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Article

Influence of Ultraviolet Radiation on the Non-Enzymatic Antioxidant System in Fenugreek

Hamed M. El-Shora[1], Ryad A. Ghazy[2], Fathy A. El-Husseiny[3], Ghada E. Zaky[4], Aya A. Attya[5]

1. Department of Botany, Faculty of Science, Mansoura University, Egypt
2,3,4. Department of Physics, Faculty of Science, Tanta University, Egypt
5. Department of Physics, Faculty of Science, Mansoura University, Egypt
*Correspondence: riyadghazy@yahoo.com, Shoraem@yahoo.com, ghada_mahmoud93@yahoo.com, Ayoya51@gmail.com

Abstract: The present study indicates that UVC priming significantly enhances the accumulation of total phenols and α-tocopherol in germinated fenugreek seeds. This increase correlates with the upregulation of key phenylpropanoid pathway enzymes (PAL, CHS, CHI, and F3H), which are essential for flavonoid biosynthesis. Additionally, UVC treatment significantly elevated levels of vital antioxidants and osmoprotectants—including ascorbic acid, proline, and reduced glutathione (GSH)—resulting in correspondingly higher DPPH and ABTS radical-scavenging capacities. Finally, metabolic profiling revealed that UVC exposure effectively alters the phytochemical composition of the seeds, inducing the synthesis of novel metabolites while downregulating others.

Keywords: UVC priming, Fenugreek germination, Phenylpropanoid pathway, Antioxidant activity, Phytochemical profiling

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Introduction

Ultraviolet (UV) radiation lies between X-rays and visible light on the electromagnetic spectrum. Although highly energetic UVC wavelengths are almost entirely absorbed by the stratospheric ozone layer, substantial amounts of UVA and a fraction of UVB radiation penetrate to the Earth's surface, exerting profound biological impacts. Within the terrestrial UV spectrum, UVB is widely regarded as the most deleterious, acting as a principal environmental risk factor for the pathogenesis of human cutaneous malignancies [1].

At the cellular level, numerous essential macromolecules—including nucleic acids, aromatic amino acids, and membrane-bound polypeptides—act as endogenous chromophores that readily absorb UV radiation. Consequently, excessive UV exposure precipitates widespread macromolecular degradation and severe cytotoxicity. UV radiation is classically categorized as a complete carcinogen due to its pleiotropic, non-selective cellular toxicity combined with its potent capacity to drive direct genomic mutagenesis [2][3].

Photosystem II (PSII) is well documented as acutely susceptible to UV-mediated photoinhibition. Primary targets of this UV-induced impairment include the manganese cluster of the oxygen-evolving complex, essential donor-side tyrosines, and the quinone electron acceptors. Disruption of these critical cofactors ultimately precipitates the enhanced breakdown and turnover of the core D1 and D2 reaction center proteins**.**

Augmented UV irradiation exerts both direct and indirect deleterious effects on cellular integrity by driving the degradation and structural modification of essential DNA, proteins, and lipids. Pathophysiologically, in plant models, this cellular damage precipitates substantial declines in photosynthetic performance, stunted growth, and altered morphological phenotypes [4]**.**

UV radiation profoundly alters the cellular landscape of plant-derived tissues. Excessive irradiance leads to severe molecular damage, characterized predominantly by membrane lipid peroxidation and inhibition of vital cellular enzymes. Susceptibility to this damage depends on the cell wall's structural properties, which determine the depth of UV penetration. Moreover, cellular vulnerability is heavily influenced by tissue complexity and genomic architecture, with variations in DNA sequence, such as low pyrimidine content, associated with increased susceptibility to UV photon absorption **[5].**

Elevated levels of harmful UV irradiance present a severe abiotic challenge for photosynthetic life. Extensive research indicates that elevated UV flux at Earth's surface stimulates excessive production of reactive oxygen species (ROS). This oxidative burst effectively perturbs cellular redox homeostasis by overriding antioxidant defense mechanisms and inflicting structural damage upon the photosynthetic apparatus [2]**[6].**

While ROS are generated continuously as inevitable metabolic byproducts, they also accumulate rapidly as a universal stress response in plants facing multifaceted environmental fluctuations. This reactive collective includes both non-radical derivatives, such as hydrogen peroxide (H_2O_2) and singlet oxygen ($^1O_2$), and highly unstable free radicals, notably the superoxide anion ($O_2\bullet^-$) and hydroxyl radical ($\bullet OH$). Individual ROS exhibit distinct physicochemical properties that dictate their intracellular stability, target reactivity, and transmembrane diffusion kinetics **[7].**

Thus, the dynamic regulation of H_2O_2-metabolizing enzymes is fundamental to bolstering plant resilience against environmental stressors **[8].** Beyond enzymatic mechanisms, a diverse suite of non-enzymatic scavengers - such as phenolics, flavonoids, proline, α-tocopherol, ascorbic acid (AsA), and reduced glutathione (GSH) - is vital for sustaining cellular redox balance. AsA and GSH act as the principal non-enzymatic antioxidants, with their steady-state levels continuously regenerated by a specific enzymatic cascade comprising ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR). Ultimately, this integrated ascorbate–glutathione (AsA–GSH) cycle functions as the most robust and efficient mechanism for H_2O_2 quenching in the plant kingdom **[2][9].**

As a rich source of bioactive compounds—including vitamins, iron, and β-carotene—fenugreek (Trigonella foenum-graecum) holds considerable therapeutic value. Preclinical studies have validated its multi-targeted pharmacological profile, demonstrating antimicrobial, antiviral, anti-inflammatory, and antioxidant effects. Notably, its haematinic activity supports its widespread use as a functional food **[10].**

The current study seeks to characterize the biochemical impact of UVC irradiation on fenugreek metabolism. We specifically aimed to determine how UVC priming modulates the activity of enzymatic and non-enzymatic antioxidant systems, ultimately evaluating its efficacy as a strategy to enhance the antioxidant bioactivity of fenugreek seeds.

Materials and Methods

Plant Material and Irradiation Setup

The experimental plant material, *Trigonella foenum-graecum* (fenugreek) seeds, was obtained from the Egyptian Ministry of Agriculture. UVC priming was conducted using a custom-designed irradiation chamber equipped with two 15 W fluorescent UVC lamps (emission range: 200–280 nm). To ensure uniform, isotropic illumination, the chamber was fully lined with reflective aluminum surfaces, as previously described by **El-bediwi et al. [11].**

Enzyme Extraction

Enzymatic extracts were prepared from germinated seeds following the protocol of **El-Shora [12].** Tissue samples were thoroughly homogenized in a chilled mortar at 4 °C using 50 mM sodium phosphate buffer (pH 7.0). The homogenate was centrifuged at 5,000 rpm for 15 min, and the resulting supernatant was recovered and utilized as the crude enzyme source for subsequent assays.

Determination of Non-Enzymatic Antioxidants

Total phenolic content was quantified using the Folin–Ciocalteu method [13]. Extracts (100 mg tissue in 100 mL deionized water) were reacted with 2N Folin–Ciocalteu reagent and 20% Na_2CO_3. After a 2-hour incubation, absorbance was measured at 765 nm, and concentrations were calculated against a gallic acid calibration curve. Total flavonoid content was determined via the aluminum chloride colorimetric assay by measuring absorbance at 415 nm [14]. Total flavonol content was assessed using the quercetin equivalent method described by **Kumarn & Karunakaran (2007)** and modified by **Mbaebie et al. (2012),** with absorbance recorded at 440 nm.

Assay of Phenylpropanoid and Flavonoid Biosynthetic Enzymes

Phenylalanine ammonia-lyase (PAL; EC 4.3.1.24) activity was measured by monitoring the conversion of L-phenylalanine to cinnamate at 290 nm [15][16]. Cinnamate-4-hydroxylase (C4H; EC 1.14.13.11) activity was quantified according to **Lamb & Rubery** by measuring the absorbance change at 290 nm after incubation at 37 °C. Chalcone synthase (CHS; EC 2.3.1.74) activity was determined spectrophotometrically at 370 nm using the method of Obinata et al. (2003) with chalcone as the substrate. Chalcone isomerase (CHI; EC 5.5.1.6) activity was assayed by monitoring the decrease in absorbance at 381 nm due to the formation of tetrahydroxychalcone [17]. Flavonoid 3-monooxygenase (F3M; EC 1.14.14.82) activity was assessed by quantifying quercetin formation from kaempferol [18].

Determination of Specific Antioxidant Metabolites

Ascorbic acid (AsA) was extracted using ice-cold trichloroacetic acid (TCA) and quantified via the 2,4-dinitrophenylhydrazine (DTC) method [19], with absorbance read at 520 nm. Free proline was determined using the acid-ninhydrin method described by **Khalil et al. [20]**, with absorbance recorded at 510 nm. Tocopherol (Vitamin E) content was assayed according to **Hira et al. [21]** using the Emmerie–Engel reaction, and absorbance was measured at 520 nm. Total and oxidized glutathione (GSSG) were quantified using the DTNB-glutathione reductase recycling assay [22]. Reduced glutathione (GSH) was calculated as the difference between total glutathione and GSSG.

In Vitro Radical Scavenging Assays

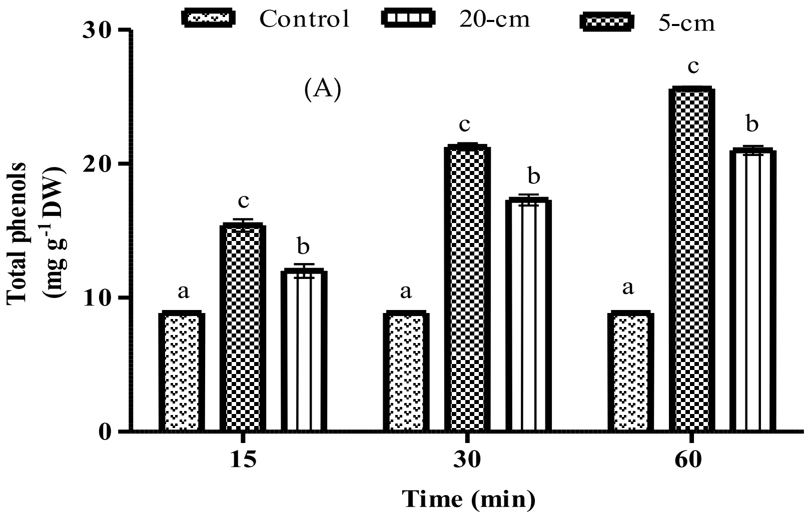
Radical scavenging capacity was evaluated using the 2,2-diphenyl-1-picrylhydrazyl (DPPH) assay as described by Valko et al. (2007), with absorbance measured at 518 nm. The ABTS radical cation decolorization assay was performed according to Awika et al. (2003), with absorbance recorded at 734 nm. For both assays, inhibition percentage was calculated relative to the control.

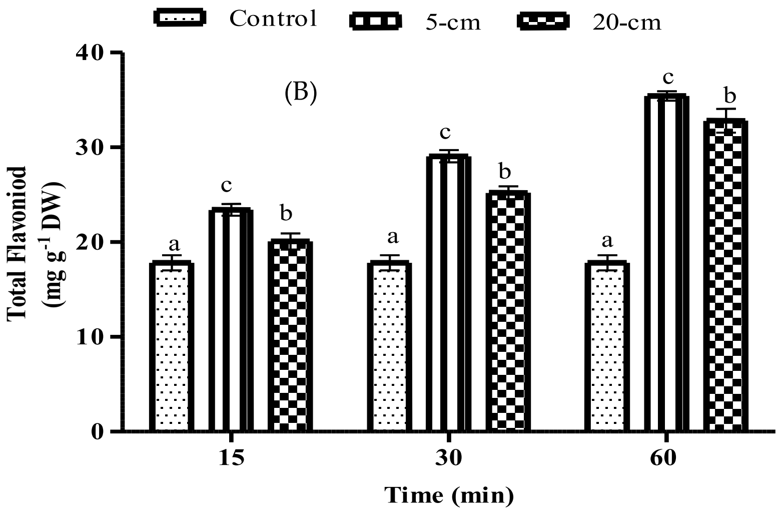
HPLC Profiling of Phenolic Compounds

Phenolic constituents were analyzed using an Agilent 1260 HPLC system equipped with an Eclipse C18 column (4.6 × 250 mm, 5 µm). Separation was achieved using a mobile phase of water (A) and 0.05% trifluoroacetic acid in acetonitrile (B) at a flow rate of 0.9 mL/min. The gradient program was: 0–5 min (80% A), 5–8 min (60% A), 8–12 min (60% A), and 12–15 min (82% A). The column was maintained at 40 °C, and elution was monitored at 280 nm [23].

Statistical Analysis: The study used a completely randomized experimental design. Data represent the mean ± standard deviation (SD) of at least three replicates. Statistical significance was evaluated via one-way analysis of variance (ANOVA) followed by Duncan's multiple range test ($p \leq 0.05$) using COSTAT software (version 6.3).

Results


Control
20-cm
5-cm
(A)
Total phenols
(mg g^{-1} DW)
30
20
10
0
a
c
b
a
c
b
a
c
b
15
30
60
Time (min)


Control
5-cm
20-cm
(B)
Total Flavoniod
(mg g^{-1} DW)
40
30
20
10
0
a
c
b
a
c
b
a
c
b
15
30
60
Time (min)

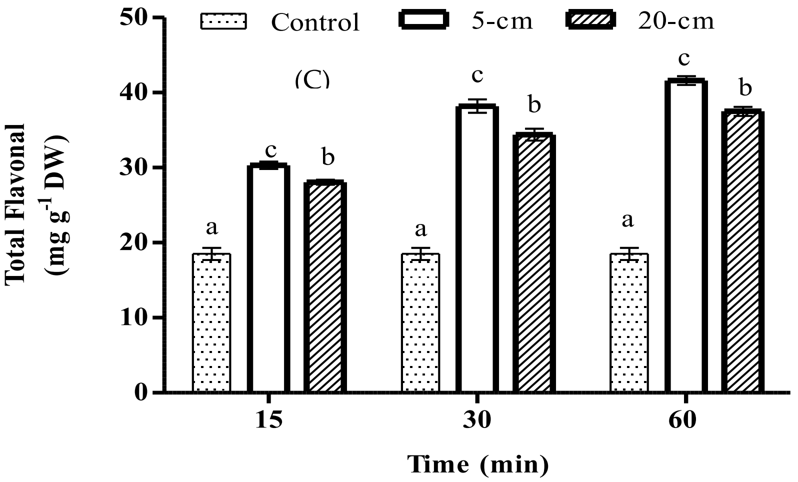

Control
5-cm
20-cm
(C)
Total Flavonal
(mg g^{-1} DW)
50
40
30
20
10
0
a
c
b
a
c
b
a
c
b
15
30
60
Time (min)

Fig. 1: Effect of UVC on the content of (A): Total phenols, (B): Total flavonoids, and (C): Total flavonols in germinated seeds of fenugreek.

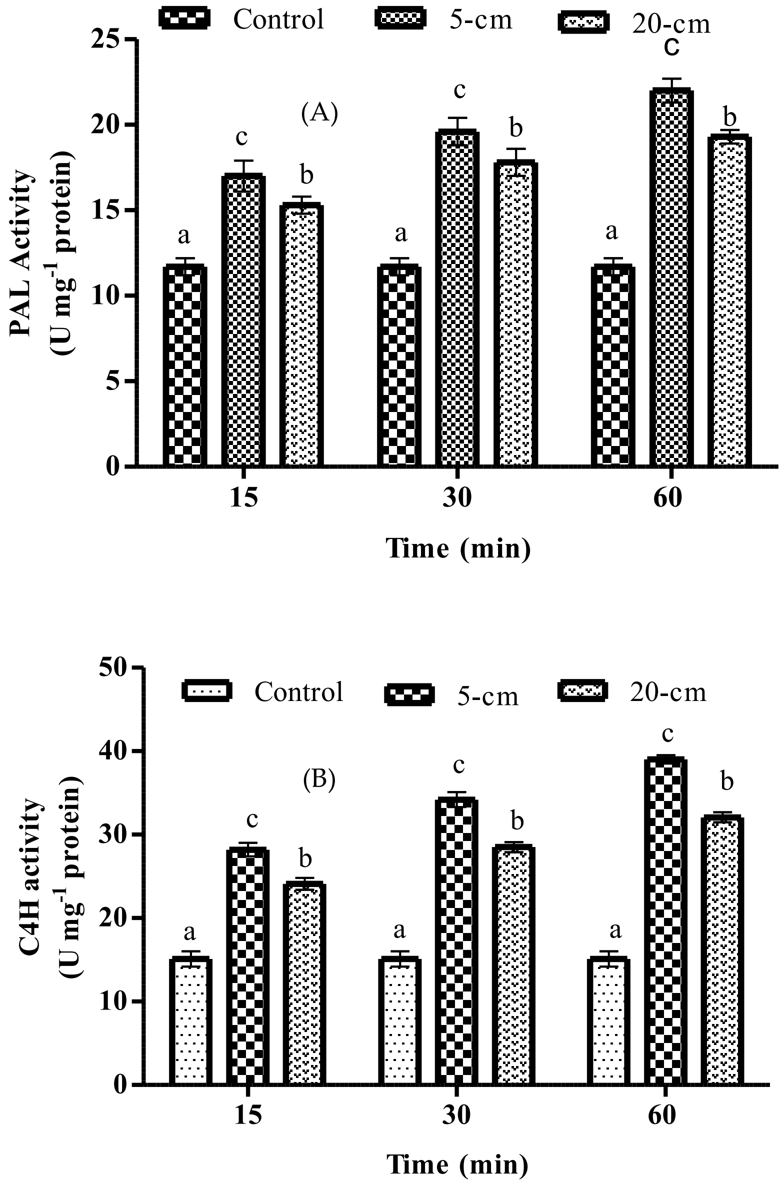
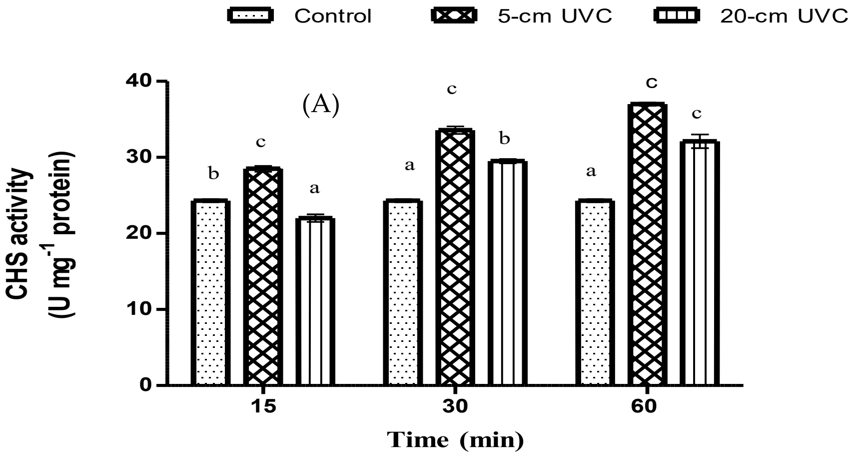
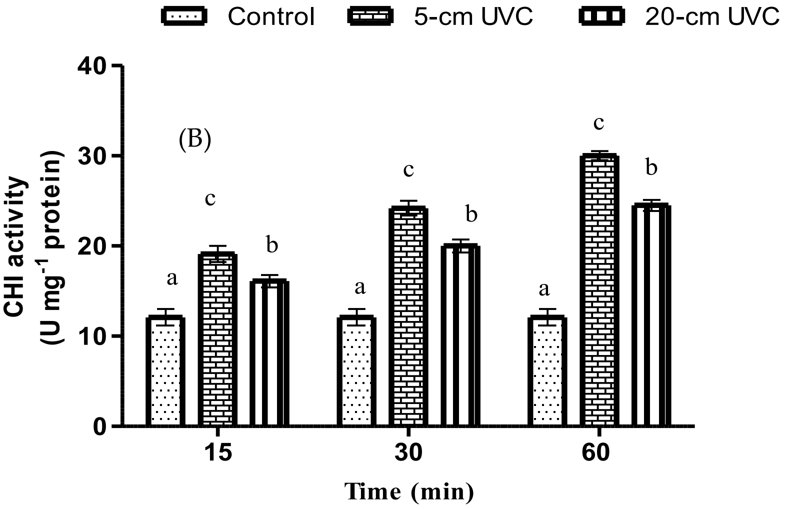


Fig. 2: Effect of UVC on the activities of (A) PAL and (B) C4H in germinated seeds of fenugreek.


Control
5-cm UVC
20-cm UVC
(A)
CHS activity
(U mg^{-1} protein)
0
10
20
30
40
b
c
a
a
c
b
a
c
c
15
30
60
Time (min)


Control
5-cm UVC
20-cm UVC
(B)
CHI activity
(U mg^{-1} protein)
0
10
20
30
40
a
c
b
a
c
b
a
c
b
15
30
60
Time (min)

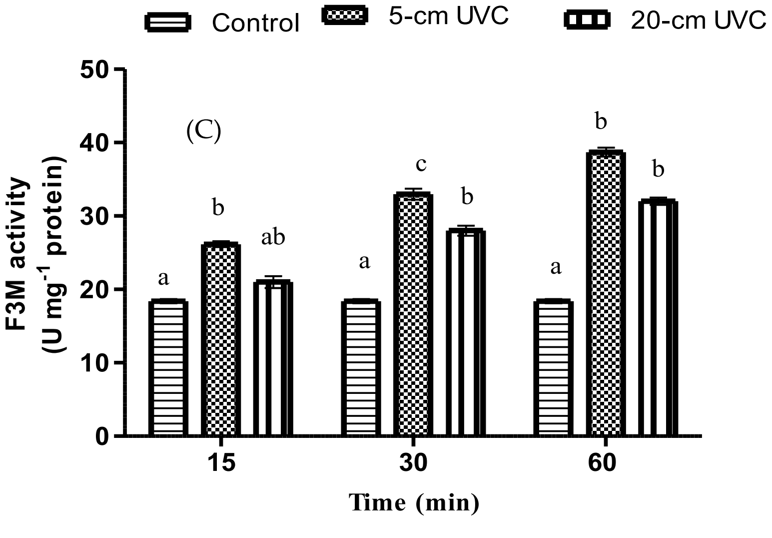

Control
5-cm UVC
20-cm UVC
(C)
F3M activity
(U mg^{-1} protein)
0
10
20
30
40
50
a
b
ab
a
c
b
a
b
b
15
30
60
Time (min)

Fig. 3: Effect of UVC on the activities of (A): CHS, (B): CHI, and (C): F3M in response to germinated seeds of fenugreek.

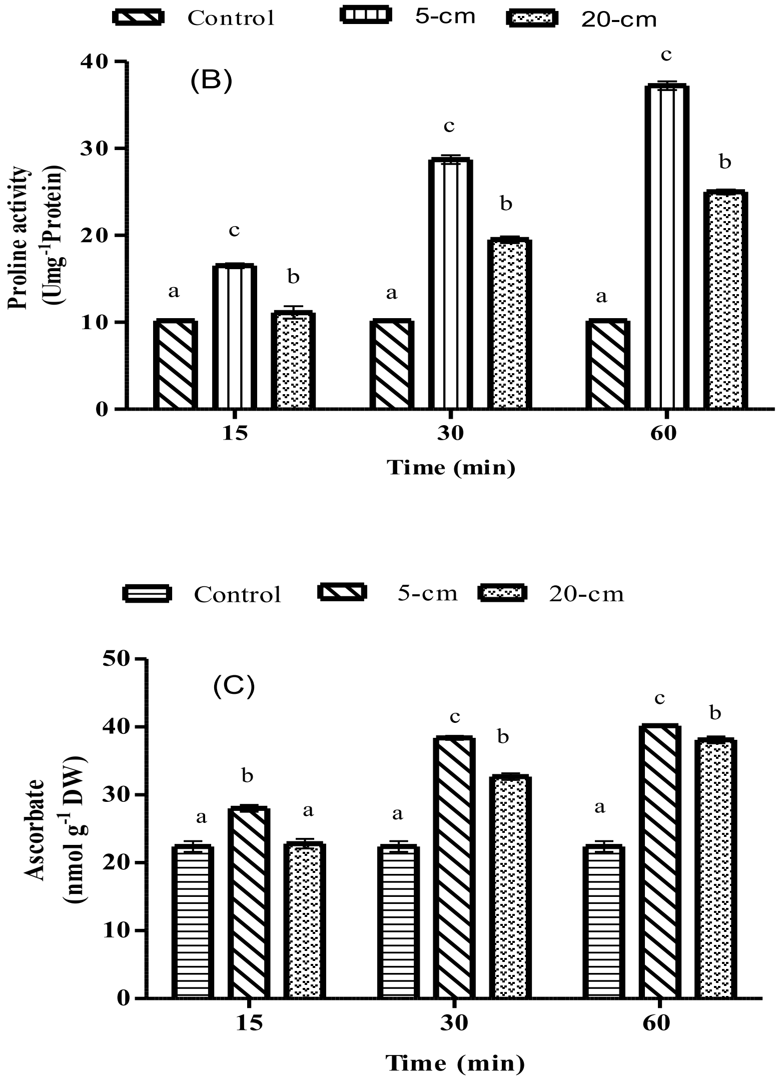


Fig. 4: Effect of UVC on the content of (A): α-tocopherol, (B): proline, and (C): ascorbate in germinated seeds of fenugreek.

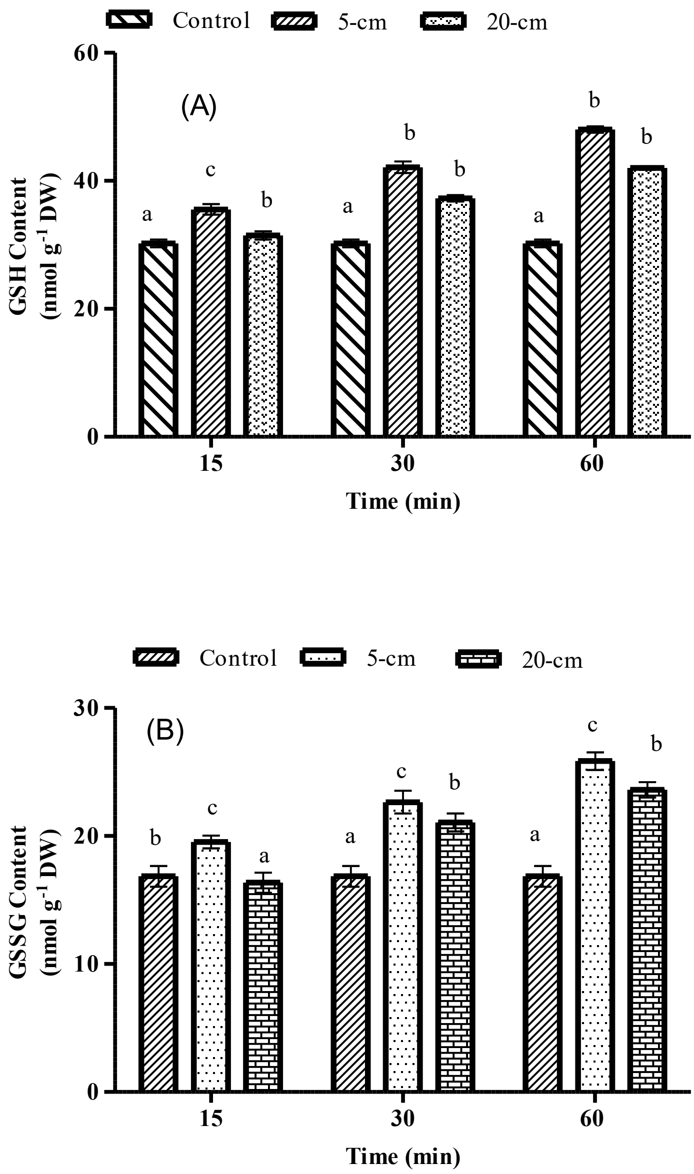
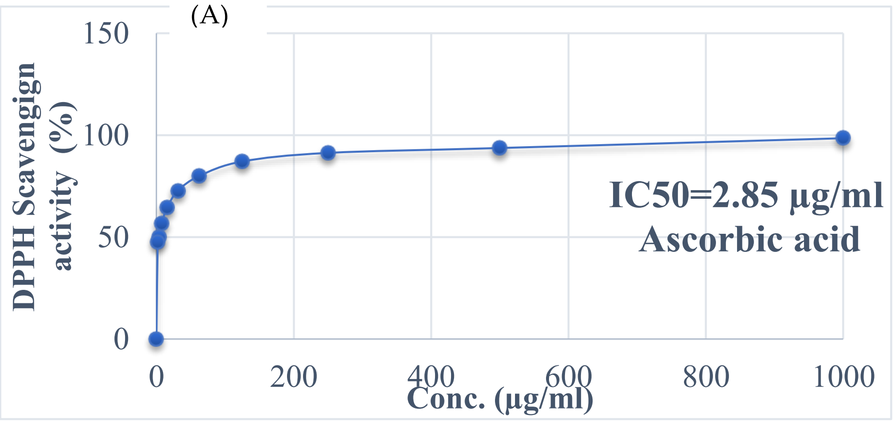


Fig. 5: Effect of UVC on the content of (A): GSH and (B): GSSG in germinated seeds of fenugreek.



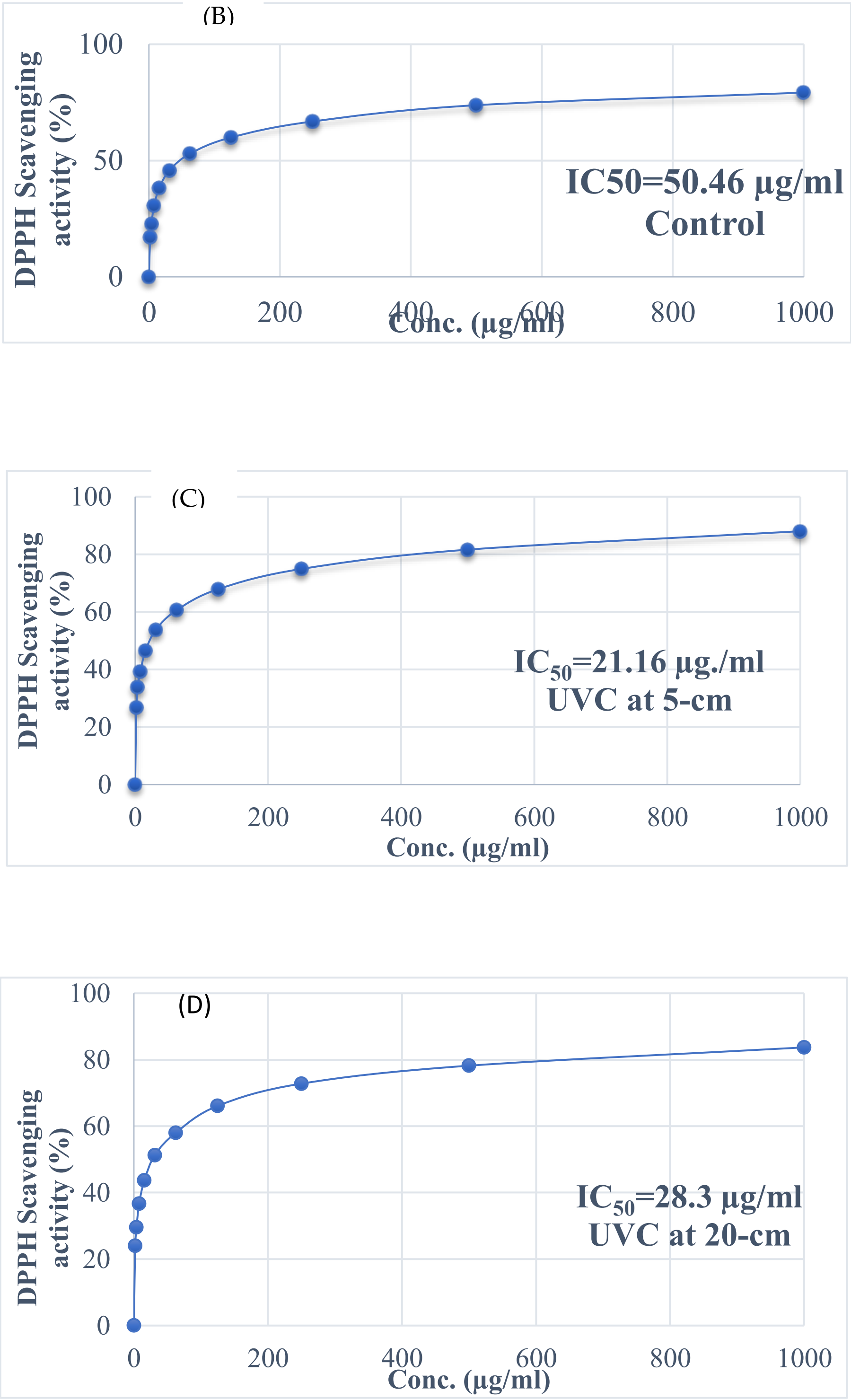
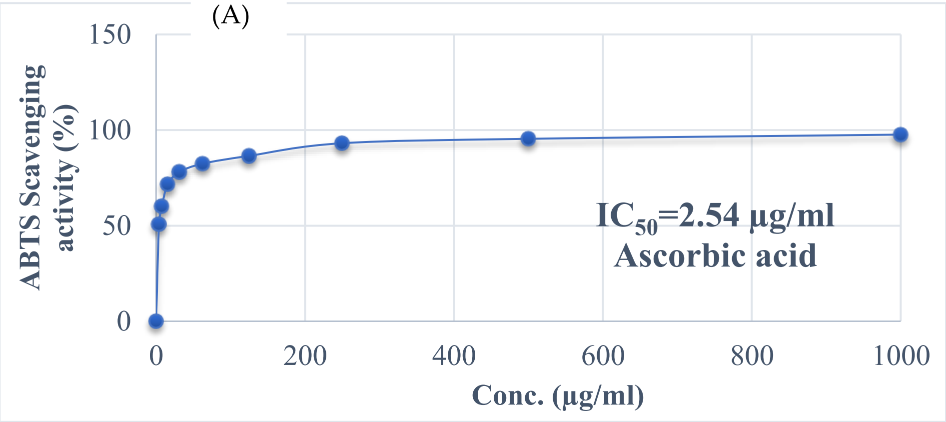
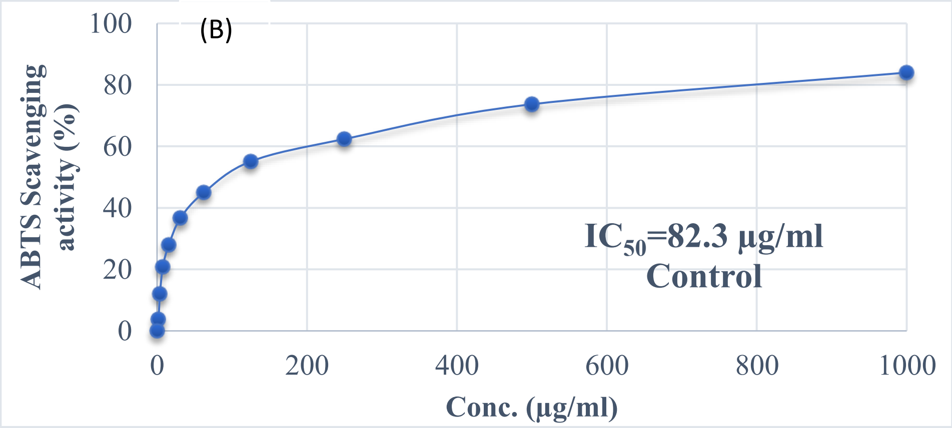
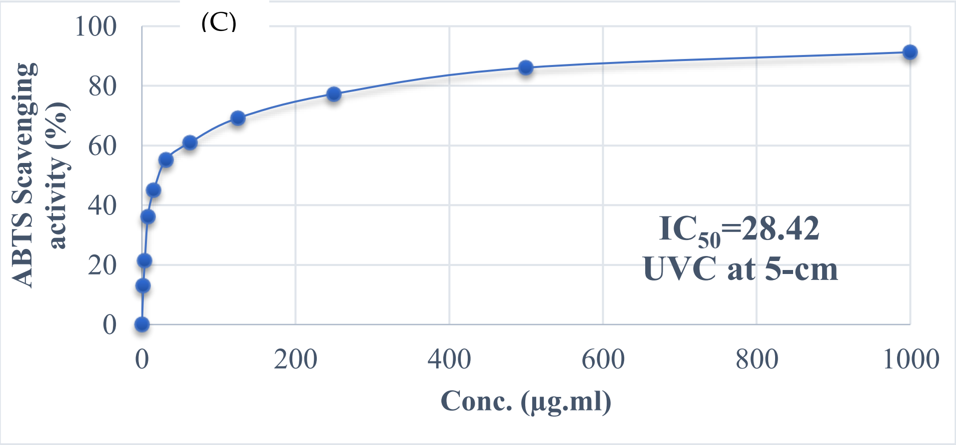


Fig. 6: DPPH scavenging activity of fenugreek (A): ascorbic, (B): control sample, (C): primed seeds with UVC from 5-cm, (D) and 20-cm.


(A)
ABTS Scavenging activity (%)
150
100
50
0
0
200
400
600
800
1000
Conc. (µg/ml)
IC50=2.54 µg/ml
Ascorbic acid


(B)
ABTS Scavenging activity (%)
100
80
60
40
20
0
0
200
400
600
800
1000
Conc. (µg/ml)
IC50=82.3 µg/ml
Control


(C)
ABTS Scavenging activity (%)
100
80
60
40
20
0
0
200
400
600
800
1000
Conc. (µg.ml)
IC50=28.42
UVC at 5-cm

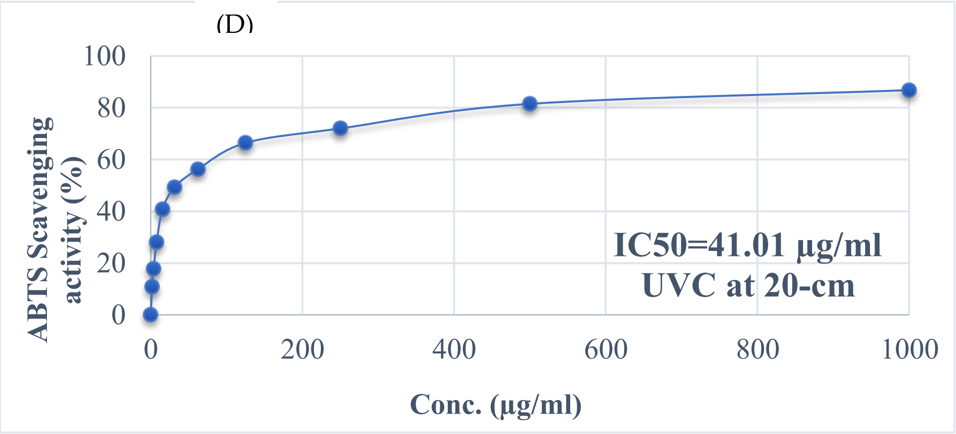


Fig. 7: ABTS scavenging activity of fenugreek (A): ascorbic, (B): control sample, (C): primed seeds with UVC from 5-cm, (D) and 20-cm.

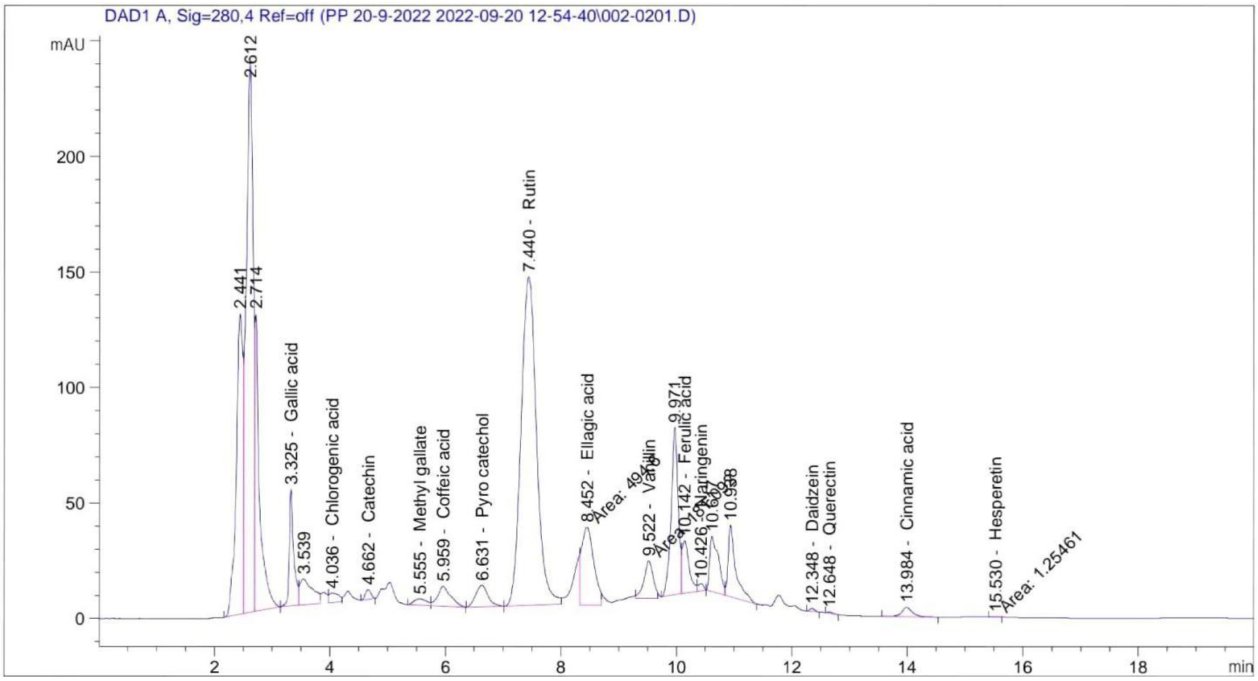


Fig. 8: HPLC profile of total phenolics from seeds of fenugreek from non- primed seeds (control) with UVC.

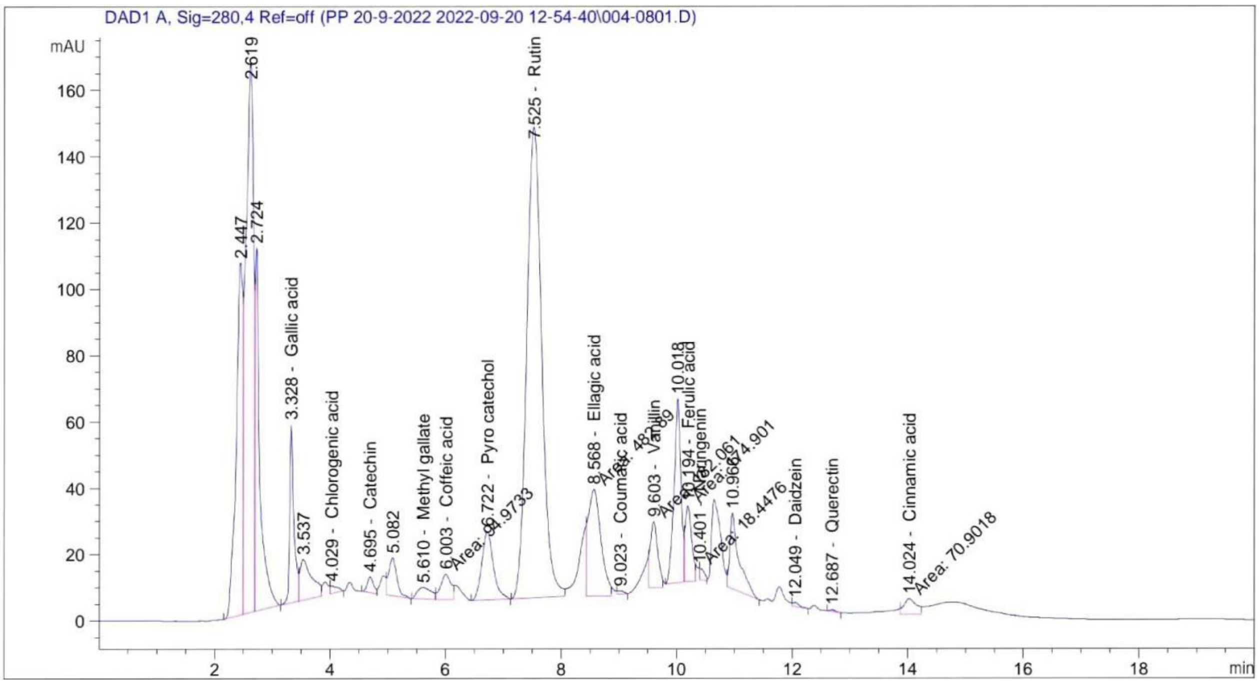


Fig.9: HPLC profile of total phenolics from seeds of fenugreek after priming with UVC at 5 cm for 15 min.

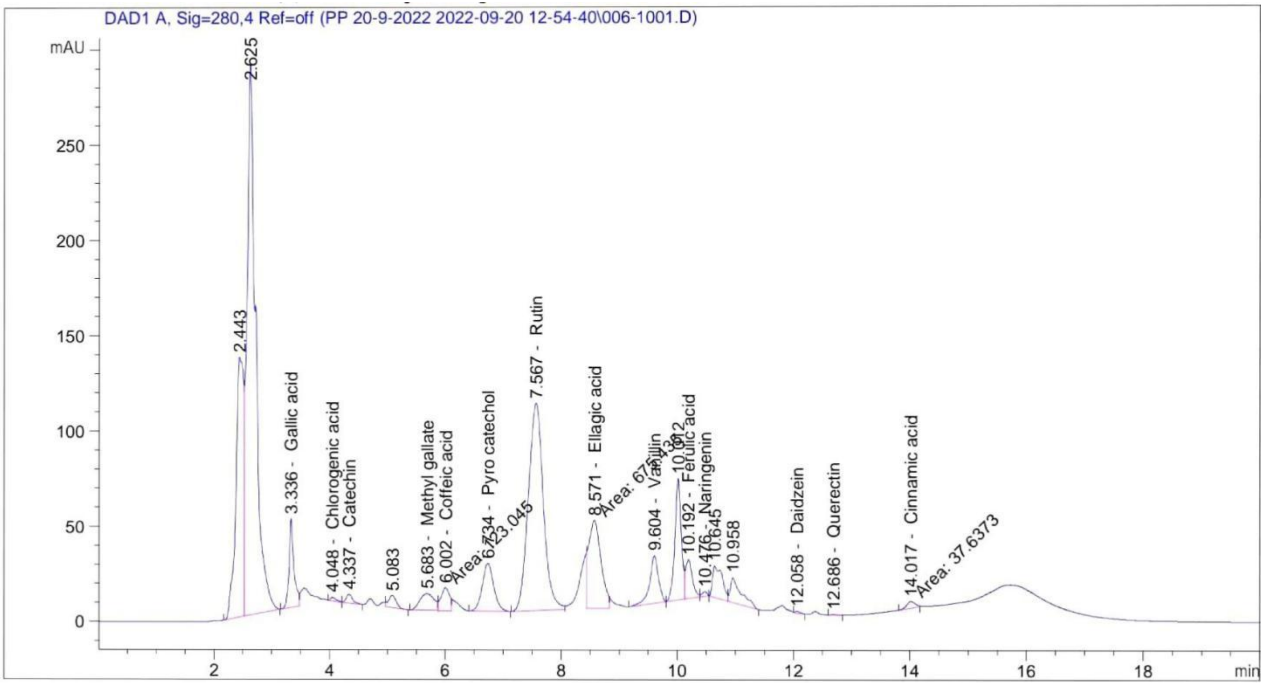


Fig.10: HPLC profile of total phenolics from seeds of fenugreek after priming with UVC at 5 cm for 60 min.

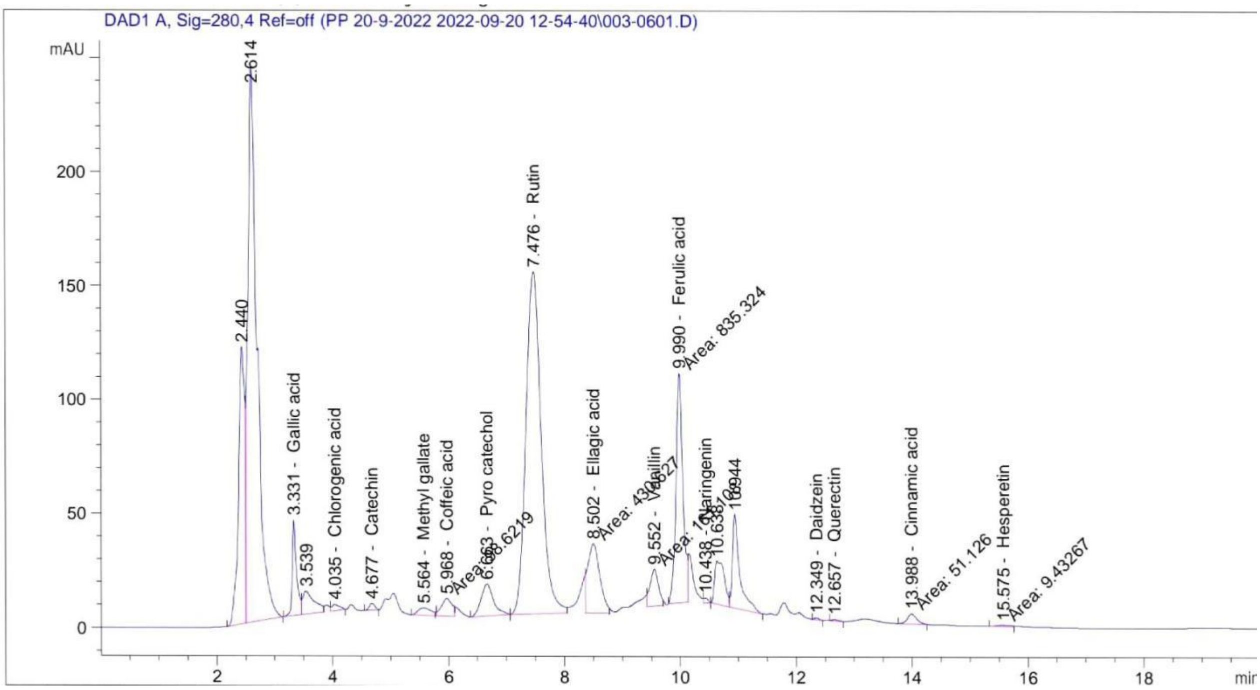


Fig. 11: HPLC profile of total phenolics from seeds of fenugreek after priming with UVC at 20 cm for 15 min.

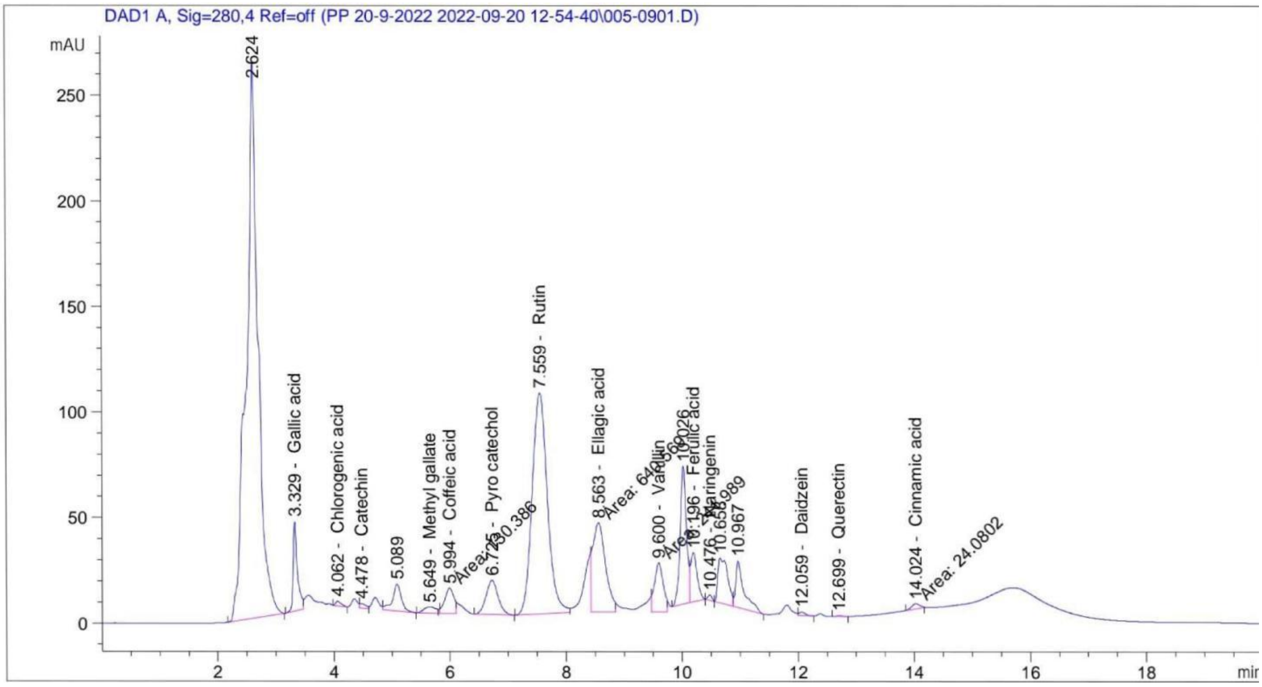


Fig. 12: HPLC profile of total phenolics from seeds of fenugreek after priming with UVC at 20 °C for 60 min.

Discussion

Ultraviolet-C (UVC) radiation is widely recognized for its cytotoxic properties, exerting both direct and indirect deleterious effects on living cells. This characteristic is routinely leveraged for effective microbial disinfection. In the agricultural context, however, plants are intrinsically vulnerable to a spectrum of abiotic stressors, including ultraviolet radiation, salinity, and drought. These environmental challenges significantly disrupt physiological homeostasis and stunt vegetative growth, ultimately culminating in substantial crop yield deficits [24].

To mitigate such environmental vulnerabilities, seed priming has emerged as a highly efficacious strategy. This pre-sowing technique augments various biochemical and physiological defense networks, thereby fortifying the adaptive capacity and resilience of seeds and developing seedlings against suboptimal environmental conditions [25].

In the current investigation, UVC priming induced a robust elevation in the total phenolic content of germinated fenugreek seeds. This observation aligns with prior literature demonstrating that low-dose UVC exposure stimulates the transcriptional activation of genes governing phenolic biosynthesis [26][27]. Furthermore, this amplified phenolic accumulation may be partially mediated by the liberation of cell wall-bound constituents and the concurrent depolymerization of complex phenolic macromolecules, such as tannins [28].

Mechanistically, phenolic compounds exhibit formidable antioxidant activity, functioning primarily as free radical scavengers via electron or hydrogen-atom donation. This activity facilitates the stabilization and resonance delocalization of unpaired electrons. Additionally, these secondary metabolites bolster cellular defense against oxidative stress by chelating transition metal ions [29]. Conversely, the observed attenuation in total phenolic concentration following prolonged UVC exposure is likely attributable to their rapid metabolic consumption. Under sustained stress, these compounds serve as primary substrates for oxidative and hydrolytic enzymes, including β-glucosidase, polyphenol oxidase, and peroxidase [30].

Biochemical analysis further revealed that UVC priming of fenugreek seeds significantly upregulated the activities of phenylalanine ammonia-lyase (PAL) and cinnamate-4-hydroxylase (C4H). As a pivotal, rate-limiting enzyme in the phenylpropanoid cascade, PAL catalyzes the deamination of phenylalanine to trans-cinnamic acid, thereby exerting foundational regulatory control over plant phenolic biosynthesis [31]. Concurrently, C4H facilitates the hydroxylation of cinnamate to 4-hydroxycinnamate, a critical downstream reaction that funnels metabolic intermediates toward the production of diverse secondary metabolites. Consequently, the pronounced accumulation of phenolic compounds in response to UVC-induced stress is closely correlated with the heightened enzymatic activity of the phenylpropanoid biosynthetic pathway, notably driven by PAL and C4H [32][33].

The elevated activity of phenylpropanoid pathway enzymes, notably PAL, indicates a profound metabolic reprogramming in germinated seeds. Specifically, this upregulation indicates a redirection of carbon flux away from primary metabolic processes, such as sucrose biosynthesis, toward secondary pathways dedicated to fortifying cellular defense and repair mechanisms against stress [34][35].

Consistent with this metabolic shift, the present study demonstrated that UVC treatments robustly stimulated flavonoid biosynthesis. Ecophysiologically, flavonoids tend to accumulate preferentially in the epidermal or outer layers of plant tissues to afford photoprotection—a distribution previously corroborated in Maradol papaya, where UVC irradiation significantly augmented peel flavonoid concentrations [36]. Biochemically, flavonoids are derived from p-coumaric acid through the action of chalcone synthase (CHS), which catalyzes the formation of chalcone, the foundational precursor of the flavonoid class. In our investigation, the activities of both CHS and the subsequent enzyme in the cascade, chalcone isomerase (CHI), were markedly induced in UVC-primed fenugreek seeds.

These observations are supported by Tiechez et al. [37], who documented that UVC exposure upregulates both CHS expression and transcripts encoding flavonol synthase (FLS), the critical enzyme governing flavonol synthesis. The resultant accumulation of flavonoids confers significant cellular protection by elevating intracellular pools of glutathione, a principal non-enzymatic antioxidant [38][39]. Furthermore, flavonoids act as potent, direct scavengers of reactive oxygen species (ROS)—specifically superoxide anions and peroxyl radicals—while concurrently modulating the activity of endogenous enzymes implicated in free radical generation [40].

Beyond the phenolic and flavonoid responses, UVC priming led to a pronounced increase in α-tocopherol content in germinated seeds. As a premier lipophilic antioxidant, α-tocopherol is instrumental in preserving the structural and functional integrity of biological membranes under oxidative stress [41]. Its exceptional antioxidant capacity is conferred structurally by three methyl substituents within its molecular framework, which optimize its ability to quench free radicals [42]. Crucially, α-tocopherol acts as a highly efficient chain-breaking agent, intercepting and terminating the propagation phase of lipid peroxidation. Because a single α-tocopherol molecule can neutralize diverse ROS through resonance energy-transfer mechanisms, its accumulation represents a cornerstone of the cellular antioxidant defense strategy [43].

The current investigation further revealed that varying intensities of UVC radiation induced a substantial increase in endogenous proline content within the germinated seeds. This observation corroborates the findings of Amal et al. [44], who documented augmented proline accumulation in stress-exposed wheat. The pronounced elevation of this amino acid is widely regarded as a pivotal adaptive mechanism for conferring enhanced tolerance to UVC-induced stress. Beyond its classical role in osmoregulation, elevated proline functions as a critical protectant against UVC-generated reactive oxygen species (ROS) [45]. The marked accumulation of free proline under such stress conditions is generally governed by three primary metabolic shifts: the upregulation of proline biosynthesis from its glutamate precursor, the inhibition of proline degradation into other soluble metabolites, and a concomitant suppression of global protein synthesis [46].

In response to environmental perturbations, plants undergo extensive metabolic reprogramming, prominently featuring the enhanced biosynthesis of compatible solutes. As a key osmoregulator, proline accumulates within the cytosol to stabilize cellular water potential, thereby preserving turgor pressure and sustaining vegetative growth. Consequently, the observed surge in proline following UVC treatment likely plays a crucial role in maintaining optimal relative water content—a physiological prerequisite for cellular turgidity and continued plant development under adverse conditions [47].

Along with proline, ascorbic acid content in germinated seeds was significantly upregulated following UVC priming. This response parallels findings in tomato, where UVC exposure induced a marked increase in ascorbic acid levels [48]. Similarly, Dwivedi et al. [49] reported enhanced ascorbate accumulation in Vigna species subjected to UVC radiation, a phenomenon potentially driven by a concurrent suppression of ascorbate peroxidase (APX) activity, as postulated by Jagadeesh et al. [50]. As a potent non-enzymatic antioxidant, ascorbate functions as a primary electron donor in myriad enzymatic and non-enzymatic reactions and is continuously recycled via the ascorbate–glutathione cycle [51]. The observed augmentation of ascorbate thus underscores the seed's adaptive resilience to environmental stressors. Mechanistically, ascorbic acid directly quenches singlet oxygen ($^1O_2$) and hydroxyl radicals (•OH), while also facilitating the detoxification of hydrogen peroxide (H_2O_2) via the Asada–Halliwell pathway.

Concomitantly, the concentration of reduced glutathione (GSH) was significantly elevated in germinated Trigonella seeds following UVC treatment. Composed of glutamate, cysteine, and glycine, GSH is the most abundant low-molecular-weight thiol in plant tissues, typically present at millimolar concentrations [52]. The cellular glutathione redox potential is fundamentally dictated by the intracellular ratio of reduced to oxidized glutathione (GSH/GSSG), a balance continuously modulated by GSH biosynthesis, catabolism, and total pool size [53]. The robust antioxidant capacity of GSH is primarily localized to the highly reactive sulfhydryl (–SH) group of its cysteine residue, which facilitates the direct scavenging of ROS [54].

During periods of oxidative stress, oxidized glutathione (GSSG) is rapidly recycled back to GSH to preserve cellular redox homeostasis [55]. This reduced pool is indispensable for stabilizing diverse enzymatic structures. It serves as an obligate substrate for the reduction of dehydroascorbate and directly neutralizes potent free radicals, including the hydroxyl radical. Through these mechanisms, GSH prevents the oxidative cross-linking of critical protein thiol groups, thereby safeguarding essential enzymes from inactivation [56][57].

Fenugreek leaves cultivated from UVC-primed seeds demonstrated robust antioxidant capacity, as quantitatively evaluated by both ABTS and DPPH radical scavenging assays [58]. The strong positive correlations observed between these scavenging activities and the total phenolic content strongly indicate that phenolic compounds are the primary agents driving the observed antioxidant efficacy [59]. Mechanistically, exposure to high-energy electromagnetic radiation, such as UVC and blue light, possesses the inherent potential to severely disrupt cellular functionality due to its elevated frequency and energy transfer. To mitigate these deleterious effects and neutralize the ensuing intracellular ROS cascade, plants upregulate the biosynthesis of diverse photoprotective compounds, a defensive response directly reflected in the enhanced DPPH scavenging capacity [59].

In the present investigation, the radical scavenging capabilities against both DPPH and ABTS exhibited a dose-dependent enhancement corresponding to the duration of UVC exposure. This progressive increase in antioxidant activity is likely driven by the irradiation-induced upregulation of PAL, leading to heightened phenolic biosynthesis under stress conditions [60]. Furthermore, UVC irradiation may induce structural perturbations in cellular and vacuolar membranes, thereby facilitating the intracellular mobilization and release of sequestered bioactive antioxidant compounds [61].

Beyond direct radical scavenging, phenolic compounds play a crucial role in the biophysical stabilization of cell membranes. They achieve this by interacting with the lipid bilayer, decreasing membrane fluidity in a concentration-dependent manner. This biophysical alteration restricts the spatial diffusion of free radicals, thereby establishing a formidable barrier against lipid peroxidation [62][63]. Furthermore, the structure-function relationship of these molecules dictates their efficacy; specifically, phenolic compounds with a greater number of hydroxyl groups generally exhibit superior ROS-scavenging capacity [64][65][66][67][68][69].

Conclusion

In brief, this study demonstrates that UVC priming significantly increases antioxidant activity in T. foenum-graecum by maximizing bioactive compound accumulation including phenolics, flavonoids, α-tocopherol, ascorbic acid, proline, and reduced glutathione. These analyses were significantly correlated with the increased expression of key enzymes involved in the biosynthesis of the phenylpropanoid and flavonoid pathways, which resulted in enhanced radical scavenging capacity as determined by DPPH and ABTS assays. The results highlight that a specific range of UVC both triggers a healthy mobilization of stress resistance that alters plant metabolism away from growth and towards antioxidant defence as well as phytochemical production. These findings have important implications of utilizing UVC priming as a cost-effective means to enhance the nutritional and functional quality of fenugreek seeds for potential applications in agriculture, food science, and nutraceutical development. However, this research also shows that the most important factors might be the duration of and intensity of UVC exposure, with the possibility of metabolic depletion of antioxidants if treated excessively. Conclusively, more studies are warranted to better optimize UVC treatment conditions, assess long-term physiological agronomic implications under field conditions, characterize the molecular mechanisms underlying stress-adaptive metabolic regulation, and evaluate the sustainability of this approach across other economically important crops

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