



ORIGINAL ARTICLE



Role of cytochrome P450 in herbicides tolerance of common bean (*Phaseolus vulgaris* L.)

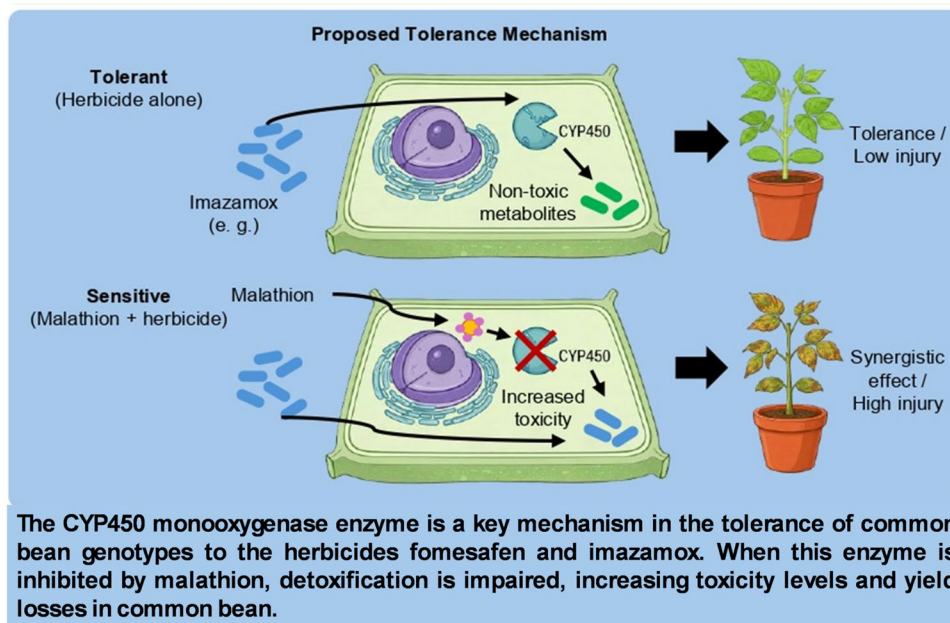
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Abstract

This study aimed to investigate the participation of cytochrome P450 in the tolerance of common bean genotypes to the herbicides fomesafen and imazamox. A completely randomized design was adopted in a 4 × 2 factorial scheme (herbicide × genotype), with three replications. The herbicide factor consisted of four levels: herbicide, malathion, herbicide + malathion, and control (no application). The following variables were evaluated: phytotoxicity (PY), plant height (PH), stem diameter (SD), number of leaves (NL), number of pods per plant (NPP), and number of grains per plant (NGP). In the first experiment, only NPP and NGP were not affected, showing no significant differences between treatments and control. In the second experiment, significant differences were observed between treatments applied to the bean genotypes. The study highlights the involvement of cytochrome P450 monooxygenase enzymes (CYP450) in the detoxification of fomesafen and imazamox. However, the application of malathion in combination with imazamox increased the sensitivity of the plants to the herbicide, acting as a key pathway in the degradation of the ALS enzyme. This led to increased plant injury and consequently reduced NPP and NGP. The study concludes that, CYP450 activity is directly in the the metabolism of the herbicides applied to the evaluated bean genotypes.

Graphical abstract



Keywords Metabolism · Selectivity · Detoxification · Tolerance · Malathion

Introduction

Common bean (*Phaseolus vulgaris* L.) is an essential legume in countries such as India, Myanmar, Latin America, and Africa, due to its high nutritional value, characterized by a high concentration of proteins, dietary fiber, minerals, and antioxidant properties (Ubersax et al., 2023). Thus, it plays a fundamental role in food security and is widely cultivated and consumed in these regions (Cortés et al., 2025). Although genetic advances in breeding programs have contributed to the improvement of the crop, common bean productivity still falls short of its maximum potential. One of the main factors limiting its production is weed interference, which poses a major challenge to sustainable agriculture and can reduce crop yield by up to 84%, as reported by (Aguiar et al., 2020). In this context, the use of herbicides has proven to be an effective strategy for controlling these competing plants, minimizing their negative impact and preventing significant yield losses, due to their broad spectrum of action, practicality, and efficiency (Dai et al., 2022).

Therefore, the plants can exhibit herbicide tolerance through different mechanisms, which are classified as target-site resistance (TSR) and non-target-site resistance (NTSR). Target-site tolerance occurs when mutations in genes that encode specific proteins modify the interaction between the herbicide and its target protein or increase the expression or copy number of these genes (Gaines et al., 2020; Pisoni et al., 2022). Non-target-site tolerance, on the other hand, involves changes in physiological processes such as absorption, translocation, sequestration, and metabolism of the herbicide, making it less harmful to the plant (Seballos et al., 2022).

However, this reinforces the idea that the main mechanism of herbicide tolerance in cultivated plants is based on metabolism (molecule degradation), which is the ability to rapidly and/or conjugatively degrade the herbicide, as well as to transform these compounds into less toxic or non-toxic components. Therefore, the plant degrades the herbicide before it causes irreversible damage (Borgato & Gonçalves Netto, 2016). This metabolic process is mediated by cytochrome monooxygenases (CYP450s), which are among the largest enzyme families responsible for plant tolerance to herbicides (Yu & Powles, 2014). These enzymes are located in the endoplasmic reticulum and are involved in the synthesis of fatty acid-derived hormones and plant secondary metabolism (Powles & Yu, 2010). They can be inhibited by organophosphate insecticides, which are used as an indirect tool to elucidate the mechanism of plant tolerance to herbicides (Matzrafi et al., 2014).

Malathion has been used for this purpose and is known for its ability to inhibit cytochrome P450 enzymes, which play a crucial role in the metabolism of various compounds,

including herbicides. Inhibition of these enzymes can affect plant tolerance to herbicides, altering their efficacy and selectivity (Carvalho et al., 2021). However, the mechanism of tolerance in common bean genotypes specifically to fomesafen and imazamox has not yet been elucidated, and there is a scarcity of research focused on this context. Based on this premise, this study aimed to elucidate the role of metabolic processes in the tolerance of common bean genotypes to these herbicides.

Materials and methods

Experimental planning and design

To investigate the role of metabolism in the tolerance of common bean genotypes to herbicides, two experiments were conducted in the greenhouse of the Institute of Breeding and Molecular Genetics (IMEGEM) at the Center for Agricultural and Veterinary Sciences of the State University of Santa Catarina (CAV/UDESC), located in Lages, Santa Catarina, Brazil. In the first experiment, a completely randomized design was employed in a 4×2 factorial arrangement (herbicides $\times$ genotypes) with three replications. The herbicide factor consisted of four levels: fomesafen (250 g a.i. ha^{-1}), malathion (1000 g a.i. ha^{-1}), fomesafen + malathion (250 + 1000 g a.i. ha^{-1}), and a control (no application). In the second experiment, the same experimental design as the first was followed, with the herbicide factor comprising four levels: imazamox (42 g a.i. ha^{-1}), malathion (1000 g a.i. ha^{-1}), imazamox + malathion (42 + 1000 g a.i. ha^{-1}), and a control (no application). The genotype factor consisted of two levels corresponding to the common bean genotypes IPR Campos Gerais (commercial cultivar) and BAF36 (accession). These genotypes were selected for their contrasting responses to herbicide effects observed in a previous field study (Joaquim Jr. et al., 2025). The CYP450 inhibitor (malathion) was applied three hours prior to herbicide application (Pagnoncelli Jr. et al., 2016). The doses of all products used are those recommended by the manufacturer.

Crop management

Sowing was performed manually in a substrate, using 5 dm^3 pots, with three seeds sown per pot at a depth of approximately 3 cm. Eight days after seedling emergence, thinning was conducted to maintain one plant per pot. Fertilization at sowing and as top dressing was based on soil analysis interpretation, following the guidelines of the Soil Chemistry and Fertility Commission, targeting a grain yield of 4000 kg ha^{-1} (CQFS-RS/SC 2016). Nitrogen top-dressing

fertilization was split and applied at the vegetative stages of the first (V3) and third (V4) fully expanded trifoliate leaf.

Herbicide application

The herbicides were applied at the stage when two to four trifoliate leaves were fully expanded, using the doses recommended for the crop according to the manufacturer. Applications were performed with a CO₂-pressurized backpack sprayer maintained at a constant pressure of 210 kPa, equipped with a boom containing four AIXR 110 015 spray nozzles spaced 50 cm apart, calibrated to deliver a spray volume of 150 L ha⁻¹. At the time of application, the temperature was 24 °C, relative humidity was 64%, and wind speed was 4.8 km h⁻¹, respectively.

Growth and phytotoxicity evaluation

Phytotoxicity (PY) was evaluated using a percentage scale from 0 to 100%, where zero indicated the absence of symptoms and 100% represented total plant death. Plant height (PH) was measured from the soil surface to the insertion of the apical bud using a measuring tape. Stem diameter (SD) was measured 3 cm above the base using a digital caliper (“INSIZE”). The number of leaves (NL) was determined by counting all fully expanded compound leaves. These variables were assessed at 7, 14, and 28 days after herbicide application (DAA), according to (Joaquim Jr. et al., 2025). At harvest, the number of pods per plant (NPP) was recorded by counting all pods from each plant, and number of grain per plant (NGP) was determined by counting the total number of grains produced by each plant.

Statistical analysis

The data were subjected to analysis of variance (ANOVA) using the F-test at a 5% significance level (error), based on the model: $y_{ijk} = u + G_i + H_j + G_i * H_j + \epsilon_{ijk}$, where: y_{ijk} : is the observed value of the response variables (PY, EP,

DC, NF, NVP e NGP); u : is the overall mean; G_i : is the effect of genotype; H_j : is the effect of herbicide; $G_i * H_j$: is the interaction effect between genotype and herbicide; ϵ_{ijk} : is the experimental error. When significant, the interaction effect between factors (herbicides x genotypes) was further explored. Subsequently, the data were subjected to orthogonal contrasts to compare structured treatment groups using the Student’s t-test. Comparisons were made between the following groups: Control vs All treatments; Herbicides vs Malathion; Herbicides and Malathion (applied separately) vs Herbicides+Malathion (mixture). Statistical analysis was performed using the “Statistical Analysis System – SAS Studio” academic version (SAS University Edition: <https://welcome.oda.sas.com/>) through the GLM procedure.

Results

Effect of cytochrome CYP450 on the metabolism of fomesafen

Table S1 presents the analysis of variance for various response variables related to plants subjected to fomesafen and different genotypes, including their interactions (G x H). The variables analyzed include phytotoxicity (%), plant height (cm), stem diameter (mm), and number of leaves, evaluated at different time points after treatment application (7, 14, and 28 days after application – DAA). The herbicide factor showed a significant effect ($p < 0.05$) at 7, 14, and 28 DAA, indicating that the different herbicide treatments impacted plant phytotoxicity at the evaluated times. The genotype factor (Gen) and the G x H interaction were not significant for this variable, suggesting that the phytotoxicity response did not vary between genotypes nor was there relevant interaction between these factors. Regarding plant height, a significant effect ($p < 0.05$) was observed for the herbicide factor at 7 and 28 DAA, indicating that herbicide treatments affected plant growth. The genotype factor was significant only at 7 DAA, showing that genotypic differences influenced plant height at early stages. The G x H interaction was not significant in any evaluation, indicating that herbicide effects were consistent across genotypes. For stem diameter and number of leaves, no significant effects were observed for any factor or interaction, indicating no influence of treatments on these variables (Table S1). For number of pods per plant (NPP) and number of grains per plant (NGP), no significant effects were found for herbicides, genotypes, or their interaction, indicating that treatments did not influence production. However, the high coefficient of variation (CV=66.42%) suggests considerable experimental variability or environmental sensitivity, which may have masked potential differences (Table 1).

Table 1 Analysis of variance (ANOVA) based on mean squares (MS) for the sources of variation Herbicides and Genotypes and their respective interaction effects on the response variables number of pods per plant (NPP) and number of grains per plant (NGP) in common bean plants subjected to fomesafen application. CAV/UDESC. Lages-SC, 2025

SV	DF	Fomesafen	
		NPP	NGP
Herb	3	93.81 ^{NS}	1945.22 ^{NS}
Gen	1	12.04 ^{NS}	416.66 ^{NS}
GxH	3	29.70 ^{NS}	642.33 ^{NS}
Error	16	34.75	767.16
Mean		8.87	40.50
CV (%)		66.42	68.38

Table 2 Analysis of variance (ANOVA) for mean squares (MS) of the sources of variation herbicides and genotypes, along with their interactions, on the response variables number of pods per plant (NPP) and number of grains per plant (NGP) in common bean plants subjected to imazamox application. CAV/UDESC, Lages-SC, 2025

SV	DF	Imazamox	
		NPP	NGP
Herb	3	165.16*	3639.37*
Gen	1	0.06 ^{NS}	7.04 ^{NS}
G×H	3	7.22 ^{NS}	90.37 ^{NS}
Error	16	11.79	204.41
Mean		6.58	27.29
CV (%)		52.16	52.38

At 7 days after application (7 DAA), a significant difference ($p=0.0014$) was observed between the control and treatments, with a 16.33% increase in phytotoxicity. No difference occurred between PPO and CYP450 applied individually. However, PPO vs PPO+CYP450 showed a significant reduction in phytotoxicity (-1.81% , $p<0.0001$), indicating a protective effect of malathion. At 14 DAA, the Control vs All contrast remained significant but reduced (2.11% , $p=0.0251$), and PPO vs PPO+CYP450 was still significant (4.17% , $p=0.0001$), maintaining the reduction in phytotoxicity. At 28 DAA, this reduction remained significant (-20.58% , $p<0.0001$), while other contrasts were not significant (Table S2). For plant height at 7 and 28 DAA, no significant differences were observed between the control and treatments or between PPO and CYP450 alone. However, PPO+CYP450 significantly increased plant height (7.5 cm and 9.6 cm at 7 and 28 DAA, respectively) compared to PPO alone (Table S2).

Effect of cytochrome CYP450 on the metabolism of imazamox

In this experiment, the source of variation Herbicides showed a significant effect ($p<0.05$) for most variables, except stem diameter, indicating influence on phytotoxicity, plant height, and number of leaves. Genotypes were significant only for plant height (7 DAA), stem diameter (7 DAA), and number of leaves (14 DAA), indicating specific and time-dependent genotypic responses. The $G\times H$ interaction was not significant for any variable, showing that genotypic responses were consistent across herbicide treatments (Table S3). For number of pods per plant (NPP) and number of grains per plant (NGP), Herbicides had a significant effect ($p<0.05$), indicating influence of treatments on productivity. However, Genotypes and the $G\times H$ interaction were not significant, suggesting similar performance among genotypes and consistent responses to treatments (Table 2).

The plants of the genotype IPR Campos Gerais exhibited moderate to severe visual symptoms of phytotoxicity in



Fig. 1 Visual evaluation of phytotoxicity and plant height in two common bean genotypes (IPR Campos gerais and BAF36) following application of fomesafen (PPO inhibitor) and imazamox (ALS inhibitor), individually and combined with malathion (cytochrome P450 inhibitor). CAV/UDESC, Lages-SC, 2025

herbicide treatments combined with the CYP450 inhibitor, especially in the ALS+CYP450 treatment. In contrast, the genotype BAF36 appeared more sensitive to the herbicide treatments, showing visibly reduced growth and greater phytotoxicity in ALS, ALS+CYP450, and PPO treatments. It was also observed that the mixture of the two products caused increased phytotoxicity in the plants. Moreover, imazamox had a greater detrimental effect on the plants compared to fomesafen (Fig. 1).

For phytotoxicity at 7 and 14 days after application (DAA), the contrasts Control vs All, ALS vs CYP450, and ALS vs ALS+CYP450 were highly significant ($p<0.0001$), indicating strong effects of herbicide application and enzyme inhibition on plant injury. Negative estimates indicated increased phytotoxicity relative to the control, reinforcing the role of CYP450-mediated metabolism in detoxifying ALS-inhibiting herbicides (Table S4). At 28 DAA, Control vs All showed a significant reduction of 28.67% in phytotoxicity without herbicide ($p<0.0001$), confirming stress caused by treatments. ALS caused 11.67% more phytotoxicity than CYP450 alone ($p=0.0465$), and ALS vs ALS+CYP450 showed a 12% increase ($p=0.0419$), indicating that CYP450 inhibition enhances herbicide toxicity (Table S4).

For plant height, significant differences occurred between ALS and ALS+CYP450 at all evaluation times, indicating cumulative effects of imazamox+malathion due to inhibited metabolism, resulting in greater toxicity and reduced

growth. Other treatments also reduced growth compared to the control at 14 and 28 DAA (Table S4). The control showed a higher number of leaves than herbicide treatments at 7, 14, and 28 DAA, with increasing differences over time, indicating cumulative phytotoxicity. ALS alone caused less reduction than CYP450 inhibition alone, while ALS+CYP450 caused progressive and significant decreases, reinforcing that CYP450 inhibition impairs detoxification and increases toxicity (Table S5). For number of pods per plant (NPP) and grains per plant (NGP), only ALS vs ALS+CYP450 was significant ($p=0.0001$ and $p=0.0004$), with higher values under ALS alone (3.6 more pods and 16.5 more grains), indicating that the combination with malathion reduced yield due to increased phytotoxicity and impaired metabolism (Table 3). These results indicate that the combination of ALS with the CYP450 inhibitor (Malathion) has a more pronounced negative effect on the number of pods and grains per plant, suggesting that the plant detoxification system mediated by CYP450 plays an important role in modulating phytotoxicity and the reproductive development of common bean plants.

Discussion

The discussion highlights the importance of herbicide tolerance in common bean for sustainable management and cultivar development, emphasizing that detoxification pathways are key to herbicide selectivity and crop productivity. Understanding these metabolic mechanisms helps explain differential responses among genotypes. Overall, the genotype IPR Campos Gerais showed greater tolerance than BAF36, with mild phytotoxicity and satisfactory growth under isolated herbicide application. However, the combination with malathion reduced plant height and increased symptoms such as chlorosis and necrosis, indicating that tolerance is partly mediated by cytochrome P450 metabolism. Orthogonal contrasts enabled precise identification of metabolic effects on phytotoxicity, showing greater impact of product mixtures compared to isolated applications. The lack of significant interaction suggests that herbicide and genotype effects act independently, supporting recommendations in integrated weed management when tolerant genotypes are used. The combination of fomesafen with malathion increased phytotoxicity and reduced plant growth compared to isolated applications, confirming that metabolic inhibition intensifies intoxication symptoms and affects vegetative development. This indicates interference in physiological processes such as photosynthesis, cell elongation, and nutrient uptake, likely due to reduced detoxification. The role of CYP450 in herbicide metabolism is well documented, and its inhibition leads to accumulation of the

Table 3 Evaluation of metabolism through orthogonal contrasts comparing herbicides for number of leaves, based on the application of malathion, a CYP450 inhibitor, in common bean genotypes. CAV/ UDESC. Lages-SC, 2025

Contrasts	Estimate	Standard Error	t Value	Pr> t
Number of pods per plant (NPP)				
Control vs All	-1.00	2.29	-0.44	0.6681
ALS vs CYP450	4.33	2.80	1.55	0.1418
ALS vs ALS+CYP450	3.63	0.54	6.73	0.0001
Number of grains per plant (NGP)				
Control vs All	16.66	9.41	1.09	0.2894
ALS vs CYP450	3.50	1.92	1.69	0.1065
ALS vs ALS+CYP450	16.53	2.22	7.58	0.0004

active compound, increasing toxicity (Ma et al., 2013). For number of pods per plant (NPP) and number of grains per plant (NGP), no significant effects were observed for herbicides, genotypes, or their interaction (Table 1), indicating that reproductive development was not compromised. Despite early phytotoxicity, the results suggest recovery over time, supporting that CYP450-mediated detoxification allows compensation of damage throughout the crop cycle.

In the study with imazamox, the results showed that CYP450 plays a key role in common bean tolerance by metabolizing herbicide. The use of malathion as an inhibitor proved effective in revealing differences in metabolic tolerance among genotypes, supporting its application in studies and breeding programs aimed at selecting more tolerant plants. Contrasts involving malathion showed stronger effects, increasing phytotoxicity, reducing leaf number, and inhibiting plant growth. These results indicate that inhibition of the CYP450 enzymatic system leads to greater accumulation of toxic compounds in the plant, impairing vegetative development, as also reported by Siminszky (2006). This corroborates the findings of (Kong et al., 2018), who reported that CYP450 inhibition compromises the plant's ability to detoxify herbicides, resulting in more severe damage.

Overall, the results suggest that the combination of imazamox and malathion has a significant impact on the development of common bean plants, affecting both growth and leaf production. This combination also indicates a reduction in the plants' capacity to metabolize herbicides through the inhibition of CYP450, increasing herbicide toxicity and impairing leaf growth and overall plant development. The significant differences found in the combination of imazamox with malathion, both for number of pods per plant (NPP) and number of grains per plant (NGP) (Table 2), suggest that inhibition of cytochrome P450 significantly compromises the plant's ability to metabolize and detoxify the herbicide, thereby enhancing its toxic effects. This aligns with previous studies indicating that the CYP450 enzyme family is strongly involved in herbicide metabolism and

constitutes an important mechanism of tolerance or resistance in various species (Pandian et al., 2020; Siminszky, 2006). The presence of malathion impairs CYP450 activity, promoting accumulation of toxic metabolites or herbicide, which causes severe damage to reproductive tissues and reduces pod and grain formation, directly affecting yield. Similar findings were reported by Kong et al. (2018), showing increased phytotoxicity and impaired reproductive development under CYP450 inhibition. Individually, the products did not show significant effects on NPP and NGP, although estimates were positive, suggesting that malathion alone is insufficient to cause strong effects without interaction with herbicides metabolized via this pathway. This reinforces the importance of metabolic interactions and enzymatic specificity in plant responses (Yuan et al., 2007).

Overall, the results confirm the essential role of oxidative metabolism via CYP450 in herbicide detoxification and maintenance of productivity in common bean. This is supported by Carvalho et al. (2021), who highlighted the role of metabolic enzymes in herbicide selectivity, and by Pagnoncelli Jr. et al. (2016), who demonstrated that selectivity in common bean is physiological, based on degradation mechanisms. Detoxification mainly involves CYP450 and glutathione S-transferase (GST), responsible for oxidation and conjugation reactions, respectively (Carvalho et al., 2021). These findings align with studies using metabolic inhibitors, such as Yun et al. (2005), who observed increased phytotoxicity in soybean with malathion-herbicide mixtures, confirming the role of CYP450 in tolerance.

This study confirmed that CYP450 enzyme activity contributes to enhanced metabolism of imazamox in common bean, demonstrated through the use of malathion as an inhibitor. The results are consistent with findings from other studies (Snipes & Seifert, 2003; Matzrafi et al., 2014; Ogliari et al., 2014; Walsh et al., 2015; Pagnoncelli Jr. et al., 2016) across different crops. The study also highlights the importance of avoiding the combined application of herbicides with organophosphate insecticides such as malathion in common bean, to prevent crop damage. Additionally, further research including greater genetic diversity and complementary physiological variables (e.g., photosynthesis, grain mass, and biomass) could improve understanding of tolerance mechanisms to fomesafen. Variation in malathion doses combined with fomesafen should also be further investigated.

To strengthen the study and address potential limitations, some improvements may be considered: (i) inclusion and deeper evaluation of the malathion-only treatment to separate its intrinsic effects from herbicide interactions; (ii) increasing the number of replicates, especially for variable traits, to improve statistical power; (iii) incorporation of physiological and biochemical analyses, such as

CYP450 activity, metabolite accumulation, and stress-related enzymes, to validate the proposed mechanism; (iv) inclusion of additional evaluation times to better understand metabolic inhibition and recovery dynamics; (v) application of molecular approaches, such as gene expression analysis of CYP450 candidates, to identify tolerance-related isoforms; and (vi) validation under field conditions to account for environmental interactions and enhance the applicability of the results. In summary, although the use of malathion allowed the identification of the role of metabolism in modulating phytotoxicity and plant development, the limitations inherent to its use as an indirect inhibitor highlight the need for complementary approaches to confirm the mechanisms involved. Nevertheless, the results presented represent a relevant advance in the understanding of metabolic tolerance in common bean, particularly by integrating physiological and yield-related responses under different chemical stress conditions.

Conclusion

The study demonstrated the involvement of cytochrome P450 (CYP450) enzymes in the detoxification of fomesafen and imazamox. However, the combination of malathion with imazamox increased common bean sensitivity, leading to greater injury and reductions in the number of pods per plant and grains per plant, indicating that CYP450 plays a key role in herbicide metabolism. These results suggest that CYP450 activity is associated with herbicide degradation in the evaluated genotypes. However, the findings are not conclusive, and further studies under multiple environments, especially field conditions, are needed to ensure robustness. Additionally, the lack of physicochemical evaluations, such as ALS and PPO enzyme activity, represents a limitation that should be addressed in future research.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s40502-026-00959-3>.

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Authors' contributions Conceptualization: CZJJ, LTSC, PHC; Data curation: CZJJ, LTSC, PHC, HAS, MBS, JLT, JLMC, AMON, AFG; Formal analysis: CZJJ, LTSC, PHC; Investigation: CZJJ, LTSC, PHC, HAS, MBS, JLMC, AMON, AFG; Methodology: CZJJ, LTSC, PHC, HAS, MBS; Project administration: CZJJ, JLMC, AMON, AFG; Software: CZJJ, LTSC; Resources: CZJJ, LTSC, PHC, JLMC, AMON, AFG; Supervision: CZJJ, LTSC, PHC, HAS, MBS, JLT, JLMC, AMON, AFG; Validation: CZJJ, LTSC, PHC, HAS, MBS, JLT, JLMC,

AMON, AFG; Preview: CZJJ, LTSC, PHC, HAS, MBS, JLT, JLMC, AMON, AFG; Writing - original draft: CZJJ, LTSC; Writing - review and editing: CZJJ, LTSC, PHC, HAS, MBS, JLT, JLMC, AMON, AFG.

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Data availability The data used in this study are available from the corresponding authors upon reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

Consent for publication Not applicable.

Ethical approval and consent to participate Not applicable.

Clinical trial number Not applicable.

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