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

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 assessments, 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

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 (Lapuiimakuni 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 (James 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).

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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 microorganisms (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 CdCl₂ (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.
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):

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

\( (1) \)

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

\( (2) \)

\[
\text{Total Chlorophyll} \text{ (mg/g FW)} = \frac{(20.2[A645] - 8.02[A663])}{(V)(W)}
\]

\( (3) \)

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

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**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).
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 G1/S transition of Cd (20–120 µmol/L), their response and level of sensitivity was different (Li et al., 2013). 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 by a reduced root length, by 63.4%, 17.3%, and 69.2%, was also reported to decrease after treatment with 200 µM Cd (Tian et al., 2017). Root growth in *S. italica* var. Jingu-21 has been reported to decrease after treatment with 200 µM Cd (Monteiro 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; Wang et 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 sulphydryl 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.
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.

**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.

**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.

**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...
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-minolevulinic 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.

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

| CD CONCENTRATION (µM) | CHLOROPHYLL-A (Mg/g) | CHLOROPHYLL-B (Mg/g) | TOTAL CHLOROPHYLL (Mg/g) | % OF REDUCTION |
|-----------------------|-----------------------|-----------------------|--------------------------|----------------|
| 0 (Control)           | 0.30 ± 0.004c         | 0.10 ± 0.001c         | 0.40 ± 0.002c            | -              |
| 0.5                   | 0.21 ± 0.003b         | 0.06 ± 0.002b         | 0.28 ± 0.001b            | 30.4           |
| 1                     | 0.12 ± 0.002a         | 0.04 ± 0.001a         | 0.16 ± 0.001a            | 60.5           |
| 1.5                   | 0.12 ± 0.002a         | 0.04 ± 0.002a         | 0.16 ± 0.002a            | 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.
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