

Article

Confirmation of the Mechanisms of Resistance to ACCase-Inhibiting Herbicides in Chinese Sprangletop (*Leptochloa chinensis* (L.) Nees) from South Sulawesi, Indonesia

Denny Kurniadie *, Ryan Widiyanto, Annisa Nadiah Aprilia and Farida Damayanti

Department of Agronomy, Faculty of Agriculture, Universitas Padjadjaran, Jl. Ir. Soekarno Km 21, Jatinangor, Sumedang 45363, West Jawa, Indonesia

* Correspondence: denny.kurniadie@unpad.ac.id

Abstract: Chinese sprangletop (*Leptochloa chinensis* (L.) Nees) is recognized as the most disturbing weed in rice fields in Africa, Australia, and Asia due to causing a significant reduction in yields. The habit of most lowland rice farmers in Indonesia is using high doses of herbicides more than once without any rotation, leading to increased weed resistance potential. Therefore, this study aimed to confirm the resistance level of *L. chinensis* to acetyl-CoA carboxylase (ACCase)-inhibiting herbicides using the whole-plant pot test method. We identified other herbicides that can control the resistant biotype and performed DNA sequencing on a sample to determine mutations present in the biotype's ACCase gene through polymerase chain reaction. The herbicide dose–response experiment showed that the *L. chinensis* from Bantimurung Subdistrict, Maros Regency, South Sulawesi, exhibited resistance to ACCase inhibitors (metamifop and cyhalofop-butyl), which is the first case of resistance to ACCase herbicides reported in Indonesia. An acetolactate synthase inhibitor (bispyribac-sodium) and a 1-deoxy-d-xylulose-5-phosphate synthase (DOXP) inhibitor (clomazone) were effective at controlling the resistant biotypes of *L. chinensis*, so could considered for use in rotation or as an ingredient in mixed herbicides. Single-nucleotide substitution of guanine for thiamine at position 6081 (TGG; susceptible, TGT; Maros) that causes a Trp₂₀₂₇Cys mutation in the target gene contributes to the resistance of the Maros biotype to ACCase inhibitors.

Keywords: ACCase; herbicides resistance; *Leptochloa chinensis*; amino acid substitution

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1. Introduction

Acetyl-CoA carboxylase (ACCase) plays an important role in fatty acid metabolism and is an attractive target for herbicides. It is a biotin-dependent enzyme and acts as a catalyst for malonyl-CoA formation from the ATP-dependent carboxylation of acetyl-CoA [1]. ACCase-inhibitor herbicides are divided into three chemical families, namely aryloxyphenoxypropionates (FOPs), cyclohexanodiones (DIMs), and phenylpyrazoles (DENS). FOPs and DIMs were introduced more than 45 years ago, while DENS were launched in 2006 and consist of a single herbicide, pinoxaden [2]. The prevention of biosynthesis causes subsequent plant death, and ACCase is the target site for ACCase-inhibitor herbicides [3,4]. ACCase herbicides have advantages such as a broad spectrum, high effectiveness in controlling grass weed species, low soil toxicity, and selectivity in major crops around the world [5–7]. Therefore, they are intensively applied over large areas in different cultivated crop for weed management, but excessive application increases the potential of developing resistant weed biotypes [1,5,7].

Chinese sprangletop (*Leptochloa chinensis* (L.) Nees) is a grassweed distributed across Africa, Asia, and Australia [8]. Generally, grass weeds are difficult to control in lowland rice fields due to their strong ecological adaptability, quick germination, and quick maturation under anaerobic environments, as well as ability to produce large amounts of seeds

[9]. The competition between *L. chinensis* and rice occurs in the middle stage of vegetative growth to the grain-filling stage [10]. Rice yields can significantly drop due to the presence of this weed, with high densities causing up to 50% reduction [11].

Cases of weed resistance to herbicides have been experienced in 72 countries, which interfere with 97 different types of crop commodities, including rice [12]. The U.S. has the highest resistance level in the world, followed by Australia and Canada. Meanwhile, in Asia, the highest level is recorded in China, followed by Japan and South Korea [12]. The cases rapidly increased from 41 in 1980 to 191 in 1995, which was triggered by the rapid resistance of weeds to the ACCase and ALS herbicides [13]. Currently, 47 biotypes are resistant to ACCase inhibitors, while there are no such reports in Indonesia [12].

Metamifop and cyhalofop-butyl are postemergent ACCase herbicides that are effective in controlling rice and cereal weeds [14]. Most Indonesian lowland rice farmers typically use high doses of herbicides more than once without any rotation, thereby elevating the resistance potential. Resistant biotypes of *L. chinensis* have been reported in China. This type of report is still absent in Indonesia, but there are cases of multiple-resistance *Eleusine indica* to glyphosate, paraquat, and 2,4-D, as well as of *Limnocharis flava* to 2,4-D [12,13].

This study aimed to confirm the occurrence of weed resistance to prevent more significant problems and to set up a management strategy in the future. Preventing the spread and development of weed resistance to various herbicides can be accomplished if the mechanism of resistant weeds is immediately confirmed. Therefore, this study aimed to confirm the resistance of *L. chinensis* resistant biotype against ACCase inhibitor herbicides (metamifop and cyhalofop) and to determine if an acetolactate synthase (ALS) inhibitor (bispyribac-sodium) and a 1-deoxy-d-xylulose-5-phosphate synthase (DOXP) inhibitors (clomazone) can control ACCase-resistant weeds. The nucleotide sequences in the ACCase gene of the resistant and susceptible biotypes were determined.

2. Material and Methods

2.1. Plant Materials

Susceptible and resistant biotypes of *L. chinensis* seeds were obtained from lowland rice cultivation areas in October 2021 in the South Sulawesi Province. The susceptible biotypes were from Cempa District, Pinrang Regency, South Sulawesi Province at 3°44'10.5" S, 119°33'43.8" E. Meanwhile, the resistant biotype was from Bantimurung District, Maros Regency, South Sulawesi Province at 4°58'21.6", S 119°38'50.4" E. The samples were gathered by collecting seeds from mature weeds, which were then cleaned and dried in the sun for one week to reduce moisture and increase maturity. Seed samples were taken from ± 50 *L. chinensis* weed propagules that were randomly distributed over the land.

2.2. Herbicides Dose–Response Experiments

These experiments were carried out using the whole-plant dose–response method [15]. To ensure the germination of only *L. chinensis*, the soil was sterilized with an autoclave at 120 °C and 15 psi for 2 h. About 10–15 seeds were sown on the surface of 3 kg of sterilized topsoil contained in earthen pots and kept in muddy conditions. In the experiment, puddles were maintained at a depth of 0.5 cm from the soil surface. Herbicides were applied 14 days after planting at the 1–2 leaf stage. Herbicides were applied at seven dose levels including 0, 0.25, 0.5, 1, 2, 4, and 8 times the herbicides' recommended dosage. Furthermore, metamifop and cyhalofop-butyl were applied at doses of 0, 31.25, 62.5, 125, 250, 500, or 1000 g a.i. ha⁻¹; cyhalofop-butyl herbicide at doses 0, 31.25, 62.5, 125, 250, 500, or 1000 g a.i. ha⁻¹ both formulated in an emulsifiable concentrate 100 g a.i. L⁻¹; bispyribac-sodium herbicide at doses 0, 5, 10, 20, 40, 80, or 160 g a.i. ha⁻¹ formulated in a suspension concentrate, 400 g a.i. L⁻¹; and clomazone herbicide at doses 0, 12, 24, 48, 96, 192, or 384 g a.i. ha⁻¹ formulated in an emulsifiable concentrate, 480 g a.i. L⁻¹. Herbicide application was carried out with a spray volume of 400 L ha⁻¹ using a semi-automatic knapsack sprayer

with a flat fan nozzle at a pressure of 138 kPa. After 28 days, *L. chinensis* was harvested for mass determination.

2.3. Statistical Analyses of the Dose–Response Experiments

The percentage of growth-reduction data was obtained from the comparison between the dry weight of herbicide-treated weeds (T) and the control, using the following equation: growth reduction (%) = $[1 - (T/C)] \times 100$. The damage percentage was determined through ANOVA, while the interaction between weed populations and herbicides doses was analyzed based on a p -value < 0.05 . When an interaction occurred, Tukey's test was used to identify significant differences.

The herbicide doses required for 50% growth reduction (GR_{50}) were obtained by a nonlinear regression using the log-logistic dose–response equation $Y = c + (d - c)/[1 + (X/GR_{50})^b]$, where c and d denote lower and upper limits, respectively; and b is the response curve slope [16]. The dose–response analysis was performed with Origin Pro 9.0 software (Originlab, 2018, Northampton, MA, USA).

2.4. Isolation of DNA and Gene Sequence

Genomic DNA was isolated from the leaves of susceptible and resistant *L. chinensis* biotypes using a Quick DNA Plant/Seed Miniprep Kit (Zymo Research, D6020, Irvine, CA, USA). A primer set, 5' TGCATACAGCGTATTGACCAG3' (forward) and 5' CTCTGACCTGAACTTGATCTC3' (reverse) [17], was employed for PCR amplification of the *ACCase* gene. The amplification was performed in a total volume of 50 μ L containing 25 μ L of MyTaq HS Red Mix (Bioline, BIO-25048, London, UK), 2 μ L of each primer (0.4 μ M), up to 50 μ L of dd H₂O, and 1 μ L DNA of *L. chinensis* (50 ng). The PCR program included denaturation at 95 °C, followed by 35 cycles of 95 °C and 55 °C, and final extension at 72 °C for 3 min, 15 s, 30 s, and 45 s, separately. Afterward, the DNA was sequenced with capillary electrophoresis and the products were translated to amino acid sequences using Snap Gene 6.1.2 software (www.snapgene.com; accessed on 22 October 2022).

3. Results

3.1. Dose–Response Experiments

Based on the ANOVA results, all herbicide treatments had significant differences in dry weight and decreased growth of *L. chinensis* at the level of $p < 0.05$. The results showed that in all tested herbicides effectively controlled the susceptible biotypes at the recommended dose. However, metamifop, cyhalofop-butyl, and bispyribac-sodium at one and two times of the recommended doses were not effective in controlling *L. chinensis* from Maros, because growth was observed 28 days after their application as indicated in Figure 1. Complete growth reduction occurred when doses four times higher than the recommendation were applied, as indicated in Table 1. Clomazone effectively subdued susceptible weeds and the Maros biotype at the recommended dose with 100% growth reduction, as presented in Figure 1 and Table 1. The growth reduction of *L. chinensis* from Maros after the application of metamifop, cyhalofop-butyl, and bispyribac-sodium at the recommended doses was 76.66, 71.95, and 60.28%, respectively.

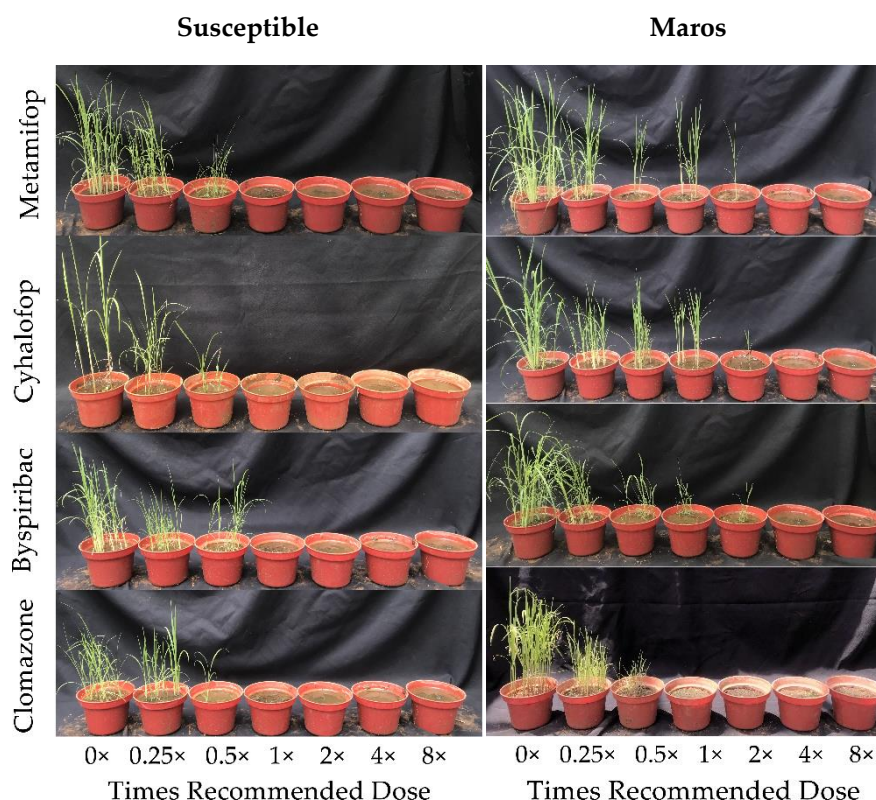


Figure 1. Effects of herbicides on susceptible and Maros biotypes of *L. chinensis*. Herbicides were applied at seven dosage levels at two weeks after sowing of *L. chinensis*: metamifop (0, 31.25, 62.5, 125, 250, 500, and 1000 g a.i. ha⁻¹), and cyhalofop-butyl (0, 31.25, 62.5, 125, 250, 500, and 1000 g a.i. ha⁻¹), bysyrribac-sodium (0, 5, 10, 20, 40, 80, and 160 g a.i. ha⁻¹), and clomazone (0, 12, 24, 48, 96, 192, and 384 g a.i. ha⁻¹).

Table 1. Effects of herbicides on the growth reduction (%) of susceptible and resistant *L. chinensis* biotypes.

Herbicide	Biotypes	Times Recommended Dose (g a.i. ha ⁻¹)						
		0	0.25	0.5	1	2	4	8
Metamifop	Susceptible	0 a,C	69.02 a,B	69.74 a,B	93.67 a,A	100 a,A	100 a,A	100 a,A
	Maros	0 a,E	39.71 a,D	67.39 a,C	76.66 b,B	89.49 b,B	100 a,A	100 a,A
Butyl-Cyhalofop	Susceptible	0 a,C	54.35 a,B	65.73 a,B	100 a,A	100 a,A	100 a,A	100 a,A
	Maros	0 a,D	19.22 b,C	46.71 b,B	61.16 b,B	90.68 a,A	100 a,A	100 a,A
Byspyribac-Sodium	Susceptible	0 a,D	56.50 a,C	70.70 a,B	100 a,A	100 a,A	100 a,A	100 a,A
	Maros	0 a,E	33.25 b,D	50.54 b,C	82.29 b,B	100 a,A	100 a,A	100 a,A
Clomazone	Susceptible	0 a,D	43.79 a,C	80.20 a,B	100 a,A	100 a,A	100 a,A	100 a,A
	Maros	0 a,C	53.26 a,B	59.39 b,B	100 a,A	100 a,A	100 a,A	100 a,A

The values in each column followed by the same lowercase letters (vertical direction) and uppercase letters (horizontal direction) are not significantly different at $p < 0.05$ according to Tukey's test for each herbicide. The susceptible biotypes were obtained from Pinrang District.

The ACCase inhibitors metamifop and cyhalofop-butyl caused the symptoms of necrosis, chlorosis, leaf curling, and cupping, while bysyrribac-sodium and clomazone induced the symptoms of chlorosis and necrosis in the plants. The four herbicides' GR₅₀ values for metamifop, cyhalofop-butyl, bysyrribac-sodium, and clomazone for the resistant and susceptible biotypes of *L. chinensis* were determined, as demonstrated in Figure 2 and Table 2. The results showed that the resistance index for Maros treated with

metamifop was 3.73, meaning about 3.73 times the recommended dose was needed to control *L. chinensis* from Maros.

The index values of Maros resistance to metamifop, cyhalofop-butyl, bispyribac-sodium, and clomazone herbicides were 3.73, 2.44, 1.86, and 0.96, respectively. Based on the index, Maros was identified as having low resistance to metamifop and cyhalofop-butyl, but was susceptible to bispyribac-sodium and clomazone as presented in Figure 2 and Table 2. The herbicides' GR₅₀ values were obtained by nonlinear regression of the log-logistic dose-response equation. The index was calculated with the ratio of resistant to susceptible biotypes of *L. chinensis*.

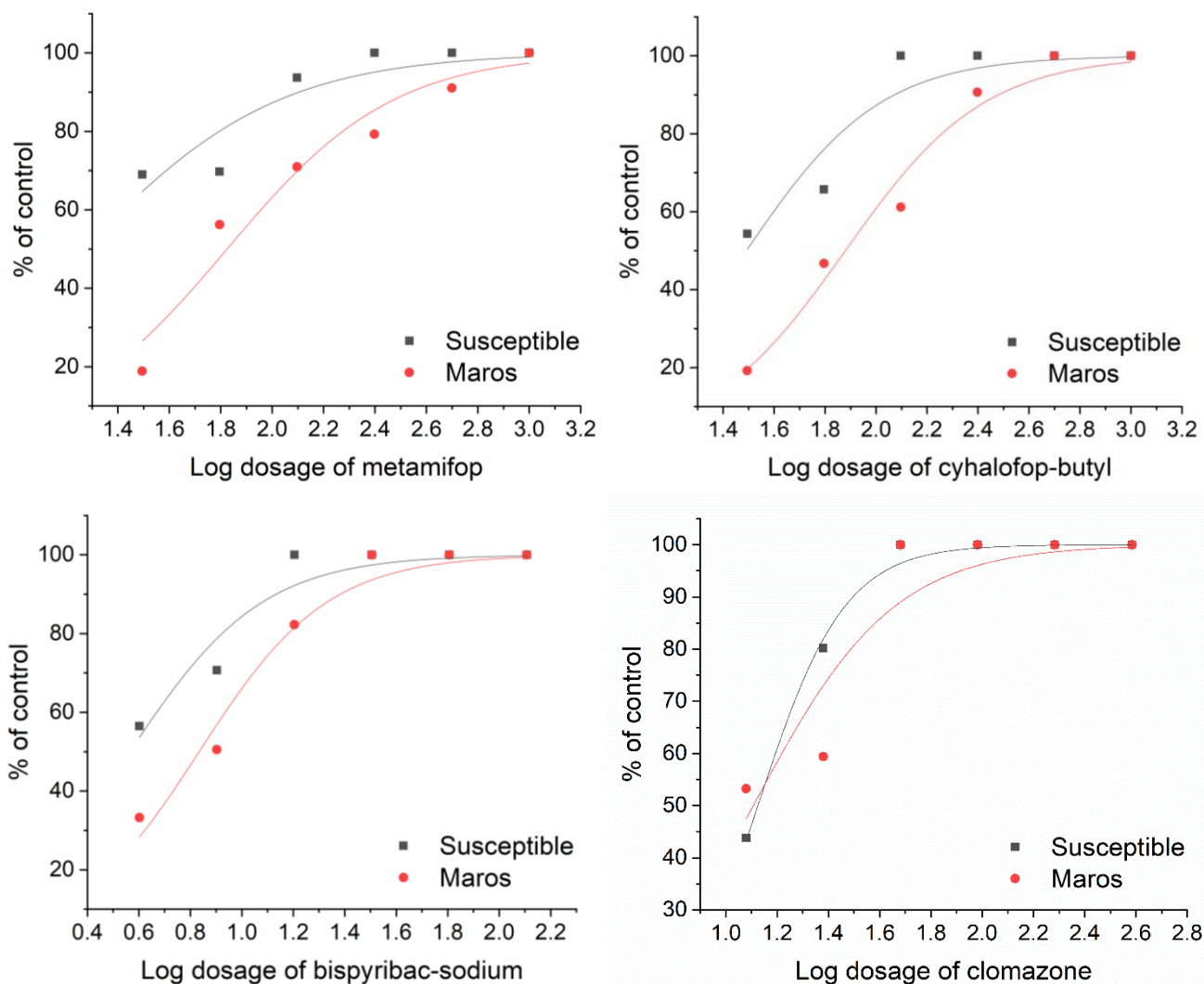


Figure 2. Growth reduction curves of susceptible and resistant biotypes of *L. chinensis* by herbicide application.

Table 2. Herbicide dose required for 50% reduction (GR₅₀) of dry biomass and resistance index.

Herbicides	<i>b</i>	<i>r</i> ²	Biotypes	GR ₅₀ (g a.i ha ⁻¹)	R/S	Resistant Category [18]
Metamifop	1.11	0.83	Susceptible	17.91 ± 6.09	1.00	-
	1.29	0.98	Maros	66.82 ± 5.54	3.73	Low
Cyhalofop-butyl	1.64	0.90	Susceptible	30.97 ± 9.65	1.00	-
	1.75	0.99	Maros	75.83 ± 26.94	2.44	Low
Bsyprbac-sodium	1.68	0.92	Susceptible	3.67 ± 0.62	1.00	-
	1.27	0.94	Maros	6.83 ± 0.73	1.86	Susceptible

Clomazone	2.57	0.83	Susceptible	13.33 ± 1.11	1.00	-
	2.36	0.86	Maros	12.79 ± 1.72	0.96	Susceptible

GR₅₀ values of herbicides were obtained by nonlinear regression using the log-logistic dose–response equation. The index was calculated as the ratio of resistant to susceptible (Pinrang) biotypes’ GR₅₀ values.

3.2. Isolation of DNA and Gene Sequencing

The base sequence of PCR-amplified DNA showed complete homology with that of the *L. chinensis* ACCase gene [16]. The gene sequence demonstrated a single nucleotide difference between the susceptible and resistant Maros biotypes at position 6081 (guanine to thymine). The *L. chinensis* from Maros exhibited a single amino acid substitution of Trp₂₀₂₇Cys (TGG; susceptible, TGT; Maros) in the ACCase gene, as presented in Figure 3. This indicated a mutation at the target site of the ACCase inhibitors.



Figure 3. Alignment of deduced amino acid sequences of ACCase gene (red: amino acid substitution in the Maros biotype that change compared to susceptible biotype).

4. Discussion

L. chinensis originating from Maros was identified with resistance to metamifop and cyhalofop-butyl. The index (R/S) level was calculated by the ratio of GR₅₀ values for resistant (R) and susceptible (S) biotypes. The results were classified as susceptible (R/S < 2), low (R/S = 2–6), moderate (R/S = 6–12), and high (R/S > 12) resistance [18]. Among the ACCase inhibitors, metamifop and cyhalofop-butyl are in the same chemical group. The majority of herbicides in the FOP chemical group are often formulated as methyl, butyl, or esters, providing lipophilicity and the potential for acceleration across cellular membranes by trapping acids [2]. The prevention of the formation process blocks fatty acid biosynthesis, which in turn culminates in the inhibition of cell division [19]. Weeds that are under stress due to herbicide application experience an initial response to this condition for survival. The repeated use of the same herbicides leads to stress and triggering of a selection process that has an impact on the evolution of weeds to become resistant. The susceptible biotypes are controlled by herbicides, while those surviving under such pressure develop to inherit their resistant properties and gain dominance [15].

L. chinensis originating from Maros was treated with ALS herbicides, namely bspyribac-sodium, and DOXP inhibitors, such as clomazone. ALS has a broad-spectrum efficiency on grass and broadleaved plants. It also inhibits the synthesis of branched-chain amino acids, e.g., valine, leucine, and isoleucine [20]. Clomazone is known for possessing a broad spectrum and the ability to stop carotenoid biosynthesis [21]. There is a need to identify the herbicide types used by farmers in the rotation process, which is one of the practices used for preventing and controlling resistant weeds. The ACCase, ALS, and

DOXP inhibitors marketed in Indonesia can control *L. chinensis*. ALS and DOXP application in single or mixed forms is expected to be the farmers' choice for controlling ACCase-inhibitor-resistant *L. chinensis* because rotating these types of herbicides tends to reduce the evolution of resistance [22]. Currently, there have been 262 cases of weeds resistance to ACCase inhibitors worldwide [12]. The population of *L. chinensis* from Zhejiang, China, was identified as being resistant to cyhalofop-butyl, with an index of 23.8 [23]. *Echinochloa crus-galli*, originating from Taehahn, South Korea, was confirmed to be resistant against metamifop, as well as ACCase and ALS inhibitors [24].

There are target site resistance (TSR) and nontarget site resistance (NTSR) mechanisms [25]. TSR is the occurrence of mutations in certain herbicides' target sites, leading to zero or lower sensitivity of the target protein during application. Meanwhile, NTSR involves reducing the herbicides' absorption/translocation and increasing their metabolism into nontoxic compounds [25]. Increased reports of weed resistance were associated with several mutations in the herbicides' target site genes in the form of amino acid substitutions caused by changes in nucleotide bases [26]. This substitution does not always occur, but changes in the nucleotide sequence can also reduce herbicides' binding to the target site enzyme [27]. The resistance of *L. chinensis* to cyhalofop-butyl is probably initiated by a particular detoxifying enzyme, which possibly has high catalytic efficiency and good substrate specificity [28,29]. This study showed that *L. chinensis* resistance to ACCase and ALS inhibitors might be related to mutations in their genes and the development of metabolic systems, which similarly occurs in other Gramineae weeds. This certainly needs to be proven through further study, but Trp⁵⁷⁴Leu substitution was reported in ALS-resistant *Echinochloa crus-galli* [30]. Additionally, *Lolium* spp. cross-resistance to ALS and ACCase is due to the metabolism of cytochrome P450 herbicides [29,31].

The sequences of the ACCase gene were compared with those of *Alopecurus myosuroides* (GenBank accession no. AJ310767). According to the alignment results, the homology between the ACCase gene fragments from *A. myosuroides* compared with Maros *L. chinensis* was 93.5% and with the susceptible biotypes was 93.9%. The ACCase gene of Maros *L. chinensis* exhibited nucleotide substitution in the susceptible sequence TGG to TGT, leading to a Trp²⁰²⁷Cys amino acid substitution. This indicated mutations in the weed's target site to prevent it from being inhibited by ACCase herbicides. Currently, several amino acid substitutions causing resistance to ACCase inhibitors have been reported, including Ile¹⁷⁸¹, Trp¹⁹⁹⁹, Trp²⁰²⁷, Ile²⁰⁴¹, Asp²⁰⁷⁸, Cys²⁰⁸⁸, and Gly²⁰⁹⁶ [29,32]. Trp²⁰²⁷Cys (TGG to TGT) is one of the mutations identified as the initiator of *L. chinensis* resistance, while others include Trp²⁰²⁷Cys (TGG to TGC), Trp²⁰²⁷Ser (TGG to TCG), and Trp²⁰²⁷Leu (TGG to TTG) [17,23,29]. Molecular analysis results associated this with a tryptophan-to-cysteine (Trp²⁰²⁷Cys) substitution in the ACCase gene, which affects the lipophilic nature of the enzymes' binding target and causes resistance (TSR) to its herbicides [7,17].

Results similar to the description above have also been reported in several weed species resistant to ACCase inhibitors, such as *A. myosuroides*, *Avena sterilis*, *Lolium rigidum*, and *A. japonicus* [14,22]. According to previous reports, substitutions of Trp²⁰²⁷Cys and Gly²⁰⁹⁶Ala in *Avena fatua* L., as well as Ile¹⁷⁸¹Leu in *A. fatua* [12,22], *A. myosuroides* [3], and *L. rigidum* [33] have occurred in the polar region at the bottom of the active CT site cavity [3]. Furthermore, increased reports of weed resistance have been associated with several mutations in the herbicides' target site genes in the form of amino acid substitutions caused by changes in nucleotide bases [27,33].

The emergence of resistance is a serious problem for weed control in crop cultivation. Resistant weeds spread and dominate an area when not controlled; for example, glyphosate-resistant *Amaranthus* can spread 300 m through pollen movement [34]. Moreover, glyphosate-resistant kochia was confirmed to appear in 2013 with a 1% distribution in maize and soybean fields in Manitoba, Canada. Within 5 years (2018), the weeds were found to have dominated several cultivated areas, including soybeans with 77% of the kochia population, 70% maize, 53% canola, 83% other oilseeds, 48% small grain cereals, 20% legumes, 50% alfalfa/grass, and 21% rough areas [35]. Resistant weeds can cause

herbicide failure, leading to wasted costs that were incurred for application. Another impact is the reduced options for the use of herbicide types, which continuously decrease once there is no proper management [15]. Preventive measures needed include rotation of the herbicides' mode of action and using them in mixed forms, plus crop rotation, which are the easiest ways to control and prevent the emergence of resistant biotypes [1,36].

5. Conclusions

This study confirmed the resistance of *L. chinensis* from Maros, South Sulawesi, to ACCase herbicides, but it can be effectively controlled by ALS and DOXP inhibitors. A single nucleotide substitution of guanine to thymine at position 6081 leading to Trp₂₀₂₇Cys mutation in the target gene, contributing to the resistance of the Maros biotype to ACCase inhibitors. *L. chinensis* resistance to ACCase inhibitors, has never been reported in Indonesia, so this is the first case, which needs to be treated as early as possible.

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