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Target-site resistance to glyphosate in *Eleusine indica* biotypes from South Sulawesi and Lampung, Indonesia

Abstract. Glyphosate is a non-selective systemic herbicide that has been widely used to control weeds by local corn farmers in South Sulawesi and Lampung Provinces of Indonesia. However, some corn farmers in these two regions were considered that glyphosate herbicide at the standard field dose no longer effective against goosegrass (*Eleusine indica*). To confirms the level of its resistance to glyphosate, seeds of *E. indica* suspected to be glyphosate-resistant were collected from corn fields in Soppeng Regency-South Sulawesi and South Lampung Regency-Lampung (designated as GR-1 and GR-2 respectively), along with a known susceptible biotype from Sumedang Regency-West Java (GS) as a comparison. By using whole-plant pot assay method in a greenhouse at the Ciparanje. A range of seven glyphosate concentrations was applied to the seedlings at the Experimental Farm, representing 0, 0.25, 0.5, 1, 2, 4, and 8 x the standard field rate. Dose–response experiment showed that GR-1 and GR-2 biotypes has a low levels resistance to glyphosate (2.57 and 2.96 folds of each) compared to susceptible biotype (GS). Sequencing results confirmed the Pro-106-Ser mutation in the *EPSPS* genes of the resistant biotypes. This specific amino acid substitution is among the most frequently documented mechanisms of resistance in weed species. Therefore, the shared mutation in the GR-1 and GR-2 biotypes likely confers this resistance. These findings serve as an early warning for corn farmers to manage and prevent further spread of *E. indica* glyphosate-resistant biotypes.

Keywords: Amino acid substitution · *EPSPS* gene · Goosegrass · Herbicide resistance

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Introduction

Regardless of the cropping system, weeds remain a major factor limiting yields. This has led to a progressive increase in herbicide application frequency within these agricultural systems (Casimero et al., 2022). Of all the herbicides, glyphosate with the IUPAC name N-(phosphonomethyl) glycine has become the most used herbicide in the world, because it has high efficacy against a broad spectrum of weeds (Duke, 2017). In 2014, glyphosate application reached volumes capable of covering 22–30% of global cultivated land, establishing it as the most extensively used pesticide in history (Benbrook, 2016). In the Indonesian agricultural sector, glyphosate constituted 73% of the total herbicide active ingredients utilized. Notably, 7% of this volume was applied during land preparation for corn cultivation (Brookes, 2019).

Goosegrass, scientifically named *Eleusine indica* (L.) Gaertn commonly known as a weed species that have strong competitive ability and seed dispersal potential (Alcántara-de la Cruz et al., 2025; Souza et al., 2024; Takano et al., 2016). Distinguished by C4 metabolism and exceptional adaptability, this species grows rapidly to a height of 30–50 cm. It completes its life cycle within approximately 120 days, during which a single plant can produce a staggering 120,000 seeds (Takano et al., 2016). The presence of *E. indica*, which also known as white crabgrass, silver crabgrass, goosegrass, wiregrass or bullgrass is recognized as a problematic weed species, capable of causing substantial yield losses of 25–90% across both annual and perennial cropping systems (Singh et al., 2025). For instance, in Brazil, corn yield reductions of 18% have been observed with goosegrass densities as low as two plants m^2, escalating to 39% losses at an infestation level of 16 plants/m^2 (Alcántara-de la Cruz et al., 2025). The management of *E. indica* infestation is further complicated by its ability to develop resistance to commonly used herbicides, as the plant is capable of rapidly dominating large areas (Souza et al., 2024).

The first case of glyphosate-resistant population of *E. indica* was detected on a four-year-old orchard in Malaysia, while glyphosate treatments from 720 to 5760 g a.i. ha^{-1} failed to control it (Lee & Ngim, 2000). Since then, glyphosate-resistant biotypes of *E. indica* have been reported in other countries, such as Philippines (Kaundun et al., 2008), USA (Mueller et al., 2011), Brazil (Takano et al., 2016), China (Chen et al., 2023a), and Indonesia (Kurniadie et al., 2023).

E. indica was one of many weeds which commonly found at corn fields in Soppeng Regency-South Sulawesi and South Lampung Regency-Lampung. Corn farmers in these two regions only used glyphosate for more than 10 years and commonly applied 2 to 3 times per year to stop or reduce growth of weeds, especially noxious weeds, before sowing the seeds of corn. However, currently the local corn farmers are being considered that the standard field dose of glyphosate no longer effective against *E. indica*. To determine the level and potential resistance mechanisms, seed samples were collected from two suspected resistant biotypes originating from these regions, along with a known susceptible biotype from Sumedang Regency-West Java as a control. The three biotypes were maintained within a greenhouse environment at the Ciparanje Experimental Farm, Faculty of Agriculture, Universitas Padjadjaran, in which their responses to various glyphosate doses were evaluated. Considering that corn in Indonesia is one of the second strategic food commodities after rice (Muliany & Amzani, 2024), the results of this study can be used as an early warning to mitigate the risk of the presence of resistant weeds in staple crop areas.

Materials and Method

Plant Growing Conditions and Seed Collection. Samples of *E. indica* seeds with suspected resistance to glyphosate were sourced from two independent corn-producing areas; each located in Soppeng Regency (4°19′32.2″ S 120°02′47.0″ E) - South Sulawesi, and South Lampung Regency (5°32′36.8″ S 105°26′28.9 E) - Lampung. These two *E. indica* biotypes (designated as GR-1 and GR-2) were considered by local corn growers as weeds that failed to be controlled by glyphosate. In addition, seeds of a wild *E. indica* at a noncropping area in Sumedang Regency (6°56′4,7″ S 107°47′20,5″ E) – West Java that previously known to be glyphosate-susceptible biotype (GS) were used for comparison in this study (Kurniadie et al., 2023).

The seeds for each *E. indica* biotype population were harvested and collected from 30 mature plants which have fully developed

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panicles, as the spikelet at the tip have dried out, but the bottom is still slightly green. Seeds underwent cleaning and a one-week sun-drying process to reduce moisture content and promote after-ripening. Samples were then stored in individual paper bags, labeled with their respective GPS coordinates, pending analysis. In mid-August 2025, located in a greenhouse at the Ciparanje, Faculty of Agriculture, Padjadjaran University, these seeds were sown into 25 cm diameter pots filled with a topsoil mix (± 30 seeds per pot of each biotype). To ensure that only seeds of *E. indica* were allowed to sprout and thrive on the soil surface in each pot, previously the potting soil had been sterilized on the autoclave at temperature 120^{o}C and maintain pressure 15 psi for 2 h. During seed germination until it had grown into a *E. indica* plant that is ready to be treated with the glyphosate herbicide, a watering pot was used for watered the plants regularly to maintained optimal soil moisture levels in each pot. Thinning out the *E. indica* plants in each pot were carried out for 21 days to leave 10 individual plant samples per pot, which constituted as an experimental unit.

Glyphosate Dose–Response Experiment. A glyphosate dose–response study was conducted using the whole-plant pot bioassay method (Burgos, 2015). This experiment was conducted as a split-plot design and had two factors, namely the glyphosate dose level and the type of *E. indica* biotype, with three replicates per treatment. Glyphosate (Roundup 486 SL, PT Monagro Kimia, Indonesia) as the whole-plots factor consisted of seven dosage levels: 0, 0.25, 0.5, 1, 2, 4, and 8× of 750 g a.i. ha^{-1} (standard field rate). The second factor was three *E. indica* biotypes (GR-1, GR-2 and GS) as subplots within the application of whole-plots factor. Therefore, distribution of 63 plots (each plot consists of ten *E. indica* plant samples) were prepared to be treated and observed.

Four weeks after sowing, glyphosate herbicide was applied according to the designed dosage for each experimental units of *E. indica plants* in the 4th – 6th leaf growth stage. Foliar treatments with these different doses of glyphosate were applied using a backpack sprayer (semi-automatic) through a single flat-fan nozzles, 400 L ha^{-1} spray volume at a pressure of 138 kPa. The next day after treatments, watering all the plants started again to maintain adequate growth until being harvested to obtained its dry weight.

The magnitude of *E. indica* above ground biomass (AGB) reduction in resistant biotypes (GR-1 and GR-2) and susceptible biotype (GS) due to the impact of each dose of glyphosate (g a.i. ha^{-1}) treatments are recorded at 28 days after treatment (DAT), and compared to untreated controls. The above ground biomass reduction assessment more appropriate to be used rather than total biomass reduction (AGB + below-ground biomass) for several practical and methodological reasons, such as a standardized metric allowing comparison across sites, species, and experiments because root biomass is highly variable to directly reflects the effect of each dose treatments. The above-ground biomass of *E. indica*' survivors in each experimental plot was cut at the base of the stem (at the soil surface), and then the dry weight was obtained by drying the living material in an oven at 80 °C for 48 h before weighing (Ma et al., 2019). The above-ground dry weight biomass reduction in each treated biotype (T) was calculated as the percentage of its growth reduction over dry weight in the untreated control (C) as shown in Equation (1):

$$\text{Biomass Reduction } (\%) = \frac{C-T}{C} \text{ x } 100\% \quad (1)$$

Statistical Analysis. The percentage of dry weight biomass reduction in both resistant (GR-1, GR-2) and susceptible (GS) biotypes was analyzed using ANOVA. The F-test was employed to identify significant differences between means at a significance level of 5%. For the variances that present significance, Duncan's Multiple Range Test (DMRT) at the 95% confidence level was applied, using SmartstatXL software version 3.6.5.4.

Resistance levels were determined by comparing the GR_{50} values; the doses resulting in a 50% reduction in dry weight compared to untreated plants of each biotype. The degree of resistance was expressed as a ratio between the GR_{50} of GR-1 or GR-2 and the susceptible GS biotype. The dose required for 50% growth reduction (GR_{50}) was estimated by fitting the percentage biomass reduction data to a non-linear log-logistic regression model. This analysis produced a sigmoid curve that was fitted to the distribution of growth reduction data (Seefeldt et al., 1995). Data were analyzed using Origin Pro 2018, where the dose–response curve was fitted to a non-linear log-logistic model using the equation:

$$y = C + \frac{D - C}{1 + (x/I_{50})^b}$$

Note: y: dry weight at herbicide dose (x), b=slope, D=upper limit, C=lower limit, I_{50}=the herbicide dose that results reduction of 50% in biomass dry weight.

The resistance index (RI) of a given biotype can then be simply calculated by dividing the GR_{50} of a suspected glyphosate-resistant biotype (GR-1 and GR-2) relatives to the GR_{50} of standard susceptible biotype (GS). The resistance index, based on GR_{50}, is more informative than the actual rate required to kill the resistant population (Heap, 1994). The classification of the level resistance is as follows: R/S > 12: high resistance, R/S = 6–12: moderate resistance, R/S = 2–6: low resistance, R/S < 2: susceptible (Ahmad-Hamdani, 2012).

***EPSPS* Gene Sequence.** Approximately 0.25 g of fresh leaf tissue was collected separately from each sensitive and suspected resistant biotype of *E. indica* when the plants reached 4th – 6th leaf stage. Furthermore, each of these fresh leaf tissues was ground into dry powder using a bead mill, and then vortexed and centrifuged at 2,200 x g for 5 minutes. The pellet obtained at the bottom of the tube was used for DNA extraction (Kaundun et al., 2008). The genomic DNA was extracted using the 'Quick-DNA Magbead Plus kit" (Zymo Research Corp., D4082, Irvine, CA, USA). Quantification of extracted DNA (genomic DNA) was performed with a NanoDrop™ spectrophotometer (Thermo Fisher Scientific). PCR amplification was performed using the "KOD FX Neo kit" (KFX-201Toyobo Co., Ltd., Japan), employed bi-directional sequencing (sequencing DNA fragments in both forward and reverse directions). Primers used to amplify a 330-bp DNA fragment were *EPSPS*-SeqF (5'-CTCTTCTTGGGAATGCTGGA-3') and *EPSPS*-SeqR (5'-TAACCTTGCCACCAGGTAGCCCTC-3'), which was previously identified as part of the *EPSPS* region.

PCR amplification was performed in a total volume reaction of 50 µL, comprising PCR buffer for KOD FX Neo (25 µL), 10.0 µL of dNTPs (2 mM), 1.5 µL of each primer (0.3 µM), 0.8 µL of KOD FX Neo polymerase, and *E. indica* genomic DNA (1 µL of) (50 ng), with the remaining volume adjusted using 10.2 µL of ddH_2O. PCR condition: 94 °C for 2 min for initial denaturation; 30 cycles of 98 °C denaturation for 10 s and 59 °C annealing for 30 s; and 72 °C final extension for 30 s. The PCR product was then loaded onto a 1% agarose gel with EPSPS _F and EPSPS _R, and sequenced using Sanger sequencing method which was performed by Thermo Fisher Scientific Inc.'s VeritiPro Thermal Cycler, 96 well (Applied Biosystems, Waltham, MA, USA, A48141).

Results and Discussion

Dose–Response Assays. Dose response assays confirmed that the suspected resistant biotypes originated from a corn field in South Sulawesi and Lampung was resistant to glyphosate. The effect of glyphosate dose treatments in Table 1 showed that the suspected resistant biotypes (GR-1 and GR-2) required 2 - 3 folds higher dose (1,500 - 3,000 g a.i ha^{-1}) to achieved an equivalent biomass reduction in susceptible biotype (GS) which was treated with 375 – 750 g a.i ha^{-1}. This indicated that GR-1 and GR-2 biotype have been exhibited a resistance mechanism to the effects glyphosate herbicide in the dose range of 187 g a.i ha^{-1} to 750 g a.i ha^{-1}. Comparable findings have been reported in the first documented case of glyphosate-resistant biotype of *E. indica* in Europe (Lodo et al., 2020).

Table 1. Percentage the biomass reduction of each *E. indica* biotypes

Biotype	Dose of Glyphosate Herbicide (g a.i ha^{-1})						
	0	187	375	750	1500	3000	6000
GS	0.00 a	88.46 b	99.76 c	100.00 c	100.00 c	100.00 c	100.00 c
(West Java)	A	C	C	B	B	A	A
GR-1	0.00 a	16.10 b	66.43 c	72.75 d	95.06 e	100.00 f	100.00 f
(South Sulawesi)	A	B	B	A	A	A	A
GR-2	0.00 a	10.59 b	58.73 c	69.68 d	94.72 e	100.00 f	100.00 f
(Lampung)	A	A	A	A	A	A	A

Note: The average value followed by the same lowercase letter in the row (dose of glyphosate herbicide) and the same uppercase letter in the column (biotype of weed) is not significantly different based on the Duncan test at the 5% level. GS = Glyphosate Susceptible, GR = Glyphosate Resistant

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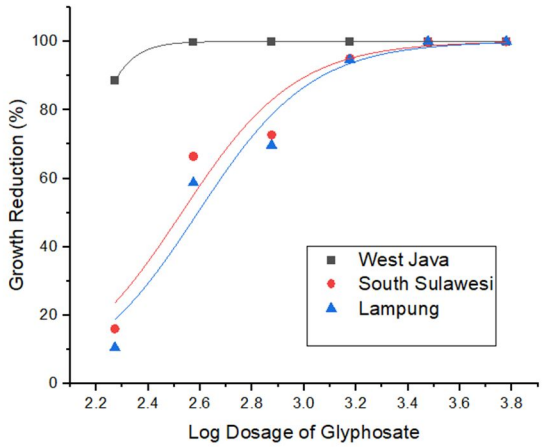

Figure 1. Application of the glyphosate herbicide causes a decrease in growth for both the susceptible (West Java) and resistant biotypes of *E. indica* (South Sulawesi and Lampung)

In the present study, the susceptible of *E. indica* were effectively eliminated at the standard field dose of 360 g a.i ha^{-1}. In contrast, 50% of the resistant biotypes survived even when the glyphosate dose was increased to 1440 g a.i ha^{-1}. In the present study, complete control of GR-1 biotype from South Sulawesi and GR-2 from Lampung was reached at the dose of 3000 g a.i ha^{-1}.

Dose-response curve (Figure 1) revealed a rightward shift in the GR-2 biotype curve compared to the susceptible biotype (GS), indicating greater tolerance to glyphosate. The GR-1 biotype also exhibited a rightward shift, though to a lesser extent, suggesting comparatively lower tolerance. Based on the fitted model, the estimated glyphosate dose required to reduce the biomass dry weight of the GR-1 and GR-2 biotype by 50% (GR_{50} value) was 338 and 390 g a.i ha^{-1} respectively, which was significantly higher than that of the GS biotype (131 g a.i ha^{-1}). On the basis of GR_{50} values (Table 2; Figure 1), the GR-1 and GR-2 biotypes was 2.57 and 2.96-fold respectively to glyphosate; compared to the GS-susceptible biotype. Based on these values, both of GR-1 and GR-2 biotypes demonstrate a decline in sensitivity to glyphosate herbicide, suggesting had a low-level of resistance (R/S value of < 4) (Ahmad-Hamdani et al., 2012). Consequently, glyphosate has become ineffective for managing these biotypes, even though they are classified within the low-resistance category. To ensure effective suppression, alternative strategies must be employed, such as rotating herbicides with different modes of action (MoA) and implementing non-chemical control methods (Ramos et al., 2021; Perotti et al., 2020; PAN, 2023; Nath et al., 2024; HRAC, 2025; Singh et al., 2025; Ravi & Kamal, 2025).

PCR Amplification and Analysis of *EPSPS* Gene. Alignment of *EPSPS* gene sequences identified a point mutation at codon 106, where a CCA-to-TCA transition resulted in a Pro-106-Ser amino acid replacement in the resistant biotypes (Table 3). This mutation confers glyphosate resistance in *E. indica* biotypes from a corn field in South Sulawesi and Lampung Provinces. The Pro-106-Ser mutation was reported as the first glyphosate-resistant in *E. indica* population (Baerson et al., 2002), and has subsequently been documented in resistant populations from Brazil (Takano et al., 2019) and China (Chen et al., 2023a). Mutations at codon 106 of EPSPS are among the most frequently reported target-site resistance mechanisms, alongside those occurring at codon 102 (Gaines et al., 2020; Kurniadie et al., 2023).

Table 2. Resistance index (RI) and GR_{50}

Biotypes	GR_{50}	r^2	RI	Resistance Level *)
GS (West Java)	131.36	1.00	1.00	Susceptible
GR-1 (South Sulawesi)	337.78	0.94	2.57	Low
GR-2 (Lampung)	389.87	0.95	2.96	Low

Note: *) = Ahmad-Hamdani et al., 2012. GS = Glyphosate Susceptible, GR = Glyphosate Resistant

Table 3. Comparison of deduced amino acid sequences of the *EPSPS* gene around position 106 in susceptible and resistant *Eleusine indica* biotypes

Biotype	Position	101	102	103	104	105	106
Susceptible *)	Sequence:	GGA	ACT	GCA	ATG	CGA	CCA
	Amino Acid:	(Gly)	(Thr)	(Ala)	(Met)	(Arg)	(Pro)
South Sulawesi	Sequence:	GGA	ACT	GCA	ATG	CGA	**TCA**
	Amino Acid:	(Gly)	(Thr)	(Ala)	(Met)	(Arg)	**(Ser)**
Lampung	Sequence:	GGA	ACT	GCA	ATG	CGA	**TCA**
	Amino Acid:	(Gly)	(Thr)	(Ala)	(Met)	(Arg)	**(Ser)**

Note: *) = The nucleotide sequence related to the amino acid position of the susceptible *E. indica* biotype is the same as the GenBank Accession reference (AY157642.1) (Takano et al., 2019)

The proline substitution by serine at position 106 in the *EPSPS* gene of resistant biotypes modifies the structural and functional conformation the active site of EPSPS, which subsequently lead to reducing its affinity for glyphosate (Han et al., 2016; Fonseca et al., 2020). This increases the inhibitory constant (Ki)—the concentration of glyphosate required to reduce EPSPS activity by 50%, as more glyphosate is required to inhibit EPSPS mutant activity with its natural substrate (PEP: phosphoenolpyruvate), under normal physiological conditions (Gaines et al., 2020). In addition, the affinity of the EPSPS mutant with Pro-106-Ser substitution tended to bind for PEP more than glyphosate compared with natural EPSPS (Chen et al., 2023b). As a result, this present study found a significant difference in the glyphosate susceptibility between the susceptible and resistant biotypes of *E. indica* occurring in corn fields from South Sulawesi and Lampung.

Conclusion

This study provides compelling evidence of emerging glyphosate resistance in *E. indica* biotypes collected from maize fields in South Sulawesi (GR-1) and Lampung (GR-2). Dose–response assays categorized these biotypes as having low-level resistance, with resistance indices of 2.6 and 3.0, respectively. Sequence analysis of the *EPSPS* gene confirmed the Pro-106-Ser substitution, a characterized target-site resistance (TSR) mutation that diminishes glyphosate's binding affinity to the enzyme's active site.

Although GR-1 and GR-2 biotypes being in low level resistance to glyphosate, the detection of this mutation highlights the potential for rapid escalation if glyphosate continues to be applied as the sole control measure. The findings underscore the importance of several management approach, including to rotate herbicides with different mode of action which is integrated with non-chemical control methods, and establish resistance monitoring programs. Therefore, these needs to be explained to local corn farmers in South Sulawesi and Lampung Provinces, so that they can involve in preventing its spread to other locations.

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