



RESEARCH ARTICLE

Comparative analysis of root system architecture and sulfur acquisition among chickpea cultivars under contrasting sulfur nutrition in hydroponic cultures

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Abstract

Sulfur (S) is an essential element for plant growth, development and defense against biotic and abiotic stresses. Sulfate assimilation in plants is demand-driven and low soil S severely impairs growth and reduces seed protein quality. Like many legumes, chickpea (*Cicer arietinum* L.) seeds are characterized by suboptimal levels of cysteine and methionine. Therefore, it is imperative to screen the cultivars for maximum sulfate assimilation and utilization efficiency. In the present study, we screened a total of sixteen chickpea cultivars based on root system architecture (RSA) under contrasting S regimes-S-starvation and S-sufficient conditions-highlighting the potential correlations between altered root plasticity, corresponding dry mass and S allocation within plants at the whole-plant level. The root morphological traits were measured and the values of RSA traits for Desi cultivars (PUSA256, PUSA547, PUSA5028 and PUSA362) and Kabuli cultivars (PUSA1003 and PUSA1053) were significantly higher even under S-starvation conditions, maximizing the concurrent increase in sulfur acquisition, indicating their sulfur efficiency. However, the fold decrease of these traits, dry mass and sulfur content at S-starvation was higher for Kabuli cultivars, coinciding with plant chlorosis, indicating their susceptibility to S-starvation stress. Additionally, cultivars such as PUSA3022, KAK2, PUSA5023, BGD112 and BGD72 displayed drastic declines in root traits and sulfur content under S-starvation, highlighting their limited capacity to adapt via root plasticity, particularly in lateral root development. These findings emphasize the importance of root morphogenetic traits in sulfur efficiency and provide a basis for breeding chickpea cultivars with improved nutrient use efficiency.

Keywords: *Cicer arietinum*; root system architecture; sulfur acquisition; sulfur efficiency; S-starvation; S-sufficiency

Introduction

Chickpea (*Cicer arietinum* L.) is one of the most extensively cultivated pulse crops in India and represents a major source of human dietary protein. Nevertheless, like other grain legumes, its protein quality is constrained by inadequate levels of sulfur-containing essential amino acids, namely methionine and cysteine (1). Sulfur nutrition plays a pivotal role in plants, with nearly 90 % of the absorbed sulfur being allocated toward the synthesis of these amino acids, which in turn constitute the sole dietary source of essential sulfur amino acids for humans and animals (2). Further, cysteine is not only used to build proteins but also serves as a key source of sulfur for many other molecules. It contributes sulfur to iron-sulfur proteins, essential coenzymes (such as coenzyme A, lipoic acid and thiamine), methyl donor, the antioxidant glutathione, defense compounds such as glucosinolates and alliin derivatives and the osmoprotectant choline-O-sulfate (3, 4). Sulfur limitation adversely affects plant growth, development and defense mechanisms, ultimately reducing crop

productivity and compromising nutritional quality (5, 6). For augmenting the levels of sulfur-containing amino acids in legume seeds, increasing sulfate assimilation and utilization efficiency is a valuable approach. It has been hypothesized that the accumulation of sulfur-poor proteins in legumes could result from their ecological adaptation to soil sulfur deficiency (7). For instance, a shift in the proteomic balance toward sulfur-poor proteins such as omega-gliadin and glutenin, at the expense of sulfur-rich proteins, was observed in wheat grown in sulfur-deprived soils.

Sulfur is absorbed mainly as sulfate ions through the root system and subsequently distributed within plants via specific sulfate transporters (8). Roots are central to plant function, contributing to nutrient and water uptake, synthesis of hormones, organic acids and amino acids and structural anchorage (9). Investigations into root-mediated nutrient acquisition are therefore critical for developing strategies to match crop productivity and optimize resource use efficiency. Root systems exhibit marked

plasticity in response to soil nutrient availability (10, 11). For instance, an apparent plasticity of root system architecture (RSA) of *Arabidopsis* was observed in homogeneous and heterogeneous provision of nitrate and phosphate, showing decreased primary root length with increasing nitrate availability while it increased with higher phosphate supply (12). Similarly, sulfur deficiency reduces fine root length, biomass and root activity, whereas adequate sulfur supply promotes lateral root development (6, 13). Sulfate application has also been shown to increase the total plant dry mass, root length and nodule biomass, as demonstrated in white clover (14). Therefore, we hypothesized that both S-starvation and S-excess may induce distinctive morphological and physiological changes in chickpea roots and leaves. These conditions likely influence sulfur uptake and metabolism differently. Assessing root system plasticity among chickpea cultivars is therefore essential to identify genotypes with superior sulfur use efficiency for breeding programs.

Materials and Methods

Plant material and growth conditions

Seeds of sixteen chickpea cultivars were surface-sterilized using 2 % (w/v) sodium hypochlorite for 2 min, rinsed thoroughly with sterile water and placed on germination paper moistened with reverse osmosis (RO) water under aseptic conditions (supplementary Table 1). After 5 days of germination, seedlings were transferred to 15 L hydroponic containers filled with Hoagland's nutrient medium (pH 6.5). The solution contained 2.4 mM calcium nitrate tetrahydrate, 3.6 mM potassium nitrate, 2 mM magnesium sulfate heptahydrate, 0.3 mM ammonium dihydrogen phosphate, 89 μ M ferrous sulfate with ethylenediaminetetraacetic acid (EDTA), 1.5 μ M cupric sulfate pentahydrate, 6 μ M zinc sulfate heptahydrate, 7.5 μ M boric acid, 6 μ M manganese chloride tetrahydrate, 1.5 μ M ammonium heptamolybdate and 0.5 μ M cobalt nitrate hexahydrate. The nutrient solution was refreshed every third day.

Plants were maintained in the National Phytotron Facility, ICAR-Indian Agricultural Research Institute, New Delhi, under controlled environmental conditions: day/night temperatures of $22 \pm 2^\circ\text{C} / 18 \pm 2^\circ\text{C}$, a 10 hr photoperiod and $45 \pm 5\%$ relative humidity. After three nutrient replacements, S-starvation treatment was imposed by replacing all sulfate salts with chloride salts of respective nutrients, while the S-sufficient condition was provided by increasing S concentration to 2 mM, standardized based on previous standardization procedures (supplementary Fig. 1 and supplementary Table 2) (6). Harvesting was carried out after six days of treatment. Fresh and dry biomass were recorded, while additional root and shoot tissues were preserved for the determination of total sulfur and sulfate anion content.

Root morphological traits

Six days after sulfur treatments, root systems were carefully spread without overlap and scanned using the WinRHIZO root scanning system (Regent Instruments, Quebec, Canada) at a resolution of 600 dpi. Parameters of root system architecture, including total root length (TRL), total root surface area (TRSA), total root volume (TRV), mean root diameter (MRD) and lateral root length (LRL) were recorded.

Estimation of total sulfur content

Dried and powdered samples (500 mg) from root and shoot tissues were digested with 5 mL of a nitric-perchloric acid mixture (4:1, v/v)

on a hot plate until dense white fumes were observed. After cooling, the digest was diluted with 25 mL of deionized water and filtered through Whatman filter paper. Sulfur concentration was determined by the turbidimetric method using acacia gum and barium chloride (15).

Sulfur efficiency (SE) was calculated as:

$$\text{SE (\%)} = \frac{\text{Dry matter yield at S starvation}}{\text{Dry matter yield at S sufficient}} \times 100 \quad (\text{Eqn. 1})$$

Quantification of sulfate ions

For sulfate determination, frozen tissues were homogenized in demineralized water (10 mL g⁻¹ fresh weight) using an Ultra-Turrax homogenizer for 30 sec at 0 °C. The homogenate was filtered through Miracloth, boiled at 100 °C for 10 min and centrifuged at 30000 \times g for 15 min at 0 °C. The supernatant was analyzed using a Shimadzu Nexera X2 UPLC system equipped with a Shim-pack Bio IEX QNP column (50 \times 4.6 mm; Shimadzu, USA). Separation was achieved with 25 mM potassium biphthalate buffer (pH 4.3) containing 0.02 % (w/v) NaN₃ as the mobile phase at a flow rate of 1 mL min⁻¹. Sulfate was detected using a Knauer differential refractometer (Model 98.00, Bad Homburg, Germany) maintained at 25 °C. Chromatographic peaks were processed using a Shimadzu Chromatopac C-R8A data processor (Kyoto, Japan), following the methods mentioned elsewhere (16, 17).

Statistical analysis

All experiments were conducted in triplicate and data are presented as mean and standard error (SE). Statistical significance was assessed using one-way analysis of variance (ANOVA), followed by Duncan's multiple range test, performed with SPSS 20.0 software (SPSS Inc., Chicago, IL, USA). GraphPad Prism 8 was used for data visualization. Significance was considered at $p < 0.05$.

Results

To determine the sulfur efficiency of chickpea cultivars, we carried out a comparative analysis of seedlings, investigating biomass production, total sulfur content and root system architecture under previously optimized S-sufficient (2 mM SO₄²⁻) and S-starvation (0 mM SO₄²⁻). The S-sufficient condition significantly improved plants growth performance, enhancing biomass and root morphology traits such as total root length (TRL), total root surface area (TRSA), total root volume (TRV) and lateral root length (LRL), except for mean root diameter (MRD), which did not differ significantly between treatments. In contrast, S-starvation consistently hindered the overall root architecture, including all the root morphological traits and biomass. It was also observed that cultivar-specific differences in these traits were evident in response to sulfur nutrition. Desi chickpea cultivars (PUSA256, PUSA547, PUSA5028 and PUSA362) displayed higher TRL, TRSA and TRV even under S-starvation conditions, whereas all the Kabuli cultivars, except PUSA1003 showed a pronounced reduction in these traits between the treatments (Table 1). Additionally, the major root parameter contributing to efficient nutrient acquisition, LRL, was markedly lower in PUSA3022, KAK2, PUSA5023, BGD112 and BGD72 (287.48 \pm 0.64, 296.03 \pm 0.58, 306.55 \pm 0.92, 327.12 \pm 0.69 and 329.94 \pm 0.52, respectively), suggesting their reduced efficiency in sulfur uptake from the rhizosphere under S-starvation. This altered root plasticity substantially influenced sulfate acquisition and plant

Table 1. Impact of contrasting sulfur treatment on root system architecture of chickpea cultivars raised in hydroponics

Cultivars	Total root length (cm)		Total root surface area (cm ²)		Average root diameter (mm)		Total root volume (cm ³)		Lateral root length (cm)	
	S-sufficient	S-starvation	S-sufficient	S-starvation	S-sufficient	S-starvation	S-sufficient	S-starvation	S-sufficient	S-starvation
BGD72	731.68±0.88	485.83±0.59	111.03±0.41	75.43±0.35	0.48±0.01	0.51±0.01	1.34±0.05	0.93±0.05	531.17±0.93	329.94±0.52
PUSA547	916.01±0.73	660.97±0.87	129.36±0.37	99.46±0.14	0.45±0.01	0.48±0.02	1.46±0.06	1.19±0.03	720.54±0.71	482.33±0.68
PUSA362	889.07±0.75	632.81±0.71	127±0.12	102.3±0.35	0.45±0.01	0.52±0.04	1.45±0.15	1.33±0.11	663.56±0.71	398.02±0.8
PUSA256	998.55±0.91	732.62±0.63	142.37±0.52	104.33±0.61	0.45±0.01	0.45±0.03	1.62±0.07	1.19±0.11	759.11±0.9	569.24±0.78
BGD112	785.84±0.96	481.64±0.39	116.93±0.52	73.73±0.46	0.47±0.01	0.49±0.04	1.39±0.07	0.91±0.13	586.95±0.91	327.12±0.69
PUSA5028	909.77±0.88	653.59±0.78	136.01±0.04	94.8±0.13	0.48±0.02	0.46±0.03	1.62±0.04	1.1±0.06	657.44±0.64	494.79±0.88
PUSA1005	774.29±0.46	563.19±0.57	111.05±0.43	80.54±0.31	0.46±0.02	0.46±0.04	1.27±0.07	0.92±0.08	599.79±0.74	429.2±0.86
PUSA391	795.06±0.76	528.62±0.8	118.8±0.88	80.5±0.05	0.48±0.03	0.49±0.03	1.42±0.13	0.98±0.05	572.5±0.58	384.3±0.52
KAK2	670.11±0.16	407.83±0.57	100.5±0.13	62.14±0.63	0.48±0.01	0.49±0.04	1.2±0.03	0.76±0.1	491.09±0.96	296.03±0.58
PUSA1053	787.99±0.87	563.47±0.88	119.36±0.48	84.01±0.37	0.48±0.01	0.47±0.02	1.44±0.06	1±0.06	574.79±0.82	415.6±0.92
PUSA1003	878.21±0.54	665.45±0.51	126.94±0.22	107.04±0.58	0.46±0.02	0.51±0.04	1.46±0.06	1.38±0.13	677.29±0.79	444.09±0.8
PUSA3000	754.83±0.59	557.53±0.38	115.98±0.53	83.29±0.32	0.49±0.02	0.48±0.03	1.42±0.08	0.99±0.07	538.07±0.71	406.6±0.57
PUSA3022	743.25±0.62	398.07±0.58	112.8±0.31	60.92±0.67	0.48±0.02	0.49±0.03	1.37±0.06	0.75±0.11	550.32±0.75	287.48±0.64
PUSA1105	735.73±0.84	550.48±0.35	113.16±0.19	87.39±0.17	0.49±0.02	0.51±0.01	1.39±0.01	1.11±0.04	537.39±0.86	391.03±0.42
PUSA2085	733.98±0.97	519.49±0.72	110.36±0.58	78.69±0.61	0.48±0.01	0.5±0.01	1.32±0.08	0.95±0.08	543.03±0.73	375.74±0.64
PUSA5023	700.42±0.69	456.62±0.83	112.36±0.37	70.51±0.64	0.5±0.04	0.49±0.04	1.44±0.07	0.87±0.12	479.29±0.94	306.55±0.92

growth, as reflected by differences in dry matter accumulation and total sulfur content in the shoot, root and whole plant among cultivars (Fig. 1 & 2). Interestingly, plant dry weight, including both shoot and root, was strongly associated with sulfur nutrition and correlated with the sulfur efficiency of cultivars. Furthermore, the significant reduction in root dry weight under S-starvation and variation in root sulfur efficiency among the cultivars highlighted the primary role of roots in acquiring nutrients from the rhizosphere.

A comparable trend in total sulfur and sulfate content was observed between the Kabuli cultivars (PUSA1003 and PUSA1053) and all the Desi cultivars under S-sufficient conditions. However, under the S-starvation, the total sulfur and sulfate content of both shoot and root decreased significantly, by more than 35 % and 30 %, respectively, in all Kabuli varieties except PUSA1003 and PUSA1053, which correlated with their pronounced chlorotic symptoms and premature defoliation after 5 days after initiation of sulfur starvation (supplementary Fig. 2). A substantial reduction in total sulfur content was also evident in PUSA5023, KAK2 and PUSA3022 under S-starvation, where S acquisition declined by approximately 50 %. This reduction was directly reflected in impaired growth parameters, including reduced plant height, stem thickness and leaf size (supplementary Fig. 2), emphasizing that Desi cultivars possess higher sulfate uptake efficiency than Kabuli cultivars. Interestingly, the relative changes in growth traits and sulfur content were consistently highest in PUSA256, PUSA547, PUSA5028 and PUSA362 in response to sulfur nutrition, suggesting their superior capacity to withstand sulfur deficiency via enhanced sulfate uptake and assimilation (Fig. 1).

Discussion

Sulfur requirements vary between plant species; among crop plants, members of the Brassicaceae are the most S-dependent family, followed by Fabaceae and Poaceae, with the relative requirement being mirrored in the S concentration of their seeds (18). Hence, the paradigm explaining how plants combat sulfur starvation remains largely empirical, allowing for the screening of cultivars with high sulfur uptake/use efficiency. In the present study, chickpea cultivars were cultivated hydroponically under S-sufficient (2 mM) and S-deficient (0 mM) conditions to assess the effects on growth and metabolism. The phenotypic symptoms of sulfur starvation are primarily observed in younger parts of plants due to their limited S mobility (supplementary Fig. 2). Further, the degree of symptoms, including chlorosis in young leaves, growth retardation, stem elongation, thin and woody stem and reduction in leaf size, depends on plant genotype (6, 19). Similarly, S-starvation in chickpea also resulted in a significant reduction in the dry weight of the shoot and root (Fig. 1A and B). The chlorotic symptoms were pronounced among Kabuli cultivars, leading to a corresponding change in the SE of cultivars (Fig. 1D). Additionally, a drastic reduction in total sulfur and sulfate content in both shoot and root was observed under S-starvation and further, it was significant among the low SE varieties, PUSA5023, KAK2 and PUSA3022 (Fig. 2).

Plant root systems serve as the primary organ for water and nutrient uptake and are capable of modifying their three-dimensional architecture in response to the water and nutrient availability and distribution in the soil (20). The architecture of root systems in response to deficiencies in nitrogen and phosphorus has been extensively investigated (10). It has been reported that nitrogen

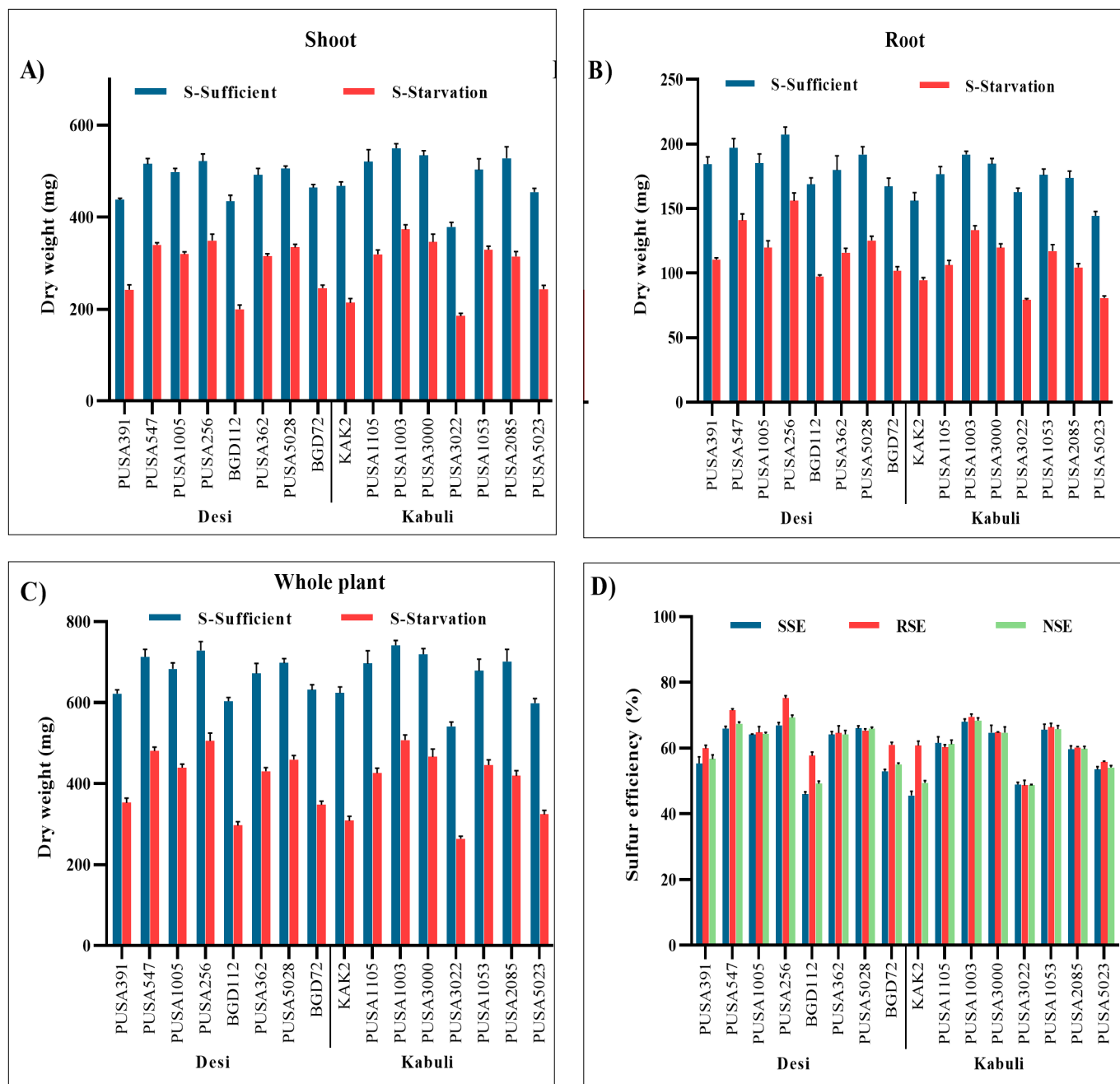
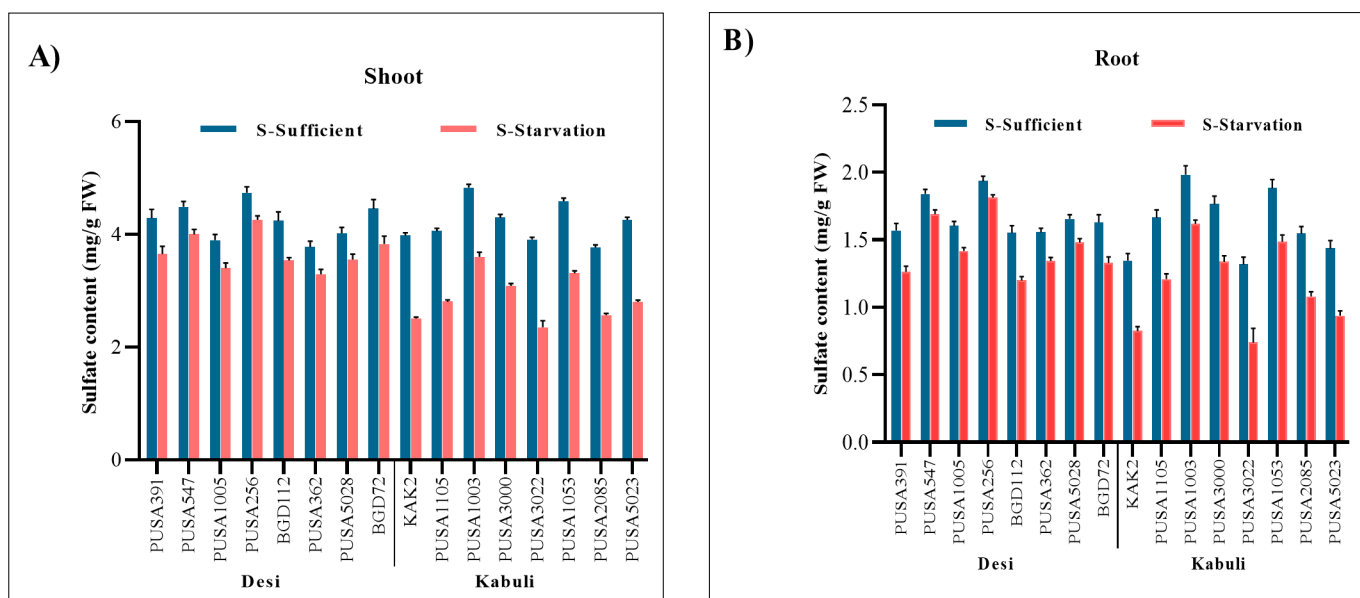


Fig. 1. Morpho-physiological responses of chickpea cultivars under S-starvation (0 mm SO_4^{2-}) and S sufficient (2 mm SO_4^{2-}). (A) shoot dry weight, (B) root dry weight, (C) total plant dry weight, (D) sulfur efficiency.



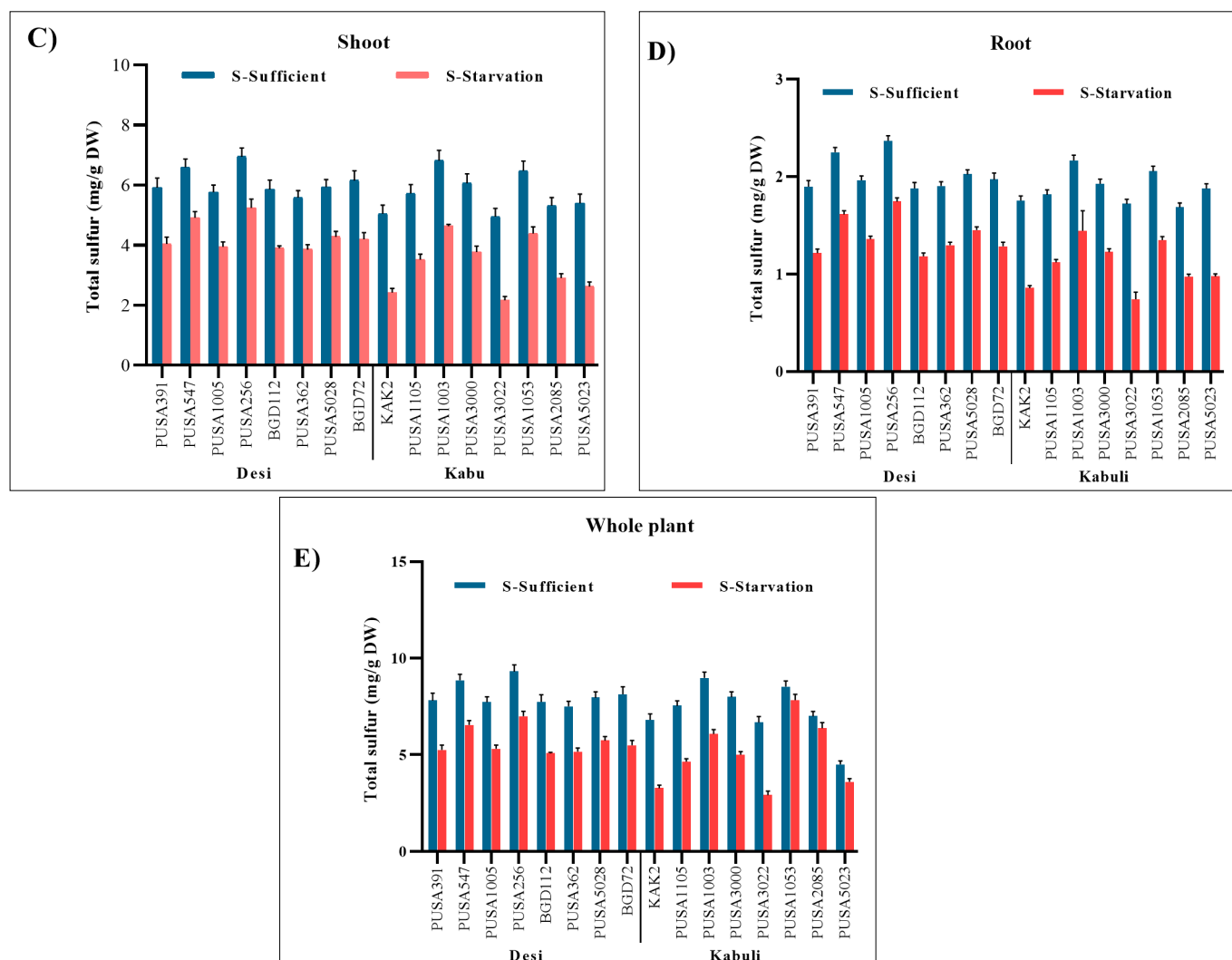


Fig. 2. Sulfur metabolic flux of chickpea cultivars under S-starvation (0 mm SO_4^{2-}) and S sufficient (2 mm SO_4^{2-}). (A) shoot sulfate content, (B) root sulfate content, (C) total shoot sulfur, (D) total root sulfur, (E) total plant sulfur.

-efficient maize cultivars exhibit significantly greater dry matter accumulation, nitrogen uptake and grain yield compared to nitrogen-inefficient cultivars grown under the same soil nitrogen levels (21). However, studies focusing on the effect of S deficiency on root system architecture have been limited (6, 18, 22, 23). In *Arabidopsis*, S-starvation significantly affected the lateral root growth in terms of both the number and density of lateral roots (24). Another critical aspect of the root system is the root surface area that the root explores. In particular, increasing the length and number of root hairs significantly increases the root surface area, which can greatly affect the plant's absorption of fixed nutrients. Lettuce and soybean treated with a high concentration of sulfur showed better root parameters than plants treated with a low concentration of sulfur (6, 23). Our results corroborate the same, where TLA, TSRA, RV and LRL values were observed to be high under S-sufficient conditions. Conversely, S-starvation limits shoot growth rather than root architecture (25). Therefore, the reprogramming of growth patterns to adapt to nutrient availability in turn depends on the developmental stage (26).

Conclusion

Alterations in RSA are a consistent response to sulfate availability and represent an effective adaptive mechanism under nutrient stress conditions. As observed in our study, S-efficient cultivars (PUSA256, PUSA547, PUSA5028 and PUSA362) exhibited

significantly higher sulfur uptake and greater root dry weight under both sulfur-sufficient and sulfur-deficient conditions compared to S-inefficient cultivars. These findings indicate that root morphogenetic traits (TRL, TRSA, TRV and LRL) are critical determinants of S accumulation efficiency in plants. Morphogenetic changes in roots, including variations in elongation and irregular branching patterns, are closely associated with auxin biosynthesis. Such plasticity in root development provides a valuable strategy for enhancing mineral nutrient uptake efficiency. Further, these S-efficient chickpea cultivars pave the way to breed for increased seed protein quality.

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Authors' contributions

NCR was involved in investigation, data curation, formal analysis, validation, visualization and writing of the original draft. DR contributed to investigation, data curation and formal analysis. DPG, SM, PKC and MD participated in investigation and data curation. NB provided resources. SG and RRR were responsible for conceptualization and methodology development. RP contributed

to investigation and CB supported the study through conceptualization and resources. RG contributed to writing, review and editing, whereas VT was responsible for conceptualization, methodology, supervision, writing, review and editing. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors do not have any conflict of interests to declare.

Ethical issues: None

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