UNIVERSIDADE FEDERAL DE SÃO CARLOS – UFSCar

CENTRO DE CIÊNCIAS DA NATUREZA – CCN

campus LAGOA DO SINO

CURSO DE GRADUAÇÃO EM ENGENHARIA AGRONÔMICA

RAJA YAMMA RODRIGUES SOUZA

Uso de jasmonatos na fitorremediação e tolerância a cádmio: uma revisão sistemática

Buri (SP)

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Trabalho de Conclusão de Curso apresentado ao Curso de Engenharia Agronômica para obtenção do título de Bacharel em Engenharia Agronômica.

Orientação: Professor Doutor Daniel Baron
Co-orientação: Doutor Cristiano Soares

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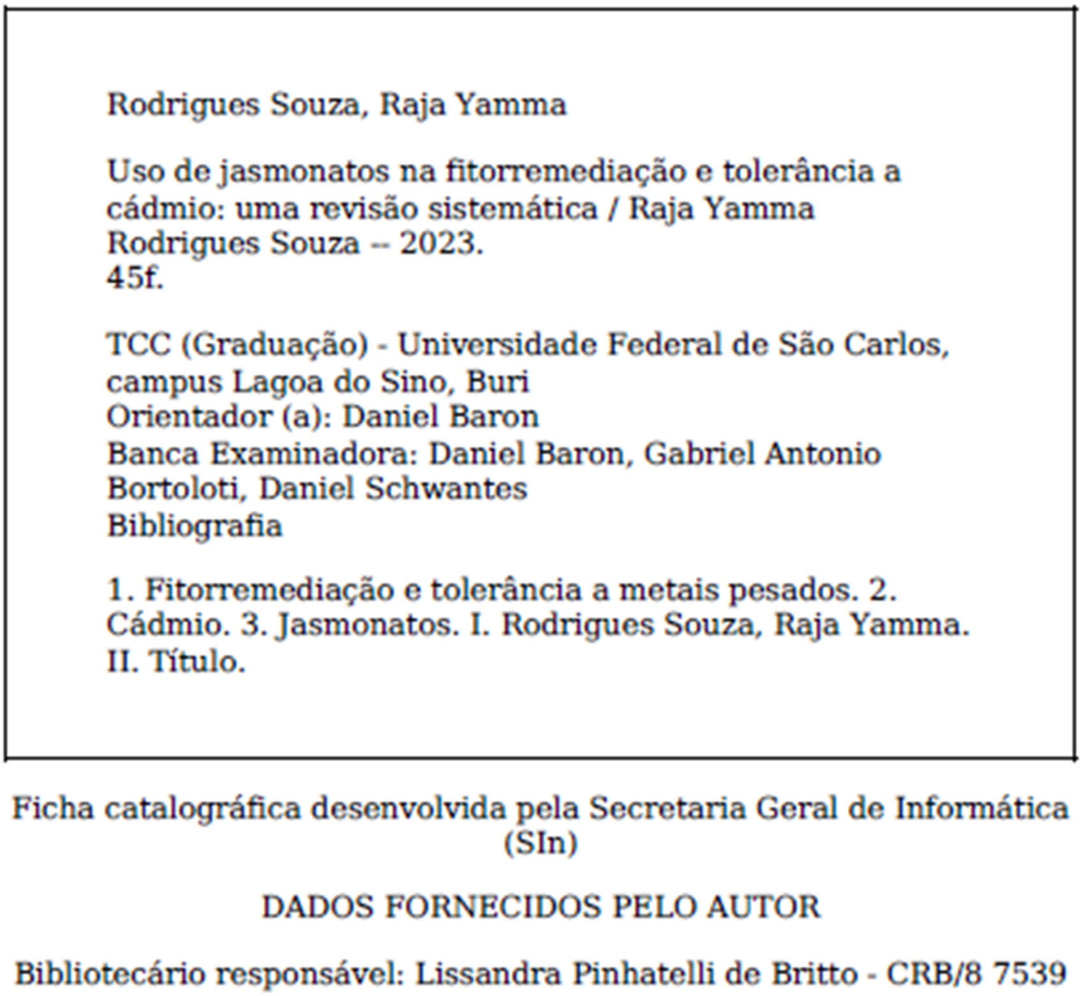

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RAJA YAMMA RODRIGUES SOUZA

USO DE JASMONATOS NA FITORREMEDIAÇÃO E TOLERÂNCIA A CD: UMA REVISÃO SISTEMÁTICA

Trabalho de Conclusão de Curso apresentado como requisito parcial à obtenção do título de Bacharel em Engenharia Agronômica pela Universidade Federal de São Carlos.

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RESUMO

RODRIGUES-SOUZA, Raja Yamma. Uso de jasmonatos na fitorremediação e tolerância a cádmio: uma revisão sistemática. 2023. 45f. Trabalho de Conclusão de Curso (Graduação em Engenharia Agronômica) – Universidade Federal de São Carlos, Buri/SP, 2023.

A emissão de cádmio (Cd) no ambiente, como resultado de atividades industriais, agrícolas e de urbanização acarretam riscos às áreas de produção agrícola e, consequentemente, a saúde humana. Entre as promissoras estratégias de descontaminação, a fitorremediação é reportada como uma solução de baixo custo e ecologicamente correta. Nesse sentido, diferentes espécies são estudadas com a finalidade de entender qual plantas são mais tolerantes a ambientes contaminados e indicas para a fitorremediação de Cd. Entretanto, apesar de várias publicações cientificas reportadas pela literatura, os efeitos da aplicação de fitorreguladores na modulação do metabolismo vegetal em condições de estresse por Cd ainda não estão totalmente elucidados. Dessa forma, o objetivo do nosso presente estudo foi investigar se a fitorremediação e a tolerância de plantas sob a aplicação exógena de jasmonato (JA) em diferentes plantas cultivadas em ambiente contaminado com Cd. Utilizamos a metodologia de revisão sistemática, por meio da definição do escopo, planejamento, identificação e busca, triagem dos artigos, avaliação da elegibilidade e interpretação e apresentação dos resultados. As publicações elegíveis indicam que a aplicação de JA em plantas cultivadas em ambiente contaminado, diminui o acúmulo de Cd e o conteúdo de malondialdeído (MDA) ao passo que aumenta a atividade antioxidante (superóxido dismutase, SOD, catalase, CAT, peroxidase, POD e ascorbato peroxidase, APX). Dessa forma, concluímos que a aplicação de JA diminui a fitorremediação e aumenta a tolerância de plantas cultivadas em ambiente com Cd. Os resultados desta revisão foram escritos no formato de artigo revisão e submetidos ao periódico científico '*Environmental Chemistry Letters*'.

Palavras-chave: metal pesado, stress oxidativo, peroxidação lipídica, antioxidantes, toxicidade do cádmio, resposta de defesa

ABSTRACT

RODRIGUES-SOUZA, Raja Yamma. Role of jasmonates in cadmium phytoremediation and plant tolerance: a systematic review. 2023. 45f. Course Completion Work (Degree in Agronomic Engineering) – Federal University of São Carlos, Lagoa do Sino *campus*, Buri/SP, 2023.

The emission of cadmium (Cd) into the environment due to industrial, agricultural, and urbanization activities poses risks to agricultural production areas and, consequently, to human health. Among the promising decontamination strategies, phytoremediation is reported to be a low-cost and environmentally friendly solution. In this sense, different species have been studied to understand which plants are more tolerant of contaminated environments and suitable for Cd phytoremediation. However, the effects of applying phytoregulators on modulating plant metabolism under conditions of Cd stress have yet to be elucidated. Therefore, this study aimed to investigate phytoremediation and plant tolerance under exogenous jasmonate (JA) application in different plants grown in a Cd-contaminated environment. We used the systematic review methodology by defining the scope, planning, identifying, and searching, screening the articles, assessing eligibility, and interpreting and presenting the results. The eligible publications indicate that the application of JA to plants grown in a contaminated environment decreases Cd accumulation and malondialdehyde (MDA) content while increasing antioxidant activity (superoxide dismutase, SOD, catalase, CAT, peroxidase, POD, and ascorbate peroxidase, APX). Thus, we conclude that applying JA decreases phytoremediation and increases the tolerance of plants grown in a Cd environment. The results of this review were written up as a review article and submitted to the scientific journal Environmental Chemistry Letters.

Keywords: heavy metal, oxidative stress, lipid peroxidation, antioxidants, cadmium toxicity, defense response

SUMÁRIO

1 BREVE INTRODUÇÃO E JUSTIFICATIVA PARA ESCOLHA DO TEMA

O cádmio (Cd) é um metal pesado tóxico listado entre os 10 elementos químicos mais perigosos da biosfera. Esse mineral está presente, naturalmente, na composição de diversas rochas, entretanto, o aumento de atividades antropogênicas como agricultura, industrialização e urbanização têm aumentado a presença deste metal pesado em ambientes aquáticos e terrestres (El-Sherbiny; Sallan, 2021; Shen et al., 2021; Wu et al., 2021). A exposição ao Cd pode causar uma série de danos em organismos animais e vegetais, promovendo processos oxidativos e limitando o desenvolvimento, conforme constatado por Lin, Lu e Wu, cujo estudo demonstrou que uma população exposta ao poluente teve maior propensão ao desenvolvimento de carcinomas (Lin; Lu; Wu, 2021; Wu et al., 2018). Assim, esse fato está relacionado a capacidade do Cd em bioacumular nas células, permitindo sua entrada na cadeia alimentar (Sharma, 2021).

Como forma de minimizar a presença de Cd no solo, a fitorremediação é reportada como uma ferramenta biotecnológica e ecologicamente sustentável que utiliza organismos vegetais para a descontaminação ambiental. A partir de mecanismos fisiológicos como a imobilização de poluentes na raiz (fitoestabilização), absorção e acúmulo nos tecidos vegetais (fitoextração) e absorção e transpiração de poluente para a atmosfera (fitovolatilização), as plantas conseguem promover a descontaminação de ambientes terrestres e aquáticos (Bortoloti; Baron, 2022). Diversas espécies são estudadas a fim de se compreender quais mecanismos e estratégias são eficientes em promover a tolerância e fitorremediação de plantas cultivadas em ambiente com Cd, tais como *Oryza sativa* L. (Ronzan et al., 2019), *Avicennia marina* L. (Yan et al., 2015), *Solanum lycopersicum* L. (Wei et al., 2021) e *Glycine max* (L.) Merril (Noriega et al., 2012).

A fim de potencializar a tolerância e fitorremediação de metais pesados (MP), diversos estudos buscam elucidar as respostas fisiológicas e bioquímicas desencadeadas por reguladores vegetais em plantas cultivadas em ambiente contaminado com Cd (Ali et al., 2018; Chen et al., 2022). Entre os fitorreguladores, os jasmonatos (JA) são uma classe de hormônios vegetais que atua na ativação e sinalização de vias do sistema de defesa vegetal, relacionados a respostas fisiológicas como fechamento estomático, inibição do crescimento radicular e síntese compostos de defesa, como os antioxidantes. Os JAs são presentes nas plantas nas formas de metil-jasmonato (MeJA) e o ácido jasmônico (AJ), em que ambos podem ser sintetizados em laboratório e utilizados em aplicações exógenas (Hewedy et al., 2023).

Diferentes estudos investigam o efeito de JAs aplicados à tolerância e fitorremediação a metais pesados. Estudos publicados por Bali e colaboradores e Yan e colaboradores relacionam a aplicação de JA a efeitos benéficos para a fitorremediação e tolerância a MPs a partir da repressão da enzima clorofilase, aumento dos níveis de enzimas antioxidantes, compostos secundários e outros fatores (Bali et al., 2019; Yan et al., 2015b). Por outro lado, Ahmad e colaboradores (Ahmad et al., 2021) e Manzoor e colaboradores (Manzoor et al., 2022) reportaram que a aplicação de jasmonato diminui o acúmulo de Cd, assim diminuindo o potencial fitorremediador e aumentando a tolerância Cd.

Dessa forma, especulamos que não exista consenso na literatura sobre as implicações da aplicação de JA em plantas cultivadas em ambiente contaminado com Cd. Nesse sentido, nosso estudo se propôs a elaborar um manuscrito de revisão sistemática da literatura com objetivo de compreender as respostas bioquímicas desencadeadas pela aplicação de JA em plantas cultivadas em ambiente contaminado, e suas implicações na tolerância e fitorremediação ao Cd.

2 HIPÓTESE

Investigar se regulador vegetal potencializa a fitorremediação de elemento químico tóxico; e

Investigar se regulador vegetal não promove a tolerância de espécies vegetais elemento químico tóxico.

3 OBJETIVOS

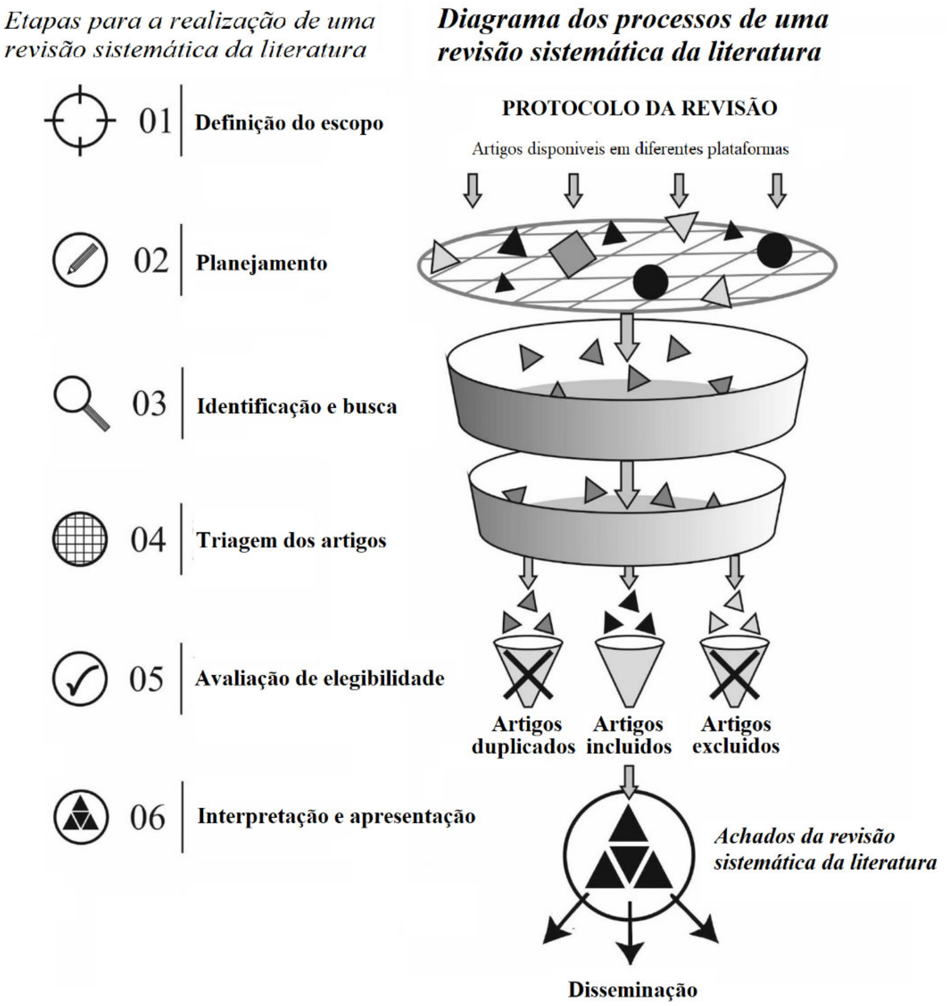
Analisar a aplicação de regulador vegetal e seus efeitos no metabolismo de diferentes espécies vegetais cultivadas em ambiente agrícola e/ou natural contaminado com metal pesado.

4 PERCURSO METODOLÓGICO

Ao verificarmos o pioneiro estudo de Grant e Booth (Grant; Booth, 2009), estes autores identificam 14 ‘modalidades de artigos de revisão’, tais como (1) revisão crítica; (2) revisão narrativa; (3) revisão de mapeamento; (4) meta-análise; (5) revisão de estudos mistos; (6) visão geral; (7) revisão sistemática qualitativa; (8) revisão rápida; (9) revisão de escopo; (10) estado da arte; (11) revisão sistemática; (12) pesquisa e revisão sistemática; (13) revisão sistematizada e (14) revisão guarda-chuva. Essas modalidades de estudo apresentam diversas abordagens de pesquisa, análise, síntese e avaliação. Em meio as categorias apresentadas, nosso presente estudo é classificado como ‘revisão sistemática de literatura’, cujas principais características são utilizar estratégias de buscas explícitas e abrangentes que detalham as bases de dados, indicar quantitativamente os dados coletados, utilizar critérios de inclusão e exclusão de forma homogênea, e classificar os resultados com base na força das evidências (Grant; Booth, 2009).

Para a realização da revisão sistemática da literatura utilizamos como principal referencial teórico metodológico o trabalho de Koutsos, Menexese e Dordas (Koutsos; Menexes; Dordas, 2019), que sugere uma metodologia específica para estudos na área de agronomia. A condução desta pesquisa foi realizada seguindo as etapas de definição do escopo, planejamento, identificação e busca, triagem dos artigos, elegibilidade, e interpretação e apresentação conforme apresentado na Figura 1.

Figura 1 - Diagrama das etapas de uma revisão sistemática de literatura.



Fonte: adaptado de Koutsos, Menexese e Dordas (2019).

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6 MANUSCRITO DE REVISÃO

Conforme estabelecido pelo Projeto Pedagógico do Curso de Bacharelado em Engenharia Agronômica (PPC, 2016 – *link* de acesso: https://www.lagoadosino.ufscar.br/cursos/arquivos/ppcs/ppc_engenharia_agronomica_2018_07.pdf), no item '9.4.2. Regulamento do Trabalho de Conclusão de Curso', estabelece que a monografia do trabalho de conclusão do curso se refere a "***um trabalho acadêmico pode ser monográfico ou de pesquisa o qual poderá ter tema inédito ou advir de pesquisa realizada pelo estudante, no âmbito de sua iniciação científica ou elaborar uma monografia a partir de situações-problema que porventura vivencie no campo de estágio***".

Considerando as justificativas apresentadas anteriormente ao longo dessa monografia, redigimos o presente TCC na modalidade '*review paper*' com os atuais avanços intelectuais, conforme as normas de publicação do periódico científico '*Environmental Chemistry Letters'* (***https://www.springer.com/journal/10311/***).

Environmental Chemistry Letters
ROLE OF JASMONATES IN CD PHYTOREMEDIATION AND PLANT TOLERANCE:
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--Manuscript Draft--

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Abstract:	The release of cadmium (Cd) into the environment due to industrial, agricultural, and urban activities can result in non-target toxicity towards flora and fauna. Phytoremediation is a cost-effective and eco-friendly strategy that can be used to mitigate Cd contamination and environmental damage. However, in most cases, phytoremediator species can still be affected by the metal exposure, so ways to boost plant tolerance without affecting the remediation potential are needed. Within this perspective, the exogenous application of PGRs, such as jasmonates (JA), can be a feasible approach. Yet, so far, these biological effects on plant metabolism under cadmium stress remain a matter of debate. Thus, the objective of the present paper was to conduct a literature review on phytoremediation and heavy metal tolerance, particularly focusing on the outcomes of JA application on plants grown in Cd-polluted settings. The systematic review methodology was adopted, which involved defining the scope and planning, identifying and searching, screening the articles, assessing eligibility, and interpreting and presenting the findings. Here, we review the role of JA application in Cd tolerance and phytoremediation from a biochemical approach, with analyses of Cd absorption, MDA content, the activity of the AOX enzymes (SOD, CAT, POD and APX), and GLT content.
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ROLE OF JASMONATES IN CD PHYTOREMEDIATION AND PLANT TOLERANCE: A SYSTEMATIC REVIEW

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HIGHLIGHTS

Exogenous JA reduces Cd phytoremediation

The use of JA increases plant tolerance to Cd

JA increases AOX enzyme activity in plants grown in a Cd environment

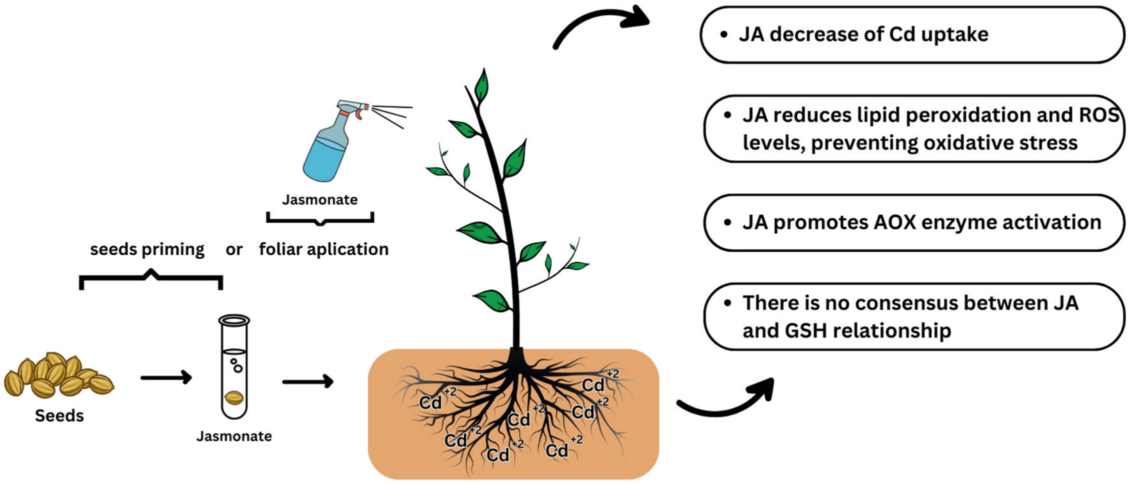
ABBREVIATION

Cd	Cadmium
JAs	Jasmonate
JA	Jasmonic acid
MeJa	Methyl jasmonate
PGR	Plant growth regulator
AOX	Antioxidante
MDA	Malondialdehyde
SOD	Superoxide dismutase
CAT	Catalase
POD	Peroxidase
APX	Ascorbate peroxidase
HM	Heavy metal
Pb	Lead
Zn	Zinc
Hg	mercury
As	Arsenic
Cu	Copper
Fe	Iron
AX	Auxins
GA	Gibberellins
CK	Cytokinins
ROS	Reactive oxygen species
AsA	Ascorbic acid
GSH	Reduced glutathione
GSSG	Oxidized glutathione
RQ	Research question
EDTA	Ethylenediaminetetraacetic acid

ABSTRACT

The release of cadmium (Cd) into the environment due to industrial, agricultural, and urban activities can result in non-target toxicity towards flora and fauna. Phytoremediation is a cost-effective, eco-friendly strategy that can mitigate Cd contamination and environmental damage. However, in most cases, metal exposure can still affect phytoremediator species, so ways to boost plant tolerance without affecting the remediation potential are needed. The exogenous application of plant growth regulators (PGRs), such as jasmonates (JAs), can be a feasible approach within this perspective. However, so far, these biological effects on plant metabolism under Cd stress remain a matter of debate. Thus, the objective of the present paper was to conduct a literature review on phytoremediation and heavy metal tolerance, particularly focusing on the outcomes of JAs application on plants grown in Cd-polluted settings. The systematic review methodology was adopted, which involved defining the scope and planning, identifying, and searching, screening the articles, assessing eligibility, and interpreting and presenting the findings. Here, we review the role of JAs application in Cd tolerance and phytoremediation from a biochemical approach, with analyses of Cd absorption, malondialdehyde (MDA) content, the activity of the antioxidant (AOX) enzymes (superoxide dismutase, SOD, catalase, CAT, peroxidase, POD, and ascorbate peroxidase, APX), and glutathione (GSH) content.

Keywords: heavy metal, oxidative stress, lipid peroxidation, antioxidants, cadmium toxicity, defense response



Graphical abstract

1. INTRODUCTION

Heavy metal (HM) naturally occurs as minerals in the composition of some rocks that form the soil. Carbonate rocks, for example, can contain traces of lead (Pb), zinc (Zn), and cadmium (Cd) without significant damage to the ecosystem (Wu et al., 2021). However, anthropogenic activities related to urbanization, agriculture, burning fossil fuels, industrialization and mining have been leading to an uncontrolled increase in HM concentrations in the environment (Shen et al., 2021). Cd is a toxic HM and its presence in the environment can affect plant growth, causing morphophysiological disorders. In this context, it is imperative to seek out species that exhibit tolerance and possess the ability to survive in environments contaminated with Cd (Ali et al., 2018). The degenerative effects of Cd are because this HM can bioaccumulate in plant and animal cells, thus impairing plant development and causing risks to human health due to increased oxidative damage (Keyster et al., 2020). This urges the need to develop and optimize technologies to decontaminate land and water areas to minimize the presence of this HM and other pollutants in the environment, as well as to promote practices that promote plant tolerance to stress conditions caused by HMs.

Among the various environmental decontamination techniques, phytoremediation stands out for being an ecologically relevant, low-cost alternative that can be used in significant territorial extensions and is capable of eliminating and mitigating the deleterious effects of numerous pollutants (He et al., 2020). Various plant species can be used in the process of phytoremediation of soils contaminated by HMs, among which are plants from the botanical families Solanaceae (e.g. *Solanum nigrum* L.), Fabaceae [e.g. *Glycine max* (L.) Merril], Poaceae (e.g. *Oryza sativa* L.), Lamiaceae (e.g. *Thymus vulgaris* L.), and others (Moori and Ahmadi-Lahijani, 2020; Noriega et al., 2012; Singh and Shah, 2014b; Rehman et al., 2017).

Some researchers are investigating whether using organic compounds, such as bioregulators, can promote phytoremediation and tolerance to HMs. In this context, several works have been undertaken to examine the effect of bioregulators, such as plant growth regulators (PGR), chelating agents, and acidifiers on the phytoremediation of contaminated soils (Al Mahmud et al., 2018; Bashri and Prasad, 2016; Mousavi et al., 2021). Among these substances, PGRs belonging to the class of auxins (AX), gibberellins (GA), cytokinins (CK), and jasmonates (JAs) are of significant interest, given their ability, even when applied in small concentrations, to modulate physiological effects (Bali et al., 2019; Ji et al., 2015; Singh et al., 2021).

Included in the family of phytohormones, JAs (jasmonic acid, JA, and methyl jasmonate, MeJA) are endogenous molecules in plants, capable of modulating different aspects of plant growth and development ('stress responses'). When plants are subjected to biotic (e.g. herbivory and diseases) and abiotic (e.g. drought, heat, and potentially toxic metals) stresses, JAs stimulate defense mechanisms such as growth inhibition and the production of AOX substances that favor tolerance to stressful conditions. These mechanisms can also be induced by exogenous applications of JAs (Ali et al., 2018). The role of this PGR in Cd phytoremediation has been the subject of research and debate among various scientists (Ahmad et al., 2017; Yan et al., 2015a).

In light of the aforementioned, our literature review aims to identify and analyze articles about using of JAs in plants cultivated in Cd-contaminated environments, specifically concerning phytoremediation or oxidative stress studies.

2. SEARCH STRATEGY, KEYWORDS, AND SELECTION CRITERIA

This manuscript is structured around four sections: (a) description of search strategies, keywords, and selection criteria; (b) presentation of the theoretical bases (topics 'cadmium', 'stress responses and tolerance to HMs', 'phytoremediation' and 'jasmonates'; (c) discussion of results (topics 'JAs vs phytoremediation - what do we know so far?', 'JAs does not potentiate the phytoremediation mechanisms of plant species grown in the presence of Cd' and 'JAs promote the tolerance of plant species grown in Cd-contaminated environments') and (d) conclusions and future prospects. The article of Koutsos, Menexese, and Dordas (Koutsos et al., 2019) was used as the primary methodological theoretical reference, providing a specific methodology for studies in agronomy. After the bibliographical survey, we proceeded with the research protocol for the systematic review article. The scope of the research was defined based on 2 hypotheses ("research question"): (i) "to investigate whether a plant growth regulator (jasmonate) does not improve the phytoremediation of a toxic chemical element (cadmium)"; and (ii) "to investigate whether a plant growth regulator (jasmonate) does not promote the tolerance of plant species to a toxic chemical element (cadmium)".

We then collected data from the databases ACS Journals Search', 'CAB Abstract' (CABI), 'JSTOR Redalyc', 'Science Direct' (Elsevier), 'SCOPUS' (Elsevier), 'Springer Link', 'Web of Science' (WOS), and 'Taylor and Francis'. To conduct our search, relevant keywords related to the study's aim were merged as per the search string: "(((phytoremediation) OR ("oxidative stress")) AND ((cadmium) OR (Cd)) AND ((jasmonate) OR ("jasmonic acid") OR ("methyl jasmonate")))". Subsequently, the articles were attached to a document manager, where duplicates were excluded. Finally, we proceeded to the eligibility and exclusion of the publications collected with online search engines, based on the following criteria: (i) Inclusion criteria: the article must have been accepted and/or published between 2012 and 2023 (until 31 May); research results that directly analyze the effects of applying JAs to plant species grown in a Cd-contaminated environment. (ii) Exclusion criteria: the article is not published in English; it is not a research article or does not address the PGR and/or target pollutant and/or phytoremediation and/or oxidative stress.

3. CADMIUM

The term "heavy metal" is used to characterize chemical elements 'metals and metalloids' (also known as "semimetals") that have metallic properties, high density, and an atomic number greater than 20g.cm^{-3} (Baron et al., 2017). Some HMs, for example, Zn, copper (Cu), and iron (Fe) are required in minute quantities by plants (mg.kg^{-1} dry matter mass) during their growth and development, so these metals are considered 'essential elements' or 'nutrients'. Other HMs such as mercury (Hg), arsenic (As), Cd, and Pb promote degenerative processes in plants even when present in small concentrations, so they are considered 'toxic elements' (Wu et al., 2018).

Cd is listed among the 10 most toxic chemical elements to living organisms and given its bioaccumulation in the environment, it can enter the food chain and cause significant damage to animals and plants (El-Sherbiny and Sallam, 2021; Sharma et al., 2022). Cd contamination resulting from mining, industry, and thermal power plants has been reported in various provinces of the Turkey (Baştabak et al., 2021). Moreover, numerous incidents of contamination outbreaks have been reported in countries located in South America (above 0.001 $mg.kg^{-1}$) (Bárbara et al., 2019), China (above 0.12 $mg.kg^{-1}$) (Wu et al., 2018) and Asia (Ngoc et al., 2020). This pollutant, in some cases, occurs in concentrations exceeding the limit set by the World Health Organization (0.01 $mg.L^{-1}$), leading to the contamination of water sources and food (Ngoc et al., 2020). An increase in the concentration of this metal in the environment can lead to a series of health problems for animal and plant organisms (Keyster et al., 2020). The ingestion of Cd can be highly harmful to human health, predisposing the human population exposed to the pollutant to cancer development, as found by Lin et al. (2021). Similarly, this pollutant can also harm other organisms (Berik et al., 2017).

In plant tissues, Cd in concentrations above 100 $mg.kg^{-1}$ causes damage to respiratory, photosynthetic, and enzymatic processes (Wu et al., 2018). This metal can cause a series morphophysiological disturbances at the beginning of embryogenesis, preventing seed germination. At advanced stages of development, Cd can cause deformations and disorganization of the most different cell types present in root tissues — such as the epidermis, cortex, and endodermis — and in leaf tissues ("translocating plants") — such as mesophyll and epidermis cell —. One of the main results of these disturbances is lower plant growth and development than would be expected for healthy plants (Hu et al., 2009; Stingu et al., 2012). In addition, the stress generated by Cd will stimulate the production of reactive oxygen species (ROS) (Rehman et al., 2018).

4. STRESS RESPONSES AND TOLERANCE TO HMs

The concept of 'stress' used in this manuscript was proposed by Lichtenthaler (1996), who defined stress in plants as any condition or substance that prevents the plant organism from fully expressing its genetic potential. Plant organisms are naturally subjected to different types of stresses (biotic and abiotic). However, depending on the intensity and time of exposure to the stress, the plant's response in terms of quality, productivity and tolerance can be positive ('eustress') or negative ('distress') (Vázquez-Hernández et al., 2019). In this condition, tolerance is as the plant's capacity to survive and maintain growth under stressful conditions.

In general, tolerance is innate in some species, allowing plants to survive within certain limits of heavy metals in the soil (Clemens, 2006). Among the plant species found in our review, Arachis hypogaea L. (Pilaisangsuree et al., 2020), Atriplex lentiformis (Torr.) S. Watson

(Ibrahim et al., 2022), Avicennia marina L. (Yan et al., 2015a), Brassica juncea L. (Per et al., 2016), Brassica napus L. (Ali et al., 2018), Cajanus cajan L (Kaushik et al., 2022), Capsicum annuum L. (Zhang et al., 2023), Capsicum frutescens L. (Yan et al., 2013), Chlorella vulgaris L. (Piotrowska-Niczyporuk et al., 2012), Cicer arietinum L. (Ahmad et al., 2021), Cucumis sativus L. (Feng et al., 2023), Glycine max L. (Noriega et al., 2012), Kandelia obovata Sheue, Liu & Yong (Chen et al., 2014), Mentha arvensis L. (Zaid and Mohammad, 2018), Oryza sativa L. (Kanu et al., 2022; Li et al., 2022; Ronzan et al., 2019; Singh and Shah, 2014ab), Pisum sativum L. (Abbas et al., 2022; Manzoor et al., 2022), Sedum alfredii L. (Chen et al., 2022), Solanum lycopersicum L. (Wei et al., 2021; Wei et al., 2022), Solanum nigrum L. (Yan et al., 2015b), Thymus vulgaris L. (Moori and Ahmadi-Lahijani, 2020), Triticum aestivum L. (Kaya et al., 2021) and Vicia faba L. (Ahmad et al., 2017) can survive in soils contaminated with Cd (Cd^{2+}), but the presence of Cd in contaminated soils lacks specific studies with plants of agronomic interest, since most of the articles study model organisms that are not necessarily used in agricultural environments. In addition, it is essential to use laboratory techniques that indirectly measure the effects of Cd on cell structure (phospholipid bilayer), such as oxidative cell damage, which can be indirectly analysed by MDA content. This condition also can be analyzed using stress indicators such as ROS and defense indicators such as AOX and can be stimulated by practices such as genetic improvement, gene editing, management, and the application of substances such as JAs (Ali et al., 2018; Kanu et al., 2022).

ROS are free radicals or molecules produced during normal metabolic processes occurring in plant cells; however, when the presence of HMs triggers a cellular electrochemical imbalance, these highly unstable compounds will be overpowered. These compounds become stable again and oxidize all kinds of biomolecules, which will promote damage to the cell and organelle membranes, nucleic acids, and chloroplast pigments, in addition to promoting lipid peroxidation and the production of malondialdehyde (Yan et al., 2015b). In response to the overproduction of ROS, plants employ a complex defense mechanism based on synthesizing various enzymatic AOX. These include superoxide dismutase (SOD, EC 1.15.1.1), catalase (CAT, EC 1.11.1.6), peroxidase (POD, EC 1.11.1.7), and ascorbate peroxidase (APX, EC 1.11.1.11). In addition, non-enzymatic AOX compounds such as ascorbic acid (AsA), phenolic compounds, proline, and glutathione (GSH) are also produced (Al Mahmud et al., 2018; Bhaduri and Fulekar, 2012). In this context, phytohormones (e.g., JAs) modulate the biochemical responses triggered by HM stress conditions, often stimulating the synthesis of AOX and promoting plant tolerance (Rahman et al., 2023).

AOX enzymes and other non-enzymatic AOX compounds can dramatically increase the efficiency of the detoxification processes of some ROS. For example, SOD simultaneously oxidizes and reduces superoxide anion (O_2^-) to hydrogen peroxide (H_2O_2) and molecular oxygen (O_2). Complementarily, CAT catalyzes the detoxification of H_2O_2 into H_2O and O_2, forms of oxygen that are not toxic to the plant (Hippler et al., 2018; Soares et al., 2019; Stephenie et al., 2020). Similarly, non-enzymatic AOX compounds such as ascorbic acid, phenolic compounds, and GSH can donate electrons to hydroxyl (OH^-), carboxylic acid ($COOH^-$), and/or H_2O_2 radicals (ROS species) to make plants tolerant to stressful conditions (Mousavi et al., 2021). GSH is a tripeptide found in the chloroplast, mitochondria, and cytosol, which contributes to plant detoxification directly by neutralizing the ROS H_2O_2 and $OH^\cdot$, and indirectly by participating in the reactions of the APX cycle. In addition, GSH is widely used to determine the tolerance of a plant under stress (Gill and Tuteja, 2010). The main AOX reactions are illustrated in Figure 1.

Our review found a significant number of methodologies addressing different metabolic pathways and their modulation by metals, but articles with molecular assessments addressing our research questions were scarce. This suggests that biomolecular approaches such as gene expression, transcription and physiological effects could be studied in model plants to explore their phytoremediation potential.

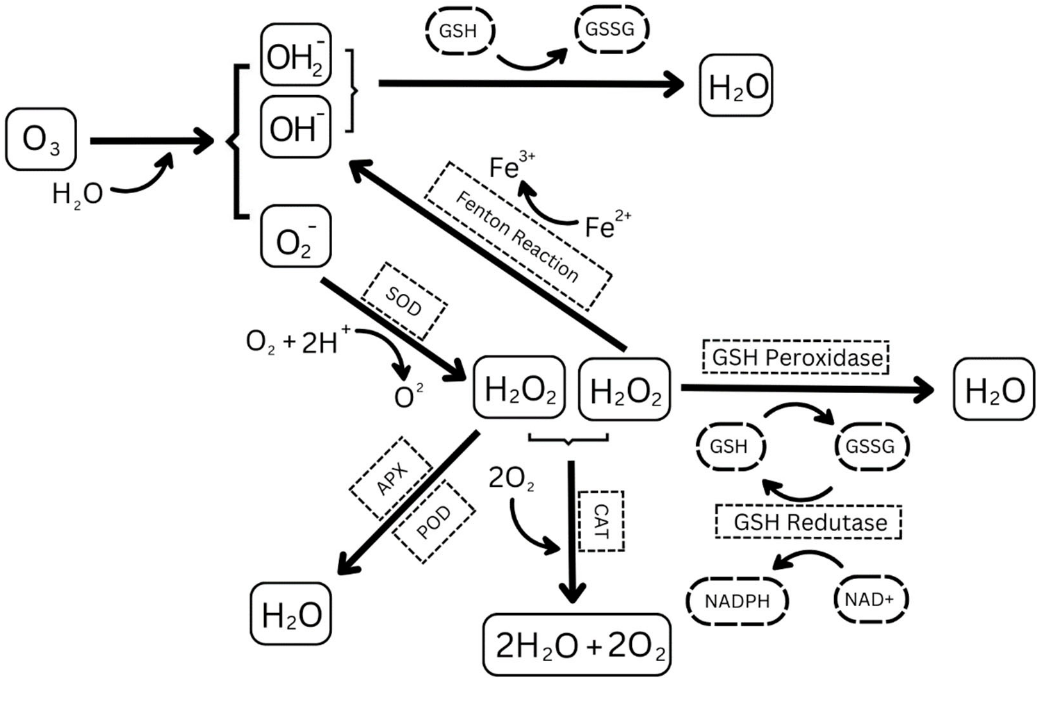


Fig 1. Illustration of the main inputs and outputs of the biochemical reactions involved in the formation of hydroxyl radicals (OH^-) hydroperoxyl (OH_2^-), superoxide anion (O_2^-) and hydrogen peroxide (H_2O_2), and the detoxification of these molecules, promoted by the antioxidants superoxide dismutase (SOD)

catalase (CAT) peroxidase (POD) ascorbate peroxidase (APX) and glutathione [reduced glutathione (GSH) and oxidized glutathione (GSSG)].

5. PHYTOREMEDIATION

Several technologies have been studied as alternatives for the environmental decontamination of HMs, including chelating agents, electric currents, thermal desorption, chemical leaching, and phytoremediation (Zheng et al., 2021). Phytoremediation is reported in the literature as a biotechnological or 'sustainable tool', as it uses plants without applying of chemical and/or synthetic compounds (He et al., 2020). Different plant species are reported for potential use in phytoremediation systems, such as *Artemisia vulgaris* L. (Antoniadis et al., 2021), *Zea mays* L. (Košnář et al., 2018), *Lolium multiflorum* L. (Cui et al., 2021), *Brassica juncea* L. (Al Mahmud et al., 2018), *Cynara cardunculus* L. (Arena et al., 2017) and *Solanum nigrum* L. (Soares et al., 2016). Through plant physiological mechanisms, such as stabilization of the pollutant in the root ('phytostabilization'), accumulation of the pollutant in root and leaf tissues ('phytoextraction') and absorption and volatility of the pollutant through the transpiration process ('phytovolatilization'), various plant species promote the decontamination of terrestrial and aquatic areas (Bortoloti and Baron, 2022). The main HM phytoremediation strategies are illustrated in Figure 2.

Our literature review found several articles that investigated the role of Cd in phytoremediation mechanisms, given its rapid and easy absorption by the root system and its movement, via the xylem towards the aerial parts via transpiration (Ran et al., 2020; Rossi et al., 2012; Rostami and Azhdarpoor, 2019). Moreover, the subsequent by-products of many plant species that are commercially exploited in the field, for example, stubble and plant leftovers from *Zea mays* L., *Brassica napus* L., and *Saccharum officinarum* L., can be used as alternative sources of energy from the production of biodiesel and other second-generation fuels (Baştabak et al., 2021). In this way, using phytoremediation in environmental decontamination can increase the quality of soils, rivers, and lakes, minimize health risks, contribute to food security, and open up new commercial opportunities through the sustainable disposal of its by-products. Although relevant, there is still no clarity among the scientific community about the physiological and biochemical responses, signaling, and mechanisms involved in the metal detoxification of plant species grown in soil contaminated with HMs, especially under the application of compounds that modulate plant metabolism, such as PGRs.

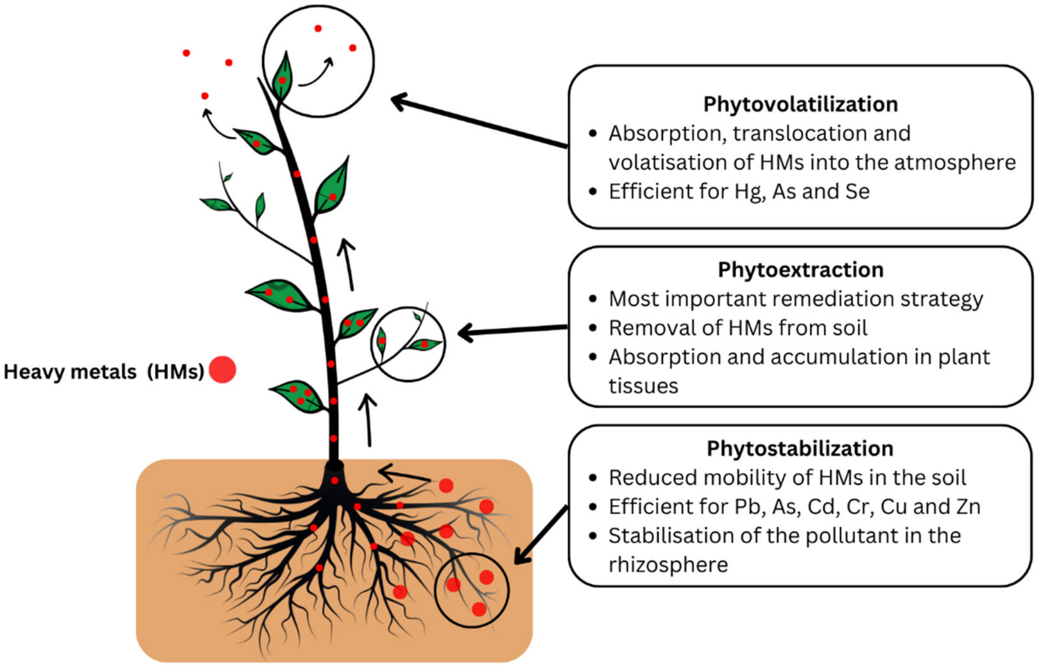


Fig. 2 Representation of the three main phytoremediation strategies for heavy metals (phytovolatilization, phytoextraction and phytostabilization).

6. JASMONATES

PGR are organic compounds that interact with plant metabolism. PGR are analogous to phytohormones but are chemically synthesized in laboratories for external application. They can be applied at low concentrations (< µM) to stimulate physiological processes. AX, GA, and CK are of interest in phytoremediation as they reportedly stimulate plant growth, while JAs directly contribute to plant defense (Bali et al., 2019; Ran et al., 2020; Singh et al., 2021). Based on the literature review carried out in this study, doses of several PGR up to 1 nM may enhance the vegetative growth and biomass yield of plants cultivated in Cd-contaminated soil (Rostami and Azhdarpoor, 2019). However, depending on concentrations and phenological stage of the plant, PGRs can cause deleterious effects on plant development, which makes further studies relevant to elucidate the effect of these compounds when used to promote phytoremediation (Piotrowska-Niczyporuk et al., 2012).

JAs are PGRs that regulate senescence, inhibiting plant growth by blocking the incorporation of glucose into cell wall polysaccharides, and acting signaling against stresses (Kim et al., 2023). When biotic (e.g. attack by herbivores) and abiotic (e.g. heavy metals) stresses are perceived, the plant immediately produces protease inhibitors, stress regulation enzymes, and other compounds. Among the JAs, the literature identifies JA and MeJA as hormones that participate in signaling plant reactions to stressful environmental changes. In addition, both can be artificially synthesized, so MeJA is the most active for exogenous applications (Hewedy et al., 2023). Different studies have sought to elucidate the signaling promoted by MeJA in the phytoremediation of soils contaminated with HMs such as Cd (Ali et al., 2018; Kaushik et al., 2022; Yan et al., 2015a). The presence of MeJA is related to an increase in the enzymatic activity of SOD, POD, CAT, and APX, and a reduction in the accumulation of H_2O_2 and malondialdehyde (MDA) in soils contaminated with HMs (Ahmad et al., 2017; Sirhindi et al., 2016). However, at low concentrations, MeJA can aggravate the inhibition of root growth caused by the high presence of the heavy metal aluminum (Al) (Wang et al., 2020; Yang et al., 2017). At concentrations above 2 µM, degenerative action has been reported in seedlings of the species *Solanum trilobatum* L., which application decreased the biomass production of this species (Shilpha et al., 2015).

Thus, we speculate that there is no consensus in the literature on the use of PGRs in the phytoremediation of HMs, and so our study analyzed original articles that used JAs in plants grown in a Cd-contaminated environment in phytoremediation and/or oxidative stress studies.

7. JAS VS PHYTOREMEDIATION - WHAT DO WE KNOW SO FAR?

Our literature review found 3,418 original research articles or review articles which, after being screened for the 'eligibility filters', resulted in 28 articles that fully met our research scope. The occurrence of these publications over the last 12 years (between 2012 and 2023) is shown in Figure 3.

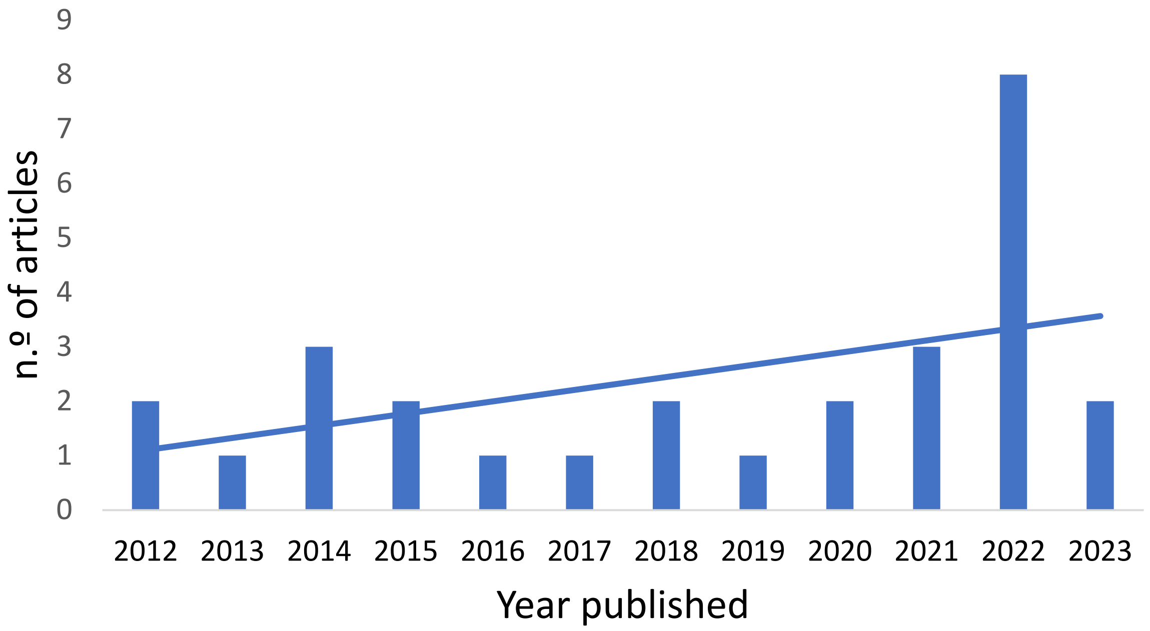


Fig. 3 – Occurrence of articles published between 2012 and 2023 that passed the inclusion and exclusion criteria mentioned in this manuscript's 'Search strategy, keywords, and selection criteria' section.

Of these publications, 20 articles address 'the effect of JAs application on the phytoremediation potential of plants grown in a Cd-contaminated environment' ('research question 1') and 28 articles address 'the effect of jasmonate application on the tolerance of plants grown in a Cd-contaminated environment' ('research question 2'), as shown in Table 1.

Table 1. Articles categorized under research question 1 (RQ1 — "Do jasmonates (JAs) enhance the phytoremediation mechanisms of plant species grown in the presence of cadmium (Cd)?"—) and research question 2 (RQ2 - "Do jasmonates (JAs) promote tolerance of plant species grown in an environment contaminated with cadmium (Cd)?").

Species	**RQ1**	**RQ2**	**References**
Arachis hypogaea L.		X	Pilaisangsuree et al., 2020
Atriplex lentiformis (Torr.) S. Watson	X	X	Ibrahim et al., 2022
Avicennia marina L.	X	X	Yan et al., 2015a
Brassica juncea L.	X	X	Per et al., 2016
Brassica napus L.	X	X	Ali et al., 2018
Cajanus cajan L		X	Kaushik et al., 2022
Capsicum annuum L.	X	X	Zhang et al., 2023
Capsicum frutescens L.		X	Yan et al., 2013
Chlorella vulgaris L.	X	X	Piotrowska-Niczyporuk et al., 2012
Cicer arietinum L.	X	X	Ahmad et al., 2021
Cucumis sativus L.		X	Feng et al., 2023
Glycine max L.		X	Noriega et al., 2012
Kandelia obovata Sheue, Liu & Yong	X	X	Chen et al., 2014
Mentha arvensis L.	X	X	Zaid and Mohammad, 2018
Oryza sativa L.	X	X	Kanu et al., 2022; Li et al., 2022; Ronzan et al., 2019; Singh and Shah, 2014a
Oryza sativa L.		X	Singh and Shah, 2014b
Pisum sativum L.		X	Abbas et al., 2022
Pisum sativum L.	X	X	Manzoor et al., 2022
Sedum alfredii L.	X	X	Chen et al., 2022
Solanum lycopersicum L.	X	X	Wei et al., 2021; Wei et al., 2022
Solanum nigrum L.	X	X	Yan et al., 2015b
Thymus vulgaris L.		X	Moori and Ahmadi-Lahijani, 2020
Triticum aestivum L.	X	X	Kaya et al., 2021
Vicia faba L.	X	X	Ahmad et al., 2017

7.1 JAS DOES NOT POTENTIATE THE PHYTOREMEDIATION MECHANISMS OF PLANT SPECIES GROWN IN THE PRESENCE OF CADMIUM

The phytoremediation potential of a phytoextractor species is measured mainly by assessing the pollutant concentration in the plant tissue. In this sense, there is strong evidence that applying JAs to plant species grown in a Cd-contaminated environment attenuates their phytoremediation potential. Throughout their life cycle, plants are in a "dilemma" between allocating their metabolites and energy reserves to plant growth or defense mechanisms promoting stress tolerance. Allocation plays a crucial role in plant health, and a proper balance benefits their full development (Wang et al., 2020). The complex signaling network modulated by phytohormones ('crosstalk') influences plants' adaptive responses to stressful conditions. In this context, JAs stand out as a group of PGR that play an essential role in regulating defense mechanisms. These include the activation of biosynthetic routes of AOX substances, protection and increased efficiency of photosynthetic structures, restoration of redox homeostasis, and transcription of genes related to increased plant tolerance to HMs (Kolupaev and Yastreb, 2021; Rahman et al., 2023). Exposure to Cd causes degenerative disorders in plant organisms including growth inhibition, chlorosis, osmotic stress, and damage to photosynthetic system (Haider et al., 2021). The application of different doses of JAs to plants grown in a Cd-contaminated environment reduced the accumulation of Cd in leaves and/or roots of plants of the species *Oryza sativa* L. (Ali et al., 2018; Kanu et al., 2022; Li et al., 2022; Ronzan et al., 2019; Singh and Shah, 2014b), *Avicennia marina* L. (Yan et al., 2015a), *Solanum lycopersicum* L. (Wei et al., 2021; Wei et al., 2022), *Cicer arietinum* L. (Ahmad et al., 2021), *Vicia faba* L. (Ahmad et al., 2017), *Pisum sativum* L. (Manzoor et al., 2022), *Solanum nigrum* L. (Yan et al., 2015b), *Brassica juncea* L. (Per et al., 2016), *Mentha arvensis* L. (Zaid and Mohammad, 2018), *Triticum aestivum* L. (Kaya et al., 2021), *Brassica napus* L. (Ali et al., 2018), *Sedum alfredii* L. (Chen et al., 2022) and *Chlorella vulgaris* L. (Piotrowska-Niczyporuk et al., 2012).

Cd uptake depends on factors such as availability (Cd^{2+}). In alkaline soils, Cd is hydrolysed and unavailable in forms such as $Cd(OH)_2$ and $Cd_3(PO_4)_2$. On the other hand, in acidic soils the phytoavailability of Cd increases, which favours accumulation and consequently toxicity (Kulsum et al., 2022). In addition to the "assimilable ionic form", the uptake of Cd in plant tissues depends on factors such as the transpiration rate of the xylem, which allows the pollutant to be absorbed and translocated. Thus, the decrease mentioned above in the accumulation of this metal may be related to the inhibitory effects of JAs, which promotes, for example, stomatal closure and consequently limits transpiration, or protective effects, which can increase dry matter mass production and decrease the Cd per dry mass ratio (mg.g^{-1}) (Wei et al., 2022). This behavior, however, was not observed in the study by Chen et al. (2014), in which the species *Kandelia obovata* Sheue. Despite reducing Cd accumulation in the leaves, the authors repot that the treatment did not reduce levels in the roots. In *Capsicum annuum* L. leaves, there was no difference in Cd accumulation between plants treated with and without JAs (Zhang et al., 2023). However, even without reducing the accumulation of this pollutant, the authors report that JAs increases tolerance due to its protective effects that induce, for example, the synthesis of AOX compounds.

In contrast, applying JAs combined with other compounds can modulate Cd absorption and thus stimulate or inhibit its accumulation. For example, using chelating agent ethylenediaminetetraacetic acid (EDTA) increases the concentration of Cd in plant tissue in *Atriplex lentiformis* (Torr.) Watson plants by forming metal-ligand complexes and increasing the chelation of the pollutant in the soil (Ibrahim et al., 2022). On the other hand, studies conducted by Zaid and Mohammad (2018) found that *Mentha arvensis* L. plants treated with the combination of JAs and nitrogen (basal nitrogen) absorbed less Cd than plants treated with JAs alone. Similarly, the combined application of JAs and sulfur (S) to *Brassica juncea* L. plants resulted in lower Cd accumulation than JAs alone (Per et al., 2016). Both effects may be related to the upregulation of the N and S assimilation pathways, which enhance nutrient efficiency, and enzymatic activity (e.g., nitrate reductase and ATP-sulfurylase) added to the protective effects of JAs, which increase AOX activity and decrease peroxidation promoted by ROS. Compiled articles and the physiological responses of plants grown with Cd and treated with and without JAs are shown in Table 3.

7.2 JAs PROMOTE THE TOLERANCE OF PLANT SPECIES GROWN IN CD-CONTAMINATED ENVIRONMENTS

The tolerance of plants grown in soil contaminated with HM can be analyzed using different indicators, such as physiological growth indices, photosynthetic rate, the enzymatic activity of AOX systems, oxidative stress markers, "omic approaches", bioaccumulation patterns, among others, as shown in Table 2. In this sense, our study aimed to assess plant tolerance based on 4 indicators, (i) Cd accumulation — discussed in 7.1 section—, (ii) lipid peroxidation, (iii) enzymatic AOX activity; (iv) non-enzymatic AOX.

Table 2. List and number of occurrences of primary methodologies used in the articles filtered based on the inclusion and exclusion criteria described in the 'Search strategy, keywords, and selection criteria′ section.

Methodologies	No. of articles	References
Antioxidant enzymes	24	Noriega et al., 2012; Piotrowska-Niczyporuk et al., 2012; Yan; Chen; Li, 2013; Singh; Shah, 2014; Singh; Shah, 2014; Chen; Yan; Li, 2014; Yan et al., 2015; Yan et al., 2015; Per et al., 2016; Ahmad et al., 2017; Ali et al., 2018; Zaid; Mohammad, 2018; Moori; Ahmadi-Lahijani, 2020; Pilaisangsuree et al., 2020; Ahmad et al., 2021; KAYA et al., 2021; Li et al., 2022; Kanu et al., 2022; Ibrahim; Ali; Eissa, 2022; Manzoor et al., 2022; Wei et al., 2022; Abbas et al., 2022; Kaushik et al., 2022, Zhang et al., 2023
Peroxidation	22	Noriega, et al. 2012; Piotrowska-Niczyporuk, Alicja et al. 2012; Yan; Chen; Li, 2013; Singh; Shah, 2014; Chen; Yan; Li, 2014; Yan et al., 2015; Yan et al., 2015; Per et al., 2016; Ahmad et al., 2017; Ali et al., 2018; Ronzan et al., 2019; Moori; Ahmadi-Lahijani, 2020; Wei et al., 2021; Ahmad et al., 2021; Kaya et al., 2021; Li et al., 2022; Kanu et al., 2022; Ibrahim; Ali; Eissa, 2022; Manzoor et al., 2022; Wei et al., 2022; Kaushik et al., 2022, Zhang et al., 2023
Cd quantification	20	Piotrowska-Niczyporuk et al., 2012; Singh; Shah, 2014; Chen; Yan; Li, 2014; Yan et al., 2015; Yan et al., 2015; Per et al., 2016; Ahmad et al., 2017; Ali et al., 2018; Zaid; Mohammad, 2018; Ronzan et al., 2019; Wei et al., 2021; Ahmad et al., 2021; Kaya et al., 2021; Li et al., 2022; Kanu et al., 2022; Ibrahim; Ali; Eissa, 2022; Manzoor et al., 2022; Wei et al., 2022; Chen et al., 2022, Zhang et al., 2023.
Non-enzymatic antioxidants	17	Noriega et al., 2012; Piotrowska-Niczyporuk et al., 2012; Yan; Chen; Li, 2013; Singh; Shah, 2014; Chen; Yan; Li, 2014; Yan et al., 2015; Per et al., 2016; Ahmad et al., 2017; Moori; Ahmadi-Lahijani, 2020; Pilaisangsuree et al., 2020; Ahmad et al., 2021; Kaya et al., 2021; Li et al., 2022; Kanu et al., 2022; Ibrahim; Ali; Eissa, 2022; Abbas et al., 2022; Kaushik et al., 2022;
Photosynthetic pigments analysis	17	Yan; Chen; Li, 2013; Singh; Shah, 2014; Chen; Yan; Li, 2014; Yan et al., 2015; Per et al., 2016; Ahmad et al., 2017; Ali et al., 2018; Zaid; Mohammad, 2018; Wei et al., 2021; Ahmad et al., 2021; Kaya et al., 2021; Kanu et al., 2022; Manzoor et al., 2022; Wei et al., 2022; Abbas et al., 2022; Chen et al., 2022; Zhang et al., 2023
Growth analysis	15	Noriega et al., 2012; Singh; Shah, 2014; Per et al., 2016; Ahmad et al., 2017; Zaid; Mohammad, 2018; Ronzan et al., 2019; Wei et al., 2021; Ahmad et al., 2021; Kanu et al., 2022; Ibrahim; Ali; Eissa, 2022; Manzoor et al., 2022; Wei et al., 2022; Abbas et al., 2022; Kaushik et al., 2022; Feng et al., 2023
Gene and protein analyses	9	Noriega et al., 2012; Piotrowska-Niczyporuk et al., 2012; Singh; Shah, 2014; Chen; Yan; Li, 2014; Ronzan et al., 2019; Pilaisangsuree et al., 2020; Wei et al., 2021; Kaya et al., 2021; Feng et al., 2023

Hormone analysis	7	Yan; Chen; Li, 2013; Singh; Shah, 2014; Chen; Yan; Li, 2014; Yan et al., 2015; Yan et al., 2015; Ronzan et al., 2019; Wei et al., 2022
Histological analyses	5	Noriega et al., 2012; Ali et al., 2018; Zaid; Mohammad, 2018; Moori; Ahmadi-Lahijani, 2020; Li et al., 2022
Cd distribution	2	Wei et al., 2021, Li et al., 2022

7.2.1 Lipid peroxidation

Exposure to Cd causes the degeneration of plant cells through the production of ROS, which oxidizes the cell wall and increases the concentration of MDA. MDA is a compound commonly used as a stress indicator in plants, formed during lipid peroxidation resulting from the breakdown of polyunsaturated fatty acids in cell membranes (Keramat et al., 2010). The protective effect stimulated by endogenous JAs also extends to lipid peroxidation because more energy is directed towards synthesing of compounds that combat oxidative stress (Ronzan et al., 2019).

Different authors have also linked the exogenous application of JAs to a reduction in lipid peroxidation. Yan et al. (2015b) found that appliyng of JA to *A. marina* grown in soil contaminated with Cd reduced the concentration of MDA to non-toxic levels when compared to the control. In *S. lycopersicum* plants grown in a Cd-contaminated environment, foliar application of MeJa at a concentration of 2.5 µmol.L^{-1} resulted in a decrease in MDA of 11.83% in the leaves and 69.94% in the roots when compared to the control without MeJa (Wei (Wei et al., 2021). Similar results were reported in a study published by Wei et al. (2022), in which individuals of *S. lycopersicum* grown up in a Cd-contaminated environment and under MeJa application at concentrations of 0.25 µM and 2.50 µM, obtained a decrease in MDA in leaves and roots of 34.29% and 34.80%, respectively, and 40.87% and 28.82%, compared to the control without the presence of MeJa. Similarly, the application of JAs is related to a decrease in MDA in plants of *K. obovata* (Chen et al., 2014), *O. sativa* (Kanu et al., 2022; Li et al., 2022; Singh and Shah, 2014b), *T. vulgaris* (Moori and Ahmadi-Lahijani, 2020), *C. arietinum* (Ahmad (Ahmad et al., 2021), *V. faba* (Ahmad et al., 2017), *P. sativum* (Manzoor et al., 2022), *C. annuum* (Zhang et al., 2023), *T. aestivum L.* (Kaya et al., 2021), *C. frutescens* (Yan et al., 2013), *B. napus* (Ali et al., 2018) and *C. cajan* (Kaushik et al., 2022). It should be noted that the studies mentioned above consistently conclude that JAs have a protective effect by promoting the synthesis of AOX compounds. These compounds detoxify cellular ROS and minimize oxidative processes triggered by Cd.

However, these results differ from those found by Ibrahim et al. (2022) in the species *A. lentiformis*, whose MDA did not differ between the treatments with and without JA, which highlights the divergence as to the effectiveness or otherwise of JAs in modulating tolerance to the stress caused by Cd. Similarly, *Solanum nigrum* L. species grown in an environment contaminated with Cd did not differ in MDA content between treatments with low concentrations and in the absence of MeJa. On the other hand, high doses (1 mM) increased the concentration of MDA under Cd stress (Yan et al., 2015a). JA application also increased MDA production in *Chlorella vulgaris* L. plants under Cd stress (Piotrowska-Niczyporuk et al., 2012). The increase in MDA content in the first case was related to the dosage, which stimulated degenerative processes related to plant senescence. In contrast, in the second case, the increase is justified by how the algae were cultivated, since the application of JA may have acidified the culture medium, thus increasing Cd bioavailability and absorption.

Thus, there is also no consensus regarding lipid peroxidation under the effect of JAs application in plants grown in a Cd-contaminated environment. To complement what has been elucidated so far, Noriega et al. (2012), Per et al. (2016), and Zaid and Mohammad (2018) also address lipid peroxidation. However, in the light of other methodologies that use, for example, quantification of thiobarbituric acid (TBARS) and hydrogen peroxide (H_2O_2), these methodologies will not be addressed in our current data collection, given the scarcity of publications for a satisfactory discussion.

7.2.2 Antioxidant enzymes

AOX enzymes play a crucial role in the detoxification of plants in stressful situations. AOX systems neutralize reactive oxygen species (ROS) by transforming them into less toxic or non-toxic compounds (Stephenie et al., 2020). The biochemical responses to the application of JAs in plants grown in a Cd-contaminated environment can be very diverse. In general, the use of this phytoregulator is related to an increase in the activity of the AOX enzymes. There are indications that, depending on the dose used, the application of MeJa to *O. sativa* grown in a Cd-contaminated environment (hydroponically and sand culture) increases SOD activity (Li et al., 2022; Singh and Shah, 2014a; Singh and Shah, 2014b). This result may also explain the decrease in MDA content in this species. Similar results were found for other species, such as *G. max* (Noriega et al., 2012), *V. faba* (Ahmad et al., 2017), *P. sativum* (Manzoor et al., 2022), *S. nigrum* (Yan et al., 2015b), *B. juncea* (Per et al., 2016), *M. arvensis* (Zaid and Mohammad, 2018), *C. annuum* (Zhang et al., 2023), *T. aestivum* (Kaya et al., 2021), *C. frutescens* (Yan et al., 2013), *P. sativum* (Abbas et al., 2022) and *C. cajan* (Kaushik et al., 2022). However, SOD activity did not vary between treatments with Cd or Cd single applications combined with MeJa or JA in plants of *T. vulgaris* (Moori (Moori and Ahmadi-Lahijani, 2020), *Cicer arietinum* L. (Ahmad (Ahmad et al., 2021) and *S. lycopersicum* (Wei (Wei et al., 2021). The *B. napus* species cultivated with Cd was the only one that indicated a decrease in SOD activity when treated with JAs (Ali et al., 2018). However, it is worth pointing out that the above results do not show a consensus on the dose-responses of JAs (as shown in Table 3). Furthermore, each of the articles in question used different plant organs and a considerable number of treatments. In this way, the indication of an increase or decrease in enzymatic activity result from of an average of extrapolated data. Thus, although the data tends to indicate that the application of JAs increases the tolerance of plants to contaminated environments, it should be borne in mind that, depending on the dosage, the results may not differ or may even decrease tolerance.

Variations in enzyme activity can also be observed in the CAT, POD, and APX enzymes, especially in treatments that evaluate PGR in different concentrations. These enzymes act in the 'secondary line' of plant defense, detoxifying H_2O_2 (the product of dismutation promoted by SOD). The species *A. marina* grown in an environment contaminated with Cd and Cu, and under application of JA at concentrations of 1 µM and 10 µM, increased APX activity (Yan et al., 2015a). In the *K. obovata* species grown in a Cd environment, the application of MeJA at a dose of 0.1 µM increased the activity of CAT and APX and decreased that of POD. In addition, 1.0 $\mu mol.L^{-1}$ JAs increased the activity of APX and CAT and did not alter the activity of POD and, finally, a dose of 10.0 $\mu mol.L^{-1}$ decreased the activity of CAT and increased the enzymatic activities of APX and POD (Chen et al., 2014). Compared to treatment with Cd, the application of JA (5 µM and 0.2 µM) and MeJa (20 mM) in *O. sativa* grown in a Cd environment (hydroponics, soil, and sand culture) increased the activity of APX, CAT, and POD (Kanu et al., 2022; Li et al., 2022; Singh and Shah, 2014a; Singh and Shah, 2014b). The literature also reports increased CAT and APX activity in *V. faba* (Ahmad et al., 2017) and *T. aestivum* plants (Kaya et al., 2021); CAT and POD in *P. sativum* (Abbas et al., 2022; Manzoor et al., 2022), *S. nigrum* (Yan et al., 2015b), *C. annuum* (Zhang et al., 2023) and *C. cajan* (Kaushik et al., 2022); and APX in *B. juncea* (Per et al., 2016). The increase in the activity of these enzymes indicates an increase in H_2O_2 scavenging reactions, thereby contributing to better ROS management inside the cells.

However, not all species show an increase in enzyme activity. For example, plants of *G. max* and *M. arvensis* grown in a Cd environment, applying of JA increased CAT activity, but did not induce any variations in APX activity (Noriega et al., 2012; Zaid and Mohammad, 2018). The opposite occurred in *C. arietinum* plants, where there was an increase in APX activity, while CAT remained stable between treatments (Ahmad et al., 2021). In *S. lycopersicum* plants grown in the presence of Cd, POD activity increased with the application of 2.5μM MeJa and decreased with doses of 0.25 and 5.0μM (Wei et al., 2021). Similarly, different Cd doses can also cause changes in the enzymatic activity of plants in the presence and absence of JAs (Ali et al., 2018). For the species *T. vulgaris, A. lentiformis, C. frutescens* and *C. vulgaris* grown in Cd-contaminated soil and under JAs application, there is no difference in the enzymatic activity of CAT and/or POD and/or APX (Ibrahim (Ibrahim et al., 2022; Moori and Ahmadi-Lahijani, 2020; Piotrowska-Niczyporuk et al., 2012; Yan et al., 2013). The non-significant differences and the decrease in the enzymatic activity of SOD, CAT, POD, or APX can be understood by the genetic variability between the plant individuals evaluated, which possibly attributes different biochemical responses to the application of JAs. In addition, a decrease in Cd absorption promoted by JAs may suppress the demand for the antioxidative apparatus (Ali et al., 2018). In general, scientific advances have been documented regarding the action of enzymatic AOX in the scavenging of free radicals triggered by the presence of heavy metals, but it is also necessary to understand the role of specialized metabolites in the detoxification of Cd with or without the addition of JA.

7.2.3 Non-enzymatic antioxidants

There is also no consensus in the literature on the effect of JAs on non-enzymatic AOX compounds in plants exposed to Cd. AsA, GSH, phenolic compounds, alkaloids, proline, glycine, and betaine are compounds that, like enzymatic AOX, donate electrons to free radicals and promote detoxification and, consequently, increased plant tolerance (Al Mahmud et al., 2018). In our review, we identified 17 publications that use non-enzymatic AOX as an indicator to discuss plant tolerance. Among these, GSH stands out among the parameters categorized as non-enzymatic, as it was the subject of investigation in 11 of these publications. GSH is a metabolite with various plants functions, such as translating signals, activating proteins, and promoting plant tolerance through different mechanisms. Phytochelatins, principal peptide involved in the complexation of HMs and responsible for reducing the induction of oxidative stress in plants, are derived from GSH (Yannarelli et al., 2007). In addition, GSH contributes directly to the detoxification of ROS by donating electron pairs to H_2O_2, $OH^{\cdot}$ and $OH_2^{\cdot}$ radicals, forming H_2O and O_2 (Gill and Tuteja, 2010). The application of JAs and the exposure of plants to HMs is usually associated with an increase in the transcription of genes related to the synthesis of different GSH isoforms, such as GSH synthase and glutathione reductase (GSSG), to promote detoxification processes and consequently tolerance (Chen et al., 2021).

However, in *O. sativa* plants exposed to Cd followed by the application of MeJa, the ratio between GSH and GSSG - GSH/GSSG - may increase, decrease, or not vary, so this response will depend directly on the cultivar, which indicates the influence of genotypic variation on GSH isoforms (Kanu et al., 2022; Singh and Shah, 2014a; Singh and Shah, 2014b). Applying of 10 μM of MeJa to *T. aestivum* grown in a Cd-contaminated environment increased the GSH/GSSG ratio (Kaya et al., 2021). On the other hand, the application of JAs to plants of *O. sativa, G. max, S. nigrum*, *B. juncea* and *C. frutescens*, grown in a Cd-contaminated environment, can or not increase GSH content, depending on the concentration of the phytoregulator (Li et al., 2022; Noriega et al., 2012; Per et al., 2016; Yan et al., 2013; Yan et al., 2015b). In contrast, the species *C. arietinum* and *C. vulgaris* showed no differences between the treatments of Cd and Cd combined with JAs for the evaluations of GSH, GSSG, and GSH/GSSG (*C. arietinum*), and total GSH content (*C. vulgaris*) (Ahmad et al., 2021; Piotrowska-Niczyporuk et al., 2012). On the one hand, the increase in the AOX activity of GSH may have been stimulated by JAs, given its role in signaling plant defense mechanisms. On the other hand, these same defense mechanisms may decrease the absorption and accumulation of Cd and reduce the stimulation of the synthesis of AOX compounds such as GSH.

GSH content will vary depending on the concentrations of Cd that the plant is exposed to. As reported by Kaushik et al (2022), the application of MeJa increased the GSH content in *C. cajan* when grown in an environment with 1mM Cd. However, it decreased when grown with 5mM Cd, so the authors indicate an interaction between the biochemical responses promoted by the application of JAs in plants grown with different doses of Cd. Thus, we speculate that there is no consensus in the scientific literature on the effects of JAs on the GLT content of plants grown in a Cd-contaminated environment, as presented in Table 3.

Table 3. Effect of jasmonate (JAs) application on plants grown in a cadmium (Cd) environment (compared to plants grown in the presence of Cd but without JAs application) on Cd accumulation, lipid peroxidation, antioxidant enzymes (superoxide dismutase, SOD, catalase, CAT, peroxidase, POD, and ascorbate peroxidase, APX) and non-enzymatic antioxidants. The second column indicates whether there was an increase, decrease or non-significance in the accumulation of Cd, lipid peroxidation, enzymatic antioxidant activity, or the content of non-enzymatic antioxidant compounds.

Analyse	Effect	Specie	Reference
Cd acumulation	Higher	*Kandelia obovata* Sheue, Liu & Yong	Chen; Yan; Li, 2014
	Not significant	*Kandelia obovata* Sheue, Liu & Yong*;* *Capsicum annuum L.;Atriplex lentiformis (Torr.) S. Watson.*	Chen; Yan; Li, 2014; Zhang et al., 2023; Ibrahim; Ali; Eissa, 2022.
	Lower	*Oryza sativa* L.; *Avicennia marina* L.; *Solanum lycopersicum* L.; *Cicer arietinum* L.; *Vicia faba* L.; *Pisum sativum* L.; *Solanum nigrum* L.; *Brassica juncea* L.; *Mentha arvensis* L.; *Triticum aestivum* L.; *Brassica napus* L.; *Sedum alfredii* L.; *Chlorella vulgaris* L.;	Kanu et al., 2022; Li et al., 2022; Ronzan et al., 2019; I. Singh & Shah, 2014b; Yan et al., 2015ab; Wei et al., 2021; Wei et al., 2022; Ahmad et al., 2021; Ahmad et al., 2017a; Manzoor et al., 2022; Per et al., 2016; Zaid & Mohammad, 2018; Kaya et al., 2021; Ali et al., 2018; Chen et al., 2022; Piotrowska-Niczyporuk et al., 2012.
Lipid peroxidation	Higher	*Solanum nigrum* L.; *Chlorella vulgaris* L.	Yan et al., 2015b; Piotrowska-Niczyporuk et al., 2012
	Not significant	*Atriplex lentiformis* (Torr.) S. Watson; *Solanum nigrum* L.	Ibrahim; Ali; Eissa, 2022; Yan et al., 2015b
	Lower	*Avicennia marina* L.; *Solanum lycopersicum* L; *Kandelia obovata* Sheue, Liu & Yong; *Oryza sativa* L.; *Thymus vulgaris* L.; *Cicer arietinum* L.; *Vicia faba* L.; *Pisum sativum* L.; *Capsicum annuum* L.; T*riticum aestivum* L.; *Brassica napus* L.; *Cajanus cajan* L.	Yan et al., 2015a; Wei et al., 2021; Wei et al., 2022; Chen et al., 2014; Li et al., 2022; Kanu et al., 2022; I. Singh & Shah, 2014b, 2014a; Moori & Ahmadi-Lahijani, 2020; Ahmad et al., 2021; Ahmad et al., 2017a; Manzoor et al., 2022; Zhang et al., 2023; Kaya et al., 2021; Yan et al., 2013; Ali et al., 2018; Kaushik et al., 2022.

Antioxidant enzimes	Superoxide dismutase (SOD)	Higher	*Oryza sativa* L.; *Glycine max* L.; *Vicia faba* L.; *Pisum sativum* L.; *Solanum nigrum* L.; *Brassica juncea* L.; Mentha *arvensis* L.; Ca*psicum annuum* L.; T*riticum aestivum* L.; *Capsicum frutescens* L.; *Pisum sativum* L.; *Cajanus cajan* L.	Li et al., 2022; I. Singh & Shah, 2014b, 2014a; Noriega et al., 2012; Ahmad et al., 2017a; Manzoor et al., 2022;Yan et al., 2015b; Per et al., 2016; Zaid & Mohammad, 2018; Zhang et al., 2023; Kaya et al., 2021; Yan et al., 2013; Abbas et al., 2022; Kaushik et al., 2022
		Not significant	*Thymus vulgaris* L.; *Cicer arietinum* L.; *Solanum lycopersicum* L.	Moori & Ahmadi-Lahijani, 2020; Ahmad et al., 2021; Wei et al., 2022.
		Lower	*Brassica napus* L.	Ali et al., 2018.
	Catalase (CAT)	Higher	*Kandelia obovata* Sheue, Liu & Yong; *Oryza sativa* L.; *Vicia faba* L.; *Triticum aestivum* L.; *Pisum sativum* L.; *Pisum sativum* L.; *Solanum nigrum* L.; C*apsicum annuum* L.; *Cajanus cajan* L.; Glycine max L.; *Mentha arvensis* L.; *Thymus vulgaris* L.	Chen et al., 2014; Kanu et al., 2022; Li et al., 2022; I. Singh & Shah, 2014b, 2014a; Ahmad et al., 2017; Kaya et al., 2021; Abbas et al., 2022; Manzoor et al., 2022; Yan, et al., 2015b; Zhang et al., 2023; Kaushik et al., 2022; Noriega et al., 2012; Zaid & Mohammad, 2018; Moori & Ahmadi-Lahijani, 2020
		Not significant	*Cicer arietinum* L.; *Thymus vulgaris* L.; *Chlorel*la vulgaris L.; *Avicennia marina* L.	Ahmad et al., 2021; Moori & Ahmadi-Lahijani, 2020; Piotrowska-Niczyporuk et al., 2012; Yan et al., 2013
		Lower	*Kandelia obovata* Sheue, Liu & Yong; *Capsicum frutescens* L.	Chen et al., 2014; Yan et al., 2013
	Peroxidase (POD)	Higher	*Kandelia obovata* Sheue, Liu & Yong; *Oryza sativa* L.; *Vicia faba* L.; *Triticum aestivum* L.; *Pisum sativum* L.; *Solanum nigrum* L.; C*apsicum annuum* L.; *Cajanus*	Chen et al., 2014; Kanu et al., 2022; Li et al., 2022; I. Singh & Shah, 2014b, 2014a; Ahmad et al., 2017; Kaya et al., 2021; Abbas et al., 2022; Manzoor et al., 2022; Yan, et al., 2015b;

			cajan L.; *Solanum lycopersicum* L.	Zhang et al., 2023; Kaushik et al., 2022; Wei et al., 2022
		Not significant	*Kandelia obovata* Sheue, Liu & Yong.	Chen et al., 2014
		Lower	*Kandelia obovata* Sheue, Liu & Yong; *Solanum lycopersicum* L.	Chen et al., 2014; Wei et al., 2022
	Ascorbate Peroxidase (APX)	Higher	*Solanum nigrum* L.; *Kandelia obovata* Sheue, Liu & Yong; *Oryza sativa* L.; *Vicia faba* L.; Triticum aestivum L.; *Brassica juncea* L.; *Cicer arietinum* L.	Yan, et al., 2015b; Chen et al., 2014; Kanu et al., 2022; Li et al., 2022; I. Singh & Shah, 2014b, 2014a; Ahmad et al., 2017b; Kaya et al., 2021; Per et al., 2016; Ahmad et al., 2021
		Not significant	*Glycine max* L.; *Mentha arvensis* L.; *Atriplex lentiformis* (Torr.) S. Watson; *Chlorella vulgaris* L.; *Capsicum frutescens* L.	Noriega et al., 2012; Zaid & Mohammad, 2018; Ibrahim et al., 2022; Piotrowska-Niczyporuk et al., 2012; Yan et al., 2013
		Lower		
Non-enzymatic antioxidants		Higher	*Oryza sativa* L.; *Triticum aestivum* L.; *Glycine max* L.; *Brassica juncea* L.; *Capsicum frutescens* L.; *Solanum nigrum* L.; *Cajanus cajan* L.	Kanu et al., 2022; Singh & Shah, 2014a; Kaya et al., 2021; Li et al., 2022; Noriega et al., 2012; Per et al., 2016; Yan et al., 2013; Yan et al., 2015b; Kaushik et al., 2022
		Not significant	*Oryza sativa* L.; *Glycine max* L.; *Brassica juncea* L.; *Capsicum frutescen*s L.; *Solanum nigrum* L.; *Cicer arietinum* L.; *Chlorella vulgaris* L.	Singh & Shah, 2014a; Li et al., 2022; Noriega et al., 2012; Per et al., 2016; Yan et al., 2013; Yan et al., 2015b; Ahmad et al., 2021; Piotrowska-Niczyporuk et al., 2012
		Lower	*Oryza sativa* L.; *Cajanus cajan* L.	Kanu et al., 2022; Kaushik et al., 2022

8. CONCLUSION AND FUTURE PROSPECTS

Cd is an HM that provokes several health problems for plant and animal organisms. In this sense, the techniques that improve phytoremediation are vital to increasing its utilization. Studies of phytoremediation and plant tolerance can provide insights into recovering contaminated areas. In our review, we put into perspective the physiological and biochemical responses of JAs utilization in plants grown in Cd-contaminated environments.

We observed that for most of the plant species studied, the application of JAs activates defense signaling pathways and thus reduces the accumulation of Cd. In addition, there is strong evidence that this protective action promoted by JAs also induces the synthesis of AOX compounds such as SOD, POD, CAT, and APX, which act in plant detoxification and promote increased tolerance to Cd-contaminated environments. The increase in detoxification and tolerance promoted by AOX compounds is also corroborated by the decrease in MDA content, which indicates a lower level of cellular oxidation.

Thus, for our 'RQ1', we accept the null hypothesis applying of JAs to plants grown in a Cd-contaminated environment does not improve phytoremediation potential. On the other hand, for 'RQ2', we accept our alternative hypothesis that applying of JAs to plants grown in a Cd-contaminated environment increases tolerance to this HM.

The signaling pathways activated by JAs are still unclear. This result indicates the need for scientific complementation that collects and analyzes information in the light of "omics" analyses (transcriptomics, proteomics, and metabolomics). These methodological approaches will contribute to understanding and comprehensive potential signaling pathways of the defense system activated by phytohormones and their role in promoting phytoremediation and plant tolerance in contaminated environments. In addition, new studies that will test the application of JAs combined with other PGRs may help to understand the hormonal crosstalk involved in signaling and activating the pathways responsible for increasing or decreasing Cd tolerance and phytoremediation.

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