J. Indian bot. Soc. (2024)

e-ISSN:2455-7218, ISSN:0019 - 4468

https://doi: 10.61289/jibs2024.12.05.396

www.indianbotsoc.org

RESEARCH ARTICLE

Differential impact of aluminium stress on photosynthetic pigment contents of certain rice (*Oryza sativa* L.) landraces from Sikkim Himalaya

Poonam Chetry and Shanti S. Sharma*

Abstract

Aluminium (Al) toxicity is a primary constraint to plant productivity on acidic soils posing a threat to global food security. Here, we have monitored the impact of Al on photosynthetic pigment (chlorophyll and carotenoids) contents of certain rice (*Oryza sativa* L.) landraces from Sikkim Himalaya with contrasting Al tolerance namely, Kalo tukmar (KT), Champasari (CP), Krishna bhog (KB) and Dhansey (DH). Seedlings were grown hydroponically with half strength Hoagland solution containing Al (0-1500 µM, pH 4.5) for 14-d and chlorophyll (a, b and total) and carotenoid contents were measured. In response to the exposure to Al, pigment levels declined in a concentration dependent manner in all the tested landraces with strong landrace-specific differences. Thus, the extent of Al-induced decline in chlorophyll and carotenoid contents was much lower in KT and CP than that in KB and DH. A decline of 42, 50, 69 and 70% in total chlorophyll content at 1500 µM Al was evident in KT, CP, KB and DH, respectively. The observations are consistent with greater Al tolerance of KT and CP as compared to KB and DH. Chl a : b ratio tended to increase due to Al with landrace and concentration specific quantitative differences; minimum effect was evident in CP. The ratio increased by 91 and 45% at 1500 µM Al in KB and KT, respectively. The increased ratios suggest a higher Al-induced decline in Chl b content than that in Chl a. The carotenoid contents were suppressed by 55 and 38% in KB and KT, respectively due to 1500 µM Al treatment. Differential response of the tested landraces to Al could be ascribed to variations in cellular management of Al burden. The findings have implications for selection of suitable landrace(s) for acidic soil conditions.

Keywords: Acidic soils, Al toxicity, Photosynthetic pigments, Rice landraces, Sikkim Himalaya

Introduction

Soil acidity is a serious constraint for the global agricultural productivity. Approximately 30-40% of the world's ice free arable lands are acidic. (Von Uexküll and Mutert, 1995). In India, acidic soils are prevalent in the sub-Himalaya belt, eastern Himalaya, coastal plains and peninsular India (Roy and Bhadra, 2014). Greater than 80% of total soil accounting to 21.26 million hectares in the North eastern region (NER) comprising eight states is acidic in nature (Majumdar *et al.* 2022). Aluminium toxicity is the most important factor affecting plant productivity on acidic soils (Kochian *et al.* 2004; Kocjan *et al.* 2024). It ranks next to water deficit stress only. Although Al is the third most abundant element (approx.. 8%) in the earth crust (Marschner, 2012), it turns toxic only at soil pH < 5.5. Under these conditions, it oxidizes to trivalent ion (Al^{3+}) that is readily taken up by plant roots causing severe phytotoxic impact. By contrast, at soil pH > 5.5, Al forms complexes with silicates, phosphate, sulfides and oxides making it unavailable to plants (Chowra *et al.* 2017). Al^{3+} primary targets the root tips causing inhibition of cell wall extensibility, cell division and cell elongation and in turn reduction of root growth (Kochian, 1995; Barcelo and Poschenreider, 2002). The Al^{3+} affected roots appear thick, stunted with brittle root hair and deformed root apices (Matsumoto, 2000). Al^{3+} interference with signal transduction pathway, ROS (H_2O_2, O_2^-) generation leading to plasma membrane lipid peroxidation and DNA damage

Department of Botany, School of Life Sciences, Sikkim University, Gangtok 737102, India.

***Corresponding Author:** Shanti S. Sharma, Department of Botany, School of Life Sciences, Sikkim University, Gangtok 737102, India., E-Mail: shantissharma@hotmail.com

How to cite this article: Chetry P, Sharma SS. (2024). Differential impact of aluminium stress on photosynthetic pigment contents of certain rice (*Oryza sativa* L.) landraces from Sikkim Himalaya. *J. Indian bot. Soc.*, Doi: 10.61289/jibs2024.12.05.396

Source of support: Nil

Conflict of interest: None.

Received: 17/11/2024 **Accepted:** 05/12/2024 **Published online**: 05/01/2025

contribute to Al^{3+} toxicity (Sharma and Dietz, 2009; Kocjan *et al.* 2024).

Al-induced suppression of root growth leads to altered water and mineral nutrient uptake that eventually affects the shoot growth. Al toxicity deleteriously affects different aspects of photosynthesis. It altered the chloroplast ultrastructure and also the activity of enzymes related to Calvin cycle (Jiang *et al.* 2008; Silva *et al.* 2012). Exposure to Al^{3+} resulted in inhibition of carbon assimilation in cereal crops (Peixoto *et al.* 2002; Silva *et al.* 2012). Likewise, Al-induced reduction in the maximum quantum yield (Fv/Fm), maximum chlorophyll flourescence (Fm), total PSII performance, the quantum yield of electron transport and oxygen-evolving complex was shown in the sensitive cultivars of citrus (Jiang *et al.* 2008). Furthermore, Al^{3+}-induced reduction in the biosynthesis of plastid pigments via altered δ-aminolevulinic acid dehydratase and δ-aminolevulinic acid synthase in Al-sensitive maize species has been reported. This eventually triggered signalling mechanisms downstream initiating drastic change to the photosynthetic apparatus at physiological and biochemical levels (Mihailovic *et al.* 2008). As such, the analysis of photosynthetic pigments (chlorophylls and carotenoids) provides a simple and reliable idea about the photosynthetic potential of concerned plant species and genotypes under deviations from optimum growth conditions such as Al toxicity.

Plants employ distinct external and internal Al detoxification strategies with marked species-specificity (Kochian *et al.* 2015; Kocjan *et al.* 2024). In the first, Al^{3+} entry into the plant roots is altogether prevented via formation of Al^{3+} complexes with organic acids (OAs) such as malate, citrate and oxalate in a species- specific manner (Delhaize *et al.* 2012; Kochian *et al.* 2015). In the second, binding of Al^{3+} to cell wall components particularly pectin is altered through changes in carbohydrate composition. In case of rice, substantially more tolerant to Al than other cereals, the involvement of OAs in Al^{3+} detoxification is only to a limited extent (Ofoe *et al.* 2023). A part of root Al burden in rice is reduced through vacuolar compartmentalization that requires a concerted action of OsNrat1, a plasma membrane transporter and OsALS1, a tonoplast transporter (Delhaize *et al.* 2012; Kocjan *et al.* 2024). A part of Al is translocated to the shoot where it directly interferes with diverse metabolic processes.

Sikkim, a small Himalayan state of NER, is known as "valley of rice" (Denzong) for its indigenous rice landraces which are grown in small areas of the state. Various aspects related to cultivation practices, genetic diversity, nutrient profile and germination characteristics of rice landraces from Sikkim have been reported (Kapoor *et al.* 2019; Chettri and Sathyanarayana, 2021; Chettri *et al.* 2021; Chetry and Sharma, 2023). The pH in the agricultural lands predominantly lies in the range below 5.5 across different parts of Sikkim. Some of these landraces likely developed tolerance owing to the prolonged exposure to prevailing abiotic stress factors including Al toxicity. The screening of 10 rice landraces from across Sikkim for Al tolerance in terms of root growth response at seedling stage in a hydroponic assay revealed strong variations in Al tolerance. Of the tested landraces, Kalo tukmar (KT) proved most Al tolerant followed by Champasari (CP) whereas Krishna bhog (KB) was most sensitive followed by Dhansey (DH) (Chetry *et al.*, unpublished data). It was of interest to examine whether the the landrace specific differences in Al toxicity observed on root growth will be reflected in the leaves in terms of photosynthetic pigment contents. Therefore, the influence of Al on the photosynthetic pigment (chlorophyll and carotenoids) contents of Al tolerant (KT and CP) and sensitive (DH and KB) rice landraces has been evaluated in a hydroponic system.

Material and methods

Seed sources: The seeds of rice (*O. sativa* L.) landraces were provided by the local farmers from different locations in Sikkim (mentioned in parentheses) in December 2018 - January 2019 and subsequent years as follows: Champasari (CP) (Turuk, Namchi), Dhansey (DH) (Upper Rumtek, Gangtok), Kalo tukmar (KT) (Pentong, Mangan) and Krishna bhog (KB) (Saramsa, Pakyong).

Al treatment in hydroponic culture

Two-day germinated seeds with water-soaked vermiculite in dark were transferred for further hydroponic culture by placing them on nylon nets fixed to O-rings placed on the plastic containers (capacity, 1 L) in a plant growth chamber (28-30 ^{0}C, 65% RH, 14 h photoperiod; PAR: 200 µmol m^{-2} s^{-1}). Half-strength Hoagland solution of following composition was used: 3 mM KNO_3, 2 mM $Ca(NO_3)_2$, 0.5 mM (NH_4) H_2PO_4,1 mM $MgSO_4$, 35 µM Fe-Na EDTA, 0.1 µM Na_2MoO_4, 0.32 µM $CuSO_4$, 0.77 µM $ZnSO_4$, 5 µM $MnCl_2$, 20 µM H_3BO_3. $AlCl_3$ stock solution was added appropriately to obtain the final concentrations of 100, 250, 500, 1000, 1500 µM Al. The pH of nutrient solution was adjusted to 4.5 with 1 N HCl and 1 N NaOH. Nutrient solution without Al supplementation served as the control. The nutrient solution was replaced every second day. The adopted hydroponic system allowed to maintain the nutrient and intended Al concentrations as well as pH. After 14 d of treatment, the shoots were harvested, rinsed properly in water followed by complete removal of adhering moisture with blotting paper. Thereafter, they were frozen with liquid nitrogen and stored at -80^{0}C until analysis for pigment contents.

Determination of chlorophyll and carotenoid contents

Approximately 100 mg leaf tissue was powdered with liquid

nitrogen, homogenized with 1 ml of acetone (80%) and the homogenate centrifuged at 10,000 rpm for 10 min. The final volume of supernatant was adjusted to 2 ml by acetone (80%) and the absorbance read at 663, 645 and 470 nm, respectively. The amount of chlorophyll and carotenoids was calculated by the following equations given by Lichtenthaler and Buschmann (2001):

$$\text{Chl a } (\mu g\ ml^{-1}) = 12.25\, A_{663}\ nm - 2.79\, A_{645}\ nm$$

$$\text{Chl b } (\mu g\ ml^{-1}) = 21.50\, A_{645}\ nm - 5.10\, A_{663}\ nm$$

$$\text{Carotenoids } (\mu g\ ml^{-1}) = \frac{1000\, A_{470}\ nm - 1.82\ Chl\ a - 85.02\ Chl\ b}{198}$$

Statistical analysis

All measurements were made in four replicates and the values are presented as arithmetic means ± SE. Based on skewness and kurtosis values, the data distribution was considered normal. The data were subjected to two-way analysis of variance (ANOVA; $p<0.001$) followed by Tukey's post-hoc test ($p<0.05$) using IBM SPSS Statistics for Windows, version 20 (IBM Corp., Armonk, NY, United States). Significantly different means are marked with different letters.

Results

Leaves from hydroponically grown seedlings of contrasting rice landraces in the presence of Al (0-1500 µM) for 14 d were analysed for pigment contents. Following observations were obtained:

Chlorophyll contents and Chlorophyll a : b ratio

The total chlorophyll contents in control were generally comparable in the tested rice landraces with some quantitative fluctuations except lower chlorophyll contents in Dhansey (DH). In response to a 14 d exposure to Al (0-1500 µM), total chlorophyll contents declined in a concentration dependent manner in all the landraces. However, the magnitude of decrease was lower in Al-tolerant landraces (KT and CP) as compared to that in Al-sensitive counterparts (KB and DH). Thus, the lowest tested Al concentration (100 µM) induced a nonsignificant reduction in chlorophyll level in KT and CP. In contrast, the inhibitory effect of this concentration was significant in case of KB and DH (Figure 1). In the Al-tolerant landraces KT and CP, the magnitude of Al-induced reduction in the chlorophyll content was 1, 11, 22, 29, 42% and 9, 19, 28, 36, 50% at 100, 250, 500, 1000, 1500 µM Al, respectively. On the other hand, in Al sensitive landrace KB, total chlorophyll declined by 17, 37, 50, 60, 69%

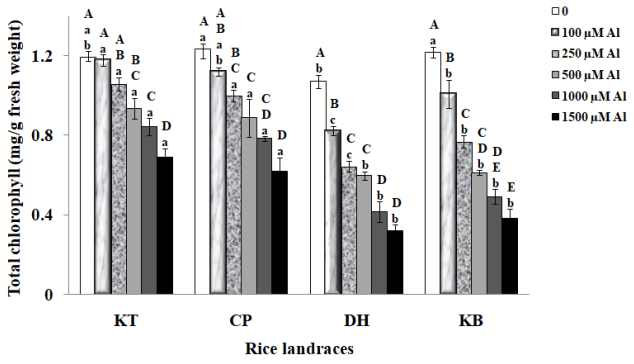

Figure 1: Total chlorophyll contents (mg/g fresh weight) of leaves of four rice (*O. sativa* L.) landraces (KT, CP, DH, KB) from Sikkim Himalaya exposed to Al (0-1500 µM; pH 4.5) in hydroponics for14 d. Values are arithmetic means of 4 replicates ± S.E.; landrace, treatment and landrace×treatment effects analyzed for significance (two-way ANOVA; $p<0.001$). Upper case letters represent significant differences among different treatments within a landrace, whereas lower case letters represent significant differences among landraces at same treatment (Tukey's test; $p<0.05$).

Table 1: Chlorophyll a (Chl a) and Chlorophyll b (Chl b) contents and Chl a: Chl b ratio of four rice (*O. sativa* L.) landraces (KT, CP, DH, KB) from Sikkim Himalaya exposed to Al (0-1500 µM; pH 4.5) in hydroponics for 14 d. Values are arithmetic means of 4 replicates ± S.E.; landrace, treatment and landrace×treatment effects analyzed for significance (two-way ANOVA; $p<0.001$). Upper case letters represent significant differences among different treatments within a landrace, whereas lower case letters represent significant differences among landraces at same treatment (Tukey's test; $p<0.05$).

Rice landrace	*Al (µM)*	*Chl a (mg/g)*	*Chl b (mg/g)*	*Chl a : b*
Kalo tukmar (KT)	0	0.80±0.01Aa	0.44±0.01Ab	1.82:1
	100	0.77±0.01ABa	0.41±0.04Aa	1.82:1
	250	0.70±0.02BCa	0.36±0.06ABa	1.94:1
	500	0.64±0.03CDa	0.30±0.06ABa	2.13:1
	1000	0.58±0.03Da	0.26±0.06ABa	2.23:1
	1500	0.50±0.02Ea	0.19±0.03Ba	2.63:1
Champasari (CP)	0	0.83±0.01Aa	0.40±0.04Ab	2.08:1
	100	0.76±0.02ABa	0.36±0.03Aa	2.11:1
	250	0.69±0.03BCa	0.31±0.00Aab	2.23:1
	500	0.62±0.02CDa	0.27±0.08ABa	2.30:1
	1000	0.55±0.00Da	0.24±0.02ABa	2.29:1
	1500	0.40±0.04Ea	0.22±0.03ABa	1.82:1
Dhansey (DH)	0	0.59±0.02Ac	0.48±0.03Aab	1.23:1
	100	0.44±0.03Bc	0.38±0.03Aa	1.16:1
	250	0.42±0.03Bb	0.22±0.04Bb	1.91:1
	500	0.40±0.02Bb	0.19±0.03Ba	2.11:1
	1000	0.26±0.01Cc	0.15±0.04Ba	1.73:1
	1500	0.20±0.02Cb	0.12±0.03Ba	1.67:1
Krishna bhog (KB)	0	0.68±0.04Ab	0.53±0.01Aa	1.28:1
	100	0.60±0.03ABb	0.40±0.04Ba	1.50:1
	250	0.50±0.03BCb	0.26±0.01Cab	1.92:1
	500	0.43±0.02CDb	0.19±0.02CDa	2.26:1
	1000	0.34±0.01DEb	0.16±0.04CDa	2.13:1
	1500	0.27±0.01Eb	0.11±0.04Da	2.45:1

at 100, 250, 500, 1000 and 1500 µM Al, respectively. In case of DH, these values were 23, 40, 44, 61 and 70%, respectively (Figure 1).

As in case of total chlorophyll, the levels of chlorophyll a and b declined due to Al treatment; magnitude of inhibition being generally greater in KB and DH than that in KT and CP (Table 1). However, there were quantitative differences in response of Chla and Chlb to Al that was reflected in differentially altered Chl a : b ratios in different landraces. In KT, Chl a : b ratio was not affected much at lower Al concentrations (100, 250 µM) but gradually increased at higher ones; an increase of 45% was evident at 1500 µM. In case of CP, the ratio was minimally affected by Al across the tested concentrations except a marginal decline at the highest tested concentration. In case of Al-sensitive KB and DH, Chl a : b ratio tended to increase at most of the tested Al concentrations. Thus, at 1500 µM Al, the ratio increased by 91 and 36% in KB and DH, respectively (Table 1).

Carotenoid contents

The carotenoid contents in control did not differ significantly among the tested rice landraces except the higher levels in KT. As in case of chlorophylls, the carotenoid levels declined due to Al treatment in a concentration dependent manner in all the four landraces. However, the magnitude of decline was greater in the Al sensitive landraces (KB and DH) particularly at higher concentration than that in the Al-tolerant counterparts particularly KT; occasionally, the extent of decline in CP resembled that in KB and DH. For example, the carotenoid contents were suppressed by 27, 40 and 55% in KB as compared to 24, 35 and 38% in KT at 500, 1000, 1500 µM Al (pH 4.5) (Figure 2).

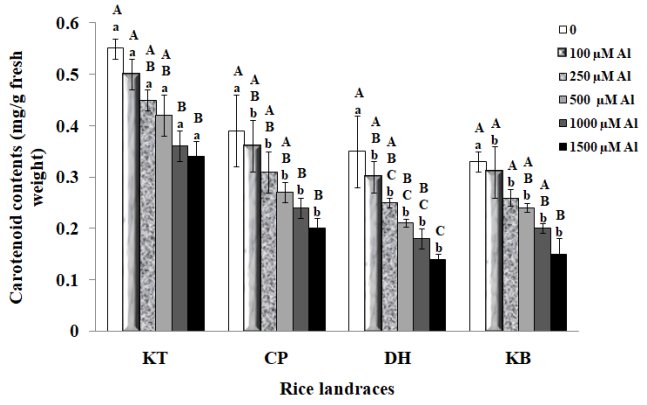

Figure 2: Carotenoid contents (mg/g fresh weight) of leaves of four rice (*O. sativa* L.) landraces (KT, CP, DH, KB) from Sikkim Himalaya exposed to Al (0-1500 µM; pH 4.5) in hydroponics for 14 d. Values are arithmetic means of 4 replicates ± S.E.; landrace, treatment and landrace×treatment effects analyzed for significance (two-way ANOVA; $p<0.001$). Upper case letters represent significant differences among different treatments within a landrace, whereas lower case letters represent significant differences among landraces at same treatment (Tukey's test; $p<0.05$).

Discussion

The present study aimed at evaluating the impact of Al toxicity on photosynthetic pigment (chlorophyll and carotenoid) contents in a couple each of Al-sensitive (KB, DH) and Al-tolerant (KT, CP) landraces of rice from Sikkim Himalaya. Differential Al tolerance of these landraces was revealed in a short-term hydroponic root growth assay (Chetry *et al.*, unpublished data). Indeed, the pigment levels are a reliable indicator of phytotoxicity of heavy metal(loids) (Gratao *et al.* 2005; Goncalves *et al.* 2009). They in turn indicate the photosynthetic potential of concerned genotype(s) under stressful growth conditions. The Al^{3+} tolerance mechanism in higher plants relies not only on the restricted uptake of Al^{3+} by roots, but also its restricted root-to-shoot translocation (Guo *et al.* 2017). Interference of Al^{3+} with diverse metabolic processes such as photosynthesis, respiration and transpiration has been reported (Yamamoto *et al.* 2002). Here, the pigment levels were markedly suppressed due to Al treatment in a concentration dependent manner. The magnitude of suppression was generally lower in case of tolerant (KT and CP) than that in sensitive (KB and DH) rice landraces except occasional deviations for carotenoids in CP. Similar Al-induced reduction in the pigment contents and photosynthesis has been reported in several plant species (Phukunkamkaew *et al.* 2021; Zhao *et al.* 2017; Jiang *et al.* 2008).

Al-induced suppression of pigment levels could inter alia be ascribed to disturbances in ionic homeostasis. Indeed, the plant growth and productivity are compromised due to the deficiencies of essential elements (P, Ca, Mg, Mo) in acidic soils (Kochian *et al.* 2015). Fe is required for chlorophyll synthesis and Al^{3+} toxicity associated accumulation of Fe in roots but not in the shoots caused Fe the deficiency symptoms in wheat (Foy and Fleming, 1982). Additionally, Al^{3+} competes with Mg^{2+}, the central constituent of chlorophyll, for active site in the chromatophores by blocking the Mg^{2+} transporters (Rengel and Robinson, 1989; Silva *et al.* 2009). Consequently, photosynthetic electron transport is inhibited which ultimately leads to lower assimilation of CO_2 in Al^{3+}-stressed plants. Toxic metal ions including Al impose a cellular redox imbalance by stimulating the generation of reactive oxygen species (ROS) and concomitantly diminishing antioxidative defence (Sharma and Dietz, 2009). Al^{3+} toxicity is known to enhance the levels of ROS (Ofoe *et al.* 2023) that might target the pigment molecules. The altered Chl a : b ratio due to Al treatment suggests the differential sensitivity of the two chlorophyll molecules to Al. Thus, enhanced Chl a, b ratio is a result of greater suppression of Chl b than that of Chl a. Carotenoids are the photosynthetic pigments that function as cellular non-enzymatic antioxidants (Strzalka *et al.* 2003). They play an important role in protecting plants subjected to various environmental stresses. Apparently, the reduced carotenoid levels in Al stressed plants weakened

the antioxidative defence affecting the pigment contents. Differential impact of Al on photosynthetic pigment levels in the tested rice landraces is inter alia due to difference in root Al uptake and root-to-shoot translocation. Also, the pigment synthesis processes including the activities of enzymes involved might have been differentially influenced by Al in the tested landraces. Further research is required for precise understanding of molecular mechanistic basis of the differences observed. The landrace specific differences in response of pigment levels to Al have implications for the photosynthetic potential and in turn productivity of the tested rice landraces under acidic soil conditions. As such, the Al tolerant rice landraces are a unique genetic resource for crop improvement.

Conclusion

In brief, the findings revealed landrace-specific differences in Al-induced suppression of pigment (chlorophyll and carotenoid) contents of certain rice landraces from Sikkim Himalaya in a hydroponic system. The magnitude of suppression was lower in KT and CP than in KB and DH. The observed differential response could be ascribed to more efficient cellular management of Al in Al-tolerant (KT and CP) vis-à-vis Al-sensitive (KB and DH) landraces. The findings revealed KT and CP as promising landraces for cultivation in acidic soils due to their superior Al tolerance as evident by a lower magnitude of reduction in photosynthetic pigment levels.

Acknowledgments

The authors are grateful to the local framers of Sikkim Himalaya for providing the seeds of rice landraces. The award of Senior Research Fellowship to PC by Council of Scientific and Industrial Research (CSIR), New Delhi is thankfully acknowledged.

References

Barcelo J and Poschenrieder C (2002). Fast root growth responses, root exudates, and internal detoxification as clues to the mechanisms of aluminium toxicity and resistance, a review. *Environ Exp Bot* **48(1):** 75-92.

Chettri D, Anandan A, Nagireddy RK, Sabarinathan S and Sathyanarayana N (2021). Genetic diversity in rice (*Oryza sativa* L.) landraces of Sikkim-Himalaya and early insight into their use in genome-wide association analysis. *Plant Genet Res* **19(4):** 347-56.

Chettri D and Sathyanarayana N (2021). Traditional rice landraces and indigenous knowledge associated with the rice cultivation in Sikkim Himalaya: An analysis based on local farming practices. *Ind J Hill Farm* **34(1):** 1-15.

Chetry P and Sharma SS (2023). Variability in seed germination and seedling growth of some rice (*Oryza sativa* L.) landraces from Sikkim Himalaya: α-amylase activity and response to gibberellic acid. *J Indian Bot Soc* **101(03):** 156-62.

Chowra U, Yanase E, Koyama H and Panda SK (2017). Aluminium-induced excessive ROS causes cellular damage and metabolic shifts in black gram *Vigna mungo* (L.) Hepper. *Protoplasma* **254:** 293-302.

Delhaize E, Ma JF and Ryan PR (2012). Transcriptional regulation of aluminium tolerance genes. *Trends Plant Sci* **17(6):** 341-348.

Foy CD and Fleming AL (1982). Aluminum tolerances of two wheat genotypes related to nitrate reductase activities. *J Plant Nutr* **11(5):** 1313-1333.

Gonçalves JF, Nicoloso FT, Becker AG, Pereira LB, Tabaldi LA, Cargnelutti D, de Pelegrin, Dressler VL, da Rocha JBT and Schetinger MRC (2009). Photosynthetic pigments content, δ-aminolevulinic acid dehydratase and acid phosphatase activities and mineral nutrients concentration in cadmium-exposed *Cucumis sativus* L. *Biol* **64:** 310-318.

Gratao PL, Polle A, Lea PJ and Azevedo RA (2005). Making the life of heavy metal stressed plants a little easier. *Funct Plant Biol* **32:** 481-494.

Guo P, Qi YP, Yang LT, Lai NW, Ye X, Yang Y and Chen LS (2017). Root adaptive responses to aluminum-treatment revealed by RNA-Seq in two Citrus species with different aluminum-tolerance. *Front Plant Sci* **8:** 330.

Jiang HX, Chen LS, Zheng JG, Han S, Tang N and Smith BR (2008). Aluminum-induced effectson Photosystem II photochemistry in Citrus leaves assessed by the chlorophyll a fluorescence transient. *Tree Physiol* **28(12):** 1863-1871.

Kapoor RKA, Chettri PK, Gopi R., Kalita H, Rao DS and Babu VR (2019). Morphometric, physico-chemical and micronutrient characterization of rice (*Oryza sativa* L.) landraces of Sikkim Himalayas. *Indian J Plant Genet Res* **32(3):** 327-339.

Kochian LV (1995). Cellular mechanisms of aluminum toxicity and resistance in plants. *Annu Rev Plant Biol* **46(1):** 237-260.

Kochian LV, Hoekenga OA and Pineros MA (2004). How do crop plants tolerate acid soils? Mechanisms of aluminum tolerance and phosphorous efficiency. *Annu Rev Plant Biol* **55(1):** 459-493.

Kochian LV, Piñeros MA, Liu J and Magalhaes JV (2015). Plant adaptation to acid soils: the molecular basis for crop aluminum resistance. *Annu Rev Plant Biol* **66(1):** 571-598.

Kocjan A, Kwasniewska J and Szurman-Zubrzycka M (2024). Understanding plant tolerance to aluminum: exploring mechanisms and perspectives. *Plant Soil*. https://doi.org/10.1007/s11104-024-06745-0.

Lichtenthaler HK andBuschmann C (2001). Chlorophylls and carotenoids: Measurement and characterization by UV-VIS spectroscopy. *Curr Protocol Food Anal Chem* **1(1):** 4-3.

Matsumoto H (2000). Cell biology of aluminum toxicity and tolerance in higher plants. *Int Rev Cytol* **200:** 1-46.

Majumdar S, Wanniang SK and Behera U (2022). Acid soil management in north eastern hill region of India. *Indian Farm* **72(3):** 12-17.

Marschner P (2012). Rhizosphere biology. In Marschner's mineral nutrition of higher plants. *Acd Press London3rd (ed*) pp.369-388.

Mihailovic N, Drazic G and Vucinic Z (2008). Effects of aluminium on photosynthetic performance in Al-sensitive and Al-tolerant maize inbred lines. *Photosynthetica* **46(3):** 476-480.

Ofoe R, Thomas RH, Asiedu SK, Wang-Pruski G, Fofana B and Abbey L (2023). Aluminum in plants: Benefits, toxicity and tolerance mechanisms. *Front Plant Sci* **13:** 1085998.

Peixoto HP, Da Matta FM and Da Matta JC (2002). Responses of

the photosynthetic apparatus to aluminum stress in two sorghum cultivars. *J Plant Nutr* **25(4):** 821-832.

Phukunkamkaew S, Tisarum R, Pipatsitee P, Samphumphuang T, Maksup S and Cha-Um S (2021). Morpho-physiological responses of indica rice (*Oryza sativa* sub. indica) to aluminum toxicity at seedling stage. *Environ Sci Pollut Res* **28:** 29321-29331.

Rengel Z and Robinson DL (1989). Competitive Al^{3+} inhibition of net Mg^{2+} uptake by intact *Lolium multiflorum* roots: I. Kinetics. *Plant Physiol* **91:** 1407–13.

Roy B and Bhadra S (2014). Effects of toxic levels of aluminium on seedling parameters of rice under hydroponic culture. *Rice Sci* **21(4):** 217-223.

Sharma SS and Dietz KJ (2009). The relationship between metal toxicity and cellular redox imbalance. *Trends Plant Sci* **14(1):** 43-50.

Silva IR, Corrêa TFC, Novais RF, Smyth TJ, Ruft T, Silva EF, Gebrim FO and Nunes FN (2009). Timing, location and crop species influence the magnitude of amelioration of aluminum toxicity by magnesium. *Rev Bras Ciênc Solo* **33:** 65–76.

Silva S, Pinto G, Dias MC, Correia CM, Moutinho-Pereira J, Pinto-Carnide O and Santos C (2012). Aluminium long-term stress differently affects photosynthesis in rye genotypes. *Plant Physiol Biochem* **54:**105-112.

Strzałka K, Kostecka-Gugała A and Latowski D (2003). Carotenoids and environmental stress in plants: significance of carotenoid-mediated modulation of membrane physical properties. *Russ J Plant Physiol* **50:** 168-173.

Von Uexküll HR and Mutert E (1995). Global extent, development and economic impact of acid soils. *Plant Soil* **171:** 1-15.

Yamamoto Y, Kobayashi Y, Devi SR, Rikiishi S and Matsumoto H (2002). Aluminum toxicity is associated with mitochondrial dysfunction and the production of reactive oxygen species in plant cells. *Plant Physiol* **128(1):** 63-72.

Zhao X, Chen Q, Wang Y, Shen Z, Shen W and Xu X (2017). Hydrogen-rich water induces aluminum tolerance in maize seedlings by enhancing antioxidant capacities and nutrient homeostasis. *Ecotoxicol Environ Saf* **144:** 369-379.