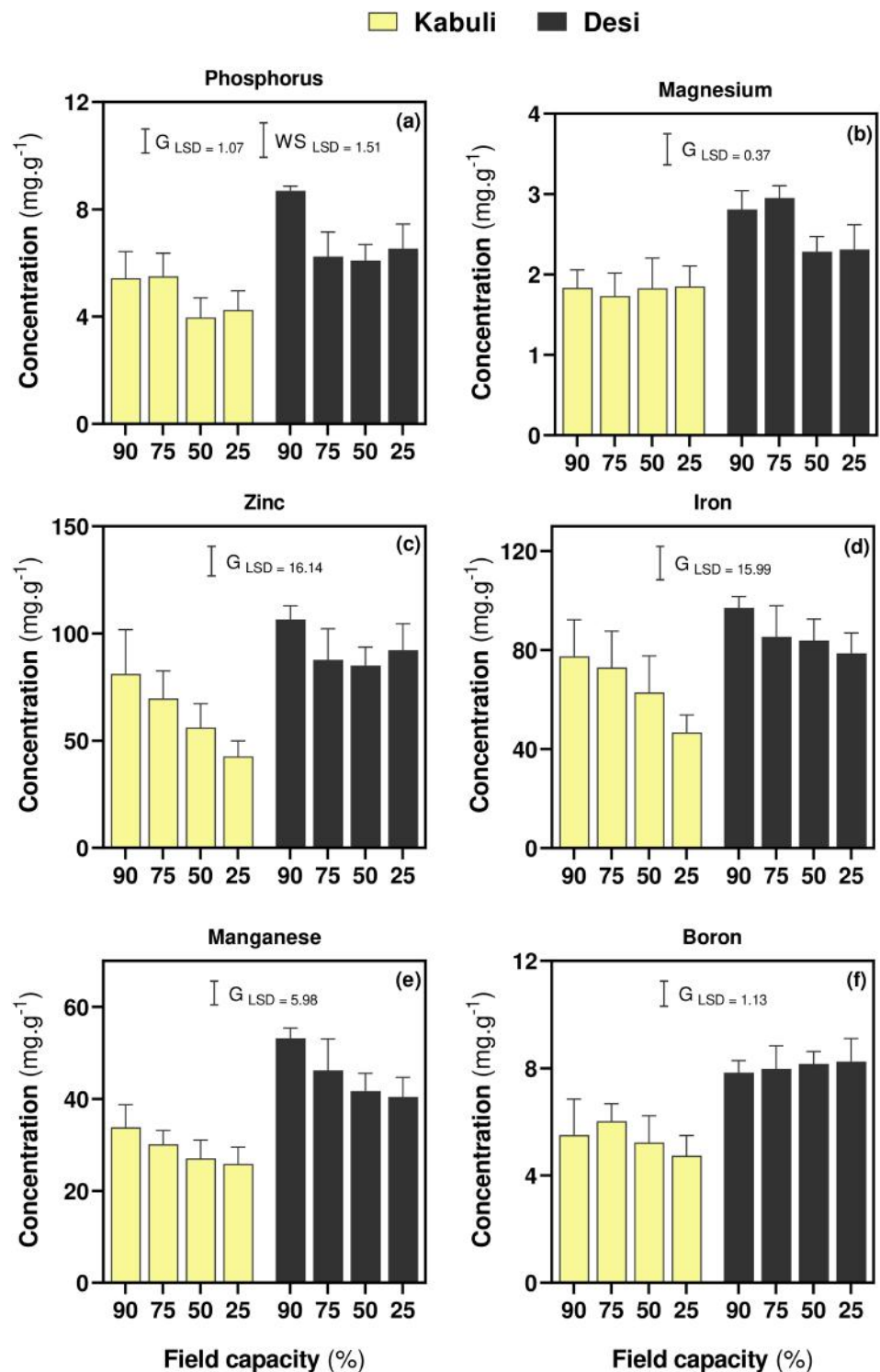
FIGURE 4 Water content (a and b) and malondialdehyde concentration (c and d) in shoots and roots of *Cicer arietinum* kabuli and desi plants grown to grain maturity at different water supplies: 90%, 75%, 50% and 25% of field capacity. Each value represents the mean \pm standard error. Bars represent Fisher's LSD ($p = .05$) for the independent effects (G—genotype, WS—water supply), as the interaction G \times WS was not statistically significant.

weight per plant also being negatively affected by root fresh and dry weights but having a positive correlation with the root water content (Figure 2). Although the number of pods and seeds per plant decreased with a decrease in water supplies (Figure 3b,c), desi, which had higher root FW and water content, produced a higher number of seeds than kabuli. This seems to corroborate that root water preservation traits are better determinants for yield in chickpeas under drought conditions (Zaman-Allah et al., 2011a, 2011b) and that desi genotypes are more efficient in sustaining higher productivity under adverse soil water conditions (Leport et al., 2006). Thus, the genus *Cicer* appears to demonstrate sufficient genetic variability to support crop improvement programmes aimed at producing larger seeds or higher seed numbers as a strategy to increase individual yield and overall crop productivity even under conditions of low water availability (Maphosa et al., 2020).

Stress-induced reactive oxygen (ROS) species play a significant role in regulating chickpea root growth and development under drought stress (Ranjan et al., 2022). These molecules are generally regarded as harmful to cell homeostasis, being neutralised by antioxidant enzymes, such as catalase, superoxide dismutase and

peroxidases (Mafakheri et al., 2011; Oberoi et al., 2014). However, they can also be beneficial for plant fitness, acting as triggers of plant defences and transiently increasing as part of the plant acclimation process (Morales & Bosch, 2019). High levels of ROS in plant cells can lead to lipid peroxidation of cell membranes, resulting in MDA accumulation and may increase or decrease in chickpeas under low water supplies depending on the plant genotype and environmental conditions (Mohammadi et al., 2011; Jameel et al., 2021). Despite the variable patterns of MDA accumulation in different chickpea genotypes, it has been proposed that drought stress at the seed-filling stage leads to higher hydrogen peroxide concentrations in plant cells, membrane instability, lipid peroxidation and MDA accumulation, to a higher extent in susceptible than in tolerant chickpea genotypes (Oberoi et al., 2014). A positive correlation has been found between MDA concentration and leaf variable fluorescence (Fv) and chlorophylls a and b, while a negative correlation was observed with leaf minimal and maximal fluorescences and shoot dry weight (Jameel et al., 2021). Here, MDA was constitutively higher in kabuli than in desi, particularly, at lower water supplies (Figure 4c,d), and positively correlated with plant growth

FIGURE 5 Concentration of phosphorus (a), magnesium (b), zinc (c), iron (d), manganese (e) and boron (f) in grains of *Cicer arietinum* kabuli and desi plants grown to grain maturity at different water supplies: 90%, 75%, 50% and 25% of field capacity. Each value represents the mean \pm standard error. Bars represent Fisher's LSD ($p = .05$) for the significant interaction genotype \times water supply.



parameters (root and shoot fresh and dry weights and shoot length and RS ratio) while having a negative correlation with plant productivity (number of pods and seeds per plant and seed weight per plant, Figure 2). This highlights the importance of plant genotype in water stress tolerance and the complex relationships between water content, lipid peroxidation and plant growth and productivity, supporting the role of MDA in stress signalling and responses to soil water content in chickpeas.

4.2 | The desi chickpea offers a richer mineral profile than kabuli, even at low water supplies

Chickpeas are an essential crop in sustainable agriculture, particularly, in semi-arid areas (Verkaart et al., 2019), but their nutritional profile can be negatively affected by water stress due to poor nutrient mobility in the soil and decreased nutrient uptake caused by impaired root growth (Samarah et al., 2004). As drought becomes more frequent in

the future, it is necessary to understand how water scarcity impacts the nutritional content of chickpeas to support human nutrition in a context of climate change. Crop irrigation at different growth stages, especially during flowering and pod-filling stages, can enhance chickpeas' nutritional properties, including protein, starch, oil and amino acid content (Varol et al., 2020). However, it is crucial to have adequate knowledge of the impact of low water supply on seed nutritional profiles to support chickpea improvement towards nutrition in drought scenarios. Gunes et al. (2006) reported significant losses in P, K, Ca, Mg, Fe, Zn, Mn and B concentrations in chickpeas grown under 40% field capacity, as compared with 60%. Seed P, K and Mg uptake was also shown to decrease in chickpeas subjected to drought stress, particularly during late growth stages (post-anthesis) (Maqbool et al., 2017). Contrastingly, other authors have reported that terminal drought stress results in increased protein, Zn, P and Ca seed concentrations (Farooq et al., 2018). A recent study evaluating 140 different chickpea genotypes growing under drought conditions seems to corroborate the latter scenario, demonstrating an average increase in grain Fe (6%) and Zn (10%) contents among all genotypes, compared to irrigated conditions (Saminieni et al., 2022). In the current work, low water supply did not impair K, Ca, Mg, Zn, Mn and B concentrations nor protein content but led to lower P concentration (Table 1, Figure 5). It has been demonstrated that drought-tolerant chickpea genotypes can absorb more nutrients than susceptible genotypes under low water supply, including P and Ca (Farooq et al., 2018; Ahmed et al., 2021). Although P and Ca were not affected by the plant genotype nor by the water supply in this study, the higher concentration of other minerals in desi plants, such as Mg, Zn, Fe, Mn and B, may provide an adaptative advantage against water stress due to their important role as co-factors in several osmoregulatory and antioxidant mechanisms (Umair Hassan et al., 2020). The higher concentration of these minerals, particularly Mg and Mn, in desi may support a higher number of pods and seeds per plant observed, likely resulting from the higher root water content and shoot dry weight observed in this genotype (Figure 2). Zinc supplementation has been demonstrated to enhance plant antioxidant activities and water use efficiency on biomass allocation, which can alleviate the effects of drought stress in chickpea plants (Khan et al., 2004; Ullah et al., 2019). However, the role of Mg and Mn supplementation in promoting plant productivity in water-poor soils is still to be uncovered. Proteins also play an essential role in plant response to drought stress by regulating various physiological processes, but the specific changes that occur in protein composition between desi and kabuli chickpeas under drought stress are not well understood. Some studies report no changes in seed protein content under water stress (Kahraman et al., 2015), which is in agreement with the current study, in which protein content was not significantly affected by the water supply (Table 1, SM Figure 1). Nevertheless, drought stress can lead to significant changes in protein expression patterns in both desi and kabuli chickpeas (Nisa et al., 2020). Under low water supply, desi chickpeas have higher levels of antioxidant enzymes, heat shock proteins and osmoprotectants, such as proline and betaine, than kabuli, although several genes involved in proline biosynthesis have also been described in kabuli

(Mahdavi Mashaki et al., 2018; Nisa et al., 2020). Overall, the specific changes that occur in protein composition in desi and kabuli chickpeas under drought stress may vary depending on the specific environmental conditions and genetic makeup of the plant. Therefore, further research is needed to better understand the impact of drought stress on the protein and mineral composition of desi and kabuli chickpeas and their ability to cope with low water availability to support the improvement of resilient genotypes that deliver higher nutritional profiles under adverse climatic conditions (Rani et al., 2020).

5 | CONCLUSION

Strategies aimed at producing nutritious food under climate change scenarios are urgently needed, including the identification of genotypes that are rich in essential nutrients with health-promoting traits even when grown under suboptimal water supplies. Here, water stress was imposed at the young plant stage, resulting in the loss of shoot and root water content and root elongation in both genotypes. Low water availability led to decreased shoot and root fresh and dry weights, but kabuli and desi seem to employ distinct biomass and water allocation strategies to cope with low water supply. Kabuli had a higher RS ratio and a lower root water content than desi, which resulted in a lower number of pods and seeds per plant, as compared with desi. This suggests that desi genotypes may sustain higher productivity under adverse soil water conditions, supporting their exploitation in crop improvement towards drought resilience. Seed P concentration was significantly affected by both plant genotype and water supply, with desi seeds having 44% higher P concentration than kabuli seeds, including at the lowest water supply. The concentration of magnesium (Mg), zinc (Zn), iron (Fe), manganese (Mn) and boron (B) in desi seeds was found to be significantly higher than that in kabuli seeds, highlighting the potential of desi chickpeas in promoting human nutrition. Understanding the physiological mechanisms behind the greater ability of desi genotypes to tolerate low water availability is crucial in developing strategies for improving crop resilience and promoting human nutrition in challenging environmental conditions. This includes investigating the genetic and metabolic pathways responsible for the observed morphological and mineral variations between different genotypes. With this knowledge, plant scientists and breeders could develop crop improvement strategies that enhance the chickpeas' nutritional value and resilience to adverse environmental conditions.

ACKNOWLEDGEMENTS

This research was financed by the European Union's Horizon 2020 Research and Innovation Programme through the project "Realising Dynamic Value Chains for Underutilised Crops" (RADIANT), Grant Agreement number 101000622 and supported by the project HSoil4Food—Healthy soils for healthy foods, co-financed by the European Regional Development Fund (FEDER) through the Northern Regional Operational, Program (NORTE-01-0145-FEDER-000066). The authors would also like to thank the scientific

collaboration under the FCT projects UIDB/50016/2020 and 2022.01903.CEECIND.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The datasets generated during this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

How to cite this article: Medeiros, J. S., Nunes da Silva, M., Carvalho, S. M. P., Santos, C. S., & Vasconcelos, M. W. (2023). Low water supply differentially affects the growth, yield and mineral profile of kabuli and desi chickpeas (*Cicer arietinum*). *Annals of Applied Biology*, 1–13. <https://doi.org/10.1111/aab.12835>