# Growth Responses of Indonesian Foxtail Millet (Setaria italica (L.) Beauv.) to Cadmium Stress

Authors: Jadid, Nurul, Puspaningtyas, Ira, Jannah, Adillatul Lathiifatun, Safitri, Chusnul Eka, and Hutahuruk, Vidya Hana Dameria

Source: Air, Soil and Water Research, 15(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/11786221221114310

# Growth Responses of Indonesian Foxtail Millet (*Setaria italica* (L.) Beauv.) to Cadmium Stress

Air, Soil and Water Research
Volume 15: 1–8

DOI: 10.1177/11786221221114310

Nurul Jadid, Ira Puspaningtyas, Adillatul Lathiifatun Jannah, Chusnul Eka Safitri and Vidya Hana Dameria Hutahuruk

Department of Biology, Institut Teknologi sepuluh Nopember, Surabaya, Indonesia

**ABSTRACT:** Cadmium (Cd) contamination is considered as one of the most important environmental and human health issues worldwide. The occurrence of Cd in air, water and soil is resulted from massive industrialization, uncontrolled agricultural system and anthropogenic activities in urban lives. The presence of Cd in soil threatens human health through food chain bioaccumulation, negatively affect soil quality and also reduce the productivity of agricultural crops. Foxtail millet (*Setaria italica* L.) is an alternative cereal food that is highly tolerant to abiotic stresses such as drought and salinity. However, the mechanism underlying its response to the stress caused by heavy metals, such as Cd, remains unclear. This study aimed to examine the effects of Cd stress on morpho-physiological responses of the foxtail millet accession *Buru Merah*, cultivated using the hydroponic method. To this end, four levels of Cd concentrations (0, 0.5, 1.0, and 1.5 µM in ABmix™ growth media) were applied for 4 weeks followed by morpho-physiological assessements, including plant height, root length, shoot and leaf number, panicle biomass measurements and chlorophyll content evaluation. Our results demonstrated that Cd stress perturbed the growth of foxtail millet on morpho-physiological parameters, particularly at the highest Cd concentration (1.5 µM). The negative effects of Cd stress included decrease in shoot length, root length, number of leaves and shoots, panicle biomass, and chlorophyll content. Furthermore, our findings showed that Cd stress affected the growth of foxtail millet in a concentration-dependent manner. Taken together, our findings might be useful for further development of strategies to increase plant tolerance to heavy metal stress and ensure sustainable food production. In addition, this study also demonstrated the importance of protecting nature from Cd contamination.

**KEYWORDS:** Agriculture, cereal food, cadmium stress, growth responses, heavy metal, foxtail millet, sustainable food production

**RECEIVED:** December 28, 2021. **ACCEPTED:** June 24, 2022.

**TYPE:** Original Research

**CORRESPONDING AUTHOR:** Nurul Jadid, Department of Biology, Institut Teknologi Sepuluh Nopember (ITS), Surabaya 60111, Indonesia. Email: nuruljadid@bio.its.ac.id

## Introduction

Foxtail millet (*Setaria italica*) is a C4 cereal plant that belongs to the Poaceae family. It has been cultivated for more than 8000 years in North China (Jia et al., 2013; Prasad, 2017). Based on data collected in the Herbarium Bogoriense, Indonesia, it is estimated that in the early 1900s, foxtail millet was distributed in some Indonesian regions such as Sulawesi, Java, South Sumatra, Kalimantan, a small part of the Sunda Islands, Maluku, and Papua (Lestari et al., 2017). Foxtail millet is generally used as a bird feed despite the fact that the plant contains high fiber but low protein (Yulita & Ridwan, 2018). In some areas, such as Buru Island, Indonesia, the plant is considered a local superior food crop consumed by the local community (Herodian et al., 2008). The seeds contain carbohydrates, ranging from 60% to 80%; vitamins; and minerals such as calcium (Ca), iron (Fe), magnesium (Mg), phosphorus (P), zinc (Zn), and potassium (K).

The nutritional content of foxtail millet is three to five times higher than that of rice and wheat (Verma et al., 2015). Foxtail millet grows in arid and semiarid habitats and has a high tolerance to marginal environmental conditions. The plant is also able to grow well on various types of soil: from sandy to clay soils, even in rocky areas on hillsides (Herodian et al., 2008). Besides its advantages as alternative food, foxtail millet has the potential for biofuel production (Zhang et al., 2012). There are several accessions cultivated by Indonesian farmers, each of which has different morphological characteristics. In Maluku, *Buru Merah* and *Buru Kuning* are the most widely developed accessions. The *Buru Merah* accession shows better performance and viability than other accessions (Nisa & Jadid, 2021).

Several previous studies have revealed that foxtail millet is highly adaptable to environmental stress conditions such as drought stress and salinity stress (Lapuimakuni et al., 2018; Nisa & Jadid, 2021). However, studies on the responses of foxtail millet to heavy metals are limited. In some areas, including Buru Island, Indonesia, this plant is cultivated near a source of water that is polluted with heavy metal (Tupan & Uneputty, 2017). Cd contamination is thought to result from abrasion process in the river, garbage disposal activities by communities, wastewater irrigation, and ship repair and painting activities (Genchi et al., 2020). Additionally, Cd contamination in soil can result from the use of chemical or non-organic fertilizers, which are often used in agriculture (Khan et al., 2017).

A previous study revealed that the use of phosphate fertilizers on agricultural land could increase Cd content in the soil which can increase soil acidulation and hence, reduce the quality of the soil. Additionally, contamination of soil with Cd results in its accumulation in plants (Cui et al., 2014; Dharma-Wardana, 2018). According to the data from the US Environmental Protection Agency (EPA), Cd is the major contaminant or pollutant, after mercury (Hg) and lead (Pb), causing environmental damage (Jamers et al., 2013). Cadmium can cause kidney disorders, and at certain concentrations, it can cause damage to other organs such as the lungs and heart (Khan et al., 2017). Moreover, heavy metal stress is a limiting factor that causes a decrease in agricultural productivity (Gupta et al., 2013).

**Figure 1.** Foxtail millet accession Buru Merah treated with Cd stress.

Cadmium is a nonessential micronutrient that is absorbed through the plant root system and transported to the aerial parts of plants (Abozeid et al., 2017). Cadmium accumulation in plants can cause changes in plant morphology and physiology (Bruno et al., 2017). The toxic effects of Cd on plants lead to chlorosis, leaf epinasty, and deformation of the chloroplast structure (Gill & Tuteja, 2011). Excessive Cd accumulation can inhibit nutrient uptake (Sánchez-Pardo et al., 2013), photosynthesis (Xue et al., 2013), cellular respiration, and nitrogen metabolism (Bruno et al., 2017). Templeton and Liu (2010) reported that Cd accumulation can inhibit enzyme activity, increase oxidative stress, and reduce antioxidant levels. Cd uptake occurs through protein transporters. However, the uptake of Cd in some other plants is non-specific (Lu et al., 2009). Most of metal ions enter *via* root cells and subsequently be detoxified in the cytoplasm. Vacuoles are act as storage organelles. Heavy metals sequestration and detoxification are important strategies for plants. These processes mainly take place in the cuticles and trichomes (Haider et al., 2021).

Many plants developed their defense mechanisms against Cd contamination in genotype-dependent manner (Haider et al., 2021). Some plants display high tolerance to Cd contamination. More than 450 species were classified as hyperaccumulators of heavy metals (Tran & Popova, 2013). Due to the negative effects of Cd contamination, an eco-friendly protocol for mitigating the contamination should be developed (Khanna, Jamwal, Gandhi, et al., 2019). The use of microbes as plant growth-promoting microorgananisms (PGPM) is now widely used by farmer, not only for reducing the Cd pollution from soils but also for improving agricultural crop productivity (Khanna et al., 2021).

The present work observed the effects of Cd stress on the morpho-physiological responses of the foxtail millet accession *Buru Merah*. In this study, four levels of Cd concentrations (0, 0.5, 1.0, and 1.5 µM in ABmix™ growth media) were applied for 4 weeks to the tested plants using hydroponic compartments. Some morpho-physiological assessments, including plant height, root length, shoot and leaves number, panicle biomass measurements, and chlorophyll content evaluation were measured. Our study showed negative impact of Cd contamination on the growth and development of foxtail millet. This also highlighted the importance of protection the biosphere from heavy metal contamination.

## Materials and Methods

### *Plant cultivation and Cd stress treatment*

Foxtail millet (accession *Buru Merah*) seeds were obtained from the Indonesian Institute of Sciences (LIPI). The 5-days germinated foxtail seeds were then transferred into hydroponic containers supplemented with the AB Mix™ medium (Figure 1). Fourteen days after planting (DAP) the foxtail millets, they were treated with $CdCl_2$ (at concentrations of 0, 0.5, 1, and 1.5 µM) for 4 weeks (Salinitro et al., 2021). Nine replicates were used for each treatment unit (Salinitro et al., 2021).

### *Morpho-physiological assessments*

Plant growth is important parameter to evaluate the effect of abiotic stress (Sher et al., 2021). In this study plant growth were represented by some morphological factors including plant height, root length, number of leaves, and number of shoots. The assessment was performed after 4 weeks of treatment (Salinitro et al., 2021). All tested plants were removed from the hydroponic containers after 4 weeks of treatment and rinsed with tap water before being photographed to demonstrate the morphological appearances and root architecture.

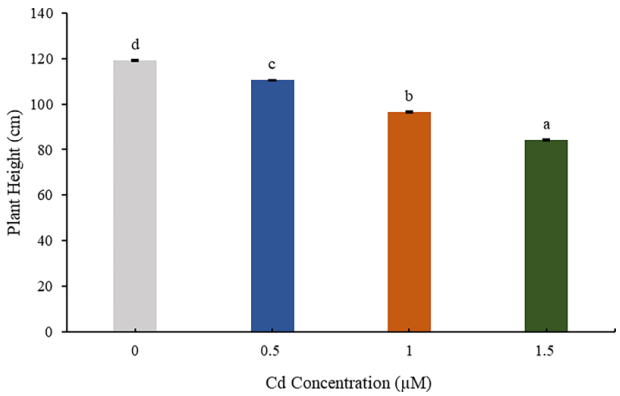


**Figure 2.** Effect of Cd stress treatment on plant height in the foxtail millet (*S. italica*) accession *Buru Merah* after 4 weeks of Cd stress treatment. Different letters indicate statistically differences at $p$ value $< .05$.


**Figure 3.** Morphological appearance of the foxtail millet (*S. italica*) accession *Buru Merah* in response to Cd stress treatment ((A) non-treated plant; (B–D) plants treated with 0.5, 1.0, and 1.5 µM, respectively).

Panicle biomass and chlorophyll content were also measured. The panicles produced from the 28 days of treatment (DAT) plants were collected and photographed. Chlorophyll content is used to indicate the photosynthesis activity of the treated plants. Therefore, it might represent plant productivity (Nisa & Jadid, 2021). Chlorophyll was measured using two-wavelength spectrophotometers to determine the absorption spectra of the chlorophyll dissolved in organic solvents. Leaves (0.1 g) from each treatment were used for chlorophyll content analysis. The sample was ground in a mortar and homogenized using 2 ml of 80% acetone (Nisa & Jadid, 2021). Subsequently, the homogenate was transferred into a measuring cup and calibrated using an 80% acetone solvent to obtain a volume of 10 ml and then centrifuged at 2,500 rpm for 10 minutes. The supernatant obtained was then quantified at 645 and 663 nm using a spectrophotometer (Nisa & Jadid, 2021). The extinction coefficient and relative absorption of chlorophyll-a and -b dissolved in the acetone were determined according to Lichtenthaler (1987). The absorbance results obtained were utilized to measure the levels of chlorophyll-a, chlorophyll-b, and total chlorophyll using the following equation (Rajput & Patil, 2017):

$$\text{Chlorophyll a}\ (\text{mg/g FW}) = \frac{(12.7[\text{A663}] - 2.69[\text{A645}])(\text{V})(\text{W})}{1000} \quad (1)$$

$$\text{Chlorophyll b}\ (\text{mg/g FW}) = \frac{(22.9[\text{A645}] - 4.68[\text{A663}])(\text{V})(\text{W})}{1000} \quad (2)$$

$$\text{Total Chlorophyll (mg/g FW)} = \frac{(20,2[\text{A645}] - 8.02[\text{A663}])(\text{V})(\text{W})}{1000} \quad (3)$$

Note:
A: absorbance value at specific wavelength
V: volume of chlorophyll extracts (mL)
W: fresh weight of the extracted tissues (g)

### *Data analysis*

All morphological measurements were conducted in triplicate, and the results were expressed as mean ± *SD*. The analysis of variance (ANOVA) test was performed using SPSS 25. Microsoft Excel 2010 (Microsoft Corporation, Redmond, WA, USA) was used for morphological and chlorophyll content data processing and interpretation. Statistical significance was indicated at $p < .05$.

## Results and Discussion

### *Effect of Cd on plant height and root length*

As assessed from the one-way ANOVA test, Cd stress at different concentrations had a significant effect ($p < .05$) on the morphological characteristics, such as plant height and root length, of *Buru Merah*. Our data demonstrated that the average height of plants treated with 0.5, 1.0, and 1.5 µM Cd was 7.4%, 19.1%, and 29.3% lower than that of the control plant (Figures 2 and 3), respectively. These results were in agreement with those of Tian et al. (2017), who reported that high concentration of Cd contamination results in decreased height in *S. italica* plant compared to that in non-treated plants. However, their responses might be genotype- and Cd concentration-dependent. In addition, Cd stress has been reported to decrease other industrial crops height such as in cotton plants (Farooq et al., 2016), *Hibiscus cannabinus* cultivars Fuhong 991, and ZM412 (Li et al., 2013). Other studies on the effect of heavy metals have also reported similar results, which was demonstrated by reduce of plant height after heavy metal treatment (Farid et al., 2013; Jadid et al., 2017). This might indicate that heavy metal contamination in soil inhibits plant growth.

In addition, Cd stress was found to cause a significant reduction in the root length of *S. italica*. The lowest average root length (14.13 cm) was observed in *S. italica* treated with 1.5 µM Cd and was approximately 45.9% lower than that of

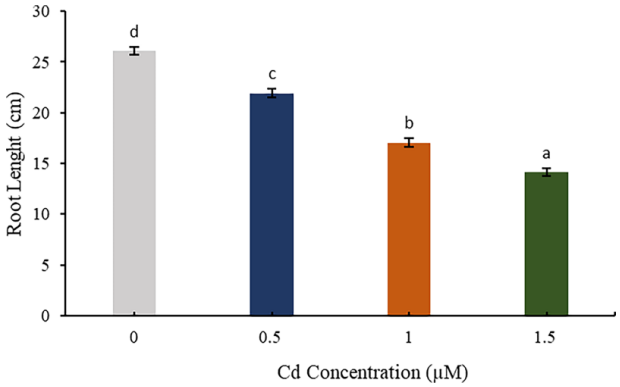


**Figure 4.** Effect of Cd stress treatment on root length of the foxtail millet (*S. italica*) accession *Buru Merah* after 4 weeks of Cd stress treatment. Different letters indicate statistically differences at $p$ value $< .05$.


**Figure 5.** Root architecture of the *S. italica* accession *Buru Merah* after Cd stress treatment for 4 weeks. ((A) non-treated plant; (B–D) plants treated with 0.5, 1.0, and 1.5 μM, respectively).

the non-treated plants (26.1 cm) (Figure 4). A minimum impact on root length (21.91 cm) was observed in *S. italica* plants treated with 0.5 μM Cd (Figure 5). Inhibition of root growth is an indicator of the effect of heavy metal stress (Jadid et al., 2017). Root growth in *S. italica* var. Jingu-21 has been reported to decrease after treatment with 200 μM Cd (Tian et al., 2017). Reduction in root growth which is demonstrated by a reduced root length, by 63.4%, 17.3%, and 69.2%, was also reported for cotton plants, *Hibiscus cannabinus* var. Fuhong 991 and ZM412, respectively, upon Cd treatment. Root length was reduced in parallel with the increase of Cd concentration (Li et al., 2013). Li et al. (2013) showed that root accumulate higher content of Cd and it was found to be "dose-dependent" and genotype-dependent. Even though all plants showed a decrease of root length after being treated with high concentration of Cd (20–120 μmol/L), their response and level of sensitivity was different (Li et al., 2013).

Cd toxicity reduce cellular division in the meristematic tissues. It will lead to reduced root length, plant height, and plant biomass. Bertels et al. (2020) demonstrated that $G_1$/S transition of the cell cycle was inhibited during Cd stress in maize. This leads to a lower proportion of cells in the S stage of plant cell cycle. In addition, Cd stress generates the production of reactive oxygen species (ROS). The accumulation of ROS might then cause an oxidative post-translational modification of cyclin D protein and A-type cyclin-dependent kinase (CDKA) (Kintlová et al., 2021).

Cd inhibits the absorption of several macro- and micronutrients, such as P, K, Ca, Fe, and Zn, required by plants via reducing the transporter selectivity (Jiang et al., 2004). Cadmium that enters root cells through these transporters further blocks the entry of other essential metal ions (Caetano et al., 2015; Thomine et al., 2000). Generally, Cd transport occurs via Fe transporters, such as Iron-Regulated metal Transporter-like protein (IRT), yellow stripe-like protein (YSL), and natural resistance-associated macrophage protein (NRAMP), located in the plasma membrane of root epidermal cells (Huang et al., 2020; Ismael et al., 2019; Takahashi et al., 2012). Therefore, similar symptoms are often observed in plants under Cd and Fe stress. Physiological disturbances observed in Fe-deficient plants might result from the perturbation of enzymatic activity and cell metabolism (Dobermann & Fairhurst, 2000; Rout & Sahoo, 2015). In addition, a previous study demonstrated that Cd absorption might interfere with Zn influx into plant cells, and subsequent Zn deficiency might decrease auxin biosynthesis in wheat (*Triticum polonicum*) (Taiz & Zeiger, 2006; Wanget al., 2017), consequently inhibiting plant root growth (Wang et al., 2017).

### *Effect of Cd on shoot and leaf number in* S. italica

Cd stress significantly affected the number of leaves and shoots in *Buru Merah* ($p < .05$). The lowest average number of leaves was 6.11 and was obtained from plants treated with 1.5 μM Cd. It was 46.08% lower than that in the non-treated plants. A decrease in the number of leaves by 35.29% and 28.43%, compared to that in control plants, was seen in *S. italica* plants treated with 0.5 and 1.0 μM Cd, respectively (Figure 6).

Similar to other parameters, *S. italica* plants treated with 1.5 μM Cd had the lowest number of shoots, which was 0.89 or 69.23% lower than that in the control plants (Figure 6). Our results indicated that the negative effect of Cd stress on the number of shoots and leaves in *Buru Merah* was dose-dependent. At higher Cd concentrations, the negative effects were more pronounced. This is in line with the results of a previous study conducted by Farooq et al. (2016), who found that a high concentration of Cd (5 μM) reduced the number of leaves of cotton plants by approximately 72.12% compared to that of non-treated plants. The low number of leaves formed in Cd-treated plants could be due to Cd-mediated inhibition of plant cell division (Abdolali et al., 2015).

Upon entering the cell, Cd interacts with the sulfhydryl group (-SH) on the cysteine residue present in the tubulin protein. This can perturb the formation of microtubules and consequently inhibit plant cell division (Abdolali et al., 2015). Monteiro et al. (2012) revealed that low concentrations of Cd treatment (1 μM) block the checkpoint process of cell division

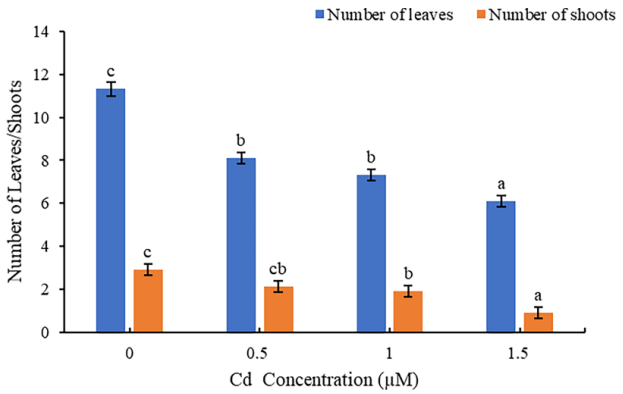


**Figure 6.** Effect of Cd stress treatment on the number of shoots and leaves in the foxtail millet (*S. italica*) accession *Buru Merah* after 4 weeks of Cd stress treatment. Different letters indicate statistically differences at $p$ value $< .05$.

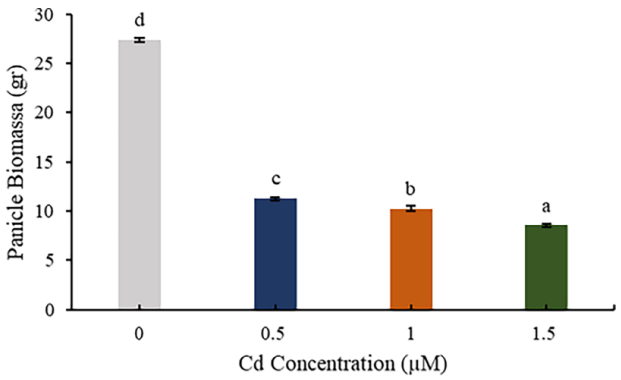


**Figure 7.** Effect of Cd stress treatment on panicle biomass of the foxtail millet (*S. italica*) accession *Buru Merah* after 4 weeks of Cd stress treatment. Different letters indicate statistically differences at $p$ *value* $< .05$.

in the G2/M phase, while at higher concentrations (10 µM), it inhibits the S phase of cell division, further affecting plant organogenesis in lettuce plant (Huybrechts et al., 2019). A study performed by Monteiro et al. (2012) demonstrated that the formation and multiplication of shoots and leaves decrease with increasing Cd concentration. Application of 10 µM Cd in lettuce (*Lactuca sativa* L.) reduced the proliferative index (PRI) by 25% compared to that in the control.

The toxicity of plant under Cd contamination is characterized by the generation of ROS. Therefore, mechanism of ROS scavenging is crucial. An increased of antioxidant enzymes such as glutathione-S-transferase (GST) as well as P450 enzymes has been described in rice and in *Medicago truncatula* (Ogawa et al., 2009; Zhang et al., 2013). In addition, production of ROS triggers upregulation of several genes which are involved in the biosynthesis of secondary metabolites (Khanna, Jamwal, Sharma, et al., 2019). It includes *Phenylalanine Amonia Lyase (PAL), Shikimate O-Hydroxycinnamoyltransferase (HCT), Cinnamoyl-CoA reductase (CCR)* (Kintlová et al., 2021).

### *Effect of Cd treatment on* S. italica *panicle biomass*

Cd treatment significantly affected *S. italica* panicle biomass ($p < .05$) (Figures 7 and 8). Treatment with 0.5, 1.0, and 1.5 µM Cd for 4 weeks decreased the panicle biomass by 58.9%, 62.55%, and 68.8%, respectively, compared to that in the control plants (Figure 7). A previous study conducted by Wei et al. (2005) showed that Cd contamination caused reduction of plant biomass of *Solatium nigrum*. Similar results were also demonstrated in Kenaf (*Hibiscus cannabinus* L. cultivar Fuhong991) and ZM412 after Cd treatment at 120 µM for 3 weeks (Li et al., 2013).

In addition, He et al. (2017) reported that cadmium (Cd) stress at a high concentration range can cause biomass reduction, chlorosis, necrosis, and disruption of homeostasis in plant organs. Consequently, it inhibits the rate of metabolism in cells, thereby reducing the productivity of plants.


**Figure 8.** Morphology of the *S. italica* panicle 28 days after treatment (DAT) ((A) non-treated S. italica plant, (B) 0.5 µM, (C) 1.0 µM, (D) 1.5 µM of Cd).

### *Effect of Cd treatment on chlorophyll content of* S. italica

In this present study, Cd treatment significantly affected the total chlorophyll content of *Buru Merah* ($p < .05$) (Table 1). The lowest chlorophyll content was observed in *S. italica* plants treated with 1.0 µM and 1.5 µM Cd (0.16 mg/g). Our statistical analysis demonstrated that there was no significant difference between the total chlorophyll contents of foxtail millets treated with 1.0 µM and 1.5 µM Cd. A decrease in chlorophyll content corroborated the morphological observations in foxtail millet leaves. We observed chlorosis symptoms in the leaves of Cd-treated foxtail millet compared to those in the green healthy leaves of control plants (Figure 9). Data on chlorophyll content were consistent with our previous data on panicle biomass. This suggests that Cd stress inhibits the photosynthesis rate of plants and consequently reduces their productivity.

A decrease in total chlorophyll levels has been observed in other studies as well—the chlorophyll content of *Pisum sativum* decreased by 31.7% after treatment with 6 mM

**Table 1.** Effect of 4 Weeks of Cd Stress Treatment on Chlorophyll Content of the *S. italica* Accession *Buru Merah*.

| CD CONCENTRATION (MM) | CHLOROPHYLL-A (MG/G) | CHLOROPHYLL-B (MG/G) | TOTAL CHLOROPHYLL (MG/G) | % OF REDUCTION |
|---|---|---|---|---|
| 0 (Control) | $0.30 \pm 0.004^{c}$ | $0.10 \pm 0.001^{c}$ | $0.40 \pm 0.002^{c}$ | - |
| 0.5 | $0.21 \pm 0.003^{b}$ | $0.06 \pm 0.002^{b}$ | $0.28 \pm 0.001^{b}$ | 30.4 |
| 1 | $0.12 \pm 0.002^{a}$ | $0.04 \pm 0.001^{a}$ | $0.16 \pm 0.001^{a}$ | 60.5 |
| 1.5 | $0.12 \pm 0.002^{a}$ | $0.04 \pm 0.002^{a}$ | $0.16 \pm 0.002^{a}$ | 61.4 |

*Note*. Results are presented as mean ± *SD*. Data value in the same column followed by the same letter are not significantly different from each other according to Post-hoc Tukey's test ($p < .05$).

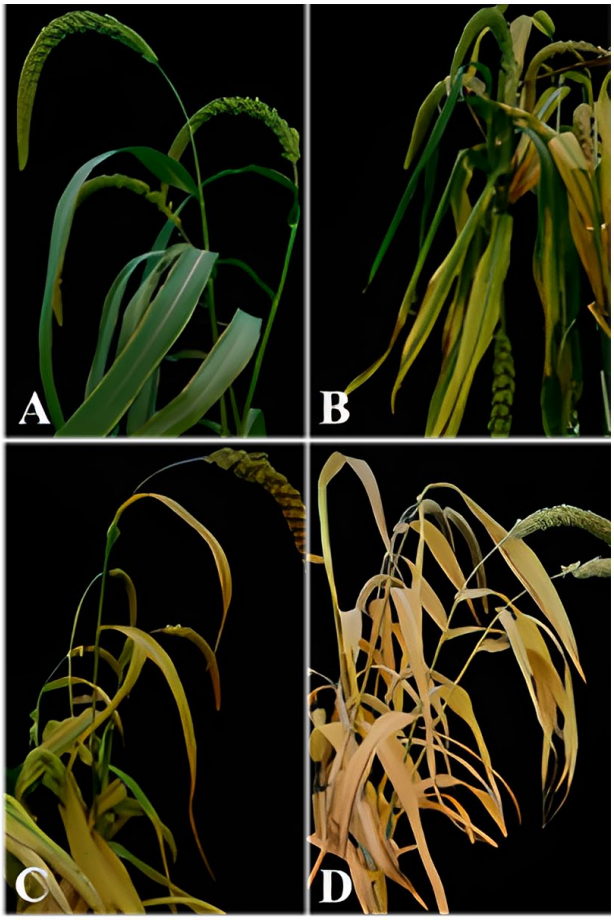


**Figure 9.** Foxtail millet *S. italica* accession *Buru Merah* after exposure to Cd in 28 DAT. (A)non-treated plants, (B) 0.5 µM Cd treatment, (C) 1.0 µM Cd treatment, and (D) 1.5 µM Cd treatment.

Cd (Januskaitene, 2012), that of corn (*Zea mays* L.) decreased by 37.3% at 20 µM Cd concentration (Wang et al., 2009), while that of *Phragmites australis* decreased by 62.7% at 100 µM Cd concentration (Pietrini et al., 2010). Exposure to Cd-contaminated soils has been reported to cause chloroplast structural abnormalities. Changes in the structure of chloroplasts in Cd-stressed plant cells are caused by swelling of the thylakoid structure. Membrane integrity of the thylakoid membrane is also affected (Baryla et al., 2001; Najeeb et al., 2011). In addition, a decrease in the number of chloroplasts, accumulation of grana, decreased levels of starch grains (SG), and accumulation of Postaglobuli (PG) have been reported in several other plants for instance, *Pircis divarticata* (75 µM Cd, 14 days after treatment (DAT)) (Ying et al., 2010), *Hordeum vulgare* (5 µM Cd, 15 HSP) (Wang et al., 2011), and Brassica (Elhiti et al., 2012). These results suggest that the effect of Cd might be species- or genotype-dependent (Parmar et al., 2013).

Cadmium can also cause changes in chlorophyll pigments by replacing the $Mg^{2+}$ ions in protoporphyrinogen. Consequently, the chlorophyll will be non-functional (Cd-Chl) (Parmar et al., 2013). Decreased chlorophyll levels can also occur due to Cd-mediated suppression of the activity of the δ-minolevunilic acid dehydratase (ALAD) enzyme, which plays an important role in chlorophyll biosynthesis (Rout & Sahoo, 2015; Sarangthem et al., 2011). In addition, some enzymes which are involved in the biosynthesis of chlorophyll are also inhibited during Cd contamination. It includes chlorophyll synthase, rubisco, protochlorophyllide reductase, and chlorophyllase (Khanna, Jamwal, Gandhi, et al., 2019).

## Conclusions

Our study focused on the effect of Cd stress on morpho-physiological characteristics of foxtail millet var. Buru Merah. Cd toxicity is characterized by reduce of some morphological parameters such as plant height, root length, number of leaves, and number of shoots. In addition, physiological parameters including panicle biomass and chlorophyll content are also affected. Highest concentration of Cd used in this study demonstrated the most reduction of both morphological and physiological parameters. Nevertheless, this study could be taken forward toward investigation of other physiological and molecular parameters underlying plant defense mechanism under Cd contamination. Also, biochemical assessment could be further conducted to enrich the understanding of the effect of Cd contamination on foxtail millet. Our study demonstrated the importance of controlling the Cd contamination in the environment. Understanding the effect of Cd contamination on plant growth and development is essential not only for sustainable management in agricultural system and global food security, but also important for environmental conservation of water resources and human health.

## Declaration of conflicting interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

## Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: The authors gratefully acknowledge financial support from the Institut Teknologi Sepuluh Nopember (ITS), Surabaya, Indonesia for this work, under project scheme of the publication writing and IPR incentive program (PPHKI).

## ORCID iD

Nurul Jadid https://orcid.org/0000-0001-9387-4919

## REFERENCES

Abdolali, A., Ngo, H. H., Guo, W., Zhou, J. L., Du, B., Wei, Q., Wang, X. C., & Nguyen, P. D. (2015). Characterization of a multi-metal binding biosorbent: Chemical modification and desorption studies. *Bioresource Technology*, 193, 477–487.

Abozeid, A., Ying, Z., Lin, Y., Liu, J., Zhang, Z., & Tang, Z. (2017). Ethylene improves root system development under cadmium stress by modulating superoxide anion concentration in *Arabidopsis thaliana*. *Frontiers in Plant Science*, 8(8), 253–260. https://doi.org/10.3389/fpls.2017.00253

Baryla, A., Carrier, P., Franck, F., Coulomb, C., Sahut, C., & Havaux, M. (2001). Leaf chlorosis in oilseed rape plants (*Brassica napus*) grown on cadmium-polluted soil: Causes and consequences for photosynthesis and growth. *Planta*, 212, 696–709. https://doi.org/10.1007/s004250000439

Bertels, J., Huybrechts, M., Hendrix, S., Bervoets, L., Cuypers, A., & Beemster, G.T.S. (2020). Cadmium inhibits cell cycle progression and specifically accumulates in the maize leaf meristem. *Journal of Experimental Botany,* 71(20), 6418–6428. https://doi.org/10.1093/jxb/eraa385

Bruno, L., Pacenza, M., Forgione, I., Lamerton, L. R., Greco, M., Chiappetta, A., & Bitonti, M. B. (2017). In *Arabidopsis thaliana* cadmium impact on the growth of primary root by altering SCR expression and auxin-cytokinin cross-talk. *Frontiers in Plant Science*, 8(1323), 1323. https://doi.org/10.3389/fpls.2017.01323

Caetano, S. M., Menezes, R., Amaral, C., Rodrigues-Pousada, C., & Pimentel, C. (2015). Repression of the low affinity iron transporter gene FET4: A novel mechanism against cadmium toxicity orchestrated by YAP1 via ROX1. *Journal of Biological Chemistry*, 290, 18584–18595. https://doi.org/10.1074/jbc.M114.600742

Cui, W., Fang, P., Zhu, K., Mao, Y., Gao, C., Xie, Y., Wang, J., & Shen, W. (2014). Hydrogen-rich water confers plant tolerance to mercury toxicity in alfalfa seedlings. *Ecotoxicology and Environmental Safety*, 105, 103–111.

Dharma-Wardana, M. W. C. (2018). Fertilizer usage and cadmium in soils, crops and food. *Environmental Geochemistry and Health*, 40, 2739–2759. https://doi.org/10.1007/s10653-018-0140-x

Dobermann, A., & Fairhurst, T. (2000). *Rice nutrient disorders and nutrients management*. Potash and Phosphat Institute of Canada and International Rice Research Institute; Oxford Geographic Prntersn Ptc Ltd.

Elhiti, M., Yang, C., Chan, A., Durnin, D. C., Belmonte, M. F., Ayele, B. T., Tahir, M., & Stasolla, C. (2012). Altered seed oil and glucosinolate levels in transgenic plants overexpressing the *Brassica napus SHOOTMERISTEMLESS* gene. *Journal of Experimental Botany*, 63, 4447–4461.

Farid, M., Shakoor, M. B., Ehsan, E., Ali, S., Zubair, M., & Hanif, M. A. (2013). Morphological, physiological and biochemical responses in different plant species to Cd stress. *International Journal of Chemical and Biochemical Sciences*, 3, 53–60.

Farooq, M. A., Ali, S., Hameed, A., Bharwana, S. A., Rizwan, M., Ishaque, W., Farid, M., Mahmood, K., & Iqbal, Z. (2016). Cadmium stress in cotton seedlings: Physiological, photosynthesis and oxidative damages alleviated by glycinebetaine. *South African Journal of Botany*, 104, 61–68.

Genchi, G., Sinicropi, M. S., Lauria, G., Carocci, A., & Catalano, A. (2020). The effects of cadmium toxicity. *International Journal of Environmental Research and Public Health*, 17(11), 3782.

Gill, S. S., & Tuteja, N. (2011). Cadmium stress tolerance in crop plants: Probing the role of sulfur. *Plant Signaling & Behavior*, 6(2), 215–222.

Gupta, D. K., Corpas, F. J., & Palma, J. M. (2013). *Heavy metal stress in Plants*. Springer.

Haider, F. U., Liqun, C., Coulter, J. A., Cheema, S. A., Wu, J., Zhang, R., Wenjun, M., & Farooq, M. (2021). Cadmium toxicity in plants: Impacts and remediation strategies. *Ecotoxicology and Environmental Safety*, 211, 111887.

Herodian, S., Sugiyono, S., & Widowati Susila, B.A. (2008). *Development of buru hotong as alternative food source*. Research report of the Institut Pertanian Bogor in cooperation with Indonesian Agency for Agricultural Research and Development. https://doi.org/10.33964/jp.v17i3.265.

He, S., Yang, X., He, Z., & Baligar, V. C. (2017). Morphological and physiological responses of plants to cadmium toxicity: A review. *Pedhosphere*, 27(3), 421–438.

Huang, X., Duan, S., Wu, Q., Yu, M., & Shabala, S. (2020). Reducing cadmium accumulation in plants: Structure-function relations and tissue-specific operation of transporters in the spotlight. *Plants*, 9(2), 1–18.

Huybrechts, M., Cuypers, A., Deckers, J., Iven, V., Vandionant, S., Jozefczak, M., & Hendrix, S. (2019). Cadmium and plant development: An agony from seed to seed. *International Journal of Molecular Sciences*, 20(16), 1–30.

Ismael, M. A., Elyamine, A. M., Moussa, M. G., Cai, M., Zhao, X., & Hu, C. (2019). Cadmium in plants: Uptake, toxicity, and its interactions with selenium fertilizers. *Metallomics*, 11(2), 255–277. https://doi.org/10.1039/c8mt00247a

Jadid, N., Maziyah, R., Nurcahyani, D. D., & Mubarokah, N. R. (2017). *Growth and physiological responses of some Capsicum frustescens varieties to copper stress* [Conference session]. AIP Conference Proceedings, 1854 (pp. 020018–1–020018–7). AIP Publishing. https://doi.org/10.1063/1.4985409.

Jamers, A., Blust, R., De Coen, W., Griffin, J. L., & Jones, O. A. H. (2013). An omics based assessment of cadmium toxicity in the green alga *Chlamydomonas reinhardtii*. *Aquatic Toxicology*, 126, 355–364.

Januskaitene, I. (2012). The effect of cadmium on several photosynthetic parameters of pea (*Pisum sativum* L.) at two growth stages. *Journal of Agriculture*, 99, 71–76.

Jia, G., Huang, X., Zhi, H., Zhao, Y., Zhao, Q., Li, W., Chai, Y., Yang, L., Liu, K., Lu, H., Zhu, C., Lu, Y., Zhou, C., Fan, D., Weng, Q., Guo, Y., Huang, T., Zhang, L., Lu, T., . . . Han, B. (2013). A haplotype map of genomic variations and genome-wide association studies of agronomic traits in foxtail millet (*Setaria italica*). *Nature Genetics*, 45(8), 957–961.

Jiang, X. J., Luo, Y. M., Liu, Q., Liu, S. L., & Zhao, Q. G. (2004). Effects of cadmium on nutrient uptake and translocation by Indian mustard. *Environmental Geochemistry and Health*, 26, 319–324.

Khan, M. A., Khan, S., Khan, A., & Alam, M. (2017). Soil contamination with cadmium, consequences and remediation using organic amendments. *The Science of the Total Environment, 601*–602, 1591–1605. https://doi.org/10.1016/j.scitotenv.2017.06.030

Khanna, K., Jamwal, V. L., Gandhi, S. G., Ohri, P., & Bhardwaj, R. (2019). Metal resistant PGPR lowered Cd uptake and expression of metal transporter genes with improved growth and photosynthetic pigments in Lycopersicon esculentum under metal toxicity. *Scientific Reports*, 9(1), 5855.

Khanna, K., Jamwal, V. L., Sharma, A., Gandhi, S. G., Ohri, P., Bhardwaj, R., Al-Huqail, A. A., Siddiqui, M. H., Ali, H. M., & Ahmad, P. (2019). Supplementation with plant growth promoting rhizobacteria (PGPR) alleviates cadmium toxicity in *Solanum lycopersicum* by modulating the expression of secondary metabolites. *Chemosphere*, 230, 628–639.

Khanna, K., Ohri, P., Bhardwaj, R., & Ahmad, P. (2021). Unsnarling plausible role of plant growth-promoting rhizobacteria for mitigating Cd-toxicity from plants: An environmental safety aspect. *Journal of Plant Growth Regulation*. Advance online publication. https://doi.org/10.1007/s00344-021-10445-9

Kintlová, M., Vrána, J., Hobza, R., Blavet, N., & Hudzieczek, V. (2021). Transcriptome response to cadmium exposure in barley (*Hordeum vulgare* L.). *Frontiers in Plant Science*, 12, 629089.

Lapuimakuni, S., Khumaida, N., & Ardie, S. W. (2018). Short Communication: Evaluation of drought tolerance indices for genotype selection of foxtail millet (*Setaria italica*). *Tropical Drylands*, 2(2), 37–40.

Lestari, L. A., Huriyati, E., & Marsono, Y. (2017). The development of low glycemic index cookie bars from foxtail millet (*Setaria italica*), arrowroot (*Maranta arundinacea*) flour, and kidney beans (*Phaseolus vulgaris*). *Journal of Food Science and Technology*, 54(6), 1406–1413. https://doi.org/10.1007/s13197-017-2552-5

Lichtenthaler, H. K. (1987). Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. *Methods in Enzymology*, 148, 350–382.

Li, F., Qi, J., Zhang, G., Lin, L., Fang, P., Tao, A., & Xu, J. (2013). Effect of cadmium stress on the growth, antioxidative enzymes and lipid peroxidation in two kenaf (*Hibiscus cannabinus* L.) plant seedlings. *Journal of Integrative Agriculture*, 12(4), 610–620.

Lu, L. L., Tian, S. K., Yang, X. E., Li, T. Q., & He, Z. L. (2009). Cadmium uptake and xylem loading are active processes in the hyperaccumulator *Sedum alfredii*. *Journal of Plant Physiology*, 166(6), 579–587.

Monteiro, C., Santos, C., Pinho, S., Oliveira, H., Pedrosa, T., & Dias, M. C. (2012). Cadmium-induced cyto- and genotoxicity are organ-dependent in lettuce. *Chemical Research in Toxicology*, 25, 1423–1434. https://doi.org/10.1021/tx300039t

Najeeb, U., Jilani, G., Ali, S., Sarwar, M., Xu, L., & Zhou, W. (2011). Insights into cadmium induced physiological and ultra-structural disorders in *Juncus effusus* L. and its remediation through exogenous citric acid. *Journal of Hazardous Materials*, 186, 565–574.

Nisa, C., & Jadid, N. (2021). Exogenous acetic acid pre-treatment increases drought tolerance of two Indonesian foxtail millet (*Setaria italica*) accessions. *Biodiversitas*, 22(4), 2117–2124. https://doi.org/10.13057/biodiv/d220460

Ogawa, I., Nakanishi, H., Mori, S., & Nishizawa, N. K. (2009). Time course analysis of gene regulation under cadmium stress in rice. *Plant and Soil*, 325, 97–108. https://doi.org/10.1007/s11104-009-0116-9

Parmar, P., Kumari, N., & Sharma, V. (2013). Structural and functional alterations in photosynthetic apparatus of plants under cadmium stress. *Botanical Studies*, 54(1), 45–46.

Pietrini, F., Zacchini, M., Iori, V., Pietrosanti, L., Ferretti, M., & Massacci, A. (2010). Spatial distribution of cadmium in leaves and its impact on photosynthesis: Examples of different strategies in willow and poplar clones. *Journal of Plant Biology*, 12, 355–363.

Prasad, M. (2017). *The foxtail millet genome*. Springer International Publishing.

Rajput, R. D., & Patil, R. P. (2017). The comparative study on spectrophotometric analysis of chlorophyll and carotenoids pigments from non-leguminous fodder crops. *International Journal of Innovative Science, Engineering and Technology*, 4(7), 140–148.

Rout, G. R., & Sahoo, S. (2015). Role of iron in plant growth and metabolism. *Reviews in Agricultural Science*, 3, 1–24. https://doi.org/10.7831/ras.3.1

Salinitro, M., Mattarello, G., Guardigli, G., Odajiu, M., & Tassoni, A. (2021). Induction of hormesis in plants by urban trace metal pollution. *Scientific Reports*, 11, 20329.

Sánchez-Pardo, B., Carpena, R. O., & Zornoza, P. (2013). Cadmium in white lupin nodules: Impact on nitrogen and carbon metabolism. *Journal of Plant Physiology*, 170(3), 265–271.

Sarangthem, J., Jain, M., & Gadre, R. (2011). Inhibition of δ-aminolevulinic acid dehydratase activity by cadmium in excised etiolated maize leaf segments during greening. *Plant Soil and Environment*, 57(7), 332–337.

Sher, A., Mudassir Maqbool, M., Iqbal, J., Nadeem, M., Faiz, S., Noor, H., Hamid, Y., Yuan, X., & Pingyi, G. (2021). The growth, physiological and biochemical response of foxtail millet to atrazine herbicide. *Saudi Journal of Biological Sciences*, 28(11), 6471–6479.

Taiz, L., & Zeiger, E. (2006). *Lecture Text Plant Physiology* (4th ed.). Sinauer Associates, Inc Publishers.

Takahashi, R., Ishimaru, Y., Senoura, T., Shimo, H., Ishikawa, S., Arao, T., Nakanishi, H., & Nishizawa, N. K. (2012). The OsNRAMP1 iron transporter is involved in Cd accumulation in rice. *Journal of Experimental Botany*, 62(14), 4843–4850.

Templeton, D. M., & Liu, Y. (2010). Multiple roles of cadmium in cell death and survival. *Chemico-Biological Interactions*, 188(2), 267–275.

Thomine, S., Wang, R., Ward, J. M., Crawford, N. M., & Schroeder, J. I. (2000). Cadmium and iron transport by members of a plant metal transporter family in *Arabidopsis* with homology to *Nramp* genes. *Proceedings of National Academy of Science of United States America*, 97(9), 4991–4996.

Tian, B., Zhang, Y., Jin, Z., Liu, Z., & Pei, Y. (2017). Role of hydrogen sulfide in the methyl jasmonate response to cadmium stress in foxtail millet. *Frontiers in Bioscience*, 22, 530–538.

Tran, T. A., & Popova, L. P. (2013). Functions and toxicity of cadmium in plants: recent advances and future prospects. *Turkish Journal of Botany*, 37, 1–13.

Tupan, C. 1., & Uneputty, P. A. (2017). Concentration of heavy metal lead (Pb) and cadmium (Cd) in water, sediment and seagrass *Thalassia hemprichii* in Ambon Island Water. *AACL Bioflux*, 10(6), 1610–1617.

Verma, S., Srivastava, S., & Tiwari, N. (2015). Comparative study on nutritional and sensory quality of barnyard and foxtail millet food products with traditional rice products. *Journal of Food Science and Technology*, 52(8), 5147–5155. https://doi.org/10.1007/s13197-014-1617-y

Wang, F., Chen, F., Cai, Y., Zhang, G., & Wu, F. (2011). Modulation of exogenous glutathione in Ultrastructure and photosynthetic performance against Cd stress in the two barley genotypes differing in Cd tolerance. *Biological Trace Element Research*, 144(1–3), 1275–1288.

Wang, H., Zhao, S. C., Liu, R. L., Zhou, W., & Jin, J. Y. (2009). Changes of photosynthetic activities of maize (*Zea mays*) seedlings in response to Cadmium stress. *Photosynthetica*, 47, 277–283.

Wang, Y., Wang, X., Wang, C., Peng, F., Wang, R., Xiao, X., Zeng, J., Kang, H., Fan, X., Sha, L., Zhang, H., & Zhou, Y. (2017). Transcriptomic profiles reveal the interactions of Cd/Zn in dwarf polish wheat (*Triticum polonicum* L.) roots. *Frontiers in Physiology*, 8, 168.

Wei, S., Zhou, Q., Wang, X., Zhang, K., Guo, G., & Ma, L. Q. (2005). A newly-discovered Cd-hyperaccumulator *Solanum nigrum* L. *Chinese Science Bulletin*, 50, 33–38.

Xue, Z. C., Gao, H. Y., & Zhang, L. T. (2013). Effects of cadmium on growth, photosynthetic rate and chlorophyll content in leaves of soybean seedlings. *Biologia Plantarum*, 57(3), 587–590.

Ying, R. R., Qiu, R. L., Tang, Y. T., Hu, P. J., Qiu, H., Chen, H. R., Shi, T. H., & Morel, J. L. (2010). Cadmium tolerance of carbon assimilation enzymes and chloroplast in Zn/Cd hyperaccumulator *Picris divaricata*. *Journal of Plant Physiology*, 167, 81–87.

Yulita, K. S., & Ridwan, R. (2018). Molecular characterization of induced mutation of jewawut (*Setaria italica* ssp. italica) from Buru Island, Indonesia using SRAP. *Biodiversitas*, 19(3), 1160–1168.

Zhang, G., Liu, X., Quan, Z., Cheng, S., Xu, X., Pan, S., Xie, M., Zeng, P., Yue, Z., Wang, W., Tao, Y., Bian, C., Han, C., Xia, Q., Peng, X., Cao, R., Yang, X., Zhan, D., Hu, J., . . . Wang, J. (2012). Genome sequence of foxtail millet (*Setaria italica*) provides insights into grass evolution and biofuel potential. *Nature Biotechnology*, 30(6), 549–554.

Zhang, Y., Liu, J., Zhou, Y., Gong, T., Wang, J., & Ge, Y. (2013). Enhanced phytoremediation of mixed heavy metal (mercury)-organic pollutants (trichloroethylene) with transgenic alfalfa co-expressing glutathione S-transferase and human P450 2E1. *Journal of Hazardous Materials*, 260, 1100–1107. https://doi.org/10.1016/j.jhazmat.2013.06.065