

Physio-anatomical modifications and element allocation pattern in *Alternanthera tenella* Colla. associated with phytoextraction of chromium

Kottakunnu Abdulrahman Firdous

Sree Neelakanta Government Sanskrit College

Padmanabhan Jayanthikumari Vivek

Sree Neelakanta Government Sanskrit College

Kizhakkepurath Neethu

Sree Neelakanta Government Sanskrit College

Mohankumar Saraladevi Resmi (✉ resmivivek@gmail.com)

Sree Neelakanta Government Sanskrit College <https://orcid.org/0000-0002-5110-6978>

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Abstract

Intensive industrial activities increased the concentration of chromium in the environment especially in the soil and water, which pose serious threat due to its cytotoxic and carcinogenic nature. Phytoremediation has evolved as an eco-friendly, cost-effective alternative for the decontamination of pollutants, and an attempt has been made to reveal the potential of Cr remediation by an invasive plant, *Alternanthera tenella* Colla in the present study. The morphological, anatomical and physiological modifications of plant tissues in response to 240 μM of $\text{K}_2\text{Cr}_2\text{O}_7$ is studied, with reference to the elemental distribution pattern and bioaccumulation potential. Assessment of growth parameters showed that Cr adversely affects the elongation of root and shoot, leaf area, and dry biomass weight. Cr influence the macro and micro-elemental distribution in plant tissues specially in roots and leaves. Plants exhibited structural modifications like increase in the thickness and diameter of the xylem walls in the root, stem and leaf tissues of Cr treated *A. tenella*. Presence of cell structural distortions and Cr deposit inclusions in the xylem wall and the inner parenchyma cells were distinct. Cr stress induced the reduction in pigment content and metabolites like proteins and soluble sugars, while proline, phenol and malondialdehyde marked a significant increase. With BCF and TF values greater than 1 and the mechanisms to cope with the metal stress, *A. tenella* proves to be an ideal candidate for phytoextraction of Cr.

1. Introduction

The increased industrial and urban activities have triggered the rate of environmental pollution with heavy metals, pesticides, microplastics, petroleum products, and persistent organic pollutants (Liu et al. 2022; Kiran et al. 2021). Heavy metals (HMs) are major inorganic environmental contaminants that are toxic to the living system. Since HMs are difficult to transform into non-toxic forms under natural circumstances and will have long-lasting effects on ecosystems, their indiscriminate discharge into the environment is posing a serious threat to human health on a global scale (Chen et al. 2020). Heavy metals like chromium (Cr), arsenic (As), cadmium (Cd), lead (Pb), and mercury (Hg) are not only cytotoxic but also mutagenic and carcinogenic in nature, therefore even very small doses of these substances can have major health effects (Dixit et al. 2015). The wide distribution of Cr in soil, water, and biological materials has made it a serious pollutant in the ecosystem over the past few decades (Gill et al. 2016). With a specific density of 7.19 g/cm^3 , Cr is the 21st most prevalent HM in the Earth's crust and ranks seventh among all metals (Economou-Eliopoulos et al. 2013). Cr ions are released into the atmosphere from industries like chrome plating, cement plants, steel production works, manufacture of dyes and paints, mining, leather tanning, the textile industry, the aircraft industry, wood preservation, mud drilling, and upon leaching from improper sanitary landfills (Haider et al. 2022; Coetzee et al. 2020). Cr has high redox potential and can exist in a range of valence states from (-II) to (IV), in which Cr (0), Cr (III), and Cr (VI) are the stable forms in nature (Jiang et al. 2015). Cr in different oxidation states shows different chemical, toxic and epidemiological characteristics, and Cr (VI) is 100 times more toxic than Cr (III) because of its higher oxidation potential, solubility, and mobility (Qianqian et al. 2022; Liang et al. 2021).

Plants absorb Cr in both its valence states, i.e., Cr (III) and Cr (VI) (Shahid et al. 2017). The cation exchange sites in plant cell walls allow the passive entry of Cr (III) (Park, 2020; Singh et al. 2013), while sulphate and phosphate carriers actively transport Cr (VI) into plant cells (Xu et al. 2021; Gill et al. 2017). Cr (III) may have beneficial effects on plant growth with an enhanced yield at low concentrations, even if it is not necessary for plants (Paiva et al. 2009; Helena, 2012). However, Cr (III) at high concentrations and Cr (VI) can have deleterious effects on plant physiological processes such as development, seed germination, mineral nutrition, photosynthesis, biomass production, metabolism, and crop productivity and eventually cause plant death (Singh et al. 2020; Sehrish et al. 2019; Anjum et al. 2017; Shahid et al. 2017; Chebeir et al. 2016; Jobby et al. 2018). Cr toxicity reduces plant growth by inducing ultrastructural modifications of the cell membrane and chloroplast, modulation in cell division and cell cycle, degradation of chlorophyll, water and minerals imbalance, affecting transpiration and nitrogen assimilation and alters enzymatic activities (Zaheer et al., 2020; Reale et al., 2016; Anjum et al., 2017; Masciarelli et al., 2017; Ugwu and Agunwamba 2020). High Cr concentrations in the soil are taken up and translocated to shoots of plants, where it is stored and eventually enter the food chain and have adverse effects on human health (Giri and Singh, 2017). It is a powerful epithelial irritant and can cause bronchitis, dermatitis, and tuberculosis (Saud et al. 2022). Therefore, it is crucial to develop effective methods for removing Cr from the environment.

Natural processes like leaching, plant absorption, erosion, and deflation can cause heavy metal depletion in the environment but the efficiency is low (Chen et al. 2020). Many physio-chemical processes, such as reverse osmosis, chemical precipitation and oxidation/reduction, ion exchange, adsorption, filtration, membrane technology, solvent extraction, evaporation, and electrochemical treatment, were developed to eliminate the HMs from the contaminated environment (Al-Alawy and Al-Ameri, 2015; Huang et al. 2017; Levchuk et al. 2018; Burakov et al. 2018; Liu et al. 2018). However, these techniques are expensive, less sustainable, and involve significant maintenance functionalities. Alternately, highly efficient biosorption and/or hyper-bioaccumulation are promising biological remediation strategies for HM removal that could restore and maintain the natural balance of the environment (Liu et al. 2018; Liu et al. 2020). Plants and microorganisms are frequently used as acceptors in biological methods (Dixit et al. 2015).

Phytoremediation offers one of the promising alternative approaches to remediate the HM contaminated sites which is sustainable, environment-friendly, and less expensive (Liu et al. 2020). Invasive alien plant species (IAPS) are one such category of plants that are most suitable for the remediation of polluted soils in industrial areas, especially riparian zones. It has been observed that some invasive plants grow more rapidly than nearby native plants in contaminated areas (Wang et al. 2020). Because they are a group of plants that can withstand or even accumulate heavy metals in their tissues (Liu et al. 2018), and have inherent benefits over native plants in terms of growth, fertility, and certain physiological traits like phenotypic plasticity and allelopathy (Davidson et al. 2015; Zheng et al. 2015).

The total biomass of plants and their ability to accumulate high concentrations of HMs in plant organs without suffering phytotoxic effects are important for efficient phytoremediation (Liu et al. 2013; Helena, 2012). According to previous studies, several species are reported for Cr phytoremediation, such as *Miscanthus sinensis* (Nie et al. 2021), *Pennisetum sinense* (Chen et al. 2020), *Prosopis laevigata* (Buendia-

Gonzalez et al. 2010), *Spartina argentinensis* (Redondo-Gómez et al. 2011), *Nopalea cochenillifera* (Adki et al. (2013), *Eichhornia crassipes* L. (Khalid and Ganjo, 2021; Ibezim-Ezeani and Ihunwo, 2020), *Jatropha curcas* L. (Martín et al. 2020; Abioye et al. 2017), *Pisum sativum* L. (Srivastava et al. 2021), *Brassica napus* (Sahay et al. 2020), *Spinacia oleracea* L. (Sharma et al. 2020; Abhilash et al. 2016), *Phragmites australis* (Romero-Hernández et al. 2017; Bonanno and Giudice, 2010), *Typha latifolia* (Yang and Shen, 2019; Demirezen and Aksoy, 2004), *Veronica aquatica* (Parikh and Unadkat, 2021), *Pistia stratiotes* (Khalid and Ganjo, 2021; Sudarshan et al. 2020; Galal et al. 2018), *Vallisneria spiralis* (Khalid and Ganjo, 2021). However, the slow growth and low biomass of the existing Cr hyper-accumulator plants which are practically insufficient for phytoremediation, limit the applicability of these plants.

Due to the accumulation of heavy metals in their biomass, a number of plant species in the Amaranthaceae family have the potential to be used in phytoremediation (Odiyi et al. 2019; Rodrigues et al. 2017). *Alternanthera tenella* Colla (Amaranthaceae) is a fast-growing, invasive alien herb widely found in India, especially in polluted areas such as industrial zones. *A. tenella* is a facultative metallophyte and has already been proven as a bioaccumulator of Cd under controlled micro-conditions (Rodrigues et al. 2017) and also showed responses to various HM stress (Chinmayee et al. 2014). However, additional studies with this species can also verify its potential use as a bioindicator and phytoremediator in areas contaminated by these heavy metals. Therefore, based on the potential for phytoremediation of several species of the Amaranthaceae family, we aimed to evaluate the changes in the anatomy and physiology of *A. tenella* induced by Cr stress and the phytoremediation potential of Cr by this species.

2. Materials and methods

2.1. Plant material

Alternanthera tenella Colla., an invasive plant species from the family Amaranthaceae, was selected for the present study. Healthy *A. tenella* stem cuttings that had a consistent size (20–30 cm) were chosen. The cuttings were kept in distilled water for a week to induce rooting. Later, the rooted plantlets were transferred to ½ strength Hoagland's solution taken in glass test tubes (25 × 150 mm) for 21 days. Throughout the experiment, plantlets were maintained in a controlled environment with 60 ± 5% relative humidity, 25 ± 3°C temperature, and a day/night cycle of 12/12 h to ensure optimal plant growth.

2.2. Chromium treatment

The ½ strength Hoagland nutrient media was supplied with K₂Cr₂O₇ at different concentrations (0–300 M) for the plantlets to absorb. The highest concentration of Cr (VI) that could result in visible damage without causing plant death was selected for treatment. *A. tenella* was able to withstand 240 µM of chromium for 21 d. So, for further study, healthy plantlets of *A. tenella* were exposed to 240 µM concentration of K₂Cr₂O₇ for 21 d under hydroponic culture conditions provided with ½ strength Hoagland medium. Plants without Cr were used as a control. The *A. tenella* samples were collected on 0 d, 7 d, 14 d, and 21 d after Cr stress treatment, and 5 biological replicates were taken for each treatment.

The leaves, stems, and leaves of the sampled plants were separated after weighing and were immediately frozen in liquid nitrogen to store for further treatment and analysis. Hereupon, $K_2Cr_2O_7$ treatments will be referred to as chromium stress (Cr).

2.3. Plant growth

The growth of *A. tenella* under different concentrations of Cr was evaluated by measuring root and shoot length, leaf area, dry weight, and tolerance index. Graph paper and a graduated scale were used to measure the leaf area and root and shoot length respectively. The roots, stems and leaves were washed with distilled water prior to measurement and then blotted dry with filter paper. For the estimation of dry weight, the fresh roots, stems, and leaves were weighed and recorded. It was then placed in an oven set at 100°C for 1 h and followed by 60°C. The sample weight was recorded every day up until a constant value was reached. The tolerance index percentage of the plantlets was calculated according to the equation given by Turner (1994).

2.4. Anatomical modifications

The fresh root, stem, and leaf samples from the control and Cr treatments were dissected on 21d and immediately fixed in a solution of 2.5% glutaraldehyde prepared in a 0.1 M phosphate buffer (pH 7.2) for 12 h at room temperature and then dehydrated by passing through alcohol series. The dehydrated samples were mounted on aluminium stubs using double-sided adhesive conducting carbon tape. After gold-palladium coating, the specimens were viewed and photomicrographed using a 20 kV scanning electron microscope (SEM, Jeol 6390LA).

2.5. Element analysis in tissues

Dehydrated root, stem, and leaf samples of *A. tenella* were examined under a high-resolution scanning electron microscope (Jeol 6390LA, Magnification: $\times 300000$) for analyzing the elemental distribution pattern. Using an Inca analyzer EDX spectrophotometer and the method described by Coccozza et al. (2008), a quantitative compositional analysis of the elements was also performed. Using EDXMA (energy dispersive X-ray microanalysis), three micro spots in the root, stem, and leaves from both control and metal-treated plantlets were analyzed. The three microspots were named spectrum 1, 2, and 3 respectively (Sarath et al. 2022a).

2.6. Photosynthetic efficiency

Photosynthetic pigments. The chlorophyll and carotenoid contents of the pigments in the leaf samples were determined according to Arnon (1941).

2.7. Metabolites

The metabolites such as total proteins, soluble sugars, total phenolics, proline and malondialdehyde content in roots, shoots, and leaves of plant samples were estimated according to the protocol of Lowry et al. (1941), Dubois et al. (1956), Bray and Thorpe (1954), Bates et al. (1973), and Li et al. (2010)

respectively. The D-glucose, bovine serine albumin, L-proline and tannic acid were used as standards for the estimation of total sugar, total proteins, proline and total phenolics respectively.

2.8. Bioaccumulation of chromium

The freshly collected samples on 21 d for Cr content determination (root, stem, and leaves) were dried at 100°C for 1 h and then placed at 60°C until a constant dry weight was achieved. Dried samples were then ground and reduced to a fine powder. About 0.2 g of dried plant samples were weighed and left in a mixed solution of nitric and hydrochloric acids (4HNO₃: 1HCl) in closed PTFE vessels, followed by digestion in a microwave oven for two hours at 200°C. The concentrations of Cr in the *A. tenella* digest were measured using an inductively coupled plasma-atomic emission spectrometer (ICP-AES) (Perkin Elmer Avio 200, USA). The phytoremediation potential of the *A. tenella* against Cr stress was calculated using different indices like biological accumulation coefficient (BAC), translocation factor (TF), and bioconcentration factor (BCF) by using the formulas of Zu et al. (2005) and Yoon et al. (2006).

2.9. Fourier transform infrared (FTIR) analysis

The dried powder of leaf, stem, and root samples was mixed with dried KBr (water-free) in a ratio of 1:150 mg (sample: KBr) and pressed under 10 tons of hydraulic pressure to create KBr discs for IR analysis. To measure the solid-state spectrum in FT-IR (JASCO 4100, Shanghai, China), the disc was positioned in the path of the instrument beam. With a resolution of 2 cm⁻¹, an IR examination was recorded in the 400–4000 cm⁻¹ range (Sarath et al. 2022a).

2.10. Statistical analysis

The results of the study were statistically examined using one-way ANOVA. All significant treatment effects were determined by using Dunnett's test at $p < 0.05$. Data are average recordings from three independent experiments, each with five replicates (i.e., $n = 15$). The data represent mean \pm standard error.

3. Results

According to the results of preliminary study (treatment with different concentrations of Cr, i.e., 0–300 μM), *A. tenella* could effectively withstand concentrations of K₂Cr₂O₇ up to 230 μM , but plantlets grown in concentrations of 240 μM and above for 21 days began to exhibit signs of stress. Therefore, for further part of the study, *A. tenella* plantlets were exposed to only the 240 μM concentration.

3.1. Plant growth

When compared to the control plantlets, all the parameters directly related to plantlet growth were significantly lowered by the Cr treatment throughout the stress period. The root length of *A. tenella* when treated with Cr showed significant reduction. The root length showed gradual decrease, i.e., from 31% on 7d to 52% on 21d in the treated plantlets. In contrast, a twofold increase in growth was observed in the control root at this time. A similar trend was observed in shoot length of the plantlets. The shoot length of

A. tenella was decreased on Cr treatment. It showed a 15% reduction on 21d than the control plantlets. The area of the newly opened leaves was measured after the Cr treatment and a reduction in leaf area was recorded. On 21d, leaf area was reduced by 17% in Cr treated plants compared to control plantlets whereas control leaves exhibited a significant increase in area throughout the stress period (Table 1).

Table 1

Growth parameters of *A. tenella* subjected to Cr stress at different time intervals compared to control. Values are the means \pm SE of the five different experiments (n = 15).

Day	Root length (cm)		Shoot length (cm)		Leaf area (cm ²)		Tolerance index (%)
	Control	Cr	Control	Cr	Control	Cr	
0	4.47 \pm 0.1	4.47 \pm 0.1	16.7 \pm 0.03	16.7 \pm 0.03	1.71 \pm 0.03	1.73 \pm 0.37	100
7	6.68 \pm 0.33	4.55 \pm 0.87	19.6 \pm 0.78	17.86 \pm 0.36	2.75 \pm 0.01	2.35 \pm 0.41	68.23 \pm 0.36
14	7.29 \pm 0.03	4.61 \pm 0.14	20.47 \pm 0.32	18.09 \pm 0.31	2.99 \pm 0.33	2.77 \pm 0.22	63.29 \pm 0.25
21	10.45 \pm 0.91	4.99 \pm 0.25	22.43 \pm 0.24	18.86 \pm 0.58	4.05 \pm 0.43	3.33 \pm 0.19	47.73 \pm 0.15

Table 2

Biomass of *A. tenella* subjected to Cr stress at different time intervals compared to control. Values are the means \pm SE of the five different experiments (n = 15).

Day	Fresh weight (g)				Dry weight (g)			
	Control		Cr		Control		Cr	
	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root
0	9.15 \pm 0.08	1.98 \pm 0.02	9.62 \pm 0.23	1.85 \pm 0.01	0.72 \pm 0.002	0.08 \pm 0.002	0.89 \pm 0.001	0.06 \pm 0.001
7	11.93 \pm 0.11	2.16 \pm 0.01	10.47 \pm 0.02	2.05 \pm 0.03	1.29 \pm 0.02	0.13 \pm 0.004	1.01 \pm 0.002	0.09 \pm 0.006
14	15.67 \pm 0.42	3.44 \pm 0.09	11.23 \pm 0.21	2.11 \pm 0.07	1.53 \pm 0.23	0.19 \pm 0.001	1.38 \pm 0.005	0.15 \pm 0.004
21	18.01 \pm 0.05	4.98 \pm 0.11	12.02 \pm 0.32	2.39 \pm 0.12	1.98 \pm 0.21	0.26 \pm 0.013	1.89 \pm 0.018	0.23 \pm 0.007

The fresh and dry weight of shoot and root of *A. tenella* also showed reduction in the Cr treatment than the control plantlets. The reduction in the fresh weight of the shoots and roots was up to 33% (in shoots) and 52% (in roots) on 21d in plantlets subjected to Cr treatment compared to the control plantlets. A similar trend of reduction was observed in the dry weight of shoot and root samples (Table 2). The tolerance index was used to measure the tolerance potential of *A. tenella* against Cr stress. The tolerance

index of Cr treated plantlets showed a gradual decrease during the entire stress period. On 21d of treatment, the tolerance index for plantlets treated with Cr was 47%, compared to 100% for control plantlets (Table 1).

3.2. Scanning Electron Microscopic (SEM) study

The SEM analysis of the root, stem and leaves of the control and Cr treated *A. tenella* plantlets on 21d indicates that the treatment with Cr caused significant structural changes especially in the vascular regions and inner pith.

Table 3
The diameter of xylem and xylem wall thickening of roots, stem and leaves of *A. tenella* (control and Cr treated). Values are the means \pm SE of the five different experiments (n = 15).

Sample	Diameter(μ m)		Thickness(μ m)	
	Control	Chromium	Control	Chromium
Root	18.616 \pm 1.97	13.81 \pm 1.36	3.06 \pm 1.18	3.35 \pm 2.14
Stem	32.08 \pm 2.06	27.495 \pm 2.61	6.52 \pm 1.26	8.49 \pm 0.89
Leaf	6.957 \pm 2.11	13.65 \pm 0.56	1.51 \pm 0.36	4.3 \pm 0.25

Root. A profound change in the thickness of the xylem wall and diameter of xylem were seen in the plantlets grown in Cr treatment compared to control plantlets. A slight increase in the thickness of the xylem vessel was observed in roots of treated plants (3.35 \pm 2.14) over control samples (3.06 \pm 1.18). But a reverse trend was seen in the diameter of the xylem. There was a decrease of 25% in the diameter of xylem in the roots of Cr treated plants from that of control (Table 3). In comparison to control plantlets, metal treated plantlets had distorted root shape and structure. When plantlets were treated with Cr, the parenchyma cells of the root cortex showed a degeneration than the control root (Fig. 1). The cortex and vascular sections in the root of the Cr treated plants showed further changes, including some depositions (Fig. 3A).

Stem. When compared to the stem of the control plants, the structure of the stem was deformed in plantlets treated with Cr. Various occlusions were seen in the xylem vessels (Fig. 2D). The loss to the structure of the pith cells near the vascular region in response to the Cr treatment was a major observation. They were highly distorted and depositions were seen inside these cells (Fig. 3B). The thickness of xylem wall was increased and the diameter of the xylem was reduced in response to the Cr. The thickness of the xylem wall increased up to 8.49 \pm 0.89 in treated plantlets as compared to the stem of control plantlets (6.52 \pm 1.26), whereas the diameter of xylem decreased from 32.08 \pm 2.06 in control plantlets to 27.495 \pm 2.61 in Cr treated plantlets (Table 3).

Leaf. The thickness of xylem wall and the diameter of the xylem was increased in response to the Cr in the leaf samples. The thickness of the xylem wall increased up to 64% in treated plantlets as compared to

the stem of control plantlets, whereas 49% increase in the diameter of xylem was observed in Cr treated plantlets than control (Table 3). There were aggregates in the xylem walls of leaves of Cr treated plants that can be assumed to be formed by the heavy metal (Fig. 4). Non-glandular trichomes and diacytic shaped stomata were present in the leaf surfaces of *A. tenella*; the stomata were spread all over the lamina (Fig. 5A,5C). The number of trichomes were highly reduced in the leaves of Cr treated plants than the control. Abaxial surface of the leaf contained more stomata. With guard cells and prominent borders, all the observed stomata were fully matured in both the leaf samples (control and treated). However, compared to the fully opened stomata in the control plants, the stomata in the Cr-treated plants appear to be just partially open and small depositions can also be seen (Fig. 5D).

3.3. Element analysis in tissues

Using EDXMA, three distinct regions of root, stem, and leaf - the epidermis and cortex (spectrum 1), endodermis and vascular tissues (spectrum 2), and the inner pith (spectrum 3), were examined in both control and Cr treated samples. The elemental (macro and micro-elements) distribution pattern in the root, stem, and leaf tissues of *A. tenella* treated with Cr showed significant changes.

Root. C, O, K, and P were found to be distributed in both of the samples studied (control and Cr treatments) among the various macro-elements. Distribution of C in the three regions of the root reduced in the case of plants subjected to Cr treatments compared to the control. The least reduction in C distribution was observed in the middle region (spectrum 2) followed by the inner region, and the highest reduction was observed in outer region (exodermis and cortex) of roots in plants exposed to Cr treatments (Table 5). In the plants treated with heavy metals, O content was reduced in the middle area and inner area of the roots, while the O distribution was slightly increased in the outer region of the roots of Cr treated plants compared to control plantlets. The K content was significantly enhanced in the plants exposed to Cr. The maximum increase was observed in the outer region (98%), followed by middle region. The P content in the roots of Cr treated *A. tenella* was also higher in all three regions than the control roots. S and Ca were present in lower quantities in all the regions of the control roots, whereas they were not detected in roots of Cr treated plantlets. Mg was found only in the outer region. Microelement distribution specifically, Fe, Al and Si were detected in the control roots; Fe in the inner region and Al, Si in the outer region. These elements were not detected in roots of Cr treated plants (Table 4).

Stem. Less number of elements were detected in the stem of both samples (control and treated) compared to the root and leaf. Cr treatment has not hindered the C and O distribution in all the three regions. The C content showed an increase in the inner region of the Cr treated plants, followed by middle region with reference to stem of control plantlets. But the C content was slightly reduced in the outer region of the stem of Cr treated plantlets than the control stem. The Cr treated plants had much higher Ca content in the stem, which can be detected in the EDXMA profile, and in the control samples, Ca content was detected only in the inner region. Microelements, Cu and Zn were present in the stem of control plantlets, but was not detected in treated samples (Table 5).

Leaf. Among the several macro-elements, C and O were found to be dispersed evenly and diffusely throughout the root tissues in both samples (control and Cr treatments). The C distribution was highly varied in the samples. While the outer region of the stem in Cr treated plants showed a reduction in C content, the middle region and lower region showed a significant increase compared to control sample. Interestingly, O distribution in the stem tissues showed a reverse trend. The outer region showed a slight increase in the O content of the stem in Cr treated plantlets, whereas the middle region and inner region showed a reduction compared to control sample. Ca content was enhanced by Cr treatment in all the three regions (Table 7). The K content showed significant reduction in the middle region of the stem in Cr treated plantlets, followed by the inner region and outer region. In plants exposed to Cr, the S content increased significantly to a level that can be seen in the EDXMA profile, and in the control samples, S content was not detected. There was a slight reduction in the P content in the inner region of stem in Cr treated plantlets than the control. P content was also detected in the outer region of the control stem. Microelement, Cl was detected in the stem tissues of both the sample, but absent in the middle region of the stem in treated sample. Similarly, Cu was not detected in the outer region of control sample but was present in other regions. The middle region of the stem of Cr treated plantlet showed a slight decrease in Cu content, while the inner region showed a slight increase. Al was present in the inner region of control stem and middle region of treated sample. Si was detected in the outer and middle regions of treated sample, while it was not detected in control. Na was present in the three regions of control stem and was not detected in treated sample. Zn content was detected in the middle region of control stem and in the outer region of Cr treated sample. Fe was also detected after Cr treatment in the outer region of stem (Table 6).

Table 4

SEM-EDX microanalysis data in the roots of *A. tenella* cultured in Hoagland solution. The macro and microelements concentrations (% weight) are shown for 3 different spots, i.e., spectrum 1 (outer region), spectrum 2 (middle region), and spectrum 3 (inner region).

Element	Control			Cr		
	Spectrum 1	Spectrum 2	Spectrum 3	Spectrum 1	Spectrum 2	Spectrum 3
C	63.69	56.04	57.49	35.71	36.96	36.19
O	33.96	41.75	40.2	37.13	37.9	35.73
K	0.24	1.08	0.31	17.29	15.83	7.76
P	0.32	0.5	0.39	9.86	9.31	5.24
S	0.47	0.26	0.18	NIL	NIL	NIL
Ca	0.31	0.36	0.28	NIL	NIL	NIL
Fe	NIL	NIL	0.55	NIL	NIL	NIL
Mg	0.22	NIL	NIL	NIL	NIL	NIL
Al	0.31	NIL	NIL	NIL	NIL	NIL
Si	0.49	NIL	NIL	NIL	NIL	NIL

Table 5

SEM-EDX microanalysis data in the stems of *A. tenella* cultured in Hoagland solution. The macro and microelements concentrations (% weight) are shown for 3 different spots, i.e., spectrum 1 (outer region), spectrum 2 (middle region), and spectrum 3 (inner region).

Element	Control			Cr		
	Spectrum 1	Spectrum 2	Spectrum 3	Spectrum 1	Spectrum 2	Spectrum 3
C	53.37	52.96	51.67	51.18	55.25	59.61
O	42.72	42.66	46.78	48.39	44.34	40.1
Ca	NIL	NIL	0.39	0.43	0.41	0.29
Cu	2.58	2.76	1.15	NIL	NIL	NIL
Zn	1.33	1.62	NIL	NIL	NIL	NIL

Table 6

SEM-EDX microanalysis data in the leaves of *A. tenella* cultured in Hoagland solution. The macro and microelements concentrations (% weight) are shown for 3 different spots, i.e., spectrum 1 (outer region), spectrum 2 (middle region), and spectrum 3 (inner region).

Element	Control			Cr		
	Spectrum 1	Spectrum 2	Spectrum 3	Spectrum 1	Spectrum 2	Spectrum 3
C	56.5	53.42	51.44	49.11	63.66	62.6
O	41.46	40.18	44.06	44.27	34.93	34.69
K	1.24	3.19	2.39	0.35	0.22	0.6
S	NIL	NIL	NIL	0.24	0.13	0.47
Cl	0.13	0.67	0.3	0.16	NIL	0.18
Cu	NIL	0.45	0.58	0.5	0.37	0.87
Al	NIL	NIL	0.13	NIL	0.24	NIL
Si	NIL	NIL	NIL	0.67	0.19	NIL
P	NIL	NIL	0.56	0.43	NIL	0.25
Na	0.39	0.41	0.53	NIL	NIL	NIL
Zn	NIL	0.8	NIL	1.47	NIL	NIL
Ca	0.28	NIL	NIL	0.41	0.26	0.28
Fe	NIL	NIL	NIL	2.05	NIL	NIL

3.4. Photosynthetic efficiency

Photosynthetic pigments. The total chlorophyll content of the control plants increased throughout the stress period. But a slight on increase in the total chlorophyll content of Cr treated plants on 7d, was followed by a gradual decrease on 14d (reduction by 61%) and on 21d (by 83%) compared to control plantlets. A similar trend was observed in the carotenoid contents of both control and treated samples (Table 7).

Table 7

The chlorophyll (in mg/g FW) and carotene content (in mg/g FW) of *A. tenella* subjected to Cr stress at different time intervals compared to control. Values are the means \pm SE of the five different experiments (n = 15).

Day	Control				Cr			
	Chl. a	Chl. b	Total Chl.	Carotenes	Chl. a	Chl. b	Total Chl.	Carotenes
0	0.4 \pm 0.05	0.14 \pm 0.02	0.53 \pm 0.07	0.23 \pm 0.02	0.4 \pm 0.05	0.14 \pm 0.02	0.53 \pm 0.07	0.23 \pm 0.02
7	0.64 \pm 0.01	0.23 \pm 0.005	0.89 \pm 0.02	0.32 \pm 0.007	0.38 \pm 0.006	0.18 \pm 0.003	0.56 \pm 0.009	0.26 \pm 0.01
14	0.97 \pm 0.21	0.3 \pm 0.001	1.27 \pm 0.02	0.4 \pm 0.001	0.33 \pm 0.006	0.16 \pm 0.003	0.49 \pm 0.009	0.22 \pm 0.01
21	1.89 \pm 0.009	0.34 \pm 0.006	2.23 \pm 0.01	0.84	0.24 \pm 0.003	0.12 \pm 0.01	0.36 \pm 0.05	0.18 \pm 0.001

3.5. Metabolites

Protein content. Significant enhancement in the total protein content was recorded in the tissues of root, stem and leaf of control plantlets. The root, stem and leaves of control plants recorded an increase in the total protein content by 68%, 80% and 59% respectively over the treated samples. The total protein content of the root, stem and leaf samples after Cr treatment showed an increase initially followed by a decrease. The changes in the total protein content were more prominent in the leaves of the treated plantlets (Table 8).

Soluble sugar. The soluble sugar content in the root tissues of *A. tenella* were less than the stem and leaves of both the control and Cr treated plantlets. In control samples, soluble sugar content increased over a treatment period of 0-21d, and a prominent increase was monitored in the stem and leaf tissues than the root tissues. In the case of Cr treated plants, the soluble sugar content decreased gradually over the treatment days after an increase in the initial phase (7d). The highest soluble sugar content in stem and leaves was recorded on 7d (nearly 2-fold) and after which the accumulation decreased significantly until 21d. All tissues of *A. tenella* treated with Cr showed a considerable reduction in the accumulation of soluble sugar compared to control samples, and the reduction peaked on 21d of stress (Table 8).

Proline. Significant enhancement in the proline content was recorded in the tissues of root, stem and leaf subjected to Cr treatment with reference to the control samples, while the proline content got reduced in the parts of control plantlets except for the leaf. A gradual increase of proline was recorded in the roots of Cr treated samples over the control plants during initial stages (0-14d), and a 3-fold increase was recorded on 21d of treatment. But in the stems and leaves, a rapid increase in total proline content was recorded on 7d itself, and respectively showed an increase of 95% and 90% on 21d with reference to the control plants (Table 8).

Total phenols. The total phenol content in *A. tenella* is less and among the different plant parts, it was observed that leaf tissues contain more phenolics. There were no significant changes in the phenolics content of the root, stem and leaf tissues of the control sample over the treatment period. However, there were slight increase in the total phenolics content in roots, stem, and leaves of Cr treated *A. tenella*, with maximum content on 14d in roots and leaves while maximum phenolics were induced in stem on 21d (Table 8).

Malondialdehyde. Lipid peroxidation in different plant parts is measured by the amount of malondialdehyde (MDA) synthesized in the tissues. There was a gradual increase in MDA content of both the samples (control and treated) over the treatment period but MDA content was drastically enhanced in the tissues of root, stem, and leaf exposed to Cr treatment, and it increased by 79%, 48%, and 50% respectively on 21d with reference to the control samples. In both the samples, maximum MDA content was observed in the leaf tissues, whereas MDA content was minimum for roots and stem in the control and treated sample respectively (Table 8).

Table 8

Data of the metabolites in the roots, stem and leaves of *A. tenella* cultured in Hoagland solution (control) and exposed to Cr stress. Values are the means \pm SE of the five different experiments (n = 15).

	Day Control			Cr		
	Root	Stem	Leaf	Root	Stem	Leaf
Total Protein (mg/g FW)						
0	2.18 \pm 0.12	3.82 \pm 0.12	7.4 \pm 0.27	2.18 \pm 0.12	3.82 \pm 0.12	7.4 \pm 0.27
7	4.88 \pm 0.06	6.28 \pm 0.54	14.14 \pm 0.17	4.89	6.9 \pm 0.12	12.58 \pm 0.25
14	6.02 \pm 0.13	8.71 \pm 0.95	18.17 \pm 0.83	4.45 \pm 0.9	3.07 \pm 0.15	15.36 \pm 0.19
21	7.65 \pm 0.11	12.98 \pm 0.36	23.76 \pm 0.47	2.41 \pm 0.08	2.51 \pm 0.9	9.58 \pm 0.25
Proline (mg/g FW)						
0	5.21 \pm 0.6	2.3 \pm 0.37	3.97 \pm 0.17	5.21 \pm 0.6	2.3 \pm 0.37	3.97 \pm 0.17
7	2.88 \pm 0.03	2.56 \pm 0.43	4.7 \pm 0.74	8.2 \pm 0.3	19.16 \pm 0.88	31.92 \pm 0.15
14	2.7 \pm 0.15	2.62 \pm 0.07	5.09 \pm 0.05	12.2 \pm 0.06	29.05 \pm 0.7	40.1 \pm 0.5
21	2.23 \pm 0.04	1.73 \pm 0.43	5.03 \pm 0.97	16.24 \pm 0.3	37.7 \pm 0.32	54.01 \pm 1.08
MDA content (mg/g FW)						
0	3.43 \pm 0.66	8.02 \pm 0.002	14.1 \pm 0.01	3.43 \pm 0.66	8.02 \pm 0.002	14.1 \pm 0.01
7	7.37 \pm 0.08	14.44 \pm 0.006	18.11 \pm 0.006	21.09 \pm 0.002	26.12 \pm 0.004	33.64 \pm 0.03
14	7.69 \pm 0.21	15.73 \pm 0.64	21.78 \pm 0.03	34.3 \pm 0.11	28.02 \pm 0.12	44.1 \pm 0.09
21	9.9 \pm 0.14	19.01 \pm 0.005	25.04 \pm 0.11	49.29 \pm 0.12	36.81 \pm 0.03	50.24 \pm 0.16
Soluble sugar (mg/g FW)						
0	1.21 \pm 0.07	3.09 \pm 0.11	5.9 \pm 0.67	1.21 \pm 0.07	3.09 \pm 0.11	5.9 \pm 0.67
7	2.19 \pm 0.005	6.25 \pm 0.13	7.4 \pm 0.06	1.89 \pm 0.4	6.67 \pm 0.08	8.04 \pm 0.18
14	3.22 \pm 0.03	6.8 \pm 0.12	8.76 \pm 0.35	1.39 \pm 0.001	6.61 \pm 0.15	7.07 \pm 0.04
21	2.17 \pm 0.16	9.71 \pm 0.11	10.47 \pm 0.006	0.91 \pm 0.1	5.01 \pm 0.7	5.97 \pm 0.04
Phenolics (mg/g FW)						
0	0.21 \pm 0.007	0.1 \pm 0.02	0.34 \pm 0.02	0.21 \pm 0.007	0.1 \pm 0.02	0.34 \pm 0.02
7	0.19 \pm 0.005	0.33 \pm 0.07	0.53 \pm 0.09	0.39 \pm 0.05	0.25 \pm 0.01	0.69 \pm 0.01
14	0.22 \pm 0.003	0.39 \pm 0.03	0.71 \pm 0.11	0.44 \pm 0.001	0.41 \pm 0.1	0.76 \pm 0.02
21	0.17 \pm 0.006	0.13 \pm 0.02	0.54 \pm 0.05	0.37 \pm 0.1	0.49 \pm 0.03	0.68 \pm 0.09

3.6. Fourier transform infrared (FTIR) analysis

The functional groups of biomolecules (carboxyl, phosphate, amide, and hydroxide) that interact with transition metals in biological samples can be identified by analysing the infrared light adsorption of the molecules. Therefore, metal cation binding in biological samples can be studied using FTIR data. The IR spectra of roots, stems, and leaves from control and Cr treated samples were compared to assess the variation in functional groups in response to heavy metal stress. After 21d of growth, control root samples had absorption peaks at 3412, 2925, 2684, 2357, 2145, 1641, 1360, 1060, and 615 cm^{-1} , whereas Cr treated root samples had absorption peaks at 3418, 2924, 2356, 2120, 1638, 1381, 1054, and 603 cm^{-1} (Fig. 6). The absorption peaks of control stem samples were at 3419, 2922, 2354, 2132, 1640, 1382, 1054, and 610 cm^{-1} and that of treated stem samples were at 3421, 2922, 2354, 2090, 1638, 1382, 1055, and 662 cm^{-1} (Fig. 7). The control leaf samples had absorption peaks at 3423, 2925, 1627, 1384, 1316, 1241, 1060, 780, and 517 cm^{-1} , while Cr treated leaf samples had absorption peaks at 2980, 1641, 1384, 1250, 1071, and 953 cm^{-1} (Fig. 8). It was observed that there are no significant changes in the absorption peaks of control and treated samples in case of root and stem tissues which means that the interaction of heavy metal ions with all functional groups was less. In case of leaf samples, the absorption peaks have some variations which shows that the dry biomass had different functional groups available for binding of heavy metal ions. No absorption peaks were observed in the 3600 – 3200 cm^{-1} range in the Cr treated sample which characterize O-H and N-H stretch, but a peak at 3423 cm^{-1} was recorded in control sample. Also, there were absorption peaks below 900 cm^{-1} in the control samples which were absent in the Cr treated leaf sample.

3.7. Bioaccumulation of chromium

The plantlets were treated with 240 μM of Cr (VI) for a period of 21d. Roots exhibited a larger accumulation of Cr than the other plant parts studied (leaves and stem). The Cr concentration in the roots of the plantlets was 179.625 mg/kg DW, respectively on 21d. The accumulation of Cr in the stem and the leaves were less as compared to the roots. The Cr concentration in the stem and leaves of the plantlets was 87.075 mg/kg DW and 98.625 mg/kg DW, respectively on 21 d. The BCF value was given by the ratio of the concentration of metal in roots of treated plant to that of medium and was found to be 16.23 for *A. tenella* under Cr treatment. BAC value measures the proportion of metal concentration in shoot (stem and leaves) to that of medium. BAC value was also high for Cr metal in *A. tenella* i.e., 15.7. BTC value provides an idea on the concentration of metal translocated from the root system to the aerial part of the plant and for *A. tenella*, it was found to be 1.03 which can make it ideal for phytoextraction of Cr.

4. Discussion

Higher concentrations of heavy metals in environment are one of the major abiotic stresses that affects the overall growth and development of plants. Cr (VI) is a highly toxic metal that inhibits various morphological, anatomical, physiological and metabolic activities in plants (Srivastava et al. 2021). *Alternanthera tenella*, is an invasive weed species that profusely grow on the riparian zone near metal

industries. Therefore, assessing the changes in the structure, metabolic processes induced by Cr (VI) stress and the tolerance potential of the *A. tenella* towards Cr turn out to be important.

4.1. Plant growth

A. tenella, when exposed to Cr, showed visible morphological parameters in terms of root length, shoot length, and leaf area. Reduction in these parameters is correlated with the increase in days of exposure to Cr. The reduction in the fresh weight and dry weight of *A. tenella* on treatment with Cr, showed the toxicity of the metal in biomass production of the plant. Roots are the primary sites for Cr toxicity since they are directly associated with heavy metal uptake. As a tolerance mechanism in plants, stress-induced root length reduction reduces the region of exposure to metal stress (Miras-Moreno et al. 2014). The reduction in root length of plants on Cr treatment was also reported in *Cicer arietinum* (Medda and Mondal, 2017), *Citrus aurantium* (Shiyab, 2019), *Pistia stratiotes* (Kakkalameli et al. 2018), *Camellia sinensis* (Tang et al. 2012), *Oryza sativa* (Ma et al. 2016; Chen et al. 2017), *Pisum sativum* (Rodriguez et al. 2011), *Arabidopsis thaliana* (Wakeel et al. 2018), and *Vigna radiata* (Singh et al. 2021). Cr (VI)-mediated root growth inhibition may result from a reduction in cell size and an inhibition of cell division in the elongated region (Peralta et al. 2001) or the chromosome distortion in root apex cells, or the stress ethylene production (Shinwari et al. 2015; Shahid et al. 2017). Plants take up Cr through roots and it gets transported to shoot, which affects the growth of stem and leaves. The Cr stress-induced decrease in shoot length may be due to ultrastructural damage in leaf mesophyll cells, which impairs photosynthesis and ultimately results in decreased shoot development (Singh et al. 2021). The reduction in shoot length and leaf area was supported by the studies on *Helianthus annuus* (Fozia et al. 2008), *Allium cepa* (Nematshahi et al. 2012), *Citrus aurantium* (Shiyab, 2019), *Camellia sinensis* (Tang et al. 2012), *Myriophyllum spicatum* (Chandra and Kulshreshtha, 2004), *Convolvulus ternata* (Rhaman et al. 2020), *Vigna radiata* (Singh et al. 2021), and *Oryza sativa* (Ma et al. 2016; Chen et al. 2017).

The phytomass get reduced as the Cr gets translocated from root to above aerial parts of the plant in *A. tenella*, as shown by the decrease in fresh weight and dry weight. This is in correlation with the reports of Del Bubba et al. (2013) in *Nicotiana langsdorffi*, Basit et al. (2022) in *Glycine max*, Qing et al. (2015) and Wakeel et al. (2018) in *Medicago sativa*, *Festuca arundinaceae*, and *Trifolium repens*, Chen et al. (2020) in *Pennisetum sinense*, Singh et al. (2021) and Jabeen et al. (2016) in *Vigna radiata*. Phyto-toxic effects of Cr on growth and biomass production have also been studied in *Brassica oleracea* (Ahmad et al. 2020), *Solanum lycopersicum* (Javed et al. 2021), *Cicer arietinum* (Singh et al. 2020), *Brassica juncea* (Handa et al. 2018), and *Brassica parachinensis* (Kamran et al. 2021). Tolerance indexes based on root length are regarded as a good metric for determining how resilient plants are to heavy metal stress (Majeed et al. 2019). The low TI value found in *A. tenella* after Cr treatment suggests that the high concentration of Cr severely inhibits root growth and interferes with cell division.

4.2. Anatomical modifications

Chromium treatment induced significant structural alterations in the plant organs (root, stem and leaves) of *A. tenella*. SEM images showed that the increased wall thickness of xylem components and

depositions were the most prominent change. Scanning micrograph of control root and shoot showed the distinct features of epidermis, cortex, vascular region and pith, but with Cr treatment these tissues get deformed. This result is in corroboration with the reports in plants like *Vigna radiata*, and *Cicer arietinum* (Ratheesh Chandra et al. 2010; Medda and Mondal, 2017). The root and stem showed more damages than the leaf, with the cell structures getting highly distorted (Fig. 3) and some depositions were also seen in the tissues. This is in accordance with the findings of Wakeel et al. (2020). Cr (VI) on passing through endodermis via symplast probably get reduced to Cr (V) which gets retained in the root cortex cells and this may be the reason for distortions in the root. Continued exposure to Cr can lead to the translocation of Cr from root to stem. At higher concentrations of Cr, ROS production is enhanced that cause oxidative damage at cellular level and this may be the reason for distortions in anatomy of stem (Shanker et al. 2005). Shanker et al. (2004) has also mentioned that the damage of root and stem tissues can be the result of cell malfunctioning induced by Cr accumulation in roots, by the displacement of Ca^{2+} ions from the binding sites in cell walls and plasma membranes. The sequestration of Cr in the root vacuoles and poor translocation from root to shoots thus alters the structure of the root (Shanker et al. 2004) and in *A. tenella*, it can be correlated with the reduced root growth. Scanning electron micrographs showed the presence of some aggregates on the cell wall of xylem elements of the Cr treated leaves (Fig. 4B). Rucinska-Sobkowiak (2016) reported that apoplast resistance to water flow is increased by cell wall thickening caused by metal deposits and/or incrusting substances in the cell walls. This will in turn eventually reduces the transportation of water and soluble mineral nutrients from the root to the shoot, and this observation can be corroborated with the decreased macro and micro-elements content detected in shoot than roots in the SEM-EDX data. Fully opened stomata were observed on the leaf surface of control plants, while the stomata in Cr treated plants were partially opened. Moreover, in *B. juncea* treated with Cr, sunken and poorly defined elliptical stomata were seen (Han et al. 2004). This may be due to rapid induction of stomata closure by abscisic acid (ABA), a signaling molecule activated under water stress to reduce the water loss from leaves (Rucinska-Sobkowiak, 2016).

4.3. Element analysis in tissues

To know the underlying mechanism of uptake of chromium and its translocation to various plant parts is important because of its toxic effects on plant and human metabolism. But the mechanism of Cr uptake in plants is not distinctly explained till date. In contrast to Cr (VI), which shares structural similarities with phosphate and sulphate and is therefore actively taken up by phosphate and sulphate transporters, plants take up Cr (III) through a passive process by diffusion at the cation exchange site of the cell wall (de Oliveira et al. 2016; Singh et al. 2013). The intake of essential minerals like calcium (Ca), magnesium (Mg), phosphorus (P), and iron (Fe) has been shown to be reduced by excessive Cr, which masks the sorption sites and forms insoluble complexes (Basile et al. 2012; Torok et al. 2001). In addition to being necessary for plant growth and development, mineral nutrients also aid in the reduction of various stresses, including heavy metal stress (Jalloh et al. 2009).

Treatment of Cr caused a reduction of C in the roots but marked an increase in leaves of *A. tenella* with reference to the control plants. The C content did not change significantly in the Cr treated stem from that

of control. The macronutrient C is a component of macromolecules, including proteins, nucleic acids, carbohydrates, and many others (Holland et al. 2005). There has been a decrease in carbon absorption due to the insufficient ability of leaves to absorb CO₂ (Barthel et al. 2011; Ruehr et al. 2009). This is related to the partially closed stomata due to Cr stress, which prevents the CO₂ needed for C fixation from entering the plant. The carbon that enters the leaf get reduced to sugars and this is correlated with the increased amount of soluble sugars in leaves of Cr treated *A. tenella*. But the translocation of these photoassimilates is reduced due to the Cr ions and hence there is less C content in the stem and roots compared to leaves (Jha and Dubey, 2004; Mishra and Dubey, 2013). The distribution of O was also affected by the Cr treatment in *A. tenella*. The O content reduced in the treated plants compared to control in all plant parts. The increased activity of antioxidant enzymes is attributed to the higher level of K in the Cr-treated roots, and K also serves as a coenzyme or activator of a number of crucial enzymes (Mengal, 2007). K⁺ ions activate a vast variety of enzymes, which encourage cell elongation and maintain osmotic balance. The presence of K was not detected in the stem tissues of both control and treated plants, but the K content was reduced in the leaves of treated plants than the control plants. Similarly, P distribution was also increased in the roots of treated plants compared to control. While the P content was detected in trace amounts in the leaf tissues of both the plant samples without any significant changes, P content was below the detection limit in the stem tissues of both samples. Phospholipids, nucleic acids, ATP, and certain coenzymes all contain P. The higher ATP synthesis due to increased mitochondrial activity and the activation of the antioxidant enzymes could account for the higher P level found in the roots of Cr-treated plantlets (Sarath et al. 2022b). The Ca content was slightly increased in the Cr treated roots compared to control. As calcium is an essential component of many signalling pathways, it is easily absorbed by roots and transported to shoots through xylem, controlling a number of physiochemical activities (Mansoor et al. 2014; Tuteja et al. 2007). Ca²⁺ has a significant influence on stomatal motility and regulates guard cell activity as a secondary messenger (Schroeder et al. 2001). When plants are under metal stress, the lowering of Ca has a significant impact on how well the stomata function (Rucińska-Sobkowiak, 2016).

Of the several micronutrients, Fe, Al, Si and Cu, Zn were present in the roots and stem respectively of control plant roots in low quantities but in the treated roots, these ions were below the detectable limit. In the leaves of Cr treated plants, S, Si and Fe content was less but was not detected in the control leaves, while Na showed a reverse trend. The changes in the distribution of Cu, Cl, Al, and Zn were not significant in the Cr treated plants compared to control. Thus, the SEM-EDX microanalysis of roots, stem and leaves of control and Cr treated plantlets showed that Cr significantly affects the distribution and content of macroelements in *A. tenella*, but do not affect the content of micronutrients. Intracellular concentrations of the important nutrients P, Ca, Mn, Mg, K, and Fe in plants are altered by Cr (VI) (Gardea-Torresdey et al. 2004). The findings of the present study can be corroborated with the reports from other plants such as *Oryza sativa* (Sundaramoorthy et al. 2010; Ahmad et al. 2011), *Citrullus vulgaris* (Dube et al. 2003), *Zea mays* (Mallick et al. 2010), *Kali turgidum* (Oliveira, 2012), and *Raphanus sativus* (Tiwari et al. 2013).

4.4. Photosynthetic efficiency

The reduction in chlorophyll content of the plantlets treated with Cr makes it easy to assess the enhanced toxicity. An increase in the total chlorophyll content of Cr treated *A. tenella* plantlets was followed by a gradual decrease during the stress period (Table 7). Chinmayee et al. (2014) had also reported similar findings in *Jatropha curcas*. The degradation of photosynthetic pigments that cause deficiency in light-harvesting capacity is caused by exposure to high levels of heavy metals (Srivastava et al. 2021). Cr stress induced reduction in chlorophyll content was reported in plants like *Citrus aurantium* (Shiyab, 2019), *Triticum aestivum* (Subrahmanyam, 2008), *Najas indica*, *Vallisneria spiralis*, and *Alternanthera sessilis* (Chandra and Kulshreshtha, 2004) showed decrease in chlorophyll content under Cr toxicity. The adverse effects of Cr on the vital photosynthetic pigments including chlorophylls were reported by Boonyapookana et al. (2002) and Henriques (2010). Gill et al. (2015) hypothesised that Cr at higher doses inhibits the activity of d-aminolaevulinic acid dehydratase, an essential enzyme in pigment synthesis that results in inhibiting chlorophyll biosynthesis. Studies on Cr stress in *Vigna radiata* (Singh et al. 2021), *Nicotiana tabacum* (Bukhari et al. 2016), *Sorghum bicolor* (Kumar et al. 2019), *Brassica juncea* (Mahmud et al. 2017; Singh et al. 2017), *Cicer arietinum* (Singh et al. 2020; Li et al. 2017), *Zea mays* (Habiba et al. 2019), *Brassica napus* (Gill et al. 2015a), and *Brassica oleracea* (Ahmad et al. 2020) have reported similar results. Since photosynthetic pigments like Chlorophyll a and b are inhibited by Cr, the net photosynthetic rate is impacted, which lowers dry biomass (Liu et al. 2008), and it validates the result in *A. tenella*. Carotenoids also followed a similar trend to that of chlorophyll in *A. tenella*. The decrease in carotenoids was reported in *Phaseolus vulgaris* by Aldoobie and Beltagi (2013).

4.5. Metabolites

The total protein content of the root, stem and leaf samples of *A. tenella* after Cr treatment showed an increase initially, followed by a gradual decrease. A significant and rapid response of metal stressed plants is the induction of protein synthesis (Hall, 2002). The increased protein content found in *A. tenella* tissues treated with Cr may be linked to the synthesis of stress proteins like phytochelatins and metallothioneins. This overproduction of "stress proteins" like phytochelatins, metallothioneins, antioxidants like glutathione (GSH), and heat shock proteins, which protect the plant from harm from toxic metal ions, is the likely cause of the increased protein content (Verma and Dubey, 2003; Mishra et al. 2006). HSPs may be produced in response to heavy metal stress to stop proteins from misfolding, aggregating, and degrading (Gupta et al. 2010). HSPs are significantly increased under conditions of metal toxicity in order to repair and stabilise the damaged proteins (Haap et al. 2016; Pochodylo and Aristilde, 2017). During extended growth, heavy metals have a negative impact on protein composition, which may be caused by the degradation and fragmentation of proteins that alters their structural and functional properties (John et al. 2009). In lettuce, increased protein breakdown and the suppression of Rubisco activity are thought to cause a decline in protein synthesis, according to Monteiro et al. (2009).

In Cr treated *A. tenella*, the soluble sugar content decreased gradually over the stress period after an initial spike. The improvement in photosynthesis is responsible for the rise in soluble sugar concentration during the initial phases of metal treatment (Sarath et al. 2022b). Sugars are the primary fuel for energy metabolism, and are important signalling chemicals (Rosa et al. 2009). Characterizing the changes in

soluble sugars and starch accumulation in leaves is essential for determining the phytotoxicity of Cr (Sinha et al. 2018). The change in the soluble sugars and starch concentration of plants when treated with Cr was reported by Rodriguez et al. (2012), and Prado et al. (2010) and their results can be corroborated with the findings of the present study. The amount of soluble sugars was high in the leaves of treated plants compared to roots in *A. tenella* and this can be due to the less translocation of carbohydrate from the synthesising sites (Jha and Dubey, 2004; Mishra and Dubey, 2013). The amount of photoassimilates produced is also decreased due to the lower leaf area and damage to the photosynthetic system (Armendariz et al. 2016).

Significantly higher proline, phenol and malondialdehyde content was observed in *A. tenella* when subjected to Cr. Accumulation of proline is one of the strategies plants adopt to counteract the toxic effect of HM stress (Clemens, 2006). Significantly increased proline contents due to Cr stress have been reported in *Sorghum bicolor* (Kumar et al. 2019), *Helianthus annuus* (Qadir et al. 2020), *Cicer arietinum* (Singh et al. 2020), *Zea mays* (Adhikari et al. 2020), *Ocimum tenuiflorum* (Rai et al. 2004). Proline is believed to have multiple roles during metal stress, such as osmoticum maintenance, scavenging of free radicals, stabilizing of membranes (Rai et al. 2004). Proline functions as a compatible solute to protect enzymes against denaturation and the scavenging of ROS in addition to osmotic control (Hussain et al. 2011). According to reports, proline is the only amino acid that builds up in plant leaves under stress conditions. Proline accumulation in tissues leads to osmotic adjustment and serves as a dependent marker for genotypes associated with stress tolerance (Ganesh et al. 2009). Increased Phenolics is another way of coping up with the metal stress in plants. Phenolics protect plant cells against HM stress by metal chelation, phenol- coupled ascorbate peroxidase activity and scavenging of reactive oxygen species (Lavid et al. 2001). Malonydialdehyde (MDA) content represents the magnitude of lipid peroxidation as an important impact of HM toxicity in plants. The increased MDA levels in the root and shoot tissues at different concentrations of Cr are considered a sign of oxidative damage due to external Cr toxicity. Increased lipid peroxidation due to Cr stress was reported in *Triticum aestivum* (Zhang et al. 2010; Ali et al. 2015), *Zea mays* (Maiti et al. 2012), *Chamomilla recutita* (Kováčik et al. 2014), *Brassica campestris* (Chandra et al. 2009), *Cicer arietinum* (Singh et al. 2020), *Brassica napus* (Gill et al. 2015b), *Zea mays* (Anjum et al. 2017; Habiba et al. 2019).

4.6. Fourier transform infrared (FTIR) analysis

FTIR is a reliable method for identifying metal-induced changes to the structural composition of the biomolecules in root and leaf sample samples (Sruthi and Puthur, 2019). FTIR results shows that dry biomass has several functional groups such carboxyl, phosphate, amide, and hydroxide that are available for binding heavy metal ions (Usman et al. 2019). O-H and N-H stretch are characterised by the broad and robust IR spectral bands spanning $3600 - 3200 \text{ cm}^{-1}$ (Panda et al. 2007). All bands in the regions $2500 - 2000 \text{ cm}^{-1}$ and $2000 - 1500 \text{ cm}^{-1}$ corresponds to absorption caused by triple bonds and double bonds respectively. All bands at the range of 1600 cm^{-1} corresponds to specific amide groups due to C = O stretch (Dumas and Miller, 2003). The regions from 1200 to 900 cm^{-1} signify C-C, C-O, and C-O-P stretch overlaps occurring mainly in cellular polysaccharides (Wolkers et al. 2004). Although, three to five major

bands were found to correspond to metal interaction in the root, stem and leaf samples of *A. tenella*, only three of these peaks, and their corresponding shifts were consistent on comparison to all tissues, and hence studied in detail.

Examining our FTIR results, root control (RoC) showed a band at 3412 cm^{-1} shifting to 3418 cm^{-1} for root treated (RoT), from 3419 cm^{-1} for stem control (SoC) to 3421 cm^{-1} for stem treated (SoT), 3423 cm^{-1} for leaf control (LoC) to no peak at $3200\text{--}3600\text{ cm}^{-1}$ region for leaf treated (LoT). These band shifts are due to cationic interaction of Cr^{2+} with the hydroxyl group for metal oxygen binding. Similar pattern was noted by Usman et al. (2019) when *Tetraena qataranse* was assessed for the accumulation of heavy metals including Cr, D'Souza (2008) when *P. tetrastromatica* was treated with and without Cd and Panda et al. (2007) following Cd and Ni adsorption by *L. sativus*. RoC showed a band at 1641 cm^{-1} shifting to 1638 cm^{-1} for RoT, from 1640 cm^{-1} for SoC to 1638 cm^{-1} for SoT, 1627 cm^{-1} for LoC to 1641 cm^{-1} region for LoT. These shifts are due to the interaction of Cr^{2+} ions with specific amide groups due to C = O stretch. There were decrease in bands intensity from RoC at 1060 to 1054 cm^{-1} for RoT, SoC from 1054 to 1055 cm^{-1} for SoT, LoC from 1060 at 1071 cm^{-1} LoT. These shifts can be attributed to strong metal binding with C-C, C-O, and C-O-P (Sheng et al. 2004). A prominent band shift was observed at RoC showing a band at 1360 cm^{-1} shifting to 1381 cm^{-1} for RoT, which corresponds to CH_3 deformation. This indicates the enhancement of hemicellulose in xylem cell walls that lead to increase in its thickness (Sarath et al. 2022a). Finally, with consistent decrease in band intensity of RoT when compared to SoT, the FTIR results were in agreement with the ICP-AES result, that *A. tenella* adsorb more Cr in the root, with further translocation to the stem and leaf.

According to FTIR data, amide, hydroxyl, phosphate, and carboxyl groups interact with one another to form bonds. Ion exchange via the carboxyl groups on the plant's surface is the primary mechanism for removing heavy metals. The interactions between the transition metals Cd, Cr, Cu, and Ni and plant biomass are mostly mediated by amino sugars (Panda et al. 2007). These sites primarily accommodate the cations H^+ , Na^+ , K^+ , Ca^{2+} , Mg^{2+} , and Fe^+ . Yet, there is a propensity for metal substitution when metals like Cr are present (Schneider et al. 2001). Hence, carboxyl and amino groups are the means via which metals interact with *A. tenella* biomass. After the cationic exchange for metals via the functional groups, modifications to the structural moieties of lignin, cellulose, and proteins affect the growth pattern of plants, photosynthetic activity, and antioxidant system (Panda et al. 2007; Kumar et al. 2017).

4.7. Bioaccumulation of chromium

An effective phytoremediation plant must be able to produce biomass even under stress. The metal accumulation in biomass, BCF, BAC, and BTC of the plants determines their potential for phytoremediation (Abou-Aly et al. 2021; Parihar et al. 2021; Budzynska et al. 2019). In the present study, a higher accumulation of Cr was observed in the roots of *A. tenella* exposed to Cr treatment (179.625 mg/kg DW) and the accumulation of Cr in the stem (87.075 mg/kg DW) and leaves (98.625 mg/kg DW) were less compared to roots. Similar observations were found in *Colocasia esculenta* (Men et al. 2018), *Diectomis fastigiata* (Mohanty and Patra, 2020), *Melia azedarach* (Yan et al. 2020), and *Pennisetum*

sinese (Chen et al. 2020), *Vigna radiata* (Jabeen et al. 2016; Singh et al. 2021), *Zea mays* (Anjum et al. 2017), *Brassica napus* (Gill et al. 2015b), *Brassica campestris* (Zhao et al. 2019), *Brassica oleracea* (Ahmad et al. 2020), *Cicer arietinum* (Singh et al. 2020), *Arachis hypogaea* (Zong et al. 2020), and *Oryza sativa* (Nagarajan and Ganesh, 2015), and *Tradescantia pallida* (Sinha et al. 2014). Sometimes, the root concentration of Cr exceeds the shoot concentration by 100 times (Shanker et al. 2005). This could be due to the low mobility of Cr in the plant roots compared to other metals or the sequestration of Cr in the vacuoles of root cells which acts as a protective mechanism and provides natural tolerance to plants against Cr toxicity (Mangabeira et al. 2011). Stress ethylene is induced by Cr in plant roots that cause strong cellular damage and is transported to shoots from roots. Since the root comes in contact with stress ethylene prior to shoot, the roots get damaged first (Shiwari et al. 2015; Shahid et al. 2017). The transport of Cr also depends on its oxidation state. The conversion of Cr (VI) to Cr (III) in plant tissues prevents further transport of Cr because Cr (III) has a propensity to attach to cell walls (Kabata-Pendias and Szteke, 2015). The present study, further proved that the concentration of Cr in shoots of the *A. tenella* (185.7 mg/kg DW) is higher than in roots (179.625 mg/kg DW).

Bioconcentration factor (BCF) and translocation factors (TF) are two important parameters used to evaluate the potential of plant to remediate a particular metal (Sinha et al. 2018). The plants such as *Dyera costulata* (Ghafoori et al. 2013), *Pluchea indica* (Sampanpanish et al. 2006), *Azolla caroliniana* (Pandey, 2012), *Amaranthus dubius* (Mellem et al. 2012), *Convolvulus arvensis* (Gardea-Torresdey et al. 2005), showed a significant translocation of Cr from roots to aerial parts and thus, suggested that these species have a high phytoremediation potential. BCF helps assess a plant's ability to translocate heavy metals from soil to plant organs (Siyar et al. 2022). TF index was applied to evaluate the ability of metals to translocate from roots to shoots. The plant with both BCF and TF values greater than 1 is a potent candidate for phytoextraction. *A. tenella* showed a very high BCF_{root} value (> 1) and $TF > 1$, and this substantiates the phytoextraction potential of *A. tenella* towards Cr. *Mesembryanthemum crystallinum* (Sliwa-Cebula et al. 2020) and *Lemna minor* (Sallah-Ud-Din et al. 2017) are plants reported for their phytoextraction potential of Cr. Plants that can absorb heavy metal ions more than 100 times that of ordinary plants, and whose leaf-to-root ratio (TF) of HM content is > 1 are called hyperaccumulators (Baker et al. 2000; Saud et al. 2022). 300 $\mu\text{g/g}$ is the plant absorption threshold for Cr (Garciahernandez et al. 1998; Van Der Ent et al. 2013). Several species have been recently identified as hyperaccumulators of Cr, like *Cannabis sativa* and *Allium griffithianum* (Sajad et al. 2020), *Spirodela polyrrhiza* (Singh and Malaviy, 2019), *Canna indica* and *Hydrocotyle umbellate* (Taufikurahman et al. 2019), *Cirsium vulgare* (Dökmeci and Adilo, 2020), *Helianthus annuus* (Ranieri et al. 2013), *Euphorbia helioscopia*, *Rumex dentatus*, *Cannabis sativa* and *Parthenium hysterophorus* (Ullah et al. 2019), *Diectomis fastigiata* and *Vernonia cinerea* (Mohanty and Patra, 2020), *Ipomoea aquatica* (Haokip and Gupta, 2020), *Vigna unguiculata* and *Arachis hypogea* (Eze et al. 2018), *Cassia tora* (Patra et al. 2021), *Origanum vulgare* (Levizou et al. 2018), *Callitriche cophocarpa* (Augustynowicz et al. 2020), *Arundo donax* (Cano-Ruiz et al. 2020), *Chrysopogon zizanioides* (Rajendran et al. 2019), triploid hybrid Napier grass (Ram et al. 2019), *Miscanthus sinensis* (Liu et al. 2009), *Oryza sativa* (Yu et al. 2019), *Vetiveria zizanioides* (Nayak et al. 2018), *Spartina argentensis* (Redondo-Gómez et al. 2011), *Eichhornia crassipes* (Mondal and Nayek,

2020), *Pteris vittata* (Kalve et al. 2011), and *Solanum viarum* (Afonso et al. 2019). However, existing hyperaccumulator plants have slow growth, low biomass or economic benefits, so they cannot be practically used for remediation. The plant under study, *Alternanthera tenella*, being an invasive fast-growing plant with $TF > 1$ thus meet the criteria for a phytoextractor plant and can be a hyperaccumulator, if the concentration of Cr translocation to shoot can be enhanced. With less economical uses, *A. tenella* is an ideal candidate for phytoremediation of Cr contaminated areas.

5. Conclusion

Morphological, anatomical and physiological modifications in *Alternanthera tenella* upon Cr treatment shows that the plant was able to withstand the stress induced by the heavy metal and can uptake Cr from contaminated soil and water. Growth retardation, higher tolerance index exhibited by the plants and changes in elemental distribution pattern shows the plant's defense against Cr toxicity. Accumulation of higher Cr content in the shoot tissues of *A. tenella* reveals the phytoextraction of Cr by this plant. With $TF > 1$, the plant even meets the criteria for a hyperaccumulator. The Cr induced enhancement in stress protein, proline and MDA content, structural modifications such as more Cr depositions in vascular regions and pith, increase in the thickness of xylem elements and modifications in the functional groups with band shifts at carboxyl and amide groups in the root, stem and leaf samples clearly demonstrated the tolerance and adaptations of *A. tenella* against Cr stress. Being a prominent industrial contaminant, it is important to limit the magnification of Cr up the trophic levels and *A. tenella* is an ideal candidate for the practical remediation of Cr contaminated soil and water. Along with its use in the replenishment of water bodies and revegetation along industrial riparian zones, *A. tenella* can also be used in constructed wetlands.

Declarations

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Author contribution

K.A. Firdous and M.S. Resmi conceived the idea and designed the experiments. K.A. Firdous and K.P. Neethu collected and analyzed the data with assistance from M.S. Resmi. K.A. Firdous led writing with input from M.S. Resmi. K.A. Firdous, M.S. Resmi and P.J. Vivek reviewed and edited further details of the manuscript. All authors read and approved the final manuscript.

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Figures

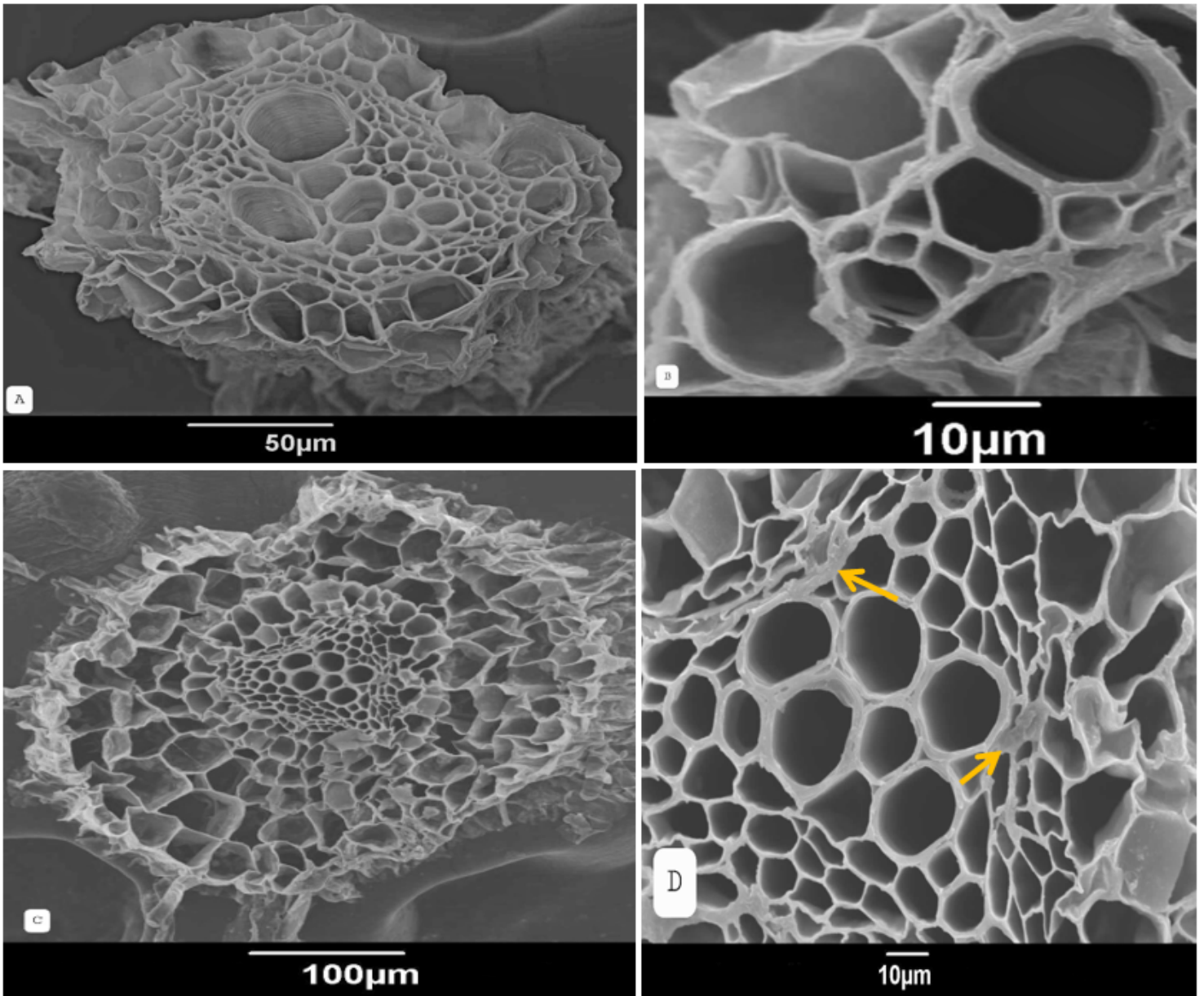


Figure 1

Scanning electron micrographs of the root of *A. tenella* (A & B – ground view and vascular region with inner pith of control sample; C & D – ground view and vascular region with inner pith of Cr treated sample)

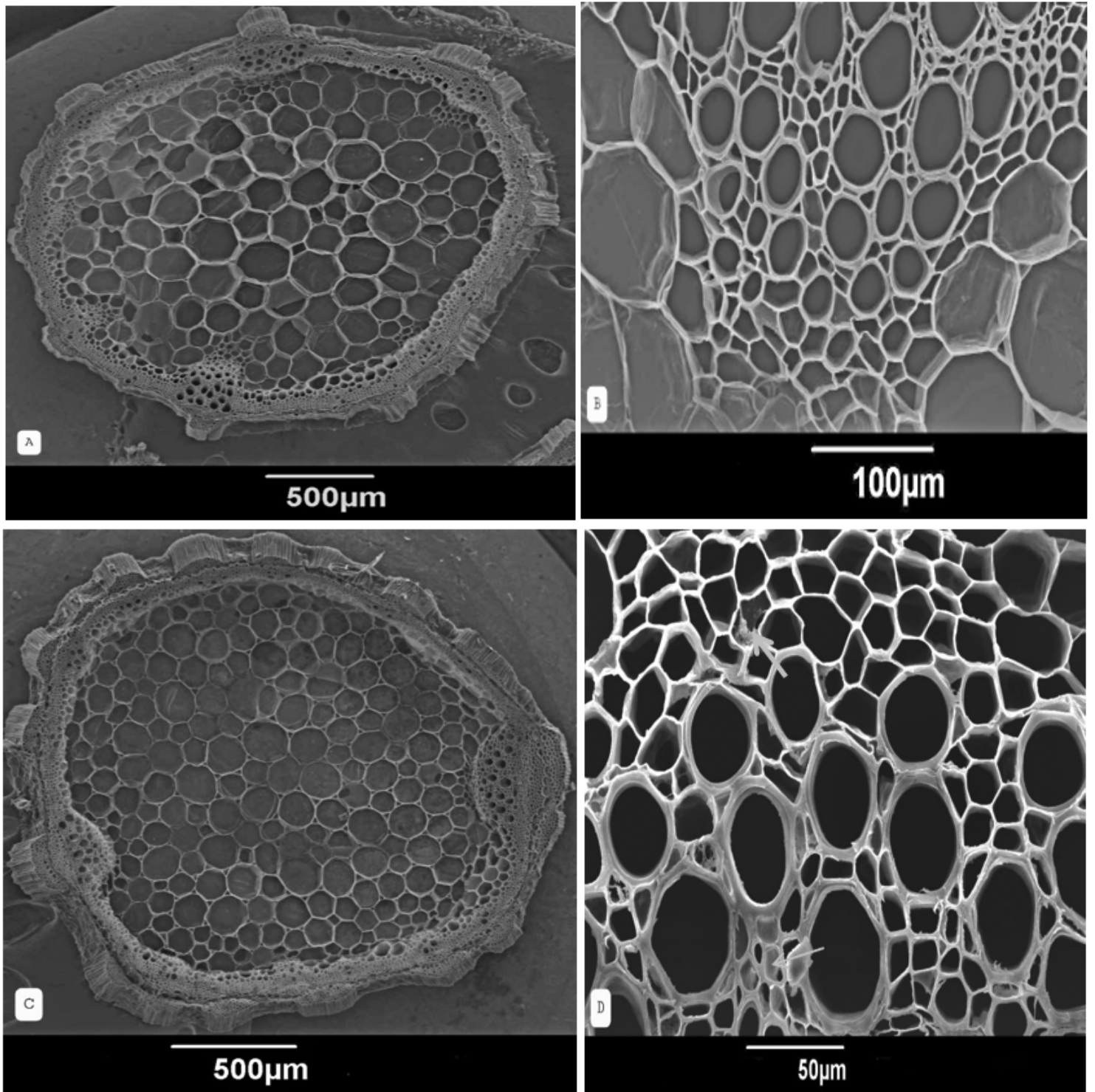


Figure 2

Scanning electron micrographs of the stem of *A. tenella* (A & B – ground view and vascular region with inner pith of control sample; C & D – ground view and vascular region of Cr treated sample)

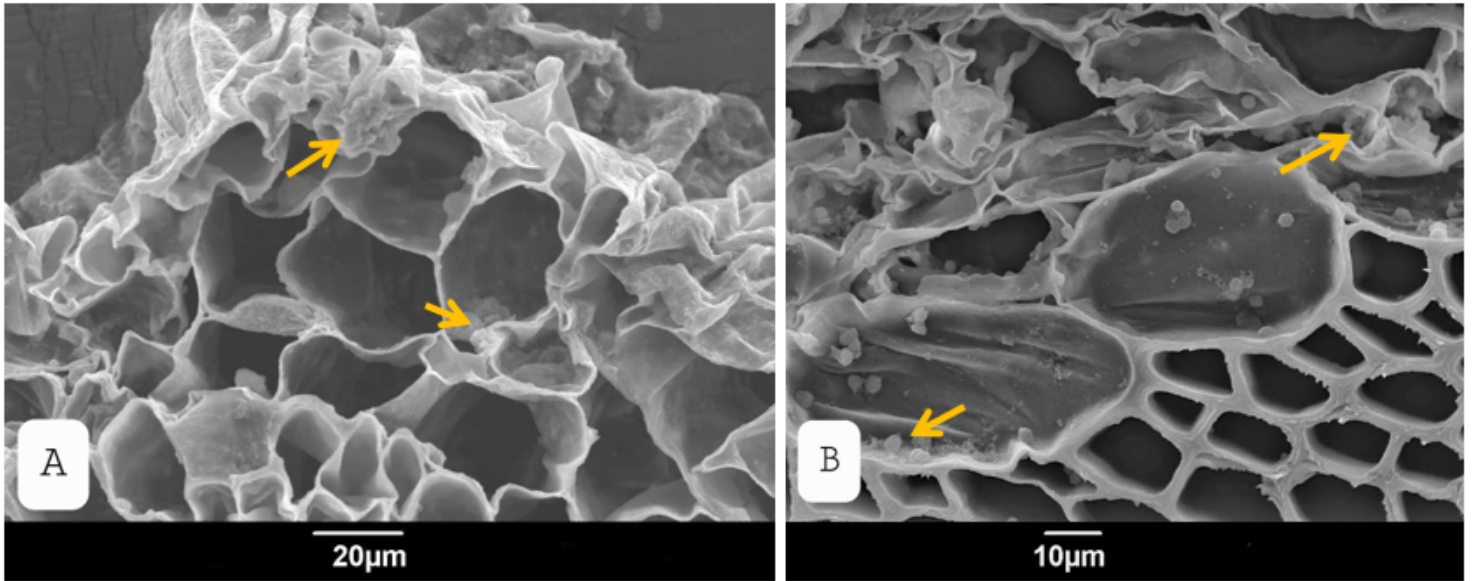


Figure 3

Scanning electron micrographs of the pith cells of Cr treated samples of *A. tenella*(A – root; B – stem)

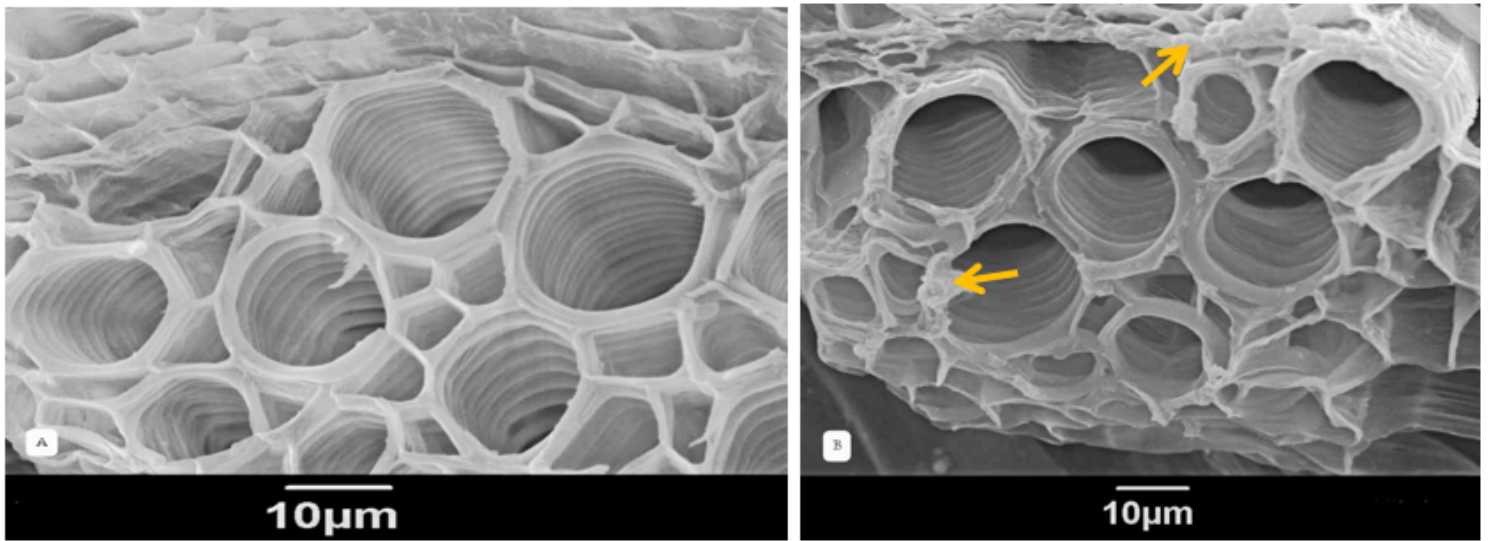


Figure 4

Scanning electron micrographs of the leaf (Xylem walls) – A. control; B - Cr treated

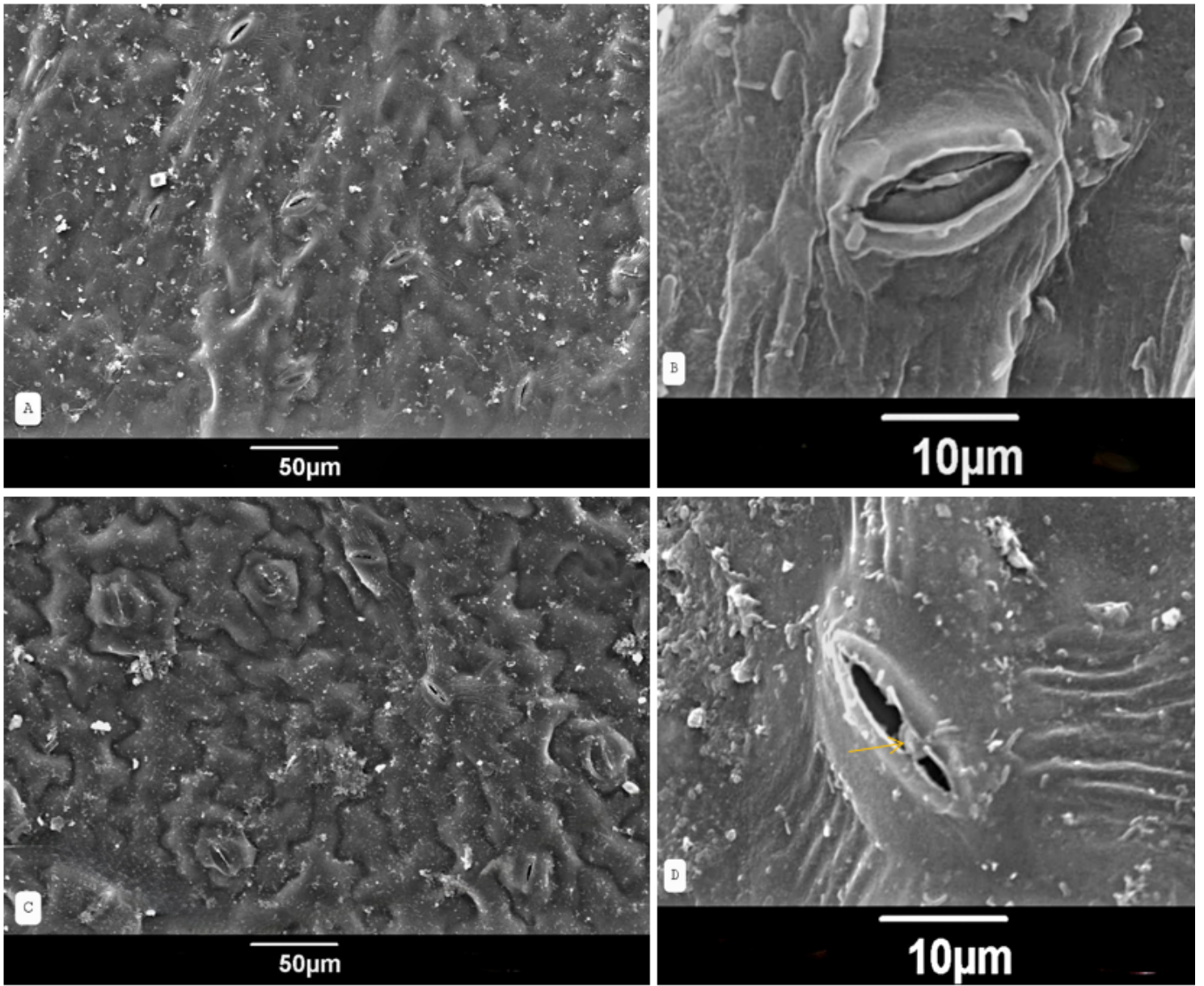


Figure 5

Scanning electron micrograph of stomata in the leaves of *A. tenella* (A, B – control; C, D – Cr treated)

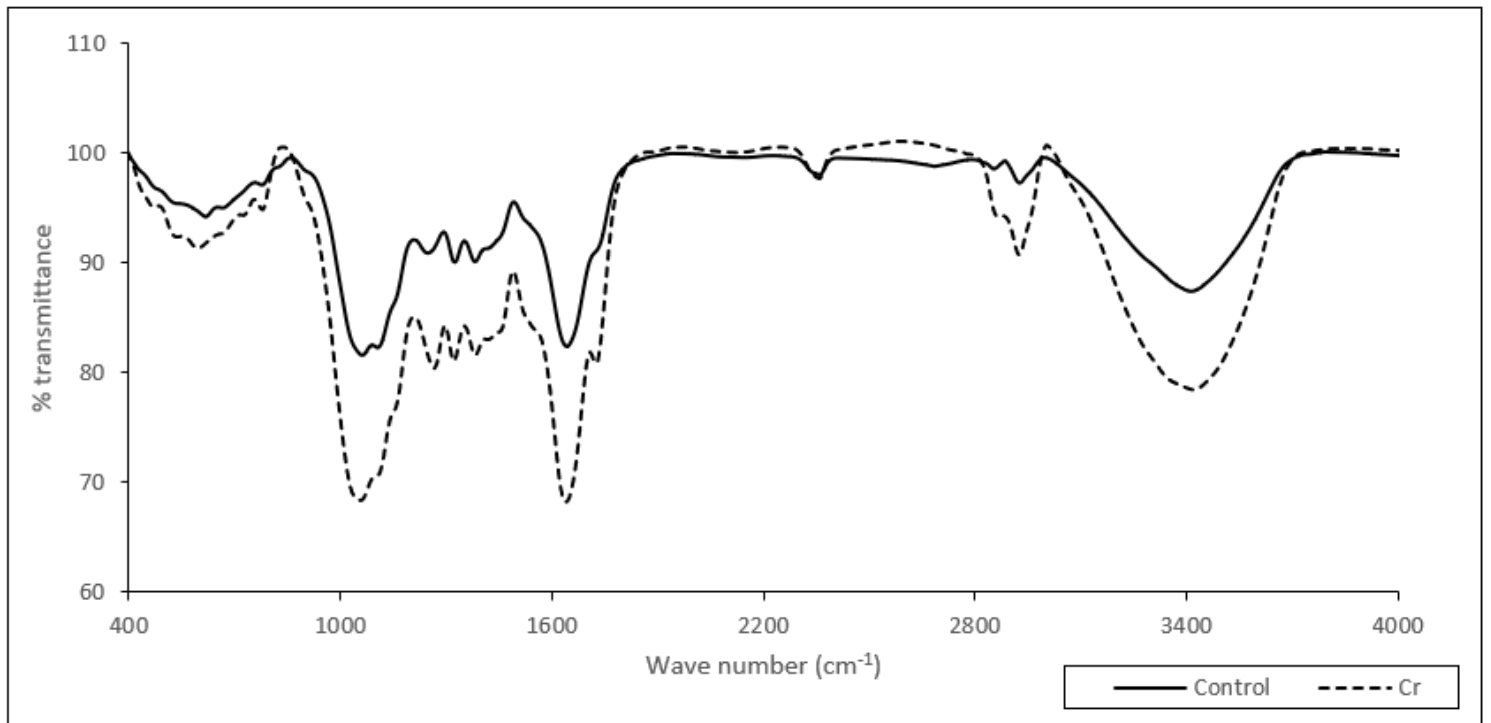


Figure 6

FTIR spectra of control and Cr treated roots

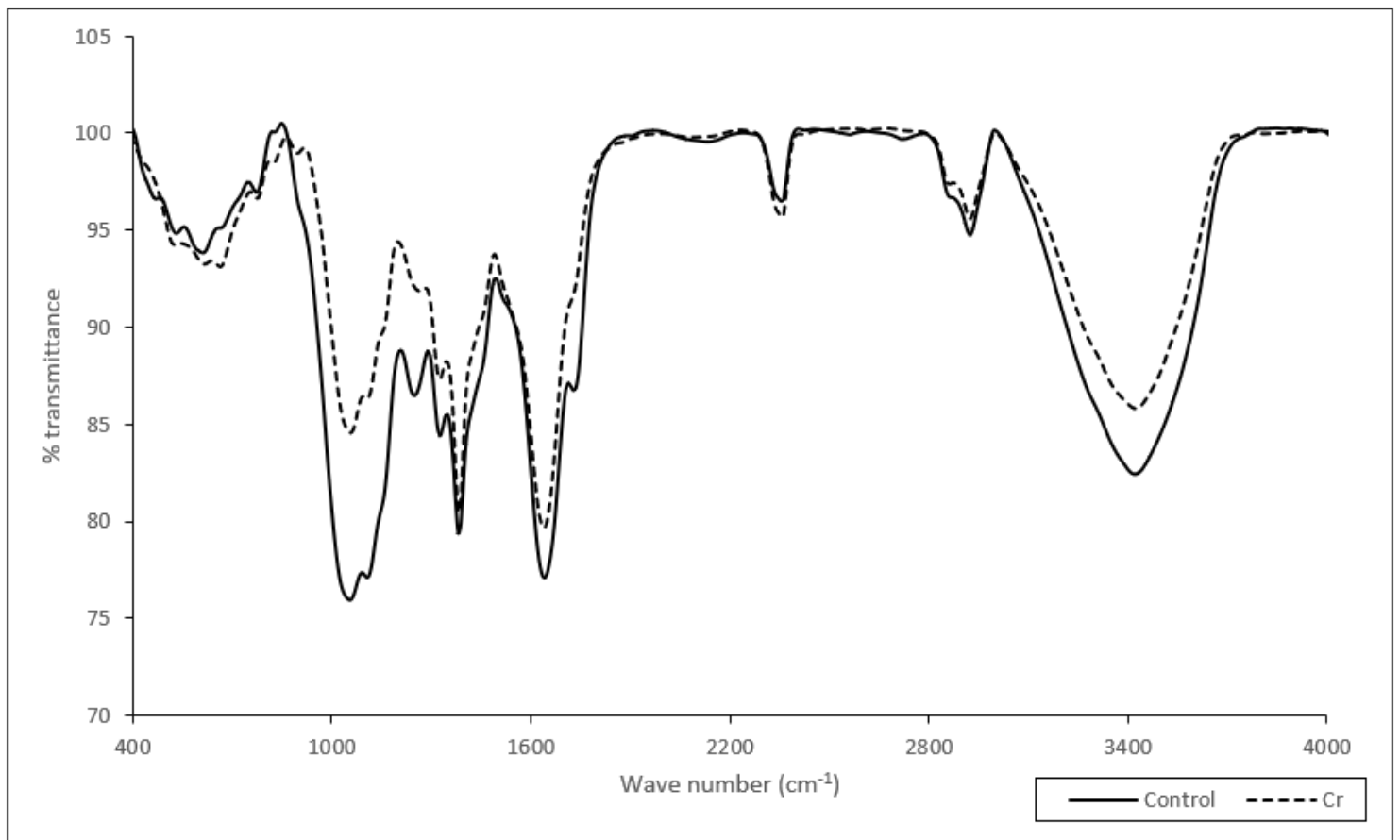


Figure 7

FTIR spectra of control and Cr treated stem

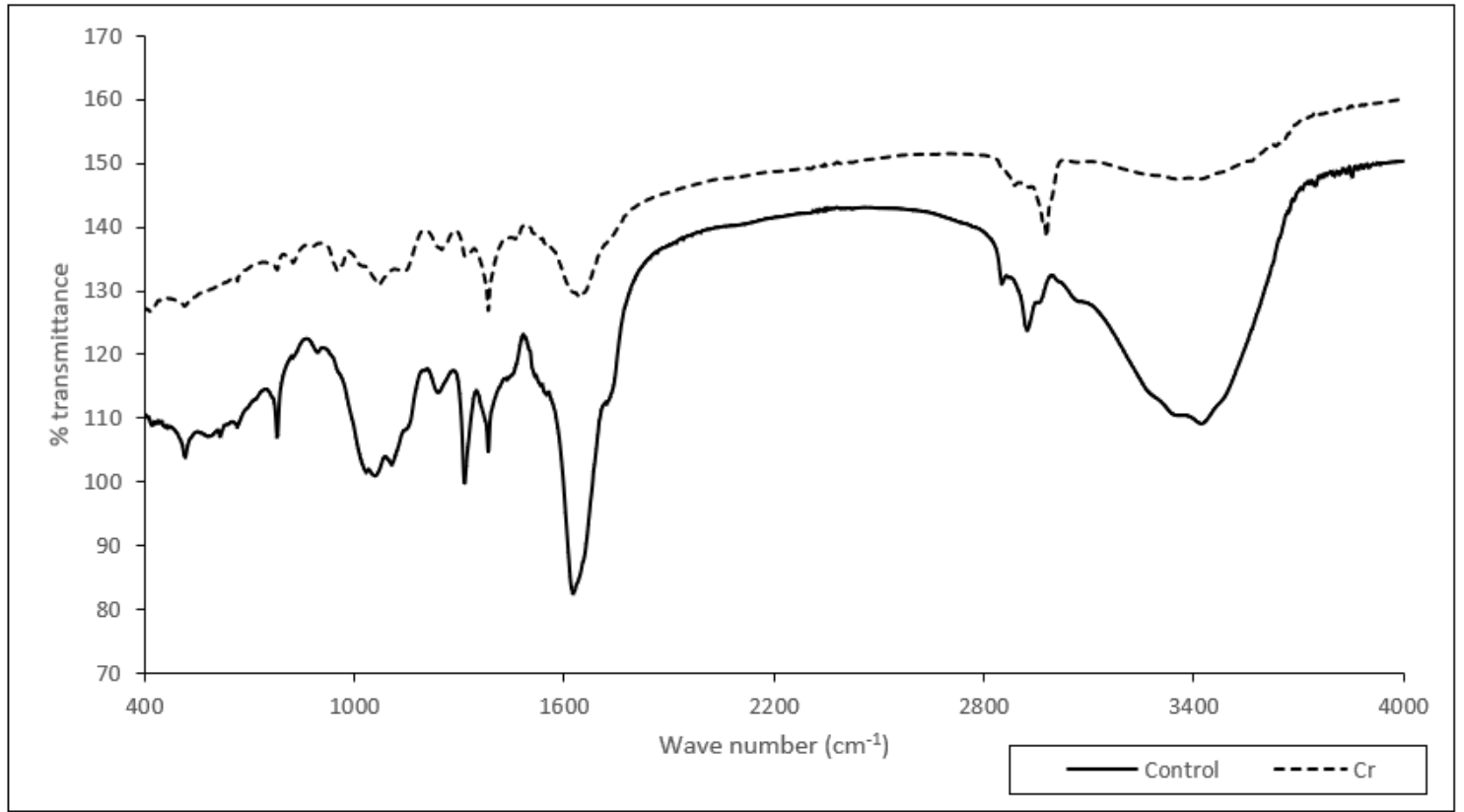


Figure 8

FTIR spectra of control and Cr treated leaf